ADVANCES IN EARLY LIFE HISTORY
STUDY OF FISH
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Trophic flexibility in larvae of two fish species (lesser sandeel, *Ammodytes marinus* and dab, *Limanda limanda*)

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SUMMARY: We investigated the trophic level of larvae of two fish species (lesser sandeel. *Ammodytes marinus*, and dab, *Limanda limanda*) in spring 2004 by means of stable isotope signatures at the Helgoland Roads Station (54°11.18'N and 07°54.00' E). The signatures were contrasted with the spring succession of phytoplankton and zooplankton. Phytoplankton biomass remained low until the middle of April, when a bloom developed. The $\delta^{15}N$ signature of the seston increased until the bloom started then decreased during the bloom. The $\delta^{15}N$ of the larvae of both fish species generally followed the development of the baseline, but the decrease in the fishes' trophic level (expressed as the $\Delta\delta^{15}N$) was larger than that of the seston, suggesting that larval fish switched their diet to lower trophic levels. For larval sandeel we found that the switch to feeding on lower trophic levels was accompanied by a decrease in nutritional condition, while this pattern was not apparent in larval dab. Hence, larval sandeel were not able to substitute the lack of high trophic level zooplankton prey with prey originating from lower trophic levels; however, at least the smaller size classes of larval dab could successfully switch diets.

Keywords: prey selection, diet switching, optimum foraging, stable isotopes, microzooplankton, niche widths.

RESUMEN: Flexivilidad trófica en larvas de dos especies de peces (aguacioso, *Ammodytes marinus* y lenguadina, *Limanda limanda*). – Mediante el análisis de isótopos estables hemos investigado el nivel trófico de las larvas de dos especies de peces (aguacioso, *Ammodytes marinus* y limanda, *Limanda limanda*) en la primavera de 2004 en Helgoland Roads Station (54°11.18'N and 07°54.00'E). Estas señales de los isótopos se contrastaron con la sucesión primaveral de fitoplancton y zooplancton. La biomasa de fitoplancton se mantuvo baja hasta mediados de abril, cuando se desarrolló un bloom. El $\delta^{15}N$ del seston se incrementó hasta que se inició el bloom y disminuyó durante el bloom. El $\delta^{15}N$ de las larvas de ambas especies siguió de modo general el de la línea de base, pero la disminución en el nivel trófico de los peces (expresada como $\Delta\delta^{15}N$) fue mayor que el del seston, lo que sugiere que las larvas de peces cambiaron su dieta a un nivel trófico inferior. Para las larvas de *A. marinus* pudimos demostrar que el cambio hacia una alimentación en niveles trófico inferiores fue acompañado por una disminución en el estado nutricional, mientras que este patrón no era evidente en las larvas limanda. Por lo tanto, larvas de *A. marinus* no fueron capaces de sustituir la falta de zooplancton de alto nivel trófico con presas procedentes de niveles tróficos inferiores, mientras que, al menos las larvas de limanda de las clases de talla menores, cambiaron de dieta con éxito.

Palabras clave: selección de presas, cambio de dieta, forrajeo óptimo, isótopos estables, microzooplancton, amplitud de nicho.

INTRODUCTION

Feeding success, especially in very young life stages of fish, most likely explains a large proportion of the observed variance in fish stock size fluctuations (Hjort, 1914; Cushing, 1990). According to the majority of the published literature, larval fish feed almost exclusively on early life stages of copepods (Last, 1978b; Pepin and Penney, 1997, 2000). This is surely an oversimplification, as it is unlikely that

(a) all species behave in a similar way, (b) other prey items are actively rejected in favour of copepod naupliar and copepodite stages, and (c) small animals with high growth rates do not show plasticity in their food preferences. It is more likely that there are both generalists and specialists, even in fish larvae. Indeed, Last (1978a) studied the diet of four flatfish species in the North Sea using gut content analysis, and reported that plaice (*Pleuronectes platessa*) larvae preyed almost exclusively on appendicularians, and flounder (*Plathichties flesus*) larvae fed on a wide range of planktonic organisms including phytoplankton, polychaete larvae, lamellibranch larvae, and copepod *nauplii*. Dab (*Limanda limanda*) larvae fed mainly on the *nauplii* and copepodite stages of a variety of copepods, while sole (*Solea solea*) larvae consumed copepodites and polychaete larvae but their main prey was lamellibranch larvae. Three of the four species had one thing in common: the initial food of all species except plaice consisted of dinoflagellates, followed by tintinnid ciliates and copepod *nauplii*. Dickmann *et al.* (2007) reported a similar pattern for sprat (*Sprattus sprattus*) larvae in the Baltic Sea, as did Pepin and Dower (2007) for at least two out of six species of fish larvae in Conception Bay, revealed by stable isotope analysis.

However, gut content analysis are prone to misinterpretations, as shown in the study by Pepin and Dower (2007) in which for at least one species (capelin) the stable isotope analysis suggests other food sources than those revealed by gut content analysis. The main problem in gut content analysis is the variability in digestion times in relation to the nature of the ingested prey item (Fukami *et al.*, 1999). Prey items containing hard structures like crustaceans can be identified better and at a longer time after ingestion than, for example, protozoan plankton like flagellates or naked ciliates (Fukami *et al.*, 1999). To overcome the discrepancy between what can be found in guts and what consumers actually feed on over longer periods is one of the main reasons for applying stable isotope analysis (Fry, 2006).

Larval stages of many fish species generally select larger prey items as they grow (Voss *et al.*, 2003), which is attributed to the maximization of energy gain per prey capture effort (Pearre, 1986). Consequently, under good feeding conditions the trophic niche width of growing larvae should remain constant (Pearre, 1986); whereas under poorer feeding conditions, niche width should increase to compensate for the lack of prey and so achieve the optimal ratio of time spent searching and capturing prey to gain energy (Werner and Hall, 1974).

The base of the food web is characterized by enormous variability in food quantity (e.g. Sommer *et al.*, 1986; Wiltshire *et al.*, 2008) and quality (Quigg *et al.*, 2003; Klausmeier *et al.*, 2004), and not only the quantitative effects, but also the qualitative ones have been shown to affect the condition of larval fish (Malzahn *et al.*, 2007a). The higher an organism feeds in the trophic cascade the lower the variability in the quality of its food. This large variability in primary production quality for higher trophic levels is caused by a large flexibility in the biochemical composition of algal cells, which depends on growth conditions (Aberle and Malzahn, 2007). The variability of food quality decreases with increasing trophic level (Boersma, 2000; Boersma and Elser, 2006; Boersma *et al.*, in press; Malzahn *et al.*, in press) due to the tendency (or the constraint) of consumers to keep their chemical and thus biochemical body composition relatively constant (Elser *et al.*, 2000).

The trophic position of an organism in its environment is reflected by its chemical and biochemical composition. One measure for the trophic position is the ratio between the heavy stable nitrogen isotope ^{15}N and the light nitrogen isotope ^{14}N. This ratio can be used as a trophic tracer (Peterson and Fry, 1987; Fry, 1988), as the stable isotope signatures of a consumer generally reflect the isotopic composition of their diets plus a relatively predictable enrichment in the heavier isotope (DeNiro and Epstein, 1981; Post, 2002). Hence, based on the predictions above, we would expect a gradual upwards shift in $\delta^{15}N$ (and hence in trophic position) of larval fish with increasing body length in the case of constant niche widths and good feeding conditions, since in marine environments larger organisms usually feed higher up in the food chain. Under poorer feeding conditions, however, it is not possible to predict in which direction the mean $\delta^{15}N$ will change, but one would expect an increase in variance as a result of broader niche widths. We further hypothesize that shifts in the trophic position of the larvae should be reflected in their condition, and a decrease in the trophic level of fish larvae is correlated with a decrease in nutritional condition.

Here, we tested this hypothesis with the help of an intensive field campaign that focused on two fish species, sandeel (*Ammodytes marinus*) and dab (*Limanda limanda*), which are known to feed on

copepod life stages and on bivalve and gastropod larvae and which rapidly increase prey size with ontogeny (Dab: Last, 1978a; Sandeel: Simonsen *et al.*, 2006).

MATERIALS AND METHODS

The isotopic signals of larval fish and seston were studied in an extensive field campaign carried out in spring 2004 to elucidate the feeding ecology of larval lesser sandeel (*Ammodytes marinus*) and dab (*Limanda limanda*). Daily ichthyoplankton samplings were taken at the Helgoland Roads Station (54°11.18'N and 07°54.00'E, German Bight, southern North Sea, at water depths of 8 m, Fig. 1). Because of the shallow depths and the strong tidal currents (up to 2 knots), the water body is mixed throughout the year. We deployed one double oblique haul from the surface to 1 m above the ground per working day, weather permitting, using a 500 μm CALCOFI ring trawl equipped with a flow meter. Larval dab and sandeel, the most abundant larval fish species in spring in the area (Malzahn and Boersma, 2007) were sorted, and length, dry weight and carbon and nitrogen isotopic composition were measured. To meet the analytical requirements for the isotope analysis, larvae were pooled to a minimum of 200 μg dry weight. Dab larvae smaller than 200 μg (approx 6 mm) and sandeel smaller than 200 μg (approx 10 mm) were pooled for the stable isotope analysis to 1 mm size classes. Larvae were analyzed as whole animals, i.e. organisms in the gut were also included in the results. This procedure is described to be reasonable for larval fish stable isotope analysis (Pepin and Dower, 2007), as the gut content rarely exceeds 2% of the fish mass (Pepin and Penney, 2000). We chose seston, particulate organic matter, as the baseline for calculating the trophic position of larval fish, as this is the most conservative measure available to us of the food web base that the larval fish act in. The use of particular zooplankton species would not have been correct, as we were interested in the trophic flexibility of larval fish, and not whether larval fish feed on a particular zooplankton species, chosen *a priori*. Hence, water samples were taken twice a week in triplicate at a depth of 2 m in the completely mixed water body of the Helgoland Roads Station. Seston was filtered in precombusted GF/F filters and was analyzed for its isotopic composition in triplicate for each sampling date. All samples were analyzed for elemental and

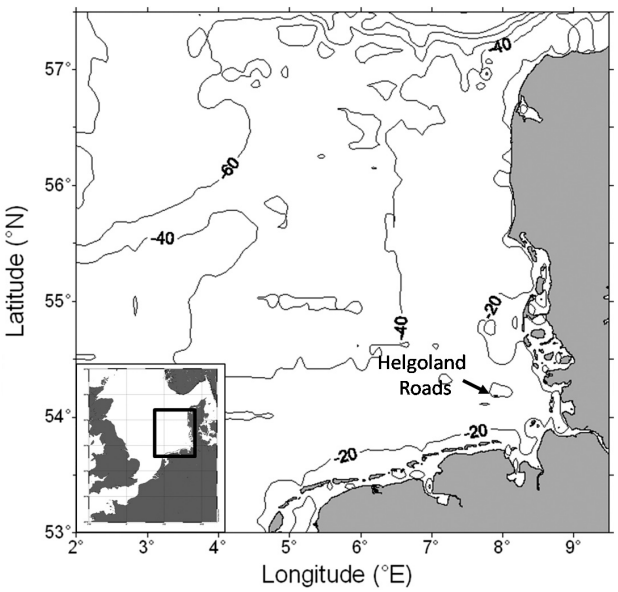

FIG. 1. – Map of the German Bight in the North Sea. The black arrow indicates the location of the Island of Helgoland.

isotopic composition at the UC Davis Stable Isotope Facility, (Davis, California, USA), using a PDZ Europa ANCA-GSL element analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). The difference between the $\delta^{15}N$ of seston and larval fishes was calculated on weekly means of both sample types and is denoted by $\Delta\delta^{15}N$.

Diatom carbon concentrations were derived from the Helgoland Roads long term monitoring program (Wiltshire and Manly, 2004). Following Malzahn *et al.* (2007b), we split the larval fish stable isotope dataset in two parts: before and after 20 April, 2004. The authors reported a drastic decrease in zooplankton densities and a synchronous increase in diatom carbon; here we are interested in the effect of such drastic changes on the stable isotope signatures of the larvae under investigation. As the trophic level of larval fish might be related to their length, $\delta^{15}N$ data along with the standard length were analyzed by means of ANCOVA. In the case of dab, larvae longer than 8 mm were excluded from the analyses as no larvae longer than 8 mm were present after 20 April, 2004. Contrasting to dab, sandeel $\delta^{15}N$ and standard length data did not meet the assumption of homogeneity of variances (Levene test) and therefore were log transformed. Stable isotope data again failed to meet variance homogeneity, but standard length did.

RNA and DNA concentrations of whole individual larvae were analyzed using a modification

of the method by Clemmesen *et al.* (2003). Samples of lesser sandeel and dab were thawed and standard length was measured using a stereomicroscope. Larvae were freeze-dried to a constant weight (16 h, using a Christ Alpha 1-4 freeze-drier at -51°C) and 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 min. Cells were disrupted by shaking in a cell mill with different sized glass beads (diameter 2 mm and 0.17 to 0.34 mm) for 15 min. The homogenate was then centrifuged at 6000 rpm at 0°C for 8 min, and the supernatant used for analysis. The amount of nucleic acid was measured fluorometrically in a microtitre fluorescence reader (Labsystems, Fluorescan Ascent) using the fluorophore Ethidium Bromide. Total nucleic acid was measured first, and RNAse was then applied to the sample to digest the RNA. After the enzyme treatment (30 min at 37°C) the remaining DNA was measured. RNA fluorescence was calculated by subtracting DNA fluorescence from the total nucleic acid fluorescence. RNA calibrations (16S, 23S ribosomal RNA, Boehringer Mannheim, 206936) were carried out each day. The DNA concentrations were calculated using the relationship between RNA and DNA fluorescence described by Le Pecq and Paoletti (1966), which is RNA:DNA = 0.46. The basis for this ratio is that there is about one binding site for ethidium bromide per five nucleotides for DNA and one per ten for RNA. All steps were carried out on ice. To investigate a relation between larval nutritional condition and the trophic level larvae feed on, we calculated weekly means of the RNA:DNA ratio for each species and contrasted them with the $\Delta\delta^{15}N$ signal of the respective species (also weekly means) by means of linear regression.

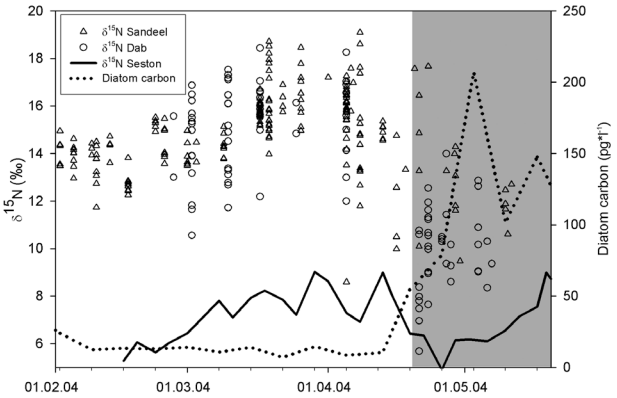

FIG. 2. – $\delta^{15}N$ signature of larval dab (*Limanda limanda*), sandeel (*Ammodytes marinus*), seston, as well as diatom carbon concentrations in spring 2004 at the Helgoland Roads Station. Fish isotopic data shown represents individual fish larvae, with the exception of dab larvae smaller than 6 mm and sandeel larvae smaller than 10 mm, which had to be pooled to achieve the analytical requirements of 200 µg carbon. Shaded area depicts the timeframe after the zooplankton breakdown.

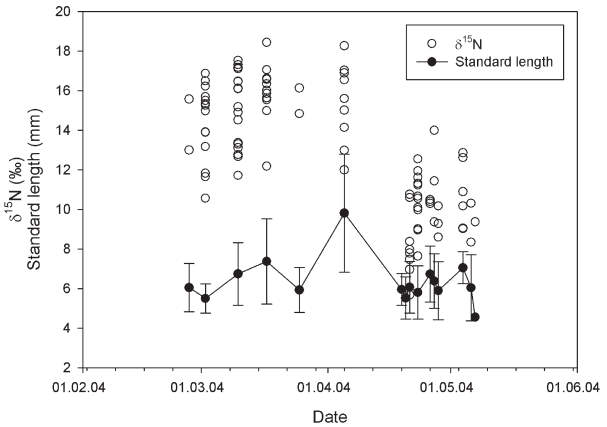

FIG. 3. – Temporal development of size and $\delta^{15}N$ of larval dab (*Limanda limanda)*. Error bars are standard deviation.

RESULTS

Diatom carbon was characterized by constantly low diatom carbon concentrations around 10 pg*l^{-1} and a rapid development of a diatom bloom in the middle of April characterized by carbon concentrations exceeding 200 pg*l^{-1}(Fig. 2).

The seston $\delta^{15}N$ signature increased from 5‰ to 8‰ until the onset of the diatom bloom in the middle of April and decreased back to 5‰ again, coinciding with the phytoplankton bloom (Fig. 2). This pattern can be interpreted as an increasing proportion of heterotrophic organisms relative to the autotroph proportion contributing to the microplankton community, which is reversed at the moment of the onset of the phytoplankton bloom. Afterwards the $\delta^{15}N$ signature increases again, indicating an enhanced development of heterotrophyis organisms feeding on the bloom. The same pattern of an increase in $\delta^{15}N$ from 13‰ to 17‰ in the pre-diatom bloom situation and a decrease down to 10‰ during the bloom could be observed in fish larvae of both species (Fig. 2). This pattern was independent of the size structure of the samples, as same-sized larvae early in the season had higher $\delta^{15}N$ signatures than those late in the season (dab: Fig. 3, sandeel: Fig. 4).

The development of zooplankton densities increased with time and drastically decreased again around 20 April. Zooplankton development is further described in Malzahn *et al.* (2007b).

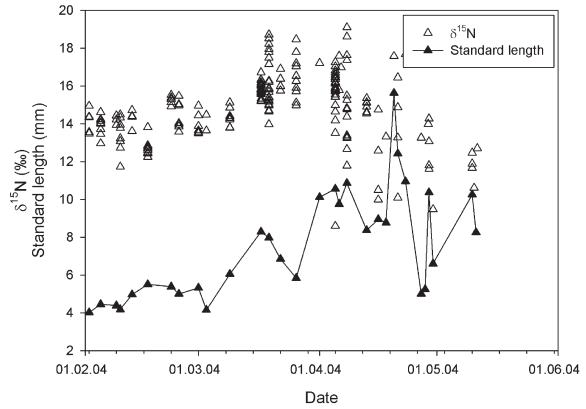

FIG. 4. – Temporal development of size and $\delta^{15}N$ of larval sandeel (*Ammodytes marinus*).

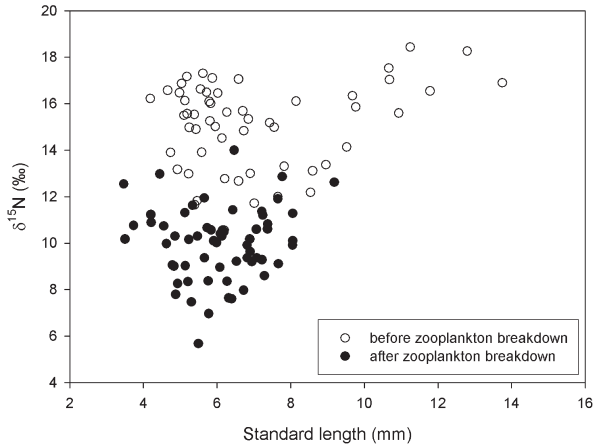

FIG. 5. – $\delta^{15}N$ signatures of larval dab (*Limanda limanda*) caught in spring 2004 at the Helgoland Roads Station plotted against mean larval size. In larvae smaller than 200 µg, (approx. 6 mm standard length) the mean size of the larvae pooled to achieve enough material for the stable isotope analysis are shown, individual data are shown for larger larvae. The dataset is divided into pre-phytoplankton bloom (before zooplankton breakdown, n=55) and phytoplankton bloom (after zooplankton breakdown, n=61).

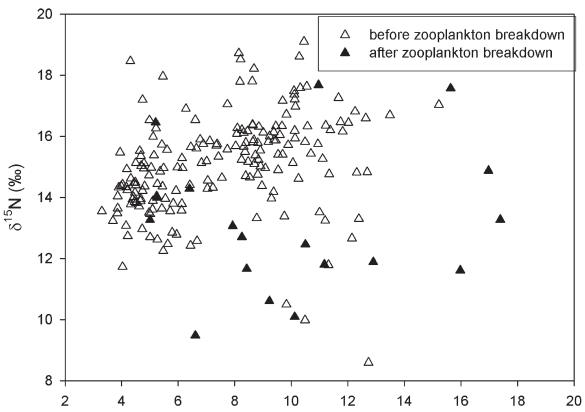

FIG. 6. – $\delta^{15}N$ signatures of larval sandeel (*Ammodytes marinus*) caught in spring 2004 at the Helgoland Roads Station plotted against larval size. In larvae smaller than 200 µg, (approx. 10 mm standard length) the mean size of the larvae pooled to achieve enough material for the stable isotope analysis are shown, individual data are shown for larger larvae. The dataset is divided into pre-phytoplankton bloom (before zooplankton breakdown, n=183) and phytoplankton bloom (after zooplankton breakdown, n=18).

TABLE 1. – Summary of the analyses of covariance (ANCOVA) on larval $\delta^{15}N$, the period of the sampling and larval standard length as covariable. Standard lengths of larval sandeel smaller than 200 µg, (approx. 10 mm standard length) and larval dab (approx. 6 mm) are the mean size of the larvae pooled to achieve enough material for the stable isotope analysis, individual data were used for larger larvae.

Species	Factor	MS	df	*F*	*p*
Sandeel	Size	41.18	1	15.69	< 0.05
	Period	84.59	1	32.24	< 0.05
	Error	2.62	198		
Dab	Size	4.67	1	1.69	0.20
	Period	575.17	1	208.58	< 0.05
	Error	2.76	95		

As we did not investigate a specific cohort of larval fish but rather the full set of size classes caught with the plankton gear, it can be ruled out that the shift was only due to the feeding habits of different larval size classes (Figs. 5 and 6). For larval dab we were able to exclude a possible size effect as the ANCOVA revealed length as a covariate to be insignificant (Table 1). However, for this analysis we excluded larvae larger than 8 mm as no such larvae were in the samples after the breakdown. Size was a significant covariate in the case of sandeel (Table 1), but linear regression analysis on size and $\delta^{15}N$ revealed it to be insignificant for both periods.

The difference between the development of the seston baseline and that of the fish larvae was that the decrease in $\delta^{15}N$ was more pronounced in larval fish than it was in the baseline signatures. This resulted in a decrease in $\Delta\delta^{15}N$ from around 8‰ to 4‰ in dab and 6‰ in sandeel (Fig. 7), a change which is generally accepted to be more than a trophic level. Enrichment relative to the seston signal was significantly lower (T-test, $p<0.05$) for larval dab but not

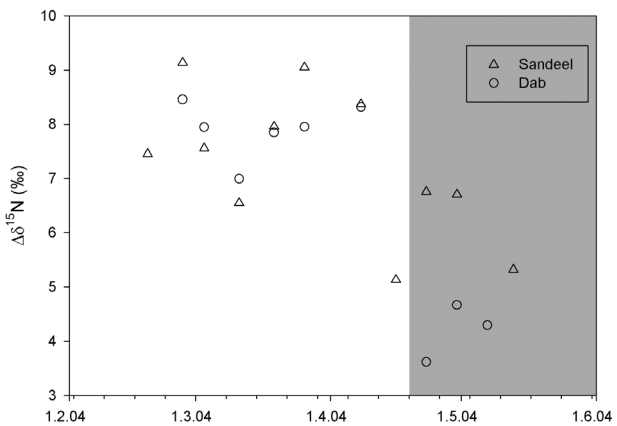

FIG. 7. – Weekly mean $\Delta\delta^{15}N$ (relative to the weekly mean seston $\delta^{15}N$) signature of larval sandeel and larval dab. Shaded area depicts the timeframe after the zooplankton breakdown.

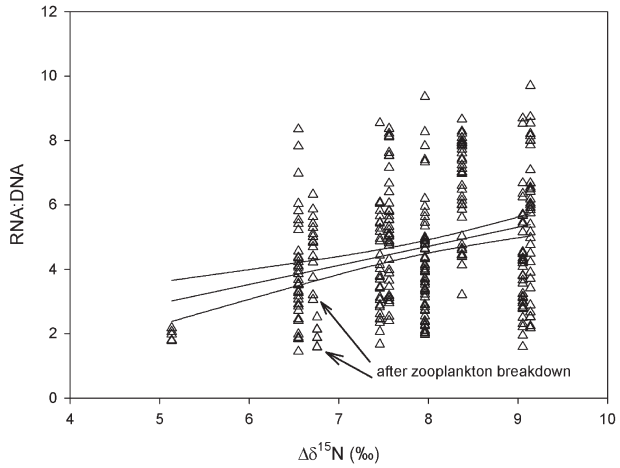

FIG. 8. – Relationship between the weekly mean $\Delta\delta^{15}N$ of the larval sandeel and the corresponding RNA:DNA ratio. The solid line is the linear regression line.

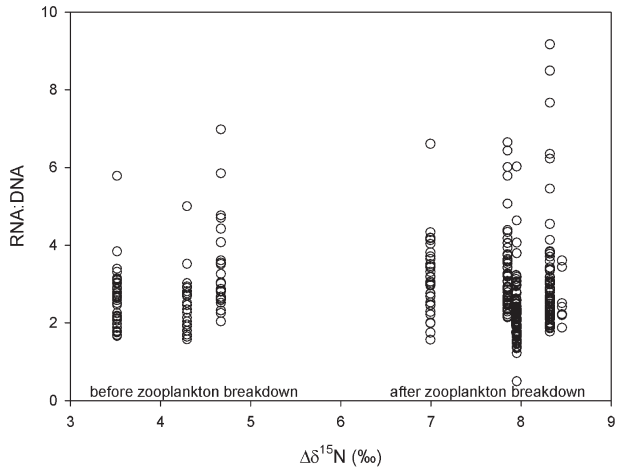

FIG. 9. – Relationship between the weekly mean $\Delta\delta^{15}N$ of the larval dab and the corresponding RNA:DNA ratio.

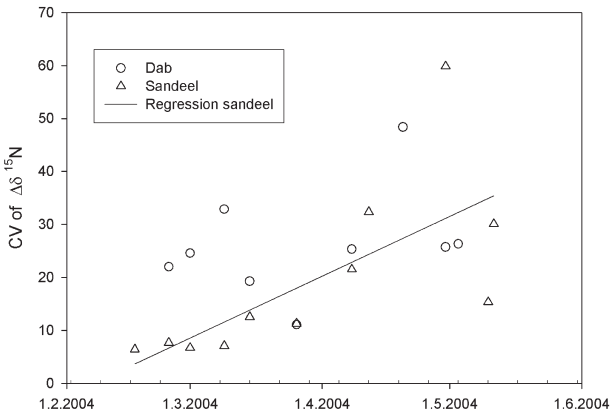

FIG. 10. – Temporal development of the coefficient of variation (CV%, calculated for each week) of the weekly mean $\Delta\delta^{15}N$ signal of larval dab and sandeel. The solid line is the regression line for sandeel.

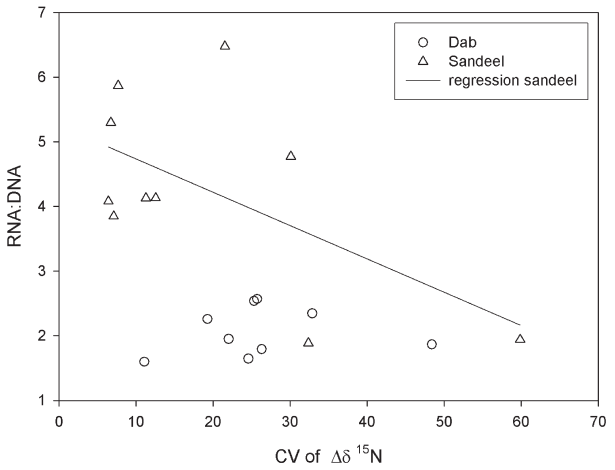

FIG. 11. – Coefficient of variation (CV%, calculated for each week) of the mean $\Delta\delta^{15}N$ signal of larval dab and sandeel on a weekly basis versus the corresponding mean RNA:DNA ratio of the larvae. The solid line is the regression line for sandeel.

for sandeel after the breakdown compared to the enrichment before the bloom (Fig. 7).

When the nutritional condition of larval sandeel was correlated with the trophic level of the larvae (here the difference between the larval and the seston δ15N), a significant positive relationship was observed (linear regression analysis, $p<0.01$, $r^2=0.10$ (Fig. 8). However, there was no relationship between the trophic level and nutritional condition of dab (Fig. 10).

The coefficient of variation (CV=standard deviation/mean*100) of the $\Delta\delta^{15}N$, a measure for niche widths, did not change over time in larval dab, while it increased significantly in larval sandeel (linear regression analysis, p=0.03, Fig. 11), showing higher values late in the season when zooplankton was scarcer. Dividing the dataset into two sets, before and after the zooplankton breakdown, revealed significant differences for sandeel (t-test, p=0.03) and no differences for dab (t-test, p=0.13). However, a correlation of these coefficients of variation with the nutritional condition of the larvae showed that the RNA:DNA ratio did significantly vary with the variability of the $\Delta\delta^{15}N$ of larval fish (Fig. 12), albeit with a significance level of p=0.07.

DISCUSSION

Until the onset of the diatom bloom, the importance of the microbial loop for the food web in early spring was clearly increasing. This was revealed by the steady increase of the seston $\delta^{15}N$ label, which could even be traced up to larval fish. The constant difference between the $\delta^{15}N$ label of seston and fish

suggests that the larvae did not change their feeding habits, but their prey did, as the prey were simply following what was on offer in the seston. The relative contribution of microzooplankton to seston increased, and hence the prey of larval fish feed more on secondary than on primary production. This is in line with Wu (1997) who showed that an increase in the $\delta^{15}N$ signatures of zooplankton with distance from the coast was caused by an increasing dominance of the microbial loop over new production. During the diatom bloom, the relative importance of the microbial loop in the system decreased, as indicated by the decrease in seston nitrogen signatures, but at the same time microbial loop members are likely to increase in their importance as food for larval fish, as indicated by the decrease in $\Delta\delta^{15}N$, which is the enrichment of the larvae in relation to the seston signal. In fast growing animals, diet switches are quickly detectable in their isotopic composition (Fry and Arnold, 1982; Herzka and Holt, 2000), which is related to high turnover rates. The decrease in the $\Delta\delta^{15}N$ signature of larval fish in late spring is clear evidence of a downward shift in trophic level of the larval fish. This may be due to a complete downward shift of all the consumer levels, or that the larvae switched diets and substituted a shortage in zooplankton prey during the diatom bloom with organisms of lower trophic levels. The alternative food sources were presumably small microzooplankton as well as some phytoplankton species.

Earlier studies on cod (Kane, 1984), dab, flounder and sole (Last, 1978a) as well as American sandeel (Monteleone and Peterson, 1986) showed that the smallest larval fish feed on phytoplankton. However, all these studies reported a rapid shift to zooplanktivory with increasing size. Here, we show that, depending on the availability of prey, large shifts in the diet of larval fish can be observed and even large individuals may be obliged to feed on algae and microzooplankton. The lack of well-conditioned larger larvae feeding on phytoplankton reported by Malzahn *et al*. (2007b) and shown for sandeel in this study, suggests that although larger larvae were able to find alternative food sources, food items like e.g. microzooplankton and phytoplankton did not support proper growth of larger individuals, while small larvae were sufficiently nourished by microzooplankton and phytoplankton. The poor ability to cope with suboptimum prey size and quality might even be a reason for the low abundances of sandeel caught after the onset of the spring bloom. The high temporal stability of phytoplankton blooms at Helgoland Roads (Wiltshire *et al.*, 2008) and the annually occurring poor feeding conditions might well be linked to the stable temporal occurrence of the sandeel larvae season reported in Malzahn and Boersma (2007).

There was a positive relationship between the trophic level and nutritional condition of sandeel. This matches classic assumptions on larval fish prey selection (Werner and Hall, 1974; Kane, 1984) being coupled to trophic upgrading mechanisms by lower consumer levels (Klein Breteler *et al.*, 1999; Tang and Taal, 2005), as with each component in a trophic chain, e.g. variability in biochemical composition ceases and approaches a constant quality. We were not able to find this pattern in larval dab. This could be explained by the finding of Last (1978a; 1978b) and Economou (1991), who reported that prey composition varied little within closely related larval fish but prey size increased with larval length, e.g. gadoids ingested larger prey than did flatfishes of a given length. This would show that flatfishes are better adapted to variable feeding conditions, than could be expected for cod in this context.

Feeding habits of larval fish are species dependent and several species have been shown to regularly prey on protozoan plankton (Fukami *et al.*, 1999). Larvae of several flatfish species live on prey originating from very low trophic levels (Last, 1978a; Pepin and Dower, 2007). It is likely that such prey species (e.g. appendicularians, ciliates, heterotrophic dinoflagellates) are flexible in their requirements of the biochemical composition of their prey, and consequently are likely to also be flexible with respect to their body composition. This in turn means that consumers of organisms that are very low in the food web are probably adapted to an unstable feeding environment. For dab, this might mean that at least smaller size classes are able to switch to lower trophic levels and handle the higher variability of prey quality without detectable growth and condition reductions. Larger size classes might in turn be seriously affected by a lack of suitable prey, indicated by the absence of larger larvae after the zooplankton breakdown.

Our prediction, based on the optimal foraging theory (Werner and Hall, 1974) that an increased prey spectrum towards the lower part of the foodweb would be reflected negatively in larval fish nutritional condition, might be wrong for at least a proportion of species and size classes. There is

growing evidence that microzooplankton plays an important role and is regularly used as prey or at least to substitute the commonly accepted crustacean based diet of larval fish (de Figueiredo *et al.*, 2005; Pedersen and Fossheim, 2008), although this is often reported concurrent with low larval growth rates (Van der Meeren and Naess, 1993). This might depend on the species under investigation, as in the case of Van der Meeren and Naess (1993) who studied cod, which showed low growth rates in the first three weeks of the investigation. Cod larvae switch to a fish based diet very early and are known to be cannibalistic. This makes it unlikely that such larvae are adapted to very small prey over such a long period as the first three weeks of their lives.

This study shows that, even though our knowledge about the feeding ecology of larval fishes is growing, there is a set of yet understudied topics open to be investigated. Species and life stage dependent selectivity for prey organisms might not necessarily mean that a forced switch away from the favourite dish must have a drastic effect on the welfare of larval fish. Effects arising from suboptimal foraging might be less serious than previously thought, as it is likely that fish are able to react flexibly as they evolve in a unstable environment.

In conclusion, the two species under investigation showed clear differences in their flexibility to react to, as well as their vulnerability to changing feeding environments. Larval sandeel seemed to stick more closely to their feeding habits, although they also showed downwards shifts in their trophic levels. Smaller dab larvae showed a strong change in their feeding habits, while we cannot judge for larger sizes, as these were not included in our samples when zooplankton prey was scarce. Contrasting to sandeel, the downwards shift in trophic level did not negatively affect the nutritional condition of dab larvae.

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