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ORIGINAL ARTICLE

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

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Abstract In order to test the temporal stability within and the reproducibility of larval fish assemblages between years, the larval fish assemblage at Helgoland Roads, North Sea (NE Atlantic) was quantitatively sampled almost daily from January 2003 to December 2005. The survey resulted in a total of 462 samples containing 50,632 larval fish of at least 42 taxa. In winter the larval fish assemblage was mainly dominated by larvae emerging from demersal eggs. This changed gradually to larvae hatching from pelagic eggs. Larvae from pelagic eggs dominated the ichthyoplankton assemblage in summer. A remarkably stable seasonality in terms of dominance patterns with recurring, season-specific fish assemblages was observed over the 3 years, despite substantial variation in environmental conditions such as a temperature difference of almost 20°C between summer and winter. The lesser sandeel (*Ammodytes marinus*), was the only species which showed significant fluctuations in abundance between the years. After removal of this species from the analysis, the dominance patterns of the remaining fish species were almost identical between years.

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Introduction

On any timescale, planktonic communities are never static. Changes in community structure might occur as a result of disturbances such as storms, or might be caused by more gradual environmental changes like seasonally driven temperature changes. The intra-annual succession in temperate marine ecosystems is characterized by slight changes in time scales of days, and by strong environmental changes in terms of months or seasons. In contrast to severe sudden processes like upwelling events, 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 the years (Edwards and Richardson 2004; Wiltshire and 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 and Richardson 2004; Malzahn et al. 2006) 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 (Köster et al. 2003; Wieland et al. 2000), otherwise abundance will be underestimated and this will result in weak larval abundance–recruitment-relationships (Bradford 1992).

The majority of lifecycles realized by marine organisms include a planktonic phase (Cowen et al. 2000). In case of fish, these are planktonic egg and larval stages, although many fishes lay demersal eggs. 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). Even without invoking changing currents one can make predictions under which conditions producing demersal or pelagic eggs is the best strategy. Egg development as well as the duration of the larval stage is highly temperature-dependent with low temperatures leading to long egg incubation times (Malzahn et al. 2003). Hence, it is likely that in different 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 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. The second hypothesis under test is a part of the match/mismatch hypothesis. 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 3 year, high temporal resolution, single location ichthyoplankton survey at Helgoland Roads, located in the North Sea (NE Atlantic).

Materials and methods

The ichthyoplankton assemblage was surveyed at a single site (54°11.18′N and 07°54.00′E, known as Helgoland Roads station) between the island of Helgoland and the adjacent dune, in the German Bight from January 2003 to December 2005. Three to five ichthyoplankton samples were taken each week, weather permitting at a mean depth of 10 m from the research vessel "Aade". The water column at the station is mixed throughout the year due to the shallow water and the strong tidal currents (up to 1.5 knots). The area is characterized by a strong seasonality with water temperatures ranging from 0–3°C in February up to 20°C in August. After subtraction of tidal currents, the residual flow 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 and Manly 2004) and the secondary production follows the phytoplankton growth (Greve et al. 2004). A second, smaller phytoplankton bloom often occurs in autumn.

Double oblique hauls were carried out using a CalCOFI ring trawl equipped with 500 µm mesh net (aperture 100 cm, length 400 cm, equipped with a flow meter) from a research vessel. The gear was deployed for 15 min per sampling. On board, the sample was gently flushed into a bucket, in which it was transferred to the Institute. As the station sampled is approximately 200 m away from the Institute and the ichthyoplankton haul was always carried out as the last deployment before heading back to the Institute, samples usually arrived at the laboratory within 15 min. Samples were sieved and transferred into a Bogorov chamber, larval fish were sorted using a stereo microscope (Olympus B061) and classified to 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, due to

their brood care habits, not a regular part of the ichthyoplankton.

In order to test seasonal changes in the contribution of demersal and pelagic eggs, a value of 0 or 1 was assigned to each species depending on egg type: demersal (0) or pelagic (1). An unweighted mean was calculated for each collection to determine general patterns and whether demersal or pelagic egg species dominated at a given time of year. For example, a collection containing two species from demersal eggs and one species from pelagic eggs would result in a value of 0.33.

A nested ANOVA was used to test for differences in larval abundance between years, months, and weeks 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. For the sake of a balanced design, 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. Weekly abundance means were the smallest hierarchical unit. 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 and Weaver 1963) and Pilou´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.)

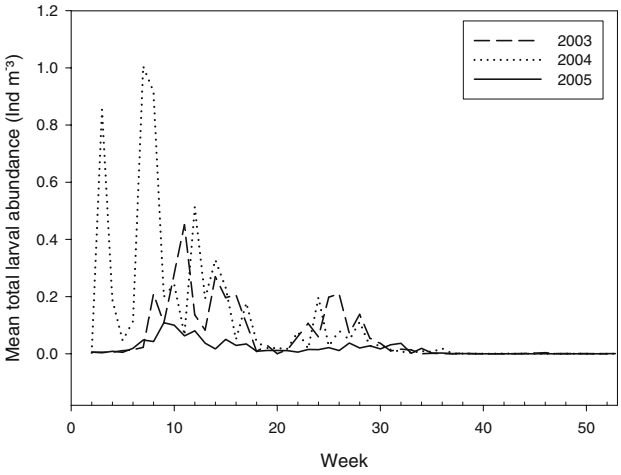

Fig. 1 Mean weekly larval abundances of the years 2003–2005

Results

During the 3 years of investigation a total of 462 samples were taken. These samples contained 50,632 larval fish of at least 42 taxa. The 3 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. 1).

The mean temperatures of the first 8 months, in which 99% of the cumulative abundance reached in all 3 years under investigation did not 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°C, 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 to 10 (6.9–4.3°C), 2005 was characterized by a decrease from 6.0 to 2.9°C (Fig. 2).

The total larval cumulative abundance showed similar shapes but differences in timing. The development of the cumulative abundance in 2004 was always 2–3 weeks ahead of those of 2005 and even 4 weeks compared to 2003. In week 10 of 2004, 55% of the total larval abundance was already caught,s while in 2005 it was 35% and in 2003 it was just 20% (Fig. 2). Removing the dominant sandeel from the cumulative abundance curves, a higher temporal match between the

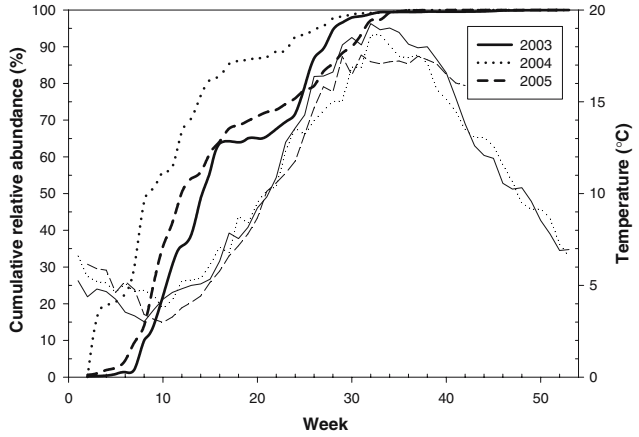

Fig. 2 Cumulative relative abundance of the total larval catch from 2003 to 2005 (total abundance scaled to 100%) and the weekly temperature means. Sandeel included. *Thick lines* are larval cumulative abundances and *thin lines* represent temperature in the different years

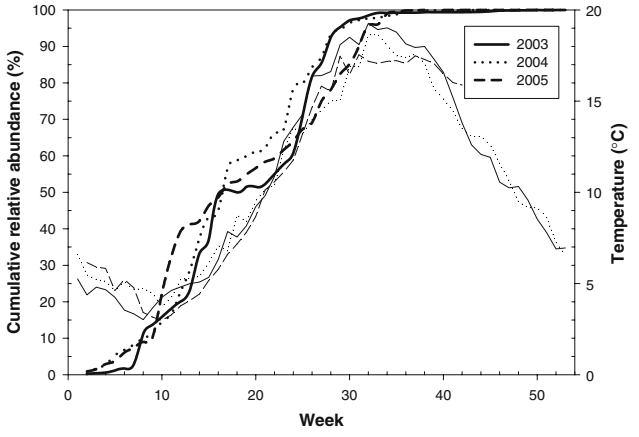

Fig. 3 Cumulative relative abundance of the total larval catch from 2003 to 2005 (total abundance scaled to 100%) and the weekly temperature means. Sandeel excluded. *Thick lines* are larval cumulative abundances and *thin lines* represent temperature in the different years

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. In sandeel, the temperature trajectory with rising temperatures seemed to play a major role (Fig. 3).

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, 8 of the 12 most abundant species showed significant variation in months nested within years. Variation between the years was significant only in case of the lesser sandeel. For sculpin, sardine and the great sandeel none of the two higher levels (weeks and months) 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 these three species. 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.

The dominance patterns clearly separated 2004 from the other 2 years. The lesser sandeel made up 75% of the total catch in 2004 (Fig. 4) while it accounted for roughly 30% in the other 2 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. 5). The rankings within the years were significantly correlated between the 3 years

Table 1 Nested ANOVA results of the 12 most abundant species of this study

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

Data analysed are weekly mean larval densities. Four values for weeks are nested within month, months are nested within years. The percentages of explained variance by each level are given. ($ns = P > 0.05$, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$)

Table 2 List of species caught during the study period

Species	Total catch	Months of occurrence	Frequence	% of total catch	Rank abundance 2003	Rank abundance 2004	Rank abundance 2005	mean Rank ± S.D.	Temperature (°C)
Ammodytes marinus	28,184	1–5	142	55.7	1	1	1	1 ± 0	2.7–10.2
Limanda limanda	4,387	1–7	150	8.7	2	2	5	3 ± 1.8	2.8–18
Agonus cataphractus	2,867	1–4	99	5.7	7	6	2	5 ± 2.7	2.8–6.6
Gobiidae spp.	2,850	4–8	132	5.6	3	3	9	5 ± 3.5	7–19.1
Trachurus trachurus	1,910	5–9	112	3.8	4	10	4	6 ± 3.5	11.1–19.1
Sardina pilchardus	1,584	5–10	69	3.1	11	11	3	8.4 ± 4.7	11.2–18.5
Callionymus lyra	1,504	4–9	122	3.0	5	4	6	5 ± 1	7–18.7
Buglossidium luteum	1,155	5–8	109	2.3	6	5	8	6.4 ± 1.6	9.9–18.8
Arnoglossus laterna	916	4–9	97	1.8	9	8	10	9 ± 1	7–19.7
Hyperoplus immaculatus	735	4–9	82	1.5	10	16	7	11 ± 4.6	6.2–18.2
Engraulis encrasicolus	682	6–8	22	1.3	n.c.	9	16	12.5 ± 5	14.6–19.1
Taurulus bubalis	639	12–3	73	1.3	17	7	12	12 ± 5	2.9–17.3
Pholis gunnellus	537	1–3	42	1.1	13	13	14	13.4 ± 0.6	2.9–6.2
Liparis spp.	505	1–6	102	1.0	16	19	11	15.4 ± 4.1	2.8–13.7
Myoxocephalus scorpius	443	1–3	41	0.9	8	14	18	13.4 ± 5.1	2.8–5.6
Gadus morhua	367	1–5	62	0.7	22	15	15	17.4 ± 4.1	2.8–7.9
Sprattus sprattus	353	4–8	59	0.7	12	18	13	14.4 ± 3.3	6–18.7
Platichthys flesus	306	2–7	34	0.6	14	12	21	15.7 ± 4.8	3.5–16.4
Indet species	202	1–9	46	0.4	15	17	26	19.4 ± 5.9	4.3–19.7
Scomber scombrus	104	6–8	27	0.2	25	21	17	21 ± 4	13–18.3
Rocklings	73	1–7	38	0.1	n.c.	20	22	21 ± 1.5	5.2–15.8
Eutrigla gurnadus	57	4–8	34	0.1	20	26	20	22 ± 3.5	7–18.7
Merlangius merlangus	52	1–5	22	0.1	18	23	23	21.4 ± 2.9	2.9–9.8
Ctenolabrus rupestris	51	6–8	24	0.1	24	27	19	23.4 ± 4.1	14.3–18.6
Trisopterus esmarkii	28	1–2	6	0.1	n.c.	22	n.c.	28.4 ± 5.6	4.5–5
Gymnammodytes semisquamatus	21	10–12	9	>0.1	21	n.c.	n.c.	30.7 ± 9.1	8.2–12.6
Clupeide indet	17	6–8	6	>0.1	30	24	n.c.	27 ± 4.3	13.2–19.7
Chirolophis ascanii	16	1–2	9	>0.1	n.c.	29	24	26.5 ± 3.6	4.5–6.2
Raniceps raninus	16	5–7	11	>0.1	27	28	27	27.4 ± 0.6	8.2–18.1
Psetta maxima	14	6–8	10	>0.1	29	31	25	28.4 ± 3.1	12.8–18.4
Belone belone	12	7–7	3	>0.1	23	30	n.c.	26.5 ± 5	15.2–17.3
Pollachius pollachius	11	5–5	2	>0.1	n.c.	25	n.c.	28 ± 4.3	8.6–10.1
Blennius spp.	9	5–10	7	>0.1	26	32	n.c.	30 ± 3.5	9.7–18.1
Pleuronectes platessa	7	2–7	4	>0.1	19	n.c.	n.c.	29 ± 14.2	3.2–14.6
Cyclopterus lumpenus	4	5–5	3	>0.1	n.c.	n.c.	28	32.7 ± 5.7	10.2–10.4
Hippoglossoides platessoides	3	6–8	3	>0.1	28	n.c.	31	29.5 ± 2.2	15.6–17.5
Microchirus variegatus	3	5–7	3	>0.1	n.c.	36	29	32.5 ± 5	11.2–15.2
Trachinus vipera	3	4–7	3	>0.1	n.c.	34	30	32 ± 2.9	7.2–16.8
Clupea harengus	2	3–3	2	>0.1	n.c.	33	n.c.	32 ± 1	5.2–5.3
Mullus surmuletus	1	7–7	1	>0.1	n.c.	38	n.c.	33.7 ± 3.8	14.8–14.8
Phycis blennoides	1	8–8	1	>0.1	n.c.	35	n.c.	32.7 ± 2.1	18.1–18.1
Scophtalmus rhombus	1	7–7	1	>0.1	n.c.	37	n.c.	33.4 ± 3.3	16.8–16.8

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
n.c. no catch

(Spearman's Rank correlation, $P < 0.05$) with correlation coefficients from 0.85 to 0.88. Dominance ranks are given in Table 2.

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 0.3–1.0. This changed 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. 6).

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 3 years and a spring cluster uniting the weeks 5–16. The spring cluster consisted of several groups, which could be divided

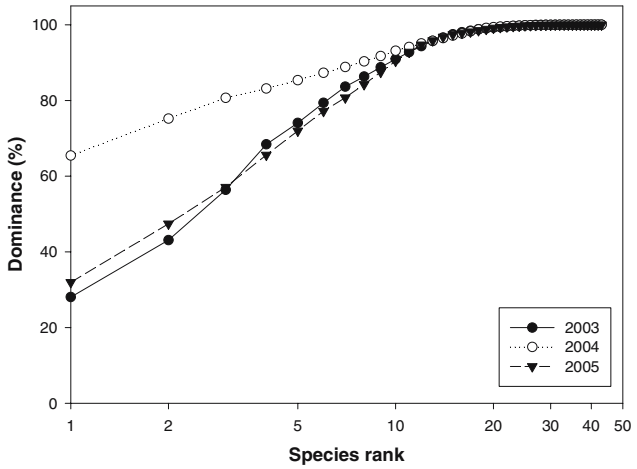

Fig. 4 Cumulative dominance plot of the 3 years of the investigation. Species sorted by dominance ranks. Lesser sandeel (*Ammodytes marinus*) included

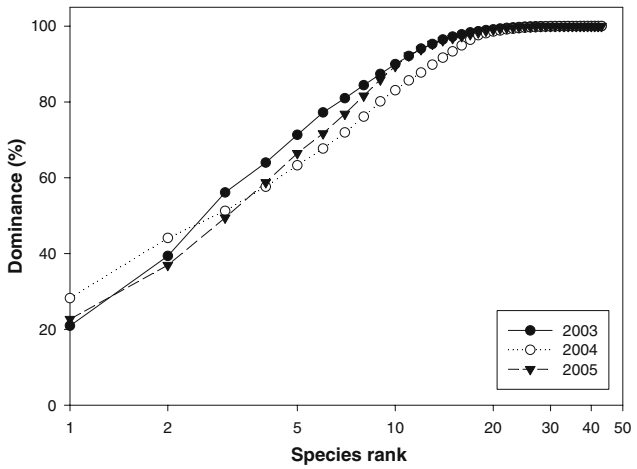

Fig. 5 Cumulative dominance plot of the 3 years of the investigation. Species sorted by dominance ranks. Lesser sandeel (*Ammodytes marinus*) excluded

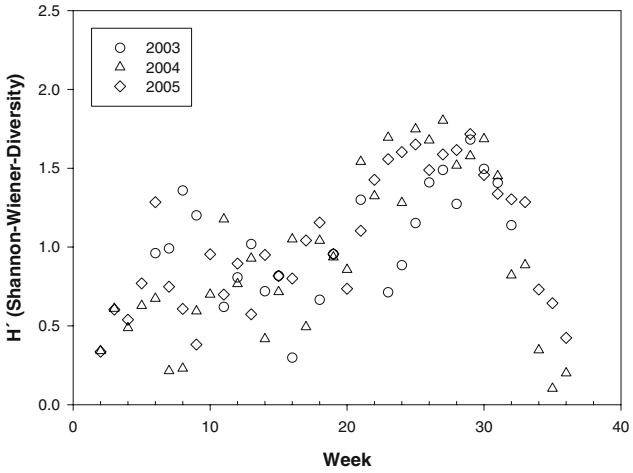

Fig. 6 Shannon Wiener diversity of the larval fish assemblage sampled from 2003 to 2005

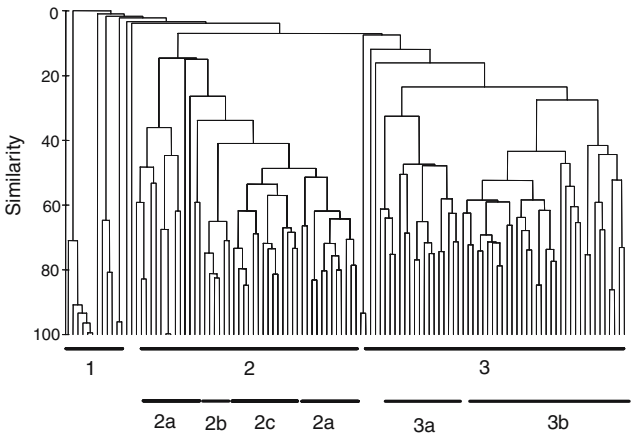

Fig. 7 Cluster analysis of Bray–Curtis similarities of samples from 2003 to 2005. Similarities are calculated using mean weekly fish larvae abundance. Data are square root-transformed. *1* Winter, *2* spring (2a spring 2003 and 2004; 2b sandeel-dominated weeks all years; 2c spring 2005), *3* summer (3a early summer; 3b late summer)

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 from the beginning of winter showed no clear cluster as catches were rare and displayed usually a single species at very low densities (Fig. 7). Figure 7 represents a cluster analysis of all data from 2003 to 2005 and because there were no obvious differences between the years, it is used as representative for the single years.

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 assemblages. The winter/spring assemblage 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

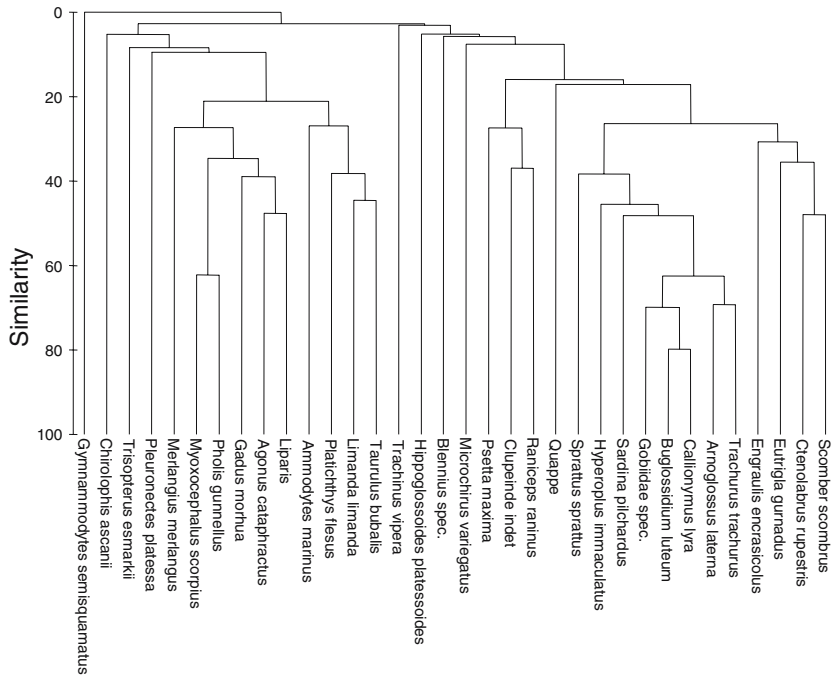

Fig. 8 Cluster analysis of larval fish assemblages for 2003–2005. Bray–Curtis similarities of mean weekly fish larvae abundance are given. Data are square root-transformed

during the 3 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 where minor abundant or not caught in all years (Fig. 8).

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, when the majority of the larvae hatched from pelagic eggs (Fig. 9).

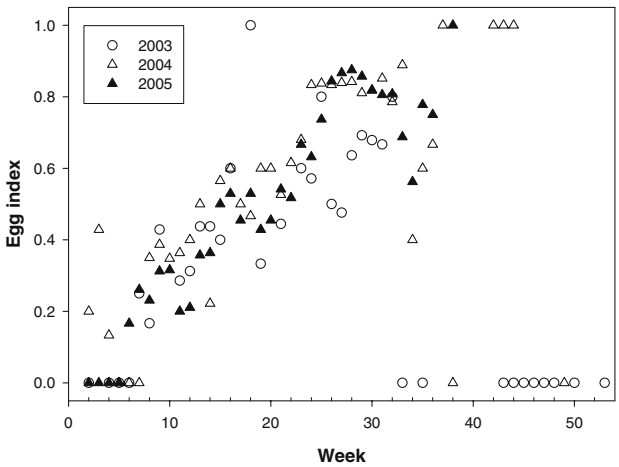

Fig. 9 Egg index corresponding to the larvae observed in the ichthyoplankton. (0 means all larvae in the sample emerged from demersal eggs; 1 means all species in the sample had pelagic eggs)

Discussion

Larval fish assemblages have been found to be influenced by a large variety of factors such as currents (Meekan et al. 2006), upwelling systems (Hutchings et al. 2002, 1998; Painting et al. 1998) 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 was not 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 assemblages 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 fishes are regulated by temperature (Baumann et al. 2006; Franco et al. 2006; Greve et al. 2005; Malzahn et al. 2003; Mello and Rose 2005; Peck et al. 2005; Sponaugle et al. 2005). 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 leading to delayed larval occurrence. Contrasting to Greve et al. (2005), 2 of the 3 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) was not able to predict sandeel seasonality by mean winter temperatures. A similar observation has been reported by Frank and Leggett (1981, 1982). They were able to demonstrate that the emergence of larvae of several species to the pelagic zone was strongly triggered by rising temperatures. Our results are not as pronounced as those reported by Frank and Legget (1981, 1982), and this can clearly be attributed to the more severe changes in water temperature in Conception Bay, Newfoundland, caused by coastal upwelling than those observed in the North Sea.

We observed some temperature-related shifts in the development of the cumulative larval abundances between the 3 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 assemblage? 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 and 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. (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 findings to the "adaptive emergence" and the "safe site" concept they established earlier (Frank and Leggett 1981, 1982). 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 Leggett (1981, 1982) 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. The gradual change from demersal to pelagic eggs observed in this study can rather be explained with the absence of such strong differences between water masses in the shallow 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 selected 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. 2006; Hinrichsen et al. 2003) and the Benguela System (Hutchings et al. 2002). Additionally, a prolonged drift phase may increase egg mortality (McGurk 1986). On the other hand, a moderate amount of dispersal is needed to explore new habitats or reach nursery grounds (Köster et al. 2003; Van der Veer et al. 1998, 2000). 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 assemblage 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 3 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. This study supports Cushing's assumption that larval fish production is fixed in time, with the exception of the lesser sandeel.

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