Shift in larval fish diets related to phytoplankton blooms revealed by stable isotope analysis

Arne M. Malzahn[1] (Arne.Malzahn@awi.de), Justus van Beusekom[2], Karen H. Wiltshire[1], Nicole Aberle[1] and Maarten Boersma[1,3]

[1]Biologische Anstalt Helgoland, Alfred Wegener Institute for Marine and Polar Research, Helgoland, Germany
[2]Alfred Wegener Institute for Marine and Polar Research, List, Germany
[3]GKSS Research Centre, Institute for Coastal Research, Geesthacht, Germany

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

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 to the light isotope ^{14}N. Nitrogen isotopes can be used as a trophic tracer (Peterson and Fry, 1987; Fry, 1988), as the stable isotope signatures of a consumer generally reflects the isotopic composition of their diets plus a relatively predictable enrichment in heavier isotopes (DeNiro and Epstein, 1981; Post, 2002). Hence, based on the predictions above, we can 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. Under poor feeding conditions, however, we predict a decrease in mean $\delta^{15}N$ coupled with an increase in variance as a result of broader niche widths.

Isotopic signals 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 and two seston samples per week were taken at the Helgoland Roads Station (54°11.18' N and 07°54.00' E, German Bight, southern North Sea). Larval fish were analysed for length and isotopic composition, and seston was analysed for isotopic composition. Additionally, diatom carbon concentrations were derived from the Helgoland Roads long term monitoring programme (Wiltshire and Manly, 2004).

Primary production was characterised by constantly low diatom carbon concentrations and a rapid development of a diatom bloom in the middle of April (Fig. 1). This diatom bloom coincided with a drastic decrease in larval fish prey abundance (Fig. 1; for further details see Malzahn *et al.*, 2007). The seston $\delta^{15}N$ signature constantly increased until the onset of the diatom bloom and decreased coinciding with the phytoplankton bloom (Fig. 1). 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. The same pattern of an increase in $\delta^{15}N$ in the pre-diatom bloom situation and a decrease during the bloom was observed in both species of larval fish, with the remarkable difference that the decrease in $\delta^{15}N$ was more pronounced than it was in the seston signatures (Fig. 1). This reduction of the $\delta^{15}N$ signature of larval fish in late spring is a clear evidence for a downwards shift in trophic level of larval fish, implying that the larvae substituted a shortage in zooplankton prey during the diatom bloom

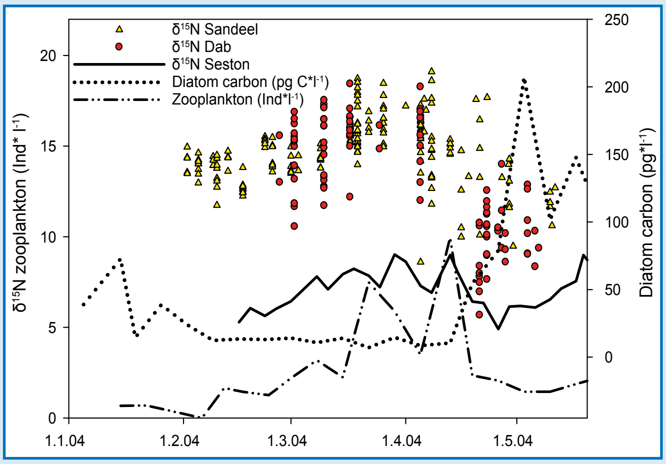

Figure 1. $\delta^{15}N$ signature of larval dab (Limanda limanda), sandeel (Ammodytes marinus), seston, diatom carbon concentrations as well as zooplankton abundance in spring 2004 at the Helgoland Roads station.

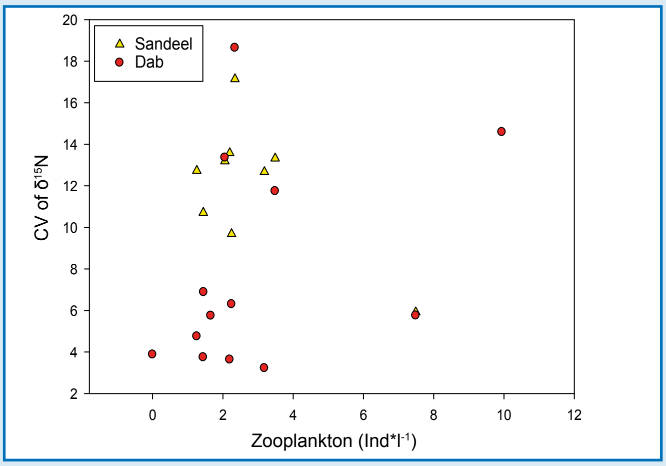

Figure 2. Coefficient of variation (CV) of the $\delta^{15}N$ signal of larval dab and larval sandeel on a weekly basis versus zooplankton densities.

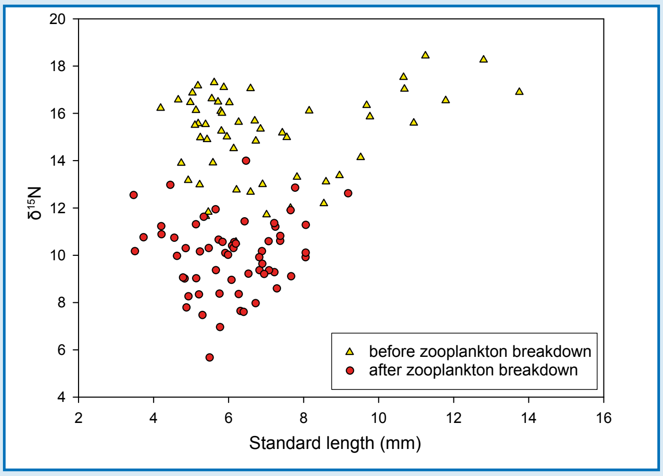

Figure 3. δ¹⁵N signatures of larval dab (Limanda limanda) caught in spring 2004 at the Helgoland Roads station plotted against larval size. The dataset is divided into pre-phytoplankton bloom (before zooplankton breakdown) and phytoplankton bloom (after zooplankton breakdown).

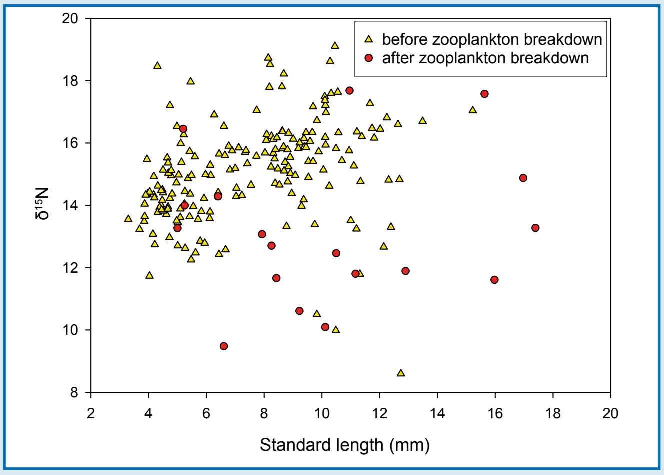

Figure 4. δ¹⁵N signatures of larval sandeel (Ammodytes marinus) caught in spring 2004 at the Helgoland Roads station plotted against larval size. The dataset is divided into pre-phytoplankton bloom (before zooplankton breakdown) and phytoplankton bloom (after zooplankton breakdown).

with organisms of lower trophic levels. The alternative food sources were presumably small microzooplankton as well as some phytoplankton species, as indicated by the fact that the difference between the seston $\delta^{15}N$ signal and that of the larval fish decreased. Linear regression analysis revealed that the variability of the $\delta^{15}N$ of larval fish, expressed as the coefficient of variation (CV=standard deviation/mean*100) of the $\delta^{15}N$ signature on a weekly basis, did not significantly vary with prey availability (Fig. 2).

As we did not investigate a specific cohort of larval fish but rather the full suite of size classes caught with the plankton gear, it can be ruled out that the shift was caused by feeding habits of different larval size-classes alone (Figs. 3 and 4). In fact, all size classes in the catches showed a downward shift in their trophic position after the breakdown of the zooplankton densities. As shown by Malzahn *et al.* (2007), low RNA:DNA ratios indicate reduced nutritional conditions in larger larval fish during times of reduced zooplankton availability. As this was not the case for smaller larvae, it can be concluded that small larvae were sufficiently nourished by microzooplankton and phytoplankton.

Prior studies on cod (Kane, 1984), dab, flounder and sole (Last, 1978) as well as American sandeel (Monteleone and Peterson, 1986) showed that the smallest larval fish can feed on phytoplankton. However, all these studies reported a rapid shift to zooplanktivory with increasing size. In this study, we showed that, depending on the availability of prey, large shifts in the diet of larval fish can be observed and that even larger individuals can be obliged to feed on algae and microzooplankton. The lack of well-conditioned larger larvae feeding on phytoplankton reported by Malzahn *et al.* (2007) suggests that although larger larvae are able to find alternative food sources, food items such as microzooplankton and phytoplankton do not support proper growth of larger individuals.

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