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On the phenology of North Sea ichthyoplankton

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The timing of fish larvae abundance was investigated at Helgoland Roads in the southern North Sea for the years 1990, 1993−1996, 1998, and 1999. From the 44 species identified, 27 were sufficiently abundant in more than 3 years and had well defined seasonal changes to calculate their phenology. The passage of the 15%, 50%, and 85% annual cumulative abundance thresholds was used to define the "start of season", "middle of season", and "end of season", respectively. The timing of a significant number of these events was correlated with the mean annual winter sea surface temperatures (SSTs) in weeks 1−10 with higher temperatures leading to earlier appearance. The timing of the end of season was also negatively correlated with the SSTs. Sole (*Solea solea*) is presented as an example of the general functional relationship.

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Introduction

It is believed that global warming will change the latitudinal, altitudinal, and temporal distribution of populations (Parmesan and Johe, 2003). Though generally sparsely investigated, a northward displacement of marine organisms has been observed (Southward et al., 1995), and a seasonal shift to earlier appearance of fish larvae has been described (Greve et al., 1996). Predictions of the seasonal timing of zooplankton populations on the species level can be made from temperature (Greve et al., 2001), and inter-decadal phenological trends for North Atlantic phytoplankton and zooplankton have been found (Edwards and Richardson, 2004).

The scientific discipline treating meteorological influences on biological processes is biometeorology (Weihe, 1997). At least two of its branches are concerned with marine ecology, i.e. climatic biogeography, which treats the impact of meteorology on the regional distribution of organisms; and phenology, which treats the impact of weather and climate on the temporal orientation of ontogenetic events (Schwartz, 2003). Thus, phenology is the study of the timing of recurrent biological processes. In temperate regions, the seasonal timing of population development varies from year to year within a limited time frame. Phenology was developed in terrestrial ecology, especially for agricultural applications. The timing of sprouting, blossoming, and harvesting permits the optimization of fertilization, pest control, and other management activities. Indeed, observation systems have been installed in many countries and by international bodies to monitor the phenology of plants and several animals (Schwartz, 2003).

Global warming has led to the expansion of the study of phenology (Sparks and Menzel, 2002; Walther et al., 2002). Though most examples are drawn from terrestrial systems, marine biota deserve equal attention (Rodwell and Rodwell, 1999; Marshall et al., 2001), if for no other reason than the commercial importance of fish. The year-class size of marine fish is greatly influenced by the timing of spawning and the resulting match−mismatch with their prey and predators (Cushing, 1990). This was confirmed recently on the basis of satellite remote sensing and a long-term data set of haddock recruitment (Platt et al., 2003).

A common obstacle limiting marine phenological studies is the requirement of long time-series of high frequency (at least weekly) observations, of which there are few in the ocean because of the considerable effort required. One such zooplankton time-series, including ichthyoplankton, has been collected near the only offshore island in the North Sea, Helgoland (Figure 1). This paper explores the changes in phenology of the ichthyoplankton using the Helgoland data set.

Methods

Since April 1974, the marine station Biologische Anstalt in Helgoland has been collecting macrozooplankton samples three times a week at Helgoland Roads (positioned about 50 km off the coast between the two small islands of Helgoland at 54° 11′ 3″N 7° 54′ 0″E) (Greve *et al.*, 2004). Tidal currents, approaching from a depth of 50 m to the south

or 30 m to the north, mix the water in the shallow, 6 m deep passage between the islands where sampling is possible under almost any wind condition. Mean residual currents pass along the German Bight counterclockwise. The river plumes of the Weser and Elbe reach as far offshore as Helgoland, so samples taken can be representative of coastal, estuarine, or stratified central North Sea water.

Macrozooplankton sampling was carried out with a 500-μm mesh Hydrobios CalCOFI net, using oblique hauls filtering approximately 100 m^3 of water based upon flow-meter readings. Samples were collected every Monday, Wednesday, and Friday. They were preserved in 4% formaldehyde, stored, and processed later to determine the abundance of meso- and macrozooplankton (Greve, 2004). Since 1993, fish larvae have been sorted, identified and counted, and then combined into a single weekly sample. Prior to this, only the sum of the total ichthyoplankton was recorded. Following an initial analysis using the years
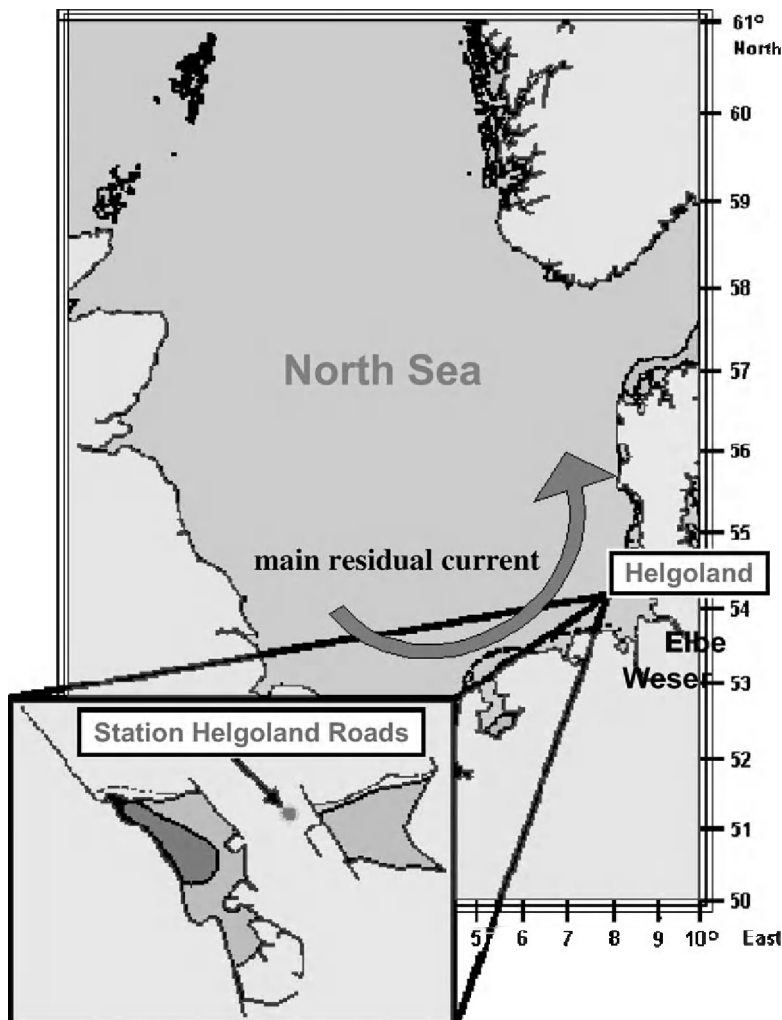

Figure 1. Sampling locations at Helgoland Roads in the North Sea.

1993–1995, it appeared that thermal control might affect the timing of ichthyoplankton occurrences. Therefore, stored samples from the extremely cold winter of 1996 and the extremely warm winter of 1990 (Figure 2) were investigated along with 1998 and 1999 samples. Inclusion of more years has been prevented by limited resources for taxonomic discrimination of the fish larvae within the routine zooplankton work, although the stored samples are available for later processing.

In all 44 species were identified over the 7 years (Table 1). From the weekly abundance measurements, a cumulative sum of values was calculated. The annual sum was set as 100%, and the week of the passage of the 15%, 50%, and 85% cumulative abundance levels for each year was determined (Figure 3). These levels were defined as the "start of season", "middle of season", and "end of season", respectively. These dates were then correlated with the mean annual sea surface temperature (SST) for weeks 1–10, calculated from measurements at the Biologische Anstalt in Helgoland.

Standard linear regressions and correlation coefficients were calculated using Microsoft Excel with a significance level of $p \leq 0.05$.

Results

Variability among the 44 species of ichthyoplankton was large. The number of samples in which there was at least one larva over the 7 years ranged from 191 (*Limanda limanda*) to 1 (e.g. *Trisopterus luscus*) (Table 1). Maximum abundance varied from 25.65 individuals m^{-3} (*Ammodytes*

marinus) to 0.005 individuals m^{-3} (*Trisopterus luscus*). Mean weekly abundance varied from 2.096 individuals m^{-3} (*Ammodytes marinus*) to 0.005 individuals m^{-3} (*Trisopterus luscus*).

The common sole, *Solea solea*, because of its large interannual variability (Figure 4), demonstrated why relative cumulative abundance thresholds were used instead of absolute abundance values to define the phenophases (see Figure 3). There are also extreme interannual differences in the seasonal timing for *Solea solea*, e.g. the "end of season" occurred in week 22 during the warm year of 1990, while there was a late "start of season" in week 27 during the cold year of 1996. Note that SST accounts for 76% of the variance in the timing of the "middle of season" for this species (Figure 5, Table 1).

The duration of occurrence also varies from species to species. The maximum number of weeks of the year during which a species was observed was 48 for Atlantic herring, *Clupea harengus*, representing an extended reproductive phase. This is believed to be due to the location of several spawning sites within or near Helgoland with different spawning times (Greve *et al.*, 2004). Another species with several annual spawning periods is *Ammodytes tobianus*. In such cases, the methodology for the determination of phenophases and phenological temperature correlations was assumed to be unreasonable and was not applied. However, in the case of species with more pronounced larval seasonal distribution, the calculation of the regression of the phenophases "start of season", "middle of season", and "end of season" with the winter SSTs was considered reasonable.

The statistical reliability of any regression relationship generally increases with the number of observations (i.e. years of data). Four years was chosen as the minimum
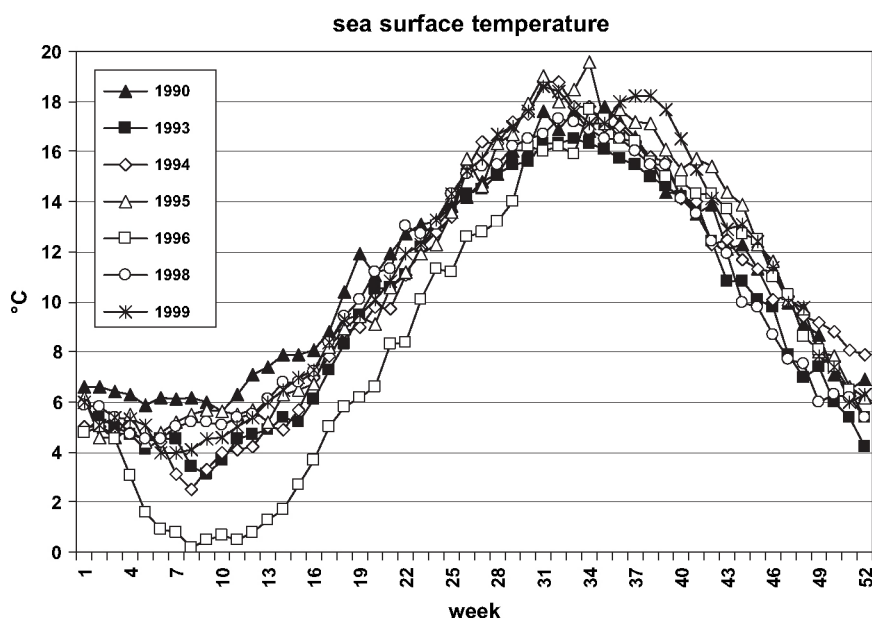

Figure 2. Sea surface temperatures (SSTs) at Helgoland in the years investigated.

Table 1. Species of fish larvae observed at Helgoland Roads: scientific names, common names, number of observations, maximum concentration observed, mean concentration observed, and variance accounted for by SST variability (r^2) for "start of season", "middle of season", and "end of season". Correlation coefficients are only given for those species with 4 or more years of data. Coefficients significant at the p = 0.05 level are shown in bold type.

Taxon	Common name	No. of samples with concentrations > 0	Maximum concentration	Mean concentration	No. of years	r^2 start of season	r^2 middle of season	r^2 end of season
Agonus cataphractus	Hooknose	152	2.911	0.199	7	0.185	**0.506**	0.421
Ammodytes marinus[*]	Lesser sandeel	173	25.649	2.096	7			
Ammodytes tobianus	Small sandeel	104	0.580	0.064	7	0.411	0.004	0.056
Arnoglossus laterna	Scaldfish	80	1.446	0.128	7	**0.849**	**0.935**	**0.750**
Belone belone	Garpike	2	0.045	0.025	2			
Buglossidium luteum	Solenette	88	1.190	0.121	7	0.419	0.368	**0.702**
Callionymus sp.	Dragonet	130	6.161	0.382	7	**0.884**	0.471	0.318
Ciliata mustela	Fivebeard rockling	1	0.197	0.197	1			
Clupea harengus[*]	Atlantic herring	79	0.272	0.028	7			
Ctenolabrus rupestris	Goldsinny-wrasse	26	0.112	0.028	6	0.517	**0.670**	**0.625**
Cyclopterus lumpus	Lumpsucker	6	0.016	0.013	3			
Echiichthys viper	Lesser weeverfish	5	0.015	0.013	3			
Engraulis encrasicolus	European anchovy	5	0.143	0.064	4	0.009	0.009	0.009
Entelurus aequoreus	Snake pipefish	2	0.025	0.020	1			
Eutrigla gurnardus	Grey gurnard	7	0.289	0.052	3			
Gadus morhua	Atlantic cod	64	0.817	0.053	7	0.034	**0.655**	**0.827**
Gaidropsarus sp.	Rockling	23	0.045	0.016	5	0.275	0.018	0.027
Gobiidae ge. sp.		171	1.209	0.125	7	0.400	0.248	0.384
Hippoglossoides platessoides	American plaice	1	0.011	0.011	1			
Hyperoplus lanceolatus	Great sandeel	54	0.602	0.079	6	**0.647**	0.432	**0.579**
Limanda limanda	Dab	191	3.087	0.198	7	0.452	0.398	**0.536**
Liparis sp.	Striped seasnail	66	0.136	0.020	7	**0.681**	**0.595**	0.311
Merlangius merlangus	Whiting	83	0.377	0.061	7	0.156	0.412	**0.579**
Microstomus kitt	Lemon sole	2	0.009	0.009	1			
Myoxocephalus scorpius	Shorthorn sculpin	83	0.365	0.048	7	0.103	0.282	0.000
Pholis gunnellus	Rock gunnel	65	0.148	0.029	7	**0.562**	**0.731**	0.053
Phrynorhombus norvegicus	Norwegian topknot	2	0.050	0.037	2			
Platichthys flesus	Flounder	47	0.592	0.053	7	0.473	0.486	0.432
Pleuronectes platessa	European plaice	25	0.072	0.018	6	**0.671**	**0.723**	0.370
Pollachius pollachius	Pollack	6	0.114	0.037	3			
Pollachius virens	Pollock	4	0.013	0.010	2			
Raniceps raninus	Tadpole fish	5	0.013	0.010	4	0.492	0.492	0.284
Sardina pilchardus	European pilchard	19	0.548	0.069	7	0.086	0.096	0.021
Scomber scombrus	Atlantic mackerel	40	0.977	0.067	6	0.271	0.332	0.440
Scophthalmus maximus	Turbot	13	0.086	0.027	4	0.609	0.240	0.632
Scophthalmus rhombus	Brill	8	0.067	0.031	2			
Solea solea	Common sole	64	0.425	0.080	7	**0.670**	**0.760**	**0.714**
Sprattus sprattus	European sprat	167	7.435	0.285	7	0.055	0.011	0.007
Taurulus bubalis	Longspined bullhead	54	0.228	0.042	7	**0.660**	**0.501**	0.483
Taurulus lilljeborgi	Norway bullhead	20	0.046	0.019	4	**0.971**	**0.941**	**0.902**
Trachurus trachurus	Atlantic horse mackerel	114	7.287	0.270	7	**0.650**	**0.863**	**0.668**
Trigla lucerna	Tub gurnard	10	0.021	0.014	3			
Trisopterus esmarki	Norway pout	2	0.030	0.026	1			
Trisopterus luscus	Pouting	1	0.005	0.005	1			

[*]Species with extended spawning durations that precluded reliable estimation of ontology.
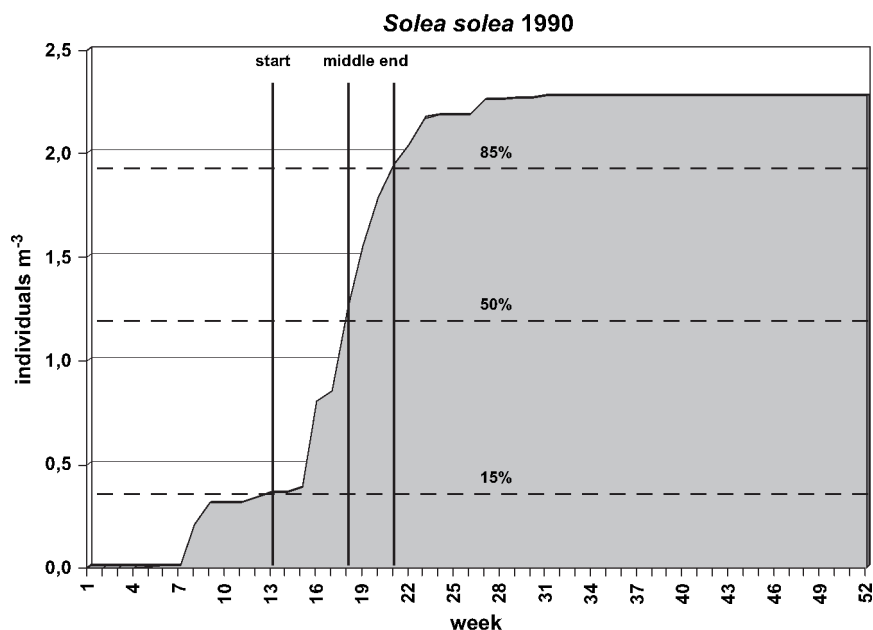
Solea solea 1990

Figure 3. Annual cumulative abundance showing the method of calculating the phenological timing (15%, 50%, and 85% thresholds) based upon data for *Solea solea* in 1990.

number of data points in this study before undertaking a regression analysis between temperature and ontology, resulting in a total of 29 species with between 4 and 7 years of data. Two of these species (*Clupea harengus*, *Ammodytes tobianus*) were deleted because of their extended spawning times, as discussed above. This left 27 species for which

regression analyses were calculated. In 11 of the 27 cases, the ''middle of season'' regressions against temperature were statistically significant. For both the ''start of season'' and ''end of season'', there were 10 significant cases (Table 1). Significance levels were based upon $n - 1$ degrees of freedom, where n varied from 4 to 7. The range of the
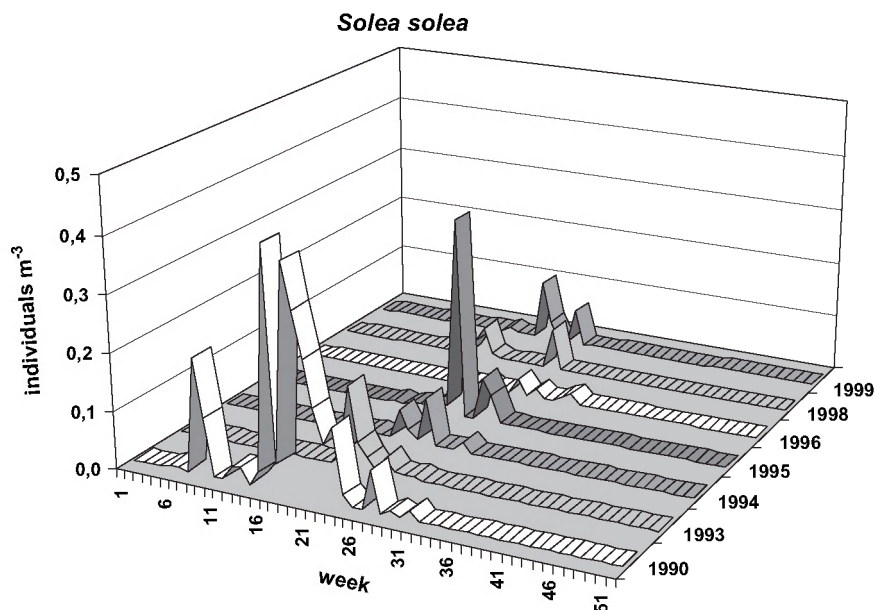
Solea solea

Figure 4. Population dynamics of the common sole, *Solea solea*, at Helgoland Roads in the years investigated.
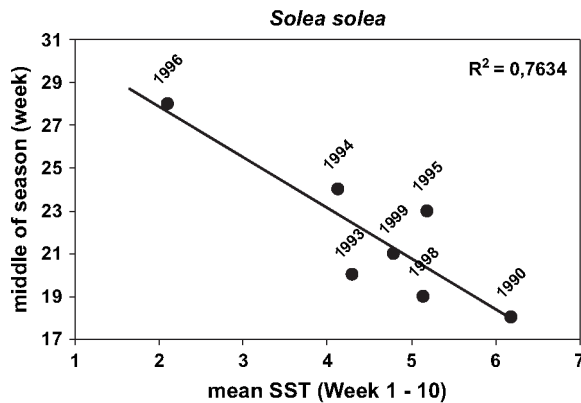
Figure 5. *Solea solea*, middle of season regression: SST to phenological timing (week).

Table 2. Range of seasonal distribution of the 24 most abundant species of fish larvae: weeks of observations and weeks of "middle of season" determination in the 7 years investigated.

Species	Range from start to end of season (weeks)	Range of middle of season (weeks)
Agonus cataphractus (Hooknose)	5−14	8−11
Ammodytes marinus (Lesser sand-eel)	4−14	6−10
Ammodytes tobianus (Small sandeel)	14−44	14−40
Arnoglossus laterna (Scaldfish)	24−33	26−33
Buglossidium luteum (Solenette)	22−35	23−32
Callionymus sp. (Dragonet)	19−28	23−28
Clupea harengus (Atlantic herring)	1−48	1−47
Ctenolabrus rupestris (Goldsinny-wrasse)	27−34	27−32
Gadus morhua (Atlantic cod)	3−19	7−17
Gobiidae ge. sp.	19−35	22−31
Hyperoplus lanceolatus (Great sandeel)	17−44	25−39
Limanda limanda (Dab)	10−26	14−23
Liparis sp. (Striped seasnail)	5−26	15−25
Merlangius merlangus (Whiting)	6−28	9−23
Micrenophrys lilljeborgi (Norway bullhead)	6−27	6−25
Myoxocephalus scorpius (Shorthorn sculpin)	4−16	7−11
Pholis gunnellus (Rock gunnel)	2−14	6−13
Platichthys flesus (Flounder)	10−21	11−19
Pleuronectes platessa (European plaice)	3−18	10−15
Scomber scombrus (Atlantic mackerel)	24−32	25−30
Solea solea (Common sole)	13−32	18−28
Sprattus sprattus (European sprat)	16−39	21−26
Taurulus bubalis (Longspined bullhead)	8−26	9−25
Trachurus trachurus (Atlantic horse mackerel)	24−32	25−30

variance in the seasonal distribution of the 24 most abundant species is given in Table 2.

The slope of the regression line varied depending upon the seasonal state (Figure 6) and from species to species (Figure 7). In some populations, as in the pelagic species *Scomber scombrus* and *Sprattus sprattus*, no influence of winter temperatures on the phenology was found, but in other pelagic species, e.g., *Trachurus trachurus*, there was a strong correlation (Table 1). The more demersal populations of *Arnoglossus laterna*, *Ctenolabrus rupestris*, *Gadus morhua*, *Hyperoplus lanceolatus*, *Taurulus lilljeborgi*, *Platichthys flesus*, *Pleuronectes platessa*, *Solea solea*, and *Taurulus bubalis* display a generally strong negative correlation with winter SSTs.

The total number of correlations undertaken between temperature and either the start, middle, or end of the season for the 27 species was 81. In 76 of these cases, the sign of the correlation was negative, providing further evidence of the significance of temperature.

Discussion

This study found that the timing of the occurrence of fish larvae is influenced by the SSTs the preceding winter, as had been determined for other zooplankton (Greve *et al.*, 2001) and anticipated by Lange and Greve (1997). The phenophases, i.e. "start of season", "middle of season", and "end of season" defined by the 15%, 50%, and 85% cumulated abundance by numbers, respectively, are generally negatively correlated with the mean SST in weeks 1−10 in the North Sea. An extension of the spawning season indicated by a positive correlation with the "end of season", as observed in terrestrial systems (Parmesan and Johe, 2003), was not seen. Such an extension might occur in the case of marine organisms with short generation times, i.e. the possibility of two or more a year. We expect that the mechanism linking temperature to the timing of fish

larval abundance is through faster gonadal development with increasing temperatures. If true, the monitoring of the gonadal state of the fish in fish markets could provide another and possibly more precise phenophase observation.

Sagarin (2001) warned against possible false conclusions concerning the advance of spring being attributed to climate. He calculated a precession of the vernal equinox of 0.78 days in 100 years on the basis of the conventions of our calendar. This trend towards earlier springs should be subtracted from observed phenological trends, but it is small relative to our observed changes and therefore was neglected.

The annual cumulative abundance-related determination of phenophases as used within the present study is suitable for populations with seasonal spawning but not for species
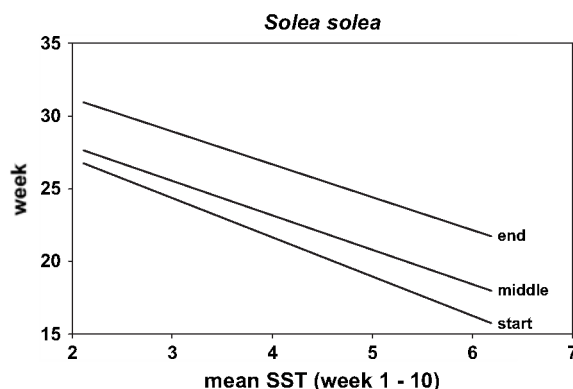
Solea solea

Figure 6. *Solea solea*, regression lines for "start of season", "middle of season", and "end of season" (for coefficients of determination see Table 1).

with extended spawning periods or with several spawning sites near the sampling area that might have different spawning times.

Besides temperature, ichthyoplankton abundance is influenced by parental abundance and their nutrition, as well as by the mortality of the eggs and larvae themselves, but none of these factors were considered in this study. In spite of this, our results indicate that predictions of the timing of the abundance of fish larvae can be made on the basis of SSTs for a period of up to half a year ahead and with

Fishlarvae Helgoland Roads

Figure 7. Regression lines for North Sea fish larvae exemplifying temporal and slope variance for a selection of 10 out of 24 species (see Table 2).

an accuracy of a single week for the "middle of season" in some species. As predictions on the seasonality of other zooplankton that are potential prey or predators of ichthyoplankton have reached a similar level of accuracy (Greve et al., 2001), match–mismatch projections and hence year-class recruitment prognoses may become possible.

Interestingly, the phenology of phytoplankton at Helgoland Roads does not follow the negative correlation with temperature described for fish larvae. The spring bloom has been delayed in spite of a warming by 1.1 °C in the period from 1962 to 2004 (Wiltshire and Manly, 2004). The increased winter abundance of copepods and phytoplankton grazing, consistent with the phenological trend observed in zooplankton, was presented as possibly influencing the delay in the phytoplankton bloom.

Improved knowledge of the sensitive early life history periods of fish and the species-specific annual development could be used as protective measures for fish populations through possible short-term reduction of the effort of commercial fisheries during spawning.

Improved predictions by prognostic models are a major objective of research. In the case of the seasonality of fish larvae, our results narrow the band of possible appearance of many species in the southern North Sea by a substantial degree. Instead of a time frame of months as displayed by FishBase (Froese and Pauly, 2003), it is possible to focus almost on a single week as the period of most probable start of season, middle of season, and end of season. Of course, these results are based on only 7 years of data, and the investigations must extend over longer periods, more locations, and further populations to ensure reliable predictive models of the responses to climate change. Also, the methodology could be improved by including an optimization procedure for detecting the phenophases. Figure 3 shows the possible uncertainties of the temporal determinations, e.g. of the start of season, which could be shifted easily by 7 weeks by minor abundance changes. Such uncertainties become less important when based on longer sampling periods.

It is anticipated that global warming will change the latitudinal, altitudinal, and temporal distribution of marine populations just as it does with terrestrial populations. To better define the phenological functional relationships of marine species, two avenues are promising. First is the determination of the physiological thermal preference zone of each species (Uhlig and Sahling, 1995) representing this functional relationship within its ecological niche (Elton, 1927). This can be determined by laboratory experiments or, it is to be hoped in the future, by genetic analysis as a molecular trigger of functional biodiversity. Second is the traditional way as practised successfully in terrestrial ecology with the development of an observation system for all major regions. Weekly phenological observations for a decade would provide the basis for marine biometeorology. As volunteer observers carry the load for terrestrial observations, we expect to find sufficient potential volunteers dwelling near the seacoast to support biometeorological
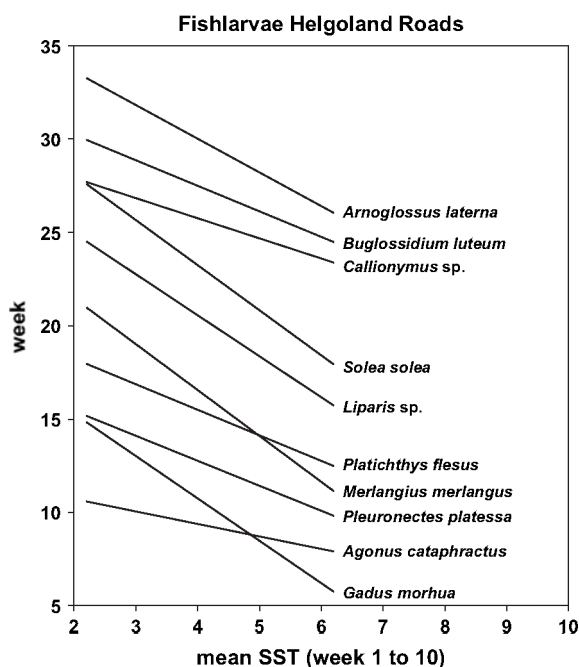
marine research and phenological studies, in particular by helping to observe changes in sea life that accompany globally changing temperatures.

The aim of the international GLOBEC programme is to advance our understanding of the structure and functioning of the global ocean ecosystem, its major subsystems, and its response to physical forcing so that a capability to forecast the responses of the marine ecosystem to global change can be developed. Biometeorology, with its disciplines phenology, thermal biology, and marine biogeography, treats such responses to global change. Generally, the field has been neglected in marine ecosystem studies until now, but offers an excellent way of monitoring the effects of climate change and as such needs to be encouraged.

Acknowledgements

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