Not to be cited without prior reference to the author

ICES CM2009/T:05

Mortality of juvenile sandeel on the Faroe Shelf due to food limitation

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Abstract

On the Faroe Shelf, sandeel (*Ammodytes marinus*) spawn around new-year. Since 1974, juvenile sandeel have been sampled during the annual 0-group surveys in late June – early July and the results show large variations, both in the number and the average length of the sandeel sampled. Here, we investigate these variations in recruitment success in relation to food availability. The food of early-life sandeel is dominated by zooplankton, which again depends on the primary production. On the Faroe Shelf, measurements of chlorophyll *a* and accumulated new primary production during spring and summer have been carried out since 1990 and this shows large inter-annual variations in the spring bloom onset and intensity. In the paper, we compare the time series from sandeel 0-group surveys with data on phytoplankton production and biomass. The results confirm that survival and condition of the early-life stages of sandeel on the Faroe Shelf is dependent on the magnitude of the primary production. Although the sandeel spawns several months before the spring bloom, the timing of the spring bloom start does not seem to have a significant influence on the number or length of juvenile sandeel during the 0-group survey. They seem to be mainly determined by the phytoplankton concentration just before the survey. Sandeel is an important food source for higher trophic levels e.g. seabirds, cod and haddock. The established link between sandeel mortality and primary production may therefore help explain a previously found link between primary production and commercially important fish stocks as well as seabirds on the Faroe Shelf.

Keywords: Sandeel, Faroe Plateau, mortality, phytoplankton, zooplankton, recruitment, condition

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Introduction

The sandeel is well known for its importance in numerous marine ecosystems. Many marine mammals, fish species, and seabirds are dependent on sandeel for both survival and recruitment (Bailey et al., 1991; Furness & Tasker, 2000; Furness, 2002; Poloczanska et al., 2004; Temming et al., 2004; Frederiksen et al., 2007).

Sandeel has a complex life cycle. The adults spend most of the year buried in sandy sediments, and only emerge to feed during daylight hours in late spring and early summer, and briefly to spawn in mid-winter. The pelagic larvae hatch in early spring, and after metamorphosis the young 0-group fish establish a diurnal rhythm similar to that of the adults. They continue feeding until late summer. Throughout its life, the sandeel feeds on zooplankton, mainly copepods (Reay 1986), but food availability is generally considered to be especially critical in the early life stages (Arnott & Ruxton, 2002; Frederiksen et al., 2006).

Copepod reproduction is highly dependent on food availability (e.g. Diel & Tande, 1992; Hirche, 1996; Niehoff et al., 1999; Maps et al., 2005; Pierson et al., 2005) and for most copepod species, phytoplankton is the main food item (Irigoien, 1998; Meyer-Harms et al., 1999). Seasonal development in primary production and phytoplankton abundance and composition is generally reflected in copepod reproduction and growth (Campbell et al., 2001; Durbin et al., 2003; Devreker et al., 2005). In high latitudes, the seasonal difference in phytoplankton production and abundance is high and therefore timing and intensity of primary production significantly influences production, composition and abundance of the entire copepod community (e.g. Gislason & Astthorsson, 1995; Gaard, 1999). The timing and the intensity of copepod reproduction is considered to be essential for survival of fish larvae, since they feed largely on copepod eggs or nauplii during their early feeding stage (e.g. McLaren & Avendaño, 1995; Michaud et al., 1996; Gaard & Steingrund, 2001; Voss et al., 2003). Furthermore, several pelagic fish stocks feed on copepods during their entire lifetime (e.g. sandeel), and their individual growth as well as stock production is highly affected by copepod availability (Jacobsen & Hansen, 2000; Holst et al., 2004; Skjoldal et al., 2004).

Many of the demersal fish species depend on food items that feed on zooplankton (e.g. sandeel, Norway pout, capelin etc.) and in several areas, clear correlations have been observed between variability in plankton, planktivorous fish and demersal fish (Gaard et al., 2002; Astthorsson & Vilhjálmsson, 2002; Temming et al., 2004; Steingrund & Gaard, 2005).

Despite its relatively small size (~10,000 km^2), the Faroe shelf contains a distinct neritic ecosystem, surrounded by an oceanic environment. The shelf water is relatively well separated from the open ocean by a persistent front that surrounds the shelf, usually between 100 and 130 m bottom depth (Figure 1) (Gaard et al., 1998; Larsen et al., 2002; Larsen et al., 2009). Tidal rectification and other effects drive a current system, which circles the islands in a clockwise direction (Hansen, 1992). Due to strong tidal currents over the shallow parts of the shelf, the water column is mixed from surface to bottom throughout the year and no summer stratification occurs in the shallow areas (Gaard, 1996; Gaard et al., 1998). The average residence time of the shelf water is estimated to be about 2–3 months, but it is highly variable and the monthly flushing rates may vary by about a factor of six (Gaard & Hansen, 2000; Gaard, 2003).

On the Faroe shelf, previous investigations have shown that the magnitude of primary production varies considerably from one year to another (Gaard et al., 2002; Debes et al., 2008a) and that this may be linked to the exchange between the waters on the shelf and off it. According to this hypothesis, years with intensive exchange in spring result in a relatively large loss of phytoplankton from the shelf due to flushing, which prevents development of an intensive spring bloom (Eliasen et al., 2005; Hansen et al., 2005). The inter-annual variations in spring bloom intensity have furthermore been shown to have strong effects on higher trophic levels, such as cod, haddock, and seabirds (Gaard et al., 2002).

Together, these results imply a link from climatic and physical oceanographic forcing to the primary production and further to higher trophic levels of the marine ecosystem on the Faroe shelf. This link has to be transmitted upwards in the food chain by some intermediate species that connect plankton to the non-planktivorous species at higher trophic levels. The sandeel is known to be an important food element for cod, haddock, and seabirds on the Faroe shelf (Gaard et al., 2002) and might play a role as this link, but this would only be relevant, if sandeel productivity can be shown to depend on the primary production. The aim of this paper is to explore potential links between the timing and magnitude of primary production and the abundance and size of the juvenile sandeel.

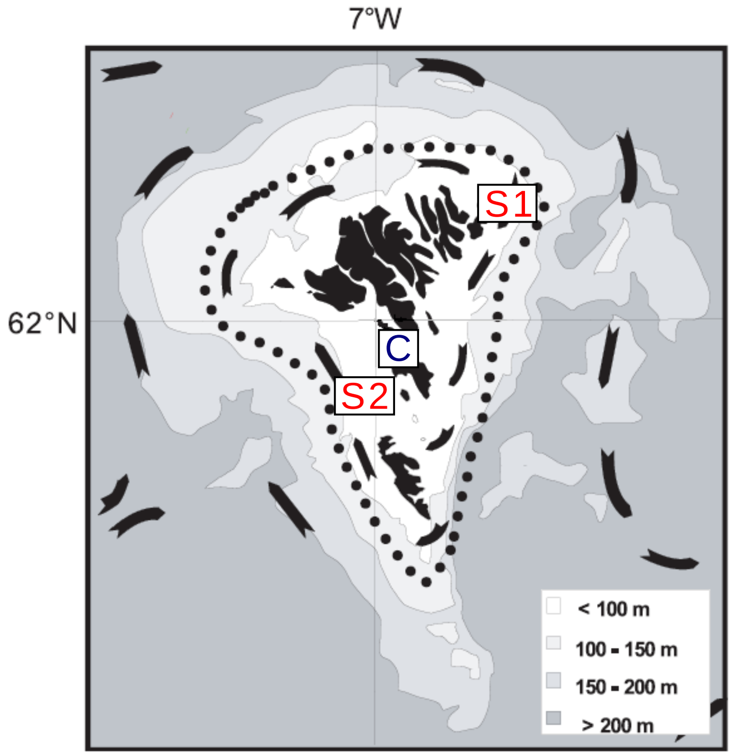

Fig. 1. Topography and main features of the flow field around the Faroes. The dotted line enclosing the light grey area around the shelf indicates the typical position of the tidal front that separates the shelf water from the open ocean. The blue and red letters refer to sampling stations (see material and methods).

Material and methods

Frequent samplings for measurement of chlorophyll *a* were carried out at a land-based station C (Figure 1). This station pumps large amounts of seawater (about 15 tonnes per minute) from 18 m depth at a location on the central shelf, where the water column always is highly mixed from surface to bottom. The samples have been collected on a weekly basis during the productive season, from April until September since 1997. Chlorophyll *a* was measured spectrophotometrically according to Parsons et al. (1984). Calculations were made according to Jeffrey & Humphrey (1975). When comparing interannual variability of chlorophyll *a* concentrations in this time series, daily concentrations are calculated based on linear interpolation between the weekly measurements.

Samples for measurement of nitrate were collected at stations that were evenly distributed on the shelf and slope in late June 1990-2009. The samples that were taken in 1990 were stored in a refrigerator and analysed a few days after sampling. In 1991-1994, they were frozen immediately after sampling and analysed ashore. Since 1995 they were analyzed onboard the same day or the next day after sampling. Nitrate + nitrite was measured on an auto-analyzer according to Grasshoff et al. (1983).

A measure of the accumulated new primary production in the shelf water ecosystem during the high productive period was calculated based on reduction of nitrate concentrations from winter levels to a fixed date (26 June each year) on station S_1 and S_2 (Figure 1) plus estimated net influx of nitrate from the surrounding off-shelf water during the same time period:

PP-index = nitrate decrease + nitrate net inflow

The inflow of nitrate is calculated as:

Nitrate net inflow = renewal rate of shelf water · ($[NO_3^-]_{offshelf}$ - $[NO_3^-]_{shelf}$)

where $[NO_3^-]_{offshelf}$ and $[NO_3^-]_{shelf}$ are the nitrate concentrations in the surrounding off-shelf and the shelf water, respectively. The average renewal rate of the shelf water is estimated to about 1/75 day^{-1} (Gaard, 2003).

The juvenile sandeel material was derived from the annual Faroese 0-group surveys in late June-early July 1974-2009. The 0-group survey is primarily designed to obtain information on the year class strength of cod but other fish species, e.g. sandeel, are caught as well. The trawl stations were on fixed positions from year to year, evenly distributed on the Faroe shelf. In total, 90 annual stations are examined and 70 of these are placed within bottom depths of 45-150 m. In order to get additional information on e.g. the horizontal distribution of the juveniles, 20 stations are placed outside the tidal front, down to about 500 m bottom depth. In 1981, the ship used in these surveys was replaced, but due to initial complications, only the length measurements were of sufficient quality for further analysis.

The juveniles were collected with a capelin trawl with 5 mm mesh size in the cod-end with a mouth opening of about 8 m (horizontally) times 4-5 m (vertically). The trawling depth was approximately 30-40 m; the exact depth was chosen based on the recordings on the echo-sounder. The towing speed was 3 knots and the duration of each haul was 30 min. The species were identified, measured and counted on board. In cases of very large catches, sub-samples were analysed and the results were then calculated to total catches. The juvenile length was measured as total length to the nearest whole mm.

Results

Large inter-annual variations are seen in the average number of juvenile sandeel caught per station, the average juvenile sandeel length, and the primary production on the Faroe shelf (Figure 2). Approximately 1800 juvenile sandeel were on average caught per station in the periods 1974-1980 and 1982-2009. The number caught varied with a factor 160, with 2007 having the lowest catch and 2008 having the highest catch (Figure 2A). Overall, the average juvenile sandeel length was 50.5 mm, but it has varied with a factor 1.8 over the last 35 years (Figure 2B). The years 1982, 1983, and 2000 had the largest specimens in June/July, while 2007 had the smallest. Since 1990, the PP- index has varied with a factor 5.6, with year 1990 being the least, and year 2000 the most, productive (Figure 2C).

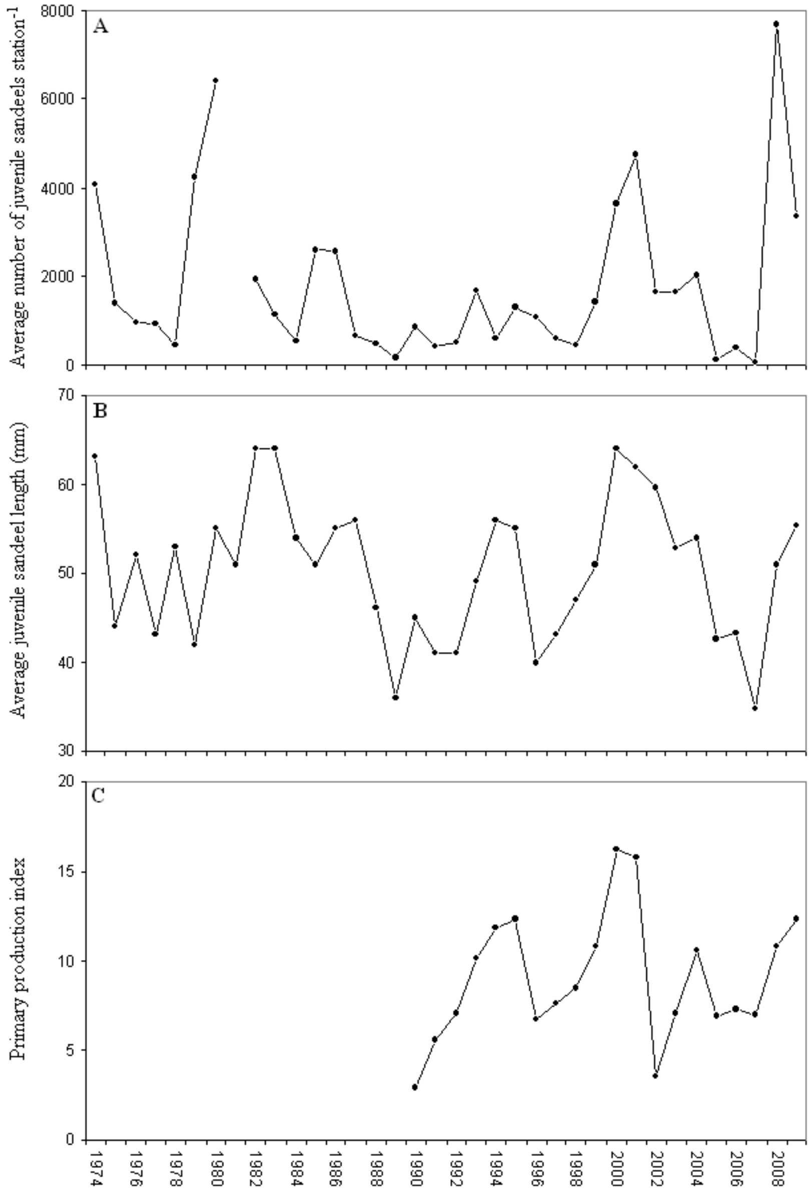

Fig. 2. Three of the four time series presented in this paper. A) Average number of juvenile sandeel caught at each station on the Faroe shelf (<100 m) in late June-early July in the periods 1974-1980 and 1982-2009. B) Average length in millimetres of the juvenile sandeel caught in late June-early July on the Faroe shelf in the period 1974-2009. C) Index on the primary production (PP-index) on the Faroe shelf in the period 1990-2009.

The seasonal development in phytoplankton concentration on the Faroe shelf shows large variations (Figure 3). Annual differences are in the date of the spring bloom onset, the spring bloom intensity and in the number of blooms.

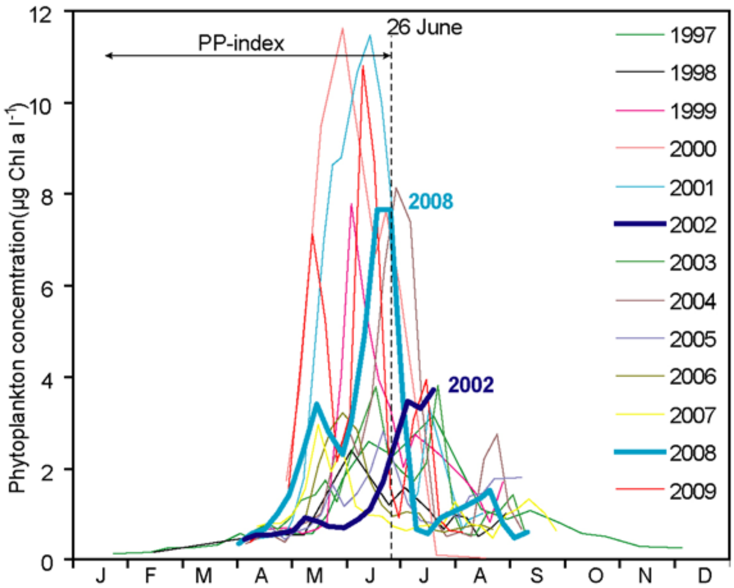

Fig. 3. A) Seasonal variation in the phytoplankton concentration (µg Chl *a* l^{-1}) on the Faroe shelf in the period 1997-2009. The horizontal arrow ending on 26 June indicates the period, over which the PP-index is calculated. The two abnormal years 2002 and 2008 are enhanced (see discussion).

Similar trends are observed in the time series presented in Figure 2, and the similarities are verified by relatively high correlation coefficients (R). The squared correlation coefficient (R^2) between the primary production index and the average number of juvenile sandeel caught per station was 0.31, which is statistically significant at the 1% level. Similarly, the R^2 between the primary production index and the average juvenile sandeel length was 0.43, which again is statistically significant at the 1% level.

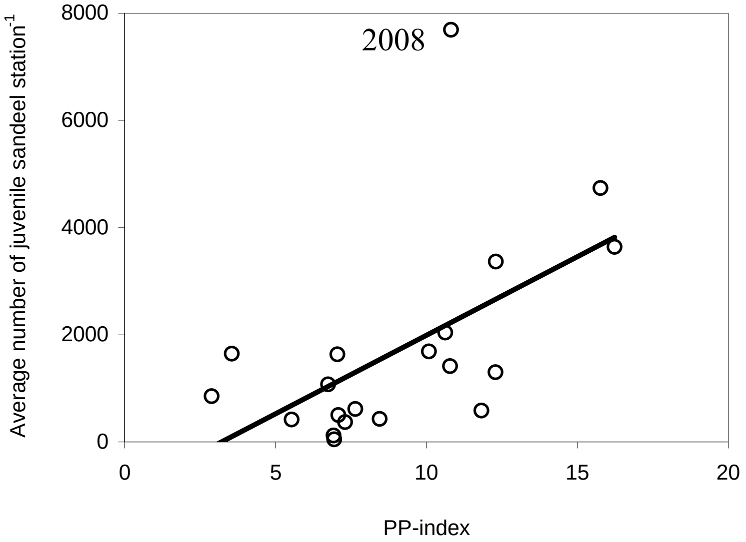

Fig. 4. Correlation between the average numbers of juvenile sandeel caught at the stations investigated and the primary production (PP) index in the years 1990-2009 (R^2 = 0.31).

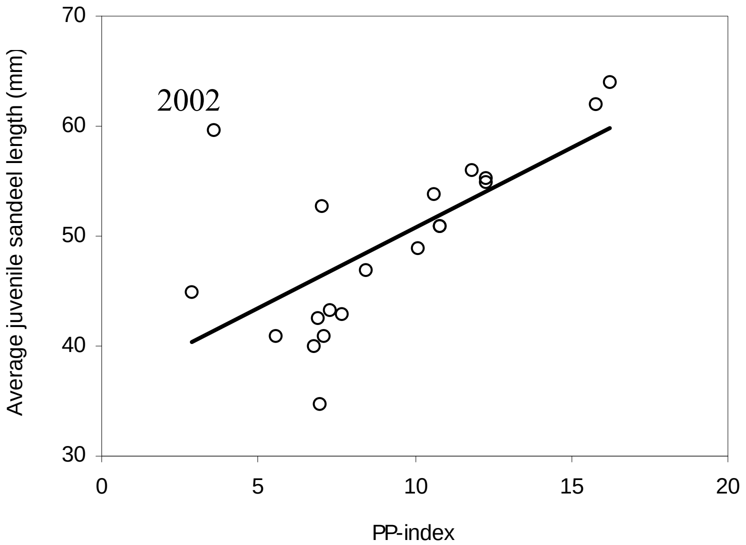

Fig. 5. Correlation between the average juvenile sandeel length and the primary production (PP) index in the years 1990-2009 (R^2 = 0.43).

The PP-index is a measure of the accumulated new production from early spring until 26 June each year. To see, whether there is a certain critical time within this period, the correlations were calculated between the sandeel series and phytoplankton concentration averaged over monthly or semi-monthly periods (Table 1). The overall conclusion is that the primary production in the last part of the period is most important for both sandeel number and length.

Table 1. The squared correlation coefficient (R^2) between the phytoplankton concentration (µg Chl *a* l^{-1}) averaged over monthly or semi-monthly periods and the average number of juvenile sandeel caught in the period 1997-2009 (middle column), and the average juvenile sandeel length (mm) in the period 1997-2009 (last column).

Phytoplankton concentration in:	Average number of juvenile sandeel R^2	Average juvenile sandeel length R^2
the second half of April	0.29	0.11
the first half of May	0.31	0.27
May	0.26	0.36
June	0.55	0.50

Discussion

The results presented (Figures 4 and 5) indicate that both sandeel number and length on the Faroe shelf are related to the magnitude of primary production. For the sandeel number, this could partly be an indirect effect, since the primary production, as mentioned in the introduction, is believed to depend on the exchange with off-shelf waters. Less exchange between the shelf and off-shelf waters should give a high primary production, but should also influence the concentration of sandeel larvae, since fewer larvae will be exported off the shelf. The observed variations in sandeel numbers (Figure 3) are, however, considerably larger than the variations in exchange rate (Gaard & Hansen, 2000), and this mechanism does not explain the good correlation between the primary production and sandeel length. Therefore a direct dependence of sandeel on the primary production in form of food limitation in years with low primary production is more likely.

As shown in Figures 4 and 5, two years seem to fall especially outside this relationship: 2008 for sandeel number and 2002 for sandeel length. We have no explanation for this, but Figure 3 shows that both these years were somewhat abnormal. In 2008, the production started early and phytoplankton biomass increased rapidly, but in mid-May, this tendency changed and the phytoplankton biomass decreased for two weeks before recovering again. The year 2002, in contrast, had an extremely late start of the spring bloom, and had a relatively high phytoplankton biomass in late June - early July.

From this, it might be tempting to conclude that sandeel length depends mainly on the phytoplankton biomass in early spring, whereas sandeel number depends more on the biomass in June-July. Table 1 indicates, however, that the phytoplankton biomass in June is most important for both the number and the average length of the sandeel caught during the 0-group cruises in June-July. This is somewhat inconsistent with the expectation that food would have a crucial importance in the early life stages of fish (Cushing, 1990; Arnott & Ruxton, 2002), but of course, factors such as drifting off the shelf, predation and unsuccessful location of suitable habitat also play relatively large roles in this period (Deurs et al., 2009).

A study in 2004 implied that a mismatch between food availability and hatching date of sandeel larvae could occur on the Faroe shelf (Eliasen, 2005). In 2004, the number of sandeel larvae peaked in late March and afterwards continually dropped in number until late April when they disappeared. The density of the smaller zooplankton, e.g. copepod nauplii, on the other hand, did not start increasing until late May (Figure 6). In spite of this, the juvenile sandeel, caught on the 0-group survey in 2004 were average both in number and length (Figure 2).

There can be several explanations for this phenomenon. First, it might be sampling bias, where the sampling gear might not have sampled the different early life stages of sandeel properly. Every 7 to 14 day in the first half of 2004, a fixed station was sampled with WP-2 (200 µm), Bongo (100 and 200 µm) and MIK (500 µm) nets. While the earliest stages of juvenile sandeel did appear in both the WP-2 and Bongo nets, the MIK net seemed to collect the later stages poorly. Secondly, investigations have revealed that the most important copepod species on the Faroe shelf begin to spawn prior to the spring phytoplankton bloom, and some food in the form of copepod eggs might thus be available earlier than expected (Eliasen, 2005; Debes & Eliasen, 2006; Madsen et al., 2008; Debes et al., 2008b).

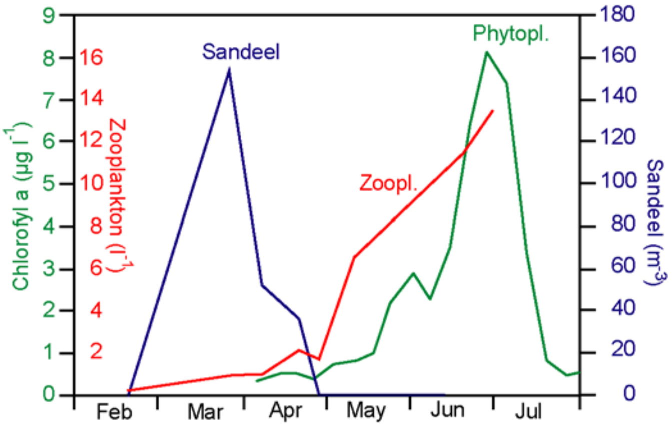

Fig. 6. Seasonal variation in the number of juvenile sandeel (blue line), the phytoplankton concentration (green line) and the number of zooplankton (red line) caught with a 100 µm net on the Faroe shelf in 2004.

The link from primary production to sandeel is also complicated by the fact that it must go through zooplankton, but the zooplankton density does not tell the full story. The species composition of the zooplankton community is also of great importance in understanding the link (Deurs et al., 2009). The study in 2004 revealed that the sandeel larvae in the earliest stages of their life are very selective. Size is, of course, a natural inhibitor for certain food items, but species related selection did also occur. As an example, the sandeel larvae tended to avoid the heavily armoured species, largely the *Temora longicornis* nauplii (Eliasen, 2005).

On longer timescales, the question arises whether high densities or larger specimens during the surveys is the best guarantee for recruitment success. A priory, a high number of juvenile sandeel would seem to be the best basis for recruitment success, but the 0-group surveys on the Faroe shelf are carried out in late June-early July and the juvenile sandeel thus still have approximately two months left to forage the water column before hibernation. Being a preferential prey species, the main goal of juvenile sandeel after hatching is to increase in size and thereby avoid a large number of potential predators (Cushing, 1990). Additionally, the juvenile sandeel do not begin their predator-avoiding burrowing behaviour before metamorphosis, and poor growth can thus potentially postpone this behaviour (Deurs et al., 2009). Larger specimens also have a wider range of food opportunities since they are able to ingest larger food elements (Monteleone & Peterson, 1986; Eliasen, 2005), and thus are better suited to enhance their lipid stores needed in the exhausting hibernation period ahead. Consequently, it is not clear to what extent juvenile abundance or size determines the recruitment success of Faroese sandeel.

Conclusions

Overall, it can be concluded that the magnitude of the spring and early summer phytoplankton production has a significant influence on both the numbers caught and the average length of juvenile sandeel during the 0-group survey in late June-early July on the Faroe shelf. The timing of the onset of the spring bloom does not seem to have as significant an influence on the numbers or lengths of juvenile sandeel, which seem to be mainly determined by the phytoplankton concentration just before the survey. A thorough investigation on the seasonal succession of the zooplankton community and sandeel feeding on the Faroe shelf is needed before a final conclusion on the importance of food in the early life stages of sandeel can be made.

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