

Animal congregation in the open ocean – a theoretical approach

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Betreff: Erklärung zur Dissertation

Hiermit erkläre ich, dass die Abhandlung dieser Doktorarbeit – abgesehen von der Beratung durch beide Betreuer – nach Inhalt und Form meine eigene Arbeit ist.

Die Arbeit hat noch nicht, weder teilweise noch vollständig, einer anderen Stelle im Rahmen eines Prüfungsverfahrens vorgelegen und ist weder veröffentlicht worden, noch sind Teile zur Veröffentlichung eingereicht worden.

Die Arbeit ist unter Einhaltung der Regeln guter wissenschaftlicher Praxis der Deutschen Forschungsgemeinschaft entstanden.

Mit freundlichen Grüßen,

Carina Ramm

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Abstract

Many aspects of the behavioural ecology of oceanic predators are little understood due to difficulties related to costs and reduced accessibility of their habitat. Often only certain parts and factors of an ecosystem can be studied. Hence it is important to compile results of previous research so as to extract the most possible information from what is available.

In the scope of this study a review of animal grouping in the oceanic environment identified possible evolutionary drivers towards congregation in cetacea which were then quantitatively evaluated by a meta-analysis of group size correlations with a number of ecological and behavioural parameters, including habitat range, migration behaviour, prey composition, foraging depth and predation risk. The latter was quantified based on vertical and horizontal overlap of cetacea habitat with that of their predators, and from both, the probability of attack during an encounter with a predator and attack fatality. Tuna-dolphin associations were qualitatively analysed with regard to fitness benefits related to predation risk, foraging and improved navigation accuracy.

Killer whales, great white sharks and broadnose sevengill sharks were identified as the main predators of oceanic whales, dolphins and porpoises. Particularly high risks of killer whale predation were estimated for gray and minke whales, humpback whales, dusky dolphins and common dolphins whereas deep-diving species such as beaked whales and pilot whales experience the lowest predation risks. White sharks inflict high predation threats to several species of small delphinids, especially melon-headed whales, rough-toothed, Fraser's, spinner, pantropical spotted, Atlantic spotted, Clymene and common dolphins. With the exception of the rough-toothed dolphin these are also the species which form congregations of the largest average sizes among cetacea.

In line with this finding the group size meta-analysis identified predation risk inflicted by white and sevengill sharks as the main evolutionary driver towards the formation of large groups in this taxon whereas alloparental care for calves and improved access to females seem to drive the selection of congregations of small size. A lack of correlation between group size and predation risk inflicted by killer whales suggests that adaptations other than gregariousness such as inconspicuousness and deep-diving are more effective in reducing predation by this species. Communal prey search, cooperative prey herding and improved navigation accuracy are suggested to represent secondary benefits of grouping.

Likewise, tuna-dolphin congregations seem to be driven by predation risk inflicted by oceanic sharks. Dolphins particularly benefit from the association with a more vulnerable species. Tuna are suggested to reduce their predation risk by raising and herding shoaling extra-guild prey to the surface which provides forage to their potential intra-guild predators. Cooperative prey herding and prey debilitation seem to be important foraging techniques across numerous oceanic predators, including sharks, billfish, certain seabirds, sea lions and cetacea.

Zusammenfassung

Durch hohe Kosten verbunden mit der Erforschung der Hochsee und geringe Zugänglichkeit dieser Gebiete sind viele verhaltensökologische Aspekte ozeanischer Prädatoren kaum bekannt. Oft können nur Teile und bestimmte Faktoren eines Ökosystems untersucht werden. Dadurch ist es wichtig Resultate vergangener Studien so effizient wie möglich zu kompilieren um mit den Informationen die verfügbar sind den größtmöglichen Einblick zu gewinnen.

Im Rahmen dieser Arbeit wurde ein Review über das Gruppenverhalten in Hochseegewässern angefertigt, der mögliche evolutionäre Haupteinflussfaktoren identifiziert. Diese sind dann quantitativ im Rahmen einer Meta-analyse von Korrelationen zwischen Gruppengröße und verschiedenen ökologischen und verhaltensspezifischen Parametern ausgewertet worden. Diese sind unter anderem Ausbreitungs- und Migrationsverhalten, Nahrungszusammensetzung, Nahrungstiefe und Prädationsgefahr. Letztere wurde auf der Basis von der Überlappung zwischen Räuber- und Beutehabitat, der Wahrscheinlichkeit, dass das Zusammentreffen mit einem Prädatör zu einem Angriff führt und der Letalität eines solchen Angriffs quantifiziert. Thunfisch-Delphin Gemeinschaften sind im Hinblick auf mit der Ernährung, der Navigationspräzision und der Prädationsgefahr zusammenhängende Fitnessvorteile qualitativ untersucht worden.

Schwertwale, weiße Haie und Breitnasen-Siebenkiemenhaie sind als Hauptprädatoren von Hochseewalen, -delphinen und -schweinswalen identifiziert worden. Schwertwale stellen besonders für Grau- und Zwergwale sowie Buckelwale, Schwarzdelphine und gewöhnliche Delphine eine große Gefahr dar, wohingegen tief-tauchende Cetacea-Arten wie Schnabelwale und Pilotwale der geringsten Prädationsgefahr ausgeliefert sind. Weiße Haie sind besonders problematisch für mehrere Arten körperkleiner Delphine einschließlich Breitschnabeldelphinen, Raubahndelphinen, Borneodelphinen, ostpazifischen Delfinen, blau-weißen Delphinen, Zügeldelphinen, Streifendelphinen und gewöhnlichen Delphinen. Mit Ausnahme der Raubahndelphine sind dies auch die Arten mit den durchschnittlich größten Gruppen innerhalb der Cetacea.

Damit übereinstimmend hat die Meta-Analyse von Gruppengrößen die Prädationsgefahr ausgehend von weißen Haien und Breitnasen-Siebenkiemenhaien als evolutionäre Hauptursache für die Bildung großen Gruppen identifiziert, wohingegen die gemeinschaftliche Aufzucht von Jungtieren und verbesserter Zugang zu Weibchen die Hauptgründe für die Selektion kleiner Gruppen sind. Das Fehlen einer Korrelation zwischen Gruppengröße und der von Schwertwalen ausgehenden Prädationsgefahr lässt vermuten, dass andere Adaptionen wie Unauffälligkeit und tiefe Tauchgänge diese Gefahr effizienter verringern als Gruppenbildung. Gemeinschaftlich Nahrungssuche, kooperatives Zusammentreiben von Nahrung und verbesserte Navigationspräzision sind sehr wahrscheinlich sekundäre Vorteile des Gruppenlebens.

Thunfisch-Delphin Gemeinschaften scheinen ebenfalls evolutionär hauptsächlich von Prädationsgefahr beeinflusst zu werden. Durch die Gemeinschaft mit einer stärker gefährdeten Art erfahren Delphine besonders große Vorteile. Thunfische reduzieren vermutlich ihre Prädationsgefahr indem sie Gruppen-bildende Nahrungsfische aus der Tiefe an die Oberfläche treiben und dadurch ihre potentielle Inner-Gilden Feinde mit Außer-Gilden Nahrung versorgen. Das gemeinschaftliche Zusammentreiben von Nahrung und die Verwundung von Nahrungsfischen scheinen wichtige Ernährungsmethoden für viele Hochseeprädatoren zu sein. Dies sind z.B. Haie, Schwertfische und anderen Istiophoriden, eigne Seevogelarten, Seelöwen und Cetacea.

Introduction

The open ocean is a vast biome, difficult and expensive to study (e.g. Baum, Worm 2009; Graham *et al.* 2010) with major aspects still poorly understood (e.g. Purcell, Arai 2001; Jensen 2008; Ritchie, Johnson 2009; Cherel *et al.* 2014; Lidgard *et al.* 2014; Saunders *et al.* 2014; Carlisle *et al.* 2015; Cox *et al.* 2016; Steward *et al.* 2016). Studies of this environment are fewer in number compared to research on land, or in neritic and limnic habitats, and are often characterized by short periods of field work, covering small aspects of the whole. It is therefore difficult to gain comprehensive insights into the functioning of offshore habitats.

Moreover, the oceanic environment is changing quickly due to anthropogenic and climatic influences (e.g. Barber, Chavez 1983; Prince, Goodyear 2006; Halpern *et al.* 2008; Baum, Worm 2009), increasing the difficulty of developing a comprehensive understanding of its functioning unbiased by human influence (Dill *et al.* 2003; Maxwell *et al.* 2013; Bost *et al.* 2015). Behavioural patterns adjust faster to a changing environment than anatomical or physiological aspects (e.g. Gittleman, Stephens 2012), and it becomes increasingly difficult to distinguish between natural animal behaviour and behavioural changes caused by anthropogenic impact.

Drawing the most information out of available data seems therefore critical. This thesis attempts to synthesize results of ecological and behavioural studies in oceanic cetacea and to relate the same to congregation in these marine mammals. Sociality varies greatly among cetacea from solitary occurrence to large congregations comprising thousands of individuals and from small cohesive groups with strong inter-individual bonds to large societies characterized by fission-fusion patterns. Hence this taxon lends itself to the study of grouping behaviour including its main evolutionary drivers as well as secondary benefits.

A more comprehensive picture of congregation and predator-prey relationships in the open ocean will improve our understanding of both, its functioning and changes induced by human influence.

A large-scale review of grouping behaviour in the oceanic environment, the quantification of predation risk experienced by cetacea, the quantitative analysis of group size correlations with ecological parameters in cetacea and the qualitative analysis of tuna-dolphin congregations represent the means by which this thesis is attempting to improve the understanding of congregation and predator-prey relationships in the oceanic realm.

In this thesis a group is defined as a unit of individuals which are in close proximity and which directly interact with one another. Solitary individuals spread out over a large area connected through information exchange, for example by means of acoustic signals are not considered a group. Oceanic waters include both, areas far from land and regions in which deep-water conditions occur close to shore as found around offshore islands and along open coast lines with small or no continental shelf.

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Chapter 1 Review of congregation in oceanic cetacea

Introduction

Little is known about many oceanic cetacea species and a compilation of available knowledge including insights gained experimentally or through the study of other ecosystems may improve this situation. Based on that idea this chapter reviews animal grouping with focus on the oceanic environment, particularly on cetacea and species which are ecologically most relevant to cetacea, including pelagic sharks, their most important non-cetacea predators and small pelagic shoaling fish and squid, the main food source of many oceanic whales, dolphins and porpoises. Prey patchiness in general and small-scale characteristics of prey patches in particular are thought to be critical to the understanding of predator-prey relationships in pelagic marine ecosystems (Benoit-Bird *et al.* 2013). Therefore, the grouping behavior of cetacea prey is expected to influence congregation in and fitness of these marine mammals.

Oceanic pelagic animals travel between different bodies of water in order to fulfil their biological needs. In contrast to coastal habitats the open ocean provides little shelter from predators, leaving animal congregation the main or only refuge, particularly in epipelagic waters. Prey search can be difficult when food patches are far apart and hard to locate. Likewise finding a mating partner is challenging when individuals are spread out over vast areas. Behavioural adaptations to these situations such as communal prey search, cooperative prey herding, navigation-related information exchange and lekking which lead to or require congregation may yield important fitness benefits.

The identification of possible congregation-related fitness benefits relevant to cetacea by this review forms the foundation for the analyses of evolutionary drivers towards grouping in cetacea and tuna-dolphin associations in the following chapters (Chaps. 3, 4).

Studies were located through ISI Web of Science, Google Scholar, PLOS ONE, BioOne, ScienceDirect, PubMed and JSTOR search engines, references of relevant papers and articles which have cited the located papers.

Reduced predation risk

Many empirical and modelling studies demonstrate the anti-predator benefits of congregation and identify predation risk as one of the main evolutionary drivers of grouping in potential prey (Seghers 1974; Milinski 1979b; Tremblay, Fitzgerald 1979; Pulliam, Caraco 1984; Godin 1986; Milinski 1986; Magurran, Pitcher 1987; Magurran 1990; Pitcher, Parrish 1993; Helfman *et al.* 1997; Leimar 1988; Krause, Ruxton 2002). However, few quantitative studies have analysed correlations between predation risk and gregariousness in the oceanic environment.

Grouping can reduce predation risk through:

- Increased vigilance efficiency
- Dilution effect
- Selfish herd effect
- Predator confusion
- Predator swamping
- Encounter dilution
- Predator inspection
- Coordinated predator evasion
- Communal defence

Encounter dilution

When the perceptual range of a predator is low, relative to its movement velocity and that of its prey, such that the predator must search the environment in order to find food, the predator's likelihood to encounter a prey group can be decreased compared to the probability of finding a solitary food item out of many scattered prey individuals (Pitcher, Parrish 1993).

This phenomenon is termed encounter dilution (Turner, Pitcher 1986). In consequence variance in the predator's feeding rate will increase with increasing prey congregation due to reduced spatial and temporal predictability of prey availability, which may induce the predator to switch to an alternative food type (Krause, Ruxton 2002; Ambrose *et al.* 2013). The vastness of the open ocean may suggest that encounter dilution could represent an important grouping benefit in this environment.

However, many congregations of pelagic shoaling fish, squid and crustacea such as:

- spawning congregations
- seasonally migrating shoals
- feeding aggregations associated with oceanographic features (fronts, eddies etc.)
- vertically migrating deep scattering layers

are predictable in time and space (e.g. Runnström 1941; Laws 1985; Quetin, Ross 1991; Mackinson *et al.* 1999; Benoit-Bird, Au, W.W.L. 2003; Makris *et al.* 2009; Wakefield *et al.* 2009; Jereb, Roper 2010; Woodson, Litvin 2015) and can be very conspicuous due to their size or behaviour (e.g. Nordeide, Kjellsby 1999; Gannon *et al.* 2005; Rowell *et al.* 2015; Putland *et al.* 2016; Wang *et al.* 2016) which not only reduces the effect of encounter dilution but facilitates the exploitation of the prey's grouping behaviour by predators (e.g. Sergeant, Fisher 1957; Quetin, Ross 1991; Toresen 1991; Östmann 1994; Haug *et al.* 1995; Similä *et al.* 1996; Benoit-Bird 2004; Gannon *et al.* 2005; Baird *et al.* 2013; Zaeschmar *et al.* 2013, 2014; Wang *et al.* 2016; Caputo *et al.* 2017).

Large cetacea congregations apply highly conspicuous acoustic and visual behaviour (e.g. Wade, Gerrodette 1993; May-Collado *et al.* 2007; Oswald *et al.* 2008; Perrin *et al.* 2009; Henderson *et al.* 2012) which is not conducive for reducing predator encounter rates. It appears that gregarious marine species tend to form congregations of a size, conspicuousness and predictability that increases, rather than decreases the encounter rate with predators but a quantitative analysis of this phenomenon in the oceanic environment is lacking.

Increased vigilance efficiency

The period between the initial detection of a predator and the predator attack accounts for a main aspect of the functional advantage of grouping in predator avoidance (Magurran 1990; Pitcher, Parrish 1993). The earlier the predator is detected the larger this time lag is, and the more efficient the prey's response can be.

Increased vigilance was found to improve predator recognition and assessment across many taxa and species (e.g. Robinson 1981; Baldellou, Henzi 1992; Cowlshaw 1997; van Schaik, van Noordwijk 1989; Cresswell *et al.* 2003). As scans for predators by group members are variable in length, and individuals typically scan independently, prey grouping increases the difficulty for a predator to predict when an individual will scan the environment (Bertram 1980; Elgar, Catterall 1981; Elcavage, Caraco 1983; Studd *et al.* 1983; Scannell *et al.* 2001) and therefore reduces the predator's ability to approach unnoticed and stage surprise attacks (e.g. Magurran *et al.* 1985). Numerous studies have shown both, the higher probability of groups to detect an approaching predator and earlier predator detection by groups compared to solitary individuals (e.g. Miller 1922; Darwin 1871; Galton 1871; Belt 1874; Powell 1974; Siegfried, Underhill 1975; Kenwood 1978; Lazarus 1979; Treherne, Foster 1980; van Schaik *et al.* 1983; Brown, Brown 1987; Godin *et al.* 1988; FitzGibbon 1990; Magurran 1990; Pitcher, Parrish 1993; Cresswell 1994; Ebensperger, Wallem 2002; Vásquez *et al.* 2002; Boland 2003; Williams *et al.* 2003; Ebensperger *et al.* 2006).

When information is transmitted within a congregation then predator detection by a single group member is sufficient to elicit an anti-predator response in the whole group (Pulliam 1973;

Pulliam *et al.* 1982; Parker, Hammerstein 1985). It then follows that an increase in congregation size facilitates a decrease in each individual's personal commitment to vigilance without enhancing the risk of failing to detect an attack and thus enables group members to dedicate more time to other survival and fitness related needs such as foraging, mating or resting (Underwood 1982; Berger, Cunningham 1988; Burger, Gochfeld 1992; Scheel 1993; Roberts 1996; Gauthier-Clerc *et al.* 1998; Lima *et al.* 1999; Blumenstein *et al.* 1999; Blumenstein, Daniel 2002). However, some predators have been found to preferentially attack less vigilant individuals (Smythe 1970; Jacobsen 1986; FitzGibbon 1989; Krause, Godin 1996a; Maldini 2003a; Quinn, Cresswell 2006) which may reduce this benefit. Hence grouping benefits related to vigilance can vary between different predator-prey systems.

Whereas these complex interrelations have been well researched in fish, birds and terrestrial mammals, studies which address vigilance in marine mammal congregations are lacking.

The major communication process of herring, *Clupea* sp., anchovy, *Engraulis* sp. and menhaden, *Brevoortia patronus*, shoals in response to detection of or attack by a predator consists of agitation waves crossing the shoal at speeds faster than these fish and attacking predators move (Godin, Morgan 1985; Axelsen *et al.* 2001; Gerlotto *et al.* 2006; Handegard *et al.* 2012; Marras *et al.* 2012). The agitation wave is the result of individual rolling movements producing a 'flash' of light when the silvery camouflage device is nullified during a rapid manoeuvre (Denton, Nicol 1966). Each neighbour receiving the flash repeats the movement leading to a flash frontline crossing the shoal at constant speed without distortion regardless the shoal's dimensions (Axelsen *et al.* 2001; Gerlotto *et al.* 2005).

The agitation wave is followed by increased homogeneity in shoal structure and synchronicity in movement (e.g. Radakov 1973; Makris *et al.* 2009) and is also used at the onset of migration (Makris *et al.* 2009). This phenomenon of individual reactions spreading across an animal congregation faster than predator approach speed was termed Trafalgar effect by Treherne, Foster (1981) who observed the propagation of anti-predator movements across flotillas of marine isopods subsequent to an approach of a model predator. Similar agitation waves have been described in swarming insects (Kastberger *et al.* 2008), bird flocks (Davis 1980; Webb 1980; Godin, Morgan 1985; Heppner 1997; Ballerini *et al.* 2008b; Procaccini *et al.* 2011) and herds of terrestrial mammals (Krause, Ruxton 2002; Couzin, Krause 2003). Procaccini *et al.* (2011) found a high positive correlation between wave formation in peregrine falcons, *Falco peregrinus*, and reduced predator success. The Trafalgar effect allows the fast spread of information which may facilitate quicker reactions to predation risk at shoal level in fish. Many pelagic shoaling fish species respond to predation threat with coordinated predator evasion manoeuvres which require highly polarized schools and movement synchronicity (see below: Coordinated predator evasion).

Predator inspection

Predator inspection is an anti-predator response in some shoaling fish species which follows the detection of the predator and seems to inquire the motivation of the predator to facilitate anticipation of attack (Pitcher 1979; Pitcher *et al.* 1986). It is therefore critical in the recognition of danger. Inspectors appear to put themselves at risk to acquire information about the predator which is then shared with other shoal members, leading to a survival benefit for the whole group. The number of inspecting individuals can vary between a single shoal member and the majority of a shoal and seems to correlate with perceived risk.

Predator inspection has not been documented in oceanic pelagic species of shoaling fish (Pitcher 1991) but has been suggested in cetacea. Off Kaikoura, New Zealand, dusky dolphins, *Lagenorhynchus obscurus* have been observed to react in two ways to the presence of killer whales, *Orcinus orca*. While the majority of the group was fleeing along the shoreline a small subset of adult individuals (mean: 6) have been observed to approach the killer whales, swimming rapidly around and in front of the same, before departing at high speed (Markowitz 2004; Srinivasan, Markowitz 2010). This behaviour has been interpreted as predator

assessment by a small 'scouting party' but may also be used for predator distraction or harassment. Further research of this behaviour and its costs and benefits has been suggested (Srinivasan, Markowitz 2010).

Predator swamping

Grouping may yield an advantage, if the predator's feeding efficiency is limited by the time to kill, consume, or digest prey as then, once a kill has been made, the remaining prey group may have a chance to escape while the predator handles its food (Darling 1938; Taylor 1976, 1979; Barnard 1984). In large prey groups such as listed above predator swamping occurs, when the prey congregation (or aggregation) is greater than the number of individuals that all local predators can consume within the time the prey congregation persists or is accessible to the predator. Predator swamping may allow part of the prey population or group to leave the area, pass through a vulnerable life-history stage or disperse (Darling 1938; Gochfeld 1980). Due to the often large size of groups formed by social oceanic species of fish, squid and crustacea (e.g. Probatov 1953; Radakov 1973; Blaxter, Hunter 1982; Mackinson *et al.* 1999; DeBlois, Rose 1996; Hamner, Hamner 2000; Hoare *et al.* 2000; Gerlotto, Paramo 2003; Gerlotto *et al.* 2004; Ritz *et al.* 2011; Benoit-Bird *et al.* 2017) or during social phases such as spawning (e.g. Makris *et al.* 2009; Jereb, Roper 2010; Wang *et al.* 2016) or migration (e.g. Godø *et al.* 2004; Fauchald *et al.* 2006; Makris *et al.* 2009) predator swamping is expected to represent an important advantage of grouping behaviour in the oceanic environment. Prey patches such as feeding aggregations, migrating shoals and spawning congregations are ephemeral. Deep-scattering layers and oceanic island boundary communities are accessible to most predators during certain times of day only due to their daily vertical migrations (Hays 2003). Predators can only consume a limited amount of these prey congregations during the time of their persistence or accessibility (e.g. Benoit-Bird, Au 2009). The biomass of mesopelagic fish associated with deep-scattering layers is huge (Irigoiien *et al.* 2014) and predator swamping combined with the dilution effect (see below) are likely the main benefits of congregation in these species.

Dilution effect

If all individuals of a group would be of equal vulnerability to a predator, the chance of a member of this congregation to be attacked would be $1/n$ with n constituting the number of individuals comprised by the group. In contrast the likelihood for a detected solitary prey individual to be targeted by a predator is 1. Consequently, prey grouping leads to a decrease in predation threat, called dilution effect, which is the stronger the larger the group. For the dilution effect to be of advantage to prey, predator consumption has to be limited to one or few food items. If predators consume whole prey groups, then there is no dilution effect. If a group of n individuals is attacked n -times more often than a single individual, even if the predator can only capture at most one prey out of a detected group, there will be no advantage to the prey in congregating since the costs related to an increased attack rate will compensate dilution benefits (Lehtonen, Jaatinen 2016). Turner, Pitcher (1986) therefore suggested to consider dilution effect and encounter dilution together when analysing group behaviour and called the combined effect of both factors attack abatement. However, factors other than detectability such as predator population size or density in a certain area also affect predation risk. If large groups are very conspicuous but the density of predators is low compared to the density of prey, then predator swamping, and the dilution effect will still render grouping beneficial even if encounter dilution is not applicable. If large groups are easily detected but predators avoid attacking large groups and prefer smaller congregations then grouping would also be beneficial independent of encounter dilution.

A limiting factor to the dilution effect is unequal predation risk among group members which may arise under a number of circumstances including:

- unequal body size of group members (e.g. most cetacea groups) in combination with size-preferences of predators due to gape limitations etc.

- variation in experience and hence catchability among group members (e.g. cetacea groups which comprise individuals of various age classes)
- variation in predation risk associated with individual positioning within a group (e.g. Parrish 1989; Romey *et al.* 2007; Morrell Romey 2008; Eshel *et al.* 2011)
- general phenotypical differences among group members in combination with the preference of a certain phenotype by the predator (e.g. Fullick, Greenwood 1979)
- differing nutrient content among group members (e.g. due to variability in health or body strength among individuals (Krause *et al.* 1998b)
- oddity (see below)
- variation in group density in combination with preference of a certain prey density by the predator (e.g. various oceanic predators preferentially feed on patches or parts of prey congregations where density is highest: Benoit-Bird, Au 2009; Benoit-Bird *et al.* 2013)
- variation in ability to fend off predators esp. in polyspecific groups (possibly in dolphin-tuna associations since only dolphins have been documented to fend off sharks)
- morphological differences related to protection from predators among polyspecific group members (e.g. sea turtles associate with tuna shoals in the tropical E-Pacific and are likely less vulnerable to predation than tuna due to their carapaces)

which lead to the preference of certain prey individuals over others (e.g. FitzGibbon 1990; Beauchamp 2017). In such cases certain individuals may benefit from association with more vulnerable group members (Mathis, Chivers 2003). More vulnerable group members may still benefit from grouping if they form a large enough portion of the group to create a dilution effect among themselves. Hence these factors do not negate the dilution effect, but rather cause risk to be diluted unequally among group members and therefore reduce the dilution effect. The previously discussed large groups encountered in oceanic waters suggest that the dilution effect is an important benefit of congregation in this environment.

The selfish herd effect

Gregarious behaviour has been suggested to represent a form of cover-seeking in which each animal tries to reduce its chance of being attacked by a predator (Williams 1964; Galton 1871). Hamilton (1971) further developed this idea assuming that a predator attacks the nearest prey individual. A selfish individual lowers its predation risk by reducing its domain of danger (DOD), the area within which it is closest to a predator, by moving towards its neighbour and by positioning itself such that other potential prey individuals are between it and the predator. Such behaviour would lead to group compaction, a commonly observed anti-predator response (e.g. Norris, Dohl 1980a; Whitehead, Glass 1985; Magurran, Pitcher 1987; Fréon *et al.* 1992; Pitcher, Parrish 1993) and is termed the 'selfish herd effect' (Hamilton 1971).

De Vos, O'Riain (2010) empirically studied both, the proportionality between the size of the DOD and the strength of predation risk, and the hypothesis that this proportionality alone embodies differential survival probability and is subject to selection pressure. Off Seal Island, South Africa, white sharks, *Carcharodon carcharias*, hunt Cape fur seals, *Arctocephalus pusillus pusillus*, in a spatially and temporally predictable pattern (Laroche *et al.* 2008). Since sharks detect their prey using surface moving silhouettes (Laroche *et al.* 2008), seal decoys with variable DOD's were used to mimic the predators' main prey. Seals do not know where a shark will attack and are arranged within a two-dimensional plane, the sea surface, exposed to white shark attacks from below. Hence, seals cannot hide behind one another but can reduce their individual DOD by moving closer to their nearest group members.

The study revealed a significant positive correlation between the size of the domain of danger and the relative predation risk of a seal decoy, measured as the proportion of total trials in which an individual decoy was attacked. These results provide evidence for an influence of individual spacing within seal groups on predation risk by white shark ambush attacks. These

results further show that the dilution effect does not apply equally to all members of a congregation due to the described variation in predation risk between individuals which depends on the size of their individual DOD.

Even though movement rules within congregations may often be more complex than suggested by Hamilton's hypothesis (Krause, Tegeder 1994; Morton *et al.* 1994; Viscido *et al.* 2002, 2005; Morrell, James 2008; Kimbell, Morrell 2015; Morrell *et al.* 2015) De Vos, O'Riain (2010) have shown experimentally and in a natural and oceanic environment that an individual affiliated to a group can reduce its risk of predation by decreasing its DOD relative to that of other group members. The same rules are most likely to apply to other surface-swimming prey species of pelagic sharks such as seabirds and cetacea.

Confusion effect

The simultaneous movement of phenotypically identical or very similar prey individuals imposes a difficulty to the predator to focus on a particular target, causing a confusion effect (Milinski 1977a) which reduces attack success (Ohguchi 1978; Landeau, Terborgh 1986; Tosh *et al.* 2006). Such confusion can be caused in two ways: by the inability of sensory channel transduction to cope simultaneously with multiple signals, and cognitive confusion due to an inability to choose among alternative targets and bring any signal locking ability into play once a target is chosen (Pitcher 1986). Predator confusion has been documented across a wide range of taxa including mammals, birds, amphibians, fish, cephalopods, insects and crustaceans (Jeschke, Tollrian 2007) and, for visual predators, seems the stronger the more agile the prey (Eibl-Eibesfeldt 1962; Humphries, Driver 1970; Ohguchi 1981).

In oceanic waters numerous predators across many taxa, including various species of cetacea, pinnipeds, diving seabirds, teleost fish, sharks and squid feed on shoaling prey after herding the same into a dense ball. This technique is often used in combination with prey debilitation such that prey once herded are stunned, injured or killed by strikes with the predator's tail (thresher sharks, cetacea) or bill (billfish). Once herded into a dense school prey debilitation targets parts of the prey group rather than single individuals and often affects more than one individual per strike (details and references below: Increased foraging efficiency) thereby overcoming the confusion effect. The effect of prey herding on predator confusion per se has, to the author's knowledge, not been studied. However, prey density after herding can be so high that sharks have been observed to 'take bites' from a herded school of fish (Bullis 1961), rather than singling out individuals. It is expected that such a high prey density renders the selection and pursue of a particular prey individual unnecessary but studies which explore and quantify the effect of prey herding on predator confusion are needed.

Oddity

The presence of phenotypically or behaviourally odd group members allows a predator to fixate on single individuals, thereby overcoming the confusion effect, and thus increases attack success (e.g. Kruuk 1972). Odd individuals benefit less from both, the dilution and confusion effects (or not at all if there is a single odd individual in a group of phenotypically similar animals) and therefore experience a higher risk of predation than non-odd group members (Kruuk 1972; Milinski 1977b; Ohguchi 1978; Landeau, Terborgh 1986; Theodorakis 1989). In line with these findings active preference for conspecifics of similar size when choosing a group is a common phenomenon in fish and squid which increases by one order of magnitude under predation threat (Krause, Godin 1994). In some cases, mixed-species shoals are abandoned under predation risk (Wolf 1985).

Experimental studies have demonstrated active congregation preferences for a number of phenotypic characters, including size (Krause *et al.* 2000a), species (e.g. Wolf 1985; Krause, Godin 1994; Magurran *et al.* 1994), parasite load (Dugatkin *et al.* 1994; Krause, Godin 1996b; Barber *et al.* 1998) and colour (McRobert, Bradner 1998) across a number of fish species including Atlantic salmon, *Salmo salar*, and rainbow trout, *Oncorhynchus mykiss*, with

individuals preferring to shoal with others that are phenotypically similar (Crook 1999; Hoare *et al.* 2000). Selection against oddity is so strong that it seems to have suppressed the evolution of sexual dimorphism in pelagic shoaling fish (Hobson 1968).

Coordinated predator evasion

The ability to perform coordinated evasive manoeuvres under predation threat is a well-developed grouping benefit in numerous pelagic shoaling fish species including clupeids, jack, tuna, sand eel and barracuda (Hobson 1968; Radakov 1973; Major 1976; Pitcher, Wyche 1983; Fréon *et al.* 1992; Pitcher, Parrish 1993; Parrish, Edelstein-Keshet 1999; Gerlotto, Paramo 2003). Tab. 1 summarizes predator evasion manoeuvres and their documented functions. Many school formations facilitate the maintenance of a minimum approach distance to the predator which, depending on the number of predators and the size of the prey school may manifest as a bend in the periphery of the school if there is only one predator attacking, or a pseudopodium in response to several predators, or a vacuole if the predator enters the prey school (Nøttestad, Axelsen 1999). These formations maintain school structure while individuals are evading one or several predators.

Hourglass can be a result of the simultaneous attack of several predators from more than one direction close to the centre of the prey group, which some predators, particularly cetacea do on propose to separate part of a prey school by splitting it off (e.g. Nøttestad, Axelsen 1999). Hourglass can also occur, when peripheral individuals at the two ends of the school swim to opposite directions which typically results in split of the prey group (Pitcher, Wyche 1983), and hourglass can be used to transfer the school from one location to another by individuals passing along the neck-like bridge (Pitcher, Wyche 1983).

Split, fountain and flash-expansion incur the disruption of the school structure often with some individuals becoming isolated and thus especially vulnerable to subsequent predation (Magurran, Pitcher 1987; Parrish 1989). Re-joining leaves confusion zones within the school which are targeted preferentially by some predators (Hobson 1968; Pitcher 1986). This increase in vulnerability has been suggested to explain the evolution of reluctance to apply these last resort behaviours (Pitcher, Wyche 1983).

Steep diving is the most common response of prey schools to visually hunting and air-breathing predators but requires early detection of the predation risk (e.g. Pitcher *et al.* 1996; Heithaus, Dill 2009; Vaughn *et al.* 2011; Wright *et al.* 2017). Once a prey school is surrounded by predators funnel formation has been documented to facilitate escape to deeper water which is counteracted by predators swimming underneath the prey school during the process of funnel formation. This predator behaviour which was observed in dusky dolphins, led to the restoration of a spherical shape of the fish school at the surface (Vaughn *et al.* 2010b, 2011).

Conclusively, the type of predator evasion applied by schooling fish depends on the number and type of predators (e.g. Pitcher *et al.* 1996; Nøttestad, Axelsen 1999; Axelsen *et al.* 2001) as well as on the length of the time lag between predator detection by the prey school and predator attack (Lima 1992; Morrell, Ruxton 2011). Predator-specific avoidance responses linked to differences in predator hunting techniques were found by numerous studies across a variety of taxa and ecosystems (Crowder *et al.* 1997; McIntosh, Peckarsky 1999; Turner *et al.* 1999; Eklov, Werner 2000; Owings *et al.* 2001; Stapley 2004; Templeton *et al.* 2005; Wirsing *et al.* 2010; Bulbert *et al.* 2015).

When faced with multiple predator types it may be most beneficial for a prey species to adopt a more general antipredator behaviour, which is effective against a wide range of predators such as grouping (Crowder *et al.* 1997; Krause, Ruxton 2002), but also evolve a range of risk-sensitive responses tailored to specific predators or attack modes (Lima, Bednekoff 1999; Relyea 2003; Kishida, Nishimura 2005) such as a variety of evasive group manoeuvres. Very

few of the group-level predator evasion manoeuvres described in Tab. 1 have been observed in cetacea (Rose, Payne 1991) which face a much narrower range of predators than small pelagic shoaling fish or squid (Chap. 2).

Table 1: Predator evasion manoeuvres

Formation	Description	Function
Bend	a bend in an otherwise circular or oval school in the area where predator is attacking	keeping minimum approach distance to a predator attacking a specific part of the school
Pseudopodium	several bends in an otherwise circular or oval school in areas where predators are attacking	keeping minimum approach distance to several predators attacking different parts of school
Vacuole	area of no fish inside the school enclosing a predator	keeping minimum approach distance to a predator which has penetrated the school
Nucleus	area of high density in a school	not described
Hourglass	school shaped like an hourglass	keeping minimum approach distance to predators attacking same part of school from >1 side, or transfer of school from one location to another by individuals passing along neck-like bridge
Funnel	cylindrical school with a height of at least twice the width	transfer of the school from one location to another esp. vertical escape to depth
Tight ball	sphere-shaped school of high density, circular movement of fish; response to prey herding	keeping minimum approach distance to predators circling the school
Split	school splits into ≥ 2 ; often followed by re-joining, joining creates confusion zone which is often attacked by predators	last resort behaviour in obligate shoaling species; can be response to predators trying to isolate part of a school
Flash expansion	'explosion' of school caused by individuals rapidly swimming to all directions	restoration of school structure; follows a reduction of inter-individual distance below a critical value; last resort behaviour
Fountain	splitting of school in front of and subsequent re-joining behind predator	last resort behaviour
Steep dive	school responds with steep dive to fast approaching predator or vessel	escape from visually hunting and air-breathing predators such as cetacea, pinnipeds, seabirds

References: Kuhlmann, Karst 1967; Hobson 1968; Pitcher, Wyche 1983; Pitcher 1986; Magurran, Pitcher 1987; Fréon *et al.* 1992; Similä, Ugarte 1993; Vabø, Nøttestad 1997; Nøttestad, Axelsen 1999; Axelsen *et al.* 2001; Gerlotto, Paramo 2003; Heithaus, Dill 2009; Paramo *et al.* 2010; Vaughn *et al.* 2011; Wright *et al.* 2017

Five out of nine types of coordinated evasion manoeuvres for which the function is known, serve the purpose of maintaining a minimum approach distance to predators. This means that attacks by predator groups from several directions have to cause compaction of the prey school. Numerous oceanic predators use this behaviour to cooperatively herd prey, thereby increasing their foraging efficiency (see below: Increased foraging efficiency). Hence behavioural adaptations which are thought to have evolved due to the effect of reducing predation risk are used by predators to facilitate predation.

More than 50% (24 out of 47) of the cetacea species included in this thesis have been documented to apply cooperative prey herding techniques across many geographic areas (Tab. 3) and this percentage may be higher since several offshore cetacea species are rarely encountered by researchers or feed at great depths. Hence their foraging behaviour is little understood. This poses the question why the forms of coordinated predator evasion listed above are so common in small pelagic shoaling fish. One approach to research this issue would be to quantitatively assess how commonly prey herding behaviour is used by cetacea and other predators of shoaling fish. To the author's knowledge only two studies have

quantified prey herding behaviour in this taxon. Bottlenose dolphins, *Tursiops truncatus*, of Little Bahama Bank have been documented to use cooperative herding techniques in 6% of feeding events (n: 94, Rossbach 1999) and 1.1% of observed groups of Commerson's dolphins, *Cephalorhynchus commersonii*, off Argentina used this behaviour (n: 4364, Coscarella et al. 2010). However, both studies were conducted in inshore or shallow water areas. Benoit-Bird, Au (2009) reported the consistent use of prey herding techniques by spinner dolphins, *Stenella longirostris*, off Hawaii and suggested that this behaviour may be critical in energy poor featureless environments in the tropical Pacific. More research is needed which quantifies the importance of prey herding in oceanic environments such as around oceanic islands where offshore conditions occur close to shore.

Communal defence

Communal defence behaviours as an advantage of group living are thought to have evolved secondarily to gregariousness and hence, are beneficial to survival but are not an evolutionary driver of congregation (Sillen-Tullberg, Leimar 1988). Communal defence has been documented in a number of baleen whale species and in sperm whales, *Physeter macrocephalus*, in response to killer whale attacks and in several delphinid species when fending off sharks.

Common dolphins which sought refuge next to a fisheries research vessel in response to a shark attack, herded juveniles against the boat while adults seemed to chase away the predators whenever one approached (AIBS 1967). Similar communal defence of young individuals by adults against sharks has been documented in Clymene dolphins, *Stenella clymene* (Springer 1967). Atlantic spotted dolphins, *Stenella frontalis*, and bottlenose dolphins have been observed to cooperatively fend off sharks at Great Bahama Bank (Herzing 2011). However, these are rather anecdotal observations. Data for any type of quantitative analysis of the significance of communal defence in delphinids are lacking.

Sperm whales targeted by killer whales either form a tight rank with heads facing their predators (e.g. Ambom et al. 1987; Gemmill et al. 2015) or form a rosette such that the animals arrange themselves in a circle, heads together, tails towards the periphery or vice versa (Nishiwaki 1962; Caldwell et al. 1966; Pitman, Chivers 1999; Pitman et al. 2001; Gemmill et al. 2015; Ponnampalam 2016). The latter has also been observed in response to harassment by short-finned pilot whales, *Globicephala macrorhynchus* (Weller et al. 1996) and false killer whales, *Pseudorca crassidens* (Palacios, Mate 1996). The same forms of rosette have been described in right whales attacked by killer whales (Payne 1992; Sironi et al. 2004; Ford, Reeves 2008). Calves are typically positioned in the centre of the rosette surrounded by adult individuals. Often the only physical defence observed is tail-slapping, or, particularly in sperm whales, none at all (Ambom et al. 1987; Pitman et al. 2001; Whitehead 2003; Ford, Reeves 2008; Gemmill et al. 2015).

Ford, Reeves (2008) suggested that baleen whales react in one of two modes when attacked by killer whales, depending on their swimming capabilities. Robust but non-hydrodynamically shaped, slow swimming but manoeuvrable species such as right, bowhead, *Balaena mysticetus*, humpback, *Megaptera novaeangliae*, and gray whales, *Eschrichtius robustus*, tend to engage in active physical defence, either as single individuals or mother-calf pairs, or as a group, whereas stream-lined fast swimming species of the genus *Balaenoptera* tend to flee by rapid directional movement away from the predators (Ford et al. 2005). If overtaken these species rarely engage in any type of defence (e.g. Ford et al. 2005; Alava et al. 2013). A similar pattern has been found in undulate species which may either try to outrun an attacking predator or fend off the predator (Mech 1966, Kruuk 1972).

In sperm whales which form matrilineal groups of related individuals, defence of calves increases the parents' fitness as well as the inclusive fitness of relatives. Large delphinid

congregations often consist of unrelated individuals or of mother-calf pairs which are unrelated to one another (Amaral 2005; Westgate 2005; Mirimin 2007; Stockin 2008; Viricel *et al.* 2008; Mirimin *et al.* 2011; Ball *et al.* 2017). However, cooperation in the defence of young individuals increases fitness if reciprocal and also increases the survival probability of other group members by maintaining a large enough group to benefit from dilution, confusion and predator swamping whereas the removal of one or several individuals from the group certainly reduces the dilution effect and may also reduce confusion and predator satiation, depending on the size of the congregation. If the survival probability of other group members is increased whether cooperation is reciprocal or not, then communal defence can be evolutionary stable even if group members are unrelated (Garay 2009).

Based on this review gregarious cetacea are most likely to benefit from the dilution and confusion effects, the selfish herd effect, predator swamping and increased vigilance efficiency. Due to the phenotypical heterogeneity of cetacea groups as a result of the common association of individuals of various size classes, cetacea pods are expected to be very large in species which experience a high risk of predation so as to counteract oddity.

Increased foraging efficiency

Possible foraging benefits derived from congregation include:

- Increased prey search efficiency
- Improved handling of shoaling prey by cooperative prey herding and prey debilitation
- Ability to capture and subdue larger prey items
- Increased prey capture success through prey escaping from one predator ending up in the search field of another (Major 1978)
- Reduction of kleptoparasitism

Increased prey search efficiency

Prey search efficiency can be increased in groups compared to single individuals through both, the ability to cover a larger search area and improved prey detection (many eyes hypothesis). Groups operate as an interacting array of sensors and effectors, gathering and analysing more information than could a lone individual (Sumpter 2010). Physical signals are converted into social cues, which amplify or attenuate group responses (Schilt, Norris 1997; Norris, Schilt 1988). Such an information transfer between individuals can produce synergism for group members which can lead to an increase in per capita foraging success with group size (e.g. Beekman *et al.* 2001; Halley, Burd 2004). If food is shared, then the entire congregation benefits from prey detection by any group member leading to a reduction in search time for affiliated individuals (Olson 1964; Treisman 1975; Eggers 1976; Sumpter 2010). In line with this finding fish (Pitcher *et al.* 1982; Pitcher 1986), sea gulls (Götmark *et al.* 1986; Hoffman *et al.* 1981) and dolphins (Norris, Prescott 1961; Saayman *et al.* 1973) were all found to locate food patches faster in larger congregations than individuals searching for prey alone or in small groups. Large prey patches often found in the oceanic environment which provide sufficient forage for numerous predator individuals and are easy to share strongly suggest that predator congregations may benefit from increased prey search efficiency.

If several prey patches are available then information transfer about prey patch quality can lead to both, a faster detection of variations in quality between the patches and faster switching to patches of higher profitability in larger compared to smaller groups (Pitcher, Magurran 1983). Hence congregation can improve foraging efficiency through faster identification of more profitable food patches.

Coordinated prey search has been observed in sperm whales (Whitehead 2003), killer whales (Ford *et al.* 1998), bottlenose dolphins (Bel'kovich *et al.* 1991), dusky dolphins (Markowitz 2004) and in common dolphins, *Delphinus delphis* (Gallo Reynoso 1991) which arrange themselves either in large spread out congregations often comprising many sub-groups (Gallo Reynoso 1991) or in a line formation of parallel individuals (Bel'kovich *et al.* 1991; Markowitz 2004). Based on these observations it has been suggested that large oceanic cetacea congregations organized in sub-groups which are traveling to the same direction spread out over a large area, often comprising several km² facilitate prey search by increasing the volume of the water column that can be searched at any one time (Norris, Dohl 1980a; Markowitz 2004). Such formations have been documented in numerous species (Tab. 2) and are typically characterized by small inter-individual distances of one to few body lengths within sub-groups (e.g. De Boer 2010) and larger inter-subgroup distances of 10's to 100s of meters (e.g. Baird *et al.* 2008b).

Table 2: Large cetacea pods organized in sub-groups spread out over several km²

Species	Area	Reference
Long-finned pilot, <i>Globicephala melas</i>	N-Atlantic	Buckland <i>et al.</i> 1991, Visser <i>et al.</i> 2014
	N-Nova Scotia	Ottensmeyer, Whitehead 2003
False killer	Hawaii	Shallenberger 1981; Baird <i>et al.</i> 2008a

Species	Area	Reference
Killer	NE-Pacific	Ford 1989; Ford <i>et al.</i> 1998, 2000; Miller 2006
Risso's dolphin, <i>Grampus griseus</i>	Gulf of Mexico	Jennings 1982
Bottlenose	South Africa	Saayman, Taylor 1973
Rough-toothed <i>Steno bredanensis</i>	Hawaii	Baird <i>et al.</i> 2008b
	Gabon	De Boer 2010
	Brazil	Lima <i>et al.</i> 2012
Spinner	Hawaii	Östman 1994; Lammers <i>et al.</i> 2006
Common	Arabian Sea off Oman	Al-Gheilani, Jayabalan 2010
	California Bight	Henderson <i>et al.</i> 2012
	New Zealand	Neumann, Orams 2003
	Mexico	Gallo Reynoso 1991
Southern right w.d., <i>Lissodelphis peronii</i>	New Zealand	Visser <i>et al.</i> 2004
Northern right w.d., <i>Lissodelphis borealis</i>	W-USA	Rankin <i>et al.</i> 2007
Burmeister's porpoi., <i>Phocoena spinipinnis</i>	SE-Pacific	Van Waerebeek <i>et al.</i> 2002
Chilean dolphin, <i>Cephalorhynchus eutropia</i>	Chile	Pérez-Álvarez <i>et al.</i> 2007

The larger the area covered by a group the more likely it would be to encounter a prey patch. Hence a larger congregation experiences a higher prey encounter rate than a smaller one (e.g. Norris, Prescott 1961; Saayman *et al.* 1973). Large congregations may then be beneficial in an environment where prey patches are scarce but large enough to provide sufficient amounts of forage to cover the energy demands of many individuals (Crook 1965).

Cooperative prey herding

Whereas the main selection pressure towards cooperative foraging in terrestrial social carnivores seems to be the ability to capture prey individuals larger than the predator itself (Kleiman, Eisenberg 1973), in the marine pelagic habitat, foraging related cooperation most often involves detection, formation or manipulation of congregations of small prey (Bartholomew 1942; Hiatt, Brock 1948; Norris, Prescott 1961; Saayman *et al.* 1973; Würsig, Würsig 1979; Hoffman *et al.* 1981; Partridge *et al.* 1983; Götmark *et al.* 1986; Goss 1888; Anderson 1991; Gallo Reynoso 1991; Similä, Ugarte 1993; Serfass 1995; Nøttestad *et al.* 2002b).

Giant trevallies, *Caranx ignobilis*, were found to be more successful hunters of shoaling prey when affiliated to a group of conspecifics (Major 1978; Schmitt, Strand 1982). Predator congregations were able to quickly break up anchovy shoals, resulting in increased numbers of prey becoming isolated and captured before an opportunity to reform or join a shoal arose.

Social river otters, *Londra canadensis*, of Prince William Sound, Alaska, were found to gain access to higher quality prey and require smaller home ranges compared to solitary individuals as a consequence of cooperative feeding on pelagic shoaling fish (Blundell *et al.* 2002). Solitary otters mainly prey upon intertidal demersal organisms such as Cottidae, Hexagrammidae, and crustaceans which are easier to capture but lower in quality (Bowyer *et al.* 1994; Anthony *et al.* 2000).

Spinner dolphins were shown to increase their access to shoaling prey by means of cooperative feeding compared to solitary foraging (Benoit-Bird, Au 2009). Hawaiian spinner dolphins which feed on shoaling prey affiliated to the boundary layer require an intake of 1.25-22 prey items/minute depending on prey size (2.5-10cm) (Benoit-Bird 2004). Animals composing the boundary community exhibit a mean length of about 5cm with a distribution

skewed toward smaller rather than larger individuals (Reid 1994). Since prey patches are large and of high caloric value (Benoit-Bird, Au 2003) dolphins are limited by time and thus foraging efficiency rather than by prey availability (Benoit-Bird 2004). In line with these findings spinner dolphins only feed in areas of the highest animal densities observed in the boundary layer, horizontally and vertically (Benoit-Bird, Au 2003) and still increase prey density by up to 200 times through cooperative herding (Benoit-Bird, Au 2009). This cooperative compaction of shoaling prey is thought to increase the number of food items which can be captured per unit time (Benoit-Bird, Au 2009). Such an increase in prey density would also enhance the efficiency of prey debilitation techniques such as ramming or hitting prey with various body parts since more prey individuals are debilitated with a single strike (e.g. Domenici *et al.* 2000).

Conclusively, cooperative prey herding provides access to high-quality shoaling prey by:

- reducing the escape probability of prey, thereby overcoming the higher manoeuvrability of smaller prey compared to larger predators (Domenici 2001; Vogel 2008)
- separating individuals from prey schools thereby overcoming the confusion effect
- increasing prey density which leads to both, a higher prey capture rate and enhanced efficiency of prey debilitation

Thus, predator individuals affiliated to groups which cooperatively herd prey may be of higher fitness than solitary conspecifics in an environment where prey grouping constitutes a common phenomenon, which suggests a selection pressure towards predator congregation in response to grouping of prey (Major 1978).

Cooperative hunting occurs when individuals coordinate actions, such that the probability of successful prey capture is increased among all participants (Sargeant *et al.* 2005). Cooperative prey herding is a foraging technique during which a group of predator individuals encircles a prey shoal by swimming around and under, thereby compacting and moving the same horizontally or vertically (Vaughn *et al.* 2010a). It is a form of prey manipulation which takes advantage of the natural schooling and flight behaviour of numerous crustacea, fish and cephalopod species (Heithaus, Dill 2009).

Herding of forage requires that the predator either circles a school of prey in increasingly tighter trajectories or drives the same against a barrier such as:

- the water surface (e.g. Würsig, Würsig 1979; Gallo Reynoso 1991; Fertl, Würsig 1995; Jefferson, Barros 1997; Acevedo-Gutiérrez 2002a; Nøttestad *et al.* 2002b; Holland 2008; Bernasconi *et al.* 2011; McDermott 2012; Domenici *et al.* 2014)
- a shoreline or a shoal (e.g. Nøttestad 2002; Neumann, Orams 2003; Burgess 2006)
- the seafloor (e.g. Rossbach 1999)
- a kelp bed (Iñíguez, Tossenberger 2007)
- a bubble net (e.g. Fertl, Würsig 1995; Burgess 2006; Kato, Perrin 2009; Wiley *et al.* 2011; Zaeschmar *et al.* 2013)
- other members of the predator group (Rossbach 1999; Neumann, Orams 2003; Burgess 2006; Gazda *et al.* 2005; Coscarella *et al.* 2010)
- anthropogenic barriers such as boats (e.g. Lodi, Hetzel 1999; Burgess 2006; Iñíguez, Tossenberger 2007; Zaeschmar *et al.* 2013).

Several types of barriers may be used simultaneously during a single prey herding event. Bubbles cause a strong avoidance reaction in shoaling fish and crustacea (Smith 1961; Blaxter, Batty 1985; Kieckhefer 1991; Akiyama *et al.* 1992; Sharpe, Dill 1997; Sharpe 2001), an effect which is used by numerous cetacea species. The white ventral colour pattern in a number of whales, dolphins and porpoises is thought to cause a flash effect when presented

to prey which scares and further herds the same (Würsig *et al.* 1990; Fertl, Würsig 1995; Heithaus *et al.* 2017).

Pelagic predators which have been documented to apply cooperative prey herding behaviour are:

- squid (Bigelow, Schroeder 1953)
- sharks, including oceanic whitetip, *Carcharhinus longimanus*, silky, *Carcharhinus falciformis*, and thresher sharks, *Alopias* sp., (Allen 1923; Strasburg 1958; Castro 1996; Aalbers *et al.* 2010)
- teleosts such as saithe, *Pollachius virens*, mackerel, *Scomber scombrus*, yellow tail amberjack, *Seriola lalandi*, dolphinfish, *Coryphaena hippurus*, bonito, *Sarda* spp., yellowfin tuna, *Thunnus albacares*, skipjack tuna, *Katsuwonus pelamis*, and Atlantic sailfish (Hiatt, Brock 1948; Alverson 1961; Schmitt, Strand 1982; Nøttestad 2002; Robinson, Tetley 2007; Holland 2008; McDermott 2012; Domenici *et al.* 2014; De Anchieta *et al.* 2015)
- seabirds, including African penguin, *Spheniscus demersus*, rhinoceros auklet, *Cerorhinca monocerata*, common murre, *Uria aalge*, American white pelican, *Pelecanus erythrorhynchos*, and the great white pelican, *P. onocrotalus*, (Goldsmith 1840; Rand 1954; Wrangham 1982; Grover, Olla 1983; Alcock 1984; Ryan *et al.* 2012)
- pinnipeds including Steller sea lion, *Eumetopias jubatus*, and Galápagos sea lion, *Zalophus wollebaeki* (Fiscus, Baines 1966; Heithaus *et al.* 2017; De Roy, Saplakoglu 2018)
- cetacea (Tab. 3)

Table 3: Species and areas for which cooperative prey herding has been documented

Species	Area	Reference
Fin whale, <i>Balaenoptera physalus</i>	Norway	Nøttestad <i>et al.</i> 2002b
	Gulf of California	Tershy 1992
	Newfoundland, Labrador	Whitehead, Carlson 1988
	NW-Atlantic	Tershy, Wiley 1992
Bryde's whale, <i>B. brydei</i>	not published	Kato, Perrin 2009
Minke whale, <i>B. acutorostrata</i>	NE-Pacific	Hoelzel <i>et al.</i> 1989; Kuker <i>et al.</i> 2005
Humpback whale	Alaska	Jurasz, Jurasz 1979; D'Vincent <i>et al.</i> 1985, Sharpe 2001
	Newfoundland, Labrador	Whitehead, Carlson 1988
	Gulf of Maine	Hain <i>et al.</i> 1982, 1995; Wiley <i>et al.</i> 2011
	Norway	Ingebrigtsen 1929
	South Africa	Cade <i>et al.</i> 2016
Balinville's beaked, <i>Mesoplodon densirostris</i>	Bahamas	Johnson <i>et al.</i> 2008
Long-finned pilot whale	Newfoundland (possibly herding)	Weilgart 1985; Weilgart, Whitehead 1990
	Norway (poss. herding)	Visser <i>et al.</i> 2014
False killer whale	New Zealand	Zaeschmar <i>et al.</i> 2013
	Gabon	Weir <i>et al.</i> 2013
Melon-headed w., <i>Peponocephala electra</i>	tropical E-Pacific	Jefferson, Barros 1997
Killer whale	Norway	Felleman <i>et al.</i> 1991; Nøttestad, Axelsen 1999; Nøttestad <i>et al.</i> 2002a; Shapiro 2008
	NE-Pacific	Ford <i>et al.</i> 1998
	Gulf of California	Brown, Norris 1956
	New Zealand	Constantine <i>et al.</i> 1998

Species	Area	Reference
Bottlenose dolphin	Florida	Gazda <i>et al.</i> 2005
	Bahamas	Roszbach 1999
	Texas	Shane 1977
	Scotland	Evans 1980
	Black Sea	Bel'kovich <i>et al.</i> 1991
	California	Leatherwood 1975; Bearzi 2006
	Mexico	Würsig 1986; Ballance 1992
	Argentina	Würsig, Würsig 1979
	New Zealand	Zaeschmar <i>et al.</i> 2013
	South Africa	Saayman <i>et al.</i> 1973
Rough-toothed dolphin	Mauritania	Addink, Smeenk 2001
	Azores	Steiner 1995
	Brazil	Lodi, Hetzel 1999
White-beaked d., <i>Lagenorhynchus albirostris</i>	NE-Atlantic	Evans 1982, 1991
Atlantic white-sided dolphin, <i>L. acutus</i>	not published	Rosster unpubl. in: Reeves <i>et al.</i> 1999
	Norway	Hamran 2014
Pacific white-sided, <i>L. obliquidens</i>	British Columbia	Heise 1996; Morton 2000
Dusky dolphin	New Zealand	Dahood, Benoit-Bird 2010; Vaughn <i>et al.</i> 2010, 2011
	Argentina	Würsig, Würsig 1980; Würsig 1986
	Namibia	Bernasconi <i>et al.</i> 2011
Fraser's dolphin, <i>Lagenodelphis hosei</i>	Caribbean	Watkins <i>et al.</i> 1994
Spinner dolphin	Fernando de Noronha	Silva <i>et al.</i> 2007
	Hawaii	Benoit-Bird, Au 2003; 2009
Atlantic spotted dolphin	Gulf of Mexico	Caldwell 1955; Siebenaler, Caldwell 1956; Springer 1957; Fertl, Würsig 1995
	Azores	Clua, Grosvalet 2001; Quéroil <i>et al.</i> 2008
Striped dolphin, <i>Stenella coeruleoalba</i>	Azores	Clua, Grosvalet 2001
Clymene dolphin	Gulf of Mexico	Fertl <i>et al.</i> 1997
Common dolphin	New Zealand	Neumann, Orams 2003; Burgess 2006
	California	Würsig 1979; Gallo 1984; Gallo Reynoso 1991
	Gulf of California	Norris, Schilt 1988
	Azores	Clua, Grosvalet 2001; Quéroil <i>et al.</i> 2008
Commerson's dolphin	N-Argentina	Coscarella <i>et al.</i> 2010
	Patagonia, Tierra del Fuego	Gewalt 1979; Mermoz 1980; Goodall <i>et al.</i> 1988; Iñíguez, Tossenberger 2007
Chilean dolphin	Chile	Crovetto, Medina 1991
Dall's porpoise, <i>Phocoenoides dalli</i>	NE-Pacific	Norris, Prescott 1961; Miller 1987; Jefferson 1991
	NW-Pacific	Miyazaki <i>et al.</i> 1984

Herding behaviour may be combined with the isolation of a part of a large prey school (Schmitt, Strand 1982; Pitcher, Wyche 1983) and with raising of fish schools from depths up to 150m while or before herding which has been documented in killer whales and dusky dolphins (Nøttestad *et al.* 2002a; Bernasconi *et al.* 2011).

Predators have been found to feed on isolated stray individuals (Kishinouye, cited in: Hiatt, Brock 1948; Bel'kovich *et al.* 1991; Addink, Smeenk 2001), or along the periphery of prey schools (e.g. Heise 1996; De Anchieta *et al.* 2015), or by penetrating the same (e.g. Heise

1996; Nøttestad 2002; Neumann, Orams 2003) or both during the same feeding event (Heise 1996).

The following types of prey have been documented to be herded by predators for feeding purposes:

- shoaling crustacea (Heise 1996; Heithaus *et al.* 2017)
- shoaling squid (Caldwell 1955; Springer 1957; Strasburg 1958; Fiscus, Baines 1966)
- small shoaling fish such as clupeids and myctophids (e.g. Alverson 1961; Fiscus, Baines 1966; Fertl, Würsig 1995; Acevedo-Gutiérrez 2002a; Nøttestad *et al.* 2002b; Bernasconi *et al.* 2011)
- large shoaling fish such as kahawai, *Arripis trutta*, yellowfin tuna and Atlantic sailfish, *Istiophorus albicans* (Weir *et al.* 2013; Zaeschmar *et al.* 2013; De Roy, Saplakoglu 2018)
- gregarious marine mammals (Brown, Norris 1956; Constantine *et al.* 1998; Ford *et al.* 1998)

Communal prey debilitation

Prey debilitation involves the impairment of prey by the predator through disorientation or injury before consumption, thereby reducing the prey's chance of escape. Several oceanic predators use prey debilitation when targeting shoals of small pelagic fish either solitarily, or communally in groups, often in combination with prey herding. Communal prey debilitation implies that several individuals debilitate prey which is then shared. Hence a predator individual may feed on prey which it has debilitated itself and on prey individuals which have been impaired by other predator group members.

Thresher sharks, which feed on small to medium-sized shoaling fish and squid (Gubanov 1972; Stick, Hreha 1989; Bedford 1992; Preti *et al.* 2001, 2008, 2012; Polo-Silva *et al.* 2007, 2013; Finotto *et al.* 2016), collectively herd and disorient, stun or kill prey before consumption with strikes of the exaggerated upper lobe of their caudal fin (Allen 1923; Budker 1971; Castro 1996; Aalbers *et al.* 2010; Oliver *et al.* 2013).

Sailfish, marlins, spearfish and swordfish debilitate small pelagic fish such as sardines, anchovies, mackerels, or jack mackerels by strikes with their extended rostra which typically results in injury of prey individuals (Gudger 1940; Talbot, Penrith 1964; Scott, Tibbo 1968; Stillwell, Kohler 1985; Frazier *et al.* 1994; Shimose *et al.* 2007; Habegger 2014; Habegger *et al.* 2015). Particularly sailfish often hunt in groups and herd their prey before debilitating the same by alternately slashing through a prey school (Nakamura 1985; Domenici *et al.* 2014; Herbert-Read *et al.* 2016). Often debilitation leads to the isolation of injured prey individuals which cannot keep up with their school. These individuals are then quickly captured by sailfish (Herbert-Read *et al.* 2016). A modelling study has shown that this form of communal prey debilitation increases per capita capture rates compared to solitarily hunting individuals (Herbert-Read *et al.* 2016).

Several cetacea species have been documented to disorient and stun prey with percussive leaps and tail slaps after cooperatively herding the same, including bottlenose dolphins (Hamilton, Nishimoto 1977; Connor *et al.* 2000b), dusky dolphins (Würsig, Würsig 1980), common dolphins (Wells *et al.* 1987; Shane 1990; Burgess 2006) and killer whales (Similä, Ugarte 1993; Nøttestad, Similä 2001; Simon *et al.* 2005; Deecke *et al.* 2011; Samarra, Miller 2015). Up to at least 33 prey individuals may be struck by a single tail slap of a killer whale (Domenici *et al.* 2000). In the NE-Pacific groups of piscivorous killer whales commonly take turns debilitating prey for up to 20min before the stunned fish is consumed by the predators (Felleman *et al.* 1991).

Ability to capture larger prey items

In solitary fish predators hunting success was found to decline linearly as the prey size to predator size ratio increases (Juanes *et al.* 2002). Grouping may be an adaptation which overcomes this effect and enables predators to more efficiently hunt large prey. By communal hunting some predators subdue prey larger than themselves which would either exceed the capabilities of or constitute too high a risk of injury for solitary individuals (Hector 1986; Gese *et al.* 1988; Bednarz 1988; Fanshawe, FitzGibbon 1993; Creel, Creel 1995).

In the oceanic environment broadnose sevengill sharks, *Notorynchus cepedianus*, use group hunting techniques to tackle large prey items such as cape fur seals, *Arctocephalus pusillus*, (Ebert 1991b). A group of 10-20 dusky sharks, *Carcharhinus obscurus*, ranging in length between 2-3m successfully attacked a ~4m long humpback whale calf over many hours which was without mother or escort, off South Africa (Dicken *et al.* 2015). A group of two smooth hammerhead sharks, *Sphyrna zygaena*, fatally attacked a solitary pantropical spotted dolphin off Brazil (Sucunza *et al.* 2015) and an 8-9m humpback whale was fatally attacked by dozens of sharks of several species including tiger, *Galeocerdo cuvier*, and bull sharks, *Carcharhinus leucas*, and bronze whalers, *Carcharhinus brachyurus*, off W-Australia (Pitman *et al.* 2015). However, such incidents remain anecdotal and the commonness and importance of grouping in sharks in general, and its effects on foraging efficiency in particular have not been quantified by any study to the author's knowledge.

The only marine predators known to regularly use communal hunting techniques to kill and feed on large prey items, sometimes exceeding their own body size are killer whales. Groups of mammal-eating killer whales regularly feed on various species of baleen whales, including blue, *Balaenoptera musculus*, fin, sei, *B. borealis*, Bryde's, minke, humpback, northern and southern right, bowhead and gray whales and also take other large-bodied species such as sperm whales, pygmy, *Kogia breviceps*, and dwarf sperm whales, *K. sima*, beaked whales, belugas, *Delphinapterus leucas*, narwhals, *Monodon monoceros*, pilot and false killer whales, dolphins, porpoises and pinnipeds (e.g. Shevchenko 1975; Yukhov *et al.* 1975; Smith *et al.* 1981; Jefferson *et al.* 1991; George, Suydam 1998; Ternullo, Black 2002; Morrice 2004; Visser *et al.* 2008; Ferguson *et al.* 2010, 2012a,b; Barrett-Lennard *et al.* 2011; Dunn, Claridge 2014; Pitman *et al.* 2015; Wellard *et al.* 2016; Chap. 2). Subduing large prey by communal hunting seems to represent the main feeding mode of mammal-eating populations. NE-Pacific offshore killer whales were suggested to regularly feed on sharks (Ford *et al.* 2011) which have also been documented to constitute an important part of the diet of some killer whales off New Zealand (Visser *et al.* 2000; Visser 2005). Species include Pacific sleeper sharks, *Somniosus pacificus*, (Ford *et al.* 2011), common thresher, *Alopias vulpinus*, smooth hammerhead (Visser 2005) and shortfin mako sharks, *Isurus oxyrinchus*, (Visser *et al.* 2000).

Communal hunting techniques are manifold in this species. However, in the NE-Pacific and in the N-Atlantic mammal-eating killer whales were found to form smaller groups than piscivorous killer whales the former comprising 2-13 individuals (e.g. Baird, Dill 1996; Ford *et al.* 1998; Baird, Whitehead 2000; Ternullo, Black 2002; Beck *et al.* 2012). Groups of >10 members have only been found typical when gray whales are attacked (Ternullo, Black 2002), small congregations of 2-3 individuals seem ideal for capturing pinnipeds and Dall's porpoises (Hoelzel 1991; Baird, Dill 1996; Baird, Whitehead 2000; Higdon *et al.* 2012). A median group size of four (mean: 6) has been found for predation on bowhead whales and seven for predation on monodontids (beluga and narwhal) (Higdon *et al.* 2012). Larger group sizes of >20 individuals have been documented in Antarctic mammal-eating killer whales, but sample size was low (Pitman, Ensor 2003; Pitman *et al.* 2011). The analysis of group size patterns in killer whales is beyond the scope of this study but foraging techniques, calf care and cultural transmission are all likely to play a role.

Avoidance of kleptoparasitism

The role of protection of captured prey from kleptoparasitism by scavengers, a known benefit of communal foraging in terrestrial carnivores such as wolves and African wild dogs (Thurber, Peterson 1993; Gorman *et al.* 1998; Vucetich *et al.* 2004; Trinkel, Kastberger 2005), has yet to be discovered in the oceanic environment. Scavenging, at least opportunistically, is thought to be one of the most common feeding tactics of various oceanic shark species (e.g. Carey *et al.* 1982; Pratt *et al.* 1982; Compagno 1984; Stevens 1984; Casey, Pratt 1985; Seagars, Henderson 1985; Cliff *et al.* 1990; Ebert 1991b; Long, Jones 1996a; Compagno *et al.* 1998; Smith, Baco 2003; Heithaus 2004; Curtis *et al.* 2006; Dicken 2008; Leclerc *et al.* 2011; Chap. 2).

Both white and tiger sharks aggregate around carrion (e.g. Heithaus 2004; Martin *et al.* 2005). White sharks have been observed scavenging a dead whale concurrently with tiger sharks (Dudley *et al.* 2000) but seemed to defend carcasses from both, conspecifics and heterospecifics in other incidents (e.g. Pratt *et al.* 1982; McCosker 1985; Long, Jones 1996a). If prey caught by broadnose sevengill sharks is not consumed quickly conspecifics as well as other shark species tend to appear and scavenge the kill (Ebert 1991b). Sevengill sharks feeding simultaneously on a carcass, side by side and without aggression, are usually of similar size, without segregation or signs of social hierarchy. However, the arrival of larger individuals would push smaller ones toward the group's periphery, away from the food source (Ebert 1991b). These observations indicate that avoidance of kleptoparasitism may play a role in grouping behaviour of sharks but information about the role of group size is lacking.

The same applies to a number of other oceanic species. Kleptoparasitism has been documented in pinnipeds and piscivorous fish (e.g. Dahood, Benoit-Bird 2010) and in a number of seabird species (e.g. Furness 1987; Garthe, Hüppop 1998; Shealer 2002). Cetacea have been observed chasing away other species from herded prey balls (Shane 1995; Acevedo-Gutiérrez *et al.* 1997; Clua, Grosvalet 2001) but especially in oceanic waters where prey patches tend to be large mono- and polyspecific groups are typically found feeding together without aggressive behaviour (e.g. Gallo Reynoso 1991; Black 1994; Bearzi 2006; Zaeschmar *et al.* 2013, 2014; Findlay *et al.* 2017), indicating that the avoidance of kleptoparasitism does not represent an important determinant of group size in oceanic cetacea.

Increased reproductive efficiency

- Reproductive benefits of grouping include:
- mate finding
- mate choice
- male access to females
- protection of young from predation
- food supply to young
- communal teaching of young

Lekking - mate choice efficiency and access to females

Lekking, the gathering of males at traditional places (leks) for mating to engage in competitive displays which attract females can lead to a number of reproductive benefits to species which mate at a set time of year.

Inter-individual competition of males for mating opportunities with females has been suggested to entail a positive correlation between the size of a lek and the average quality of males present (Sutherland 1996). The best male of a large group was found to be, on average, fitter than the best male of a small congregation (Janetos 1980; Kokko 1997).

If males have to compete for the most profitable sites on a lek, then individual positioning on a lek provides a measure of male quality to females such that higher-quality males occupy central locations (e.g. Bro-Jørgensen 2002). This correlation can be used by females to facilitate decision making towards a mating partner and hence, can increase a females fitness, if her young have higher chances of survival due to reproduction with a high-quality male (Fiske *et al.* 1998; Kokko *et al.* 1999a,b). As a consequence, copulations are not evenly distributed between males but skewed such that some individuals attract more females than their fair share (Bradbury *et al.* 1985; Mackenzie *et al.* 1995; Kokko *et al.* 1998, 1999a).

In some species females are more attracted to, and more likely to copulate during each visit of larger leks, leading to a positive correlation between the average number of copulations per male and lek size (Sutherland 1996). Lekking would then increase the fitness of desirable males but may reduce the fitness of less successful individuals due to competition for females. However, the enhanced total number of females copulating may compensate for this imbalance such that even less preferred individuals achieve more copulations by remaining in the lek than they would from dispersing (Widemo, Owens 1995; Kokko 1997).

In cetacea lekking has only be suggested in piscivorous killer whales which form congregations of up to 100 individuals (Bigg *et al.* 1987; Ivkovich *et al.* 2007) that seem to facilitate mating (Matkin *et al.* 1997; Filatova *et al.* 2009). A mating system similar to leks in which males attract females by singing or gain excess to the same by direct competition in coalitions has been proposed in humpback whales (Clapham 1996). However, this lekking behaviour occurs across large areas, Hence, the spatial characteristic of classic leks is absent and the term 'floating lek' has been adopted instead.

Male and female sperm whales gather in certain areas such as the Azores and Galápagos to both feed and reproduce (Whitehead 1993; Pinela *et al.* 2009). Females seem to approach males but displays by males have not been described and fights between males competing for females are rare (Whitehead 1993; Christal, Whitehead 1997; Gordon *et al.* 1998; Whitehead 2003; Coakes, Whitehead 2004).

Smaller odontoceti of tropical and subtropical regions typically reproduce year-round (e.g. Norris, Dohl 1980b; Perrin *et al.* 1985; Perryman, Lynn 1993; Ferrero, Walker 1995; Danil, Chivers 2007; Lares, Chivers 2009) and therefore lack the temporal requirements of lekking.

Male coalitions - access to females

Access to oestrus females is a main driver for sociality in males (Wrangham 1980; Clutton-Brock 1989; Kappeler, Schaik 2002). Males of numerous mammalian species including lions, *Panthera leo*, (Bertram 1975; Packer *et al.* 1990, 1991), cheetahs, *Acinonyx jubatus*, (Caro

1994) and baboons, *Papio* sp. (Noë 1994) form alliances to gain access to, or defend, females. Lion male coalitions were found to retain a harem for longer than single individuals (Bertram 1975).

Access to females is an important determinant of fitness in cetacea, as females give birth to a single calf at a time and have long inter-birth intervals (Whitehead, Mann 2000). In situations where females form relatively stable congregations, coalitions of males may exclude other males from accessing a group of females (Gowans *et al.* 2008). It is therefore not surprising that males of several delphinid populations and species form alliances, including bottlenose dolphins (e.g. Connor *et al.* 2000b), Atlantic spotted dolphins (Elliser, Herzing 2014b) and spinner dolphins (Johnson, Norris 1994).

Male bottlenose dolphins form alliances consisting of a varying number of individuals who in turn may form moderately strong associations with one to two other alliances (2nd and 3rd order alliances) (Elliser, Herzing 2014b; Connor, Krützen 2015; Connor *et al.* 2017). The function of these associations seems to be increased efficiency in competition for females which often involves defence against, or attack of other alliances (Connor *et al.* 1992). Alliances are formed in certain geographical areas including Australian waters (Moller *et al.* 2001), Doubtful Sound, New Zealand (Lusseau *et al.* 2003), Sarasota Bay, Florida (Owen *et al.* 2002), and the Bahamas (Parsons *et al.* 2003). Alliance size has been suggested to depend upon male competitive ability as well as the number of males competing for a mating partner (Whitehead, Connor 2005) and may vary within a single social network across small spatial scales (Connor *et al.* 2017).

Male alliances consist of closely related individuals in some populations (Krützen *et al.* 2003; Parsons *et al.* 2003), and of randomly related members in others (Möller *et al.* 2001; Owen 2003) and may last for several years when individuals form strong bonds or may be short-term with lower levels of association (Wiszniewski *et al.* 2012). Alliances with a high level of inter-individual relatedness do not persist longer than alliances between unrelated individuals (Wiszniewski *et al.* 2012). In Atlantic spotted dolphins of Little Bahama Bank male alliances not only defend females against conspecific males but also fend off attempted approaches and copulations by male bottlenose dolphins which seems to explain a larger size of alliances in this population (Herzing, Johnson 1997; Herzing, Elliser 2013; Elliser, Herzing 2016).

According to modelling studies males should always form alliances in order to improve competitiveness for females, unless the rate at which receptive females encounter males is low, with the average number of males per receptive period being less than one (Whitehead, Connor 2005; Connor, Whitehead 2005). Yet in many species and populations such associations are not found (e.g. Möller 2012) indicating that not all factors affecting the effectiveness of male alliances are understood (Connor *et al.* 2017). High food competition and large discrepancies in resource-holding capabilities among males may render alliances inefficient (e.g. Noë 1994) as could a lack of effective male dominance over females combined with female choice for particular males and promiscuity favouring sperm competition between males over defence of females (Whitehead, Connor 2005).

Alloparental care

Grouping beyond the mother-calf pair may be required for efficient care for calves in species or populations for which fitness is related to social learning, teaching, calf protection and alloparental care.

A number of studies on various mammalian species found that mothers prioritize the safety of their young over foraging efficiency (Kohlmann *et al.* 1996; Main *et al.* 1996) and form groups of a size which is optimal for offspring survival (e.g. Packer *et al.* 1990; Schmidt, Mech 1997; Courchamp *et al.* 2002). House mice, *Mus musculus*, are more successful in pup rearing when affiliated to a communal nest than single females which has been ascribed to the fact that a

given female suckles not only her own offspring but also those of her breeding partners even when the latter are unrelated and unfamiliar (König 1994).

Similar alloparental care has been documented in a number of oceanic cetacea species including sperm (Best *et al.* 1984; Gordon 1987; Mesnick 2001; Gero 2005; Gero, Whitehead 2007; Gero *et al.* 2009), killer (Bigg *et al.* 1987; Waite 1988) and pilot whales (Augusto *et al.* 2017), belugas (Bel'kovitch, Sh'ekotov 1993; Leung *et al.* 2010; Krasnovaa *et al.* 2014), bottlenose (Caldwell, Caldwell 1966; Mann, Smuts 1998; Gaspar *et al.* 2000; Sakai *et al.* 2016), spinner (Johnson, Norris 1994) and Atlantic spotted dolphins (Herzing 1996; Weinpress, Herzing 2015) and was found to involve adult males in addition to females in killer whales (Bigg *et al.* 1990), pilot whales (Augusto *et al.* 2017), bottlenose (Lusseau 2007) and Atlantic spotted dolphins (Weinpress, Herzing 2015).

Alloparental care may include:

- escorting of calves by individuals other than a parent (e.g. Caldwell, Caldwell 1966; Bigg *et al.* 1987, Gordon 1987; Arnbom, Whitehead 1989; Gordon *et al.* 1998; Gero *et al.* 2009)
- disciplining of young (Weinpress, Herzing 2015)
- allosuckling (Best *et al.* 1984; Gordon 1987; Smolder 1988; Gaspar *et al.* 2000; Gero 2005; Gero, Whitehead 2007; Gero *et al.* 2009; Leung *et al.* 2010; Sakai *et al.* 2016)
- protection of calves from predation while their mother is foraging (Arnbom, Whitehead 1989; Bel'kovitch, Sh'ekotov 1993; Herzing 1996; Whitehead 1996)
- social learning of calf-caring skills (Mann, Smuts 1998)
- complete adoption of calves which have lost their mother (Gaspar *et al.* 2000; Sakai *et al.* 2016).

In sperm whales alloparental care and the protection of offspring have both been identified as main drivers of sociality (Arnbom, Whitehead 1989; Weilgart *et al.* 1996; Whitehead 1996; Lettevall *et al.* 2002). Calves cannot keep up with the mother's diving capabilities and are therefore left at the surface with other adult individuals which are thought protect calves from potential predators while their mother is foraging (Whitehead 1996; Connor *et al.* 1998).

Protection of young from predation while the mother is foraging has also been suggested as a main benefit of alloparental care in beluga whales (Bel'kovitch, Sh'ekotov 1993) and Atlantic spotted dolphins (Herzing 1996). However, studies which quantify the significance of grouping for successful rearing of calves and which identify the optimal group size for alloparental care are lacking.

In bottlenose dolphins escorting of calves by individuals other than the mother has been found to benefit juvenile individuals in learning care-giving skills rather than benefiting mothers (Mann, Smuts 1998). Inexperienced females that never raised young before were more likely to escort new-borns than were experienced females, and mothers foraged less when their young were accompanied by escorts than when mothers were with her calves. This study emphasizes the importance of the quantification of potential benefits of alloparental care.

In pilot whales the amount of alloparental care was found to vary between years such that during a 3-year study 85.7% of calves, 80.6% of calves and 63% of calves had alloparents (Augusto *et al.* 2017). Within- or between-year alloparental care reciprocity was lacking, suggesting that alloparental care is a by-product of this species' social structure and entails a very small cost to the alloparent's fitness (Augusto *et al.* 2017). Adoption of unrelated calves by adult female bottlenose dolphins even across species, further indicates that kinship and social relationships may not play an important role in alloparental care in cetacea (Gaspar *et al.* 2000; Sakai *et al.* 2016).

Few accounts of group size in species with alloparental care are available. In the White Sea beluga females with calves form groups of 2-8 individuals (Bel'kovitch, Sh'ekotov 1993; Krasnovaa *et al.* 2014). Very rarely are congregations with calves of up to 17 individuals observed (Bel'kovitch, Sh'ekotov 1993). Social units of sperm whales which have been suggested to be evolutionarily driven by alloparental care (Weilgart *et al.* 1996; Whitehead 1996; Lettevall *et al.* 2002; Gero *et al.* 2013) typically consist of 7-12 individuals (e.g. Whitehead, Kahn 1992; Coakes, Whitehead 2004; Jaquet *et al.* 2005; Gero *et al.* 2009; Jaquet, Gendron 2009; Whitehead *et al.* 2012). Sexually mature males which very rarely participate in calf care do not form long-term bonds and seldom congregate (Lettevall *et al.* 2002). In Atlantic spotted dolphins of Little Bahama Bank which were found to provide alloparental care to their young (Herzing 1996; Weinpress, Herzing 2015) groups containing calves average 13 individuals whereas groups without calves comprise about 6 individuals (Elliser, Herzing 2014a).

Alloteaching of young has been suggested in killer whales (Guinet, Bouvier 1995). Thereby the adult individual seemed to teach the calf the prey capture technique of intentional stranding on pinniped breeding beaches used by mammal-eating killer whales off the Crozet Archipelago and off Punta Norte, Argentina.

The only study which has quantitatively assessed teaching in cetacea found that Atlantic spotted dolphin mothers consistently chase prey significantly longer and make significantly more referential body-orienting movements in the direction of the prey during foraging events when their calves are present than when their calves are absent, regardless of whether they were foraging alone or with another non-calf dolphin. However, all observations involved only the mother-calf pair (Bender *et al.* 2009). Young coastal bottlenose dolphins (Mann, Sargeant 2003) and sperm whales (Whitehead 2003) likewise appear to learn foraging techniques predominantly from their mothers. Anecdotal accounts of possible teaching related to foraging in rough-toothed dolphins involved two individuals (Lodi, Hetzel 1999; Addink, Smeenk 2001).

Calves of dusky and common dolphins have been observed to be present during or participate in prey herding (e.g. Würsig, Würsig 1980; Burgess 2006), which may be related to learning behaviour, but studies dedicated to the transmission of cooperative prey herding techniques from adults to offspring are lacking despite the fact that prey herding is implemented by most oceanic cetacea species (Chap. 3). Foraging mostly occurs solitarily or in small groups or sub-groups in cetacea. Further studies on this subject should explore whether or not group or sub-group size changes in the presence of calves to identify the effect of teaching and learning on group size. Unfortunately, most accounts of possible teaching and of other forms of calf care in the literature do not mention the size of groups on which the observations were made.

Conclusively these studies indicate that congregation is likely to increase calf fitness through alloparental care, but the group size required for these fitness benefits is below 15. Hence alloparental care does not explain the formation of larger groups.

Calf protection

Since calves are preferentially attacked by sharks (Chap. 2) dilution and confusion effects and predator swamping are reduced (Beauchamp 2017) unless congregations are very large containing many young individuals such that calves alone can generate dilution and confusion. Hence if calf protection is the main evolutionary driver for congregation in cetacea then pods containing calves should be much larger than those which do not. Species which reproduce year-round would be expected to form consistently large groups whereas species with seasonal calving should form large pods only during calving season.

Calves or mother-calf pairs tend to be pooled in sub-groups in common dolphins (Chivers *et al.* 2016), spinner dolphins (Norris, Dohl 1980a), pantropical spotted dolphins (Kasuya *et al.* 1974), striped dolphins (McBride, Hebb 1948; Kasuya 1972; Williams *et al.* 2002) and large

congregations of narwhals (Marcoux *et al.* 2009). These sub-groups can either be randomly distributed across the pod (Marcoux *et al.* 2009; Chivers *et al.* 2016) or may be herded to central locations by adult individuals (McBride, Hebb 1948; Kasuya 1972; Kasuya *et al.* 1974; Norris, Dohl 1980a; Williams *et al.* 2002). The pooling of calves in sub-groups is expected to reduce predation risk through increased dilution and confusion effects, predator swamping and reduced oddity.

If calves are typically unrelated then large congregations reduce the risk for adults that a related calf is killed by a predator and may consequently increase the inclusive fitness of adult individuals affiliated to the pod. This is particularly true for adult females since males seem to rarely be related to calves associated with their groups (Amaral 2005; Westgate 2005; Mirimin 2007; Stockin 2008; Viricel *et al.* 2008; Mirimin *et al.* 2011). A high level of unrelatedness between mother-calf pairs of large congregations has been revealed through genetic analysis of both, individuals involved in mass-strandings of N-Atlantic and New Zealand common (Westgate 2005; Mirimin 2007; Stockin 2008; Viricel *et al.* 2008), and in N-Atlantic white-sided dolphins (Amaral 2005; Mirimin *et al.* 2011) and N-Atlantic common dolphins sampled in their natural environment (Ball *et al.* 2017). Females of these pods consistently shared the same reproductive state and are accompanied by calves of similar age. Juveniles above age 2-3 were missing. Preferential associations of females with other females of similar reproductive state has also been found in common and Indo-Pacific bottlenose dolphins (Wells *et al.* 1987; Möller, Harcourt 2008) striped dolphin off the Pacific coast of Japan (Miyazaki, Nishiwaki 1978).

The more calves are affiliated to the pod the stronger is the dilution effect and the smaller the risk of every calf to become the target of a predator attack. The more unrelated calves are present the less likely it is that a related calf is killed by a predator. This may drive the formation of large congregations of unrelated individuals in oceanic waters.

It would then follow that these congregations are initiated by adult females with calves which associate with other females of similar reproductive state. Lactating females are also the individuals with the highest energy requirements (Trivers 1972; Emlen, Oring 1977) and hence would be expected to lead these groups (Fischhoff *et al.* 2007; Conradt *et al.* 2009; Sumpter 2009). Affiliated adult males may benefit from both much reduced predation risk through association with more vulnerable young and females and continuous mating opportunities. These fitness benefits of all associated individuals may make large oceanic congregations an evolutionarily stable strategy in areas where sufficient amounts of prey can be found to cover the energy needs of such groups.

Besides the formation of large groups other behavioural adaptations can reduce predation risk of calves. Examples are calving seasonality and habitat shifts. A distinct seasonal peak in calving for bottlenose dolphins in Little Bahama Bank despite its tropical latitude was found to coincide with an inverse seasonal peak in the risk of predation by sharks inferred by the incidence of fresh shark-bite wounds (Fearnbach *et al.* 2012). Hence the authors suggested that predation risk by sharks may be a selective force for calving seasonality in this area.

Examples for habitat shifts during calving season are New Zealand dusky and Hector's dolphins which both occur close to shore when groups comprise young calves and are distributed more offshore during the rest of the year (Cipriano 1985; Slooten *et al.* 2006). In these species shelter provided by shallow coastal waters is thought to reduce predation risk of calves (Weir *et al.* 2008b; Markowitz 1012). Balaenopterid whales predominantly calf in oceanic waters far from land (Ford, Reeves 2008) which likely reduces predation by killer whales due to lower densities of this species in these areas (Forney, Wade 2006). Dall's porpoises, too show a seasonal habitat shift from offshore to coastal areas in synchrony with calving (e.g. Miyashita, Kasuya 1988).

The largest suggested habitat shift in response to predation risk to calves is the long-distance migration from temperate, subpolar and polar feeding areas to tropical breeding areas in several baleen whale species (Ford, Reeves 2008). These migrations have been suggested

to represent a behavioural adaptation to killer whale predation on calves (Corkeron, Connor 1999; Ford, Reeves 2008).

Group decision making and increased navigation accuracy

Theoretical (Larkin, Walton 1969; Torney *et al.* 2009; Guttal, Couzin 2010; Codling, Bode 2014; De Luca *et al.* 2014) and empirical (Biro *et al.* 2006; Flack *et al.* 2012; Berdahl *et al.* 2013; Mueller *et al.* 2013; Irisson *et al.* 2015; Berdahl *et al.* 2016b) work across many animal taxa suggests that consensus decision-making, the process of reaching a consensus at group level when choosing between two or more mutually exclusive actions (Conradt, Roper 2005; King *et al.* 2008; Sueur, Petit 2008a,b) in animal groups can significantly improve navigation accuracy. In line with the 'many wrongs principle' (Simmons 2004; Berdahl *et al.* 2013) by which averaging over many independent estimates tends to suppress outliers, collective navigation was found to be more accurate than solitary navigation even when all group members have limited navigational ability and there are no leaders (Bergmann, Donner 1964; Wallraff 1978; Tamm 1980; Conradt, Roper 2005; Codling *et al.* 2007; King, Cowlshaw 2007; Dell'Arciccia *et al.* 2008; Faria *et al.* 2009). In congregations sensory, memory and inherited information is pooled, and individual navigational errors are suppressed or reduced by interactions between group members (Simmons 2004). Quorum sensing arises at the group level from individuals modulating their speed and direction in response to external information and through social interactions, only requiring rudimentary cognition. In this way groups are more efficient than single individuals in retrieving information from the environment (Conradt 2011; Ward *et al.* 2011; Berdahl *et al.* 2013).

With quorum sensing the probability that an individual adopts the same choice as others in the group increases in a non-linear fashion with the number of individuals that have already made that choice. Even though this can lead to all individuals making the wrong decision, in a large group chances are that at least some individuals possess the right information and act as leaders in those situations (Couzin *et al.* 2005; Sumpter *et al.* 2008; Ward *et al.* 2011). Modeling studies based on empirical observations have shown that the level of improvement in a group's navigation accuracy compared to a solitary individual depends on the group's social structure such that social networks, a number of individuals interconnected via social ties between them (Krause *et al.* 2015), lead to more precise navigation than leaderless groups, but the highest accuracy is achieved when individuals are organized such that each individual has a strong connection with one other group member only (Bode *et al.* 2012b; Flack *et al.* 2015; Franks *et al.* 2015). In this way a predetermined chain along which movement decisions cascade emerges (Flack *et al.* 2015). The more members are connected, the more the group resembles a homogeneous network and becomes similar to a no-social-structure situation. As a consequence, there is little improvement in navigation accuracy in highly connected social networks compared to leaderless groups.

Several studies have shown that collectively migrating groups can be led by a small proportion of actively navigating individuals, while the greater part of the group adopts socially facilitated movement behaviour, as long as the navigating group members possess a combination of navigational knowledge and an influential social network position (Guttal, Couzin 2010; Bode *et al.* 2012a; Zafeiris, Vicsek 2013). Since leadership is determined by knowledge (e.g. Ben-Yashar, Nitzan 1997), experience (e.g. Flack *et al.* 2012) or motivational differences (e.g. Smith *et al.* 2015) in many species, different group members may emerge as leaders on different occasions (distributed leadership) (Ben-Yashar, Nitzan 1997; Pyritz *et al.* 2011; Strandburg-Peshkin *et al.* 2015). Typical leaders are older individuals (Feist, McCullough 1976; Maransky; Bildstein 2001; Krause 2002; Couzin, Krause 2003; McComb *et al.* 2001, 2011; Brent *et al.* 2015), individuals with central positions in their social network (see below) or lactating females (Fischhoff *et al.* 2007; Smith *et al.* 2015).

In Doubtful Sound, New Zealand, bottlenose dolphin pods which show high fission-fusion dynamics the most socially connected individuals which frequently move between groups, and

therefore are expected to be best informed, appear to lead the decision-making process related to shifts in behaviour states, particularly traveling (Lusseau 2007; Lusseau, Conradt 2009). These few decision-making individuals are believed to be more knowledgeable regarding the behaviour of potential competitors due to their position in the social network. The consensus is mediated to other group members by non-vocal signals which can be communicated globally within the dolphin pod. These signals are side-flopping during which a dolphin clears the body entirely from the water and lands on its side and which is only performed prior to the onset of traveling; upside down lobtailing implying that the dolphin rolls over to expose its ventral side at the water surface followed by repeated slapping of the water surface with the dorsal side of the tail which is only observed before the pod concludes traveling (Lusseau 2003). These signals seem to always be performed by one member of the group and do not travel far underwater compared to vocalizations. Thus, the signals are only heard by group members but not by other groups. In line with these findings Couzin *et al.* (2006) suggested that individuals which interconnect communities should play a key role in information transmission in a population as a whole. In herring individuals which behave more independently of the shoal and move between shoals have been found to be particularly influential on shoal behaviour (Romey 1996). In guppy social networks fish of intermediate body lengths that cannot be clearly assigned to any particular community tend to take up this position.

In salmon postreproductively aged females lead groups during shoal movements in foraging grounds, especially during difficult years when salmon abundance is low (Brent *et al.* 2015). Small sets of leaders effectively influence the behaviour of large oceanic fish shoals related to the onset of spawning migrations, accurate navigation towards a target and foraging (Reeb 2000; Swaney *et al.* 2001; Makris *et al.* 2009). Leader-follower relationships have also been found in groups of sharks (Jacoby *et al.* 2016) and indicate the potential for significantly improved navigation accuracy as a consequence of grouping.

Individuals with a highly interconnected local neighbourhood were found to have the strongest influence on change in shoal behaviour in shiners (Rosenthal *et al.* 2015). It is those individuals near the front and side periphery of groups that are both most capable of propagating, and the most sensitive to, social cues (Rosenthal *et al.* 2015). In line with these findings adult male killer whales usually occupy a position far out on the wings of traveling pods and were suggested to communicate signals from this position to the pod as a whole (Norris, Dohl 1980a).

Populations of animals with a several year lifespan and seasonal migration are not expected to be homogeneously informed. Rather individuals which have participated in the migration before would be expected to navigate more accurately and hence, would provide good leaders. Many pelagic fish species, including clupeids, capelin and tuna fall into this category, so do migrating species of sea turtles, seabirds, pinnipeds and cetacea.

The latter include baleen whales, male sperm whales, killer whales, and possibly southern bottlenose whales (Chap. 3). Baleen and killer whales were found to navigate oceanic realms with high accuracy as the following factors indicate:

- the ability to maintain straight paths in the open ocean (Garrigue *et al.* 2010; Horton *et al.* 2011; Silva *et al.* 2013; Fossette *et al.* 2014; Kennedy *et al.* 2014; Riekkola *et al.* 2018)
- a high level of directedness of the migration path towards a remote destination (Mate *et al.* 2007; Bailey *et al.* 2009; Durban, Pitman 2012; Kennedy *et al.* 2014)

- continued active course adjustments in response to even slight deviations from the correct heading (Horton *et al.* 2011)

Many cetacea species lead nomadic lives and often cover substantial distances within few days (e.g. Evans 1974; Leatherwood, Ljungblad 1979; Perrin *et al.* 1979; Scott, Cattanach 1998; Bloch *et al.* 2003). It is to be expected that these movements involve travel between predictable but ephemeral feeding opportunities associated with high-density deep-scattering layers, a main forage base of oceanic odontoceti (Bertrand *et al.* 1999; Dagorn *et al.* 2000; Ballance *et al.* 2006), as well as with fish or squid spawning congregations (e.g. Sergeant, Fisher 1957; Wang *et al.* 2016). Travel between such areas may require good navigation abilities but little is known about the movement patterns of nomadic species.

In cetacea, leadership behaviour in combination with complex social structures from not-well understood fission-fusion patterns of large oceanic delphinid congregations (Möller 2012; Martien *et al.* 2017) to stable mixed-sex and matrilineal groups with strong and long-lasting bonds between few individuals (e.g. Bigg *et al.* 1990; Whitehead 2003; McSweeney *et al.* 2009; Oremus *et al.* 2013) all suggest a high potential for improved navigation accuracy by grouping. Yet all species which carry out long-distance migrations travel either solitarily or in small groups.

Northern elephant seals, *Mirounga angustirostris*, have been documented to migrate solitarily along almost exactly the same paths during successive oceanic migrations (Le Boeuf *et al.* 2000; Block *et al.* 2011) and maintain a highly directed course even at night and independent of ocean currents (Davis *et al.* 2001; Matsumura *et al.* 2011). Southern, *Mirounga leonine*, and northern elephant seals undertake directed trips of 1000-3000km between breeding and foraging locations, arriving on the same beaches they used for breeding the previous season (Le Boeuf *et al.* 2000; Biuw *et al.* 2007).

Albatrosses solitarily and accurately return to their breeding islands after long-distance foraging trips, even with magnets attached to their heads (Mouritsen *et al.* 2003; Bonadonna *et al.* 2005) and replacement experiments with white-chinned petrels, *Procellaria aequinoctialis*, have shown that individuals find their way to the correct destination accurately and solitarily (Benhamou *et al.* 2003a,b). Highly synchronized migrations in shearwaters, *Puffinus tenuirostris*, and Arctic terns, *Sterna paradisaea*, through narrow oceanic corridors even though there was no indication that tracked birds travelled together in the same flocks (Shaffer *et al.* 2006; Egevang *et al.* 2010) further suggest navigational skills.

Sea turtles on the other hand achieve a low level of navigation accuracy and seem to use both, search behaviour to find oceanic islands and course correction during the last phase of migration once coastal waters have been reached (Hays *et al.* 2014). High inter-individual variation in navigation accuracy (Hays *et al.* 2014) indicates that learning by repetition may improve navigational abilities. However, in contrast to baleen whales, sea turtles do not seem to regularly assess their position at sea in relation to their destination and consequently do not correct their course when deviating from the optimal route, e.g. due to current, until coastal waters are reached (Lohmann *et al.* 2008; Sale, Luschi 2009).

Many pelagic shark species, including porbeagle, *Lamna nasus*, blue, *Prionace glauca*, shortfin mako, silky, white and tiger sharks travel over vast distances, sometimes thousands of kilometres (e.g. Casey, Kohler 1992; Boustany *et al.* 2002; Bonfil *et al.* 2005; Bonfil 2008; Bruce *et al.* 2006; Nakano, Stevens 2008; Werry *et al.* 2014; Ferreira *et al.* 2015; Francis *et al.* 2015), but clear migration paths have only been identified in N-Pacific white sharks, suggesting a nomadic lifestyle. Frequent deviation from straight-line movement indicates low navigation accuracy in porbeagle sharks (Francis *et al.* 2015).

Migratory small pelagic shoaling fish typically move between spawning, wintering and feeding areas (Harden Jones 1968) along migratory routes which remain consistent over many years. Several species appear to develop migratory habits during an early stage of adult life which remain consistent even when the environment changes (Corten 2001). It has been suggested that migration patterns are learned by social transfer of information from old to young individuals (Rose 1993; Harden Jones 1968; Hourston 1982; McQuinn 1997; Alerstam 2006; Fernö *et al.* 2008), a process called guided learning (Helfman, Schultz 1984; Brown, Laland 2003). A change of migration pattern is usually initiated by a recruiting year-class that lacks the guidance of older herring at the time it has to start its first migration. The new migration route then becomes habitual and is adopted by following generations (Corten 2001).

Tab. 4 summarizes the patterns of grouping and navigation accuracy and shows that pelagic fish which migrate in large shoals are able to navigate with great accuracy when stocks are large. Among solitarily migrating species navigation accuracy is low in some taxa and high in others. These findings indicate that oceanic species have adapted to the problem of navigation in more than one way and different techniques are applied by different taxa.

Table 4: Gregarious versus solitary migration

Gregarious migration	Navigation accuracy	Solitary migration	Navigation accuracy
Salmonids	high when abundance is high	Large pelagic sharks	low, nomadic without clear paths
Mackerel	high	Sea turtles	low
Clupeids	high when abundance is high	Albatrosses	high
Plaice, <i>Pleuronectes platessa</i>	high	Baleen whales	high
		Elephant seals	high

Ref. for gregariousness: Fernö *et al.* 1998; Misund *et al.* 1998; Block *et al.* 2001, 2005; Fauchald *et al.* 2006; Juan-Jordá *et al.* 2013; Braun *et al.* 2015; Westley *et al.* 2015; Berdahl *et al.* 2016b; Chap. 3

Ref. for navigation accuracy: Casey, Kohler, 1992; Hunter *et al.* 2003; Godø *et al.* 2004; Lohmann *et al.* 2008; Nakano, Stevens 2008; Sale, Luschi 2009; Horton *et al.* 2011; Saunders *et al.* 2011; Costa *et al.* 2012; Weimerskirch *et al.* 2012; Hays *et al.* 2014; Kennedy *et al.* 2014; Francis *et al.* 2015; Mate *et al.* 2015; Berdahl *et al.* 2016b

Shifts in migration routes and destinations after stock collapse in several species of pelagic shoaling teleosts indicate either an importance of grouping in navigating accurately or the unnecessary of migration when population size is small, or both (Dragesund 1970; Rottingen 1992). In herring feeding migration recommenced and spawning areas became larger as stocks began to increase and the specie's range extended as recovery progressed (Dragesund *et al.* 1997).

The idea of young fish following older and therefore larger fish seems in disagreement with size-assortment in pelagic shoals (Peuhkuri 1997; Croft *et al.* 2009), which would be expected to limit contact between younger and older individuals. However, shoals often form clusters separated only by short inter-shoal distances (Mackinson *et al.* 1999; Haugland, Misund 2004) indicating that inter-group communication may be important. DeBlois, Rose (1996) found an internal structure characterized by size-differential sub-groups within a more than 20km long shoal of migrating Atlantic cod, *Gadus morhua*, with larger individuals occupying positions in the front of the group as expected when older and hence larger shoals or sub-groups are leading the migration. Using an evolutionary model of migrant populations Guttal, Couzin (2010) showed that when interactions among organisms are relatively inconspicuous, such as when migrants do not form coherent groups, they may nevertheless provide vital social cues

that aid migration. A model for collective motion addressing this situation has shown that long-distance interactions can lead to higher global alignment of the entire population (Buscarino *et al.* 2006). In line with these findings Barbaro *et al.* (2009) suggested that quorum-sensing is more efficient when very large numbers of individuals spread out over large areas exchange information about navigation-related sensory input. Both collective memory and quorum sensing of and between shoals of synchronously migrating pelagic fish seem to play an important role in navigation accuracy (e.g. Larkin, Walton 1969; Corten 2001; Ward *et al.* 2008; Barbaro *et al.* 2009).

Baleen whales which typically travel in groups of 1-3 individuals (Chap. 3) may increase navigation accuracy through long-distance communication between individuals. Gray whales were found to increase their calling rates during migration, especially at night (Guazzo *et al.* 2017). A higher night-time compared to daytime call frequency has also been reported in blue, humpback and north Pacific right whales (Au *et al.* 2000; Wiggins *et al.* 2005; Munger *et al.* 2008). Baleen whales are capable of communicating over hundreds of kilometres and slow clicks of sperm whales have an active space of at least up to 60km (Payne, Webb 1971; Sirovic *et al.* 2007; Clark 1995; Madsen *et al.* 2002; Tsuchiya *et al.* 2004; Tran *et al.* 2014). These findings indicate both, that inter-individual information exchange does not require grouping in these species and that information exchange over large distances may be more valuable for navigation than the formation of cohesive localized groups seen in many delphinid species (Chap. 3).

Klimley *et al.* (2001) found that white sharks searched for prey independently but remained close enough to each other to sense and exploit a kill made by any one of them by joining in on the kill to feed. Hence even though traveling solitarily inter-individual distances may be such that information exchange is facilitated, possibly not only regarding prey but also navigation. White sharks are the only pelagic shark species for which a migratory pattern has been identified. In the N-Pacific white sharks migrate seasonally from Guadalupe Island and California to an offshore area between the American continent and Hawaii (Boustany *et al.* 2002; Weng *et al.* 2007; Domeier, Nasby-Lucas 2008; Jorgensen *et al.* 2010).

Luschi (2013) suggested that an inherited biological compass enables seabirds to navigate accurately and successfully across the open ocean (Luschi 2013). This compass is likely combined with various navigational cues the use of which is learned by experience and repetition as has been shown in homing pigeons which travel along more efficient and increasingly stereotyped routes as experience increases (Meade *et al.* 2005). Similarly, in migrating raptors navigation accuracy was found to be positively correlated with the number of times an individual completes a trip (Thorup *et al.* 2003), and course correction during the final stages of migration indicate challenges in accurate navigation at least in some individuals (Klaassen *et al.* 2011).

Conclusively, navigation techniques vary between taxa, but navigational accuracy can be improved mainly in three ways: (1) through congregation when groups or sub-groups are spread out and information exchange happens over large areas, (2) by solitary migration in combination with long-distance communication, and (3) through repetition of migration and learning from older cohorts or individuals. Number 3 may apply on its own or in combination with number 1 or 2.

This review further indicates that long-distance communication may be of greater importance for navigational accuracy than grouping in cetacea. However quantitative studies are lacking, so is an understanding of the importance of grouping for navigation accuracy in migrating versus nomadic populations or species.

Increased hydrodynamic efficiency

Individuals affiliated to groups can increase their hydrodynamic efficiency by a number of mechanisms. These are:

- Vortices generated within a fish school may reduce the relative velocity for a given absolute velocity of an individual if school members synchronize their swimming behaviour (Weihs 1973, 1975; Liao 2007). Hence, the schooling fish needs to work less to swim at the same absolute speed compared to a solitary individual.
- The presence of other school members to both sides of an individual creates a channel in which flow velocity is enhanced between individuals in the direction of swimming and hence thrust efficiency is increased (Weihs 1973, 1975). This effect is the stronger the smaller the distance between neighbouring individuals (Daghooghi, Borazjani 2015).
- Wakes generated by neighbouring individuals provide lift if a school consists of several horizontal planes of fish in close vertical proximity. This is useful in negatively buoyant fish (Weihs 1973, 1975).
- dolphin neonates gain hydrodynamic benefits through Bernoulli suction when positioned close to, ideally 0.2 body lengths from their mother (drafting, Fish, Rohr 1999; Weihs 2004, Shoele, Zhu 2015)

The first three mechanisms were suggested for fish schools but apply to cetacea in similar ways since propulsion underlays the same principles except tail movement is vertical rather than horizontal. Hence individuals are expected to stagger differently to optimize hydrodynamic efficiency. Both animal groups are discussed in more detail below.

Weihs 1973, 1975; Hemelrijk *et al.* 2014

Fish

Endurance of fish can increase 2-6 times when individuals are organized in schools compared to singletons (Weihs 1973). Studies on a variety of species found a reduction in tail beat frequency, typically of ~10%, in individuals occupying trailing positions compared to the front of the school over a wide range of velocities (Zuyev, Belyayev 1970; Fields 1990; Herskin, Steffensen 1998; Svendsen *et al.* 2003; Killen *et al.* 2012). Reductions in tail beat frequency of up to 28.5% have been documented in grey mullets, *Liza aurata* (Marras *et al.* 2015). Ashraf *et al.* (2017) found a reduced stroke rate in schooling versus solitary tetra fish, *Hemigrammus bleheri* and oxygen consumption can be reduced by up to about 20% in schools of hydrodynamically ideally positioned fish compared to solitary movement (Herskin, Steffensen 1998; Marras *et al.* 2015).

According to Weihs (1973, 1975) maximum energy savings are predicted to occur when neighbours are situated 0.3 body lengths apart in the same horizontal dimension and effectively disappear when neighbours are one body length apart. A more recent modelling study suggested that such close positioning is disadvantageous, and individuals should be further apart (Hemelrijk *et al.* 2014). However, there is agreement in that hydrodynamic benefits decrease with increasing inter-individual distance from a certain small inter-individual distance onward (Weihs 1973, 1975; Hemelrijk *et al.* 2014). In line with these findings Pitcher, Partridge (1979) documented inter-individual distance in herring, cod and saithe to decrease as schools accelerated. Newlands, Porcelli (2008) found inter-individual distances of 0.3-0.9 body lengths in schools of Atlantic bluefin tuna, *Thunnus thynnus*. Individuals maintained a fixed number of neighbours at certain angles and distances, presumably to improve their ability to search for and detect prey while schooling. Reduced energy expenditure has been suggested as the main benefit gained by schooling in Atlantic bluefin tuna (Partridge *et al.* 1983; Newlands, Porcelli 2008).

Whereas Weihs (1975) suggested that units of at least six individuals have to swim in a diamond pattern at the same vertical plane as their neighbours for hydrodynamic efficiency to be improved, Abrahams, Colgan (1985) found benefits to occur even in pairs of fish. Ashraf *et al.* (2017) found side by side swimming in a phalanx configuration to be energetically more advantageous than a diamond shape. The diamond shape does not seem to be important for the channelling effect (Daghooghi, Borazjani 2015).

In both scenarios the ideal positioning of individuals at the same vertical plane causes considerable blockage of the individuals' visual fields by their neighbours and therefore represents the least beneficial structure with regard to vigilance efficiency (Abrahams, Colgan 1985). If sensory capabilities of individuals of a school are to be pooled so as to enhance the likelihood of detecting environmental stimuli including predators and food, then neighbouring individuals should be staggered on different vertical planes (Abrahams, Colgan 1985). This trade-off is expected to lead to deviations from a hydrodynamically ideal arrangement of individuals under predation threat or when hungry. Such deviations may affect the whole school (e.g. Partridge, Pitcher 1979; Partridge *et al.* 1980; Abrahams, Colgan 1985; Pitcher, Parrish 1993), or parts of it due to intra-school variations in hydrodynamic and foraging efficiency as well as predation risk and oxygen supply (McFarland, Moss 1967; Moss, McFarland 1970; Steffensen 1993; Domenici *et al.* 2002; Svendsen *et al.* 2003; Killen *et al.* 2011; Trenchard, Perc 2016). Especially in the oceanic environment other parameters such as predation risk and foraging requirements are expected to be prioritized over hydrodynamic efficiency in many situations to maximize fitness and the study of individual arrangement and inter-individual distances in wild fish school may be useful in identifying the main benefit of grouping in different species.

Cetacea

When neonate dolphins swim very close to their mother the water flow between mother and calf increases with dolphin speed, leading to a drop in pressure between mother and neonate while pressure above the new-born increases. In this way suction is created which reduces the calf's energy requirements for swimming by about 90% at velocities up to 2.4 m/s when the calf is positioned close to the mother's nose (Weihs 2004). Due to increased drag the mother's sustainable swimming speed simultaneously reduces to 76% of her solitary capabilities (Noren 2008). Few hours after birth the calf switches to the echelon position within 10cm of the mother's mid-lateral flank, where energy savings are still > 60%, but decrease with increasing distance from the mother to ~25% at 30cm (Weihs 2004). Older calves often swim in close proximity underneath the mother's tailstock, called infant position. Here energy savings are limited to a 24% reduction in fluke stroke amplitude compared to solitary swimming whereas stroke frequency and swim speed are not affected (Noren, Edwards 2001).

Fish *et al.* (2013) suggested that echelon swimming in foraging adult bowhead whales may entail hydrodynamic benefits and increased foraging efficiency. However, little is known about hydrodynamic benefits arising from grouping in cetacea beyond mother-calf pairs. Most cetacea species porpoise during high-speed swimming (e.g. Breese, Tershy 1993; Ford, Reeves 2008; Deakos *et al.* 2010; Visser *et al.* 2010; Wellard *et al.* 2016), a behaviour which consists of serial leaps in which the animal leaves and re-enters the water during continuous swimming (Fish 2006). To the author's knowledge no studies have addressed an ideal group structure which would maximize efficiency for this type of movement.

Odontocetes have been suggested to gain hydrodynamic benefits when swimming in tight synchronous congregations (e.g. Henderson *et al.* 2012; Senigaglia *et al.* 2012). In long-finned pilot whales the commonly observed synchronization of movement was suggested to allow rapid coordinated responses of individuals, with multiple functions including reaction to disturbance (Senigaglia *et al.* 2012). Pods of common dolphins were found to maintain small inter-individual distances when swimming fast but are spaced more widely when moving slowly, across a large range of group sizes in line with a negative correlation between inter-individual distance and hydrodynamic efficiency (2-1000, \bar{x} : 207, n: 61, Henderson *et al.* 2012).

30.1% of fast traveling pods were tightly spaced, compared to 10.7% of moderate and 4.6% of slowly swimming groups. The authors further found fast traveling groups to be large whereas slower pods were of a wide range of sizes.

Tight spacing and synchronous movements are common in small traveling groups of odontocetes and in sub-groups of larger congregations across many species (Norris, Dohl 1980a; Heimlich-Boran 1988; Ponganis *et al.* 1995; Pitman *et al.* 1999; Hastie *et al.* 2003; Shirihai, Jarrett 2006; Kuczaj, Yeater 2007; Dulau-Drouot *et al.* 2008; Weir *et al.* 2008a; De Boer 2010; Senigaglia, Whitehead 2011). Group compaction in response to attack by predators (Brown, Norris 1956; Norris, Dohl 1980b; Ljungbald, Moore 1983; Best *et al.* 1984; Whitehead, Glass 1985; Arnborn *et al.* 1987) may facilitate increased flight speed. However, group compaction under high levels of predation threat or under attack represents a common phenomenon whether the anti-predator response involves flight or not. For example, humpback, gray, southern right and sperm whales typically increase group density when approached by mammal-eating killer whales, but rarely flee from these predators unless a solitary individual is attacked (App. 4: Tab. 5). Instead group compaction is related to defence behaviour in these species.

Large congregations of oceanic delphinids typically comprise individuals of highly variable swim speed such as a combination of adult males, pregnant females, mother-calf pairs and sub-adults (e.g. Bearzi *et al.* 2003; Jankowski 2005; De Boer 2010; Rankin *et al.* 2011). Smaller groups of matrilineal species such as sperm, killer and pilot whales also contain individuals of various age and body size (e.g. Ford *et al.* 2000; Ottensmeyer, Whitehead 2003; Whitehead 2003). Such a group composition, lacking the size assortment found in fish (Auster *et al.* 1992; Peuhkuri 1997; Croft *et al.* 2009), is not hydrodynamically efficient and indicates that grouping is driven by factors other than hydrodynamic benefits, even though even though hydrodynamic advantages may still arise secondarily from grouping. Life history traits vary greatly between cetacea and pelagic shoaling fish and selection for parental care, which is carried out by all cetacean species is stronger than selection pressure towards hydrodynamic efficiency/assortment by body size in these marine mammals.

In fish reduction of predation risk is prioritized over hydrodynamic efficiency such that school members position themselves in a vertically staggered manner which increases vigilance efficiency when under risk of predation but swim in the same horizontal plane when predators are absent in line with a hydrodynamically beneficial school structure (Abrahams, Colgan 1985). A higher importance of behavioural adaptation to predation risk than to hydrodynamic efficiency would also be expected in cetacea, especially in the oceanic environment. The only exception is the killer whale which does not seem to have natural predators. Hence the killer whale might be a very suitable species for the study of group density – hydrodynamic efficiency relationships.

Group size

Theoretically group size is optimal when benefits to the average member are maximal relative to a loner. Equilibrium or critical group size corresponds to the number of individuals for which benefits to the average group member equal those of a loner (Parrish, Edelman-Keshet 1999). When considering a fitness increase with enhancing group size till an arbitrary size of 20 individuals, and a critical group size of 54, and each potential member has a choice between remaining alone or joining the group, the second arrival will do better by affiliating the solitary individual than by being alone. The same argument holds for each individual that arrives until the optimal group size of 20 is obtained. The 21st individual will still increase its fitness by joining the group, and so will every further potential member until a group size of 53 is reached which is why groups larger than optimal size are expected to be found in nature (Sibly 1983; Clark, Mangel 1984; Pulliam, Caraco 1984). For the 54th individual joining implies the same fitness as foraging alone. However, beyond the size of 20, affiliation of new individuals entails a decrease in fitness for all members which have joined previously. Therefore, the group would be expected to split before comprising 53 individuals.

In some species or situations group members may actively prevent newly arriving individuals from joining. For the 21st individual affiliation implies a large fitness increase, whereas the loss for the other members is small. Therefore, exclusion of the arrival is unlikely, but the more individuals join after the optimal group size is obtained, the more likely resistance by the group is and the less the arrival's fitness increase entailed by joining is worth fighting for affiliation. This situation changes if individuals are genetically related. Theoretically, in this case a new arrival may reject joining a group if the benefit to its own direct fitness is exceeded by a reduction in its inclusive fitness caused by a decrease in the direct fitness of related individuals already in the group. Therefore, increasing relatedness would be expected to lead to a decrease in group size towards the optimum. However, the group might allow another individual to join, if the arrival is related to its members, and each group member's loss in direct fitness is more than compensated for considering their inclusive fitness due to the increase in direct fitness of the joiner. Consequently, if entry to the group is controlled by the joiner, the characteristic group size should decrease with relatedness, but should increase with the degree of relationship, if affiliation is controlled by the group (Krause, Ruxton 2002). Practically optimal group size depends on the interplay of numerous parameters some of which are discussed below, and is in constant change due to the inconsistency of many of these parameters across time and space.

Predation risk

Group size related anti-predator benefits vary between predator-prey systems and depend on prey and predator behaviour including predator hunting techniques (e.g. Cresswell, Quinn 2010), attack rates, attack-to-kill ratio (Creel, Creel 2002), and flight and defence mechanisms in prey (e.g. Krause, Ruxton 2002). The following correlations between group size and predation have been found to select for large congregations when applicable to the predator-prey system in question:

- positive correlation between group size and strength of the dilution effect (Pulliam *et al.* 1982; Dehn 1990; Packer, Abrams 1990; Fairbanks, Dobson 2007; Beauchamp, Ruxton 2008)
- decrease in the predator's attack success rate with increasing prey group size (Kenwood 1978; Treherne, Foster 1982; Martin *et al.* 2005; Cresswell, Quinn 2011)
- predator preference of small compared to large groups (Calvert *et al.* 1979; FitzGibbon 1990)
- positive correlation between prey capture time and congregation size (Gillett *et al.* 1979; Ruxton *et al.* 2007)

- increased and earlier predator detection in large compared to small groups (Kenwood 1978; Pulliam *et al.* 1982; Parker, Hammerstein 1985; Dehn 1990; Beauchamp 2003, 2017)

Predation related costs of grouping in general and of large groups in particular are:

- increased attack rate with increasing group size until a maximum attack rate is reached (Creel, Creel 2002; Hebblewhite, Pletscher 2002; Cresswell, Quinn 2011)
- increased predator encounter rate (Uetz, Hieber 1994; Krause, Godin 1995; Hebblewhite, Pletscher 2002; Creel, Creel 2002)
- increased detection of prey by predators particularly at small prey group sizes (Lima, Dill 1990)
- increased cost of oddity in large compared to small groups given a skewed phenotype ratio (Krakauer 1995)
- increased foraging competition leading to reduced time devoted to vigilance and therefore increased predation risk (Elgar 1989; Blumstein *et al.* 2001; Beauchamp, Ruxton 2003; Roberts 2003; Fortin *et al.* 2004a,b; Dalerum *et al.* 2008)

These costs, too, do not apply equally to all predator-prey systems which involve prey grouping. Several benefits and costs of larger compared to smaller groups may apply simultaneously. For example, Cresswell, Quinn (2011) found the attack rate by sparrowhawk, *Accipiter nisus*, targeting redshanks, *Tringa tetanus*, to increase up until a group size of 55 even though attack success rate decreased with increasing prey group size. Attack success declines exponentially in small prey groups and then decreases less and less quickly as prey congregation size increases until it remains evenly low for groups consisting of more than 69 redshanks. Combined with the dilution effect, the individual redshank mortality risk per attack was found to be reduced by 95% when a group size of 30 is obtained, compared to solitary occurrence (Cresswell, Quinn 2011). This study emphasizes the importance of assessing all components of predation risk rather than focusing on single parameters.

In general species exposed to high predation risk were found to form larger groups than those living under low predation threat (Crook 1965; Jarman 1974; Seghers 1974) and groups of the same species are often larger in high-risk areas than in less risky habitat (e.g. Hill, Lee 1998; Hass, Valenzuela 2002; Ebensperger *et al.* 2012) or during times when predation risk is high compared to times of low risk (e.g. Hager, Helfman 1991; Ashley *et al.* 1993; Krause, Godin 1994; Tegeder, Krause 1995; Hoare *et al.* 2004). A large optimal group size would be expected when predation risk is the main driver for congregation and the dilution effect and predator swamping are the main factors leading to reduced predation threat in groups compared to solitary individuals. Since the latter seems to apply to gregarious cetacea as discussed before, very large groups would be expected if predation risk represents the main evolutionary driver for grouping in this taxon. This is especially true in oceanic species which predominantly feed on prey distributed in large patches such as associated with vertically migrating deep-scattering layers.

However, if the main driver for grouping is different from predation risk, then large congregations may be formed even if they do not entail a reduction in predation. More so, large colonies of cliff swallows, *Petrochelidon pyrrhonota*, experience a higher predation risk than congregations comprising a small number of individuals (Brown, Brown 1996) and in mongoose the size and composition of groups does not differ between populations with different predation regimes (Clutton-Brock *et al.* 1999). Such results can also arise from non-adaptiveness of grouping in general or non-adaptiveness of congregation beyond a certain group size in the species or population studied.

Foraging efficiency

Numerous studies across various taxa found group sizes to be small or congregations to disperse during foraging or when animals are food-deprived, including various fish and cetacea species (e.g. Krause 1993a; Soury 1996; Reeb, Saulnier 1997; Scott, Cattanach 1998; Benoit-Bird *et al.* 2004; Markowitz 2004; Brownell Jr. *et al.* 2009). These findings indicate increased competition for forage in larger compared to smaller congregations (Krause 1993a; Reeb, Saulnier 1997) which in turn can reduce time available for any other kind of behaviour thereby leading to further costs of grouping when individuals are struggling to meet their energy requirements (Dalerum *et al.* 2008).

The formation of large groups may also lead to an increased need to travel so as to locate sufficient amounts of forage to cover the group's energy demands as a result of exploitative competition (e.g. Milton 1984; Janson 1988; Wrangham *et al.* 1993; Chapham *et al.* 1995; Janson, Goldsmith 1995; Gillespie, Chapman 2001). Such increased costs must then be compensated by other benefits for grouping to be beneficial (Chapman, Chapman 2000a).

On the other hand, under conditions of efficient collective sensing and information exchange increasing group size reduces the time an individual has to spend vigilant for predators and hence increases time available for foraging (Pulliam 1973; Lagory 1986; Elgar 1989; Lima, Dill 1990; Quenette 1990; McNamara, Houston 1992; Roberts 1996; Hunter, Skinner 1998; Beauchamp 2008). A positive correlation between the strength of the dilution effect and group size can further facilitate a reduction in vigilance in larger groups (Bertram 1978; Pulliam *et al.* 1982; Dehn 1990; Packer, Abrams 1990; McNamara, Houston 1992; Fairbanks, Dobson 2007; Beauchamp, Ruxton 2008). However, vigilance is affected by grouping in complex ways and an unchanged or a higher level of individual vigilance can be required in larger groups compared to small ones when:

- predators are attracted to large prey congregations (Howe 1979; Parrish, Edelstein-Keshet 1999; Hebblewhite, Pletscher 2002)
- quorum sensing is inefficient (McNamara, Houston 1992) or information about approaching predators is not exchanged quickly enough and therefore benefits of direct predator detection are so large relative to indirect detection by other individuals that group members rely on their own vigilance (Lima 1994; FitzGibbon 1989; van der Post *et al.* 2013)
- increased vigilance for group members is necessary to maintain group affiliation, or a certain position within the group relative to others, or to keep a certain distance to competitors or to avoid aggression (Treves 2000; Beauchamp 2001; Favreau *et al.* 2010)

These interrelations explain why a significant number of studies has not found a direct effect of group size on vigilance, or even found a higher level of vigilance in larger groups (Lima 1995; Treves 2000; Laundré *et al.* 2001; Beauchamp 2003).

Further documented foraging benefits of large groups are:

- more efficient localization and exploitation of prey when forage is distributed in large but scarce patches (Pitcher *et al.* 1982; Clark, Mangel 1984; Pitcher 1986; Travis *et al.* 1995; Beekman *et al.* 2001; Brashares, Arcese 2002; Halley, Burd 2004)
- increased ability to defend prey from kleptoparasites (Cooper 1991; Fanshawe, FritzGibbon 1993; Langley 2001)

Conclusively, whether large group sizes are beneficial, costly or neutral with regard to foraging depends on a number of factors including:

- the level of competition for food and hence forage availability and distribution
- the necessity to monitor other group members
- the amount of time which has to be devoted to vigilance for predators which may be higher, lower, or unchanged in large compared to small congregations
- the necessity to defend prey from kleptoparasites.

Typically, the optimal group size for foraging is smaller than the optimal congregation size with regard to predation risk (Krause, Ruxton 2002).

Navigation accuracy

Navigation accuracy was found to improve with increasing group size given a fixed proportion of leaders (Couzin *et al.* 2005; Sumpter *et al.* 2008) and is higher in years of higher animal abundance (e.g. Berdahl *et al.* 2016b; Westley *et al.* 2015). Smaller populations contain a higher proportion of straying individuals which can lead to fast colonization of new areas rather than fidelity to established ones (Berdahl *et al.* 2016b). In some but not all species, migratory distance is positively correlated with group size (Beauchamp 2011).

Couzin *et al.* (2005) revealed that the larger the congregation the smaller the proportion of informed individuals needed to guide the group. Hence when the number of informed individuals in the population is low larger groups are advantageous so as to ensure that every group includes at least the necessary minimum number of informed individuals for accurate navigation.

Much empirical work on binary decision-making by animal groups shows that larger groups are often able to choose the superior option more accurately (Sumpter *et al.* 2008; Ward *et al.* 2008, 2011; Arganda *et al.* 2012).

Conclusively, whether group size affects congregation benefits positively or negatively depends on many factors, including behavioural adaptations of the species in question, predator density and hunting technique, the distribution and abundance of forage and the social structure of congregations. Generally, larger groups entail a stronger dilution effect and increased communal prey search efficiency and navigation accuracy, but regarding other parameters such general statements cannot be made.

Conclusions

Conclusively congregation may lead to fitness benefits related to predation risk, foraging, reproduction, information exchange and navigation accuracy and may increase hydrodynamic efficiency. Most relevant to cetacea are the dilution and confusion effects as well as predator swamping and possibly increased vigilance efficiency, but also communal prey search and cooperative prey herding, information exchange, calf-care and access to females.

Behavioural studies can provide insight into the complex interplay of these factors. However, most ethological accounts of oceanic cetacea in the scientific literature are mere descriptions of a certain type of behaviour. More studies on the quantitative importance of behavioural traits related to predation risk, foraging, calf care and mating are needed.

Group density can provide valuable insights regarding predation risk (e.g. McBride, Hebb 1948; Norris, Dohl 1980a,b; Magurran, Pitcher 1987; Fréon *et al.* 1992) and hydrodynamic efficiency (e.g. Weihs 1973, 1975; Hemelrijk *et al.* 2014) and can be estimated in the field from inter-individual distances (e.g. Baird *et al.* 2008b) which are rarely reported in cetacea literature and should receive more attention.

Two very common behaviour adaptations to foraging in the oceanic environment are cooperative prey herding and prey debilitation which are often used in combination and are applied by species across numerous taxa. The interplay between predators which use, and prey which are affected by these foraging techniques represents an important research field, especially in a quickly changing environment such as the open ocean. Top- and meso-predator densities are strongly influenced by anthropogenic changes (e.g. Worm, Myers 2003; Frank *et al.* 2005; Kitchell *et al.* 2006; Casini *et al.* 2008, 2009) which may lead to alterations in the adaptiveness of behavioural traits (e.g. Lourenco; Casey 2013; Wong, Candolin 2015).

Hydrodynamic grouping benefits beyond the mother-calf pair have received little attention in cetacea. The effect of group size on hydrodynamic efficiency in cetacea and the implications of grouping on the combined movement through air and water during porpoising represent interesting future research fields.

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Chapter 2: Predation risk in oceanic cetacea

Abstract

Little is known about predation risk of cetacea in oceanic waters. In this chapter a quantitative predation risk analysis is attempted which consists of five parts: (1) the identification of predators based on predator stomach content analyses, field observations of predation events on cetacea, and an evaluation of active versus passive predation in important shark predators, (2) the discussion of exposure to predators in the open ocean environment, (3) the estimation of relative frequency of encounters between cetacea and their predators based on habitat overlap between prey and predator, which was derived from horizontal and vertical distribution patterns of both, (4) the estimation of predator fatality consisting of the rate of attack upon encounter and the portion of attacks leading to a kill, and (5) the calculation of predation risk based on points 3 and 4.

Results identify killer whales, *Orcinus orca*, and white sharks, *Carcharodon carcharias*, as the most important predators of cetacea in offshore waters. Bluntnose sixgill, *Hexanchus griseus*, and broadnose sevengill sharks, *Notorynchus cepedianus*, impose a significant predation risk to some species, and in some areas. Shortfin mako, *Isurus oxyrinchus*, oceanic whitetip, *Carcharhinus longimanus*, dusky, *Carcharhinus obscurus*, and tiger sharks, *Galeocerdo cuvier*, are minor cetacea predators in oceanic waters. Large quantities of cetacea remains have been found in stomachs of Greenland shark, *Somniosus microcephalus*, Pacific sleeper, *Somniosus pacificus*, and southern sleeper sharks, *Somniosus antarcticus*, but the former two species seem to predominantly scavenge, rather than actively prey on whales and dolphins. Southern sleeper sharks are likely to actively hunt cetacea at a higher level but show no or little habitat overlap with most species.

Killer whales prey heavily on gray whales, *Eschrichtius robustus*, in the NE-Pacific, and take humpback, *Megaptera novaeangliae*, and minke whales, *Balaenoptera acutorostrata/B. bonaerensis*, at significant numbers in some areas and at certain times of year. Dusky dolphins, *Lagenorhynchus obscurus*, and common dolphins, *Delphinus delphis*, also face high risks of predation by these predators. Sperm whales, *Physeter macrocephalus*, and hourglass dolphins, *Lagenorhynchus cruciger*, were estimated to experience the lowest overall predation risks among toothed whales.

Introduction

Killer whales and large pelagic sharks have been identified as predators of cetacea by numerous studies (e.g. Jefferson *et al.* 1991, Ford *et al.* 1998 Heithaus 2001a).

Killer whales were suggested to pose a level of risk to baleen whales which has influenced the evolution of life history traits, behaviour and morphology in this sub-order (Ford Reeves 2008). These predators are also known to feed on a variety of toothed whales, including sperm (Arnbom, Whitehead 1989; Jefferson *et al.* 1991; Morrice 2004) and beaked (Wellard *et al.* 2016) whales, dolphins (Shevchenko 1975; Ternullo, Black 2002; Best *et al.* 2010; Coscarella *et al.* 2015) and porpoises (Nishiwaki, Handa 1958; Ford *et al.* 1998; Saulitis *et al.* 2000; Ternullo, Black 2002).

Killer whales form a variety of populations throughout the world's oceans, some of which prey exclusively on marine mammals, others prey on a large variety of food items including marine mammals, and some populations feed exclusively on fish. The N-Atlantic comprises two mammal-eating populations, A and B, of which A predominantly feeds on fish but occasionally switches to marine mammals. Population B consists of two sub-populations of which one preys on fish and marine mammals, whereas the other exclusively takes marine mammals. A third population C, feeds on fish (Wellard *et al.* 2016, review). In Antarctic waters two out of four killer whale populations prey on marine mammals: type A killer whales occurring offshore and in pack ice, and type B's (Gerlache killer whales) which mainly prey on seals and penguins, but also take minke whales (Pitman, Durban 2010, 2012; Durban *et al.* 2017). In the NE-Pacific transient killer whales feed exclusively on marine mammals, whereas resident and offshore

killer whales prey on different trophic levels of fish (Ford *et al.* 1998, 2011). Residents and transient killer whales both also occur in the NW-Pacific off Kamchatka (Burdin *et al.* 2005). In the Canadian arctic killer whales prey predominantly, if not exclusively on marine mammals, esp. belugas, *Delphinapterus leucas*, and narwhals, *Monodon monoceros*, followed by bowhead whales, *Balaena mysticetus*, and phocid seals (Ferguson *et al.* 2010). Off New Zealand and Patagonia killer whales feed on a large variety of prey, including teleosts, elasmobranchs, penguins, seals and cetacea, indicating a very generalist diet (Visser 1999, 2000; Iñíguez *et al.* 2002; Goodall *et al.* 2007; Häussermann *et al.* 2013). Beaked and humpback whales seem to be regular prey of killer whales off western Australia (Pitman *et al.* 2015; Wellard *et al.* 2016).

In his review of shark interactions with dolphins, Heithaus (2001a) suggested white, tiger, bull, sixgill and sevengill sharks to be major predators of these marine mammals, whereas dusky and oceanic whitetip sharks occasionally prey on cetacea. He further suspected shortfin mako, Pacific sleeper and Greenland sharks to feed on delphinids. Tiger sharks are known to affect spatial and temporal distribution of dolphins in coastal areas (Heithaus, Dill 2002). However, few analyses contain quantitative information on predation risk experienced by whales, dolphins and porpoises. Since predation risk has long been suggested to represent one of the major drivers of grouping it is analysed here in more detail, as a base for the analysis of group size correlation with predation threat in the following chapter.

The following cetacea species were included in the analysis (Tab. 1):

Table 1: Cetacea species

English name	Scientific name	English name	Scientific name
Blue whale	<i>Balaenoptera musculus</i>	Pygmy killer whale	<i>Feresa attenuata</i>
Fin whale	<i>B. physalus</i>	Melon-headed whale	<i>Peponocephala electra</i>
Sei whale	<i>B. borealis</i>	Killer whale	<i>Orcinus orca</i>
Bryde's whale	<i>B. edeni</i>	Risso's dolphin	<i>Grampus griseus</i>
Minke whale	<i>B. acutprostrata</i> , <i>B. bonaerensis</i>	Bottlenose dolphin	<i>Tursiops sp.</i>
Southern right whale	<i>Eubalaena australis</i>	Rough-toothed dolphin	<i>Steno bredanensis</i>
Humpback whale	<i>Megaptera novaeangliae</i>	White-beaked dolphin	<i>Lagenorhynchus albirostris</i>
Gray whale	<i>Eschrichtius robustus</i>	Atlantic white-sided dolphin	<i>L. acutus</i>
Sperm whale	<i>Physeter macrocephalus</i>	Pacific white-sided dolphin	<i>L. obliquidens</i>
Pygmy sperm whale	<i>Kogia breviceps</i>	Hourglass dolphin	<i>L. cruciger</i>
Dwarf sperm whale	<i>Kogia sima</i>	Dusky dolphin	<i>L. obscurus</i>
Cuvier's beaked whale	<i>Ziphius cavirostris</i>	Fraser's dolphin	<i>L. hosei</i>
Baird's beaked whale	<i>Berardius bairdii</i>	Spinner dolphin	<i>Stenella longirostris</i>
Arnoux's beaked whale	<i>B. arnuxii</i>	Pantropical spotted dolphin	<i>S. attenuata</i>
Blainville's beaked whale	<i>Mesoplodon densirostris</i>	Atlantic spotted dolphin	<i>S. frontalis</i>
Gervais' beaked whale	<i>M. europaeus</i>	Striped dolphin	<i>S. coeruleoalba</i>
Sowerby's beaked whale	<i>M. bidens</i>	Clymene dolphin	<i>S. clymene</i>
Pygmy beaked whale	<i>M. peruvianus</i>	Common dolphin	<i>Delphinus delphis</i>
Longman's beaked whale	<i>Indopacetus pacificus</i>	Commerson's dolphin	<i>Cephalorhynchus commersonii</i>
Southern bottlenose whale	<i>Hyperoodon planifrons</i>	Southern right whale dolphin	<i>Lissodelphis peronii</i>
Northern bottlenose whale	<i>H. ampullatus</i>	Northern right whale dolphin	<i>L. borealis</i>

English name	Scientific name	English name	Scientific name
Long-finned pilot whale	<i>Globicephala melas</i>	Dall's porpoise	<i>Phocoenoides dalli</i>
Short-finned pilot whale	<i>G. macrorhynchus</i>	Burmeister's porpoise	<i>Phocoena spinipinnis</i>
False killer whale	<i>Pseudorca crassidens</i>		

Materials and methods

Predation risk was assessed by the following steps, based on Lima, Dill (1990):

- Identification of predators on cetacea
- Discussion of time spent exposed to predators
- Estimation of relative frequency of encounters with predators
- Estimation of death rate upon predator encounter/predator fatality
- Calculation of predation risk

1. Predator identification

Studies in which encounters between cetacea and predators and predator stomach content analyses are published were located through ISI Web of Science, Google Scholar, PLOS ONE, BioOne, ScienceDirect, PubMed and JSTOR search engines, references of relevant papers and articles which have cited the located papers using the following key words:

- (name of cetacea species) shark attack
- (name of shark species) hunting feeding
- (name of shark species) stomach content
- killer whale feeding
- killer whale predation
- killer whale stomach content
- pilot whale harassing
- false killer whale harassing

The same publications were searched for information about active predation versus scavenging in all those shark species in which cetacea remains were found in $\geq 5\%$ of stomachs. Indicators of active predation used for this analysis are:

- direct observations in the field,
- occurrence of scars and wounds inflicted by sharks on living cetacea,
- observations of attacks on other living fast-moving prey of similar size,
- cetacea constituting a large portion of shark stomach contents/ accounting for most of the diet of a shark species, since it is unlikely that a large portion of the diet can be covered by carcasses alone (Heithaus 2001a).
- the presence of cetacea flukes or vertebrae in shark stomachs (Cockcroft et al. 1989), since scavenging sharks are expected to consume only fat-rich portions of a carcass, not bony material (e.g. Carey *et al.* 1982; Klimley 1994, cited in Heithaus 2001a).

Due to limited data on cetacea, studies about shark predation on pinnipeds were searched for further information about the importance of active predation. Relevant papers were localized using the key words:

- shark feeding seal

Since pelagic sharks are generalist predators (e.g. Ebert 1994; Cortés 1999; Bianucci *et al.* 2000; Malcolm *et al.* 2001; Crespi-Abril *et al.* 2003; Dudley *et al.* 2005; Sigler *et al.* 2006; Yano *et al.* 2007; Mendonça 2009; Lopez *et al.* 2010; Hussey *et al.* 2012; Dicken *et al.* 2017) it is

assumed that predation is not limited to the cetacea species for which attacks have been observed, or remains have been identified in stomach contents, but is rather directed towards available species up to a certain maximum cetacea body size, as long as distributional ranges overlap. The lack of documented predation on a number of cetacea species is suggested to reflect a lack of data due to the offshore distribution and inconspicuous behaviour of many species included in this analysis, rather than indicating non-existence of predation risk. The only exception is the killer whale, who indeed does not seem to have any natural predators. To the authors knowledge predation on killer whales has not been documented. Cannibalism seems extremely rare if existent at all (Jefferson *et al.* 1991). Based on these assumptions expected shark predators of the different toothed whale species were identified according to their body size (Tab. 5). Shark predation on living baleen whales is based on documented predation only, rather than on body size.

Killer whales show dietary specialization between populations towards either marine mammals or shoaling fish or large predatory fish in some areas but seem to rarely specialize on certain species of whales or dolphins (e.g. Ford *et al.* 1998; Dahlheim, White 2010; Ferguson *et al.* 2012a). Hence based on App. 4: Tabs. 2, 3 which show killer whale predation on all cetacea size classes of both sub-orders, it is assumed that this predator represents a predation threat to all whale, dolphin and porpoise species included in this analysis.

Since this predator identification is based on stomach content analyses and field observations of predation events, the existence of further predator species, for which predation on cetacea has never been documented is possible. Even though the most robust measure of stomach content analysis in fish, frequency of occurrence, has been used (Baker *et al.* 2014), stomach contents represent a snapshot-like insight into the diet of animals (Duffy, Jackson 1986). The composition of stomach contents may vary greatly temporally and locally, esp. in generalist predators such as large pelagic sharks which adjust their diet to prey availability (e.g. Cliff *et al.* 1989, 1996; Ebert 1991a; Yano *et al.* 2007; Barnett *et al.* 2010b; Abrantes, Barnett 2011; Courtney, Foy 2012). Stable isotope analyses indicate a large variability in the feeding ecology of Pacific sleeper sharks with a wider range of prey than stomach content analyses suggest (Courtney, Foy 2012). The importance of baleen whales in the diet of killer whales can change depending on the availability of calves (Ternullo, Black 2002; Matkin *et al.* 2007). Variation in digestion times of different types of prey can bias an assessment of the importance of a prey species in a predator's diet (Hyslop 1980; Jackson, Ryan 1986; Jackson *et al.* 1987). Identification of cetacea prey remains to species level is often impossible (e.g. Shevchenko 1975; Cliff *et al.* 1989, 1996; Bianucci *et al.* 2000; Crespi-Abril *et al.* 2003; Sigler *et al.* 2006). The combination of stomach content analyses with field observations partially dissolves these issues. However, studies which applied either method have included only a subset of predator species and areas. The extrapolation from these data to other offshore cetacea and predator species for an estimation of predation risk has to be interpreted with care, and future study results will improve our understanding in this issue.

Parasites and predators which only take small bites out of their prey, such as cookiecutter sharks, *Isistius brasiliensis*, have not been included in this predation risk analysis.

2. Exposure to predators

Exposure to predators is briefly discussed based on predator attack and prey escape techniques. The lack of shelter in the offshore environment provides few possibilities to reduce predator exposure. With the accumulation of information about the portion of time spent at depth by deep-diving cetacea species more accurate quantitative estimates of exposure of these species to epipelagic killer whales will be possible.

3. Estimation of relative predator encounter rate

Due to the lack of data regarding absolute encounter rates between cetacea and their predators this analysis uses estimates of relative encounter rates, based on habitat overlap. Density estimates of relevant whale, dolphin and shark species are only available for a subset of areas and species. Therefore, this analysis of predation threat is based on the overlap of predator and cetacea habitat. It is assumed that a species which has more predators will encounter a predator more often than a species which has less predators. It is further assumed that a great overlap in distributional range between prey and predator leads to more encounters between the two.

The estimation of overlap in horizontal habitat range between cetacea and their predators is based on the analysis of distribution maps. Cetacea distribution maps in Shirihai, Jarrett (2006) show a grid of 40° latitude by 40° longitude squares. The number of squares inhabited by every cetacea species was counted. Shark distribution maps provided by 'fishbase' were used to assess habitat overlap. These maps show the distribution of shark species in more detail than the available cetacea maps. Hence when maps of a shark species were laid over the map of cetacea species to estimate habitat overlap, a smaller grid of 20° latitude by 20° longitude was used, and squares which are shared by cetacea and shark predators were counted for every species included in this analysis. The relative overlap in horizontal habitat range between predator and prey, x , was then calculated from:

$$x = \frac{n_p}{4n} \quad (1)$$

n : number of squares inhabited by the cetacea species
 n_p : number of squares shared by predator and prey

The number of squares inhabited by the cetacea species is multiplied by four due to the variation in grid size used to estimate n and n_p .

The calculation of the relative overlap in vertical habitat range between predator and prey species is based on Tab. 7 and was calculated as:

$$y = \frac{l_p}{l} \quad (2)$$

l : number of vertical layers inhabited by prey species
 l_p : number of vertical layers shared with predator

The total overlap in habitat, including horizontal and vertical aspects, was calculated as:

$$o = xy \quad (3)$$

o : percent habitat overlap
 x : relative overlap in horizontal habitat range between predator and prey
 y : relative overlap in vertical habitat range between predator and prey

An additional parameter, h , describes the overlap in horizontal range of cetacea prey species with high-density killer whale areas, based on Tab. 11:

low level of overlap	$h = 1/3$
medium level of overlap	$h = 2/3$
high level of overlap	$h = 1$

leading to the relative encounter rate, e_k , of cetacea prey species with killer whales of:

$$e_k = h o_k \quad (4)$$

Some species of shark predators and cetacea show a strong association with slope habitat. The distributional maps used for sharks (fishbase) reflect this association. The distributional maps used for cetacea are more general. Therefore, slope associated cetacea species encounter slope inhabiting sharks more often than reflected by the calculations of habitat overlap. Vice versa, association with deep oceanic waters or offshore shelf waters in cetacea reduces encounter rates with slope associated sharks. To account for this a slope association factor, s , was introduced.

Based on the preferred habitat of cetacea species and their shark predators, slope association in cetacea, s_c , and sharks, s_s , was defined as:

$s_c = 0.5$ in species which show strong slope association

$s_c = 0$ in species which occupy a variety of habitats, including slopes

$s_c = -0.5$ in species which do not associate with slopes/avoid slopes

Slope association, s , was then calculated as:

$$s = s_c s_s \quad (5)$$

By doing that slope association, s , is:

- positive when either both, shark and cetacea are associated with slopes, or shark and cetacea are both not slope-associated.
- 0 when shark and/or cetacea inhabit a variety of habitats, including slopes.
- negative when either the shark is slope-associated but the cetacea is not, or vice versa.

Relative encounter rate, e_s , of cetacea species with their shark predators was then calculated as:

$$e_s = o + (os). \quad (6)$$

Rather than assuming an overall random distribution of cetacea and sharks in offshore waters, these estimates contain density components due to the incorporation of slope association in the analysis of habitat overlap between cetacea and sharks, and by consideration of high versus low density killer whale areas when estimating the habitat overlap with whale, dolphin and porpoise prey species. However, this analysis does not consider non-random distribution caused by preferred association with or avoidance of ephemeral and/or non-stationary oceanographic phenomena such as eddies, frontal areas and up- or downwelling events.

4. Estimation of death rate upon encounter

Death rate upon encounter consists of two components: the probability that an encounter leads to an attack, and the probability that an attack results in a kill (attack fatality).

The percentage of encounters leading to an attack, a , was derived from both, reviews on predation risk in cetacea, and encounters between killer whales and cetacea prey derived from dedicated survey data. When extracted from reviews the percentage of encounters leading to an attack was calculated as:

$$a = \frac{\text{number of encounters of killer whales and cetacea prey leading to an attack}}{\text{total number of documented encounters of killer whales with cetacea prey species}} \quad (7)$$

References and values are given in App. 4: Tab. 4. Attack rates upon encounter derived from reviews must be interpreted with care. If encounters which lead to an attack are more likely to be published than non-aggressive encounters, then that tendency would also be reflected by the results presented in App. 4: Tab. 4 and would lead to an over-estimation of the percentage of encounters that result in an attack. The same applies vice versa which would lead to an under-estimation of attack rate.

For shark predators attack rates upon encounter are not available due to the difficulty of observing encounters which do not lead to an attack. However, a correlation between the importance of cetacea in the diet of a shark species, and the percentage of encounters leading to an attack would be expected. Such a correlation has been found in terrestrial predators such as cougars feeding on ungulates (Knopff *et al.* 2010). Higher attack rates lead to a higher portion of ungulates ingested by cougars. To estimate attack rates upon encounter with Greenland, Pacific sleeper, southern sleeper, bluntnose sixgill, broadnose sevengill and white sharks stomach content data were analysed in combination with information on the importance of scavenging on cetacea.

According to the results of that analysis each shark species was assigned one of the following values for attack rate:

low attack rate upon encounter	a = 0.02
medium attack rate upon encounter	a = 0.1

These values were derived from the mean frequency of occurrence of cetacea in stomach contents of the two groups of shark species, which are 2% for shortfin mako, dusky and tiger sharks, and 15% for white, Greenland, Pacific sleeper, southern sleeper, bluntnose sixgill and broadnose sevengill sharks. In the latter set of species the percentage has been modified according to importance of scavenging versus active predation.

Unfortunately, a quantification of active predation versus scavenging was not possible due to the lack of relevant data. Assumptions about the extent of active predation had to be made based on few qualitative study results (Tab. 4).

Attack fatality, f , was calculated from the number of attacks with known outcome and the number of fatal attacks, both based App. 4: Tabs. 2, 3.

$$f = \frac{\text{number of fatal attacks}}{\text{number of attacks with known outcome}} \quad (8)$$

Since this calculation is based on low sample sizes, attack fatality was further compared with rates of scars inflicted by cetacea predators as an additional measure of predator fatality. Low levels of scars inflicted by predators can mean both, a high level of predator fatality or the lack of predation by the predator on a potential prey species. A high scar rate indicates low attack fatality (e.g. Norris *et al.* 1994, Heithaus 2001a). Hence, scar rates are best used as a measure of predator fatality in combination with the percentage of encounters leading to an attack. If that percentage is low, then a low scar rate reflects the lack of attacks. If the percentage of encounters leading to an attack is high, then a low scar rate indicates a high attack fatality. The main difference between the two measures of attack fatality is that the percentage of attack leading to a kill as used here, is an indicator for attack fatality at group level whereas scar rates reflect the outcome of predation attempts at the level of the individual.

In baleen whale species which respond to killer whale attacks by fight, namely southern right, humpback and gray whales (Ford, Reeves 2008), wounds and scars can be acquired while defending other group members. That means individuals may acquire scars without being the target of an attack such as mothers defending their calves. It also means that scars can be acquired even though an attack was fatal at group level, for example when a mother or escort defends a calf which is killed in the scope of the attack. The same applies to sperm whales.

Scar rates therefore need to be interpreted with care in these species when used as an indicator of attack fatality.

Death rate upon encounter was calculated as:

$$d = fa \quad (9)$$

5. Estimation of predation risk

Predation risk was calculated from encounter rate and death rate upon encounter for each predator-prey pair. Subsequently predation risks inflicted by all shark predators were added up to obtain an overall shark predation risk estimate for every cetacea species.

Predation risk inflicted by killer whales, r_k , was calculated as:

$$r_k = e_k d_k \quad (10)$$

and likewise shark predation risks, r_{si} , for every shark species as:

$$r_{si} = e_{si} d_{si} \quad (11)$$

for every shark species.

e_k : relative encounter rate with killer whales

e_s : relative encounter rate with sharks

d_k : death rate upon encounter with killer whales

d_s : death rate upon encounter with sharks

i : shark species

Overall shark predation risk, r_s , is:

$$r_s = \sum(e_{si} d_{si}) \quad (12)$$

Results

1. Predator identification

This analysis identifies predators of offshore cetacea species and analyses the importance of whales and dolphins as prey to their predators.

By review of shark and killer whale stomach content analyses and field observations of predation events (App. 4: Tabs. 2, 3) the following predators have been identified for cetacea in offshore waters:

- killer whale
- false killer whale
- pygmy killer whale
- shortfin pilot whale
- great white shark
- shortfin mako shark
- oceanic whitetip shark
- dusky shark
- bronze whaler/copper shark
(*Carcharhinus brachyurus*)
- tiger shark
- smooth hammerhead shark (*Sphyrna zygaena*)
- blue shark (*Prionace glauca*)
- Greenland shark
- Pacific sleeper shark
- southern sleeper shark
- bluntnose sixgill shark
- broadnose sevengill shark

No predation records have been found for the following offshore cetacea species:

- Arnoux's beaked whale
- Blainville's beaked whale
- Gervais' beaked whale
- Sowerby's beaked whale
- pygmy beaked whale
- Longman's beaked whale
- southern bottlenose whale
- pygmy killer whale
- melon-headed whale
- killer whale
- rough-toothed dolphin
- Atlantic white-sided dolphin
- hourglass dolphin
- Commerson's dolphin
- northern right whale dolphin
- Burmeister's porpoise

Shark species documented to attack living cetacea in addition to scavenging are summarized in Tab. 2.

Table 2: Shark species known to attack and prey on living cetacea

Species	Reference
Great white shark	Arnold 1972; Corkeron <i>et al.</i> 1987; Long 1991; Long, Jones 1996a; Bianucci <i>et al.</i> 2000; Celona <i>et al.</i> 2006; Pitman <i>et al.</i> 2015
Shortfin mako shark	Santos-Monteiro <i>et al.</i> 2006; Silva Jr. <i>et al.</i> 2007; Porsmoguer <i>et al.</i> 2015
Oceanic whitetip shark	Leatherwood <i>et al.</i> 1973, related to purse-seine fishing
Dusky shark	Dicken <i>et al.</i> 2015
Tiger shark	Corkeron <i>et al.</i> 1987; Wells 1991; Darling 2001; Maldini 2003b; Bornatowski <i>et al.</i> 2012
Pacific sleeper shark	Crovetto <i>et al.</i> 1992; Sigler <i>et al.</i> 2006
Broadnose sevengill shark	Ebert 1991b

Bull sharks are cetacea predators in many coastal areas (e.g. Cockcroft *et al.* 1989; Heithaus 2001a) but do not inhabit offshore waters (Compagno *et al.* 2005) and are therefore not included in this predation risk analysis. Cetacea remains are occasionally found in blue shark stomachs but no attack on living cetacea by this species has been observed. A single study found baleen whale remains to occur in 15% stomachs off S-Brazil (Tab. 2). The authors suggested that these food items have been scavenged. The same study did not find any mysticeti remains in 116 stomachs from waters off NE-Brazil (Vaske *et al.* 2009). Markaida, Sosa-Nishizaki (2010) reviewed 34 studies on blue shark diet, none of which lists marine mammals as a main prey. Numerous studies have not found any cetacea remains in blue shark stomachs (e.g. Mearns *et al.* 1981; Seki 1993, n: 32; Clarke *et al.* 1996, n: 195; McCord, Campana 2003, n: 231; Fujinami *et al.* 2018, n: 221). Cetacea remains found in few stomachs of bronze whalers are most likely to reflect scavenging, rather than active predation (Cliff, Dudley 1992). Hammerhead sharks form large shoals in deep offshore waters (Klimley 1985; Vooren *et al.* 2005), which can potentially harm cetacea. However only a single attack has been observed in the wild and stomach content and stable isotope analyses do not indicate predation on marine mammals (Galvan-Magaña *et al.* 1989; Bolaño Martínez 2009, n: 445; Ochoa-Díaz 2009, n: 136; Gonzalez-Pestana *et al.* 2017, n: 485). All of these species are thought to be very minor predators on cetacea, if active predators at all, and are no further considered in this predation risk analysis.

Table 3: Frequency of occurrence of cetacea remains in stomachs of large pelagic sharks [%]; in braces: number of stomachs containing cetacea remains/sample size

Shark species	Mysticeti	Dolphins	Unid. cetacea
Great white shark	25% (71/225)	9% (41/440)	23% (15/66)
Shortfin mako shark	-	1% (11/878)	-
Oceanic whitetip shark	-	-	-
Dusky shark	-	-	2% (1/49)
Tiger shark	-	2% (18/859)	-

Blue shark	15% (11/106)	4% (44/1037)	-
Greenland shark	18% (14/76)	14% (3/22)	-
Pacific sleeper shark	-	25% (1/4)	11% (18/171)
Southern sleeper shark	-	-	25% (3/12)
Bluntnose sixgill shark	-	13% (9/69) but 29% (6/21) in ind. > 2m	-
Broadnose sevengill shark	-	6% (22/342)	-

Stomach content analyses indicate that tiger, dusky and shortfin mako sharks are occasional cetacea predators (Tab. 3). Cortés (1999) found marine mammal remains in 3 out of 468 (0.6%) dusky shark stomachs, suggesting a low predation rate of this species on cetacea. Of the only two studies which found high portions of cetacea in the diet of tiger sharks one was carried out in an area with bather protection nets off South Africa (Dicken *et al.* 2017). Since sharks are well known for attacking and preying on various cetacea species when entangled in nets (see below), and the tiger sharks were found to congregate around baleen whale carcasses related to these nets (Dicken *et al.* 2017), the high portion of cetacea found in tiger shark stomachs is most likely anthropogenically caused. The other study examined the stomachs of tiger sharks caught in gill nets off North Carolina and the authors pointed out that 6 of the 7 sharks with dolphins in their stomachs may have preyed on individuals caught in the same net (Bell, Nichols 1921).

Oceanic whitetip sharks have only been seen to prey on dolphins when group structure of the latter was dissolved by purse-seine fishing activity and dolphins were exhausted and confused. Cortés (1999) found marine mammal remains in 4 out of 108 (4%) stomachs of oceanic whitetip sharks. The author did not differentiate between pinnipeds and cetacea. Backus *et al.* (1956) did not find cetacea remains in 41 stomachs from individuals of the Gulf of Mexico, the Caribbean and E-USA, and stable isotope analyses identified oceanic squid (44%) and teleosts (43-47%) as main prey items in this species (Madigan *et al.* 2015). These findings indicate that oceanic whitetip sharks rarely prey on cetacea.

White sharks heavily prey on cetacea in a number of areas. Dolphins are the primary prey of white sharks off S-Australia (Bruce 1992), and cetacea account for one third of of the diet of white sharks in the Mediterranean (Bianucci *et al.* 2000). Off South Africa marine mammals, esp. cetaceans are the most common prey in white sharks > 2.5m body length (Cliff *et al.* 1989, 1996). Results of stomach content analyses presented in Tab. 2 confirm this dietary reliance on whales and dolphins. The highest frequency of occurrence of cetacea remains was found in stomachs of > 3.2m long great white sharks from S-Australian waters (44%F, Bruce 1992, n: 16).

Stomach content analyses further identify all three species of sleeper sharks included in this analysis, as well as bluntnose sixgill sharks and broadnose sevengill sharks as important predators of whales and dolphins (Tab. 3). Whether these species attack living cetacea or are merely scavengers is largely unknown (e.g. Heithaus 2001a). The large portion of cetacea remains in stomachs of all three species of sleeper sharks and of bluntnose sixgill sharks suggests active predation by these species. However, these results are based on small sample sizes. Therefore, any relevant information has been collected from the literature to further investigate the level of active predation versus scavenging. Results are presented in Tab. 4.

Table 4: Level of active predation versus scavenging in sleeper sharks

Species	Information	Reference
Greenland shark	active predation on seals caught in nets	Templeman 1963
	new-born harbour porpoise, <i>Phocoena phocoena</i> , found in Greenland shark stomach, suggesting active predation during birth	Williamson 1963 (stomach content analysis)
	main prey off N-Baffin Island: scavenged whaling offal, discarded fish + seal meat 4 narwhals + 1 beluga attacked in nets, sharks removed chunks of skin/blubber from carcasses	Beck, Mansfield 1969 (stomach content analysis)

Species	Information	Reference
	fresh remains of a ringed seal, <i>Phoca hispida</i> , found in stomach of Greenland shark which was bitten across the chest and swallowed whole suggest active predation	Ridoux 1998 (ringed seal homing experiment)
	marine mammals (at least 3 pinniped species) are 2nd most important prey incl. fresh remains, suggesting active predation, N-Atlantic	Yano <i>et al.</i> 2007 (stomach content analysis)
	heavy and active predation on 5 seal species off Sable Island, Nova Scotia	Lucas, Natanson 2010 (seal wound + carcass analysis)
	6 of 33 stomachs of Greenland sharks caught off Svalbard contained scavenged minke whale offal from whaling operations (18%F, 5%N, 3%M)	Leclerc <i>et al.</i> 2011, 2012 (stomach content analysis)
	active predation on belugas around breathing holes in Arctic ice suggested by observations of large pieces of blubber bitten out of living individuals	MacNeil <i>et al.</i> 2012 (review on Greenland shark)
	active predation on harp and bearded seals, <i>Erignathus barbatus</i> , off southern Greenland	Nielsen <i>et al.</i> 2014 (stomach content analysis)
Pacific sleeper shark	fresh and complete southern right whale dolphin calf and genital area of adult found in Pacific sleeper shark stomach in Chilean waters, suggesting predation on living dolphin as mother was giving birth	Crovetto <i>et al.</i> 1992 (stomach content analysis)
	individuals of TL 150-350cm removed more soft tissue from whale carcass over 1.5-month period than any other species, tissue removal continued for months	Smith <i>et al.</i> 2002, Smith, Baco 2003 (whale fall experiment)
	blubber from filter-feeding baleen whales identified as most important source of energy and lipid, Gulf of Alaska, active predation very unlikely blubber accounted for > 75% of energy ingested,	Schaufler <i>et al.</i> 2005 (fatty acids analysis)
	of 21 cetacea pieces found in Pacific sleeper shark stomachs 3 were scavenged, 4 likely scavenged, 3 fresh when consumed, 11 unknown	Sigler <i>et al.</i> 2006 (stomach content analysis)
Southern sleeper shark	several dead seals found in stomachs were very fresh and suggest active predation on living individuals; dietary importance of giant squid, a large, fast-moving squid, suggests ability to actively attack agile prey	Yano <i>et al.</i> 2007 (stomach content analysis)
	1 living southern elephant seal, <i>Mirounga leonina</i> , with southern sleeper shark bite wound observed at Macquarie Island in 19 years of research	Van Den Hoff, Morrice 2008
Bluntnose sixgill sharks	observations of sixgill sharks attacking large, fast-swimming prey incl. swordfish, <i>Xiphias gladius</i> , and marlin off South Africa, indicating ability to catch living cetacea	Ebert 1990 (field observations)
Broadnose sevengill sharks	17% of stomachs from individuals in Uruguayan waters contained franciscana dolphin, <i>Pontoporia blainvillei</i> , remains	Praderi 1985 (stomach content analysis)
	active predation on South African fur seal, <i>Arctocephalus pusillus</i> , solitarily and by cooperative group hunting, and on small cetaceans by cooperative group hunting; scavenges opportunistically	Ebert 1991b: (coastal field observations)
	marine mammals account for 1/3 of diet in ind. TL: >220cm off California, and South Africa	Ebert 2002 (stomach content analysis)

Species	Information	Reference
	marine mammals, incl. cetacea (15%F), represent ≥30% of total biomass consumed by sevengill sharks off Patagonia indicating active predation; 1 stomach contained the fluke and caudal peduncle of a dolphin	Crespi-Abril <i>et al.</i> 2003 (stomach content analysis)

Tab. 4 further confirms that marine mammals are important prey of Greenland sharks. Active predation on seals has been documented for various areas and can be so extensive that top-down control of the ringed seal population off Sable Island by this shark species has been suggested (Lucas, Natanson 2010). Even though this predator heavily scavenges on whaling offal when available, a switch to active predation on toothed whales when carcasses are unavailable, and opportunistic predation on odontoceti are indicated by observations of attacks on living belugas and narwhals in nets, and on belugas around breathing holes, as well as by fresh remains of a new-born harbour porpoise found in the stomach of a Greenland shark. However, it seems that this species covers a much higher portion of its diet by both, scavenging on cetacea and active predation on seals than by predation on living cetacea.

In spite of the scarcity of information the feeding ecology of Pacific sleeper sharks seems very similar to that of the Greenland shark. Heavy scavenging activity on whale carcasses and the importance of baleen whale blubber as a source of fat show the extensive use of cetacea carcasses when available. The fresh remains of a new-born southern right whale dolphin in the stomach of a Pacific sleeper shark indicate opportunistic active predation on small cetacea, which was further confirmed by Sigler *et al.* (2006) who found this species to both, scavenge and actively prey on cetacea, but scavenged cetacea remains accounted for a higher proportion of stomach contents than pieces ingested by active predation. The lack of bony material of baleen whales in stomachs of Pacific sleeper sharks indicates that the use of these large mammals as a food source is most likely limited to scavenging.

Southern sleeper sharks seem to actively prey on seals as well as on a number of other living fast-moving prey suggesting active predation on small cetacea. Scavenging may be less important to this sleeper shark species, but more information is needed.

Knowledge of feeding habits of bluntnose sixgill sharks is also very limited. The predation of this species on other fast-moving prey suggests the ability to actively attack small cetacea, which have been found in stomachs of these sharks in large proportions off South Africa and in Turkish waters. However, the use of satellite telemetry revealed that in Hawaiian waters most active foraging happens at night at water depths of 200-300m (Comfort, Weng 2015) which is below the night-time feeding depth of most small offshore cetacea species (e.g. Benoit-Bird, Au 2003; Benoit-Bird *et al.* 2004; Scott, Chivers 2009). During the day sixgill sharks are typically found at a depth of 600-700m, only overlapping with the vertical range of deep-diving toothed whales, most of which are of medium to large body size. It seems that predation pressure by this species on cetacea may depend on habitat characteristics. More studies investigating sixgill shark foraging are needed.

Broadnose sevengill sharks prey on cetacea to an extent which cannot be explained by scavenging alone, at least in some areas. Active predation has been observed on pinnipeds as well as cetacea, and the use of cooperative group hunting techniques suggest that marine mammals are regularly actively preyed on. Scavenging seems to play a minor role in this shark species.

Conclusively these results suggest that southern sleeper, bluntnose sixgill and broadnose sevengill sharks may regularly actively prey on cetacea whereas Pacific sleeper and Greenland sharks predominately feed on carcasses of these marine mammals.

Stomach content analyses identify the killer whale as a major predator of minke whales, dolphins and Dall's porpoises (Tab. 5).

Table 5: Frequency of occurrence of cetacea remains in stomachs of killer whales

Species	Frequency of occurrence [%]	Number of stomachs containing cetacea	Sample size n
Balaenopterid whales exc. minke	1	4	390
Minke whale	62	56	90
<i>Kogia</i>	4	1	26
Beaked whales	2	6	364
Pilot whales	1	3	364
Dolphins	31+	14+	45
Dall's porpoise	18	66	376

Tab. 6 shows which predators are expected to feed on cetacea based on cetacea body size. It forms the base for the quantitative analysis of predation risk.

Attacks by shortfin pilot whales, and pygmy and false killer whales on other cetacea species seem extremely infrequent and have therefore not been included in the following predation risk analysis.

Table 6: Predators on odontoceti species based on cetacea body size

Body size class	Cetacea species	Documented predators
10-20m	sperm whale, Baird's beaked whale	killer whale, white shark, dusky shark, tiger shark
4-10m	Cuvier's beaked, Arnoux's beaked, Blainville's beaked, Longman's beaked, southern + northern bottlenose, long- + short-finned pilot, false killer whales	killer whale, white shark, dusky shark, tiger shark, Greenland shark
≤ 4m	<i>Kogia</i> , Gervais' beaked, Sowerby's beaked, pygmy beaked pygmy killer, melon-headed whales, Risso's, bottlenose, rough-toothed, white-beaked, Atlantic + Pacific white-sided, hourglass, dusky, Fraser's, spinner, pantropical + Atlantic spotted, Clymene, common, Commerson's, southern + northern right whale dolphins, Dall's, Burmeister's porpoises	killer whale, white shark, shortfin mako, oceanic whitetip shark, dusky shark, tiger shark, Greenland shark, Pacific sleeper shark, southern sleeper shark, bluntnose sixgill shark, broadnose sevengill shark

2. Exposure to predators

Exposure to predators in offshore waters is constant for any cetacea species whose diving capabilities are limited to the epi- and mesopelagic realms since this environment does not provide shelter. The only exceptions are offshore areas close to shore, such as the coastline of South Africa, New Zealand and Hawaii, where deep water, offshore conditions and offshore species can be found in great proximity to land and escape in shallow water can provide temporary relief from exposure to killer whales and sharks. Deep-diving species may escape predation from killer whales and some shark species by steep and fast decent beyond their predator's reach. However, smaller deep-diving species such as dwarf and pygmy sperm whales may expose themselves to predation risk from sleeper, sixgill and sevengill sharks at depth.

With the exception of sperm whales, and likely most beaked whale species, predation threat is nearly imminent in offshore waters due to the lack of shelter. Even though sperm whales have been suggested to benefit from their deep-diving capabilities when attacked by killer whales (e.g. Jefferson *et al.* 1991), evidence for this type of anti-predator behaviour is lacking. Instead, male sperm whales have been shown to prematurely interrupt foraging dives and gather with conspecifics on the surface when exposed to killer whale sounds (Curé *et al.* 2013). Groups of sperm whales which include calves cannot escape by deep dives due to the limited diving capabilities of young individuals (Whitehead 2003). Vertical overlap in habitat

between cetacea and their various predators was included in the estimation of encounter probability (Tab. 7) and accounts for time spent sheltered from predation.

3. Relative encounter rate with predators

For practical reasons results of the relative encounter rates of cetacea with sharks are presented first and will be followed by the estimation of encounter rates of whales, dolphins and porpoises with killer whales.

Large pelagic sharks

Fig. 1 shows the overlap in distributional range between cetacea and their shark predators. Only predator-prey relationships which are thought to include active predation are considered here.

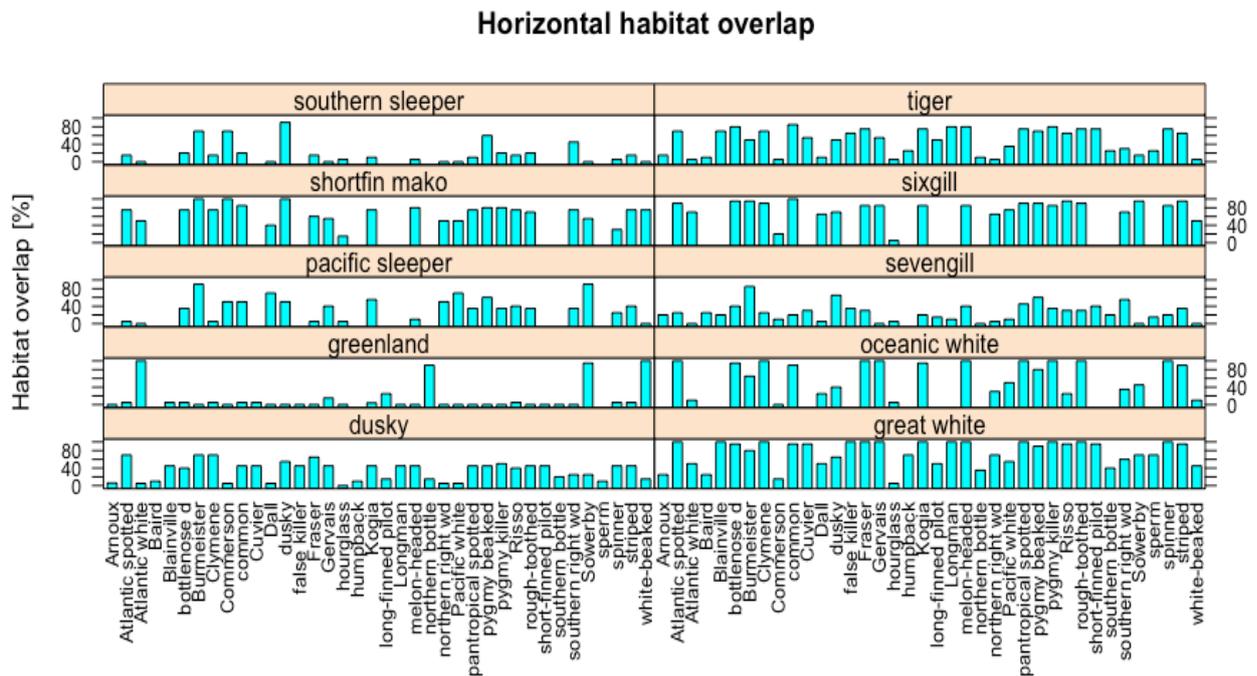


Figure 1: Overlap in horizontal distribution between shark predators and cetacea prey (x • 100) in %

Tab. 7 shows the vertical habitat of oceanic cetacea and their predators, which was quantified from the number of vertical layers shared with the predator divided by the number of vertical layers inhabited by the cetacea prey species (Fig. 2).

Table 7: Vertical habitat of cetacea and their predators

Habitat	Shark species ^a	Cetacea species ^b
Epi-pelagic	killer whale, white, shortfin mako, oceanic whitetip, dusky, tiger, Greenland, Pacific sleeper, sevengill	blue, fin, sei, Bryde's, minke, southern right, humpback, gray, sperm, <i>Kogia</i> , Cuvier's beaked, Baird's beaked, Arnoux's beaked, Blainville's beaked, Gervais' beaked, Sowerby's beaked, pygmy beaked, Longman's beaked, southern + northern bottlenose, long- + short-finned pilot, false killer, pygmy killer, melon-headed, Risso's, bottlenose, rough-toothed, white-beaked, Atlantic + Pacific white-sided, hourglass, dusky, Fraser's, spinner, Pantropical spotted, Atlantic spotted, striped, Clymene, common, Commerson's, southern + northern right w.d., Dall's, Burmeister's
Meso-pelagic	white, shortfin mako, oceanic whitetip, dusky,	blue, fin, Bryde's, humpback, sperm, <i>Kogia</i> , Cuvier's beaked, Baird's beaked, Blainville's beaked, Gervais' beaked, Sowerby's beaked, pygmy beaked, Longman's beaked, southern + northern

Habitat	Shark species ^a	Cetacea species [•]
	Greenland, Pacific sleeper, southern sleeper, sixgill, sevengill	bottlenose, long- + short-finned pilot, false killer, pygmy killer, melon-headed, Risso's, bottlenose, rough-toothed, white-beaked, Pacific white-sided, hourglass, Fraser's, striped, southern right w.d., Dall's
Bathypelagic	Greenland, Pacific sleeper, southern sleeper, sixgill	sperm, <i>Kogia</i> , Cuvier's beaked, Baird's beaked, Blainville's beaked, Gervais' beaked, Sowerby's beaked, pygmy beaked, southern + northern bottlenose, long- + short-finned pilot, Risso's dolphin

^a References: Compagno *et al.* 2005; Jorgensen *et al.* 2012; Hoffmayer *et al.* 2014; Holmes *et al.* 2014, Howey *et al.* 2016; Vaudo *et al.* 2016

[•] References: App. 2 (based on foraging depth and parts of water column which have to be traversed to commute between surface (for breathing) and feeding depth)

Fig. 2 shows the overlap in vertical habitat between sharks and cetacea.

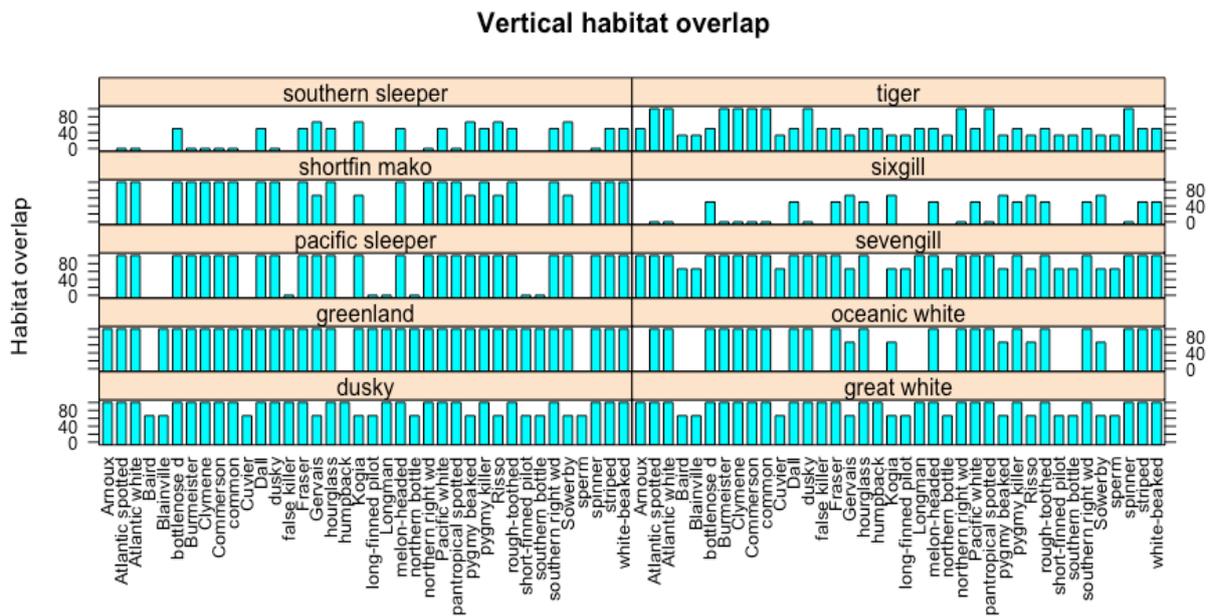


Figure 2: Overlap in vertical distribution between sharks and cetacea species ($y \cdot 100$) in %

Tab. 8 shows the preferred horizontal habitat of sharks and cetacea which was used as a base for the calculation of the slope association factor, s . Pacific sleeper, southern sleeper and bluntnose sixgill sharks occur predominantly in slope habitat, whereas Greenland and broadnose sevengill sharks inhabit a variety of habitats, including slopes. White, shortfin mako, oceanic whitetip, dusky and tiger sharks are not typically associated with slope habitat. A slope association factor has been assigned to every species accordingly (Tab. 10). Slope association in cetacea was analysed in the same manner (Tab. 9).

Table 8: Overlap in preferred habitat between sharks and cetacea

Habitat association	Shark species [•]	Cetacea species ^a
Offshore shelf waters	white, shortfin mako, dusky, tiger, Greenland, (Pacific sleeper), broadnose sevengill	minke, southern right whale, humpback, gray whale, pygmy sperm, false killer whale, bottlenose, rough-toothed, white-beaked, Atlantic + Pacific white-sided, dusky, Atlantic spotted, spinner, common, Commeron's, southern right whale dolphin, Burmeister's + Dall's porpoise
Slope	Greenland, Pacific sleeper, southern sleeper, bluntnose	minke, southern right, sperm, dwarf + pygmy sperm whale, Cuvier's beaked, Blainville's beaked, Longman's beaked, general beaked, long- + short-

Habitat association	Shark species•	Cetacea species ^a
	sixgill, broadnose sevengill	finned pilot, false + pygmy killer, melon-headed whale, Risso's, bottlenose, Atlantic + Pacific white-sided, dusky, Fraser's, Atlantic spotted, striped, Clymene, common, southern right whale dolphin
Deep oceanic waters	white, shortfin mako, oceanic whitetip, tiger	southern right whale, humpback, sperm, dwarf + pygmy sperm, melon-headed whale, rough-toothed, Atlantic white-sided, hourglass, Fraser's, spinner, pantropical spotted, striped, Clymene, common, northern + southern right whale dolphin, Dall's porpoise

• References: Compagno *et al.* 2005; fishbase

^a References: Moore *et al.* 2000; Waring *et al.* 2001; Cañadas *et al.* 2002; MacLeod, Zuur 2005; Anderson *et al.* 2006; Dolar *et al.* 2006; Garaffo *et al.* 2007; Ingram *et al.* 2007; Kiszka *et al.* 2007; Azzellino *et al.* 2008; Doksæter *et al.* 2008; MacLeod *et al.* 2008; McSweeney *et al.* 2009; Perrin *et al.* 2009; West *et al.* 2011; Santora 2012; Baird *et al.* 2013; Weir *et al.* 2013; Rosso *et al.* 2014; Abecassis *et al.* 2015; Claridge *et al.* 2015; Rayment *et al.* 2015; Di Tullio *et al.* 2016; Palmer *et al.* 2017

Tab. 9 shows slope association values for cetacea.

Table 9: Slope association, s_c , in cetacea species which have shark predators

Cetacea species	s	Cetacea species	s	Cetacea species	s
Minke whale	0	Northern bottlenose	0.5	Fraser's dolphin	0
Southern right whale	0	Long-finned pilot	0.5	Spinner dolphin	-0.5
Humpback whale	-0.5	Short-finned pilot	0.5	Pantropical spotted	-0.5
Sperm whale	0	False killer whale	0	Atlantic spotted	0
<i>Kogia</i>	0	Pygmy killer	0.5	Striped dolphin	0
Cuvier's beaked	0.5	Melon-headed	0	Clymene dolphin	0
Baird's beaked	0.5	Risso's	0.5	Common dolphin	0
Arnoux's beaked	0.5	Bottlenose	0	Commerson's	-0.5
Blainville's beaked	0.5	Rough-toothed	-0.5	Southern right w.d.	0
Gervais' beaked	0.5	White-beaked	-0.5	Northern right w.d.	-0.5
Sowerby's beaked	0.5	Atlantic white-sided	0	Dall's porpoise	-0.5
Pygmy beaked	0.5	Pacific white-sided	0	Burmeister's	-0.5
Longman's beaked	0.5	Hourglass dolphin	-0.5		
Southern bottlenose	0.5	Dusky dolphin	0		

Tab. 10 shows slope association values for shark species which prey on cetacea. The resulting slope association factor for each predator-prey pair was directly incorporated in the estimation of relative encounter rates between cetacea and their shark predators, e_s .

Table 10: Slope association, s_s , in sharks

Shark species	s	Shark species	s	Shark species	s
White shark	-0.5	Tiger shark	-0.5	Bluntnose sixgill	0.5
Shortfin mako	-0.5	Greenland shark	0	Broadnose sevengill	0
Oceanic whitetip	-0.5	Pacific sleeper shark	0.5		
Dusky shark	-0.5	Southern sleeper	0.5		

The combined analysis of vertical and horizontal habitat overlaps, as well as slope association, resulted in the following estimates of relative encounter rates between sharks and their cetacea prey (Fig. 3).

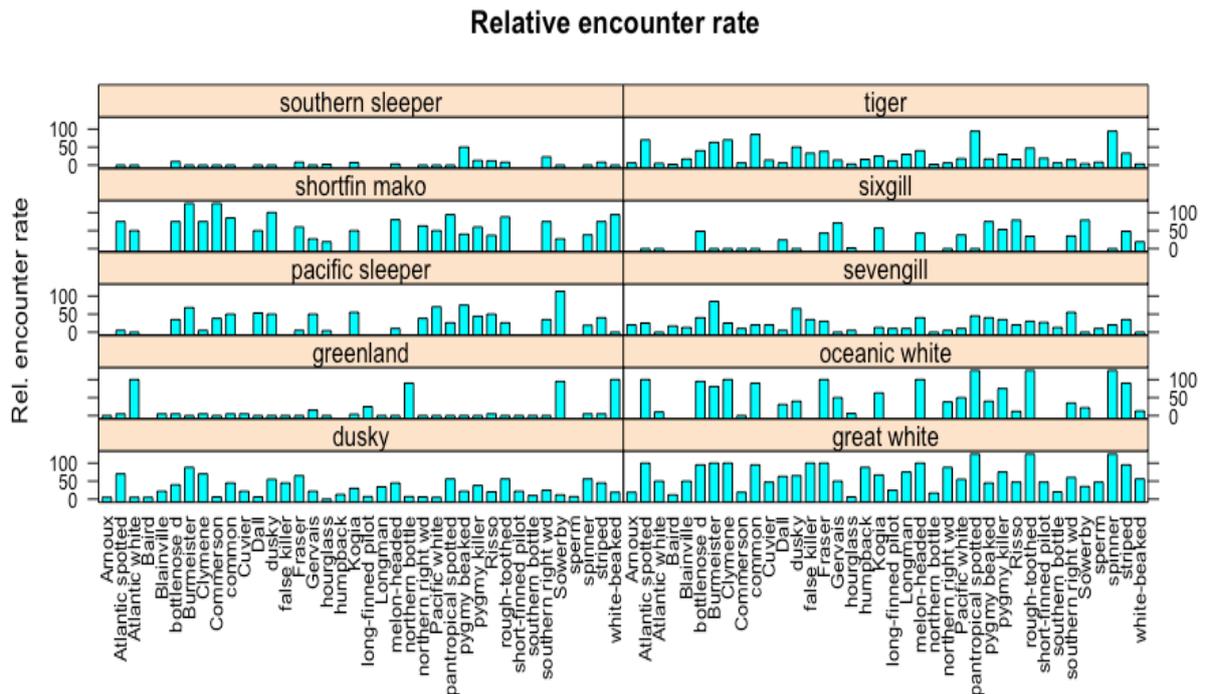


Figure 3: Relative encounter rate ($e_s \cdot 100$) in %

Killer whales

The killer whale's horizontal range overlaps to 100% with that of every other cetacea species included in this analysis. The major variation in predation risk inflicted by this predator lays in its reduced density in tropical and subtropical compared to temperate, sub-polar and polar waters, and in its reduced density in areas > 200km from land (Forney, Wade 2006). Hence, species with a predominantly tropical and subtropical distribution should experience less predation by killer whales than species with temperate to polar distribution. Species which rarely approach land should be exposed to a lower risk of killer whale predation than species which live under oceanic conditions close to shore, such as dusky dolphins off New Zealand, or common dolphins off South Africa. A value for the level of overlap of high-density killer whale areas with horizontal range of cetacea prey species, h , was assigned to every cetacea prey species accordingly (Tab. 11).

Table 11: Overlap of cetacea horizontal range with high-density killer whale areas

Level of overlap	Cetacea prey species ^a	h
Low	sei, Bryde's, pygmy sperm, Cuvier's beaked, Blainville's beaked, Gervais' beaked, Longman's beaked, pygmy killer, melon-headed whale, Risso's, rough-toothed, hourglass dolphin, Fraser's, spinner, pantropical spotted, Atlantic spotted, striped, Clymene dolphin	1/3
Medium	blue, fin, southern right, sperm, dwarf sperm, Baird's beaked, Arnoux's beaked, Sowerby's beaked, pygmy beaked, southern + northern bottlenose whale, short-finned pilot, false killer whale, bottlenose, Atlantic white-sided, common, southern + northern right whale dolphin, Burmeister's porpoise	2/3
High	minke, humpback, gray, long-finned pilot whale, white-beaked, Pacific white-sided, dusky, Commerson's dolphin, Dall's porpoise	1

^a References on cetacea distribution: Shirihi, Jarrett 2006; Perrin *et al.* 2009

The overall overlap, o , in vertical and horizontal habitat between killer whales and cetacea prey species is shown in Fig. 4.

Habitat overlap and relative encounter rate

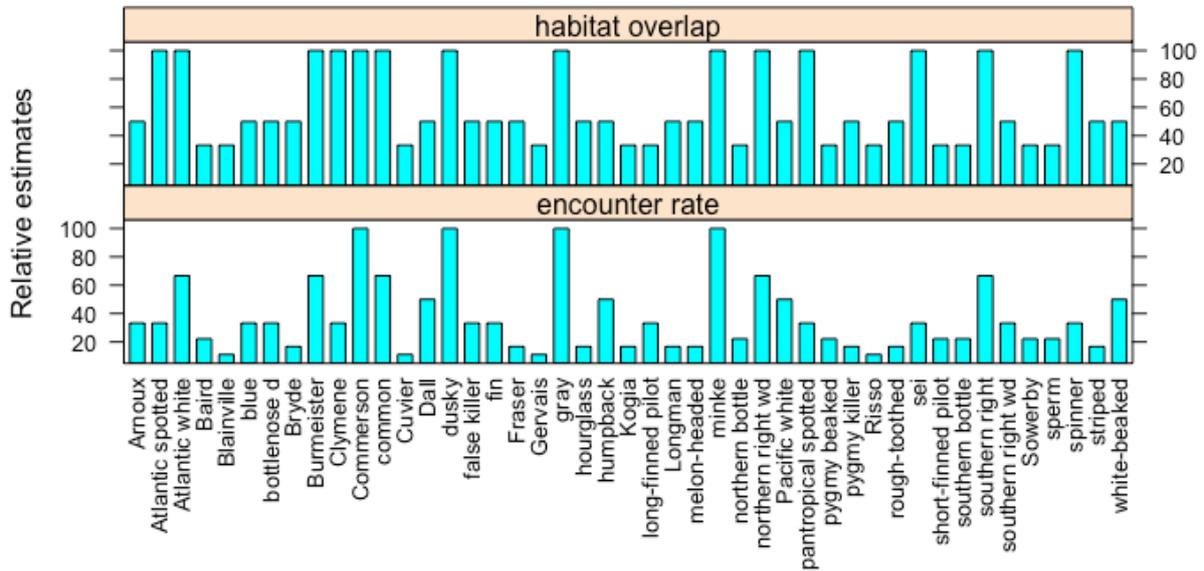


Figure 4: Percent habitat overlap killer whale - cetacea prey, o , and relative encounter rate, $e_k = ho$

4. Estimation of death rate upon encounter/predator fatality

The analysis of predator fatality consists of two components: the percentage of encounters leading to an attack, and the percentage of attacks resulting in the death of the prey species.

Killer whales

Results of both components of killer whale fatality are shown for each cetacea species for which data were available (App. 4: Tab. 4). However, due to small sample sizes, in balaenopterids and dolphins the combined results across species are likely to more realistically reflect killer whale fatality than the numbers presented for single species. Hence numbers derived from pooled balaenopterids and dolphins were used for further analysis of predation risk. In accordance with body size similarity in predation risk, pilot whale data were used for the estimation of predation risk in false killer whales, whereas dolphin data were applied to pygmy killer whales and melon-headed whales.

Scar rates show that the estimate of attack rate upon encounter provided above is too high in blue whales, and the percentage of attacks leading to a kill was estimated too high in sei, humpback and sperm whales. Humpback whale scar rates reflect the geographic variation in attack rate upon encounter indicated by the high variation in estimates of this parameter derived from different publications (App. 4: Tab. 4: column 2). Scar rates are in agreement with fatality estimates in fin, gray and minke whales and in dusky dolphins. Details on scar rates used in App. 4: Tab. 4, including sample size and study area, can be found in Tab. 12.

Table 12: Rates of scars inflicted by killer whales, n: number of identified individuals

Species	Scar rate [%]	Sample size n	Area
Blue whale	0	150+	Sri Lanka
	4	27	SE-Australia
Fin whale	53	not publ.	Southern Ocean
Sei whale	24	not publ.	Southern Ocean
Minke whale	6	not publ.	Southern Ocean
Humpback whale	12-15	1364	Caribbean
	<1	13	Cape Verde

Species	Scar rate [%]	Sample size n	Area
	17-29	1114	Gabon
	24	54	Namibia
	35	107	W-South Africa
	14-15	5793	N-Atlantic
	9-11	2206	Gulf of Maine
	16-18	4107	E-Canada
	22	163	Greenland
	11	464	W-Greenland
	8-13	367	Iceland
	3-8	161	Norway
	6-8	448	S-Japan
	5-9	734	Alaska (incl. Aleutians), W-Canada
	22	237	SW-Alaska
	20	694	W-USA
	23-40	899	Mexico
	15-18	1291	Hawaii
	18-20	392	American Samoa, Tonga
	31	166	New Caledonia
	17	1436	SE-Australia
	16	1287	W-Australia
	38	8	New Zealand
	1	164	Antarctic Peninsula
	9	33	Oman
Gray whale	18	317	California
	34	not publ.	Okhotsk Sea
Sperm whale	65	not publ.	Southern Ocean
	21	190	Galápagos
Dusky dolphin	0.09	1171	Kaikoura, New Zealand

Ref.: App. 4: Tab. 1

Large pelagic sharks

Quantitative analyses of the percentage of encounters of cetacea with sharks which lead to an attack are non-existent. The approach used here is based on the positive correlation between attack rate upon encounter and portion of prey found in stomach contents, combined with information about the importance of scavenging on cetacea in the different shark species. Stomach content analyses indicate that the percentage of encounters leading to an attack are low in oceanic whitetip, dusky, shortfin mako and tiger sharks (Tab. 3). Stomachs of the latter three species contained significantly less cetacea remains than stomachs of white, sleeper, sixgill and sevengill sharks (one-tailed Welch's $t(7) = 2.8$, $\alpha < 0.025$). The Shapiro-Wilk test revealed that data for shark species with large portions of cetacea in stomach contents show normal distribution ($\alpha = 0.01$) whereas stomach content data across the remaining species do not ($\alpha > 0.05$). However, the prerequisite of normal distribution can be loosened for large sample sizes (Altman, Bland 1995). The total amount of stomachs analysed for each of the two groups are 1187 and 1693, respectively. The combination of stomach content data with information on the importance of scavenging (Tab. 3) further suggest low attack rates in Greenland and Pacific sleeper sharks, medium attack rates in white, southern sleeper, bluntnose sixgill and broadnose sevengill sharks on odontoceti except for the sperm whale, and low attacks rates on all species of baleen whales and in sperm whales (Tab. 13). No shark species is expected to attack cetacea during most encounters since all species feed on a large variety of prey, rather than showing specialization on cetacea.

Table 13: Attack rate upon encounter, a , of sharks with odontoceti, exc. sperm whale

Attack rate upon encounter	Shark species	Based on	Assigned value for a [%]
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Low	oceanic whitetip, dusky, shortfin mako, tiger shark	stomach content data	3
	Greenland and Pacific sleeper shark	combination of stomach content data + importance of scavenging on cetacea	
Medium	white, southern sleeper, bluntnose sixgill, broadnose sevengill shark	combination of stomach content data + importance of scavenging on cetacea	10
High	-	prey generalism rather than specialization on cetacea	-

Attack fatality estimates are shown in Tab. 14. Due to low sample sizes attack fatality was pooled across dolphins. This value has also been applied to *Kogia*, pygmy killer and melon-headed whales, and porpoises for the calculation of death rate upon encounter, d (Tab. 15). The attack fatality estimate for beaked whales has been applied to pilot and false killer whales. Details on scar rates are summarized in Tab. 16.

Table 14: Attack fatality of sharks: f = number fatal attacks / number of attacks with known outcome (n)

Cetacea species	Shark species	f [%]	Sample size n	Scar rate [%]	Indication of scarring
Humpback	tiger, white, dusky, bull, copper	80	5+ (all calves)	< 1	low a
<i>Kogia</i>	white	0	2	-	-
Beaked whales	white	50	2	-	-
Risso's	white	100	1	-	-
Bottlenose	white	83	6	1-69	high f offshore, low f inshore
Pacific white-sided	white, unid.	50	2	-	-
<i>Stenella</i> dolphins	white, oceanic whitetip, tiger, shortfin mako, unid.	100	8	1-15	high f
common dolphin	white, mainly shortfin mako	50	4+	-	-
southern right w.d.	Pacific sleeper shark	100	1	-	-
Dolphins	white, shortfin mako, oceanic whitetip, tiger, Pacific sleeper	82	22+	1-69	high f offshore, low f inshore
Dall's porpoise	white	100	1	-	-

Dolphin scar rates consistently indicate a low attack fatality in inshore waters and suggest a high attack fatality offshore, whereas the low shark scar rate in humpback whales is likely attributable to a low attack rate upon encounter. The high attack fatality estimate in this species may be caused by the very low sample size, and only applies to calves. Estimates of death rate upon encounter with sharks are shown in Tab. 15.

Table 15: Death rate upon encounter, d

Cetacea species	Shark species	a [%]	f [%]	d [%]
Baleen + sperm whale calves	all shark species	2.0	80	1.6
Beaked, pilot, false killer whales	oceanic whitetip, dusky, shortfin mako, tiger, Greenland, Pacific sleeper sharks	2.0	50	1.0
	white, southern sleeper, sixgill, sevengill sharks	10.0		5.0
<i>Kogia</i>, pygmy killer, melon-headed, dolphins, porpoises	oceanic whitetip, dusky, shortfin mako, tiger, Greenland, Pacific sleeper sharks	2.0	82	1.6
	white, southern sleeper, sixgill, sevengill sharks	10.0		8.2

These values are intended for sharks of a length TL > 2.5m and are expected to be higher if only large mature individuals are considered.

Table 16: Rates of scars form pelagic sharks; n: number of identified ind. (Ref.: App. 4: Tab. 1)

Species	Scar rate [%]	Sample size n	Area
Humpback whale	< 1	865	E-Brazil
False killer whale	1	71	Aruba (S-Caribbean)
Bottlenose dolphin	1	76	Aruba (S-Caribbean)
	10-19	145	South Africa (caught in gill nets)
	22	86	W-Florida (Sarasota) inshore
	31*	151	W-Florida (Sarasota) inshore
	37	334	E-Australia inshore mostly white and tiger sharks
	69	138	W-Australia (Shark Bay) inshore mostly tiger shark
	0	106	Adriatic Sea
Dusky dolphin	0.17	1171	New Zealand (Kaikoura)
Spinner dolphin	13	418	Fernando de Noronha (SW-Atlantic)
Atlantic spotted dolphin	15	92	North Bimini
	1	179	Aruba (S-Caribbean)

*Urian *et al.* 1998

5. Calculation of predation risk

Predation risk was calculated from estimates of relative encounter rate with predators and predator fatality. Fig. 6 shows predation risk inflicted by the various shark species which prey on cetacea. Fig. 5 provides estimates of killer whale inflicted predation risk for each cetacea species included in this analysis.

These results indicate a high variability in shark and killer whale predation risk for different cetacea species. Killer whale predation risk varies between 1.3 in southern right whales and 63 in gray whales, whereas overall shark predation risk ranges from 0.1 in minke whales to 9.2 in Burmeister’s porpoises. The white shark inflicts the highest predation risk of all potential shark predator species to most cetacea.

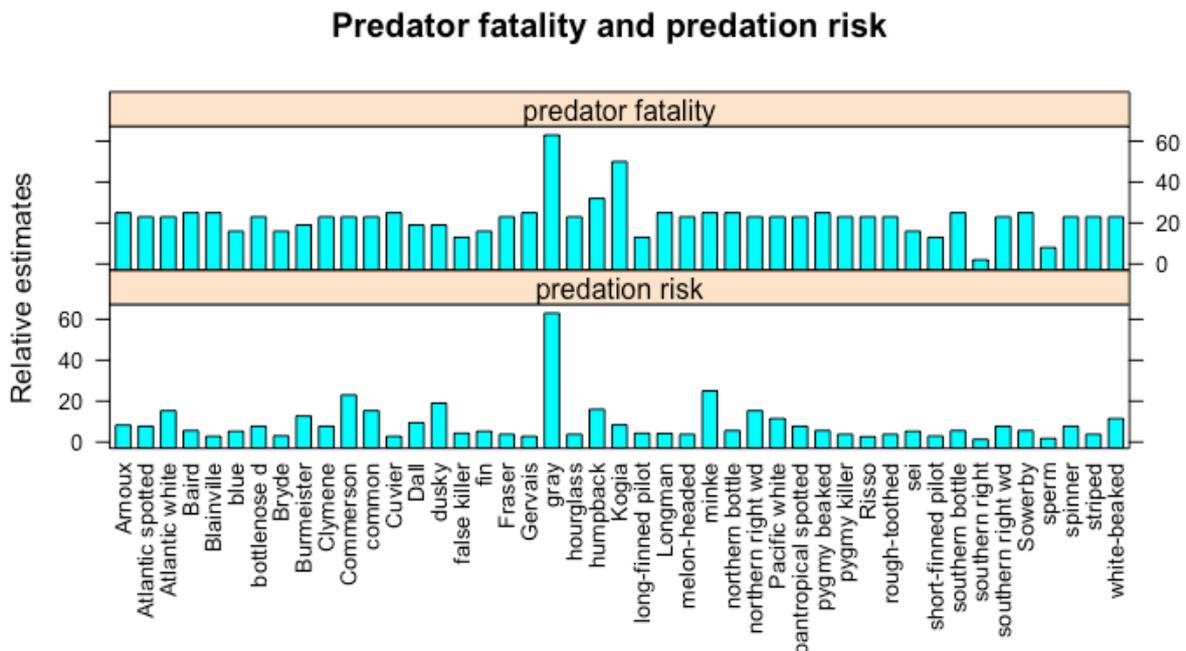


Figure 5: Predation risk inflicted by killer whales, r_k , ($r_k = e_k d_k$)

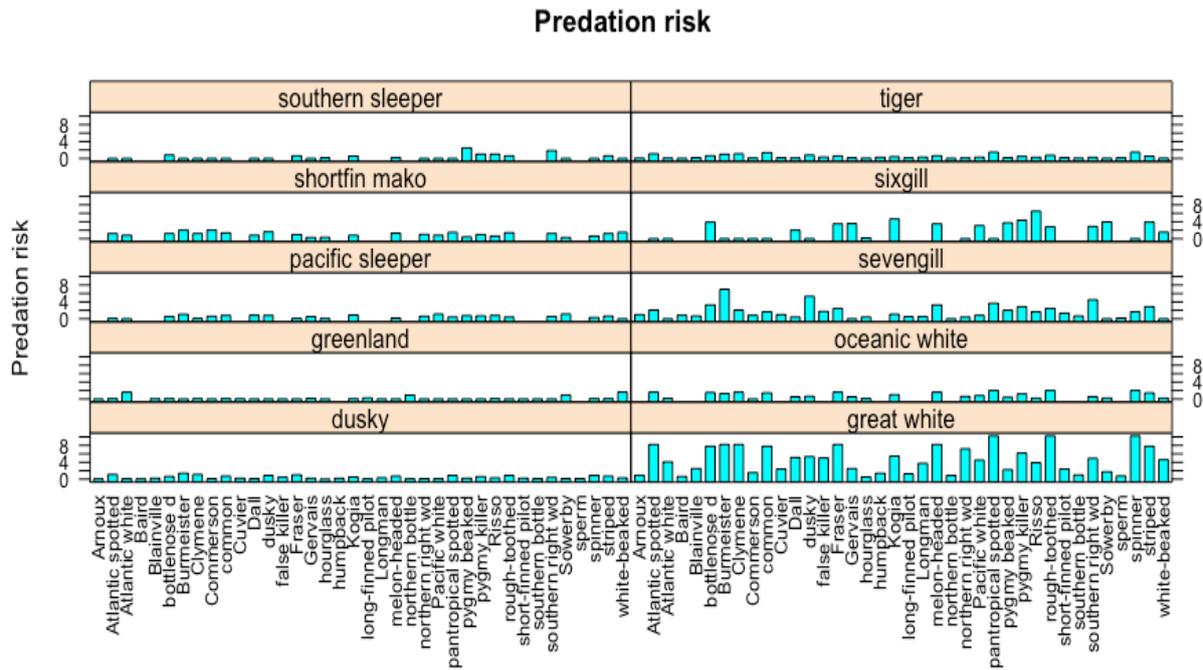


Figure 6: Predation risk inflicted by sharks, r_s

Discussion

It seems logical that the nature of an encounter between killer whales and another cetacea species largely depends on whether or not the killer whale pod in question belongs to a mammal-eating ecotype. None of the studies cited above for the percentage of encounters leading to an attack differentiates between different ecotypes of these mammals. For example, an encounter of a group of Dall's porpoises with a group of resident killer whales off British Columbia will obviously not lead to an attack (even though harassment has been observed) since that population feeds on fish. Pilot whales have even been found to be attracted to killer whale foraging sounds in areas where the latter predominantly feed on herring (Curé *et al.* 2012). Hence the numbers presented above are likely to partially reflect the encounter rate of cetacea with different ecotypes of killer whales, rather than the level of predation risk arising from encounters with mammal-eating killer whales. That means the actual percentage of encounters with mammal-eating killer whales leading to an attack is likely higher than Tab. 16 suggests. More research is needed on the risk of attack caused by an encounter of mammal-eating killer whales with other cetacea species.

An analysis of 103 interactions between mammal-eating killer whales (MEKW) and humpback whales found that humpbacks approach the former more often (37% encounters) than vice versa (26%) (Pitman *et al.* 2017). This is in spite of the fact that most encounters initiated by the killer whales result in an attack. In 87% of the encounters initiated by humpback whales the MEKW were already attacking or feeding on prey different from humpbacks. MEKW in turn only attacked humpback whales when no other prey was observed in the area (Pitman *et al.* 2017). This study shows the complexity of killer whale interactions with other cetacea species.

A high geographic variability in killer whale predation on humpback whales is indicated by both, large differences in scar rates between areas (Tab. 12) and a high variation in attack rate upon encounter between studies conducted in different regions (App. 4: Tab. 4). The percentage of encounters leading to an attack ranges from 20% off Angola and in the Gulf of Guinea (Weir *et al.* 2010) to 69% off western Australia, where 3 calves were killed in 6 days in the scope of 8 attacks, suggesting that at least dozens of humpback whales are taken by

killer whales annually (Pitman *et al.* 2015). Orcas selectively target calves off western Australia whereas attacks on all age classes have been observed in other areas (Jefferson *et al.* 1991; Visser 1999, 2000; Lawson *et al.* 2007; Ford, Reeves 2008). Scar rates vary between <1% off Cape Verde and up to 40% off Mexico, most likely reflecting the geographic variation in killer whale attack rates, rather than variable attack fatality.

High attack rates on gray whales upon encounter with killer whales, and medium to high attack fatality presented here, are in line with a high rate of killer whale predation on this species found by other studies. Killer whale attacks on gray whales have been observed in calving/mating grounds in the Gulf of California, at many points along the migration route between Mexico and Alaska, and on the feeding grounds in the Bering and Chukchi seas (Melnikov, Zagrebin 2005). Barrett-Lennard *et al.* (2005) suggested that mortalities of up to 35% of the average annual calf production of California gray whales may be attributable to killer whales. Eastern Aleutian island transient killer whales seem to exclusively prey on juvenile gray whales in May (Ternullo, Black 2002; Krahn *et al.* 2007; Matkin *et al.* 2007), and 18 kills in the scope of 19 observed predation attempts show that attack fatality may be as high as 95% in that area (Matkin *et al.* 2005). These results indicate that gray whales are a main prey species of killer whales in the NE-Pacific. However, little is known about killer whale predation on gray whales in the NW-Pacific. Predator fatality may be different and studies on killer whale predation are needed for that area.

A low attack rate upon encounter of southern right whales with killer whales is in line with accounts of high predation on Antarctic minke whales (Yukhov *et al.* 1975; Pitman, Ensor 2003) and pinnipeds (Pitman, Durban 2012; Reisinger *et al.* 2011) by mammal-eating killer whales in the Southern ocean, and predation on a large variety of food items, including various baleen and toothed whale species, pinnipeds and birds, in South American waters (Hoelzel 1991; Häussermann *et al.* 2013; Capella *et al.* 2014) and off South Africa (Best *et al.* 2010). The low attack fatality (Tab. 15; Ford, Reeves 2008) may indicate a high efficiency of the typically cooperative defence in this species (Ford, Reeves 2008). Out of 9 attacks/harassments by killer whales on southern right whales with known outcome cited in Ford, Reeves (2008) none were fatal. Southern right whales further predominantly inhabit offshore waters far from land during summer months (Shirihai, Jarrett 2006), where killer whale density is low (Forney, Wade 2006), whereas humpback and gray whales occasionally occupy oceanic and offshore shelf areas, but are often found in coastal, and sometimes very shallow water.

Scar rates and field observations of killer whale attacks on minke whales, both indicate a high attack fatality for this species (App. 4: Tab. 4; Tab. 12), which may however be lower in some coastal areas (Ford *et al.* 2005; Matkin *et al.* 2005). An attack rate upon encounter of 28% is in line with findings of regular predation on this species in the NE-Pacific (Jefferson *et al.* 1991; Ford *et al.* 2005), NW-Pacific (Mironova *et al.* 2002) and NW-Atlantic (Sergeant, Fisher 1957; Jefferson *et al.* 1991; Lawson *et al.* 2007). In the eastern Aleutian Islands minke whales account for 28% of the diet of transient killer whales during late summer (Matkin, Saulitis unpubl. data, cited in: Krahn *et al.* 2007). However, stomach content analyses (Tab. 4) suggest that the attack rate upon encounter may be high in Antarctic waters where few data on field observations of killer whale - minke whale encounters are available. Minke whale remains were recovered from 84% of 44 stomachs off killer whales caught in the Southern Ocean, south of 50°S (Shevchenko 1975). Yukhov *et al.* (1975) found minke whale remains in 75-100% of killer whale stomachs from the Indian ocean sector of Southern Ocean, 53-55°S, and in 73% killer whale stomachs from the Amundsen Sea. Minke whales seem to be a major prey item of type A killer whales (offshore form) in southern sub-polar and polar waters (Pitman, Ensor 2003).

Other balaenopterid whale species seem to experience much lower predation risks from killer whales. This may be related to large body length and consequently high escape speeds in

these species but is also a reflection of the offshore distribution of these species. This is particularly true for Bryde's and sei whales which are typically found in deep oceanic water. Out of 280 killer whale attacks observed on baleen whales, 108 were with certainty directed towards calves (App. 4: Tab. 2). In many cases groups containing calves were targeted but in non-fatal attacks, or attacks with unknown outcome it was often not clear whether or not the presence of calves was the reason for the attack. Non-fatal predation attempts and successful predation by killer whales on adult individuals has been observed in all baleen whale species included in this study (App. 4: Tab. 2; Best 1982; Bloch, Lockyer 1988; Silber *et al.* 1990; Jefferson *et al.* 1991; George, Suydam 1998; Visser 1999; Sironi *et al.* 2004; Ford *et al.* 2005; Lawson *et al.* 2007; Ford, Reeves 2008; Boyce 2013; Häussermann *et al.* 2013).

In spite of a number of observed killer whale attacks on sperm whales, and an unexpectedly high attack fatality, sperm whales seem to face a low risk of predation from these predators. Attacks typically last several hours (e.g. Weir *et al.* 2010; Whitt *et al.* 2015) and are hence more likely to be observed than killer whale attacks on many other cetacea species. Sperm whales spend long periods of time at depth to feed, out of the reach of killer whales, contributing to a low estimate of predation risk. The presence of calves can change that situation since young individuals have lower diving capacities and are often left at the surface accompanied by one or few adults while the majority of the group is foraging at depth (Whitehead 1996). 12 out of 18 attacks (67%) for which the age of the targeted individual or group was known, were either directed toward calves or involved sperm whale groups comprising one or more calves or young individuals. However, females and calves are typically found in tropical and subtropical regions where killer whale density is lower than at higher latitudes.

Killer whale scar rates of 65% in the Southern Ocean indicate a low attack fatality in adult male sperm whales which mainly inhabit high latitude waters, where killer whale density is high (Best 1979; Caldwell *et al.* 1966; Rice 1989; Whitehead 2003). A scar rate of 21% off Galápagos may reflect a lower killer whale density in tropical waters but could also indicate higher attack fatality on female and young individuals, or both. Killer whale attacks on sperm whales analysed by this study include both, single males and groups of females and juveniles. Consequently, attack fatality in adult male sperm whales may be lower than the estimate presented in App. 4: Tab. 4 (54%).

The long duration of attacks often prevents the determination of the outcome since researchers have to leave the area before the attack ends. Hence in 11 out of 24 documented killer whale attacks on sperm whales it is not known whether or not a kill occurred.

Few studies provide information on predation risk in pygmy and dwarf sperm whales (*Kogia*). All 5 observed attacks by killer whales were successful, leading to an attack fatality estimate of 100%. However, both species of the genus *Kogia* carry out prolonged foraging dives, outside the range of killer whales, reducing risk of predation by this species. Pygmy sperm whales occupy deep oceanic water, typically far from land whereas dwarf sperm whales enter coastal areas. Resulting differences in predation risk are likely.

Dwarf sperm whales were suggested to adjust group size and habitat use to killer whale predation risk, a learned behavioral response which indicates more than just occasional predation (Dunphy-Daly *et al.* 2008; Dunn, Claridge 2014). *Kogia* seems to be important prey of killer whales in the Bahamas. Killer whale density, however is low in this area (Dunn, Claridge 2014).

Two observed attacks by white sharks were both unsuccessful, but an overlap in habitat of *Kogia* with nine out of ten shark species known to attack cetacea leads to a high estimate of shark predation risk. Sharks are the final host for larval cestodes (Cheung 1993, Caira, Healy 2004), such as *Phyllobothrium delphini*, which are commonly found encysted in dwarf sperm whale blubber (Nagorsen 1985; Cardona-Maldonado, Mignucci-Giannoni 1999; Goold, Clarke 2000). In order for these parasites to be transmitted, shark predation and scavenging of dwarf sperm whale carcasses must be relatively frequent (Dunphy-Daly *et al.* 2008).

Few information of killer whale predation on beaked whales is available. Especially the Arnoux's beaked whale is data deficient. Estimates of relative encounter rates in this study have been made under the assumption that this species occurs in epi- and mesopelagic waters, but since neither tracking nor prey data are available this is uncertain. Beaked whales spend long periods of time out of the reach of epipelagic killer whales. A long-term tagging study revealed that Cuvier's beaked whales dive for up to 137.5min to depths of almost 3000m, and surface for no longer than about 3min between dives. Extended surface times are uncommon and almost exclusively occur at night (Schorr *et al.* 2014). Deep diving combined with inconspicuous surface behaviour has been suggested to represent a response to predation pressure from epipelagic predators like killer whales (Aguilar de Soto 2006). Nevertheless, killer whale predation has been documented for Cuvier's, Baird's, strap-toothed and possibly Gray's beaked whales, and for northern bottlenose whales (App. 4: Tab. 3). Out of 5 observed attacks all have been successful, indicating a high attack fatality. Killer whale playback sounds were found to elicit avoidance responses in Blainville's beaked whales (Tyack *et al.* 2011; Allen *et al.* 2014). Variation in time spent at depth versus surface time between species may alter risk of predation by killer whales and should be included in future studies of predation risk in ziphiids as well as other deep-diving cetacea. However, currently dive and surface times are known for only a small subset of beaked whale species and were therefore not added as an additional parameter in this analysis.

Only two shark attacks on beaked whales have been documented, both by white sharks, of which one was fatal. However beaked whales are difficult to observe due to both, the large proportion of time spent at depth and inconspicuous surface behaviour. Attacks, especially by deep-water sharks may not be uncommon. This is particularly suggested in species of small body size, including Gervais', Sowerby's and pygmy beaked whales.

Attack rates on pilot whales upon encounter with killer whales may vary dramatically between areas. An estimate of 0% was found for long-finned pilot whales in the Strait of Gibraltar where killer whales predominantly feed on bluefin tuna (e.g. Guinet *et al.* 2007; Esteban *et al.* 2016), whereas the analysis of the nine encounters cited in Jefferson *et al.* (1991) lead to an estimate of 56% of encounters leading to an attack. Bloch, Lockyer (1988) found killer whales to frequently mix with pilot whales in Faroese waters, likely feeding on a common food source. More studies of killer whale predation on pilot whales are needed. Shark attacks on pilot whales have not been directly observed but scars attributed to attempted predation by unidentified sharks were found on several individuals in New Zealand waters (Zaeschmar, J. pers. comm.). Pilot whales seem to face a low overall predation risk.

Only one killer whale attack on false killer whales has been observed, none in pygmy killer whales and melon-headed whales. The last two species inhabit deep oceanic waters, usually far from land, which reduces both, actual killer whale predation risk and the likelihood of attacks being observed. False killer whales approach land in some regions, especially where under-water slopes occur close to shore such as off New Zealand and Hawaii. All three species dive to depths beyond the reach of killer whales which reduces relative encounter rates with killer whales. Shark attacks have not been documented but especially white sharks may inflict a significant predation risk to these species.

Most dolphins species face a significant predation risk from sharks (Fig. 6). The attack fatality estimate is high (82%, Tab. 15), which is also indicated by low scar rates in offshore compared to coastal populations (Tab. 16). The only exceptions are hourglass and Commerson's dolphins which share their habitat with few relevant shark species due to their sub-polar and polar distributions. Hourglass dolphins are further suggested to face a low predation risk from killer whales. Even though killer whales are generally abundant in (sub-)polar waters hourglass dolphins may face low encounter rates with these predators due their oceanic deep-water distribution (Tab. 13). Vertical habitat is also only partially shared between the two species (Tab. 7). No attacks have been observed. Risso's dolphins were estimated to face the lowest risk of predation from killer whales of all dolphin species. These animals are deep divers which spend

considerable time outside the vertical range of killer whales, and inhabit deep water, typically far from land where killer whale density is low. Dolphin species which occupy oceanic waters close to shore in temperate and sub-polar areas face the highest risks of killer whale predation. These include dusky dolphins off New Zealand, and Commerson's dolphins off Patagonia. Killer whale predation on Commerson's dolphins has not been observed but the species shows a strong avoidance reaction to the presence of these predators (Iñíguez, Tossenberger 2007). Killer whales are likely the main predator of this species (Harmer 1922) in offshore waters, where this species has been observed occasionally in large pods (Goodall *et al.* 1988; Coscarella *et al.* 2010). However, Commerson's dolphins predominantly inhabit coastal areas where shallow shorelines provide shelter from killer whale predation (Goodall *et al.* 1988; Coscarella *et al.* 2010; Dellabianca *et al.* 2016). The risk estimate presented here is to be applied to offshore areas only and would have to be corrected based on the time spent in inshore versus offshore waters to gain an overall species estimate of predation risk. That estimate would be lower than calculated in the scope of this analysis. Dusky dolphins remain in proximity to shore when killer whale density is high, and nursery groups composed of females and calves respond dramatically to the presence of these predators (Srinivasan 2009), all in line with a high risk of predation. Common dolphins are targeted by mammal-eating killer whales in a number of areas, including New Zealand (Visser 1999, 2000), Patagonia (Coscarella *et al.* 2015), California (Ternullo, Black 2002) and Gulf of California (Brown, Norris 1956; Breese, Tershy 1993). Attack rates on dolphins upon encounter with killer whales show high variation and more research on predation rates is needed.

Estimated percentages of Dall's porpoise in the diet of transient killer whales vary by region, and amount to 5% in Glacier Bay area, Alaska (Matkin *et al.* 2005), 6% in inshore waters of British Columbia and SE-Alaska (Ford *et al.* 1998), 10% in Monterey Bay, California (Ternullo, Black 2002), and 50% in Prince William Sound (Saulitis *et al.* 2000). Offshore off Prince William Sound transient killer whales feed almost exclusively on Dall's porpoises (Saulitis *et al.* 2002). These geographical differences seem to correlate with two parameters: the availability of alternative prey and attack fatality. In Monterey Bay Dall's porpoises are killed by quick surprise attacks, leading to very high rates of success (Ternullo, Black 2002), whereas transient killer whales observed in inshore waters of British Columbia and offshore off Prince William Sound often involve high-speed chases over several kilometres, lasting up to 43min (Ford *et al.* 1998; Saulitis *et al.* 2000). Attack fatality was only 39% off British Columbia (n: 18, Ford *et al.* 1998) and 67% offshore off Prince William Sound. The high level of predation on Dall's porpoises in the latter area was suggested to reflect a decline in harbour seal density since the early 90s (Saulitis *et al.* 2000).

The killer whale attack fatality of 72% across Dall's porpoise habitat estimated in this study seems in line with an average of publications cited above. Attack rates upon encounter are further expected to vary between areas depending on the relative density of mammal-eating versus fish-eating killer whales. Resident killer whales frequently interact in non-predatory ways with Dall's porpoises, while transients do not (Saulitis *et al.* 2000). The majority of killer whales in the eastern Aleutian Islands are of the resident ecotype (Matkin *et al.* 2005). Similarly, a high number of non-aggressive interactions between killer whales and Dall's porpoises in the Prince William Sound area (n: 47, versus 18 attacks) suggests a higher density of residents than of transients (Saulitis *et al.* 2000). The attack rate upon encounter based on results of Saulitis *et al.* (2000) is 28% (n: 65), which is very similar to the estimate of 26% derived from Jefferson *et al.* (1991) for this analysis.

Only 1 shark attack on Dall's porpoises has been observed, by a white shark, which was fatal. Overall predation risk based on habitat overlap was estimated lower than in most dolphin species. Very little is known about Burmeister's porpoises and predation risk estimates presented here are solely based on habitat overlap with killer whales and sharks, and on predator fatality data derived from studies on Dall's porpoises and dolphins.

Killer whale predation on cetacea has been documented all around the Pacific, Bering sea, Chukchi sea, Arctic, all over N- and S-Atlantic, Caribbean, Gulf of Mexico, Gibraltar, N- and E-Indian ocean, Southern Ocean and around Antarctica (App. 4: Tabs. 2, 3).

The high fatality of killer whales attacks on cetacea overall (App. 4: Tab. 4) suggests a high hunting efficiency of these predators. Killer whales are the single most important natural cause of mortality in most cetacea species analysed in this study. More killer whale predation studies are particularly needed in sub-polar and polar areas where killer whales are abundant, but survey times have been small. Killer whales increasingly frequent the high arctic (Higdon, Ferguson 2009; Ferguson *et al.* 2010) and are known to prey on belugas (Vladykov 1944; Perrin 1982; Higdon *et al.* 2012, 2013), narwhals (Steltner *et al.* 1984; Campbell *et al.* 1988; Jefferson *et al.* 1991; Higdon *et al.* 2012) and bowhead whales (Perrin 1982; George *et al.* 1994; Finley 2001; Higdon *et al.* 2012). A recent study has shown that the presence of killer whales strongly alters the behaviour and distribution of narwhals in the Canadian arctic (Breed *et al.* 2017), and more research is needed which investigates interactions between both species in this quickly changing environment.

It is undeniable that cetacea are important prey for several shark species in some areas. However, living cetacea account for only a small percentage of the diet of most shark predators. The only exceptions are great white sharks, bluntnose sixgill sharks and broadnose sevengill sharks. Cetacea estimated to face the highest white shark predation risks are rough-toothed dolphins, spinner dolphins and pantropical spotted dolphins. The latter two species are known to form large mixed-species congregations in the eastern tropical Pacific, often involving yellowfin, *Thunnus albacares*, or skipjack tuna, *Katsuwonus pelamis* (Chap. 4), an area where white sharks concentrate, esp. in waters off Guadalupe Island and California year-round, and in the 'Cafe' area between Baja Peninsula and Hawaii, as well as around the Hawaiian Islands during spring (Boustany *et al.* 2002; Weng *et al.* 2007; Domeier, Nasby-Lucas 2008; Jorgensen *et al.* 2010; fishbase). Even though white shark abundance seems low even in core areas of this species (Chapple *et al.* 2011), predator encounter rates may be high in the eastern tropical Pacific due to a narrow mixed layer above an extended oxygen minimum zone which lead to the concentration of most top predators within the upper 50m of the water column. These findings lead to the question whether white shark predation risk represents a driver towards the formation of these large dolphin congregations (Chap. 3 and 4).

Cetacea which experience the highest predation risk from bluntnose sixgill sharks are Risso's dolphins, species of the genus *Kogia*, pygmy killer whales, Sowerby's beaked whales, bottlenose dolphins and striped dolphins, due to vertical and horizontal habitat overlap and shared slope association. Broadnose sevengill sharks may be important predators of Burmeister porpoises, dusky dolphins and southern right whale dolphins. Very little is known about predation of both species on cetacea. Unidentified dolphin remains were found in stomachs of bluntnose sixgill sharks between 1.2 and 6.0m total length, caught off South Africa and Turkey (Ebert 1994; Kabasakal 2006). Field observations and stomach content analyses identified broadnose sevengill sharks as predators of southern right whales off South Africa, bottlenose dolphins off S-Tasmania and dusky dolphins off Patagonia and South Africa (App. 4: Tabs. 1-3). Remains of unidentified dolphins and small odontoceti were found in stomachs of individuals from Namibia, South Africa, Patagonia and California.

Other species which face an overall high shark predation risk are melon-headed whales, Fraser's, Atlantic spotted, Clymene and common dolphins.

Active predation by sharks on cetacea is typically directed towards:

- sick (Ridgway, Dailey 1972; Stroud, Roffe 1979; Darling 2001) or young (Cockcroft *et al.* 1989; Paterson *et al.* 1993; Long, Jones 1996a; Mazzuca *et al.* 1998; Santos-Monteiro *et al.* 2006; Bornatowski *et al.* 2012; MacNeil *et al.* 2012; Melillo-Sweeting *et al.* 2014; Dicken *et al.* 2015; Pitman *et al.* 2015; Porsmoguer *et al.* 2015) individuals

- individuals in vulnerable situations such as during birth (e.g. Williamson 1963; Best *et al.* 1984; Crovetto *et al.* 1992) or during purse seine tuna fishing activity (Leatherwood *et al.* 1973)
- individuals entangled by, or caught in nets and other fishing gear (Bell, Nichols 1921; Templeman 1963; Beck, Mansfield 1969; Brownell 1975; Praderi 1985; Cockcroft *et al.* 1989; Cockcroft 1991; Darling 2001; Dicken *et al.* 2017)
- individuals separated from their group (Leatherwood *et al.* 1973; Cockcroft *et al.* 1989; Mann, Barnett 1999; Maldini 2003a,b; Mann, Watson-Capps 2005; Gibson 2006).

Predation by sharks on baleen whales is often interpreted as scavenging due to both, the size of these cetacea, and observations of heavy predation on baleen whale carcasses (e.g. Bornatowski *et al.* 2012). However, active predation and attempts thereof by large pelagic sharks on humpback whales, particularly calves, have been documented by a number of studies and for various areas, incl. waters off Brazil, Australia, Hawaii and South Africa (Paterson *et al.* 1993; Mazzuca *et al.* 1998; Darling 2001; Naessig, Lanyon 2004; Bornatowski *et al.* 2012; Dicken *et al.* 2015; Pitman *et al.* 2015; App. 4: Tab. 2). Tiger sharks were observed attacking living but entangled adults off Hawaii (Darling 2001). A group of ~10-20 dusky sharks (2-3m length) attacked a single humpback whale calf for 5 1/2h off South Africa. The calf was presumed to have drowned from exhaustion when it stopped surfacing (Dicken *et al.* 2015). A beached southern right whale calf was found in South Africa with numerous sevengill shark bites taken out of it (Ebert 1991b). These observations show that active predation by sharks on cetacea is not limited to species of small body size.

Interactions between small or medium sized white and tiger sharks with cetacea were found to be principally directed toward small toothed whale species (Slipp, Wilke 1953; Day, Fisher 1954; Arnold 1972; Corkeron *et al.* 1987; Bianucci *et al.* 2000; Dicken *et al.* 2017), particularly small to medium sized delphinids (Casey, Pratt 1985). As body size increases mysticeti and beaked whales become important prey (e.g. Long, Jones 1996a,b; Bianucci *et al.* 2000) which is further indicated by a positive correlation between trophic level and body size of large pelagic sharks (Arnold 1972; Mearns *et al.* 1981; Stillwell, Kohler 1982; Cliff *et al.* 1989; Cliff, Dudley 1991; Ebert 1994; Lowe *et al.* 1996; Cortés 1999).

However, the attack fatality estimate of 80% (Tab. 15) which was applied to all other baleen whales and sperm whales due to a lack of data, is based on a very low sample size, and is likely an over-estimate.

A high level of geographic and temporal variation in the importance of cetacea in the diet of large pelagic sharks is reflected by a number of studies which did not find whale or dolphin remains in stomachs of species which heavily prey on cetacea in other areas. These include Pacific sleeper sharks in the Bering Sea, the Gulf of Alaska (Yano *et al.* 2007, n: 16; Yang, Page 1999, n: 11) and the NW-Pacific (Orlov, Moiseev 1999, n: 148), southern sleeper sharks off southern Africa (Yano *et al.* 2007, n: 3), Greenland sharks in the N-Atlantic (Yano *et al.* 2007, n: 39) and in coastal Greenland waters (Nielsen *et al.* 2014) and bluntnose sixgill sharks off NE-Sicily (Celona *et al.* 2005, n: 23). High seasonal and decadal shifts in the diet regarding mammals and elasmobranch prey have been documented in tiger sharks off South Africa (Dicken *et al.* 2017).

Variation in attack rate upon encounter likely arises from inter-species variation in anti-predator behaviour. While most cetacea species flee from their predators at high speed (e.g. Lowry *et al.* 1987; Breese, Tershy 1993; Dahlheim, Towell 1994; Constantine *et al.* 1998; Saulitis *et al.* 2000; Visser 1999, 2000; Ternullo, Black 2002; Ford *et al.* 1998, 2005; Ford, Reeves 2008; Alava *et al.* 2013; Pitman *et al.* 2015), gray whales, sperm whales, species of the genus *Kogia* and beaked whales often respond with motionlessness to the presence of killer whales, or quietly sink below the water surface and dive (Gaskin 1964, 1971; Caldwell *et al.* 1966; Willis, Baird 1998; Dahlheim, Heyning 1999). Such inconspicuous behaviour combined with the prevalence of small group sizes may reduce detectability and therefore

lower attack rates compared to cetacea which form large pods and show a high level of surface and vocal activity such as spinner, common, dusky and spotted dolphins.

Attack success rate may vary between species which flee from predators versus cetacea which use defensive behaviour. Bottlenose, Atlantic spotted, Clymene and common dolphins have been observed to fend off sharks (AIBS 1967; Springer 1967; Herzing 2011) and humpback, southern right and gray whales actively defend themselves against killer whales (Payne 1992; Sironi *et al.* 2004; Ford, Reeves 2008). Unfortunately, the analysis of variation in fatality between shark predator species was hampered by a lack of data. Further research is needed for an improved estimation of both, attack rate upon encounter and attack fatality of shark predators.

Lastly, it is possible that more predators than identified by this study pose a risk to cetacea in offshore waters. Istiophorids such as marlins may occasionally attack vulnerable individuals of small cetacea species, and it is conceivable that adult giant squid, *Architeuthis* sp. And other large squid species, may pose a threat to deep-diving cetacea, such as species of the genus *Kogia*, beaked whales and Risso's dolphins, but no information is available on this issue.

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Chapter 3: Group size in oceanic cetacea

Abstract

Congregation behaviour in cetacea has been linked to a variety of parameters including predation risk, foraging and reproduction but quantitative analyses of the phenomenon are scarce and incomplete. Particularly in open oceanic waters many cetacea species can be encountered in pods of hundreds, sometimes of thousands of individuals, but variability in group size is large both, between and within species. This study attempts to identify the main evolutionary driver or drivers of congregation in oceanic whales, dolphins and porpoises through the comparative approach based on the quantitative analysis of correlations between predation risk, foraging-, reproduction-, and migration-related parameters, based on six hypotheses.

Cetacea phylogeny indicates that a large average group size of > 50 individuals is typical only in some evolutionarily young species. These large congregations were found to represent a behavioural adaptation to predation risk inflicted by sharks. A number of alternative adaptations to predation risk in oceanic cetacea causes the inconsistency in group size across species. Intra-specific group size variation is related to spatial and temporal variations in predation risk as well as to the presence or absence of calves. Calves are found in larger congregations than adults across many odontoceti species. A large difference in size between groups which contain calves compared to those which do not was linked to the protection of calves from predators, whereas small group size variations are likely related to alloparental care. Alloparental care and male alliances which increase access to females were found to drive the formation of small congregations of up to 15 individuals, whereas predation risk is the main driver towards larger groups.

Cooperative prey herding, communal prey search, improved navigation accuracy and hydrodynamic efficiency were identified as consequences, rather than causes of congregation in oceanic cetacea. Large congregations require a higher supply of forage than small pods, leading to the exploitation of grouping behaviour to increase access to prey. Large group size is facilitated by small body size, distribution of prey in large patches, a large home range, epi- and or mesopelagic foraging and acoustic communication signals of medium range.

This study shows that despite the limited availability of data for oceanic cetacea the analysis of group size alone can provide valuable and important insight into evolutionary and ecological interrelations between grouping behaviour in cetacea and their environment.

Introduction

Large groups can entail increased effectiveness of the dilution effect and predator swamping, greater predator detection distances, higher prey capture times for predators, and may lead to increased mitigation and predator confusion as well as reduced predator encounter rates compared to small groups or solitary occurrence (Chap. 1). Hence, fitness benefits of congregation due to reduced predation risk may increase with increasing pod size (e.g. Jarman 1974; Hager, Helfman 1991; Krause, Godin 1994; Tegeder, Krause 1995; Hoare *et al.* 2004; Cresswell, Quinn 2011).

Foraging efficiency may change with varying congregation size due to alteration of prey search efficiency, the ability to handle grouped prey, accuracy of navigation between profitable foraging areas, the ability to capture larger prey items, ability to fend off kleptoparasites, competition for food, or time available for foraging (Chap. 1). Larger groups may also enhance navigation accuracy during migration and facilitate alloparental care and access to mating partners in a vast open environment (Chap. 1).

Using the comparative approach, this study attempts to find out which of these factors are main evolutionary drivers towards congregation in oceanic cetacea. Davies *et al.* (2012) listed a number of limitations of early comparative studies which are that (1) alternative hypotheses have not been considered in a rigorous manner, (2) ecological variables have often not been quantified, (3) cause and effect were not disentangled, (4) alternative solutions to the same problem and non-adaptiveness of differences have not been considered, and (5) independent data points were not properly identified, biasing statistical analyses. Attempts were made to consider these points as much as possible.

Analyses are based on interrelations between group size and the following parameters:

- phylogenetic relationships
- body size
- predation threat
- geographic group size variation
- foraging depth
- shoaling tendency of prey
- home range size/migration pattern
- active space of acoustic signals
- group size seasonality
- presence of calves

These parameters were quantified as much as possible. Group size, body size, predation threat, shoaling tendency of prey and active space were analysed as continuous variables, whereas foraging depth, migration/movement pattern, group size seasonality and the presence/absence of calves are discrete variables. Phylogenetic analyses of group size, body size, foraging depth and migration/movement pattern were carried out to avoid bias caused by dependent data points and in an attempt to disentangle cause and effect. Alternative adaptive solutions to congregation are identified and discussed where applicable.

Hypotheses, which were derived in Chap. 1, include all main recognized possible drivers towards grouping which may apply to oceanic cetacea and for which data are available. Hypotheses are:

1. Communal prey-search hypothesis: Nomadic species with reduced local knowledge about prey distribution which move between ephemeral prey concentrations form larger groups than cetacea which show site-fidelity. This hypothesis would be supported by a positive correlation between group size and home range size.
2. Cooperative prey-herding hypothesis: Cetacea species whose diet includes a high portion of shoaling prey are more likely to congregate, and form larger congregations, than species which predominantly consume solitary prey. This hypothesis would be supported by a positive correlation between group size and the portion of shoaling prey in the diet.
3. Predation-risk hypothesis: Cetacea which experience a high predation threat form large congregations whereas species exposed to a low risk of predation occur solitarily or in small groups. This hypothesis would be supported by positive correlations between group size and predation risk inflicted by killer whales and sharks.
4. Calf protection hypothesis: Groups which contain calves are of much larger size than groups which do not comprise calves. Species with calving seasonality form larger groups in autumn than in spring.
5. Access to females hypothesis: Cetacea congregate in autumn and occur solitarily in spring.
6. Navigation accuracy hypothesis: Migration distance positively correlates with group size in migrating species and nomadic cetacea consistently form groups of large size whereas resident species with small home ranges consistently form small congregations or occur solitarily.

Hydrodynamic efficiency as a possible driver for congregation in cetacea is not quantitatively analysed here since this factor has a stronger relationship with group density than with group

size (Weihs 1973; Pitcher, Partridge 1979; Marras *et al.* 2015). In fish congregation-related hydrodynamic benefits were found in groups consisting of as few as two individuals (Abrahams, Colgan 1985). Information about group density is sparse in the cetacea literature. Moreover, a high group density may often be related to selfish herd effects which are difficult to disentangle from hydrodynamic benefits since both factors apply simultaneously for example when groups are fleeing from predators or traveling in offshore waters under unknown or high perceived levels of predation risk. A high group density has also been linked to eaves-dropping on conspecifics' echolocation signals in groups of tight highly synchronized moving rough-toothed dolphins (Götz *et al.* 2006). Many oceanic odontoceti react with group compaction to the presence of research platforms such as ships and aircraft which increases the difficulty of unbiased data collection. However, the typical composition of cetacea groups indicates that factors other than hydrodynamic efficiency evolutionarily drive congregation behaviour in this taxon (Chap. 1).

Body size and foraging depth were used to further analyse group size relationships with feeding constraints and behaviour. Active space has been included in the analysis to assess if this parameter may limit group size in species which only produce sounds of short acoustic range. Analyses of geographic variations in group size were used to further evaluate correlations between congregation and predation risk.

Species included in this study are listed in Tab. 1.

Table 1: Species studied

English name	Scientific name	English name	Scientific name
Blue whale	<i>Balaenoptera musculus</i>	Pygmy killer whale	<i>Feresa attenuata</i>
Fin whale	<i>Balaenoptera physalus</i>	Melon-headed whale	<i>Peponocephala electra</i>
Sei whale	<i>Balaenoptera borealis</i>	Killer whale	<i>Orcinus orca</i>
Bryde's whale	<i>Balaenoptera edeni</i>	Risso's dolphin	<i>Grampus griseus</i>
Minke whale	<i>Balaenoptera sp.</i>	Bottlenose dolphin	<i>Tursiops sp.</i>
Southern right whale	<i>Eubalaena australis</i>	Rough-toothed dolphin	<i>Steno bredanensis</i>
Humpback whale	<i>Megaptera novaeangliae</i>	White-beaked dolphin	<i>Lagenorhynchus albirostris</i>
Gray whale	<i>Eschrichtius robustus</i>	Atlantic white-sided dolphin	<i>Lagenorhynchus acutus</i>
Sperm whale	<i>Physeter macrocephalus</i>	Pacific white-sided dolphin	<i>Lagenorhynchus obliquidens</i>
Pygmy sperm whale	<i>Kogia breviceps</i>	Hourglass dolphin	<i>Lagenorhynchus cruciger</i>
Dwarf sperm whale	<i>Kogia sima</i>	Dusky dolphin	<i>Lagenorhynchus obscurus</i>
Cuvier's beaked whale	<i>Ziphius cavirostris</i>	Fraser's dolphin	<i>Lagenodelphis hosei</i>
Baird's beaked whale	<i>Berardius bairdii</i>	Spinner dolphin	<i>Stenella longirostris</i>
Arnoux's beaked whale	<i>Berardius arnuxii</i>	Pantropical spotted dolphin	<i>Stenella attenuata</i>
Blainville's beaked whale	<i>Mesoplodon densirostris</i>	Atlantic spotted dolphin	<i>Stenella frontalis</i>
Gervais' beaked whale	<i>Mesoplodon europaeus</i>	Striped dolphin	<i>Stenella coeruleoalba</i>
Sowerby's beaked whale	<i>Mesoplodon bidens</i>	Clymene dolphin	<i>Stenella clymene</i>
Pygmy beaked whale	<i>Mesoplodon peruvianus</i>	Common dolphin	<i>Delphinus delphis</i>
Longman's beaked whale	<i>Indopacetus pacificus</i>	Commerson's dolphin	<i>Cephalorhynchus commersonii</i>

English name	Scientific name	English name	Scientific name
Southern bottlenose whale	<i>Hyperoodon planifrons</i>	Southern right whale dolphin	<i>Lissodelphis peronii</i>
Northern bottlenose whale	<i>Hyperoodon ampullatus</i>	Northern right whale dolphin	<i>Lissodelphis borealis</i>
Long-finned pilot whale	<i>Globicephala melas</i>	Dall's porpoise	<i>Phocoenoides dalli</i>
Short-finned pilot whale	<i>Globicephala macrorhynchus</i>	Burmeister's porpoise	<i>Phocoena spinipinnis</i>
False killer whale	<i>Pseudorca crassidens</i>		

Most of these species rarely approach land whereas others are sometimes found associated with inshore waters and occur offshore at other times. The latter include dusky, spinner and Commerson's dolphins and both porpoises. In species for which coastal inshore and oceanic offshore populations exist, such as bottlenose, rough-toothed and Atlantic spotted dolphins, only data collected in offshore waters were included in this analysis. Arctic bowhead whales, *Balaena mysticetus*, belugas, *Delphinapterus leucas*, and narwhals, *Monodon Monoceros*, were not included despite their seasonal oceanic distribution due to the lack of group size estimates during winter when these species occupy offshore waters.

Materials and methods

Data collection

Literature was reviewed for information on group size (App. 1), movement/migration patterns, foraging depth (App. 2), prey composition (App. 3: Tab. 1) and active space of sounds produced by the species listed above. Key words used for the literature research through ISI Web of Science, Google Scholar, PLOS ONE, BioOne, ScienceDirect, PubMed and JSTOR search engines are:

Table 2: Key words used for literature research

Parameter	Keywords used
Group size, season, calf presence	cetacea survey, cetacea abundance estimation, [name of cetacea species] group size
Movement pattern, migration distance	[name of cetacea species] migration movement, [name of cetacea species] genetic population structure, [name of cetacea species] distribution home range
Foraging depth	[name of cetacea species] tagging telemetry, [name of cetacea species] dive depth, [name of cetacea species] foraging behaviour
Diet composition	[name of cetacea species] stomach contents, [name of cetacea species] feeding prey, [name of cetacea species] diet foraging
Prey shoaling	[name of prey species] school shoal, [name of prey species] deep sound scattering layer, [name of prey species] aggregation
Active space	cetacea acoustic range, whistle active space, whale long range communication, dolphin communication

References of relevant papers and articles which have cited the located papers were also included in the literature research. Cetacea body sizes were derived from Perrin *et al.* (2009) and Shirihai, Jarrett (2006). Data on cetacea prey composition were derived from publications which are based on large sample sizes except for cetacea species for which dietary information is scarce in the literature. In such cases every available publication was used.

'Fishbase' provided information on shoaling behaviour of some cetacea prey species but further research was necessary (Tab. 2). According to Benoit-Bird *et al.* (2017) deep scattering layers consist of shoals of various fish and squid species which show typical predator avoidance behaviour known for epipelagic shoaling fish. Based on this finding species which are typically affiliated to deep-scattering layers, such as numerous myctophids were

categorized as shoaling. References for prey shoaling behaviour are summarized in App. 3: Tab. 2. The analysis of correlation between group size and predation threat is based on predation risk estimates in Chap. 2.

Only data collected in offshore/oceanic waters, including areas where offshore conditions persist in close proximity to shore, have been used. Group size data comprise accounts of sample sizes ≥ 5 except for species for which very few data were available, or the study comprises an area which is rarely sampled. In these cases, group sizes derived from smaller samples were included. Only data from studies which identified the researched cetaceans to species level were used, except for the genus *Kogia*. Dwarf and pygmy sperm whales are so difficult to distinguish at sea that the majority of publications does not provide species-level data.

Many study results on group size and prey composition were found published by several papers or reports. To ensure that any set of data was included in this analysis once only the sample area and time of sampling were compared between publications by the same author(s). Hence publications of group size or prey data which were published by several papers or reports can only be found once in the appendix tables.

Data analyses

Group size parameters derived from published records comprise range, arithmetic mean (\bar{x}), standard deviation (SD), sample size (n) and additional information such as on the presence of calves, cetacea behaviour or seasonal variations in group size. Measures of variance other than SD such as standard error or coefficient of variation were converted into SD. If raw data were published instead of statistics then mean, SD and sample size were derived from these data.

Based on references in App. 1 for which at least means and sample size were available, species were a-posteriori assigned to four different group size categories (Tab. 3), according to their overall group size mean, $\bar{x}_{(total)}$ (Tab. 4).

Table 3: Group size categories.

Group size category	Mean group size
small:	1-5
medium:	6-20
large:	21-100
very large:	> 100

Calculation of the overall mean group size, $\bar{x}_{(total)}$, for each species, weighted by sample size, n_i , of each published record was calculated as:

$$\bar{x}_{(total)} = \sum_{i=1}^a \frac{\bar{x}_i \cdot n_i}{n_i} \quad (1)$$

\bar{x}_i : mean group size as in reference

$\bar{x}_{(total)}$: total mean across all references included in the calculation

$n_{(total)}$: total sample size of all references included in the calculation

i: number of reference

a: total number of references

Overall group size standard deviation, $SD_{(total)}$, for each species:

$$SD_{(total)} = \sqrt{\sum_{i=1}^n (SD_i^2 \cdot n_i) / n_{total} + \sqrt{\sum_{i=1}^n (n_i \cdot [\bar{x}_i - \bar{x}_{(total)}]^2) / (n_{(total)} - 1)} \quad (2)$$

s_i : SD in reference

The first part of the term calculates an average of SD's derived from published references. The second half of formula calculates the SD between published references based on the total group size mean of the species. The total range, mean, standard deviation and sample size across all group size references for each species are listed in Tab. 4.

Positive correlation between total group size means and SD identified during data analysis was further analysed using Pearson's coefficient of correlation and the following t-test for significance:

$$t = r \cdot \sqrt{(n - 2)/(1 - r^2)}, \quad df = n - 2 \quad (3)$$

df: degrees of freedom

Based on unequal sample sizes between group size categories and highly inhomogeneous variances Welch's ANOVA and the Games-Howell post hoc test (Shingala, Rajyaguru 2015) were used to analyse group size differences between categories with species as independent data points.

Normal distribution of data is given based on the central limit theorem which states that the means of random samples from any distribution will themselves have a normal distribution. Since this study is based on means derived from published records, normal distribution can be assumed.

For phylogenetic analysis a consensus tree was downloaded from <http://10kTrees.fas.harvard.edu>. Based on this tree all species included in this analysis were assigned to 1 of 14 phylogenetic groups of related species (Fig. 3). These groups were used as independent data points for analyses of correlations between group size and the following parameters: body size, foraging depth and home range size/migration pattern.

For analysis of group size correlation with migration pattern and home range size cetacea species were classified as seasonally migrating over long distances, or nomadic, or resident with either small or large home ranges. Long-distance migrations are characterized by consistent seasonal movements over thousands of kilometres between summer feeding and winter breeding areas along specific migration routes. Nomadic species typically cover large areas in short periods of time, often traveling > 100km per day, without the regular temporal and geographic patterns of migration, and show very low re-sighting rates of individuals in any particular area. Resident species occupy a certain home range which is rarely left. This home range can either be large, covering thousands of square kilometres or small, covering hundreds of square kilometres or less.

Significance of correlation between home range size and group size at species level was tested with Welch's ANOVA followed by the Games-Howell post hoc test, due to very inhomogeneous variances and unequal sample sizes. Species were used as independent data points based on similarity of results at species and phylogenetic levels.

The evaluation of the portion of shoaling prey in cetacea diet was based exclusively on stomach content analyses since field observations of feeding events are often biased towards predation on shoaling prey which tends to be easier observable than predation on more inconspicuous solitary food items. Field observations were only used as additional support of the results.

To quantify the portion of shoaling prey in the diet of oceanic cetacea percent by number (%N) was used whenever available since this measure was provided by most papers. If not available, then either percent by mass (%M) or percent by volume (%V) were used. This was necessary because results of stomach content analyses are published in highly variable ways in the literature. Frequency of occurrence (%F) was not included in the quantitative assessment of shoaling prey.

Information about the social behaviour of prey species is scarce for most non-epipelagic types of forage, particularly for squid and crustacea prey of deep-diving cetacea, namely the sperm whale, both members of the genus *Kogia*, all beaked whales and the Risso's dolphin. The sperm whale was excluded from the analysis for that reason. The portion of shoaling prey in the diet of beaked whales and *Kogia* may be under-estimated and results have to be interpreted with care. Moreover, many cephalopod species pass pelagic gregarious life stages but live a benthic, solitary life once a certain body size is reached. However, general trends of inter-species differences became apparent during the analysis which is why deep-diving whales were included in spite of these difficulties.

Since cetacea stomachs frequently contain hard remains of prey items such as squid beaks, fish otoliths and eye lenses it is possible that prey composition data on which this analysis is based are biased towards species which contain such materials.

Predation risk data calculated in chap. 2 for killer whales and various shark species were tested for correlation with cetacea group size using Pearson's correlation coefficient, r , and two-tailed t-tests of significance as in formula 3. Species were used as independent data points.

Areas of an extended oxygen minimum zone and a high density of white, *Carcharodon carcharias*, and broadnose sevengill sharks, *Notorynchus cepedianus*, were identified based on Karstensen *et al.* (2008) and 'fishbase'. Cetacea group sizes were then compared between these regions and areas where either shark density is low, or the oxygen minimum zone is narrower such that predators are less restrained to a shallow epipelagic corridor which tends to increase encounter rates between predator and prey and thus predation risk. Group size data were derived from App. 1.

The influence of calf presence in a group has been evaluated by the compilation of study results which compared the size of groups containing calves with the size of congregations without calves in various species of cetacea.

For the assessment of seasonal group size variation, the results of several studies which analysed this parameter were compiled. Seasonal changes in congregation size were compared across species and within species between different study areas when such data were available.

Active space is the effective range over which a communication signal can be detected by a conspecific (Marten, Marler 1977). A bar diagram shows the interrelations between active space and cetacea group size.

A scatter plot of cetacea group size against body size shows a lack of a clear negative or positive correlation between both parameters, in spite of a two-way pattern of interrelation. Therefore, body size has not been analysed any further statistically. To ensure that results hold across odontoceti, rather than being caused by a high number of species in one particular phylogenetic group the correlation analysis has been conducted at the levels of both, species and phylogenetic group. The method of independent contrasts was used to test for coevolution between body size and group size.

For the analysis of group size correlation with cetacea foraging depth species were assigned to three different categories according to their primary foraging depth which are (1) epipelagic, (2) epi-/mesopelagic and (3) meso-/bathypelagic. Due to a large overlap in mean group sizes the first two categories were pooled into one for phylogenetic and statistical analyses. Significance of results was determined with the Games-Howell post hoc test. Species were used as independent data points based on similarity of results at species and phylogenetic levels.

Geographic group size variations were analysed based on the intra- and interspecific comparison of mean pod size between studies conducted at different latitudinal zones and, interspecifically, in two different ocean basins, the N-Atlantic and the N-Pacific. Data were derived from App. 1. Welch's t was used to test significance of results due to inhomogeneous variances.

Congregation sizes were also compared between related species of the southern versus norther hemispheres with similar latitudinal distribution based on App. 1. Statistical analyses were not applied due to the inconsistency of results which show no clear trend in groups size variation.

To assess the influence of shark predation risk on sociality in cetacea variation in congregation size between areas of extended oxygen minimum zones and regions with a deeper and weaker oxygen minimum layers was reviewed.

Results

Results are presented for each parameter and are summarized in Tab. 18.

Groups of small size, averaging 1-5 individuals, were found to be formed by all baleen whale species included in this analysis, both species of the genus *Kogia*, most beaked whale species, Dall's porpoises and Commerson's dolphins.

Medium group sizes, averaging 6-20 members, are typical for sperm whales, three species of beaked whales, killer whales, pygmy killer whales, Risso's, rough-toothed, white-beaked and hourglass dolphins and for Burmeister's porpoises.

Large groups of an average of 21 to 100 individuals are formed by both species of pilot whales, false killer whales, bottlenose, Atlantic and Pacific white-sided, dusky, Atlantic spotted, striped, Clymene and northern right whale dolphins.

Very large pods, exceeding an average of 100 members are typical for melon-headed whales, Fraser's, spinner, pantropical spotted, common and southern right whale dolphins. Group size estimates for southern right whale dolphins are based on a very small sample size (n: 16) and may be an over-estimate due to the better detectability of large groups.

Table 4: Group size meta-analysis based on App. 1.

Group size category	$\bar{X}_{(total)}$	SD _(total)	Range	n _(total)	Species
Small	1	1	1-60	5268	Blue whale
	2	2	1-81	4100	Fin whale
	2	2	1-12	676	Sei whale
	2	1	1-15	1273	Bryde's whale
	2	0.7	1-20	10317	Minke whale
	2	2	1-15	840	Southern right whale
	2	1	1-95	7255	Humpback whale
	2	1	1-16	1262	Gray whale
	2	1	1-15	800	<i>Kogia</i>
	3	5	1-90	1444	Cuvier's beaked whale
	4	3	1-11	305	Blainville's beaked whale
	3	2	2-9	6	Gervais beaked whale
	1	0.2	1-2	10	Sowerby's beaked whale
	2	-	-	17	Pygmy beaked whale
	2	1	1-20	1738	Southern bottlenose whale
	4	3	1-22	2477	Northern bottlenose whale
	2	15	1- 100s	5438	Commerson's dolphin
4	3	1-3000	3768	Dall's porpoise	
2	2	1-3000	46993	Total category	
Medium	12	-	1-1000s	App. 1	Sperm whale
	9	10	1-33	95	Baird's beaked whale

Group size category	\bar{X} (total)	SD(total)	Range	n(total)	Species
	14	25	1-75	17	Arnoux's beaked whale
	16	29	1-100	68	Longman's beaked whale
	18	15	2-120 ^c	97	Pygmy killer whale
	7	9	1-1000s	2920	Killer whale
	17	33	1-4000 ^d	3629	Risso's dolphin
	14	11	1-109	610	Rough-toothed dolphin
	7	16	1-1500	2401	White-beaked dolphin
	8	7	1-100	284	Hourglass dolphin
	7	15	1-150	28	Burmeister's porpoise
		12	18	1-4000	10137
Large	22	34	1-1000s	2215	Long-finned pilot whale
	23	35	1-1500	1661	Short-finned pilot whale
	24	36	1-470	271	False killer whale
	33	47	1-10000	8676	Bottlenose dolphin
	38	89	1-2500	1848	Atlantic white-sided dolphin
	79	183	1-6000	3415	Pacific white-sided dolphin
	54	179	1-1000s	324	Dusky dolphin
	39	70	1-650	2215	Atlantic spotted dolphin
	56	107	1-2136	9840	Striped dolphin
	71	27	1-1000	302	Clymene Dolphin
	28	59	1- >2000	267	Northern right whale dolphin
		41	62	1-10000	29777
Very large	240	257	1-2000 ^e	160	Melon-headed whale
	156	182	3-2500	215	Fraser's dolphin
	127	189	1-1200	3580	Spinner dolphin
	148	164	1-2233	4353	Pantropical spotted dolphin
	101/ 144	190/ 186	1-4000	8050/ 5116	Common dolphin total/ excl. Azores
	298	245	3-1000	16	Southern right whale dolphin
		145	124	1-4000	16374

^c Leatherwood *et al.* 1984

^d Kruse *et al.* 1999; Baird 2009

^e Jefferson *et al.* 2008

Most species occur in groups of a wide range of sizes which is reflected by large standard deviations despite high sample sizes. A positive linear correlation between mean group size and standard deviation (Pearson's $r = 0.9$, two-tailed $t(42) = 13.18$, $\alpha < 0.0001$, based on values in Tab. 4) shows that species which form large groups do not do so consistently (Fig. 1). Rather the range of observed group sizes becomes increasingly wider from the first to the fourth group size category and an increasing portion of groups is of large size.

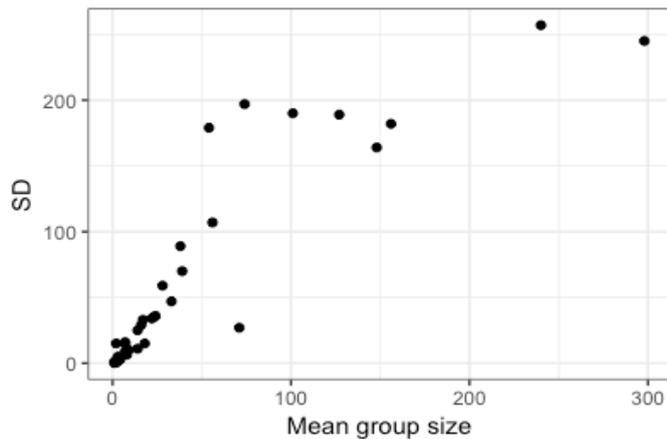


Figure 1: Positive correlation between mean group size of different cetacea species and its standard deviation (Pearson's $r = 0.9$, two-tailed $t(42) = 13.18$, $\alpha < 0.0001$).

According to Taylor's power law mean population density positively correlates with its variance or SD (Taylor *et al.* 1978). If an increase in both, mean group size and population density entail an increase in their variation, then a positive correlation between mean population density and mean group size in cetacea is expected. That is, a higher density of individuals leads to the formation of larger groups rather than more groups of a consistent size.

This expected interrelation was analysed using density and group size data for blue, fin, and humpback whales, short-beaked common and Pacific white-sided dolphins and Dall's porpoises derived from Campbell *et al.* (2015). These data were collected off southern California through visual line-transect surveys during thirty-seven California Cooperative Oceanic Fisheries Investigations (CalCOFI) cruises from July 2004 to November 2013, and include seasonal, annual and overall group size and density estimates for the species listed above. Fig. 2 shows a positive correlation between group size and density across species (Pearson's $r = 0.93$, two-tailed $t(52) = 18.1$, $\alpha < 0.0001$). This correlation is consistent across years, seasons and overall.

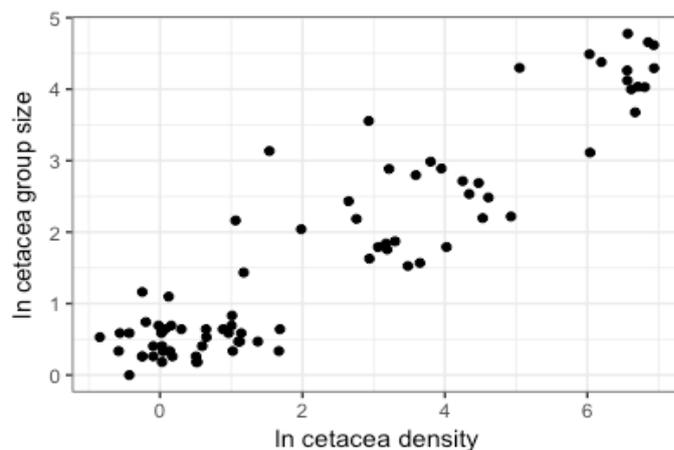


Figure 2: Correlation between cetacea group size and density (both natural log transformed), data from Campbell *et al.* 2015, Pearson's $r = 0.93$, two-tailed $t(52) = 18.1$, $\alpha < 0.0001$

Welch's ANOVA yielded significant differences in group size means between group size categories ($F(3, 12.7) = 33.1$, $\alpha < 0.001$), indicating that at least one group size category is significantly different from the others. The Games Howell post hoc test (Shingala, Rajyaguru 2015) produced significant differences between group size means of species affiliated to the small and medium as well as medium and large categories, but not between large and very large group size means (Tab. 5).

Table 5: Games-Howell statistics, df: degrees of freedom, k = 4

Group size categories	df	t	q(k,df,α)/√2	α
small versus medium	10.54	7.17	5.66	< 0.001
large versus very large	10.93	4.77	4.40	< 0.005
medium versus large	5.31	3.01	3.69	> 0.05

Phylogeny

Based on the phylogenetic tree in Fig. 3 cetacea were assigned to phylogenetic groups of related species (Tab. 6) which are represented by different colours in Fig. 3. Due to considerable mean group size variety within several phylogenetic groups which may veil interrelations between congregation size and other parameters all further analyses were carried out at species level. In addition, a group size analysis based on phylogenetic groups was conducted in parameters which show strong correlation with phylogeny which are body size, foraging depth and migration/movement pattern to identify possible differences between results at species and phylogenetic levels.

A comparison between group size and phylogenetic positions of species shows that only phylogenetically young species form groups averaging more than 20 members, indicating that the formation of large groups is a behavioural trait that developed comparatively recently from ancestors which formed small congregations. The phylogenetic tree also shows that large group size has evolved several times independently (Fig. 3).

Within the blackfish phylogenetic group, the melon-headed whale represents a strong outlier with regard to its mean group size of 240. All other species within this group form congregations averaging 17-24 individuals.

Table 6: Phylogenetic groups

Phylog. group	Species affiliated to phylogenetic group
Baleen	blue, fin, sei, Bryde's, minke, humpback, gray whale
Right whale	southern right whale
Sperm	sperm whale, dwarf + pygmy sperm whale (<i>Kogia</i>)
Beaked	Cuvier's, Blainville's, Gervais, Sowerby's, pygmy beaked whale, bottlenose whale
Berardius	Baird's, Arnoux's beaked whale
Longman	Longman's beaked whale
Killer	killer whale
Blackfish	pilot whales, false killer, pygmy killer, melon-headed whale, Risso's dolphin
Albirostris	white-beaked dolphin
Steno	rough-toothed dolphin
Acutus	Atlantic white-sided dolphin
Dolphin 1	Pacific white-sided, hourglass, dusky, Commerson's, north. + south. right whale dol.
Dolphin 2	bottlenose, Fraser's, spinner, pantropical spotted, Atlantic spotted, striped, Clymene, common dolphin
Porpoise	Dall's, Burmeister's porpoise

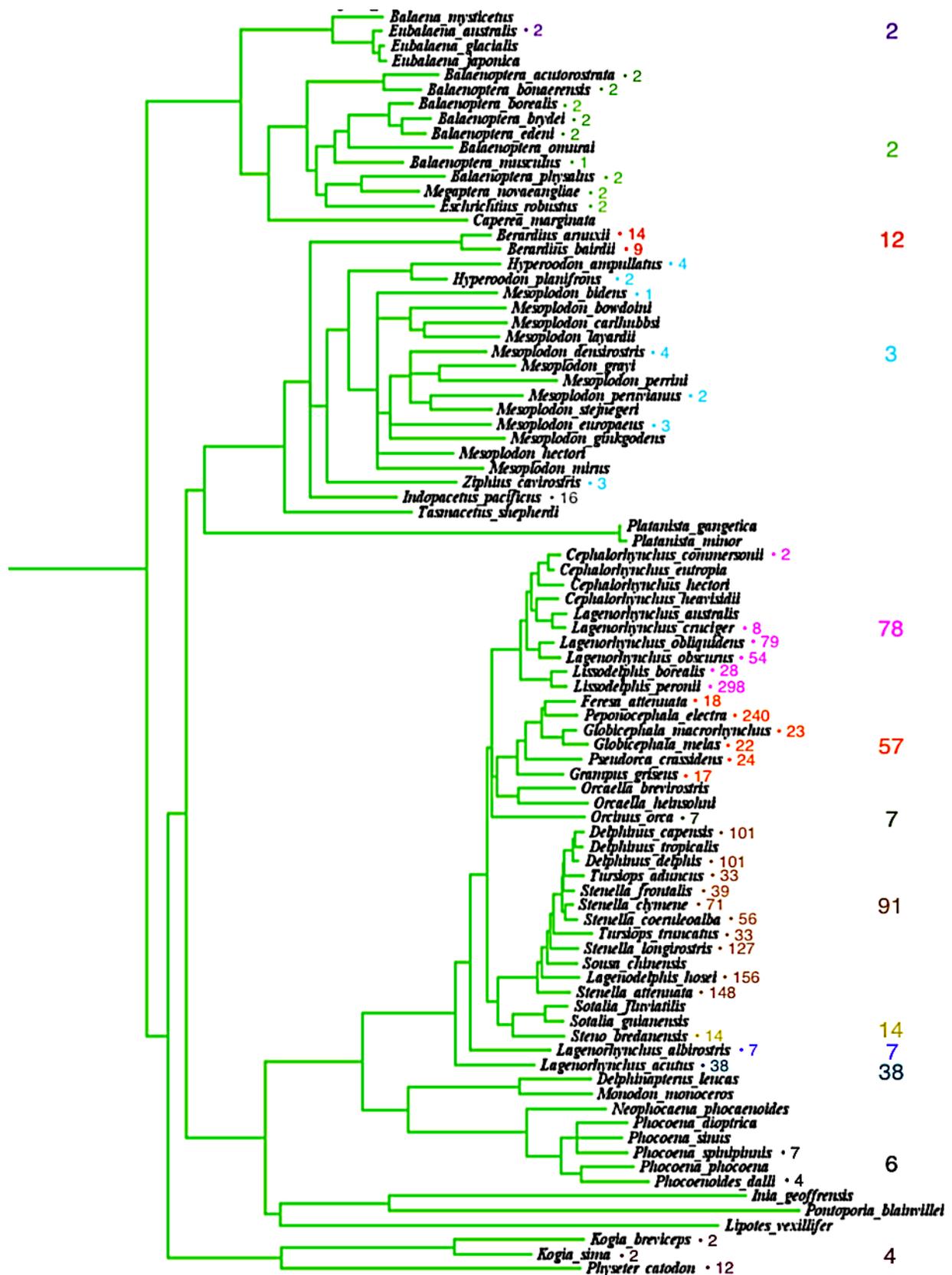


Figure 3: Cetacea phylogeny, downloaded from <http://10kTrees.fas.harvard.edu>; included species show mean group size behind name; mean group size of phylogenetic group on right edge of figure

Home range size and migration pattern

Tab. 7 summarizes migration behaviour and home range of oceanic cetacea. Resident populations of false and pygmy killer whales, and melon-headed whales range over a large area whereas most beaked whales and rough-toothed dolphins show a remarkable level of small scale-site fidelity. Therefore the 'resident' category was divided into resident with small home range and resident with large home range. Species for which migration behaviour is unknown were not included in this analysis (Tab. 7).

Table 7: Cetacea migration behaviour

Species	Migration behaviour	Species	Migration behaviour
Blue whale	seasonal l.-d. migration	Pygmy killer	resident, small home range
Fin whale	seasonal l.-d. migration	Melon-headed	resident, small/large home range, nomadic ^m
Sei whale	seasonal l.-d. migration	Risso's	nomadic ^{o,m}
Bryde's whale	less defined seasonal l.-d. migration*	Bottlenose d.	resident, nomadic ^{*m}
Minke whale	seasonal l.-d. migration	Rough-toothed	resident, small home range
Southern right w.	seasonal l.-d. migration	White-beaked	nomadic
Humpback whale	seasonal l.-d. migration	Atlantic white-sided	nomadic
Gray whale	seasonal l.-d. migration	Pacific white-sided	nomadic ^{m,o*}
Sperm whale	nomadic, seasonal l.-d. migration ^a	Hourglass	unknown
<i>Kogia</i>	resident ^o , nomadic	Dusky	resident ^o , small home range
Cuvier's beaked	resident, small home range	Fraser's	unknown
Baird's beaked	resident ^o , small home range	Spinner	resident, nomadic
Arnoux's beaked	unknown	Pantrop. spotted	nomadic
Blainville's beaked	resident, small home range	Atlantic spotted	nomadic [*]
Gervais' beaked	resident, small home range	Striped	nomadic
Sowerby's beaked	unknown	Clymene	nomadic
Pygmy beaked	unknown	Common	nomadic ^{m,o}
Longmans beaked	unknown	Commerson's	resident ^o
S. bottlenose w.	possibly seasonal l.-d. migr.	Southern right w.d.	unknown, likely nomadic ^{*m}
N. bottlenose w.	resident, small home range	Northern right w.d.	Nomadic ^{m,o}
Long-finned pilot	nomadic	Dall's	resident large home range ^{o,m}
Short-finned pilot	nomadic*	Burmeister's	likely resident ^m
False killer whale	resident, large home range		

References: Amano, Kuramochi 1992; Ferrero, Walker 1993, 1996; Sekiguchi *et al.* 1993; Black 1994; Mate *et al.* 1994; Rossbach, Herzing 1999; Escorza-Treviño, Dizon 2000; Chivers, Scott 2002; Whitehead 2003; Hayano *et al.* 2004; Huggins *et al.* 2005; Dunphy-Daly *et al.* 2008; Hartman *et al.* 2008, 2014; Silva *et al.* 2008; McSweeney *et al.* 2009; Olsen *et al.* 2009; Perrin *et al.* 2009; Andrews *et al.* 2010; Glover *et al.* 2010; Quéroutil *et al.* 2010; Aschettino *et al.* 2012; Pitman, Brownell 2012; De Boer *et al.* 2013; Schorr *et al.* 2014; Stevens 2014; Viricel, Rosel 2014; Bertulli 2015; Claridge *et al.* 2015; Oudejans *et al.* 2015; Niemeyer 2016; Viricel *et al.* 2016; Baird *et al.* 2011, 2017; Ball *et al.* 2017; Palmer *et al.* 2017

- (some) coastal populations are resident

- ^a ♂: nomadic+seasonal migration, no clear migr. routes, ♀ resident or nomadic at low latitudes year-round
- ^o seasonal inshore-offshore migration has been documented
- ^m seasonal short-distance migration has been documented

Satellite tagging studies indicate that oceanic populations with larger home ranges than indicated in Tab. 7 may exist in Cuvier's beaked whales (Baird *et al.* 2011) and pygmy killer whales (Brownell *et al.* 2009) but comparative intra-specific group size estimates between populations of varying home range are not available to date for these species. The following analysis is therefore based on data presented in Tab. 7.

The smallest mean group sizes were found in species which carry out long-distance migrations (l-d migr). Resident species with small home ranges (res shr) form congregations of small to intermediate size. Nomadic species and resident species with large home ranges both form groups of highly variable average size, ranging from 2 to > 100. Based on this data similarity, which likely reflects a smooth transition between both movement types in nature, these two distribution patterns were treated as one category for further analysis, which includes all species with large home ranges (lhr) whether nomadic or resident (Fig. 4).

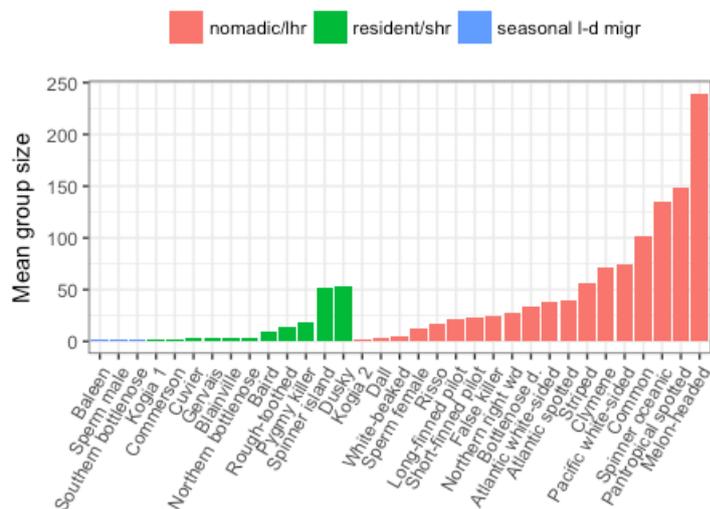


Figure 4: Cetacea group size correlation with movement pattern, island-associated and truly oceanic spinner dolphins are distinguished, so are male and female sperm whales

Analysis at the level of phylogenetic groups rather than species yields the same result (Fig. 5). Thus, statistical analysis was carried out at species level. The phylogenetic group Dolphin 1 contains resident and nomadic species and therefore appears twice in Fig. 5.

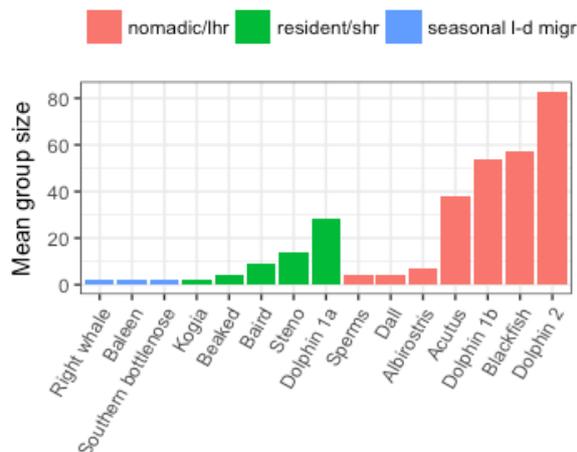


Figure 5: Cetacea group size correlation with movement pattern for phylogenetic groups

Seasonal short-distance migrations are carried out by species of all group size levels and are therefore not analysed any further.

Results of Welch's ANOVA are summarized in Tab. 8 and indicate that at least one movement category is significantly different from the other two. Large standard deviations reflect the previously described increase in SD with increasing mean group size, and a high variation in group size in both the small and the large home range categories.

Table 8: Welch's ANOVA, \bar{x} : mean group size across species affiliated to the movement category

Movement category	\bar{x}	SD	range of species \bar{x} 's	n	Welch's F statistics
long-distance migration	2	0.3	1-2	9	F(2, 15.7) = 10.9 $\alpha < 0.005$
resident, small home range	15	20	2-54	10	
large home range	47	44	4-240	18	

The Games-Howell post hoc test did not produce significant differences in pod size between species which occupy small versus large home ranges (Tab. 9), indicating that home range size is not a determinant of group size in oceanic cetacea. Species which carry out long-distance migrations form congregations of significantly lower size than species which occupy large home ranges and move between areas in a nomadic manner. These results contradict the communal prey-search hypothesis.

Table 9: Games Howell statistics, df: degrees of freedom, k = 3

Group size categories	df	t	$q(k,df,\alpha)/\sqrt{2}$	α
l-d migr versus res shr	9.01	1.98	4.31	$\alpha > 0.05$
res shr versus lhr	25.50	2.63	3.50	$\alpha > 0.05$
l-d migr versus lhr	17.00	4.33	3.68	$\alpha < 0.005$

Portion of shoaling prey in diet

The correlation between group size and the portion of shoaling prey in the diet identifies three different species groups but no clear correlation between both factors (Fig. 6, left):

- (1) dietary portion of shoaling prey < 45% and group size < 25: Cuvier's and Baird's beaked whale, northern and southern bottlenose whales and Risso's dolphin.
- (2) dietary portion of shoaling prey > 55 and $\leq 88\%$, group size increasing with percentage of shoaling prey: *Kogia*, Gervais and Sowerby's beaked whales, long- and

short-finned pilot whales, melon-headed whale, bottlenose dolphin, white-beaked dolphin, Atlantic and Pacific white-sided dolphins, dusky, spinner, pantropical spotted, striped, common and northern right whale dolphins.

- (3) dietary portion of shoaling prey $\geq 90\%$, group size < 50 : baleen whales, false and pygmy killer whale, rough-toothed dolphin, Atlantic spotted dolphin, Burmeister's porpoise. Dall's porpoise (shoaling prey: 85%, group size: 4) and Commerson's dolphin (mainly feeding on shoaling prey, group size: 2) were also included in this category.

The lack of a positive correlation between group size and the dietary portion of shoaling prey contradicts the cooperative prey-herding hypothesis.

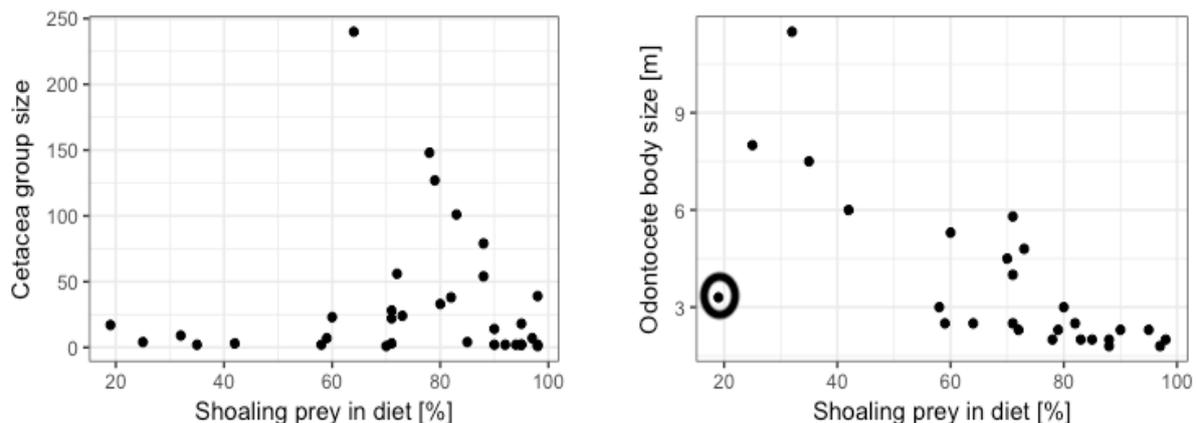


Figure 6: Cetacea group size interrelation with dietary portion of shoaling prey (left), correlation between odontoceti body size and shoaling prey (right) ($r = -0.84$; $t(24) = 7.45$, $\alpha < 0.0005$, excl. outlier). Encircled: Risso's dolphin.

Even though shoaling tendency of prey may be underestimated in species which heavily prey on deep-sea squid including beaked whales, Risso's dolphins and kogiids these results suggest that the diets of odontoceti species of large body size which are Cuvier's and Baird's beaked whales and both bottlenose whales contain less shoaling species, and likely more benthic prey of larger body size than is the case in smaller-bodied cetacea. Cetacea of small body size, including most dolphin and both porpoise species heavily prey on shoaling fish, squid and crustacea in oceanic waters, regardless of their typical group sizes. The negative correlation between odontoceti body size and the dietary portion of shoaling prey further confirms these findings (Fig. 6). Pearson's correlation coefficient is $r = -0.84$, excluding the Risso's dolphin ($t(24) = 7.45$, $\alpha < 0.0005$).

Analysis of the group size-shoaling prey interrelation for species of similar body size of 2.0-2.5m, including 13 odontoceti species, did not yield a correlation between both factors further indicating that group size is not determined by the portion of shoaling prey in the diet of cetacea.

Due to a lack of diet information or information on the shoaling tendency of prey, the following species were excluded from this analysis:

- gray whale
- sperm whale
- Arnoux's beaked whale
- Blainville's beaked whale
- Longman's beaked whale
- killer whale
- hourglass dolphin
- Clymene dolphin
- southern right whale dolphin

The gray whale was excluded because dietary data were only found for coastal but not for offshore areas. The killer whale was excluded due to its complexity of ecotype variety. This species lends itself to an ecotype- or population-based analysis of foraging-related effects on group size which goes beyond the scope of the thesis.

Tab. 10 summarizes group and sub-group sizes during prey herding in various cetacea species and shows that the number of cooperating individuals is typically < 15.

Table 10: Sub-group size during feeding

Species	Sub-group size	Reference
Fin whale	1-10	Tershy 1992; Nøttestad <i>et al.</i> 2002b
Bryde's whale	1	Kato, Perrin 2009
Minke	1	Hoelzel <i>et al.</i> 1989; Kuker <i>et al.</i> 2005
Humpback whale	1-10	e.g. Ingebrigtsen 1929; Hain <i>et al.</i> 1982; D'Vincent <i>et al.</i> 1985; Whitehead, Carlson 1988; Sharpe 2001; Wiley <i>et al.</i> 2011
Blainville's beaked	1	Johnson <i>et al.</i> 2008
False killer	few	Zaeschmar <i>et al.</i> 2013; Weir <i>et al.</i> 2013
Killer	2-12	Steiner <i>et al.</i> 1979; Similä, Ugarte 1993; Nøttestad, Axelsen 1999; Nøttestad, Similä 2001; Ford <i>et al.</i> 2000
Bottlenose	2-32	Bel'kovich <i>et al.</i> 1991; Rossbach 1999; Gazda <i>et al.</i> 2005; Zaeschmar <i>et al.</i> 2013
Rough-toothed	2-8	Addink, Smeenk 2001; De Boer 2010
Atlantic white-sided	2-15	Haase 1987; De Boer 1989; Leopold, Couperus 1995; Hamran 2014
Pacific white-sided	2-10	Heise 1996
Dusky	2-5	Benoit-Bird <i>et al.</i> 2004; Dahood, Benoit-Bird 2010
Spinner	2-28	Benoit-Bird, Au 2003, 2009
Common	2-4	Clua, Grosvalet 2001
	5-50	Neumann, Orams 2003
Commerson's	5-10	Coscarella <i>et al.</i> 2010

Predation risk

Predation risk inflicted by killer whales does not correlate with cetacea group size (Fig. 7, left). However, only species which experience a low killer whale predation risk average congregation sizes of > 100. A moderate correlation was found between congregation size and predation threat by sharks (Pearson's $r = 0.43$, two-tailed $t(38) = 2.92$, $\alpha < 0.01$). All cetacea species which form large or very large groups are exposed to high risks of predation by sharks (Fig. 7, right), but not all species which are under high risk of shark predation form large groups, indicating that more than one behavioural adaptation to shark predation risk has evolved within this taxon. Species which form small to medium-sized groups may experience any level of predation risk. However, low-risk species consistently form small groups.

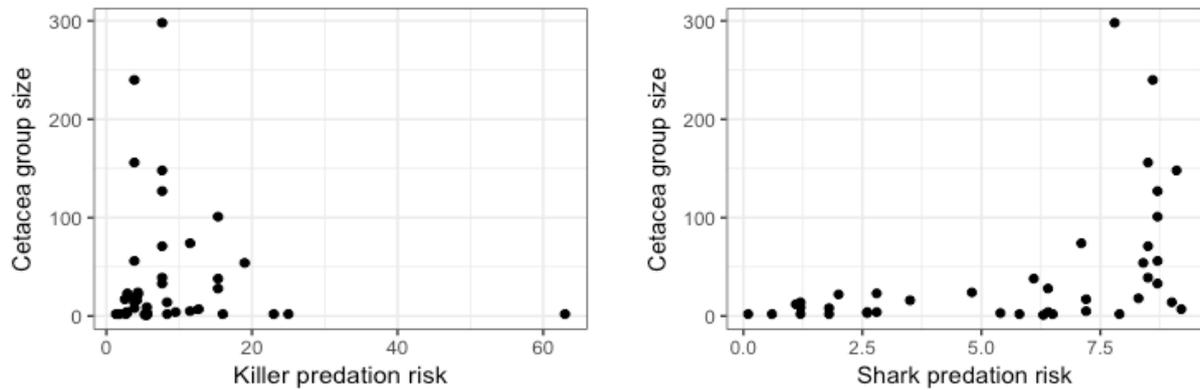


Figure 7: Lack of correlation between killer whale predation risk and cetacea group size (right). Positive correlation between overall shark predation risk and cetacea group size (left) (Pearson's $r = 0.43$, two-tailed $t(38) = 2.92$, $\alpha < 0.01$).

To determine which shark species are responsible for the correlation between cetacea group size and overall shark predation threat, risks inflicted by particular species were analysed. Positive correlations were found between congregation size and predation risk inflicted by both, white sharks and broadnose sevengill sharks (Fig. 8).

This correlation is linear in broadnose sevengill sharks (Pearson's $r = 0.73$, two-tailed $t(36) = 6.33$, $\alpha < 0.001$ incl. Burmeister's porpoise; Pearson's $r = 0.89$, two-tailed $t(35) = 11.8$, $\alpha < 0.001$ excl. Burmeister's porpoise) and exponential in white sharks (Pearson's $r = 0.53$; two-tailed $t(36) = 3.79$, $\alpha < 0.001$ incl. outliers, Pearson's $r = 0.6$ excl. outliers). These correlations support the predation risk hypothesis.

Outliers and correlations of intermediate strength both further indicate that some species have developed alternative anti-predator adaptations unrelated to group size which is to be expected when species with large average congregation sizes are phylogenetically young.

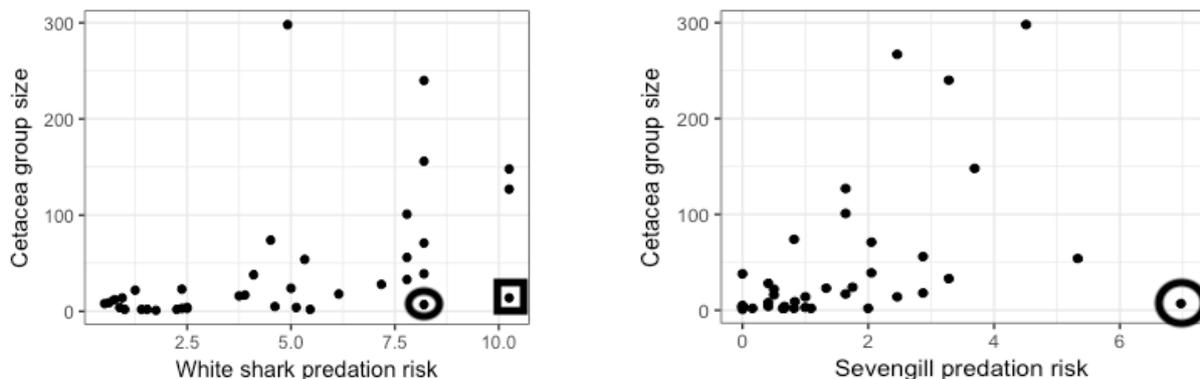


Figure 8: Positive correlation of cetacea group size with predation risk by both, white sharks (Pearson's $r = 0.52$; two-tailed $t(36) = 3.79$, $\alpha < 0.001$ incl. outliers; $r = 0.6$ excl. outliers) and sevengill sharks ($r = 0.73$, two-tailed $t(36) = 6.33$, $\alpha < 0.001$ incl. outlier; $r = 0.89$, two-tailed $t(35) = 11.8$, $\alpha < 0.001$ excl. outlier). Outliers: circled: Burmeister's porpoise, squared: rough-toothed dolphin.

A weak correlation between cetacea group size and predation risk by oceanic whitetip sharks, *Carcharhinus longimanus*, was found to be insignificant (Pearson's $r = 0.39$; two-tailed $t(24) = 2.06$, $\alpha > 0.05$). Cetacea group size does not correlate with predation risk inflicted by shortfin mako, *Isurus oxyrinchus*, dusky, *Carcharhinus obscurus*, tiger, *Galeocerdo cuvier*, Greenland, *Somniosus microcephalus*, Pacific sleeper, *Somniosus pacificus*, southern sleeper, *Somniosus antarcticus*, and bluntnose sixgill sharks, *Hexanchus griseus* (Pearson's $r < 0.3$). It should be noted that these are results for offshore waters. Predation risk may be different for inshore species and populations.

The comparison of group size in gregarious delphinids between areas of high white shark and broadnose sevengill shark density or an extended oxygen minimum zone and regions of low risk from these predators suggests that congregations are largest where the oxygen minimum zone is strong and thick combined with a high density of white sharks, particularly in most parts of the tropical E-Pacific, in the Gulf of California, off Galápagos and in the northern Indian Ocean. Group size is also large in regions of high predation risk by sevengill sharks, regardless of the thickness and strength of the oxygen minimum zone, including New Zealand, South Africa, outer shelf and slope regions of the SW-Atlantic, waters off Japan, W-USA and Galápagos (App. 1). Smaller groups have typically been documented in areas where the oxygen minimum zone is thinner, including most parts of the Atlantic Ocean (excl. Gulf of Guinea area), the Gulf of Mexico and the Caribbean Sea, La Reunion in the southern Indian Ocean and waters off the Marianna Islands, French Polynesia and Hawaii in the Pacific. No correlation between group size and oxygen minimum zone and/or shark density has been found in species of the genus *Kogia*, beaked whales, pilot, false killer and killer whales and rough-toothed dolphins.

Presence of calves

Group size does not differ in correlation with calf presence in baleen whales with the only exception of the humpback whale. In this species mother-calf pairs may be accompanied by an additional adult individual, an escort, in some geographic areas (App. 6). In odontoceti pods containing neonates or calves are often larger than those which only comprise adults and sub-adults (Fig. 9). These results are significant in Risso's, bottlenose, Atlantic white-sided and Atlantic spotted dolphins (significances provided by literature, see: App. 6). However very large groups necessary for calves to benefit from the dilution effect (Chap. 1) are only formed by Atlantic white-sided dolphins out of the species for which data were available. In Atlantic white-sided dolphins more than 50%, but not 100% of the pods labelled as calves actually contained calves (App. 6). Hence the actual difference in size between congregations in which calves were present and those without calves may be higher than Fig. 9 indicates. In all other species the increase in groups size is rather small and congregations are hardly large enough for the dilution and confusion effects and predator swamping to work. Hence the calf protection hypothesis is only partially supported.

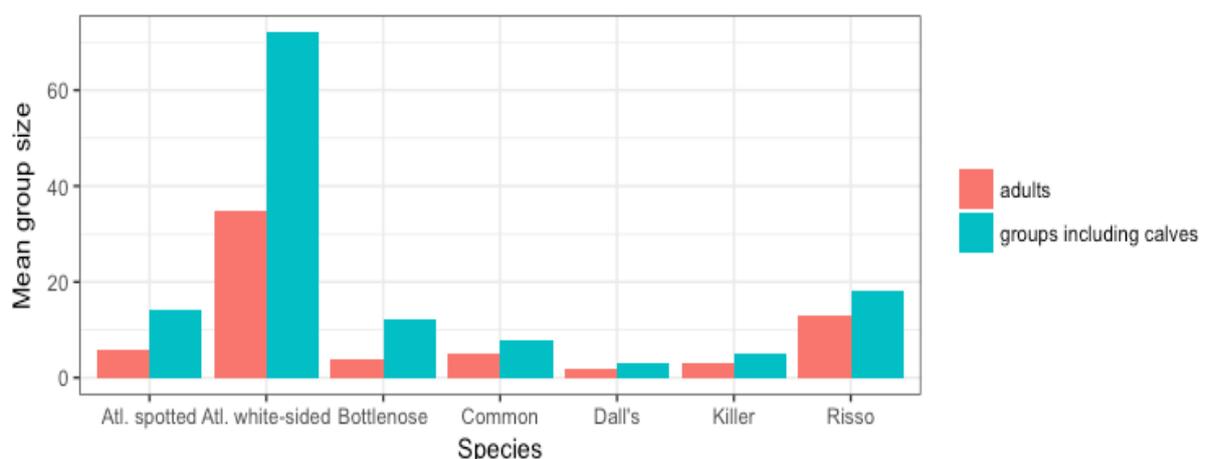


Figure 9: Groups size with and without calves

In false killer whales five out of six sightings included calves and the mean group size estimated by Weir *et al.* (2013) is higher than the species average. However, the researchers did not encounter more than one group without calves. Hence a direct comparison of group size with and without calves was not possible. In long-finned pilot whales Ottensmeyer, Whitehead (2003) documented a higher mean size of congregations in which calves were

present compared to the average across all observed groups, but a comparison of group size with versus without calves was not provided (App. 6).

Gaspari (2004) found striped dolphin calves distributed across all group sizes in the Mediterranean Sea. However, no clear data analysis of group size with and without calves was presented, in both Risso's and striped dolphins (App. 6).

Season

In odontoceti a number of studies found significant differences in group size between seasons. The nature of this variation changes between years (e.g. Gaspari 2004; Azzellino *et al.* 2008), geographic areas and species (App. 5). Figs. 10, 11 show group size variation between summer and winter for bottlenose, striped and common dolphins. The former two species show a consistently higher group size in summer compared to winter across all areas for which data were found. Common dolphins form larger groups in summer off New Zealand and San Clemente Island (California), whereas congregations off S-California average a higher number of individuals in winter (both California studies: short-beaked common dolphin, New Zealand: *Delphinus sp.*).

Risso's dolphins studied off San Clemente Island and Commerson's dolphins off Argentina both formed larger groups in winter than in summer (App. 5).

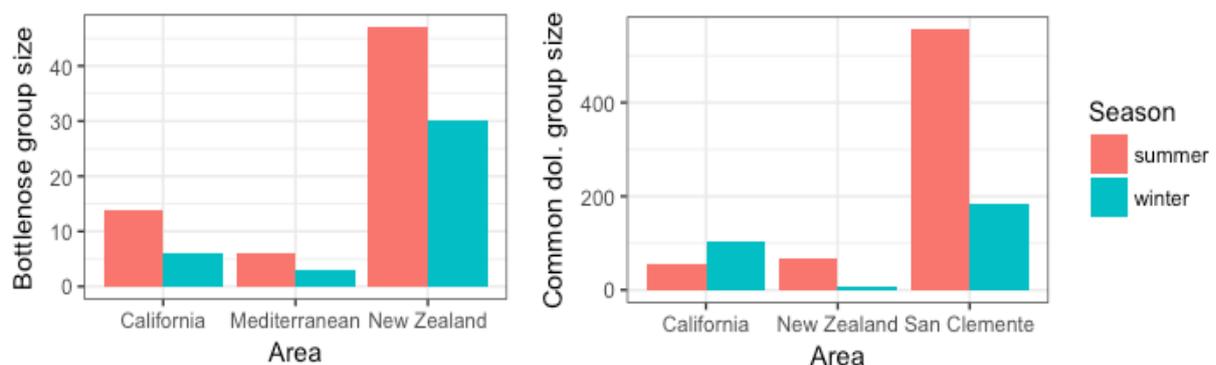


Figure 10: Group size variation between summer and winter in bottlenose and common dolphins.

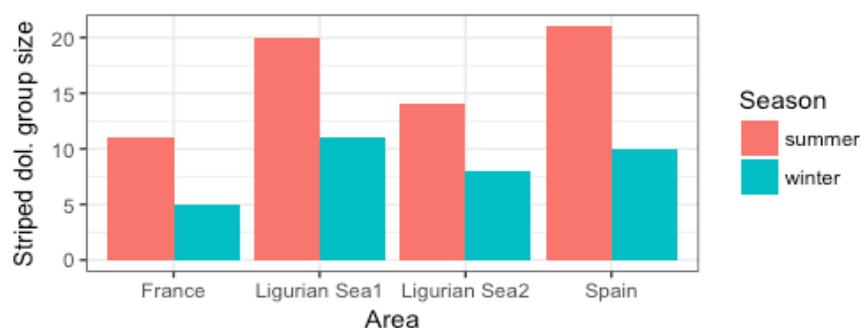


Figure 11: Group size variation between summer and winter in striped dolphins.

Group size variation between spring and autumn shows that congregations are typically larger in spring, particularly in species which form pods averaging > 20 individuals (large and very large groups) (Fig. 12). An exception are common dolphins in the SW-Atlantic outer shelf and slope area which form larger group in autumn but pods average > 100 individuals year-round. Dall's porpoises and Pacific white-sided dolphins occur in slightly larger congregations in autumn (App. 5). A larger group size in autumn compared to winter supports the calf protection and contradicts the access to females hypothesis.

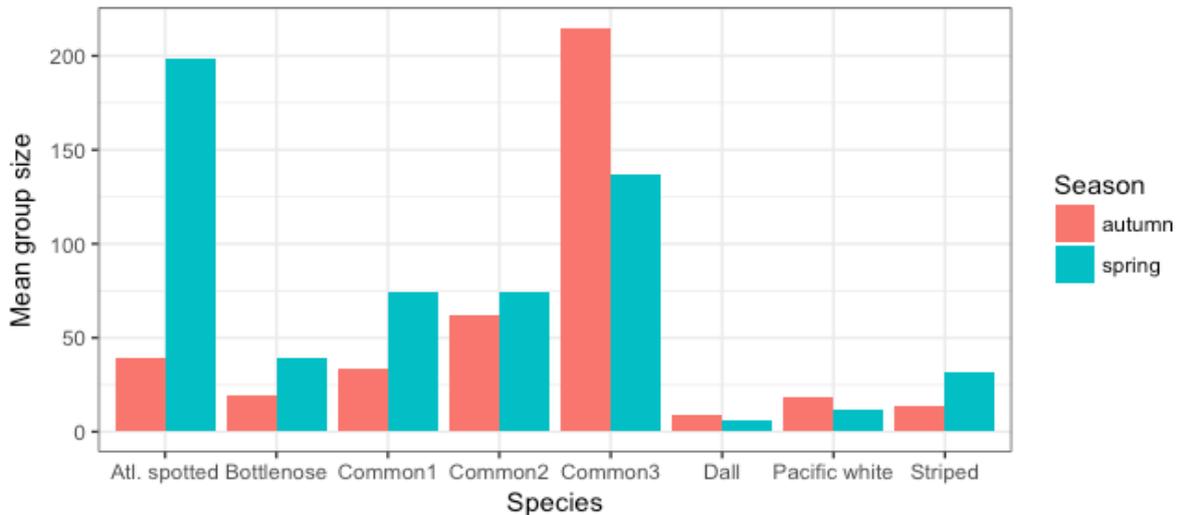


Figure 12: Group size variation between spring and autumn.

Migration distance

Long-distance migrations are carried out by most populations of all included baleen whale species, by adult male sperm whales, killer whales and possibly southern bottlenose whales. Maximum migration distances derived from telemetry and photo-ID studies are listed in Tab. 11. Average migration distances are unknown. However, a large-scale telemetry study on humpback whales has shown that migrations of 1000s of kilometres are typical, rather than an exception (Riekkola *et al.* 2018).

Migrations in Bryde’s whales were found to be diffuse between (sub)tropical and temperate regions, lacking a consistent winter-summer pattern (Murase *et al.* 2016). Therefore, this species is not included in the analysis.

Tab. 11 shows that all species included in this analysis cover thousands of kilometres during their migrations, often across the open ocean. Baleen whales, southern bottlenose whales and male sperm whales all travel solitarily or in groups averaging two individuals. Killer whales form groups averaging seven individuals but do not migrate over larger distances than most baleen whale species and male sperm whales. These results indicate that group size is not determined by migration distance and therefore do not support the navigation accuracy hypothesis.

Table 11: Maximum recorded migration distances

Species	Area	Distance [km]	Reference
Blue	Galapagos - S-Chile	5200	Torres-Florez <i>et al.</i> 2015
	central America - Alaska	5200	Bailey <i>et al.</i> 2009
Fin	Azores - E-Greenland/W-Iceland	4000	Silva <i>et al.</i> 2013
Sei	Azores - Labrador	3000	Olsen <i>et al.</i> 2009
Minke	Antarctica - Togo	8300	Segniagbeto <i>et al.</i> 2014
Southern right	South Africa - Antarctica	3000	Mate <i>et al.</i> 2010
Humpback	Cook Islands - Antarctica	8000	Riekkola <i>et al.</i> 2018
Gray	Chukchi Sea - Gulf of California	10000	Guazzo <i>et al.</i> 2017
	Sakhalin Island (E-Russia) - Mexico	11000	Mate <i>et al.</i> 2015
Southern bottlen.	Brazil/South Africa - Antarctica	4000+	Nemoto <i>et al.</i> 1980
Sperm whale	Azores - Norway	4400	Steiner <i>et al.</i> 2012
Killer whale	Antarctic Peninsula - Brazil	4700	Durban, Pitman 2012

Active space

Tab. 12 provides an overview of the active space of different types of sounds produced by cetacea. Most delphinids communicate with whistles (e.g. Lammers *et al.* 2006) and hence have an acoustic range of up to 6-10km. A lack of whistles has been reported in species of the genus *Cephalorhynchus*, including the Commerson's dolphin (Watkins *et al.* 1977; Dziedzic, De Buffrenil 1989; Dawson 1991; Morisaka, Connor 2007), in hourglass dolphins (Morisaka, Connor 2007), northern right whale dolphins (Oswald *et al.* 2008), both *Kogia* species and in porpoises (Schevill *et al.* 1962; Herman, Tavolga 1980; Watkins, Wartzok 1985; Tyack 1986; Ridgway, Carder 2001; Madsen *et al.* 2005), which are thought to communicate through click-based pulsed sounds of shorter range (Herman, Tavolga 1980; Popper 1980; Overstrom 1983; Herzing 1988; Dawson 1991). Echolocation clicks have an acoustic range of about 200-400m depending on the noise level.

The active space of long-range signals amounts to 8-12km in pilot whales, 16-26km in killer whales, 60km in sperm whales, and 100s-1000s of kilometres in baleen whales, depending on species and noise level (Schevill *et al.* 1962), with the largest acoustic ranges measured in fin and blue whales.

Deep-diving beaked whales are thought to use rasps to coordinate group dispersion and reunion, which may be audible to other individuals at substantial ranges, given the deep-water sound speed profile that tends to focus sound transmission in a deep-water channel (Medwin, Clay 1998) but quantitative active space measurements are lacking.

Table 12: Active space of cetacea acoustic signals

Species	Sound type	Active space	Reference
Blue/fin whale	low-frequency calls	100s-1000s of km	Payne, Webb 1971; Sirovic <i>et al.</i> 2007; Clark 1995; Tsuchiya <i>et al.</i> 2004
Sperm whale	slow click	60km	Madsen <i>et al.</i> 2002; Tran <i>et al.</i> 2014
	usual click	16km	Madsen <i>et al.</i> 2002
	creak click	6km	Madsen <i>et al.</i> 2002
Beaked whales	rasp	unknown, likely several km	Aguilar de Soto <i>et al.</i> 2011; Dunn <i>et al.</i> 2013
Pilot whales	pulsed call	8-12km	Nemiroff, Whitehead 2009; Pérez <i>et al.</i> 2016
Killer whale	pulsed call	10-16km+, max.: 26km	Miller 2006
	short-range call	5-9km	Miller 2006
Bottlenose dolphin	whistle	20-25km	Janik 2000b
		740m, max.: 5.7km	Jensen <i>et al.</i> 2012
Rough-toothed dolphin	whistles, broadband clicks	mean detection range of recording device: 3.8km	Rankin <i>et al.</i> 2015
White-beaked dolphin	whistle	min: 140m (167dB), max.: 10.5km (118dB)	Rasmussen <i>et al.</i> 2006
Spinner dolphin	whistle	6.3-9.3km (153.9dB)	Heenehan <i>et al.</i> 2016
Indo-Pacific humpback dolphin	whistle	6.6km (143.2dB)	Zhi-Tao <i>et al.</i> 2016
Dolphin	jaw pop	660-1040m, max.: 2km	Finneran <i>et al.</i> 2000
	breach	340-840m, max.: 1.6km	Finneran <i>et al.</i> 2000
	tail slap	max.: 90-180m	Finneran <i>et al.</i> 2000
False killer whale	echolocation click	238m*	Thomas, Turl 1990
Pygmy killer whale	echolocation click	100-400m*	Madsen <i>et al.</i> 2004
Bottlenose dolphin	echolocation click	346m*	Au <i>et al.</i> 2007

*based on the distance at which a fish or artificial equivalent thereof can still be detected times two, since successful detection implies that the echo of the original signal could be perceived

Fig. 13 shows that the seven species which only produce click-based sounds of an acoustic space in the range of hundreds of meters form small to medium-sized groups with an average of nine members. Species which use whistles for communication form groups of any size with an average ranging from 7-298 across 18 species, indicating that large group size may require, and is facilitated by the ability to produce whistles. Species which produce acoustic signals of a range of 10km and more form congregations of an average size of 2-23. Baleen whales which most commonly occur solitarily or in pairs utilize the furthest ranging sounds. These results suggest that baleen, sperm, pilot, killer and possibly beaked whales may be able to exchange information with other individuals via acoustic signals without the necessity to form cohesive groups.

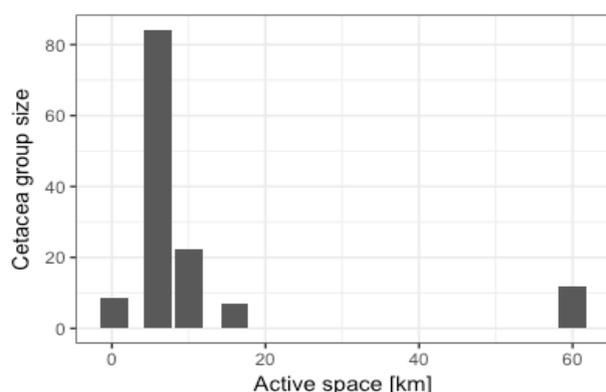


Figure 13: Group size as a variable of active space in odontoceti.

Body size

Cetacea vary in body length from an average of 1.5m in the Commerson's dolphin to 27m in the Antarctic blue whale. The largest odontoceti is the sperm whale with a mean length of 11m in females and 16m in males. The smallest mysticeti species, the minke whale, reaches an average length of 8.5m (Tab. 13).

Table 13: Mean adult body size

Cetacea species	Mean body size [m]	Cetacea species	Mean body size [m]	Cetacea species	Mean body size [m]
Blue whale	27.0	Sowerby's beaked	4.5	Pacific white-sided	2.0
Fin whale	22.0	Pygmy beaked	3.5	Hourglass dolphin	1.8
Sei whale	16.5	Longman's beaked	6.0	Dusky dolphin	1.8
Bryde's whale	13.0	Southern bottlenose	7.5	Fraser's dolphin	2.3
Minke whale	8.5	Northern bottlenose	8.0	Spinner dolphin	2.3
Southern right whale	14.0	Long-finned pilot	5.8	Pantropical spotted	2.0
Humpback whale	14.5	Short-finned pilot	5.3	Atlantic spotted	2.0
Gray whale	13.5	False killer whale	4.8	Striped dolphin	2.3
Sperm whale	12.5♀ 16.5♂	Pygmy killer	2.3	Clymene dolphin	2.0
<i>Kogia</i>	3.0	Melon-headed	2.5	Common dolphin	2.0
Cuvier's beaked	6.0	Risso's	3.3	Commerson's	1.5
Baird's beaked	11.5	Bottlenose	3.0	Southern right w.d.	2.5
Arnoux's beaked	9.0	Rough-toothed	2.3	Northern right w.d.	2.5
Blainville's beaked	5.0	White-beaked	2.5	Dall's porpoise	2.0
Gervais' beaked	4.0	Atlantic white-sided	2.5	Burmeister's	1.8

References: Shirihai, Jarrett 2006; Perrin *et al.* 2009

Fig. 14 shows two patterns of interrelation between group size and body size in odontoceti. Small groups are formed by species of any body size. However, species of > 3m body length all occur in congregations averaging < 25 members. Species of ≥ 7.5 m length average group sizes of < 15 individuals. These include all baleen whales, the sperm whale, both bottlenose whales, and Baird's and Arnoux's beaked whales. Species of small body length occur in congregations of any size, but groups of more than 100 individuals are regularly encountered only in species of ≤ 2.5 m average length. In mysticeti which form groups of an average of 1 to 2 members regardless of their length no correlation was found between body size and group size. These results indicate that small body size facilitates the formation of large groups whereas large body size requires small groups.

Logarithmic transformation of data further confirmed a lack of a clear positive or negative correlation between both parameters. The analysis of group size by phylogenetic groups as opposed to species yields very similar results although less clear since some phylogenetic groups contain species of a variety of body and group sizes (Fig. 14, right). This indicates that the pattern detected at species level holds across cetacea and is not caused by a high number of species in one particular phylogenetic group. Independent contrasts between body size and groups size do not show a correlation implying that these two traits are not linked by coevolution.

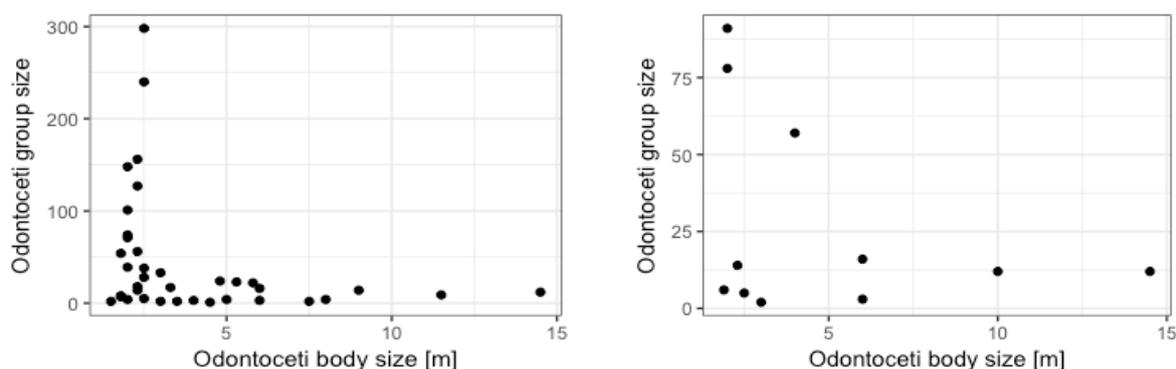


Figure 14: Two-way interrelation between mean group size and body size in toothed whales by species (left) and by phylogenetic group (right).

Foraging depth

Cetacea foraging depth shows a high level of inter-specific variation such that several baleen whale and dolphin species are restricted to epipelagic waters whereas sperm whales, both species of the genus *Kogia*, beaked and pilot whales, and Risso's dolphins either use the whole water column to cover their energy needs, or feed exclusively at meso- and bathypelagic depths (Tab. 14). Foraging depths listed as epi-, meso- and bathypelagic are meant to describe the vertical range of feeding, not foraging habitat. Many cetacea species are benthic as well as pelagic feeders.

Table 14: Main foraging depths

Species	Foraging depth	Species	Foraging depth
Blue whale	epi-/mesopelagic	Pygmy killer	epi-/mesopelagic
Fin whale	epi-/mesopelagic	Melon-headed	epi-/mesopelagic
Sei whale	epipelagic	Risso's	meso-/bathypelagic
Bryde's whale	epi-/mesopelagic	Bottlenose	epi-/mesopelagic
Minke whale	epipelagic	Rough-toothed	epi-/mesopelagic
Southern right whale	epipelagic	White-beaked	epi-/mesopelagic
Humpback whale	epi-/mesopelagic	Atlantic white-sided	epipelagic
Gray whale	epipelagic	Pacific white-sided	epi-/mesopelagic
Sperm whale	meso-/bathypelagic	Hourglass dolphin	epi-/mesopelagic
<i>Kogia</i>	meso-/bathypelagic	Dusky dolphin	epipelagic

Species	Foraging depth	Species	Foraging depth
Cuvier's beaked	meso-/bathypelagic	Fraser's dolphin	epi-/mesopelagic
Baird's beaked	meso-/bathypelagic	Spinner dolphin	epipelagic
Arnoux's beaked	unknown	Pantropical spotted	epipelagic
Blainville's beaked	meso-/bathypelagic	Atlantic spotted	epipelagic
Gervais' beaked	bathypelagic	Striped dolphin	epi-/mesopelagic
Sowerby's beaked	bathypelagic	Clymene dolphin	epipelagic
Pygmy beaked	bathypelagic	Common dolphin	epipelagic
Longman's beaked	epi-/mesopelagic	Commerson's	epipelagic
Southern bottlenose	bathypelagic	Southern right w.d.	epi-/mesopelagic
Northern bottlenose	meso-/bathypelagic	Northern right w.d.	epipelagic
Long-finned pilot	meso-/bathypelagic	Dall's porpoise	epi-/mesopelagic
Short-finned pilot	meso-/bathypelagic	Burmeister's	epipelagic
False killer whale	epi-/mesopelagic		

References: App. 2

Based on Tab. 14 cetacea were divided into three categories for the analysis of correlation between group size and foraging depth: (1) species which exclusively feed in epipelagic waters, (2) species which use epi- and mesopelagic parts of the water column, and (3) species which feed either exclusively at bathypelagic depths or at bathy- and mesopelagic depths. Results show a high variability in group size within epi- and epi-/mesopelagic foraging species and a high overlap between these two categories, whereas deep-diving meso-/bathypelagic feeders form small congregations (Fig. 15).

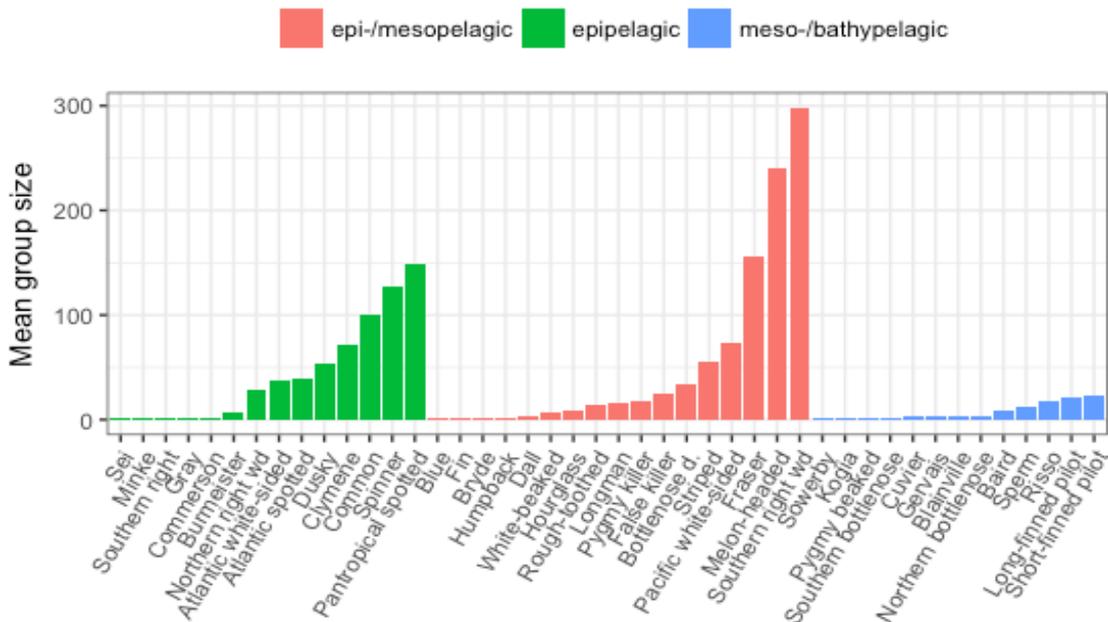


Figure 15: Mean group size correlation with foraging depth in cetacea species

Due to the large overlap in group size between species foraging in the epipelagic and epi-/mesopelagic realms, and a mix of epipelagic and epi-/mesopelagic species in almost every phylogenetic group, both categories were treated as one for phylogenetic and statistical analyses. Results show that the pattern detected at species level holds true for phylogenetic groups. Large mean group sizes are only found in species which forage at epi- or epi- and mesopelagic depths (Fig. 16).

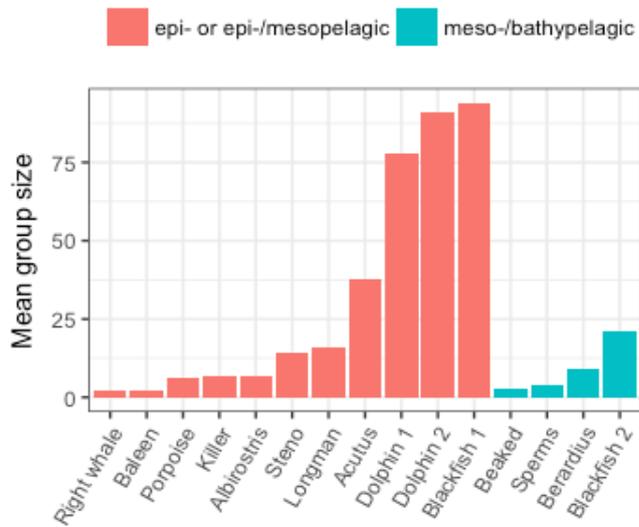


Figure 16: Correlation between group size and foraging depth for phylogenetic cetacea groups

The Games Howell post hoc test produced significant group size differences between both foraging depth categories (Tab. 15).

Table 15: Games-Howell statistics, df: degrees of freedom, k = 2

Group size categories	df	t	q(k,df,α)/√2	α
epi- + epi-/mesopelagic versus meso-/bathypelagic	24.96	3.51	3.09	< 0.005

Geographic group size variation

Group size comparisons between different latitudinal zones indicate little or inconsistent intraspecific variation between (sub)tropical and temperate climate zones (Fig. 17). All species for which temperate and (sub)polar group size estimates were available form congregations of small size and no significant intraspecific group size differences between these latitudes were found.

Interspecifically mean group size overlaps between low and middle latitudes such that species which occur in congregations of small and medium size occur in both climate zones. However, pods averaging > 75 individuals are only formed by four (sub)tropical species which are absent from temperate waters. These are melon-headed whales, spinner, pantropical spotted and Fraser's dolphins.

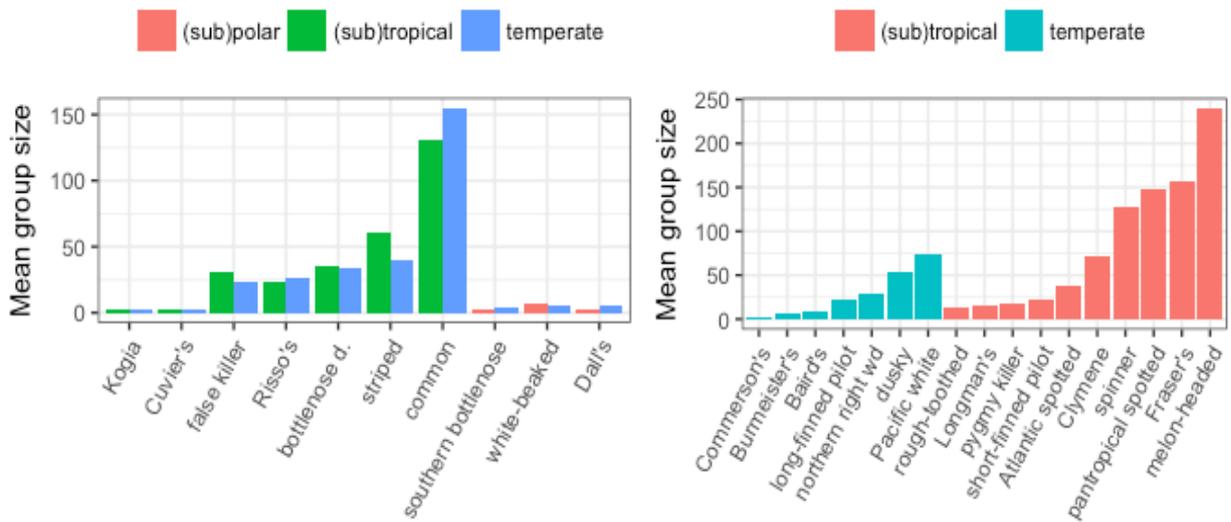


Figure 17: Latitudinal group size differences within (left) and between species (right)

Comparison of congregation size between N-Pacific and N-Atlantic found groups of significantly larger average sizes in the former compared to the latter ocean basin in Risso's, bottlenose (offshore form), Fraser's, striped, pantropical spotted and common dolphins (Fig. 18). Welch's t produced consistent significances of these results (Tab. 16).

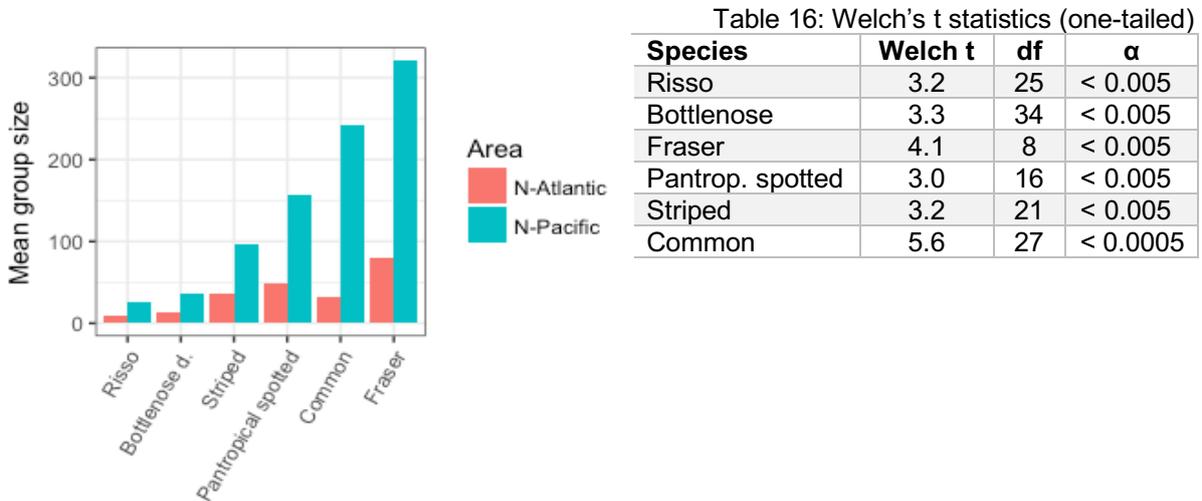


Figure 18: Higher average group size in central and N-Pacific compared to N-Atlantic

A comparison of pod sizes between related species of the southern and northern hemisphere shows inconsistent results, indicating that group size is determined by factors unrelated to hemisphere (Tab. 17).

Table 17: Comparison of group size between closely related species of southern and northern hemispheres

Southern hemisphere		Northern hemisphere	
Species	Group size \bar{x}	Species	Group size \bar{x}
Arnoux's beaked whale	14	Baird's/Sowerby's beaked w.	9 / 1
Southern bottlenose whale	2	Northern bottlenose whale	4
Hourglass dolphin	8	Atlantic white-sided dolphin	38
Dusky dolphin	54	Pacific white-sided dolphin	74
Southern right whale dolphin	298	Northern right whale dolphin	28
Burmeister's porpoise	7	Dall's porpoise	4

Summary of results

Overall results are summarized in Tab. 18.

Table 18: Summarized results: corr: correlation, gs: group size, sign.: significant, pel.: pelagic

Hypothesis	Parameter	Results
Communal prey-search	home range size	lack of corr. between gs and home range size, hypothesis not supported ; sign. smaller gs in long-dist. migrating species than in nomadic species
Cooperative prey-herding	% shoaling prey in diet	lack of corr. between gs and portion of shoaling prey in diet; hypothesis not supported
Predation-risk	predation risk	sign. positive corr. between shark predation risk and gs; lack of corr. between killer whale predation risk and gs hypothesis supported for sharks only
Calf protection	gs with/without calves, spring - autumn gs variation	in odontoceti: groups with calves sign. larger than groups without calves but in most species not large enough for calf protection; in delphinids: gs tends to be larger in autumn than spring; hypothesis partially supported by results
Access to females	spring - autumn gs variation	in delphinids: gs tends to be larger in autumn than spring; hypothesis not supported
Navigation accuracy	migration distance	lack of corr. between gs and migration distance; hypothesis not supported
-	active space	ability to produce whistles facilitates large gs; long-range sounds facilitate communication without grouping
	body size	2-way interrelation with gs, small body size facilitates large groups; positive corr. between body size and portion of shoaling prey in diet in odontoceti
	foraging depth	sign. smaller gs in bathypel. feeders than epi-/mesopel. feeders; epi-/mesopelagic feeding facilitates large gs
	geographic gs variation	in delphinids: gs sign. larger in N-Pacific than N-Atlantic; lack of latitudinal and hemispheric gs variation
	summer-winter gs variation	in delphinids: summer gs > winter gs in some and vice versa in other species and areas, tendency for larger groups in summer

Discussion

Communal prey-search hypothesis

Hypothesis: Nomadic species with reduced local knowledge about prey distribution which move between ephemeral prey concentrations form larger groups than cetacea which show site-fidelity.

Nomadic cetacea and resident cetacea which occupy large home ranges form on average larger congregations (\bar{x} : 47) than resident species which occupy a small home range (\bar{x} : 15). However, this difference is not significant due to large variation in group size within, and overlap of congregation sizes between both categories. Therefore, this analysis does not support the communal prey search hypothesis.

Average congregation size varies between 2-240 in cetacea with a large home range, and between 2-54 in resident species, indicating that a large home range facilitates but does not require a large group size, and large group size is only one of several possible adaptations to a nomadic lifestyle which has been selected for in some but not all nomadic cetacea species. The same pattern is apparent across phylogenetic groups of related species. All three distinguished movement patterns include phylogenetic groups which form very small congregations. The findings that movement and migration patterns in cetacea show a phylogenetic correlation - most phylogenetic groups contain only one movement pattern across all species affiliated to that group - and that large group size can only be found in phylogenetically young species whereas a nomadic lifestyle is applied by species of variable phylogenetic age, further suggest that large group size is only one of several possible adaptations to a nomadic lifestyle which secondarily facilitates communal prey search.

The analysis of active space of sounds produced by cetacea provides further support. Whistles, the communication sounds produced by many odontocete species (e.g. May-Collado *et al.* 2007), have an active space of several kilometre (Janik 2000b; Rasmussen *et al.* 2006; Jensen *et al.* 2012; Heenehan *et al.* 2016), especially in a low-noise tropical open ocean environment where large congregations are found with highest consistency. This implies that individuals could be distributed over wider areas than observed in most delphinid species and still exchange foraging-related information. To search the largest possible volume of water group members should be spaced so as to fully use their echolocation detection range of about 100-400m (Thomas, Turl 1990; Madsen *et al.* 2004; Au *et al.* 2007). Hence, sub-groups with distances of 10s to 100s of meter from each other (Baird *et al.* 2008) may be close to optimally spaced but individuals within sub-groups are not. To maximize prey search efficiency individuals would also be expected to spread out the further the larger the size of the prey patches typical for the area which is searched.

Inter-individual communication between widely spaced individuals and food calling in response to prey detection have both been documented in various cetacea species. For example, sperm whales use creak sounds to signal a prey encounter (Miller *et al.* 2004) which can be detected by conspecifics up to at least 6km away (Madsen *et al.* 2002). Whitehead (2016) described groups of 10-50 sperm whales spread out over several kilometres when foraging off Galápagos which were slowly traveling and turning synchronously despite large inter-individual distances, indicating information exchange about travel speed and trajectory. In bottlenose dolphins bray-calls have been correlated with animals swimming quickly towards the caller's location (Dos Santos *et al.* 1990, 1995; Janik 2000a). This species seems to share information about prey patch characteristics acoustically through sounds which are always used in combination with food calls (King, Janik 2015). Food-calling has been suggested in blue, fin (Croll *et al.* 2002) and humpback whales (Jurasz, Jurasz 1979; D'Vincent *et al.* 1985; Sharpe 2001; Fournet *et al.* 2018) based on feeding-related sound production, but the purpose of these sounds is still a matter of debate (e.g. Fournet *et al.* 2018). These findings show complex behavioural and acoustic adaptations related to communal prey search and further suggest that cohesive groups are not a requirement for collective prey search.

Conclusively communal prey search is suggested to be an effect of rather than a cause for the formation of cohesive groups. A group's foraging requirements are higher than those of a solitary individual. Hence more prey needs to be found to cover the energy demands of all associated individuals and prey search becomes a higher priority. Therefore, grouping behaviour is used to increase the efficiency of prey search.

Cooperative prey-herding hypothesis

Hypothesis: Cetacea species whose diet includes a high portion of shoaling prey are more likely to congregate, and form larger congregations, than species which predominantly consume solitary prey.

The lack of correlation between group size and the portion of shoaling prey in the diet of oceanic cetacea species contradicts the cooperative prey herding hypothesis. In fact, several species which heavily rely on shoaling prey to cover their energy needs and for which prey herding behaviour has been documented (Chap. 1) occur solitarily or in very small groups of < 10 individuals. These include baleen whales, Commerson's dolphins and Dall's and Burmeister's porpoises.

Field observations and the large variation in mean group size of cooperatively prey herding species both indicate that this foraging technique is efficiently applied even by solitary individuals and is most often carried out by small groups or groups. Large pods typically split into smaller sub-groups for feeding rather than herding prey as a cohesive unit. Even though groups of up to 50 individuals have been observed to cooperatively herd prey, such large collaborations seem rare. Sub-groups mostly comprise 1-15 individuals, even when large shoals of prey are herded (e.g. Clua, Grosvalet 2001). Larger sub-group sizes were recorded in killer whales (22-46 individuals) and rough-toothed dolphins (10-20 individuals) when prey schools were not only herded but also lifted to the surface from depths of up to 150m (Nøttestad *et al.* 2002a; Bernasconi *et al.* 2011).

Shoaling fish, squid and crustacea represent the most important food source of oceanic cetacea. The only species in which larger, solitary and often benthic prey may be of greater importance than small shoaling species are sperm whales (e.g. Whitehead 2003; Joyce *et al.* 2017), large- and medium-sized beaked whales and Risso's dolphins.

Cooperative prey herding neither explains the formation of groups comprising > 20 individuals, nor the high variability in group size between and within many cetacea species which apply this technique. The formation of small groups may increase the ability to maintain herded prey schools at the surface for longer compared to solitary foraging (Vaughn *et al.* 2010b; 2011), and larger groups may be able to herd prey schools of low initial density more efficiently than small ones (Benoit-Bird, Au 2009), but cooperative prey herding does not appear to be the evolutionary driver of grouping behaviour in oceanic cetacea. Rather results of this study indicate that congregations form in response to factors other than prey type and foraging technique, and grouping behaviour is secondarily used for cooperative prey herding.

Predation-risk hypothesis

Hypothesis: Cetacea which experience a high predation threat form large congregations whereas species exposed to a low risk of predation occur solitarily or in small groups.

The positive correlations between group size and white shark, broadnose sevengill shark and overall shark predation risks in oceanic cetacea support the predation risk hypothesis, whereas a lack of correlation between congregation size and killer whale predation risk indicates that gregariousness does not affect the risk inflicted by these predators.

A positive correlation between group size and high-shark-risk areas such as regions of an extended oxygen minimum zone and/or high density of white and broadnose sevengill sharks further supports the predation risk hypothesis related to sharks.

The four species which account for the higher encounter rate of large groups in tropical and subtropical areas compared to temperate regions of the Pacific, and which consistently occur in congregations averaging > 100 individuals (spinner, pantropical spotted and Fraser's

dolphins and the melon-headed whale) all experience a low risk of predation from killer whales due to the low density of these predators in areas far from shore and at low latitudes (Forney, Wade 2006). Northern and southern right whale dolphins which rarely approach land and hence, also occupy areas of low killer whale density regularly occur in large congregations in temperate seas, further indicating that congregation is not an adaptation to killer whale predation risk.

Killer whales seem to regularly attack large groups of small odontocetes (Ternullo, Black 2002; Morrice 2004; Best *et al.* 2010; Pitman *et al.* 2015) including dusky, common and Pacific white-sided dolphins, and their sophisticated techniques of prey herding and of isolating individuals from their groups (Chap. 1) may render large group size an ineffective adaptation to killer whale predation risk. Acoustic signals necessary to maintain cohesion of large delphinid groups are used by mammal-eating killer whales to localize cetacea pods (Jefferson *et al.* 1991; Barrett-Lennard *et al.* 1996; Deecke *et al.* 2005). This interrelation is thought to restrict vocalization when perceived predation risk is high across many odontoceti species (Tyack, Clark 2000; Morisaka, Connor 2007; Oswald *et al.* 2008; Aguilar de Soto *et al.* 2011; Rankin *et al.* 2013) which in turn limits group cohesion and size. Hence, anti-predator mechanisms other than the formation of large groups such as long, deep dives beyond the reach of killer whales and small group size in combination with inconspicuous acoustic and surface behaviour which decrease detection by these predators may be more effective in reducing killer whale predation. Visually inconspicuous behaviour in direct response to the presence of killer whales has been documented in gray whales (Dahlheim, Heyning 1999), sperm whales (Gaskin 1964; Caldwell *et al.* 1966), *Kogia* (Willis, Baird 1998) and beaked whales (Gaskin 1971).

In line with a positive correlation between shark predation risk and congregation in cetacea bottlenose dolphins of Shark Bay, Australia, occur in larger groups when tiger shark predation threat is high compared to areas and times of low risk (Heithaus, Dill 2002). A dramatic increase in group size in Indo-Pacific bottlenose dolphins from an average of 18 to 76 in the time period from 2008 to 2016 in Algoa Bay, South Africa, was suggested to be related to an increase in predation risk by great white sharks (Bouveroux *et al.* 2018). Commerson's dolphins which experience a high shark predation risk, yet form small groups averaging two individuals inhabit more sheltered coastal areas and only occasionally venture into oceanic waters. These findings further emphasize the influence of shark predation risk on congregation behaviour in cetacea.

A reduction in the rate of predation at night in combination with greater food availability was suggested to select for smaller group sizes at night across various ecosystems (Clark, Mangel 1986; Mangel 1990; Beauchamp 2007). In line with this finding many delphinid species which experience a high risk of predation from sharks (Chap. 2) congregate during the day and disperse into small sub-groups at night when feeding and when risk inflicted by visual predators is reduced (e.g. Norris *et al.* 1994; Scott *et al.* 2012; Markowitz 2004; Garaffo *et al.* 2007, 2011).

The exponential increase in cetacea group size at high levels of predation risk inflicted by white sharks suggests that the dilution effect and predator swamping play an important role in reducing predation by these elasmobranchs. The dilution effect was found to work conjointly with collective predator detection in lowering the perception of predation risk, particularly in large groups (Beauchamp 2017). Thus, increased vigilance efficiency and dilution may represent the main mechanisms behind fitness benefits related to cetacea congregation when shark predation risk is high.

This study suggests that oceanic cetacea have developed a number of anti-predator adaptations including large body size, long dives beyond the reach of epipelagic predators, inconspicuous behaviour, high escape speed, defence which may or may not be communal,

large group size and association with shallow coastal waters during the day (App. 4: Tab. 5). All species included in this analysis apply a combination of these adaptations, rather than a single one. Table 19 summarizes which species were documented to use which adaptations. Communal defence has been documented for several delphinids and is typically directed against sharks. Defence by baleen whales is mostly directed towards killer whales and is applied solitarily and in groups (App. 4: Tab. 5).

Table 19: Adaptations to predation risk

Predation risk adaptation	Species applying this adaptation	Predation risk adaptation	Species applying this adaptation	
Large body size	Blue whale	High escape speed	Blue whale	
	Fin whale		Fin whale	
	Sei whale		Sei whale	
	Bryde's whale		Bryde's whale	
	Minke whale		Minke whale	
	Southern right whale		delphinids	
	Humpback whale		Dall's porpoise	
	Gray whale		(Communal) defence	Southern right whale
	Sperm whale			Humpback whale
	Baird's beaked whale			Gray whale
Arnoux's beaked whale	Sperm whale			
Bathypelagic long dives beyond reach of epipelagic predators	Sperm whale	Large group size	Bottlenose dolphin	
	<i>Kogia</i>		Atlantic spotted dolphin	
	Cuvier's beaked whale		Clymene dolphin	
	Baird's beaked whale		Common dolphin	
	Arnoux's beaked whale		Long-finned pilot whale	
	Blainville's beaked whale		Short-finned pilot whale	
	Gervais' beaked whale		False killer whale	
	Sowerby's beaked whale		Melon-headed whale	
	Pygmy beaked whale		Bottlenose dolphin	
	Longman's beaked whale		Atlantic white-sided dolphin	
	Southern bottlenose whale		Pacific white-sided dolphin	
	Northern bottlenose whale		Dusky dolphin	
	Long-finned pilot whale		Fraser's dolphin	
	Short-finned pilot whale		Spinner dolphin	
Risso's dolphin	Pantropical spotted dolphin			
Inconspicuous behavior	Sei whale	Shore-association and only partial use of offshore habitat	Atlantic spotted dolphin	
	<i>Kogia</i>		Striped dolphin	
	Cuvier's beaked whale		Clymene dolphin	
	Baird's beaked whale		Common dolphin	
	Arnoux's beaked whale		Southern right whale dolphin	
	Blainville's beaked whale		Northern right whale dolphin	
	Gervais' beaked whale		Minke whale	
	Sowerby's beaked whale		Humpback whale	
	Pygmy beaked whale		Gray whale	
	Southern bottlenose whale		Rough-toothed dolphin*	
	Northern bottlenose whale		White-beaked dolphin	
	Rough-toothed dolphin		Dusky dolphin	
	Pygmy killer whale		Spinner dolphin*	
	Dall's porpoise		Commerson's dolphin	
	Burmeister's porpoise		Burmeister's porpoise	

References: surface behaviour: Shirihai, Jarrett 2006, communal defence + high escape speed: App. 4: Tab. 5

* some populations

Tab. 20 summarizes expected foraging and predation-related benefits and drawbacks of large versus small groups in oceanic cetacea.

Table 20: Expected group size benefits and drawbacks related to predation and foraging in oceanic cetacea

Group size	Benefits	Drawbacks	Typically associated with
large	dilution effect ↑ confusion effect ↑ vigilance efficiency ↑ predator swamping ↑	predator encounter rate ↑ detection by predators ↑ forage requirements ↑	conspicuous surface and acoustic behaviour; limited to cetacea of small body size
small	predator encounter rate ↓ detection by predators ↓ forage requirements ↓	dilution effect ↓ confusion effect ↓ vigilance efficiency ↓ predator swamping ↓	inconspicuous surface and acoustic behaviour, small inter-individual distance, often combined with deep diving

Conclusively, shark predation risk is suggested to represent a main evolutionary driver towards congregation in cetacea. Particularly large delphinid groups seem to be driven by this parameter.

Calf protection hypothesis

Hypothesis: Groups which contain calves are of much larger size than groups which do not comprise calves. Species with calving seasonality form larger groups in autumn than in spring.

A larger mean group size in autumn than in spring in several delphinids with calving seasonality supports the calf protection hypothesis. Odontoceti pods with calves are typically larger than those without calves but both, group sizes and group size differences are too small to reduce predation risk through confusion and dilution effects, and predator swamping except for the Atlantic white-sided dolphins. Most species which form congregations averaging > 100 individuals such as melon-headed whales, spinner, pantropical spotted and common dolphins reproduce year-round in (sub)tropical areas (e.g. Norris, Dohl 1980; Larese, Chivers 2009). Hence a seasonal group size change is not expected.

These results indicate that congregation may play an important role in calf protection in some species but overall, considering the populations and species for which relevant data were available, results of this study rather indicate that calf care may be an important evolutionary driver towards grouping. In this case groups would also be expected to be larger when calves are present but alloparental care seems to require groups of < 15 individuals (Chap. 1).

The following accounts of increased group size when calves were present are unlikely to be related to reduced predation risk:

- Blainville's beaked whale: group size increase from 3 to 6 and 9 off La Gomera (Canary Islands) (Ritter, Brederlau 1999)
- Long-finned pilot whale: group size increase from 20 to 23 off N-Nova Scotia (Ottensmeyer, Whitehead 2003)
- Killer whale: group size increase from 3 to 5 in the Magellan Strait (Capella *et al.* 2014)
- Risso's dolphin group size increase from 13 to 17 off the Azores (Hartman *et al.* 2014)
- bottlenose dolphin: group size increase from 4 to 12 off Croatia (Bearzi *et al.* 1997)
- Atlantic spotted dolphin: group size increase from 6 to 14 at Little Bahama Bank (Elliser, Herzing 2014)
- common dolphin: group size increase from 5 to 9 off S-Australia (Filby *et al.* 2010)

- Dall's porpoise: group size increase from 2 to 3 off W-Canada (Jefferson 1987)

Alloparental care explains these group dynamics much better than calf protection. A number of coastal bottlenose dolphin communities form larger groups when calves are present (Johnson, Norris 1986; Wells 1991; Mann *et al.* 2000; Reynolds *et al.* 2000; Kerr *et al.* 2005; Gibson, Mann 2008a,b; Gibson *et al.* 2013). Such nursery groups are composed of mother-calf pairs and additional adult females which look after calves while their mothers are foraging (Johnson, Norris 1986). These groups are thought to facilitate social learning rather than being selected for by anti-predator benefits (Gibson, Mann 2008b).

To better understand the role of grouping for calf protection more research is needed studying group size differences related to the presence of calves in species which form large congregations such as common dolphins in some areas, northern and southern right whale dolphins and Pacific white-sided dolphins. However only a strong shift from very small to large group size between groups without and with calves would indicate that calf protection is a main driver for congregation. If species form large groups whether calves are present or not, then general predation risk would be the evolutionary driver.

To the authors knowledge, humpback whales represent the only baleen whale species which increases group size in response to calf presence in some areas. Southern hemisphere humpback whale mother calf pairs are sometimes accompanied by an escort during migration off Australia, in breeding areas including Tonga, Ecuador and Colombia, and on Antarctic feeding grounds. The escort assists in defending the calf from attacks by killer whales (Chittleborough 1953; Naessig, Lanyon 2004; Pitman *et al.* 2015, 2017).

In humpback whales defence of calves can involve unrelated and unassociated individuals as documented off Alaska, California and Antarctica (review: Pitman *et al.* 2017). Adult humpbacks may join an attacked calf or mother-calf pair from more than 1 mile away (D'Vincent *et al.* 1989) indicating that communal defence does not necessarily require a tight group, esp. in species of large body size which cannot be killed within short periods of time. Similar behaviour of attacked conspecifics being joined by nearby individuals has been documented in sperm whales (Pitman *et al.* 2001).

Attacks on baleen and sperm whales often last hours (Brennan, Rodriguez 1994; George, Suydam 1998; Pitman *et al.* 2001; Matkin, Saulitis 2002; Ford, Reeves 2008; Pitman *et al.* 2017; Whitt *et al.* 2015). Hence approach by additional individuals from a wider area is still helpful, which may not be the case in small odontocetes such as *Kogia*, dolphins and porpoises which are often killed within minutes (Dahlheim, Towell 1994; Constantine *et al.* 1998; Ford *et al.* 1998; Visser 1999; Ternullo, Black 2002; Pitman *et al.* 2003; Dunn, Claridge 2014). Attack times of up to 43min have been recorded in Dall's porpoises (Saulitis *et al.* 2000, 2002).

If mean group size is small, even a slight increase may improve the group's ability to communally defend young individuals from sharks, a behaviour which has been observed in Clymene and common dolphins (AIBS 1967; Springer 1967).

Navigation accuracy hypothesis

Hypothesis: Migration distance positively correlates with group size in migrating species and nomadic cetacea consistently form groups of large size whereas resident species with small home ranges consistently form small congregations or occur solitarily.

The results of this analysis do not support the navigation accuracy hypothesis. Long-distance migrations are carried out by most baleen whale species, male sperm whales, killer whales and possibly southern bottlenose whales. All of these species migrate over 1000s of

kilometres often predominantly across open oceanic waters (Olsen *et al.* 2009; Mate *et al.* 2010, 2015; Steiner *et al.* 2012; Silva *et al.* 2013; Fossette *et al.* 2014; Kennedy *et al.* 2014; Riekkola *et al.* 2018), yet occur solitarily or in groups averaging two individuals, except for killer whales which form congregations of a mean size of seven members.

Group size does not increase during migration (e.g. Brueggeman *et al.* 1987; Shane 1994; Brown, Corkeron 1995) despite the lack of foraging during all or major parts of migration as indicated by the straight-line movement detected by many telemetry studies (Garrigue *et al.* 2010; Horton *et al.* 2011; Silva *et al.* 2013; Fossette *et al.* 2014; Kennedy *et al.* 2014; Riekkola *et al.* 2018). Hence, group formation is not expected to be limited by forage supply during travel. These findings confirm that accurate navigation does not require grouping in cetacea (Chap. 1). Instead information exchange via long-distance communication may play a role in increased navigation accuracy (e.g. Guazzo *et al.* 2017).

The migration pattern is highly variable between species, populations and individuals and may range from non-migrating populations and individuals (Mizroch *et al.* 2009; Simon *et al.* 2010; Geijer *et al.* 2016) or an interruption of migration in some years (Kennedy *et al.* 2014) to movements of > 10000km each way, particularly when migration does not only involve N/S movement but an ocean is crossed W/E at the same time (e.g. Mate *et al.* 2015). Migrations may include foraging stops in productive areas between lines of straight travel (Silva *et al.* 2013) or may be carried out non-stop (Durban, Pitman 2012). When not foraging movement typically follows a direct trajectory (e.g. Olsen *et al.* 2009; Horton *et al.* 2011; Silva *et al.* 2013; Fossette *et al.* 2014; Kennedy *et al.* 2014; Riekkola *et al.* 2018).

Phylogenetically there is some indication that long-distance migration is an older trait than grouping behaviour. Migration in baleen whales is thought to have evolved about four million years ago in the late Pliocene (Bianucci *et al.* 2006; Marx, Fordyce 2015), whereas congregation seems to be an evolutionarily new development with the possible exception of matrilineal groups of sperm whales which are nomadic but do not seasonally migrate between feeding and breeding areas. The consistent formation of large groups is limited to some of the phylogenetically young delphinid species, none of which carry out long-distance migrations along definable paths.

Whether or not information exchange plays a significant role for navigation accuracy in cetacea could be studied by the use of telemetry. If communication is important then individuals which start migrating first would be expected to navigate less accurately than individuals which follow and use acoustic signals or cues of 'leaders' to improve their navigation accuracy. Hence, first migrators of the season would have to be localized along their migratory paths and would have to be equipped with a tracking device. For comparison some individuals which migrate later during the season would also have to be tagged and tracked. This approach only works when the whole population migrates. Otherwise vocalizing individuals which have remained at a feeding or breeding ground year-round may provide navigational cues or signals to migrating individuals via low-frequency sounds. If information exchange plays an important role in baleen whale migrations, then individuals which start migrating first would also be expected to be experienced individuals which have repeatedly travelled between feeding and breeding areas before and would therefore be good leaders (Chap. 1).

The high intra- and inter-specific variation in group size of nomadic cetacea when traveling indicates that grouping is not required by these species to accurately navigate between different parts of the ocean. In fact, very small groups or solitary individuals spread out over a large area combined with long-distance communication may be more efficient in picking up large-scale navigation cues in oceanic waters such as the location of oceanographic features, changes in seafloor relief etc. than cohesive groups.

Conclusively, the following points contradict the hypothesis that increased navigation accuracy represents an evolutionary driver for grouping in cetacea:

- Lack of correlation between migration distance and group size
- Solitary whales are able to accurately navigate the open ocean
- The ability of long-distance migration without grouping is consistent across various marine vertebrates (Chap. 1).
- High variability in mean group size among nomadic cetacea species.
- Phylogenetically migration and hence the ability to successfully navigate the open ocean seems to have evolved earlier than the formation of large groups in cetacea.
- Inter-individual information exchange during migration does not require the formation of groups due to the ability of most oceanic cetacea to communicate over large distances.

Access to females hypothesis

Hypothesis: Cetacea congregate in autumn and occur solitarily in spring.

When females are spread out over vast areas such as in oceanic odontocetes then there are few ways for males to gain sufficient and reliable access: lekking, long-term association with one or several females (mate guarding) or travel between groups of females. Of these, lekking, the gathering of males at traditional places (leks) during the mating season to engage in competitive displays that attract females, would lead to the formation of groups for mating purposes including access to females.

However, the typically larger group sizes found in spring compared to autumn do not support this hypothesis. This result does not exclude that small male alliances of few individuals are evolutionarily driven by access to females since a seasonal occurrence of congregations of such few members would likely go undetected by this study.

Access to females is difficult to quantify and results of this study, which are solely based on observed seasonal changes in group size have to be interpreted with care since non-biological factors such as variations in cetacea density in the study area due to seasonal movements of part of the population, or seasonal differences in food supply could produce pod size variations similar to what has been found by this study.

Summer and autumn are expected to represent the main mating period in seasonally calving small delphinids and porpoises based on documented peaks in calving and a gestation period between 9 and < 12 months (LeDuc 2009). Mating has been observed during these months in many cetacea species but, quantitative analyses of seasonal mating peaks are lacking in oceanic cetacea due to the difficulty of collecting such data. Nevertheless, further support of a lack of correlation between mating and group size is summarized below.

Lekking results in synchronous mating and birth across a population (e.g. Clutton-Brock *et al.* 1992) which may not be desirable in oceanic areas without shelter, where calves are exposed to killer whale and shark predators which tend to specialize in prey of a certain type when available in high quantity at certain predictable times (e.g. Norris, Prescott 1961; Ternullo, Black 2002; Barrett-Lennard *et al.* 2005; Laroche *et al.* 2008; Pitman *et al.* 2015). Calves are more vulnerable than adults and are preferentially targeted by oceanic sharks (Chap. 1). Several records indicate that females are targeted by sharks during birth of their young (e.g. Williamson 1963; Best *et al.* 1984; Crovetto *et al.* 1992). Hence synchronous births are expected to reduce rather than increase fitness in the oceanic environment.

Permanent association of males with one or few females for mating purposes seems rare among cetacea (Willis, Dill 2007). Congregations of sperm whales comprise females, their young offspring and additional adult and sub-adult females whereas males occur solitarily or in small bachelor groups depending on their age (Gaskin 1968; Whitehead, Weilgart 2000;

Whitehead 2003). Mature males move between female congregations when both sexes meet in certain areas of intermediate latitude such as the Azores or Galápagos (e.g. Christal, Whitehead 1997; Whitehead 2003). The year-round occurrence of female groups despite latitudinal sex segregation between mature individuals (Whitehead, Weilgart 2000) suggests that grouping is driven by factors other than mating. This is in line with the previously discussed correlation between killer whale predation threat and group size in this species. Social segregation between males and females has also been documented in northern bottlenose whales (Gowans *et al.* 2001, 2008).

In pilot and killer whales both sexes remain associated with their natal groups after reaching sexual maturity (Bigg *et al.* 1990; Oremus *et al.* 2013). However, due to high level of relatedness among these individuals, males and females affiliated to the same congregation are not expected to mate one another. Instead mating seems to take place during temporary associations of several pods and temporary dispersal of males between pods (Pilot *et al.* 2010; Chap. 1), indicating that the formation of groups is not related to mating.

Small delphinids of tropical and sub-tropical waters such as spinner, pantropical spotted, Fraser's and Clymene dolphins, and melon-headed whales tend to reproduce year-round (e.g. Perrin *et al.* 1985; Perryman, Lynn 1993; Ferrero, Walker 1995; Danil, Chivers 2007) and form groups, often of large size throughout the year. Social structure in these species is not well understood and study results found in the literature are controversial (Möller 2012). However, particularly large congregations are often polyspecific. False killer whales, bottlenose, rough-toothed, Atlantic and Pacific white-sided, spinner, pantropical, common dolphins can all be found in mixed-species groups (e.g. Perrin 1969; Leatherwood, Reeves 1983; Scott, Chivers 1990; Au 1991; Hall 1998; Gannier 2000, 2002; Frantzis, Herzing 2002; Shirihai, Jarrett 2006; Oswald *et al.* 2008; Zaeschmar *et al.* 2013, 2014). Melon-headed whales are often associated with Fraser's dolphins. These polyspecific congregations cannot be explained by access to females.

The following points indicate that access to females does not represent an evolutionary driver towards grouping in cetacea beyond male coalitions:

- Lack of group size correlation with expected mating season
- Congregations are formed year-round in at least some species with calving seasonality, including matrilineal groups of sperm whales despite latitudinal sex-segregation among adults of this species throughout part of the year.
- High level of relatedness within groups of pilot and killer whales unless several matrilines associate to form larger congregations.
- Variable patterns in group size variation between months, seasons and years among delphinids of small body size, unrelated to reproduction.
- Cetacea groups are often polyspecific. Especially large congregations frequently contain more than one species.
- Permanent association of males with one or few females for mating purposes seems rare among cetacea. Males typically travel between females or groups of females rather than remaining associated with the same (e.g. Connor *et al.* 2000a; Whitehead 2003; Amano *et al.* 2014).

Conclusions

The outcome of this analysis is summarized in Tab. 21.

Grouping is suggested to increase reproductive efficiency through alloparental care and by increasing male access to females through the formation of small alliances. Groups averaging > 20 individuals are driven by shark predation risk whereas communal prey search, cooperative prey herding, improved navigation accuracy and hydrodynamic efficiency are all

suggested to represent secondary benefits of congregation in cetacea. Killer whale predation risk does not correlate with congregation size.

Alloparental care has been suggested to represent a strong evolutionary driver towards sociality in sperm and pilot whales (e.g. Arnborn, Whitehead 1989; Augusto *et al.* 2017) and may be more common than suggested by the literature due to the difficulty in studying related behaviour in the oceanic environment. The detection of alloparental care requires individual identification of calves and adults and repeated re-sightings of these individuals which is often impossible offshore.

Table 21: Conclusive results

Parameter		Evolution. driver?	Required group size
Reproductive efficiency	access to females (Chap. 1)	yes	< 15
	alloparental care	yes	
Predation risk	calf protection from predators	possibly in some species	the bigger the better
	general protection from predation	yes	
Foraging efficiency	communal prey search	no	the bigger the better
	cooperative prey herding	no	< 20
Other	navigation accuracy	no	the bigger the better
	hydrodynamic efficiency (Chap. 1)	no	few individuals

These results do not exclude the possibility that some large congregations represent a non-adaptive response to a high availability of forage in a certain area as observed in baleen whales at feeding grounds (e.g. Nowacek *et al.* 2011) and in long-finned pilot whales of the Southern Ocean where group size was found to increase with latitude to up to 200 in polar waters (Miyazaki, Kato 1988). Correlations between group size and body size indicate that a small body size facilitates the formation of large congregations whereas a large body size requires a solitary lifestyle. When forage supply is exceptionally high then large species may be encountered in larger pods than usual.

Results further suggest that a large group size is facilitated by:

- availability of large prey patches
- epi-/ and/or mesopelagic foraging
- large home range
- acoustic communication signals of medium range

and is limited by forage supply. Group size limitation by forage in baleen whales further indicated by a positive correlation between pod size and prey shoal size in fin and humpback whales which has been documented off Newfoundland and Labrador (Whitehead, Carlson 1988).

The sperm whale is an exception from the lack of correlation between group size and killer whale predation risk. Sperm whales have been documented to increase group size in response to killer whale attacks such that conspecifics close to a targeted group of sperm whales would join the congregation (Pitman *et al.* 2001). Typically, a rank or rosette formation facilitates protection of vulnerable individuals (App. 4: Tab. 5) and larger groups may be more effective for this type of anti-predator behaviour. Group size in this species is larger in the Pacific where several social units are often observed together compared to the Atlantic where a group most often comprises a single social unit (Whitehead 2003). This variation between ocean basins has been suggested to reflect different levels of predation risk inflicted by killer whales which are caused by cultural foraging-related differences between Atlantic and Pacific

killer whales (Whitehead *et al.* 2012). Whereas sperm whales strongly react to the presence of killer whales in the Pacific, both species seem to ignore one another in the N-Atlantic. Attacks have not been observed in this area in spite of a larger survey effort than in the Pacific and despite killer whale predation on other cetacea species (Whitehead *et al.* 2012). These findings show that killer whale predation risk may have a strong influence on group size in sperm whales. Defending themselves and their young against killer whales may be the primary function of the association of several social units to form larger groups in this species (Whitehead, Weilgart 2000; Pitman *et al.* 2001; Whitehead 2003; Whitehead *et al.* 2012).

The interplay between and variation of the discussed parameters likely causes the high variability in group size observed in oceanic waters. Many taxa use grouping facultatively corresponding to the strength of perceived predation risk, such that congregation is initiated or enhanced in response to heightened threat (Rand 1967; Foster, Treherne 1981; Watt *et al.* 1997; Viscido, Wetthey 2002; Laroche *et al.* 2008). Similar interrelations have been documented in cetacea (e.g. Heithaus, Dill 2002).

The positive correlation between group size and animal density which has also been documented in pelagic fish (Niwa 2004; Hensor *et al.* 2005; Guttal, Couzin 2010) and terrestrial ecosystems (e.g. Dell, Hobday 2008; Cresswell, Quinn 2011) implies further variance in pod size.

Conclusively group size variation is caused by a number of parameters including:

- animal density
- variation in predation risk
- variation in forage supply
- reproductive state
- species
- age
- gender

Results of this study have to be interpreted with care since parts of the analyses are based on few studies and limited data. Whereas body size is a well-known parameter for most species included in this study and sample sizes are high for group size estimates and geographic variations of the same, migration distance, predation risk, shoaling behaviour of meso- and bathypelagic prey species, foraging depth and active space of acoustic signals need further research. Home range size is well known for some species and populations, but recent studies indicate the existence of further unresearched populations which appear to have larger home ranges than their better studied counterparts.

However, considering how little is known about most oceanic cetacea species results of this analysis provide novel insights into congregation and its evolutionary drivers in these marine mammals which will improve the understanding of ecological and behavioural interactions of cetacea with their environment.

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Chapter 4: Tuna-dolphin congregation

Abstract

Tuna-dolphin associations have long been a matter of debate. Predation risk, foraging benefits and the 'meeting point' hypothesis have been suggested to explain these polyspecific congregations, but results of different studies are controversial. This chapter provides a thorough qualitative analysis of the different hypotheses based on a large-scale literature review and includes recent findings such as improved navigation accuracy as a grouping benefit.

Possible evolutionary drivers are systematically analysed based on the comparison of sensory capabilities, predation risk, group structure and diving- and foraging-related behaviour in tuna and dolphins.

Results suggest that the association is driven by mutual anti-predator benefits such that dolphins experience reduced predation risk due to association with a more vulnerable species, and tuna may be attacked less aggressively when in congregation with dolphins compared to monospecific occurrence.

It is further suggested that tuna reduce their risk of predation by supplying potential intra-guild predators such as pelagic sharks and billfish with extra-guild prey by herding and raising patches of small shoaling fish to the surface. Shedding light on animal grouping patterns is an important part of understanding the functioning of the open ocean.

Introduction

In the eastern tropical Pacific yellowfin tuna, *Thunnus albacares*, and predominantly pantropical spotted dolphins, *Stenella attenuata*, but also spinner, *S. longirostris*, and common dolphins, *Delphinus* sp., are frequently encountered in tight polyspecific congregations (e.g. Perrin 1969; Au 1991; Hall 1998). This region is characterized by a thin mixed layer, usually extending less than 60m from the surface down in vast areas (Green 1967), vertically followed by the world's most extensive and most hypoxic oxygen minimum zone (OMZ) (Knauss 1963; Wyrki 1964; Joseph, Greenough 1979; Scott *et al.* 1999; Helly, Levin 2004; Fiedler, Lavín 2006; Fiedler, Talley 2006). The latter consists of cold water, relative to other tropical areas, high salinity and low content of dissolved oxygen (Prince, Goodyear 2006). Suboxic conditions of $< 4.5 \mu\text{mol/kg}$ (0.1 ml/l) (Warren 1995; Morrison *et al.* 1999) prevail in part of the eastern tropical Pacific (Karstensen *et al.* 2008). It has been reasoned that these oceanographic features result in a distinct 'oxythermal floor' of warm and oxygen-rich water with high surface chlorophyll, above the thermocline which concentrates many top- and meso-predators within a vertically narrow corridor, thereby increasing encounter rates between predators and prey (e.g. Prince, Goodyear 2006; Prince *et al.* 2010; Hoolihan *et al.* 2011; Carlisle *et al.* 2016).

Congregation of spotted dolphins and yellowfin tuna is most prevalent in waters characterized by a mixed layer of about 45m depth, and a very low oxygen concentration below (Scott *et al.* 2012). To the west of the eastern tropical Pacific the thermocline deepens to about 150m and the OMZ thins markedly (Knauss 1963; Sprintall, Cronin 2001; Tomczak 2001). Simultaneously tuna-dolphin congregations become uncommon (Scott *et al.* 2012). Consequently, the oceanographic features of the eastern tropical Pacific have been suggested to promote congregation of dolphins and tuna (Green 1967; Perrin *et al.* 1976; Au, Perryman 1985; Au, Pitman 1986; Edwards 1992; Norris *et al.* 1994). A shallow thermocline in combination with a thick OMZ is thought to restrict vertical movements of yellowfin tuna (Cayré 1991; Edwards 1992; Brill 1994; Brill, Lutcavage 2001; Prince, Goodyear 2006) leading to the assimilation of tuna and dolphin habitat, which facilitates congregation. Although tight, these congregations are neither permanent nor obligatory (e.g. Carey, Olson 1982; Scott *et al.* 2012). This is also indicated by a significant proportion of un-associated/school sets on tuna

in the eastern tropical Pacific fishing industry, meaning catches of tuna un-associated with any dolphin species (e.g. Polacheck 1988).

To a smaller extent dolphins and tuna group in tropical waters of the western Indian ocean (De Silva, Boniface 1991; Ballance, Pitman 1998) and the eastern tropical and subtropical Atlantic (e.g. Simmons 1968; Levenez *et al.* 1980; Pereira 1985; Donahue, Edwards 1996). Both areas are characterized by a shallow thermocline and marked OMZ, although not as hypoxic as in the eastern tropical Pacific, and not suboxic (Tomczak 2001; Prince, Goodyear 2006; Prince *et al.* 2010). The OMZ of the eastern Atlantic holds oxygen minimum values of about 17 $\mu\text{mol/kg}$ in the south Atlantic and more than 40 $\mu\text{mol/kg}$ in the north Atlantic (Karstensen *et al.* 2008). According to purse-seine logbooks the frequency of tuna-dolphin associations is low in most areas of the NE-Atlantic and Indian oceans (Escalle *et al.* 2015, 2016).

Associations of spinner and pantropical spotted dolphins and yellowfin tuna around many oceanic islands such as the Maldives (Anderson, Shaan 1999; Anderson 2005), Sri Lanka (De Silva, Boniface 1991; Leatherwood, Reeves 1991; Nanayakkara *et al.* 2014), Fernando de Noronha (Sazima *et al.* 2006; Silva *et al.* 2007), the Azores and surrounding seamounts (Clua, Grosvalet 2001; Silva *et al.* 2002; Morato *et al.* 2008), Hawaii (Shallenberger 1981), the Philippines, Indonesia and New Guinea (Dolar 1994; Hampton, Bailey 1999) are thought to be promoted by a shallow thermocline in the lee of some islands (e.g. McManus *et al.* 2008). Spotted, spinner and common dolphins, and associated tuna, all show a pattern of increasing group size in the morning and throughout the day, and dispersal in the late afternoon or night, although variability in re-grouping and dispersal times is high (Scott, Cattanach 1998). In line with these findings Sharp (1978) found that catches per set of yellowfin tuna were greater in the afternoon than in the morning and fishermen observed yellowfin and skipjack tuna, *Katsuwonus pelamis*, of the eastern tropical Pacific to scatter at dusk and congregate during predawn hours (Scott *et al.* 1999). This pattern may represent a response to prey behaviour, or perceived predation threat, or a combination of both (e.g. Scott, Cattanach 1998; Scott *et al.* 2012). Several theories about the evolutionary driver towards tuna-dolphin association have been brought forward by previous studies but conclusive results remain controversial. Tab. 1 summarizes main studies and reviews on tuna-dolphin congregation together with proposed drivers of the association.

Table 1: Key publications about tuna-dolphin congregation; ETP: trop. E-Pacific

Reference	Species involved in association	Area	Suggested driver
Au, Perryman 1985 Au, Pitman 1986	spinner, pantropical spotted dolphins, yellowfin, skipjack tuna	ETP	tuna raising prey to surface, tuna follows dolphins
Au 1991	spinner, pantropical spotted dolphins, yellowfin tuna, sharks	ETP	foraging-related benefits
Edwards 1992	pantropical spotted dolphins, yellowfin tuna	ETP	no driver identified, hydrodynamics discussed, tuna follows dolphins
Scott, Cattanach 1998	spinner, pantropical spotted, common dolphins, yellowfin tuna	ETP	predation risk, prey distribution
Fréon, Dagorn 2000	associations of fish with objects, mammals, topographic structures	tropics worldwide	no driver identified, meeting point hypothesis
Das <i>et al.</i> 2000	Striped, <i>Stenella coeruleoalba</i> , common dolphin, albacore tuna	Bay of Biscay	possibly foraging related benefits
Clua, Grosvalet 2001	common, Atlantic spotted dolphins, <i>S. frontalis</i> , Bluefin, <i>Thunnus thynnus</i> , yellowfin tuna	Azores	foraging related benefits to tuna

Scott <i>et al.</i> 2012	pantropical spotted dolphins, yellowfin tuna	ETP	not foraging-related, likely driven by predation risk
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The following hypotheses have been derived from both, the results of these previous studies and the identification of possible drivers towards grouping in Chap. 1:

Hypotheses

- Tuna dolphin congregations increase foraging efficiency.
- Mixed grouping of tuna and dolphins yields important anti-predator benefits.
- The association yields improved navigation accuracy.
- The 'meeting point' hypothesis explains tuna-dolphin congregation.

Since tuna-dolphin congregations involve two separate species, reproductive benefits can be excluded as an evolutionary driver. Hydrodynamic reasons can also be excluded since tuna swim deeper in the water column than dolphins. The congregation is consequently vertically assorted by species.

Due to a lack of data, the hypotheses are analysed qualitatively rather than quantitatively based on:

- the comparison of sensory capabilities of tuna and dolphins
- differences in predation risk between affiliated species
- differences in group structure between tuna and dolphins
- the comparison of diving- and foraging-related behaviour of affiliated species

to identify possible benefits to one or both associates.

Based on these analyses, the relevance of possible predation- foraging- and navigation-related advantages of grouping identified in Chap. 1 to tuna-dolphin associations is systematically discussed.

Material and methods

Key publications about tuna-dolphin congregation were identified. Conclusions of these papers about the evolutionary driver of the association are summarized in Tab. 1. Based on both, these conclusions and part 1 of this thesis several hypotheses regarding the main evolutionary driver of tuna-dolphin associations were formulated and facilitating factors of the tuna-dolphin congregation were identified. The hypotheses are systematically discussed based information in the scientific literature about dolphin and tuna foraging, predation threat, distribution, grouping patterns and navigation. Sensory capabilities were compared to identify potential benefits in prey search, navigation accuracy and vigilance efficiency to either species.

Relevant publications were located through ISI Web of Science, Google Scholar, PLOS ONE, BioOne, ScienceDirect, PubMed and JSTOR search engines, references of relevant papers, and articles which have cited the located papers. The following key words have been used for the literature search: tuna dolphin association, purse seine dolphin sets, pantropical spotted dolphin diet, yellowfin stomach content, tuna behaviour, tropical Pacific oceanography, oxygen minimum zone, dolphin sense perception, tuna sense perception, tuna diving, spotted dolphin diving, shark tuna predation, shark dolphin predation and intra-guild predation.

Results

Scott *et al.* (2012) identified two aspects related to the formation of tuna-dolphin associations which are:

- factors facilitating grouping,
- main evolutionary driver(s) of the association.

Facilitation factors are reviewed before possible evolutionary drivers are analysed.

Facilitating factors

For the congregation of tuna and dolphins to develop and last diets, depth preferences, home ranges, or at least day ranges and optimal swim speed of the associated species all have to be similar. The associated species must further be able to find one another. The latter is facilitated by the thin mixed layer which leads to increased encounter rates. The shallow thermocline promotes propagation of dolphin sounds such as jaw pops, breaches and tail slaps, and yellowfin tuna may detect these sounds at distances of several hundred meters to 2km depending on the background noise level (Finneran *et al.* 2000; Schaefer, Oliver 2000). This is consistent with suggested acoustic detection of FAD's by smaller tuna (Babaran *et al.* 2008). Dolphin breaches and jaw pops have a horizontal detection range of 340-840m and 660-1040m. Tail slaps can be detected at distances of 90-180m from the source. The maximum audible range for breaches and jaw pops may be approximately 1600m and 2000m in a quiet environment (Finneran *et al.* 2000).

1. Depth preferences

Yellowfin tuna shoals are typically found near the thermocline during daylight hours which, in the eastern tropical Pacific, corresponds to a depth of 20-60m (Spear *et al.* 2001; Scott *et al.* 2012). Since spinner and common dolphins occur close to the surface during the day (Evans 1974), and pantropical spotted dolphins at a depth of 15-20m below, habitat of the latter matches that of yellowfin tuna the best. In line with these findings spinner dolphins and tuna seem to associate more often in areas where the mixed layer is the shallowest (15-20m) and the oxygen minimum zone underneath is most hypoxic (Scott *et al.* 2012). Common dolphins tend to inhabit cooler, upwelling-modified waters which is thought to cause the generally low encounter rate of yellowfin tuna associated with common dolphins (Au, Perryman 1985; Reilly 1990; Fiedler, Reilly 1994; Reilly, Fiedler 1994; Ballance *et al.* 2006).

2. Home range

Offshore pantropical spotted dolphins occupy vast home ranges, and sometimes travel >100km/day (Leatherwood, Ljungblad 1979; Perrin *et al.* 1979; Scott, Cattnach 1998; Scott, Chivers 2009). For tuna some studies suggest a significant level of site fidelity and long-term association with certain areas or FAD's (e.g. Brill *et al.* 1999; Itano, Holland 2000; Schaefer *et al.* 2007), others found a combination of residency and extended travel (Schaefer *et al.* 2007), with high variations in association strength with FAD's between years (Stehfest *et al.* 2013). Since absolute energy intake increases with body size (Beukema 1968; Allen, Wootton 1984) larger tuna have higher foraging requirements than smaller individuals and are therefore expected to range further to cover these (McNab 1963; Calder 1974; Harestad, Bunnell 1979), by travel between areas where foraging conditions are expected to be beneficial. However, dolphins generally seem to range further than yellowfin tuna, which means that some level of 'compromising' must take place when both species travel in association.

3. Swim speed

Tuna is only found in congregation with marine mammals from a body size of about 55cm onward (Edwards 1992). Smallest tuna congregate around floating objects, medium-sized individuals tend to form free-swimming shoals with conspecifics (e.g. Schaefer *et al.* 2009). Edwards (1992) argued that it would not be energetically efficient for small yellowfin or skipjack tuna to congregate with dolphins as optimal cruising speeds would differ too much between fish and mammals. She found a strong overlap in body size between neonate to first year dolphins and age-III yellowfin tuna, the age class most often associated with dolphins, since

both species grow from about 85cm to 125cm body length during these respective years. This resemblance in body length may imply similar optimum swimming speeds in both species and therefore no additional hydrodynamic costs for the tuna when associated with dolphins (Edwards 1992).

However, even though spotted dolphins maintain a swimming speed which allows calves to remain affiliated with the group, which is below the optimal swimming speed of adult individuals (Perrin *et al.* 1979), the pod is still likely to travel faster than the travel speed of neonates per se. This is due to increased hydrodynamic efficiency in the neonate when swimming close to its mother, as often observed (Weihs 2004; Noren, Edwards 2011; Noren 2008). Hydrodynamic interactions simultaneously increase the calf's and reduce the mother's optimal swimming speeds so that the actual travel velocity is somewhere in between the mother's and the calf's optimum, depending on the position of the calf in relation to its mother (Weihs 2004; Noren, Edwards 2011; Noren 2008). Consequently, optimal swimming speeds of tuna and dolphins do not necessarily match. Differences in morphology and propulsion, relative muscle weight, muscle temperature, and the ratio of white to red muscle tissue (Wardle 1975; Brill, Dizon 1979; Fish 1998; Leavy, Bonner 2009; Yan *et al.* 2013) between tuna and dolphins may also affect swimming speed. Further research is needed to shed light on hydrodynamic aspects of tuna-dolphin associations.

If the association incurs a cost to one species then that species would be expected to benefit from the association in other ways. Therefore, costs of tuna-dolphin congregation can indirectly shed light on the main evolutionary driver of the association and on the question which species follows the other and hence initiates the polyspecific congregation.

4. Diet

Daytime forage of large yellowfin tuna of the tropical E-Pacific primarily consists of shoaling scombrid and nomeid fish (Scott, Cattanch 1998), that of spotted dolphins of vertically migrating cephalopods (in the morning) and epipelagic flying fish, scombrids, nomeids, and crustaceans (Perrin *et al.* 1973; Robertson, Chivers 1997; Scott *et al.* 2012), indicating some prey overlap between the species.

Scott *et al.* (2012) found scombrids, particularly frigate tunas, *Auxis* spp., to dominate the fresh food remains in yellowfin stomachs during the day. Other epipelagic congregations of non-vertically migrating small fish such as the stomiiform *Vinciguerria nimbaria* and the nomeid *Cubiceps pauciradiatus* (bigeye cigarfish) are preyed on when available (Bard, P ezennec 1991; Bard *et al.* 2002; Potier *et al.* 2007). Since small scombrids, clupeids, and carangids have similar oxygen needs as tuna (Roberts 1975, 1978; Brill 1996), habitat compression constrains both predator and prey to near-surface waters (Prince, Goodyear 2006).

Both tuna and dolphins, feed on deep scattering layer associated species at night (Alverson 1963; Perrin *et al.* 1973; Robertson, Chivers 1997).

Diets of albacore tuna, striped and common dolphins which occur in association in the Bay of Biscay (Das *et al.* 2000), were found to be species-differential with fish ranking first in tuna, second in common dolphin and third in striped dolphin prey composition (Hassani *et al.* 1997). In both dolphin species cephalopods represent more important food than fish and the piscivorous proportion of the food intake is almost exclusively comprised of mesopelagic species of the families myctophidae and sternoptychidae in the NE-Atlantic. Albacore feeds primarily on the sternoptychid *Maurollicus muelleri* and to a lesser extent on crustacea (Hassani *et al.* 1997).

Prey overlap is higher between common dolphins and albacore than between striped dolphins and the tuna. Whereas tuna caught out of monospecific shoals, or in congregation with common dolphins had predominantly preyed on fish, stomachs of albacore caught in the same set nets as striped dolphins contain a high portion of squid (Hassani *et al.* 1997). Hence tuna

seem to alter feeding behaviour when associated with striped dolphins. Such 'compromising' indicates that the tuna benefits from the association which leaves two possible explanations:

- the tuna is gaining access to a different but profitable forage or
- the tuna is gaining a benefit different from foraging which is worthwhile altering diet.

Possible evolutionary drivers

Hypothesis 1: Tuna dolphin congregations increase foraging efficiency.

According to Edwards (1992) dolphins would not be able to meet daily energy requirements when relying on tuna for forage due to higher food requirements of the former. He reasoned that dolphins are therefore unlikely to gain a foraging benefit from the polyspecific congregation. For the same reason tuna may benefit by following dolphins since tuna would then be associating with a predator that is searching for the same or similar prey, but which must encounter that prey either more often or in larger patches than required by the tuna (Edwards 1992). Since in oceanic waters prey patches, once found, are typically big enough to provide large predator assemblages with prey (Reilly, Fiedler 1994; Fiedler, Lavín 2006; Fiedler, Talley 2006; Scott *et al.* 2012), the limiting factor is prey encounter rate. This leads to the question whether the association of dolphins and tuna increases prey encounter rate.

Prey encounter rate

Pooling of sensory information can lead to an increase in prey detection and thus encounter rate, particularly in polyspecific associations with differing sensory capabilities between species (Chap. 1).

Tuna strongly react to chemical cues such as odour when searching for prey (Atema *et al.* 1980; Southwood *et al.* 2008) and were suggested to form chemical search images (Atema, Derby 1981). Prey odour is typically used to detect the general direction of food which is then located and caught by visual cues (Atema *et al.* 1980). Olfactory and gustatory cues are known to be used by various fish species to detect prey, conspecifics and predators (Hara 1994). Little is known about chemoreception in dolphins (Kremers *et al.* 2016a,b). Behavioral studies suggest that dolphins are able to detect airborne odours and discriminate between different flavours, but the under-water sense of smell seems reduced (Kremers *et al.* 2016b), indicating that dolphins could potentially benefit from the exploitation of the tuna's chemoreception.

Both species share a well-developed sense of vision, adapted to their respective hunting depths (Southwood *et al.* 2008; Nachtigall 1986; Fasick, Robinson 2016; Kremers *et al.* 2016a). The tuna's highest sensitivity to light is in the violet-blue (426nm) and blue (483nm) range (Loew *et al.* 2002), indicating adaptation to epi- and meso-pelagic depths. A high temporal resolution facilitates detection of fast moving animals in both tuna and dolphins (Nachtigall 1986; Fritsches unpubl., cited in: Southwood *et al.* 2008; Kremers *et al.* 2016a). Visual acuity in dolphins is high (Herman *et al.* 1975), and distance estimation is well developed (Mobley, Helweg 1990). The importance of vision for foraging may be the reason while yellowfin tuna mainly feed during the day, whereas many offshore dolphin species predominantly hunt at night and during twilight hours, using their echolocation system (e.g. Benoit-Bird *et al.* 2004; Benoit-Bird, Au 2009b). Diel vertical migration entails a higher epipelagic prey abundance at night than during the day in oceanic waters.

Tuna respond to sound in the frequency range of 50-1100Hz, with highest sensitivity between 200Hz and 500Hz (Iverson 1967; Southwood *et al.* 2008) and a lowest source level perceived of 83db (re 1 μ bar) at 500Hz (Finneran *et al.* 1999), whereas the dolphins extremely well developed auditory perception covers a much wider frequency range and shows greater acuity. Species of the genus *Stenella* show cutoff frequencies above 120kHz and highest sensitivity around 40kHz (Greenhow 2013; Greenhow *et al.* 2016). The lower hearing threshold is about 1kHz in bottlenose dolphins, *Tursiops truncatus* (Nachtigall *et al.* 2000), and

the lowest source level perceived is -55db (re 1 μ bar) at 50kHz (Johnson 1966). Both thresholds are likely similar in *Stenella* species. Directional hearing is well developed (Kremers *et al.* 2016a). Tuna and dolphins use their passive listening capabilities for prey detection (e.g. Barros 1993; Gannon *et al.* 2005; Ramage-Healey *et al.* 2006), but only dolphins are capable of echolocation. Hence, a potential basis for the association of tuna with dolphin pods is the dolphins' ability to more efficiently locate concentrations of prey, particularly deep scattering layer organisms (Au 1993; Norris *et al.* 1994) by using their bio-sonar system (Moore, Patterson 1983; Moore, Pawloski 1990; Moore *et al.* 2008; Finneran *et al.* 2014), which is highly adapted to foraging needs (e.g. Madsen, Surlykke 2013; Jensen *et al.* 2015).

Vigilance-related differences in sensory capabilities between dolphins and tuna are summarized in Tab. 2.

Table 2: Comparison of relevant sensory capabilities in yellowfin tuna and pantropical spotted dolphins

Sense	Yellowfin tuna	Pantropical spotted dolphin
Olfaction/Chemoreception	well developed; strongly react to chemical cues and components of prey	under-water olfaction reduced, detect airborne odours, discriminate between flavours
Acoustic reception	frequency range: 50-1100Hz highest sensitivity: 200-500Hz lowest source level heard: 83db (re 1 μ bar) at 500Hz	frequency range: ~1-120kHz highest sensitivity: ~ 40-50kHz lowest source level heard: -55db (re 1 μ bar) at 50kHz
Vision	well developed; highest sensitivity to light of violet-blue (426nm) and blue (483nm) range; high temporal resolution	high visual acuity, excellent distance estimation, high temporal resolution

In the eastern tropical Pacific, where the association is strongest, yellowfin tuna are thought to be primarily day-time feeders, while pantropical spotted and spinner dolphins mainly forage at night-time and during twilight hours (Reintjes, King 1953; Alverson 1963; Shomura, Hida 1965; Fitch, Brownell 1968; Perrin *et al.* 1973; Norris, Dohl 1980; Ortega-García *et al.* 1992; Buckley, Miller 1994; Perrin, Hohn 1994; Richard, Barbeau 1994; Roger 1994; Robertson, Chivers 1997; Fiedler *et al.* 1998; Scott, Cattnach 1998; Galván-Magaña 1999; Román-Reyes 2005; Scott *et al.* 2012; Silva *et al.* 2016). Stomach fullness in both dolphin species was found to be high in the morning but then sharply declines between noon and 1pm, with close to zero full stomachs in the afternoon (Scott, Cattnach 1998). Hence feeding times of pantropical spotted and spinner dolphins do not match the afternoon peaks in group size found in tuna-dolphin congregations (Scott, Cattnach 1998), and only partly overlap with those of tuna.

Schaefer *et al.* (2007) found that yellowfin tuna encounter sufficient forage within the mixed layer when utilizing habitats close to the coast or islands where the thermocline is at a depth of about 100m, but in the offshore eastern tropical Pacific where the mixed layer is narrower than 100m concentrations of forage are far less abundant during the day (Blackburn *et al.* 1970; Petitgas, Levenez 1996; Haugland, Misund 2004; Olsen *et al.* 2007). The authors therefore hypothesize that yellowfin tuna forage on organisms of the deep scattering layers at night above the thermocline and during the day below thermocline. Tuna seem to utilize deep water and engage in night-time foraging when necessary to meet energy requirements but predominantly feed above the thermocline and during the day when sufficient forage is available within the mixed layer. Vice versa dolphins have been documented to forage in association with tuna by several studies (Reilly 1990; Sazima *et al.* 2006; Nanayakkara *et al.* 2014) and seem to engage in day-time feeding opportunistically.

The exploitation of the dolphins' superior prey search capabilities has been documented in other species, including seabirds which follow pods of varying species of small odontoceti (e.g. Evans 1982; Au, Pitman 1986; Martin 1986; Pitman, Balance 1992; Pitman 1993; Clua,

Grosvalet 2001; Hebshi *et al.* 2008; Vaughn *et al.* 2008; Degradi *et al.* 2013), and California sea lions, *Zalophus californianus*. In Santa Monica Bay, California, the latter were found in association with bottlenose dolphins in 18.6% of 201 sightings, including in- and offshore waters, and with common dolphins in 45.9% of 98 sightings exclusively in offshore areas (Bearzi 2006; see also: Shane 1994). The sea lions initiate and end the polyspecific congregation and spend a significant amount of time following and feeding with the dolphins. Sea lions join dolphins during traveling, exploit the same food source when associated with the odontocetes and split from the latter immediately after feeding, indicating that the pinnipeds take advantage of the dolphins' prey detection abilities.

Access to forage

In the eastern tropical Pacific, yellowfin tuna have been documented driving prey toward the surface, thereby facilitating surface feeding in other species such as dolphins, seabirds and sharks which have been observed to feeding on the same prey patch (Au, Perryman 1985; Au, Pitman 1986). The authors therefore suggest that the tuna's ability to drive prey to the surface may entail a foraging benefit to dolphins (Au, Pitman 1986, 1988). In line with this conclusion telemetry studies revealed that yellowfin tuna spend most of their time above the thermocline but undertake occasional dives below, sometimes in access to 150m in various parts of the tropical E-Pacific (Carey, Olson 1982; Holland *et al.* 1990; Block *et al.* 1997; Brill *et al.* 1999; Schaefer *et al.* 2007).

In line with Au, Pitman (1986, 1988) tropical seabirds, which depend on sub-surface predators driving prey toward the surface and thereby in an accessible depth range (Erdman 1967; Colblentz 1985; Harrison *et al.* 1991; Spear *et al.* 2001; Jaquemet *et al.* 2004; Hebshi *et al.* 2008; Goyert *et al.* 2014; Miller *et al.* 2018), especially during day-time hours, are predominantly associated with those dolphin species that in turn associate with tuna in the eastern tropical Pacific (Au, Pitman 1986), suggesting that tuna provide foraging opportunities (Jaquemet *et al.* 2004; Hebshi *et al.* 2008). For the same reason seabird flocks are thought to associate with tuna shoals around the Christmas Islands and in the Mozambique Channel, both Indian Ocean (Ashmole, Ashmole 1967; Weimerskirch *et al.* 2004). Tunas, particularly skipjack and yellowfin, are believed to be the most important sub-surface predators to provide seabirds with forage in tropical and sub-tropical waters (Ashmole, Ashmole 1967; Harrison, Seki 1987; Au, Pitman 1988; Ballance, Pitman 1999; Weimerskirch *et al.* 2004). These are also the predominant tuna species found in congregation with dolphins.

Hypothesis 2: Grouping of tuna and dolphins yields anti-predator benefits.

A number of oceanic shark and billfish species prey on both, tuna and dolphins (Leatherwood *et al.* 1973; Scott, Cattanch 1998; Galván-Magaña 1999; Heithaus 2001; Maldini 2003; Santos-Monteiro *et al.* 2006; Bocanegra-Castillo 2007; Felando, Medina 2011; Hunsicker *et al.* 2012). Hence several potential predators are shared within the congregation (Scott, Cattanch 1998).

Dolphins experience predation threat predominantly from large pelagic sharks including great white, bluntnose sixgill, *Hexanchus griseus*, broadnose sevengill, *Notorynchus cepedianus*, and sleeper sharks and to a lesser extent tiger, *Galeocerdo cuvier*, shortfin mako, *Isurus oxyrinchus*, oceanic whitetip, *Carcharhinus longimanus*, and dusky, *C. obscurus*, sharks (Chap. 2) of which white, sevengill, shortfin mako, oceanic whitetip, tiger and dusky sharks occur in areas of extended oxygen minimum zones.

Yellowfin and skipjack tuna are preyed upon by both billfish and sharks to an extent that Hunsicker *et al.* (2012) suggested to categorize these species as meso- rather than top-predators in the eastern tropical Pacific. Pelagic sharks are abundant in this area and are often caught in association with tuna (Strasburg 1958; Au 1991; Arenas *et al.* 1992; Román-Verdesoto, Orozco-Zöllner 2005; Hall, Roman 2013), particularly silky, *Carcharhinus falciformis*, and oceanic whitetip sharks (Au 1991; Román-Verdesoto, Orozco-Zöllner 2005; Bonfil 2008; Hall, Roman 2013; Duffy *et al.* 2015). Marlins and sailfish, *Istiophorus* sp., are

also incidentally taken during tuna purse-seine fishing operations and hence seem to follow tuna shoals, but in lower numbers than sharks (Hall, Roman 2013).

Skipjack and yellowfin tuna have been documented in stomachs of shortfin mako (Lopez *et al.* 2009; Horn *et al.* 2013), blue, *Prionace glauca* (Lopez *et al.* 2010; Preti *et al.* 2012), hammerhead, *Sphyrna* sp. (Hunsicker *et al.* 2012) and tiger (Dicken *et al.* 2017) sharks, swordfish, *Xiphias gladius* (Gorni *et al.* 2012), sailfish (Hunsicker *et al.* 2012; Tsai *et al.* 2015) and blue marlin, *Makaira nigricans* (Brock 1984; Shimose *et al.* 2006; Vaske *et al.* 2011). Among scombrids which account for more than 50% of silky shark diet, skipjack and yellowfin tuna were found to be the dominant species preyed upon (Hunsicker *et al.* 2012; Duffy *et al.* 2015), whereas dolphins were not found in the stomachs of these predators (Cabrera-Chávez-Costa *et al.* 2010; Duffy *et al.* 2015; Varghese *et al.* 2016; Filmlalter *et al.* 2017; Flores-Martínez *et al.* 2017).

Oceanic whitetip sharks seem to predominantly prey on squid in some areas (Madigan *et al.* 2015; Howey *et al.* 2016) but were suggested to prefer scombrids, including tuna when available (Bullis 1955; Backus *et al.* 1956; Madigan *et al.* 2015). Several studies found that scombrids account for a major portion of oceanic whitetip shark diet (Backus *et al.* 1956; Bullis 1961; Compagno 1984; Cortés 1999), whereas marine mammals account for only about 4% of the food intake (Cortés 1999; see also: Stevens 1984).

Hence, sharks and billfish are thought to have the potential to play an important role in regulating tuna populations (Hunsicker *et al.* 2012) and may therefore constitute a driving force for selection pressure towards avoidance of predation. Predation pressure by sharks on delphinids is comparatively lower and limited to fewer shark species. Whereas tuna represent a common food source for several pelagic shark and billfish species, dolphins are taken rather opportunistically when individuals stray from their group or when a calf becomes separated from its mother (e.g. Cockcroft *et al.* 1989; Mann, Barnett 1999; Mann, Watson-Capps 2005; Gibson 2006, Chap. 2). Conclusively these results show that tuna are more vulnerable to predation than dolphins and would therefore benefit more from a reduction in predation risk.

The oceanic conditions in the eastern tropical Pacific lead to increased encounter rates between sharks, billfish and tuna since all depend on warm oxygen-rich water to meet their physiological demands (Holland *et al.* 1990; Holts, Bedford 1990; Block *et al.* 1992; Brill *et al.* 1993; Pepperell, Davis 1999; Graves *et al.* 2002; Gunn *et al.* 2003; Kerstetter *et al.* 2003; Prince, Goodyear 2006; Dutton 2010) and are therefore restricted to the narrow mixed layer (Prince, Goodyear 2006; Stramma *et al.* 2012). Improved detection of tuna by visually hunting predators (Braun *et al.* 2015) compared to the greater depths at which tuna occur in other areas, further increases predation risk.

Vigilance efficiency

Just as the pooling of information and complementation of differing sensory systems in polyspecific groups can increase prey search efficiency, it can also improve predator detection (e.g. Diamond 1981; Heymann, Buchanan-Smith 2000). Since the affiliated species are not trying to find, but rather attempting to avoid predators inter-individual distances should be small particularly when perceived predation risk is high, yet individuals should be staggered in a way which allows vigilant behaviour (Abrahams, Colgan 1985) and peripheral individuals are expected to regularly scan the environment for predators.

Since sensory systems differ between tuna and dolphins as described above (see: prey encounter rate), improved predator detection when traveling in association is conceivable as long as the affiliated species share their information which requires some form of signalling or eavesdropping on predation threat related cues. Scott *et al.* (2012) suggested that both species may benefit from the association by monitoring each other's alarm responses. This form of mutualism has previously been described for terrestrial polyspecific congregations

involving birds (e.g. Goodale, Kotagama 2005, 2008) and mammals (e.g. McKee Shriener 1998; Trefry, Hik 2009; Makenbach *et al.* 2013).

Dolphins have been anecdotally reported to signal predator detection by alarm calls, but little is known about vocalization and signalling in tuna and other pelagic fish. Bigeyes, *Pempheris adspersa*, a nocturnal planktivorous reef fish emit contact calls which facilitate the maintenance of group cohesion (van Oosterom *et al.* 2016). Alarm calls or acoustic cues which could be used by other individuals as indicators of increased predation risk have also been documented in teleosts. Longspine squirrelfish, *Holocentrus rufus*, emit short sounds and grunts in response to predator detection (Winn *et al.* 1964) and west African bichir, *Polypterus retropinnis*, emit a moaning sound when frightened (Ladich, Tadler 1988). Tuna seem to vocalize but the function of these sounds is not known (Kuznetsov 1975; Allen, Demer 2003). However, signalling does not need to involve sound. A sudden reduction in inter-individual distance, the most common response to predation threat in fish and delphinids (e.g. McBride, Hebb 1948; Norris, Dohl 1980a; Pitcher, Parrish 1993; Tsagarakis *et al.* 2012), may be sufficient as an indicator of predator detection.

Hypothesis 3: The association yields improved navigation accuracy.

Consensus decision-making in animal groups can significantly improve navigation accuracy regardless of the navigational abilities of its members (Biro *et al.* 2006; Torney *et al.* 2009; Flack *et al.* 2013; Berdahl *et al.* 2013; Mueller *et al.* 2013; Codling, Bode 2014; De Luca *et al.* 2014; Irisson *et al.* 2015; Berdahl *et al.* 2016). Positive correlation between navigation accuracy and group size (Chap. 1) may explain the formation of groups containing hundreds or thousands of individuals.

Socially structured groups yield a higher level of improvement in navigation accuracy than a homogeneous network (Chap. 1). There is evidence that both, yellowfin tuna shoals and pantropical spotted dolphin pods show a non-random group composition and a certain level of stability. Klimley, Holloway (1999) suggested active shoal mate choice in yellowfin tuna, based on a significant co-occurrence of particular individuals in the FAD array around Oahu, Hawaii. Some tagged individuals returned simultaneously to the FAD of tagging, up to 5 months after their departure.

Cooperation such as in herding of shoaling prey was suggested to facilitate the formation of long-term bonds in offshore odontoceti species, including dolphins (Gowans *et al.* 2008). On the other hand, pods of pelagic spotted dolphins seem highly dynamic in nature, with changing size and membership over the course of a day (Scott, Cattanach 1998; Chivers, Scott 2002). However, increasing evidence suggests that large pods of odontoceti, including pantropical spotted dolphins, consist of subgroups (Goodall *et al.* 1988; Gowans *et al.* 2008; Pérez-Álvarez *et al.* 2007; Würsig, Würsig 2010; Lima *et al.* 2012; Sucunza *et al.* 2015) which show a higher level of stability (Norris, Dohl 1980; Scott, Perryman 1991; Pryor, Shallenberger 1995; Baird *et al.* 2008). In bottlenose, rough-toothed and southern right whale dolphins, *Lissodelphis peronii*, of different deep-water environments leader-follower relationships have been documented (Rose, Payne 1991; Lusseau 2003, 2007; Lusseau, Conradt 2009; De Boer 2010). These group patterns indicate a base for improved navigation accuracy by congregation in both, tuna and dolphins.

Comparison of navigation-related sensory capabilities (Tab. 3) reveals that mechano- and thermoreception are well developed in both, dolphins and tuna but whereas tuna and pelagic fish in general possess a more acute sense of olfaction and chemoreception than dolphins (Atema *et al.* 1980; Kobayashi, Fujiwara 1987; Hara 1994; Hirvonen *et al.* 2000; Døving, Stabell 2003), dolphins have superior hearing capabilities which can aid in the detection of fish spawning aggregations or feeding aggregations of other cetacea (e.g. Putland *et al.* 2016; Wang *et al.* 2016, Tab. 2). These differences can form a base for mutual exchange of sensory information. The simultaneous use of several senses to successfully navigate during migration

and other large-scale movements has been suggested for birds (Able, Able 1996; Muheim *et al.* 2006; Nevitt, Bonadonna 2005) and marine pelagic migrants (Costa *et al.* 2012).

Table 3: Further comparison of sensory capabilities in yellowfin tuna and pantropical spotted dolphins

Sense	Yellowfin tuna	Pantropical spotted dolphin
Magnetoreception	discriminate between altered and normal, magnetic fields	indicated, but primary magnetoreceptors not identified
	use of magnetoreception for navigation unclear in both species	
Somatosensory perception incl. thermo- and mechanoreception	thermo- and mechanoreception well developed; lower pressure threshold: 10mg/mm ²	thermo- and mechanoreception well developed, skipjack tuna perceive temp. changes of 1°C

Even though yellowfin tuna of different age classes navigate precisely between FADs that are up to 18km apart (Brill *et al.* 1999), little is known about long-distance navigational mechanisms and skills. A study by Willis *et al.* (2009) suggested a navigational function of spike dives in southern bluefin tuna, *Thunnus maccoyii*. These dives have a characteristic shape, last from 16min to > 1h, and can exceed 500m in depth when not limited by seafloor relief, and are typically carried out during dusk and dawn. The authors suggest that tuna may use polarized light cues in a similar way to birds to obtain true geographic reference information and calibrate one or more other compasses. These dives could also provide magnetic cues, information about temperature stratification, or bathymetric cues related to navigation. The rapid descent and ascent of these dives may provide the tuna with a direct vertical profile of one or more environmental variables. Yellowfin tuna were also documented to engage in occasional deep dives, sometimes in excess of 1000m, in the eastern tropical Pacific (Fink, Bayliff 1970; Bayliff, Rothschild 1974; Bayliff 1979, 1984; Schaefer *et al.* 2007) and the Indian Ocean (Dagorn *et al.* 2006). None of the dolphin species which associate with tuna seem able to dive to such depths and, hence, could potentially benefit from the use of additional navigational cues when affiliated to a tuna shoal. Maximum dive depths recorded are 213m for pantropical spotted dolphins (Baird *et al.* 2001) and 257m in common dolphins (Evans 1994).

Hypothesis 4: ‘Meeting point’ hypothesis

The ‘meeting point’ hypothesis states that floatsam, large animals such as whale sharks, *Rhincodon typus*, and baleen whales, and fish-aggregating devices (FAD’s) may serve as a cue that allows tuna and other species to congregate and has been suggested to explain the shoaling behaviour of pelagic tunas (Fréon, Misund 1999; Fréon, Dagorn 2000). Scott *et al.* (2012) proposed to extend this hypothesis to mobile dolphin pods as an explanation for the association between both taxa. However, this hypothesis neither explains why there is a selection pressure towards congregation nor why tuna-dolphin congregations are only encountered in few areas. Since this analysis is approaching congregation from an evolutionary perspective the ‘meeting point’ hypothesis is not discussed further.

Discussion

Hypothesis 1: Tuna dolphin congregations increase foraging efficiency.

Prey encounter rate

Even though tuna are endowed with better developed chemoreception, chemical cues can only be detected downstream of their source, whereas echolocation is useful in all directions. Furthermore, the thermocline serves as a barrier for chemical substances, preventing the detection of mesopelagic prey. Echolocation sounds, too, are attenuated or blocked by this horizontal front but, due to the narrow mixed layer, even shallow dives surmount this barrier and facilitate downward echolocation. Tuna on the other hand, would have to be at the same depth as their prey to detect chemical cues unless there is an upward moving current. Sojourn

below the thermocline for an extended period of time is prevented by the low oxygen content and temperature of the water in the eastern tropical Pacific.

The same conditions also limit the daytime depth of vertically migrating meso-mesopelagic prey (Wishner *et al.* 1998; Fernández-Álamo, Färber-Lorda 2006; Koslow *et al.* 2011; Bianchi *et al.* 2013), potentially placing the same within the range of the dolphin's echolocation system. The comparison of daytime diving depth of tagged individuals with the depth of the thermocline reveals whether or not dolphins regularly briefly break through this barrier. Tagging studies in pantropical spotted dolphins have not detected dives below 30m and hence below the thermocline during the day (Chivers, Scott 2002). Rather, pantropical spotted dolphins remain within the mixed layer (e.g. Silva *et al.* 2016) and seem to predominantly engage in travel as indicated by their tracks which often contain segments of directional swimming for long periods of time (Leatherwood, Ljungblad 1979; Perrin *et al.* 1979; Scott, Chivers 2009).

It is perceivable that dolphins and tuna both benefit from the association, if the former acoustically locate prey at greater depth and the tuna then drive that prey toward the surface. This would imply that the dolphins would have to signal the discovery of a prey patch and thereby prompt the tuna to dive for the prey. Signalling a change from one behavioural state to another has been observed in pods of bottlenose (Lusseau 2003, 2007) and southern right whale dolphins (Rose, Payne 1991), and initiation of a course direction by tail-slapping of few individuals has been documented in rough-toothed dolphins, *Steno bredanensis* (De Boer 2010). Such a communication between tuna and dolphin seems sophisticated. However, complex cooperative feeding techniques involving signalling within and between species have been documented for several fish species (Arnegard, Carlson 2005; Bshary *et al.* 2006; Strübin *et al.* 2011; Lönnstedt *et al.* 2014; Vail *et al.* 2014), showing the capability for advanced collaboration. Since OMZ waters are known to reduce the daytime depth of diel vertical migration species (Wishner *et al.* 1998; Fernández-Álamo, Färber-Lorda 2006; Koslow *et al.* 2011; Bianchi *et al.* 2013), including such as myctophid fish (Maas *et al.* 2014), an important prey item in pantropical spotted dolphins (e.g. Robertson, Chivers 1997, Wang *et al.* 2003), such mesopelagic prey patches may be within echolocation range of the dolphins and high enough in the water column for tuna to drive food patches toward the surface. More research is needed on the use of signals in dolphins and tuna when associated.

If prey search efficiency is to be maximized dolphins and tuna should be spaced according to their forage detection ranges such that the inter-individual distance is larger than the detection range for searched prey so as to minimize overlap in scanned volumes of water between neighbouring animals. A threshold detection range of 113m was measured for a bottlenose dolphin locating a 7.62cm-diameter water-filled stainless steel sphere (target strength of -28dB) when exposed to snapping shrimp noise in Kaneohe Bay, Oahu, Hawaii (Au, Snyder 1980). In both, the same area and species the 50% correct detection threshold for a 2.54cm solid steel sphere was measured to equal 74m (target strength of -42dB) (Murchison 1980). Thomas, Turl (1990) measured a target detection threshold range of 119m for a false killer whale, *Pseudorca crassidens*, locating a 7.62cm diameter water-filled stainless steel sphere. The maximum and minimum distances to which bottlenose dolphins are able to detect a cod in a noise-limited environment was calculated to be 93m and 70m, respectively, and increases to 173m and 107m in a quiet setting (Au *et al.* 2007). Consequently, dolphins should be positioned ≥ 100 m apart in order to maximize prey search efficiency, considering the typically low background noise in open tropical oceans. Since prey patches are often large and are therefore expected to be detected easier than single prey individuals, the optimal inter-individual distance may be even larger. Such large inter-individual distances have not been observed at day-time when the tuna-dolphin association is strongest.

Conclusively, the apparent lack of day-time dives below the thermocline in pantropical spotted dolphins, varying feeding times between tuna and dolphins and inter-individual distances far below the expected optimum for prey search all indicate that tuna-dolphin congregations are not driven by communal prey search. However, the superior prey detection capabilities of

dolphins due to their echolocation system provides an important benefit to these marine mammals and tuna are known to find less forage in oceanic than in coastal waters. It cannot be excluded that some form of signalling and cooperation has developed between the associated species for example if only certain individuals dive below the thermocline to scan for prey patches and such individuals have not been tagged.

Access to forage

It seems logic that raising prey patches from deep water would be costlier for dolphins than for tuna since dolphins would have to commute between the surface and depth to breath until the prey ball has been raised sufficiently due to their limited dive durations (\bar{x} : 1.5-1.9min, Scott, Chivers 2009; Silva *et al.* 2016). However, this suggestion is in disagreement with the night-time feeding behaviour in pantropical spotted dolphins. Fishermen of the tropical E-Pacific (cited in: Donahue, Edwards 1996) observed pantropical spotted dolphins to remain at the periphery of the association apparently not foraging, while tuna were feeding during the day. Au, Pitman (1986) on the other hand reported tuna and dolphins feeding together on the same prey patches at day time. Hence it cannot be excluded that pantropical spotted dolphins may benefit from day-time feeding opportunities, but it is unlikely that this advantage represents a main driver for the tuna-dolphin association.

Hypothesis 2: Grouping of tuna and dolphins yields anti-predator benefits.

Vigilance efficiency

Since dolphins are most vulnerable to shark attacks from behind and below (Arnold 1972; Ainley *et al.* 1985; Cockcroft *et al.* 1989; Mead, Potter 1990; Scott, Cattanach 1998), any alarm responses by deeper swimming tuna could reduce predation. However, it seems unlikely that tuna gain a benefit from improved detection of sharks by association with dolphins since sharks are believed to attack tuna by ambush from below, too (Bullis 1961; Myrberg 1987), and tuna swim deeper in the water column than dolphins. Hence the more vulnerable species is more exposed to predation by sharks. The omnipresence of silky and oceanic whitetip sharks around tuna shoals seems to deem alarm calls to these species futile.

Billfish have not been reported to preferentially attack from below (Domenici *et al.* 2014) and tuna could potentially benefit from improved detection of these predators by the dolphins' echolocation system, if dolphins signal in response to approaching istiophorids. However, since these predators follow tuna-dolphin congregations, too, predation threat seems ubiquitous.

General anti-predator grouping benefits

Given the conspicuous behaviour of large dolphin congregations, particularly in tropical and subtropical areas (Oswald *et al.* 2008, Chap. 3) it is unlikely that encounter dilution plays a significant role in reducing predation threat of dolphins or tuna when associated. Encounter rates with sharks and billfish are high especially under OMZ conditions.

The most obvious anti-predator benefit from association of dolphins and tuna seems to be the dilution effect which is the stronger the more individuals are affiliated to a group. However, if sharks or billfish preferentially attack tuna then the dilution effect for tuna associated with dolphins would be as high or as low as for tuna affiliated to a monospecific shoal. Dolphins would not dilute the tuna's risk of falling prey to these predators by dilution (Beauchamp, Ruxton 2008; Lima, Bednekoff 2011; Schmitt *et al.* 2014).

Vice versa the less vulnerable species (dolphins) may benefit from congregation with a more vulnerable species (tuna) (Sinclair 1985; FitzGibbon 1990; Mathis, Chivers 2003) since sharks and billfish are likely to target the latter when presented with the choice between both types of prey but may attack dolphins when tuna are not available.

Dolphins and tuna are phenotypically different leading to oddity. However, a positive correlation between the number of dolphins and the number of tunas affiliated to a congregation indicates a consistent ratio of both species (Au, Pitman 1986, 1988; Scott, Cattanach 1998; Perkins, Edwards 1999) under which conditions oddity is negligible (Landeau, Terborgh 1986). Hence, both species may benefit from predator confusion. Since both, tuna and dolphins form large groups in areas of extended OMZ's (Scott *et al.* 2012; Chap. 3) it is questionable though whether or not the confusion effect is higher in associations of both species than in monospecific groups. Research of the effect of group size on predator confusion and oddity has produced controversial results (e.g. Krakauer 1995 versus Ruxton *et al.* 2007).

Predator swamping likely reduces predation risk in large congregations of tuna and dolphins but, as discussed before for the dilution effect, would not be different between monospecific and polyspecific groups if tuna are taken preferentially.

Conclusively, dolphins are suggested to gain a survival benefit by associating with a more vulnerable species. Tuna are unlikely to increase their fitness through any of the discussed parameters.

Reducing intra-guild predation by providing extra-guild prey to potential intra-guild predators?

Several pelagic shark and istiophorid species, including blue, silky and shortfin mako sharks, swordfish, blue and striped marlin, *Kajikia audax*, feed on a large variety of prey of various size, including small shoaling fish and squid as well as larger intra-guild (IG) prey such as tuna or marine mammals (Clarke *et al.* 1996; McCord, Campana 2003; Shimose *et al.* 2006; Vaske *et al.* 2009; Lopez *et al.* 2009, 2010; Ferretti *et al.* 2010; Abitia-Cárdenas *et al.* 2011, 2012; Gorni *et al.* 2012; Preti *et al.* 2012; Duffy *et al.* 2015).

IG-prey typically shows avoidance behaviour towards IG-predators (Heithaus 2001; Janssen *et al.* 2007; Choh *et al.* 2010) through the use of areas where IG-predators are rare (e.g. Major, Sherburne 1987; Theberge, Wedeles 1989; Durant 1998; Sergio *et al.* 2003; Choh *et al.* 2010), or by occupying habitat with structural complexity, which provides means to escape or to avoid detection (Janssen *et al.* 2007), or by temporally avoiding IG-predators when they are most active (e.g. Arjo, Pletscher 1999). In the tropical E-Pacific with its extensive OMZ none of these mechanisms are applicable.

However, when extra-guild (EG) prey is plentiful then IG-predation is expected to be reduced because the IG-predator's energy needs are met with EG-prey which is typically of higher profitability with regard to the ratio of energy content to handling time or risk of injury, than IG-prey (e.g. Charnov 1976; Schausberger, Croft 2000; Matsumura *et al.* 2004; Kagata, Katayama 2006; Provost *et al.* 2006). Although the nutrient composition of IG-prey per se can be favourable (Denno, Fagan 2003; Matsumura *et al.* 2004), capturing, subduing and killing the same may be energetically costly. Hence EG-prey is expected to be used when available, but predators may switch to IG-prey when necessary to meet energy demands. Such a negative correlation between IG-predation and density or availability of EG-prey has been found across a large variety of taxa and ecosystems (Crombie 1943; Ulyette 1950; Kruuk 1972; Schaller 1972; Eaton 1979; Lonsdale *et al.* 1979; Turner 1983; Yen 1983; Mabelis 1984; Polis, McCormick 1987; for review: Polis *et al.* 1989).

It then follows that tuna could reduce their risk of IG-predation by providing EG-prey to potential IG-predators such as sharks and billfish following the congregation. Such a scenario would lead to a:

- short-term decrease in predation threat during and after the feeding event. If IG-predators, which represent a threat through asymmetric IG-predation when food-deprived, tend to

stay in loose association with their potential IG-prey after a feeding event, then the latter experience reduced predation threat subsequent to the feeding event for the time period of reduced hunger level in potential IG-predators.

- long-term decrease in predation threat. As long as the assemblage persists, and prey encounter rates and patch size are sufficient to meet energy demands of the affiliated individuals, tuna and dolphins experience reduced IG-predation threat as sharks and billfish prey on small pelagic shoaling fish and squid instead of members of the tuna-dolphin congregation. Consequently, tuna and marine mammals affiliated to the conjoint assemblage benefit from sharing encountered prey patches with those predators which would otherwise represent an asymmetric IG-predation threat.

IG-predation risk increases when insufficient EG-prey is encountered and when IG-predators have previously eaten IG-prey (Magalhães *et al.* 2004). Thus, behaviour patterns which lead to a consistent supply of EG-prey to potential IG-predators should be selected for, particularly in tuna due to the higher vulnerability to predation.

Hence tuna are suggested to reduce their predation risk by increasing the access of IG-predators to EG-prey through raising patches of shoaling prey to the surface. Every EG-feeding event reduces the risk of IG-predation and hence the tuna's predation risk. As the hunger level of the assemblage rises tuna predation threat increases and sharks or billfish will either switch to IG-prey or the supply of EG-prey will again reduce the tuna's predation risk (Fig. 1). The purpose of the tuna-dolphin association would then be to maintain the small loop illustrated in Fig.1, and to avoid the big loop.

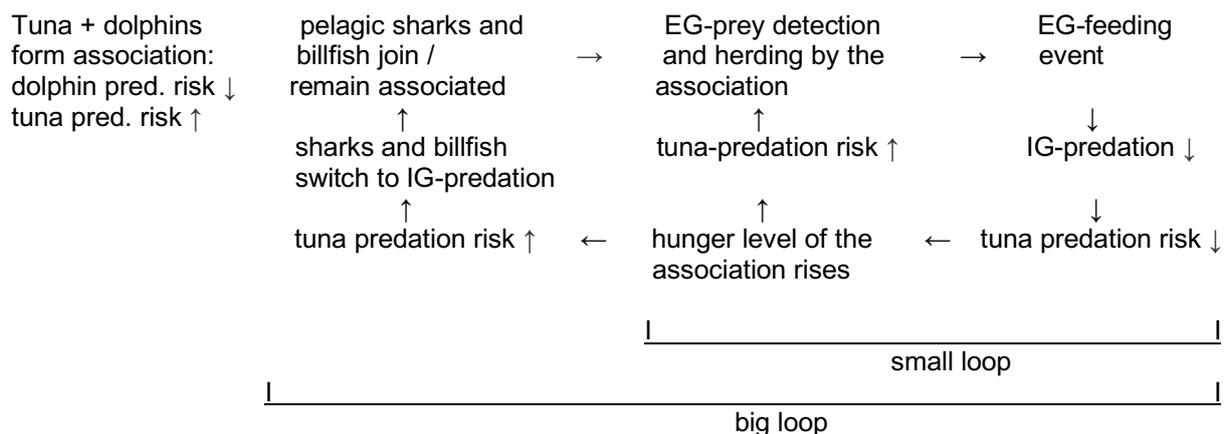


Figure 1: The tuna-dolphin association is thought to reduce the dolphins' predation risk and tends to switch the tuna's situation from the big loop toward the small loop, thereby keeping the tuna's predation risk lower than it is in un-associated shoals.

The strength of the association between tuna and dolphins indicates a mutual relationship. Tuna were documented to follow the dolphins when the latter are chased by fishermen (Au, Pitman 1986) and have been suggested to 'home in' on dolphins, thereby initiating the association (Finneran *et al.* 2000). It is conceivable that the dolphins' echolocation system, the most prominent difference in sensory capabilities between dolphins and tuna, increases prey detection and thereby facilitates a more consistent supply of EG-prey. However, the fact that pantropical spotted dolphins do not seem to dive below the thermocline during the day (Chivers, Scott 2002) contradicts this hypothesis.

Pods of small delphinids including common, Clymene, *Stenella clymene*, and Atlantic spotted dolphins have been observed fending off sharks communally (AIBS 1967; Springer 1967; Herzing 2011) and it seems logical that sharks approach groups of dolphins less aggressively than they interact with monospecific tuna shoals. Sharks predominantly attack cetacea in vulnerable situations such as during birth or when individuals become entangled in fishing

gear or when calves stray from their group (Chap. 2), whereas tuna are preyed on heavily by several species as discussed before. Hence, rather than attacking the group of dolphins and tuna sharks as they would for monospecific tuna shoals they follow the association waiting for individuals to become separated. This would explain why tuna follow dolphins even when the latter are chased by fishermen.

Tunas may benefit by the enlargement of the group when joining dolphins if sharks or billfish avoid attacking large congregations. Such an interrelation has been found in the terrestrial environment. Thomson's gazelles, *Gazella thomsoni*, in mixed and therefore larger groups with Grant's gazelles, *G. granti*, are less vulnerable to predation by cheetahs, *Acinonyx jubatus*, than when associated in monospecific congregations, as cheetahs tend to avoid targeting large groups which entail improved predator detection, and a lower attack success rate for the predator (FitzGibbon 1990).

In line with this theory tuna and dolphins dissolve their association and spread out to feed at night when EG-prey is available in epipelagic waters and hence predation risk is low. In deep water off the Bahamas Atlantic spotted dolphins of all age classes including new-borns were found to feed on vertically migrating prey affiliated to deep-scattering layers in the presence of tiger sharks at night, even though tiger shark attacks on the same species have been reported during the day in shallow waters which are thought to be used as a refuge to reduce predation risk (Herzing, Elliser 2014). Hence the availability of EG-prey seems to reduce predation risk in dolphins.

By association with a tuna-dolphin congregation sharks and billfish benefit from increased consistency in food supply by taking advantage of both species' capabilities in finding, raising and herding EG-prey, and the constant presence of tuna and dolphins as potential IG-prey. Since large pelagic sharks, including sixgill and oceanic whitetip sharks, occasionally prey on istiophorids (e.g. Jolley, Irby 1979; Compagno 1984; Ebert 1990) billfish may, like dolphins, further benefit from associating with tuna by grouping with a more vulnerable species, thereby reducing their own risk of predation by sharks.

Avoidance of potential IG-predators by IG-prey was found to decrease with increasing density of EG-prey due to both, reduced IG-predation risk and reduced IG-competition (St-Pierre *et al.* 2006; Grassel *et al.* 2015). The eastern tropical Pacific is not only characterized by high encounter rates with various pelagic sharks and billfish species but is also a productive area due to the influence of upwelling, and therefore provides large patches of vertically migrating shoaling prey (Reilly, Fiedler 1994; Fiedler, Lavín 2006; Fiedler, Talley 2006; Scott *et al.* 2012). Hence, increasing the encounter rate of sharks and billfish with EG-prey may facilitate the use of the eastern tropical Pacific and other areas with an extended OMZ as suitable habitat by dolphins and tuna. Mutualistic relationships often increase the ecological range and niche breadth of participating species compared to monospecific occurrence (Begon *et al.* 2006).

Tuna-dolphin congregations should be the larger the more food-deprived the assemblage is, so as to benefit from the dilution effect and predator swamping when associated sharks and billfish switch to IG-prey. Food deprivation is most likely when EG-prey is distributed in large but sparse patches which are difficult to find. Inter-individual distances are expected to be small under such conditions as each group member is expected to reduce its personal domain of danger (Hamilton 1971).

Oceanic whitetip sharks, one of the two pelagic shark species most often found in association with tuna-dolphin congregations, were also documented to associate with short-finned pilot whales, *Globicephala macrorhynchus* (Gannon *et al.* 1997a,b; Mintzer *et al.* 2008), and frequently follow these mammals into the deep (Bonfil *et al.* 2008). A dietary overlap between the species seems to promote grouping (Madigan *et al.* 2015).

Conclusively, dolphins reduce their predation risk through congregation with a more vulnerable species and tuna benefit if sharks approach less aggressively when dolphins are associated with a tuna shoal. Tuna also reduce their predation risk by raising patches of small shoaling fish to the surface, thereby providing EG-prey to following sharks and billfish. Such mutual benefits may render the tuna-dolphin association an evolutionarily stable strategy in areas where encounter rates with pelagic sharks and billfish are high.

This theory explains why dolphins may remain at the periphery of prey patches without feeding when associated with tuna in the tropical E-Pacific (Donahue, Edwards 1996).

Hypothesis 3: The association yields improved navigation accuracy.

Pantropical spotted dolphins are nomadic and movements of >100km/day have been documented (Leatherwood, Ljungblad 1979; Perrin *et al.* 1979; Scott, Cattanch 1998; Scott, Chivers 2009) whereas tuna shows a high level of site fidelity (e.g. Brill *et al.* 1999; Itano, Holland 2000; Schaefer *et al.* 2007) and only occasional extended travel (Schaefer *et al.* 2007).

The higher longevity in dolphins of 20-50 years (Small, DeMaster 1995; Venn-Watson *et al.* 2015) compared to <10 years in yellowfin tuna (Lehodey, Leroy 1999; Nurdin *et al.* 2016), combined with a larger day and home range, and the affiliation of individuals of most age classes (except for immature females) to large oceanic pods compared to tuna shoals which typically consist of one age class, suggest that dolphin pods are endowed with more knowledge and experience related to the location and onset of favourable foraging areas, and other migration and movement related factors (Chap. 1). Therefore, following dolphins may lead to a more reliable and steady success in search for locations which provide sufficient forage such as fronts, eddies and upwelling systems which vary in strength and profitability across time and space. Some cetacea were found to navigate large distances with high precision (Mate *et al.* 2007; Bailey *et al.* 2009; Horton *et al.* 2011; Durban, Pitman 2012; Kennedy *et al.* 2014).

These findings reveal a potential for improved navigation accuracy through association of dolphins and tuna. Information exchange about, and improved navigation to, profitable feeding sites may yield benefits for one or both species. Since dolphins range further, live longer and possess more sophisticated cognitive capabilities it is more likely that tuna gain an advantage from association with dolphins than vice versa. However, more studies are needed which explore the process of decision-making in dolphins and tuna, or other pelagic fish species.

In cetacea improved navigation accuracy does not seem to be a driver for grouping and does not require congregation (Chap. 3). Delphinids are capable of communicating acoustically over up to 6km, possibly 10km, in the quiet environment of the tropical open ocean (Rasmussen *et al.* 2006; Jensen *et al.* 2012; Heenehan *et al.* 2016). Hence individuals can exchange information without forming groups. However, this does not exclude the possibility that congregation between dolphins and tuna benefits navigation accuracy.

Conclusions

Even though data for a quantitative analysis are lacking results indicate that tuna-dolphin congregation is driven by predation risk in areas of an extended OMZ where encounter rates with tuna and dolphin predators are high. Dolphins are suggested to gain anti-predator benefits by association with a more vulnerable species. Tuna are not expected to experience reduced predation risk by congregation with these marine mammals in such a direct way. Rather improved prey detection through sensory pooling and the tuna's prey herding techniques which bring small pelagic shoaling fish and squid toward the surface may increase access to EG-prey for pelagic sharks and billfish, which often follow tuna shoals and tuna-dolphin congregations. The satiation of these potential IG-predators with EG-prey would then in turn reduce predation risk particularly for tuna.

Predation risk as the main driver for tuna-dolphin congregation is in line with a large group size of spinner and pantropical spotted dolphins when associated with tuna (Au, Perryman 1985) since large monospecific congregations of oceanic delphinids were also found to be driven by predation risk (Chap. 3). Both occur in areas where predator encounter rates are high due to an extended oxygen minimum zone (Scott *et al.* 2012; Chap. 3).

Association of tuna and dolphin may improve navigation accuracy to suitable feeding habitat through the pooling of sensory and memorized information whereby tuna are likely to benefit from the dolphins superior acoustic and cognitive capabilities and from the marine mammals' echolocation system. Finneran *et al.* (2000) suggested that tuna may home on dolphin-produced sounds as part of their foraging strategy in the absence of nearby prey. However, dolphins may also take advantage of the tuna's more acute chemoreception and capability to carry out deep dives which were suggested to be related to navigation.

Tuna tend to leave an area in response to both, changes in current patterns and the location of FAD's in relation to physical or oceanographic features (Dempster, Kingsford 2003), which in turn affect prey distribution and may lead to the necessary to cover larger areas until a new suitable habitat has been located. Hence the facultative nature of the tuna-dolphin association may reflect variation in predation threat and/or the tuna's varying need to travel in search for better foraging conditions. Observations of tuna which seem to leave their FAD's when dolphins appear to join the same (Moreno *et al.* 2007) supports the idea that the former home-in on the mammals as suggested by Finneran *et al.* (2000).

In areas where the thermocline is at greater depth than in the tropical E-Pacific tuna inhabit deeper water leading to both, a separation of dolphin and tuna habitat and reduced vulnerability to visually hunting predators in tuna. The association becomes less common. The mutual benefits described may also explain the somewhat contradictory suggestions in the literature about who follows whom in this association. Anderson (2005) found dolphins to follow tuna whereas other studies suggest that tuna follow dolphins (Au, Perryman 1985; Au Pitman 1986; Edwards 1992).

Tuna-dolphin associations in areas unrelated to oxygen minimum zones such as congregation of common and striped dolphins with albacore tuna in the Bay of Biscay (Das *et al.* 2000) may be driven by different parameters and have to be studied separately. This analysis applies to the association of pantropical and spinner dolphins with skipjack and yellowfin tuna in areas with extended oxygen minimum zones.

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Conclusions

This study provides new insight into grouping behaviour in oceanic predators, by analysing its evolutionary basis and interrelations with ecological parameters and behavioural traits. Congregation in oceanic cetacea is most likely to affect predator-prey interactions for example through the apparent importance of prey herding and prey debilitation techniques across numerous species and areas. Dietary analyses and the level of behavioural adaptation to the exploitation of shoaling prey across species and areas suggest that shoaling fish, squid and crustacea represent the most important food source in baleen whales and small to medium-sized odontoceti.

Dilution, confusion and selfish herd effects, as well as predator swamping seem to play an important role in reducing predation risk in small pelagic shoaling fish, squid and crustacea. The same factors may lead to large average group sizes in gregarious (sub)tropical delphinids due to the oddity effect caused by an unequal body size of group members.

The most important oceanic elasmobranch predators of cetacea are great white sharks and broadnose sevengill sharks which were estimated to inflict high risks of predation to melonheaded whales, rough-toothed, Fraser's, spinner, Atlantic and pantropical spotted, Clymene and common dolphins. These are also the species which form pods of the largest average size among cetacea.

In line with these findings, predation risk is also suggested to represent the main driver for tuna-dolphin associations. The latter are most likely to particularly benefit by congregating with a species which is more vulnerable to predation by sharks.

The role of communal defence and its quantitative importance, particularly in these large pods is little understood and future research may provide insights as to how this behaviour may effect predation threat experienced by tuna when associated with dolphins.

Congregation in small groups appears to be primarily driven by both, alloparental care for young and increased access to females. Lekking is rare among cetacea and does not seem to be related to large congregations documented in small delphinids. Many cetacea species show extended mating and calving periods spanning few months in polar species to a whole year in tropical and subtropical odontoceti. Long calving periods may reduce predation risk by counteracting a possible specialization of predators to a sudden large supply of a certain prey source, namely calves.

Migration often implies travel through areas of high or unknown predation risk. Chapter 3 shows that among cetacea species have adapted in various ways to the threat of predation. Similarly, different taxa apply different modes of navigation (Chap. 1) and only some migrate in groups. Based on the identification of predation risk as a main evolutionary driver towards congregation in oceanic cetacea a similar pattern may be expected more broadly such that species or taxa which experience a high risk of predation travel in large congregations whereas others which are less influenced by predators migrate solitarily or in small groups.

Sea turtles possess a protective carapace, likely rendering these species invaluable for many predators. Sea turtles are rarely preyed on by killer whales which, together with large pelagic sharks, would be the species most likely to impose predation risk to these marine reptiles (e.g. Ford *et al.* 1998, 2011). A review of numerous papers on stomach content analyses in sleeper, bluntnose sixgill, broadnose sevengill, shortfin mako, salmon, porbeagle, dusky and blue sharks did not produce any records of sea turtles as prey. Oceanic whitetip and great white sharks rarely feed on these reptiles (e.g. Compagno 1984; Hussey *et al.* 2012).

Migrating seabirds spend much time in the air and therefore away from predators and hence are expected to experience a low risk of predation, too. Killer whales and large pelagic sharks

such as tiger and great white sharks have few natural predators. Interestingly all these species or species groups seem to migrate in small congregations or solitarily (Durban, Pitman 2012; Chap. 1) whereas pelagic shoaling fish and some delphinids of small body size which are exposed to risk from various predators travel in large groups (Chap. 2, 4).

This indicates that predation risk may play an important role in oceanic migration behaviour which should be analysed in a quantitative manner. The fact that sea turtles and possibly sharks achieve low navigation accuracies unless a certain migration has been carried out many times by an individual may further suggest that navigation accuracy is a secondary grouping benefit.

A higher efficiency in communal prey search, cooperative prey herding, and navigation accuracy, as well as hydrodynamic benefits are all suggested to represent secondary advantages of, and possibly necessities in response to congregation.

Both theory (Niwa 1994; Guttal, Couzin 2010) and observation (Hensor *et al.* 2005) in pelagic fish species suggest that reduced population density leads to smaller groups in collectively moving populations rather than fewer groups of the same size. The same correlation between animal density and group size was found in cetacea (Chap. 3) indicating that not just congregation size, but also the number of groups is subject to natural selection.

In fish, shoals have been found to be inter-connected by information exchange (Chap. 1) and the active space of cetacea some sounds (Chap. 3) as well as behavioural studies which found cetacea to disperse over large areas and re-join after several days (e.g. Baird *et al.* 2008; Scott, Chivers 2009) suggest the same in these marine mammals.

In migrating shoaling fish these findings have been linked to the occupation of an area of a certain size which facilitates the detection of migration-related cues such as changes in water temperature or in the chemical composition of the water (Chap. 1). Cetacea may use their grouping behaviour in similar ways such that a certain number of groups is spread out over a very large area and exchange of group members as in societies with a fission-fusion pattern of individual group affiliation may then facilitate information exchange regarding navigation accuracy or prey search through the formation of more, but smaller groups as opposed to few large ones.

Several oceanic cetacea species have received comparatively little research attention. These include sei whales, Atlantic white-sided, hourglass, Clymene and northern and southern right whale dolphins as well as Burmeister's porpoises. Most of these species are difficult to research due to their offshore occurrence. Geographic areas which lend themselves to the study of these species such as oceanic islands or continental edges where oceanic conditions occur close to shore need to be identified.

Several baleen whale species were estimated to experience a high predation risk by killer whales, the only cetacea species in which the ability to capture large prey items seems to represent a significant grouping benefit. Particularly gray and minke whales are an important food source of mammal-eating populations.

In the southern hemisphere a predatory interrelation between southern right whales and kelp gulls, *Larus dominicanus*, has strongly increased in recent years. Kelp gulls have been found to inflict large wounds to the dorsal body of right whales which strongly affect behaviour, health and likely survival in this species (Fazio *et al.* 2015; Marón *et al.* 2015; Fiorito *et al.* 2016). Adaptation of baleen whales to predation is little understood and should be a focus of future research.

The influence of body size on group size in cetacea likewise lends itself to further investigation. Even though there is evidence that body size is a limiting factor to group size in baleen whales, congregations remain small even during migration periods of little or no foraging, and even in

species and areas for which killer whale predation risk is high during migration such as gray whales of the NE-Pacific.

Bryde's and sei whales occur solitarily or in very small groups in areas where extensive prey patches related to deep-scattering layers facilitate the formation of large congregations in delphinids. Both feed on shoaling fish and have been documented to conjointly feed on prey balls. There may be phylogenetic reasons for a limited group size such that the formation of larger groups has not developed among baleen whales and has therefore not been subject to natural selection.

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Appendix 1: Group size of cetacea species

Table 1: Odontoceti group size: ind.: individual(s), sign.: significant, typ.: typical, unid.: unidentified, incl.: including, unpubl.: unpublished

Species/Reference	Group size	Area	Group characteristics
Kogia/ Au, Pitman 1988	\bar{x} : 2, SD: 1, n: 30	trop. E-Pacific	
Wade, Gerrodette 1993	\bar{x} : 2, SD: 0.2, n: 95	trop. E-Pacific	
Mangels, Gerrodette 1994	1-4, \bar{x} : 2, SD: 1, n: 38	E-Pacific	pygmy \bar{x} : 1, SD: 0, n: 2 dwarf 1-4, \bar{x} : 2, SD: 1, n: 31
Barlow 1995	\bar{x} : 1, n: 2	California	pygmy sperm whale
Ballance <i>et al.</i> 1996	1-4, \bar{x} : 2, SD: 0.2, n: 20	N/NW-Indian Ocean	
Davis, Fargion 1996	1-7, \bar{x} : 2, SD: 0.2, n: 83	Gulf of Mexico	
Barlow <i>et al.</i> 1997	\bar{x} : 3, SD: 2, n: 21	California	dwarf sperm whale
Mullin, Fulling 2003	\bar{x} : 2, SD: 0.3, n: 8	SE-USA	
Anderson 2005	1-6, \bar{x} : 2, SD: 1.7, n: 74	Maldives	dwarf sperm whale
Barlow 2006	\bar{x} : 2, n: 7	Hawaii	pygmy \bar{x} : 1, n: 2 dwarf \bar{x} : 2, n: 5
Claridge 2006	1-15, \bar{x} : 3, SD: 2, n: 141	Great Abaco Island (Bahamas)	pygmy 1-2, \bar{x} : 1, SD: 1, median: 1, n: 8, dwarf 1-15, \bar{x} : 3, SD: 2, median: 2, n: 133
Maze-Foley, Mullin 2006	1-8, \bar{x} : 2, SD: 0.4, n: 133	Gulf of Mexico	
Barlow, Forney 2007	\bar{x} : 1, n: 5	W-USA	
Dunphy-Daly <i>et al.</i> 2008	1-12, median: 3, n: 54	Great Abaco Island (Bahamas)	dwarf sperm whale
Jackson <i>et al.</i> 2008	\bar{x} : 2, n: 37	trop. E-Pacific	pygmy \bar{x} : 1, n: 3, dwarf \bar{x} : 2, n: 31
Palka 2012	\bar{x} : 2, SD: 0.5, n: 32	NE-USA	pygmy \bar{x} : 2, SD: 0.4, n: 12, dwarf \bar{x} : 2, SD: 1, n: 13
Baird <i>et al.</i> 2013	1-8, \bar{x} : 3, SD: 0.4, median: 2, n: 74	Hawaii	dwarf sperm whale, thought to be island-associated population
Cuvier's beaked whale/ Holt, Jackson 1987	1-2, \bar{x} : 2, SD: 0.5, n: 5	trop. E-Pacific	
Wade, Gerrodette 1993	\bar{x} : 2, SD: 0.2, n: 91	trop. E-Pacific	
Mangels, Gerrodette 1994	1-5, \bar{x} : 2, SD: 1, n: 32	E-Pacific	
Barlow 1995	\bar{x} : 2, n: 7	California	
Davis, Fargion 1996	1-4, \bar{x} : 1, SD: 0.1, n: 7	Gulf of Mexico	
Barlow <i>et al.</i> 1997	1-7, \bar{x} : 2, SD: 1, n: 21	California	
Mignucci-Giannoni 1998	1-3, \bar{x} : 2, n: 8	Caribbean Sea	single ind.: 62.5% of sightings
Carretta <i>et al.</i> 2000	\bar{x} : 2, n: 3	San Clemente Island, California	
Ritter 2001	1-3, \bar{x} : 2, SD: 1, n: 4	La Gomera (Canary Islands)	
Palacios, Salazar 2002	\bar{x} : 3, median: 3, n: 22	Galápagos Islands	
Carrillo 2003	1-4, \bar{x} : 3, SD: 1, n: 4	Tenerife (Canary Islands)	
Jackson <i>et al.</i> 2004	1-3, \bar{x} : 1, SD: 1, n: 7	trop. E-Pacific	
Anderson 2005	1-4, \bar{x} : 2, SD: 0.4, n: 17	Maldives	

Species/Reference	Group size	Area	Group characteristics
Claridge 2006	1-5, \bar{x} : 2, SD: 1, median: 2, n: 18	Great Abaco Island (Bahamas)	
MacLeod, D'Amico 2006	1-15, \bar{x} : 2, SD: 2, n: 189	throughout range	
Maze-Foley, Mullin 2006	1-4, \bar{x} : 2, SD: 0.3, n: 15	Gulf of Mexico	
Barlow, Forney 2007	\bar{x} : 3, n: 17	W-USA	
Kiszka <i>et al.</i> 2007	\bar{x} : 2, SD: 1, n: 60	Azores, English Channel	
Moulins <i>et al.</i> 2007	1-11, \bar{x} : 2, SD: 2, n: 247	Ligurian Sea (Mediterranean)	mature ind. typically solitary (n: 87)
Azzellino <i>et al.</i> 2008	1-8, \bar{x} : 4, SD: 2, median: 4, n: 24	Ligurian Sea (Mediterranean)	significant variation in group size between years and areas
Gannier, Epinat 2008	1-5, \bar{x} : 2, SD: 1, median: 1, n: 11	Mediterranean Sea	
Jackson <i>et al.</i> 2008	\bar{x} : 2, n: 16	trop. E-Pacific	
Falcone <i>et al.</i> 2009	2-15, \bar{x} : 4, SD: 2, n: 24	Clemente Island, California	long encounter durations
Hildebrand 2009	1-90, \bar{x} : 4, SD: 13, n: 302	S-California	
Ford <i>et al.</i> 2010	1-2, \bar{x} : 1, SD: 0.5, n: 3	W-Canada	
Gannier 2011	1-5, \bar{x} : 3, SD: 1, n: 22	Mediterranean Sea	2 sightings included calves, 4 sightings included juveniles
Palka 2012	\bar{x} : 2, SD: 0.4, n: 36	NE-USA	
Baird <i>et al.</i> 2013	1-5, \bar{x} : 2, SD: 1, median: 2, n: 64	Hawaii	breaching regularly
Moore, Barlow 2013	\bar{x} : 2, SD: 0.2, n: 112	W-USA	
Silva <i>et al.</i> 2014	1-4, \bar{x} : 2, SD: 1, n: 43	Azores	
Correia <i>et al.</i> 2015	1-6, \bar{x} : 3, SD: 2, n: 13	Portugal (E-Atlantic)	
Baird's beaked whale/ Smith <i>et al.</i> 1986	\bar{x} : 4, n: 2	W-USA	
Brueggeman <i>et al.</i> 1987	4-5, \bar{x} : 5, n: 2	Aleutians, Alaska	
Mangels, Gerrodette 1994	4-19, \bar{x} : 13, SD: 6, n: 5	E-Pacific	
Barlow 1995	4, n: 1	California	
Barlow <i>et al.</i> 1997	3-11, \bar{x} : 8, SD: 4, n: 3	California	
Dawson <i>et al.</i> 1998	3-33, \bar{x} : 16, SD: 13, n: 3	W-USA	
Wade <i>et al.</i> 2003	\bar{x} : 8, n: 11	Gulf of Alaska, Aleutians	
Jackson <i>et al.</i> 2004	1-6, \bar{x} : 3, SD: 2, n: 3	trop. E-Pacific	
Barlow, Forney 2007	\bar{x} : 9, n: 15	W-USA	
Matkin <i>et al.</i> 2007	\bar{x} : 9, n: 10	Aleutians, Alaska	
Jackson <i>et al.</i> 2008	\bar{x} : 8, n: 8	trop. E-Pacific	
Barlow 2010	\bar{x} : 11, n: 5	W-USA	
Ford <i>et al.</i> 2010	4-7, \bar{x} : 5, SD: 1, n: 3	W-Canada	
Moore, Barlow 2013	\bar{x} : 10, SD: 9, n: 24	W-USA	
Arnoux's beaked whale/ Ponganis <i>et al.</i> 1995	5-15, n: several	Southern Ocean	tight pods
Rogers, Brown 1999	1-47, \bar{x} : 7, SD: 5, n: 15	Southern Ocean	joining, splitting and exchange of ind. between pods observed

Species/Reference	Group size	Area	Group characteristics
Friedlaender <i>et al.</i> 2010	50-75, \bar{x} : 63, SD: 13, n: 2	Antarctic Peninsula	Pods consisting of sub-groups
Blainville's beaked whale / Ritter 2001; Ritter, Brederlau 1999	1-9, \bar{x} : 3, SD: 2, n: 26	La Gomera (Canary Islands)	calves observed regularly
Gannier 2000	2-4, \bar{x} : 3, n: 4	Society Islands (S-Pacific)	
Carrillo 2003	1-10, \bar{x} : 5, SD: 2, n: 57	Tenerife (Canary Islands)	calves present in 10 sightings
Anderson 2005	2-6, \bar{x} : 4, n: 3	Maldives	
Claridge 2006	1-11, \bar{x} : 4, SD: 2, median: 4, n: 111	Great Abaco Isl. (Bahamas)	
MacLeod, D'Amico 2006	1-8, \bar{x} : 4, SD: 2, n: 31	throughout range	
McSweeney <i>et al.</i> 2007	1-9, \bar{x} : 4, SD: 2, median: 3, n: 19	Hawaii	
Hermans, Pistorius 2008	1-8, \bar{x} : 3, n: 8	Aldabra Atoll, Indian Ocean	
Baird <i>et al.</i> 2013	1-11, \bar{x} : 4, SD: 2, median: 3, n: 45	Hawaii	including pods of both and island-associated and an oceanic population
Gervais' beaked whale / Gillespie <i>et al.</i> 2009	9, n: 1	Bahamas	pod consisting of 3 sub-groups of 3, 2 and 4 ind.; no calves
Palka 2012	\bar{x} : 2, SD: 2, n: 5	NE-USA	
Sowerby's beaked whale / Palka 2012	\bar{x} : 1, SD: 0.2, n: 10	NE-USA	
Pygmy beaked whale / Barlow <i>et al.</i> 1997	2, n: 1	California	
Jackson <i>et al.</i> 2008	\bar{x} : 2, n: 16	trop. E-Pacific	
Longman's beaked whale / Pitman <i>et al.</i> 1999	1-100, \bar{x} : 19, SD: 22, n: 41	Indo-Pacific	Pods tight, larger pods in W-Pacific (mean: 29, n: 15) than in E-Pacific (mean: 9, n: 17)
Anderson <i>et al.</i> 2006	1-40, \bar{x} : 7, SD: 11, n: 22	N- and W-Indian Ocean	
Barlow 2006	21, n: 1	Hawaii	
Jackson <i>et al.</i> 2008	3, n: 1	trop. E-Pacific	
Rankin <i>et al.</i> 2011	88, n: 1	Hawaii	3 - 5 calves present; no other sightings within 100km; evasive behaviour to ship, incl. split into sub-groups
Nanayakkara <i>et al.</i> 2014	4, n: 1	Sri Lanka	traveling
Martin, Nimak-Wood 2016	~20, n: 1	Kenya	tight pod, no calves visible, traveling, breaching, interacting with a pod of ~50 bottlenose dolphins
Southern bottlenose whale / Miyazaki, Kato 1988	1-10, \bar{x} : 2, n: 320	Southern Ocean	some pods were Arnoux's beaked whale, high density along pack ice, 3 mother-calf pairs
Findlay <i>et al.</i> 1992	1-15, \bar{x} : 5, SD: 3, n: 47	southern Africa	
Sekiguchi <i>et al.</i> 1993	1-12, \bar{x} : 4, SD: 2, n: 138	South Africa	species identification uncertain

Species/Reference	Group size	Area	Group characteristics
Branch, Butterworth 2001	\bar{x} : 2, SD: 0.2, n: 1032	Southern Ocean	
MacLeod, D'Amico 2006	1-20, \bar{x} : 2, SD: 2, n: 201	throughout range	
Northern bottlenose whale/ Gray 1882	typ. 4-10, males solitary	N-Atlantic	often several groups of 4-10 visible in an area
Gowans <i>et al.</i> 2001	1-14, \bar{x} : 3, SD: 2, n: 1281	Gully (S off Nova Scotia)	Pods often consist of members of several age- and sex classes, long-term bonds between mature and sub-adult males, calves in 3.9% of pods, typically 1 calf/pod
Weir <i>et al.</i> 2001	\bar{x} : 2, n: 12	N-Scotland	
Whitehead, Wimmer 2005	\bar{x} : 4, n: 154	S-Nova Scotia/Scotian shelf	
MacLeod, D'Amico 2006	1-22, \bar{x} : 4, SD: 2, n: 895	throughout range	
Silva <i>et al.</i> 2014	1-13, \bar{x} : 6, SD: 2, n: 135	Azores	
Long-finned pilot whale/ Miyazaki, Kato 1988	3- ~200, \bar{x} : 67, n: 20	Southern Ocean	pod size increasing with latitude, 9 out of 13 closely examined pods contained mother-calf pairs
Buckland <i>et al.</i> 1991	mostly < 50; > 100 seen occasionally	N-Atlantic	Pods often consist of sub-groups and are spread out over large areas
Kasamatsu, Joyce 1995	\bar{x} : 73, SD: 33, n: 23	Southern Ocean	
Kingsley, Reeves 1998	\bar{x} : 9, SD: 12, n: 18	Gulf of St. Lawrence	
Abend, Smith 1999	1-1000s, \bar{x} : 8-50, n: 33	Greenland	
Hooker <i>et al.</i> 1999	\bar{x} : 11, SD: 13, n: 54	Gully (S off Nova Scotia)	
Weir <i>et al.</i> 2001	\bar{x} : 14, n: 121	N-Scotland	
Ottensmeyer, Whitehead 2003	2-135, \bar{x} : 20, SD: 17, median: 15, n: 249, groups with calves: 5-135, \bar{x} : 23, SD: 18, median: 18, n: 197	N-Nova Scotia	larger pods organized in sub-groups and spread out over an area spanning several km ² , 78.3% of groups contained calves
López <i>et al.</i> 2004	\bar{x} : 12, SD: 22, n: 7	Galicia (N-Spain)	
Cañadas <i>et al.</i> 2005/ Cañadas, Sagarminaga 2000	1-350, \bar{x} : 30, SD: 41, n: 350	S-Spain (Mediterranean)	
Jankowski 2005	1-135, \bar{x} : 15, SD: 13, median: 11, n: 934, 90.6% < 30	NW-Nova Scotia	calves present in 69.3% of encounters, large groups are rare
Kiszka <i>et al.</i> 2007	1-30, \bar{x} : 7, SD: 5, n: 134	Azores, English Channel	
De Stephanis <i>et al.</i> 2008	1-160, \bar{x} : 33, SD: 32, n: 122	Strait of Gibraltar	
Laran <i>et al.</i> 2010	\bar{x} : 28, SD: 8, n: 6	Ligurian Sea (Mediterranean)	
Oudejans 2014	1-25, \bar{x} : 6, SD: 6, n: 16	NE-Atlantic	calves present in 6 sightings

Species/Reference	Group size	Area	Group characteristics
Visser <i>et al.</i> 2014	60-80, \bar{x} : 70, n: 8	N-Atlantic	Pods organized in sub-groups of 1-30 ind. spread out over several km ² ; 7 groups included calves
Fontaine <i>et al.</i> 2015	1-300, \bar{x} : 53, n: 131	Kerguelen	
Di Tullio <i>et al.</i> 2016	\bar{x} : 98, SD: 35, n: 17	SW-Atlantic outer shelf/ slope	
Laran <i>et al.</i> 2017	\bar{x} : 2, n: 5	NW-Mediterranean	
Short-finned pilot whale/ Holt, Jackson 1987	2-107, \bar{x} : 18, SD: 22, n: 21	trop. E-Pacific	
Breese, Tershy 1993	2-9, \bar{x} : 6, SD: 2, n: 8	Gulf of California	
Mangels, Gerrodette 1994	6-119, \bar{x} : 23, SD: 22, n: 25	E-Pacific	
Davis, Fargion 1996	2-50, \bar{x} : 19, SD: 4, n: 20	Gulf of Mexico	
Barlow <i>et al.</i> 1997	15-325, \bar{x} : 70, SD: 79, n: 16	California	incl. 6 mixed-species pods
Mignucci-Giannoni 1998	1-100, \bar{x} : 11, n: 66	Caribbean Sea	1-3 ind. 50%; 4-7 ind. 19.6%; 8-20 ind. 15.2%; 25-100 ind. 15.2%
Gannier 2000	10-35, \bar{x} : 26, SD: 12, n: 5	Society Islands (S-Pacific)	
Ritter 2001	5-53, \bar{x} : 24, SD: 11, n: 111	La Gomera (Canary Islands)	
Gerrodette, Forcada 2002b	\bar{x} : 20, n: 370	trop. E-Pacific	
Palacios, Salazar 2002	\bar{x} : 18, median: 15, n: 131	Galápagos Islands	
Anderson 2005	3-100, \bar{x} : 18, SD: 29, n: 74	Maldives	
Barlow 2006	\bar{x} : 27, n: 25	Hawaii	
Claridge 2006	3-14, \bar{x} : 6, SD: 5, median: 4, n: 5	Great Abaco Island (Bahamas)	
Ferguson <i>et al.</i> 2006	\bar{x} : 18, n: 117	trop. E-Pacific	
Maze-Foley, Mullin 2006	3-85, \bar{x} : 25, SD: 4, n: 18	Gulf of Mexico	
Barlow, Forney 2007	\bar{x} : 18, n: 5	W-USA	
Jackson <i>et al.</i> 2008	\bar{x} : 18, n: 57	trop. E-Pacific	
Oswald <i>et al.</i> 2008	\bar{x} : 20, SD: 13, n: 18	E-Pacific	
Fulling <i>et al.</i> 2011	5-43, \bar{x} : 18, SD: 9, n: 5	Mariana Islands	
Kanaji <i>et al.</i> 2011	8-1500, \bar{x} : 128, median: 40, n: 42	Japan	
Baird <i>et al.</i> 2013	1-195, \bar{x} : 20, SD: 16, median: 18, n: 502	Hawaii	
Kendall-Bar <i>et al.</i> 2016	2-200, \bar{x} : 36, SD: 23, n: 20	California, Mexico (Pacific)	
False killer whale/ Kasuya 1971	2-200, \bar{x} : 55, n: 6	Japan	
Findlay <i>et al.</i> 1992	1-50, \bar{x} : 16, SD: 23, n: 6	southern Africa	
Breese, Tershy 1993	20-100, \bar{x} : 42, SD: 24, n: 11	Gulf of California	
Mangels, Gerrodette 1994	13-353, \bar{x} : 183, SD: 170, n: 2	E-Pacific	
Anderson 2005	1-100, \bar{x} : 36, SD: 15,	Maldives	

Species/Reference	Group size	Area	Group characteristics
	n: 12		
Ferguson <i>et al.</i> 2006	\bar{x} : 11, n: 19	trop. E-Pacific	
Maze-Foley, Mullin 2006	3-70, \bar{x} : 28, SD: 7, n: 11	Gulf of Mexico	
Jackson <i>et al.</i> 2008	\bar{x} : 12, n: 16	trop. E-Pacific	
Reeves <i>et al.</i> 2009d	2-470, median: 195, n: 14	Hawaii	
Fulling <i>et al.</i> 2011	2-26, \bar{x} : 10, SD: 4, n: 10	Mariana Islands	
Baird <i>et al.</i> 2013	1-35, \bar{x} : 16, SD: 9, median: 16, n: 47	Hawaii	Pods of one oceanic and two resident populations around Hawaiian Islands
Weir <i>et al.</i> 2013	10-100, \bar{x} : 35, SD: 34, median: 24, n: 6	Gabon, Côte d'Ivoire (W-Africa)	calves present during at least 5 sightings
Bradford <i>et al.</i> 2014	\bar{x} : 56, n: 44	Hawaii	
Silva <i>et al.</i> 2014	3-20, \bar{x} : 10, SD: 6, n: 78	Azores	
Zaeschmar <i>et al.</i> 2014	20-150, \bar{x} : 47, SD: 29, n: 47; single-species pods: 20-50, \bar{x} : 35, SD: 13, n: 4; mixed-species total: 28-400, \bar{x} : 120, SD: 65, n: 43	N-New Zealand	feeding often on large shoals of fish, traveling, 43 pods associated with common bottlenose dolphins, very low encounter rate
Pygmy killer whale/ Hansen <i>et al.</i> 1994	\bar{x} : 11, n: 3	Gulf of Mexico	
Mangels, Gerrodette 1994	10-16, \bar{x} : 13, SD: 3, n: 2	E-Pacific	
De Boer 2000	18, n: 1	Indian Ocean	
Williams <i>et al.</i> 2002	\bar{x} : 12, SD: 0, n: 2	Bay of Biscay	
Anderson 2005	9-30, \bar{x} : 17, SD: 9, n: 4	Maldives	
Barlow 2006	\bar{x} : 16, n: 3	Hawaii	
Claridge 2006	30, n: 1	Great Abaco Island (Bahamas)	
Ferguson <i>et al.</i> 2006	\bar{x} : 30, n: 23	trop. E-Pacific	
Maze-Foley, Mullin 2006	4-84, \bar{x} : 19, SD: 7, n: 10	Gulf of Mexico	
Jackson <i>et al.</i> 2008	\bar{x} : 25, n: 9	trop. E-Pacific	
Oswald <i>et al.</i> 2008	\bar{x} : 15, SD: 18, n: 2	E-Pacific	
McSweeney <i>et al.</i> 2009	4-33, median: 13, n: 11	Hawaii	
Baird <i>et al.</i> 2013	2-25, \bar{x} : 10, SD: 7, median: 10, n: 37	Hawaii	
Melon-headed whale/ Wade, Gerrodette 1993	\bar{x} : 200, SD: 40, n: 14	trop. E-Pacific	often in association with large pods of Fraser's dolphins, forming some of the largest mixed-species pods observed
Davis, Fargion 1996	30-400, \bar{x} : 141, SD: 28, n: 10	Gulf of Mexico	4x associated with Fraser's dolphins, group size Fraser's: 17-45
Reeves <i>et al.</i> 1999a	up to 300	French Polynesia	
Gannier 2000	50-120, n: 4	Society Islands (S-Pacific)	
Laran, Gannier 2001	n: 30-120, \bar{x} : 90, SD: 30, n: 3	Marquesas (S-Pacific)	

Species/Reference	Group size	Area	Group characteristics
Anderson 2005	30-1200, \bar{x} : 412, SD: 218, n: 12	Maldives	
Huggins <i>et al.</i> 2005	17-800, \bar{x} : 305, SD: 189, n: 18	Hawaii	
Dolar <i>et al.</i> 2006	Tañon Strait: 40-210, \bar{x} : 143, n: 2; Sulu Sea: 7-52, \bar{x} : 34, n: 6	Philippines	
Claridge 2006	120-500, \bar{x} : 310, SD: 269, n: 2	Great Abaco Island (Bahamas)	
Ferguson <i>et al.</i> 2006	\bar{x} : 258, n: 5	trop. E-Pacific	
Gero, Whitehead 2006	4-20, \bar{x} : 12, SD: 7, n: 5	Dominica (Caribbean)	
Maze-Foley, Mullin 2006	22-275, \bar{x} : 100, SD: 16, n: 17	Gulf of Mexico	
Dulau-Drouot <i>et al.</i> 2008	100-1000, \bar{x} : 477, SD: 324, n: 11	La Réunion (Indian Ocean)	often associated with Fraser's dolphins
Jackson <i>et al.</i> 2008	\bar{x} : 396, n: 2	trop. E-Pacific	
Baird <i>et al.</i> 2013	1-800, \bar{x} : 252, SD: 168, median: 240, n: 53	Hawaii	large groups encountered year-round, two populations
Killer whale/ Condy <i>et al.</i> 1978	1-25, \bar{x} : 4, SD: 3, n: 281	Marion Island (Southern Ocean)	
Bloch, Lockyer 1988	up to thousands	Faroe Islands	
Miyazaki, Kato 1988	1-345, \bar{x} : 21, n: 146, 77% of pods \leq 20 individuals	Southern Ocean	single adult males encountered regularly in oceanic areas; high density of large groups along ice edge
Morton 1990	trans.: 1-12, \bar{x} : 5, n: 39 resid.: 3-39, \bar{x} : 11, n: 55	British Columbia nearshore	significance in size difference: $t = 4.88$; $p < 0.01$
Findlay <i>et al.</i> 1992	1-12, \bar{x} : 5, SD: 3, n: 56	southern Africa	
Breese, Tershy 1993	1-14, \bar{x} : 6, SD: 4, n: 21	Gulf of California	1-2 adult males per pod
Mangels, Gerrodette 1994	2-9, \bar{x} : 6, SD: 2, n: 10	E-Pacific	
Barlow 1995	\bar{x} : 4, n: 3	California	
Kasamatsu, Joyce 1995	\bar{x} : 9, SD: 1, n: 128	Southern Ocean	
Barlow <i>et al.</i> 1997	1-14, \bar{x} : 5, SD: 4, n: 7	California	
Mignucci-Giannoni 1998	1-25, \bar{x} : 8, n: 6	Caribbean Sea	2 types of pods: 1-3 ind. (67%) and 12-25 ind. (33%)
Branch, Butterworth 2001	\bar{x} : 12, SD: 6, n: 299	Southern Ocean	
Keith <i>et al.</i> 2001	1-28, \bar{x} : 3, SD: 0.1, n: not published	Marion Island (Southern Ocean)	predominantly nearshore
Weir <i>et al.</i> 2001	\bar{x} : 5, n: 44	N-Scotland	
Palacios, Salazar 2002	\bar{x} : 3, n: 38	Galápagos Islands	
Pinedo <i>et al.</i> 2002	\bar{x} : 3, SD: 1, n: 9	Brazil	
Wade <i>et al.</i> 2003	2-90, \bar{x} : 18, SD: 18, n: 59	Gulf of Alaska, Aleutian Islands	residents: 4-90, \bar{x} : 22, SD: 18, n: 39; transients: 2-13, \bar{x} : 5, SD: 3, n: 14; offshore: 40-60, \bar{x} : 50, SD: 10, n: 2
Jackson <i>et al.</i> 2004	1-7, \bar{x} : 3, SD: 2, n: 9	trop. E-Pacific	
Anderson 2005	5-11, \bar{x} : 6, SD: 1, n: 9	Maldives	

Species/Reference	Group size	Area	Group characteristics
Ferguson <i>et al.</i> 2006	\bar{x} : 5, n: 41	trop. E-Pacific	
Maze-Foley, Mullin 2006	1-12, \bar{x} : 7, SD: 1, n: 13	Gulf of Mexico	
Barlow, Forney 2007	\bar{x} : 7, n: 23	W-USA	
Foote <i>et al.</i> 2007	\bar{x} : 8, n: 91	NE-Atlantic	
De Stephanis <i>et al.</i> 2008	3- 13, \bar{x} : 8, SD: 4, n: 33	Strait of Gibraltar	
Jackson <i>et al.</i> 2008	\bar{x} : 8, n: 17	trop. E-Pacific	
Oswald <i>et al.</i> 2008	\bar{x} : 6, SD: 5, n: 11	E-Pacific	
Best <i>et al.</i> 2010	1-20, \bar{x} : 3, SD: 3, n: 723	South Africa	offshore, mostly beyond 200m isobath
Ford <i>et al.</i> 2010	northern resident: 3-30, \bar{x} : 12, n: 20 transient: 1-23, \bar{x} : 7, n: 36	W-Canada	
Weir <i>et al.</i> 2010	1-17, \bar{x} : 6, SD: 3, n: 32	trop. E-Atlantic off Africa	coastal and oceanic, no difference in group size between habitats, mainly traveling
Barrett-Lennard <i>et al.</i> 2011	Unimak Island \bar{x} :10, SD: 8, n: 64 E-Aleutians \bar{x} : 5, SD: 3, n: 37	Aleutians, Alaska	transient killer whales
Beck <i>et al.</i> 2012	Scotland: 1-15, \bar{x} : 5-6, SD: 3, n: 60; Iceland: 2-80, \bar{x} : 15, SD: 12, n: 38	Scotland (nearshore), Iceland	feeding on herring off Iceland and on seals in Scotland; Scottish pods more consistent in size than those of Iceland
Higdon <i>et al.</i> 2012	1-100, \bar{x} : 8, median: 4, n: 246	Canadian Arctic	
Häussermann <i>et al.</i> 2013	1-60, \bar{x} : 5, n: 119	Chilean Patagonia	without 2 outliers of 30 and 60: 1-15, \bar{x} : 4, n: 117
Capella <i>et al.</i> 2014	1-16, \bar{x} : 4, SD: 4, n: 63	Magellan Strait	with calves 2-16, \bar{x} : 5, SD: 3, n: 43 without calves \bar{x} : 3, SD: 2, n: 20
Dunn, Claridge 2014	1-12, \bar{x} : 4, SD: 3, n: 34	Bahamas	traveling, feeding (on cetacea)
Fearnbach <i>et al.</i> 2014	3-120, median: 15, n: 331	Gulf of Alaska, Aleutian Islands, Bering Sea	fish-eating killer whales traveling and feeding together, likely multiple matriline
Risso's dolphin/ Leatherwood <i>et al.</i> 1980	1-220, \bar{x} : 23, SD: 38, n: 184	eastern N-Pacific	
Jennings 1982	3-25, \bar{x} : 11, SD: 6, n: 11	Gulf of Mexico	1 add. pod of a minimum of 157 ind. consisted of 18 sub-groups of 1-25 ind., \bar{x} : 9, SD: 6, spread over 18.1km
Smith <i>et al.</i> 1986	\bar{x} : 21, n: 8	W-USA	
Holt, Jackson 1987	1-78, \bar{x} : 16, SD: 20, n: 18	trop. E-Pacific	
Findlay <i>et al.</i> 1992	1-80, \bar{x} : 11, SD: 13, n: 43	southern Africa	
Notarbartolo di Sciarra <i>et al.</i> 1993	3-55, \bar{x} : 17, SD: 16, n: 12	Italy	
Wade, Gerrodette 1993	\bar{x} : 12, SD: 1.2, n: 194	trop. E-Pacific	small groups

Species/Reference	Group size	Area	Group characteristics
Mangels, Gerrodette 1994	1-332, \bar{x} : 36, SD: 61, n: 82	E-Pacific	
Shane 1994	1-100, \bar{x} : 13, SD: 14, median: 10, n: 72	Santa Catalina Island, California	mostly traveling; density increased as density of pilot whales decreased
Barlow 1995	\bar{x} : 18, n: 28	California	
Forney <i>et al.</i> 1995	\bar{x} : 48, n: 19	California	
Ballance <i>et al.</i> 1996	4-500, \bar{x} : 48, SD: 18, n: 49	N/NW-Indian Ocean	
Davis, Fargion 1996	1-78, \bar{x} : 10, SD: 2, n: 83	Gulf of Mexico	
Barlow <i>et al.</i> 1997	2-1600, \bar{x} : 96, SD: 252, n: 41	California	incl. 6 mixed-species pods
Baldwin <i>et al.</i> 1999	2-500, \bar{x} : 50, n: 43	Oman	
Carretta <i>et al.</i> 2000	\bar{x} : 33, n: 23	San Clemente Island, California	summer: \bar{x} : 27, n: 7; winter: \bar{x} : 36, n: 16
Ritter 2001	6-18, \bar{x} : 11, SD: 4, n: 6	La Gomera (Canary Islands)	
Palacios, Salazar 2002	\bar{x} : 14, median: 7, n: 117	Galápagos Islands	
Mullin, Fulling 2003	\bar{x} : 15, SD: 4, n: 18	SE-USA	
Gaspari 2004	2-70, \bar{x} : 15, SD: 13, n: 117	Ligurian Sea (Mediterranean)	84% of sightings consisted of pods of 2-20 ind.; pod size varied significantly between years (Kruskal-Wallis H: 16.63, p: 0.01, n: 105), but not between months
Jackson <i>et al.</i> 2004	2-37, \bar{x} : 11, SD: 9, n: 28	trop. E-Pacific	
Anderson 2005	2-300, \bar{x} : 33, SD: 69, n: 184	Maldives	
Cañadas <i>et al.</i> 2005	\bar{x} : 13, SD: 11, n: 62	Alborán Sea (Mediterranean)	
Gannier 2005	2-35, \bar{x} : 13, n: 19	Mediterranean Sea	
Barlow 2006	\bar{x} : 17, n: 7	Hawaii	
Ferguson <i>et al.</i> 2006	\bar{x} : 19, n: 189	trop. E-Pacific	
Gómez de Segura <i>et al.</i> 2006	1-18, \bar{x} : 4, median: 2, n: 15	E-Spain (Mediterranean)	
Maze-Foley, Mullin 2006	1-40, \bar{x} : 10, SD: 1, n: 147	Gulf of Mexico	
Barlow, Forney 2007	\bar{x} : 22, n: 110	W-USA	
Azzellino <i>et al.</i> 2008	1-130, \bar{x} : 37, SD: 31, median 28, n: 43	Ligurian Sea (Mediterranean)	
Gómez de Segura <i>et al.</i> 2006	1-80, \bar{x} : 22, n: 17	SE-Spain	
Jackson <i>et al.</i> 2008	\bar{x} : 19, n: 48	trop. E-Pacific	
Oswald <i>et al.</i> 2008	\bar{x} : 14, SD: 21, n: 41	E-Pacific	
Pereira 2008	1-180, \bar{x} : 12, SD: 10, n: 74, excl. 4 pods of 55-180 socializing ind.	Azores	77% traveling, 13% socializing, 5% feeding; calves observed for 11 sightings
Hildebrand 2009	1-50, \bar{x} : 16, SD: 13, n: 17	S-California	
Laran <i>et al.</i> 2010	April-September: \bar{x} : 10, SD: 4; October-March: \bar{x} : 11, SD: 5; n(total): 10	Ligurian Sea (Mediterranean)	

Species/Reference	Group size	Area	Group characteristics
Bearzi <i>et al.</i> 2011 (review)	1-130; \bar{x} : 17, SD: 18, n: 402	Mediterranean Sea	sub-groups formed
Fortuna <i>et al.</i> 2011	1-10, \bar{x} : 4, SD: 3, n: 11	Adriatic Sea (Mediterranean)	
De Boer <i>et al.</i> 2012	1-6, \bar{x} : 2, SD: 1, n: 96	Bardsey Island, W-Wales, UK	offshore area, but shallow water; calves and juveniles seen regularly
Palka 2012	\bar{x} : 7, SD: 2, n: 112	NE-USA	
Silva <i>et al.</i> 2014	1-45, \bar{x} : 10, SD: 8, n: 722	Azores	
Di Tullio <i>et al.</i> 2016	\bar{x} : 78, SD: 108, n: 9	SW-Atlantic outer shelf/ slope	7 sightings < 50 individuals
Hammond <i>et al.</i> 2017	\bar{x} : 7, n: 75	NE-Atlantic	
Laran <i>et al.</i> 2017	\bar{x} : 3, n: 23	NW-Mediterranean	winter \bar{x} : 2, n: 15, summer \bar{x} : 4, n: 8
Bottlenose dolphin /Saayman, Taylor 1973	3-1000, \bar{x} : 140, SD: 206, n: 93	South Africa (Eastern Cape)	typically dispersed in sub-groups over several km ²
Würsig 1978	8-22, \bar{x} : 15, SD: 3, n: 191	Argentina	
Smith <i>et al.</i> 1986	\bar{x} : 17, n: 6	W-Greenland	
Holt, Jackson 1987	1-633, \bar{x} : 77, SD: 129, n: 26	trop. E-Pacific	
Scott, Chivers 1990	1-10000, \bar{x} : 57, median: 10, n: 3170	trop. E-Pacific	1-10: 52%, 11-49: 38%, 50+: 10%, mixed-species pods: 24% (mainly short-finned pilot whale, pantropical spotted and spinner dolphins)
Breese, Tershy 1993	Pods < 5km offshore: \bar{x} : 9, SD: 7, n: 66, pods \geq 5km offshore: \bar{x} : 110, SD: 63, n: 5	Gulf of California	
Wade, Gerrodette 1993	\bar{x} : 23, SD: 5, n: 298	trop. E-Pacific, often nearshore	
Jefferson, Lynn 1994	3-20, \bar{x} : 10, SD: 7, n: 6	Caribbean, Gulf of Mexico	
Mangels, Gerrodette 1994	1-2233, excl. pod of 2233: \bar{x} : 29, SD: 51, n: 155	E-Pacific	
Barlow 1995	\bar{x} : 7, n: 14	California	
Forney <i>et al.</i> 1995	\bar{x} : 18, n: 8	California	
Ballance <i>et al.</i> 1996	2-750, \bar{x} : 53, SD: 21, n: 41	N/NW-Indian Ocean	
Davis, Fargion 1996	1-90, \bar{x} : 12 SD: 1, n: 166	Gulf of Mexico	
Barlow <i>et al.</i> 1997	2-500, \bar{x} : 69, SD: 87, n: 70	California	incl. 17 mixed-species pods
Bearzi <i>et al.</i> 1997	1-65, \bar{x} : 7, SD: 7, median: 5, n: 787	Adriatic Sea (Croatia)	Pods of adults only 1-17, \bar{x} : 4, SD: 3, n: 415 Pods with \geq 1 juv. 2-31, \bar{x} : 7, SD: 4, n: 176 Pods with \geq 1 calf: 2-65, \bar{x} : 12, SD: 8, n: 196 differences significant
Mignucci-Giannoni 1998	1-50, \bar{x} : 8, n: 147	Caribbean Sea	single ind. 24.9%; 2-4 ind. 31.0%; 5-10 ind. 18.6%; 11-

Species/Reference	Group size	Area	Group characteristics
			19 ind. 14.5%; 20-39 ind. 7.6%; 40-50 ind. 3.4%; summer, fall \bar{x} : 6; spring, winter \bar{x} : 8
Hooker <i>et al.</i> 1999	\bar{x} : 11, SD: 13, n: 7	Gully (S off Nova Scotia)	
Carretta <i>et al.</i> 2000	\bar{x} : 10, n: 14	San Clemente Island, California	summer: \bar{x} : 14, n: 8, winter: \bar{x} : 6, n: 6; inshore: \bar{x} : 8, n: 10 offshore: \bar{x} : 3, n: 4
Laran, Gannier 2001	1-35, \bar{x} : 12, SD: 5, n: 6	Marquesas (S-Pacific)	
Ritter 2001	1-80, \bar{x} : 14, SD: 13, n: 230	La Gomera (Canary Islands)	
Weir <i>et al.</i> 2001	1-30, \bar{x} : 6, n: 21	N-Scotland	\bar{x} : 13 for offshore sightings in September + October
Palacios, Salazar 2002	\bar{x} : 33, median: 15, n: 366	Galápagos Islands	
Mullin, Fulling 2003	\bar{x} : 12, SD: 3, n: 31	SE-USA	
Jackson <i>et al.</i> 2004	4-37, \bar{x} : 15, SD: 11, n: 11	trop. E-Pacific	
López <i>et al.</i> 2004	\bar{x} : 14, SD: 11, n: 21	Galicia (N-Spain)	
Anderson 2005	1-170, \bar{x} : 15, SD: 39, n: 197	Maldives	
Cañadas <i>et al.</i> 2005	\bar{x} : 27, SD: 29, n: 248	S-Spain	
Claridge 2006	1-50, \bar{x} : 11, SD: 17, median: 3, n: 8	Great Abaco Island (Bahamas)	
Ferguson <i>et al.</i> 2006	\bar{x} : 24, n: 274	trop. E-Pacific	
Gómez de Segura <i>et al.</i> 2006	2-40, \bar{x} : 11, median: 7, n: 19	E-Spain (Mediterranean)	
Maze-Foley, Mullin 2006	1-220, \bar{x} : 21, SD: 3, n: 151	Gulf of Mexico	
Barlow, Forney 2007	\bar{x} : 12, n: 38	W-USA	
Kiszka <i>et al.</i> 2007	\bar{x} : 14, SD: 12, n: 110	Bay of Biscay	
De Stephanis <i>et al.</i> 2008	1-200, \bar{x} : 24, SD: 33, n: 63	Strait of Gibraltar	
Dulau-Drouot <i>et al.</i> 2008	10-100, \bar{x} : 48, SD: 31, n: 19	La Réunion (Indian Ocean)	
Hermans, Pistorius 2008	15-50, \bar{x} : 32, n: 9	Aldabra Atoll (Indian Ocean)	
Jackson <i>et al.</i> 2008	\bar{x} : 24, n: 149	trop. E-Pacific	
Oswald <i>et al.</i> 2008	\bar{x} : 41, SD: 61, n: 67	E-Pacific	single-species: \bar{x} : 27, SD: 70, n: 34
Hildebrand 2009	5-456, \bar{x} : 66, SD: 117, n: 13	S-California	
Larese, Deakos 2010	1-60, \bar{x} : 7, n: 57	Palmyra Atoll	
Fortuna <i>et al.</i> 2011	1-48, \bar{x} : 4, SD: 6, n: 126	Adriatic Sea (Mediterranean)	coastal and offshore waters
Palka 2012	\bar{x} : 15, SD: 4, n: 91	NE-USA	
Baird <i>et al.</i> 2013	1-200, \bar{x} : 9, SD: 16, median: 5, n: 227	Hawaii	
Pleslić <i>et al.</i> 2013	\bar{x} : 7, SD: 24, n: 569	Adriatic Sea (Mediterranean)	calves often present
Holcer <i>et al.</i> 2014	\bar{x} : 4, SD: 1, n: 61	Adriatic Sea (Mediterranean)	coastal and offshore waters

Species/Reference	Group size	Area	Group characteristics
Zaeschmar <i>et al.</i> 2014	5-250, \bar{x} : 63, SD: 43, n: 36	N-New Zealand, shelf waters	foraging, traveling in association with false killer whales
Aïssi <i>et al.</i> 2015	\bar{x} : 3, SD: 2, n: 15	central Mediterranean	
Correia <i>et al.</i> 2015	2-35, \bar{x} : 9, SD: 7, n: 32	Portugal (E-Atlantic)	
Oudejans <i>et al.</i> 2015	1-74, \bar{x} : 22, SD: 19, n: 51	Ireland	distinct coastal and offshore communities
Di Tullio <i>et al.</i> 2016	\bar{x} : 37, SD: 8, n: 33	SW-Atlantic outer shelf/ slope	
Laran <i>et al.</i> 2017	\bar{x} : 4, n: 57	NW-Mediterranean	winter \bar{x} : 3, n: 39 summer \bar{x} : 6, n: 18
Rough-toothed dolphin/ Wade, Gerrodette 1993	\bar{x} : 15, SD: 3, n: 135	trop. E-Pacific	small groups; everywhere in study area in low density
Mangels, Gerrodette 1994	2-58, \bar{x} : 10, SD: 12, n: 22	E-Pacific	
Davis, Fargion 1996	3-48, \bar{x} : 11, SD: 3, n: 17	Gulf of Mexico	
Mignucci-Giannoni 1998	3-30, \bar{x} : 10, n: 8	Caribbean Sea	3-4 ind. 25%; 5-10 ind. 50%; 15-30 ind. 25%; associated with humpback whales in 4 sightings
Barlow <i>et al.</i> 1997	5-17, \bar{x} : 11, SD: 4, n: 6	California	incl. 1 mixed-species pod
Gannier 2000	1-35, \bar{x} : 11, SD: 11, n: 32	Society Islands (S-Pacific)	
Laran, Gannier 2001	5-12, \bar{x} : 8, SD: 2, n: 4	Marquesas (S-Pacific)	
Pitman, Stinchcomb 2002	10-20, n: 4	W-Costa Rica	feeding on Mahimahi
Ritter 2002	1-50, \bar{x} : 17, SD: 12, n: 137	Canary Islands	calves present: n: 13, juveniles present: n: 39, juveniles + calves: n: 8
Anderson 2005	6-40, \bar{x} : 22, SD: 13, n: 5	Maldives	
Barlow 2006	\bar{x} : 17, n: 18	Hawaii	
Ferguson <i>et al.</i> 2006	\bar{x} : 15, n: 120	trop. E-Pacific	
Maze-Foley, Mullin 2006	2-28, \bar{x} : 14, SD: 2, n: 21	Gulf of Mexico	
Baird <i>et al.</i> 2008b	2-109, median: 7, n: 72	Hawaii	larger groups comprised of sub-groups of 2–10 ind. separated from other sub-groups by 10's -100's m; longer encounter durations resulted in detection of more scattered sub-groups; often associated with melon-headed whales; no quantification of calf presence
Jackson <i>et al.</i> 2008	\bar{x} : 10, n: 76	trop. E-Pacific	
Oswald <i>et al.</i> 2008	\bar{x} : 22, SD: 28, n: 8	E-Pacific	\bar{x} : 12, SD: 11, n: 6
De Boer 2010a	at least 50, n: 1	Gabon	traveling, foraging incl. cooperative prey-herding; sub-groups of 2-8 individuals varied from tight to loose (2-5 body lengths), 6 juveniles + 2 calves present

Species/Reference	Group size	Area	Group characteristics
White-beaked dolphin/ Kingsley, Reeves 1998	\bar{x} : 9, SD: 8, n: 17	Gulf of St. Lawrence	
Reeves <i>et al.</i> 1999b	up to 1500	throughout range	large groups rare; groups of juveniles seem to travel separately from mixed groups of adults and calves
Lien <i>et al.</i> 2001	10-several hundred	Atlantic	Pods of several hundred esp. in NE-Atlantic; smaller groups of 10-20 individuals typical in NW-Atlantic
Weinrich <i>et al.</i> 2001	\bar{x} : 4, n: 495	N-Scotland	
Compton <i>et al.</i> 2007	3-6, \bar{x} : 4, n: 5	N-Atlantic	
Simrad, Gowans 2008	\bar{x} : 8, SD: 5, n: 12	Halifax area, nearshore	50.0% of groups contained young
Pike <i>et al.</i> 2009b	1-100, \bar{x} : 6, n: 400	Iceland	
Hansen, Heide-Jørgensen 2013	1-15, \bar{x} : 5, n: 55	W-Greenland	
Fall, Skern-Mauritzen (2014)	1-150, \bar{x} : 8, n: ~180	Barents Sea	
Bertulli 2015	1-300, \bar{x} : 9, SD: 16, n: 1119	Iceland	20% pods included immatures
Hammond <i>et al.</i> 2017	\bar{x} : 4, SD: 1, n: 118	NE-Atlantic	
Atlantic white-sided dolphin/ Winn, Edel 1982	2-500, \bar{x} : 42, n: 215	N-Atlantic: Nova Scotia to Cape Cod	
Kingsley, Reeves 1998	\bar{x} : 8, SD: 9, n: 44	Gulf of St. Lawrence	often several of these pods were loosely associated in larger groups, but were recorded separately
Hooker <i>et al.</i> 1999	\bar{x} : 9, SD: 8, n: 148	Gully (S off Nova Scotia)	
Weinrich <i>et al.</i> 2001	2-2500, \bar{x} : 52, SD: 91, n: 985	S-Gulf of Maine (NE-USA)	June/July \bar{x} : 35, SD: 45, calves rare; August/September \bar{x} : 72, SD: 111, calves present in > 50% of pods
Weir <i>et al.</i> 2001	\bar{x} : 16, n: 290	N-Scotland	
Macleod <i>et al.</i> 2003	1-20, \bar{x} : 5, SD: 3, n: 79	Scotland continental slope	
Wall <i>et al.</i> 2006	1-60, \bar{x} : 13, SD: 11, n: 31	W-Ireland	1 calf encounter in a pod of 10 ind.
Compton <i>et al.</i> 2007	2-600, \bar{x} : 55, n: 34	N-Atlantic	
Waring <i>et al.</i> 2008	3-60, \bar{x} : 15, n: 7	Middle Atlantic Ridge	
Palka 2012	\bar{x} : 15, SD: 2, n: 15	NE-USA	
Pacific white-sided dolphin/ Sullivan, Houck 1979	6-720, \bar{x} : 236, n: 7	N-California	sightings 11-161km offshore
Leatherwood <i>et al.</i> 1984	1-6000, \bar{x} : 88, SD: 366, n: 1269	NE-Pacific	seasonal and latitudinal group size variation
Smith <i>et al.</i> 1986	\bar{x} : 150, n: 7	W-Greenland	coastal and offshore sightings
Stacey, Baird 1991	1-1000, \bar{x} : 62, median: 15, n: 156	W-Canada	
Buckland <i>et al.</i> 1993	1-400, \bar{x} : 30, n: 69	N-Pacific	

Species/Reference	Group size	Area	Group characteristics
Black 1994	1-4000, \bar{x} : 203, SD: 395, n: 443	Monterey Bay, California + adjacent waters	50.6% of groups contained 50 or fewer individuals, large group size associated with under-water canyon; traveling: \bar{x} : 438, SD: 463; resting: \bar{x} : 367, SD: 295; feeding: \bar{x} : 204, SD: 269; socializing: \bar{x} : 167, SD: 224; milling: \bar{x} : 116, SD: 203
Dahlheim, Towell 1994	1-500, \bar{x} : ~36, n: 55	SE-Alaska	
Mangels, Gerrodette 1994	1-1245, excl. pod of 1245: \bar{x} : 59, SD: 196, n: 19	E-Pacific	
Shane 1994	1-30, \bar{x} : 10, SD: 8, median: 8, n: 43	Santa Catalina Island, California	mostly traveling
Barlow 1995	\bar{x} : 31, n: 12	California	
Forney <i>et al.</i> 1995	\bar{x} : 152, n: 21	California	
Heise 1996	\bar{x} : 103, SD: 129, n: 92	W-Canada	groups organized in sub-groups
Carretta <i>et al.</i> 2000	\bar{x} : 24, n: 26	San Clemente Island, California	
Morton 2000	1-1000, \bar{x} : 62, n: 127	British Columbia deep nearshore waters	group size distribution: 1-10: 18%, 11-50: 42%, 51-100: 25%, 101-200: 9%, 201-500: 5%, >500: 1%
Jackson <i>et al.</i> 2004	1-1267, \bar{x} : 16, SD: 21, n: 23, excl. pod of 1267	trop. E-Pacific	
Barlow, Forney 2007	\bar{x} : 79, n: 71	W-USA	
Oswald <i>et al.</i> 2008	\bar{x} : 32, SD: 44, n: 23	E-Pacific	single-species: \bar{x} : 9, SD: 10, n: 16
Hildebrand 2009	1-100, \bar{x} : 14, SD: 20, n: 48	S-California	
Ford <i>et al.</i> 2010	1-1500, n: 183	W-Canada	80% of pods with < 50 ind.
Henderson <i>et al.</i> 2011	3-200, \bar{x} : 36, SD: 2, median: 25, n: 525	S-California Bight	pod of 200 foraging in sub-groups, then fusing for travel; fast/moderately traveling pods larger than slow pods
Campbell <i>et al.</i> 2015	\bar{x} : 18, SD: 36, n: 107	S-California	winter \bar{x} : 15, SD: 18, spring: \bar{x} : 12, SD: 14, summer \bar{x} : 35, SD: 72, fall \bar{x} : 18, SD: 20
Hourglass dolphin/ Miyazaki, Kato 1988	2- ~100, \bar{x} : 19, n: 21	Southern Ocean	group size increasing with latitude, one mother-calf pair encountered
Kasamatsu, Joyce 1995	\bar{x} : 7, SD: 1, n: 110	Southern Ocean	
Goodall 1997	1-16, \bar{x} : 6	South American sector of Antarctic and sub-Antarctic	feeding, traveling
Branch, Butterworth 2001	\bar{x} : 8, SD: 5, n: 105	Southern Ocean	
Dellabianca <i>et al.</i> 2012	1-12, \bar{x} : 5, SD: 3, median: 5, n: 19	Patagonian Shelf, Atlantic Southern Ocean	distinct coastal and oceanic groups, no calves observed, all sightings in or close to areas of high productivity

Species/Reference	Group size	Area	Group characteristics
Santora 2012	2-6, except for 2 pods of 15 and 25 individuals, \bar{x} : 5, SD: 5, n: 29	N-South Shetland Islands, Drake passage	
Dusky dolphin/ Cipriano 1985	1- >1000, typically 100-400, \bar{x} : 250, n: 43	New Zealand, Kaikoura	larger daily range and occur further offshore in winter
Findlay <i>et al.</i> 1992	2-800, \bar{x} : 35, SD: 104, n: 100	southern Africa	no seasonal variation in group size
Oswald <i>et al.</i> 2008	\bar{x} : 40, SD: 36, n: 4, excl. pod of 1167	trop. E-Pacific	all pods within 2h, no whistles detected
Markowitz 2004	thousands	New Zealand, Kaikoura	resting, socializing diurnally, often mixed-species pods; dispersal as moving offshore in afternoon before feeding starts, re-grouping in morning; noisy leaps esp. when groups are large and spread out
Elwen <i>et al.</i> 2010	\bar{x} : 17, median: 6, max: 500, n: 177	South Africa, nearshore	large pods are associated with strong upwelling
Fraser's dolphin/ Miyazaki, Wada 1978b	400-500, n: 1	off Nauru	
Holt, Jackson 1987	17-533, \bar{x} : 365, SD: 209, n: 4	trop. E-Pacific	
Findlay <i>et al.</i> 1992	7-1000, \bar{x} : 183, SD: 277, n: 14	southern Africa	
Wade, Gerrodette 1993	\bar{x} : 395, SD: 79, n: 25, max: 1500	trop. E-Pacific	
Jefferson, Leatherwood 1994	3-2500	throughout range	typ. in large pods, often associated with melon-headed whales
Anderson 2005	40-1000, \bar{x} : 215, SD: 266, n: 14	Maldives	
Barlow 2006	\bar{x} : 333, n: 2	Hawaii	
Claridge 2006	40-150, \bar{x} : 95, SD: 78, n: 2	Great Abaco Isl. (Bahamas)	
Ferguson <i>et al.</i> 2006	\bar{x} : 440, n: 11	trop. E-Pacific	
Gero, Whitehead 2006	10-125, \bar{x} : 59, SD: 40, n: 6	Dominica (Caribbean)	
Maze-Foley, Mullin 2006	34-117, \bar{x} : 65, SD: 26, n: 3	Gulf of Mexico	
Dulau-Drouot <i>et al.</i> 2008	50-300, \bar{x} : 158, SD: 111, n: 6	La Réunion (Indian Ocean)	typically in tight pods, often associated with melon-headed whales
Jackson <i>et al.</i> 2008	\bar{x} : 73, n: 2	trop. E-Pacific	
Weir <i>et al.</i> 2008	60-150, \bar{x} : 110, SD: 37, n: 3	Gulf of Guinea, Angola	typ. in tight pods
Rinaldi, Rinaldi 2011	\bar{x} : 72, n: 123	Caribbean	
Spinner dolphin/ Holt, Jackson 1987	7-633, \bar{x} : 183, SD: 160, n: 34	trop. E-Pacific	
Wade, Gerrodette 1993	\bar{x} : 121, SD: 15, n: 390, max: 1700	trop. E-Pacific	often in mixed-species pods with pantropical spotted dolphins of >300 individuals
Mangels, Gerrodette 1994	4-830, \bar{x} : 187, SD: 184, n: 43	E-Pacific	
Östmann 1994	6-300, \bar{x} : 77, SD: 51, n: 134, mostly 21-100	Hawaii	pod size seems limited by food, pods consist of sub-

Species/Reference	Group size	Area	Group characteristics
			groups, calves occ. observed swimming with females other than mother
Poole 1995	4-92, \bar{x} : 31, SD: 3, n: 249	Mo'orea, French Polynesia	most and largest pods in lee of island
Ballance <i>et al.</i> 1996	2-1200, \bar{x} : 170, SD: 30, n: 66	N/NW-Indian Ocean	
Davis, Fargion 1996	9-215, \bar{x} : 60, SD: 24, n: 14	Gulf of Mexico	
Barlow <i>et al.</i> 1997	1-925, \bar{x} : 212, SD: 274, n: 20	California	incl. 11 mixed-species pods
Mignucci-Giannoni 1998	1-500, \bar{x} : 54, n: 37	Caribbean Sea	1-5 ind. 32.5%; 6-10 ind. 18.9%; 11-30 ind. 18.9%; 31-100 ind. 18.9%; 200 ind. 5.4%; 500 ind. 5.4%
Gannier 2000	3-100, \bar{x} : 34, SD: 23, n: 43	Society Islands (S-Pacific)	
Laran, Gannier 2001	2-100, \bar{x} : 30, SD: 6, n: 17	Marquesas (S-Pacific)	
Gerrodette, Forcada 2002a	1-600, \bar{x} : 122, n: 591	trop. E-Pacific	
Palacios, Salazar 2002	\bar{x} : 502, median: 200, n: 303	Galápagos Islands	
Anderson 2005	6-750, \bar{x} : 58, SD: 142, n: 466	Maldives	
Ferguson <i>et al.</i> 2006	\bar{x} : 101, n: 194	trop. E-Pacific	\bar{x} : 109, n: 138 eastern spinner dolphin \bar{x} : 83, n: 56 whitebelly spinner dolphin
Maze-Foley, Mullin 2006	6-800, \bar{x} : 152, SD: 31, n: 40	Gulf of Mexico	not associated with pantropical spotted dolphins, islands, banks or coastal waters
Dulau-Drouot <i>et al.</i> 2008	5-200, \bar{x} : 51, SD: 45, n: 28	La Réunion (Indian Ocean)	feeding pods significantly larger (\bar{x} : 124) than resting pods (\bar{x} : 16); no significant correlation between group size and distance to shore
Hermans, Pistorius 2008	100-500, \bar{x} : 69, n: 60	Aldabra Atoll, Indian Ocean	
Jackson <i>et al.</i> 2008	\bar{x} : 169, n: 177	trop. E-Pacific	incl. eastern spinner, whitebelly and southwestern spinner
Oswald <i>et al.</i> 2008	\bar{x} : 230, SD: 200, n: 41	E-Pacific	single-species: \bar{x} : 123, SD: 132, n: 11
Baird <i>et al.</i> 2013	1-185, \bar{x} : 39, SD: 35, median: 28, n: 198	Hawaii	7 out of 8 pods over >1000m depth had only 1-3 individuals mixed with >30 pantropical spotted dolphins; a coastal and an oceanic population
Hill <i>et al.</i> 2013	\bar{x} : 33, n: 55	Mariana Islands	
Costa 2015	1-350, \bar{x} : 43, SD: 36, n: 125	Red Sea	larger group size when encountered in resting areas than otherwise
Condet, Dulau-Drouot 2016	6-250, \bar{x} : 57, median: 50, n: 240	La Reunion (Indian Ocean)	no sign. group size variations across behavioural states

Species/Reference	Group size	Area	Group characteristics
Di Tullio <i>et al.</i> 2016	\bar{x} : 315, SD: 70, n: 15	SW-Atlantic outer shelf/ slope	
Pantropical spotted dolphin/ Holt, Jackson 1987	7-633, \bar{x} : 169, SD: 142, n: 47	trop. E-Pacific	
Wade, Gerrodette 1993	\bar{x} : 128, SD: 11, n: 604, max.: 2400	trop. E-Pacific	most abundant cetacean species around Hawaii
Hansen <i>et al.</i> 1994	\bar{x} : 34, n: 98	Gulf of Mexico	
Jefferson, Lynn 1994	2-60, \bar{x} : 22, SD: 21, n: 10	Caribbean, Gulf of Mexico	
Mangels, Gerrodette 1994	18-2233, excl. pod of 2233: \bar{x} : 137, SD: 112, n: 49	E-Pacific	
Davis, Fargion 1996	3-225, \bar{x} : 49, SD: 10, n: 127	Gulf of Mexico	
Barlow <i>et al.</i> 1997	6-925, \bar{x} : 166, SD: 225, n: 34	California	incl. 13 mixed-species pods
Laran, Gannier 2001	2-150, \bar{x} : 32, SD: 8, n: 23	Marquesas (S-Pacific)	
Gerrodette, Forcada 2002a	1- >600, \bar{x} : 114, n: 1332	trop. E-Pacific	
Palacios, Salazar 2002	\bar{x} : 474, median: 250, n: 519	Galápagos Islands	
Mullin, Fulling 2003	\bar{x} : 78, SD: 19, n: 6	SE-USA	
Anderson 2005	4-500, \bar{x} : 161, SD: 251, n: 58	Maldives	
Moreno <i>et al.</i> 2005	3-250, n: 44	Brazil	
Barlow 2006	\bar{x} : 70, n: 14	Hawaii	
Claridge 2006	2-30, \bar{x} : 12, SD: 12, median: 7, n: 9	Great Abaco Island (Bahamas)	
Ferguson <i>et al.</i> 2006	\bar{x} : 131, n: 293	trop. E-Pacific	
Gero, Whitehead 2006	3-200, \bar{x} : 58, SD: 62, n: 28	Dominica (Caribbean)	
Maze-Foley, Mullin 2006	3-650, \bar{x} : 71, SD: 4, n: 381	Gulf of Mexico	no association with tuna
Dulau-Drouot <i>et al.</i> 2008	3-150, \bar{x} : 79, SD: 43, n: 10	La Réunion (Indian Ocean)	
Jackson <i>et al.</i> 2008	\bar{x} : 95, n: 209	trop. E-Pacific	
Oswald <i>et al.</i> 2008	\bar{x} : 180, SD: 118, n: 66	E-Pacific	single-species: \bar{x} : 106, SD: 118, n: 35
Fulling <i>et al.</i> 2011	1-115, \bar{x} : 64, SD: 37, n: 17	Mariana Islands	
Baird <i>et al.</i> 2013	1-350, \bar{x} : 65, SD: 50, median: 55, n: 398	Hawaii	leaping frequently
Di Tullio <i>et al.</i> 2016	\bar{x} : 104, SD: 43, n: 7	SW-Atlantic outer shelf/ slope	
Herzing, Elliser 2016	7-150, \bar{x} : 57, SD: 45, n: 14	SE-Florida	
Atlantic spotted dolphin/ Davis, Fargion 1996	3-55, \bar{x} : 21, SD: 4, n: 30	Gulf of Mexico	
Mignucci-Giannoni 1998	1-50, \bar{x} : 14, n: 26	Caribbean Sea	1-4 ind. 30.8%; 5-10 ind. 34.6%; 11-29 ind. 15.4%; 30-50 ind. 19.2%
Roden, Mullin 2000	19-48, \bar{x} : 30, SD: 3, n: 8	N-Caribbean	
Ritter 2001	1-650, \bar{x} : 83, SD: 182, n: 103	La Gomera (Canary Islands)	

Species/Reference	Group size	Area	Group characteristics
Moreno <i>et al.</i> 2005	2-200, \bar{x} : ~27, n: 37	Brazil	90% groups < 50 individuals
Claridge 2006	1-30, \bar{x} : 10, SD: 7, median: 9, n: 68	Great Abaco Island (Bahamas)	
Maze-Foley, Mullin 2006	1-68, \bar{x} : 26, SD: 3, n: 35	Gulf of Mexico	
Palka 2012	\bar{x} : 24, SD: 10, n: 22	NE-USA	
Elliser, Herzing 2014	1-56, \bar{x} : 11, SD: 9, n: 251, 68% < 11	Bahamas (coastal/ shallow water)	groups significantly larger with calves: \bar{x} : 14, SD: 10, n: 143, than without: \bar{x} : 6, SD: 5, n: 108, F: 9.26, P < 0.005
Herzing, Elliser 2014	1-15, \bar{x} : 7, SD: 4, n: 48	Bahamas offshore	all during night-time feeding
Silva <i>et al.</i> 2014	1-500, \bar{x} : 42, SD: 56, n: 1399	Azores	
Read <i>et al.</i> 2014	\bar{x} : 26, SD: 4, n: 93	off Onslow Bay, NC (E-USA)	
Correia <i>et al.</i> 2015	2-25, \bar{x} : 11, SD: 6, n: 13	Portugal	
Papale <i>et al.</i> 2016	4-250, \bar{x} : 50, SD: 45, n: 90	Canary Islands	
Di Tullio <i>et al.</i> 2016	\bar{x} : 139, SD: 33, n: 40	SW-Atlantic outer shelf/ slope	spring: \bar{x} : 199, n: 25 autumn: \bar{x} : 39, n: 15
Striped dolphin/ Miyazaki Nishiwaki 1978	8-2136, \bar{x} : 267, n: 531	Japan	
Holt, Jackson 1987	1-1540, \bar{x} : 100, SD: 124, n: 47, excl. pod of 1540	trop. E-Pacific	
Miyashita 1992	\bar{x} : 121, n: 183	Japan	pods moving south are larger than those moving north earlier in the year
Wade, Gerrodette 1993	\bar{x} : 61, SD: 6, n: 799	trop. E-Pacific	much smaller pods than other small delphinids but very high encounter rate
Mangels, Gerrodette 1994	5-1450, \bar{x} : 113, SD: 215, n: 92	E-Pacific	
Barlow 1995	\bar{x} : 59, n: 21	California	67% pods > 100 ind.
Ballance <i>et al.</i> 1996	10-175, \bar{x} : 43, SD: 7, n: 37	N/NW-Indic	
Davis, Fargion 1996	4-150, \bar{x} : 41, SD: 8, n: 29	Gulf of Mexico	
Hooker <i>et al.</i> 1999	\bar{x} : 13, SD: 3, n: 29	Gully (S off Nova Scotia)	
Gordon <i>et al.</i> 2000	\bar{x} : 20, median: 10, n: 161	Ligurian Sea (Mediterranean)	pod size sign. higher offshore (depth > 2000m) than inshore (< 2000m); offshore: \bar{x} : 22, median: 12, n: 124 inshore: \bar{x} : 13, median: 6, n: 37
Ritter 2001	9-80, \bar{x} : 38, SD: 21, n: 27	La Gomera (Canary Islands)	
Gerrodette, Forcada 2002b	\bar{x} : 53, n: 1405	trop. E-Pacific	
Palacios, Salazar 2002	\bar{x} : 182, median: 50, n: 247	Galápagos Islands	
Jackson <i>et al.</i> 2004	18-508, \bar{x} : 188, SD: 169, n: 6	trop. E-Pacific	

Species/Reference	Group size	Area	Group characteristics
Gaspari 2004	2-200, \bar{x} : 17, n: 1492	Ligurian Sea (Mediterranean)	pod size varied sign. between years (Kruskal-Wallis H: 23.49, $p < 0.005$, n: 1327), and between months (H: 18.55, $p: 0.000$, n: 1327); largest pods in July/August; calves present in coastal + pelagic waters across all pod sizes
Anderson 2005	3-200, \bar{x} : 48, SD: 69, n: 41	Maldives	
Cañadas <i>et al.</i> 2005	\bar{x} : 58, SD: 80, n: 863	S-Spain	
Barlow 2006	\bar{x} : 43, n: 15	Hawaii	
Ferguson <i>et al.</i> 2006	\bar{x} : 55, n: 471	trop. E-Pacific	
Gómez de Segura <i>et al.</i> 2006	1-100, \bar{x} : 16, median: 7, n: 162	E-Spain (Mediterranean)	spring \bar{x} : 32, median: 30, n: 19, summer \bar{x} : 21, median: 11, n: 31, autumn \bar{x} : 14, median: 7, n: 52, winter \bar{x} : 10, median: 6, n: 60 no significant variation in density between seasons
Maze-Foley, Mullin 2006	8-150, \bar{x} : 46, SD: 5, n: 51	Gulf of Mexico	
Barlow, Forney 2007	\bar{x} : 49, n: 73	W-USA	
Kiszka <i>et al.</i> 2007	1-250, \bar{x} : 33, SD: 35, n: 187	Bay of Biscay	
Azzellino <i>et al.</i> 2008	1-240, \bar{x} : 26, SD: 30, median: 16, n: 389	Ligurian Sea (Mediterranean)	pods significantly smaller in July and September, group size correlation with latitude and longitude but pods of 1-5 ind. are equally distributed in study area, significant variation in group size between years
De Stephanis <i>et al.</i> 2008	1-2000, \bar{x} : 130, SD: 222, n: 118	Strait of Gibraltar	
Jackson <i>et al.</i> 2008	\bar{x} : 52, n: 139	trop. E-Pacific	
Oswald <i>et al.</i> 2008	\bar{x} : 73, SD: 163, n: 90	E-Pacific	single-species: \bar{x} : 45, SD: 40, n: 77
Waring <i>et al.</i> 2008	3-25, \bar{x} : 10, n: 12	Middle Atlantic Ridge	
Lauriano <i>et al.</i> 2009	1-35, \bar{x} : 8, SD: 7, n: 37	Ligurian Sea (Mediterranean)	
Laran <i>et al.</i> 2010	April-September: \bar{x} : 20, SD: 2; October-March: \bar{x} : 11, SD: 1; n(total): 243	Ligurian Sea (Mediterranean)	
Dimatteo <i>et al.</i> 2011	\bar{x} : 41, SD: 6, n: 41	S-Italy	
Fortuna <i>et al.</i> 2011	1-85, \bar{x} : 13, SD: 15, n: 85	Adriatic Sea (Mediterranean)	
Fulling <i>et al.</i> 2011	7-44, \bar{x} : 27, SD: 9, n: 10	Mariana Islands	
Panigada <i>et al.</i> 2011	summer: 1-170, \bar{x} : 14, SD: 23, n: 274, winter: 1-57, \bar{x} : 8, SD: 6, n: 114	Ligurian Sea (Mediterranean)	larger groups in summer likely due to higher food abundance
Palka 2012	\bar{x} : 46, SD: 10, n: 65	NE-USA	
Baird <i>et al.</i> 2013	2-110, \bar{x} : 28, SD: 23, median: 25, n: 29	Hawaii	leaping frequently

Species/Reference	Group size	Area	Group characteristics
Silva <i>et al.</i> 2014	3-150, \bar{x} : 43, SD: 31, n: 194	Azores	
Aïssi <i>et al.</i> 2015	3-100, \bar{x} : 18, SD: 20, n: 17	central Mediterranean	
Laran <i>et al.</i> 2017	\bar{x} : 9, n: 307	NW-Mediterranean	winter \bar{x} : 5, n: 138 summer \bar{x} : 11, n: 169
Panigada <i>et al.</i> 2017	\bar{x} : 12, n: 707	W- and S-Italy	
Clymene dolphin/ Mullin <i>et al.</i> 1994b	\bar{x} : 42, SD: 5, n: 29	Gulf of Mexico	calves present in 45% of pods
Davis, Fargion 1996	2-200, \bar{x} : 40, SD: 12, n: 30	Gulf of Mexico	
Fertl <i>et al.</i> 2003	1-1000, \bar{x} : 76, SD: 11 median: 47, n: 105	W-Atlantic	
Mullin, Fulling 2003	\bar{x} : 110, SD: 41, n: 2	SE-USA	
Maze-Foley, Mullin 2006	2-325, \bar{x} : 90, SD: 11, n: 44	Gulf of Mexico	
Moreno <i>et al.</i> 2005	8-300, n: 13	Brazil	
Weir <i>et al.</i> 2014	3-1000, \bar{x} : 73, SD: 12 median: 48, n: 92	trop. E-Atlantic off Africa	mostly traveling, 91 sightings were monospecific pods
Common dolphin/ Smith <i>et al.</i> 1986	\bar{x} : 200, n: 43	W-USA	pods < 20 more frequent than any other group size class
Holt, Jackson 1987	18-1540, \bar{x} : 351, SD: 329, n: 31	trop. E-Pacific	
Lens 1991	\bar{x} : 19, n: 36	N-Atlantic	
Findlay <i>et al.</i> 1992	1-1000, \bar{x} : 267, SD: 287, n: 52	southern Africa	
Breese, Tershy 1993	1- >1500, \bar{x} : 129, SD: 138, n: 88	Gulf of California	often in feeding associations with Bryde's whales (prey: Pacific sardine)
Wade, Gerrodette 1993	\bar{x} : 380, SD: 65, n: 209, max: 4000	trop. E-Pacific	
Mangels, Gerrodette 1994	1-1675, \bar{x} : 199, SD: 277, n: 249	E-Pacific	long-beaked 6-1675, \bar{x} : 272, n: 50; short-beaked 2-1450, \bar{x} : 181, n: 177
Barlow 1995	1-662, \bar{x} : 112, n: 129	California	short-beaked \bar{x} : 112, n: 116, 34% pods > 100 ind. long-beaked: \bar{x} : 155, n: 5, 80% pods > 100 ind.
Forney <i>et al.</i> 1995	\bar{x} : 515, n: 27	California	
Ballance <i>et al.</i> 1996	15-1700, \bar{x} : 221, n: 16	N/NW-Indic	
Barlow <i>et al.</i> 1997	17-1200, \bar{x} : 289, SD: 287, n: 26	California	short-beaked 17-1200, \bar{x} : 273, SD: 306, n: 15; long-beaked 20-800, \bar{x} : 309, SD: 256, n: 11
Mignucci-Giannoni 1998	1-50, \bar{x} : 9, n: 12	Caribbean Sea	1-3 ind. 66.8%; 7-15 ind. 6.9%; 25-29 ind. 6.9%; 30-50 ind. 19.4%
Hooker <i>et al.</i> 1999	\bar{x} : 16, SD: 26, n: 104	Gully (S off Nova Scotia)	short-beaked common dolphin
Carretta <i>et al.</i> 2000	\bar{x} : 354, n: 61	San Clemente Island, California	winter: \bar{x} : 183, n: 33; summer: \bar{x} : 556, n: 28
Ritter 2001	3-225, \bar{x} : 36, SD: 43, n: 44	La Gomera (Canary Islands)	
Weir <i>et al.</i> 2001	\bar{x} : 14, n: 74	N-Scotland	

Species/Reference	Group size	Area	Group characteristics
Palacios, Salazar 2002	\bar{x} : 253, median: 115, n: 456	Galápagos Islands	
Bearzi <i>et al.</i> 2003	typically: 50-70; 100-600 common in some areas	Mediterranean Sea	feeding, traveling, socializing, calves present year-round at least in some areas
Barlow <i>et al.</i> 2004	3-125, \bar{x} : 33, SD: 32, n: 22	Hawaii	
Jackson <i>et al.</i> 2004	1-1267, \bar{x} : 87, SD: 186, n: 85	trop. E-Pacific	
López <i>et al.</i> 2004	\bar{x} : 37, SD: 129, n: 95	Galicia (N-Spain)	
Cañadas <i>et al.</i> 2005	\bar{x} : 59, SD: 86, n: 754	S-Spain	short-beaked common dolphin
Ferguson <i>et al.</i> 2006	\bar{x} : 258, n: 152	trop. E-Pacific	long-beaked \bar{x} : 412, n: 23; short-beaked \bar{x} : 230, n: 129
Wall <i>et al.</i> 2006	1-300, \bar{x} : 20, SD: 41, n: 63	W-Ireland	large groups consisting of sub-groups calves/juv. present in 6 encounters
Barlow, Forney 2007	\bar{x} : 163, n: 507	W-USA	
Kiszka <i>et al.</i> 2007	1-600, \bar{x} : 38, SD: 74, n: 329	Bay of Biscay	group size highly variable
De Stephanis <i>et al.</i> 2008	1-250, \bar{x} : 36, SD: 42, n: 113	Strait of Gibraltar	
Jackson <i>et al.</i> 2008	\bar{x} : 217, n: 128	trop. E-Pacific	
Oswald <i>et al.</i> 2008	\bar{x} : 209, SD: 502, n: 140	E-Pacific	long-beaked \bar{x} : 565, SD: 563, n: 11 short-beaked \bar{x} : 185, SD: 356, n: 124
Waring <i>et al.</i> 2008	1-30, \bar{x} : 9, n: 26	Middle Atlantic Ridge	
Hildebrand 2009	1-1000, \bar{x} : 76, SD: 142, n: 107	S-California	
Al-Gheilani, Jayabalan 2010	15-several thousand, \bar{x} : 135, SD: 87, n: 18, excl. 1 pod of 1000s	Arabian Sea off Oman (N-Indic)	long-beaked common dolphin, mostly traveling, occ. feeding (n: 2) spread out over wide area
Barlow 2010	\bar{x} : 199, n: 117	W-USA	long-beaked \bar{x} : 535, n: 7 short-beaked \bar{x} : 178, n: 110
Carretta <i>et al.</i> 2011	\bar{x} : 455, n: 56	California	
Henderson <i>et al.</i> 2012	2-1000, \bar{x} : 207, SD: 9, median: 120, n: 61	S-California Bight	traveling, foraging; larger pods traveling faster; pods either very spread out when slow or tight when fast; fast traveling pods with highest rates of all call types
Palka 2012	\bar{x} : 18, SD: 4, n: 151	NE-USA	short-beaked common dolphin
Silva <i>et al.</i> 2014	1-500, \bar{x} : 27, SD: 36, n: 2934	Azores	
Campbell <i>et al.</i> 2015	\bar{x} : 71, SD: 148, n: 437	S-California	short-beaked common dolphin; winter \bar{x} : 105, SD: 213, spring \bar{x} : 74, SD: 113, summer \bar{x} : 56, SD: 115, fall \bar{x} : 62, SD: 85
Correia <i>et al.</i> 2015	1-120, \bar{x} : 14, SD: 23, n: 37	Portugal (E-Atlantic)	

Species/Reference	Group size	Area	Group characteristics
Chivers <i>et al.</i> 2016	48-2334, \bar{x} : 551, median: 439, n: 34	NE-Pacific	calves tend to be clustered together and the clusters are randomly placed within pods
Di Tullio <i>et al.</i> 2016	\bar{x} : 151, SD: 58, n: 27	SW-Atlantic outer shelf/ slope	spring \bar{x} : 137, SD: 65, n: 22; autumn \bar{x} : 215, SD: 140, n: 5
Commerson's dolphin/ Goodall <i>et al.</i> 1988	1- hundreds, \bar{x} : 7, SD: 17, n: 302	Argentina, Chilean Patagonia	occasional large congregations in various locations and seasons
Coscarella <i>et al.</i> 2010	\bar{x} : 2, n: 5048 \bar{x} (coop. feeding): 6, max: 30, n: 48; pods > 100 individuals recorded offshore	Argentina	number of ind. in scan area (~30km ²): \bar{x} : 18, SD: 26, n: 479, max.: 218 summer \bar{x} : 13, SD: 16 winter \bar{x} : 19, SD: 27 (sign.) > 20% pods > 20+ ind.
Dellabianca <i>et al.</i> 2016	1–20, \bar{x} : 2, SD: 2, median: 2, n: 88	Patagonia	
Southern right whale dolphin/ Gaskin 1968	infrequent sightings of very large pods	New Zealand	
Miyazaki, Kato 1988	all < 40, \bar{x} : 30, n: 3	Southern Ocean	always associated with other species (hourglass dolphin, fin + pilot whales)
Van Waerbeek <i>et al.</i> 1991	20-1000, \bar{x} : 368, SD: 111, n: 10	off Chile	traveling, feeding
Cruickshank, Brown 1981	3-300, n: 8	off SW-Africa	
Rose, Payne 1991	200-300, n: 2	off Namibia	very large pods seem monospecific
Visser <i>et al.</i> 2004	> 500, n: 1	> 15km SE off Kaikoura, NZ	spread out over ca. 2km ²
Northern right whale dolphin/ Smith <i>et al.</i> 1986	\bar{x} : 165, n: 5	W-USA	
Buckland <i>et al.</i> 1993	1-100, \bar{x} : 15, n: 21	N-Pacific	
Jefferson <i>et al.</i> 1994	\bar{x} : 100-200, range: 1- >2000	throughout range	
Mangels, Gerrodette 1994	8-101, \bar{x} : 37, SD: 29, n: 9	E-Pacific	
Barlow 1995	\bar{x} : 19, n: 15	California	
Forney <i>et al.</i> 1995	\bar{x} : 19, n: 31	California	
Carretta <i>et al.</i> 2000	\bar{x} : 12, n: 11	San Clemente Island, California	
Jackson <i>et al.</i> 2004	2-80, \bar{x} : 17, SD: 19, n: 36	trop. E-Pacific	
Barlow, Forney 2007	\bar{x} : 29, n: 60	W-USA	
Rankin <i>et al.</i> 2007	non-vocal pods: 2-15, \bar{x} : 7, n: 13 vocal pods: 6-63, \bar{x} : 27, n: 7	off W-USA, within EEZ	spread out in sub-groups; 7 of 20 single-species pods produced click and pulsed sounds, no whistles detected
Oswald <i>et al.</i> 2008	\bar{x} : 28, SD: 35, n: 36	E-Pacific	single-species: \bar{x} : 15, SD: 16, n: 28
Hildebrand 2009	1-100, \bar{x} : 21, SD: 29, n: 10	S-California	
Barlow 2010	\bar{x} : 24, n: 8	W-USA	
Ford <i>et al.</i> 2010	20- >200, n: 5, pod size \geq 200: n: 3	W-Canada	always associated with Pacific white-sided dolphins

Species/Reference	Group size	Area	Group characteristics
Dall's porpoise/ Sullivan, Houck 1979	2-30	California	congregation of ~1000 ind. observed 16km offshore
Morris <i>et al.</i> 1983	typ. 2-20, mode: 4, > 200 observed; 1 pod of ~3000 ind. off SE- Alaska	Gulf of Alaska	
Smith <i>et al.</i> 1986	\bar{x} : 6, n: 29	W-USA	
Jefferson 1987	1-6, \bar{x} : 3, SD: 1, n: 68	Johnstone Strait (W-Canada)	adults only: 1-4, \bar{x} : 2, SD: 1, n: 23; pods with calves 2-6, \bar{x} : 3, SD: 1, n: 29
Brueggeman <i>et al.</i> 1987	1-8, \bar{x} : 3, n: 50	Aleutians, Alaska	
Steward <i>et al.</i> 1987	1-6, \bar{x} : 3, SD: 1, n: 42	N- Pacific/Aleutians	
Miyashita, Kasuya 1988	1-70, excl. pod of 70, \bar{x} : 7, SD: 2, n: 274	Japan	dalli type: 1-34, \bar{x} : 8, SD: 2, n: 138; truei type: 1-70, \bar{x} : 6, SD: 0.5, n: 136
Buckland <i>et al.</i> 1993	1-25, \bar{x} : 4, n: 998	N-Pacific	
Mangels, Gerrodette 1994	1-13, \bar{x} : 4, SD: 3, n: 16	E-Pacific	
Barlow 1995	\bar{x} : 3, n: 69	California	
Forney <i>et al.</i> 1995	\bar{x} : 3, n: 38	California	
Carretta <i>et al.</i> 2000	\bar{x} : 3, n: 8	San Clemente Island, California	
Wade <i>et al.</i> 2003	\bar{x} : 4, n: 592	Gulf of Alaska, Aleutians	
Jackson <i>et al.</i> 2004	1-15, \bar{x} : 3, SD: 2, n: 104	trop. E-Pacific	
Matkin <i>et al.</i> 2007	\bar{x} : 4, n: 521	Aleutians, Alaska	non-fatal harassment by orcas during 3 of the sightings -> high speed escape
Barlow, Forney 2007	\bar{x} : 4, n: 214	W-USA	
Oswald <i>et al.</i> 2008	\bar{x} : 3, SD: 2, n: 101	E-Pacific	
Barlow 2010	\bar{x} : 4, n: 20	W-USA	
Ford <i>et al.</i> 2010	1-50, \bar{x} : 4, n: 482	W-Canada	inshore and offshore sightings, 10 sightings of > 15 ind.
Friday <i>et al.</i> 2012	typically 2-4	E-Bering Sea	very small group size in- and offshore
Campbell <i>et al.</i> 2015	\bar{x} : 6, SD: 4, n: 142	S-California	winter \bar{x} : 7, SD: 4, spring: \bar{x} : 6, SD: 4, fall \bar{x} : 9, SD: 7
Burmeister's porpoise/ Van Waerebeek <i>et al.</i> 2002	78% sightings: 1-4, \bar{x} : 7, SD: 15 excl. 2 large pods (40, 150), median: 2, n: 28	SE-Pacific	pod of 150 structured in sub- groups of 1-5 individuals, widely dispersed, extended ~0.5 nm to each side of the boat, both large pods likely connected

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Sperm whale group size

In sperm whales most surveys yield an underestimate of group sizes due to the long diving times and staggered dives in this species (e.g. Whitehead 2003). Often only part of the group is visible at the surface at any time. Therefore, long observation times are necessary for an accurate estimate of the number of individuals affiliated to a pod.

The typical mean group size in female sperm whale groups is ~28 in the E-Pacific, ranging from 27 off Ecuador to 31 off northern Chile, and 8 in the N-Atlantic ranging from < 7 off Dominica to 12 in the Sargasso Sea (Whitehead, Kahn 1992; Coakes, Whitehead 2004; Jaquet *et al.* 2005; Gero *et al.* 2009; Jaquet, Gendron 2009; Whitehead *et al.* 2012). In the Atlantic Ocean groups mostly comprise one social unit whereas in the Pacific 2-3 social units form larger groups (Whitehead 2003). Adult males lead solitary lives (e.g. Whitehead 2003; Whitehead *et al.* 2012; Silva *et al.* 2014). Range: 1-thousands. For this analysis a group size mean of 12 has been used.

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Table 2: Baleen whale group sizes: ind.: individual

Species	Group size	Reference
Blue whale/ <i>Balaenoptera musculus</i>	\bar{x} : 2, n: 20	Smith <i>et al.</i> 1986
	1-44, excl. pod of 44: \bar{x} : 2, SD: 0.9, n: 81	Mangels, Gerrodette 1994
	\bar{x} : 2, n: 49	Barlow 1995
	1-4, \bar{x} : 2, SD: 1, n: 9	Barlow <i>et al.</i> 1997
	\bar{x} : 1, SD: 0, n: 5	Kingsley, Reeves 1998
	\bar{x} : 1, SD: 0.5, n: 8	Hooker <i>et al.</i> 1999
	\bar{x} : 1, n: 9	Carretta <i>et al.</i> 2000
	\bar{x} : 2, SD: 0.3, n: 75	Branch, Butterworth 2001
	1-7, \bar{x} : 2, SD: 0.8, n: 261	Gill 2002
	1-2, \bar{x} : 1, SD: 0.3, n: 12	Barlow <i>et al.</i> 2004
	1-12, \bar{x} : 3, n: 47, group size does not correlate with presence of calves	Hucke-Gaete <i>et al.</i> 2004
	1-6, \bar{x} : 2, SD: 1, n: 13	Jackson <i>et al.</i> 2004
	1-2, \bar{x} : 1, SD: 0.2, n: 14	Anderson 2005
	\bar{x} : 2, n: 198	Barlow, Forney 2007
	1-60, \bar{x} : 1, n: 3346 + 250 (review)	Branch <i>et al.</i> 2007
	1-3, \bar{x} : 1, SD: 1, median: 1, n: 38	Oleson <i>et al.</i> 2007
	\bar{x} : 2, n: 57	Jackson <i>et al.</i> 2008
	1-25, \bar{x} : 1, SD: 1, n: 438	Hildebrand 2009
	\bar{x} : 1, SD: 0, n: 6	Ford <i>et al.</i> 2010
	1-3, \bar{x} : 2, SD: 0.7, n: 163	Silva <i>et al.</i> 2014
	\bar{x} : 2, SD: 3, n: 136	Campbell <i>et al.</i> 2015
	1-5, \bar{x} : 2, SD: 1, n: 33	Miller <i>et al.</i> 2015
	Fin whale/ <i>Balaenoptera physalus</i>	1-5, \bar{x} : 2, SD: 0.2, n: 74; 86% pods in clusters of 2-10 pods in a 3-5nmi radius
\bar{x} : 2, n: 76		Lens 1991
1-6, \bar{x} : 2, SD: 0.1 n: 68		Buckland <i>et al.</i> 1992
traveling: 2-10, median: 2, n: 197 feeding: median: 5, n: 44, feed in coordinated groups of 2-4 individuals		Tershy 1992
1-81, \bar{x} : 4, SD: 11, n: 61		Mangels, Gerrodette 1994
\bar{x} : 2, n: 21		Barlow 1995
1-4, \bar{x} : 2, SD: 1, n: 10		Barlow <i>et al.</i> 1997
\bar{x} : 2, SD: 2, n: 18		Kingsley, Reeves 1998
\bar{x} : 1, SD: 1, n: 32		Hooker <i>et al.</i> 1999
\bar{x} : 1, n: 21		Carretta <i>et al.</i> 2000
\bar{x} : 3, SD: 1.6, n: 102		Branch, Butterworth 2001
\bar{x} : 2, n: 276		Wade <i>et al.</i> 2003
1-15, \bar{x} : 1, SD: 5, n: 8		Barlow <i>et al.</i> 2004
1-30, \bar{x} : 2, SD: 4, n: 45		Jackson <i>et al.</i> 2004
\bar{x} : 2, SD: 2, n: 80		Williams <i>et al.</i> 2006
\bar{x} : 2, n: 214		Barlow, Forney 2007
1-30, \bar{x} : 5, n: 13		Compton <i>et al.</i> 2007
\bar{x} : 2, n: 15	Matkin <i>et al.</i> 2007	
1-6, \bar{x} : 2, SD: 1, median: 1, n: 107	Azzellino <i>et al.</i> 2008	

Species	Group size	Reference
	significant group size variation between months and years, larger pods in July and August (summer)	
	1-50, \bar{x} : 3, SD: 0.2, n: 78	Heide-Jørgensen <i>et al.</i> 2008
	\bar{x} : 1, n: 8	Jackson <i>et al.</i> 2008
	1-2, \bar{x} : 1, n: 12	Waring <i>et al.</i> 2008
	1-5, \bar{x} : 2, SD: 0.7, n: 299	Hildebrand 2009
	\bar{x} : 3, n: 62	Barlow 2010
	1-7, \bar{x} : 2, n: 257	Ford <i>et al.</i> 2010
	\bar{x} : 1, SD: 0.2, n: 85	Laran <i>et al.</i> 2010
	\bar{x} : 2, SD: 0.1, n: 7	Rone <i>et al.</i> 2010
	1-30, \bar{x} : 2, n: 280	Moore, Barlow 2011
	1-7, \bar{x} : 3, n: 26	Scheidat <i>et al.</i> 2011
	\bar{x} : 1, n: 10	Matsuoka <i>et al.</i> 2012
	\bar{x} : 1, SD: 0.2, n: 53	Palka 2012
	1-7, \bar{x} : 3, SD: 3, n: 190	Silva <i>et al.</i> 2014
	\bar{x} : 2, SD: 3, n: 262	Campbell <i>et al.</i> 2015
	1-6, \bar{x} : 2, n: 129, group size does not correlate with presence of calves	Aniceto <i>et al.</i> 2016
	\bar{x} : 1, SD: 0.1, n: 984	Hammond <i>et al.</i> 2017
	\bar{x} : 1, n: 51, winter \bar{x} : 1, n: 12 summer \bar{x} : 1, n: 39	Laran <i>et al.</i> 2017
	1-4, \bar{x} : 1, SD: 0.1, n: 66	Panigada <i>et al.</i> 2017
Sei whale/ <i>Balaenoptera borealis</i>	1-6, \bar{x} : 2, n: 105	Cattanach <i>et al.</i> 1993
	\bar{x} : 1, SD: 0, n: 3	Hooker <i>et al.</i> 1999
	\bar{x} : 1, SD: 0.2, n: 31	Branch, Butterworth 2001
	1-4, \bar{x} : 2, SD: 1, n: 5	Ritter 2001
	1-2, \bar{x} : 1, SD: 0.4, n: 8	Barlow <i>et al.</i> 2004
	1-4, \bar{x} : 1, n: 53	Waring <i>et al.</i> 2008
	\bar{x} : 1, n: 7	Barlow, Forney 2007
	1-10, \bar{x} : 3, SD: 1, n: 4	Heide-Jørgensen <i>et al.</i> 2008
	1-4, \bar{x} : 2, SD: 1, n: 20	Iñíguez <i>et al.</i> 2010
	1-4, \bar{x} : 1, SD: 0.2, n: 16	Fulling <i>et al.</i> 2011
	\bar{x} : 1, SD: 0.3, n: 11	Palka 2012
	1-8, \bar{x} : 2, SD: 0.1, n: 162	Hakamada, Matsuoka 2014
	1-7, \bar{x} : 3, SD: 2, n: 186	Silva <i>et al.</i> 2014
	1-12, \bar{x} : 4, SD: 2, median: 3, n: 65	Acevedo <i>et al.</i> 2017
Bryde's whale/ <i>Balaenoptera edeni</i> , <i>B. brydei</i>	1-7, 52% single ind., 27% pairs, 18% > 2, n: 73 feeding: 1/3 observations, rest: traveling, resting; in pelagic waters: associations with common dolphins, sailfish, brown boobies common, occasionally with blue marlin, hammerhead, thresher, carcharhinid sharks, tuna, other sea bird species	Notarbartolo di Sciara 1980
	traveling: median: 1, 93% solitary, n: 195; feeding: median: 3, n: 91, individuals feed independently	Tershy 1992
	1-5, \bar{x} : 2, SD: 1, n: 16	Mangels, Gerrodette 1994
	1-5, \bar{x} : 2, SD: 1, n: 19	Barlow <i>et al.</i> 1997
	\bar{x} : 2, n: 76, 13 mother-calf pairs	Shimada, Miyashita 2001
	\bar{x} : 2, n: 294	Gerrodette, Forcada 2002b
	\bar{x} : 2, SD: 1, median: 1, n: 316	Palacios, Salazar 2002
	1-2, \bar{x} : 1, SD: 1, n: 14	Barlow <i>et al.</i> 2004
	1-15, \bar{x} : 2, SD: 1, n: 36	Anderson 2005
	1-5, \bar{x} : 2, SD: 0.3, n: 14	Maze-Foley, Mullin 2006

Species	Group size	Reference
	\bar{x} : 2, n: 22	Jackson <i>et al.</i> 2008
	1-2, \bar{x} : 2, SD: 0.4, n: 25	Steiner <i>et al.</i> 2008
	1-3, \bar{x} : 1, SD: 0.2, n: 18	Fulling <i>et al.</i> 2011
	\bar{x} : 1, n: 137	Matsuoka <i>et al.</i> 2012
Minke whale/ <i>Balaenoptera acutorostrata</i>	\bar{x} : 1, n: 172	Donovan, Gunnlaugsson 1989
	\bar{x} : 1, SD: 0.3, n: 43	Kingsley, Reeves 1998
	\bar{x} : 1, SD: 0.5, n: 8	Hooker <i>et al.</i> 1999
	\bar{x} : 2, SD: 0.3, n: 8570	Branch, Butterworth 2001
	\bar{x} : 1, n: 130	Weir <i>et al.</i> 2001
	\bar{x} : 1, SD: 0, n: 96	Wade <i>et al.</i> 2003
	1-2, \bar{x} : 1, SD: 0.3, n: 7	Jackson <i>et al.</i> 2004
	\bar{x} : 1, SD: 1, n: 75	Williams <i>et al.</i> 2006
	1-9, \bar{x} : 3, SD: 2, median: 2, n: 41	Ainley <i>et al.</i> 2007
	\bar{x} : 1, n: 18	Barlow, Forney 2007
	1-4, \bar{x} : 1, n: 44	Compton <i>et al.</i> 2007
	\bar{x} : 1, n: 42	Matkin <i>et al.</i> 2007
	1-2, \bar{x} : 1, SD: 0.0, n: 42	Heide-Jørgensen <i>et al.</i> 2008
	1-4, \bar{x} : 1, n: 594	Pike <i>et al.</i> 2009a
	1-6, \bar{x} : 1, n: 117	Andriolo <i>et al.</i> 2010
	1-20, \bar{x} : 2, n: 72	De Boer 2010b
	1-7, \bar{x} : 2, n: 94	Scheidat <i>et al.</i> 2011
	\bar{x} : 1, SD: 0.1, n: 37	Palka 2012
	1-4, \bar{x} : 2, SD: 1, n: 25	Correia <i>et al.</i> 2015
	\bar{x} : 1, n: 90	Hammond <i>et al.</i> 2017
Southern right whale/ <i>Eubalaena australis</i>	1-10, \bar{x} : 2, median: 2, n: 649, no correlation with calf presence, cow-calf pairs segregated from other ind.	Best <i>et al.</i> 2003 coastal and offshore
	1-15, \bar{x} : 2, SD: 2, n: 125	Carroll <i>et al.</i> 2014
	1-3, \bar{x} : 2, SD: 0.6, n: 66	Danilewicz <i>et al.</i> 2016
Humpback whale/ <i>Megaptera novaeangliae</i>	1-8, \bar{x} : 2, SD: 0.1, n: 98; 63% solitary; 64% pods were in clusters of 2-20 pods covering a 3-4nmi radius	Brueggeman <i>et al.</i> 1987
	\bar{x} : 4, n: 10	Barlow 1995
	\bar{x} : 2 migrating to breeding ground \bar{x} : 3 migrating to feeding ground, overall: 1-7, \bar{x} : 2, median: 2, SD: 1, n: 562	Brown, Corkeron 1995
	\bar{x} : 2, n: 8	Forney <i>et al.</i> 1995
	\bar{x} : 2, SD: 1, n: 14	Kingsley, Reeves 1998
	\bar{x} : 2, n: 1293; single ind. 43.2%; pairs 37.5%; trios 9.2%, ≥ 4 ind. 10.1%	Mignucci-Giannoni 1998
	\bar{x} : 2, SD: 1, n: 38	Hooker <i>et al.</i> 1999
	1-4, \bar{x} : 2, SD: 1, n: 35	Gannier 2000
	\bar{x} : 2, SD: 0.3, n: 342	Branch, Butterworth 2001
	\bar{x} : 2, n: 407	Wade <i>et al.</i> 2003
	1-80, \bar{x} : 2, SD: 3, n: 37, excl. pod of 80	Jackson <i>et al.</i> 2004
	\bar{x} : 2, SD: 0.8, n: 129	Williams <i>et al.</i> 2006
	\bar{x} : 2, n: 129	Barlow, Forney 2007
	1-6, \bar{x} : 2, n: 31	Compton <i>et al.</i> 2007
	\bar{x} : 4, n: 834	Matkin <i>et al.</i> 2007
	1-6, \bar{x} : 2, SD: 1, n: 68	Dulau-Drouot <i>et al.</i> 2008
	1-95, \bar{x} : 3, SD: 0.4, n: 21	Heide-Jørgensen <i>et al.</i> 2008
	1-10, \bar{x} : 2, n: 215, incl. 30 mother-calf-pairs	Hermans, Pistorius 2008

Species	Group size	Reference
	\bar{x} : 2, n: 11	Jackson <i>et al.</i> 2008
	1-35, \bar{x} : 2, n: 1700 119 sightings (7%) of > 3 ind.	Ford <i>et al.</i> 2010
	1-11, \bar{x} : 2, n: 53	Scheidat <i>et al.</i> 2011
	\bar{x} : 1, n: 32	Matsuoka <i>et al.</i> 2012
	\bar{x} : 1, SD: 0.2, n: 26	Palka 2012
	1-7, \bar{x} : 3, SD: 1, n: 41 calves present in 8 sightings	Nøttestad <i>et al.</i> 2014
	\bar{x} : 2, SD: 1, n: 192	Campbell <i>et al.</i> 2015
	\bar{x} : 2, SD: 0.0, n: 929	Bortolotto <i>et al.</i> 2016
Gray whale/ <i>Eschrichtius robustus</i>	1-16, \bar{x} : 2, SD: 0.4, n: 392; spring migration \bar{x} : 3, SD: 0.5, n: 39, autumn migration \bar{x} : 2, SD: 0.1, n: 243	Brueggeman <i>et al.</i> 1987
	1-7, \bar{x} : 2, SD: 1, median: 1, n: 195 (migrating along offshore corridors)	Shane 1994
	\bar{x} : 4, n: 25	Forney <i>et al.</i> 1995
	\bar{x} : 3, n: 31	Carretta <i>et al.</i> 2000
	1-7, median: 1, n: 171	Shelden, Laake 2002
	\bar{x} : 6, n: 22	Wade <i>et al.</i> 2003
	\bar{x} : 1, n: 18	Matkin <i>et al.</i> 2007
	1-11, \bar{x} : 2, median: 1, n: 383	Meier <i>et al.</i> 2007
1-10, \bar{x} : 2, SD: 1, median: 2, n: 196	Laake <i>et al.</i> 2009	

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Appendix 2: Foraging depth

Table 1: References for foraging depth by species.

Species	References
Blue whale	Lagerquist <i>et al.</i> 2000; Croll <i>et al.</i> 2001; Acevedo-Gutiérrez <i>et al.</i> 2002; Oleson <i>et al.</i> 2007; Calambokidis <i>et al.</i> 2008; Hildebrand 2009; Goldbogen <i>et al.</i> 2011; Watwood, Buonantony 2012; Hazen <i>et al.</i> 2015, Mate <i>et al.</i> 2017
Fin whale	Panigada <i>et al.</i> 1999; Croll <i>et al.</i> 2001; Acevedo-Gutiérrez <i>et al.</i> 2002; Goldbogen <i>et al.</i> 2006; Watwood, Buonantony 2012; Mate <i>et al.</i> 2017
Sei whale	Baumgartner, Fratantoni 2008; Horwood 2009; Ishii <i>et al.</i> 2016
Bryde's whale	Alves <i>et al.</i> 2010; Watwood, Buonantony 2012;
Minke whale	Gales <i>et al.</i> 2013; Friedlaender <i>et al.</i> 2014
Southern right whale	Argüelles <i>et al.</i> 2016
Humpback whale	Dolphin 1987a,b; Dietz <i>et al.</i> 2002; Goldbogen <i>et al.</i> 2008; Witteveen <i>et al.</i> 2008; Hazen <i>et al.</i> 2009; Simon <i>et al.</i> 2012; Friedlaender <i>et al.</i> 2013; Baumgartner <i>et al.</i> 2015; Burrows <i>et al.</i> 2016
Gray whale	Watwood, Buonantony 2012
Sperm whale	Watkins <i>et al.</i> 1993, 2002; Amano, Yoshioka 2003; Johnson, Tyack 2003; Whitehead 2003; Zimmer <i>et al.</i> 2003; Drouot <i>et al.</i> 2004; Miller <i>et al.</i> 2004; Watwood <i>et al.</i> 2006; Davis <i>et al.</i> 2007; Johnson <i>et al.</i> 2009; Aoki <i>et al.</i> 2012; Claridge <i>et al.</i> 2015; Joyce <i>et al.</i> 2016, 2017; Dunn <i>et al.</i> 2017; Guerra <i>et al.</i> 2017; Irvine <i>et al.</i> 2017; Mate <i>et al.</i> 2017
<i>Kogia</i>	Au, Pitman 1988; Watwood, Buonantony 2012
Cuvier's beaked whale	Johnson <i>et al.</i> 2004; Tyack <i>et al.</i> 2006; Baird <i>et al.</i> 2006b, 2008c; Schorr <i>et al.</i> 2014; Claridge <i>et al.</i> 2015; Joyce <i>et al.</i> 2016, 2017; Baird <i>et al.</i> 2017; Dunn <i>et al.</i> 2017
Baird's beaked whale	Ohizumi <i>et al.</i> 2003; Minamikawa <i>et al.</i> 2007; Stimpert <i>et al.</i> 2014
Blainville's beaked whale	Johnson <i>et al.</i> 2004, 2008, 2009; Madsen <i>et al.</i> 2005; Tyack <i>et al.</i> 2006; Baird <i>et al.</i> 2006b, 2008c; Arranz <i>et al.</i> 2011; Hazen <i>et al.</i> 2011; Claridge <i>et al.</i> 2015; Joyce <i>et al.</i> 2016, 2017; Dunn <i>et al.</i> 2017
Gervais' beaked whale	Gillespie <i>et al.</i> 2009; Claridge <i>et al.</i> 2015
Sowerby's beaked whale	Wenzel <i>et al.</i> 2013
Pygmy beaked whale	Reyes <i>et al.</i> 1991*
Longman's beaked whale	Yatabe <i>et al.</i> 2010
Southern bottlenose whale	Sekiguchi <i>et al.</i> 1993
Northern bottlenose whale	Hooker, Baird 1999; Miller <i>et al.</i> 2015
Long-finned pilot whale	Desportes, Mouritsen 1993; Baird <i>et al.</i> 2002; Heide-Jørgensen <i>et al.</i> 2002; Johnson <i>et al.</i> 2009; Visser <i>et al.</i> 2014
Short-finned pilot whale	Baird <i>et al.</i> 2003b; Aguilar de Soto <i>et al.</i> 2008; Jensen <i>et al.</i> 2011; Au <i>et al.</i> 2013; Claridge <i>et al.</i> 2015; Joyce <i>et al.</i> 2016; Quick <i>et al.</i> 2017
False killer whale	Cummings, Fish 1971; Baird 2009a; Oleson <i>et al.</i> 2010; Watwood, Buonantony 2012; Minamikawa <i>et al.</i> 2013
Pygmy killer whale	O'Dwyer <i>et al.</i> 2015*
Melon-headed whale	Jefferson, Barros 1997; Claridge <i>et al.</i> 2015; Joyce <i>et al.</i> 2016, 2017
Killer whale	Baird 1994; Nøttestad, Similä 2001; Baird <i>et al.</i> 2003a; Shapiro 2008; Miller <i>et al.</i> 2010; Wright <i>et al.</i> 2017
Risso's dolphin	Wells <i>et al.</i> 2009; Soldevilla <i>et al.</i> 2010; Au <i>et al.</i> 2013; Arranz <i>et al.</i> 2016; Benoit-Bird 2016
Bottlenose dolphin	Reynolds <i>et al.</i> 2000; Klatsky <i>et al.</i> 2007
Rough-toothed dolphin	Wells <i>et al.</i> 2008; Jefferson 2009
White-beaked dolphin	Camphuysen, Webb 1999; Fall, Skern-Mauritzen 2014
Atlantic white-sided dolphin	Doksaeter <i>et al.</i> 2008
Pacific white-sided dolphin	Kajimura <i>et al.</i> 1980; Dailey <i>et al.</i> 1994
Hourglass dolphin	Fernández <i>et al.</i> 2003; Santora 2012

Species	References
Dusky dolphin	Benoit-Bird <i>et al.</i> 2004; Würsig <i>et al.</i> 2007
Fraser's dolphin	Dolar <i>et al.</i> 2003
Spinner dolphin	Fitch, Brownell 1968; Norris <i>et al.</i> 1994; Benoit-Bird, Au 2003; Dolar <i>et al.</i> 2003; Au <i>et al.</i> 2013
Pantropical spotted dolphins	Baird <i>et al.</i> 2001; Chivers, Scott 2002; Scott, Chivers 2009; Scott <i>et al.</i> 2012
Atlantic spotted dolphin	Griffin 2005; Herzing, Elliser 2014
Striped dolphin	Blanco <i>et al.</i> 1995; Archer, Perrin 1999; Minamikawa <i>et al.</i> 2003; Doksaeter <i>et al.</i> 2008
Clymene dolphin	Fertl <i>et al.</i> 1997
Common dolphin	Ohizumi <i>et al.</i> 1998; Doksaeter <i>et al.</i> 2008; Simonis <i>et al.</i> 2017
Commerson's dolphin	Goodall <i>et al.</i> 1988; Coscarella <i>et al.</i> 2010
Southern right whale dolphin	Baker 1981
Northern right whale dolphin	Watwood, Buonantony 2012
Dall's porpoise	Baird, Hanson 1998; Hanson, Baird 1998
Burmeister's porpoise	Goodall <i>et al.</i> 1995; Reyes, van Waerebeek 1995; García-Godos <i>et al.</i> 2007*

* based on depth range of prey species according to fishbase

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Appendix 3: Shoaling tendency of cetacea prey

Table 1: Prey composition of offshore cetacea species, ML: mantle length, shoaling species or species groups are marked with an 's', %F: % frequency of occurrence, %N: percent by number, %M: percent by mass, %V: percent by volume, '%': paper did not specify type of percentage

Cetacea species	Area	Prey	Reference
Blue whale	Antarctica	euphausiids (s) (98% stomachs contained excl. euphausiids)	Nemoto 1970: stomach content analysis, n: 1203 (with food: 529)
	N-Pacific	euphausiids (s) (98%), copepods (s)	Nemoto, Kawamura 1977: stomach content

Cetacea species	Area	Prey	Reference
			analysis, n: 971 (with food: 467)
	N-Atlantic, N-Pacific	euphausiids (s): N-Atlantic: <i>Meganyctiphanes norvegica</i> , <i>Thysanoessa raschii</i> , <i>T. inermis</i> , <i>T. longicaudata</i> ; N-Pacific: <i>Euphausia pacifica</i> , <i>T. inermis</i> , <i>T. longipes</i> , <i>T. spinifera</i> , <i>Nyctiphanes symplex</i>	Sears, Perrin 2009: review
Fin whale	Antarctica	euphausiids (s) (100%F, 99% stomachs contained excl. euphausiids)	Nemoto 1970: stomach content analysis, n: 35139 (with food: 16261)
	N-Pacific	euphausiids (s), copepods (s) (64% stomachs contained excl. euphausiids, 26% excl. copepods)	Nemoto, Kawamura 1977: stomach content analysis, n: 29575 (with food: 19511)
	W-Iceland	euphausiids (s)	Víkingsson 1997: stomach content analysis, n: 1524 (with food: ~50%)
Sei whale	South Africa	euphausiids (s) (esp. <i>Euphausia lucens</i> , <i>E. recurva</i>), copepods (s) (esp. <i>Neocalanus tonsus</i> , <i>Calanoides carinatus</i> , <i>Clausocalanus arcuicornis</i>), Megalopa larvae	Best 1967: stomach content analysis, n: 892 (with food: 472)
	Antarctica	euphausiids (s), copepods (s), amphipods (s) (59% stomachs contained excl. euphausiids, 25% excl. copepods, 15% excl. amphipods)	Nemoto 1970: stomach content analysis, n: 26182 (with food: 10037)
	N-Pacific	copepods (s), euphausiids (s) (83% stomachs contained excl. copepods, 13% excl. euphausiids)	Nemoto, Kawamura 1977: stomach content analysis, n: 21713 (with food: 12048)
	Japan	copepods (s) (37%F), Japanese anchovy (s) (27%F), euphausiids (s) (20%F), Pacific saury <i>Cololabis saira</i> (s) (9%F), <i>Scomber</i> sp. (6%F) (incl. chum mackerel <i>Scomber japonicus</i> (s), spotted mackerel <i>S. australasicus</i> (s))	Konishi <i>et al.</i> 2009: stomach content analysis, n: 489 (with food: 489)
Bryde's whale	N-Pacific	Euphausiids (s), fish (89% stomachs contained excl. euphausiids, 11% excl. fish)	Nemoto, Kawamura 1977: stomach content analysis, n: 109 (with food: 27)
	SW-Pacific, SW-Indic (Madagascar)	euphausiids (s) esp. <i>Euphausia diomedea</i> , <i>E. recurva</i> , <i>Thysanoessa gregaria</i> , <i>E. sibogae</i>	Kawamura 1980: stomach content analysis, n: 459 with food: 234
	Japan	Japanese anchovy (s) (55%F), euphausiids (s) (37%F), <i>Scomber</i> sp. (5%F), north Pacific lightfish <i>Maurollicus japonicus</i> (s) (3%F); 92% stomachs contained a single prey species	Konishi <i>et al.</i> 2009: stomach content analysis, n: 393 (with food: 393)
Minke whale	Antarctica	Antarctic krill (s) (94-100%M)	Ichii, Kato 1991: stomach content analysis, n: 273

Cetacea species	Area	Prey	Reference
	NE-Atlantic	krill (s) (esp. <i>Thysanoessa</i> sp.), herring (s), capelin <i>Mallotus villosus</i> (s), cod <i>Gadus morhua</i> (s), <i>Benthoosema glaciale</i> (s), haddock <i>Melanogrammus aeglefinus</i> (s), variation with season and area	Haug <i>et al.</i> 1996, (2002): stomach content analysis, n: 133, (289) (with food: 113)
	NW-Pacific	Japanese anchovy (s) (44%N), Pacific saury (s) (37%N), krill (s) (17%N), 90% stomachs contained a single prey species	Tamura, Fujise 2002 stomach content analysis, n: 498 (with food: 426)
	Japan	Japanese anchovy (s) (38%F), Pacific saury (s) (37%F), euphausiids (s) (12%F), Alaska pollock <i>Gadus chalcogrammus</i> (s) (5%F), <i>Todarodes pacificus</i> (s) (2%F), <i>Berryteuthis anonychus</i> (s) (2%F), copepods (s) (1%F), <i>Scomber</i> sp. (1%F)	Konishi <i>et al.</i> 2009: stomach content analysis, n: 740 (with food: 740)
	Antarctica	Antarctic krill (s) (> 90%M in offshore areas)	Tamura, Konishi 2009: stomach content analysis, n: 6777
	Iceland	Atlantic herring (s), sand eel <i>Ammodytes</i> sp. (s), capelin (s), haddock (s), euphausiids (s)	Vikingsson <i>et al.</i> 2014: stomach content analysis, n: 190 (with food: 190)
Southern right whale	South America Atlantic side	north of 40°S main prey: copepods (s) (92%), south of 50°S main prey: krill (s) (99%), in between: krill (71%), copepods (24%)	Rowntree <i>et al.</i> 2008: stomach content analysis, n: 249
Humpback whale	N-Pacific	euphausiids (s), fish (77% of stomachs contained excl. euphausiids, 17% excl. fish, esp. Atka mackerel (s) <i>Pleurogrammus monopterygius</i>)	Nemoto, Kawamura 1977: stomach content analysis, n: 458 (with food: 308)
	NW-Pacific	fish in neritic areas, plankton in oceanic areas	Filatova <i>et al.</i> 2013: stable isotope analysis, n: 111
Sperm whale	New Zealand	<i>Nototodarus sloanei</i> (s) (8%F), <i>Histioteuthis cookiana</i> (13%F), <i>Architeuthis</i> sp., <i>Moroteuthis</i> sp. (47%F), onychoteuthids (24%F), Hapuku wreckfish <i>Polyprion oxygeneios</i> (8%F), pink cusk-eel <i>Genypterus blacodes</i> (10%F), orange roughy <i>Hoplostethus</i> sp. (s), mainly feed on squid of small to moderate size, occ. take large ind.	Gaskin, Cawthorn 1967: stomach content analysis, n: 133 (with food: 118)
	Japan n: 3364 (with food: 2030)	<i>Histioteuthis dofleini</i> , <i>Octopoteuthis</i> sp., <i>Onykia robusta</i> (s), <i>Ommastrephes bartrami</i> (s), cod (s), rockfish	Kawakami 1980: review
	Kurile Islands n: 360 (with food: 360)	<i>Gonatopsis borealis</i> (s), <i>Berryteuthis magister</i> (s), <i>Gonatus fabricii</i> , <i>Galiteuthis armata</i> , <i>Histioteuthis</i> sp.	
	Bering Sea n: 1251 (with food: 1248)	<i>Onykia robusta</i> (s), <i>Gonatopsis borealis</i> (s), <i>Gonatopsis makko</i> , <i>Gonatus magister</i> , <i>Gonatus fabricii</i> , <i>Galiteuthis armata</i>	

Cetacea species	Area	Prey	Reference
	W-Canada, W-USA n: 178 (with food: 104)	<i>Onykia robusta</i> (s), <i>Gonatopsis borealis</i> (s), <i>Gonatus fabricii</i> , skate, sardine (s), rockfish, shark	
	Peru, Chile	<i>Histioteuthis</i> sp., <i>Chiroteuthis</i> spp., <i>Octopoteuthis</i> sp., <i>Dosidicus gigas</i> (s)	
	general	occas. take large squid incl. <i>Moroteuthis robusta</i> , <i>Architeuthis</i> sp., and sharks but mostly feed on small-medium sized prey	
	W-Iceland, E-Greenland	lumpfish, cephalopds incl. cranchiids (57%N, 25%M), histioteuthids (26%N, 38%M); 94% cephalopods eaten are oceanic, neutrally buoyant, and 84% of these are ammoniacal	
<i>Kogia</i>	South Africa	<i>Histioteuthis</i> sp. (pygmy: 32%V, dwarf: 48%V), <i>Lycoteuthis lorigera</i> (s) (13%V, 18%V), <i>Merluccius</i> sp. (17%V, 8%V), <i>Ommastrephes bartramii</i> (s) (8%V, 3%V)	Sekiguchi <i>et al.</i> 1992: stomach content analysis, n: 38 (with food: 30, pygmy sperm whale n: 20, dwarf sperm whale n: 10)
	NE-Atlantic	<i>Histioteuthis reversa</i> (s) (68%N, 57%M), <i>H. bonnellii</i> (s) (1%N, 7%M), <i>Todarodes sagittatus</i> (s) (3%N, 10%M), <i>Teuthowenia megalops</i> (s) (2%N, 2%M), <i>Polybius henslowii</i> (s) (6%N, 7%M) <i>H. reversa</i> ML: <5-70mm	Santos <i>et al.</i> 2006: stomach content analysis, n: 14 (with food: 14, all pygmy sperm whale); Galicia n: 5, France n: 7, Scotland n: 2
	Hawaii	<i>Stigmatoteuthis hoylei</i> (s) (100%F, 20%N, 35%M), <i>Taonius pavo</i> (s) (86%F, 17%N, 7%M), <i>Liocranchia reinhardti</i> (s) (71%F, 4%N, 9%M), <i>Leachia</i> sp. (14%F, 6%N, 1%M), <i>Sthenoteuthis oualaniensis</i> (s) (29%F, 1%N, 5%M), the decapod <i>Pasiphaea tarda</i> (43%F, 10%N, 2%M), giant red mysid <i>Neognathophausia ingens</i> (s) (57%F, 5%N, 1%M)	West <i>et al.</i> 2009: stomach content analysis, n: 7 (all pygmy sperm whale)
	Bay of Biscay (NE-Atlantic)	<i>Histioteuthis reversa</i> (s) (69%N, 60%M), swimming crab <i>Polybius</i> spp. (s) (9%N, 11%M), <i>Todarodes sagittatus</i> (s) (4%N, 9%M), <i>Histioteuthis bonnellii</i> (s) (2%N, 6%M)	Spitz <i>et al.</i> 2011: stomach content analysis, n: 10 (pygmy sperm whale n: 9, dwarf sperm whale n: 1)
Cuvier's beaked whale	South Africa	<i>Moroteuthis knipovitchi</i> (6%N, 25%M), <i>M. robsoni</i> (6%N, 14%M), <i>Teuthowenia</i> sp. (s) (16%N, 8%M), <i>Octopoteuthis</i> sp. (16%N, 7%M), giant red mysid (s) (15%N), <i>Chiroteuthis</i> sp. (10%N), <i>Pholidoteuthis boschmai</i> (8%N), <i>Onychoteuthis banksii</i> (s) (8%M), <i>Taningia danae</i> (7%M), <i>Moroteuthis</i> sp. (7%M)	Sekiguchi <i>et al.</i> 1992, Sekiguchi 1994: stomach content analysis, n: 4 (with food: 4)
	Greece	<i>Octopoteuthis sicula</i> (47%N), <i>Histioteuthis bonnellii</i> (s) (40%N)	Lefkaditou, Pouloupoulos

Cetacea species	Area	Prey	Reference
			1998: stomach content analysis, n: 7
	Canary Islands	<i>Taonius pavo</i> (s) (24%N, 11%M), <i>Histioteuthis reversa</i> (s) (15%N, 7%M), <i>Histioteuthis</i> type A (5%N, 10%M), <i>Mastigoteuthis schmidtii</i> (s) (14%N, 7%M), <i>Octopoteuthis sicula</i> (7%N, 15%M), <i>Chroteuthis veranyi</i> (5%N, 3%M), prey size: 15-305mm	Santos <i>et al.</i> 2007: stomach content analysis, n: 7
	Bay of Biscay (NE-Atlantic)	<i>Teuthowenia megalops</i> (s) (27%N, 23%M), <i>H. reversa</i> (s) (33%N, 27%M), <i>H. bonnellii</i> (s) (2%N, 4%M), giant octopod <i>Haliphron atlanticus</i> (10%N, 10%M), <i>Galiteuthis armata</i> (10%N, 8%M), <i>Todarodes sagittatus</i> (s) (2%N, 8%M)	Spitz <i>et al.</i> 2011: stomach content analysis, n: 10
	N-Pacific	<i>Octopoteuthis deletron</i> (27%N, 20%M), <i>Gonatopsis borealis</i> (s) (13%N, 36%M), <i>Taonius borealis</i> (21%N, 9%M), <i>Vampyroteuthis infernalis</i> (14%N, 12%M), <i>Gonatus onyx</i> (8%N, 1%M), <i>Galiteuthis phyllura</i> (5%N, 2%M), the macrourid fish <i>Albatrossia pectoralis</i> (1%N, 12%M)	West <i>et al.</i> 2017: stomach content analysis, n: 16 (with food: 16)
Baird's beaked whale	Japan	Honshu: longfin codling <i>Laemonema longipes</i> (44%N, 80%F), popeye grenadier <i>Coryphaenoides cinereus</i> (15%N, 78%F), longfin grenadier <i>Coryphaenoides longifilis</i> (14%N, 71%F), <i>Coryphaenoides acrolepis</i> (5%N, 60%F), <i>Gonatus</i> sp. (8%N, 83%F) esp. <i>Eogonatus tinro</i> (4%N, 63%F), <i>Taonius borealis</i> (4%N, 76%F), <i>Galiteuthis phyllura</i> (1%N, 32%F) Hokkaido: <i>Berryteuchis magister</i> (s) (32%N, 100%F), <i>Gonatus madokai</i> (15%N, 95%F), <i>Gonatus berryi</i> (10%N, 85%F), <i>Eogonatus tinro</i> (14%N, 90%F) prey length: 23-560mm	Walker <i>et al.</i> 2002: stomach content analysis, n: 127 (with food: 127 incl. n: 107 off Honshu and n: 20 off Hokkaido)
Gervais' beaked whale	Curaçao (Caribbean)	Sloane's viperfish <i>Chauliodus sloani</i> (s) (37%N), giant red mysid <i>Neognathophausia ingens</i> (s) (34%N), <i>Octopoteuthis</i> spp. (11%N)	Debrot, Barros 1992: stomach content analysis, n: 1
	U.S. Virgin Islands	giant red mysid (s)	Rossairo-Delestre <i>et al.</i> 1999: stomach content analysis, n: 1
Sowerby's beaked whale	Azores	<i>Diaphus</i> sp. (s) (20%N, 100%F), <i>Lampanyctus</i> sp. (s) (15%N); melamphids (13%N), <i>Opisthoproctus soleatus</i> (10%N), <i>Diretmus argenteus</i> (s) (5%N)	Pereira <i>et al.</i> 2011: stomach content analysis, n: 10 (with food: 10)

Cetacea species	Area	Prey	Reference
	Bay of Biscay (NE-Atlantic)	blue whiting <i>Micromesistius poutassou</i> (s) (20%N, 25%M), pouting <i>Trisopterus luscus</i> (s) + poor cod <i>T. minutus</i> (s) (27%N, 13%M), European hake <i>Merluccius merluccius</i> (s) (3%N, 12%M), swimming crab <i>Polybius</i> spp. (s), <i>Sepia</i> sp. (3%N, 8%M), whiting (4%N, 7%M)	Spitz <i>et al.</i> 2011: stomach content analysis, n: 3 coastal/shelf feeding
	western N-Atlantic	shortbeard codling <i>Laemonema barbatulum</i> (s) (35%, 100%F), <i>Lobianchia gemellarii</i> (s) (13%, 100%F), marlin-spike <i>Nezumia bairdii</i> (11%, 100%F), <i>Lampanyctus</i> sp. (s) (8%, 100%F), longfin hake <i>Phycis chesteri</i> (7%, 88%F)	Wenzel <i>et al.</i> 2013: stomach content analysis, n: 11 (with food: 8)
Southern bottlenose whale	Tierra del Fuego (Argentina)	cranchiids (67%N), neoteuthids (16%N), enoplateuthids (9%N)	Clarke 1986: stomach content analysis, n: 1
	South Africa	<i>Histioteuthis</i> spp. (22%N), <i>Taonius pavo</i> (s) (17%N), <i>Galiteuthis glacialis</i> (11%N), <i>Chiroteuthis</i> spp. (9%N), <i>Gonatus antarcticus</i> (8%N, 7%M), <i>Mesonychoteuthis hamiltoni</i> (23%M), <i>Kondakovia longimata</i> (13%M)	Sekiguchi <i>et al.</i> 1993: stomach content analysis, n: 2
	Tierra del Fuego (Argentina)	<i>Histioteuthis eltaninae</i> (24%N of cephalopods, 5%M), <i>Taonius pavo</i> (s) (53%N, 3%M), <i>Kondakovia longimana</i> (3%N, 66%M), <i>Gonatus antarcticus</i> (9%N, 10%M)	Clarke, Goodall 1994: stomach content analysis, n: 2
	Herd Island (Southern Ocean)	<i>Psychroteuthis glacialis</i> (50%N, 8%M), <i>Kondakovia longimana</i> (3%N, 55%M), <i>Taonius pavo</i> (s) (6%N, 6%M), <i>Galiteuthis glacialis</i> (12%N, 5%M), <i>Liochranhia</i> sp. (11%N, 6%M), <i>Gonatus antarcticus</i> (6%N, 7%M) prey ML: 75-355mm	Slip <i>et al.</i> 1995: stomach content analysis, n: 1
Northern bottlenose whale	Iceland (n: 46), Labrador (n: 108)	Iceland: <i>Gonatus fabricii</i> ; Labrador: <i>Gonatus fabricii</i> , fish	Benjaminsen, Christensen 1979: stomach content analysis, n: 154
	Faroe Islands	<i>Gonatus fabricii</i> (90%F), <i>Taonius</i> sp. (90%F), <i>Megalocranchia</i> sp. (80%F), <i>Teuthowenia</i> sp. (s) (90%F), <i>Octopoteuthis</i> sp. (60%F)	Bloch <i>et al.</i> 1996: stomach content analysis, n: 10
	NE-Atlantic	<i>Gonatus</i> spp. (31%N, 53%M), <i>Teuthowenia</i> sp. (s) (31%N, 20%M), <i>Taonius pavo</i> (s) (33%N, 19%M), <i>Histioteuthis</i> sp. (2%N, 6%M)	Fernandez <i>et al.</i> 2014: stomach content analysis, n: 10
Long-finned pilot whale	NW-Atlantic	Atlantic mackerel (s) (71%M), <i>Loligo pealeii</i> (s) (29%M); ind. caught by mackerel fishing vessels -> mackerel may be over-represented	Overholtz, Waring 1991: stomach content analysis, n: 5 (with food: 5), may be short-finned pilot whale
	South Africa	<i>Todarodes angolensis</i> (s) (81%M), <i>Lycoteuthis lorigera</i> (s) (13%M)	Sekiguchi <i>et al.</i> 1992: stomach content

Cetacea species	Area	Prey	Reference
			analysis, n: 5 (with food: 5)
	Tierra del Fuego (Argentina)	<i>Loligo gahi</i> (s) (31%N, 7%M), <i>Histioteuthis eltaninae</i> , (29%N, 5%M), <i>Moroteuthis ingens</i> (s) (17%N, 52%M), <i>Brachioteuthis riisei</i> (s) (8%N, 9%M)	Clarke, Goodall 1994: stomach content analysis, n: 4
	E-USA	<i>Loligo pealeii</i> (s) (68%N), ommastrephid squid (s) (17%N), <i>Histioteuthis reversa</i> (s) (7%N), Atlantic mackerel (s) (likely biased, 4%N)	Gannon <i>et al.</i> 1997a: stomach content analysis of ind. incident. caught in mackerel fishery, n: 30 (with food: 30)
	New Zealand	<i>Nototodarus gouldi</i> (s) (35%N, 87%M), <i>Chiroteuthis</i> sp. (40%N, 1%M)	Beatson <i>et al.</i> 2007b: stomach content analysis, n: 16 (with food: 11)
	Bay of Biscay (NE-Atlantic)	benthic ocotopods (15%N, 21%M), <i>Todarodes sagittatus</i> (s) (22%N, 17%M), <i>Histioteuthis reversa</i> (s) (13%N, 11%M), <i>Histioteuthis bonnellii</i> (s) (4%N, 11%M), <i>Galiteuthis armata</i> (14%N, 9%M), eel <i>Conger conger</i> (5%N, 8%M), Atlantic horse mackerel (s) (5%N, 4%M), salps (9%N, 8%M)	Spitz <i>et al.</i> 2011: stomach content analysis, n: 11
Short-finned pilot whale	California	<i>Loligo opalescens</i> (s) (99%), <i>Onykia robusta</i> (s), <i>Histioteuthis dofleini</i>	Seagars, Henderson 1985: stomach content analysis, n: 1
	Canary Islands	cranchiids (67%N: <i>Megalocranchia</i> sp., <i>Cranchia scabra</i> , <i>Taonius</i> sp.), cycloteuthids (9%N esp. <i>Cycloteuthis</i> sp.), ommastrephids (s) (6%N: European flying squid (s)) histioteuthids, pholidoteuthids	Hernández-García, Martín 1994: stomach content analysis, n: 2 (with food: 2)
	North Carolina (E-USA)	<i>Brachioteuthis riisei</i> (s) (28%N), <i>Taonius pavo</i> (s) (12%N), <i>Histioteuthis reversa</i> (s) (9%N), the fish <i>Scopelogadus beanii</i> (s) (25%N)	Mintzer <i>et al.</i> 2008: stomach content analysis, n: 27 (with food: 11)
False killer whale	South Africa	<i>Thysanoteuthis rhombis</i> (50%M), <i>Todarodes angolensis</i> (s) (47%M)	Sekiguchi <i>et al.</i> 1992: stomach content analysis, n: 13 (with food: 13)
	Strait of Magellan, Chile	<i>Martialia hyadesi</i> (ommastrephid) (s) (45%N, 57%M, 81%F), <i>Illex argentines</i> (s) (50%N, 17%M, 76%F), <i>Macruronus magellanicus</i> (s) (7%N, 33%M, 57%F), <i>Todarodes fillipovae</i> (s) (2%N, 19%M, 24%F), <i>Moroteuthis ingens</i> (s) (1%N, 7%M, 14%F); prey size: 74-862mm	Alonso <i>et al.</i> 1999: stomach content analysis, n: 25 (with food: 21)
	Hawaii	yellowfin tuna (s), albacore (s), skipjack (s), broadbill swordfish, mahi mahi (s), wahoo <i>Acanthocybium solandri</i> , lustrous pomfret <i>Eumegistus illustrus</i>	Baird 2009a: field observations (small sample size)

Cetacea species	Area	Prey	Reference
Pygmy killer whale	Cape Verde (W-Africa)	myctophids (s), deepbody boarfish <i>Antigonia capros</i> (s) (together 95%N)	O'Dwyer <i>et al.</i> 2015: stomach content analysis, n: 2 (with food: 2)
	Gulf of California	purpleback flying squid <i>Sthenoteuthis oualaniensis</i> (s)	Elorriaga-Verplancken <i>et al.</i> 2016: stable isotopes, stomach content analysis, n: 3 (with food: 2)
Melon-headed whale	South Africa	<i>Loligo reynaudii</i> (s) (100%)	Sekiguchi <i>et al.</i> 1992: stomach content analysis, n: 1
	Bay of Biscay (NE-Atlantic)	<i>Sepia</i> spp. (19%N, 55%M), blue whiting (s) (18%N, 4%M), European hake (s) (10%N, 5%M), <i>Trisopterus</i> spp. (s) (29%N, 8%M), ommastrephid squid (s) (4%N, 19%M)	Spitz <i>et al.</i> 2011: stomach content analysis, n: 2 (with food: 2)
	Hawaii (oceanic)	<i>Lampadena urophaos</i> (s) (15%N), <i>Lampanyctus nobilis</i> (s) (7%N), <i>Diaphus fragilis</i> (s) (4%N); <i>Chauliodus macouni</i> (s) (6%N, 8%M), enoploteuthids (13%N, 19%M) incl. <i>Enoploteuthis reticulata</i> (4%N, 9%M); <i>Cycloteuthis sirventi</i> (8%M)	West <i>et al.</i> 2015: stomach content analysis, n: 6
Risso's dolphin	South Africa	<i>Octopus</i> sp. (44%V), South African anchovy (s) (19%V), <i>Todaropsis eblanae</i> (s) (10%V), <i>Octopoteuthis</i> sp. (10%V)	Sekiguchi <i>et al.</i> 1992: stomach content analysis, n: 18 (with food: 11)
	W-Mediterranean	<i>Argonauta argo</i> (46%N, 79%F), <i>Histioteuthis bonnellii</i> (s) (8%N, 36%F), <i>Ancistroteuthis lichtensteinii</i> (7%N, 50%F), <i>Todarodes sagittatus</i> (s) (6%N, 50%F), <i>Illex coindetti</i> (s) (5%N, 29%F); ML: 16.2-432mm	Blanco <i>et al.</i> 2006: stomach content analysis, n: 15 (with food: 15)
	Santa Catalina Basin (off California)	dolphins feeding within mono-specific schools, each ~20-150m across and affiliated with deep-scattering layers, feeding primarily within schools with an acoustic frequency response characteristic of squid	Benoit-Bird <i>et al.</i> 2017: AUV-based echosounder observations, n: 425
Bottlenose dolphin	South America Pacific (offshore)	myctophids (s), anchoveta (s), South Pacific hake (s), Pacific sardine (s), Pacific jack mackerel <i>Trachurus symmetricus</i> (s), <i>Leuroglossus</i> sp. (s)	Van Waerebeek <i>et al.</i> 1990: stomach content analyses, n: 23 (with food: 20), neritic samples excl.
	USA Atlantic (oceanic)	mesopelagic fish esp. myctophids (s), pelagic squid	Barros, Odell 1990; Mead, Potter 1995: stomach content analyses, n: 18
	Peru	<i>Lampanyctus parvicauda</i> (s) (45%F, 39%N), barracuda <i>Sphyraena</i> sp. (23%F, 14%N), Peruvian pilchard <i>Sardinops sagax</i> (s) (41%F, 13%N), lumptail searobin <i>Prionotus stephanophrys</i> (5%F, 10%N), blue	García-Godos <i>et al.</i> 2007: stomach content analysis, n: 22

Cetacea species	Area	Prey	Reference
		jack mackerel <i>Trachurus murphyi</i> (s) (32%F, 4%N), Peruvian anchovy (23%F, 4%N)	
	Greece (Mediterranean)	European pilchard (s), round sardinella (s)	Bräger <i>et al.</i> 2016: collection of 1227 fish scales in 257 feeding events
Rough-toothed dolphin	E-Pacific n: 4, Hawaii n: 2	mahimahi <i>Coryphaena hippurus</i> (s)	Pitman, Stinchcomb 2002: field observations, n: 6
	SE-Brazil	largehead hairtail <i>Trichiurus lepturus</i> (s)	Di Benedetto <i>et al.</i> 2001: stomach content analysis, n: 3 (with food: 2)
	throughout range	mahi mahi (s), longspine snipefish <i>Macroramphosus scolopax</i> (s); stomachs of few stranded individuals contained: silverside <i>Atherinomorus insularum</i> (s), saury <i>Cololabis adocetus</i> (s), smelt <i>Atherinops</i> sp. (s), <i>Trichiurus lepturus</i> (s), ommastrephid (s), <i>Onychoteuthis borealijaponica</i> (s), <i>Loligo</i> (s), octopus	West <i>et al.</i> 2011: review based on stomach content analyses + field observations
White-beaked dolphin	Newfoundland (E-Canada)	cod (s) (100%)	Dong <i>et al.</i> 1996: stomach content analysis, n: 20 (with food: 20)
	Scotland	haddock (20%N, 43%M), whiting <i>Merlangius merlangus</i> (s) (35%N, 24%M), cod (s) (2%N, 11%M)	Canning <i>et al.</i> 2008: stomach content analysis, n: 22 (with food: 22)
	Dutch North Sea	whiting (s) (31%N, 38%M), cod (s) (7%N, 56%M), gobies (55%N, 1%M)	Jansen <i>et al.</i> 2010: stomach content analysis, n: 45 (with food: 45)
	W-Ireland	Atlantic horse mackerel (s) (50%N), blue whiting (s) (11%N)	Hernández-Milián 2014: stomach content analysis, n: 6 (with food: 3)
Atlantic white-sided dolphin	Ireland	Atlantic mackerel (s) (67%M), silvery pout <i>Gadiculus argenteus</i> (s) (71%F, 9%M), ommastrephids (s) (9%M)	Couperus 1997a,b: stomach content analysis, n: 49
	New England (NE-USA)	silver hake <i>Merluccius bilinearis</i> (35%F), Atlantic hagfish <i>Myxine glutinosa</i> (27%F), spoonarm octopus <i>Bathypolypus bairdii</i> (23%F), red hake <i>Urophycis chuss</i> (23%F), haddock <i>Melanogrammus aeglefinus</i> (13%F), <i>Ceratocopelus maderensis</i> (s) (2%F), Atlantic herring (s) prey length: 8.5-489.1mm	Craddock <i>et al.</i> 2009: stomach content analysis, n: 62 (with food: 62) mostly trace remains in stomachs
	W-Ireland	blue whiting (s) (24%N, 37%M), <i>Trisopterus</i> spp. (s) (34%N, 12%M), Atlantic mackerel (s) (4%N, 21%M)	Hernández-Milián 2014: stomach content analysis, n: 41 (with food: 24)

Cetacea species	Area	Prey	Reference
		silvery pout (s) (12%N, 4%M), whiting (s) (6%N, 10%M)	
Pacific white-sided dolphin	W-USA	<i>Loligo opalescens</i> (s) (64%F), <i>Onychoteuthis borealijaponica</i> (s) (45%F), <i>Abraliopsis</i> sp. (s) (36%F), northern anchovy (s) (58%F), North Pacific hake <i>Merluccius productus</i> (s) (33%F), Pacific saury (s) (28%F), salmon <i>Oncorhynchus</i> spp. (s) (23%F); prey length: 109-405mm	Kajimura <i>et al.</i> 1980: stomach content analysis, n: 44
	central N-Pacific	<i>Ceratoscopelus</i> sp. (s) (52%F, 29%N), <i>Symbolophorus</i> sp. (s) (58%F, 11%N), <i>Onychoteuthis borealijaponica</i> (s) (85%F, 9%N), <i>Diaphus theta</i> (s) (52%F, 9%N), <i>Notoscopelus japonica</i> (s) (30%F, 8%N), <i>Leuroglossus schmidti</i> (s) (30%F, 5%N), <i>Bathylagus</i> spp. (24%F, 5%N), <i>Abraliopsis felis</i> (s) (58%F, 4%N)	Walker, Jones 1993: stomach content analysis, n: 33 (with food: 33)
	W-USA	market squid <i>Loligo opalescens</i> (s), gonatid squid incl. <i>Gonatus</i> spp., <i>Abraliopsis</i> sp. (s), <i>Onychoteuthis borealijaponica</i> (s), <i>Symbolophorus californiensis</i> (s), northern anchovy (s)	Preti <i>et al.</i> 2016: stomach content analysis, n: 25
Dusky dolphin	New Zealand	myctophids, <i>Nototodarus</i> sp. (s), hoki <i>Macruronus novaezelandiae</i> (s), also: red codling <i>Pseudophycis bachus</i> , <i>Moroteuthopsis</i> spp., <i>Teuthowenia</i> sp. (s)	Cipriano (1985, 1992): stomach content analysis, n: 24 (with food: 18)
	South Africa	Cape horse mackerel (s) (30%V), <i>Merluccius</i> sp. (18%V), <i>Todarodes angolensis</i> (s) (13%V), <i>Lampanyctodes hectoris</i> (s) (12%V), South African pilchard (s) (5%V)	Sekiguchi <i>et al.</i> 1992: stomach content analysis, n: 37 (with food: 31)
	Patagonia	Argentine anchovy <i>Engraulis anchoita</i> (s) (80%F, 39%N, 46%M), Argentine hake <i>Merluccius hubbsi</i> (s) (48%F, 5%N, 26%M), <i>Loligo gahi</i> (s) (84%F, 21%N, 5%M), <i>Illex argentinus</i> (s) (68%F, 31%N, 21%M)	Alonso <i>et al.</i> 1998: stomach content analysis, n: 25 (with food: 25)
	Peru	sample 1: Argentine anchovy (s) (71%F, 50%N), <i>Lampanyctus parvicauda</i> (s) (12%F, 24%N), blue jack mackerel <i>Trachurus picturatus</i> (s) (57%F, 17%N), Peruvian pilchard (s) (20%F), Chilean silverside (s) (16%F); sample 2: <i>Normanichtys crockery</i> (s) (61%F, 76%N), anchovy (s) (96%F, 17%N)	García-Godos <i>et al.</i> 2004: stomach content analysis, n: 66 (2 samples from ind. landed in 2 different ports)
	Patagonia	Argentine anchovy (s) (100%F, 85%N, 60%M), <i>Loligo sanpaulensis</i> (s) (60%F, 6%N, 4%M), silver warehou <i>Seriolaella porosa</i> (s) (60%F, 1%N, 8%M), Argentine hake	Romero <i>et al.</i> 2012: stomach content analysis, n: 31 (with food: 30)

Cetacea species	Area	Prey	Reference
		(s) (40%F, 4%N, 10%M), <i>Illex argentinus</i> (s) (40%F, 1%N, 11%M)	
	Argentina	Argentine anchovy (s), butterfish <i>Stromateus brasiliensis</i>	De Castro <i>et al.</i> 2016: stable isotope analysis, n: 45
Fraser's dolphin	Sulu Sea, Philippines	<i>Lampadena luminosa</i> (s) (76%F, 12%N), <i>Ceratoscopelus warmingii</i> (s) (43%F, 14%N), <i>Diaphus parri</i> (s) (30%F, 5%N), viperfish <i>Chauliodus sloani</i> (s) (42%F, 7%N), <i>Abraliopsis lineata</i> (s) (41%F, 31%N), <i>Octopoteuthis</i> sp. (32%F, 6%N), <i>Onycboteuthis banksi</i> (s) (35%N, 13%N), <i>Histioteuthis miranda</i> (27%F, 9%N), <i>Chiroteuthis</i> sp. (35%F, 9%N), <i>Nototodarus</i> c.f. <i>philippinensis</i> (s) (30%F, 6%N), <i>Leachia dislocata</i> (16%F, 5%N)	Dolar <i>et al.</i> 2003: stomach content analysis, n: 28 (with food: 24), fish and squid prey analysed separately, each amounting to 100%
Spinner dolphin	tropical Pacific	<i>Diogenichthys</i> sp. (s) (100%F, 61%N), <i>Bregmaceros</i> sp. (100%F, 15%N), <i>Scopelogadus bispinosus</i> (s) (50%F, 8%N), <i>Lampanyctus parvicauda</i> (s) (100%F, 6%N), <i>Vinciguerria</i> sp. (s) (75%F, 2%N), <i>Abraliopsis affinis</i> (s) (100%F, 3%N), ommastrephids (s) (75%F, 1%N)	Perrin <i>et al.</i> 1973: stomach content analysis, n: 27 (with food: 12)
	Sulu Sea, Philippines	<i>Ceratoscopelus warmingii</i> (s) (91%F, 28%N), <i>Diaphus parri</i> (s) (98%F, 20%N), <i>Myctophum asperum</i> (s) (69%F, 8%N), <i>Diaphus lutkeni</i> (s) (69%F, 4%N), <i>Symbolophorus evermanni</i> (s) (71%F, 4%N), <i>Larizpanyctus alatus</i> (s) (47%F, 4%N), <i>Abraliopsis</i> sp. (s) (71%F, 79%N) <i>Enoplateuthis</i> sp. (22%F, 6%N)	Dolar <i>et al.</i> 2003: stomach content analysis, n: 38 (with food: 33), fish and squid prey analysed separately, each amounting to 100%
	Fernando de Noronha (SW-Atlantic)	small pelagic fish affiliated to shoals of hundreds of individuals, likely scad + flying fish (s), small ommastrephid (s) + cranchiid squid	Silva Jr. <i>et al.</i> 2007: visual field observations, n: 34; vomit, n: 11, and stomach content analyses, n: 2
Pantropical spotted dolphin	tropical Pacific	<i>Onykia</i> sp. (s) (97%F, 56%N), ommastrephids (s) (100%F, 26%N), <i>Abraliopsis affinis</i> (s) (100%F, 11%N)	Perrin <i>et al.</i> 1973: stomach content analysis, n: 120 (with food: 110)
	eastern tropical Pacific	ommmastrephids (s) (65%F, 9%N), <i>Lampanyctus parvicauda</i> (s) (30%F, 14%N), other <i>Lampanyctus</i> sp. (s) (4%N), <i>Symbolophorus</i> spp. (s) (35%F, 8%N), <i>Diaphus splendidus</i> (s) (13%F, 4%N), <i>Diaphus</i> sp. (s) (4%N), <i>Myctophum</i> sp. (s) (4%N), <i>Lampadena luminosa</i> (s) (8%F, 3%N), <i>Abraliopsis affinis</i> (s) (47%F, 10%N), <i>Cubiceps pauciradiatus</i> (s) (24%F, 6%N), exocoetids (s)	Robertson, Chivers 1997: stomach content analysis, n: 428 (with food: ≥ 354)

Cetacea species	Area	Prey	Reference
		(19%F, 2%N), <i>Bregmaceros bathymaster</i> (6%F, 4%N)	
	Taiwan	<i>Myctophum asperum</i> (s) (42%F, 20%N), <i>Diaphus schmidti</i> (s) (47%F, 13%N), <i>Diaphus watasei</i> (s) (29%F, 5%N), <i>Enoploteuthis chunii</i> (s) (67%F, 26%N), <i>Abraliopsis lineata</i> (s) (44%F, 3%N), Japanese anchovy (s) (18%F, 3%N), <i>Trichiurus lepturus</i> (s) (11%F, 3%N) prey length: 26.5-656.5mm	Wang <i>et al.</i> 2003: stomach content analysis, n: 45 (with food: 45)
Atlantic spotted dolphin	SE-Brazil	<i>Doryteuthis plei</i> (s) (100%F, 95%N, 98%M), rough scad <i>Trachurus lathami</i> (s) (11%F, 70%N, 15%M), Atlantic cutlassfish <i>Trichiurus lepturus</i> (s) (22%F, 12%N, 73%M), <i>Merluccius hubbsi</i> (s) (11%F, 6%N, 9%M), red porgy <i>Pagrus pagrus</i> (s) (22%F, 6%N, 2%M), Argentine anchovy <i>Engraulis anchoita</i> (s) (11%F, 6%N, 1%M)	Lopes <i>et al.</i> 2012: stomach content analysis, n: 9 (with food: 9), squid and fish analysed separately, each amounting to 100%
Striped dolphin	South Africa	<i>Loligo reynaudii</i> (s) (74%M), hake (s) (8%M), <i>Sthenoteuthis</i> sp. (s) (8%M), Cape horse mackerel <i>Trachurus capensis</i> (s) (4%M)	Sekiguchi <i>et al.</i> 1992: stomach content analysis, n: 11 (with food: 11)
	W-Mediterranean Sea	<i>Albraliopsis pfefferi</i> (s) (52%F, 25%N, 8%M), <i>Onychoteuthis banksii</i> (s) (36%F, 19%N, 25%M), <i>Todarodes sagittatus</i> (s) (60%F, 5%N, 16%M), <i>Todaropsis eblanae</i> (s) (32%F, 5%N, 14%M), <i>Brachioteuthis riisei</i> (s) (40%F, 22%N, 5%M), <i>Octopoteuthis sicula</i> (48%F, 7%N, 7%M), <i>Ancistrocheirus lesueurii</i> (32%F, 3%N, 11%M)	Blanco <i>et al.</i> 1995: stomach content analysis, n: 28
	NE-Atlantic	<i>Teuthowenia megalops</i> (s) (84%F, 11%N, 32%M), <i>Histioteuthis reversa</i> (s) (80%F, 5%N, 5%M), <i>Histioteuthis corona</i> (36%F, 1%N, 8%M), <i>Brachioteuthis riisei</i> (s) (77%F, 10%N, 0.2%M), <i>Notoscopelus kroeyeri</i> (s) (75%F, 14%N, 8%M), <i>Lobianchia gemellarii</i> (s) (46%F, 8%N, 6%M), <i>Lampanyctus</i> spp. (s) (54%F, 8%N, 2%M), <i>Ceratoscopelus maderensis</i> (s) (53%F, 6%N, 3%M)	Ringelstein <i>et al.</i> 2006: stomach content analysis, n: 60
	eastern tropical Pacific	<i>Lampanyctus parvicauda</i> (s) (60%F, 12%N), <i>Parvilux ingens</i> (s) (34%F, 7%N), <i>Notoscopelus resplendens</i> (s) (23%F, 6%N) <i>Scopelogadus bispinosus</i> (s) (51%F, 6%N), <i>Melamphaes</i> sp. (s) (26%F, 5%N), other <i>Lampanyctus</i> sp. (s) (5%N), <i>Lampadena luminosa</i> (s) (23%F, 3%N), <i>Abraliopsis affinis</i> (s) (46%F, 8%N), ommastrephids (31%F, 4%N)	Perrin <i>et al.</i> 2008: stomach content analysis, n: 131 (with food: 104)

Cetacea species	Area	Prey	Reference
	W- and S-Ireland	<i>Histioteuthis reversa</i> (s) (14%N, 67%M), <i>Benthoosema glaciale</i> (s) (28%N, 3%M), <i>Notoscopelus kroeyeri</i> (s) (8%N, 4%M), <i>Diaphus effulgens</i> (s) (8%N, 2%M), <i>Diaphus raffinesquii</i> (s) (6%N, 1%M), <i>Notostomus</i> spp. (s) (3%N, 1%M), <i>Teuthowenia megalops</i> (s) (3%N, 3%M)	Hernández-Milián 2014: stomach content analysis, n: 27 (with food: 27)
Common dolphin	South Africa	South African pilchard (s) (69%F, 48%N, 48%M), chub mackerel (s) (13%F, 2%N, 14%M), bluefish <i>Pomatomus saltatrix</i> (s) (15%F, 2%N, 9%M), African scad <i>Trachurus delagoa</i> (s) (14%F, 5%N, 4%M), salema <i>Sarpa salpa</i> (12%F, 2%N, 8%M), myctophids (s) (5%F, 10%N, 0.3%M), <i>Loligo</i> sp. (s) (29%F, 10%N, 8%M)	Young, Cockcroft 1994, 1995: stomach content analysis, n: 297 (sardine-run associated)
	Portugal	European pilchard (s) (81%F, 27%N, 43%M), blue whiting (s) (31%F, 24%N, 16%M), <i>Macroramphosus</i> sp. (s) (24%F, 9%N, 3%M), <i>Trachurus</i> sp. (s) (45%F, 5%N, 7%M), sand smelt <i>Atherina</i> sp. (s) (12%F, 5%N, 11%M), <i>Alloteuthis</i> sp. (s) (33%F, 5%N, 2%M)	Silva, Sequeira 1996; Silva 1999: stomach content analysis, n: 50 (with food: 42)
	New Zealand	jack mackerel <i>Trachurus novaezelandiae</i> (s), kahawai <i>Arripis trutta</i> (s), yellow-eyed mullet <i>Aldrichetta forsteri</i> (s), <i>Cheilopogon pinnatibarbus</i> (s), parore <i>Girella tricuspidata</i> (s), garfish <i>Hyporamphus ihi</i> (s)	Neumann, Orams 2003: field observations, n: 68 (short-beaked common dolphin)
	Peru	Peruvian anchovies (s) (81%F, 71%N), South Pacific hake <i>Merluccius gayi gayi</i> (s) (14%F, 4%N), Chilean silverside <i>Odontesthes regia</i> (s) (18%F, 4%N), blue jack mackerel <i>Trachurus picturatus</i> (s) (16%F), Peruvian pilchard <i>Sardinops sagax</i> (s) (16%F), <i>Vincigerria lucetia</i> (s) (8%F, 8%N), <i>Lampanyctus parvicauda</i> (s) (8%F, 7%N)	García-Godos <i>et al.</i> 2004, 2007: stomach content analysis, n: 117 (with food: 117, long-beaked common dolphin)
	NE-Atlantic (oceanic)	<i>Myctophum punctatum</i> (s) (72%F, 29%N), <i>Notoscopelus kroeyeri</i> (s) (77%F, 22%N), Atlantic horse mackerel (s) (63%F, 37%N), <i>Arctozenus risso</i> (s) (47%F, 3%N), <i>Brachioteuthis riisei</i> (s) (65%F, 4%N)	Brophy <i>et al.</i> 2007, Pusineri <i>et al.</i> 2007: stomach content analysis, n: 58 (with food: 43, short-beaked common dolphin, stranded ind. with neritic diet not incl.)
	New Zealand, North Island	<i>Nototodarus</i> spp. (s) (15%N, 36%M), <i>Lampanyctus australis</i> / <i>Lampanyctodes hectoris</i> (s) (42%N, 3%M), jack mackerel <i>Trachurus</i>	Meynier <i>et al.</i> 2008: stomach content analysis, n: 53 (with food: 37)

Cetacea species	Area	Prey	Reference
		spp. (s) (3%N, 11%M), anchovy <i>Engraulis australis</i> (s) (4%N, 1%M), eel <i>Conger wilsoni</i> (2%N, 10%M); 80% prey <100mm long	
	W-USA	<i>Abraliopsis</i> sp. (s), <i>Gonatus</i> spp., <i>Ceratoscopelus townsendi</i> (s), <i>Symbolophorus californiensis</i> (s), <i>Onychoteuthis borealijaponica</i> (s), <i>Lampanyctus ritteri</i> (s), Pacific saury (s)	Preti <i>et al.</i> 2016: stomach content analysis, n: 259 (short-beaked common dolphin)
	W-USA	market squid (s), northern anchovy (s), <i>Gonatus</i> spp., California lizardfish <i>Synodus lucioceps</i> , <i>Symbolophorus californiensis</i> (s), Pacific sardine (s)	Preti <i>et al.</i> 2016: stomach content analysis, n: 49 (long-beaked common dolphin)
Commerson's dolphin	Tierra del Fuego	Fuegian spratt <i>Sprattus fuegensis</i> (s), Patagonian grenadier <i>Macruronus magellanicus</i> (s), <i>Patagonotothen tesellata</i> (s), <i>P. sima</i> , <i>P. cornucula</i> , Patagonian blenny <i>Eleginops maclovinus</i> , silversides <i>Odontheistes</i> spp. (s), <i>Loligo gahi</i> (s), <i>Illex argentines</i> (s), red octopus <i>Enteroctopus megalocyathus</i> , squat lobster <i>Munida gregaria</i> (s), marine crab <i>Halicarcinus planatus</i> , euphausids (s)	Riccaldelli <i>et al.</i> 2013: review, stable isotope analysis
Northern right whale dolphin	central N-Pacific	<i>Ceratoscopelus</i> sp. (s) (63%F, 15%N), <i>Diaphus theta</i> (s) (61%F, 11%N), <i>Lampanyctus jordani</i> (s) (47%F, 8%N), <i>Notoscopelus japonica</i> (s) (39%F, 9%N), <i>Stenobrachius</i> spp. (s) (50%F, 8%N), <i>Leuroglossus schmidtii</i> (s) (31%F, 6%N), <i>Abraliopsis felis</i> (s) (63%F, 7%N), <i>Onychoteuthis borealijaponica</i> (s) (90%F, 7%N)	Walker, Jones 1993: stomach content analysis, n: 72 (with food: 72)
	W-USA	<i>Abraliopsis</i> sp. (s), <i>Gonatus</i> spp., <i>Diaphus theta</i> (s), <i>Onychoteuthis borealijaponica</i> (s), other gonatids, <i>Symbolophorus californiensis</i> (s), market squid (s), California smoothtongue <i>Leuroglossus stilbius</i> (s), <i>Ceratoscopelus townsendi</i> (s), <i>Triphoturus mexicanus</i> (s)	Preti <i>et al.</i> 2016: stomach content analysis, n: 56
Dall's porpoise	S-Sea of Okhotsk (NW-Pacific)	Japanese pilchard <i>Sardinops sagax melanostictus</i> (s) (72%N), <i>Beryteuthis magister</i> (s) (17%N), Walleye pollock <i>Theragra chalcogramma</i> (s) (6%N)	Walker 1996: stomach content analysis, n: 85
	Sea of Japan off Hokkaido (Japan)	walleye pollock (s) (37%M), <i>Todarodes</i> sp. (s) (30%M), Atka mackerel (s) (17%M), Japanese sand lance (s) (8%M), Japanese anchovy (s) (7%M)	Ohizumi, Miyazaki 1998: stomach content analysis, n: 30 (with food: 30)
	NW-Pacific, Bering Sea	<i>Gonatopsis borealis</i> (s) (85%F, 27%N), <i>Gonatus pyros</i> (78%F,	Fiscus, Jones 1999: stomach content

Cetacea species	Area	Prey	Reference
		19%N), <i>Gonatus berryi</i> (71%F, 12%N), <i>Eogonatus tinro</i> (64%F, 5%N), <i>Gonatus</i> spp. (49%F, 9%N)	analysis, n: 100 (with food: 100, all beaks)
	temperate + subarctic N-Pacific, Bering Sea	<i>Bathylagus ochotensis</i> (3%N, 14%F), <i>Scopelosaurus harryi</i> (s) (0.1%N, 9%F), <i>Protomyctophum thompsoni</i> (s) (14%N, 60%F), <i>Diaphus theta</i> (s) (24%N, 53%F), <i>Stenobrachius leucopsarus</i> (s) (10%N, 51%F), <i>Stenobrachius nannochir</i> (s) (1%N, 20%F), <i>Lampanyctus jordani</i> (s) (4%N, 26%F), <i>Gonatopsis borealis</i> (s) (7%N, 66%F)	Ohizumi <i>et al.</i> 2003b: stomach content analysis, n: 326 (with food: 321)
Burmeister's porpoise	throughout range	anchovy (s), hake (s), anchovita (s), drum, jack mackerel (s), silverside, sardine (s), weakfish <i>Cynoscion</i> sp., rudderfish <i>Centrolophus niger</i> , <i>Loligo gahi</i> (s), euphausiids (s), mysids (s)	Goodall <i>et al.</i> 1995: stomach content analyses, n: 168
	Peru	anchovy (s) (89%N, 78%M), Chilean silverside <i>Odontesthes regia</i> (s) (7%N, 0%M), mote sculpin <i>Normanichthys crockeri</i> (s) (<1%N, 8%M), South Pacific hake <i>Merluccius gayi</i> (s) (1%N, 8%M)	García-Godos <i>et al.</i> 2007: stomach content analysis, n: 69

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Table 2: References for shoaling behaviour of cetacea prey

Species	Reference
euphausiids	e.g. Kalish <i>et al.</i> 1986; Ritz <i>et al.</i> 2011; Knutsen <i>et al.</i> 2017
copepods	Burd <i>et al.</i> 1992; Knutsen <i>et al.</i> 2017
amphipods	Knutsen <i>et al.</i> 2017
swimming crab <i>Polybius</i> spp.	González-Gurriarán <i>et al.</i> 1993; Romanov <i>et al.</i> 2009
<i>Neognatophausia</i> sp.	Wilson, Boehlert 1993
<i>Munida gregaria</i>	Diez <i>et al.</i> 2012
blue whiting	Madirolas 1999; Petitgas 2010
whiting	Skov <i>et al.</i> 2000
Atka mackerel	Poltev, Shubin 2011; Poltev, Mukhametov 2013
Atlantic mackerel	Petitgas 2010
European hake	Korta <i>et al.</i> 2015
South Pacific hake	Gatica <i>et al.</i> 2015
North Pacific hake	Hamel <i>et al.</i> 2015
Argentine hake	Vaz-dos-Santos, Schwingel 2015
hoki	Livingston <i>et al.</i> 2015
orange roughy	Williams, Koslow 1997; Kloster <i>et al.</i> 2002
<i>Normanichthys crockeri</i>	Landaeta <i>et al.</i> 2010
flying fish (exocoetids)	Parin 1983; Churnside <i>et al.</i> 2017
shortbeard codling	Ross, Quattrini 2007
<i>Patagonotothen tessellata</i>	Moreno, Jara 1984
red porgy	Manooch, Hassler 1978
<i>Maurollicus japonicus</i>	Hamano 1993; Fujino <i>et al.</i> 2005
<i>Maurollicus muelleri</i>	Dalpadado, Gjøsaeter 1987; Kaartvedt <i>et al.</i> 2009; Peña <i>et al.</i> 2014
<i>Polyipnus</i> sp.	Ross <i>et al.</i> 2010; Olivar <i>et al.</i> 2017
<i>Benthoosema glaciale</i>	Gjosater, Kawaguchi 1980; Sigurðsson <i>et al.</i> 2002; Godø <i>et al.</i> 2009
<i>Notoscopelus kroeyeri</i>	Sigurðsson <i>et al.</i> 2002; Heino <i>et al.</i> 2011
<i>Myctophum</i> sp.	Raman, James 1990; Ross <i>et al.</i> 2010; Catul <i>et al.</i> 2011
<i>Myctophum punctatum</i>	Sigurðsson <i>et al.</i> 2002; Catul <i>et al.</i> 2011; Heino <i>et al.</i> 2011
<i>Myctophum asperum</i>	Ross <i>et al.</i> 2010; Olivar <i>et al.</i> 2017
<i>Protomyctophum thompsoni</i>	Kalish <i>et al.</i> 1986; Beamish <i>et al.</i> 1999
<i>Chauliodus sloani</i>	Sigurðsson <i>et al.</i> 2002; Heino <i>et al.</i> 2011; Olivar <i>et al.</i> 2012
<i>Scopelogadus beanii</i>	Sigurðsson <i>et al.</i> 2002; Heino <i>et al.</i> 2011
<i>Ceratoscopelus warmingii</i>	Barnett 1983; Karuppasamy <i>et al.</i> 2010; Catul <i>et al.</i> 2011
<i>Ceratoscopelus townsendi</i>	Lara-Lopez <i>et al.</i> 2012; Davison <i>et al.</i> 2015
<i>Ceratoscopelus maderensis</i>	Olivar <i>et al.</i> 2012; Peña <i>et al.</i> 2014
<i>Diaphus</i> sp.	Raman, James 1990; Ross <i>et al.</i> 2010; Olivar <i>et al.</i> 2017
<i>Diaphus theta</i>	Kalish <i>et al.</i> 1986; Lara-Lopez <i>et al.</i> 2012; Davison <i>et al.</i> 2015
<i>Diaphus fragilis</i>	Karuppasamy <i>et al.</i> 2010; Ross <i>et al.</i> 2010
<i>Diaphus effulgens</i>	Williams, Koslow 1997
<i>Diaphus raffinesquii</i>	Ross <i>et al.</i> 2010; Olivar <i>et al.</i> 2017

<i>Symbolophorus californiensis</i>	Kalish <i>et al.</i> 1986; Catul <i>et al.</i> 2011; Lara-Lopez <i>et al.</i> 2012; Davison <i>et al.</i> 2015
<i>Stenobranchius leucopsarus</i>	Kalish <i>et al.</i> 1986; Beamish <i>et al.</i> 1999; Lara-Lopez <i>et al.</i> 2012
<i>Stenobranchius nannochir</i>	Rogachev <i>et al.</i> 2000; Sinclair, Stabeno 2002
<i>Triphoturus mexicanus</i>	Lara-Lopez <i>et al.</i> 2012; Davison <i>et al.</i> 2015
<i>Lampanyctodes hectoris</i>	Hulley 1986; Catul <i>et al.</i> 2011; Gauthier <i>et al.</i> 2014
<i>Lampanyctus ritteri</i>	Catul <i>et al.</i> 2011
<i>Lampanyctus nobilis</i>	Ross <i>et al.</i> 2010; Olivar <i>et al.</i> 2017
<i>Lampanyctus jordani</i>	Rogachev <i>et al.</i> 2000
<i>Lampanyctus</i> sp.	Barnett 1983; Heino <i>et al.</i> 2011; Olivar <i>et al.</i> 2012; Peña <i>et al.</i> 2014
<i>Lampadena urophaos</i>	Barnett 1983; Davison <i>et al.</i> 2015
<i>Diogenichthys</i> sp.	Raman, James 1990
<i>Lobianchia gemellari</i>	Barnett 1983; Ross <i>et al.</i> 2010; Catul <i>et al.</i> 2011
<i>Vinciguerria</i> sp.	Ménard, Marchal 2003 Karuppasamy <i>et al.</i> 2010; Davison <i>et al.</i> 2015
<i>Leuroglossus stilbius</i>	Davison <i>et al.</i> 2015
<i>Arctozenus risso</i>	Davison <i>et al.</i> 2015
<i>Lestrolepis intermedia</i>	Ross <i>et al.</i> 2010
<i>Melamphaes</i> sp.	Ross <i>et al.</i> 2010
<i>Epigonus</i> sp.	Williams, Koslow 1997; Ross <i>et al.</i> 2010
<i>Diretmus argenteus</i>	Williams, Koslow 1997
<i>Scopelosaurus harryi</i>	Khoruzhiy 2011
ommatrephids	Dunning, Wormuth 1998; Jereb, Roper 2010; Vijai <i>et al.</i> 2017
<i>Loligo</i> sp.	Bernard 1980; Jereb, Roper 2010
<i>Histioteuthis reversa</i>	Quetglas <i>et al.</i> 2000, Shea <i>et al.</i> 2017
<i>Histioteuthis bonnellii</i>	Roper <i>et al.</i> 1984
<i>Stigmatoteuthis hoylei</i>	Voss <i>et al.</i> 1998; Jereb, Roper 2010
<i>Onychoteuthis banksii</i>	Clarke 2006; Jereb, Roper 2010; Ariza <i>et al.</i> 2016
<i>Onychoteuthis borealijaponica</i>	Jereb, Roper 2010
<i>Berryteuthis anonychus</i>	Jereb, Roper 2010
<i>Berryteuthis magister</i>	Ormseth 2014
<i>Gonatopsis borealis</i>	Jereb, Roper 2010
<i>Gonatus steenstrupi</i>	Clarke 2006
<i>Taonius pavo</i>	Clarke 2006
<i>Teuthowenia megalops</i>	Clarke 2006; Heino <i>et al.</i> 2011
<i>Teuthowenia</i> sp.	Williams, Koslow 1997
<i>Abraliopsis</i> sp.	Williams, Koslow 1997; Shea <i>et al.</i> 2017
<i>Lycoteuthis lorigera</i>	Williams, Koslow 1997
<i>Brachioteuthis riisei</i>	Clarke 2006; Quetglas <i>et al.</i> 2014
<i>Liocranchia reinhardtii</i>	Clarke 2006
<i>Mastigoteuthis schmidti</i>	Clarke 2006
<i>Onykia</i> sp.	Potier <i>et al.</i> 2014
<i>Enoploteuthis chunii</i>	Jereb, Roper 2010

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Appendix 4: Predation on cetacea

Table 1: References used for predation risk assessment: sample size of stomach content analyses reflects non-empty stomachs

Species	Reference	Predation information
Baleen whales/Mysticeti		
Blue whale	Tarpy 1979	group of ~30 <u>killer whales</u> non-fatally attacked and bit pieces of blubber out of sub-adult blue whale in Gulf of California in a collaborative manner, n: 1
	Jefferson <i>et al.</i> 1991	3 further attacks: group of 5 <u>killer whales</u> successfully attacked adult blue whale in Antarctica; pod of 11 killer whales chased blue whale cow-calf pair off S-Australia; single blue whale non-fatally attacked by group of 5 killer whales in Monterey Bay, California, n: 3
	Shaughnessy 2000	single blue whale attacked by group of 2 <u>killer whales</u> , outcome unknown, Antarctica, n: 1
	Ternullo, Black 2002	several observations of non-fatal harassment of blue whales by <u>killer whales</u> in Monterey Bay, California, n: several
	Pitman <i>et al.</i> 2007	group of ~19 <u>killer whales</u> observed feeding on blue whale calf off Nicaragua, n: 1
	Ford, Reeves 2008	3 non-fatal attacks by groups of 4-12 <u>killer whales</u> on single blue whale (n: 1), pair (n: 1) and group of 4 ind. (n: 1) off California (n: 1) and in Gulf of California (n: 2); n: 3
	Boyce 2013	group of ~25 <u>killer whales</u> attacked single blue whale in Gulf of California, most likely fatal; orcas attacked fluke and took turns pushing blue whale under water in attempt to immobilize and drown the ind.; large junks of blubber and muscle bitten out of blue whale esp. in dorsal caudal peduncle area, n: 1
	Gemmell <i>et al.</i> 2015	observation of blue whale in poor health with severe injuries most likely inflicted by <u>killer whales</u> , off S-Sri Lanka, n: 1; no blue whales with killer whale rake marks observed off Sri Lanka, n: 150+ identified ind.

Species	Reference	Predation information
Fin whale	Shevchenko 1975	marks of <u>killer whale</u> bites found in 53% of fin whales studied in Southern Ocean
	Bloch, Lockyer 1988	single fin whale attacked by group of <u>killer whales</u> for 1/2h off Faroe Islands, no kill observed, n: 1
	Vidal, Pechter 1989	fin whale pair attacked by pod of 3 <u>killer whales</u> , unknown outcome, in Gulf of California, n: 1
	Jefferson <i>et al.</i> 1991	13 attacks or chases with unknown outcome, at least 4 on single fin whales, at least 1 of them adult, 1 on 3 fin whales, by pods of 2-30 <u>killer whales</u> off Greenland (n: 8), E-USA (n: 1), Alaska (n: 1), W-Canada (n: 1), Gibraltar (n: 1); 1 fatal attack by 2 killer whales on a single fin whale off W-Greenland, n: 14
	Ford, Reeves 2008	single fin whale killed and fed on by group of 16 <u>killer whales</u> ; single fin whale attacked by group of 7 killer whales, outcome unknown; both Gulf of California, n: 2
	Best <i>et al.</i> 2010	fin whale tongue found in <u>killer whale</u> stomach, South Africa, 26 stomachs analysed
Sei whale	Nishiwaki, Handa 1958	out of 364 <u>killer whale</u> stomachs from ind. off Japan 2 contained sei whale remains
	Shevchenko 1975	marks of <u>killer whale</u> bites found in 24% of the sei whales studied in Southern Ocean
	Gaskin 1982	<u>killer whale</u> attack on a female sei whale with calf, n: 1
	Goodall <i>et al.</i> 2007	group of 9 <u>killer whales</u> chased 2 sei whales, 1 stranded itself and was found dead next morning; group of 6 killer whales chased sub-adult sei whale which stranded itself, found dead next morning; both Tierra del Fuego, n: 2
	Best <i>et al.</i> 2010	sei whale tongue found in <u>killer whale</u> stomach from South Africa, 26 stomachs analysed, n: 1
	Häussermann <i>et al.</i> 2013	group of 2 <u>killer whales</u> attacked single adult sei whale in inshore waters of Chilean Patagonia, outcome unknown, n: 1
Bryde's whale	Silber <i>et al.</i> 1990	group of ~15 <u>killer whales</u> attacked + killed Bryde's whale in a coordinated manner in N-Gulf of California, n: 1
	Brennan, Rodriguez 1994	group of 10 <u>killer whales</u> attacked group of 5 Bryde's whales off Galápagos, 1 Bryde's whale was killed and preyed on by orcas, n: 1
	Ford, Reeves 2008	fatal attack by group of ~20 <u>killer whales</u> on single adult ind.; 3 non-fatal attacks by groups of 10-20 killer whales on adult single ind.; all Gulf of California, n: 4
	Best <i>et al.</i> 2010	group of 3 <u>killer whales</u> attacked Bryde's whale calf off South Africa, outcome unknown, n: 1
	Alava <i>et al.</i> 2013	observation of successful <u>killer whale</u> attack on a Bryde's whale off Galápagos, n: 1
Minke whale	Sergeant, Fisher 1957	a <u>killer whale</u> from Newfoundland waters contained minke whale flesh in its stomach
	Hancock 1965	group of 7 <u>killer whales</u> fatally attacked and ate minke whale off Vancouver Island (W-Canada), n: 1
	Jonsgård 1968b	<u>killer whale</u> scars on minke whales which survived attack(s)

Species	Reference	Predation information
	Shevchenko 1975	minke whale remains found in 84% of 44 <u>killer whale</u> stomachs analysed S of 50°S (Southern Ocean); marks of killer whale bites found in 6% of the minke whales studied, indicating that minke whales often do not survive killer whale attacks
	Yukhov <i>et al.</i> 1975	in November <u>killer whale</u> stomach contents consist excl. of minke whales in Indian ocean sector of Southern Ocean 53-55°S, in December pred. minke but 2 out of 8 stomachs also contained seal; minke remains also found in orca stomachs 60°S; fish remains in Ross sea stomachs but pred. minke remains in 8 of 11 stomachs from Amundsen sea -> minke whales are main prey of killer whales in Southern Ocean
	Budylenko 1981	<u>killer whale</u> attacks on minke whales in S-Atlantic
	Best 1982	single minke whale fatally attacked by pod of ~10 <u>killer whales</u> off Durban, South Africa, n: 1
	Perrin 1982	<u>killer whale</u> predation on minke whales in Antarctica, Indian ocean, NE-Pacific and NW-Atlantic
	Berzin, Vladimirov 1983	<u>killer whale</u> predation on minke whales in Antarctica
	Hall 1986	fatal attack by 6-7 <u>killer whales</u> on minke whale off Alaska, n: 1
	Lowry <i>et al.</i> 1987	minke whale chased by pod of 7 <u>killer whales</u> off Aleutians (near Dutch Harbour), minke whale beached itself to escape orcas and died, n: 1
	Wenzel, Sears 1988	group of 3 <u>killer whales</u> fatally attacked single minke whale in N-Gulf of St. Lawrence, n: 1
	Jefferson <i>et al.</i> 1991	11 fatal attacks on minke whales by pods of 3-50 <u>killer whales</u> off Greenland (n: 6), Alaska (n: 2) in Bering Sea (n: 1) and Gulf of St. Lawrence (n: 1), at least 6 of these were on single individuals; 2 attacks with unknown outcome in southern hemisphere (n: 1) and off Ross Island (Antarctica, n: 1), n: 13
	Guinet <i>et al.</i> 2000	fatal attack by <u>killer whales</u> on minke whale calf, Crozet Archipelago, n: 1
	Matkin, Saulitis 2002	90-minute fatal attack by 13 transient <u>killer whales</u> on minke whale off SE-Alaska, n: 1
	Mironova <i>et al.</i> 2002	2 fatal, predatory <u>killer whale</u> attacks on minke whales off Kamchatka, n: 2
	Pitman, Ensor 2003	type A <u>killer whales</u> (Antarctica, offshore form) seem to prey primarily on Antarctic minke whales
	Wade <i>et al.</i> 2003	predation on minke whale by group of 3 <u>killer whales</u> (male, female, sub-adult), W-Alaska near Shumagin Islands, n: 1
	Morrice 2004	attack and predation on minke whale by pod of 9 <u>killer whales</u> in Antarctic waters, n: 1
	Ford <i>et al.</i> 2005	transient <u>killer whale</u> attacks (groups of 2-13) on single minke whales in coastal waters of NE-Pacific, n: 9, some fatal (n: 5); typically prolonged chases on a straight heading at velocities of 15-30 km/h; in 4 instances minke

Species	Reference	Predation information
		whale gradually outdistanced the killer whales, which abandoned the attack after 0.5-1h; successful predation on minke whales in coastal waters is rare compared to pinnipeds and small cetaceans, the main prey of transient killer whales
	Matkin <i>et al.</i> 2005	1 of 43 (2%) predatory kills of W-coast transient <u>killer whales</u> involved minke whales, Alaska n: 2
	Goodall <i>et al.</i> 2007	group of 6 <u>killer whales</u> attacked single minke whale of Tierra del Fuego (Argentina), minke whale killed and consumed; single minke beached itself in scope of killer whale attack (9 ind.), was found dead next morning, n: 2
	Lawson <i>et al.</i> 2007	<u>killer whale</u> groups killed and ate single minke whales off Newfoundland and Labrador, n: 5+; single killer whale and single minke whale cooperatively herding herring off Labrador, n: 1
	Matkin, Saulitis unpublished data, in: Krahn <i>et al.</i> 2007	E-Aleutian transient <u>killer whales</u> feed on minke whales (28%) during late summer
	Matkin <i>et al.</i> 2007	2 fatal attacks by <u>killer whales</u> in Aleutian Islands, n: 2
	Ford, Reeves 2008	1 fatal and 1 non-fatal attack by <u>killer whales</u> off British Columbia; non-fatal: minke fled to offshore water, n: 2
	Best <i>et al.</i> 2010	parts of minke whale calves found in at least 2 out of 26 examined <u>killer whale</u> stomachs, South Africa
	Ferguson <i>et al.</i> 2012a	<u>killer whale</u> predation on minke whales reported by 1 of 105 interviewees in Nunavut (N-Baffin isl.)
	Leclerc <i>et al.</i> 2012	6 out of 33 stomachs of <u>Greenland sharks</u> caught off Svalbard contained scavenged minke whale offal (18%F, 5%N, 3%M) from whaling operations
	Pitman, Durban 2012	predation by type B Antarctic <u>killer whales</u> on a minke whale, n: 1
	Bertulli <i>et al.</i> 2013	pod of <u>killer whales</u> fatally attacked and preyed on minke whale off N-Iceland, n: 1
	Lydersen <i>et al.</i> 2016	14 of 76 (18%) stomachs of immature <u>Greenland sharks</u> from Svalbard contained minke whale remains (5%N, 2%M)
Southern right whale	Sorensen 1950	<u>killer whale</u> attack on single southern right whale off Campbell Island, New Zealand, outcome unknown, n: 1
	Cummings <i>et al.</i> 1972	group of 5 <u>killer whales</u> attacked group of 2 right whales off Argentina; attack ended unsuccessfully after 25min
	Ebert 1991b	beached southern right whale calf found in South Africa with numerous <u>broadnose sevengill shark</u> bites taken out of it, n: 1
	Jefferson <i>et al.</i> 1991	3 non-fatal attacks by small pods of <u>killer whales</u> on right whales off South Africa (n: 1) and Argentina (n: 2), n: 3; encounters between killer whales and other cetacea without evidence of predatory intent documented for 26 cetacea species

Species	Reference	Predation information
	Sironi <i>et al.</i> 2004	6 non-fatal attacks by <u>killer whales</u> on single ind. (n: 2) and groups (n: 4) of right whales; 2 attacks with unknown outcome on single ind.; all off Valdés peninsula (Argentina) n: 8; 63 out of 112 encounters (56%) between killer whales and right whales involved no apparent changes in the behaviour of either species; shift of right whale distribution away from areas of high density of killer whales during recent decades and subsequent reduction in observed encounters
	Ford, Reeves 2008	attack by <u>killer whales</u> on mother-calf pair, calf possibly killed, attack lasted 3h, defence of calf by mother; killer whale attack on right whale group with unknown outcome, lasted 3h; both off South Africa; 3 non-fatal attacks by killer whales on mother-calf pairs off South Africa (n: 1) and Valdés peninsula (n: 2); n: 5
	Best <i>et al.</i> 2010	group of 7-8 right whales (incl. 2 calves) attacked by group of 3-4 <u>killer whales</u> off South Africa; killer whales split right whale group in 2, were then driven away by helicopter, n: 1
	Ott <i>et al.</i> 2017	fatal <u>killer whale</u> attack on a calf in Brazilian waters, n: 1
Humpback whale	Chittleborough 1953	group of 4-5 <u>killer whales</u> attack group of 3 humpbacks (calf, 2 adults) off Australia, apparently non-fatal, adult humpback (not mother) fended orcas off with fluke, n: 1
	Hoyt 1983	humpback calf attacked and possibly killed by group of <u>false killer whales</u> off Hawaii, n: 1
	Whitehead, Glass 1985	2 non-fatal attacks on humpbacks by pods of 10-17 <u>killer whales</u> off Newfoundland (E-Canada), injury of humpbacks observed in 1 incident, n: 2
	Katona <i>et al.</i> 1988	small group of <u>killer whales</u> attacked humpback calf accompanied by mother in Caribbean, orcas repeatedly breached onto calf, presumably to drown it, n: 1; 14% of 3365 humpbacks photographically identified in N-Atlantic bear parallel scars, likely attributable to orcas
	D'Vincent <i>et al.</i> 1989	2 <u>killer whales</u> attacked humpback calf belonging to a pod of cooperatively lunge-feeding individuals in Chatham Strait, Alaska, 2 of adult humpbacks separated attacked calf from orcas; killer whales attacked juvenile humpback which was joined + defended by 2 adults off Alaska; both non-fatal, n: 2
	Jefferson <i>et al.</i> 1991	1 fatal attack on single humpback by single <u>killer whale</u> off Greenland; 9 attacks of unknown outcome by pods of up to 90 killer whales on single ind. (n: 1+), 2 ind. (n: 1), group of 3 ind. (n: 1), off Greenland (n: 4), SE-Alaska (n: 1), E-USA (n: 2), in Gulf of California (n: 1) and NW-Atlantic (n: 1), n: 10
	Paterson <i>et al.</i> 1993	calf stranded alive bearing 2 large <u>shark bites</u> , calf was re-floated but died within few hours, off E-Australia, n: 1

Species	Reference	Predation information
	Flórez-González <i>et al.</i> 1994a	group of 10 <u>killer whales</u> attacked 3 humpbacks (calf, mother, female escort) off Colombia (Pacific) by separating calf from adults, ramming and biting adults but non-fatal, n: 1
	Flórez-González <i>et al.</i> 1994b	harassment of adult humpback by <u>false killer whales</u> off Colombia (Pacific), non-fatal, n: 1
	Steiger, Calambokidis 1995	<u>killer whale</u> predation on humpbacks off California, Oregon and Washington
	Mazzuca <i>et al.</i> 1998	several humpback whale calves died due to <u>shark</u> attacks off Hawaii, 1972-1996, based on second hand reports, n: several
	Visser 1999	single humpback whale attacked by group of 3 <u>killer whales</u> off New Zealand (n: 1)
	Visser 2000	group of 6 <u>killer whales</u> attacked single humpback whale off New Zealand; 1 further attack off New Zealand described in Beale 1994, n: 2
	in: Darling 2001	<u>tiger sharks</u> observed following sick humpback calves and attacking living but entangled adults off Hawaii, n: several
	Paterson, Paterson 2001	presumed <u>killer whale</u> on calf attack off Queensland, Australia, n: 1
	Matkin, Saulitis 2002	8 attacks by 1-17 <u>killer whales</u> on humpbacks off SE-Alaska, lasting from 26 min-4h, outcome unknown, n: 8
	Mironova <i>et al.</i> 2002	3 fatal, predatory <u>killer whale</u> attacks on humpback whales off Kamchatka, n: 3
	Morrice 2004	humpbacks attacked by group of 5 <u>killer whales</u> , outcome unknown; killer whales feeding on humpback whale; both off S-Australia, n: 2
	Naessig, Lanyon 2004	group of 7 <u>killer whales</u> successfully attacked and killed humpback calf affiliated to 2 adult humpbacks off New South Whales, Australia, n: 1; 17% of 1436 individually identified humpbacks show scars attributable to killer whales 1% of the 1436 humpbacks acquired killer whale scars after 1st sighting -> calves targeted by killer whales, not adults; <u>shark</u> bites on four living humpback whales
	Baird <i>et al.</i> 2006a	<u>killer whales</u> observed feeding on a humpback whale carcass, presumably killed by the orcas, off Hawaii, n: 1
	Lawson <i>et al.</i> 2007	<u>killer whales</u> attacked and harassed young and adult humpbacks off Newfoundland and Labrador, n: 3
	Matkin <i>et al.</i> 2007	fatal attack by <u>killer whales</u> in Aleutian Islands, n: 1
	Mehta <i>et al.</i> 2007	<u>killer whale</u> scars found on 22% of humpbacks off Greenland (n: 163), 16-18% E-Canada (n: 1447), 10-11% Gulf of Maine (n: 700), 13% Iceland (n: 69), 8% Norway (n: 49), 21-22% SW-Alaska (n: 237), 40% Mexico (n: 377), 18% Hawaii (n: 79), 1% Antarctic Penin. (n: 164), 16% W-Australia (n: 1287), 38% New Zealand (n: 8), 18-31% tropical SW-Pacific (n: 558), 12-13% Caribbean (n: 1364), 0% Cape Verde (n: 13), 9% Oman (n: 33);

Species	Reference	Predation information
		\bar{x} : 15% for N-Atlantic high latitude feeding areas; \bar{x} : 14% in low-latitude breeding areas blue whale: 4% off SE-Australia (n: 27)
	Ford, Reeves 2008	<u>killer whale</u> attack on single adult humpback with unknown outcome off Alaska; 5 non-fatal attacks by groups of killer whales on single adult ind. (n: 2), single juvenile (n: 2), and group of 5 incl. calf (n: 1); single killer whale harassed humpback mother-calf pair off South Africa, killer whales left in response to mother's tail slaps, non-fatal, n: 7
	Steiger <i>et al.</i> 2008	15% N-Pacific humpbacks show <u>killer whale</u> rake marks; BC, Alaska, Aleutian area: 5-9% (n: 734), S-Japanese islands: 6-8% (n: 448); W-USA: 20% (n: 694), Mexico: 23-31% (n: 562); Hawaii: 15-18% (n: 1212)
	Weir <i>et al.</i> 2010	group of 3-4 <u>killer whales</u> circling pair of adult humpbacks > 1h off Gabon (W-Africa), outcome unknown; group of 10 killer whales harassing humpback mother-calf pair for 6.5h off Cameroon with unknown outcome; n: 2; 17% of humpbacks off Gabon show scars on flukes, presumably caused by killer whale attacks
	Bornatowski <i>et al.</i> 2012	3 living humpback whales (< 1%) with bite scars from large <u>sharks</u> off E-Brazil; 35 out of 150 (22%) dead ind. with tiger shark bites inflicted before or after death; 2 field observations of tiger sharks scavenging on humpbacks; humpback whale calf stranded alive with severe tiger shark bite marks, estimated length of shark: 265cm (based on bite circumference), n: 1
	Elwen <i>et al.</i> 2014	<u>killer whale</u> scar rates: Gabon: 29% (n: 432), Namibia: 24% (n: 54), W-South Africa: 35% (n: 107), no sign. difference between regions
	McCordic <i>et al.</i> 2014	<u>killer whale</u> scar rate, E-Canada: 17% (n: 2660), W-Greenland: 11% (n: 464), Gulf of Maine: 9% (n: 1506), Iceland: 8% (n: 298) Norway: 3% (n: 112)
	Dicken <i>et al.</i> 2015	single humpback whale calf attacked by group of ~10-20 <u>dusky sharks</u> (2-3m length) for 5 1/2h off South Africa, calf presumed to have drowned from exhaustion when it stopped surfacing, n: 1
	Pitman <i>et al.</i> 2015	observations of 14 kills during 22 separate attacks of <u>killer whales</u> on neonate humpback whales on their calving grounds and during northbound migration off W-Australia + 2 attacks of unknown outcome; 3 calves killed in 6 days in the scope of 8 attacks on humpback calves; likely at least dozens taken annually; orcas attacked selectively and exclusively calves; n: 24 humpback 'escorts' vigorously assisted mothers in protecting their calves from attacking killer whales
	Pitman <i>et al.</i> 2015	observation of a <u>white shark</u> attempting to attack a humpback calf off W-Australia; shark

Species	Reference	Predation information
		approached from directly behind the whales but left when humpback 'escort' defended calf; 8-9m humpback fatally attacked by dozens of sharks, incl. <u>tiger+bull sharks</u> , <u>bronze whalers</u>) off Coral Bay, W-Australia; n: 2 during and after at least 5 of 14 humpback calf kills off W-Australia numerous large sharks (2-4+m) gathered within minutes at the attack site to feed on the carcass
	Saulitis <i>et al.</i> 2015	4 non-fatal transient <u>killer whale</u> attacks on sub-adult humpbacks (n: 2) and cow-calf pairs (n: 2) and 1 attack of unknown outcome on pair of ind. of unknown age (n: 1) in Cook Inlet- Kodiak island region (Alaska), all by groups of 10-11 orcas, n: 5; 17 partially consumed humpback whale carcasses found in same area
	Denkinger unpublished, in: Pitman <i>et al.</i> 2017	group of 2 male <u>killer whales</u> attacked group of 3 humpbacks (calf, mother, escort) off Ecuador, by breaching on calf and separating calf from adults, ramming adults, n: 1
	Donoghue unpublished, in: Pitman <i>et al.</i> 2017	2 <u>killer whales</u> attacked group of 3 humpbacks (calf, mother, escort) off N-Tonga by biting the fluke of 1 of the adults, n: 1
	Evans unpublished, in: Pitman <i>et al.</i> 2017	humpback whale calf harassed by <u>killer whales</u> but successfully defended by adult humpbacks off Seward, Alaska, n: 2
Gray whale	Pike, MacAskie 1969	<u>killer whales</u> attacked pair of gray whales off Haida Gwaii (W-Canada), outcome unknown, n: 1
	Rice, Wolman 1971	non-fatal attack of pod of 6 <u>killer whales</u> on group of 3 gray whales in Monterey Bay, California; 18% of gray whales examined at California whaling station (n: 317) show evidence of killer whale attack, n: 1
	Baldrige 1972	successful attack of a group of 5-6 <u>killer whales</u> on gray whale calf in Monterey Bay, California, n: 1
	Perrin 1982	<u>killer whale</u> predation on gray whale in Pacific arctic and sub-arctic
	Ljungblad, Moore 1983	fatal attack by pod of 10-12 <u>killer whales</u> on gray whale; non-fatal attack (chasing) by pod of 16 killer whales on group of several gray whales, both N-Bering Sea, n: 2
	Lowry <i>et al.</i> 1987	pod of 8 <u>killer whales</u> feeding on gray whale most likely killed by the orcas in NE-Chukchi Sea, n: 1
	Jefferson <i>et al.</i> 1991	7 fatal attacks by pods of 1-7 <u>killer whales</u> on at least 2 single gray whales, 1 mother-calf pair, 1 group of 3 gray whales, with a total of at least 7 gray whales killed, incl. 4 calves, in Baja California (n: 1), off California (n: 5), Alaska (n: 1); 3 non-fatal attacks by pods of 5-7 killer whales on groups of 2-6 gray whales off California; 1 killer whale attack of unknown outcome on single large gray whale off California; n: 11

Species	Reference	Predation information
	Goley, Straley 1994	gray whale mother calf pair attacked by group of at least 17 <u>killer whales</u> in Monterey Bay, California, calf and possibly mother killed, n: 1
	Ford <i>et al.</i> 1998	2 apparently non-fatal attacks by transient <u>killer whales</u> on mother-calf pairs in NE-Pacific, n: 2
	George, Suydam 1998	3 fatal attacks on single gray whales by groups of 3-10 <u>killer whales</u> off Alaska, 1 attack lasted several hours; 10 dead, stranded young gray whales examined 1987-1995 had injuries inflicted by killer whales, incl. missing body parts (tongues), Alaska, n: 13
	Ternullo, Black 2002	out of 84 transient <u>killer whale</u> feeding events observed in Monterey Bay, California, 25 (30%) were on gray whale calves, n: 25; gray whales are significant seasonal food source, esp. calves; once a mother/calf pair was detected, orcas formed group, then pursued gray's until these slowed down and were surrounded by the orcas, up to 6h may pass from initial attack to kill with ramming, biting, pulling on pectoral fins, and attempts to separate mother and calf, if successful calf is drowned and preyed on
	Barrett-Lennard <i>et al.</i> 2005	predation by transient <u>killer whales</u> may be responsible for mortalities of up to 35% of average annual calf production of California gray whales (uncertainty about assumptions underpinning the estimate)
	Matkin <i>et al.</i> 2007; Matkin, Saulitis unpublished data, in: Krahn <i>et al.</i> 2007	18 fatal and 1 non-fatal attack by <u>killer whales</u> off Aleutian Islands, n: 19; E-Aleutian transient <u>killer whales</u> seem to excl. prey on juvenile gray whales in May, but feed on northern fur seals (58%) minke whales (28%), Steller sea lions (14%) later in summer
	Ford, Reeves 2008	attack by <u>killer whales</u> on mother-calf pair with unknown outcome, off British Columbia; 5 non-fatal attacks by killer whales on mother-calf pairs (n: 4) and a single ind.; n: 6
	Weller 2009	nearly 34% of all gray whales photo ID'ed possess <u>killer whale</u> tooth rakes in Okhotsk Sea
	Barrett-Lennard <i>et al.</i> 2011	E-Aleutian transient <u>killer whales</u> feed seasonally on migrating gray whale calves and subadults; 4 fatal attacks, 3 non-fatal attacks off Unimak, n: 7
Unid. mysticeti	Shaughnessy 2000	unid. large whale attacked by single <u>killer whale</u> near Possession island, NE-Australia, outcome unknown, n: 1
	Vaske <i>et al.</i> 2009	unid. baleen whales accounted for 4%N, 40%M, 15%F of diet <u>blue sharks</u> off S-Brazil, remains found in 11 out of 106 stomachs, scavenging likely; no mysticeti remains found in 116 stomachs from waters off NE-Brazil
	Hussey <i>et al.</i> 2012	stomach content analysis of <u>white sharks</u> off South Africa, n: 225: unid. mysticeti 25%F, 14%N, 35%M in ind. > 285cm
Toothed whales/Odontoceti		
Sperm whale	Shevchenko 1975	<u>killer whale</u> attack on sperm whale group with calves, unknown outcome, n: 1;

Species	Reference	Predation information
		marks of killer whale bites found in 65% of the sperm whales studied in Southern Ocean
	Yukhov <i>et al.</i> 1975	<u>killer whale</u> attack on pod of female sperm whales with calves in Southern Ocean, outcome unknown, n: 1
	Perrin 1982	<u>killer whale</u> predation on sperm whale in Caribbean, no quantitative information
	Best <i>et al.</i> 1984	<u>killer whales</u> and <u>sharks</u> circling pod of sperm whales incl. 1 female giving birth off Durban, South Africa, non-fatal, n: 1
	Arnbom <i>et al.</i> 1987	seemingly unsuccessful attack of a pod of ~20 sperm whales by a group of 15-25 <u>killer whales</u> off Galápagos, n: 1
	Arnbom, Whitehead 1989	21% sperm whales (n: 190) off Galápagos show tooth marks from <u>killer whale</u> attacks
	Jefferson <i>et al.</i> 1991	out of 39 analysed encounters between <u>killer whales</u> and sperm whales, 6 involved attack (unknown outcome n: 3, non-fatal n: 3); 2nd hand reports of killer whale attacks on new-borns off Kuril Islands, n: several
	Brennan, Rodriguez 1994	a sperm whale affiliated to a loose pod of 12 individuals was attacked by several <u>killer whales</u> off Galápagos, sperm whale was wounded and may have been killed, n: 1
	Palacios, Mate 1996	group of 25 <u>false killer whales</u> observed harassing group of 20-25 sperm whales off Galápagos, non-fatal but injury to flukes and fins of sperm whales, sperm whales ended encounter by diving, n: 1
	Weller <i>et al.</i> 1996	group of 12 sperm whales, incl. 2 calves, non-fatally attacked by group of 30-45 <u>short-finned pilot whales</u> in the Gulf of Mexico; 5 incidents of non-fatal harassment of sperm whales by groups of 12-50 short-finned pilot whales off Galápagos and Ecuador, n: 6
	Mignucci-Giannoni 1998	attack by <u>killer whales</u> on a pod of sperm whales; killer whale attack on unid. species of large whale; both with unknown outcome, both in Caribbean Sea, n: 1
	Pitman, Chivers 1999	<u>killer whales</u> attack pod of sperm whales off California, n: 1
	Visser 1999	sperm whale washed ashore dead after being attacked and heavily wounded by <u>killer whales</u> ; a wounded sperm whale was harassed by killer whales, both off New Zealand, n: 2
	Pitman <i>et al.</i> 2001	a fatal attack by ~35 <u>killer whales</u> on group of ~9 female and sub-adult sperm whales, at least 1 sperm whale died and was partially eaten, at least 3-4 more individuals were mortally wounded; non-fatal attack by a group of ~5 killer whales on a group of ~ 50 sperm whales, both attacks off California, n: 2
	Morrice 2004	<u>killer whale</u> attack and predation on sperm whales (n: 3); killer whale predation on sperm whale calf (n: 1); all off S-Australia, n: 4
	Weir <i>et al.</i> 2010	group of 5 <u>killer whales</u> harassed pod of 18-20 sperm whales for > 1h off Angola, blood-filled spray observed 2x, outcome unknown, n: 1

Species	Reference	Predation information
	Gemmell <i>et al.</i> 2015	pod of 5-6 <u>killer whales</u> attacked pod of ~5 sperm whales, incl. 1+ calf, off S-Sri Lanka, injury of at least 1 sperm whale, outcome unknown, n: 1
	Whitt <i>et al.</i> 2015	group of 5 <u>killer whales</u> non-fatally attacked group of 19 sperm whales, incl. 2 calves; orcas abandoned area after several hours, Gulf of Mexico, n: 1
<i>Kogia</i> pygmy sperm w.	Perrin 1982	<u>killer whale</u> predation on pygmy sperm whale in Caribbean and Indian ocean
pygmy sperm whale	Long 1991	<u>white shark</u> bite mark on caudal peduncle of living pygmy sperm whale which stranded off California, n: 1
dwarf sperm whale	Long, Jones 1996a	dwarf sperm whale non-fatally attacked by <u>white shark</u> off California, n: 1
pygmy + dwarf sperm whale	Willis, Baird 1998	scars from <u>shark</u> attacks, incl. white shark, found on stranded and living ind.
dwarf sperm whale	Dunphy-Daly <i>et al.</i> 2008	<u>shark</u> predation and scavenging of dwarf sperm whale carcasses must be relatively frequent off Bahamas, based on parasite occurrence; <u>killer whale</u> predation off Bahamas
dwarf sperm whale	Best <i>et al.</i> 2010	head and incomplete skeleton of juvenile, and incomplete skeleton of adult <i>Kogia sima</i> found in <u>killer whale</u> stomach from South Africa, n: 1 (out of 26 analysed stomachs)
pygmy + dwarf sperm whale	Dunn, Claridge 2014	predation by pods of 3-7 <u>killer whales</u> on pygmy (n: 1) and dwarf (n: 2) sperm whales and unid. <i>Kogia</i> (n: 1) in Bahamas, n: 4; lack of vocalization by killer whales in Bahamas suggested to represent stealth behaviour
Beaked whales Cuvier's, Baird's beaked whale	Nishiwaki, Handa 1958	out of 364 <u>killer whale</u> stomachs from ind. off Japan 2 contained Cuvier's beaked whale remains, 4 Baird's beaked whale remains
Northern bottlenose whale	Jonsgård 1968a	pod of <u>killer whales</u> kills and eats single bottlenose whale off Svalbard, n: 1
Cuvier's, Stejneger's beaked whale	Long, Jones 1996a	juvenile Stejneger's beaked whale non-fatally attacked (n: 1) and juvenile Cuvier's beaked whale fatally attacked (n: 1) by ~5m long <u>white sharks</u> off California, n: 2
Blainville's beaked whales	Dunn, Claridge 2014	group of 4 <u>killer whales</u> passed within 1km of 3 pods of Blainville's beaked whales, no attack, n: 3
<i>Mesoplodon</i> sp.	Gemmell <i>et al.</i> 2015	group of 2 <u>killer whales</u> attacked, injured, and possibly killed single mesoplodont beaked whale off S-Sri Lanka, n: 1
<i>Mesoplodon</i> sp., strap-toothed beaked whale <i>M. layardii</i> (n: 1)	Wellard <i>et al.</i> 2016	4 attacks by <u>killer whale</u> groups of 5-20 ind. on 1 strap-toothed beaked whale and 3 ind. of either same species or Gray's beaked whale, orcas observed injuring + drowning beaked whales by pushing ind. under water, 1 ind. skinned alive, use of coordinated group behaviour by orcas; all in Bremer sub-basin (SW-Australia), n: 4
Pilot whales	Nishiwaki, Handa 1958	out of 364 <u>killer whale</u> stomachs from ind. off Japan 3 contained short-finned pilot remains
	Bloch, Lockyer 1988	pod of 50 <u>killer whales</u> attacked group of ~200 long-finned pilot whales, pilot whales seemed to escape in shallow water;

Species	Reference	Predation information
		group of <10 killer whales attacked group of pilot whales, many ind. mortally wounded, n: 2
	Jefferson <i>et al.</i> 1991	1 observation of killer whales feeding on long-finned pilot whales off NE-USA, n: 1
	Visser 1999	2 <u>killer whales</u> cornered 1 long-finned pilot whale and ate it off New Zealand, n: 1
	Zaeschmar, J. pers. comm.	pilot whales bear scars from bites of unid. <u>sharks</u> off New Zealand
False killer whale	Visser <i>et al.</i> 2010	group of ~8 <u>killer whales</u> attacked group of 50-60 false killer whales, incl. ~15 calves and 3-5 bottlenose dolphins in Bay of Islands, New Zealand, 5 false killer whales were attacked, with at least three rammed from below, forcing them out of the water, at least 1 calf was killed and fed on by orcas, n: 1
	Luksenburg 2014	<u>shark</u> bite marks found in 1 out of 71 photo-ID'ed ind. (1%) off Aruba (S-Caribbean)
Dolphins Common dolphin	Brown, Norris 1956	pod of 15-20 <u>killer whales</u> attacked pod of ~100 common dolphins in Gulf of California, at least 1 dolphin killed, n: 1
Clymene dolphin	Springer 1967	unid. <u>shark</u> attacked pod of possible Clymene dolphins in Gulf of Mexico, cooperative defence of young by adult dolphins, n: 1
bottlenose, spotted dolphin	Wood <i>et al.</i> 1970	dolphin remains recovered from <u>shark</u> stomachs, incl. bottlenose and spotted dolphins
Bottlenose dolphin	Arnold 1972	<u>white shark</u> predation on bottlenose dolphin in Bay of Fundy
Common dolphin	Ridgway, Dailey 1972	adult but sick common dolphin stranded alive with fresh <u>shortfin mako shark</u> bite wounds, California, n: 1
spinner, pantropical spotted, common dolphin	Leatherwood <i>et al.</i> 1973	scavenging on dead spinner, pantropical spotted and common dolphins by <u>mako, hammerhead and oceanic whitetip sharks</u> common during purse-seining activities in eastern tropical Pacific; fatal attacks by oceanic whitetip and unid. sharks on spotted (n: 3) and spinner (n: 1) dolphins; non-fatal attacks by mako sharks on common dolphins also observed; n: 4
	Shevchenko 1975	dolphin remains found in 47% of 19 analysed <u>killer whale</u> stomachs in waters 30°-50°S-Pacific, unid. small toothed whales found in 16% of the 19 stomachs
Pacific white-sided dolphin	Stroud, Roffe 1979	sick white-sided dolphin attacked by <u>shark</u> off Oregon, then stranded, n: 1
pantropical spotted, spinner, common dolphin	Perryman, Foster 1980	<u>pygmy and false killer whale and pilot whale</u> attacks on pantropical spotted, spinner and common dolphins related to purse-seine fishing for yellowfin tuna in tropical E-Pacific, n: 23
<i>Stenella</i> sp., striped, common dolphin	Perrin 1982	<u>killer whale</u> predation on dolphins in Caribbean (<i>Stenella</i> sp.), NE-Pacific (striped, common dolphins) and NW-Pacific (striped dolphin)
	Stillwell, Kohler 1982	3 out of 399 <u>shortfin mako shark</u> stomachs analysed contained cetacea remains, likely from dolphin or porpoise, NW-Atlantic
	Stevens 1984	dolphin remains found in <u>tiger shark</u> stomachs from ind. caught off New South Whales, Australia;

Species	Reference	Predation information
Bottlenose dolphin	Corkeron <i>et al.</i> 1987	<u>shark</u> bite scar rate of 37% off E-Australia (Moreton Bay), scars mainly from white and tiger sharks, n: 334 photo-ID'ed dolphins, no significant difference between sexes
	Rice, Saayman 1987	pod of 5 <u>killer whales</u> kills dolphin affiliated to small group; 2 attacks with unknown outcome by 1 and 2 killer whales on dolphin pods, all off South Africa, n: 3
	Cawthorn 1988	<u>broadnose sevengill sharks</u> prey on Hector's dolphins off New Zealand according to stomach content analysis
Bottlenose dolphin	Cockcroft <i>et al.</i> 1989	<u>bull, tiger, great white, dusky sharks</u> identified as dolphin predators (1% of >6000 stomachs contained dolphin remains, mostly from young dolphins); 10% (28 of 145) bottlenose dolphins of all age classes caught in gill nets off Natal (South Africa) exhibited scars or wounds from shark bites
Dusky dolphin	Ebert 1991a	of 232 stomachs of <u>broadnose sevengill sharks</u> from South African and Namibian waters 6% contained delphinids which accounted for 5%N and 10%M, incl. dusky dolphin off W-cape (1%N, 5%M, 1%F of 73 stomachs); portion of delphinid prey varied from 12%N, 29%M, 13%F off E-cape (S-Africa) to none off central Namibia
	Ebert 1991b	fatal attacks and predation on small cetaceans by cooperatively hunting <u>broadnose sevengill sharks</u> off California and Namibia, n: several
	Bruce 1992	dolphins are the primary prey of <u>white sharks</u> off S-Australia; 44% of stomachs containing dolphin remains (n: 16), cetacea typ. in diet of sharks > 320cm
Southern right whale dolphin	Crovetto <i>et al.</i> 1992	complete fetus + genital area of an adult female southern right whale dolphin found in stomach of 3.6m <u>Pacific sleeper shark</u> captured off central Chile, freshness of prey indicative of active predation, n: 1
	Simpfendorfer 1992	7 of 558 (1%) <u>tiger sharks</u> caught in NE-Australia had consumed dolphins; 9%F for sharks > 3m
Common dolphin	Breese, Tershy 1993	2 non-fatal <u>killer whale</u> predation attempts on common dolphins in Gulf of California + 2 attacks with unknown outcome, n: 4; killer whales did not change behaviour when passing balaenoterid whales within 100m, neither did balaenopterids (incl. 2♀ + calves) Gulf of California, n: 9, 2 subadult Bryde's whales approached and swam with groups of 3 killer whales > 20min
Pacific white-sided dolphin	Dahlheim, Towell 1994	group of 15 transient <u>killer whales</u> fatally attacked and preyed on 1 Pacific white-sided dolphin affiliated to group of 5-6, off SE-Alaska, chase + kill took < 5min; two add. 2. hand observations of predation on Pacific white-sided dolphins by killer whales off SE-Alaska, n: 3

Species	Reference	Predation information
	Ebert 1994	3 of 48 stomachs (6%) of <u>bluntnose sixgill sharks</u> (1.2-2.0m long) contained delphinids which accounted for 4%N, 5%M; 2 of 9 stomachs of sixgill sharks > 2m contained delphinids which accounted for 18%N, 9%M; South Africa
	Norris <i>et al.</i> 1994	scars from <u>shark</u> attacks found in several Hawaiian spinner dolphins, nearshore; shark attacks seem frequent
Risso's, Pacific white-sided, dusky dolphin	Long, Jones 1996a	Risso's dolphin fatally attacked (n: 1) and Pacific white-sided dolphin non-fatally attacked (n: 1) by <u>white sharks</u> off California, n: 2; dusky dolphins bear scars from healed shark bites + shark-damaged dorsal fins off New Zealand
	Lowe <i>et al.</i> 1996	10 out of 217 <u>tiger shark</u> stomachs from Hawaiian waters contained unid. dolphin remains; only ind. > 2m preyed on dolphins
Bottlenose dolphin	Bearzi <i>et al.</i> 1997	0% <u>shark</u> bite scar rate on bottlenose dolphins of the Adriatic Sea
Dusky dolphin	Constantine <i>et al.</i> 1998	within 11 days of research off Kaikoura, New Zealand, a pod of 4 <u>killer whales</u> chased single dusky dolphins (n: 4) and ind. affiliated to groups of 15, 150 and 200 on 4 days, resulting in 7 fatal captures, incl. 2 juveniles, n: 7; herding behaviour observed during 2 attacks
Pacific white-sided dolphin	Ford <i>et al.</i> 1998	1 fatal and 3 non-fatal attacks by transient <u>killer whales</u> on Pacific white-sided dolphins off British Columbia, n: 4
Bottlenose dolphin	Wells <i>et al.</i> 1999	<u>shark</u> bite scar rate of 22% off W-Florida
Bottlenose, common, <i>Stenella</i> sp.	Bianucci <i>et al.</i> 2000	predation by <u>white sharks</u> on unid. dolphins (n: 13), bottlenose (n: 4), common (n: 1), and <i>Stenella</i> (n: 1) dolphins in the Mediterranean Sea, 1889-1997, incl. observation of predation, scavenging, shark stomach content analysis
Bottlenose, dusky, common dolphin	Visser 1999, 2000	<u>killer whale</u> attacks and predation on bottlenose (n: 1, fatal), dusky (n: 9, in 3 occasions 3 dolphins killed, in 3 occasions 2 dolphins killed, in 2 occasions 1 dolphin killed, 1 non-fatal), common dolphins (n: 4, at least 2 fatal), and unid. dolphins (n: 1, several dolphins killed) off New Zealand, n: 17
Bottlenose dolphin	Heithaus 2001b	shark bite scars found on 74% (95 of 128) of non-calves, most scars inflicted by <u>tiger sharks</u> , Shark Bay, Australia
	Simpfendorfer <i>et al.</i> 2001	1 <u>tiger shark</u> stomach out of 84 from 118 to 361cm FL long ind. contained dolphin, W-Australia
Pacific white-sided, long-beaked common dolphin	Ternullo, Black 2002	out of 84 feeding events of transient <u>killer whales</u> observed in Monterey Bay, California, 3 (4%) involved Pacific white-sided and 3 (4%) long-beaked common dolphins, n: 6; killer whales typically followed dolphin groups of 100-2000+ ind. for a while before choosing and killing an ind. that fell behind
Dusky dolphin	Crespi-Abril <i>et al.</i> 2003	marine mammals represent at least 30% of total biomass consumed by <u>broadnose sevengill</u>

Species	Reference	Predation information
		<u>sharks</u> in Patagonian shelf water; n: 20 stomachs, TL: 107-244cm; 3 stomachs (15%) contained unid. cetacea remains incl. 1 small cetacea (likely dusky dolphin), 1 fluke and caudal peduncle of unid. dolphin, blubber from a mysticeti whale; TL of ind. with cetacean remains: 147-210cm;
Pantropical spotted dolphin	Maldini 2003	attack and predation by 3.5-4m <u>tiger shark</u> on living juvenile pantropical spotted dolphin which was affiliated to a pod of 30-50 conspecifics off Hawaii, n: 1
Pantropical spotted dolphin	Pitman <i>et al.</i> 2003	fatal attack by pod of <u>killer whales</u> on pod of spotted dolphins in Gulf of Mexico, 3 dolphins were isolated from group by orcas, 1 dolphin killed, n: 1
	Markowitz 2004	2 predation events on dusky dolphins by <u>killer whales</u> off Kaikoura, New Zealand; group of 6 killer whales chased group of 15 adults, 3 juveniles, and 2 calves for 1h45min, killer whales remained just behind and roughly 500m offshore of the dolphins and eventually left; n: 3
	Morrice 2004	3 records of attacks by groups of 3-5 <u>killer whales</u> on large pods of unid. dolphins off S-Australia, outcome unknown, n: 3
Bottlenose dolphin	Celona <i>et al.</i> 2006	living adult bottlenose dolphin with 2 fresh bites from > 4m great <u>white shark</u> encountered off Lampedusa island (Mediterranean), n: 1
	Kabasakal 2006	dolphin remains found in 4 out of 12 stomachs of <u>bluntnose sixgill sharks</u> from Turkish waters, TL of sharks containing dolphin: 360-600cm
Pantropical spotted dolphin	Santos-Monteiro <i>et al.</i> 2006	predation by 2.1m <u>shortfin mako shark</u> on pantropical spotted dolphin calf in central Atlantic, complete dolphin was recovered from shark stomach, most likely not a scavenging event, tail attached to rest of body by skin only, almost completely bitten off, n: 1
White-beaked dolphin	Lawson <i>et al.</i> 2007	<u>killer whales</u> attacked and preyed on white-beaked dolphins off Newfoundland/Labrador, n: 3
Spinner dolphin	Silva Jr. <i>et al.</i> 2007	predation by sharks, incl. <u>shortfin mako</u> , on spinner dolphins off Fernando de Noronha (SW-Atlantic) indicated by bite marks; 55 of 418 dolphins with shark-inflicted injuries; observation of 1 adult ind. being killed by group of 3 unid. <u>carcharhinid sharks</u> of 1.5-2m length, n: 1
	Yano <i>et al.</i> 2007	unid. dolphin remains found in 1 of 4 stomachs (25%F, 5%N) of <u>Pacific sleeper sharks</u> off Japan; 16 ind. from Bering Sea + Gulf of Alaska did not contain cetacea remains
common dolphin	anonymous 2008	fatal <u>killer whale</u> attack and predation on common dolphin off South Africa, n: 1
Risso's dolphin	Hartman <i>et al.</i> 2008	wounded individuals observed, thought to be attacked by <u>sharks</u> or <u>killer whales</u> off Azores
Striped, bottlenose dolphin	Mendonça 2009	delphinids made up 22%F, 22%N, 22%M of <u>blue shark</u> stomach contents (n: 137), of which

Species	Reference	Predation information
		striped dolphin was 75%F, 75%N, 98%M, bottlenose dolphin 25%F, 25%N, 2%M; length of sharks: 79-258cm, NE-Atlantic
	Weller 2009	proportion of dolphins with <u>shark</u> bite scars or wounds is considerably higher in nearshore than in offshore areas
Bottlenose dolphin	Barnett <i>et al.</i> 2010c	5 out of 60 stomachs of the <u>broadnose sevengill shark</u> off S-Tasmania contained bottlenose dolphin remains
	Best <i>et al.</i> 2010	various dolphin body parts found in at least 5 out of 26 analysed <u>killer whale</u> stomachs from South Africa, remains of other small odontoceti in add. 2 stomachs
Bottlenose dolphin	Lopez <i>et al.</i> 2010	stomachs of <u>blue sharks</u> from Chilean waters contained bottlenose dolphin remains (3%N, 10%M, 4%F), n: 172
Common dolphin	Markaida, Sosa-Nishizaki 2010	6 out of 614 <u>blue shark</u> stomachs from ind. off N-Mexico contained common dolphin remains (0.2%N, 7%M, 1%F), blubber: 1 out of 614
Bottlenose dolphin	Zaeschar, Halliday, Visser unpub., in: Visser <i>et al.</i> 2010	3 bottlenose dolphins (coastal form) attacked and killed by <u>killer whales</u> off New Zealand, n: 3
Bottlenose dolphin	Barnett <i>et al.</i> 2010b; Abrantes, Barnett 2011	bottlenose dolphin remains accounted for 3%N and 6%M of <u>broadnose sevengill shark</u> stomach content in samples from Norfolk Bay (n: 29), SE-Tasmania; sharks from other areas off S+E-Tasmania had not preyed on cetacea
Risso's, bottlenose, common dolphin	Hussey <i>et al.</i> 2012	stomach content analysis of <u>white sharks</u> off South Africa: Risso's d.: ind. 235-285cm: 0%N, 4%M, 1 out of 49 stomachs), bottlenose d.: (ind > 285cm: 5%N, 13%M, 1 out of 12 stomachs), common d.: (ind. <185 cm: 2%N, 6%M, 1 out of 38 stomachs; ind. 185-235cm: 5%N, 1%M, 1 out of 126 stomachs; ind > 285cm: 5%N, 1%M, 1 out of 12 stomachs), unid. dolphins: ind. 185->285cm: 3%N, 6%M, 29 of 187)
	MacNeil <i>et al.</i> 2012	3 out of 22 (14%) <u>Greenland shark</u> stomachs contained remains of unid. dolphin or porpoise off Iceland
Short-beaked common dolphin	Preti <i>et al.</i> 2012	1 out of 238 <u>shortfin mako shark</u> stomachs from ind. off California contained ~2kg common dolphin remains
Common dolphin	Rogers <i>et al.</i> 2012	1 out of 52 <u>shortfin mako shark</u> stomachs from ind. off S-Australia contained ~3.5kg common dolphin remains (0.5%N, 19%M, TL of sampled ind.: 94-267cm)
White-beaked dolphin	Bertulli <i>et al.</i> 2012	3 out of 90 individuals bearing possible tooth marks from <u>killer whales</u> off Iceland
Atlantic spotted, Fraser's dolphin	Dunn, Claridge 2014	pods of 6 and 7 <u>killer whales</u> observed preying on Atlantic spotted (n: 1) + Fraser's (n: 1) dolphins in Bahamas, n: 2
Dusky dolphin	Kügler, Orbach 2014	out of 1171 photo ID'ed dolphins off Kaikoura, New Zealand, 2 (0.17%) had scars attributed to shark bites and 1 (0.09%) had <u>killer whale</u> scars
Atlantic spotted, bottlenose dolphin	Luksenburg 2014	<u>shark</u> bite marks found in 1 out of 179 (1%) photo-ID'ed Atlantic spotted and 1 out of 76 (1%) bottlenose dolphins off Aruba (S-Caribbean)

Species	Reference	Predation information
Atlantic spotted dolphin	Melillo-Sweeting <i>et al.</i> 2014	at least 14 out of 92 (15%) individually identified Atlantic spotted dolphins bear scars from <u>shark</u> attacks off North Bimini; individuals acquired scars as calves (n: 7), juvenile (n: 1), sub-adult (n: 1) or adult (n: 1) (unknown: 4)
Dusky, common dolphin	Coscarella <i>et al.</i> 2015	fatal attack by group of 6 <u>killer whales</u> on unid. dolphin; fatal attack on dusky dolphin by group of 5 killer whales; 1 fatal and 1 non-fatal attack on common dolphin by group of ~15 killer whales; all off Patagonia, Argentina, n: 4
	Herreria 2015	unid. dolphin most likely fatally attacked by <u>killer whales</u> in Hauraki Gulf, New Zealand, n: 1
Spinner dolphin	Pitman <i>et al.</i> 2015	group of 7-8 <u>killer whales</u> killed and ate at least 2 dolphins out of a small pod off W-Australia, n: 1
Common, striped dolphin	Porsmoguer <i>et al.</i> 2015	<u>shortfin mako shark</u> stomach content revealed that 6 out of 96 juvenile sharks preyed on newborn dolphins near Azores; 3 out of the 6 were genetically identified as common (n: 2) and possibly striped dolphin (n: 1)
Pantropical spotted dolphin	Sucunza <i>et al.</i> 2015	group of 2 <u>smooth hammerhead sharks</u> fatally attacked solitary dolphin off Brazil, n: 1
White-beaked dolphin	Galatius, Kinze 2016	<u>killer whales</u> observed hunting white-beaked dolphins in Pentland Firth, Scotland, outcome unknown, n: 1
Dall's porpoise	Nishiwaki, Handa 1958	out of 364 <u>killer whale</u> stomachs from ind. off Japan 64 contained Dall's porpoise remains
	Barr, Barr 1972	group of 2 <u>killer whales</u> attacked and preyed on Dall's porpoise in NE-Pacific, n: 1
	Morton 1990	Dall's porpoise harassed by transient <u>killer whales</u> off British Columbia, n: 1
	Jefferson <i>et al.</i> 1991	4 fatal attacks by <u>killer whales</u> off Alaska; 9 attacks by killer whales on Dall's with unknown outcome off SE-Alaska (n: 3), British Columbia (n: 5) and Washington (n: 1); 1 non-fatal attack by transient killer whales off SE-Alaska, n: 14; many records of Dall's porpoises approaching killer whales to play
	Long, Jones 1996a	Dall's porpoise fatally attacked by <u>white shark</u> off California, 3 bites, n: 1
	Ford <i>et al.</i> 1998	7 fatal and 11 non-fatal (incl. 9 high-speed chases) attacks by transient <u>killer whales</u> , attacks were fatal when orcas caught up to porpoise and rammed it from beneath or landed on it following a high leap; 4 non-fatal attacks by resident killer whales on calves (n: 3) and an adult (n: 1); all in NE-Pacific, n: 22
	Saulitis <i>et al.</i> 2000	transient <u>killer whales</u> observed killing and preying on Dall's porpoises in offshore Prince William Sound, Alaska, n: 12; offshore foraging: orcas traveled for 1+ km beneath surface at times, often during dives of 10+ min; when prey detected: coordinated chase, prey shared among group members, attacks lasted up to 43 min; harassment of Dall's without predation n: 6

Species	Reference	Predation information
		non-aggressive interactions between Dall's and residents, n: 47 minke whale swam among residents for > 3h
	Saulitis <i>et al.</i> 2002	almost all prey killed during offshore foraging by Prince William Sound transient <u>killer whales</u> are Dall's porpoises; attacks involve a coordinated effort of group members (mean group size: 5) lasting up to 40 minutes
	Ternullo, Black 2002	of 84 predation events by transient <u>killer whales</u> observed in Monterey Bay, California, 8 (10%) were on Dall's porpoises; all surprise attacks, n: 8
	Heise <i>et al.</i> 2003	Dall's porpoise remains found in 2 out of 12 analysed <u>killer whale</u> stomachs from Alaska
	Matkin <i>et al.</i> 2005	2 of 43 (5%) predatory kills of W-coast transient <u>killer whales</u> involved Dall's porpoises, Alaska n: 2
	Matkin <i>et al.</i> 2007	3 non-fatal attacks by <u>killer whales</u> in Aleutian Islands, n: 3
Cetacea in general	Stevens 1984	cetacea remains found in stomachs of <u>blue sharks, shortfin makos and oceanic whitetip sharks</u> caught off New South Whales, Australia
	Tricas, McCosker 1984	stomach contents off 33 <u>white sharks</u> from S-Australia showed 12%F of cetacea prey
	Cliff, Dudley 1992	cetacea account for 1%M of <u>bronze whaler</u> diet off South Africa based on examination of 413 stomachs, incl. common dolphin, unid. dolphin, unid. mysticeti, likely all scavenged
	Cliff <i>et al.</i> 1989, 1996	cetacea account for 21%M of <u>white shark</u> diet off South Africa based on examination of 91 stomachs of predominantly immature sharks; cetacea accounted for 31%M of shark stomach contents 1983-1988 and 4%M 1989-1993 indicating temporal variation in importance of cetacea as prey; marine mammals, esp. cetaceans, were most common prey in sharks > 2.5m and incl. common + bottlenose dolphins, unid. toothed and baleen whales
	Cortés 1999	based on stomach content analyses, <u>oceanic shark</u> species in which marine mammals account for ≥ 4% of the diet include oceanic whitetip (4%, n: 108), tiger shark (5%, n: 1209), false catshark (8%, n: 14), white shark (21%, n: 259), bluntnose sixgill (9%, n: 106), broadnose sevengill (36%, n: 313), Pacific sleeper shark (17%, n: 13)
	Bianucci <i>et al.</i> 2000	1/3 of 33 examined <u>white shark</u> stomachs from Mediterranean Sea contained cetacea remains
	Heithaus 2001a	regular <u>shark</u> predators of cetacea: white, tiger, bull, sixgill and sevengill sharks; bullshark coastal; occasional predators: dusky and oceanic whitetip sharks; suspected predators: shortfin mako, Pacific sleeper and Greenland sharks
	Ebert 2002 (incl. data from Ebert 1991a)	marine mammal prey in diet of <u>broadnose sevengill sharks</u> off southern Africa + California based on stomach contents: <120cm (n: 71): no

Species	Reference	Predation information
		marine mammals in diet; 120-180cm (n: 110): 17%N, 33%M; 180-220cm (n: 110): 22%N, 28%M; >220cm (n: 74): 30%N, 42%M (n: 365)
	Schaufler <i>et al.</i> 2005	cetacean blubber identified as important prey item in <u>Pacific sleeper sharks</u> of Gulf of Alaska (fatty acids analysis)
	Celona <i>et al.</i> 2006	cetacea preyed on by <u>white sharks</u> in Mediterranean Sea include fin and sperm whales, bottlenose and common dolphins
	Sigler <i>et al.</i> 2006	17 (10%) out of 165 <u>Pacific sleeper shark</u> stomachs from Gulf of Alaska contained unid. cetacea (3%N, 31%M), few remains were genetically identified as gray whale; out of 21 cetacea pieces 3 were scavenged, 4 likely scavenged, 3 fresh when consumed, 11 unknown
	Yano <i>et al.</i> 2007	unid. cetacea remains found in 3 of 12 <u>southern sleeper shark</u> stomachs (27%F, 8%N) from Tasman sea + Macquarie island (SW-Pacific); 3 ind. from South Africa + Namibia did not contain cetacea remains
	Ferguson <i>et al.</i> 2012a	according to 105 interviews in 11 Nunavut communities marine mammals are main prey of <u>killer whales</u> in Canadian arctic, incl. all phocid seals, esp. ringed seals, but also harp, bearded and hooded seals (in descending order of frequency), and most commonly occurring cetaceans, esp. narwhal (63 interviewees 60%), beluga (55, 52%) and bowhead whales (48, 46%, esp. Foxe Basin)
	Preti <i>et al.</i> 2012	unid. cetacea found in 1 out of 114 stomachs of blue sharks (1%F, 0.1%N, 3%M) off California
	Rogers <i>et al.</i> 2012	1 out of 49 <u>dusky shark</u> stomachs from ind. off S-Australia contained unid. cetacea remains (2%N, <0.1%M, TL of sampled ind.: 96-256cm)
	Dicken <i>et al.</i> 2017	628 stomachs of PCL: 94-335cm <u>tiger sharks</u> analysed from ind. off South Africa: myticeti, important prey in large ind.; unid. dolphin: 19%F, 5%N, 7%M, unid. whale: 8%F, 2%N, 13%M; cetacea prey found included: bottlenose (1%F, 0.2%N, 1%M), short-beaked common (1%F, 0.3%N, 2%M), sperm whale (0.5%F, 0.1%N, 0.5%M), humpback (1%F, 0.2%N, 2%M) and minke (<1%M) whales esp. mysticeti likely scavenged from carcasses related to bather protection nets

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Table 2: Predation on baleen whales summarized based on Table 1: the 'stomach content' column shows how many stomachs out of a certain sample size contained remains of the cetacea species; semicolons separate results of different references

Species	predator	fatal attacks	non-fatal attacks	attacks outcome unknown	predator stomach contents	areas of documented attacks/ predation
Blue whale	killer whale	3	7+	2	-	California, Gulf of California, Nicaragua, Antarctica, S-Australia, Sri Lanka
	no blue whales with killer whale rake marks observed off Sri Lanka, n: 150+ identified ind.					
cow-calf, calf portion	killer whale	1	2	-	-	Gulf of California, S-Australia, Nicaragua
Fin whale	killer whale	2	1	14	1 of 26 stomachs	N-Pacific, Gulf of California, W-Canada, Alaska, E-USA, W-Greenland, Faroe Islands, Gibraltar, South Africa
	marks of killer whale bites found in 53% of fin whales studied in Southern Ocean					
Sei whale	killer whale	2	-	3	1 of 26; 2 of 364 stomachs	NW-Pacific, Tierra del Fuego, Chilean Patagonia, South Africa
	marks of killer whale bites found in 24% of sei whales studied in Southern Ocean					
cow-calf, calf portion	killer whale	1	-	-	-	Tierra del Fuego
Bryde's whale	killer whale	4	3	1	-	Galápagos, Gulf of California, South Africa
cow-calf, calf portion	killer whale	-	-	1	-	South Africa
Minke whale	killer whale	40+	5	2	1 of 1; 37 of 44; 2 of 26; 8 of 8 8 of 11 stomachs	Kamchatka, NE-Pacific, Aleutian Islands, Bering Sea, Alaska, British Columbia, N-Baffin Island, NW-Atlantic, Gulf of St. Lawrence, Newfoundland, Greenland, N-Iceland, S-Atlantic, South Africa, Indic, Tierra del Fuego, Antarctic, Crozet archipelago
	cow-calf, calf portion	killer whale	1	-	-	2 of 26

Species	predator	fatal attacks	non-fatal attacks	attacks outcome unknown	predator stomach contents	areas of documented attacks/ predation
	<p>in November killer whale stomach contents consist excl. of minke whales in Indian ocean sector of Southern Ocean 53-55°S, in December pred. minke; minke remains also found in orca stomachs 60°S, and in most stomachs from Amundsen sea -> minke whale is main prey of marine mammals-eating killer whales in Southern Ocean;</p> <p>marks of killer whale bites in 6% of minke whales in Southern Ocean -> attacks often fatal;</p> <p>minke whales account for 28% of diet of transient killer whales in E-Aleutian islands in late summer</p>					
	Greenland shark	-	-	-	14 of 76	Svalbard
Southern right w. cow-calf, calf portion	killer whale	2+	14	4	-	New Zealand, South Africa, Argentina, Brazil
	killer whale	1	3	1	-	South Africa, Argentina, Brazil
	broadnose sevengill shark	1 (calf)	-	-	-	South Africa
Humpback whale	killer whale	24+	25	33	-	Kamchatka, Aleutian Islands, Alaska, Australia, New Zealand, N-Tonga, Ecuador, Colombia, Hawaii, W-USA, Gulf of California, Caribbean, NW-Atlantic, Newfoundland, E-USA, Greenland, South Africa, Gabon, Cameroon
	<p>14% of 3365 humpbacks photo-ID'ed in N-Atlantic bear scars, likely from orcas; killer whale scar rate E-Canada: 17% (n: 2660), W-Greenland: 11% (n: 464), Gulf of Maine: 9% (n: 1506), Iceland: 8% (n: 298) Norway: 3% (n: 112)</p> <p>killer whale scars found on 22% of humpbacks off Greenland, 16-18% E-Canada, 10-11% Gulf of Maine, 13% Iceland, 8% Norway, 21-22% SW-Alaska, 40% Mexico, 18% Hawaii, 1% Antarctic penin., 16% W-Australia, 38% New Zealand, 18-31% tropical SW-Pacific, 12-13% Caribbean, <1% Cape Verde, 9% Oman; \bar{x}: 15% for N-Atlantic high latitude feeding areas; \bar{x}: 14% in low-latitude breeding areas</p> <p>15% N-Pacific humpbacks show killer whale rake marks: BC, Alaska, Aleutian area: 5-9%, S-Japanese islands: 6-8%; Washington, California, Mexico, Baja Cal. area: 20-31%; Hawaii: 15-18%;</p> <p>17% of 1436 photo-ID'ed humpbacks off SE-Australia with killer whale scars, sex determined for 46 ind. of which 40 were females and 6 males;</p> <p>17% of humpbacks off Gabon show scars on flukes presumably from killer whales; Gabon: 29%, Namibia: 24%, W-South Africa: 35%</p>					
cow-calf, calf portion	false killer whale	-	1	1	-	Hawaii, Colombia
	killer + false killer whale	16	20	8+	-	Alaska, Colombia, Ecuador, Hawaii, N-Tonga, E-, W-Australia, South Africa, Cameroon, Caribbean, Newfoundland/Labrador
	14 out of 15 fatal killer whale attacks on humpback calves were observed in W-Australia					
	tiger shark	1 (calf)	-	several	-	Hawaii, E-Brazil
	3 living humpbacks (< 1%) with bite scars from large sharks; 35 of 150 (22%) dead ind. with tiger shark bites					E-Brazil

Species	predator	fatal attacks	non-fatal attacks	attacks outcome unknown	predator stomach contents	areas of documented attacks/ predation
	inflicted before or after death; 2 observations of tiger sharks scavenging on humpbacks					
	white shark	-	1 (calf)	-	-	W-Australia
	dozens of tiger + bull sharks, bronze whalers	1 (sub-adult)	-	-	-	W-Australia
	dusky shark	1 (calf)	-	-	-	South Africa
	unid. shark	several	-	-	-	Hawaii, E-Australia
Gray whale	killer whale	71+	16	3	-	Pacific arctic + sub-arctic, Bering Sea, Aleutian Islands, Alaska, British Columbia, California, Baja California, Korea
cow-calf, calf portion	killer whale	45	9	1	-	NE-Pacific, Aleutian Islands, Alaska, British Columbia, California, Baja California
	18% of gray whales examined at California whaling station show killer whale bite marks; nearly 34% gray whales photo ID'ed in Okhotsk sea possess killer whale tooth rakes; transient killer whale predation may be responsible for mortalities of up to 35% of average annual calf production of California gray whales; E-Aleutian transient killer whales seem to exclusively prey on juvenile gray whales in May					
unid. mysticeti	killer whale	-	-	1	-	NE-Australia
	blue shark	unid. mysticeti account for 4%N, 40%M, 15%F of 106 stomachs, scavenging likely				S-Brazil
	white shark	unid. mysticeti account for 25%F14%N, 35%M of stomach content of sharks > 285cm TL, n: 225 non-empty stomachs				South Africa

Table 3: Predation on toothed whales

Species	predator	fatal attacks	non-fatal attacks	attacks outcome unknown	predator stomach contents	areas of documented attacks/ predation
Sperm whale	killer whale	7	6	11	-	S-Sri Lanka, Angola, Caribbean, Gulf of Mexico, California, Galápagos, New Zealand, S-Australia, Southern Ocean
	false killer whale	-	1	-	-	Galápagos
	short-finned pilot whale	-	6	-	-	Gulf of Mexico, Galápagos, Ecuador
	marks of killer whale bites found in 65% of the sperm whales studied in Southern Ocean; 21% sperm whales off Galápagos show tooth marks from killer whale attacks					

Species	predator	fatal attacks	non-fatal attacks	attacks outcome unknown	predator stomach contents	areas of documented attacks/ predation
Kogia	killer whale	5	-	-	1 of 26 stomachs	Caribbean, South Africa, Indian ocean
	white shark	-	2	-	-	California
	white shark and killer whale attacks both involved dwarf and pygmy sperm whales					
Beaked whales	killer whale	5	-	1	6 of 364 stomachs	S-Sri Lanka, SW-Australia, Japan, Svalbard
	white shark	1	1	-	-	California
	species involved: Cuvier's, Baird's, Stejneger's, strap-toothed beaked whales, <i>Mesoplodon</i> sp., northern bottlenose whale					
Pilot whales	killer whale	3	2	-	3 of 364 stomachs	New Zealand, Japan, Faroe Islands, NE-USA
	all attacks were on long-finned pilot whales, stomach contents involve short-finned pilot whale					
	pilot whales bear scars from bites of unid. sharks off New Zealand					
False killer whale	killer whale	1	-	-	-	New Zealand
Risso's dolphin	white shark	1	-	-	1 of 49 (<0.5%N, 4%M)	California, South Africa
Bottlenose dolphin	killer whale	4	-	-	-	New Zealand
	broadnose sevengill shark	-	-	-	5 of 60	S-Tasmania
	white shark	5	1	-	1 of 12 (5%N, 13%M)	Bay of Fundy, Mediterranean, South Africa
	bull, tiger, white, dusky shark	-	-	-	~75 of >6000	South Africa
	10-19% (28 of 145) bottlenose dolphins of all age classes caught in gill nets off Natal (South Africa) exhibited scars or wounds from shark bites; shark bite scar rates of 22% off W-Florida, and up to ~37% off E-Australia (incl. coastal areas); 0% shark bite scares in Adriatic Sea					
	blue shark	-	-	-	25%N, 2%M of 137; 5 of 172	NE-Atlantic, Chile
White-beaked dolphin	killer whale	1	1	1	-	Newfoundland/Labrador
Pacific white-sided dolphin	killer whale	7	3	-	-	SE-Alaska, British Columbia, California
	unid. shark	1	-	-	-	Oregon (W-USA)
	white shark	-	1	-	-	California
Dusky dolphin	killer whale	27	2	-	-	New Zealand, Patagonia
	broadnose sevengill shark	-	-	-	1 of 73 (1%N, 5%M); 1 of 20	South Africa, Patagonia
	shark scar rate: 0.17%, killer whale scar rate: 0.09% off Kaikoura, New Zealand					
Fraser's dolphin	killer whale	1	-	-	-	Bahamas
	killer whale	2	-	-	-	W-Australia

Species	predator	fatal attacks	non-fatal attacks	attacks outcome unknown	predator stomach contents	areas of documented attacks/ predation
Spinner dolphin	oceanic whitetip + unid. shark	1	-	-	-	trop. E-Pacific
	shortfin mako shark	-	bite marks	-	-	Fernando de Noronha (SW-Atlantic)
	unid. carcharhinid sharks	1	-	-	-	
Pantropical spotted dolphin	killer whale	1	-	-	-	Gulf of Mexico
	oceanic whitetip + unid. shark	3	-	-	-	trop. E-Pacific
	tiger shark	1	-	-	-	Hawaii
	shortfin mako shark	1	-	-	-	central Atlantic
	smooth hammerhead shark	1	-	-	-	Brazil
spinner, pan. spotted, common d.	pygmy, false killer, pilot whale	23	-	-	-	trop. E-Pacific
Atlantic spotted dolphin	killer whale	1	-	-	-	Bahamas
	unid. sharks	at least 14 out of 92 (15%) photo ID'ed Atlantic spotted dolphins bears scars from attacks of unid. sharks off North Bimini				
Clymene dolphin	unid. shark	-	-	1	-	Gulf of Mexico
Stenella sp.	white shark	1	-	-	-	Mediterranean
Common dolphin	killer whale	8	3	4	-	California, Gulf of California, New Zealand, South Africa, Patagonia
	white shark	1	-	-	3 of 176 (2%N, 4%M)	Mediterranean, South Africa
	shortfin mako shark	1	several	-	1 of 238; 1 of 52 (0.5%N, 19%M); 2 of 96	trop. E-Pacific, California, S-Australia
	blue shark	-	-	-	8 of 614 (0.2%N, 7%M)	N-Mexico
Southern right whale dolphin	Pacific sleeper shark	1	-	-	-	central Chile
Unid. dolphin	killer whale	4+	-	5	9 of 19; 5+ of 26	30°-50°S Pacific, S-Australia, New Zealand, South Africa, Patagonia
	Pacific sleeper shark	-	-	-	1 of 4 (5%N)	Bering Sea, Gulf of Alaska
	broadnose sevengill shark	-	-	-	14 of 232 (5%N, 10%M);	South Africa, Namibia, Patagonia

Species	predator	fatal attacks	non-fatal attacks	attacks outcome unknown	predator stomach contents	areas of documented attacks/ predation
					1 of 20	
		portion of delphinid prey varied from 12%N, 29%M, 13%F off E-cape (S-Africa) to none off central Namibia (n: 232)				
	bluntnose sixgill shark	3 of 48 stomachs (6%) of sharks 120-200m long contained dolphin (4%N, 5%M); 2 of 9 stomachs (22%) of sharks >2m contained dolphin (18%N, 9%M); 4 of 12 stomachs of 360-600cm long sharks contained dolphin remains				South Africa, Turkey
	white shark	-	-	-	7 of 16; 29 of 187 (3%N, 6%M)	S-Australia, South Africa
	dolphins thought to be primary prey of white sharks > 320cm off S-Australia					
	shortfin mako shark	-	-	-	4 of 93	Azores
	tiger shark	-	-	-	10 of 217; 1 of 84; 7 of 558	Hawaii, W-Australia, Florida
	proportion of dolphins with shark bite scars or wounds considerably higher in nearshore than in offshore areas					
Dall's porpoise	killer whale	38	15	10	64 of 364; 2 of 12	NE-Pacific, Aleutian Islands, Alaska, British Columbia, Washington, California, Japan
	white shark	1	-	-	-	California
unid. small odontoceti	killer whale	-	-	-	3 of 19; 2 of 26	30°-50°S Pacific, South Africa
	shortfin mako shark	-	-	-	3 of 399	NW-Atlantic
	Greenland shark	-	-	-	3 of 22	Iceland
	broadnose sevengill shark	several	-	-	-	California, Namibia
unid. cetacea	Pacific sleeper shark	-	-	-	17 of 165 (3%N, 31%M)	Gulf of Alaska
	southern sleeper shark	-	-	-	3 of 12	Tasman sea, Macquarie island
	white shark	-	-	-	4 of 33; 11 of 33; 4-31%M (n: 91)	S-Australia, South Africa, Mediterranean Sea
	dusky shark	-	-	-	1 of 49 (2%N, <0.1%M)	S-Australia
	bronze whaler	-	-	-	1%M (n: 413)	South Africa
	blue shark	-	-	-	1 of 114 (0.1%N, 3%M)	California

Table 4: Killer whale fatality: underlined references are derived from dedicated surveys (as opposed to review-based); $f = a/n$, death rate upon encounter, $d = af$ (references: Chapter 2)

Species	% encounters leading to attack a	f [%]	n	d [%]	Scar r. [%]	Indication of scarring
Blue whale	67% (Jefferson <i>et al.</i> 1991, n: 6)	30	10	20	0-4	low a ^a
Fin whale	41% (Jefferson <i>et al.</i> 1991, n: 37)	67	3	27	53	high a, medium f
Sei whale	13% (Jefferson <i>et al.</i> 1991, n: 16)	100	2	13	24	low a, medium f
Bryde's whale	50% (Jefferson <i>et al.</i> 1991, n: 2)	57	7	29	-	-
Balaenopterids exc. minke	0% (Breese, Tershy 1993, n: 9) \bar{x}: 31% (n: 70)	50	22	16	0-53	varies with species
Minke whale	23% (Jefferson <i>et al.</i> 1991, n: 73) 83% (Lawson <i>et al.</i> 2007, n: 6) \bar{x}: 28% (n: 79)	89	45	25	6	high f
Southern right whale	<u>11% (Sironi <i>et al.</i> 2004, n: 112)</u> 89% (Jefferson <i>et al.</i> 1991, n: 9) \bar{x}: 17% (n: 121)	13	16	2	-	-
Humpback whale	49% (Jefferson <i>et al.</i> 1991, n: 43) <u>20% (Weir <i>et al.</i> 2010, n: 5)</u> <u>69% (Pitman <i>et al.</i> 2015, n: 35)</u> <u>26% (Pitman <i>et al.</i> 2017, n: 103)</u> \bar{x}: 39% (n: 186)	83+	49	32	<1-40	low a in some areas, high a in other areas, medium f
Gray whale	77% (Jefferson <i>et al.</i> 1991, n: 31)	82+	87	63	18-34	medium to high f
Sperm whale	15% (Jefferson <i>et al.</i> 1991, n: 39)	54	13	8	21-65	a varies between areas, low f
<i>Kogia</i>	<u>50% (Dunn, Claridge 2014, n: 8)</u>	100	5	50	-	-
Beaked whales	25% (Jefferson <i>et al.</i> 1991, n: 12)	100	5	25	-	-
Pilot whales	56% (Jefferson <i>et al.</i> 1991, n: 9) 0% (De Stephanis <i>et al.</i> 2015, n: 15), \bar{x}: 21% (n: 24)	60	5	13	-	-
False killer	-	100	1	-	-	-
Risso's	-	100	1	-	-	-
Bottlenose	-	100	4	-	-	-
White-beaked	-	50	2	-	-	-
Pacific white- sided	-	70	10	19	-	-
Dusky	11% (Jefferson <i>et al.</i> 1991, n: 9) 52% (Visser 1999, n: 21) <u>3% (Markowitz 2004, n: 33)</u> \bar{x}: 21% (n: 63)	93	26	19	0.09	high f
Fraser's	-	100	1	-	-	-
<i>Stenella</i>	-	100	4	-	-	-
Common	75% (Jefferson <i>et al.</i> 1991, n: 4) <u>67% (Visser 1999, n: 6)</u> \bar{x}: 70% (n: 10)	72	11	50	-	-
Southern right w.d.	-	100	1	-	-	-
Dolphins	27% (n: 73)	86+	65+	23	-	-
Dall's porpoise	26% (Jefferson <i>et al.</i> 1991, n: 62)	72	53	19	-	-

^a % of encounters leading to attack in this species suggests that the low scar rate reflects high fatality. However, the % of encounters leading to an attack is based on a review not dedicated to the estimation of this parameter and includes only 6 samples. It seems most unlikely that killer whale attacks on blue whales are typically fatal, as also suggested by an attack fatality of 30%. Hence the low scar rate is interpreted as a low attack rate.

Table 5: Anti-predator behaviour documented in oceanic cetacea

Species	Anti-predator behaviour	Reference
Blue whale	high-speed flight on straight course, no defence	Ford, Reeves 2008
Fin whale	high-speed flight on straight course, no defence	Ford, Reeves 2008
Sei whale	defence by tail-slapping, often no defence	Ford, Reeves 2008; Häussermann <i>et al.</i> 2013
Bryde's whale	high-speed flight on straight course, no defence	Alava <i>et al.</i> 2013
Minke whale	high-speed flight typically toward open water, no defence	Lowry <i>et al.</i> 1987; Ford <i>et al.</i> 2005
Southern right whale	formation of compact group with little or no inter-individual distance or rosette formation; defence with fluke and flippers	Payne 1992; Sironi <i>et al.</i> 2004; Ford, Reeves 2008
Humpback whale	formation of tight, compact group; vigorous defence with fluke, flippers, head or whole body	Whitehead, Glass 1985; D'Vincent <i>et al.</i> 1989; Ford, Reeves 2008
	1 escort accompanying mother-calf pair during migration which helps defend the calf from attack	Chittleborough 1953; Pitman <i>et al.</i> 2015
Gray whale	snorkelling: exhale underwater, barely expose blowholes at surface to inhale	Dahlheim, Heyning 1999
	formation of tight, compact group; defence with fluke or whole body	Ford, Reeves 2008
Sperm whale	sinking below water surface in response to predation risk	Gaskin 1964; Caldwell <i>et al.</i> 1966
	rosette formation or formation of tight rank, heads facing their predators; rosette sometimes with tails towards predators; often no other defence but tail-slapping observed	e.g. Arnbom <i>et al.</i> 1987; Pitman <i>et al.</i> 2001; Gemmell <i>et al.</i> 2015
	facing teeth/open mouth towards killer whales as a possible threat display towards the attackers	Gemmell <i>et al.</i> 2015
	flight	Visser 1999
<i>Kogia</i>	invisible descent beneath surface upon approach; motionless logging at surface	Willis, Baird 1998
Beaked whales	when approached to 90m: (1) ind. sinks slowly beneath surface, rising and blowing again when ~180m from ship, or (2) dive with lateral half roll which brings 1 flipper clear of water, but not flukes followed by long dive, ind. either not seen again or surfaced after ~1-5min ≥ 400m from ship	Gaskin 1971
	flight (strap-toothed beaked whale), no defence	Wellard <i>et al.</i> 2016
	split of group into sub-groups departing to different directions (Longman's beaked whale)	Rankin <i>et al.</i> 2011
Pilot whales	synchronized swimming	Senigaglia <i>et al.</i> 2012
False killer whale	flight in tight group formation, moving synchronized	Visser <i>et al.</i> 2010
Bottlenose d.	high-speed flight	Visser 1999
Pacific white-sided dolphin	high-speed flight	Dahlheim, Towell 1994; Ternullo, Black 2002
Dusky dolphin	high-speed flight; lack of response (possibly due to failure of predator detection)	Würsig, Würsig 1980; Constantine <i>et al.</i> 1998; Visser 1999
Spinner dolphin	high-speed flight	Pitman <i>et al.</i> 2015
	split of group into sub-groups departing to different directions	Norris, Dohl 1980b
Pantropical spotted dolphin	formation of compact groups or sub-groups; evasive manoeuvres, flight	Sucunza <i>et al.</i> 2015
Atlantic spotted, bottlenose d.	cooperatively fend off sharks	Herzing 2011

Clymene dolphin	cooperative defence of young by adults against sharks	Springer 1967
Common dolphin	herding of juveniles against boat while adults chase away potential predators	AIBS 1967
	high-speed porpoising flight	e.g. Breese, Tershy 1993; Visser 1999, 2000
Southern right whale dolphin	flash expansion (sudden departure of individuals to various directions); flight	Rose, Payne 1991
Dall's porpoise	high-speed flight, often over several kilometres and for an observed maximum duration of 43min	Baird, Dill 1995; Ford <i>et al.</i> 1998; Saulitis <i>et al.</i> 2000
	fastest swimming small cetacean species (\geq 55km/h in short bursts)	Shirihai, Jarrett 2006

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Appendix 5: Seasonal group size variation

Table 1: Seasonal variation in cetacea group size: incl.: including, sign.: significant, ind.: individual(s)

Species	Area	Season	\bar{x}	SD	n	Reference
Blue whale	S-California	Spring	1	0.5	18	Lomac-MacNair, Smultea 2016
		Summer	2	1.4	51	
Fin whale	Ligurian Sea (Mediterranean)	sign. larger pods in July/August			107	Azzellino <i>et al.</i> 2008
	NW-Mediterranean	Summer	1	0.1	39	Laran <i>et al.</i> 2017b
Winter		1	0	12		
Bryde's whale	N-New Zealand	Spring	1	0.3	12	Dwyer <i>et al.</i> 2016
		Summer	1	0.4	22	
		Autumn	1	0.4	13	
		Winter	1	0.6	19	
Risso's dolphin	San Clemente Island, California	Summer	27	-	7	Carretta <i>et al.</i> 2000 no significance reported
		Winter	36	-	16	
	Ligurian Sea (Mediterranean)	sign. annual but not monthly pod size variation			117	Gaspari 2004
Bottlenose dolphin	San Clemente Island, California	Summer	14	-	8	Carretta <i>et al.</i> 2000
		Winter	6	-	6	
	N-New Zealand	Spring	39	24	10	Dwyer <i>et al.</i> 2016
		Summer	47	24	10	
		Autumn	19	16	9	
		Winter	30	14	7	
	NW-Mediterranean	Summer	6	4	18	Laran <i>et al.</i> 2017b incl. inshore and offshore data
		Winter	3	3	39	
Atlantic white-sided	S-Gulf of Maine (NE-USA)	June/July	35	45	985	Weinrich <i>et al.</i> 2001
		August/Sept.	72	111		
Pacific white-sided dolphin	S-California	Spring	12	14	107	Campbell <i>et al.</i> 2015
		Summer	35	72		
		Autumn	18	20		
		Winter	15	18		
Dusky dolphin	southern Africa	no seasonal variation			100	Findlay <i>et al.</i> 1992
Atlantic spotted dolphin	SW-Atlantic outer shelf/slope	Spring	199	-	25	Di Tullio <i>et al.</i> 2016, result significant
		Autumn	39	-	15	
Striped dolphin	Ligurian Sea (Mediterranean)	June	19	-	219	Gaspari 2004, sign. annual pod size variation
		July	16	-	482	
		August	21	-	530	
		September	14	-	235	Azzellino <i>et al.</i> 2008, sign. annual pod size variation
		monthly variation in pod size highly variable between years			389	
		April-Sept.	20	2	243	
	E-Spain (Mediterranean)	October-March	11	1	274	Panigada <i>et al.</i> 2011
		Summer	14	23		
		Winter	8	6		
		114				
	NW-Mediterranean	Spring	32	-	19	Gómez de Segura <i>et al.</i> 2006, sign. test not provided
		Summer	21	-	31	
Autumn		14	-	52		
Winter		10	-	60		
NW-Mediterranean	Summer	11	5	169	Laran <i>et al.</i> 2017b	
	Winter	5	3	138		
Striped/common dolphin (combined)	NE-Atlantic shelf	Summer	17	4	79	Laran <i>et al.</i> 2017a
		Winter	9.5	1	246	
	NE-Atlantic slope	Summer	14	1	306	
		Winter	10	1	91	
	oceanic NE-Atlantic	Summer	18	2	167	
		Winter	19	7	22	

Species	Area	Season	\bar{x}	SD	n	Reference
	English Channel	Summer	3.5	2	4	
		Winter	10.5	4	23	
Common dolphin	N-New Zealand	Spring	74	118	4	Dwyer <i>et al.</i> 2016
		Summer	67	50	10	
		Autumn	34	33	26	
		Winter	8	12	36	
	San Clemente Island, California	Summer	556	-	28	Carretta <i>et al.</i> 2000
		Winter	183	-	33	
	S-California	Spring	74	113	437	Campbell <i>et al.</i> 2015 (short-beaked common dolphin)
		Summer	56	115		
		Autumn	62	85		
		Winter	105	213		
SW-Atlantic outer shelf/slope	Spring	137	65	22	Di Tullio <i>et al.</i> 2016	
	Autumn	215	140	5		
Commerson's dolphin	Argentina	Summer	13	16	479	Coscarella <i>et al.</i> 2010, seasonal difference in # of ind. in <u>scan area</u> sign.
		Winter	19	27		
Dall's porpoise	S-California	Spring	6	4	142	Campbell <i>et al.</i> 2015
		Autumn	9	7		
		Winter	7	4		

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Appendix 6: Group size related to presence/absence of calves

Table 1: Correlation of group size with presence/absence of calves

Species	Mean group size	Area	Calves	Reference
Blue whale	1-12, \bar{x} : 3, n: 47	S-Chile	group size does not correlate with presence of calves	Hucke-Gaete <i>et al.</i> 2004
Fin whale	1-6, \bar{x} : 2, n: 129	Bay of Biscay	group size does not correlate with presence of calves	Aniceto <i>et al.</i> 2016
Southern right whale	1-10, \bar{x} : 2, median: 2, n: 649	South Africa, coastal, offshore	group size does not correlate with presence of calves	Best <i>et al.</i> 2003
Humpback whale	\bar{x} : 2	Australia	use of an escort which accompanies mother-calf pair during migration and defends calf from attack	Chittleborough 1953; Pitman <i>et al.</i> 2015, 2017
Blainville's beaked whale	2-9, \bar{x} : 3, SD: 2, n: 23	La Gomera (Canary Islands)	2 largest groups of 6 and 9 ind. contained 1 calf each; no calves in smaller pods, n: 6	Ritter, Brederlau 1999
Long-finned pilot whale	2-135, \bar{x} : 20, SD: 17, median: 15, n: 249	N-Nova Scotia	78% of groups contained calves; pods with calves: 5-135, \bar{x} : 23, SD: 18, median: 18, n: 197	Ottensmeyer, Whitehead 2003
	60-80, \bar{x} : 70, n: 8	N-Atlantic	7 pods with calves; mean of 70 > overall species mean of 22	Visser <i>et al.</i> 2014
False killer whale	10-100, \bar{x} : 35, SD: 34, median: 24, n: 6	Gabon, Côte d'Ivoire (W-Africa)	calves present in at least 5 sightings; mean of 35 > overall species mean of 24	Weir <i>et al.</i> 2013

Species	Mean group size	Area	Calves	Reference
Killer whale	1-16, \bar{x} : 4, SD: 4, n: 63	Magellan Strait	calves 2-16, \bar{x} : 5, SD: 3, n: 43; no calves \bar{x} : 3, SD: 2, n: 20	Capella <i>et al.</i> 2014
Risso's dolphin	2-70, \bar{x} : 15, SD: 13, n: 117	Ligurian Sea (Mediterranean)	sign. group size variation between years, not months despite seasonal calving peak	Gaspari 2004
	overall average not published, n: 694	Azores	calves < 1 year: 1-61, \bar{x} : 17, SD: 16, n: 107; calves > 1 year: 1-62, \bar{x} : 19, SD: 17, n: 160; adults + sub-adults: 1-61, \bar{x} : 13, SD: 10, n: 427, sign. smaller than calf groups, more widely dispersed and distributed further offshore	Hartman <i>et al.</i> 2014
Bottlenose dolphin	1-65, \bar{x} : 7, SD: 7, median: 5, n: 787	Adriatic Sea (Croatia)	adults only: 1-17, \bar{x} : 4, SD: 3, n: 415; \geq 1 juv.: 2-31, \bar{x} : 7, SD: 4, n: 176; \geq 1 calf: 2-65, \bar{x} : 12, SD: 8, n: 196, difference sign.	Bearzi <i>et al.</i> 1997
Atlantic white-sided dolphin	2-2500, \bar{x} : 52, SD: 91, n: 985	S-Gulf of Maine (NE-USA)	June/July \bar{x} : 35, SD: 45, calves rare; August/Sept. \bar{x} : 72, SD: 111, calves present in > 50% of pods, difference sign.	Weinrich <i>et al.</i> 2001
Atlantic spotted dolphin	1-56, \bar{x} : 11, SD: 9, n: 251, 68% < 11	Bahamas (coastal/shallow)	groups significantly larger with calves: \bar{x} : 14, SD: 10, n: 143, than without: \bar{x} : 6, SD: 5, n: 108, F: 9.26, P < 0.005	Elliser, Herzog 2014
Striped dolphin	2-200, \bar{x} : 17, n: 1492	Ligurian Sea (Mediterranean)	calves present in coastal and pelagic waters and across all group sizes	Gaspari 2004
Common dolphin	2-21, \bar{x} : 5, SD: 4, n: 108	S-Australia, shallow habitat	immature ind. in larger groups: neonates \bar{x} : 9, SD: 6, n: 10; calves \bar{x} : 7, SD: 4, n: 56; adults only \bar{x} : 5, SD: 4	Filby <i>et al.</i> 2010
Dall's porpoise	1-6, \bar{x} : 3, SD: 1, n: 68	Johnstone Strait (W-Canada)	pods with calves: 2-6, \bar{x} : 3, SD: 1, n: 29; adults only: 1-4, \bar{x} : 2, SD: 1, n: 23	Jefferson 1987

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