

Larval fish dynamics in changing environments

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Chapter 1

General introduction

Planktonic organisms have by definition a very limited ability to choose their habitat by active migration to favourable habitats. They are constantly exposed to external forces, which themselves are highly dynamic, such as wind and temperature. Even more important, however, are the influences of these abiotic parameters on key factors such as food availability or physiological processes like growth and reproduction. As an evolutionary consequence of the inability to escape unfavourable conditions like neustonic organisms do by simply swimming away, planktonic organisms have developed sophisticated mechanisms to cope with varying conditions. In the case of autotrophic organisms, these comprise varying light intensities which are tackled by restructuring or activating and deactivating of pigments (Falkowski & Raven 1997) or several adaptations to fluctuating nutrient levels (Klausmeier et al. 2004). In the case of heterotrophs, these are the storage of energy in the form of lipids in food-rich times (Sargent & Falk-Petersen 1988), and the production of resting eggs in unfavourable conditions as done by daphniids during the clear-water phases in summer in freshwater systems (Alekseev & Lampert 2001) or by copepods during the winter in many marine systems (Uye 1985). Another adaptation is the wide range of trophic levels zooplankters can prey upon. Especially copepods can feed on autotrophs, microzooplankton as well as on their own conspecifics and congeners. This maximises the chance of finding food in a variety of different environmental situations. The planktonic stages of fish have still other adaptations to the highly variable conditions: they simultaneously exploit internal (yolk) and external food sources and rapidly develop to enhance their swimming ability, which significantly improves both their escape as well as their hunting abilities. Whereas the reactions of crustacean zooplankters to different environmental conditions are fairly well-studied, and the effects of temperature and feeding environment are well established, this information is largely lacking for the next trophic level, the larval fish. Hence, in this thesis I concentrate on the reaction of larval fish to changes in the environmental conditions, especially since the larval phase of many fish is pivotal in the regulation of year-class strength.

The German Bight is a typical example for a highly variable marine ecosystem. It is part of the North Sea, a temperate marine shelf sea of the North East Atlantic. The water temperature varies from a mean minimum temperature of 2°C in winter to 18°C as the mean maximum temperature in summer (Wiltshire & Manly 2004). Day length varies from 7 to 17 hours and the area is frequently hit by storms in the winter half year, while the summer is usually calm. This leads to a mixed water body in winter and a certain degree of stratification during the summer months (Haren & Howarth 2004). The dissolved nutrient levels vary from

2 $\mu\text{mol l}^{-1}$ phosphate in winter to below the detection limits in late spring, nitrate decreases from 100 $\mu\text{mol l}^{-1}$ to virtually zero and silicate usually decreases from 30 $\mu\text{mol l}^{-1}$ to zero in late spring as a result of primary production. The mean diatom day, a proxy for the occurrence of the spring diatom bloom is usually found between the middle of February and the middle of March (Wiltshire & Manly 2004), with carbon concentrations of the phytoplankton as high as 1000 $\mu\text{g l}^{-1}$ (Wiltshire, pers. comm.). Zooplankton densities are very low during winter and they increase rapidly in response to increasing primary production (Greve et al. 2004). Overall, the biotic and abiotic processes involved in structuring the North Sea ecosystem around Helgoland show a high variability and seasonality. The way in which larval fish cope with such a magnitude of variability is the overall subject of this thesis.

In the following, the introduction will continue with a review of hypotheses developed to explain the large variations in year-class strength of many fish species, including some examples of studies supporting the single concepts. This is followed by a description of several attempts to include larval stages of fish into studies on the recruitment of fishes, which leads to a description of possible causes for the general failure to predict recruitment by the use of larval fish proxies. This leads to the introduction of alternative larval fish measures and how they might potentially be implemented into recruitment studies. This introduction ends with a description of the structure of this thesis and how the single chapters fit into the topics addressed in this introduction.

Concepts of year-class strength regulation

Even though larval fish are to a certain degree adapted to environmental variability the effects of such variable conditions on larval survival are limited, as mortality rates in the early life history of fish are very high, and large inter-annual fluctuations in year-class strength are known to occur in fish stocks. As this is such a relevant issue, especially in economically exploited stocks, many researchers have studied potential mechanisms determining year-class strength regulation through larval survival. These are briefly introduced here. Hjort (1914) was the first to recognize that there was a possible link between early life stages of fishes and the large variation in year-class strength. He pointed out that the larval phase is of utmost importance for consecutive year-class strength and hypothesized that larval mortality is not constant but that there are critical periods with elevated vulnerability. He speculated that one of these periods might be the transition phase from internal to external feeding. In his second important contribution to the understanding of year-class fluctuations Hjort (1926) stressed the possible impact of losses of larvae caused by unfavourable drift patterns to food-poor offshore areas on consecutive year-class strength. He stated: "I had myself to leave the possibilities and their respective influence [starvation mortality at first feeding

larvae vs. transport to unfavourable regions], if any, on the formation of the stock undecided, and the final decision in this matter may *still* be said to be open for discussion” (my italics). This was over eighty years ago, and although our knowledge on recruitment of fish has expanded enormously, the concluding statement made by Hjort is still very valid today.

Several additional concepts to those developed by Hjort were put forward to disentangle the myriad of factors behind year-class variation. The possible regulation of population size by density-dependent mechanisms was introduced by Solomon (1949), who reported the possibility of density-dependent mortality and density-dependent fecundity as natural regulators of animal populations. This aspect was picked up by Ricker (1954) and Beverton and Holt (1957), who considered density-dependent mortalities more important than density-dependent mechanisms acting on growth or fecundity. Cushing reverted to Hjort’s findings on seasonality of food availability and larval occurrence in the plankton, formulating his match/mismatch hypothesis (Cushing 1974). He showed that in temperate marine systems the hatch of fish species is temporally rather constant with a standard deviation of 5 to 10 days of peak spawning, but that the periods of maximum primary production and subsequently zooplankton production are highly variable. Hence, he hypothesized that the year-class strength of fish populations is regulated by a temporally match or mismatch between the timing of larval production and timing of primary production and the subsequent growth of zooplankton which can be utilized as food by larval fish. Support from field studies for his hypothesis is given in Cushing’s update of his match/mismatch hypothesis (Cushing 1990) in which he extends his hypothesis from temperate marine systems to specific areas of mesotrophic subtropical and tropical seas. The equator-wards extension of his approach is mainly focused on upwelling systems, which act similar to spring blooms in temperate marine systems by a temporary outburst of biomass in upwelling situations. In case of coastal systems, the problem of advective losses in severe upwelling situations was addressed by several authors (Bakun & Parrish 1982, Cury & Roy 1989, “optimum environmental window concept”) and there is evidence that recruitment depends on upwelling events in the absence of turbulence which is the case under moderate upwelling conditions. In offshore systems, however, high wind stress leads to local divergence. Such conditions enable an upward flux of cold, nutrient-rich deepwater to the surface, enhancing plankton production. Tunas, for example, are known to exploit such local and temporal restricted upwelling events in the Pacific to meet their feeding demands as well as the demands of their larvae. Yamanaka (1978) established a relationship between water temperature and year-class strength for four tuna stocks in the Pacific. He found a higher proportion of strong year-classes at lower temperatures, and thus, a strong correlation to years with high upwelling activity.

As an alternative, Sinclair offered his “member/vagrant hypothesis” (Sinclair 1988). This hypothesis mainly states that regulation of population sizes can be attributed to spatial

processes alone and that there may be no need to introduce “energy processes” like mortality due to starvation, predation or diseases. Sinclair reasons that staying a member of a given population is most important. This can only be achieved by being retained in a restricted geographically area. Although prey densities are also important, Sinclair argues that, on the population level, it does not matter whether the larva that has become a vagrant (which means being dispersed out of the restricted area) was a feeding one or one that will die since it is anyhow lost for the population. Obviously, support for this explanation also exists, most notably for anchovy in the South African Benguela current. Here, Hutchings et al. (2002) attribute most of the year-class variability to larval losses to offshore regions by advective mechanisms. Sinclair’s hypothesis has recently received strong support from studies of mitochondrial DNA of cleaner gobies in the Caribbean (Palumbi & Warner 2003, Taylor & Hellberg 2003). The authors found distinct genetic populations of these gobies between island groups as well as within the waters of the same island. The striking aspect of these studies is the fact that the planktonic larval phase of the species lasts three weeks, a period that is long enough for the larvae to drift a distance of several hundreds of kilometres. Nevertheless, these populations are distinct and locally very restricted, which is attributed to hidden mechanisms of dispersal avoidance by the larvae. There is evidence for the existence of retention mechanisms, as larvae of these species are commonly found further inshore than the larvae of other comparable reef fishes.

Simultaneously to the publication of Cushing’s match/mismatch hypothesis, Lasker (1975) was able to show that only increased prey densities in the chlorophyll layer compared to the low prey densities in the rest of the water column during stratified situations were able to maintain larval growth. These findings were based on on-board experiments, where surface water and water from the chlorophyll maximum was offered as a food source to larval northern anchovy (*Engraulis mordax*). In these experiments only the higher densities of prey typically found in the chlorophyll maximum layer were enough to ensure a sufficient food supply. Furthermore, a validation and ecological significance for Lasker’s hypothesis was reported as the stratified water body was mixed by a storm and obliterated the chlorophyll layer. Water from all depths did not contain sufficient numbers of prey to maintain growth in the experiments of the two following days. The findings led to the stable ocean hypothesis (Lasker 1981), which is supported by several studies (Cury & Roy 1989, Lough & Mountain 1996) and has been implemented into population dynamic models (Megrey et al. 1996).

In addition to these more general hypotheses and concepts, some more local hypotheses on fishes’ adaptations to their environment were put forward. Frank and Leggett (Frank & Leggett 1981, 1982a, 1983) set up a concept for capelin (*Mallotus villosus*) as well as larvae of other fish species in Conception Bay (Newfoundland), that hatch from demersal eggs. Their “safe-site concept” states that there are favourable and unfavourable periods for a larva

to enter the plankton. The bad period is characterized by prevailing offshore winds, which are responsible for upwelling events. These cold water masses feature low prey densities and high invertebrate abundances. The safe-site period is characterized by onshore winds which bring warm water to the coast, leading to a high density of suitable prey organisms and low predator densities. The adaptive emergence strategy states that larvae from demersal eggs emerge during these safe-site situations, triggered by rapidly rising temperatures. Furthermore, Gronkjaer and Clemmesen (1997) reported the necessity of ascending to the surface for Baltic cod larvae in the Bornholm Basin to reach areas of low predation and high food concentrations.

In short, many theories exist on larval survival and recruitment, none of them is so general that it can be used in every case, and all of these concepts have their advantages and disadvantages.

Application of larval fish proxies in recruitment studies

Until now, only a few attempts were satisfying in linking dynamics of early life stages of fish to population dynamics. Those that were used are mixtures and combinations of the concepts introduced above. These include studies on Baltic cod (*Gadus morhua*); (Köster et al. 2001), on North Sea plaice (*Pleuronectes platessa*) (Van der Veer et al. 1998) and on South African anchovy (*Engraulis capensis*) (Hutchings 1992, Hutchings et al. 1998, Painting et al. 1998, Hutchings et al. 2002). Köster et al. (2001) were able to explain 69% of the observed variability in 0-group year-class strength of Baltic cod by linking it to larval abundance. Van der Veer et al. (1998) demonstrated that inter-annual variability in dispersal of plaice eggs and larvae from the spawning area in the Southern Bight of the North Sea towards the Dutch coastal nursery areas was a key factor in determining year-class strength of plaice. Hutchings et al. (Hutchings 1992, Hutchings et al. 1998, Hutchings et al. 2002) also showed that a successful egg and larval transport from the spawning grounds at the Agulhas Bank to the nursery ground in the north of South Africa determines later recruitment.

However, all the studies share one major problem: the calculation of mortality rates and abundances of the different live stages of fish are derived from field surveys. A good temporal and spatial match between the surveys and larval production as well as a good knowledge of spatio-temporal variation is imperative for obtaining reliable results. Even two of the successful applications of larval proxies into recruitment studies report of years of total miscalculations. In both instances, the surveys didn't match the production period or area because of a delayed spawning season (Köster et al. 2001) or did not match the area of egg dispersal (Huggett et al. 1998, Painting et al. 1998). The risk of a lack of match between larval production and surveys can be minimized by a good knowledge about the ecology of the target species. For many marine ecosystems including the North Sea, detailed

information on the timing and duration of larval fish in the ichthyoplankton is mostly lacking (but see von Westernhagen et al. 2002, but see Greve et al. 2005). Chapter 2 of this thesis contributes to fill this gap.

Alternative larval proxies including survival probability

None of the three above-mentioned examples for the successful link between early life stages of fish and subsequent recruitment goes further than using “simple” measures like larval abundances, even if it is clear that mortality is not constant over the larval development (Hjort 1914). Mortality in the field is caused by either predation or starvation. The actual predation pressure is very hard to study in marine systems but as predation is believed to be a function of fitness (Elliott & Leggett 1998) and fitness is believed to be a function of nutritional condition (Frank & Leggett 1982b, Peterson & Wroblewski 1984), there is hope to overcome the predation problem indirectly by means of condition indices. Pepin et al. (1999) were the first to demonstrate condition-selective mortality in a field study. Numerous studies on larval condition have been conducted, using histological measurements (Johnston et al. 1975, Ehrlich et al. 1976), nucleic acid-based indices (Clemmesen 1994, 1996, Suthers et al. 1996, Clemmesen et al. 2003, Clemmesen & Röhrscheidt 2004), protein-based indices (Buckley 1982, Goolish et al. 1984, Mathers et al. 1993, McLaughlin et al. 1995a, Gronkjaer et al. 1997, Buckley et al. 2004), lipids (Ehrlich 1974) as well as digestive enzymes (Govoni 1986, Segner et al. 1989, Troschel et al. 1991, Segner et al. 1993). Ferron and Leggett (1994) reviewed this topic extensively and concluded that nucleic acid- and protein-based indices are the most promising ones. The most-widely accepted method as a proxy for fish condition has been the normalisation of RNA content to DNA content expressed as the RNA:DNA ratio. Typically when RNA:DNA, RNA:protein, protein/DNA and RNA concentrations are correlated with recent growth, RNA:DNA ratios explain the largest part of the variance (Malloy & Targett 1994). The basic idea is that the amount of DNA per cell is constant, whereas the amount of RNA varies with the feeding situation and thus reflects growth very well. In addition to defining the nutritional situation of the organisms, the RNA:DNA ratio can also be applied as a proxy for growth rate and survival probability if water temperatures are known. This approach has been validated in many laboratory and field studies (Buckley 1984, Clemmesen 1994, Theilacker et al. 1996, Gronkjaer et al. 1997, Rooker et al. 1997, Caldarone et al. 2003, Caldarone 2005). Estimation of recent growth or condition from larval nucleic acid content requires, however, normalisation and adjustment for larval age, developmental stage or size (Buckley et al. 1999). Most field studies revealed a high degree of variation between individuals, but the general outcome was that usually a high proportion of good-conditioned larvae are caught (Ferron & Leggett 1994, Clemmesen 1996, Chicharo 1997, Chicharo et al. 2003). Nevertheless, there are also studies that found

no clear link between the nutritional condition of larval condition and prey densities. McGurk et al. (1992) found no relationship between the condition of sandeel and pacific herring caught at Port Moller (Alaska) to either temperature or prey abundance. Caldarone et al. (2003) also found no relationship between prey densities and RNA:DNA ratios in a laboratory experiment, although their interpretation was different. This shows, that there is an urgent need for studies designed to explain the degree of dependence on prey densities and other factors affecting larval condition. To gain a better understanding of mechanisms influencing larval nutritional condition, and therewith survival, the work described in Chapter 3 was carried out.

The role of food quality

In addition to food availability and hydrographic conditions, the availability of nutrients is an important agent in controlling planktonic processes in aquatic systems. During phytoplankton blooms the nutrient availability for primary producers decreases drastically with the duration of the bloom. Algae do not keep the nutrient ratios within individuals constant i.e. they are not homeostatic (Sterner & Elser 2002). This enables them to adapt their physiology to unstable nutrient conditions by adjusting their anabolic strategies to the available nutrient levels. Under phosphorus-rich conditions, algae allocate the assembly machinery (ribosomes, P-rich), whereas under phosphorus-poor situations the investment into the resource acquisition machinery is enhanced (nutrient uptake proteins and mitochondria, N-rich) (Klausmeier et al. 2004). This ultimately leads to a high variability of nutrient ratios in algae and they therefore represent a food source of variable quality for herbivores. In contrast, zooplankton organisms retain their elemental composition to a high degree, displaying a strong homeostasis (Sterner & Elser 2002). Under the assumption that an animal is not energy-limited, food with high C:nutrient ratios creates costs due to the need of having to deal with ingested excess carbon. These costs rise with an increase in the difference between producer and consumers C:nutrient ratios and may be paid by a decrease in growth and reproductive rates (Boersma 2000, Boersma et al. 2001, Boersma & Kreutzer 2002).

Algae serve as the base for most aquatic food webs not only by transforming CO₂ into highly energetic molecules, but also by constructing essential food components like fatty acids and pigments (Partali et al. 1985, Anderson et al. 2003). Essential fatty acids are needed e.g. for the maintenance of membrane fluidity (Farkas et al. 2001), they act as precursors for longer chained fatty acids (Olsen 1999, von Elert 2002), or as precursors for hormones and play a role in gene expression as e.g. DHA regulates genes involved in skeletal development (Cahu et al. 2003). Pigments play a major role as antioxidants (Hairston 1976, Edge et al. 1997) and in vision.

Poor food quality can influence primary consumers in two ways; on the one hand by the alterations in biochemical composition of the consumers as these are mostly not homeostatic when it comes to biochemical molecules, and on the other hand by decreased growth and reproductive rates (DeMott et al. 1998, Elser et al. 2000). For secondary consumers (e.g. larval fish) this can result either in variable prey qualities, if primary consumers adjust their biochemical composition to their food, or in prey quantity if the primary consumers compensate low food quality by low growth and reproductive rates. During the succession of a spring bloom this means that a fish larva potentially encounters low numbers of prey of high nutritional quality during the early bloom while during the decaying period of the bloom a high prey abundance of low food quality is encountered. Thus, high prey availability does not necessarily mean a high larval growth. In view of Cushing's match/mismatch hypothesis, this means that the match window between larval fish, a suitable quantity of prey items as well as their quality might be smaller or even shifted in time than it would be expected from prey quantity alone (Fig. 1).

The incorporation of food quality aspect into concepts on early life stages of fishes has a high potential to improve the existing models and to increase our knowledge on fish population dynamics in general. The incorporation of food quality may explain the failure of the above-cited studies to link condition indices to prey densities. Hence, there is an urgent need to understand processes regulating nutritional quality in the planktonic realm and to assess the relative importance of the impact of variable food quality on zooplankton and consequently on larval fish survival. A first promising step to improve our understanding on the role of food quality in food webs is described in Chapter 4.

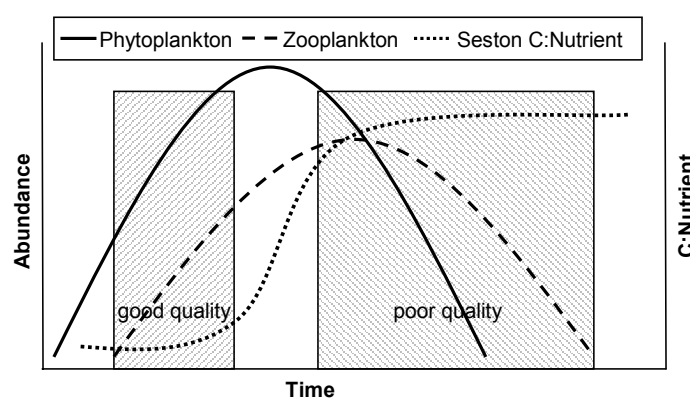


Fig. 1 Schematic sketch of a reasonable match between primary and secondary production. Larval fish feeding on zooplankton would face food of varying quality indicated by the Carbon:nutrient ratio.

Structure of the thesis

The above-cited concepts on the regulatory mechanisms of larval survival and subsequent year-class strength can be boiled down to Hjort's two main statements: factors related to feeding or drift patterns. This thesis takes up the food-related thread and mainly tests the validity of Cushing's match/mismatch hypothesis (Cushing 1974, 1990). As it consists of several assumptions, no study following a single approach can serve to test it. The first assumption of the theoretical framework of Cushing is that the timing of larval fish production is temporally fixed to a great extent. This can only be tested by a field survey over several years, and the results are given in Chapter 2 of this thesis.

Chapter 2 is based on a three years ichthyoplankton survey featuring a temporal resolution of at least three samples per week at Helgoland Roads, a fixed station near the Island of Helgoland in the German Bight, North Sea. A detailed description of the larval fish community and recurring assemblages, the occurrence, duration and peak abundance is given to gain knowledge about the degree of variability, but also about stability within and between years.

The second assumption of Cushing's hypothesis is the necessity of a temporal match between larval and prey production, i.e. the dependence of larval fish on high prey concentrations to survive the larval stages. This hypothesis is tested in Chapter 3 by the use of a high temporal resolution set of environmental data and of data on the nutritional condition of larval dab and sandeel, covering the complete occurrence of larvae of these two species in the ichthyoplankton.

The low dependence of larval fish nutritional condition on prey availability shown in Chapter 3 and in several other studies (examples cited in (Sinclair 1988)) leads to investigations on other food-related aspects such as food quality. The vast majority of field and laboratory studies in fisheries oceanography on growth and survival of larval fish focussed on food in terms of abundance. Chapter 4 deals with an extension of Cushing's hypothesis. His work was based on abundance only, but not only food quantity but also food quality varies with time (Fig. 1). In this chapter, two experiments on the propagation of food quality signals through tri-trophic food chains are used to test the hypothesis that food quality effects of mineral-limited algae are compensated by primary consumers and hence play no role for larval fish nutrition.

This thesis leads from observations of variation on the population level to variation in the nutritional condition on the individual level in field samples, to the lowermost level causing variable nutritional conditions, the effects of mineral nutrients assessed in laboratory experiments. Due to the unique three-pronged approach of investigating larval abundance, condition and the factors that lead to changes in fish densities and conditions, this study is a major step forward towards a better understanding of processes that govern survival of larval fish and hence improves our ability to understand and successfully predict recruitment and year-class strength in fish.

Chapter 2

Year-to-year variation in larval fish assemblages of the Southern North Sea

In order to test the temporal stability within and the reproducibility of larval fish assemblages between years, the larval fish community at Helgoland Roads, North Sea (NE Atlantic) was quantitatively sampled on an almost daily basis from 2003 to 2005. The survey resulted in a total of 462 samples containing 50.000 larval fish of at least 42 species. The larval fish assemblage was mainly dominated by larvae emerging from demersal eggs in winter. This changed gradually to larvae hatching from pelagic eggs. These larvae dominated the ichthyoplankton community in summer. A remarkably stable seasonality with recurring, season-specific fish assemblages was observed over the three years, despite substantial variation in environmental conditions. After removal of the lesser sandeel (*Ammodytes marinus*) from the analysis, the most abundant larvae in the samples, and the only species which showed significant fluctuations in abundance between the years, the dominance patterns of the remaining fish species were also very close.

2.1 Introduction

On any timescale, planktonic communities are never static. Changes in community structure might occur as a result of disturbance events such as storms, or be caused by more gradual environmental changes. The intra-annual succession in temperate marine ecosystems is characterized by slight changes in timescales of days, but by strong environmental changes in terms of months or seasons. These changes happen regularly and predictably. Environmental signals such as light and nutrients for phytoplankters or temperature and food availability for zooplankters are the main forcing factors of the seasonal succession of plankton communities. These factors can vary substantially between years (Edwards & Richardson 2004, Wiltshire & Manly 2004) and therefore open windows for different phytoplankton and zooplankton species adapted best to the combinations of the different factors. The level of response to e.g. temperature changes varies between functional groups and trophic levels (Edwards & Richardson 2004) and temporal mismatches between producers and consumers may be the consequence. Cushing (1974, 1990) proposed in his match/ mismatch hypothesis that fish year-class strength could be regulated by these mechanisms, i.e. a match or mismatch between the production of larval fish and their food. While holoplanktonic organisms can be found in the plankton, at least in small numbers, throughout the year, meroplanktonic organisms like the larvae of most fish species have a temporally limited occurrence in the planktonic community. Greve et al. (2005) used the strong coupling of temperature and the phenology of most fish species to predict the occurrence of several meroplanktonic species on the basis of the ambient temperatures, and was very successful in doing so, as long as the occurrence of the different species is of a short to moderate duration. Together with the observations of Köster et al. (2001), who showed that larval fish abundance can be used as a recruitment predictor this is a major step forward in our understanding of recruitment and year-class strength determination of marine fish. However, knowledge of the duration of the planktonic larval fish stages is essential to be able to implement these findings properly into recruitment models. For the design and interpretation of fish larvae surveys it is vitally important to match the period of larval occurrence in the plankton (Wieland et al. 2000, Köster et al. 2003), otherwise abundance will be underestimated and this will result in weak larval abundance-recruitment-relationships (Bradford 1992).

The majority of marine organisms exhibit life stages exposed to be dispersed by currents (Cowen et al. 2000). In the case of fish, these are planktonic eggs and larvae, or in case of species with demersal eggs, only the larval stages. In general, species with pelagic eggs tend to reproduce in the proximity to consistent hydrographic phenomena such as gyres and fronts that increase food abundance (Harden Jones 1968, Loeb 1980). In contrast, the

strategy of spawning demersal eggs bets more on local conditions at the time of larval emergence as the drift period is shortened by the time of egg incubation. Dispersal can have positive and negative effects on the survival probability and recruitment success of larval fish (Sinclair 1988). For example, Hutchings (1992) showed that recruitment of South African anchovy relies on a successful transport to nursery grounds and that unfavourable winds can result in a massive loss of larvae to offshore waters. Even without invoking changing currents one can make predictions whether producing demersal or pelagic eggs is the best strategy under which conditions. Egg development as well as the duration of the larval stage is highly temperature-dependent with low temperatures leading to long egg incubation times. Hence, it is likely that in different spawning seasons pelagic and demersal eggs have different success rates. Because developmental rates are low in winter, a moderate drift time can be realized by the combination of demersal eggs and planktonic larvae; in summer, however, pelagic eggs might prolong the pelagic phase by the time of egg incubation. We thus hypothesize that a large proportion of larval fish caught in winter should hatch from demersal eggs and that this changes gradually to pelagic eggs in summer.

Cushing's match/mismatch hypothesis (Cushing 1974) on fish year-class strength regulation is based on two main assumptions: (1) The timing of food production is variable and (2) The timing of larval production is fixed in time. In this study we investigate this second assumption of the match/mismatch hypothesis using a three year, high temporal resolution, single location ichthyoplankton survey at Helgoland Roads, located in the North Sea (NE Atlantic).

2.2 Material and Methods

The ichthyoplankton community was surveyed over a three year period at 54°11.18'N and 07°54.00'E, which is known as Helgoland Roads. Weather-permitting, the station was sampled on a work daily basis, usually resulting in three to five samples per week. The station is located between the Island of Helgoland and the adjacent dune in the German Bight, North Sea. The water depth at the station is approximately 10 m and the water column is mixed throughout the year due to strong tidal currents (up to 1.5 knots). The area is characterized by a strong seasonality. The water temperature ranges from 0-3°C in February up to 20°C in August. After subtraction of tidal currents, the residual flow direction in the area is northerly from the English Channel to the Northern North Sea. The salinity varies between 30 and 33. Usually, a spring phytoplankton bloom develops in early March (Wiltshire & Manly 2004) and the secondary production follows the phytoplankton growth (Greve et al. 2004). A second, smaller phytoplankton bloom often can be found later in the year.

For the larval surveys, a CalCOFI ring trawl with a 500 μm mesh net (aperture 100 cm, length 400 cm, equipped with a flow meter) was towed for 15 min from a research vessel. The samples were transferred to the laboratory, fish larvae were sorted out immediately and classified to the species level according to Halbeisen (1988) and Russel (1976). Larval abundance was normalized to larvae m^{-3} . Members of the family Syngnathidae (pipefishes and seahorses) were excluded from the analyses as they are not a regular part of the ichthyoplankton and occurred only occasionally after storms.

In order to test seasonal changes in the contribution of demersal and pelagic eggs, the attributes “demersal” and “pelagic” were assigned to each species of larvae found during this study. A value of zero or one was attributed to demersal and pelagic eggs respectively. Afterwards, the mean for each sampling was calculated. To detect general patterns rather than the influence of single dominant species, no weighting for larval abundance was done, i.e. a sample containing 20 larval sandeel emerged from benthic eggs and a single larval cod hatched from a pelagic egg would result in a value of 0.5.

A nested ANOVA was used to test for differences in larval abundance between years as well as months, in a similar way as this was done by Witting et al. (1999). The 12 most abundant species of the study were used for the analysis. The weeks used for the analysis were not calendar weeks but were established using 7 day intervals from the first day of the year on, months were intervals of 4 weeks, making them slightly different from calendar months. Only the months in which larvae of a certain species were caught were included in the corresponding analysis except in the case of *Arnoglossus laterna* and *Sardina pilchardus*. For the first, month 4 and 5 were omitted as in both only one specimen was caught. Month 10 was excluded from the sardine analysis for the same reason. The larval abundance data were log-transformed prior to the analysis. The variance components for each hierarchical level were calculated following Sokal and Rohlf (1995).

The abundance dominance rank for each species was calculated by the percentage contribution of each species to the total abundance of the given year. The coefficient of variation of the ranks between the years was calculated by the division of the standard deviation of the ranks by the mean rank multiplied by 100. Spearman rank correlations were calculated for the detection of variability in dominance rankings between the years. Species diversity was investigated using Shannon Wiener diversity (Shannon & Weaver 1963) and Pielou’s evenness (Pielou 1969). Community analyses were conducted by calculating Bray-Curtis similarities of square root-transformed weekly mean abundance data. The similarities were entered in a hierarchical cluster analysis. The calculations of diversity measures, similarities and clusters were done using the software package PRIMER 5.0 (© 2001 Primer-E Ltd.). ANOVA and Spearman’s rank correlations were calculated by the software package Statistica 6.1 (StatSoft, Inc.)

2.3 Results

During the three year of investigation a total of 462 samples were taken. These samples contained 50,632 larval fish of at least 42 species. The three years of the investigation differed strongly in terms of total larval abundance. 2003 and 2004 showed two pronounced abundance peaks from the mid of February to the end of April and a second peak in June and July. Additionally, 2004 exhibited high abundances in the middle of January. 2005 generally showed lower catches and no pronounced abundance peaks (Fig. 2).

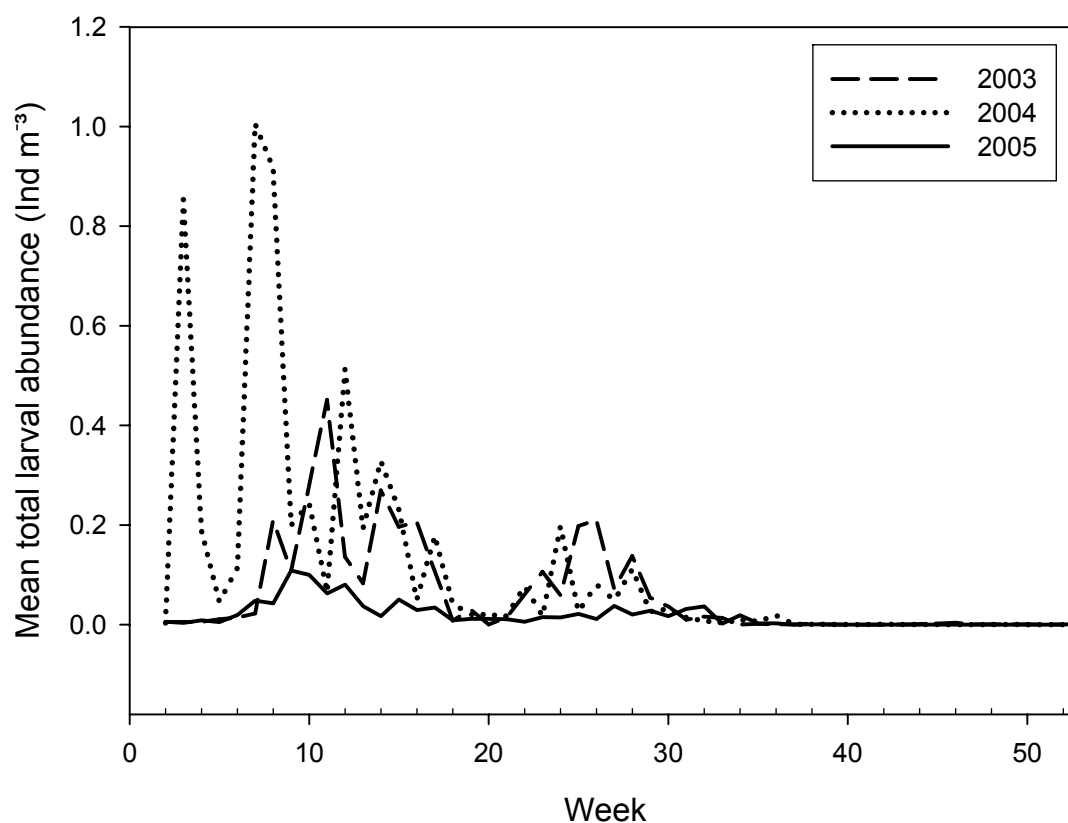


Fig. 2 Mean weekly larval abundances of the years 2003-2005.

The mean temperatures of the first 8 months, in which 99% of the cumulative abundance was reached in all three years under investigation didn't show significant differences (9.9°C in 2003, 9.9°C in 2004 and 9.7°C in 2005). In contrast, the mean winter temperatures (week 1-10) showed more pronounced differences, with 2003 showing the coldest winter and 2004 and 2005 being more similar (4.0, 4.8 and 4.8 respectively). A major difference between winter 2004 and 2005 was the temperature trajectory. While 2004 showed only a slight

decrease in temperature from week 1-10 (6.0°C to 4.3°C), 2005 was characterized by a decrease from 6.9°C to 2.9°C (Fig. 3).

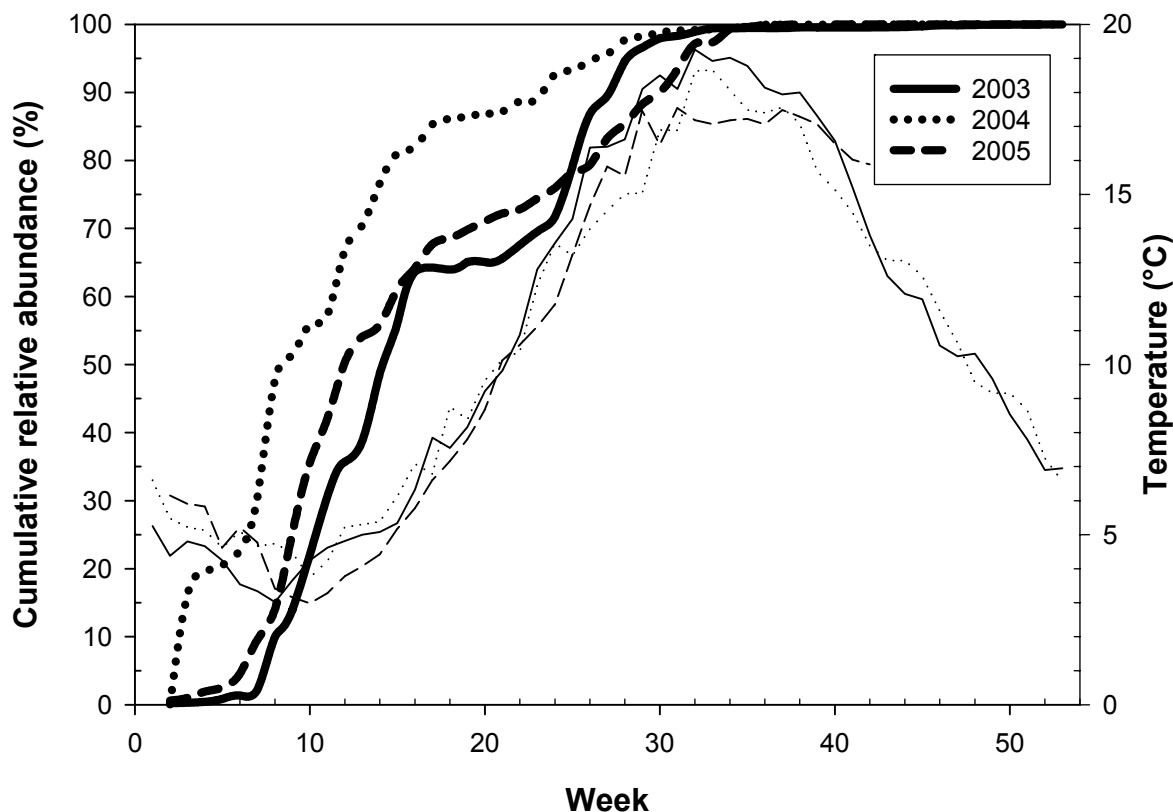


Fig. 3 Cumulative relative abundance of the total larval catch from 2003-2005 (total abundance scaled to 100%) and the weekly temperature means. Sandeel included. Thick lines are larval cumulative abundances and thin lines represent temperature in the different years.

The total larval cumulative abundance showed similar shapes but differences in timing. The development of the cumulative abundance in 2004 was always two to three weeks ahead of those of 2005 and even one week longer compared to 2003. In week 10 of 2004, 55% of the total larval abundance was already caught, while in 2005 it was 35% and in 2003 it was just 20% (Fig. 3). Removing the dominant sandeel from the cumulative abundance curves, a higher temporal match between the years was observed. As the 2004 and 2005 curves were virtually congruent, it seems that in species other than sandeel the development of the cumulative abundance seemed to be triggered by mean temperatures rather than by temperature trajectory (Fig. 4)

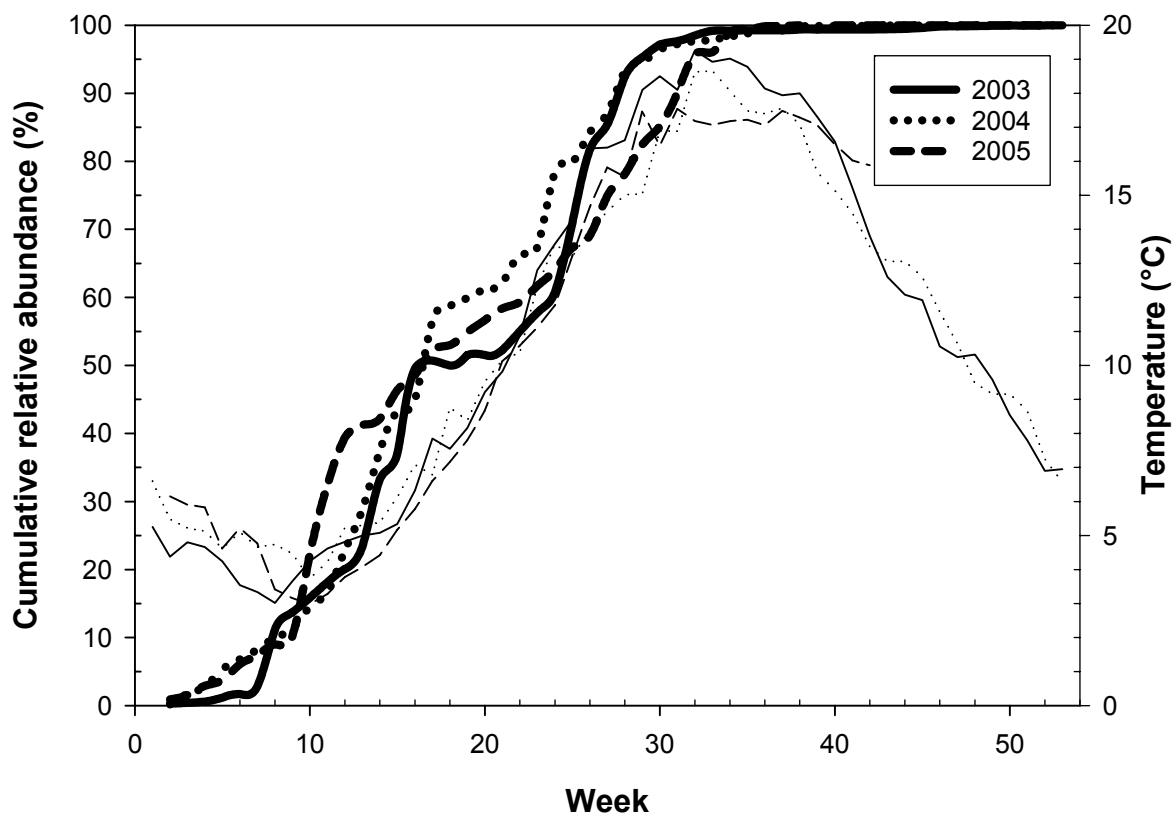


Fig. 4 Cumulative relative abundance of the total larval catch from 2003-2005 (total abundance scaled to 100%) and the weekly temperature means. Sandeel excluded. Thick lines are larval cumulative abundances and thin lines represent temperature in the different years.

A nested ANOVA was used to test for temporal differences in larval abundance. The lowest level of the nested ANOVA explained the largest part of the total observed variation (Table 1). Nevertheless, eight of the twelve most abundant species showed significant variation in months nested within years. Variation between the years was significant only in case of the lesser sandeel. In three of the twelve species none of the two higher levels explained a significant part of the observed variation. This implies no significant differences between years and between months within years and hence, a high degree of temporal stability for sculpin, sardine and the great sandeel. The great sandeel and the sardine showed comparable results in the ANOVA, but the CV in the first species was just half of that observed in sardine, giving the great sandeel the highest predictability of the species addressed in this study.

Table 1 Nested ANOVA results of the 12 most abundant species of this study. Data analysed are weekly mean larval densities. 4 values for weeks are nested within month, months are nested within years. The percentages of explained variance by each level are given. (ns= $p>0.05$, * = $p<0.05$, ** $p<0.01$, *** $p<0.001$).

	Year	Month within year	Week within month and year	Month range	Mean density (Ind 100 m ⁻³)	CV%
<i>Ammodytes marinus</i>	23.2 *	13.4 ns	63.4	1-5	64.5	90.4
<i>Limanda limanda</i>	0.1 ns	52.6 ***	47.3	1-7	17.1	80.5
<i>Sardina pilchardus</i>	>0.1 ns	6.6 ns	93.4	6-9	15.9	114.1
Gobiidae spp.	7.2 ns	31.8 **	61.0	4-8	11.3	77.9
<i>Trachurus trachurus</i>	>0.1 ns	75.0 ***	25.0	6-9	8.8	81.4
<i>Agonus cataphractus</i>	>0.1 ns	43.4 **	56.6	1-4	8.5	31.2
<i>Callionymus lyra</i>	>0.1 ns	49.2 ***	50.8	4-9	6.1	52.0
<i>Myoxocephalus scorpius</i>	1.2 ns	11.5 ns	87.3	1-3	6.0	106.9
<i>Buglossidium luteum</i>	>0.1 ns	35.5 **	64.5	5-8	5.7	56.0
<i>Arnoglossus laterna</i>	>0.1 ns	53.8 ***	46.2	4-9	3.9	46.1
<i>Hyperoplus immaculatus</i>	>0.1 ns	6.7 ns	93.3	4-10	3.7	64.3
<i>Taurulus bubalis</i>	4.2 ns	30.1 **	65.7	3-7	3.2	82.6

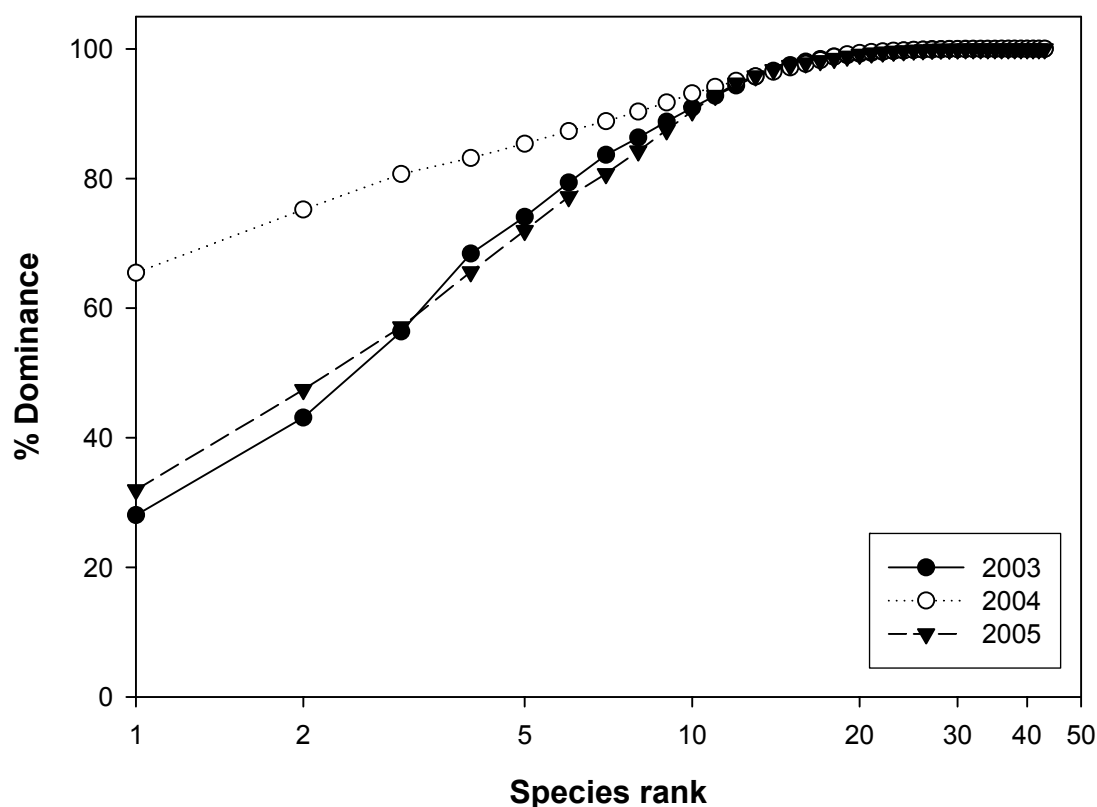


Fig. 5 Cumulative dominance plot of the three years of the investigation. Species sorted by dominance ranks. Lesser sandeel (*A. marinus*) included.

The dominance patterns clearly separated 2004 from the other two years. The lesser sandeel made up 75% of the total catch in 2004 (Fig. 5) while it accounted for roughly 30% in the other two years. In 2003 and 2005 the ten most dominant species accounted for 90% of the total catch; in the sandeel-dominated 2004 it took only eight species to reach the same level. Excluding sandeel from the dominance analysis revealed remarkably similar curves (Fig. 6). The rankings within the years were significantly correlated between the three years (Spearman's Rank correlation, $p < 0.05$) with correlation coefficients from 0.85 to 0.88. Dominance ranks are given in Table 2.

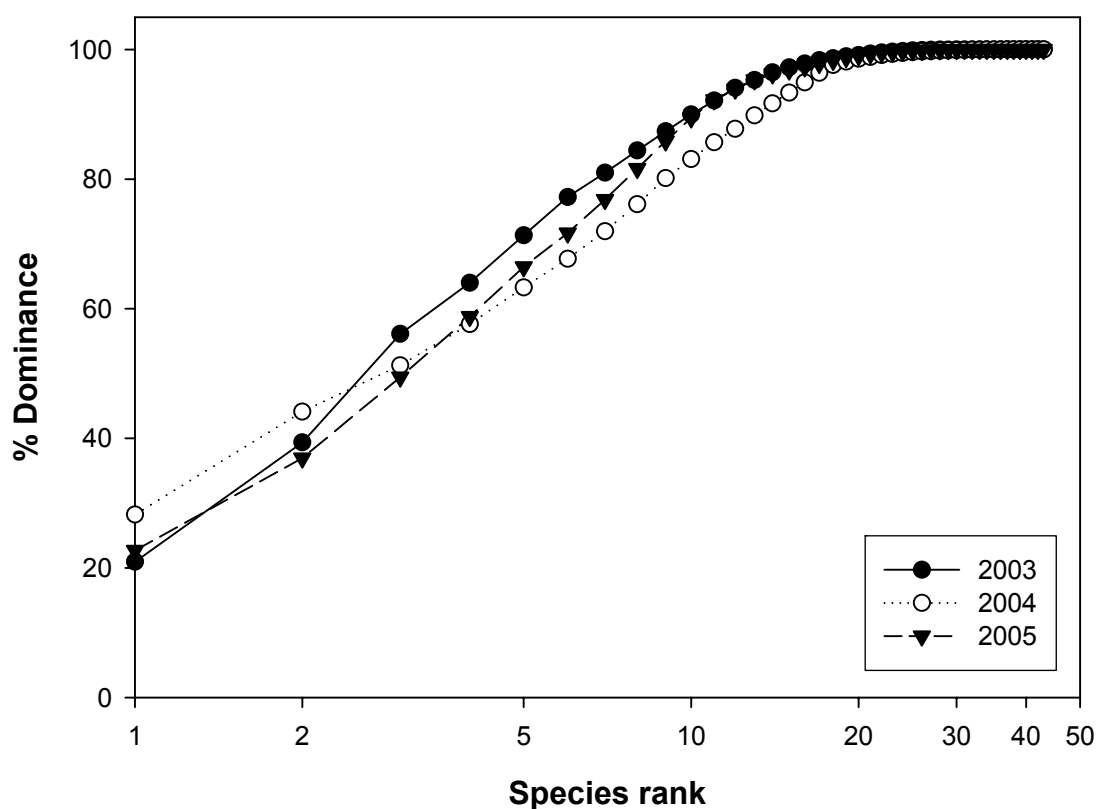


Fig. 6 Cumulative dominance plot of the three years of the investigation. Species sorted by dominance ranks. Lesser sandeel (*A. marinus*) excluded.

Table 2 List of species caught during the study period. Given are the total catch (individuals), the months of occurrence in the ichthyoplankton, the amount of hauls containing the given species (Freq.), the relative contribution to the total catch (%), the rank of the contribution to the total abundance for each year, the mean rank of the contribution to the total yearly abundance and the temperature range in which larvae of a given species were caught.

Species	Total catch	Months of occurrence	Frequency	% of total catch	Rank abundance			mean Rank \pm S.D.	Temperature (°C)
					2003	2004	2005		
<i>Ammodytes marinus</i>	28,184	1-5	142	55.7	1	1	1	1 \pm 0	2,7 - 10,2
<i>Limanda limanda</i>	4,387	1-7	150	8.7	2	2	5	3 \pm 1.8	2,8 - 18
<i>Agonus cataphractus</i>	2,867	1-4	99	5.7	7	6	2	5 \pm 2.7	2,8 - 6,6
Gobiidae spp.	2,850	4-8	132	5.6	3	3	9	5 \pm 3.5	7 - 19,1
<i>Trachurus trachurus</i>	1,910	5-9	112	3.8	4	10	4	6 \pm 3.5	11,1 - 19,1
<i>Sardina pilchardus</i>	1,584	5-10	69	3.1	11	11	3	8.4 \pm 4.7	11,2 - 18,5
<i>Callionymus lyra</i>	1,504	4-9	122	3.0	5	4	6	5 \pm 1	7 - 18,7
<i>Buglossidium luteum</i>	1,155	5-8	109	2.3	6	5	8	6.4 \pm 1.6	9,9 - 18,8
<i>Arnoglossus laterna</i>	916	4-9	97	1.8	9	8	10	9 \pm 1	7 - 19,7
<i>Hyperoplus immaculatus</i>	735	4-9	82	1.5	10	16	7	11 \pm 4.6	6,2 - 18,2
<i>Engraulis encrasicolus</i>	682	6-8	22	1.3	n.c.	9	16	12.5 \pm 5	14,6 - 19,1
<i>Taurulus bubalis</i>	639	12-3	73	1.3	17	7	12	12 \pm 5	2,9 - 17,3
<i>Pholis gunnellus</i>	537	1-3	42	1.1	13	13	14	13.4 \pm 0.6	2,9 - 6,2
<i>Liparis</i> spp.	505	1-6	102	1.0	16	19	11	15.4 \pm 4.1	2,8 - 13,7
<i>Myoxocephalus scorpius</i>	443	1-3	41	0.9	8	14	18	13.4 \pm 5.1	2,8 - 5,6
<i>Gadus morhua</i>	367	1-5	62	0.7	22	15	15	17.4 \pm 4.1	2,8 - 7,9
<i>Sprattus sprattus</i>	353	4-8	59	0.7	12	18	13	14.4 \pm 3.3	6 - 18,7
<i>Platichthys flesus</i>	306	2-7	34	0.6	14	12	21	15.7 \pm 4.8	3,5 - 16,4
Indet species	202	1-9	46	0.4	15	17	26	19.4 \pm 5.9	4,3 - 19,7
<i>Scomber scombrus</i>	104	6-8	27	0.2	25	21	17	21 \pm 4	13 - 18,3
Rocklings	73	1-7	38	0.1	n.c.	20	22	21 \pm 1.5	5,2 - 15,8
<i>Eutrigla gurnadus</i>	57	4-8	34	0.1	20	26	20	22 \pm 3.5	7 - 18,7
<i>Merlangius merlangus</i>	52	1-5	22	0.1	18	23	23	21.4 \pm 2.9	2,9 - 9,8
<i>Ctenolabrus rupestris</i>	51	6-8	24	0.1	24	27	19	23.4 \pm 4.1	14,3 - 18,6
<i>Trisopterus esmarkii</i>	28	1-2	6	0.1	n.c.	22	n.c.	28.4 \pm 5.6	4,5 - 5
<i>Gymnammodytes semisquamatus</i>	21	10-12	9	>0.1	21	n.c.	n.c.	30.7 \pm 9.1	8,2 - 12,6
<i>Clupeide</i> indet	17	6-8	6	>0.1	30	24	n.c.	27 \pm 4.3	13,2 - 19,7
<i>Chirolophis ascanii</i>	16	1-2	9	>0.1	n.c.	29	24	26.5 \pm 3.6	4,5 - 6,2
<i>Raniceps raninus</i>	16	5-7	11	>0.1	27	28	27	27.4 \pm 0.6	8,2 - 18,1
<i>Psetta maxima</i>	14	6-8	10	>0.1	29	31	25	28.4 \pm 3.1	12,8 - 18,4
<i>Belone belone</i>	12	7-7	3	>0.1	23	30	n.c.	26.5 \pm 5	15,2 - 17,3
<i>Pollachius pollachius</i>	11	5-5	2	>0.1	n.c.	25	n.c.	28 \pm 4.3	8,6 - 10,1
<i>Blenius</i> spp.	9	5-10	7	>0.1	26	32	n.c.	30 \pm 3.5	9,7 - 18,1
<i>Pleuronectes platessa</i>	7	2-7	4	>0.1	19	n.c.	n.c.	29 \pm 14.2	3,2 - 14,6
<i>Cyclopterus lumpenus</i>	4	5-5	3	>0.1	n.c.	n.c.	28	32.7 \pm 5.7	10,2 - 10,4
<i>Hippoglossoides platessoides</i>	3	6-8	3	>0.1	28	n.c.	31	29.5 \pm 2.2	15,6 - 17,5
<i>Microchirus variegatus</i>	3	5-7	3	>0.1	n.c.	36	29	32.5 \pm 5	11,2 - 15,2
<i>Trachinus vipera</i>	3	4-7	3	>0.1	n.c.	34	30	32 \pm 2.9	7,2 - 16,8
<i>Clupea harengus</i>	2	3-3	2	>0.1	n.c.	33	n.c.	32 \pm 1	5,2 - 5,3
<i>Mullus surmuletus</i>	1	7-7	1	>0.1	n.c.	38	n.c.	33.7 \pm 3.8	14,8 - 14,8
<i>Phycis blennoides</i>	1	8-8	1	>0.1	n.c.	35	n.c.	32.7 \pm 2.1	18,1 - 18,1
<i>Scopthalmus rhombus</i>	1	7-7	1	>0.1	n.c.	37	n.c.	33.4 \pm 3.3	16,8 - 16,8

The Shannon Wiener diversity of the larval fish assemblage showed an annual recurring pattern. The first part of the year was characterized by a relatively low diversity in the range of 0.3 to 1.0. This changed roughly at the end of May to values around 1.5 and was more or less constant until the middle of August. Afterwards the diversity decreased dramatically indicating the end of the larval fish production season (Fig. 7).

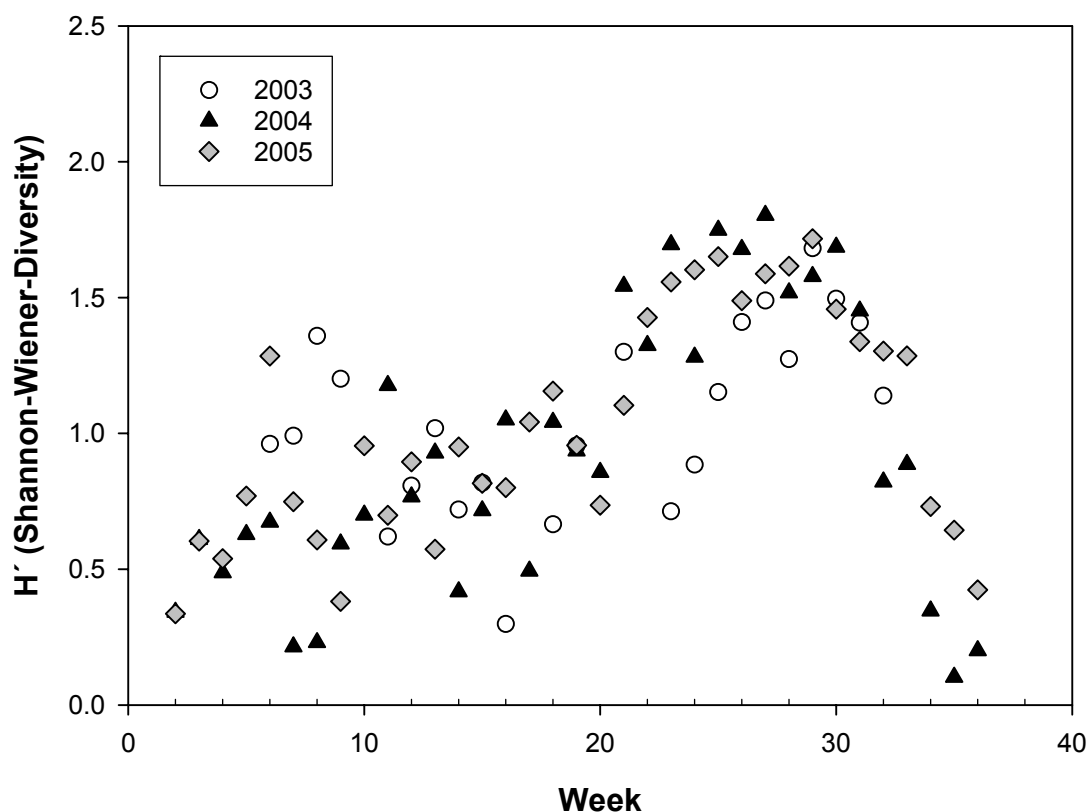


Fig. 7 **Shannon Wiener diversity of the larval fish community sampled from 2003-2005**

The clustering of samples revealed two distinct clusters at a similarity of 10%. These were a winter/spring and a summer cluster. The winter/spring cluster itself could further be separated into a distinct January group, consisting of weeks 2-5 of all the three years and a spring cluster uniting the weeks 5 to 16. The spring cluster consisted of several groups, which could be divided into a distinct sandeel-dominated group from 2004, a big cluster representing the whole spring 2005 and a last cluster consisting of spring samples from 2003 and 2005. These latter two clusters were separated at a similarity of roughly 50%. The summer cluster could be divided into an early summer group, ranging from May to mid-June (weeks 18- 25), and a later summer group aggregating weeks 25-35 (mid-June to end of August). Samples from autumn and the beginning of winter showed no clear cluster as catches were rare and displayed usually a single species at very low densities (Fig. 8). Fig. 8

represents a cluster analysis of all data from 2003-2005 and because there were no obvious differences between the years, it is used as representative for the single years.

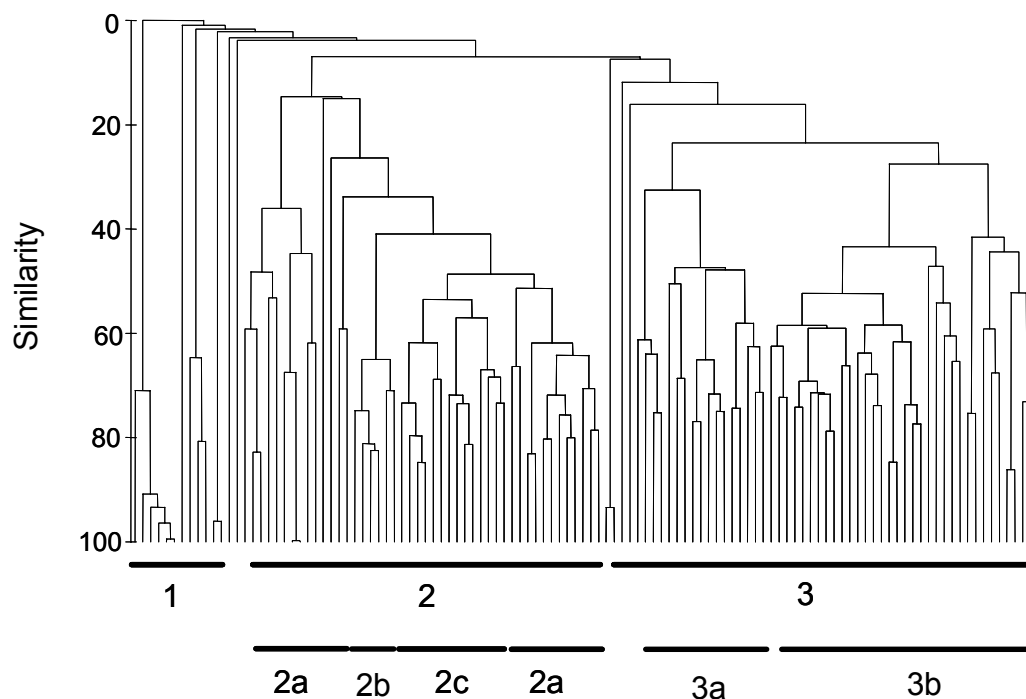


Fig. 8 Cluster analysis of Bray-Curtis similarities of samples from 2003- 2005. Similarities are calculated using mean weekly fish larvae abundance. Data are square root-transformed. 1: winter; 2: spring (2a spring 2003 & 2004; 2b sandeel-dominated weeks all years; 2c spring 2005); 3: summer (3a early summer; 3b late summer)

Cluster analysis on the species caught revealed stable, recurrent species assemblages over the years. Again, two main clusters represented distinct winter/spring and summer larval fish communities. The winter/spring community could be broken down to two groups. One always contained seasnail species (the two native species *Liparis liparis* and *L. montagui* were not discriminated in this study), the rock gunnel *Pholis gunnellus* and the sculpin *Myoxocephalus scorpius*. The second always contained the lesser sandeel *Ammodytes marinus*, dab *Limanda limanda* and the bullhead *Tauruulus bubalis*. Hooknose, cod, plaice, whiting and flounder (*Agonus cataphractus*, *Gadus morhua*, *Pleuronetes platessa*, *Merlangius merlangus*, and *Platichthys flesus*) could be found in both clusters during the three years. The summer cluster was always composed of solenette, dragonet, gobies, scaldfish, pilchard and horse mackerel (*Buglossidium luteum*, *Callionymus lyra*, undetermined Gobiidae, *Arnoglossus laterna*, *Sardina pilchardus* and *Trachurus trachurus*) and some other species, which were minor abundant or not caught in all years (Fig. 9).

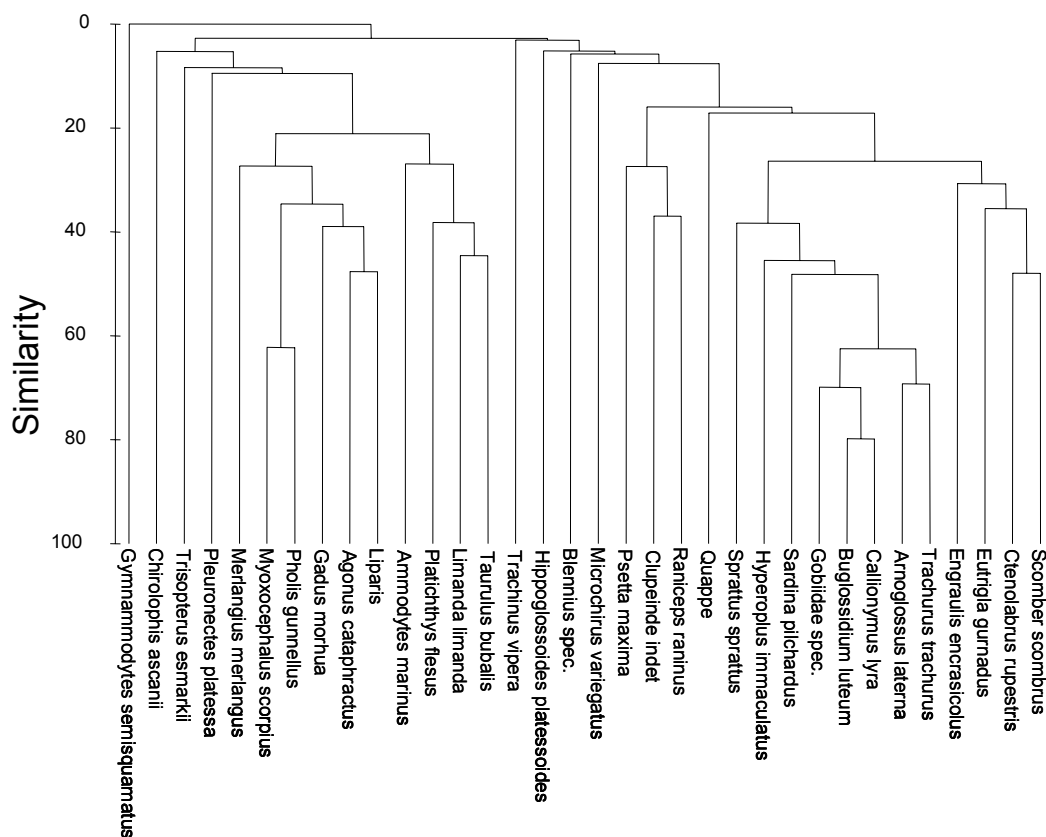


Fig. 9 Cluster analysis of Bray-Curtis similarities of larval fish assemblages for 2003-2005. Bray-Curtis similarities of mean weekly fish larvae abundance are given. Data are square root-transformed

Larvae collected during the monitoring campaign showed a clear trend in egg types (demersal vs. planktonic). In winter, most of the larvae emerged from demersal eggs. This changed gradually until summer, where the majority of the larvae hatched from pelagic eggs (Fig. 10).

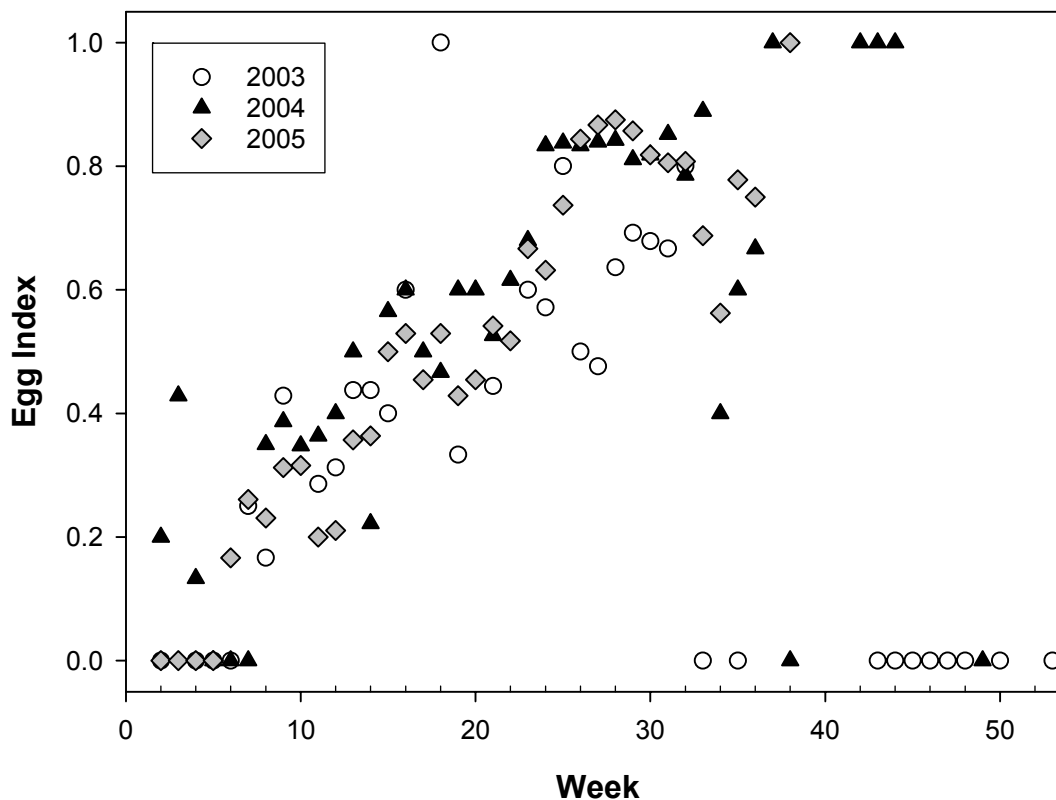


Fig. 10 Egg index corresponding to the larvae observed in the ichthyoplankton. (0 means all larvae in the sample emerged from demersal eggs; 1 means all species in the sample had pelagic eggs.)

2.4 Discussion

Larval fish communities have been found to be influenced by a large variety of factors such as currents (Meekan et al. 2006), upwelling systems (Hutchings et al. 1998, Painting et al. 1998, Hutchings et al. 2002) or haline fronts (Grioche et al. 1999, Munk et al. 2002). Implicitly, this means that to find significant differences between areas the variation within areas must be relatively low. This has not been made explicit in any of the studies cited above. Hence, the aim of our study was to look at the temporal stability of larval fish communities within one locality. Furthermore we wanted to investigate whether the premise of Cushing's match/mismatch hypothesis that larval fish production is temporally constant really holds.

Processes in poikilotherm organisms are regulated by temperature. In this study we showed that the winter temperature influenced the succession of total larval fish abundance in the ichthyoplankton. The relative cumulative abundance showed pronounced differences between the years of observation with the coldest year led to delayed larval occurrence. Contrasting to Greve et al. (2005), two of the three years showed a pronounced difference in

the cumulative abundance despite the same mean winter temperatures. This could be explained by differences in temperature trajectory between the years. The exclusion of the dominant species, the lesser sandeel, suggests a development which is triggered by the mean temperature rather than by temperature trajectory. This indicates that the hatch of the lesser sandeel is triggered by temperature rather than by cumulative temperatures and may be used as an explanation why Greve et al. (2005) were not able to predict sandeel seasonality by mean winter temperatures. A similar observation has been reported by Frank and Leggett (1981, 1982a). They were able to demonstrate that the emergence of larvae of several species to the pelagial was strongly triggered by rising temperatures. Our results are not as pronounced as those reported by Frank and Leggett (1981, 1982a), and this may be attributed to the more severe changes in water temperature in Conception Bay, Newfoundland, than those observed in the North Sea.

We observed some temperature-related shifts in the development of the cumulative larval abundances between the three years of observation, which were solely attributable to lesser sandeel. Leaving sandeel out of the analysis we observed no differences between the years when adding all of the caught fish together.

What about the different species in the larval community? The results of the nested ANOVAs indicated that the largest part of the observed variability in the temporal abundance distribution of single species was within the two lower levels, weeks and months. This implied a strong stability between years, which is further corroborated by the results from the cluster analysis. Only in the case of the lesser sandeel, the abundances differed significantly between years. Additionally, the cluster analysis revealed clear, distinct species assemblages and a recurring seasonality. A relatively low inter-annual variation as well as a high stability of species assemblages was also described in the few studies comparing assemblages between years for different temperate marine areas (Allen & Barker 1990, Witting et al. 1999). Variation between years was highest in spring as shown by the distinct spring 2005 cluster and the clustering of the strongly sandeel dominated samples in spring 2004. The summer situation did not display distinct groups of different years, suggesting similar recurring abundances and reflecting the stable dominance patterns.

The two diversity states found in spring and summer are characterized by differences in species richness. The summer assemblage consisted of 7-10 species, while the spring assemblage usually comprised 3-5 species. The only other study carried out in the German Bight (von Westernhagen et al. 2002) sampled the pelagic eggs of fish rather than their larvae, between 1984 and 2000. Von Westernhagen et al. (von Westernhagen et al. 2002) reported a positive relationship between the amount of species collected and the water temperature during their sampling period from February to July. When we concentrated on the same period as the authors cited above, we also observed this relationship, but

incorporating the species-poor late summer and autumn samples clearly disturbed the correlation between temperature and species richness.

In this study we showed a clear succession of larvae emerged from demersal eggs in winter to larvae hatched from pelagic eggs in summer. Richards (1959) observed a similar trend of changes in egg types from demersal to pelagic with ongoing season for the Long Island waters (USA) as we described it for Helgoland Roads in the North Sea. The proportion of larvae emerged from demersal eggs in the cold season was somewhat higher in this study compared to the 60% Richards (1959) reported. Frank and Legget (1983) observed a similar pattern in Conception Bay, Newfoundland, and attributed these finding to the “adaptive emergence” and the “safe site” concept they established earlier (Frank & Leggett 1981, 1982a). The “safe site” concept states that there are favourable and unfavourable times for a larva to enter the plankton. The bad one in the case of Frank and Legget (1981, 1982a) is characterized by prevailing offshore winds, which are responsible for upwelling events. These cold water masses contain low prey densities and high invertebrate abundances. The safe site is characterized by onshore winds bringing warm water to the coast, which is rich in suitable prey organisms and shows low predator densities. The adaptive emergence strategy then states that larvae from demersal eggs emerge in these safe site situations, triggered by rapidly rising temperatures. These concepts are reflected in rapid changes in the abundance of larvae hatched from pelagic or demersal eggs and can therefore not explain the more gradual change from demersal to pelagic observed in our study. This can be explained with the absence of such strong differences between water masses in the North Sea. At the Helgoland Roads station, changes in abiotic and biotic features of the water masses due to changes in prevailing wind directions are only detectable in rare and very harsh weather conditions and therefore, the evolutionary mechanism selecting for rapid reactions acting on the Newfoundland species probably did not work on the species in our study. Nevertheless, we observed the change from demersal to pelagic eggs, but in our case it is more likely that long egg incubations at low temperatures combined with pelagic eggs would be a unfavourable strategy because it makes the fate of these pelagic eggs unpredictable in terms of drift patterns. A drift period of several weeks in the North Sea might well result in a drift out of the shallow North Sea, which would mean the end e.g. for sandeel larvae, which are dependent on suitable sandbanks at the end of their drift phase. Advection has indeed been shown to be a major cause of egg and larval losses e.g. in the Baltic Sea (Baumann et al., Hinrichsen et al. 2003) and the Benguela System (Hutchings et al. 2002). Additionally, a prolonged drift phase may increase egg mortality (McGurk 1986). A second explanation might be the harsh conditions in the shallow North Sea in winter. Bunn (2000) discussed the potential of egg mortality caused by mechanical stress due to storms for several species with pelagic eggs and concluded that wind-induced stress may be a cause of massive mortality

for pelagic fish eggs. Hence, frequent storms in winter will lead to a mixed water body and may increase the risk of eggs being mechanically damaged by wave action, which may also favour demersal eggs in winter. On the other hand, a moderate amount of dispersal is needed to explore new habitats or reach nursery grounds (Van der Veer et al. 1998, Van der Veer et al. 2000, Köster et al. 2003). This seems to be achieved by a compensation of the decrease of the duration of the planktonic phase caused by warmer water and by the preference towards pelagic eggs with rising temperatures.

In summary, the larval fish community around Helgoland is remarkably stable in terms of the occurrence of the different meroplanktonic fish larvae as well as the species composition despite changes in environmental conditions. The larval fish assemblages could clearly be separated into several recurring seasonal assemblages over the three years of investigation. The dominance patterns were also stable and showed little variation from year to year and a clear succession from demersal eggs in winter to pelagic eggs in summer was shown. In conclusion, this study supports Cushing's assumption that larval fish production is fixed in time, with the exception of the lesser sandeel.

Chapter 3

Changing environments and the nutritional condition of larval dab and lesser sandeel

We investigated the nutritional condition of larval fish caught in daily ichthyoplankton hauls carried out from February to June 2004. We concentrated on larvae of dab (*Limanda limanda*) and lesser sandeel (*Ammodytes marinus*) in order to contrast early life stages of iteroparous and nearly semelparous fish. Larvae were analysed for length, weight and their RNA:DNA ratio as a proxy for the condition of the larvae. The relationship between larval nutritional condition and larval size gave indication for condition selective mortality due to a loss of poorly-conditioned larvae at larger size-classes. In larval sandeel, well conditioned larvae were present in all size-classes, whereas in larval dab the maximum larval condition rose with size. Variability in both standard length and condition was high in the two species during their planktonic stage. Both species showed a good nutritional condition in the early-mid-season and declines in condition in late April. This was more pronounced in larval dab, which showed a higher dependency on feeding conditions than larval sandeel did. Together these findings gave indication for a more conservative strategy of early life stages of the nearly semelparous sandeel.

3.1 Introduction

The only noteworthy parental care numerous larval fish species get is the amount of resources contained in the egg. This initial parental gift to their descendents varies among species and between pelagic and demersal eggs. Demersal eggs are usually larger in size, and the energy content of the eggs is positively related to egg size. Furthermore, demersal eggs are richer in energy than pelagic eggs of the same size (Loenning et al. 1988). Larvae that hatch from the more energy-rich demersal eggs have thus a better ability to cope with unfavourable nutritional conditions than larvae which emerge from smaller eggs (Miller et al. 1988, Einum & Fleming 2000, Fuiman 2002). Moreover, the variability in environmental conditions should select for larger egg sizes (McGinley et al. 1987). One could hypothesise that short-lived species, with only one or two spawning events during their lifetime should have an evolutionary history such that a specific proportion of larval survival is guaranteed under all circumstances. This is because the relative importance of a single spawning event is higher compared to long-lived species, which have a more iteroparous life-history. We thus hypothesize that short-lived species, living in highly variable environments, should have adapted to more conservative reproductive strategies through the production of larger eggs, longer spawning periods and longer transition phases from internal to external feeding to ensure that at least subsets of their offspring will survive.

There are many ways to assess performance of fish larvae, such as enzyme activity, otolith growth or the ratio between RNA:DNA in tissue. In this study, we assessed the condition of larval fish by means of the analysis of the ratio between RNA and DNA content in the organisms, a method commonly used in larval ecology and fisheries research. The general assumption is that the amount of DNA per cell is constant, while the amount of RNA per cell varies with anabolic activity. It has the advantage that it integrates the feeding history over a period of approx. three days (Clemmesen 1987, 1994), which makes it robust against short-term effects as shown for digestive enzymes (Ferron & Leggett 1994). The RNA:DNA ratio can be used in several ways; it can be used as a tool to investigate the nutritional condition and survival potential in laboratory experiments (Clemmesen 1987, 1994, 1996, St. John et al. 2001) as well as in field studies (Bulow 1987, Gronkjaer et al. 1997, Gronkjaer & Sand 2003) by comparing the ratios itself. Another widespread and promising use is its predictive power for protein growth as long as species-specific models are available (Buckley 1984, Buckley et al. 1984, Caldarone et al. 2003, Buckley et al. 2004). One shortcoming, however, is the temperature dependence of the RNA:DNA ratio itself. Higher RNA:DNA ratios at lower temperatures are believed to be a compensatory mechanism for the reduced efficiency of the anabolic machinery (Goolish et al. 1984). This makes comparisons over a wide range of temperatures, and hence the use in field studies, difficult as the same RNA:DNA ratio may

mean a different condition at different temperatures. Indeed, Malzahn et al. (2003) reported significant differences in RNA:DNA between larval coregonid fish reared under *ad libitum* food supply at two different temperatures (8°C and 18°C). However, albeit significant, the differences in RNA:DNA were only around 0.03 °C⁻¹, whereas studies with different food levels often report differences in the RNA:DNA ratio ranging from 1 to 3 in comparisons between fed and unfed larvae (McNamara et al. 1999, Suneetha et al. 1999, Rossi-Wongtschowski et al. 2003). Hence, the RNA:DNA ratio as a measure of nutritional condition can be used for larvae with a different thermal background.

Our hypothesis that shorter-lived species are more conservative translates directly into the prediction that larvae of short-lived species should be more independent of the current feeding conditions. We tested this prediction by contrasting larval stages of lesser sandeel (*Ammodytes marinus*) and dab (*Limanda limanda*), investigating their condition in the light of the prevailing environmental conditions. The lesser sandeel (*A. marinus*) is a short-lived species. It comprises up to one third of the total fishery yield in the North Sea (Arnott & Ruxton 2002) and it is a major food source for several predatory fish (Carruthers et al. 2005) and bird species (Furness & Tasker 2000, Rindorf et al. 2000, Furness 2002, Oro & Furness 2002). Sandeels normally reproduce in their second year; they produce large demersal eggs and because of extremely high natural mortalities, they do not become much older than three years. As a contrast to the larval performance of the short-lived lesser sandeel we chose the temporally co-occurring dab (*L. limanda*), which spawns several times during their 10 years lifespan, producing smaller pelagic eggs. It is generally accepted that in flatfish the relative importance of the larval stages is of minor importance compared to the density-dependent mechanisms acting on the settled juveniles, which normally dampens year-class strength variations (Van der Veer et al. 2000). Hence, we would expect that lesser sandeel larvae grow better and show less starvation symptoms under various biological and physical conditions than larval dab.

3.2 Material and Methods

The ichthyoplankton community was surveyed on a work daily base at 54°11.18'N and 07°54.00'E, which is known as "Helgoland Roads". The station is located between the island of Helgoland and the adjacent dune in the German Bight, North Sea. A CalCOFI ring trawl equipped with 500 µm mesh net (aperture 100 cm, length 400 cm, equipped with a flow meter) was towed for 15 min from a research vessel. For a detailed description of the sampling and the fish caught during the surveys see Chapter 2. Water depth at the station is app. 10 m and the water column is mixed throughout the year due to strong tidal currents (up

to 1.5 knots). The samples were transferred to the laboratory and fish larvae were sorted out immediately, classified and stored in -80°C for later biochemical analyses. Zooplankton samples were taken using a $150\ \mu\text{m}$ mesh net (aperture 17cm, length 100cm, equipped with a flow meter), hauled vertically through the water column by hand. Zooplankton samples were taken weekly from 15.Jan 2004 to 12.Feb 2004 and two times a week from 17.Feb 2004 until 29. Jun 2004. Zooplankton data were pooled to suitable prey organisms for larval fish based on their size, where all zooplankton smaller than $300\ \mu\text{m}$ were considered as potential food sources for larval fish. As different size-classes of fish larvae were present in all catches, no further division into specific plankton size-classes was conducted. Suitable prey organisms are given in Table 3. Weekly means of diatom carbon were calculated from daily phytoplankton counts following Hillebrand et al. (1999). Sea surface temperature was measured daily using a mercury thermometer.

The analysis of RNA and DNA concentrations was performed using a modification of the method of Clemmesen (1993) and Belchier et al. (2004). Samples of lesser sandeel and dab were thawed and measured for standard length using a stereomicroscope. Larvae were freeze-dried to constant weight (16 hours, using a Christ Alpha 1-4 freeze-dryer at -51°C) and were weighed to the nearest $0.0001\ \text{mg}$ (Sartorius microbalance SC2). The freeze-dried larvae were rehydrated in Tris-SDS-buffer (Tris 0.05M , NaCl 0.01M , EDTA 0.01M , SDS 0.01%) for 15 minutes. Cells were disrupted by shaking in a cell mill with different sized glass beads (diameter $2\ \text{mm}$ and $0.17\text{-}0.34\ \text{mm}$) for 15 minutes. The homogenate was then centrifuged at $6000\ \text{rpm}$ at 0°C for 8 min, and the supernatant used for the analysis. The amount of nucleic acids was measured fluorometrically in a microtiter fluorescence reader (Labsystems, Fluorescan Ascent) using the fluorophor ethidiumbromide. Total nucleic acids were measured first. Subsequently, RNase was applied to the sample in order to digest the RNA. After the enzyme treatment (30 min at 37°C) the remaining DNA was measured. The RNA fluorescence was calculated by subtracting the DNA fluorescence from the total nucleic acid fluorescence. RNA calibrations were set up on every day of measurement. The DNA concentrations were calculated using the relationship between RNA and DNA fluorescence described by Le Pecq and Paoletti (1966). All steps were done on ice.

The approach of this paper was to detect small changes in condition, which can potentially be lost in statistical approaches based on means. These changes are normally found at the extremes of distributions and they have usually only minor influences on common statistical tests. Hence, for the detection of these small-scale changes in distribution patterns of the parameters analysed, a nonparametric approach proposed by Pepin et al. (1999) and Evans (2000) was used. This approach examines how the probability distribution of a random variable Y depends on some other variable X , without any assumptions about the form of the distributions or about the form of the dependence. The goal is achieved by estimating

cumulative probability distributions and by computing local influences of X on Y. This is based on the idea of locally weighted estimates of the cumulative probability distribution by kernel smoothing (Pepin et al. 1999, Evans 2000). In this study the scatter between the 10th percentile (lower extreme) and the 90th percentile (upper extreme) of the distribution was analysed. This was done by the creation of 500 synthetic datasets originated by randomly assigning pairs of variables (length and RNA:DNA ratio) from the original dataset and by performing Monte Carlo simulations revealing the probability that the patterns of change in the cumulative probability distribution of the original data are caused by chance alone.

3.3 Results

Environmental conditions:

The water temperature dropped from 6°C in the beginning of January to 3°C in early March and increased again to 12°C until the end of May (Fig. 11). Zooplankton data were pooled to suitable prey organisms for larval fish according to Table 3. Total potential prey densities showed an increase from January to the middle of April from 1.2 to 10 individuals litre⁻¹. This increase was followed by a steep drop in density to around two zooplankton litre⁻¹ within just one week around the 20. Apr 2004 (Fig. 11). The collapse of zooplankton abundance was directly followed by a sharp increase in phytoplankton biomass from 25 to 230 µg diatom carbon litre⁻¹, which indicates top down mechanisms acting on phytoplankton growth in spring 2004.

Table 3 **List of zooplankters combined to suitable prey for larval fish in this study**

Asteroidea (Gastrula)
Aphroditidae (Larvae)
Polychaeta (Trochophora)
Gastropoda (Veliger)
Evadne sp.
Podon sp.
Bryozoa (Larvae)
Balanidae (Nauplia)
Copepoda, (Nauplia)
Copepoda, (Copepodites)

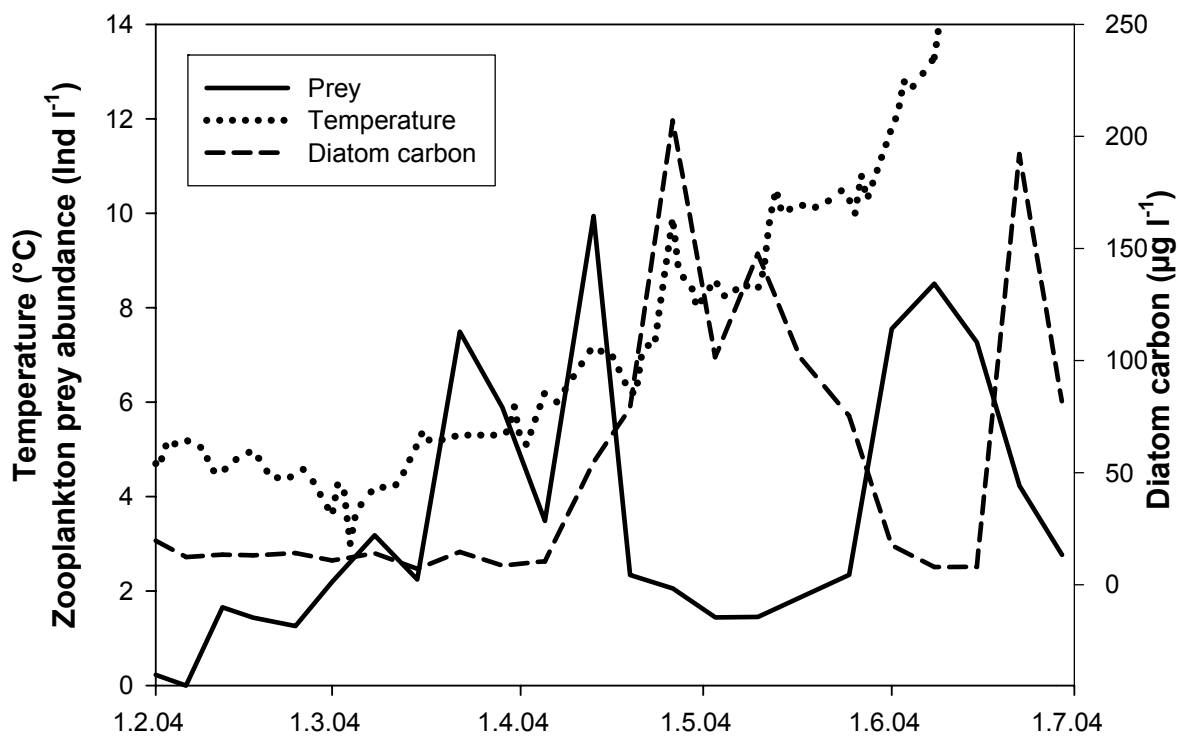


Fig. 11 Development of zooplankton prey, temperature and diatom carbon.

Species occurrence:

Larval dab were first caught at the end of February and their mean abundance in 2004 was 0.2 individuals m^{-3} . Two distinct peaks in dab abundance were observed in the middle of March and at the end of April with densities of up to 1 larva m^{-3} . From April on until late June, when the last dab larva was caught the abundance remained low. Lesser sandeel larvae first occurred in the ichthyoplankton in early February. In general, February was characterized by high sandeel numbers in the catches ranging from 2 to 50 individuals m^{-3} . A second peak in sandeel abundance was observed in late March and early April with densities of up to 8 individuals m^{-3} . Thereafter, numbers remained low with 0.01 to 0.1 larvae m^{-3} until the last larva was caught in the middle of May (Fig. 12).

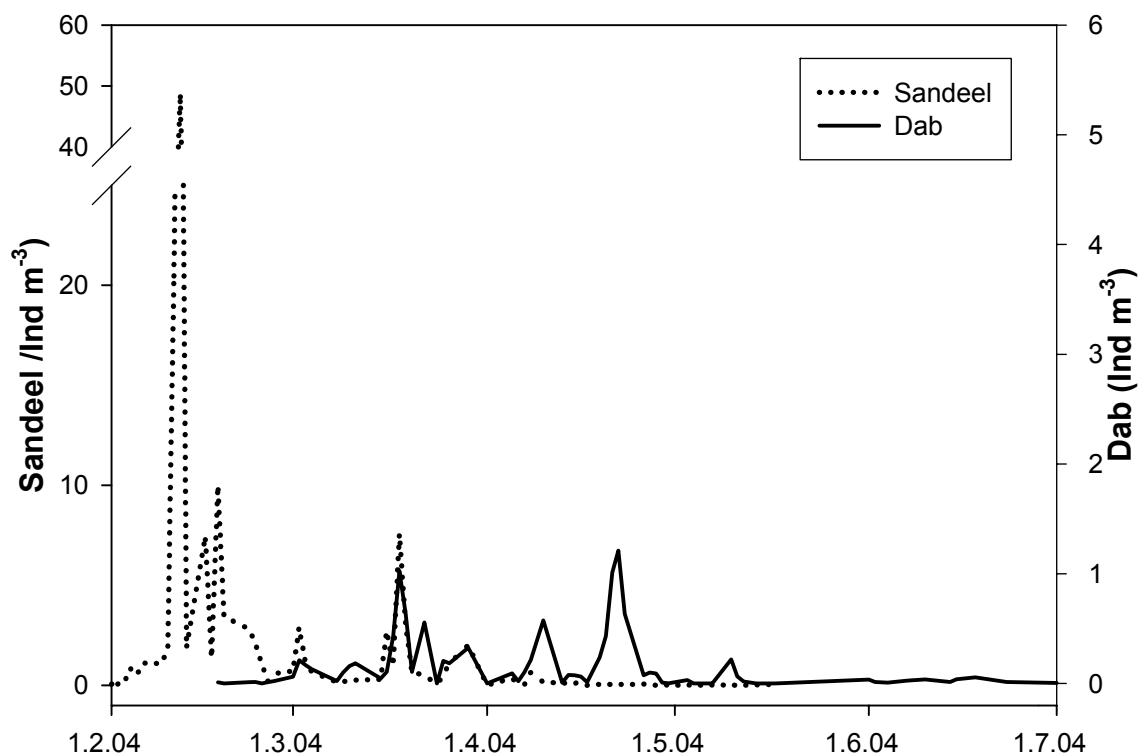


Fig. 12 Abundance of lesser sandeel (*A. marinus*) and dab (*L. limanda*) larvae. Note the different scales for the two species.

Nutritional condition of dab

A total of 419 larval dab were analysed for their standard length, dry weight and their RNA:DNA ratio. Variability in the standard length of larval dab was high but fairly constant throughout the whole period of their occurrence in the plankton as was the variability in RNA:DNA ratios (Fig. 13). None of the flatfish larvae analysed in this study showed a beginning asymmetry as a sign for forthcoming settlement. A high proportion of better-conditioned larvae were found in the middle of the sampling period. This caused a steady elevation of the 90th percentile until the middle of April. While the lower parts of the RNA:DNA ratio distribution, indicated by the 10th and 50th percentile, decreased just slightly from the 20th of April onwards, better-conditioned larvae were missing later in the season. This resulted in a sharp decrease of the 90th percentile. As a result, the mean RNA:DNA ratio decreased.

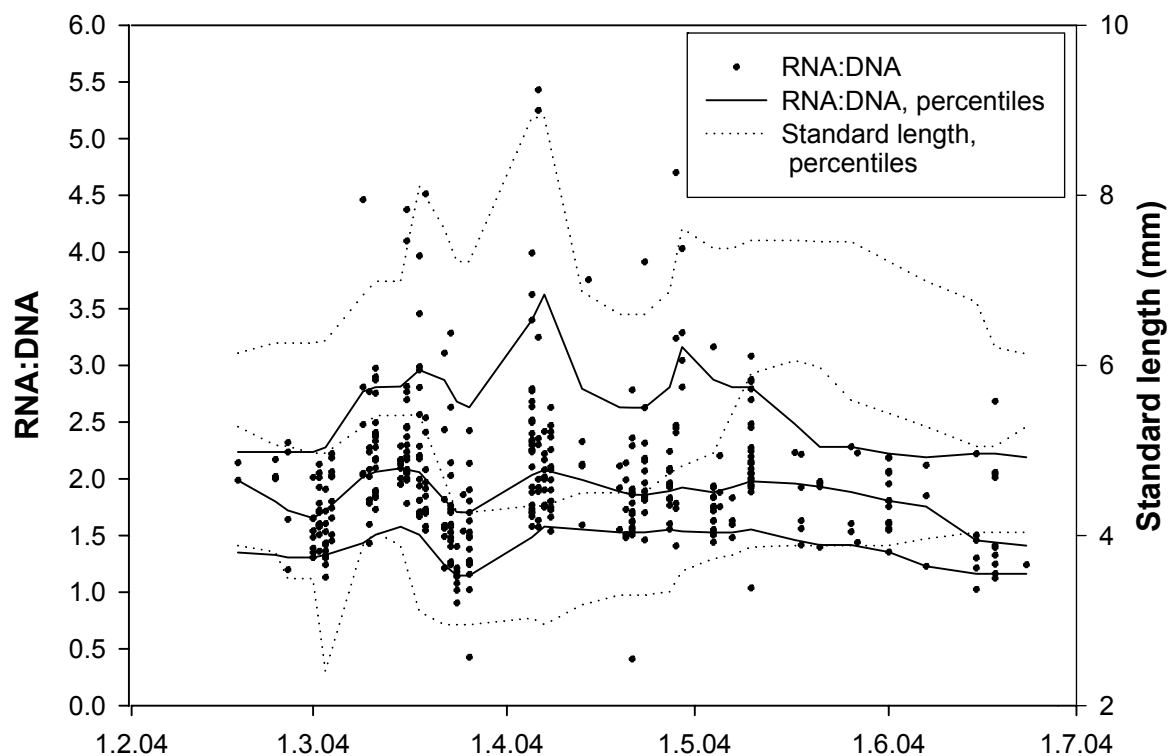


Fig. 13 RNA:DNA ratio and standard length of larval dab (*L. limanda*) over time. Solid (RNA:DNA ratio) and dotted (standard length) lines from bottom to top: 10th, 50th, 90th percentile.

In order to distinguish between periods of high and low food availability (before and after the 20th of April, see also Fig. 11), the slopes of the regression lines resulting from RNA:DNA and length data from the 46 larvae caught within the two weeks prior and the 78 larvae caught within two weeks after the breakdown in zooplankton abundance were compared. The standard length of the larvae was included into the analysis to investigate whether all size-classes were affected in the same way by the reduction of zooplankton prey. The temperature difference between the two weeks was 2.1°C. Significantly different slopes were shown with the higher slopes observed in larvae caught before the breakdown in food availability at the 20th of April (0.53 vs. 0.18) (Fig. 14; $p < 0.01$). The exclusion of two small larvae (4.5 and 3.8 mm) with unusually high RNA:DNA ratios (3.9 and 4.7 respectively) from the dataset of the food deprived weeks resulted in a r^2 of 0.40 and a slope of 0.2. Further analyses of the RNA:DNA ratio in larvae smaller than 4 mm, before and after the food deprivation revealed no significant difference in RNA:DNA ratios (t-test, $p > 0.05$) which means that larger larvae were affected by the decrease in prey availability, while smaller larvae were not.

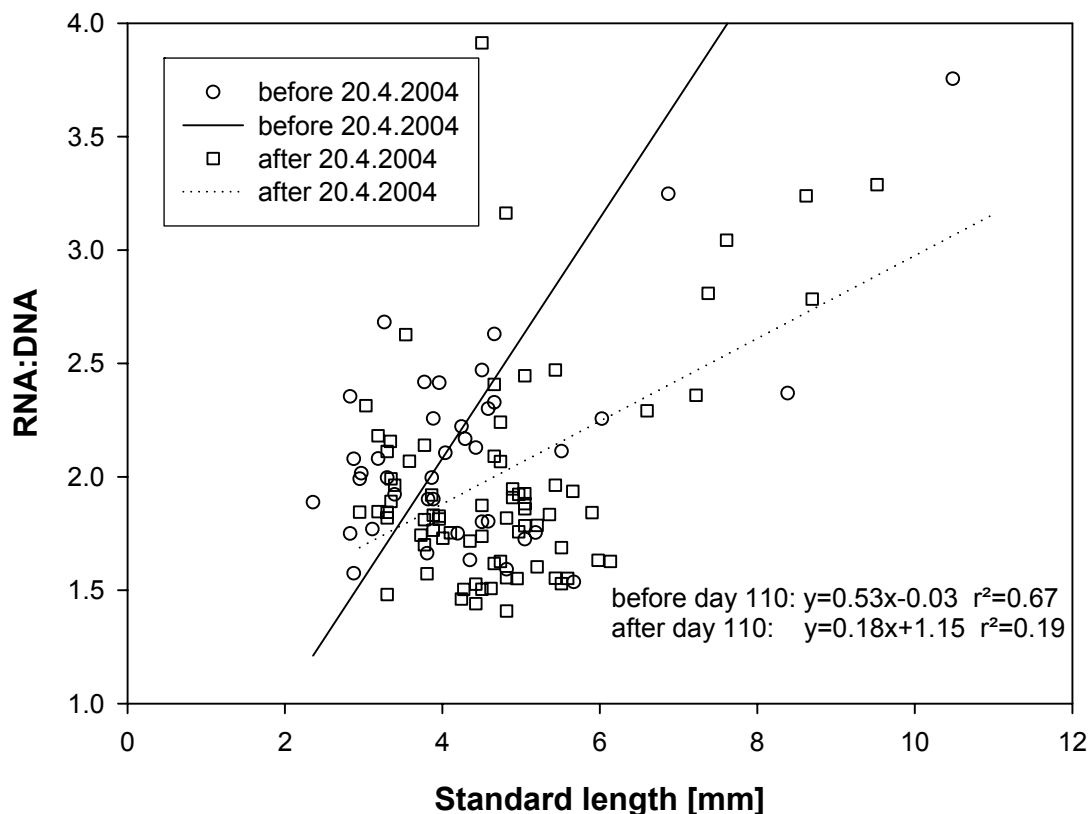


Fig. 14 Relationship of RNA:DNA ratio and standard length in larval dab (*L. limanda*) divided into the categories all data, before and after day 20.4.2004.

Nutritional condition of sandeel

In contrast to the dab size distribution, the variability and the standard length of the 366 sandeel larvae analysed increased with time. A constant supply with small larvae kept the 10th percentile at roughly 5 mm while the 50th and 90th percentile increased until the middle of April, reaching values between 11 and 14 mm (50th and 90th percentile respectively)(Fig. 15). Late in the season a decrease in larval length due to a lack of larger larvae in the catches was observed. The RNA:DNA ratios in larval lesser sandeel were highly variable throughout the season, ranging from 2 to 9. The data density later than the middle of April is low, but nevertheless, no RNA:DNA ratio greater than 4 was found in the 16 larvae caught in the last 30 days of the sandeel season, which was well below the mean RNA:DNA for the whole season (Fig. 15).

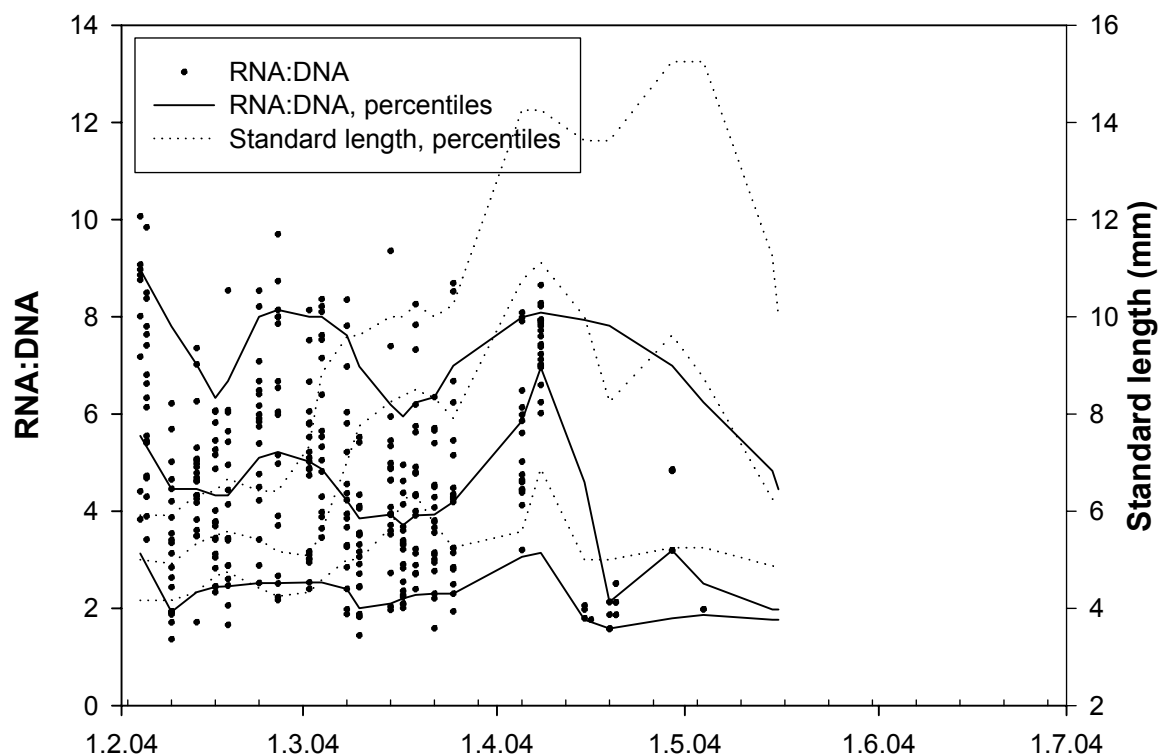


Fig. 15 RNA:DNA ratio and standard length of larval lesser sandeel (*A. marinus*) over time. Solid (RNA:DNA ratio) and dotted (standard length) lines from bottom to top: 10th, 50th, 90th percentile.

Inter-specific comparisons

Analysis of the relationship between larval size and their RNA:DNA ratios revealed a different pattern for the two species. In both species the 50th percentile increased with larval size. This elevation was caused by the loss of poor-conditioned sandeel larvae whereas the maxima ratios remained constant (Fig. 16). Larval dab also showed a loss of poor-conditioned larvae but contrasting to sandeel, a massive increase in the RNA:DNA ratios maxima with size was observed (Fig. 17).

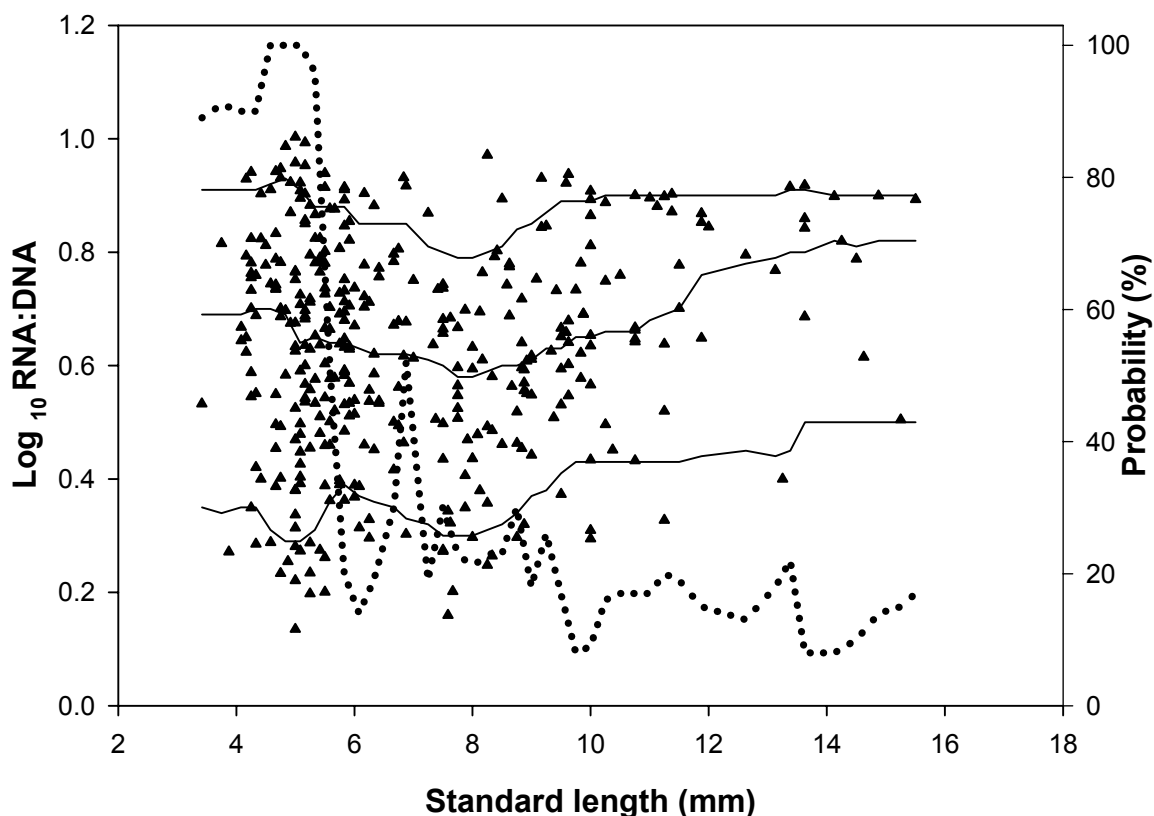


Fig. 16 RNA:DNA ratio and standard length of larval sandeel (*A. marinus*) over time. Solid lines from bottom to top: 10th, 50th, 90th percentile. The dotted line is the probability of measuring the estimated scatter between the 10th and the 90th percentile relative to a randomization of the data (right y-axis).

The probability that the observed relations between length and RNA:DNA ratio are produced by chance alone (dotted lines in Fig. 16 & Fig. 17) ranged between 5 and 20 % for larger sandeel, which means that indeed in larger sandeel size-classes only the better-conditioned animals were found. For dab, a probability of nearly 100 % at the larger size-classes was calculated, which means that the scatter was significantly higher than the average scatter of the dataset. This reflects the large scatter and the evenly distributed RNA:DNA ratios observed in larger size-classes. It was obvious, that this elevation in scatter was caused by the gain of extremely well-conditioned larvae which were not present in the population at smaller size-classes.

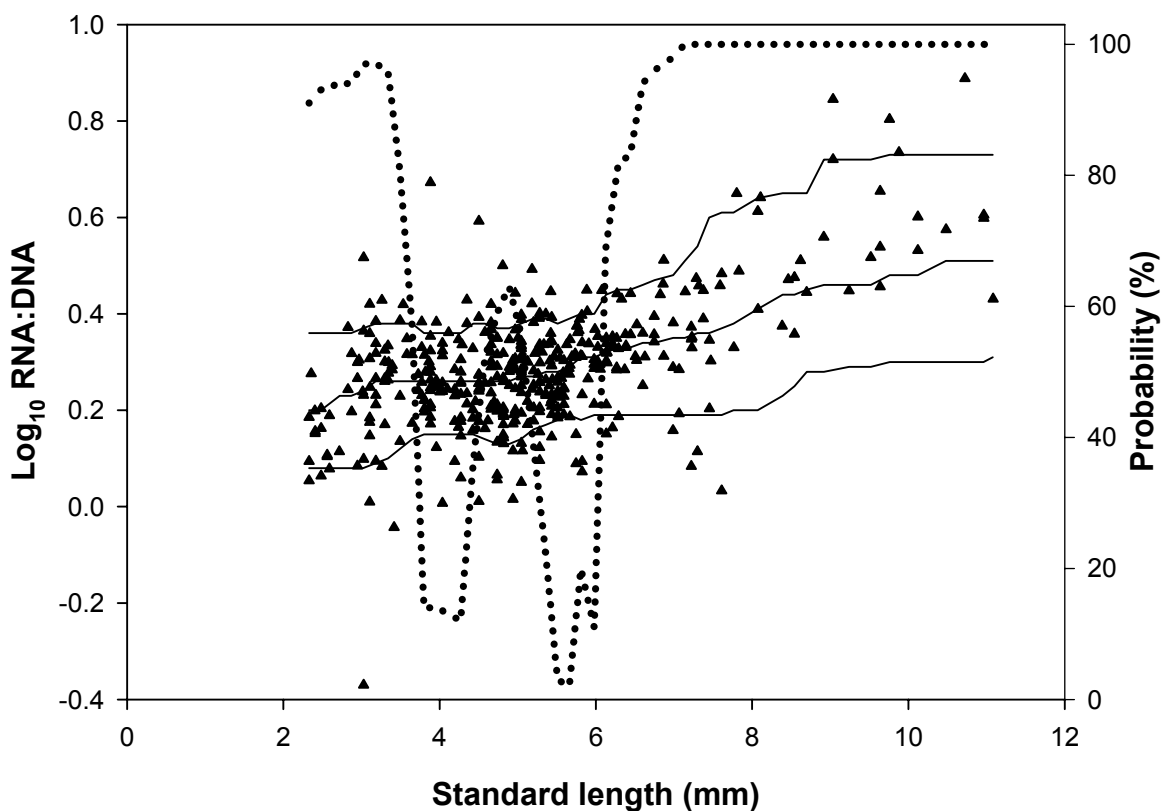


Fig. 17 RNA:DNA ratio and standard length of larval dab (*L. limanda*) over time. Solid lines from bottom to top: 10th, 50th, 90th percentile. The dotted line is the probability (in percent) of measuring the estimated scatter relative to a randomization of the data (right y-axis).

3.4 Discussion

This study provides insights into the early life history of two fish species of contrasting reproductive strategies in the North Sea. Both species are characterized by a similar seasonality and the manner in which they cope with strongly changing environments. Both species have a prolonged hatching season compared to other species in this region Chapter 2, which presumably represents a bet-hedging strategy to deal with a high variability in environmental conditions. Since feeding conditions are variable intra- and inter-annually, this bet-hedging seems a good strategy. In 2004, the larvae that hatched before mid-April seemed to be the winners. However, as the timing of the zooplankton peak is in general highly variable (Greve et al. 2004), it is likely that in other years larvae that hatch at different times are the survivors.

Nevertheless, low food availability at low temperatures early in the season does not necessarily mean that this characterizes a bad situation. Since growth is, however, accelerated by temperature, low temperature conditions results in a slow growth, leading to a longer duration of the most-vulnerable larval stages and a prolonged phase of a high predation risk. Later in spring, temperature and food availability usually rises; a pattern which this is well-reflected by the higher condition for both dab and sandeel shown for early April. In 2004, we observed a drastic reduction in food availability from the middle of April to the end of May. This may have had several consequences for the larval fish. On the one hand, the larvae ran the risk of starvation while on the other hand the risk of predation increased with decreasing condition of the larvae. Late during season, larvae faced better feeding conditions after the recovery of the zooplankton abundance. However, the larval condition did not react to such an increase in prey abundance. This could be the result of changes in nutritional quality of the zooplankton as food for larval fish (as shown in Chapter 4), but also a result of higher temperatures, which were potentially outside the optimal temperature range for the larvae of investigation. Thus, during this period, they were not able to transfer the plenteousness of food effectively into growth.

Consequently, only a short period of the year yielded favourable conditions for the larval fish species in our study, a pattern which was already proposed by Hjort (1914) and later by Cushing (1974, 1990). In fact, several studies concentrating on growth rates or hatch date distribution derived from otolith readings revealed similar results. Hovenkamp and Witte (1991) as well as Baumann et al. (2003) found the highest growth rates and thus the highest survival probability of larval plaice (*Pleuronectes platessa*) and radiated shanny (*Ulvaria subbifurcata*) at intermediate temperatures. Wright and Bailey (1996) compared the observed hatch dates of larval sandeel and back-calculated hatch dates derived from otolith microstructures of juvenile sandeel in three consecutive years. They found that the survivors'

hatch dates were rather different between years; an early hatch was favoured in 1990, a late hatch in 1991 and an intermediate hatch date were advantageous in 1992. They concluded that there is an indication for a seasonal cycle of growth opportunity in the three years of investigation, that inter-annual differences occur and that a coupling of hatching and the onset of secondary production may be an important factor for year-class variability. The results of our study also showed a strong seasonality of the development of larval condition, but contrasting to Cushings' (1974, 1990) predictions, the period of highest larval condition was not at the peak of food availability but two to three weeks earlier.

In general, a low food availability is known to lead to a reduced growth and an increased mortality in larval fish (Clemmesen 1987, McGurk et al. 1992, Clemmesen 1994, McLaughlin et al. 1995b, Theilacker et al. 1996, Gwak & Tanaka 2001, St. John et al. 2001). In this study, low RNA:DNA ratios were found being linked to poor feeding conditions only at times of an extreme decrease in food availability. By the division of data into two weeks before and two weeks after the breakdown of the prey abundance, the slope of the length-condition-regression was significantly higher than the one of the two food-deprived weeks. The temperature difference during this four-week timeframe was within the window of direct comparability of RNA:DNA ratios (Caldarone et al. 2003) and thus, it is unlikely that temperature-related effects can serve as explanation for the results. In fact our findings show that larger larvae suffered from poor feeding conditions while smaller larvae showed no significant decline with the decrease in prey abundance. Suneetha et al. (1999) reported less serious starvation effects in small herring larvae (*Clupea harengus*) than in bigger ones and attributed this finding to benefits derived from leftover yolk. This fits well to our findings that smaller larvae were not affected by the decline in zooplankton prey densities. They might have thus benefited from their ability to exhaust two sources of energy, internal yolk reserves as well as external food. Additionally, young stages of larval fish are known to feed on phytoplankton in the first days of external feeding (Last 1978, Kane 1984, Monteleone & Peterson 1986). It can be hypothesized that smaller larvae may have switched food sources in order to exploit the rapidly increasing diatom biomass, a phenomenon which is additionally supported by our unpublished results on isotopic signatures of the larvae.

The relationship between maximum larval nutritional condition and size showed a diametral pattern in the two species under investigation. Larval dab showed a clear increase of condition with size. Similar patterns were shown by Clemmesen et al. (2003) for Atlantic cod larvae in mesocosm studies and by Gronkjaer et al. (1997) for wild cod larvae from the Baltic Sea. The pattern of displaying the same maximum condition at all larval size-classes, as reported for lesser sandeel in this study, was previously reported by Pepin et al. (1999) for several species originated from Conception Bay, Newfoundland. In their study, they demonstrated condition-dependent mortality by showing that the maximum condition

remained constant with growth, but that the poorly-conditioned larvae were missing at larger size-classes. The species with the clearest signal in the investigation of Pepin et al. (1999) were short-living one. The production of larvae that are already at maximum condition at the time of hatch can be interpreted as a more conservative strategy when compared to the strategy of producing larvae that are far from their maximum possible condition at hatch and that first have to develop a good condition.

Larval sandeel, as a representative for a short-lived fish species, did not show a strong dependency on high prey densities and they performed well under various food/temperature conditions. Only at the end of the season a breakdown of larval growth coincided with decreasing prey levels. In general, high temperatures are considered as counterproductive for sandeel production. Arnott and Ruxton (2002) found a negative correlation between sandeel recruitment and water temperature in the North Sea, with strongest effects in the southern part of the North Sea, which represents the southernmost distribution limit of this species. In contrast, a positive relationship between condition and prey availability was found in dab, the representative of a long-lived species. This can be taken as an indication for a higher dependency of dab larvae on environmental conditions.

Our hypothesis that short-lived species have more conservative reproductive strategies than long-lived forms is supported by the fact that that sandeels produce large and energy-rich eggs as well as by their long transition time from internal to external feeding. To summarize, these characteristics display a relatively high independence of sandeels from environmental factors like temperature or prey densities thus enabling this short-lived fish species to produce extremely well-conditioned larvae.

Chapter 4

Primary production under nutrient limitation indirectly affects larval fish condition

It has become increasingly clear that food quality plays a very important role in aquatic systems. The main investigations, however, were carried out at the interface between primary producers (algae) and primary consumers (zooplankters). Here, we conducted laboratory experiments to track the cascading impact of algal mineral limitations through food webs. We used tri-trophic food chains, under the hypothesis that the homeostasis of the primary consumers is not strong enough to completely dampen negative limitation effects of the primary producer and that these negative effects affect the next higher trophic level. The cryptophyte *Rhodomonas salina* was cultured under nutrient sufficient as well as N- and P-limited conditions. Subsequently, the copepod *Acartia tonsa* was reared to the fifth naupliar stage on these manipulated algae and fed to two different age classes of larval herring. The effect of nutrient limitations was traced through the food chain by measures of the stoichiometry, fatty acids analysis and the RNA:DNA ratio of the herring as an indicator for larval fish condition. Fatty acids showed significant differences between the treatments in algae as well as copepods and so did the stoichiometry of the two lower trophic levels. Our hypothesis was supported, as the larval herring showed a significant response to the treatments, growing best on copepods reared on N- limited algae and worst on the P-limited food chain.

4.1 Introduction

Phytoplankton blooms are never a stable and predictable food source for primary consumers. The phytoplankton biomass often rises in the order of 3 magnitudes (Irigoien et al. 2005) within days. This does, however, not necessarily mean that the edible part of the seston rises significantly, as blooms often comprise those phytoplankton species that manage to avoid predation due to special avoidance mechanisms like spines, thick cell-walls, layers of mucus (Irigoien et al. 2005, Mitra & Flynn 2005) or form colonies, like e.g. *Phaeocystis* species. In the case of an exploitable phytoplankton bloom, however, the rising food availability enhances reproductive activity in the holoplankters participating in the exploitation of the bloom. Depending on the life history strategy of the consumers, the bloom can be utilized by several generations as shown for daphniids in freshwater systems (Sommer et al. 1986), just by the standing stock of consumers, for example in the case of copepods with an annual life-cycle which target their main reproductive output to coincide with the bloom (Mauchline 1998), or by a mixture of older individuals and their offspring as is the case with many copepod species with a shorter generation time (Sommer et al. 2003). Blooms are either terminated by bottom-up or top-down mechanisms, which is by the depletion of nutrients and subsequent sedimentation (Sommer et al. 1986) or by grazing pressure leading to a clear-water phase (Sommer et al. 1986, Alekseev & Lampert 2001). Interestingly, the exact mechanisms of bloom termination in many oceanic blooms are still unresolved.

Nevertheless, nutrient concentrations do decrease during the course of a bloom, and the low availability of nutrients at the peak of bloom situations leads to reduced phytoplankton growth rates, maintained mostly by the very limited regeneration of nutrients from the decaying algal material and ultimately this leads to drastic changes in food availability for the organisms that feed on the bloom-forming species. Apart from the dramatic decrease of primary production in decaying bloom situations, consequently leading to lower food availability for the herbivore biomass, algal quality as food for the herbivores is also likely to deteriorate. This is caused by decreases in edibility as a result of altered cell-wall morphology (Van Donk et al. 1997), changes in the stoichiometry of the macronutrients in the algae as a result of nutrient depletion, and biochemical changes in the algae such as changes in amino acids, proteins and fatty acids (Ahlgren & Hyenstrand 2003). The direct consequence of the nutrient depletion in algae is that the nutrient ratios are deviating more and more from Redfield ratios. This ultimately leads to a high variability of nutrient ratios in algae and they therefore represent a food source of variable quality for herbivores. Contrasting, zooplankton organisms retain their elemental composition to a high degree, displaying a strong homeostasis (Sterner & Elser 2002). Under the assumption that an animal is not energy-

limited, food with high C:nutrient ratios ultimately creates costs due to the need of having to deal with ingested excess carbon. These costs rise with an increase in the difference between producers' and consumers' C:nutrient ratios. Zooplankters seem to pay these costs by reduced growth and reproductive rates (Boersma 2000, Boersma et al. 2001, Boersma & Kreutzer 2002).

The reproductive phase in fish is normally not initiated by an enhanced primary production (but see Walsh et al. 1978). The more common strategy of many fish species is to try to synchronize the hatch of their larvae with enhanced primary and secondary production by the timing of spawning (Cushing 1974, 1990, 1995). As the onset of the spring bloom is hard to predict for reproducing fish, batch spawning over a prolonged period is a common reproductive strategy in temperate marine systems to match favourable feeding conditions for the offspring. This led Cushing to propose the match/mismatch hypothesis (Cushing 1974, 1975) stating that fish year-class strength depends to a large proportion on a match between the occurrence of larval fish and peak production of suitable food sources. This aspect has been in the focus of aquatic ecology since decades and several studies confirmed and widened the applicability of this hypothesis (Cushing 1990, and references herein). Nevertheless, even in the case of a perfect match between larval occurrence and high productivity, the time span of plenty for the larvae is limited as bloom situations last mostly no longer than 1-2 weeks, which is shorter than the pelagic phase of most larval fish. Following Hjort's critical life stage concept (Hjort 1914) this does not necessarily mean that larval fish suffer in post-bloom situations, as they become efficient predators very rapidly. A bloom and the following high zooplankton abundance may be interpreted as a boost in growth, channelling the early larvae through the first critical days of their lives.

Brett (1993) stated in a dispute on ecological stoichiometry held in "Limnology and Oceanography" in 1993, that carnivores should be limited by food quantity rather than by food quality, as the stoichiometric needs are similar to the stoichiometry of their prey. Furthermore, relatively strong homeostasis of herbivore zooplankters (Hessen 1990, Andersen & Hessen 1991, Sterner & Elser 2002) should act as a buffer for effects of mineral limitations on the primary production level, and such differences should therefore not be transferred through food webs to higher trophic levels. Recent evidence, and more detailed investigations have, however, shown that homeostasis in planktonic animals is far from perfect (Plath & Boersma 2001). This variability is usually neglected using the argument that the differences observed in zooplankters are at least one order of magnitude lower than those observed in primary producers (Sterner et al. 1998). Nevertheless, 50% differences in zooplankton C:nutrient ratios have been observed depending on their food (Carrillo et al. 2001, Boersma & Kreutzer 2002, Acharya et al. 2004). Hence, given the argument of Brett (1993) that stoichiometric needs of secondary consumers and the stoichiometry of prey are

normally so finely tuned, this means that there is ample opportunity for quality differences between prey of different nutritional status to be transferred to the next trophic level. Hence, we hypothesize that mineral limitation effects are indeed channelled through the food web and that their negative effects can be observed at higher trophic levels.

In order to test this hypothesis, we conducted two experiments to track the impact of mineral limitation through a tri-trophic food chain, from primary producers to primary and secondary consumers.

4.2 Material and Methods

In order to simulate the response of several trophic levels to succession patterns during phytoplankton blooms, algae, copepods and larval herring were reared under three nutrient regimes.

A stock culture of *Rhodomonas salina* was cultivated in enriched seawater, following Guillard and Ryther (1962). For our experiments, we cultivated algae at 18°C under a 16/8 hours (light/dark) light regime in enriched natural seawater (salinity ~15), as well under phosphorous- and under nitrogen- limitation. Prior to the experiment, the entire volume of water used in the experiments was 0.2 µm sterile filtered and stored cold and dark until use. The first treatment simulated a non-limited bloom situation and consisted of f/2-enriched seawater (f/2 in the following), as described by Guillard and Ryther (1962), the other two treatments simulated decaying bloom situations under N- or P-limitation. The algae of the two limitation treatments were enriched with just one macronutrient (no P- or N-addition; -P and -N in the following) and could therefore only utilize the natural P- or N-sources present in the seawater at the moment of filtration. Several tests on algal growth rates were done prior to the experiments to detect the “carrying capacity” of the three different media and to define the duration until the algae were properly limited by the element of choice in the different treatments. Concentrations of algae were determined using fluorometric measurements (Turner, 10-AU-005-CE) at an excitation wavelength of 436 nm and an emission wavelength of 680 nm. Prior to the experiments a cell number-fluorescence relationship was set up using flow cytometer counts at 7 concentrations ranging from 0.05 to 1.7 10⁶ cells ml⁻¹.

To ensure constant food quality, new cultures of each of the treatments were inoculated every day with roughly 0.2 10⁶. cells ml⁻¹ for the -N treatment and 0.3 for the -P and f/2 treatment. Algae were harvested at densities of app. 0.5, 1.0 and 1.3 10⁶. cells ml⁻¹ (-N, -P and f/2 respectively) after the predefined growth phase of 6 days for -N and 7 days for f/2 and -P. These were the maximum densities possible with the natural N- or P-sources contained in the seawater.

Eggs of the calanoid copepod *Acartia tonsa* had been produced in 200 l cylindrical tanks, where the animals were cultivated at 18°C at a 12/12 light cycle. Copepods were fed on a mixture of the algae *Rhodomonas salina*, *Dunaliella sp.* and the flagellate *Oxhyrris sp.* Eggs were siphoned from the bottom of the tanks daily and stored in seawater at 4°C for later use. No eggs older than three months were used in the experiments.

The stored eggs were incubated in fresh seawater. The hatch rate of the eggs was around 20%. The copepods used for the experiments were reared from the egg to the fifth naupliar stage in 5 l plastic bags at 18°C at densities of 1500 ind. l⁻¹. The cultured algae were fed to the copepods at app. 1.0 mg carbon l⁻¹ d⁻¹ on five consecutive days. In order to guarantee that the algal deficiencies were not changed by uptake of nutrients during the incubations with the copepods, the copepods were reared in artificial, N- and P-free seawater (hw-Marinemix, www.hw-wiegandt.de). Copepods were first fed 48 hours after adding the eggs to the rearing bags, assuming two days for the development from the egg to the first feeding second naupliar stage. Copepods were harvested after seven days of cultivation when app. 80% of all the animals was in their 5th naupliar stage and app. 20 % in the fourth. For each day of the feeding experiment, three new copepod bags were started to ensure a constant food quality for the secondary consumers, the larval herring *Clupea harengus*.

Herring larvae were obtained by means of artificial fertilisation. Adult ripe Baltic herring *Clupea harengus* were purchased from a local fisherman. The fish were transported immediately to the institute and kept on ice the whole time. Female fish were strip-spawned on glass plates. The eggs were applied in single rows to ensure a good oxygen supply during the incubation phase and the glass plates were placed in a plastic box. Milt was stripped to the eggs and activated by the addition of seawater. Fertilization was allowed for five minutes; afterwards the eggs were washed and transferred to the incubation containers. Eggs were incubated in a flow-through system, using 4 µm pre-filtered natural seawater at 13°C. The first hatch took place on the night of day 10; peak hatch took place the following night. Only larvae from the hatch peak were used in the experiments. Larvae were transferred to cylindrical 200 l stock tanks. The stock tanks were operated as a flow-trough system and gently supplied with pre-filtered water. Experiment 1 was started using 4 days post-hatch larvae, which had no feeding experience. The larvae in the stock tanks were fed from day 4 on *Brachionus plicatilis* reared on *Nannochloropsis sp.* *B. plicatilis* were taken from routine cultures of the facility. Experiment 2 was started using 9 days post-hatch larvae.

Experiments:

20 larvae each were transferred to 1 l glass beakers filled with GF/F filtered seawater. The four treatments (-P, -N, f/2 and starving) were replicated 10 times in Experiment 1 and three times in Experiment 2. Both experiments were conducted at 15°C and ran for 6 days. Larvae

were fed different qualities of food around noon for the duration of five days. Food density in the experimental containers was 1 copepod ml⁻¹, which is higher than the densities that are usually reported for food-saturated growth in larval herring (Clemmesen 1994). This was corroborated by the fact that in all of the experimental vessels copepods were still present after one day of feeding. The experiments were terminated on the morning after the 5th day of feeding. More than 80% of the water was replaced daily. Water was changed before feeding to ensure that the vast majority of uneaten prey organisms were in the experimental container for a maximum of 24 hours. This was essential in order to avoid alterations of the body composition of the copepods due to starvation and hence to assure a constant food quality over the trial period.

Analytical procedures:

The nutritional condition of larval herring was assessed by means of the analysis of the ratio between RNA and DNA content in the organisms, a method commonly used in larval fish ecology and fisheries research. The analysis of RNA and DNA concentrations was performed using a modification of the method by Clemmesen (1993) and Belchier et al. (2004). Larval herring were thawed and measured for standard length using a stereomicroscope. Larvae were freeze-dried to constant weight (16 hours, using a Christ Alpha 1-4 freeze-dryer at -51°C) and were weighed to the nearest 0.0001 mg (Sartorius microbalance SC2). The freeze-dried larvae were rehydrated in Tris-SDS-buffer (Tris 0.05M, NaCl 0.01M, EDTA 0.01M, SDS 0.01%) for 15 minutes. Cells were disrupted by shaking in a cell-mill with different sized glass beads (diameter 2 mm and 0.17-0.34 mm) for 15 minutes. The homogenate was then centrifuged at 6000 rpm at 0°C for 8 min, and the supernatant used for the analysis. The amount of nucleic acids was measured fluorometrically in a microtiter fluorescence reader (Labsystems, Fluorescan Ascent) using the fluorophor ethidiumbromide. Total nucleic acids were measured first and subsequently RNase was applied to the sample in order to digest the RNA. After the enzyme treatment (30 min at 37°C) the remaining DNA was measured. The RNA fluorescence was calculated by subtracting the DNA fluorescence from the total nucleic acid fluorescence. RNA calibrations were set up every measurement day. The DNA concentrations were calculated using the relationship between RNA and DNA fluorescence described by Le Pecq and Paoletti (1966). For the analysis of carbon and nitrogen contents of the algae, an estimated amount of 150 µg algal carbon was filtered on precombusted Whatmann GF/F filter. For the analysis of copepod carbon and nitrogen, 500 individuals were counted into tin capsules. For the C and N content of the fish larvae, we pooled four individuals to ensure enough material for the analysis and packed them into tin capsules. The elemental analyses were done using a Fison 1500N CHN analyser. Phosphorus was analysed as orthophosphate after acidic

oxidative hydrolysis with 5% H₂SO₄ (Grasshoff et al. 1999). Unfortunately, P data of the algae are only available for Experiment 1. For that reason the copepod C:P ratios of Experiment 1 and 2 were pooled, as no significant difference was found between the ratios of both experiments. C:N- and C:P ratios are given as the molar ratio.

The fatty acids of algae and copepods were measured as fatty acid methyl esters (FAMES). Lipids were extracted from the samples by dichloromethane/methanol in an ultrasound bath for 30 min. Water soluble fractions were removed after centrifugation by washing with 0.88% KCl buffer. The water phase was removed and the organic remainder was evaporated using nitrogen gas. The esterification was done using methanolic sulphuric acid at 70°C for 30 min. The FAMES were washed from the methanolic sulphuric acid using n-Hexane. Excess n-Hexane was evaporated using nitrogen gas. All chemicals used were suprasolv or GC grade. FAMES were analysed by gas chromatography using a Varian CP 8400 gas chromatograph equipped with a DB-225 column (J&W Scientific, 30 m length, 0.25 mm ID, 0.25 µm film). The injector temperature was set to 250°C. The column oven was set to 60°C, which was held for 1 min after injection. The oven was heated to 150°C at 15°C min⁻¹, then to 170°C at 3°C min⁻¹, and finally to 220°C at 1°C min⁻¹, which was held for 21 min. The carrier gas was helium at a constant pressure of 12 psi. The flame ionisation detector was set to 300°C and the total run time was 82 min sample⁻¹. The injection of the 1 µl aliquots of the samples was done in a split less mode. FAMES were quantified using calibrations set up for each fatty acid separately and a known amount of C 23:0 was added at the first step of the preparation as an internal standard.

C:N and RNA:DNA ratios were statistically analysed by means of a two factorial ANOVA with treatment and experiment as independent variables and C:N or RNA:DNA as the dependent variable. Fatty acids and C:P ratios were analysed by one-factorial ANOVA using treatment as factor and the various fatty acid proxies or the C:P ratio as the dependent variable. Duncan's tests for unequal n were used as post hoc test.

4.3 Results

Algal molar C:N differed significantly between treatments in both experiments. We were able to create similar values in both experimental runs, so that the factor "Experiment" had no significant influence in the two-way ANOVA. Algae grown under N-limitation showed the highest C:N ratios, while f/2 and P-limited algae showed significantly lower C:N ratios (~ 10, ~ 7.5 and ~8.0; p< 0.05). Copepod C:N ratio showed significant differences between treatments. In Experiment 1, copepods fed on N- as well as P-limited algae showed significantly higher C:N ratios in comparison with those copepods fed on non-limited algae. In Experiment 2, no differences were found due to the unexpectedly low C:N ratios in the N-

limited treatment (Fig. 18). The only significant difference in herrings' C:N ratio was between the start groups of Experiment 1, which were yolk sac larvae, and all other treatments (4.6 vs. 5.4). The other groups did not differ and showed remarkably low variation. The C:P ratio also differed significantly between treatments in algae (f/2~ 230, -N~180 and -P~ 580) as well as in copepods (f/2~ 180, -N~186 and -P~ 280). The -P treatment created significantly higher C:P ratios in algae and in copepods than the f/2 and the -N treatments did ($p < 0.01$). The latter two did not differ significantly (Fig. 19).

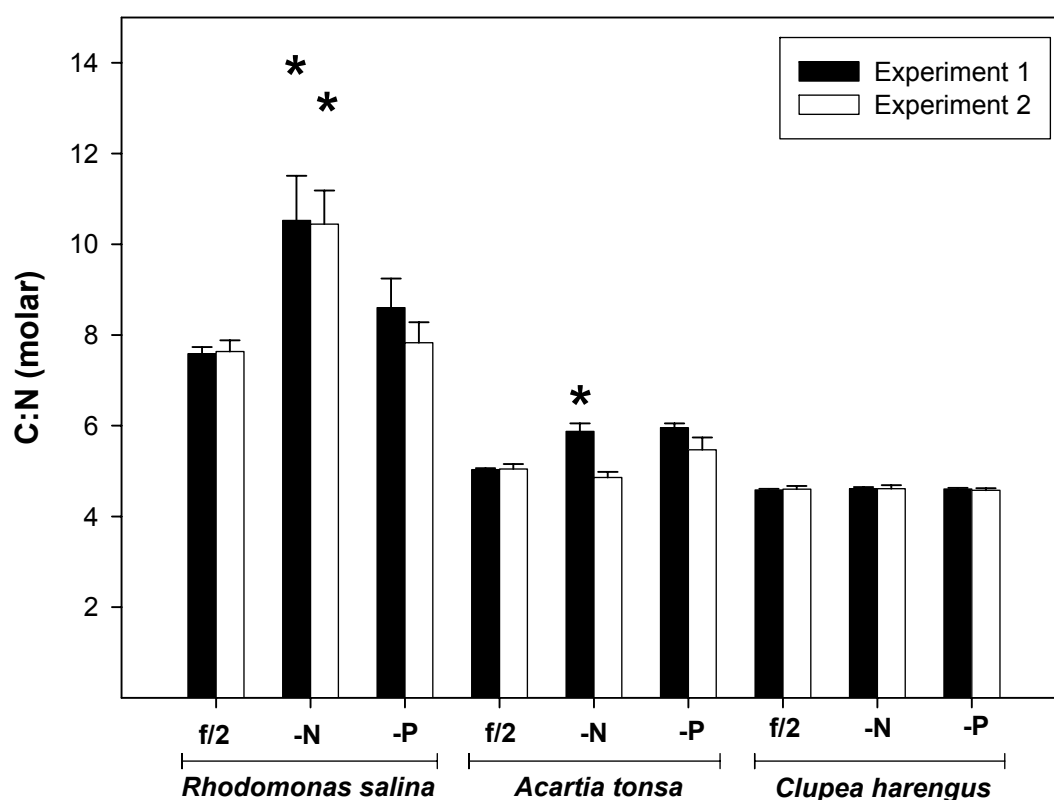


Fig. 18 Molar C:N ratio of *R. salina* cultured under nutrient-sufficient (f/2), N-limited (-N) and P-limited (-P) conditions. C:N ratios of the copepod *A. tonsa* reared on the different *R. salina* cultures and C:N ratios of larval herring (*C. harengus*), reared on the copepods from both experiments. Error bars: 1 standard error. * marks significant differences ($p < 0.05$) from the other treatments of the given species and experiment.

The different mineral limitation treatments caused different fatty acid spectra in the algae (Table 5). The -P treatment showed not only the highest concentration of fatty acids ($\mu\text{g FA mg carbon}^{-1}$), but also the highest amount and proportion of unsaturated fatty acids, Omega 3 and Omega 6 fatty acid concentrations as well as the lowest percentage of saturated fatty acids in the experiment (all $p < 0.05$ to f/2 and no differences to -N). Exactly the same pattern was found for copepods reared on different algae treatments (Table 5).

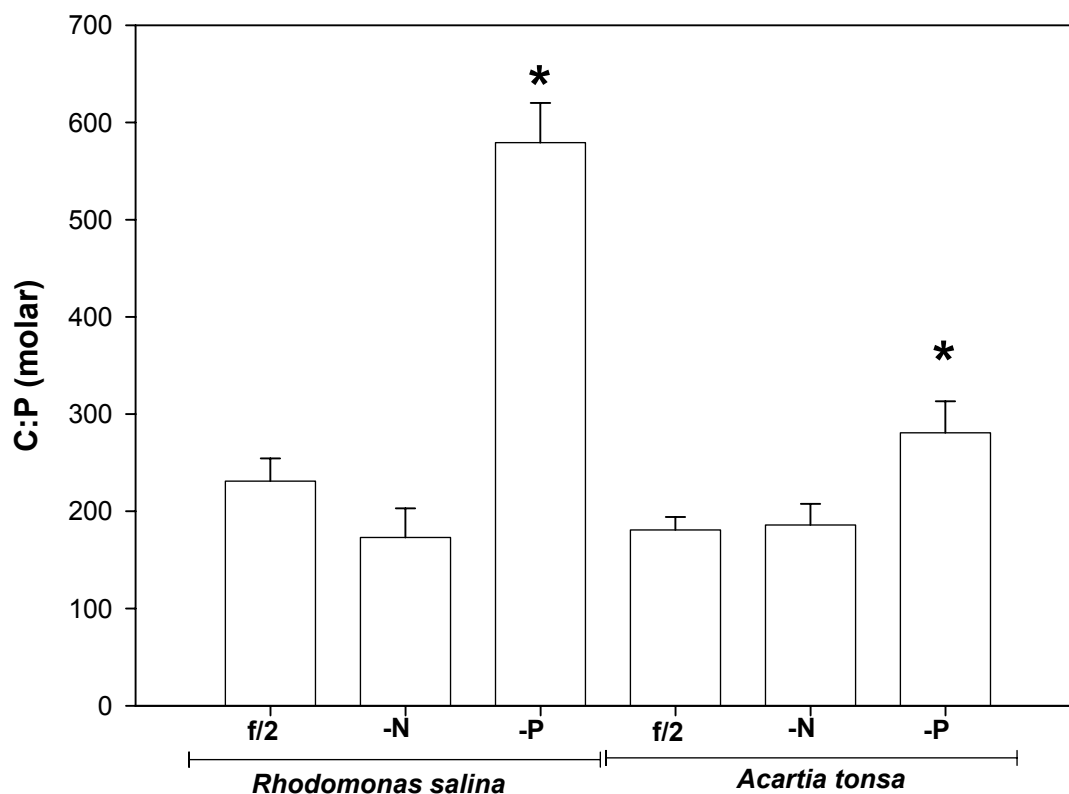


Fig. 19 Molar C:P ratio of *R. salina* cultured under nutrient-sufficient (f/2), N-limited (-N) and P-limited (-P) conditions and the C:P ratios of the copepod *A. tonsa* reared on the different *R. salina* cultures. Error bars: 1 standard error. * marks significant differences ($p < 0.05$) from the other treatments of the given species.

In general it can be said that for both higher trophic levels, the best food quality in terms of fatty acids was produced under P-limitation, followed by the N-limited conditions. The f/2 cultivated algae seemed to be of the poorest food quality. On the other hand, in stoichiometric terms f/2 produced the highest food quality and the respective limitation created food of the worst quality. This enabled us to distinguish differential effects of nutrient and biochemical originated food quality.

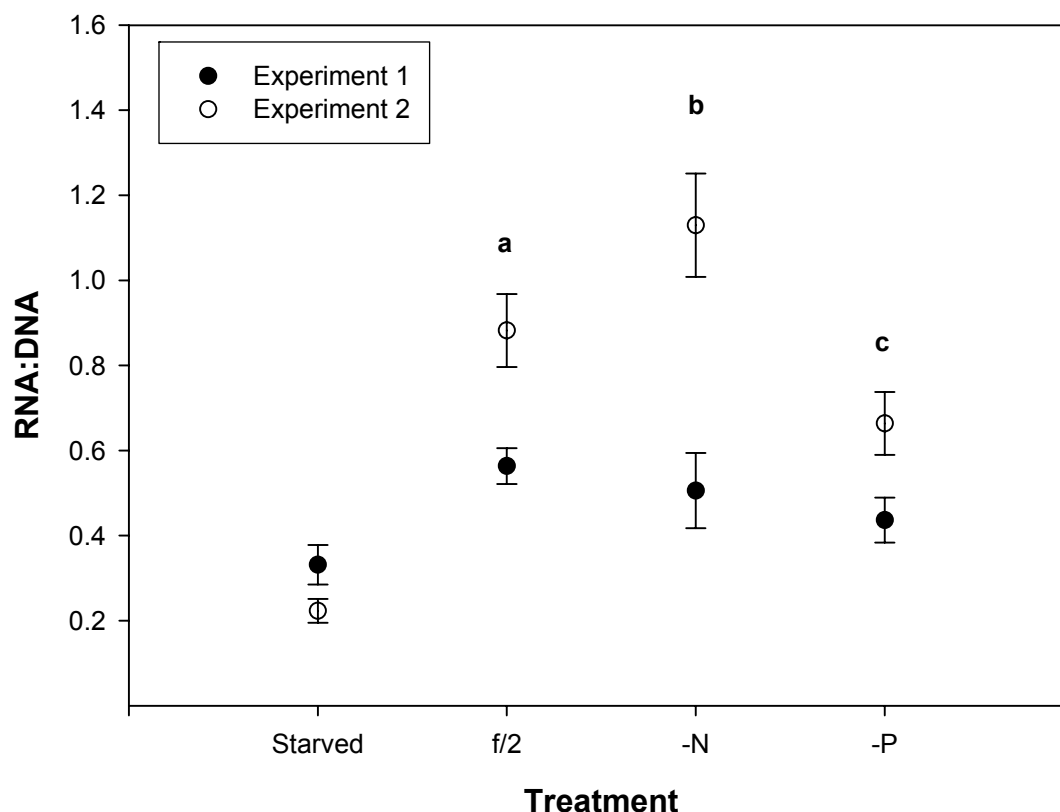


Fig. 20 RNA:DNA ratios of larval herring (*C. harengus*) reared on copepods which were fed on *R. salina* cultured under nutrient-sufficient (f/2), N-limited (-N) and P-limited (-P) conditions. Error bars: 1 standard error. Significant differences between treatments are indicated with different letters for Experiment 2. In both experiments, all fed treatments were significant different from the corresponding starving group.

Table 4 Summary table of the analysis of variance with experiment and treatment as independent factors and the RNA:DNA ratio as the dependent variable.

	MS	df	F	p
Experiment	3.13743	1	31.9402	< 0.001
Treatment	2.34235	3	23.8460	< 0.001
Exp. * Treat.	0.82783	3	8.4277	< 0.001
Error	0.09823	251		

The age of the larvae had a significant impact on the RNA:DNA ratio with older larva showing generally a better condition (Table 4). For young larvae (Experiment 1), no significant differences between the treatments were detected. All fed treatments showed significantly different values than the starved larvae of Experiment 1. Older larvae of Experiment 2 showed the same pattern as those of experiment one, but these patterns were more pronounced and differences were significant. All fed treatments differed significantly in their RNA:DNA ratios from each other (Duncan's Test $p < 0.05$). The N-limited treatment showed the highest RNA:DNA ratios, followed by the f/2 treatment. The -P treatment showed the

poorest nutritional condition of the fed groups. All three fed treatments differed significantly from the corresponding food-deprived groups (Fig. 20).

Table 5 Fatty acid composition of *R. salina*, grown under nutrient-sufficient (f/2), N-deficient (-N) and P-deficient (-P) conditions and the fatty acid composition of *A. tonsa*, reared on different algal treatments. Values are means of 19 samples per algal treatment and 10 samples per copepod treatment. Values are given in $\mu\text{g mg}^{-1}$ C (standard errors in brackets), and as a percentage of the total fatty acid content

	<i>Rhodomonas salina</i>						<i>Acartia tonsa</i>					
	f/2		-N		-P		f/2		-N		-P	
	$\mu\text{g mgC}^{-1}$	%	$\mu\text{g mgC}^{-1}$	%	$\mu\text{g mgC}^{-1}$	%	$\mu\text{g mgC}^{-1}$	%	$\mu\text{g mgC}^{-1}$	%	$\mu\text{g mgC}^{-1}$	%
C 16:0	19.06 (4.42)	34.58	68.82 (42.25)	43.75	36.72 (13.71)	28.93	47.26 (13.84)	60.83	67.98 (32.52)	56.71	70.43 (32.02)	49.47
C 16:1 n7	0.66 (0.32)	1.18	3.38 (6.71)	2.21	7.12 (8.76)	3.4	0.59 (0.27)	0.76	1.08 (0.5)	0.91	2.83 (1.68)	1.88
C 16:2n4	0	0	0	0	0	0	0	0	0	0	0	0.00
C 17:0	0.47 (0.23)	0.84	0.94 (0.52)	0.62	0.58 (0.68)	0.47	2.41 (1.11)	3.06	1.69 (1.09)	1.34	2.64 (1.47)	1.81
C 17:1 n7	0.1 (0.08)	0.18	0.26 (0.31)	0.18	0.14 (0.17)	0.13	0.26 (0.27)	0.30	0.42 (0.61)	0.41	0.69 (0.66)	0.51
C 18:0	2.92 (1.14)	5.31	8.51 (7.01)	5.5	3.25 (0.8)	3.49	10.47 (3.75)	13.23	12.15 (8.5)	9.52	13.3 (9.53)	8.81
C 18:1 n9	4.46 (2.77)	7.23	13.18 (7.91)	8.96	12.91 (7.77)	8.24	6.41 (2.6)	8.53	11.43 (4.71)	10.15	12.39 (5.22)	9.46
C 18:1n7	0	0	0	0	0	0	0	0	0	0	0.58 (1.82)	0.59
C 18:2 n6	4.03 (3.11)	6.02	7.93 (4.38)	5.11	19.96 (18.63)	9.65	0.81 (1.06)	0.88	1.78 (3.38)	1.14	6.56 (4.35)	4.21
C 18:2 n9	0.4 (0.43)	0.76	0.62 (0.64)	0.39	0.39 (0.49)	0.39	0.2 (0.18)	0.33	0.25 (0.18)	0.21	0.78 (0.47)	0.52
C 18:3 n3	11.15 (7.98)	16.53	18.18 (12.56)	12.43	40.78 (31.37)	20.52	2.43 (2.61)	2.70	5.1 (4.56)	3.84	10.45 (7.45)	6.67
C 18:3 n6	0.85 (0.88)	1.23	1.16 (0.6)	0.76	2.12 (1.9)	1.09	0.12 (0.19)	0.13	0.27 (0.29)	0.20	0.57 (0.4)	0.37
C 18:3n4	0	0	0	0	0	0	0	0	0	0	0	0
C 18:4n3	0	0	0	0	0	0	0	0	0	0	0	0
C 20:0	0.21 (0.09)	0.38	0.28 (0.15)	0.24	0.2 (0.11)	0.2	0.57 (0.15)	0.75	0.75 (0.6)	0.57	0.7 (0.36)	0.49
C 20:1 n9	0.07 (0.09)	0.14	0.23 (0.21)	0.14	0.16 (0.18)	0.09	0.03 (0.06)	0.03	0.21 (0.22)	0.15	0.21 (0.15)	0.14
C 20:2 n6	0.05 (0.05)	0.08	0.08 (0.08)	0.06	0.05 (0.06)	0.03	0.09 (0.12)	0.09	0.11 (0.09)	0.09	0.32 (0.19)	0.21
C 20:3 n3	0.03 (0.07)	0.03	0.11 (0.09)	0.08	0.14 (0.15)	0.07	0.07 (0.08)	0.08	0.03 (0.03)	0.03	0.03 (0.05)	0.02
_20_3 n6	0.1 (0.09)	0.18	0.14 (0.16)	0.09	0.23 (0.49)	0.6	0.02 (0.03)	0.03	0.04 (0.03)	0.04	0.03 (0.06)	0.02
C 20:4 n6 (ARA)	1.16 (0.71)	2.01	1.2 (0.92)	0.82	0.96 (0.81)	0.82	0.6 (0.37)	0.80	0.78 (0.6)	0.73	1.03 (0.56)	0.77
C 20:4n3	0	0	0	0	0	0	0	0	0	0	0	0
C20:5 n3 (EPA)	8.83 (7.31)	12.78	10.7 (5.78)	7.54	16.2 (10.65)	9.06	2.23 (2.79)	2.44	3.39 (3.59)	2.65	5.81 (3.35)	3.90
C 21:0	0	0	0	0	0	0	0.04 (0.06)	0.05	0.07 (0.07)	0.06	0.02 (0.03)	0.02
C 22:0	0.08 (0.03)	0.13	0.11 (0.07)	0.08	0.09 (0.06)	0.09	0.31 (0.13)	0.40	0.46 (0.66)	0.29	0.4 (0.19)	0.28
C 22:1 n9	0.06 (0.06)	0.11	0.01 (0.03)	0.01	0.01 (0.02)	0.01	0.17 (0.14)	0.20	0.07 (0.07)	0.05	0.23 (0.11)	0.16
C 22:2 n6	0	0	0	0	0	0	0	0	0.03 (0.04)	0.03	0.01 (0.03)	0.01
C 22:5n3 (DPA)	0	0	0	0	0	0	0	0	0	0	0	0
C 22:6 n3(DHA)	6.62 (4.92)	9.71	16.52 (17.3)	10.78	23.82 (39.08)	12.31	3.25 (3.34)	3.71	13.06 (12.3)	10.15	12.52 (8.25)	9.13
C 24:0	0.27 (0.14)	0.47	0.29 (0.13)	0.23	0.28 (0.18)	0.39	0.42 (0.18)	0.58	0.56 (0.57)	0.42	0.46 (0.25)	0.32
C 24:1 n9	0.05 (0.12)	0.11	0.03 (0.05)	0.02	0 (0.01)	0.01	0.09 (0.08)	0.10	0.38 (0.21)	0.32	0.33 (0.16)	0.23
total FA	57.54 (22.65)		144.75 (55.93)		146.16 (90.22)		78.05 (25.18)		120.31 (53.44)		136.74 (58.75)	
sum saturated	23 (5.2)	41.71	78.96 (49.43)	50.41	41.11 (14.16)	33.58	61.47 (18.11)	78.90	83.66 (43.19)	68.91	87.94 (42.7)	61.20
sum unsaturated	34.54 (22.05)	58.29	65.79 (32.15)	49.59	105.05 (78.6)	66.4	16.58 (9.57)	21.10	36.65 (21.54)	31.09	48.8 (17.82)	38.80
sat/unsat	0.96 (0.65)	0.85	1.68 (1.54)	1.41	0.98 (1.61)	0.91	4.39 (1.78)	4.27	2.62 (1.13)	2.58	1.82 (0.42)	1.63
n 3	26.63 (19.86)	39.06	45.51 (26.65)	30.84	80.96 (67.49)	41.97	7.98 (8.78)	8.93	21.58 (19.71)	16.66	28.81 (13.91)	19.72
n 6	6.19 (4.4)	9.52	10.52 (5.28)	6.83	23.32 (20.85)	12.19	1.64 (1.48)	1.93	3.01 (3.47)	2.22	8.52 (5.15)	5.60
n 3/n 6	4.26 (1.76)	4.26	5.28 (5.25)	5.28	6.47 (10.36)	6.47	4.55 (2.24)	4.55	10.1 (7.31)	10.10	3.83 (1.55)	3.83

4.4 Discussion

Consumers have to take up their nutrients from their food. At the interface between primary production and herbivore grazers, the nutrient supply and demand often show dramatic imbalances in terrestrial as well as aquatic systems (Elser et al. 2000). The biochemical reworking of the ingested food creates costs which rise with increasing carbon/nutrient ratios. These costs may even exceed the benefit of ingesting food and may lead to a rejection of poor quality food (Mittra & Flynn 2005). As nutrients are needed for metabolic processes and for the construction of various structures, algae have adapted their physiology to unstable nutrient conditions by adjusting their anabolic strategies to the available nutrient levels. Under P-rich conditions, algae invest in assembly machinery such as ribosomes (P-rich), whereas in P-poor situations the investment in the resource acquisition machinery (nutrient uptake proteins and mitochondria, N-rich) is enhanced (Klausmeier et al. 2004). This

ultimately leads to a high variability of nutrient ratios in algae and they therefore represent a food source of variable quality for herbivores.

It is still under debate whether the changes of quality of phytoplankton as food for zooplankters are direct, i.e. mineral limitations directly affect growth and reproduction (Urabe et al. 1997, Boersma 2000, Plath & Boersma 2001), or whether accompanying changes such as changes in the fatty acid spectrum (Müller-Navarra 1995) are responsible for the observed quality effects. Algal fatty acid compositions as well as their concentrations are known to change drastically under mineral limitation (Müller-Navarra 1995) and this is considered to represent food of poor quality. Park et al. (2002), however, reported no effects of nutritional limitation on different fatty acid measures (total fatty acids, unsaturated fatty acids, n6, n3 and EPA) in several algal species cultivated on various C:P ratios. In our study, the cryptophyte *Rhodomonas salina* produced significantly more total fatty acids, unsaturated fatty acids, EPA and DHA under both, N- and P-limitation, and thus in our case the limited algae showed enhanced food quality. This could explain the observations of (Augustin & Boersma in press) who observed increases in reproductive output of *Acartia* species fed N-limited algae. Similar, but not as pronounced findings were shown by Jonasdottir (1994), who presented fatty acid profiles for three algal species in relation to their growth phase; the differences between early exponential growing and senescent cultures were not large, but the trends were the same for *Thalassiosira weissflogii* and *Rhodomonas lens*. The most realistic view of fatty acid profiles of algae under nutrient limitation may be that given by Reitan et al. (1997) who summarized that increasing nutrient limitations may lead either to an increase or decrease of fatty acid levels, depending on the algal species.

For a long while common knowledge has been that zooplankters, despite feeding on food sources of highly variable nutrient stoichiometry, maintain a large degree of homeostasis, i.e. they keep their nutrient ratios constant (Hessen 1990, 1992, Sterner 1997, Anderson et al. 2005). Even though this has recently been contested by such authors as Plath & Boersma (2001), DeMott et al (1998) and Sterner et al (1993) who reported variation in the body C:P of freshwater zooplankton (mainly *Daphnia*), the general opinion is still that changes in stoichiometry only play a small role in comparison to the much larger ranges in algae. Our results contradict this concept, as the copepods dampened the variation of carbon:nutrient ratios of their food, but not to a degree suggested by homeostasis theory derived from freshwater crustacean zooplankters (Andersen & Hessen 1991). It remains unclear whether this is caused by differences between systems (e.g. marine and freshwater), by differences between taxonomic groups (copepods vs. cladocerans) or simply by different interpretations of data.

In our experiments the C:P ratios of the algae were similar to those reported by the above-cited studies, but the dampening effects of the consumers, in our case copepods, were not

as pronounced. We found significantly higher C:P ratios in copepods grown on P-limited algae, but unaffected C:N ratios of copepods grown on N-limited algae. The apparent contrasts in C:P ratios might be explained by differences between daphnids and copepods. A high variability in C:P ratios is reported for several copepod species taken from field samples. Variability was high between species, within species between seasons as well as within species between developmental stages (Gismervik 1997). In addition, differing P-demands occur in young and older daphnids and therefore comparable results for inter-developmental stage variability of C:P ratios was reported by Boersma (2000). DeMott (2003) doubts the findings of Boersma as he found the opposite, but nevertheless, he also reported variation between life stages. In any case, the data reported by Gismervik (1997) in combination with our data suggests a less strong homeostasis in copepods than in daphnids. Consequently, copepods represent changing nutritional values to their consumers.

In this study, the copepod fatty acid composition reflected well those of their diets, a pattern which is in good correspondence to studies by Sargent and Falk-Petersen (1988), and enabled the use of fatty acids as trophic markers (Peters et al. 2006). This was likely because long-chained unsaturated fatty acids like EPA and DHA can not be synthesized *de novo* by copepods. Different levels of fatty acids are known to influence growth in larval fish. St. John et al. (2001) were able to demonstrate significant effects of dietary EPA as well as DHA levels on larval cod growth. Additionally, Sterner (1993) reported lower growth rates but higher lipid levels in *Daphnia sp.* reared on limited *Scenedesmus sp.*. Growth rates of the copepods were not monitored in our study; however a similar amount of copepods of all treatments reached the fifth naupliar stage within the same time. Thus, the copepods reared on P-limited algae represented the best food offered to larval herring in terms of fatty acids in our experiments.

The C:N ratios of the larval herring showed no response to the different diets offered. Indeed, in contrast to the findings of Von Westernhagen et al. (1998) who proposed that the C:N ratio may be a useful indicator of condition in marine fish larvae, there is doubt that the C:N ratio is a valid predictor for condition of larval fish (Ferron & Leggett 1994). The C:N ratio mostly reflects the ratio of lipids to proteins. The storage of lipids is not common in larval fish as the energy taken up with food is usually directly channelled into growth (Kioerboe et al. 1987). The RNA:DNA ratio is a valid predictor for nutritional condition of larval fish. This has been validated in many laboratory and field studies (Buckley 1984, Clemmesen 1994, Theilacker et al. 1996, Gronkjaer et al. 1997, Rooker et al. 1997, Caldarone et al. 2003, Malzahn et al. 2003, Caldarone 2005). The RNA:DNA ratio of herring larvae in our experiments revealed that the N-limited food chain produced the best nourished larvae. This is contrary to the predictions which could be drawn from the fatty acid profiles, where the P-limited food chain displayed the best food quality. Aquaculture studies (Vielma et al. 2002) have shown that it is very well possible for fish to be limited by phosphorus. Despite this fact, almost no studies exist investigating this in an ecological context (but see Hood et al. 2005). Schindler and Eby

(1997) demonstrated the possibility of fish growth rates being P-limited by means of model exercises. Three out of 186 cases showed P-limited growth rates while another five cases were probably close to limitation. This study focussed on freshwater fish, where benthivorous fishes permanently subsidize the pelagial by excreting nutrients originating from the benthos. The authors further included several piscivorous fish species in which short term P-limitation due to seasonal nutrient depletion of the water column is very unlikely. The three cases they reported were for vendace, a zooplanktivorous whitefish species and for sockeye salmon fry, also exhibiting an obligate planktivorous feeding habit. Contrasting to the dominant P-rich cladocerans, marine systems are dominated mainly by copepods, which have a much higher N:P ratio than cladocerans (50 for calanoid copepods and 15 for *Daphnia* Elser et al. 1996). In terms of phosphorus content, planktivorous fish in marine systems are therefore more regularly faced by food of lower quality than their freshwater relatives are. Additionally, the fertilizing impact of benthivorous fish is obviously of minor importance in the majority of marine systems. Consequently, this potentially makes marine fish more susceptible to P-limitation. The copepods in our experiments reared on P-starved algae showed the best fatty acid contents, but at the same time the worst C:P ratio. In combination with food in excess, our results suggest that larval herring reared on the P-starved food chain displayed P-limited growth. These findings correspond well to the findings of Boersma (2000), who demonstrated for *Daphnia sp.* that both mineral and biochemical limitations of food play a role in the growth and population dynamics of zooplankters, but that mineral requirements need to be met first.

CONCLUSIONS

The long-accepted hypothesis, that effects of mineral limitation at the primary producer level are compensated by the stoichiometric needs of primary consumers and hence are not transported through food webs in terms of food quality must be rejected in favour of our hypothesis that effects of nutrient limitation indeed cascades through trophic levels. Larval herring reared on a P-starved food chain showed a significantly lower condition than their counterparts reared on N-starved or nutrient-sufficient food chains. This could not be explained with biochemical components of the food, as the fatty acid profiles of the P-limited food chain displayed a significantly higher food quality than the N-limited or nutrient sufficient food chains did and is more likely to be caused by P-limitation of the larvae.

These findings may have implications for the predictions of fish population dynamics using larval proxies, as larval fish might have lower growth rates at the end of bloom situations than the actual prey availability would suggest. Hence, larval fish growth in the field is not likely to be limited by food quantity only, but also by food quality.

Chapter 5

General discussion

The life cycle of fish is complex and consists of several distinct phases, each of them influenced by different processes and hence the size of a fish stock is determined by a variety of forces. Based on that, Paulik (1973) proposed not to concentrate on “simple” attempts to link stock to recruitment but to partition the life of a fish into the main phases and to understand the mechanisms which are essential for each life stage. Ultimately a better understanding of the different stages should lead to improved predictions of recruitment and year-class strength. Unfortunately, this approach has seldom been completely implemented in recruitment studies mainly because of the obvious difficulties such an approach involves. The consideration of the whole life cycle requires fundamental knowledge of the mechanisms acting on the particular life stages. As the necessary knowledge comes from multiple scientific disciplines, it can only be assembled from the work of many scientists, who are doing research on their respective topics of the different life-stages of fish. This thesis addressed several questions on larval life stages of fish to contribute to the pool of knowledge to ultimately come to a complete understanding of fish recruitment.

The questions addressed in this thesis were: (1) what are the seasonal patterns of fish larval assemblages at Helgoland Roads and what are the factors influencing species diversity and abundance; (2) what are the factors controlling nutritional condition of larval fish; and (3) to which extent does food quality influence the growth and condition of larval fish?

These questions were addressed at different levels of organisation in this thesis, ranging from species assemblages in Chapter 2 (question 1) through single species populations in Chapter 3 (question 2) to the individual level in Chapter 4 (question 3).

Each chapter contains a specific discussion of the results. This general discussion will bring the results of the single chapters in a context with published work but will focus on four main topics of larval fish studies in a broader manner than discussed in the single chapters. These questions are:

- 1) What are the general motivations to study larval fish?
- 2) What can we learn from monitoring surveys?
- 3) Why conduct field process studies on larval fish?
- 4) How can experimental work on larval fish extend our understanding of processes acting in the field?

1) What are the general motivations to study larval fish?

As described above one of the main missing links in fisheries research is the predictive link between standing stocks of adult fish and recruitment. If we were able to predict recruitment from standing stocks properly, there would be no need to study larval fish, other than out of pure scientific interest. As it is, predicting year-class strengths is still in its infancy, despite the constant interest in the topic for the past 100 years or so. Therefore, there is a strong need to study larval proxies, whereby the value of year-class strength predictions rises with the time between the forecast and the actual exploitation of the target (Heath 1992, Painting et al. 1998). A longer duration between the forecast and the fishing allows more time to adjust management strategies like mesh size adjustments or changes in the target species of the fleet among others. The processing industry also benefits from early forecasts as they can adjust their production capacities and strategies to the availability of fish on the market. Two good examples for the need and implementation of early and reliable forecasts are the South African anchovy fishery, where this has worked very well and the fishery for sandeel in the North Sea, the yields of which have plummeted in recent years.

The South African anchovy fishery lands between 0.4 and 1.5 million tons per annum and is a major branch of South Africa economics (FAO). This target species is a short-lived small pelagic fish, which spawns at an age of one year. Spawning takes place from November to January at the Agulhas Bank, off the southernmost tip of South Africa. Eggs and larvae are then transported northwards by a coastal jet current to the nursery areas in the north-west of South Africa. The fishery consists to 70% of young of the year fish, and the total allowable catch (TAC) is fixed in January on the base of echo-surveys targeting the brood stock, so virtually at a time when the incoming year-class is still in the larval stage (Hutchings 1992, Fowler & Boyd 1998, Hutchings et al. 1998, Painting et al. 1998, Hutchings et al. 2002). This means that fast and near-time predictions with a high accuracy are necessary as from the biological point of view there is no real chance to adjust the TAC effectively to save the stock in case of an overestimation of harvestable biomass and from an economic point of view the industry needs a certain degree of planning certainty. For the management of the stock of the anchovy indirect larval proxies proved to be useful (Boyd et al. 1997, cited in Painting et al. 1998). The first is a confirmation of Sinclair's member/vagrant hypothesis (Sinclair 1988). The south-easterly wind anomaly during the larval transport is strongly correlated to subsequent year-class strength. In years with high south-easterly wind speeds a huge proportion of larvae is lost to food deprived offshore waters. The second proxy is partly a confirmation of Cushing's match/mismatch hypothesis (Cushing 1974, 1990). It is the oil to meal ratio derived from adult anchovies caught at the nursery grounds prior to the arrival of the larvae. The oil to meal ratio reflects the feeding conditions at the nursery area which shows a positive correlation with recruitment.

A second example is the Danish sandeel fishery. Sandeel is also a small fish which school at daytime and feed on zooplankton while they dwell into the sediment at night and during winter. Sandeels spawn in winter and, thereafter, the larvae hatch and initiate their pelagic life phase in early spring. After several weeks in the plankton they settle at appropriate sandy habitats and enter their sediment dwelling life phase (Holland et al. 2005). As soon as they emerge from the sediment during the following spring season they are recruited to the fishery. This means that an early recruitment forecast is necessary as the fishery relies mainly on the incoming year-class (ICES 1999, 2006). The sandeel stocks in the North Sea are in a serious state at present since they have been in decline for several years now. Despite the historical minimum of the stocks, the first real management approaches were initiated only in 2004 by significantly reducing the TAC, by compiling a plan to be responsive to a possible recruitment failure and to adjust fisheries in 2005 (ICES 2005, 2006). A real-time monitoring was conducted in spring 2005 which showed that the incoming year-class was again very weak. This led to a closure of fishery with severe economical consequences for the fleet and the processing industry such as a massive fishmeal and oil shortage for the pharma-, cosmetic- and the aquaculture industry. The use of proper larval proxies would have prevented the economic disaster for the fleet and the industry by leaving more time to develop alternative plans (more information at www.ices.dk and www.999.dk). One possible measure could be an index of successful larval drift to suitable sand bank habitats for the larvae to settle. The biggest problem in setting up such a proxy is our lack of knowledge of the range of sandeels' active habitat choice.

In general, a broader knowledge on larval fishes temporal, spatial as well as growth and survival dynamics may provide required explanatory power to accurately manage fisheries. To broaden this knowledge we need proper implementation of a combination of monitoring, field experiments and laboratory experiments. This is exactly what was aimed for in this thesis.

2) What can we learn from monitoring surveys?

Basic Monitoring approaches are often considered time-consuming and sometimes even trivial enterprises with a low potential of producing publishable results. Nevertheless, routine monitoring programs sampling all trophic levels as well as abiotic information serve as a secure basis for a broad scale of studies ranging from phenological studies on single species via studies on population structure and species assemblages to the impact of global change in aquatic ecosystems and they are thus essential for the detection of such major events like regime shifts.

On a small scale, such monitoring approaches can be used to predict the seasonal occurrence of different species. Phenological studies published by Greve et al. (Greve et al.

2004, Greve et al. 2005) demonstrated that predictions on the appearance and the duration of species occurrence in the zooplankton are possible and that such phenologies are linked to the mean temperature during winter. This holds true for most of the fish species under investigation in Chapter 2, but for the lesser sandeel the temperature trajectory seemed to be of more importance than the mean temperatures. Provided that forecasts like these show a high degree of reliability, match situations between zooplankton production and larval fish occurrence in the plankton can be predicted. These predictions can then be used to test hypothesis like Cushing's match/mismatch hypothesis in the field with a comparatively low sampling effort, by sampling at those times that are predicted to have a match or a mismatch situation based on the models and sample food densities and larval growth proxies.

The level of species assemblages is investigated in Chapter 2, which is based on a three year monitoring approach and mainly focussed on the stability of species occurrence and larval fish assemblages. It supports Cushing's assumption that the occurrence of larval fish of a given species is relatively fixed in time, as the largest part of the observed variability in larval fish abundance over the three year monitoring was found within weeks, the lowest temporal unit analysed, whereas the variability on the next higher level, within months, was small. Similar robust temporal ichthyoplankton communities were reported by Witting et al. (1999). These authors also found the largest variability of larval fish abundance between weeks within months in an estuary in southern New Jersey/USA. Despite the robust pattern of species composition described in Chapter 2, there was large inter-annual variability of the total larval abundance. The maximum larval abundance was roughly 10 times higher in 2004 than it was in 2005, which was almost exclusively attributable to the mass occurrence of the lesser sandeel in spring 2004. Relatively high inter-annual variability in larval abundance was reported from lakes ecosystems (Hamley et al. 1983) as well as marine systems (Peterman et al. 1988, Miller & Shanks 2005). On the species level, the inter-annual variability in abundance was very low, as the lesser sandeel accounted for the majority of the variability in spring and gobiidae species made up the largest part of the variation in summer. A similar result was reported by Allen and Barker (1990), who showed that the inter-annual variability was highest in *Gobiosoma* species, the most dominant taxon in their study. After the exclusion of the lesser sandeel from the analysis, a remarkable similarity of the annual dominance curves between the years could be shown, contributing to the finding that the larval fish assemblage at Helgoland Roads is relatively stable between years after the extraction of just one single dominant species. The impact of the lesser sandeel was also detectable in the cluster analysis shown in Chapter 2. Clear spring and summer clusters were present, whereby the spring cluster showed a higher degree of heterogeneity. Within the spring cluster three subdivisions were observed, which were mainly caused by the presence or the absence of lesser sandeel. This pattern was not found in the summer

cluster. In summer, only two sub-groups were observed, and these showed no inter-annual pattern, but were attributed to a succession from an early summer to a late summer species assemblages which were similar in the three years of observation. Allen and Barker (1990) reported a similar pattern with higher variation in winter and spring species assemblages than those they observed in summer. They attributed their finding to differences in weather conditions between the years and the resulting increase in freshwater runoff in rainy years, as their study took place in an estuary. The more stable results in summer observed in this thesis could also be attributed to the generally higher diversity found in summer. Nevertheless, there was some temporal variation at the level of weeks, which could be explained by temperature. This was concurrent with phenological hypothesis (Parmesan & Yohe 2003, Greve et al. 2005), which predicts an earlier occurrence or biomass peak with higher temperatures. In comparison to the variability of several months in the onset of the phytoplankton spring bloom in the three years (Wiltshire, pers. comm.), the variability in larval occurrence can be considered to be low.

Exactly these phenological shifts are contributing to a large extent to the body of evidence for the existence and impact of climate change on aquatic communities (Beaugrand et al. 2003, Beaugrand 2004, Edwards & Richardson 2004) as well as on terrestrial polar and tropical ecosystems (Hughes 2000, Walther et al. 2002). A good example of climate-induced change is the major regime shift in the North Sea which was detected by analysing the datasets of the continuous plankton recorder (Beaugrand (2004). In this study the author was able to show that total phytoplankton biomass, copepod biomass as well as diversity and recruitment in flatfish and gadoid fish species showed significant shifts in the early 1980s. Weijerman et al. (2005) also reported substantial regime shifts that occurred in the North Sea and in the Wadden Sea in 1979, 1988 and 1998. These regime shifts were elucidated by interpreting biological data series, but the causes of these changes lie in earlier shifts in a number of environmental factors. Salinity and weather conditions played an important role in the 1979 shift, while in the 1988 shift, temperature and weather conditions were the predominant factors. The high resolution (work daily) of the long-term Helgoland Roads dataset on temperature, nutrients, phytoplankton and zooplankton assemblages allowed the detection of significant shifts in the timing of the phytoplankton spring bloom that were in good correlation to rising winter temperatures (Wiltshire & Manly 2004). The use of extensive datasets of zooplankton and fish species assemblages enabled Alheit et al. (2005) to show synchronous regime shifts on zooplankton by alterations of dominance patterns as well as in fish by biomass fluctuations in the North Sea and in the neighbouring Baltic Sea. Other major regime shifts in marine and terrestrial systems are reviewed by Walther et al. (2002). The level of response to temperature changes varies between functional groups and trophic levels (Edwards & Richardson 2004) and temporal mismatches between producers and

consumers may be the consequence. Experimental evidence for negative effects of trophic mismatch is discussed in detail later in this chapter, field studies dealing with the impact of such mismatches on larval fish are discussed under point three of this discussion.

3) Why conduct field process studies on larval fish?

Larval fish surveys are regularly conducted in marine areas throughout the world. Only some of them include the more sophisticated study of larval nutritional condition even if these can contribute to our understanding of mechanisms acting regulatory on larval fishes in the field. Chapter 3 reports indications for food limited growth and the impact of a disparity between prey densities and ambient temperatures on larval fish nutritional condition. After the decrease in prey densities in April 2004 only poorly conditioned larvae of dab and sandeel occurred in the catches. Nevertheless, prey densities after the breakdown were even higher than those in the middle of March, when well-conditioned larvae of both species could be found in the population. This interpretation of food-limited growth bases on bioenergetic considerations and experimental work on sockeye salmon and other species (Brett 1979) which indicated that the relation between growth and temperature is dome shaped and that the optimum temperature for growth shifts to lower temperatures if ration is restricted. As the temperature was around 4°C in March compared to 7-10°C after the food breakdown, the findings given in Chapter 3 could well be explained by the shift of optimum growth towards lower temperature with decreasing ration and thus, this can be considered as an indication for ration-restricted growth at higher temperatures late in the season.

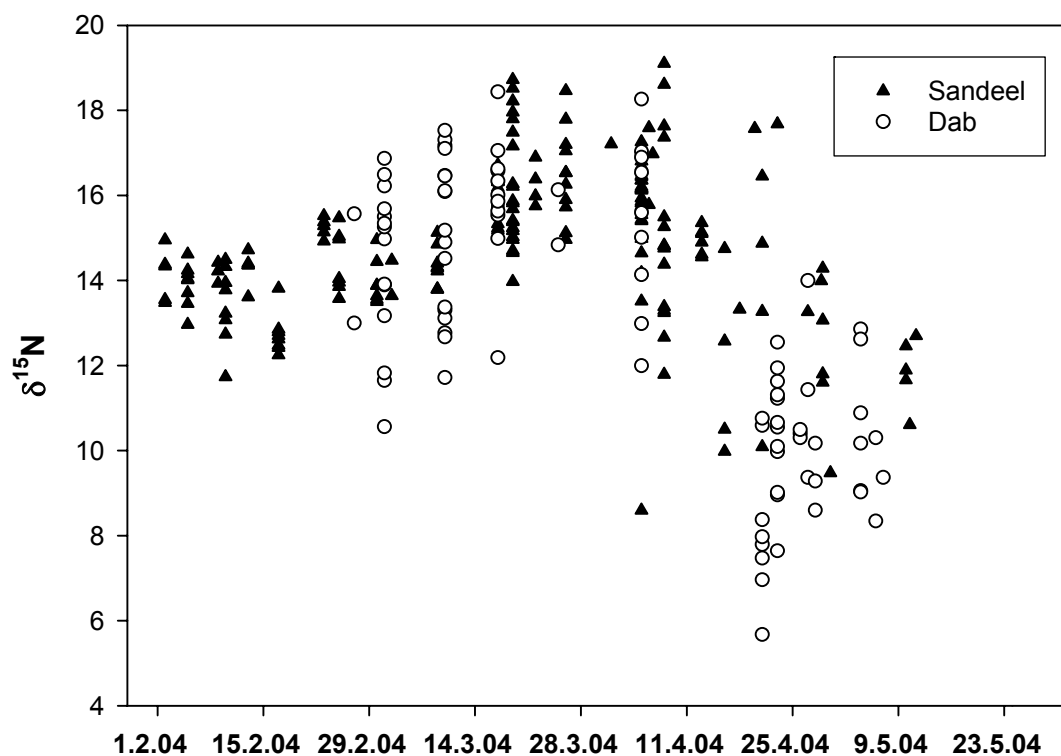


Fig. 21 $\delta^{15}\text{N}$ signature of larval dab (*Limanda limanda*) and sandeel (*Ammodytes marinus*) caught in spring 2004 at the Helgoland Roads station

Additionally to the samples taken for the study described in Chapter 3, samples of larval dab and sandeel for the analysis of stable isotopes were taken. The analyses were out-sourced, and as the results arrived late, they could not be included in Chapter 3. Due to their additional explanatory value they are briefly presented in this discussion. The enrichment of the stable nitrogen isotope ^{15}N can be used as a trophic tracer (Peterson & Fry 1987, Fry 1988), as the stable isotope signatures of a consumer generally reflects the isotopic composition of their diets and enriches the heavier isotopes in a relatively dependable manner (DeNiro & Epstein 1981, Post 2002). The reduction of the ^{15}N signature in late spring shown in Fig. 21 is clear evidence for a downwards shift in larval trophic level, which indicates that the larvae substituted the shortage in zooplankton by the phytoplankton bloom as an alternative.

That this shift is not only caused by feeding habits of different larval size-classes is shown in Fig. 22 and Fig. 23. It is obvious that all size classes in the catches showed a downward shift in their trophic position. As shown in Chapter 3, the larger larvae suffered significantly at these times of reduced zooplankton availability indicated by the low RNA:DNA ratios. This was not found in small larvae, so it could be concluded that small larvae were sufficiently

nourished by phytoplankton and possible remains of their yolk. That larval fish feed regularly on phytoplankton in the smallest size-classes was shown for cod (Kane 1984), dab, flounder and sole (Last 1978) as well as American sandeel (Monteleone & Peterson 1986), but all studies reported a rapid change to zooplanktivory with size. The lack of well conditioned larger larvae feeding on phytoplankton suggests alterations in larval nutritional demands which make zooplankton food imperative. Additionally, the quality of the phytoplankton as food for higher trophic levels deteriorates in an ongoing bloom. The Chl.a/N as well as the Chl.a/P ratio increased within the bloom, indicating a shortage of both nutrients for algal growth (Fig. 24). It was shown in Chapter 4 that mineral limitations affect the quality of the primary production itself as well as the nutritional value of consumers feeding on the algae. Consequently I conclude that this reduced food quality affects larval condition negatively. The same mechanism could be expected to act in late spring 2004. This means that the nutritional condition of larval fish in late spring 2004 was not only affected by a shortage in zooplankton prey, but also by a decrease in the quality of the alternative food source, the diatom bloom.

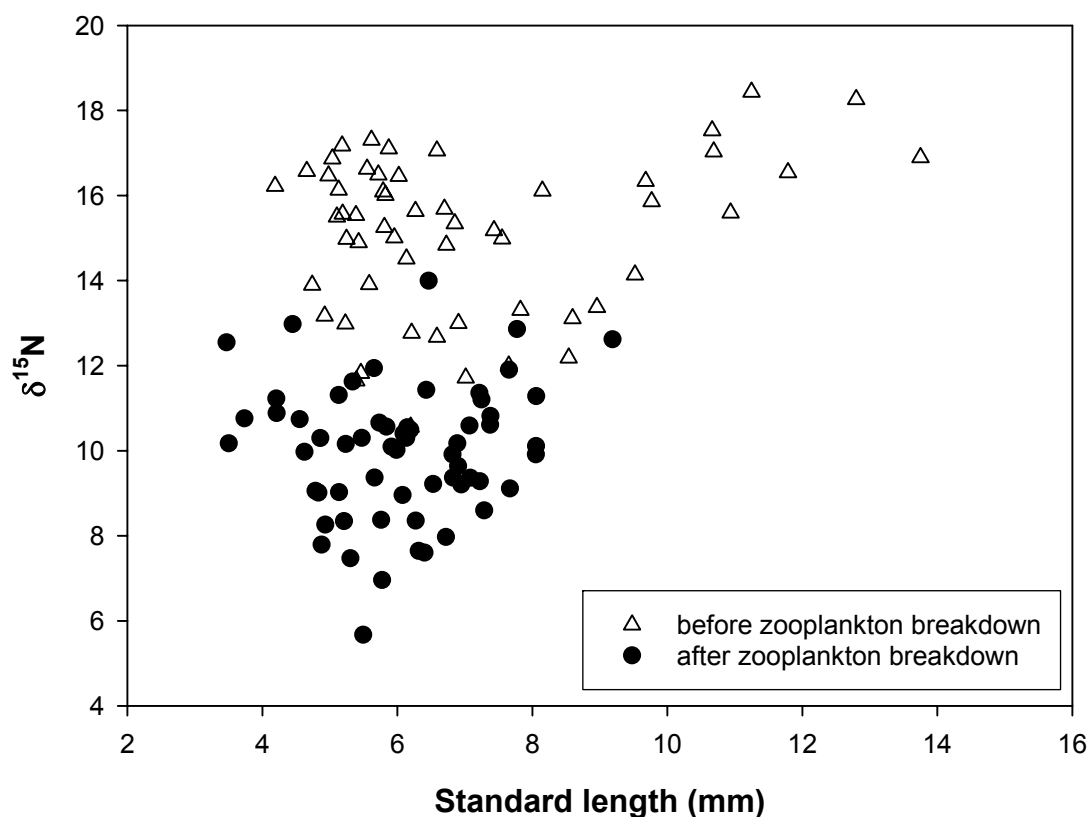


Fig. 22 $\delta^{15}\text{N}$ signatures of larval dab (*Limanda limanda*) caught in spring 2004 at the Helgoland Roads station plotted against larval size. The dataset is divided in pre-phytoplankton bloom (before zooplankton breakdown) and phytoplankton bloom (after zooplankton breakdown).

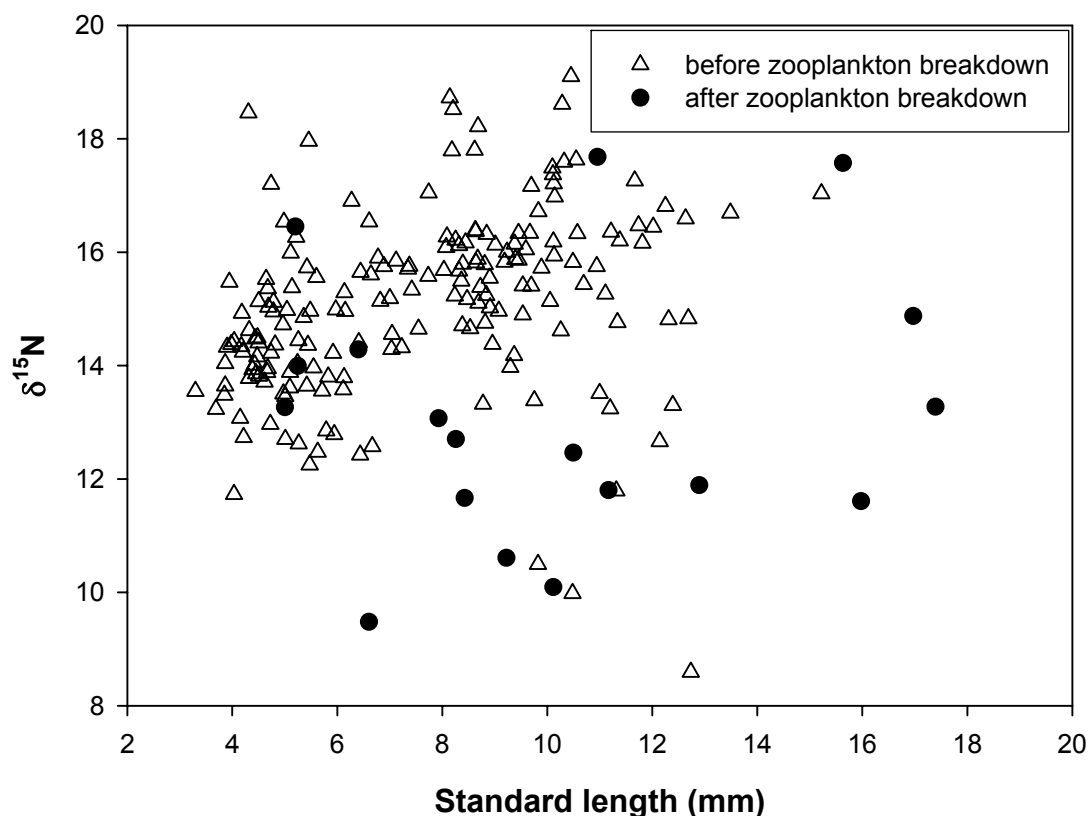


Fig. 23 $\delta^{15}\text{N}$ signatures of larval sandeel (*Ammodytes marinus*) caught in spring 2004 at the Helgoland Roads station plotted against larval size. The dataset is divided in pre-phytoplankton bloom (before zooplankton breakdown) and phytoplankton bloom (after zooplankton breakdown).

Another example for the inclusion of larval fish condition in field studies is the Georges Bank area. From that area, confirmation of the “Food-limited growth hypothesis” (Anderson 1988) was reported by Buckley and Lough (1987) and Buckley et al. (2004), who were able to show food-limited growth for larval cod and haddock in several years on Georges Bank. The observed growth rates in the field were well below those derived from laboratory experiments at the given water temperatures (Caldarone et al. 2003).

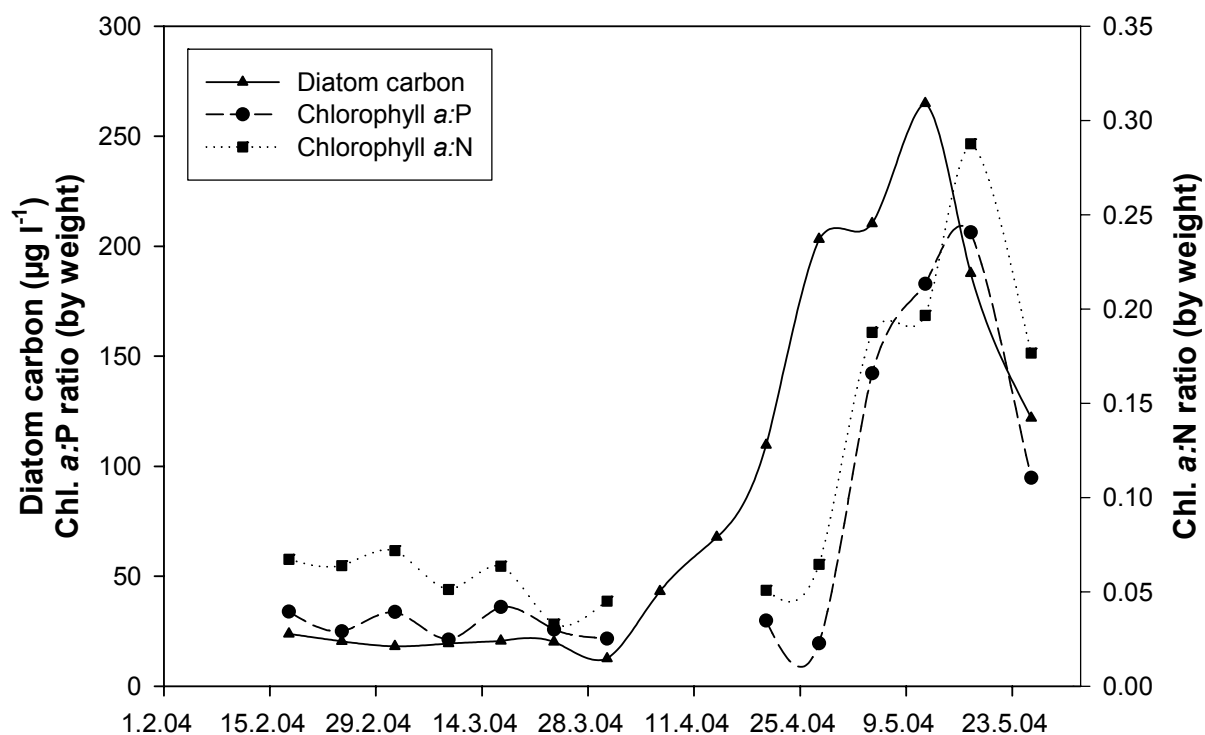


Fig. 24 Development of diatom carbon and the ratios of chlorophyll a to organic phosphorus and nitrogen in spring 2004 at the Helgoland Roads station

The demonstration of food-limited growth and a further understanding of the relationships among temperature, food availability and growth are critical steps in establishing the physical and biological factors that control fish production. Food-limited growth is implicit in many of the hypotheses advanced to explain recruitment variability (Anderson 1988). If food were not limiting in the sea, then the match/mismatch (Cushing 1974, 1990) and the growth/mortality hypotheses (Ware 1975), among others, could be rejected. The effect of growth on stage duration (Houde 1987) and the inverse relationship between larval growth and mortality rates observed for cod and haddock both in culture (Buckley et al. 1993) and in the North-West Atlantic (Campana et al. 1989) suggest that food limitation may affect survival as well as growth. Selection for fast growth during the larval stage was demonstrated for Atlantic cod on the Scotian Shelf from otolith microstructure analysis (Meekan & Fortier 1996). Larvae surviving the first 90 days of life were considerably larger at age than the population sampled earlier in the larval period. A strong correlation between otolith radius (juvenile size) at age 90 days and cohort abundance (year-class size) demonstrated the importance of rapid growth for survival and eventual recruitment of cod on Georges Bank (Campana 1996). This implies that survival is dependent on food availability, i.e. well nourished larvae have a higher probability to survive the larval stage. In turn, this means that mortality is negatively correlated to condition.

Evidence for condition-selective mortality is given in Chapter 3 of this thesis from the study on the nutritional condition of larval dab and sandeel caught in the North Sea in spring 2004. We found an increase of the mean RNA:DNA ratio with size, which was caused by a significant loss of poorly conditioned larvae in the larger length-classes in larval sandeel rather than by a gain of better conditioned larvae. This pattern combined with the lower number of larger larvae in the catches implies that the increase of the mean condition is caused by a loss of poorly conditioned larvae due to starvation or predation rather than that poorly conditioned larvae enhanced their condition with size. Similar findings are published by Pepin et al (1999). The authors also demonstrated clear evidence for condition-selective mortality by showing a significant loss of poorly conditioned larvae at larger length classes for several species of marine fish larvae coinciding with mortality rates.

Despite this evidence, the concept of condition-dependent mortality is still debated as there is also evidence that condition does not play a role. Elliott and Legget (1998) published an experimental study on the effects of larval nutritional condition and the survival of the larvae in the presence of a predator. The hypothesis that was tested was that better conditioned larvae should experience lower mortality rates and consequently the surviving population should show skewed distribution patterns towards larvae of better condition. In their study the hypothesis was rejected, as no differences between the condition frequency distribution of the experimental groups and the control were found. This study was heavily attacked by Suthers (2000), who stressed the misleading interpretation of the results and doubted the applicability of these findings to natural conditions in the planktonic realm as the experimental design of the study contained some serious flaws in the experimental design. Nevertheless, the experiment showed that well conditioned larvae are also exposed to heavy predation pressure, thus the level of response we are working at might be very hard to detect. This dispute about the value of experimental work leads directly to the last of the 4 main questions guiding through this general discussion.

4) How can experimental work on larval fish extend our understanding of

A large body of laboratory experiments on larval fish has been carried out to (1) establish and validate the potential use of methods in larval fish ecology and recruitment studies (Clemmesen 1987, 1993, 1996); (2) to establish laboratory calibrations for e.g. condition measures to various biotic and abiotic conditions for a better understanding of field data derived growth rate calculations; (3) to directly test ecological hypothesis (reviewed by Ferron & Leggett 1994); and (4) to establish needs of commercially interesting fish in aquaculture settings (Rodriguez et al. 1998, Izquierdo et al. 2000, Fountoulaki et al. 2003).

Examples for the development and validation of methods was given e.g. by Buckley (1984), who showed that the RNA:DNA ratio is a useful predictor for the nutritional condition of larval

fish, as well as Clemmesen (1993) who developed a fluorometric method for single larvae measurements.

The above-mentioned findings on larval cod and haddock on Georges Bank (Buckley et al. 2004, Lough et al. 2005) were made possible by the extensive knowledge derived from laboratory experiments. The calculations of protein growth rates of larvae caught in the field was only possible as the species-specific laboratory calibrations were available (Caldarone et al. 2003, Caldarone 2005) or by the use of a more general model derived from several temperate marine fish species if a specific model is not available for the species under study (Buckley et al. 1984).

The “food-limited growth” hypothesis (Anderson 1988) was experimentally tested for several species of larval fish. This hypothesis is a major part of the hypotheses of Hjort (1914), Cushing (1974), Lasker (1981) and Ware (1975) on year-class regulating mechanisms. The dependence of larval fish condition on feeding levels has successfully been shown for a wide range of species like herring (Clemmesen 1994), red drum (Johnson et al. 2002) coregonid fishes (Steinhart & Eckmann 1992), rainbow trout (Weber et al. 2003), cod (Clemmesen & Doan 1996) and many others. All the ecologically oriented laboratory studies have one thing in common, when carrying out experiments with different food treatments, these treatments manipulated feeding levels (quantity) only whereas the effect of food quality was neglected so far. This is unfortunate, as especially the aquaculture literature shows that food quality effects can be very important (Coutteau & Sorgeloos 1997, Izquierdo et al. 2000, Navarro et al. 2001).

Experiments with larval fish can be used in a more sophisticated way in order to experimentally test ecological hypothesis. Although such approaches have a high potential to increase our knowledge on higher trophic levels and predator-prey interactions in experimental aquatic ecology such studies are scarce. The above cited study designed to test the “condition-selective mortality” hypothesis (Elliott & Leggett 1998) is one of the few examples. Additionally, St. John et al. (2001) tested the influence of diatoms on growth and survival of larval fish. The authors tested a potential negative effect of different algal diets, as it was hypothesised that diatoms produce aldehydes as a chemical defence against their predators, and that these aldehydes negatively influencing copepods (Ianora et al. 1995, Ianora et al. 2004). The study showed a clear effect of essential fatty acids on the growth of larval Atlantic cod, but the hypothesis of negative effects on larval fish growth caused by diatom aldehydes could be rejected. Another example is presented in Chapter 4 of this thesis, where the RNA:DNA ratio of larval herring was successfully used to test a hypothesis derived from ecological stoichiometry. In ecological stoichiometry it is generally accepted that the ratio of carbon to nutrients varies in primary producers with the ambient nutrient availability but that primary consumers show a high degree of homeostasis, i.e. they keep

their carbon to nutrient ratio constant (Sterner & Elser 2002), even if this effort reduces growth and reproduction (Boersma 2000). Furthermore, the nutritional value of a food item rises with its similarity to the consumers C:nutrient demand. The fact that the similarity of the C:nutrient ratios in primary and secondary consumers is high made Brett (1993) pose that secondary consumers must rather be energy limited than limited by nutrients. This reasoning is well accepted and it is mainly for this reason that no studies exist so far to test effects of mineral limitation on higher trophic levels. However, Chapter 4 clearly shows that this hypothesis, that mineral limitation effects are dampened below detection by primary consumers and that they therefore play no role for secondary consumers should be rejected. The results of these experiments could also be discussed in a broader context, refining Cushing's match/mismatch hypothesis (Cushing 1974, 1990) as addressed in the general introduction of this thesis. Fig. 1 shows a classical match situation between the production of predators and prey. A measure for food quality is added to the graph, which partitions the classical match into two sections: The first is characterized by sufficient food of a high quality, the second by sufficient food of a lower quality. Clear evidence for food quality differences under nutrient limitations are given in Chapter 4, as significant differences in the C:Nutrient ratios as well as in the fatty acid profiles of algae transferred into the copepods that fed on the algae. Similar findings on varying nutritional quality of primary production under nutrient limitation has been published elsewhere (Boersma 2000, Plath & Boersma 2001, Boersma & Kreutzer 2002, Anderson et al. 2004, Becker & Boersma 2005). The reduced larval condition observed in poor food quality seston represented by the P-limited food chain of the experiment probably decreases the predictive power of the match/mismatch hypothesis and may have implications on our understanding of factors that control growth of larval fish, survival and subsequent recruitment. On a different scale, this could mean that fish stocks will be threatened even harder by global change processes as different species and trophic levels respond on different scales (Walther et al. 2002, Parmesan & Yohe 2003, Edwards & Richardson 2004), with organisms with short generation times and high dispersal abilities show the fastest response. Compared to phyto- and zooplankton organisms fishes are slow in their ability to react on large scale changes and hence, the magnitude of not matching suitable conditions may be more seriously than for animals which are able to react promptly to e.g. changes in their food availability. Fish may therefore under the predicted rapid environmental changes being hurt more seriously than lower trophic levels (Intergovernmental Panel on Climate Change Third Assessment Report 2001).

Chapter 4 is the first study to show the potential of mineral limitation on larval fish growth in the planktonic realm and broadens our view of larval fish nutrition. Furthermore, food quality differences were successfully detected even over three trophic levels and this should give no impulses into the research on larval fish conditions.

Conclusions & Future perspectives

In this thesis hypotheses about stability of ichthyoplankton species assemblages and their occurrence were confirmed. The presented results have a high potential of improving the design of surveys or to detect community shifts in comparison to previous or future studies. Also some degree of intra- and inter-annual variability was shown, which makes longer time series desirable. Only long term datasets on as many measures as possible can improve our understanding of mechanisms structuring the ichthyoplankton communities.

A high degree of variability in nutritional condition on the level of the individual as well as a relatively high but inter-specific variable degree of independence of larval nutritional condition from the available food densities was shown in this study. This has been discussed to be an adaptation of the species under investigation to the prevailing environmental situation. The variability might also be attributed to food quality differences.

The inability to link larval condition to prey densities could also well be a problem of the different scales on which the comparisons are based on. On the one hand, the nutritional condition of larval fish are assessed on the level of the individual, on the other hand these data are compared with bulk parameters like total prey densities. In many cases such measures are sensitive enough to be used to explain variation in larval fish condition. In other cases the prey field the individual larvae might have faced will be strongly under- or overestimated. To take the maximum advantage of the measurement of proxies from individual larval fish, it is desirable to adjust other variables intended to be used together with larval fish in analysis to the level at which the larval data are derived from. Thus it seems to be necessary to derive feeding history also on the individual level. This could be achieved by the use of different biochemical measures at individual larvae. The use of e.g. fatty acids as trophic markers has shown to be useful in larval fish ecology, but the link between individual feeding history and the individual nutritional condition has not been done yet. The knowledge of individual feeding history is also very likely to be of a high potential in the light of the findings reported in Chapter 4. It was clearly shown that poor food quality can influence the nutritional condition of larval fish, even under ad libitum feeding conditions. On the level of bulk measures, this implies that a higher proportion of the observed variability in larval fish nutritional condition might be explained by the inclusion of food quality to multiple regression approaches. To be able to include food quality measures routinely into scientific surveys, more information is needed about e.g. the degree of dependence of larval fish's condition on individual food components (essential fatty acids, minerals, phospholipids) and which measure would be the one with the highest explanatory power.

I conclude that based on the results of this thesis, food quality measures should be included to a larger extend in ecologically orientated larval fish research, as it will contribute to a better understanding of processes governing larval fish growth and subsequent recruitment.

Chapter 6

Summary

This thesis integrates different approaches in larval fish ecology. These approaches are community analyses on a three year single station ichthyoplankton sampling with a high frequency, field evaluations of larval fish condition on a selection of species as well as laboratory experiments to investigate the impact of mineral-limited phytoplankton and the propagation of the limitation signal to higher trophic levels i.e. primary consumers and larval fish.

The underlying hypothesis of Chapter 2 was that larval fish communities are stable in their occurrence between years, and that there are season-specific assemblages with a high degree of inter-annual repeatability. This hypothesis was tested by the use of a three year high frequency (min. 3 samples week⁻¹), single location monitoring programme at the Helgoland Roads station in the German Bight, North Sea, Northeast Atlantic. The hypothesis proved to be true, as the diversity patterns between years were similar. In general, the dominance patterns did not differ between years. This was, however, only true when as long as lesser sandeel, the only species within this study which showed significant inter-annual differences in abundance and season-specific similarities, were excluded from the analysis. Inter-annual variability in dominance patterns was low and variation between years was significant only for one species, the lesser sandeel *Ammodytes marinus*. Most of the variation in larval fish abundance on a species level was found within weeks and only a smaller part of the variation was found between months.

A clear succession from larvae emerging from demersal eggs in winter to larvae hatching from pelagic eggs in summer was shown. This pattern can be interpreted as an adaptation to low water temperatures and harsh weather conditions in the German Bight during winter. The presented results suggest that predictions on larval fish occurrence at specific times of the year can be considered as robust. Nevertheless, regular larval fish and egg surveys are needed to detect large-scale alterations in spawning time as it is e.g. documented for the stocks of cod in the Baltic Sea.

The investigation presented in Chapter 3 aimed at elucidating fluctuation patterns in larval fish condition under natural conditions. Nutritional conditions of lesser sandeel (*Ammodytes marinus*) and dab (*Limanda limanda*) larvae caught in the field were investigated for the whole duration of their occurrence in the plankton in 2004. For this purpose RNA:DNA ratios served as an ideal tool to proof the hypothesis that short-lived fishes (sandeel) with only one

to two spawning events must have more conservative reproductive strategies and adaptations to environmental variability than long-lived species (dab) with several reproductive cycles. Larval fish nutritional condition showed a high degree of variation although density-dependent impacts of prey items were only observed when drastic changes in prey availability occurred late in the season. In this context, dab larvae showed the highest degree of vulnerability to changing food conditions. Both species showed a positive relationship between larval size and condition. Interestingly, the increase in mean condition with size was of a diametral nature: While well-conditioned larvae of all size-classes were found in the sandeel population, this was not the case for dab larvae. In case of this species, only larger size-classes produced well-conditioned larvae. This means that the increase in condition with larval size in sandeel was mainly due to a lack of poorly-conditioned larvae at larger size-classes. This was also true for dab, but in case of dab larvae the increase in mean condition was related to a real gain in condition with size. The loss of poorly-conditioned larvae in both species can be interpreted as an indication for condition-selective mortality.

The hypothesis that short-lived species are characterized by more conservative reproductive strategies than long-lived forms was additionally supported by the facts that sandeels produce large and energy-rich eggs as well as by their long transition time from internal to external feeding. Furthermore, their nutritional condition displayed a relatively high independence from environmental factors like temperature or prey densities thus enabling this short-lived fish species to produce extremely well-conditioned larvae.

State-of-the-art assumptions of ecological stoichiometry are considered in Chapter 4. These are: (1) Good quality food sources are the ones that meet the nutrient demand of a their consumers while food quality decreases with an increasing distance to the nutrient demand of the consumer and (2) Herbivores are homeostatic and consequently low-quality food is buffered at the interface between primary production and primary consumption.

We doubt the hypothesis that secondary consumers are not affected by nutrient limitation on the primary producer level due to a dampening of herbivores. Laboratory experiments were carried out to test the hypothesis that mineral limitation signals are mediated from herbivores to carnivores' and that such limitation patterns are detectable even on higher trophic levels. In order to test this hypothesis, we used a tri-trophic food chain approach where algae grown under nutrient-limited and nutrient-sufficient conditions served as the basis of the food web. The food chain consisted of the cryptophyte *Rhodomonas salina*, nauplii of the calanoid copepod *Acartia tonsa* and larvae of the herring *Clupea harengus*. Astonishingly, the results of the limitation experiments showed that the long-believed hypothesis about the dampening effect of herbivores must be replaced by our new findings proofing that such limitation signals

are indeed passed on to consumers thus affecting higher trophic levels considerably. Significant differences in the copepods' C:nutrient ratios, however, showed that the homeostasis of the copepods was not strict. This resulted in a reduced nutritional condition of herring larvae preying upon copepods grown on P-limited diets. This was particularly surprising since the fatty acid profiles pointed at a good quality of algae grown under P-limited conditions. The results show that fish larvae can be altered by P-limitation on the primary producer and consumer level and that the growth rates of larval fish can be directly affected by abiotic forcing on the lowermost food-web levels, like e.g. in fully P-limited ecosystems or during decaying bloom situations.

Chapter 7

Zusammenfassung

Die vorliegende Arbeit vereint unterschiedliche wissenschaftliche Ansätze der Fischlarvenökologie. In dieser Arbeit werden Fragen zur Ökologie von Fischlarven auf drei unterschiedlichen Ebenen bearbeitet: Auf der Gemeinschaftsebene mit Hilfe einer dreijährigen, hochfrequenten Beprobung von Ichthyoplanktongemeinschaften, auf Populationsebene, bei der der Ernährungszustand von Larven zweier Fischarten aus Feldbeprobungen in Abhängigkeit von Umweltparametern untersucht wurde und auf Individualebene, bei der der Einfluss von nährstofflimitierten Algen und die Weitergabe des Limitationssignals an höhere trophische Ebenen untersucht und auf den Ernährungszustand von Fischlarven übertragen wurde.

Kapitel 2 beschäftigt sich mit der Hypothese, dass Fischlarvengemeinschaften ein relativ hohes Maß an Stabilität in Bezug auf ihre Saisonalität haben. Diese Hypothese wurde mit Hilfe eines dreijährigen Datensatzes getestet. Dieser Datensatz basierte auf mindestens drei Beprobungsterminen pro Woche, die immer auf der gleichen Station, der Helgoländer Reede, genommen wurden. Diese Station befindet sich in der Deutschen Bucht der Nordsee. Die Hypothese wurde angenommen, da sich Muster in Diversität und Dominanz der Fischlarvengemeinschaft, nach dem Ausschluss des Kleinen Sandaals (*Ammodytes marinus*), stark ähnelten. Der Kleine Sandaal war die einzige Fischart, deren Abundanz zwischen den Jahren einen signifikanten Unterschied zeigte. Für die anderen Arten aus dieser Untersuchung konnten keine signifikanten Unterschiede in den Abundanzen zwischen den Jahren festgestellt werden. Die größte Variationsbreite lag hierbei zwischen den einzelnen Wochen. Eine Similaritätsanalyse der Proben zeigte eine klare Gruppierung nach Jahreszeiten und nicht nach unterschiedlichen Jahren; ein kleiner Teil der erklärten Variabilität lag auf der Ebene der Monate. Die Fischlarvengemeinschaft zeigte eine klare Sukzession von Larven, die aus demersalen Eiern geschlüpft waren hin zu Larven, welche aus pelagischen Eiern stammten. Mit dem Anstieg der Temperatur konnte ein Übergang von demersal zu pelagisch beobachtet werden. Dieser wurde als Anpassung an die kalten Wintertemperaturen und die widrigen Wetterbedingungen in der Deutsch Bucht im Winter interpretiert.

Die Ergebnisse dieser Untersuchung zeigten ein hohes Maß an Ähnlichkeit zwischen den Jahren. Trotz der hieraus resultierenden hohen Vorhersagbarkeit sollten jedoch regelmäßige Eier- und Larvenuntersuchungen durchgeführt werden um großskalige Veränderungen, wie z.B. die Verschiebung der Laichzeit beim Ostseedorsch, zu detektieren.

Die in Kapitel 3 beschriebene Untersuchung wurde durchgeführt, um das Maß an Variabilität des Ernährungszustandes von Fischlarven unter natürlichen Bedingungen zu untersuchen. Hierzu wurden exemplarisch die Larven des Kleinen Sandaals (*Ammodytes marinus*) sowie die der Kliesche (*Limanda limanda*) ausgewählt. Ihr Ernährungszustand wurde über den gesamten Zeitraum des Vorkommens der Larven im Ichthyoplankton mit Hilfe von RNA:DNA Verhältnissen untersucht. Dieser Untersuchung lag die Hypothese zugrunde, dass kurzlebige Fischarten, die sich nur ein- bis zweimal fortpflanzen, konservativere Reproduktionsstrategien entwickelt haben sollten, als sie bei langlebigen Fischarten zu erwarten wären. Als Modellorganismus für kurzlebige Arten diente in dieser Untersuchung der Kleine Sandaal, als Vertreter einer langlebigen Art diente die Kliesche. Das RNA:DNA Verhältnis beider Fischarten zeigte ein hohes Maß an Variabilität; eine ausgeprägte Reaktion auf das Futterangebot zeigte sich erst spät in der Saison, als eine drastische Nahrungsverknappung zu beobachten war. Die Kliesche zeigte hierbei eine stärkere Reaktion auf die Nahrungsknappheit von Ressourcen als der Sandaal. Beide Arten zeigten eine positive Entwicklung ihres Ernährungszustandes mit zunehmender Körperlänge. Interessanterweise wurde der Anstieg des mittleren Ernährungszustandes bei beiden Arten auf gegenläufige Art und Weise erreicht: Beim Sandaal waren in allen Längensklassen sehr gut konditionierte Larven zu finden, der Anteil der schlecht Ernährten verringerte sich jedoch deutlich mit zunehmender Körperlänge, wohingegen bei der Kliesche zwar ebenfalls ein Wegfall von schlecht ernährten Larven in den größeren Längensklassen zu verzeichnen war, der Hauptanteil der Verbesserung der mittleren Kondition wurde aber durch das Hinzukommen von gut konditionierten Larven bestritten. Der Verlust von schlecht ernährten Larven wurde als Hinweis auf ernährungsbedingte Sterblichkeiten gewertet.

Die Hypothese, dass kurzlebige Arten konservativere Fortpflanzungsstrategien haben, wird im Falle des Kleinen Sandaals durch die Produktion von großen, energiereichen Eiern, eine lange Übergangsphase von interner Ernährung durch Dotter zu externer Nahrungsaufnahme und ihrer relativ hohen Unabhängigkeit von Umweltsignalen wie Futterdichten und Temperatur unterstützt. Im Gegensatz zur Produktion von schlecht konditionierten Larven, welche erst eine gute Kondition erreichen müssen, kann die Produktion von sehr gut konditionierten Larven zusätzlich als konservativ gewertet und zur Stützung der Hypothese herangezogen werden.

In der in Kapitel 4 vorgestellten Studie werden langgehegte Annahmen der ökologischen Stöchiometrie bearbeitet. Zwei der heute gültigen Grundannahmen sind: (1) Gleichen sich die Nährstoffverhältnisse von Nahrung und Konsument, kann die Nahrung als qualitativ hochwertig angesehen werden; je weiter die Verhältnisse voneinander abweichen desto

schlechter ist somit die Nahrungsqualität, und (2) Herbivore Organismen sind homöostatisch und puffern schlechte Nahrungsqualität bereits an der Schnittstelle zwischen Primärproduktion und Primärkonsument ab. Das bedeutet in der Theorie, dass sich Nahrungsqualitätsunterschiede nicht auf höhere trophische Ebenen übertragen, da sie bereits auf der Ebene der Herbivoren abgepuffert werden. In dieser Studie stellen wir diese Theorie in Frage und stellen die Hypothese auf, dass Nahrungsqualitätsunterschiede auf Primärproduzentenebene sehr wohl über trophische Ebenen hinweg weitergegeben werden und somit direkte Auswirkungen auf karnivore Organismen haben. Um diese Hypothese zu testen wurden im Experiment kurze Nahrungsketten etabliert. Diese Bestanden aus der Cryptophyceae *Rhodomonas salina*, Nauplien des calanoiden Copepoden *Acartia tonsa* und Larven des Herings (*Clupea harengus*), wobei die Cryptophyceen unter verschiedenen Nährstofflimitationen gezüchtet wurden. Die bisherige Theorie bzgl. des Abpufferns von Qualitätsunterschieden an der Schnittstelle zwischen Primärproduzenten und Herbivoren musste zugunsten der neuen Hypothese verworfen werden. Das Maß an Homöostase von Copepoden war nicht so hoch, dass die unterschiedlichen Kohlenstoff/Nährstoff-Verhältnisse der Algen komplett abgepuffert werden konnten. Als Folge davon zeigten die Copepoden signifikante Unterschiede in ihren Kohlenstoff/Nährstoff-Verhältnissen, die Heringslarven zeigten signifikante Unterschiede in ihrer Kondition. Diese Unterschiede weisen auf eine direkte Phosphor-Limitierung der Heringslarven hin, da die Fettsäurespektren der mit P-limitierten Algen gefütterten Copepoden auf eine eigentlich gute Nahrungsqualität hindeuteten. Diese Ergebnisse lassen die Vermutung zu, dass eine Limitation des Wachstums von Fischlarven durch den Einfluss von abiotische Bedingungen auf Ebene der Primärproduzenten und Konsumenten wahrscheinlich ist und dass dies negative Folgeerscheinungen für Organismen höherer trophischer Ebenen, wie z.B. Fischlarven, beinhaltet. Dies trifft im Freiland v.a. auf generell phosphorlimitierte Systemen sowie auf den Endverlauf von Blütensituationen zu.

Chapter 8

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Description of the scientific contributions to the multiple-author manuscripts

1) Year-to-year variation in larval fish assemblages of the Southern North Sea.

Arne Malzahn & Maarten Boersma

All analyses, the text writing and graphical presentation were done by Arne Malzahn under the supervision of PD Dr. Maarten Boersma.

2) Changing environments and the nutritional condition of larval dab and lesser sandeel

Arne Malzahn, Catriona Clemmesen, Silke Laakmann, Karen Wiltshire, Maarten Boersma

All analyses, the text writing and graphical presentation were done by Arne Malzahn under the supervision of PD Dr. Maarten Boersma. Prof. Dr. Karen Wiltshire provided phytoplankton data. Silke Laakman provided zooplankton data. Dr. Catriona Clemmesen provided lab space and fruitful discussion.

3) Primary production under nutrient limitation indirectly affects larval fish condition

Arne Malzahn, Nicole Aberle-Malzahn, Catriona Clemmesen, Maarten Boersma

All analyses, the text writing and graphical presentation were done by Arne Malzahn under the supervision of PD Dr. Maarten Boersma. Dr. Nicole Aberle-Malzahn assisted during the experiments and measured the nutrient data. Dr. Catriona Clemmesen provided lab space and fruitful discussion.

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Helgoland, den 19.03.2006

Arne Malzahn

Erklärung

Hiermit erkläre ich, dass die vorliegende Dissertation selbstständig von mir angefertigt wurde und dass sie nach Form und Inhalt meine eigene Arbeit ist. Sie wurde keiner anderen Stelle im Rahmen eines Prüfungsverfahrens vorgelegt. Dies ist mein einziges und bisher erstes Promotionsverfahren. Die Promotion soll im Fach Fischereibiologie erfolgen. Des Weiteren erkläre ich, dass ich Zuhörer bei der Disputation zulasse.

Kiel, den 20.3.2006

Arne Malzahn