

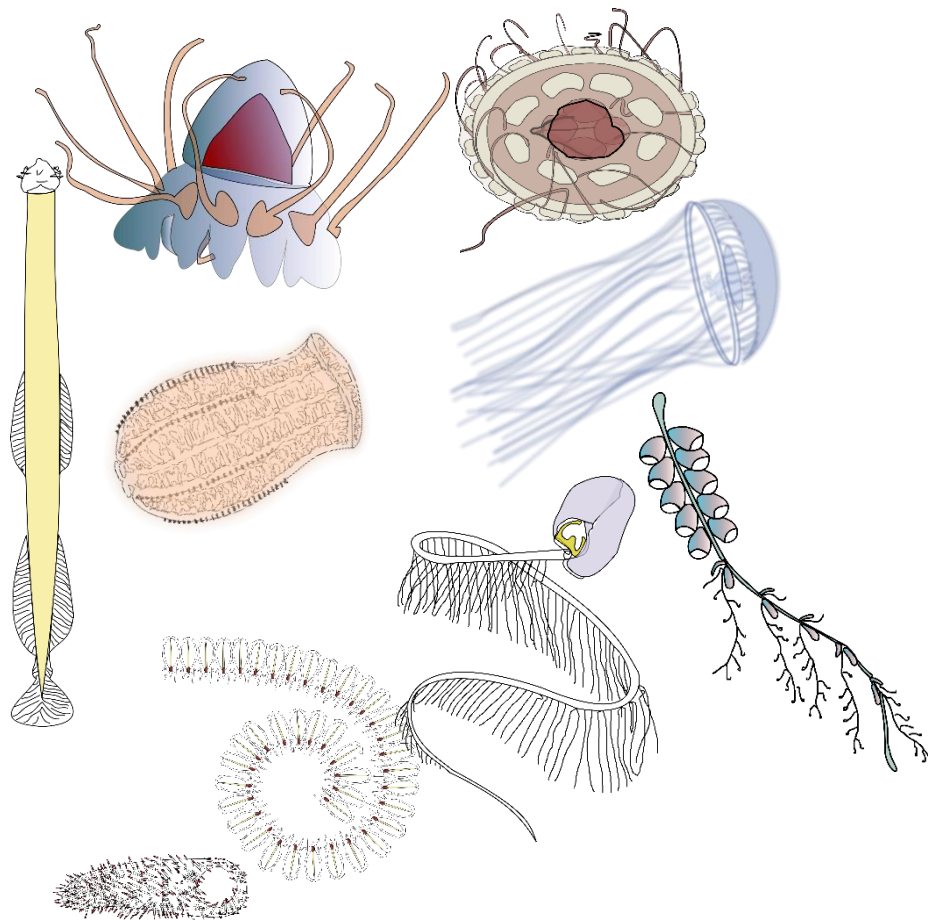
The role of gelatinous zooplankton in coastal and oceanic food webs: life history strategy and trophic ecology

Dissertation

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Summary

Gelatinous zooplankton (GZ) are comprised of diverse taxonomic groups. The population outbreaks of some GZ species occurring in marine ecosystems have drawn increasing attention because of their eco-economic consequences in recent decades. In this context, many ecological questions about GZ have not been well documented. This dissertation aims to investigate essential biomolecules transfer and consequences on life history traits of a model organism *Aurelia aurita* under the combined effects of food quality, food quantity, and temperature. Besides, large-scale stable isotope data were assembled in order to discover the general community structure of GZ in the oceanic food web (the “jelly web”).

The dissertation structures in the form of five chapters. The first chapter gives a general introduction to GZ in marine food webs and basic theory of bio-tracers. The sub-topics of the first chapter include a) GZ and “jellyfish bloom”; b) Life history traits of GZ; c) GZ in food webs; d) Trophic markers in ecological research, and e) Research objectives. Chapter 2 displays and discusses the role of food quality combined with food quantity and temperature affecting essential biomolecules transfer in a three-trophic-level food chain encompassing *A. aurita* polyps. The results showed that the fatty acid (FA) composition of polyps could be tracked back to their prey. Contents of different FA groups in prey resulted in a similar relative composition in polyps excepted for one component, arachidonic acid (ARA). It revealed a potential to use ARA as a FA marker to discover trophic relationship between polyps and their predators. Moreover, the ratio of saturated FA and unsaturated FA (SFA: UFA) of polyps was found to be altered by environmental temperature which reflects an adaption to seasonal changes and maybe related to their life history strategy. Chapter 3 is a follow-up study, which stresses these environmental factors influencing on life history traits of the moon jelly, *A. aurita*, polyps. Highly unsaturated FA (HUFA) as food quality indicators were found positively affecting polyp’s survival (especially under heat wave scenarios) and asexual reproduction. This emphasizes a potential bias of those studies which did not take food quality effect into account. For example, previous studies were potentially underestimating budding reproduction of polyps for up to 34.5 %. Moreover, both strobilation rate and ephyra production affected by food quality. Based on these findings, a novel tolerance curve for polyps has been suggested.

In Chapter 4, the trophic ecology of oceanic GZ is presented. By applying stable isotope (SI) analysis in the eastern tropical Atlantic (ETA), the general jelly web structure and isotopic niche differentiation of different GZ taxonomic groups in the overall pelagic food web was assessed. Most notably, GZ covered a large proportion in the whole food web and occupying at least 3 trophic levels. A constancy isotopic niche partitioning of different taxonomic groups was found in different habitats. However, distinct niche overlaps also indicated potential competition in some groups. Finally, chapter 5 summarized the findings from the experimental and field studies on GZ and put forwarded outlooks for further GZ ecology research in both coastal and oceanic food webs. In summary, this dissertation stresses food quality as an important factor playing critical roles on essential biomolecules transfer in food webs and explaining polyps' life history strategies under multiple stressors. Furthermore, as GZ play diverse and critical roles in aquatic food webs, the trophic “dead-end” concept of GZ should be reassessed.

Zusammenfassung

Gelatinöses Zooplankton (GZ) besteht aus einer Vielzahl verschiedener taxonomischer Gruppen. Blüten von einigen dieser Gruppen haben in den letzten Jahrzehnten durch ihre erheblichen ökologischen und ökonomischen Auswirkungen, große Aufmerksamkeit auf sich gezogen. Dennoch ist über GZ bis jetzt nur verhältnismäßig wenig bekannt und viele Fragen sind immer noch unbeantwortet. Ziel dieser Dissertation ist es den Transfer von essentiellen Biomolekülen und „Life History Traits“ unter Kombination verschiedener Effekte wie Nahrungsqualität, Nahrungsquantität und Temperatur, anhand des Model-Organismus *Aurelia aurita* zu untersuchen. Um die allgemeine Rolle des GZ im ozeanischen Nahrungsnetz zu verstehen, dem sogenannten „Jelly-Web“, wurde zusätzlich ein breiter Datensatz an stabilen Isotopen gesammelt.

Diese Dissertation beinhaltet 5 Kapitel. Das erste Kapitel gibt mit den Unterthemen a) GZ und Quallen Blüten, b) „Life History Traits“ von GZ, c) GZ in Nahrungsnetzen, g) Trophische marker in der Ökologie und e) Forschungs-Ziel, eine allgemeine Übersicht über GZ in marinen Nahrungsnetzen und die grundsätzliche Theorie der Biomarker. Das zweite Kapitel befasst sich mit den Auswirkungen von Nahrungsqualität kombiniert mit Nahrungsquantität und Temperatur, auf den Transfer von Biomolekülen in einem drei-stufigem trophischem System, welches Polypen von GZ beinhaltet. Die Ergebnisse zeigen, dass sich die Fettsäurekomposition der Polypen bis zu ihrer Beute zurückverfolgen lässt. Die Mengen verschiedener Fettsäuregruppen in der Beute spiegeln sich in der relativen Fettsäurekomposition der Polypen wieder, mit Ausnahme von Arachidonsäure (ARA). Dies zeigt, dass ARA möglicherweise als Fettsäuremarker genutzt werden kann um Räuber-Beute-Beziehungen zwischen anderen Organismen und Polypen zu untersuchen. Das dritte Kapitel beschäftigt sich mit einer Folge-Studie, der zuvor im zweiten Kapitel diskutierten Ergebnisse. Hierbei geht es um die Auswirkungen von Umweltfaktoren auf die „Life History Traits“ von Ohrenquallen *A. aurita* Polypen. Zusätzlich dazu wurde ein positiver Einfluss, von hoch ungesättigten Fettsäuren (HUFAs), welche auch als Indikatoren für die Nahrungsqualität gelten, auf das Überleben der Polypen (besonders unter Hitzestress) und ihre asexuelle Reproduktion, beobachtet. Dies zeigt, dass der Aspekt der Nahrungsqualität in bisherigen Studien übersehen wurde. Frühere Studien wurden unterschätzt, die aufkeimende Vermehrung von Polypen könnte bis zu 34,5% betragen. Darüber hinaus, wird eine neue Toleranzkurve für Polypen vorgeschlagen.

In Kapitel 4 wurde die trophische Ökologie von ozeanischem GZ im östlichen tropischen Atlantik mit Hilfe von stabilen Isotopenanalysen, untersucht. Die grundlegende Struktur des Jelly-Webs und die isotopische Nischendifferenzierung von verschiedenen taxonomischen GZ Gruppen innerhalb des pelagischen Nahrungsnetzes wurden ermittelt. Hierbei ist erwähnenswert, dass das GZ einen großen Anteil des Nahrungsnetzes mit abdeckt und mindestens drei verschiedene trophische Stufen besetzt. Es wurde eine konstante isotopische Nischenaufteilung der verschiedenen taxonomischen Gruppen in verschiedenen Habitaten beobachtet. Trotzdem zeigen klare Nischenüberlappungen auch Grund zur Annahme, dass einige dieser Gruppen in Konkurrenz miteinander stehen. Das fünfte Kapitel fasst alle Ergebnisse der experimentellen und Feldstudien über GZ zusammen und gibt eine Aussicht auf zukünftige Forschungen zu GZ, sowohl in den Nahrungsnetzen der Küsten, als auch des offenen Ozeans.

Zusammenfassend, betont diese Dissertation die Rolle von Nahrungsqualität als ein bedeutender Faktor für den Transfer von essentiellen Biomolekülen in Nahrungsnetzen und erklärt die „Life History“ Strategie von Polypen unter dem Einfluss von multiplen Stressoren. Des Weiteren, zeigt sie, dass GZ eine wichtige und mannigfaltige Rolle in Nahrungsnetzen spielt, weshalb das „Sackgassen“ Konzept für GZ überdacht und reformiert werden sollte.

Chapter 1 General introduction

1.1 Gelatinous zooplankton and “jellyfish bloom”

Gelatinous zooplankton (GZ) are fragile organisms with a low carbon content per unit volume. Their taxonomic groups include, but are not limited to, scyphomedusae, hydromedusae, siphonophores, ctenophores, tunicates, and chaetognaths. They are ubiquitous in coastal and oceanic environments, distributed from tropic to polar regions and from the surface to the deep ocean (Robison et al. 2005; Condon et al. 2012; Décima et al. 2018). These invertebrates have a high rate of reproduction and are enable to form massive bloom (“jellyfish bloom”) under their optimum environmental conditions. Increasing trends of GZ population have been observed in many marine ecosystems (Brotz et al. 2012). Further, the ecological role of GZ has attracted more attention because their bloom cause sometimes vast ecological and economic problems (Gibbons and Richardson 2013; Brodeur et al. 2016; Bosch-Belmar et al. 2017). In particular, fundamental research on GZ ecology has now received more attentions, including morphological development process in their life history and population dynamics under the impacts of environmental factors such as temperature, salinity, nutrition, etc. (Lucas 1996; Barz and Hirche 2005; Barz and Hirche 2007). However, population growth of GZ was found not to be always be consistent between years

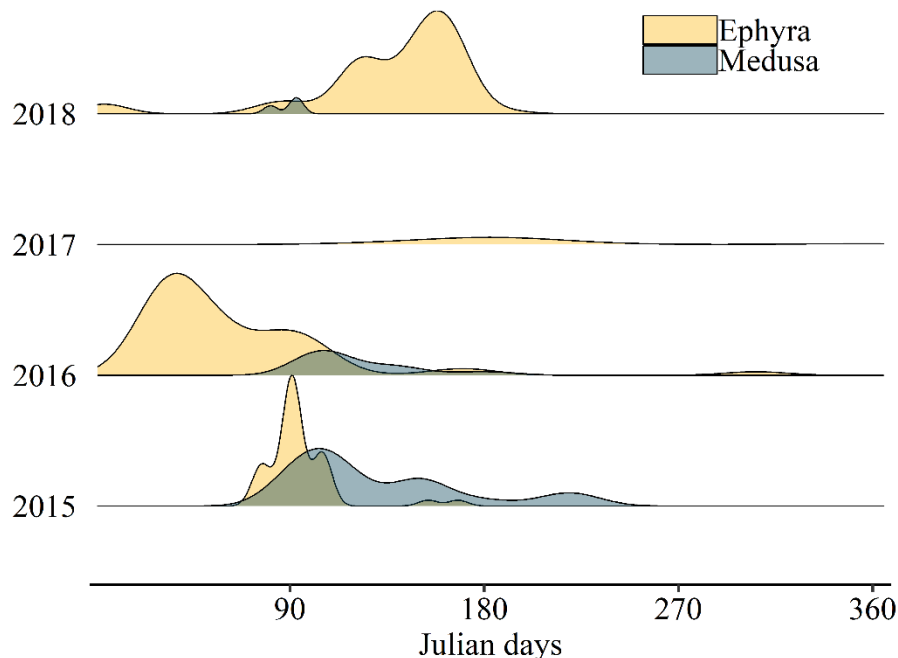


Fig. 1.1 Population dynamics of the moon jelly *Aurelia aurita* in the western Baltic Sea (Chi et al, unpublished).

or locations. For example in 2017, the “jelly-free” situation was observed in the western Baltic Sea with only small abundances of larvae stage (ephyra) of the moon jelly *Aurelia aurita* (Fig. 1.1). To understand GZ population dynamics, more research should be conducted to detect these variations, including their life history. The relationship between multiple environmental factors and jellyfish bloom have been widely investigated by focusing on the pelagic adult stage (Attrill et al. 2007; Brotz et al. 2012; D'Ambrosio et al. 2016), while investigation of combination effects of biotic- and abiotic- factors on regulating life history of GZ and of underlying mechanisms driving the rise and fall of jellyfish bloom in the context of global oscillations are still lacking.

1.2 Life history traits of gelatinous zooplankton

Scyphomedusae are an important gelatinous taxon and the majority of coastal species in this group possess a metagenic life cycle which involves a pelagic medusa stage, and a benthic polyp stage (Berrill 1949; Arai 1997), for instance, *Aurelia sp.* (Arai 1997), *Cyanea sp.* (Brewer 1989; Brewer and Feingold 1991), *Nemopilema nomurai* (Kawahara et al. 2006), and *Catostylus mosaicus* (Pitt 2000). These species have been made responsible to initiate “jellyfish bloom” resulting from extensive population rises (Daryanabard and Dawson 2008; Brotz et al. 2012; Boero 2013). In their typical life cycle, mature medusae release pelagic planulae larvae, which settle on substrates and develop into polyps. Benthic polyps can asexually expand their population *via* budding production and can also develop pelagic ephyrae *via* strobilation, which then further grow up to medusae. Under some extreme conditions, polyps can produce podocysts to maintain their population (Arai 2009).

Even though the pelagic medusa stage has been mainly blamed for problems of jellyfish bloom, their recruitment is highly dependent to the benthic polyp stage. Thus, to understand the fluctuations of GZ population, we need to investigate the relationship between benthic polyps' life history traits and environmental factors. Main life history traits of polyps include body size (mass), growth rate, survival, budding production, strobilation rate, ephyra production, podocysts production, and podocyst hatching rate. These life history traits are affected by multiple factors and their combinations. For example, prey concentrations (Han and Uye 2010; Lesniewski et al. 2015; Wang et al. 2015a), temperature (Feng et al. 2015a; Pascual et al. 2015; Hubot et al. 2017), light (Custance 1964; Liu et al. 2009), dissolved oxygen (Condon et al. 2001; Ishii et al. 2008), polyp density (Purcell et al. 2009), and salinity (Holst and Jarms 2010). However, food quality as a potential factor regulating polyps' life history has not been systematically investigated yet.

1.3 Gelatinous zooplankton in food webs

Unlike fish, the trophic importance of GZ has not been well explored, but rather overlooked for decades. Only recently, their outbreaks caused dramatically eco-economic consequences and, thus, launching more investigation efforts.

In marine ecosystems, some GZ have a significant top-down control on the community composition of mesozooplankton (Behrends and Schneider 1995). They were observed to consume up to 26-30% of the standing stock of zooplankton per day (Brodeur et al. 2002; Uye and Shimauchi 2005), which markedly impacted energy transfer and food web structure (Purcell 1997). In particular, GZ influenced fish population stock *via* competing for food or directly by feeding on fish larvae (Möller 1984; Purcell 1985; Lynam et al. 2005). Previous studies confirmed a trophic overlap between GZ and fish (Purcell & Grover, 1990, Purcell & Sturdevant 2001). Besides, aggregates of herbivorous pelagic tunicates such as salps and pyrosomes could remove substantial amounts of phytoplankton standing stock (Harbison and Gilmer 1976; Drits et al. 1992; Perissinotto et al. 2007). Thus, GZ as effective predators are involved in marine food webs and greatly determine energy flow, especially under jellyfish bloom conditions.

On the other hand, GZ comprise more than 90 % of water and low nutritional value of their body tissue (Omori 1969; Hays et al. 2018). Their predators potentially need to consume large volume of biomass to meet their metabolic demands (Hays et al. 2018). Thus, they were rarely recognized as an intermediate trophic level and consequently have been considered as trophic “dead-ends” (Hansson and Norrman 1995; Verity and Smetacek 1996; Lynam et al. 2006). However, with the development of new technologies, e.g., remotely operated underwater vehicles (ROVs), bio-tracers, DNA metabarcoding, substantial evidences for GZ as prey for carnivores at higher trophic levels accumulated. A wide range of jellyfish-feeders have drawn scientific attention in recent years such as turtles (Carman et al. 2014), seabirds (Sato et al. 2015; Thiebot et al. 2017), and many fishes (Cardona et al. 2012; D'Alelio et al. 2017). In most cases, GZ are consumed by opportunistic feeders, yet some carnivores such as adult leatherback turtles and larvae stage of tuna, which were found unique in feeding solely on GZ (Llopiz et al. 2010; Fossette et al. 2011). Moreover, some jelly-feeders were found to selectively feed on the more energy-rich tissues, i.e. gonads and oral arms (Milisenda et al. 2014; Nakamura et al. 2015). Despite the large water content of gelatinous zooplankton, their prey values have been recognized.

Meanwhile, GZ are also linked to the bacterioplankton community and benthic ecosystem. Mucus particles and fecal pellets produced by GZ have been suggested as important origin of macroscopic aggregates (“marine snow”) (Alldredge and Silver 1988; Ransom et al. 1998; Turner 2002). Released dissolved organic matter (jelly-DOM) are metabolized by respiration of bacterial communities (Condon et al. 2011). Moreover, accumulates of gelatinous carcasses sinking through the water column during post-bloom export carbon to deep water, which could alter biogeochemical cycling in benthic ecosystems (Lebrato et al. 2013; Chelsky et al. 2015; Sweetman et al. 2016).

Taken together, GZ not only have an active ecological role in the marine pelagic food webs but their function greatly extends to benthic food webs. They cover a wide range of taxonomic groups and their feeding guild can be herbivore consumers or omnivores/carnivores predators. On the other hand, GZ are potentially serve as prey for other top predators. Nevertheless, due to the limitations of sampling methods in the open ocean and their fragile nature, the general food web structure of GZ (“jelly web”) including its ecological role in the oceanic food web is still not clear.

1.4 Trophic biomarkers in ecological research

Predator-prey interactions are the core research focus in trophic ecology and food web dynamics. Approaches such as *in situ* observations and stomach content analysis (SCA) provide directly evidence of trophic linkages. However, their limitations are obvious, for example, results obtained from *in situ* observations may enlarge the impact of opportunistic feeding and SCA just reveal a snapshot of the recently consumed diet and underestimate those prey easy to digest (Iverson et al. 2004). Based on the “you are what you eat” concept in trophic ecology (DeNiro and Epstein 1976; Kohn 1999; Bradshaw et al. 2003), fatty acids and stable isotopes (i.e., trophic biomarkers) provide insights into a long-term of trophic interactions among predators and preys (Budge 1999; Dalsgaard et al. 2003; Ju et al. 2004; Fry 2006). Trophic biomarkers have been applied in GZ ecology just in recent decades (Pitt et al. 2009).

1) Fatty acid

Fatty acids (FAs) are biochemical compounds consisting of straight carbon atom chains with 0-6 double bonds, a methyl terminal and an acid group terminal at two ends, separately (Iverson 2009). They have a structural function in membrane phospholipids (Fig. 1.2), and energetic and nutritional functions as cellular energy storage (Desvillettes et al. 1997).

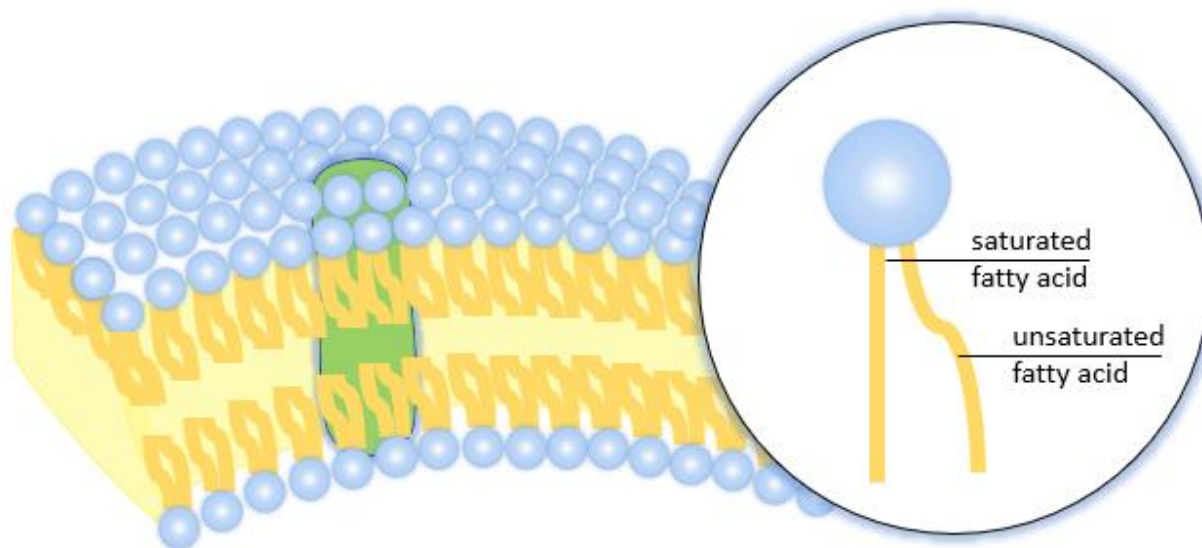


Fig. 1.2. Diagram of fatty acid in a cell membrane structure.

According to the length of the carbon atom chain and the number of double bonds, FA can be grouped as saturated FA (SFA), monounsaturated FA (MUFA), polyunsaturated FA (PUFA), and highly unsaturated FA (HUFA). Among them, HUFAs are FAs comprise more than 20 carbon atoms and more than 2 double bonds, such as arachidonic acids (ARA; 20:4 ω 6), eicosapentaenoic acid (EPA; 20:5 ω 3), and docosahexaenoic acid (DHA; 22:6 ω 3).

Phototrophic organisms can synthesize linoleic acid (LIN; 18:2 ω 6) and α -linolenic acid (ALA; 18:3 ω 3) *de novo* from stearic acid (18:0) (Gurr and Harwood 1991). LIN and ALA can serve as precursors to be further bio-converted to long-chain unsaturated fatty acids, such as EPA and DHA (Arts et al. 2009) (Fig. 1.3). In contrast, many animals are unable to synthesize these FA precursors, but exhibit capacities of bioconversion or accumulate these essential compounds from diets. Thus, FAs could provide quantitative and qualitative insights into energy flow in food webs (Iverson 2009). Because FAs accumulate over time and represent an integration of the dietary intake, being transferred, biosynthesized, and modified into predators' tissue in a conservative manner, enable them to be a trophic marker (Dalsgaard et al. 2003; Iverson et al. 2004), which can be used to investigate tropho-dynamics in food webs (Wilson et al. 2010; Salvo et al. 2017). Moreover, the degree of FA unsaturation contributes to maintaining cell membrane structure and certain FAs are precursors for tissue hormones (Müller-Navarra 2008). Especially, HUFAs, e.g. ARA, EPA, and DHA, play critical roles for the fitness of organisms and energy flow in food webs (Brett and Müller-Navarra 1997; Copeman et al. 2002; Kainz et al. 2004; Parrish 2009). They are thought to

be semi-essential for many aquatic animals, contributing to organisms' optimum survival, growth and reproduction (Brett and Müller-Navarra 1997; Ballantyne et al. 2003; Ravet and Brett 2006).

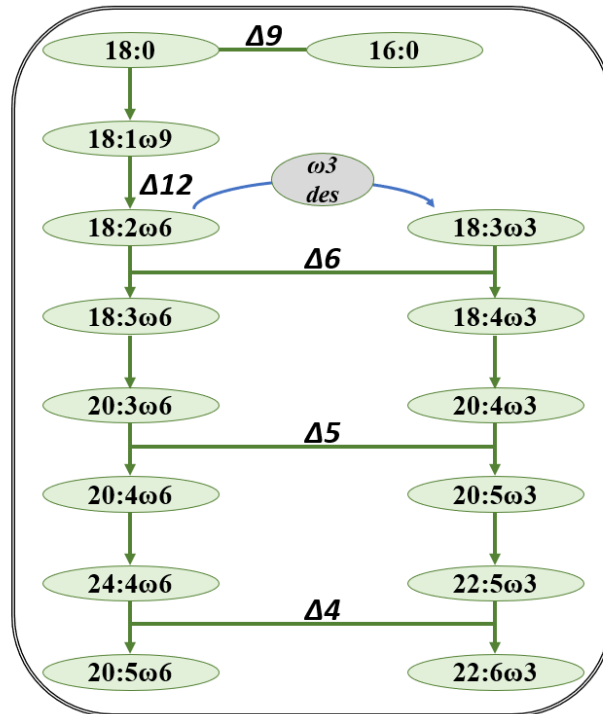


Fig. 1.3 Diagrammatic representation of the proposed pathways of PUFA synthesis *via* different desaturases ($\Delta 4$, $\Delta 5$, $\Delta 6$, $\Delta 9$, $\Delta 12$). (modified from Desvilettes and Bec (2009))

Moreover, because FAs could be transferred through the phytoplankton-zooplankton interface (Müller-Navarra et al. 2000) and due to the functional importance of essential FAs, the concentration of HUFA in prey consequently can serve as food quality indicators for consumers (Park et al. 2002). Thus, analyzing the FA composition can provide crucial information on the prey's nutritional conditions as well as predators' feeding history. FA analysis has been recently applied in GZ ecology and their trophic role in food web studies (Nelson et al. 2000; Fukuda and Naganuma 2001; Milisenda et al. 2018).

2) Stable isotope

Stable isotopes (SIs) are non-radioactive isotopes of elements with different numbers of neutrons in the nucleus and consequently different atomic masses (Sulzman 2007). The most widely used stable isotope elements in ecology are nitrogen (^{15}N) and carbon (^{13}C), they are commonly expressed as $\delta^{15}\text{N}$ (‰) and $\delta^{13}\text{C}$ (‰) indicating the ratio of heavy to light isotope and relative to a standard (Peterson and Fry 1987):

$$\delta X = \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \times 1000$$

Where δ is the isotopic notation, X is the heavy element (^{15}N or ^{13}C), R is the ratio of the heavy isotope to light isotope for this element ($^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$). The international standard for $\delta^{13}\text{C}$ measurements is the Vienna Peedee Belemnite (VPDB), and atmospheric nitrogen is used as the standard for $\delta^{15}\text{N}$ measurements (Fry 2006).

The variances in stable isotope ratios of organisms' tissues can reflect their diet, being generally stepwise enriched at each trophic level (Fry 2006). For example, $\delta^{13}\text{C}$ is a conservative tracer denoting different photosynthetic pathways in primary producers and, therefore, serves as for food sources determination and is widely used for reflecting energy flow in ecosystems (Fry and Sherr 1989). $\delta^{15}\text{N}$ varies with stepwise enrichment along trophic transfer, thus, it can be used as a robust indicator of trophic positions of organisms in food webs (McCutchan et al. 2003). Therefore, SI analysis provides a temporal and spatial insight into trophic interactions in food webs. The application of SI analysis can help to answer core ecological questions such as characterizing trophic relationships and constructing food webs, understanding the ecology of invasive species, investigating life history ecology, and animal migrations (Fry 2006; Boecklen et al. 2011). Recently, SI analysis has been widely applied to determine the trophic ecology of GZ. For example, to reveal ontogenetic and temporal dietary shifts in the moon jelly *Aurelia aurita* (Graham and Kroutil 2001; Fleming et al. 2015; Javidpour et al. 2016) and isotopic niche partitioning between fish and GZ (Nagata et al. 2015).

Due to the fragile nature of GZ and their short digestion time (Jackson et al. 1987; Arai et al. 2003), traditional trophic research methods such as SCA are limited in its application in GZ. FA and SI analyses being used as bio-trophic markers can reflect an integrated long-term trophic ecology of those organisms and, thus, provide an alternative approach of understanding the dietary composition of GZ and their trophic relationship with other organisms in food webs.

1.5 Research objectives

The aim of my PhD project was to investigate the trophic ecology of GZ by experimental methods and field sampling in coastal and oceanic food webs. To understand life history strategies and their trophic roles in food webs, both FA and SI analyses were performed. In this dissertation, three major questions have been discussed:

I. How are essential biomolecules transferred in the benthic stage (polyp) of the moon jelly *Aurelia aurita* (Cnidaria: Scyphozoa)?

Certain FAs have been recognized as essential biomolecules regulating the fitness of organisms. Even though FA as biomarkers have been widely used in aquatic ecology, analysis of their transfer in the food chain involving jellyfish polyps is lacking. Meanwhile, the polyp stage has been suggested to be critical to determine the pelagic population. Thus, understanding the relationship of FA composition between polyps and their food sources is important. Moreover, the effects of biotic- and abiotic- environmental factors on FA transfer processes from prey to polyps were assessed.

II. What is the effect of food quality and its interplay with food quantity and environmental temperature on life history traits of *A. aurita* polyps?

Due to the metagenic life cycle of scyphomedusae, their life history traits are complex. Temperature and food concentration received the main attention in polyp ecology studies. However, food quality as an important aspect of food condition affecting life history traits of polyps has not been documented. Thus, to understand polyp life history traits under different environmental conditions, I conducted a multi-factorial experiment taking food quality, food concentration, and temperature into consideration.

III. What are the trophic niche characteristics of the “jelly web” in oceanic food webs?

Since the general structure of the “jelly web” and their trophic niche characteristics in oceanic food webs have been not described, I conducted a field study applying SI analysis on different GZ taxonomic groups in the eastern tropical Atlantic. In this chapter, an overview of “jelly web” is discussed. Furthermore, isotopic niche differentiation and overlap regarding geographic and sizes dependency within taxonomic groups were quantified.

Chapter 2 Tracking fatty acids from phytoplankton to jellyfish polyps under different stress regimes: a three trophic levels experiment

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Abstract

The impacts of biochemicals driving food web processes are under investigation for just the last few decades. In addition, as jellyfish are drawing increasing attentions because of their mass developments and of their potential capacity of driving food web structures and energy flow by “top-down” and “bottom-up” controls. We here show that the provision with the biochemical complex thiamin (vitamin B₁) to the common phytoplankton *Rhodomonas baltica* altered its fatty acid (FA) pattern toward ω 3-highly-unsaturated FAs (ω 3-HUFA) and that this pattern was further transferred up to the zooplankton consumer, the copepod *Acartia tonsa*. However, polyps of the Jellyfish *Aurelia aurita* feeding on *A. tonsa* only had a low relative ω 3-HUFA content, especially due to a reduction in 22:6 ω 3 (DHA), but elevated levels of 20:4 ω 6 (ARA). The high proportion of the ω -6 HUFA, ARA in polyps may provide evidence for preferential conversion of ARA in polyps, eventually from DHA in a so far unknown pathway. In contrast to *A. tonsa*, newly hatched *A. salina nauplii* used as food for *A. aurita* polyps were almost devoid of HUFA, but contained high levels of C₁₈ polyunsaturated FAs (C₁₈-PUFA). Consequently, polyps feeding on them contained few HUFA, while high levels of C₁₈-PUFA predominated. This suggests that *A. aurita* polyps cannot efficiently convert ω 3 C₁₈-PUFA to ω 3-HUFA. In addition, besides a decrease in saturated FAs, especially an increase in HUFA in *A. aurita* polyps with decreasing temperature was observed, for which the dietary provision with HUFA seemed to be critical. Altering the FA pattern

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as a response of temperature reflects an adaptation to seasonal changes and may be related to their life history plasticity.

Keywords: biomolecules, thiamin, fatty acids, *Aurelia aurita*, polyp, food chain, food quality

2.1 Introduction

Solar Energy that is fixed by primary producers is transferred to higher trophic levels *via* predator-prey interactions reallocating biomolecules (such as carbohydrates, lipids, proteins and nucleic acids) through metabolic pathways. The syntheses rates of these essential or semi-essential biomolecules and the transfer efficiencies among food chains will determine the trophic structures of food webs and might regulate ‘bottom-up’ control to higher trophic levels (Hairston Jr and Hairston Sr, 1993). In addition, these bio-compounds are critically important for organisms’ fitness by regulating their metabolism, growth, and reproduction, and can serve as indicators of dietary nutritional conditions (Gulati and DeMott 1997; Park et al. 2002; reviewed by Müller-Navarra 2008). Despite their importance, there are still plenty of open questions regarding the biosynthesis and transfer efficiency of biomolecules in marine food web, including fatty acids (FAs).

FAs in aquatic organisms serve as intermediate energy storage (Lee et al. 2006) but can also be limiting components to support somatic growth (Müller-Navarra et al. 2000) and enhancing immune-competency (Arts and Kohler 2009). Besides, FAs are structurally and functionally important lipid molecules (Colombo et al., 2016), which, on the one hand, benefit to sustain membrane fluidity and, on the other hand, are also needed as precursors for tissue hormones (Vance and Vance 2008). Certain highly unsaturated FA (HUFA), such as eicosapentaenoic acid (EPA; 20:5 ω 3) and docosahexaenoic acid (DHA; 22:6 ω 3) play critical roles for the fitness of organisms, determining food quality and, thus, carbon energy transfer efficiency to higher trophic levels (Brett and Müller-Navarra 1997; Müller-Navarra et al. 2004; Persson and Vrede 2006). For example, it has been shown that fish larvae require a high level of DHA and arachidonic acids (ARA; 20:4 ω 6) for optimal growth and survival (Izquierdo 1996; Sargent et al. 1999; Copeman et al. 2002; Yuan et al. 2015). Likewise, another HUFA, the natural dietary content of EPA, was found to be well related to the growth rate and egg production of the freshwater zooplankton *Daphnia* (Müller-Navarra 1995; Müller-Navarra et al. 2000).

Despite caveats regarding quantitative assessments (Budge et al. 2006), FAs can be used as trophic markers (FATMs), helping to improve our understanding of so far unknown mass transfer through predator-prey interactions (e.g., Dalsgaard et al. 2003), especially for the nutritionally critical lipids as shown for fish (Kirsch et al. 1998; Budge et al. 2002), and marine mammals (Iverson et al. 1997; Thiemann et al. 2008). FA composition of prey was shown to be involved in the extent of competition in predators and its seasonal succession (Klein Breteler et al. 2005; McMeans et al. 2015). However, although FA tracers were widely used in aquatic food webs from algae *via* zooplankton to fish, both in freshwater (e.g., Ahlgren et al. 1997; McMeans et al. 2015) and marine systems (Rossi et al. 2006), understanding of FAs transfer in food webs involving jellyfish is still poor.

In recent decades, population increases of jellyfish were reported to cause numerous social-economic and ecological issues (Richardson et al. 2009; Brotz et al. 2012). Although there are indications that they may serve as prey for many top predators such as some fish (Miyajima et al. 2011), penguins (Thiebot et al. 2016) and sea turtles (Carman et al. 2014), on the other hand, they can also heavily prey on fish larvae (Lynam et al. 2005) and mesozooplankton (Behrends and Schneider 1995), therefore being a competitor for fish. In particular, scyphomedusae exhibit a metagenic life cycle, which involves a sexual pelagic medusae stage and an asexual benthic polyp stage (Arai 1997). Expansions of polyp populations by asexual reproduction (budding) and success for producing ephyrae larvae (strobilation) determine population recruitment of pelagic medusae. This benthic-pelagic coupling process depends on abiotic factors and also food availability (Lucas et al. 2012). So far, studies have been carried out on energy and nutrient flow in jellyfish by bio-tracers (reviewed by Pitt et al. 2009), but no single study exists which explored FA transfer towards jellyfish (polyps). In order to evaluate whether the FATM concept can be applied as a natural bio-tracer in a food chain involving jellyfish, and, on the other hand, predict fitness of jellyfish, we need to know the extent of the variability in jellyfish FA composition, and the factors driving this variability.

Thus, the object of the present study was to track FAs alteration and transfer in a three-trophic-level food chain, consisting of a primary producer, the phytoplankton *Rhodomonas baltica* (Karsten, 1898), a primary consumer, the anostracan *Artemia salina* (Linnaeus, 1758) and copepod *Acartia tonsa* (Dana, 1849), and polyps of jellyfish *Aurelia aurita* (Linnaeus, 1758) as predators. There are two primary aims of this study 1) to track FA composition of the predator polyps back

to their dietary FA composition, and 2) to assess the effects of environmental temperature and food availability on FA transfer processes.

2.2 Materials and Methods

2.2.1 Experiment set up

A. aurita polyps were obtained from permanent cultures of the Christian-Albrechts University, Kiel (Germany), originally collected from the North Sea (Helgoland, Germany), and kept at 20 °C and salinity of 30 psu. Prior to the experiment, polyps were fed with newly hatched *A. salina* nauplii and kept in filtered seawater (0.2 µm) exchanged twice a week. To prepare the experiment, polyps were removed carefully from the substrates and were placed individually in 6-well polycarbonate plates. We manipulated three experimental temperatures, 13 °C, 20 °C and 27 °C, which mimic autumn/spring, average summer, and a heat wave scenario, respectively (Meehl and Tebaldi 2004; Wiltshire and Manly 2004; Garrabou et al. 2009). Three food concentrations of high (20 µg C polyp⁻¹), medium (5 µg C polyp⁻¹) and low (1.5 µg C polyp⁻¹) were considered to represent excess, average and starvation food supply (Han 2009) and offered every other day for polyps.

We provided three types of zooplankton prey with different HUFA content, a) *A. salina* nauplii (thereafter *Art*), were hatched from commercial traded eggs (Great Salt Lake, USA), and unfed nauplii were directly used for feeding polyps. b) copepodites of *A. tonsa* (thereafter *Aca*⁽⁺⁾) that were fed with standard *R. baltica* stock and c) copepodites of *A. tonsa* (thereafter as *Aca*⁽⁻⁾) fed with *R. baltica* cultures lacking thiamin (vitamin B₁). Our standard *R. baltica* stock (thereafter *Rhodo*⁽⁺⁾), applied Provasoli's enrichment medium modified by U. Sommer, while in the stock medium of the other phytoplankton treatment (thereafter *Rhodo*⁽⁻⁾), no thiamin was added. Both *R. baltica* were cultured at 20 °C under 100 µmol photons m⁻² s⁻¹ light conditions. To manipulate two different qualities of *A. tonsa*, newly hatched nauplii were cultured at 20 °C, under dark condition, and were fed daily with *Rhodo*⁽⁻⁾ and *Rhodo*⁽⁺⁾, respectively at concentrations adjusted to be above the food limitation level for this copepod species, i.e. > 600 µg C L⁻¹ (Kiørboe et al. 1985). Thus, we supplied three food types (i.e., *Aca*⁽⁻⁾, *Aca*⁽⁺⁾, and *Art*) for feeding polyps, thereafter pol_(Aca-), pol_(Aca+), and pol_(Art), respectively. Overall, we applied a three-factorial design (i.e., temperature, food quality and food quantity) in which each factor had three levels. Each combination of food quality, food quantity, and temperatures at 20 °C and 27 °C comprised 12 replicates (n = 108, respectively). Given the fact that strobilation might potential happen at 13 °C and to ensure enough

materials for further analysis, each treatment was replicated 18 times for this specific temperature level ($n = 162$). The experiment lasted for 30 days.

2.2.2 Fatty acids analysis

At the end of the experiment, triplicate samples from each treatment of phytoplankton, zooplankton, and polyps were analyzed for FA composition. To prepare FA samples, 10 ml of each phytoplankton treatment was filtered on GF/F filters (Pore size: 0.7 μm). Zooplankton samples were prepared by pooling ca. twenty individuals per each sample. Polyps were put into tin capsules individually. All samples were prepared and stored at $-80\text{ }^{\circ}\text{C}$ prior to FA analyses.

Samples were analyzed as FA methyl esters (FAMES) using a gas chromatograph (GC; Thermo Fisher Scientific, Germany). The procedure of preparing FAMES was modified after Christie's (1989) method. In detail, FAs were extracted at $-20\text{ }^{\circ}\text{C}$ for 12 hours with a 1:1:1 (volume) mixture solvent of chloroform/dichloromethane/methanol. 100 μl of FA 19:0 and 21:0 were added to each sample respectively at the beginning of the extraction procedure, and serving as internal standards. In the first cleaning up procedure, we used a 1 mol L^{-1} potassium chloride solution; the lower liquid phase was collected, and dried sodium sulfate was added to remove possible residual water. Samples were transferred to glass cocoons and 100 μl toluene and 200 μl methanol (supplemented with 1 % concentrated sulphuric acid) were added for esterification, which took place at $50\text{ }^{\circ}\text{C}$ for 12 hours. Thereafter, FAMES were cleaned up with a 5 % sodium chloride solution and n-hexane. Upper phases were transferred to new cocoons and evaporated, thereafter the extractive FAMES were re-dissolved in 100 μl n-hexane for analysis. FAMES were analyzed using a GC with hydrogen as the carrier gas. Peaks were integrated using the Chromcard software (Thermo Fisher Scientific, Germany), and identified with Supelco 37 FAME mixture (Sigma-Aldrich, USA). In this study, detected FA components including 14:0, 16:0, 18:0, 18:1 ω 9, 18:2 ω 6, 18:3 ω 6, 18:3 ω 3, 20:0, 20:1 ω 9, 20:2 ω 6, 20:4 ω 6, 20:3 ω 3, 22:0, 20:5 ω 3, 22:1 ω 9, 24:0, 24:1 ω 9, and 22:6 ω 3.

2.2.3 Statistics analysis

FA results were presented as percent of total FAs (% TFA), and single FAs were summed to the respective FA groups, i.e., saturated FA (SFA), monounsaturated FA (MUFA), polyunsaturated FA (PUFA), and HUFA. First, to assess the success of the food quality manipulation of the different zooplankton types, one-way ANOVA was applied to compare FA groups (i.e., SFA, MUFA, PUFA, and HUFA) among phytoplankton or zooplankton treatments. Second, to compare

the effect of food types on overall FA composition of *A. aurita* polyps, permutational multivariate analysis of variance (PERMANOVA, permutation = 999) (Anderson 2001) on Bray-Curtis similarity matrix was performed. Comparisons of the FA composition of different trophic levels (i.e., phytoplankton, zooplankton and polyps) was restricted to polyps cultured at 20 °C and fed high food concentration, because phytoplankton and zooplankton were cultured at 20 °C and two types of *A. tonsa* were fed in excess. All detected FA components and calculated FA groups were included in the PERMANOVA model, respectively. Prior to model fitting, the multivariate homogeneity of FA components and FA groups dispersion from different food quality levels was tested. There was no statistically significantly different dispersion of both FA components data ($df = 2, F = 1.03, P = 0.31$) and FA groups data ($df = 2, F = 1.27, P = 0.27$) which met assumption of PERMANOVA tests.

To follow single FAs from phytoplankton *via* zooplankton to polyps in a controlled setting, we focused on those FAs in organisms of the three experimental trophic levels which contributed most to differences of the polyps' FA composition in each pair-wise comparison, after similarity percentage (SIMPER) analysis (Table 2.2), i.e., 16:0, 18:0, 18:1 ω 9, 18:3 ω 3 (ALA), 20:4 ω 6 (ARA), 20:5 ω 3 (EPA), and 22:6 ω 3 (DHA). In addition, we also included 18:2 ω 6 (LIN) in the final analysis which was not included by SIMPER results, but it can be an important intermediate for FA elongation to ARA (Desvillettes and Bec 2009), similar to ALA as a precursor for EPA and DHA (Vance and Vance 2008). The selected FA components among different trophic levels and different food quality treatments were tested by ANOVA. At last, a beta regression model extended with precision sub-model (Ferrari and Cribari-Neto 2004; Cribari-Neto and Zeileis 2010) was applied to analyze polyps' FA composition under the combination of food quality, food quantity, and temperature. A stepwise backward selection method via an Akaike information criterion (AIC) index was performed to select adequate models.

All statistical test, data explorations, and data visualizations were performed using R software (Version 3.3.3) (R Core Team 2017). The PERMANOVA tests and beta regressions were performed using R package *vegan* (Oksanen et. al, 2017) and *betareg* (Cribari-Neto and Zeileis 2010), respectively. All data visualizations were performed using the R package *ggplot2* (Wickham 2016).

2.3 Results

2.3.1 FA composition of phytoplankton and zooplankton treatments

The supply of thiamin to the growth medium of *R. baltica* had a positive effect on the relative PUFA, and especially HUFA content (Table 2.1, Fig. 2.1). Along the experimental food chain, the relative HUFA contents in *Aca*⁽⁻⁾ and *Aca*⁽⁺⁾ differing in the thiamin provision of their food were even more significantly different (Table. 2.1, Fig. 2.1). Compared to the two types of copepods, the share of HUFA in *Art* (4.2%), was significantly lower than that presented in *Aca*⁽⁺⁾ (48.7%) and even in *Aca*⁽⁻⁾ (32.8%). The differences could be observed in SFA and MUFA, as well (Table 1, Fig. 1). In contrast, the relative PUFA content was not that different, PUFA in *Art* (51.4%) was higher than in *Aca*⁽⁻⁾ (40.1%) but similar to *Aca*⁽⁺⁾ (52.3%).

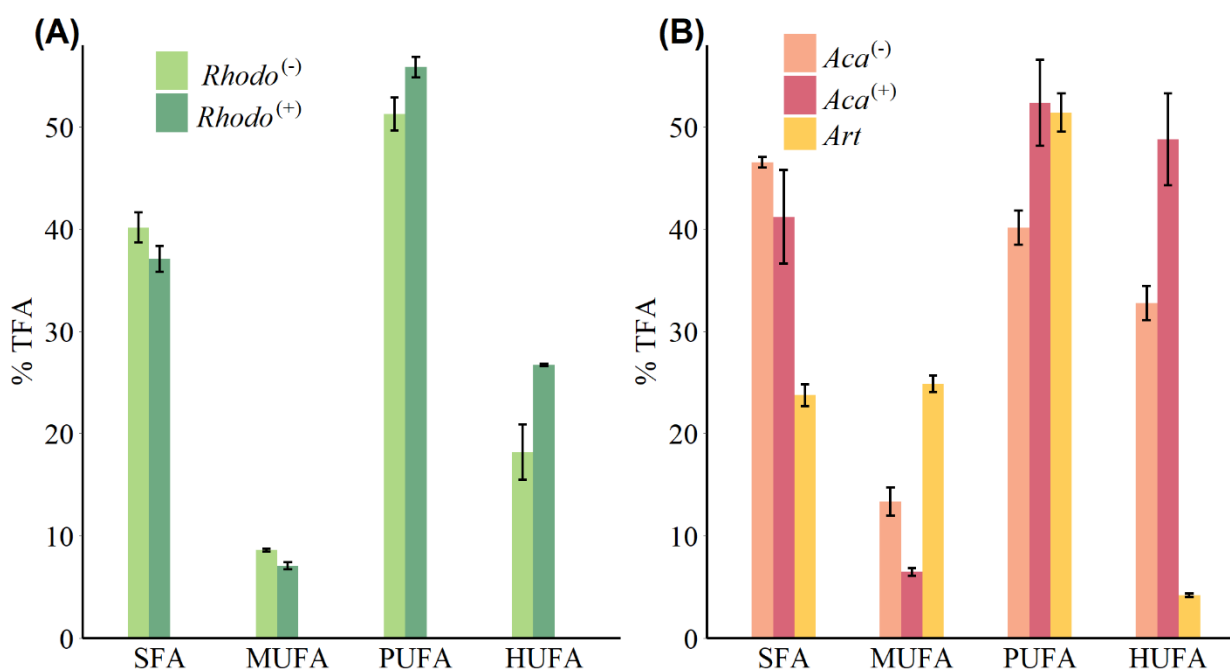


Fig. 2.1 FAs groups composition of phytoplankton (A) and zooplankton (B) (mean \pm SE). *Rhodo*⁽⁻⁾: *R. baltica* cultured in lacking thiamin medium; *Rhodo*⁽⁺⁾: *R. baltica* cultured in supplied thiamin medium; *Aca*⁽⁻⁾: *A. tonsa* fed with *Rhodo*⁽⁻⁾; *Aca*⁽⁺⁾: *A. tonsa* fed with *Rhodo*⁽⁺⁾; *Art*: newly hatched *A. salina* nauplii.

2.3.2 Following FA components along different trophic levels

The PERMANOVA test showed that FA components and FA groups from polyps were significantly different among the three food quality treatments (Table 2.2, Fig. 2.2). As showed above, thiamin supplied phytoplankton treatments contributed a higher HUFA content, especially

EPA and DHA, which could be tracked at the next trophic level in the experiment. *Rhodo*⁽⁻⁾ contained less DHA compare to *Rhodo*⁽⁺⁾. Alterations in the share of DHA were most pronounced

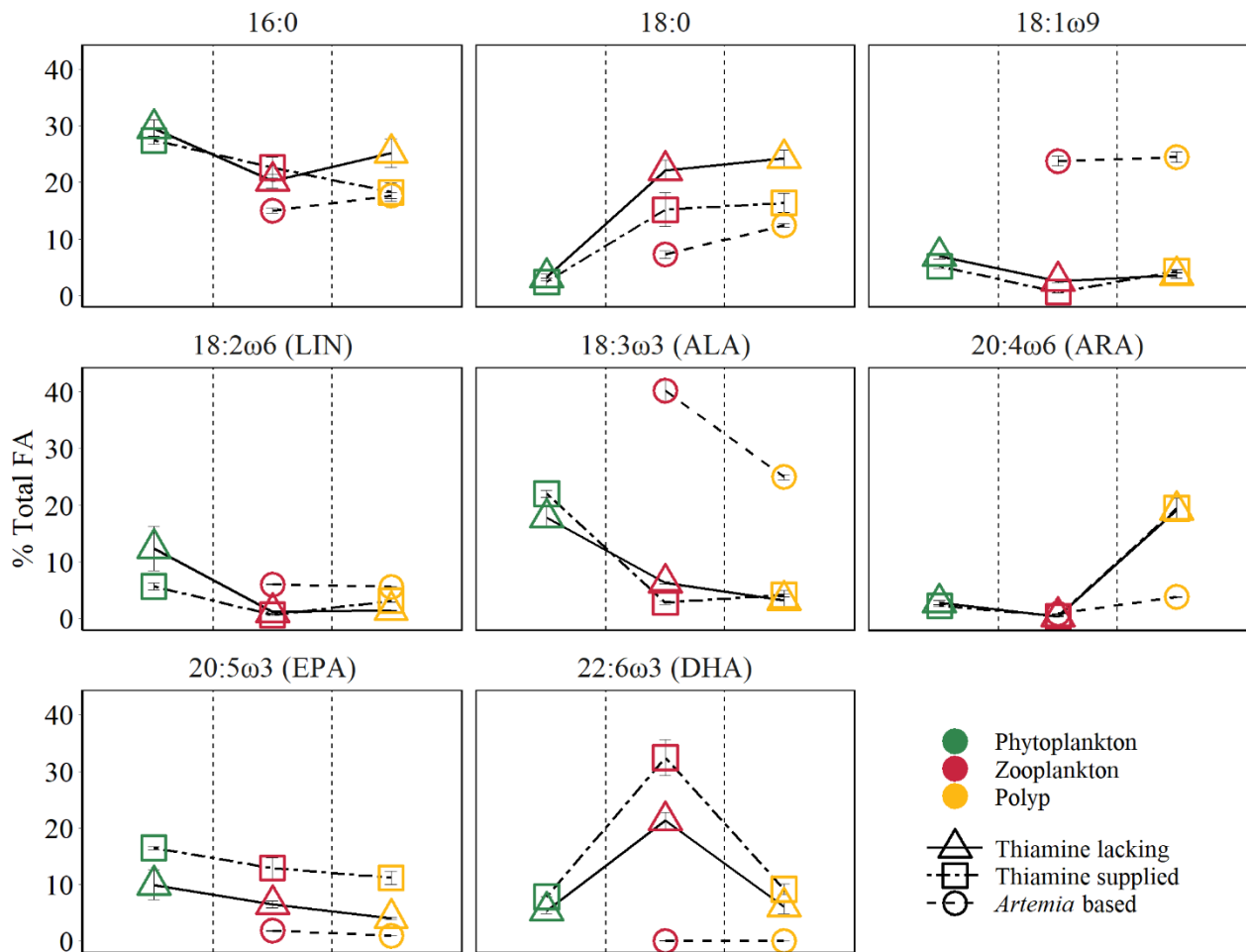


Fig. 2.2 Main FA composition of different trophic levels (mean \pm SE). The points colors denote different trophic levels, the points shapes denote different treatments.

in *A. tonsa*, following the same pattern as their food. DHA in polyps, however, was not that significantly different (Table 2.1). On the other hand, the differences in EPA were not significant in two phytoplankton, but significantly different in copepod and polyps (Table 2.1, Fig. 2.2). *Aca*⁽⁻⁾ contained less EPA than *Aca*⁽⁺⁾, and similarly, $\text{pol}_{(\text{Aca}^-)}$ contained less EPA than $\text{pol}_{(\text{Aca}^+)}$. Moreover, $\text{pol}_{(\text{Aca}^-)}$ contained more 18:0, but less LIN than $\text{pol}_{(\text{Aca}^+)}$. In particular, Fig. 2.2 shows that the relatively high levels of MUFA and PUFA in *Art* which were also mirrored in $\text{pol}_{(\text{Art})}$ were due to the extremely high levels of 18:1 ω 9 and ALA, respectively.

Following trophic levels to compare the relative FAs contents among treatments, the differences seemed to be also component-specific (Table 2.1, Fig. 2.2). For example, $Aca^{(-)}$ and $Aca^{(+)}$ had lower 16:0 but higher 18:0 than their food. These two SFAs contents were not significantly different from zooplankton to polyps, except those increased from *Art* to $pol_{(Art)}$ (Table 2.1, Fig. 2.2). In addition, all unsaturated C₁₈-FAs decreased from phytoplankton to zooplankton, either slightly (18:1 ω 9), moderately (LIN) or sharply (ALA), and their contents were also similar from zooplankton to polyps, with exception of ALA which decreased significantly from *Art* to $pol_{(Art)}$ (Table 2.1, Fig. 2.2). Interestingly, ARA content was low in phytoplankton and zooplankton, it was obviously elevated in polyps, even for $pol_{(Art)}$. EPA content decreased smoothly along food chain, while DHA content was significantly high in copepod treatments than their prey and predators. *Art* and $pol_{(Art)}$ contained extremely low EPA and DHA (Table 2.1, Fig. 2.2).

2.3.3 FA composition of polyps under different temperature and food conditions

The FA composition of polyps was significantly affected by temperature, prey FA composition and food availability (Table 2.3, Fig. 2.3). Increasing temperature led to high level of SFA which consequently caused relatively lower levels of unsaturated FAs (UFA, i.e., MUFA, PUFA, HUFA) (Table 2.3, Fig. 2.3). However, this effect was not very strong for those polyps which had a low FA content anyway, e.g., for MUFA in $pol_{(Aca^{-})}$ and $pol_{(Aca^{+})}$, and HUFA in $pol_{(Art)}$. Food type also had effects on FA composition of polyps. The FA composition of $pol_{(Art)}$ were significantly different from that of $pol_{(Aca^{-})}$ and $pol_{(Aca^{+})}$, while the latter two treatments had a similar FA groups composition (Table 2.3, Fig. 2.3). Interestingly, when offered prey at higher abundance, polyps had a lower SFA content, but higher UFA content (Table 2.3, Fig. 2.3).

Interaction effects of these three factors dependent on the FA groups. For example, the SFA content of $pol_{(Art)}$ were significant lower than $pol_{(Aca^{-})}$ (ANOVA, $F_{(1,4)} = 60.6$, $P < 0.001$) and $pol_{(Aca^{+})}$ (ANOVA, $F_{(1,4)} = 20$, $P < 0.001$) at low temperature, but similar at the highest temperature (ANOVA, $F_{(1,4)} = 2.5$, $P = 0.2$ and $F_{(1,4)} = 2.1$, $P = 0.2$). Overall, the relative HUFA content in polyps was affected by the interaction of temperature-quantity and quality-quantity. No effect of temperature-prey FA composition and their three-way interactions could be detected (Table 2.3; Fig. 2.3). In particular, the HUFA content of polyps cultured at 20 °C, seems to be similarly affected by either medium concentration of food rich in HUFA ($Aca^{(+)}$) or by high food concentration of moderate HUFA content food ($Aca^{(-)}$) (ANOVA, $F_{(1,4)} = 1.45$, $P = 0.3$). Likewise,

Table 2.1. FA composition (% total FA, mean \pm sd) of organisms from three trophic levels at 20 °C treatments. Within trophic level, not sharing the same superscript letters representing FA contents significantly different ($P < 0.05$, in bold face), those items with two letters are compare with the first and second treatment, respectively. (Σ SFA: sum up 14:0, 16:0, 18:0, 20:0, 22:0, 24:0; Σ MUFA: sum up 18:1 ω 9, 20:1 ω 9, 22:1 ω 9, 24:1 ω 9; Σ PUFA: sum up LIN, ALA, ARA, 20:3 ω 3, EPA, DHA; Σ HUFA: subset of PUFA, sum up ARA, 20:3 ω 3, EPA, DHA.)

Fatty acids (%)	Phytoplankton		Zooplankton			Polyps		
	<i>Rhodo</i> ⁽⁻⁾	<i>Rhodo</i> ⁽⁺⁾	<i>Aca</i> ⁽⁻⁾	<i>Aca</i> ⁽⁺⁾	<i>Art</i>	Pol _(Aca-)	Pol _(Aca+)	Pol _(Art)
16:0	29.6 (2.5) ^a	27.4 (1.3) ^a	20.2 (2.1) ^a	22.6 (3.2) ^a	15.0 (0.8)^b	25.2 (4.4)^a	18.3 (2.9) ^a	17.7 (0.9)^{ba}
18:0	3.2 (1.0) ^a	2.4 (1.2) ^a	22.1 (3.1)^a	15.2 (5.1) ^a	7.2 (1.1)^{ba}	24.3 (2.4)^a	16.4 (2.9) ^b	12.5 (0.5)^{cb}
Σ SFA	40.2 (2.5) ^a	37.1 (2.2) ^a	46.5 (0.9) ^a	41.2 (7.9) ^a	23.8 (1.9)^b	53.5 (6.2)^a	37.7 (6.1) ^b	33.1 (1.)^{cb}
18:1 ω 9	7.0 (0.9)^a	5.2 (0.7)^b	2.6 (0.70) ^a	0.6 (0.3) ^a	23.8 (1.5)^b	3.6 (1.0) ^a	4.3 (0.5) ^a	24.5 (1.6)^b
Σ MUFA	8.6 (0.3)^a	7.1 (0.6)^b	13.4 (2.4)^a	6.5 (0.7)^b	24.9 (1.4)^c	9.1 (3.1) ^a	11.1 (6.1) ^a	27.8 (1.8)^b
18:2 ω 6 (LIN)	12.4 (6.8) ^a	5.7 (1.0) ^a	1.1 (0.3) ^a	0.6 (0.2) ^a	6.0 (0.1)^b	1.4 (0.1)^a	3.1 (0.5)^b	5.6 (0.1)^c
18:3 ω 3 (ALA)	17.8 (3.2) ^a	22.0 (1.1) ^a	6.3 (0.3) ^a	2.8 (0.5) ^a	40.3 (3.5)^b	3.2 (2.9) ^a	4.1 (0.5) ^a	25.0 (0.8)^b
20:4 ω 6 (ARA)	2.8 (0.6) ^a	2.23 (0.2) ^a	0.3 (0.1) ^a	0.4 (0.2) ^a	0.8 (0.1)^b	19.2 (3.6) ^a	19.4 (3.0) ^a	3.8 (0.1)^b
20:5 ω 3 (EPA)	10.0 (4.5) ^a	16.5 (0.5) ^a	6.5 (1.1)^a	12.9 (3.2) ^b	1.8 (0.1)^{cb}	4.1 (0.3)^a	11.2 (2.1)^b	0.9 (0.02)^c
22:6 ω 3 (DHA)	5.3 (0.9)^a	7.9 (0.1)^b	21.3 (2.6)^a	32.4 (5.6)^b	0.1 (0.04)^c	6.1 (2.1) ^a	9.2 (1.6) ^a	0.03 (0.1)^b
Σ PUFA	51.3 (2.8) ^a	55.8 (1.7) ^a	40.1 (2.9)^a	52.3 (7.3) ^a	51.4 (3.2)^{ba}	37.4 (3.8) ^a	51.3 (6.2)^b	39.2 (0.8)^{ac}
Σ HUFA	18.2 (4.7)^a	26.7 (0.2)^b	32.8 (2.9)^a	48.8 (7.8)^b	4.2 (0.3)^c	32.1 (2.2)^a	42.4 (3.3)^b	7.8 (0.1)^c

Table 2.2. Bray-Curtis distances based Non-parametric PERMANOVA and SIMPER test for assemblages of polyps' FA composition. The five most contributions of FA component (more than 70 %) to the differences of FA components composition and all FA groups were listed from SIMPER test results.

Pair-wise comparison	FA components	Contributions %	PERMANOVA test	FA groups	Contributions %	PERMANOVA test
Pol _(Aca-) - Pol _(Aca+)	18.0	18.89	<i>F</i> = 34.96, <i>df</i> = 2, <i>R</i> ² = 0.92, <i>P</i> < 0.01	SFA	48.64	<i>F</i> = 16.98, <i>df</i> = 2, <i>R</i> ² = 0.85, <i>P</i> < 0.01
	20.5ω3	17.09				
	16.0	16.54		MUFA	8.85	
	20.4ω6	7.69				
	22.6ω3	7.46		PUFA	42.51	
	sum	67.67				
Pol _(Aca-) - Pol _(Art)	18.3ω3	21.90		SFA	49.06	
	18.1ω9	21.06				
	20.4ω6	15.50		MUFA	44.82	
	18.0	11.92				
	16.0	7.53		PUFA	6.12	
	sum	77.91				
Pol _(Aca+) - Pol _(Art)	18.3ω3	22.43		SFA	14.72	
	18.1ω9	21.67				
	20.4ω6	16.84		MUFA	49.48	
	20.5ω3	11.05				
	22.6ω3	9.85		PUFA	35.80	
	sum	81.84				

Table 2.3. Beta regression coefficients of FA groups composition of polyps under temperature, food quality and food quantity effects. Significant results ($P < 0.05$) are written in bold face.

Response	Covariate	Estimate	Standard error	Z	P
SFA	Mean submodel (logit link)				
SFA ~ temperature + quality + quantity + temperature: quantity + quality: quantity temperature (AIC = -194.66)	intercept	-0.477	0.181	-2.638	0.008
	temperature	0.037	0.010	3.644	<0.001
	qualityPol _(Aca+)	0.015	0.110	0.139	0.890
	qualityPol _(Art)	-0.645	0.106	-6.090	<0.001
	quantityMedium	-0.192	0.259	-0.740	0.459
	quantityHigh	-0.727	0.261	-2.781	0.005
	temperature:quantityMedium	0.020	0.015	1.332	0.183
	temperature:quantityHigh	0.032	0.015	2.161	0.031
	qualityPol _(Aca+) :quantityMedium	-0.380	0.159	-2.392	0.017
	qualityPol _(Art) :quantityMedium	-0.418	0.155	-2.697	0.007
	qualityPol _(Aca+) :quantityHigh	-0.440	0.159	-2.771	0.006
	qualityPol _(Art) :quantityHigh	-0.293	0.154	-1.907	0.057
	Precesion submodel (log link)				
	intercept	6.797	0.540	12.586	<0.001
	temperature	0.142	0.027	-5.264	<0.001
MUFA	Mean submodel (logit link)				
MUFA ~ temperature + quality + quantity + quality: quantity temperature (AIC = -339.35)	intercept	-1.805	0.115	-15.711	<0.001
	temperature	-0.009	0.005	-1.822	0.069
	qualityPol _(Aca+)	-0.146	0.109	-1.335	0.182
	qualityPol _(Art)	0.693	0.094	7.373	<0.001
	quantityMedium	-0.185	0.115	-1.607	0.108
	quantityHigh	-0.491	0.120	-4.110	<0.001
	qualityPol _(Aca+) :quantityMedium	0.224	0.159	1.409	0.159

Table 2.3 Continued

	qualityPol _(Art) :quantityMedium	0.316	0.138	2.286	0.022
	qualityPol _(Aca+) :quantityHigh	0.339	0.167	2.038	0.042
	qualityPol _(Art) :quantityHigh	0.779	0.141	5.545	<0.001
	Precesion submodel (log link)				
	intercept	6.780	0.544	12.460	<0.001
	temperature	-0.087	0.027	-3.040	0.001
PUFA	Mean submodel (logit link)				
	intercept	-0.168	0.189	-0.888	0.374
	temperature	-0.002	0.011	-2.686	0.007
PUFA ~ temperature + quality +	qualityPol _(Aca+)	0.076	0.129	0.589	0.556
quantity + temperature: quantity	qualityPol _(Art)	0.263	0.109	2.506	0.012
+ quality: quantity temperature	quantityMedium	0.316	0.255	1.237	0.216
+ quality + quantity	quantityHigh	1.087	0.224	4.858	<0.001
(AIC = -204.06)	temperature:quantityMedium	-0.022	0.015	-1.415	0.157
	temperature:quantityHigh	-0.042	0.013	-3.114	0.002
	qualityPol _(Aca+) :quantityMedium	0.242	0.176	1.413	0.158
	qualityPol _(Art) :quantityMedium	0.194	0.141	1.375	0.169
	qualityPol _(Aca+) :quantityHigh	0.283	0.152	1.859	0.063
	qualityPol _(Art) :quantityHigh	-0.221	0.124	-1.792	0.073
	Precesion submodel (log link)				
	intercept	7.301	0.665	10.975	<0.001
	temperature	-0.145	0.028	-5.175	<0.001
	qualityPol _(Aca+)	-1.093	0.377	-2.897	0.004
	qualityPol _(Art)	-0.786	0.399	-1.967	0.049
	quantityMedium	0.265	0.380	0.696	0.486
	quantityHigh	0.914	0.378	2.241	0.016

Table 2.3 Continued

HUFA	Mean submodel (logit link)				
	intercept	-0.437	0.203	-2.156	0.031
HUFA ~ temperature + quality +	temperature	-0.038	0.011	-3.296	0.001
quantity + temperature: quantity	qualityPol _(Aca+)	0.048	0.190	0.405	0.686
+ quality: quantity temperature	qualityPol _(Art)	-0.872	0.128	-6.812	<0.001
(AIC = -239.49)	quantityMedium	0.374	0.287	1.304	0.192
	quantityHigh	1.107	0.281	3.944	<0.001
	temperature:quantityMedium	-0.021	0.016	-1.261	0.207
	temperature:quantityHigh	-0.034	0.016	-2.143	0.032
	qualityPol _(Aca+) :quantityMedium	0.117	0.169	0.691	0.490
	qualityPol _(Art) :quantityMedium	-0.125	0.185	-0.678	0.498
	qualityPol _(Aca+) :quantityHigh	0.213	0.161	1.322	0.186
	qualityPol _(Art) :quantityHigh	-0.864	0.183	-4.730	<0.001
	Precesion submodel (log link)				
	intercept	6.571	0.541	12.147	<0.001
	temperature	-0.122	0.027	-4.523	<0.001

low concentrations of HUFA-rich food ($Aca^{(+)}$) contributed more than high concentrations of HUFA-poor food (Art) (ANOVA, $F_{(1,4)} = 100.6$, $P < 0.001$).

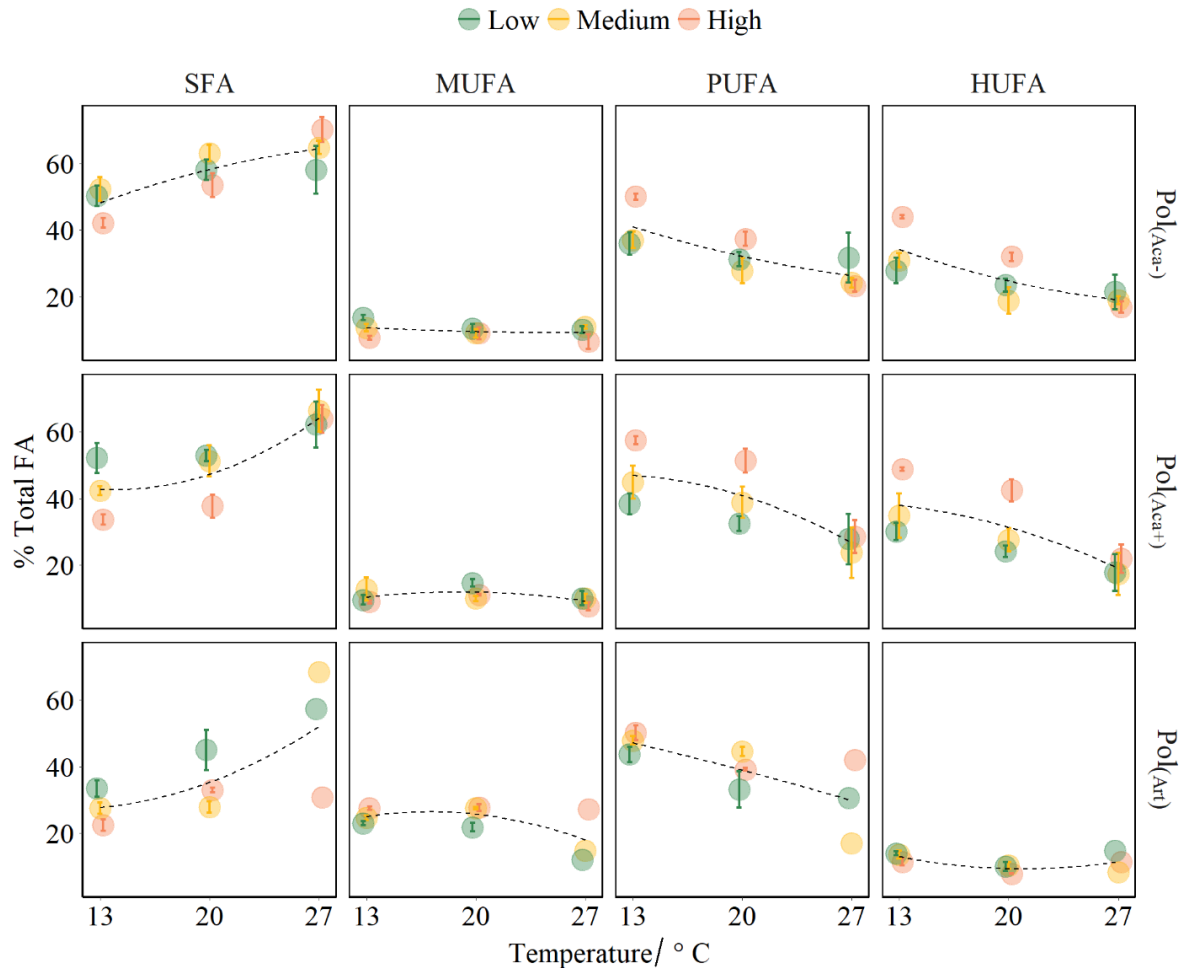


Fig. 2.3. FA groups of polyps affected by temperature, food quality and food quantity treatments (mean \pm SE). The points colors denote food different concentrations. Fitted curves using method “loess” (span = 2) from R package ggplot2. Pol_(Aca⁻): polyps fed with $Aca^{(-)}$; Pol_(Aca⁺): polyps fed with $Aca^{(+)}$; Pol_(Art): polyps fed with Art .

2.4 Discussion

Jellyfish are drawing increasingly attentions because of a perceived incidence of mass developments and of their potential capacity of driving food webs structure (West et al. 2009) and their importance in global biogeochemical cycles (Vargas et al. 2002; Lebrato et al. 2013). Yet little empirical studies can be found in the literature on the dynamic of essential or semi-essential biomolecules (e.g., FAs) in gelatinous zooplankton and their transfer along food chains dominated by jellyfish. Our study provided the first insights into the dynamic of critical biochemical substances such as vitamin B₁ and ω 3-HUFA in a system encompassing a common phytoplankton,

zooplankton, and jellyfish.

2.4.1 FA composition of phytoplankton and zooplankton

Our results could clearly show that the provision of phytoplankton *R. baltica* with thiamin (vitamin B₁) had a significant effect on its FA composition, and especially HUFA content. Differences between both thiamin treatments, suggest that the conversion from ALA to DHA is dependent on thiamin provision in this VB₁ auxotrophic phytoplankton. Thiamin deficiency resulted in high MUFA and low HUFA relative content in *R. baltica*. It is known that thiamin plays a critical role in energy metabolism (Lonsdale 2006). Thiamin diphosphate (TPP) which serves as a cofactor of enzymatic reactions to form acetyl CoA in glucose catabolism is the link between thiamin metabolism and FA synthesis (Lonsdale 2006). Acetyl CoA is a main source to biosynthesize FAs (Wakil 1960). Thus, an adequate supply of thiamin can improve an organisms' capacity of synthesizing FAs (Boxer and Stetten Jr 1944). For example, in a medical trial, FA synthesis of thiamin-deficient treatments was only 13% of trials receiving thiamin (Volpe and Marasa 1978). However, in aquatic sciences, the association between thiamin supply and the level of FA synthesis has not been well studied yet. Keeping in mind that *ca.* 22% of eukaryotic algae are thiamin auxotroph and that HUFA may limit secondary production, our finding may have important implications in critical roles of regulating both food web structure and dynamics due to the role of phytoplankton as primary producer, and zooplankton as link to higher trophic levels (Arrigo 2005; Finkel et al. 2009; Steinberg and Landry 2017). The level of nutrient supply (i.e., N, P, thiamin etc.) and synthesized biochemical molecules (i.e., fatty acids, amino acids, etc.) determines phytoplankton abundance and prey quality for zooplankton. Effects of zooplankton are potentially transmitted up to higher trophic levels and control their performances indirectly (i.e., growth rate, reproduction, etc.). Therefore, there are abundant potentials for further progress in determining the importance of vitamins in general, and thiamin, in particular, to shape marine food web under future ocean scenarios.

Moreover, when feeding on *Rhodo*⁽⁻⁾, *Aca*⁽⁻⁾ also had strongly reduced DHA and EPA contents. Thus, the relative HUFA content could be followed up to the next trophic level, i.e., the common herbivorous zooplankton *A. tonsa*, was highly diet dependent. However, also contrasting patterns were found for other FA components. For example, *Aca*⁽⁻⁾ and *Aca*⁽⁺⁾ had lower 16:0 but higher 18:0 than their food, indicating that they had likely elongated 16:0 to 18:0. Furthermore, in both treatments, relative DHA contents in *A. tonsa* increased relative to levels in their food while ALA

levels decreased, indicating some conversion from ALA via EPA to DHA as shown by Ridgway and McLeod (2015). From the differences between both thiamin treatments, we suggest that the conversion from ALA to DHA seems to be dependent on thiamin provision in the B₁ auxotrophic phytoplankton. However, for a more mechanistic explanation on how certain FA components are regulated by thiamin supply, further studies are needed which specifically should explore the association of thiamin with HUFA. This is not only critical for understanding FA pathways but also their transfer in food webs with practical implications for aquaculture (Woodbury 1943). We also emphasize the great difference in the DHA content between *A. tonsa* and *A. salina*. The latter is an often-used food source for young fish in aquaculture settings. Our finding suggests that natural food, even when co-limited by vitamin B₁, is of higher food quality than commercially used *A. salina* food supply.

2.4.2 FA composition of polyps affected by dietary FA

FA composition of polyps mostly reflected that of their diet, except for a much lower DHA and a higher relative ARA content in polyps than in *A. tonsa*. DHA could have been converted to ARA, but this would imply a biochemical pathway not related to the ALA-EPA pathway (Bell and Tocher 2009), but transforming an ω 3-HUFA into an ω 6-HUFA. In contrast, it seems that ω 3-HUFA (EPA and DHA) in polyps were retrieved from the diet, which is most probably true for the other specific FAs, such as 16:0, 18:0, 18:1 ω 9, and LIN. A lower relative ALA content of pol_(Art) compared to their diet may indicate that some of the ALA provided by *Art* were converted by the polyp, but not to ω 3-HUFA as those levels were stable and below the levels when feeding on copepod. However, polyps feeding on ALA-rich *Art* had still a manifold higher ALA content themselves compared to polyps feeding on both copepod diet, indicating low conversion in jellyfish polyps.

In our study, the ω 6-HUFA ARA was found to be a major HUFA component of polyps, which may have implications for the jellyfish life history and food web processes. Unlike the ω 3-HUFA EPA and DHA, for which beneficial effects to resist environmental stress in fish (Sargent et al. 1999), enhance growth and reproduction in zooplankton (Sundbom and Vrede 1997; Abrusán et al. 2007; Müller-Navarra 2008), the functional importance of ARA in aquatic food webs is less documented with exceptions of few studies from fishery (Yuan et al. 2015). ARA concentration in fish tissue seems to be diet dependent, and functionally regulating fish larval growth, survival,

immune function and resistance to stress (reviewed by Bell and Sargent, 2003). For example, recent studies showed that an adequate ARA supply (independently or combined with DHA) were positively associated with survival and growth of fish larvae (Yuan et al. 2015; Rombenso et al. 2016). Therefore, dietary ARA-deficiency might impact the nutritional state and performances of fish larvae in the field. If ARA is similarly important for the performance of polyps (i.e., survival, growth, and asexual reproduction) this may determine pelagic dynamics of medusae retrieved by strobilation (Lucas et al. 2012). The emerging question is whether this ability of biosynthesizing ω -6 in polyps will be beneficial in the competition with other benthic organisms, and for the medusae stage competing with fish larvae for common prey, making them resistant to nutritional imbalance and cope with insufficient food conditions. Above that, ARA or the ARA/DHA ratio may serve as a trophic marker for cnidarians when studying trophic interactions between polyps and their predators, for example, in nudibranchs.

2.4.3 FA composition of polyps affected by temperature and food conditions

In line with the membrane fluidity concept (Singer and Nicolson 1972; Pruitt 1990), polyps had a high level of PUFA at the lower experimental temperatures, representing autumn/spring conditions, while containing more SFA at the higher temperature, reflecting a heat wave scenario. Thus, low-temperature-dependent retention of PUFA might be an adaptation of polyps to maintain their physiological activities while overwintering. In contrast, heat waves lead to enhanced SFA in cellular lipids. Higher melting points of SFA (Knothe and Dunn 2009) may help organisms to resist cellular heat injury. Thus, cnidarians have the ability to control their cellular lipids' saturation degree, which is beneficial for the acclimatization to temperature shifts, and may ensure the plasticity of jellyfish polyps' life history traits.

Our results support the general concept that organisms can adapt to temperature shifts by altering the UFA: SFA ratio. For example, phytoplankton were found to increase the level of lipid unsaturation significantly when temperature decreased (Thompson 1996; Jiang and Gao 2004). This pattern was confirmed as well as for zooplankton (Werbrouck et al. 2016) and fish (Laurel et al. 2012). Above that, our study addresses that the UFA: SFA regulation in polyps is connected with the FAs obtained from the food; either of high nutritional value at low concentration or at high rations to compensate for a nutritional inferior quality. Comparing HUFA in polyps feeding on *A. tonsa* with those feeding on *A. salina* may reveal *A. salina* to be inferior to *A. tonsa*, especially at low temperatures because of the lower HUFA content. In addition, *A. tonsa* is

dominating zooplankton in most coastal waters and it fulfills the polyps essential FAs requirements. The capacities of the polyp to biochemically regulate the degree of unsaturation, enable seasonal adaption and show the plasticity of a potentially important life history trait for jellyfish polyps. As a next step, it would be essential to know whether HUFA are transferred to jellyfish's medusae stage as an important link to the pelagic food web.

2.5 Conclusions

In this study, we followed the FA composition in a three-level food chain encompassing the common marine plankton *R. baltica* (as primary producer) and *A. tonsa* (as a primary consumer), and the polyps of jellyfish *A. aurita*. We found vitamin B₁ induced alterations of the FA, especially HUFA composition at the primary producer level being transferred to the primary consumer level. Further up the food chain, HUFA of jellyfish polyps were influenced by the diet with similar relative levels for EPA, but strongly reduced DHA levels when feeding on *A. tonsa*. In contrast, ARA levels increased in the expense of DHA, making a conversion likely. However, this would biochemically imply a conversion of a ω 3-HUFA to a ω 6-HUFA in jellyfish polyps. Whether ARA can even be used as a potentially FATM for jellyfish needs to be clarified in the future. Comparing FA composition of *A. aurita* polyps feeding on *A. tonsa* with those feeding on *A. salina*, revealed that *A. salina* was inferior because of a much lower HUFA content than in *A. tonsa*. As the high relative content of C₁₈-PUFA in *A. salina* was mirrored in the polyps feeding on them, it suggests that conversion along the ω 3 route is only minor in jellyfish polyps. In addition, our results on jellyfish polyps towards temperature changes are consistent with other studies which found low temperature induced high content of UFA, while high temperature is connected with an elevation of SFA. We could show that the degree of HUFA increase at decreasing temperatures is connected to the dietary provision with HUFA, Therefore, more efforts are needed to investigate the functions of FAs and other biomolecules related to jellyfish life history traits, and including the pelagic medusae stage.

Chapter 3 Food quality matters: interplay among food quality, food quantity and temperature affecting life history traits of *Aurelia aurita* (Cnidaria: Scyphozoa) polyps

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Jamileh Javidpour ^{1,4}

Abstract

Understanding the interaction between organisms' life history traits and environmental factors is an essential task in ecology. In spite of the increasing appreciation of jellyfish as an important component in marine ecosystem, there are still considerable gaps in understanding how the phase transition from the benthic polyp to the pelagic medusa stage is influenced by multiple environmental factors, including nutrition. To investigate survival, growth, and phase transition of *Aurelia aurita* polyps, we designed a factorial experiment manipulating food quantity (20 $\mu\text{g C}$, 5 $\mu\text{g C}$ and 1.5 $\mu\text{g C polyp}^{-1}$ every other day), food quality (*Artemia salina* and two dietary manipulated *Acartia tonsa*), and temperature (13 °C, 20 °C, and 27 °C). Temperature was the key factor determining phase transition of polyps and negatively affecting their survival rate and growth at 27°C, which reflected a summer heatwave scenario. Furthermore, at polyps' optimum tolerance temperature (20°C) in our study, budding reproduction benefits from high food concentrations. Interestingly, polyps fed with food containing high level highly unsaturated fatty acid (HUFA) were able to compensate for physiological stress caused by the extreme temperature, and could enhance budding reproduction at optimum temperature. Moreover, benthic-pelagic

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coupling (strobilation) was determined by temperature but affected significantly by food conditions. Mild temperature together with optimum food conditions contributes to inducing more polyps, which may potentially bring about great ephyrae recruitments during overwintering. In contrast, heatwave events can potentially regulate plankton community structure accompanied by changes of nutritional conditions of primary and secondary producers and thus, negatively affect the population dynamics of polyps. We suggest a novel polyp tolerance curve, which can help to understand jellyfish population dynamics in different seasons and ecosystems. This sets up a baseline for understanding how anticipated global warming and food conditions may affect the population size of benthic polyps and consequently pelagic medusae.

Keywords: life history, multiple stressors, asexual reproduction, phase transition, tolerance curve, jellyfish

3.1 Introduction

Dense aggregations and population outbreaks of jellyfish have been reported from several coastal areas (Kawahara et al. 2006; Daryanabard and Dawson 2008; Licandro et al. 2010), which may cause environmental and socio-economic problems (Purcell 2012; Boero 2013). Most of the reports on jellyfish bloom refer to the class Scyphozoa. In general, this group exhibits a metagenic life cycle (Arai 1997), involving pelagic stages (ephyra, medusa, and planula) and benthic stages (polyp, strobila, and podocyst). Take the moon jelly *Aurelia aurita* for example, matured medusae release planula larvae, which then settle on hard substrates and develop into polyps. Benthic polyps can expand the population size *via* budding reproduction and produce pelagic juvenile medusae (ephyrae) through strobilation. Polyp population size, strobilation rate and ephyra production of each strobila can directly contribute to medusa recruitment. Recently, benthic polyp stage of scyphozoans has attracted increasing attentions (reviewed by Lucas et al., 2012), as their recruitment success is considered to play a critical role in massive population occurrence of medusae in summer (Gröndahl 1988a; Lucas 2001). Moreover, population size of polyp varies greatly with changing environments (Liu et al. 2009; Purcell et al. 2009; Han and Uye 2010). Among a variety of environmental factors, temperature and food conditions have been revealed to be principle factors determining polyps' fitness and asexual reproduction (Willcox et al. 2007; Purcell et al. 2012).

In the literature on polyp ecology, the relative importance of food conditions has been subject to considerable discussion (Han and Uye 2010; Wang et al. 2015a). However, most of the experiments preferentially used *Artemia sp.* as the major food source (e.g., Feng et al. , 2015; Han and Uye, 2010; Wang et al. , 2015), which does not reflect the natural food type. For example, the biochemical composition of prey, e.g., vitamin content (such as thiamin) and fatty acids (FAs), as food quality determinants, have received little attention in jellyfish polyp studies so far. Thiamin is involved in several metabolic pathways, e.g. as a cofactor in production of Acetyl Coenzyme A, which is in turn essential in carbohydrate metabolism and FAs synthesis (Lonsdale 2006; Manzetti et al. 2014). In contrast, the impact of thiamin on life history traits and biochemical cycles has been largely overlooked (Giovannoni 2012). In addition, some essential ω 3 polyunsaturated fatty acids, including the highly unsaturated fatty acids (HUFA) eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), play important roles for many aquatic organisms, such as sustaining membrane fluidity or serving as precursors for tissue hormones (Müller-Navarra 2008). Thus, HUFA play a critical role that enable organisms to achieve optimal health and reproduction (Arts et al. 2009). Moreover, HUFA as essential dietary components could flow in food webs *via* trophic transfer (Brett and Müller-Navarra 1997). The ecological implications of using HUFA content to indicate overall food quality, which in turn is used to estimate proper functioning drivers of ecosystem stability, encompass two aspects. First, the biosynthesis ability of HUFA and its transfer efficiency to higher trophic levels vary in different primary producers (Taipale et al. 2013; Strandberg et al. 2015). Second, HUFA content of the same species has seasonal and spatial shifts regulated by temperature and stoichiometry (Brett et al. 2000; Hartwich et al. 2012; De Moura et al. 2016). Thus, alterations of HUFA in primary producers will consequently alter herbivores' growth and reproduction *via* changing community structure and bio-chemicals composition (Jónasdóttir 1994; Müller-Navarra and Huntley 2013). The same processes will potentially affect development at higher trophic levels, such as fishes (e.g., Sargent et al., 2002).

The objective of the present study was to address knowledge gaps in the ecological role of food quality involved in life history strategy of scyphozoans, especially in their benthic life stages. Furthermore, we studied the combined effects of food quality and food quantity under different temperature regimes on the overall outcome of benthic-pelagic coupling.

We hypothesized that higher food quality can 1) improve polyps' survival rates under extreme temperatures such as heatwaves; 2) contribute to larger individual size; and 3) affect budding reproduction and strobilation. To test these hypotheses, we designed a factorial feeding experiment on polyps of a cosmopolitan species, *A. aurita* (Linnaeus, 1758), under different temperature and food regimes, the latter differing in quality and in quantity.

3.2 Materials and methods

3.2.1 Polyp preparation

A. aurita polyps were obtained from permanent cultures of the Christian-Albrechts University, Kiel (Germany); they were originally collected from the North Sea population (Helgoland, Germany), and kept at 20 °C with a salinity of 30. Prior to the experiment, polyps were fed with newly hatched *A. salina* nauplii, and water was changed with filtered seawater (0.2 µm filter) twice a week. In preparation for the experiment, polyps were detached carefully from their substrate with forceps and were placed individually in each well (growth area: 8,87 cm², volume: 4 ml) of 6-well polycarbonate culture plates. To allow polyps to attach to the plates, they were kept in climate cabins at 20 °C for 5 days without any feeding or water exchange. Polyps were kept under dark conditions during both the acclimation time and the entire of the experiment, as light influences polyps' asexual reproduction (Custance 1964; Liu et al. 2009).

3.2.2 Temperature manipulation

The experiment consisted of three temperature levels, 13 °C, 20 °C, and 27 °C, ensured through temperature-controlled climate cabins. The temperatures 13 °C and 20 °C represented late autumn/early spring and common summer temperatures in the study area, respectively (Wiltshire and Manly 2004). The highest temperature, 27 °C, served as an unusual summer heatwave scenario (Meehl and Tebaldi 2004; Garrabou et al. 2009). Polyps were randomly distributed in climate cabins, and were acclimated by increasing or decreasing 1 °C d⁻¹ to the test temperatures. During the experiment, water was exchanged every second day with filtered and autoclaved North Sea water. After water exchange, polyps were fed with the respective prey items.

3.2.3 Food quality manipulation

Three types of food were chosen to perform this treatment: a) *Artemia salina* nauplii (thereafter as *Art*); b) copepodites of *Acartia tonsa* (thereafter as *Aca*⁽⁺⁾) that were fed with standard *Rhodomonas baltica* stock, in a culture medium modified after Provasoli (1963) (thereafter *Rhodo*⁽⁺⁾); and c) *A.*

tonsa (thereafter as *Aca*⁽⁻⁾) fed with *R. baltica* cultures that lacked thiamin (vitamin B₁) in their medium (thereafter *Rhodo*⁽⁻⁾). *R. baltica* were cultured at 20 °C and under 100 μmol photons m⁻² s⁻¹ light condition. To manipulate *A. tonsa*'s food quality as prey for polyps, newly hatched nauplii were cultured in separate buckets in a climate room under 20 °C, and were fed daily with the two types of algae *Rhodo*⁽⁺⁾ and *Rhodo*⁽⁻⁾, respectively. All food concentrations were adjusted to be above the food limitation level for this copepod species, i.e. > 600 μg C L⁻¹ (Kiørboe et al. 1985). Similar size of copepodites were collected for feeding polyps. Thus, in summary, the experiment consisted of three food quality treatments for polyps, i.e. polyps fed with *Art* (thereafter pol_(Art)), polyps fed with *Aca*⁽⁻⁾ (thereafter pol_(Aca-)), and polyps fed with *Aca*⁽⁺⁾ (thereafter pol_(Aca+)).

Thiamin analysis was conducted with a high-performance liquid chromatography (HPLC) according to the method by Pinto et al. (2002), with modifications according to Sylvander et al. (2013). FAs in the samples were analyzed as FA methyl esters (FAMES) using a gas chromatograph (GC; Thermo Fisher Scientific, Germany) described in detail by Chi et al. (2018).

3.2.4 Food quantity

For each food quality, three levels of high (20 μg C polyp⁻¹), medium (5 μg C polyp⁻¹) and low (1.5 μg C polyp⁻¹) food concentrations were offered every other day based on previous studies (Han and Uye 2010; Wang et al. 2015a). Detailed calculation regarding the number of individuals given per treatment is provided in Suppl. Table 1. The highest food concentration provided an excess food supply to polyps, and remaining food was removed during water exchange. The medium food concentration was representative of polyps' average food level, and the low food concentration represented starvation conditions. These food concentrations ensured that some food items were left over at high concentration, while all preys were consumed before the next feeding event at medium and low food concentrations.

Each combination of food quality, food quantity, and temperature involved 12 replicates. As polyps' strobilation was expected to occur at 13 °C, causing a loss of some individuals for the final assessments, we added 6 more replicates in both food quality and food quantity at 13°C, resulting in a total of 18 replications at this specific temperature, and leading to a total of n = 378. When all polyps had attached to the plates, their initial diameters (1.04 ± 0.26 mm) were measured under a microscope equipped with a camera and scaling system, and we started to feed and change water as described above. The experiment lasted for 30 days.

3.2.5 Data collection

Following each feeding time, polyps' status was checked. Those polyps had decomposed were recorded as dead and survival rates were calculated based on the number of vital polyps. The diameters of the polyps' cone-shaped calyces were measured every 6th day to denote somatic growth. To avoid disturbances on polyps, diameters were measured by taking photos before feeding and water exchange. An average of the maximum and minimum dimensions of the calyx was calculated if it was not round. Before each time feeding and water exchange, a total number of buds were counted. In our study, we refer to "buds" as individuals produced by mother polyps in the form of "polyp-to-polyp" (Schariti et al., 2014). To avoid any intraspecific competition, new buds produced during the treatments were recorded and removed from the original cultures. When signs of strobilation occurred, polyps were regarded as strobilae and were no longer included in calyx diameter measurements. Numbers of ephyrae released by each strobila were recorded as well.

3.2.6 Statistical methods

Data were checked for outliers, homogeneity, and collinearity in both response and explanatory variables before applying statistical models (Zuur et al. 2010). Generalized linear models (GLMs) were used to analyze response variables, namely survival rate, somatic growth, budding reproduction, and strobilation rate, separately. The explanatory variables, temperature, food quality, food quantity, and time (only for survival rate) were included in the GLMs, and treated as factorial variables. We first fitted GLMs regarding different response variables with all explanatory factors and their interactions, and then selected the optimum models by applying a stepwise backward selection method *via* an Akaike information criterion (AIC) index (Zuur et al. 2009). For the survival rate data, time was included in the GLM, taking a binomial family distribution into account. Somatic growth data were fitted with Gaussian family distribution. Because a relatively large number of polyps that were fed low food quantity did not produce buds, we treated budding reproduction data in two ways, first by modeling presence/absence data and fitting it with a binomial distribution, and secondly by taking the numbers of produced buds in the GLM, and fitting a Poisson distribution. Strobilation success occurred in different food treatments, so we modeled strobilation rate data by applying binomial family distribution in the GLM, while

ephyrae production of each strobila was described by mean \pm SD. Tukey's post-hoc test was applied when explanatory variables had a significant effect on responses.

All GLMs, data explorations, and data visualizations were performed using R software, version 3.3.3. (R Core Team, 2017).

3.3 Results

3.3.1 Meeting food quality assumptions

We analyzed the biochemical composition (i.e., thiamin and FA content) of phytoplankton and zooplankton. Thiamin contents were higher in *Rhodo*⁽⁺⁾ stock cultures (average 36.74 ± 4.86 pmol mg C⁻¹), than in *Rhodo*⁽⁻⁾ (15.33 ± 2.04 pmol mg C⁻¹, $F_{(1,4)} = 59.9$, $p < 0.005$), indicating that the food quality manipulation was successful. Thiamin levels also tended to be higher in *Aca*⁽⁺⁾ (60.02 ± 9.61 pmol mg C⁻¹) than *Aca*⁽⁻⁾ (45.27 ± 11.38 pmol mg C⁻¹), although not significantly different ($F_{(1,4)} = 2.82$, $p = 0.17$). On the other hand, the HUFA content in our study was not only significantly different between the two manipulated *R. baltica* (ANOVA, $F_{(1,4)} = 26.8$, $p < 0.01$), but also among the three types of zooplankton prey (ANOVA, $F_{(2,6)} = 64.6$, $p < 0.001$). For the detailed fatty acid composition of phytoplankton and zooplankton, please see the previous publication of Chi et al. (2018). In general, HUFA content was higher in *Rhodo*⁽⁺⁾ ($26.7 \pm 0.2\%$) and *Aca*⁽⁺⁾ ($48.8 \pm 7.8\%$), than in *Rhodo*⁽⁻⁾ ($18.2 \pm 4.7\%$) and *Aca*⁽⁻⁾ ($32.8 \pm 2.9\%$), while *Art* contained the least HUFA ($4.2 \pm 0.3\%$). Thus, the manipulations of three food types involving different HUFA content levels guaranteed different food quality for feeding polyps. The three food quality treatments in this experiment denote three HUFA content levels from low to high, i.e., HUFA levels of $Art < Aca^{(-)} < Aca^{(+)}$.

3.3.2 Survival

Polyp survival was affected significantly by experimental temperature, food quality, food quantity, experimental time, and the interaction of food quality and quantity (Table 3.1). Temperature was the main factor that determined survival rate of polyps. At low and intermediate temperatures, all polyps survived (100 %), independent of food quality or quantity. However, survival rate dropped at the highest temperature (27 °C), though it was interestingly food dependent (Fig. 3.1). In general, polyps fed low food concentration had a higher survival rate than those fed medium (Tukey's test, $z = -2.9$, $p = 0.01$) and high concentrations (Tukey's test, $z = -3.4$, $p = 0.002$), with no significant differences between high and medium concentrations (Tukey's test, $z = -0.5$, $p = 0.86$). $Pol_{(Art)}$ had

a lower rate of survival than $pol_{(Aca-)}$ (Tukey's test, $z = 3.1$, $p = 0.005$) and $pol_{(Aca+)}$ (Tukey's test, $z = 2.9$, $p = 0.009$). Survival rates were not significantly different between $pol_{(Aca-)}$ and $pol_{(Aca+)}$ (Tukey's test, $z = -0.5$, $p = 0.88$) over the experimental time. However, critical mortality at high temperature treatments occurred from the 12th experimental day onwards (Tukey's test, $z = -3.1$, $p = 0.015$). Surprisingly, the mortality rate in $pol_{(Aca-)}$ was somewhat lower (16.7%) than $pol_{(Aca+)}$ when fed at medium and high food concentration. At the end of this experiment, the lowest survival rate (8.3 %) occurred at 27 °C × high food concentration × $pol_{(Art)}$ treatment.

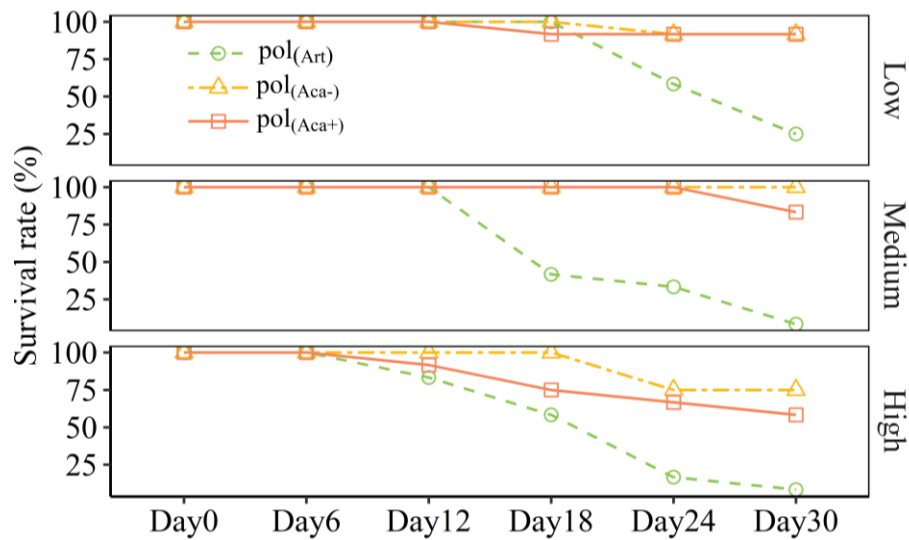


Fig. 3.1. Survival of *A. aurita* polyps (%) under different food regimes at high temperature (27 °C) during the time of the experiment. (Note: all polyps in different food regimes survived to 100% under 13 °C and 20 °C).

3.3.3 Somatic growth

Temperature had a negative effect on polyps' growth (Table 3.1, Fig. 3.2). Polyps cultured at high temperature grew to significantly smaller diameters (0.93 ± 0.25 mm) compared to those at medium (1.55 ± 0.33 mm, Tukey's test, $z = -4.7$, $p < 0.001$) and low temperature (1.81 ± 0.33 mm, Tukey's test, $z = -4.8$, $p < 0.001$). An overall significant effect of food quality on growth could be detected (Table 3.1). However, pair-wise comparisons between food quality treatments were not significantly different. Diameters of $pol_{(Aca+)}$ (1.52 ± 0.46 mm) and $pol_{(Art)}$ (1.70 ± 0.36 mm)

Table. 3.1. Statistical outputs from GLMs selected by a stepwise backward method on different functional responses and explanation variables. (the meanings of symbols used, ~ model formulae, × inclusion of main effects plus interactions between explanatory variables, + inclusion of an explanatory variable).

Functional Responses	Model	Family	Variables	Df	χ^2	P-value
Survival	survival ~ temperature + quality + quantity + time + quality × quantity (AIC = 290.1)	Binomial	temperature	2	245.9	< 0.001
			quality	2	75.1	< 0.001
			quantity	2	17.2	< 0.001
			time	5	174.6	< 0.001
			quality × quantity	4	11.6	0.02
Growth	diameter ~ temperature × quality × quantity (AIC = -45.2)	Gaussian	temperature	2	31.1	0.001
			quality	2	1.0	< 0.001
			quantity	2	11.6	< 0.001
			temperature × quality	4	1.2	< 0.001
			temperature × quantity	4	1.0	< 0.001
			quality × quantity	4	0.1	0.57
temperature × quality × quantity	8	1.1	< 0.01			
Budding	buds ~ temperature + quality + quantity + temperature × quality + temperature × quantity + quality × quantity (AIC = 1470.4)	Poisson	temperature	2	286.0	< 0.001
			quality	2	48.0	< 0.001
			quantity	2	431.9	< 0.001
			temperature × quality	4	13.4	< 0.01
			temperature × quantity	4	15.5	< 0.01
			quality × quantity	4	39.2	< 0.001
Strobilation	strobila ~ temperature + quality + quantity + quality × quantity (AIC = 137.4)	Binomial	temperature	2	74.2	< 0.001
			quality	2	13.8	< 0.01
			quantity	2	13.8	< 0.001
			quality × quantity	4	38.1	< 0.001

The statistically significant results ($P < 0.05$) are written in bold.

ultimately grew to similar sizes, while $\text{pol}_{(\text{Aca-})}$ grew to relatively smaller sizes (1.42 ± 0.48 mm); however, the size difference was not statistically significant. Food quantity had a positive effect on growth, as expected (Table 3.1, Fig. 3.2), i.e. polyps grew to larger diameters at high food concentration (1.86 ± 0.45 mm) than at medium (1.46 ± 0.35 mm, Tukey's test, $z = 5.5$, $p < 0.001$) or at low concentration (1.30 ± 0.35 mm, Tukey's test, $z = 6.6$, $p < 0.001$). The interactions among these three factors showed significant effects on growth (Table 3.1). At the end of the experiment, noticeably larger diameters could be observed in polyps fed a high food concentration of these three prey items at 13 °C, while smaller diameters were observed in polyps fed a low food concentration at 27 °C.

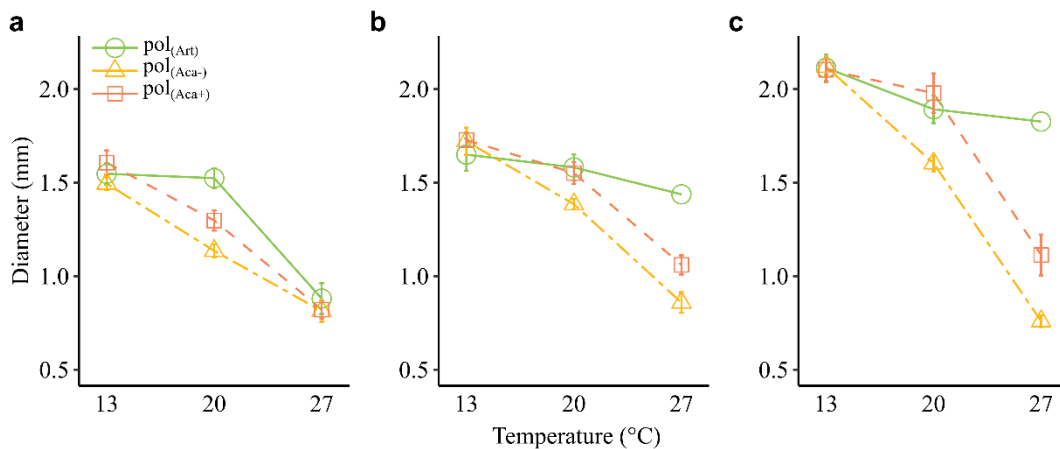


Fig. 3.2. Final calyx diameter (mean \pm SE) of *A. aurita* polyps under different food conditions and temperatures. Letters denote food quantity (a: Low, b: Medium, c: High).

3.3.4 Budding reproduction

Temperature, food quality, and food quantity influenced budding reproduction (Table 3.1). Budding reproduction was limited at high temperature (1.1 ± 1.7 ind polyp⁻¹), but was favored at low (3.7 ± 2.7 ind polyp⁻¹, Tukey's test, $z = -3.1$, $p = 0.006$) and intermediate temperatures (4.8 ± 3.6 ind polyp⁻¹, Tukey's test, $z = -3.4$, $p = 0.002$). Overall, the number of buds produced was dependent on food quality (Table 3.1, Fig. 3.3). $\text{Pol}_{(\text{Aca+})}$ produced significantly more buds on average (4.2 ± 3.3 ind polyp⁻¹) compared to $\text{pol}_{(\text{Aca-})}$ (3.0 ± 2.8 ind polyp⁻¹, Tukey's test, $z = 3.2$, $p = 0.004$) and $\text{pol}_{(\text{Art})}$ (2.7 ± 3.0 ind polyp⁻¹, $z = 6.0$, Tukey's test, $p < 0.001$); budding reproduction of the latter two treatments was also significantly different from each other (Tukey's test, $z = 3.4$, $p = 0.004$). Food quantity had a positive effect on budding production (Table 3.1, Fig. 3.3), leading to a significantly higher bud production when polyps were fed high food concentration (5.5 ± 3.5

ind polyp⁻¹) than when fed medium (3.4 ± 2.3 ind polyp⁻¹, Tukey's test, $z = 7.2$, $p < 0.001$) or low (1.0 ± 1.2 ind polyp⁻¹, Tukey's test, $z = 8.9$, $p < 0.001$) food concentrations. Moreover, two-way interactions of temperature, food quality, and quantity showed significant effects on the number of bud production (Table 3.1). Overall, the most buds were produced by pol_(Aca+) that were fed the high food concentration at 20 °C (10.1 ± 3.1 ind polyp⁻¹), while pol_(Art) fed the low food concentration at 27 °C had no budding success.

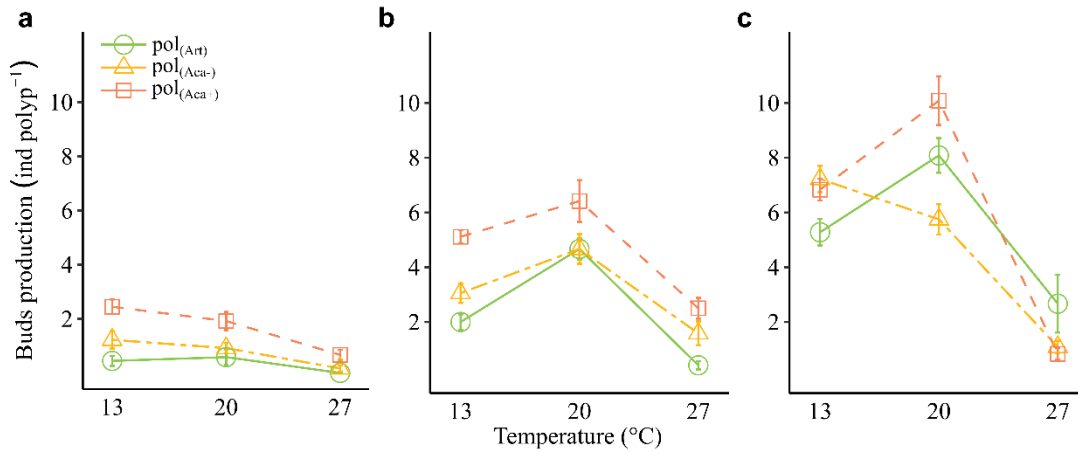


Fig. 3.3. A total number of buds (mean \pm SE) produced by *A. aurita* polyps under different food conditions and temperature regimes. Letters denote food quantity (a: Low, b: Medium, c: High).

3.3.5 Strobilation

Temperature, food quality and quantity all affected strobilation success (Table 1). In the present study, strobilation only occurred at 13 °C, as expected (Fig. 4a). Interaction of food quality and

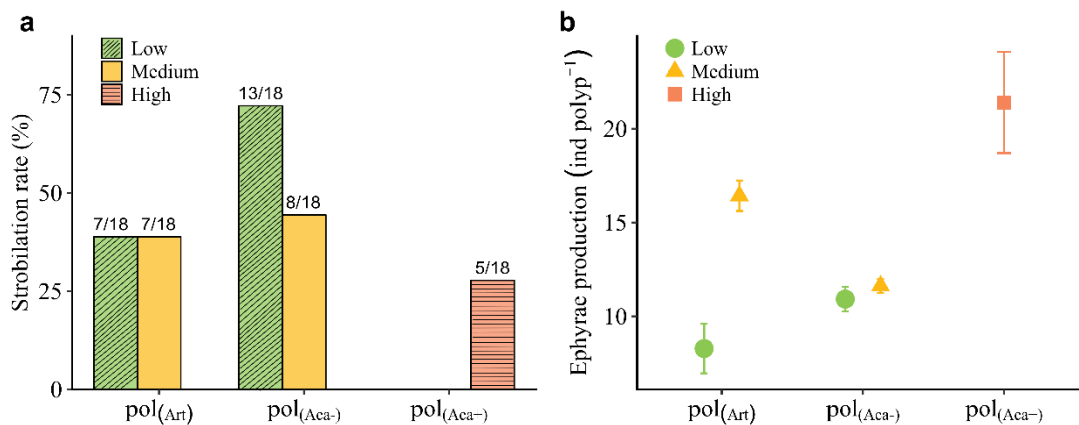


Fig. 3.4. (a) Strobilation rate (%) and (b) ephyrae production (ephyrae inds polyp⁻¹, mean \pm SE) of polyps at 13 °C. Numbers on top of bars represent the number of strobilae in n=18 replicates.

quantity also influenced strobilation success (Table 1). $Pol_{(Aca-)}$ and $pol_{(Art)}$ strobilated at medium (44.4 % and 38.9 %, respectively) and low (72.2 % and 38.9 %, respectively) food concentrations, whereas $pol_{(Aca+)}$ strobilated with 27.8 % success when fed at a high concentration. The number of ephyrae released from each strobila differed between food sources and food concentrations (Fig. 4b). Maximum production of ephyrae (21.4 ± 6.0 ephyrae $polyp^{-1}$) was recorded in $pol_{(Aca+)}$ fed a high food concentration. $Pol_{(Aca-)}$ released 11.6 ± 1.1 and 10.9 ± 2.4 ephyrae $polyp^{-1}$ at medium and low food concentrations, respectively. Meanwhile, $pol_{(Art)}$ released 16.4 ± 2.1 and 8.3 ± 3.5 ephyrae $polyp^{-1}$ at medium and low food concentrations, respectively.

3.3.6 Podocyst

Podocysts were found at 27 °C treatments when we analyzed the photographic data (Suppl. Fig. 3.1). Some of them hatched into new polyps, which were subsequently removed from the cultures and were not included in budding reproduction. We didn't collect podocysts, or measure their production and hatching rates.

3.4 Discussion

Prior studies have noted the importance of temperature and food concentration on jellyfish polyps' life history traits and phase transition (Ishii and Watanabe 2003; Purcell 2007; Han and Uye 2010). However, there have been very few empirical investigations studying the importance of food quality on this benthic-pelagic coupling process (but see Purcell et al. , 1999). Our results suggest that polyps' survival was independent of food conditions at temperatures prevailing in late autumn/early spring and at common summer temperatures within the experimental time, but did under heatwave scenarios. It is somewhat surprising that polyps could compensate part of the stress when fed with elevated HUFA containing food ($Aca^{(+)}$ and $Aca^{(-)}$). Although high HUFA containing food could not significantly contribute to somatic growth, but promoted polyp asexual reproduction (buds' production). This finding verifies an earlier experimental study indicating that polyp produced more buds when fed ciliates compared to fed *Artemia sp.*, while polyps' growth was not affected (Kamiyama 2013). These results imply that we should re-discuss the outcome of previous experiments measuring asexual reproduction that only applied *Artemia sp.* as a major food source. In addition, further empirical studies are required considering prey food quality to understand its effect on polyps' life history traits enabling us to predict physiological performances in fluctuating and multifactorial environments.

3.4.1 Polyp survival and somatic growth

In our study the overall survival rate of polyps was 100 % at 13°C and 20°C regardless of food conditions during the experimental time, but not at the highest temperature of 27°C. Polyp's survival, thus, seems to be independent of their nutritional state within the experimental duration. However, fewer polyps survived when facing an extreme heatwave scenario, indicating that this high temperature was close to the polyps' maximum tolerance range and that polyps suffered from physiological stress. Interestingly, detrimental effects of high temperatures on survival were eased by high HUFA containing food when comparing pol_(Art) with pol_(Aca-) and pol_(Aca+). It is somewhat surprising that a slight difference in the survival rate between pol_(Aca-) and pol_(Aca+) was noted in the last day of the experiment. Therefore, a note of caution is due since we did not control other sources of bias such as bacterial activities under elevated temperature.

Heatwaves might have negative effects on polyp populations especially in shallow temporal coastal waters where heating is most pronounced during summer season. A recent study reported that heatwaves will become very frequent and extreme under global warming (Frölicher et al. 2018). Irreversible changes in organisms may result under extreme heatwaves because of decreasing dissolved oxygen (Matear et al. 2000), immunocompetence or HUFA content of organisms (Roth et al. 2010). To manipulate the nutritional states of the prey, we altered the level of thiamin in phytoplankton which changed the HUFA contents in the zooplankton prey. The mechanism of how heatwaves would affect different nutritional levels in food webs has been rarely quantified. For example, it is known that the thiamin profile in phytoplankton is affected by temperature and species composition (Sylvander et al. 2013; Fridolfsson et al. 2018) and it has been suggested that thiamin deficiency can be a wide-spread phenomenon in several of bird and fish populations in the Northern Hemisphere (Balk et al. 2016). It was also approved that HUFA content generally decreased with warming temperature (Thompson 1996; Sushchik et al. 2003). Thus, not only polyps would suffer from heatwaves directly, but they will face lower food quality in terms of FA profile under warming scenarios (Fuschino et al. 2011), which may reduce their survival significantly. Thus, the combined effect of lower prey quality and increased temperature would play a crucial role in population performance of jellyfish (especially scyphomedusae) as consequences of heatwaves. It is worth noting that effects of heatwaves on organism's physiology are multidimensional. For example, besides negative effects on nutritional conditions found in this

study, depletion of dissolved oxygen or elevated bacterial activities may also be critical for polyps' survival (Ishii et al. 2008).

Once polyps attach to substrates, they feed and ingest prey to support individual somatic growth. The fact that polyps survived and grew to larger diameters at lower temperatures well agrees with previous studies (Han and Uye 2010). As polyps in temperate zones are known to be the overwintering phase, they are pre-adapted to cold conditions. Large body size potentially contributes to greater performance and fitness of organisms in general (Kingsolver and Huey 2008). In this study, high food quantity guaranteed polyps obtaining sufficient energy to support somatic growth, while high HUFA containing food didn't improve somatic growth. It, therefore, implies that HUFA content of food was not the direct factor determining polyps' somatic growth.

3.4.2 Benthic population recruitment

Budding is an important asexual reproduction mode of polyps, mainly occurring after a phase of somatic growth, to increase the population size of the benthic stage. We show here that budding production was highest under the intermediate temperature, representing summer conditions. It seems that budding can contribute to the expansion of polyp populations mainly during warmer seasons, while an extreme heatwave in summit summer could inhibit it and even cause mortality. Similar to Cargo and Schultz (1967), we found that polyps may produce inactive podocysts to survive severe heatwaves and start building a new polyp population after hatching from those cysts. On the other hand, under the representative temperature for late autumn/early spring (13 °C), budding production was inhibited, and polyps were in transit to the strobilation mode.

In line with previous studies (Han and Uye 2010; Wang et al. 2015a), our study also found that polyp budding was favored at medium and high food supply. Moreover, our study highlights the importance of food quality influencing this process besides temperature and food quantity. More buds were produced when fed high HUFA containing food. Therefore, former studies that applied *Artemia sp.* as a food source might have greatly underestimated (*ca.* 34.5 %) its effect on bud production and thus the vegetative reproduction potential of the sessile stages. Thus, to better mimic food supply in the field, we suggest using copepod as experimental food supply instead of *Artemia sp.* Future research should consider species-specific and population-specific responses.

3.4.3 Pelagic population recruitment

Strobilation that leads to ephyrae production is a benthic-pelagic coupling process and its success directly determines the potential abundance of medusae. Although a low temperature was indicated as a positive trigger for strobilation, the optimum range is quite narrow and extremely low temperature (5 °C) in winter can inhibit strobilation (Holst 2012). Consistent with previous studies on *A. aurita* from populations of temperate regions (Lucas 2001), strobilation occurred only at the designed late autumn/early spring temperature (13 °C) in this study. Although temperature *per se* seems to be the important stimulus inducing strobilation, many studies find the shift of temperature, rather than a constant temperature, being the stimulus (reviewed by Lucas, 2012). Thus, it could be hypothesized for temperate regions, that strobilation is favored twice a year, i.e., at temperature decreases in autumn and increases in spring, but not under extreme winter temperatures. Further warming after spring might limit strobilation and make conditions in favor of budding mode again (Sokołowski et al. 2016).

Moreover, previous investigations highlighted the importance of nutritional preparation for strobilation success and the need for a short starvation time (Thiel 1962; Ishii and Watanabe 2003; Purcell 2007). Therefore, it is no surprise that strobilation occurred at medium and low food concentrations in $pol_{(Art)}$ and $pol_{(Aca-)}$ in our study. Contrary to this expectation, strobilation also occurred at $pol_{(Aca+)}$ fed high food concentration. We cannot fully explain why polyps did not follow the same pattern observed for $pol_{(Art)}$ and $pol_{(Aca-)}$ but rather start to strobilate when given a high concentration of high HUFA containing food. Meanwhile, it is accepted that food quantity significantly affects the number of ephyrae produced by individual strobila (Hernroth and Gröndahl 1983; Purcell et al. 1999; Wang et al. 2015b), which could be verified in our study.

As found for budding, we demonstrate here that food quality and quantity can interplay in ephyra production as well. As ephyrae production showed inconsistent results when food quantity and quality combined, further investigations are needed to understand the mechanism behind it. In contrast to budding reproduction, which was significantly promoted by HUFA-rich copepod prey, strobilation was also affected by food quality; however, the interaction between food quality and quantity should be further investigated.

3.4.4 Tolerance curve

Polyps of *A. aurita* are highly tolerant to a wide range of environmental conditions, among which

temperature plays an important role on polyps' survival and determines different phase transitions (Lucas et al. 2012). According to Shelford's Law of Tolerance, each organism tolerates a certain range of environmental factors between a minimum and maximum limit with a defined optimum range. Outside of this optimum range, organisms will suffer from physiological stress, leading to high mortality (Shelford 1911). Based on this theory, we combined results from the current study and previous publications, put forward the hypothesis that polyps' temperature tolerance curve includes food effects (Fig. 3.5).

At an intermediate temperature, polyps seem to experience their performance optimum, with high survival and propagation rates *via* budding reproduction. Below and above that optimum temperature range, budding reproduction is limited, and polyps face physiological stress both under low (e.g. below 9 °C, Fitt and Costley, 1998; Höhn et al., 2017) and high temperatures (e.g. 27 °C, this study) and even more extreme temperatures, leading to high mortality (Fig. 3.5).

Strobilation is likely to be a response to physiological stress when polyps encounter decreasing/increasing temperatures accompanied by food scarcity before and after overwintering (Ishii and Watanabe 2003). As temperatures increase after spring, polyps from the temperate region shift from strobilation to budding mode. At very low winter temperatures, polyps' physiological activities are limited (Höhn et al. 2017), strobilation is not induced, and high mortality may occur if temperature further decreases. Likewise, extremely high temperatures, which may prevail at summer summit, may be outside of polyps' maximum physiological tolerance and lead to high mortality. Under these circumstances, podocysts, as a resting stage of polyps, are produced as an adaptation to severe high temperatures (but see Gröndahl, 1988b) and could increase survival rate of polyp populations. However, when temperature continues to increase to even more extreme levels, podocysts will not survive (Cargo and Schultz 1967).

According to our findings, food conditions can significantly alter the temperature tolerance curve of polyps (Fig. 3.5, dashed lines). Maximum experimental temperatures (for example, 27 °C in our study) combined with high food concentrations (dashed line) were likely stressful to polyps, leading to the highest recorded mortality rates. Interestingly, higher HUFA containing food could compensate for this effect and might extend the maximum tolerance range (dot-dash line). Effects

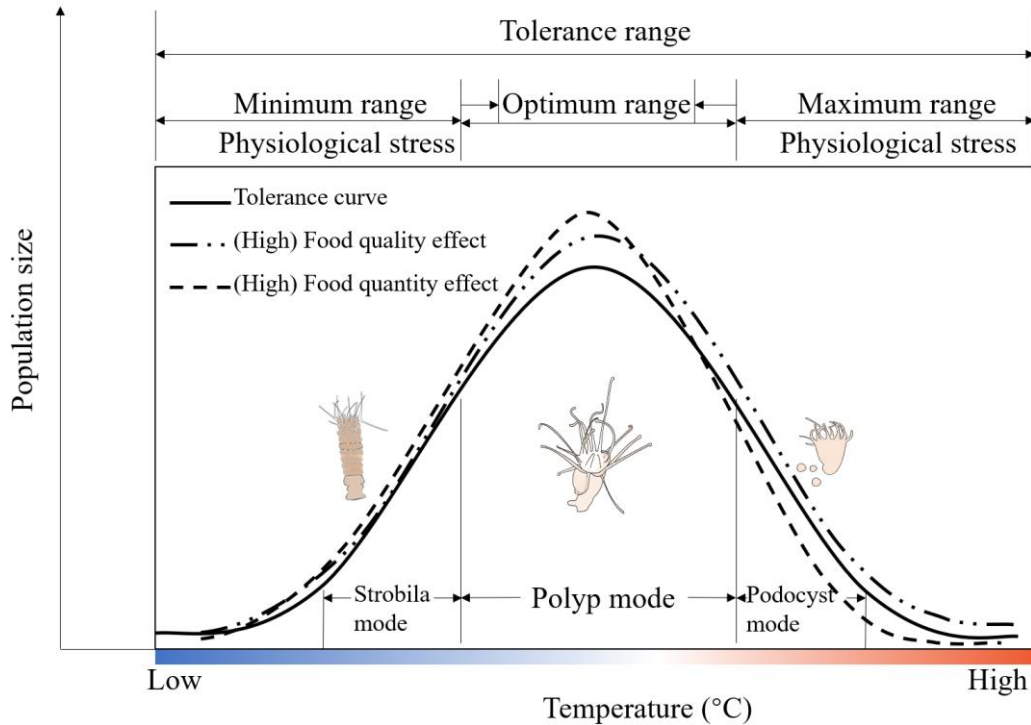


Fig. 3.5. Survival tolerance curves of polyps under different temperature regimes (solid line), food quantity (dotted line) and food quality (dot-dashed line) effects.

of food quality/quantity on polyps' survival and asexual reproduction could not be validated by this study for the minimum temperature tolerance range; thus, further research is needed.

In addition to the general survival tolerance curve (Fig. 3.5), a similar tolerance curve could be defined separately for each of the benthic life stages by considering an optimum, minimum and maximum physiological stress range. As described above, polyps experience their highest budding rates within the optimum temperature range (around 20°C in this study), promoted by a high concentration of high HUFA containing food. When temperature shifts seasonally to within either the minimum or maximum range, the budding phase is limited and, strobilae (at lower temperatures) or podocysts (at higher temperatures) will be triggered. Even though strobilation rate was irrespective of food conditions in our study, once strobilation was initiated, the ephyra production should also follow this bell-shaped curve pattern. This is exemplified in the work undertaken by Purcell (2007) on an *A. labiata* population from Puget Sound. In that study, polyps were estimated to increase ephyrae production by 8.8 % -11.3 % for each 1 °C of warming within a yearly field temperature range up to 15 °C; above this point, ephyrae production dropped by 0.4 % per 1 °C warming. Again, food availability and type seem to interplay with the temperature

tolerance curve, producing a more variable pattern. For example, once strobilation is triggered within its optimum temperature range, better food conditions (higher food concentration and high food quality) could support the production of more ephyrae. Food quality affects polyp's asexual reproduction may more conspicuous under food scarce condition, e.g. overwintering, at which time zooplankton accumulate high concentration of HUFA (Hartwich et al. 2012).

Jellyfish bloom seems to be promoted when the combined environmental factors (mainly temperature, food quality, and food quantity) fit the polyps' optimum tolerance range that best supports-bloom conditions. Modest cooling temperatures and optimum food conditions during late autumn and early spring contribute to a long-lasting strobilation optimum, inducing polyps to produce more ephyrae at a high strobilation rate. In contrast, harsh winters and sub-optimal food conditions may lead to minimum production, resulting in the minimal or even absence of jellyfish population.

3.5 Conclusion

The main goal of the current study was to elucidate effects of food quality on polyps' life history traits. Our findings suggest that changes in the nutritional conditions of prey might significantly affect the survival and life history traits of polyps. Furthermore, interactions between temperature and food conditions might determine the recruitment success of pelagic medusae from benthic polyps. Whether or not these factors have simultaneous effects on polyps and medusae recruitments depend greatly on the scale of environmental fluctuations. More importantly, under ocean warming scenarios more frequent and long-lasting heatwave events can potentially regulate plankton community structure, and may be accompanied by changes to the nutritional conditions of primary and secondary producers. Heatwaves, may thus negatively affect the population dynamics of jellyfish not only by direct physiological stress but also through the effect of food quality. To be able to fit a more generalized polyp tolerance curve, further research is needed to quantitatively examine the links between environmental factors (including, but not limited to, temperature and food conditions) and jellyfish's life history traits in consideration of different species and populations.

Chapter 4 Tackling the jelly web: new insights into the trophic ecology of gelatinous zooplankton in oceanic food webs of the eastern tropical Atlantic

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Abstract

Gelatinous zooplankton (GZ) occur both in high biomass and high taxonomic diversity in oceanic food webs, yet their ecological role remains incompletely understood due to the difficulties to sample and accurately assess the usually fragile organisms in this group. A dedicated sampling effort in the eastern tropical Atlantic (ETA) resulted in the collection of a wide variety of GZ taxa, including hydromedusae, scyphomedusae, siphonophores, ctenophores, and pelagic tunicates. We here provide one of the first large-scale assessments of GZ community within oceanic food webs (“jelly web”) of the ETA based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope (SI) analysis. The ETA jelly web covered a large proportion of the isotopic niche space of the entire food web at all analyzed locations, spanning > 3 trophic levels ranging from herbivores to higher predators, and a large range of dietary sources. Moreover, the different groups of GZ showed significant isotopic niche differentiation. Differences in the patterns of vertical isotopic space differentiation among taxa were found, pointing to vertical segregation in some taxonomic groups but mixing in others. Furthermore, some extent of isotopic niche overlap may reveal potential for competition among some taxa. These patterns highlight the complexity of the jelly web, and showed that “jellyfish is

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not equal to jellyfish”, indicating the diverse roles of GZ in oceanic food webs on different trophic levels and as both predator and prey. Our analyses also showed a size dependency of stable isotope variations in some GZ taxonomic groups which is a common phenomenon observed in, e.g., fishes. The integration of GZ in oceanic food web models thus requires careful consideration. Data sets presented here also provide a baseline to which to relate future observations of GZ communities in the ETA in the light of climate change and overfishing.

Keywords: gelatinous zooplankton, the eastern tropical Atlantic, trophic ecology, stable isotope, jellyfish

4.1 Introduction

The pelagic ocean constitutes the largest living habitat on earth but it is also the least known environment (Robison 2004). The basic understanding of oceanic food webs is that primary production *via* photosynthesis takes place in the sunlit surface layer by phytoplankton. The phytoplankton-based organic matter is then utilized by microbial communities and by herbivorous zooplankton (Fenchel 1988; Sommer et al. 2002), which are in turn consumed by carnivores such as gelatinous zooplankton (GZ), ichthyoplankton, planktivorous fishes and squids (Robison 2009). Energy and matter can further be transferred to higher trophic levels (e.g. large predatory fishes, sea turtles, and seabirds) (Houghton et al. 2006; Carman et al. 2014; Thiebot et al. 2016). Degrading matter from all trophic levels can link to the microbial loop (Lenz 1992; Caron 1994), or sink to benthic communities (Yamamoto et al. 2008; Chelsky et al. 2016).

Within the oceanic food webs, GZ constitute one of the most diverse, abundant and widely distributed groups (Condon et al. 2012), occupying habitats ranging from epipelagic layer to the deep sea and from polar region to tropical area (Madin et al. 1997; Brotz et al. 2012; Mapstone 2014). Taxonomic groups of gelatinous zooplankton include, but are not limited to, hydromedusae, scyphomedusae, siphonophores, ctenophores, pelagic tunicates (here after as tunicates) and chaetognaths (Hamner et al. 1975; Purcell 2012; Nogueira Júnior et al. 2018). In recent decades, the ecology of GZ has received more scientific attention because many species in this group have experienced increases in population size (Brotz et al. 2012), including events of mass occurrence, so-called “jellyfish bloom” (Licandro et al. 2010; Brotz et al. 2012; Boero 2013). The massive

biomass results in shifts of ecological community structure and energy transfer (Nielsen et al. 1997; West et al. 2009; D'ambra et al. 2013).

The evidence is accumulating that GZ occupy key positions in food webs as both predators and prey. For example, a database consisting of 27 years of annotated ROV underwater observations showed that GZ such as narcomedusae, siphonophores and ctenophores were key predators in the central California deep pelagic food web (Choy et al. 2017). The same study also observed that tunicates, siphonophores, hydromedusae and ctenophores could serve as prey items for other predators. In their function as both predator and prey, feeding interactions between GZ groups, and between GZ and non-GZ groups were relevant. Moreover, understanding of energy fluxes and trophic interaction in marine food webs has often been achieved based on stomach content analysis (SCA) (Hyslop 1980). Due to their watery and fragile body structure as well as their patchy distributions, GZ taxa are difficult to sample and preserve (Omori and Hamner 1982; Pugh 1989; Pierce 2009), thus, they are frequently not observed or underestimated in SCA studies due to its fragility and easy digestibility (Arai et al. 2003). As a consequence, a quantitative understanding of the ecological roles of GZ is lacking for many taxonomic groups and species within this group and for many oceanic locations, which is reflected in often oversimplified or inaccurate representation in food web models (reviewed by Pauly et al. 2009).

Besides SCA and direct *in situ* observations, stable isotope (SI) analysis has been utilized in studies of GZ feeding ecology (Pitt et al. 2009). An organism's SI value provides time-integrated signals in which the SI ratios of a predator's tissues reflect its average diet and trophic level (Fry 2006). In this context, carbon isotopes are suitable tracers of material at the base of food webs and possible food sources, whereby nitrogen isotopes can indicate the trophic positions of organisms in food webs (McCutchan et al. 2003). By describing the variability in food sources and trophic levels of individuals within a specific species, the trophic niche of this species within a community can be characterized (Bearhop et al. 2004; Newsome et al. 2007). Consequently, SI studies of many species within the same community can help to elucidate the structure of food webs and ultimately energy flow (Fry 1981; Fry 2006).

The eastern tropical Atlantic (ETA) is one of the most biologically active regions of the world oceans because of its shallow thermocline and strong upwelling (Picaut 1985). In recent years, there has been a strong increase in research cruise activities to improve biological and oceanographic understanding of this oceanic region. This includes studies of oxygen minimum

zones (OMZ) (Teuber et al. 2013), the role of seamounts as biodiversity hotspots (Hanel et al. 2010; Denda et al. 2017), and matter flux of organism in mesoscale eddies (Christiansen et al. 2018) Previous studies have shown that GZ in the ETA are highly abundant and diverse (Neitzel 2017), but no studies have formally addressed the characteristics of GZ community structure in this area.

In this study, our goal was to obtain a comprehensive SI dataset of an oceanic GZ community to date, and the first such dataset for the ETA, and thus to advance the understanding of the position and role of GZ in oceanic food webs (“jelly web” in the following). The specific objectives of our study were 1) to analyze SI values of a wide range of taxa of GZ, as well as other species and food web components of oceanic food webs in the ETA, and thus to provide an overview of the jelly web; 2) to quantify the isotopic niche width of different GZ taxonomic groups, as well as niche differentiation and overlaps in the context of the overall jelly web; 3) to assess the role of geographic, hydrographic and topographic variability (including seamount and open ocean habitat) and depth differences, as well as the presence of size dependency within taxonomic groups, in explaining variability within taxonomic groups. Based on these analyses, we aimed to obtain a SI baseline dataset against which to measure future datasets to assess e.g., effects of climate change, overfishing and potential increases in GZ, and to outline future research directions needed to further improve the understanding of GZ using SI and other dietary tracers.

4.2 Methods

4.2.1 Sampling

Sampling was conducted during November and December 2015 onboard R/V “MARIA S. MERIAN” cruise (MSM49) at 8 stations (Latitude 12°00.00’N to 18°05.00’ N, Longitude 20°00.00’W to 24°00.00’W) in Cape Verdean waters in the ETA, including a shallow seamount (100-3300 m) and its northwestern and southeastern slopes, a cyclonic eddy, and 4 oceanic stations (Fig. 4.1). The sampling focused on the collection of gelatinous organisms from the epi- and mesopelagic layers (0-1000 m). In addition, other food web components from different trophic levels were sampled. Of which seston were collected as the baseline of the food web including phytoplankton in the shallow areas and degrading organic matter. Moreover, different meso- and macro- zooplankton groups including crustaceans, fish larvae, polychaetes and squids were sampled (Table 4.1).

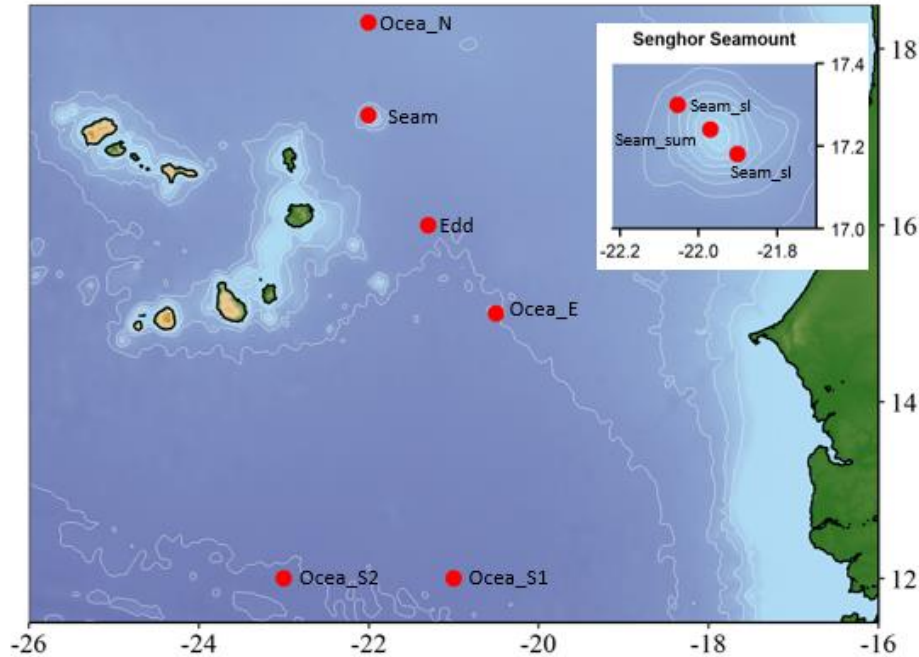


Fig. 4.1. Sample collection sites in the eastern tropical Atlantic (cruise: MSM49). The stations included summit (Seam_sum) and two slopes (Seam_sl) of a seamount, a cyclonic eddy (Edd), and four oceanic stations from the north (Ocea_N), the east (Ocea_E), and the south (Ocea_S1, Ocea_S2). Insert: Senghor Seamount.

Seston sampling: Water samples were taken at four depths (25, 200, 400, 1000 m) at each station using a CTD rosette (SEB 19 plus) equipped with 24 Niskin sampling bottles and oxygen sensors (Table 4.1). 3L of seawater were filtered through GF/F (Whatman; pore size: 0.7 μm) to obtain seston samples. For each depth, we prepared 3 replicates.

Meso- and macro- zooplankton sampling: Net sampling was conducted using two types of multiple opening/closing nets and environmental sampling systems (MOCNESS), one with 1 m^2 (3 nets, mesh size: 2 mm; and 6 nets, mesh size: 335 μm) and one with 10 m^2 opening (5 nets, mesh size: 1.5 mm), towed at a speed of 2 kn. Sampling depth intervals were targeted at 0-50, 50-100, 100-200, 200-400, 400-600, and 600-1000 m. Samples from replicate hauls at the same depth and station were pooled for analyses. Representative species of GZ are displayed in Fig. 4.2.

Zooplankton identification and storage: All specimens from net catches were identified to the lowest possible taxonomic levels and classified in taxonomic groups as described in Table 4.1 using online identification keys (WoRMS) and identified by experienced specialists. Samples included six taxonomic groups of GZ, i.e., chaetognaths, hydromedusae, siphonophores, ctenophores, scyphomedusae, and pelagic tunicates (Table 4.1, Figure 4.2). All samples were then

Table 4.1. Overview of sampling stations and specimens distribution.

	Ocea_N	Seam_sl1	Seam_sum	Seam_sl2	Edd	Ocea_E	Ocea_S1	Ocea_S2	Sum up
Bottom depth (m)	3300	1000	100	1000	4000	4200	4700	4900	
Longitude	18°05.00' N	17°14.24' N	17°09.99' N	17°09.14' N	16°08.81' N	15°00.00' N	12°00.00' N	12°00.00' N	
Latitude	22°00.00' W	22°00.71' W	21°57.59' W	21°54.68' W	21°20.52' W	20°30.00' W	21°00.00' W	23°00.00' W	
Gelatinous zoopl.	85	48	16	47	43	54	92	66	451
Chaetognaths		2	4	5	2	4	8	9	34
0-400		1	4	5	2	4	2		18
400-1000		1					6	9	16
Ctenophores	13	14	2	9	9	11	16	9	83
0-400	9	7	2	3	7	9	2	3	42
400-1000	4	7		6	2	2	14	6	41
Hydromedusae	24	5	1	11	6	14	14	7	82
0-400	13	4	1	6	2	6	4	2	38
400-1000	11	1		5	4	8	10	5	44
Scyphomedusae	23	7		9	11	2	7	1	60
0-400	4	2							6
400-1000	19	5		9	11	2	7	1	54
Siphonophores	15	10	2	4	3	19	35	28	116
0-400	13	10	2	4	3	15	30	25	102
400-1000	2					4	5	3	14
Tunicates	10	10	7	9	12	4	12	12	76
0-400	9	10	7	8	12	3	12	12	73
400-1000	1			1		1			3
Seston	12	12	3	9	12		12		60
Seston_25	3	3	3	3	3		3		18
Seston_deep	9	9		6	9		9		42
Zooplankton	9	18	19	16	16	28	15	27	148
Amphipod	9	3	3	3	8	14	11	13	64
0-400	7	3	3	3	7	11	7	10	51

Table 4.1 Continued

400-1000	2				1	3	4	3	13
Copepod		1	1	1	3	1	1	1	9
0-400		1	1	1	1		1	1	6
400-1000					2	1			3
Giant_Copepod		11		5	3	2	1	3	25
0-400					1			1	2
400-1000		11		5	2	2	1	2	23
Decapod_larvae			2	3					5
0-400			2	3					5
Shrimp		3							3
0-400		2							2
400-1000		1							1
Gastropod				1	1	3		6	11
0-400				1	1	3		5	10
400-1000								1	1
Krill		2	6	3		6		1	18
0-400			6	2				1	9
400-1000		2		1		6			9
Ostracoda					1	1	1	3	6
0-400							1		1
400-1000					1	1		3	5
Polychaete		1	7			1	1		10
0-400		1	7				1		9
400-1000						1			1
Squid	3	3	4	3	5	2	5		29
Squid larvae			1		1	1	1		4
Fish larvae		6	2	6	2	3	2	2	23
0-400		3	2	3	2	2	2	1	15
400-1000		3		3		1		1	8
Sum up	109	90	45	81	79	88	127	95	714

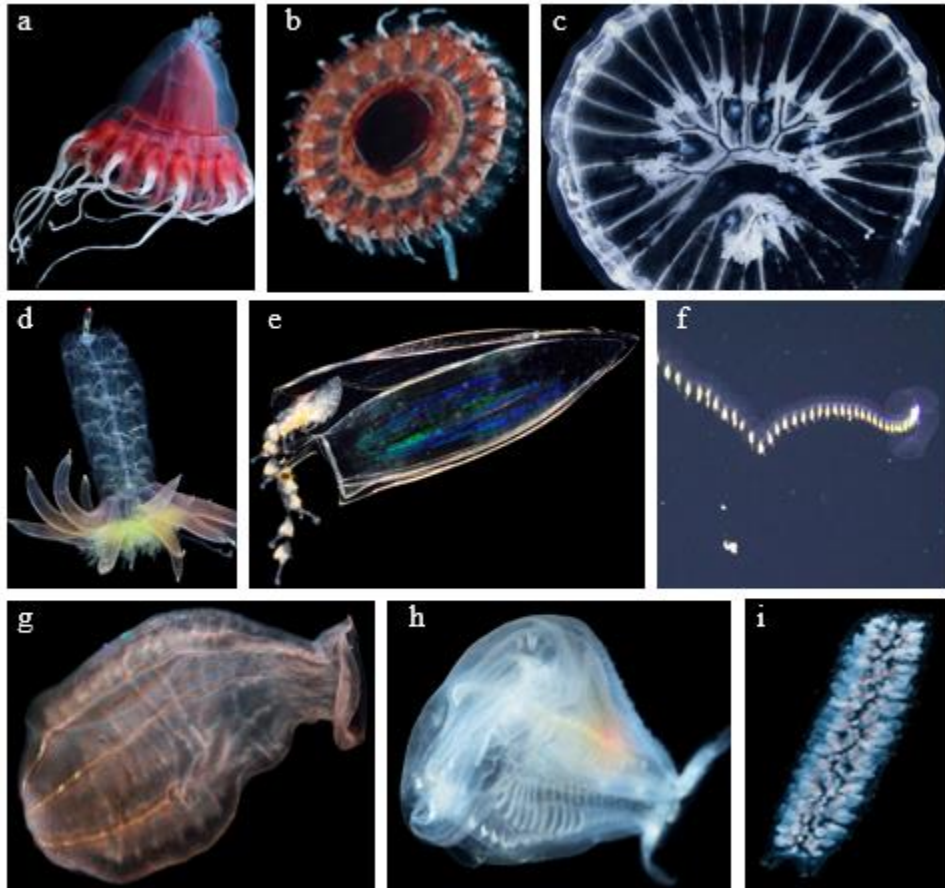


Fig. 4.2. Representative gelatinous specimens from net catching for stable isotope analysis in this study (photos by: Solvin Zankl (a, b, c, d, e, f, h, I, j); Henk-Jan Hoving (g)). Scyphomedusae: a) *Periphylla periphylla*, b) *Atolla wyvillei*; Hydromedusa: c) *Zygocanna vagans*; Siphonophores: d) *Physophora hydrostatica*, e) *Diphyida sp.*, f) *Praya dubia*; Ctenophore: g) *Beroe sp.*; Tunicates: h) *Thetys vagina*, i) *Pyrostremma sp.*

measured (GZ: bell diameter or length to the nearest mm; other organisms: total length to the nearest mm) and rinsed with artificial seawater. GZ samples and other zooplankton organisms with a body size >5 mm were stored individually, whereas chaetognaths and organisms with a body size < 5 mm were pooled (5 individuals per Eppendorf tube). Samples were then immediately frozen and kept at -80 °C until further analysis.

4.2.2 SI analysis

Sample preparation: Seston samples on GF/F filters were freeze-dried. A small round piece (diameter ~ 5 mm) of each filter was then cut out and wrapped in tin foil prior to analysis. All animal samples were freeze-dried and ground to a fine powder. Then, $250 \pm 75 \mu\text{g}$ dry weight

subsamples were weighed into tin capsules (HEKAtech; diameter × height: 3.2 × 4 mm) for SI analysis.

Sample analysis: All seston and zooplankton samples were analyzed for carbon (C) and nitrogen (N) isotope composition and C: N values using a high sensitivity isotope ratio mass spectrometer connected with an elemental analyzer system and a gas chromatography (GC) column suitable for low biomass measurements (Hansen and Sommer 2007). The results were expressed as $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, indicating the ratio of heavy to light isotope and relative to a standard (Peterson and Fry 1987) as follows:

$$\delta X = \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \times 1000$$

, where δ is the isotopic notation, X refers to the heavy element (^{15}N or ^{13}C) and R is the ratio of the heavy isotope to light isotope for this element ($^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$). The international standard for $\delta^{13}\text{C}$ measurement was Vienna Peedee Belemnite (VPDB), and atmospheric nitrogen for $\delta^{15}\text{N}$ measurement (Fry 2006).

Lipid correction of $\delta^{13}\text{C}$ isotope values: Prior to data analysis, lipid correction was carried out according to Post et al. (2007) for specimens with high C:N (> 3.5) ratios, using the formula:

$$\delta^{13}\text{C}_{\text{normalized}} = \delta^{13}\text{C}_{\text{untreated}} - 3.32 + 0.99 \times \text{C:N}$$

where $\delta^{13}\text{C}_{\text{normalized}}$ was used for further analysis in this study, $\delta^{13}\text{C}_{\text{untreated}}$ are the raw data, and C:N is the bulk carbon to nitrogen ratio.

4.2.3 Statistical analysis

Overview and general isotopic differences: The general isotopes differences ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) among gelatinous taxonomic groups were analyzed using generalized linear models (GLMs), with either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values as response variables, and taxonomic groups, sampling station and depth (0-400 m versus 400-1000 m) as potential explanatory variables.

Isotopic niches: SI analysis is a useful tool to reveal an organisms' trophic niche characteristics (Bearhop et al. 2004; Newsome et al. 2007; Baltensperger et al. 2015). Isotopic differences among species or taxonomic groups point to different trophic niches, and isotopic variation reflects their respective niche width (Bearhop et al. 2004; Newsome et al. 2007). To infer characteristics and overlap of isotopic niches of different GZ groups, the standard ellipse area (SEA) was calculated

(Jackson et al. 2011). SEAs have been used as a robust measure to compare isotopic space by Bayesian inference (Jackson et al. 2011; Syväranta et al. 2013). Pair-wise overlaps of SEAs to infer isotopic niche overlaps were calculated according to Jackson and Parnell (2017).

Differences in isotopic niches and causes of variability among groups: To assess differences in isotopic niches among GZ taxonomic groups and species, and to explore possible causes of variability within the groups, we conducted GLMs, with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ as response variables, and taxonomic group, species, sampling location, depth, and body size as potential explanatory variables. Because of sampling limitations and natural patchiness of taxa, sample sizes were not balanced and the different datasets did not always allow us to assess all explanatory variables. Thus, species with the best available sample sizes were selected to represent different taxonomic groups. GLMs were fitted in “gaussian” family and the optimum models were selected *via* the Akaike information criteria (AIC). The models with the lowest AIC values were judged to be the best fitting ones.

All data visualizations were performed in “ggplot2” R package (Wickham 2016) and statistic modelling was conducted with basal command in R software (R Core Team 2017). Characteristics of isotopic SEAs were performed in “SIBER” package in R (Jackson and Parnell 2017).

4.3 Results

4.3.1 Overview of the overall food web

SI values of the oceanic pelagic food web in the ETA occupied a large space between 0.45 ‰ and 12.66 ‰ in $\delta^{15}\text{N}$, -23.66 ‰ and -14.58 ‰ in $\delta^{13}\text{C}$ (Fig. 4.3). Within this food web, seston presented two distinct clusters by $\delta^{15}\text{N}$ values, one for seston collected at shallow depth (25 m) represented by lower values, and one for seston from all other depths with higher values. Regarding non-GZ, the isotope values ranged between 3.78 ‰ and 12.66 ‰ in $\delta^{15}\text{N}$, -22.33 and -14.61 ‰ in $\delta^{13}\text{C}$. Giant copepods (10.30 ± 1.47 ‰, expressed by mean \pm SD and thereafter) and squids (9.81 ± 0.81 ‰) had the highest $\delta^{15}\text{N}$ values on average, and small calanoid copepods (6.38 ± 1.24 ‰), krill (6.96 ± 1.62 ‰), and decapod larvae (5.16 ± 0.64 ‰) had the lowest $\delta^{15}\text{N}$ values on average. Miscellaneous fish larvae and amphipods varied greatly in both $\delta^{13}\text{C}$ (-19.57 ± 1.67 ‰ and -18.51 ± 1.53 ‰) and $\delta^{15}\text{N}$ (7.39 ± 2.40 ‰ and 6.76 ± 1.75 ‰) values.

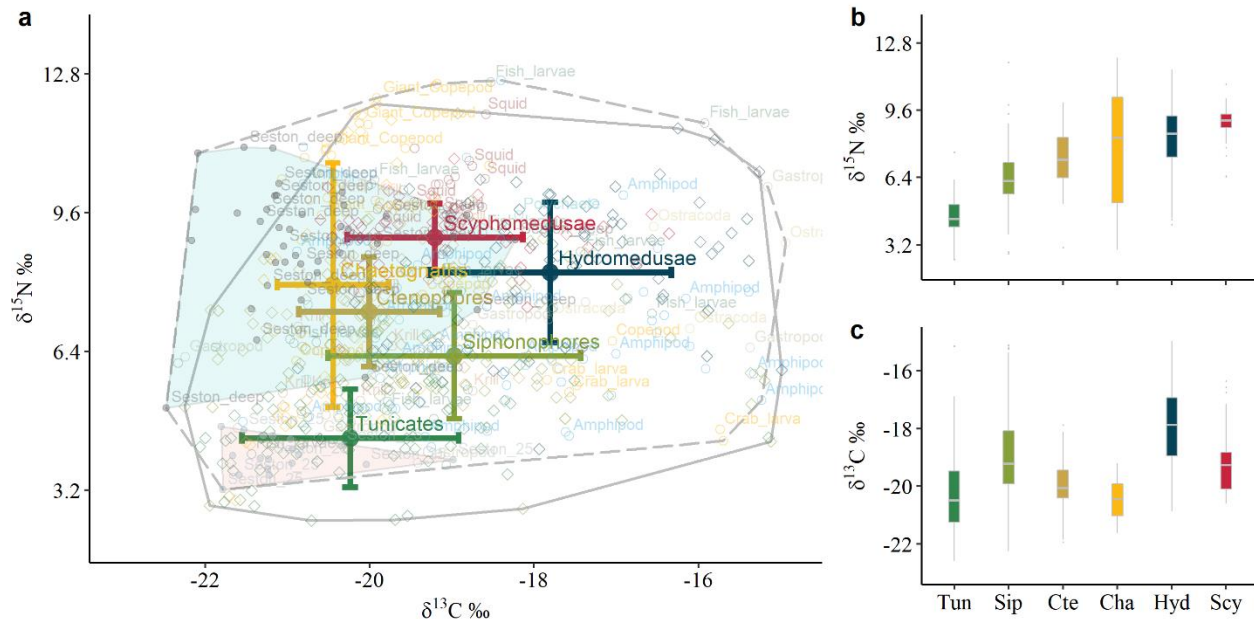


Fig. 4.3. Overview of gelatinous zooplankton stable isotope values in food webs (a) (The convex hull in grey color and solid line denotes the whole food web excluded GZ, that with dashed line stands for the jelly web; The convex hull filled with light blue color denotes seston in deep (> 25 m), that filled with light pink color stands for seston in surface (25 m)); and stable isotope values variation in $\delta^{13}\text{C}$ (b) and $\delta^{15}\text{N}$ (c) of different gelatinous zooplankton taxonomic groups. (Cha= Chaetognaths, Cte= Ctenophores, Hyd= Hydromedusae, Scy= Scyphomedusae, Sip= Siphonophores, Tun= Tunicates).

4.3.2 The jelly web within the oceanic food webs

As listed in the sample table and the representative species displayed in Fig. 4.2, six taxonomic groups of GZ were collected at different depths and stations (Table 4.1). In general, tunicates and siphonophores were mostly collected from the shallower layer (0-400 m) and scyphomedusae were sampled from deeper waters (400-1000 m), whereas other groups were found in both depth layers, i.e., ctenophores, hydromedusae, and chaetognaths.

Within the overall food web, the GZ community spanned different trophic positions and SI values ranged from 0.45 ‰ to 12.10 ‰ in $\delta^{15}\text{N}$, and -22.60 ‰ to -14.58 ‰ in $\delta^{13}\text{C}$. These values cover nearly the whole overall isotopic space occupied by the entire food web. This was also indicated by the largely overlapping convex hull areas of the jelly web and the overall food web (without GZ) (Fig. 4.3).

The lowest $\delta^{15}\text{N}$ values were displayed by tunicates with values of 4.40 ± 1.13 ‰, and the highest $\delta^{15}\text{N}$ values of 9.03 ± 0.78 ‰ were measured in scyphomedusae. Chaetognaths displayed a surprisingly large range in $\delta^{15}\text{N}$ of 9.13 ‰ (2.97 ‰ to 12.10 ‰), while other groups covered lower

ranges, e.g., scyphomedusae with 4.4 ‰ (6.44 to 10.84 ‰) (Fig. 3b). For $\delta^{13}\text{C}$, chaetognaths and tunicates showed the lowest values and smallest variations, i.e., -20.45 ± 0.68 ‰ and -20.24 ± 1.32 ‰, respectively. Hydromedusae displayed the highest $\delta^{13}\text{C}$ values and large variation, i.e., -17.80 ± 1.47 ‰ (Fig. 4.3c).

4.3.3 Geographic and depth differences

Differences in baselines: $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of seston, used here as a measure of the isotopic baseline, varied significantly in different geographic stations and depths. The samples collected from the surface layer (25 m) displayed significantly lower $\delta^{15}\text{N}$ values compared to those from all deeper layers (> 100 m) (Table 4.2). $\delta^{15}\text{N}$ values of seston also differed significantly among geographic stations. Seston $\delta^{13}\text{C}$ did not differ significantly between depths, however, marginally differed among stations on average and significantly differed among stations at the surface (Table 4.2).

Vertical and horizontal consistency and differences in the jelly web: The comparison of the jelly web structure between the shallow (0-400 m) and deep (400-1000 m) layers for two oceanic features, two slopes of a seamount (Seam_sl) and an open ocean station (Ocea_S1), revealed both commonalities and differences.

Although the community composition of GZ differed between the two depths (Table 4.1), the jelly web was always characterized by a large range in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, spanning large proportions of the respective overall food webs at both depths for both features (Fig. 4.4).

In shallow layers, isotopic values of most GZ taxonomic groups showed similar positioning among the seamount and open ocean locations. Tunicates and chaetognaths had the lowest $\delta^{15}\text{N}$ values, while ctenophores had the highest $\delta^{15}\text{N}$ values. Hydromedusae and siphonophores were positioned in between the above groups (Fig. 4.4 a & c). Only two scyphomedusae individuals were collected in the shallow layer at the seamount, in contrast to exclusively deep catches for all other specimens in this group, and these individuals displayed higher $\delta^{15}\text{N}$ values than ctenophores.

The “jelly web” in the deeper layers showed both similarities and differences in comparison to the shallow layers (Fig. 4.4 b & d). For one, mirroring the pattern observed for seston, $\delta^{15}\text{N}$ values of copepods ($t_{(9.37)} = 2.83$, $p = 0.02$) and chaetognaths ($t_{(31.33)} = 5.76$, $p < 0.001$) were significantly higher in the deep than in the shallow layer (Fig. 4.5c). Similarly, $\delta^{15}\text{N}$ values of hydromedusae in average were lower in the shallow than in the deep layer, though the differences were not as

pronounced as in chaetognaths (Fig. 4.5b). However, the difference pattern was not consistent with stations, i.e., it was significant different at the seamount ($t_{(13.71)} = -4.12$, $p = 0.001$) but not in the

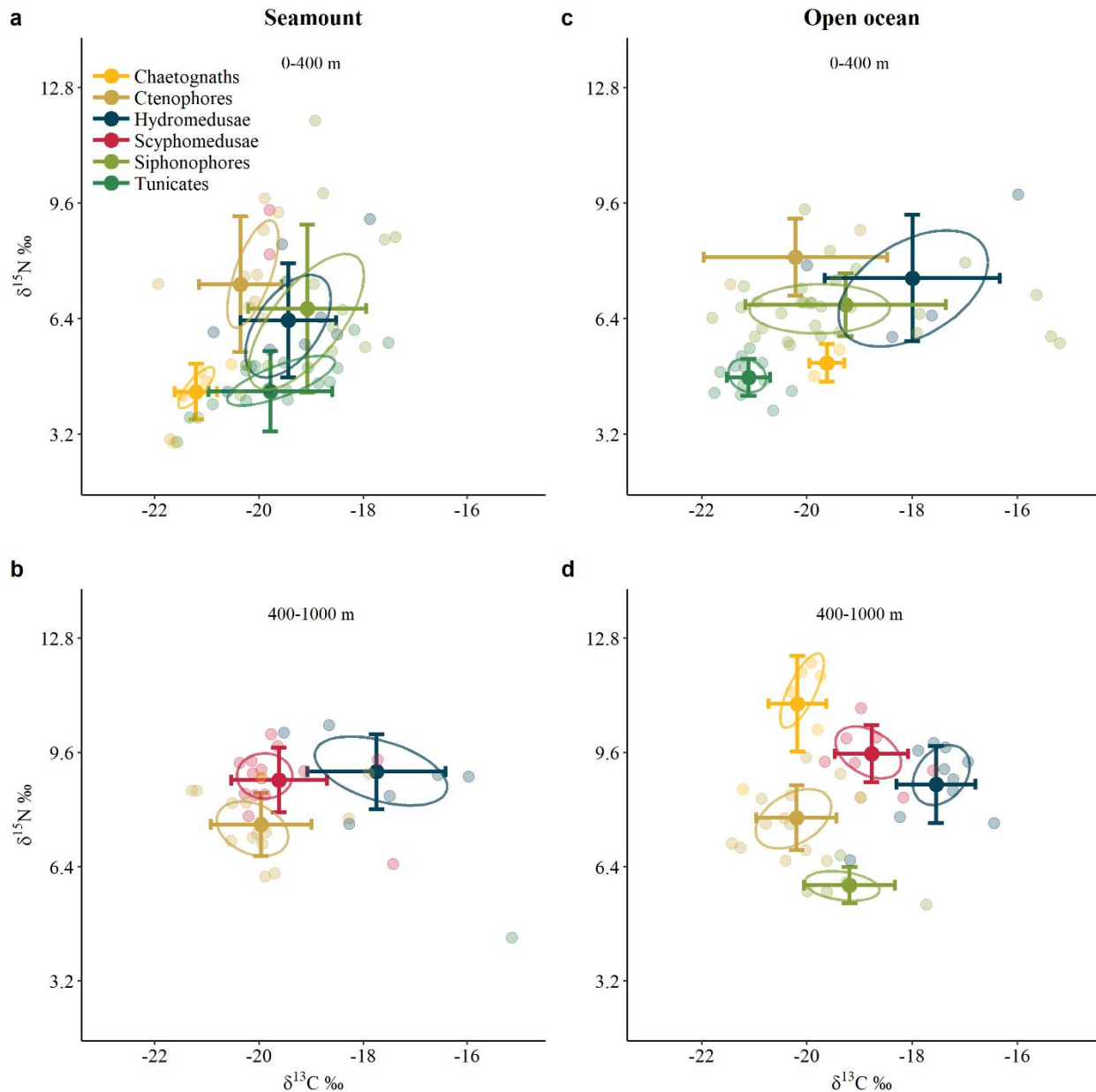


Fig. 4.4. Overview of the jelly web by illustrating stable isotopic bi-plots ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, ‰, mean \pm SD) and standard ellipse areas (SEAs) of 6 gelatinous taxonomic groups in shallow (0-400 m) and deep (400-1000 m) layers in seamount and open ocean habitats.

open ocean ($t_{(3.95)} = -1.26$, $p = 0.28$). $\delta^{15}\text{N}$ values of ctenophores, in contrast, did not show major shifts between the two different depth layers ($t_{(75.77)} = 1.49$, $p = 0.14$; Fig. 4.5a). $\delta^{13}\text{C}$ values between shallow and deep layers were similar for ctenophores ($t_{(80.81)} = -1.58$, $p = 0.12$), but

different to some extent for other, e.g. for hydromedusae at the seamount (-19.44 ± 0.92 ‰ in shallow versus -17.74 ± 1.33 ‰ in deep, $t_{(7.91)} = -2.76$, $p = 0.03$).

Comparing the same depth layer between the seamount and open ocean location, some differences existed in $\delta^{13}\text{C}$ values. The $\delta^{13}\text{C}$ values of chaetognaths in the seamount shallow layers (-21.21 ± 0.41 ‰) were smaller than that in the open ocean shallow layer (-19.62 ± 0.33 ‰, $t_{(2.15)} = -5.53$, $p = 0.03$). In contrast, $\delta^{13}\text{C}$ values of tunicates were larger in the shallow layers of the seamount (-19.78 ± 1.19 ‰) than of the open ocean (-21.11 ± 0.41 ‰, $t_{(22.58)} = 4.36$, $p < 0.001$).

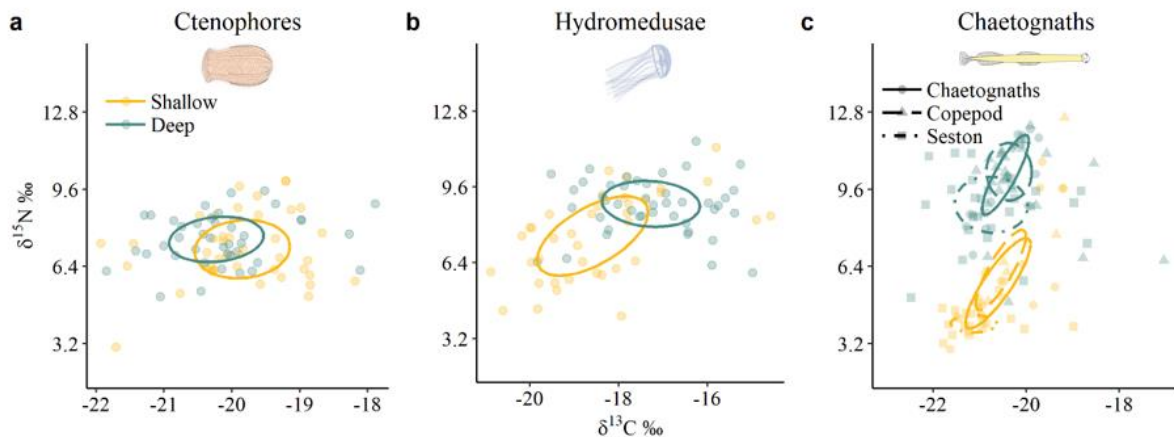


Fig. 4.5. Interpretation stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) variations caused by depth difference in ctenophore (a), hydromedusae (b), and chaetognaths (c). Points color denotes different depth layers (Deep = 400-1000 m; For Chaetognaths and copepod, Shallow= 0-400 m, for seston, Shallow= 25 m), ellipses are calculated by SEA.

4.3.4 Isotopic space partitioning and overlap within the jelly web

The overall jelly web was partitioned into distinctly different isotopic niches in different taxonomic groups, as indicated by SEA differentiation (Fig. 4.4). This niche partitioning was evident at the different depths at both the seamount and open ocean stations. In the shallow layer, tunicates occupied the lowest isotopic space, ctenophore occupied the highest isotopic space and followed by hydromedusae and siphonophores. In the deep layer, chaetognaths occupied the highest isotopic space and scyphomedusae shared almost the same level as hydromedusae, followed by ctenophores and siphonophores.

In addition to the overall differentiation, the isotopic niche width of different GZ taxonomic groups varied, and overlaps in SEA between certain taxonomic groups were present (Fig. 4.4). For example, in the shallow layer at the seamount feature, the SEA of siphonophores was largest and displayed distinct overlap with hydromedusae (Fig. 4.4a). Siphonophores and tunicates, as well as

Table 4.2. Outputs of GLMs of stable isotopes of different species gelatinous zooplankton collected from different depth and stations

Organisms/seston	Response variables	Models	Variables	Df	χ^2	P-value
Seston (in general)	$\delta^{15}\text{N}$	$\delta^{15}\text{N} \sim \text{Station} + \text{Depth}$	Station	5	57.19	0.02
			Depth	1	86.4	< 0.001
	$\delta^{13}\text{C}$	$\delta^{13}\text{C} \sim \text{Station} + \text{Depth}$	Station	5	9.41	0.05
			Depth	1	0.62	0.4
Seston (surface)	$\delta^{15}\text{N}$	$\delta^{15}\text{N} \sim \text{Station}$	Station	5	22.81	0.65
	$\delta^{13}\text{C}$	$\delta^{13}\text{C} \sim \text{Station}$	Station	5	9.39	0.003
Chaetognaths	$\delta^{15}\text{N}$	$\delta^{15}\text{N} \sim \text{Station} + \text{Depth}$	Station	6	148.01	< 0.001
			Depth	1	56.03	< 0.001
			Station	6	10.22	< 0.001
	$\delta^{13}\text{C}$	$\delta^{13}\text{C} \sim \text{Station} + \text{Depth}$	Depth	1	0.15	0.36
			Station	7	21.65	0.007
			Depth	1	0.01	0.92
Ctenophores	$\delta^{15}\text{N}$	$\delta^{15}\text{N} \sim \text{Station} + \text{Depth} + \text{Size} + \text{Station:Depth} + \text{Station:Size} + \text{Depth:Size}$	Size	1	4.59	0.04
			Station: Depth	6	11.54	0.11
			Station: Size	7	30.24	< 0.001
			Depth: Size	1	0.04	0.85
			Station	7	4.66	0.38
			Depth	1	0.02	0.85
	$\delta^{13}\text{C}$	$\delta^{13}\text{C} \sim \text{Station} + \text{Depth} + \text{Size} + \text{Station:Depth} + \text{Station:Size} + \text{Depth:Size}$	Size	1	2.5	0.04
			Station: Depth	6	10.66	0.01
			Depth: Size	1	1.6	0.11
			Station	7	31.8	0.01
Hydromedusae	$\delta^{15}\text{N}$	$\delta^{15}\text{N} \sim \text{Station} + \text{Size} + \text{Depth} + \text{Depth:Size}$	Depth	1	34.12	< 0.001
			Size	1	4.27	0.11
			Depth: Size	1	23.44	< 0.001
			Station	7	29.22	0.02
	$\delta^{13}\text{C}$	$\delta^{13}\text{C} \sim \text{Station} + \text{Depth} + \text{Size}$	Station	7	29.22	0.02

Table 4.2 Continued

			Depth	1	20.36	< 0.001
			Size	1	4.99	0.09
Scyphomedusae	$\delta^{15}\text{N}$	$\delta^{15}\text{N} \sim \text{Station} + \text{Size}$	Station	6	12.46	< 0.001
			Size	1	3.37	0.003
	$\delta^{13}\text{C}$	$\delta^{13}\text{C} \sim \text{Station} + \text{Size}$	Station	6	13.86	< 0.001
			Size	1	25.68	< 0.001
Siphonophores	$\delta^{15}\text{N}$	$\delta^{15}\text{N} \sim \text{Station} + \text{Species} + \text{Size}$	Station	7	56.9	< 0.001
			Species	5	14.25	0.16
			Size	1	0.28	0.69
			Species:Size	5	3.68	0.84
	$\delta^{13}\text{C}$	$\delta^{13}\text{C} \sim \text{Station} + \text{Species} + \text{Size}$	Station	7	37.77	0.002
			Species	5	67.02	< 0.001
			Size	1	5.96	0.06
Tunicates	$\delta^{15}\text{N}$	$\delta^{15}\text{N} \sim \text{Station} + \text{Species} + \text{Size}$	Species:Size	5	4.59	0.73
			Station	7	2.87	0.95
			Species	1	6.56	0.2
			Size	1	2.22	0.03
	$\delta^{13}\text{C}$	$\delta^{13}\text{C} \sim \text{Station} + \text{Species} + \text{Size}$	Species:Size	1	7.91	0.01
			Station	7	28.63	< 0.001
			Species	1	7.31	0.005
			Size	1	22.37	< 0.001
			Species:Size	1	13.64	< 0.001

Significant results ($P < 0.05$) are written in bold face.

hydromedusae and tunicates also showed partial overlap in SEAs. In this context, chaetognaths were isolated from other gelatinous taxonomic groups, without any SEA overlap. In contrast, GZ in the deep layer of the seamount habitat had relatively more segregated isotopic spaces (Fig. 4.4b). Similarly, a relatively large isotopic space overlap was observed between siphonophores and hydromedusae in the shallow layer of the open ocean station (Fig. 4.4c), while SEAs of all GZ taxonomic groups were partitioned in deep layer (Fig. 4.4d). Overall, SEAs appeared to show more overlap in the shallow layer and at the seamount, and stronger differentiation in the deeper layer and open ocean (Fig. 4.4).

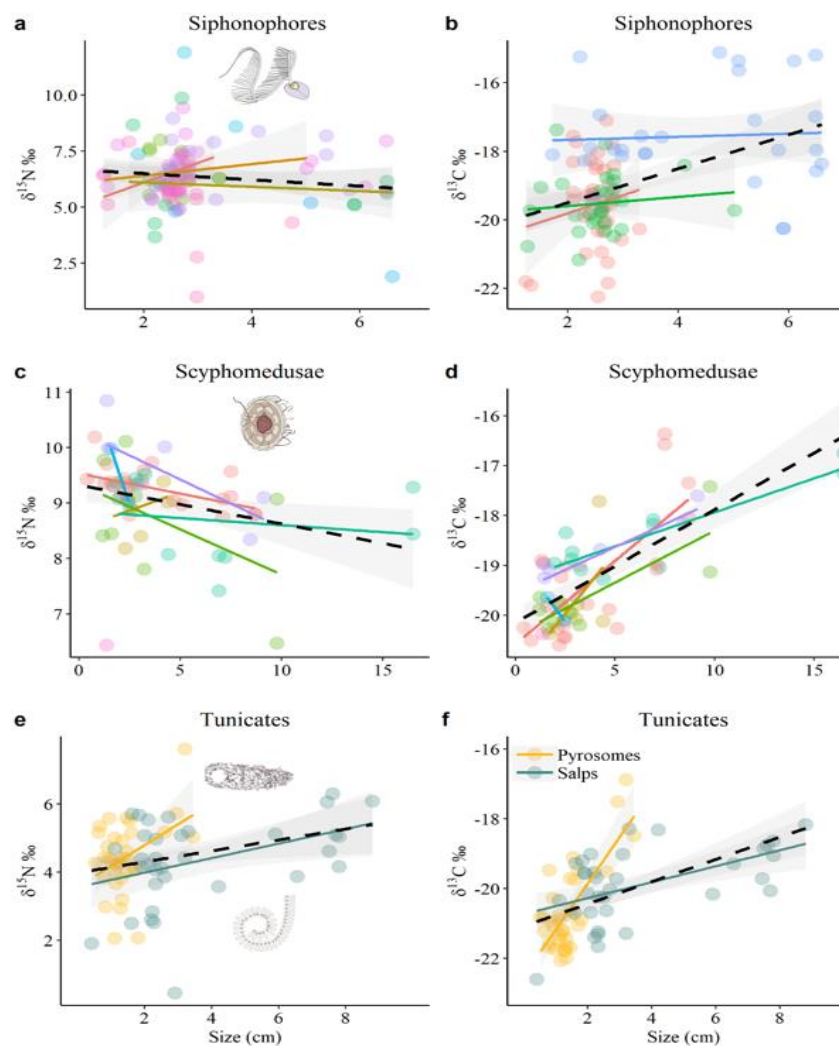


Fig. 4.6. Ontogenetic shifts of stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) values in siphonophores (a, b), scyphomedusae (c, d), and tunicates (e, f). Dashed lines denote regression line in a general pattern, colored lines denote regression lines in different stations (a-d) or inter-specific within the group (e, f).

4.3.5 Stable isotope shifts caused by size dependency

Variation of SI values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) correlated to size were detected in ctenophores, scyphomedusae, and tunicates, as well as marginally in $\delta^{13}\text{C}$ of hydromedusae and siphonophores, whereas no shifts were detected in $\delta^{15}\text{N}$ of hydromedusae and siphonophores (Fig. 4.6, Table 4.2). Chaetognaths were not included in the ontogenetic test due to their small variance in size (mean \pm SD: 3.57 ± 0.67 cm). As shown in Fig. 4.6, while all $\delta^{13}\text{C}$ values increased with size, the group of siphonophores, scyphomedusae, and tunicates presented different ontogenetic shift patterns in $\delta^{15}\text{N}$, i.e., no shifts, decreasing and increasing in $\delta^{15}\text{N}$, respectively.

For the groups represented by >2 species in reasonable sample sizes, we also analyzed differences within the taxonomic group. $\delta^{13}\text{C}$ values of the group siphonophores and both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of tunicates presented significantly inter-specific differences in ontogeny (Table 4.2).

4.4 Discussion

The ecological roles and importance of GZ in oceanic food webs remain incompletely understood, due to the difficulties to sample and accurately assess these usually fragile organisms. Based on a unique sample set of GZ taxa from the ETA, we here provided one of the first large-scale assessments of the “jelly web” within oceanic food webs based on SI analysis. Notably, the jelly web covered a large proportion of the isotopic niche space of the entire food web, spanning >3 trophic levels ranging from herbivores to higher predators, and a large range of dietary sources. Moreover, the different groups of GZ showed significant isotopic niche differentiation. Our data illustrate the diverse roles that GZ have in the oceanic food webs of the ETA.

4.4.1 Characterization of the jelly web structure

The large range in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of GZ indicates that the general jelly web was comprised of different trophic levels and that GZ species play an ecological role throughout the entire food web. In particular, there was a span of almost 12 ‰ in $\delta^{15}\text{N}$ values of the jelly web, which would represent 3-5 trophic levels assuming a fractionation rate of 2.3 to 3.4 ‰ (Post 2002; McCutchan et al. 2003). This points to a role of GZ on all trophic levels of the food web except top predators and confirms the putative role as both predators and prey (Lynam et al. 2005; West et al. 2009; Choy et al. 2017). At the same time, the large range of $\delta^{13}\text{C}$ values indicates that the jelly web integrated a high diversity of food sources and points to complex food web linkages (DeNiro and Epstein 1978; Hentschel 1998). The low trophic position of tunicates (here salps and pyrosomes)

was consistent with their trophic function as herbi- and bacterivorous filter-feeders (Madin and Purcell 1992; Pakhomov et al. 2006; Ishak et al. 2017; Conley et al. 2018) and the high position of scyphomedusae, hydromedusae and ctenophores with their role as predators (Purcell 1997; Riisgård 2007; Stowasser et al. 2012).

Overall, these findings stand in stark contrast to the traditional view that GZ constitutes a single functional group (reviewed by Pauly et al. 2009) and confirms more recent findings that found diverse roles within oceanic food webs (Choy et al. 2017).

4.4.2 Trophic niche differentiation and overlap in the jelly web

Characterizing trophic niche differentiation and links between resource utilizing and competition have long been of central interest to ecologists (Abrams 1980) and can provide insights into the mechanisms allowing the coexistence of competing species (Hutchinson 1959). In spite of this, trophic niche differentiation of GZ communities has rarely been characterized. The strong niche differentiation and consistent presence of this pattern in the shallow and deep layer and at different oceanic features observed here underscore that different GZ groups can play distinctly different roles in oceanic food webs. It can thus be suggested that “jellyfish is not equal to jellyfish”. This confirms recent findings summarizing 27 years of visual observations in the central California deep pelagic food web that showed distinctly different diets for different groups of GZ (Choy et al. 2017), but extends previous information by providing a more quantitative view of trophic positions and food sources for an entire GZ community within a larger food web.

Overall, the position of GZ groups in the jelly web in our study and the relative trophic level that can be inferred from this, in many cases support previous studies on the feeding ecology of individual species or groups. For example, tunicates (here referring to salps) are highly effective filter-feeders. Previous studies showed that salps could retain particles from 4 μm to 1 mm (Madin 1974; Harbison and McAlister 1979; Alldredge and Madin 1982). Their food sources include e.g. dinoflagellates, diatoms, radiolarians, foraminiferans, coccolithophorids and other detritus (Alldredge and Madin 1982; Vargas and Madin 2004). The low trophic level indicated for salps (and other tunicates) in our study, with values matching those of surface seston, agrees well with this prior classification as a primary consumer. Similarly, the intermediate trophic level and overlapping SEAs of siphonophores and hydromedusae agree with the prior classification as carnivorous predators sharing a similar diet composition (Biggs 1977; Purcell 1989; Colin et al.

2003). Finally, scyphomedusae with the two dominant species *Atolla wyvillei* and *Periphylla periphylla* occupied the highest trophic level in the jelly web in our study, and these species have been classified as prominent predators in the mesopelagic community (Hunt and Lindsay 1998).

Despite of the large amount of trophic differentiation among taxonomic groups, there were also niche overlaps among specific groups of GZ. This included, e.g., overlapping SEAs of tunicates and hydrozoans (siphonophores and hydromedusae) in shallow layers of the seamount station, and is consistent with *in situ* observations showing that hydrozoans compete with tunicates for food resources or directly prey on salps (Hamner et al. 1975; Purcell 1981; Larson et al. 2009). This highlights that both competition and correspondingly, functional redundancy (Pianka 1974; Wissinger 1992; Héroult et al. 2008), are additional features that need to be added to the complexity and functioning of the jelly web. Other phenomena such as intraguild predation of GZ on other GZ (Polis et al. 1989; Purcell 1991; Choy et al. 2017), which is likely to increase the number of functional links in the food web further, are difficult to elucidate with our data set. In summary, these findings underscore that the role of GZ in oceanic food webs is diverse and substantial than is currently considered in oceanic food web models.

4.4.3 Vertical and horizontal consistency and differences in the jelly web

Niche differentiation within the jelly web enables us to explain significant proportions of variability in the SI dataset. The analysis of differences related to, geographic location (including seamount and open ocean habitat), depth differences, as well as the presence of size dependency within taxonomic groups, offered additional opportunities to shed light on factors affecting isotopic variation among and within taxonomic groups in the jelly web.

Spatial differences in SI values among taxonomic groups were consistently present. Spatial variations of SI might be attributed to 1) variations in baseline SI values and 2) spatially discrete population of organisms (Harvey and Kitchell 2000). In this study, the $\delta^{13}\text{C}$ values of seston showed marginal spatial differences. In addition, fluorescence data collected in the same cruise showed that the maximum primary production occurred between depths of 25 and 50 m (Christiansen et al. 2016). The phytoplankton-based surface seston is more meaningful to be used as food web baseline. In addition, those seston showed significant spatial differences in $\delta^{13}\text{C}$. Thus, spatial variations of SI in baseline potentially act as a key factor of SI variations in GZ. Spatial differences in SI values among taxonomic groups can be explained by differences in habitat and

prey composition. Nevertheless, these two mechanisms may act simultaneously and lead to variable SI values.

The vertical niche differentiation firstly might be the result of the vertical differences in composition of GZ. Vertical gradients in species distributions and occurrences are frequently observed in marine systems (Lampert 2005). Mesoscale ocean features such as fronts and eddies may induce or strengthen vertical ecological zonation in the ETA (Hausse et al. 2016; Christiansen et al. 2018). This phenomenon is commonly driven by food sources composition. For example, tunicates consume phytoplankton-based seston (Alldredge and Madin 1982; Perissinotto et al. 2007; Décima et al. 2018) and occupying the lower trophic level is consistent with their distribution in the shallow layer. While phytoplankton is consumed by grazers or decomposed with increasing depth, seston in deeper layers might accumulate more macroscopic aggregates produced by zooplankton, so-called marine snow (Shanks and Trent 1980; Alldredge and Silver 1988), and can thus be considered as zooplankton-based seston. Yet again, this would be consistent with the more enriched $\delta^{15}\text{N}$ values of seston in deeper layers, representative of a higher trophic level. Thus, the vertical differences in seston baseline could be reflected in copepods which known partly feed on seston (Kleppel 1993). The similar pattern in chaetognaths was further demonstrated by the isotopic values of copepods which serve as the main food source for chaetognaths (Gibbons and Stuart 1994; Marazzo et al. 1997; Froneman et al. 1998). The contrasting lack of isotopic differences between shallow and deep layers for ctenophores in our study may point to stronger vertical connectivity *via* migrations, which would prevent vertical differentiation.

These findings highlight that due to the complexity of niche differentiation in the GZ community, more detailed information on the distribution and their roles in food webs at different depths should be addressed in each taxa level to better assess and understand the jelly web.

4.4.4 Trophic niche shifts in different sizes

In general, an ontogenetic shift in isotopic values indicates the potential dietary shifts (Frazer et al. 1997) and may reveal that organisms are able to prey on more diverse food and at multiple trophic positions in food webs during ontogenetic development (Kim et al. 2012). That has been reported previously, for example, in GZ in coastal areas (Fleming et al. 2015), in squids (Golikov et al. 2018), and in fishes (Hyndes et al. 1997; De la Morinière et al. 2003; Kim et al. 2012).

“Jellyfish is not equal to jellyfish”: In the present study, increasing $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of ctenophores, scyphomedusae, and tunicates were associated with increasing body size whereas not for siphonophores and hydromedusae. Meanwhile, an inter-specific difference of SI values existed between pyrosomes (represented by *Pyrostremma agassizi*) and salps (several species), in particular when they grow to larger sizes. That indicates they may use different basal food sources even though they represent the same feeding guild within the taxonomic groups. A recent study suggested different trophic levels between pyrosomes and salps (Décima et al. 2018), which showed pyrosomes occupied a lower trophic position and showed a herbivorous feeding. By contrast, the trophic position of salps was more similar to other mesozooplankton such as copepods, ostracods which displayed substantial omnivory/carnivory. Thus, this also indicates that it is necessary to include GZ groups as different compartments in food web models.

“Jellyfish is not equal to fish”: Changes of $\delta^{15}\text{N}$ values in different sizes were not always shifting to higher trophic levels. In the case of scyphomedusae (dominated by *Atolla wyvillei*), their $\delta^{15}\text{N}$ values decreased significantly with body size. This shift in $\delta^{15}\text{N}$ values may reflect a dietary shift in *A. wyvillei*, however, in a pattern which is different from fishes. In many fishes, $\delta^{15}\text{N}$ values increasing with age were attributed to shifts in dietary preference and foraging behaviour (Grey 2001; Jensen et al. 2012), for example, their diet may switch from zooplankton to fish prey with ontogenetic development (Post 2003).

Alternatively, the decreasing $\delta^{15}\text{N}$ values in larger sizes of *A. wyvillei* might be associated with energy and matter allocation with regard to their life history strategic decisions. We observed gonad maturation in larger individuals (Fig. 4.7). A similar allocation of SI was observed in the moon jelly *Aurelia aurita* in which $\delta^{15}\text{N}$ values decreased during the growth phase and when the individual reached maturity (Javidpour et al. 2016). There might be a mechanism of nitrogen isotope allocation or changes toward reproduction and tissue turnover phases that fuel catabolism in GZ in a specific part of the life cycle.

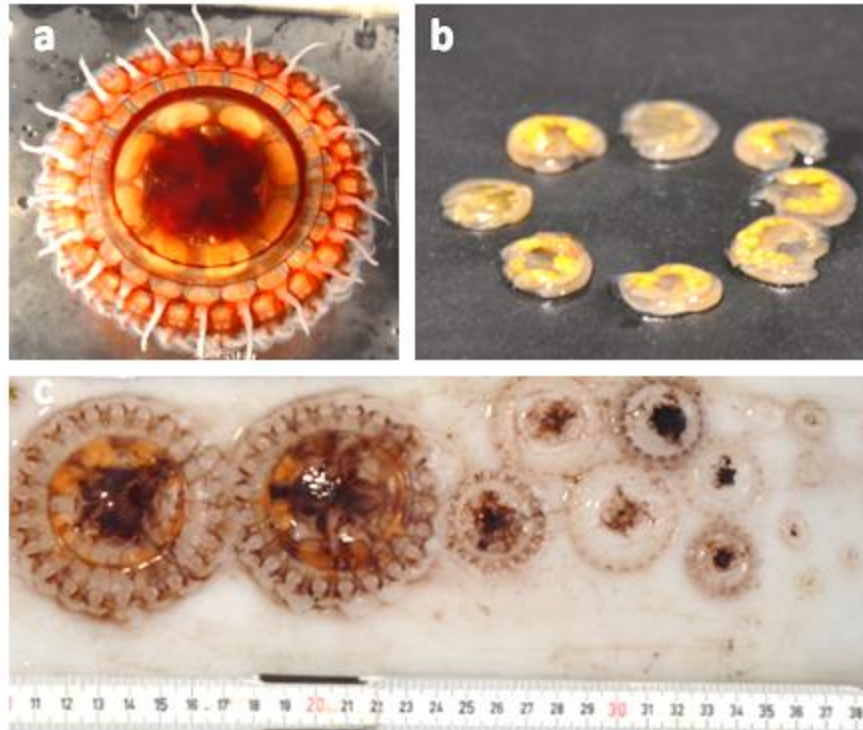


Fig. 4.7. (a) Photos showing *Atolla sp.* with developed gonad tissue, (b) isolated gonad tissue, (c) gonad appeared in larger sizes. Photos were taken by X. Chi.

4.4.5 The vision for future studies

This study shapes a general figure for the “jelly web” in oceanic food webs using SI analysis. Although a huge attempt was made to collect more than 700 specimens to be analysed individually applying high sensitivity SI measurement (Hansen and Sommer 2007), one should notice that net sampling may result in a bias towards collection for sturdier GZ and under-sampling the rare and fragile species (Larson et al. 1991). Thus, sample collection for this study could not be representative of the complete jelly web members. For example, we observed ctenophores other than *Beroe sp.* or hydromedusae not represented in our net samples during *in situ* video survey (Hoving et al. 2018). Thus, to obtain an optimum food web sampling we suggest to a) sampling frequently to gain a better taxonomic coverage due to the patchy distribution of GZ and b) performing a combination of methods to build a comprehensive picture of the jelly web by combining different trophic tracer approaches such as fatty acid and SI analyses and/or different survey methods, e.g. manned submersible or remotely-operated vehicles (ROVs) (Choy et al. 2017), unmanned aerial vehicles (UAVs) (Schaub et al. 2018) and acoustic methods (Båmstedt et al. 2003).

Chapter 5 General discussions and outlooks

Overall in this dissertation, I studied biomolecules such as fatty acids (FAs) transfer through the phytoplankton-zooplankton interface and further to the consumer, polyps of the moon jelly *Aurelia aurita* (Chapter 2). From this chapter, I found that FA composition patterns of primary producers could be reflected in polyps. In general, polyps had a relatively low ω 3-FAs comparing to their prey but elevated levels of a ω 6-FA (i.e. ARA). Polyps were also found to alter the ratio of saturated FA and unsaturated FA (SFA: UFA) under different temperature and food conditions, which might be as an adaptation to seasonal changes. Moreover, life history traits of polyps were investigated taking food properties (quality and quantity) as well as environmental temperature into account (Chapter 3). In this chapter, temperature was the key factor of regulation polyps' life history strategy. Food properties (both quality and quantity) had great impacts on the polyp population size, as well as on the pelagic medusae recruitment *via* the benthic-pelagic coupling. Based on these findings, a novel tolerance curve for polyps has been suggested. In addition, I analyzed the general trophic structure of the "jelly web" applying stable isotope (SI) analysis in the oceanic food webs of the eastern tropical Atlantic (Chapter 4). This chapter revealed that GZ covered a large proportion of the general oceanic food web and occupied at least three trophic levels. Notably, significant isotopic niche differentiation and to some extent, isotopic niche overlaps were observed among GZ communities in different oceanic habitats. Last but not least, diverse ecological roles of GZ in oceanic food webs were discussed.

5.1 Fatty acids transfer in gelatinous zooplankton involved food chain

Food condition has been recognized as a key factor for supporting an organism's survival, growth, and reproduction. In general, it refers to two aspects: food quantity and its quality. Food quantity regards to its availability, which often varies seasonally in the field. In aquatic systems, examples include the seasonal biomass variation of phytoplankton and zooplankton which are considered as prey for higher trophic levels such as fishes (Jürgens and Stolpe 1995). Food quality could be defined as three aspects (review by Müller-Navarra 2008): 1) Physical and biological properties: e.g. particle size, ingestion and assimilation properties. 2) nutritional compositions, e.g. amino acids, FAs; and 3) whether toxins are present.

As for polyp feeding ecology, there are plenty of papers that studied food quantity affecting polyps' fitness (Han and Uye 2010; Lesniowski et al. 2015; Wang et al. 2015a). In contrast, effects of food quality have not well documented. In this dissertation, certain FAs have been addressed as essential biomolecules and highly unsaturated fatty acids (HUFAs) were applied as food quality indicators. The first highlight of this study is the relationship between thiamin supply and FA composition of the primary producers. Even though thiamin as an essential biomolecule in aquatic food webs has drawn attention for ecology studies (Giovannoni 2012; Sylvander 2013; Balk et al. 2016), the evidence on its transfer and function along marine food webs are still missing. In this dissertation, the results supported that thiamin provision might be involved in the FA synthesis in primary producers and could be further transferred to higher trophic levels, which in turn would drive shifts in food web structure and biogeochemical cycles. Secondly, the FA composition of the predator, *A. aurita* polyps, could be tracked back to their zooplankton prey. In contrast, the relative content of ARA in *A. aurita* showed a significantly distinct higher value than that in prey, which implies an unknown synthetic pathway in polyps. Following this finding, ARA could potentially serve as a FA marker to track the ecological roles of polyps in benthic ecosystems. Thirdly, the results describing the temperature effect on the FA composition of polyps were consistent with the findings of studies on other aquatic organisms such as algae, copepods, and fish (Sushchik et al. 2003; Laurel et al. 2012; Garzke et al. 2016). Here the results showed that the ratio of UFA: SFA of the polyp's prey, including copepods, is of critical importance. As polyps are overwintering organisms and energy supply during the winter season is relatively low due to low prey abundance. However, rare but high-quality prey (in respect of high UFA concentration) could compensate the energy insufficiency for the benthic overwintering population of *A. aurita* polyps. Even though the relationship between FA composition and polyps' life history traits need to be further investigated, in any case, we cannot overlook the importance of food quality, as it acts simultaneously with food quantity in the determination of an organism's fitness.

To summarize, the nutritional status of prey can be transferred through the phytoplankton-zooplankton interface further to higher trophic levels (Boersma et al. 2008), but this process depends on environmental temperature conditions. Thus, high food quality of prey, simultaneously with sufficient food quantity under optimum abiotic conditions, is important to meet the nutritional requirement of organisms and potentially alter the functioning and biochemical balance of the marine ecosystem.

5.2 Consequences of multiple stressors on the life history strategy of polyps

Life history traits development is fundamental in determining organism's life-history strategies (Ansell et al. 1994) and they are determined by trophic resources and environmental conditions (Thorson 1950; Ansell et al. 1994). As a follow-up study of Chapter 2, in Chapter 3, the potential effects of both food conditions (quality and quantity) and temperature were studied on the life history traits of polyps. Survival rate, somatic growth, and asexual reproduction (budding and strobilation) were assessed as the main traits of polyp's life history. In general, food quantity and temperature showed consistency with previous studies on polyp ecology, i.e. high food quality supported larger body size and more buds production, temperature had a negative effect on growth but positively affecting budding reproduction (Han and Uye 2010; Wang et al. 2015a). Polyps showed distinct life history plasticity attribute to temperature and certain life history modes (polyp, strobila, and podocyst) could be maintained under certain temperature ranges. In this chapter, at medium temperature (20 °C), the polyp mode could be maintained, while at low (13 °C) or high temperature (27 °C), polyp mode could potentially shift to the strobila or podocyst modes. In particular, polyps encountered severe mortality when a heatwave scenario was mimicked. To a large extent, both food quality and food quantity played critical roles at each life stage. A suitable food condition could optimize polyps' survival and growth. Moreover, it could act as a co-stimulate factor to induce strobilation and podocysts production.

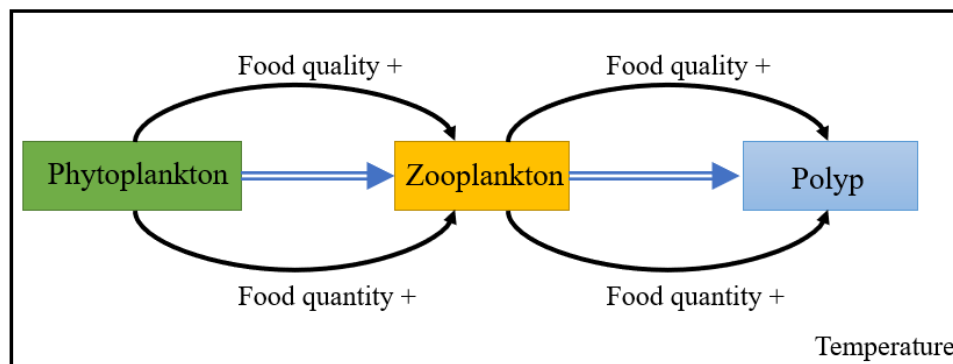


Fig. 5.1 The concept of superposition and limitation functions of food quality and food quantity on polyp's life history traits.

In this study, food quality was manipulated in two aspects: 1) different species and 2) different nutritional status. This corresponds to two food quality conditions similar to the field: 1) prey community composition differences and 2) prey chemical composition differences. These two

food quality aspects usually vary seasonally (Müller-Navarra and Lampert 1996). As an important complementary result to previous studies, the importance of food quality has been reinforced. Specifically, higher food quality could compensate heatwave stress leading to less mortality and support high production of budding and ephyrae production. Again, a co-function with food quantity plays an important role (Fig. 5.1). According to results from Chapter 2, in the respect of essential FA composition (i.e., HUFA) of polyps, a food source in low quantity but with high quality could be compared to a food source in high quantity but with low quality. Production capacity will be underestimated if food quality is overlooked. As mentioned above, in practice, this finding could be a possible explanation of polyp's overwintering survival strategy when deficiency food conditions are encountered.

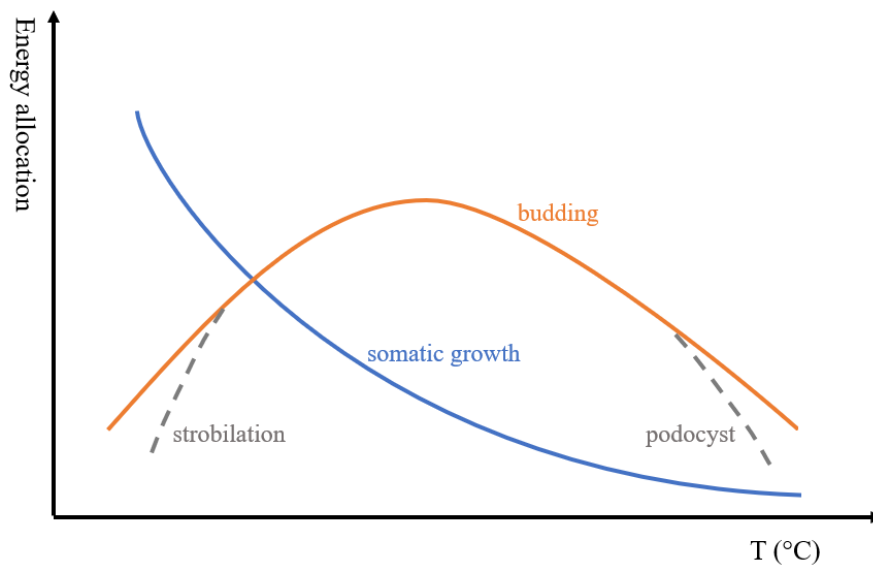


Fig. 5.2 Schematic cutline of energy allocation in polyp life history. Digested energy is allocated between somatic growth and budding reproduction. In certain food and temperature circumstances, the energy could be shunted by strobilation and podocyst production.

Nevertheless, the complexity of polyp's life history traits directed me towards the question on a more mechanistic understanding of energy allocation in each life stage (Fig. 5.2). Energy supplied from digested prey first meets the acquirement of basic metabolic demands for survival. In a sufficient food condition, spare energy could support the two vital activities of polyps, i.e. somatic growth and budding reproduction. This process, however, is also temperature dependent. At low temperature, more energy shunt to grow polyps to a larger size, while at medium temperature, spare energy could support more budding production. However, under the heatwave condition,

both activities will be limited because of the physiological stress on metabolisms from high temperature. As mentioned above, the effect of food condition is interrelated between food quality and quantity. Moreover, in low and high temperature, parts of energy could be shunted to strobilation and podocyst production, respectively. Nevertheless, to better understand polyps' life history strategy, further research is required to identify the energy thresholds for survival, somatic growth, and asexual reproduction under different food and temperature combinations.

5.3 The general figure of the “jelly web” in oceanic food webs

Chapter 4 provided the first large-scale assessments of the “jelly web” within oceanic food webs by applying SI analysis. Most notably, the jelly web covers nearly the whole isotopic space in the oceanic food webs of ETA, occupying at least three trophic levels and potentially consuming a large range of dietary sources. Further analysis of isotopic niche differentiation among GZ taxonomic groups confirmed their important role in different habitats. Moreover, significant isotopic niche overlaps were found between some specific taxonomic groups, revealing the potential predator-prey interactions or food sources competitions. Thus, once can argue that “jellyfish is not equal to jellyfish” drawn from distinct variations of SI values between different taxonomic groups. To sum up, findings provided through this work prove that the “jelly web” is more complex than previously defined and renounce the application of GZ as an average single trophic level, which is applied in most theoretical studies (reviewed by Pauly et al, 2009).

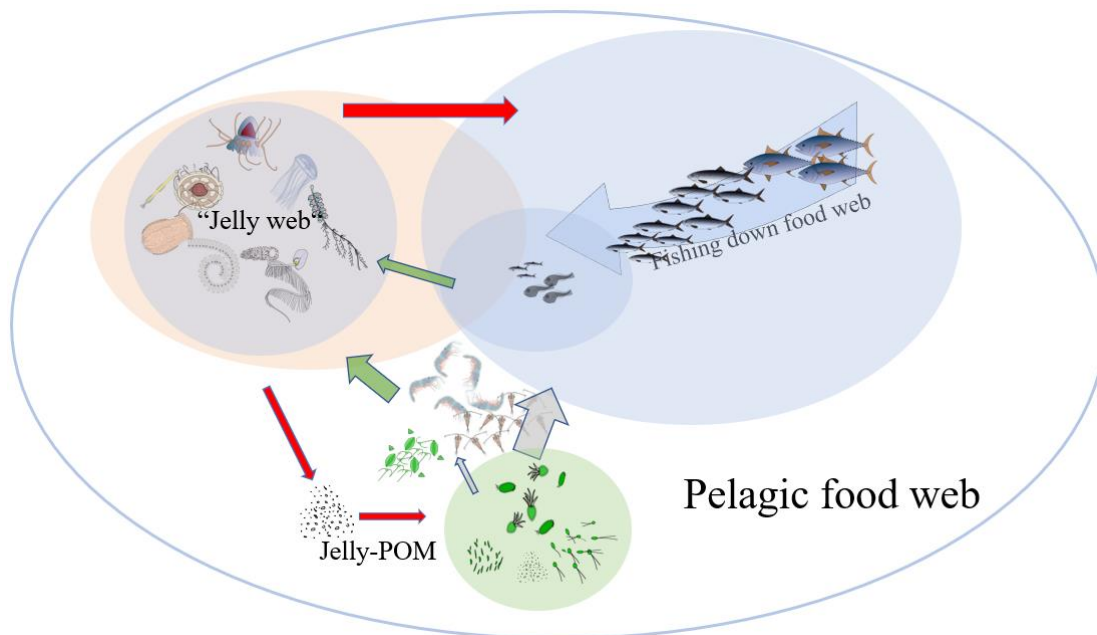


Fig. 5.3 Paradigm shifts in the “jelly web” and linkage with other food web elements.

Besides those remarkable isotopic niche characteristics within the “jelly web”, the aggregates of jellyfish small particles (jelly-POM) also links to the microbial loop (Bruland and Silver 1981; Lebrato et al. 2013) and the dead jellyfish bodies (jelly-falls) export carbons to benthic food webs (Fortier et al. 1994; Lebrato et al. 2012) (Fig. 5.3). In particular, in the context of “fishing down food webs” (Pauly et al. 1998) and jellyfish bloom conditions, whether the “jelly web” will expanding and consequently occupy more niche space should be examined under variable environmental conditions. Furthermore, compared to crustaceans, gelatinous organisms are easier to digest (Jackson et al. 1987; Arai et al. 2003) and cost less energy for their predators to capture which enables them to be a valuable food source, especially under bloom circumstances (Hays et al. 2018). Taken together, the trophic “dead-end” concept of GZ could be reformed. Nevertheless, the linkage of the jelly web, the microbial loop, fishes and the other food web elements should be integrated to generate a general concept of food web structure, which is critical for maintaining the stability of marine communities.

5.4 Outlook

Food quality as an important food condition indicator has been received special attention in this dissertation, with regards to FA transfer and determination of polyp’s life history traits. Moreover, the general structure and isotopic characteristics of the “jelly web” have been investigated. Following findings from these studies, further research directions could be addressed to GZ trophodynamics.

Bio-tracers applying in polyps’ trophic ecology studies: In this dissertation, FAs transfer was investigated in the benthic polyp stage. From the results of Chapter 2 and Chapter 3, certain FA or FA groups could be potentially used as a trophic marker in predation-prey interaction studies, as well as indicate food quality conditions of prey. A further question needs to be answered is whether the FA composition pattern in polyps can be further transferred to their pelagic stage *via* strobilation, i.e., the relationship of FA composition between polyps and ephyrae. Another research gap regarding polyps’ ecology is their ecological role in benthic systems. The findings of potential FA bio-marker, ARA, can be applied to address the trophic link between polyps and their predators. These studies should be addressed directly towards the question of life history and trophic ecology of polyps regarding biological adaptations and ecological mechanisms in benthic food webs.

The linkage between multiple environmental factors and life history strategy of polyps: *A. aurita*'s life history plasticity makes it an ideal model organism to unfold questions regarding the relationship between life history strategies and environmental factors. As discussed in the chapters, the polyp mode in the benthic stage has been received more attention. However, studies regarding strobila and podocyst modes need to be further described. Especially, food quality affecting polyps' life history traits was addressed in this dissertation, however, due to the experimental operation limitation, only three temperatures tested. I suggest conducting separate studies which take more detail regimes of food properties (both quality and quantity) and temperature to detect thresholds of environmental factors for each life history modes, thus, to frame a more detail figure for the concept of "tolerance curve".

Further research of the "jelly web": The general structure of the jelly web described in this thesis has only provided a pilot study in the level of taxonomic groups. To further understand coexistence and competition within the "jelly web" and the relationship with other food web elements, some other critical studies should be addressed: 1) even though a size dependency in variations of stable isotope values were detected in some taxonomic groups, further studies should be conducted in species level, which may link stable isotope variations to ontogenetic shifts in their life history; 2) due to the fragile nature and patchy distributions, net catching of GZ cannot stand for the complete "jelly web", thus, a combination of complementary approaches, including bio-tracers (FA and SI), SCA, eDNA, and *in situ* observations (blue water diving or ROV) should be applied to generate a more complete understanding of the trophic figure of the "jelly web" and further in the whole oceanic food webs.

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Chapter 2 Tracking fatty acids from phytoplankton to jellyfish polyps under different stress regimes: a three trophic levels experiment

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Authors: Xupeng Chi, Jamileh Javidpour, Ulrich Sommer, Doerthe C. Mueller-Navarra

Contributions: XC and JJ designed the experiment, XC implement the experiment and analyzed fatty acids samples. XC, JJ, US, and DM-N analyzed data, discussed the results, and wrote the paper.

Chapter 3 Food quality matters: interplay among food quality, food quantity and temperature affecting life history traits of *Aurelia aurita* (Cnidaria: Scyphozoa) polyps

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Contributions: XC and JJ designed the experiment, XC implement the experiment, SH analyzed thiamin samples, all authors discussed the results and wrote the paper.

Chapter 4 Tackling the jelly web: new insights into the trophic ecology of gelatinous zooplankton in the eastern tropical Atlantic oceanic food webs

To be submitted to *Limnology and Oceanography*.

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Contributions: XC, FL and AD collected the samples, XC and TH analyzed stable isotope samples, BC and HJH organized the cruise, XC, JD and JJ analyzed the data, all authors wrote the manuscript.

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Research Interests

- Population dynamics and ecology of gelatinous zooplankton. Consequences of environmental change on upgrading and transferring of essential biomolecules (vitamin, fatty acids, etc.) in “jelly webs” and their roles in history strategy of gelatinous zooplankton.
- Trophic structure and niche characteristics of marine food webs and especially the role of gelatinous zooplankton in different oceanic features (e.g., seamount, oxygen minimum zone (OMZ), and eddy) of tropical and polar regions.
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Publications

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Chi, X., Dierking, J., Hoving, H., Lüskow, F., Denda, A., Christian, B., Sommer, U., Hansen, T., Javidpour, J. *Tackling the jelly web: new insights into the trophic ecology of gelatinous zooplankton in Eastern tropical Atlantic oceanic food webs*. (Submitted to Limnol Oceanogr)

Stenvers, V and **Chi, X.**, Javidpour, J. *Seasonal Variability of the Fatty Acid Composition in Aurelia aurita: Implications for Gelativorous Food Web Studies*. (To be submitted to J Plankton Res).

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Lüskow, F., Hoving, H. J., Christiansen, B., **Chi, X.**, Silva, P., Neitzel, P., Jaspers, C. *Distribution and biomass of gelatinous zooplankton in relation to an oxygen minimum zone and a shallow seamount in the Eastern Tropical Atlantic Ocean*. (under review at Mar Biol Res).

Christiansen, B., Buchholz, C., Buchholz, F., **Chi, X.**, Christiansen, S., Denda, A., Fabrizio, E., Hauss, H., Hoving, H. J. T., Janßen, S., Kaufmann, M., Kronschnabel, A., Lischka, A., Lüskow, F., Martin, B., Merten, V., Silva, P., Pinheiro, N., Springer, B., Zankl, S. and Zeimet, T. (2016) *SEAMOX: The Influence of Seamounts and Oxygen Minimum Zones on Pelagic Fauna in the Eastern Tropical Atlantic Cruise No. MSM49 November 28 - December 21, 2015 Las Palmas de Gran Canaria (Spain) - Mindelo (Republic of Cape Verde)*. Maria S. Merian-Berichte, MSM49. DFG-Senatskommission für Ozeanographie, Bremen, Germany, 42 pp. doi: 10.2312/cr_msm49.

Conferences and workshops

30.05-03.06, 2016. 5thInternational Jellyfish Bloom Symposium. Barcelona, Spain. *Combined effects of food quality, food quantity and temperature on somatic growth, asexual reproduction and fatty acid composition of Aurelia aurita polyps*. Poster presentation.

13.09-15.09, 2017. Youmares 8, Ecosystems dynamics in a changing world: regime shifts and resilience in marine communities. Kiel, Germany. Oral presentation.

15.02-17.02, 2017. Plankton biodiversity, dynamic eco-physiology, and ecosystem function. Bremen, Germany. JAMSTEC-ZMT workshop.

Teaching experiences

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Declaration

I, Xupeng Chi, hereby declare that the dissertation submitted, entitled “The role of gelatinous zooplankton in coastal and oceanic food webs: life history strategy and trophic ecology” was written independently by me and only using the sources listed. The content and design of this thesis, apart from the supervisor’s guidance, is my own work. The thesis has not been submitted either partially or wholly as a part of a doctoral degree to another examining body and is my first and only doctoral procedure. Chapter 2 and Chapter 3 of this thesis were published in the peer reviewed journals in 2018. The authors' share of the manuscripts is explained in the section "Author contributions". This work has been prepared respecting the Rules of Good Scientific Practice of the German Research Foundation. I have not been deprived of an academic degree.

Kiel, 16.02.2019

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