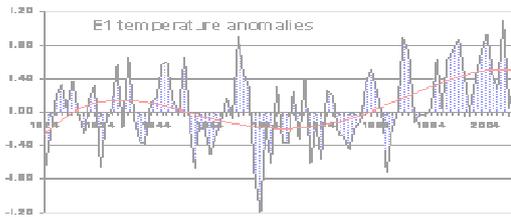
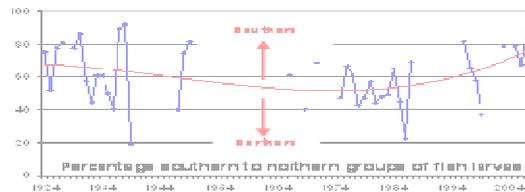
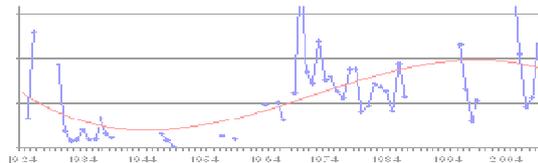
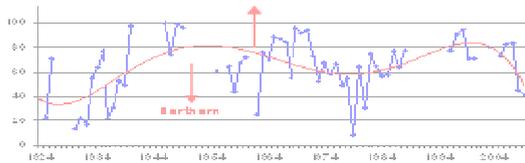


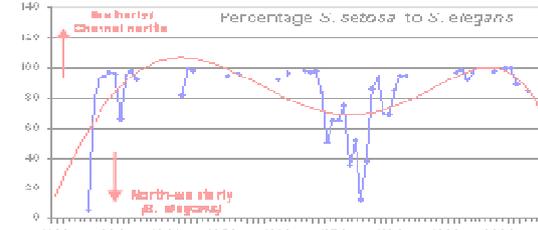
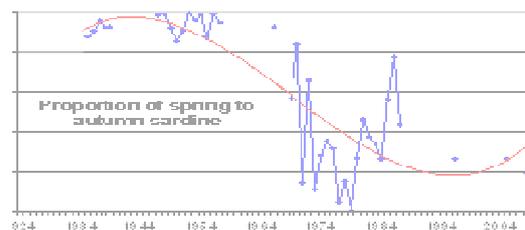
# The Russell Cycle



## An update and review of trends in zooplankton and fish larvae off Plymouth 1924-2009



### Steve Coombs and Nick Halliday



### Marine Biological Association Occasional Publication No 24

## Foreword

Regular plankton sampling off Plymouth by the Marine Biological Association (MBA) has been carried out from the early 1900s. A number of publications have described the results and investigated the environmental relationships, most recently by Southward *et al.* (2005), which includes a summary to 2001 and a comprehensive reference list.

Much of the sample analysis and description of the results was carried out by Sir Frederick Russell and Professor Alan Southward (AJS), the latter having completed the organisation and transfer of the paper records to digital files.

The current authors have transferred the main data files of AJS on zooplankton and fish larvae to the MBA long-term database (including various editing and checking against original analysis records and published data) together with adding the data for 2002-2009. The data are available to external researchers on request ([info@mba.ac.uk](mailto:info@mba.ac.uk)).

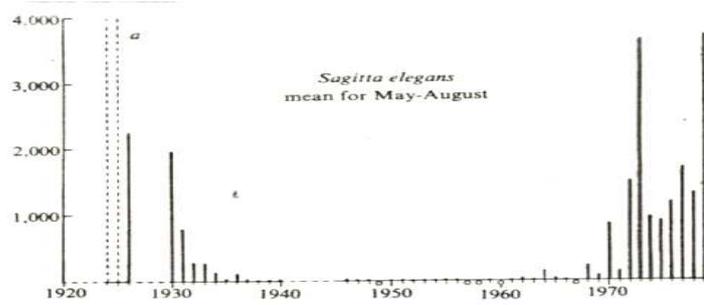
In this report the updated time-series are reviewed in the context of earlier work, particularly with respect to the Russell Cycle. It is not intended as an exhaustive analysis.

Brief details of the sampling and comments on data processing are given in an Appendix.

## Historical Perspective

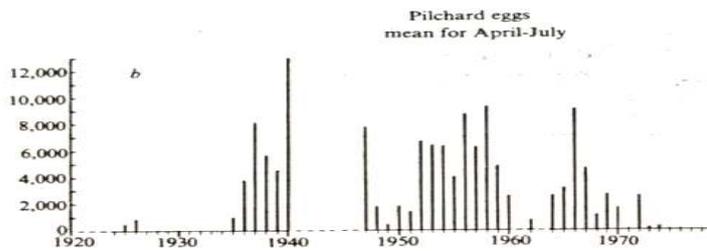
The term “Russell Cycle” was first applied by Cushing and Dickson (1976) to describe a series of changes in the plankton off Plymouth and other associated biological events from the 1930s to the 1970s. In subsequent years the term has been used rather loosely to describe the continuing changes, with non-linear relationships/rectification etc. being used to account for various inconsistencies. However, it was recognized that it was not a simple cycle (Southward *et al.*, 2005) and that the explained interactions, such as temperature control, were rather weak (Southward, 1963 and 1984). Nevertheless, the Russell Cycle is still frequently quoted, with implications both that it is a continuing cycle and that the underlying mechanisms are well understood.

Much of the original basis for the Russell cycle was summarised in Southward (1980) where a marked alternation was shown from the pre-1930s situation of high abundance of *Sagitta elegans*, low sardine (*Sardina pilchardus*; also known as pilchard) eggs and high abundance of fish larvae (Fig. 1) to a reverse situation in the 1940-1970s. This was then followed by a return to the original situation post the 1970s (essentially to 1979, this being the end of the time series at that time). Russell (1973) and Russell *et al.* (1971) showed these changes were consistent through all groups of fish larvae and were graphically characterised by alternations of high and low plankton volume in net tows (Fig. 1).

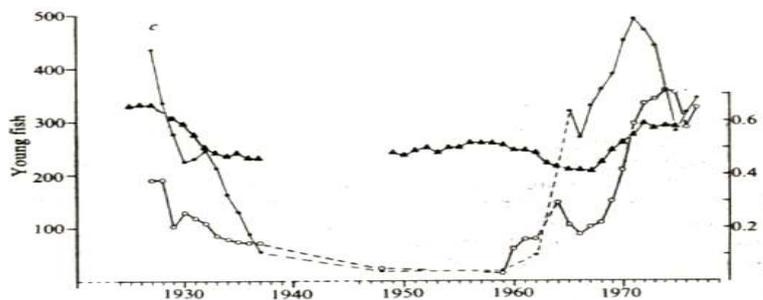


**Fig. 1. Historical presentations of Russell Cycle data**

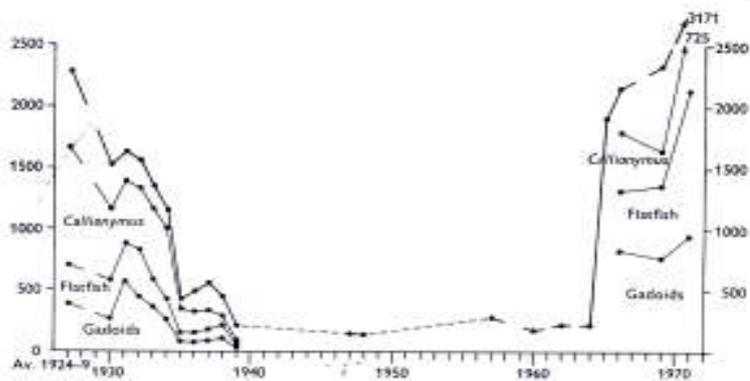
*Sagitta elegans*  
1920-1979  
(Southward, 1980)



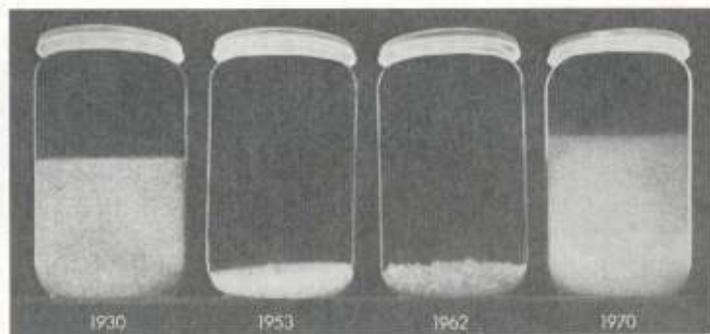
Pilchard (sardine)  
eggs 1920-1979  
(Southward, 1980)



Fish larvae and  
winter phosphate  
1920-1979  
(Southward, 1980)



Fish post-larvae  
1924-1971  
(Russell, 1973)



Plankton biovolume  
1930-1970  
(Russell *et al.*, 1971)

## Results 1924-2009

### *Fish larvae*

For total fish larvae the period of low abundance from the mid/late-1930s to the mid-1960s is clear (Fig. 2a). Thereafter the increase continued to at least the mid-1980s with highly variable levels post the mid-1990s. The changes in abundance were fairly consistent through all groups of fish larvae (Fig. 2b).

Clupeid larvae (sprat in the spring, sardine in summer and autumn) comprise 51% of total fish larvae. Sardine spawning increased from the mid-1930s, resulting in a marked increase in the proportion of clupeids of total fish larvae (Fig. 3); there was a slight decline around the late-1960s, thereafter remaining at intermediate levels.

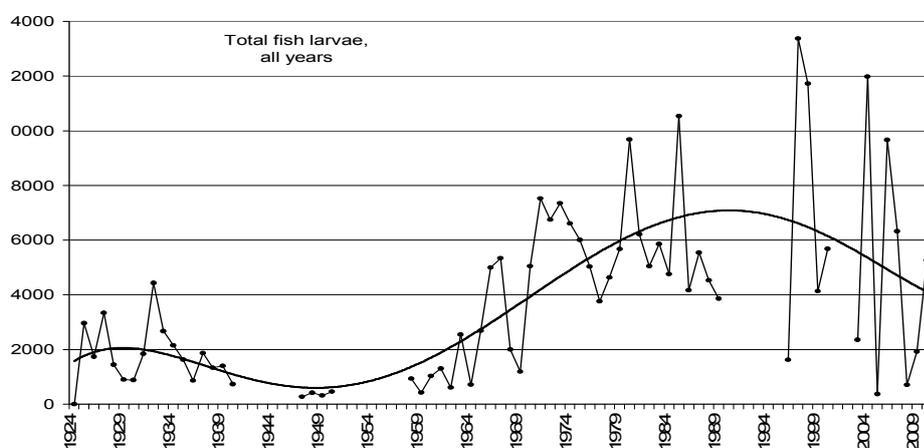


Fig. 2a.  
Total fish larvae,  
1924-2009.

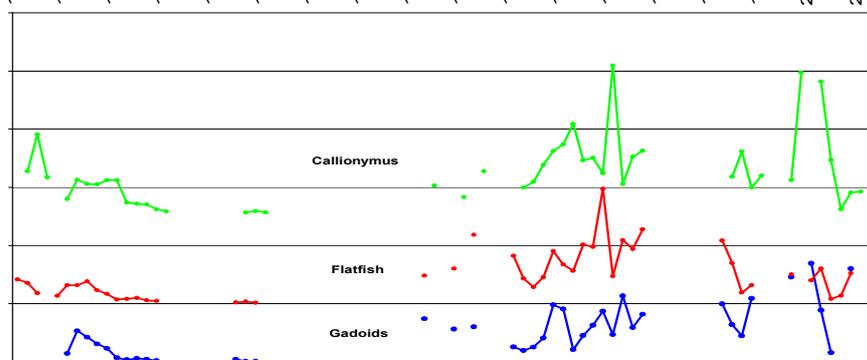


Fig. 2b.  
Examples of various  
fish groups  
(excluding poorly  
sampled years),  
1924-2009.

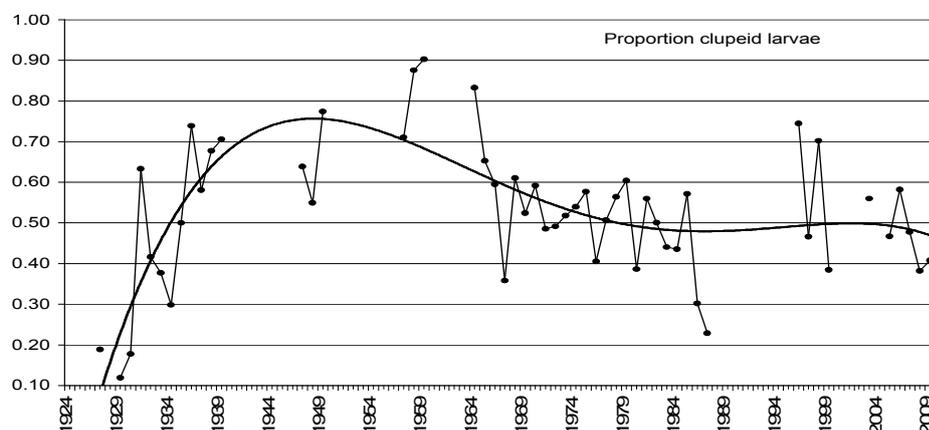


Fig. 3.  
Clupeid larvae as a  
proportion of total  
fish larvae,  
1924-2009.

Fish larvae grouped into characteristically northern and southern species (Table 1) both showed similar long-term trends in abundance as for total fish larvae.

Plotted as the percentage of southern to northern fish larvae (Fig. 4), the results show rather variable numbers before the 1970s, then possibly a slightly more northerly influence in the 1970s and 1980s, followed by a consistently high southerly character from 2003.

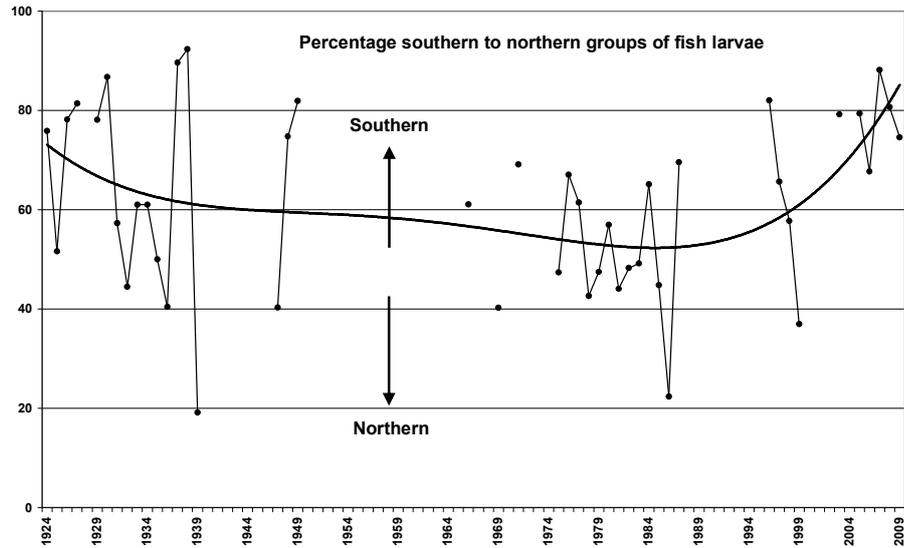


Fig. 4 Percentage of southern to northern groups of fish larvae (excluding poorly sampled years), 1924-2009.

Table 1. Species included in geographical groups of fish larvae.

Southern species	Northern species
<i>Capros aper</i>	<i>Trisopterus esmarkii</i>
<i>Trachurus trachurus</i>	<i>Phrynorhombus norvegicus</i>
<i>Labrus bergylta</i>	<i>Gadus morhua</i>
<i>Labrus mixtus</i>	<i>Clupea harengus</i>
<i>Arnoglossus spp.</i>	<i>Liparis montagui</i>
<i>Microchirus variegatus</i>	<i>Lebetes scorpiodes</i>
<i>Crenilabrus melops</i>	<i>Chirolophis ascanii</i>
<i>Cepola rubescens</i>	
<i>Dicentrarchus labrax</i>	
<i>Pegusa lascaris</i>	
<i>Trachinus vipera</i>	
<i>Blennius gattorugine</i>	

## *Fish eggs*

The trend in abundance of total fish eggs is similar to that for sardine eggs (Fig. 5), which represent around 50% of all fish eggs. There was a period of high abundance of sardine eggs from the mid-1930s to around the mid-1960s and thereafter a significant decline around the 1970s and 1980s. There was a possible increase post the mid-1990s but with rather variable levels.

Sardine has two spawning periods, one in spring/summer and a later autumn peak. Spring/summer spawning dominated until the mid-1970s after which autumn spawning has been generally higher (Fig. 6).

Abundance of other fish eggs, i.e. excluding sardine eggs, showed a somewhat increasing trend in abundance over the entire period 1924-2009 with a few notable years of high abundance in the mid to late 1960s (Fig. 7).

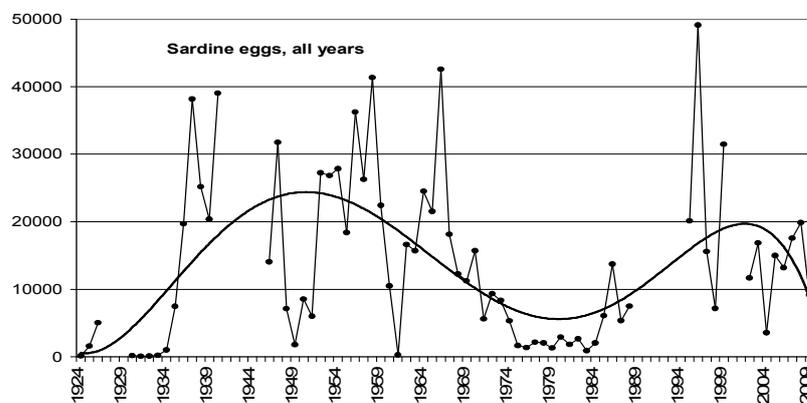


Fig. 5. Abundance of sardine eggs for combined spring/summer and autumn spawning, 1924-2009.

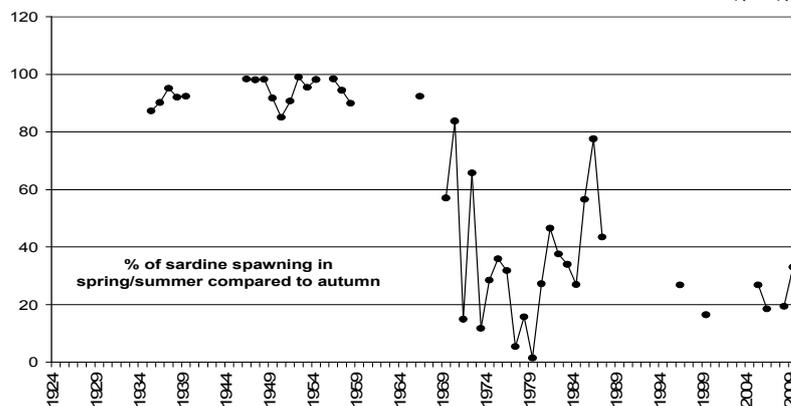


Fig. 6. Relative proportions of spring/summer and autumn abundance for sardine eggs, 1924-2009.

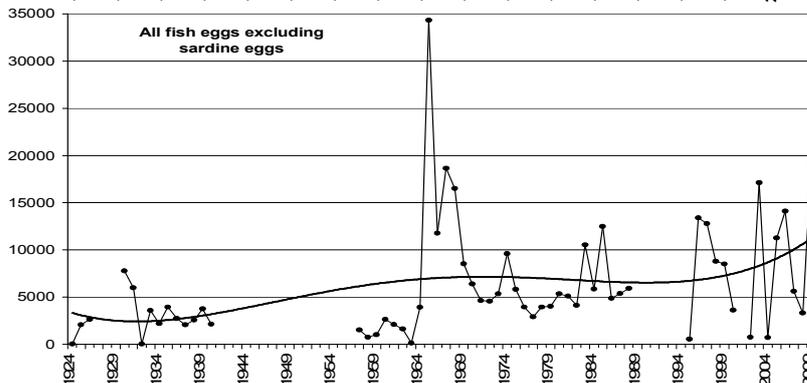


Fig. 7. Abundance of fish eggs excluding sardine eggs, 1924-2009.

## Zooplankton

Zooplankton abundance was converted from numerical counts of the different species/groups to settled volume using individual volume conversion factors for each group and observed settled volume to count ratios.

The results were comparable with the historical photos of plankton settled volume showing the high-low-high alternation of plankton biomass from the 1920s (although rather limited data in that period) to the 1970s (Fig. 8; c.f. Fig. 1). Thereafter, biomass generally remained fairly high with some indication of a dip from the mid-1970s to the end-1990s. The changes were fairly consistent across the main zooplankton groups (Fig. 9).

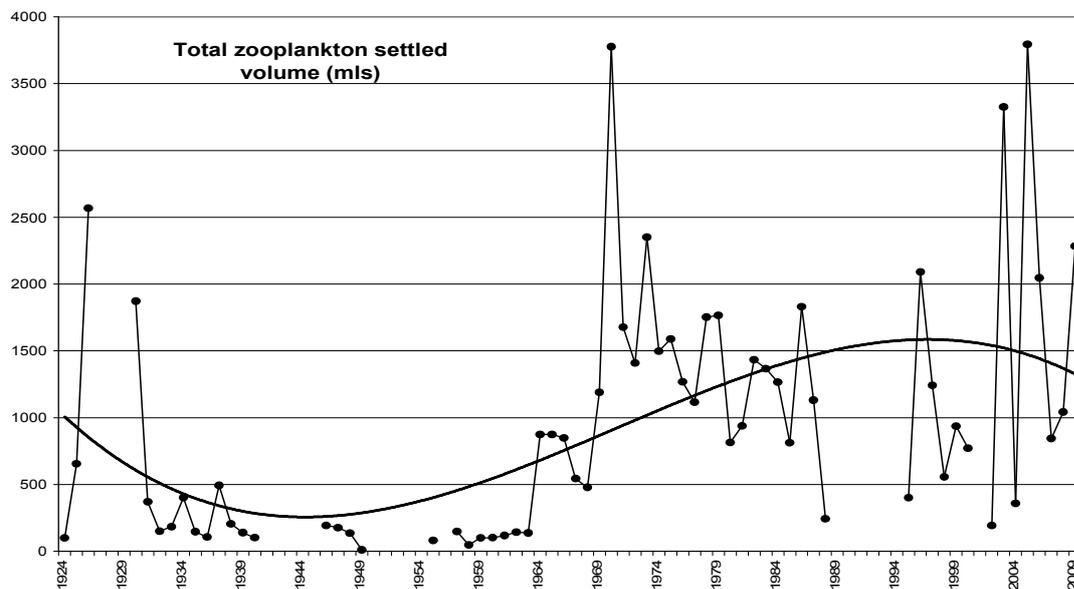


Fig. 8. Total zooplankton settled volume, 1924-2009.

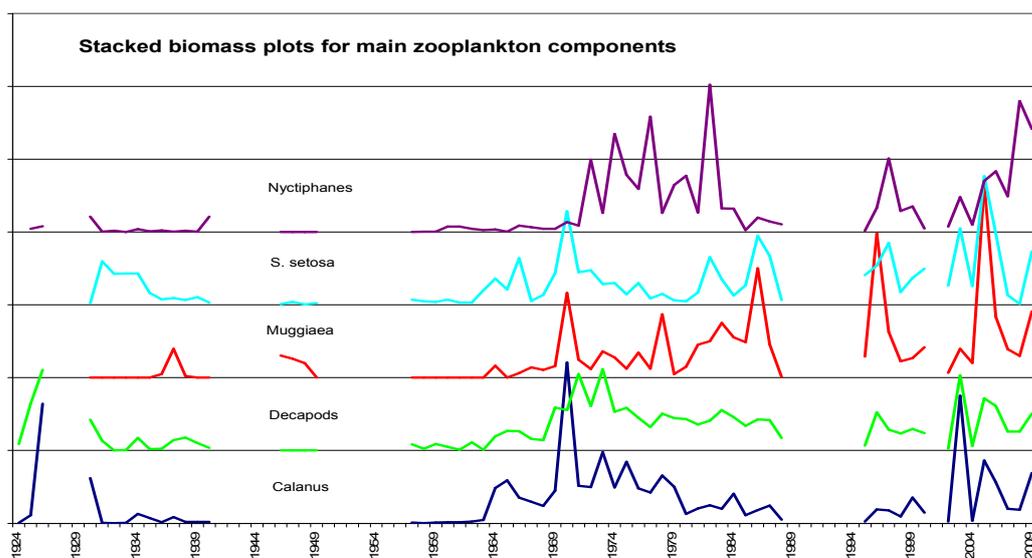


Fig. 9. Settled volume of main zooplankton components (representing 87% of total zooplankton volume), 1924-2009.

Since there has been little long-term variation in plankton composition, the changes in biomass mirrored the changes in abundance by numerical count e.g. *Calanus* (Fig. 10; probably entirely *C. helgolandicus*), which represents 30% of plankton biomass.

During the period of low zooplankton biomass from the mid-1930s until the late-1960s, sardine eggs were one of the few groups in a phase of abundance (Fig. 5) and hence comprised a significant proportion of plankton biomass at that time (Fig. 11).

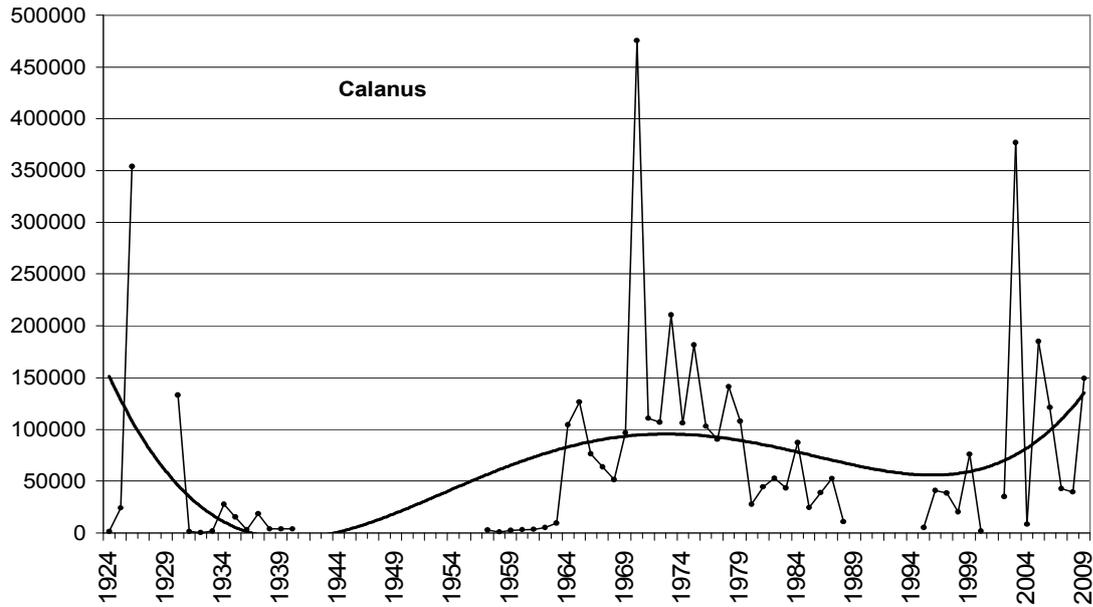


Fig. 10. Abundance of *Calanus*, 1924-2009.

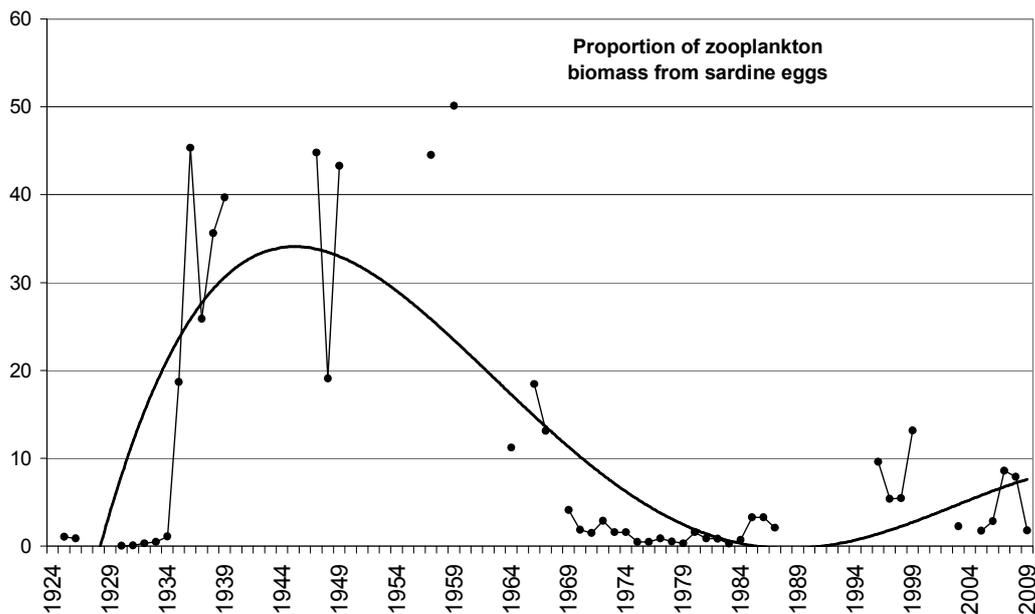


Fig. 11. Sardine eggs as a proportion of total zooplankton biomass (excluding poorly sampled years), 1924-2009.

### Indicator groups and species

Zooplankton grouped into north-westerly or broadly westerly/south-westerly groups (Southward *et al.*, 2005; Table 2) both showed similar changes in abundance as for overall plankton abundance, i.e. high-low-high 1930s to 1970s, then an increasing trend post 2000, Fig. 12, c.f. Fig. 8.

The ratio of south-westerly to north-westerly plankton (Fig. 13, with equal weighting for each species) showed an increasing southerly influence through the 1930s to the late 1940s, then rather variable indices, perhaps with the mid-1960s to mid-1970s being more south-westerly in character and the late 1970s and early 1980s being more north-westerly.

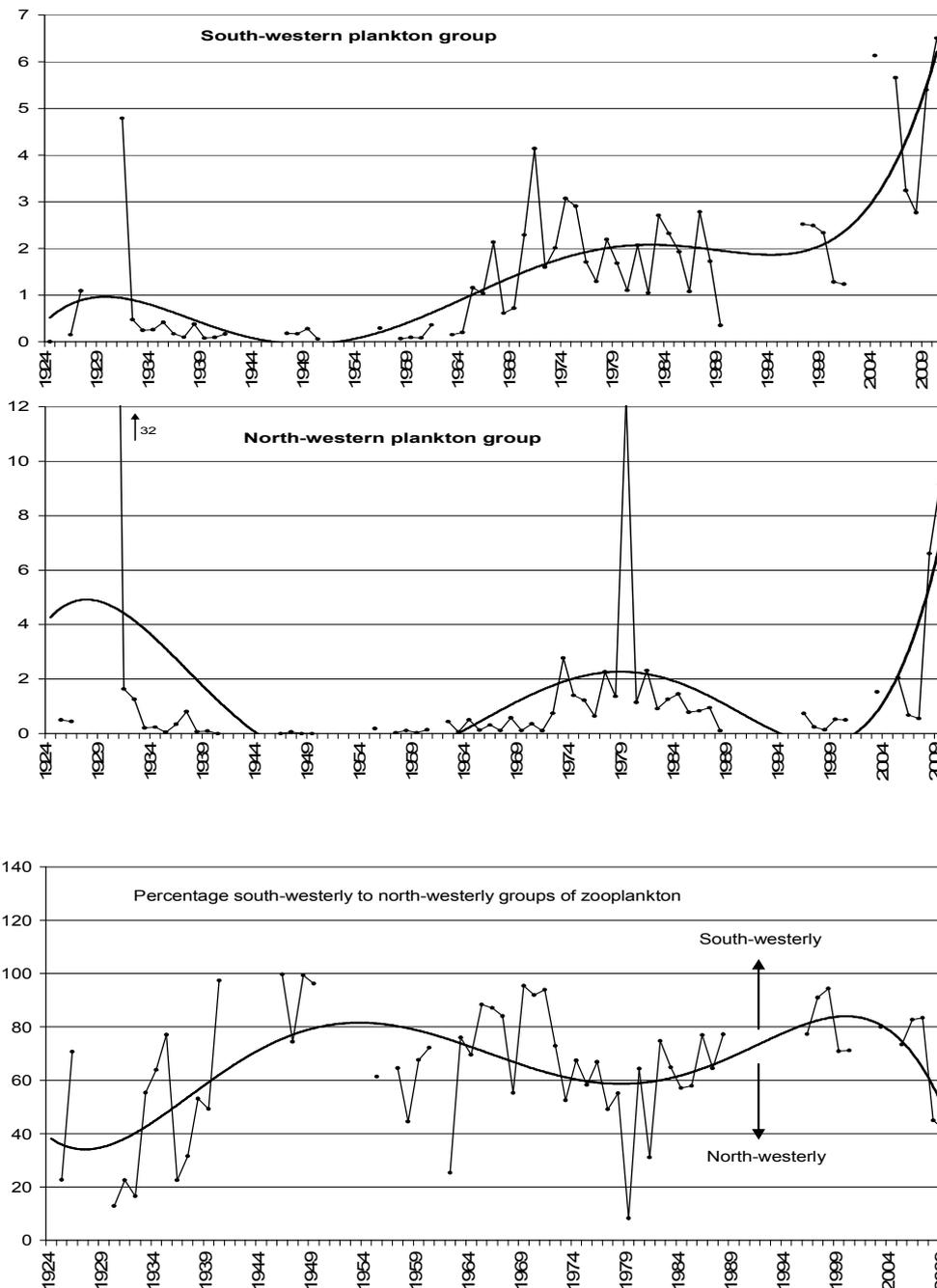


Fig. 12. Abundance of south-westerly and north-westerly plankton groups (excluding poorly sampled years), 1924-2009.

Fig. 13. Percentage south-westerly to north-westerly plankton (excluding poorly sampled years), 1924-2009.

Changes in abundance of *S. elegans* (north-westerly indicator, present in spring/summer) and the more abundant *S. setosa* (temperate/Channel species, present in autumn/winter) both showed the characteristic high-low-high cycle from the 1920s to the 1970s, after which *S. setosa* continued in relatively high abundance, whereas *S. elegans* tended to return to lower levels. The relative changes in species dominance (Fig. 14) shows the north-westerly (*S. elegans*) dominance in the mid-1970s to mid-1980s (and possibly before about the mid-1930s, but rather sparse data here).

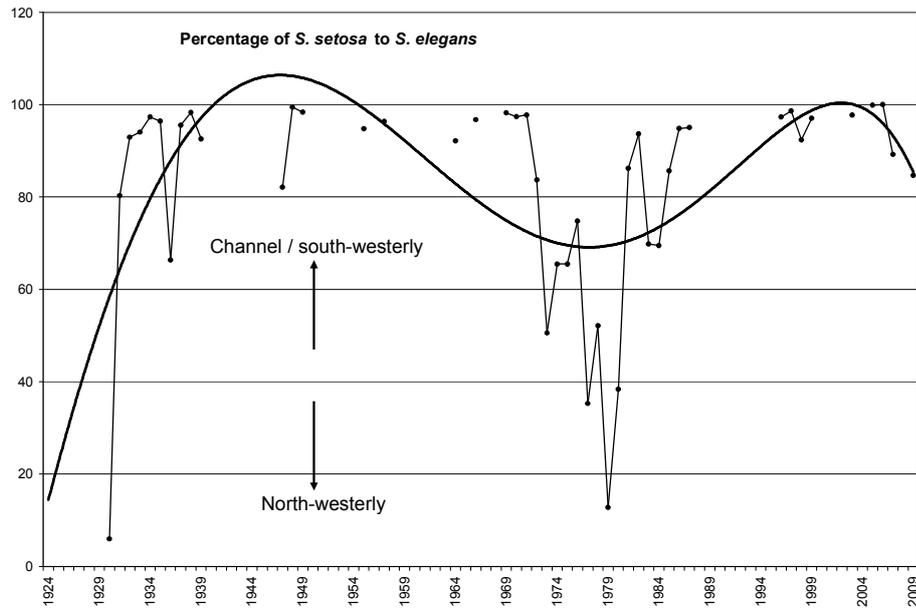


Fig. 14. Percentage of *S. setosa* to *S. elegans* (excluding poorly sampled years), 1924-2009.

Table 2. Species included in geographical groups of zooplankton.

Westerly / South-westerly species	North-westerly species
<i>Liriope tetrphylla</i>	<i>Aglantha digitalis</i>
<i>Muggiaea atlantica</i>	<i>Nanomia spp.</i>
<i>Sagitta setosa</i>	<i>Tomopteris helgolandica</i>
<i>Calanus spp. (helgolandicus)</i>	<i>Sagitta elegans</i>
<i>Candacia armata</i>	<i>Ethemisto gracilipes</i>
<i>Eucalanus crassus</i>	<i>Limacina retroversa</i>
<i>Euchaeta hebes</i>	
<i>Centropages typicus</i>	
<i>Nyctiphanes couchii</i>	

## Timing

The seasonal timing of occurrence was measured as the centre of gravity of monthly weighted abundance for each year.

The trend for clupeid larvae (sprat and sardine, representing 51% of all larvae), showed an alternating sequence of relatively earlier occurrence in the 1930s and 1990s and later occurrence in the 1920s (possibly), throughout much of the 1950s-1980 and after 2005 (Fig. 15). The main difference in this pattern for the other (non-clupeid) larvae was an underlying continuous trend towards earlier occurrence.

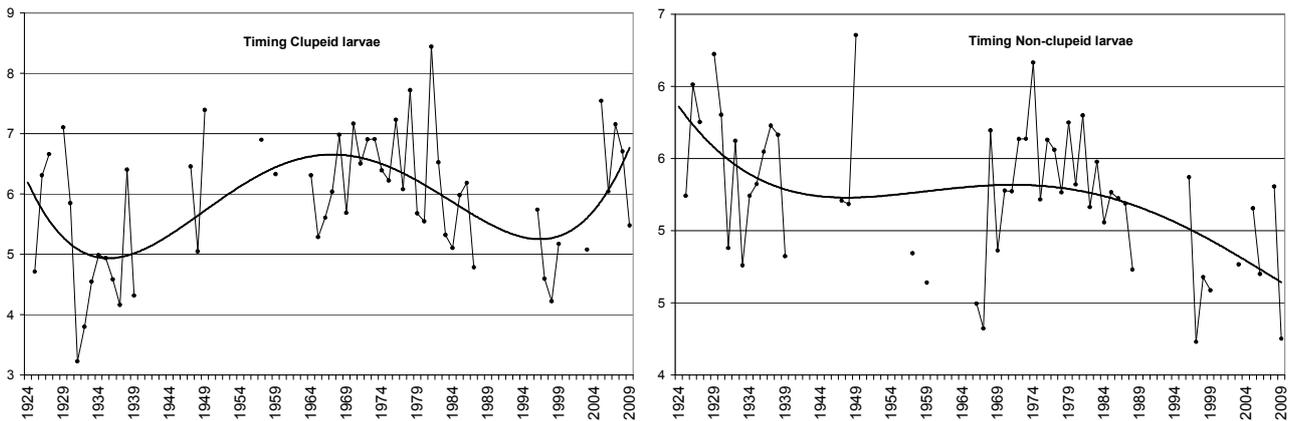


Fig. 15. Annual weighted timing of clupeid larvae and other fish larvae (excluding poorly sampled years), 1924-2009.

Sardine eggs showed a move to later spawning (see above, Fig. 6) from around 1970. For the other (non-sardine) eggs there was a similar, but less marked, pattern (Fig. 16) with a later occurrence post-1970 compared with the 1930s (although lack of data 1940-1960s).

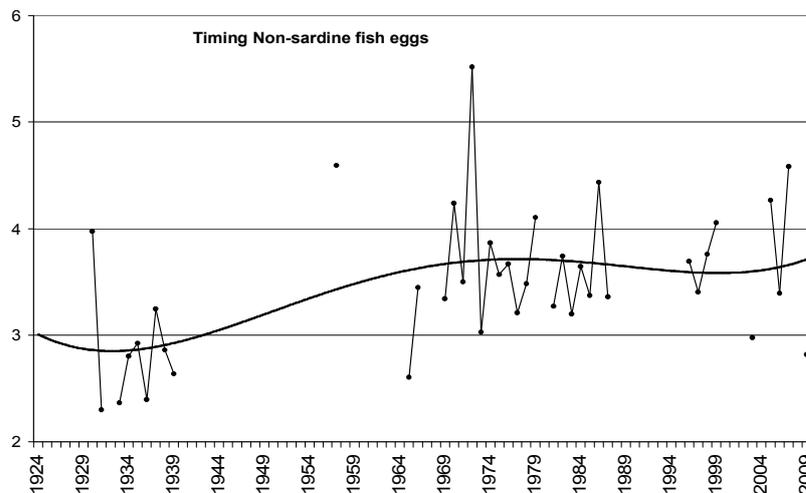


Fig. 16. Annual weighted timing for other (non-sardine) eggs (excluding poorly sampled years), 1924-2009.

For the heterogeneous group of total zooplankton, there were no clear trends in timing (Fig. 17), although a higher variability in timing was apparent, particularly in the 1920s and 1930s, outside the more stable 1960s to 1980s.

Considering *Calanus* alone (Fig. 18), there is evidence of a period of earlier occurrence around the mid-1980s to mid-2000s.

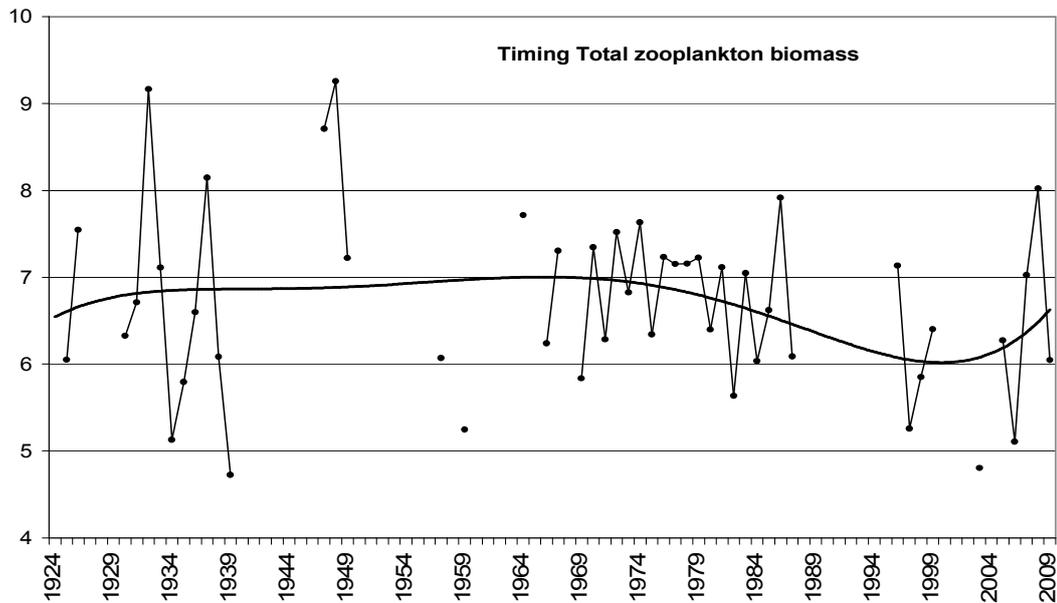


Fig. 17. Annual weighted timing of total zooplankton biomass (excluding poorly sampled years), 1924-2009.

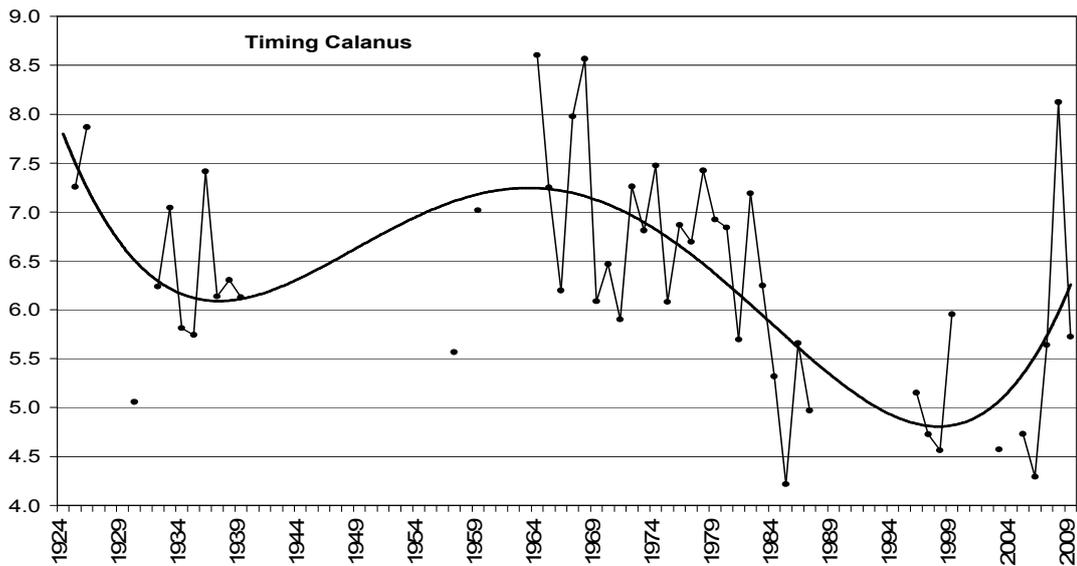


Fig. 18. Annual weighted timing of *Calanus* (excluding poorly sampled years), 1924-2009.

## Physical data

The trend in temperature anomalies at station E1 (Figs. 19a and b) show generally positive anomalies from the mid-1920s to about 1950, followed by more generally negative values to the mid-1980s and a marked positive trend from then onwards.

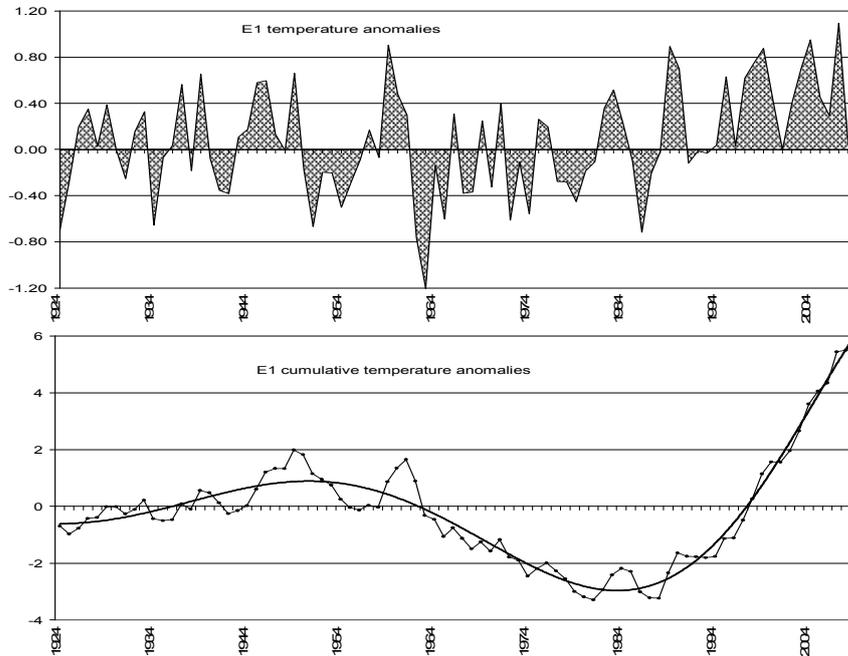


Fig 19 (a)  
E1 temperature anomalies  
°C

Fig 19 (b)  
E1 cumulative  
temperature anomalies  
°C

As an index of meteorological and oceanographic forcing, winter North Atlantic Oscillation (NAO) values were relatively positive from the mid-1920s to about the early 1950s, then rather variable until about the early-1980s, after which values were mostly positive (Fig. 20).

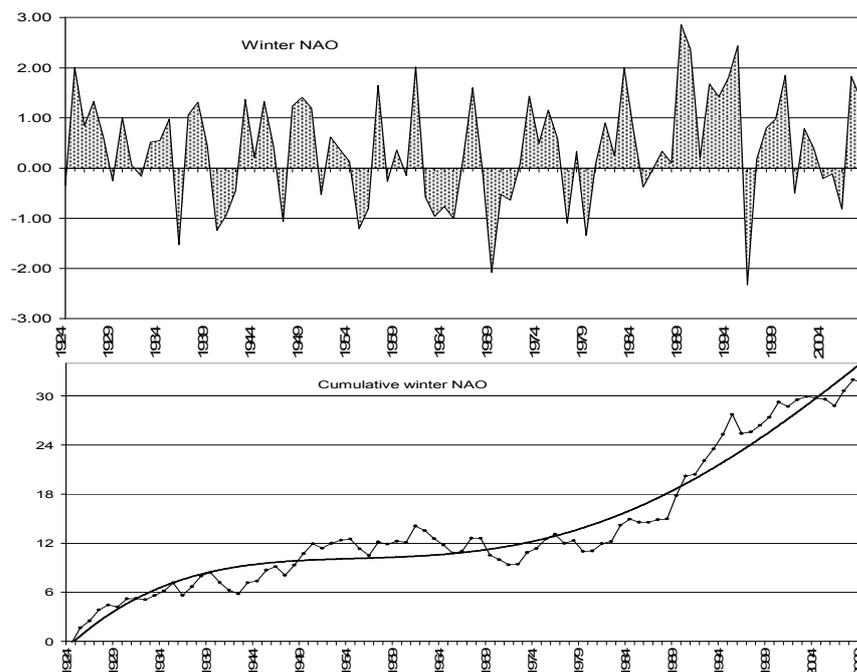


Fig 20 (a)  
Winter NAO index

Fig 20 (b)  
NAO cumulative plot

A similar pattern as for E1 temperature was observed in the Atlantic Multidecadal Oscillation (AMO) index, but with a smoother progression (Fig. 21). This showed an alternation from a positive phase from the late-1920s to the mid 1960s, then a negative phase until the mid-1990s, after which positive values resumed.

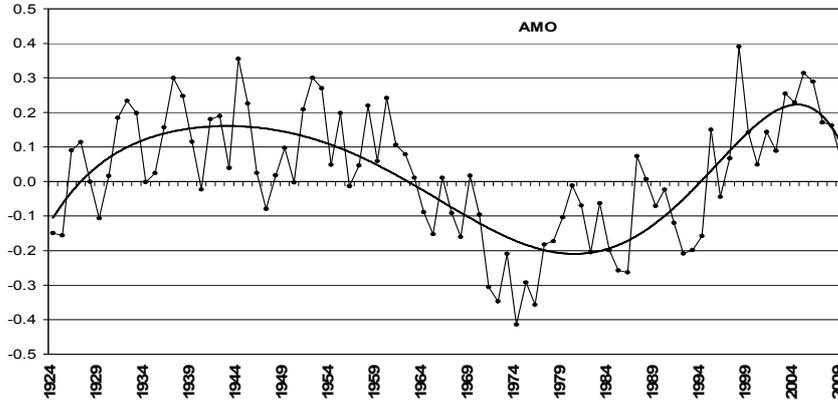


Fig 21  
Annual mean  
AMO index

## Correlations and interrelationships

Disregarding relationships due to coincidence of data in different datasets (such as the between total fish larvae and the southern group of larvae, or plankton volume and *Calanus*), the main conclusions from both the year-to-year correlations (Table 3) and the more general trends were:

- There were no significant correlations of plankton with E1 temperature (Table 3). In particular, there was no relationship with north-westerly/south-westerly plankton or north/south fish larval groups, thus not supporting any simple temperature/plankton interaction.
- Similarly, considering the trends in north/south fish larvae and E1 temperature (Figs. 4 and 19), the only slight positive indication was between the higher proportion of more southern fish larvae post-2003 and continuing rising temperatures for the same period. For the trends in north-westerly/south-westerly plankton and E1 temperature (Figs. 13 and 19), there was a positive relationship only for the period of slight warming in the 1930s-1940s.
- For individual plankton groups, the ratio between *S. elegans* and *S. setosa* (representing more northerly conditions; Fig. 14) was positively related in trend with the cooler mid-1970s to the mid-1980s (Fig. 19).
- For the AMO index (essentially, N. Atlantic temperature) there was a significant inverse relationship with the northern group of fish larvae (Table 3). In terms of trend, the AMO was similar to all-year sardine egg abundance (positive, Fig. 22) and to plankton biomass and total fish larvae (negative, Fig. 23).
- Winter NAO was positively related to E1 temperature (Table 3), as previously documented (increased westerly winds being associated with positive NAO). This might also be expected to result in a positive relationship between NAO and southern fish species and south-westerly plankton, but this was not the case. However, the NAO was negatively related with total fish larvae, implying better survival of fish larvae with less westerly weather influence.
- Total fish larvae, plankton volume and the south-westerly zooplankton group were all positively interrelated (Table 3; Fig. 23). The mean length of fish larvae taken in the YFT is around 12 mm, which represents an age several weeks post-spawning and hence much of the density independent mortality has already occurred (supported by lack of relationship with fish eggs, see below). Since mortality of fish larvae is generally linked to food availability, with higher food abundance promoting faster growth and lower mortality, the relationship between plankton volume and numbers of fish larvae supports this view; in particular, that a preponderance of south-westerly plankton is more favourable for higher plankton biomass and hence larval survival. (A qualification of this conclusion is that the plankton catch of the fairly coarse mesh YFT is a rather poor measure of food availability and includes a significant contribution from potential predators such as *Muggiaea*).
- Fish eggs showed no relationships of interest and, notably, were not linked to total fish larvae (Table 3), indicating that the abundance of fish larvae, as taken by the YFT at several weeks of age, has been highly modified by mortality rates through the egg and earlier larval stages.
- The lack of any relationship between fish eggs and plankton biomass (Table 3; Figs 5, 7 and 8) does not support the hypothesis that spawning success is a reflection of food availability to the adults in the same year as spawning (nor for plankton biomass in the previous year, as checked separately).

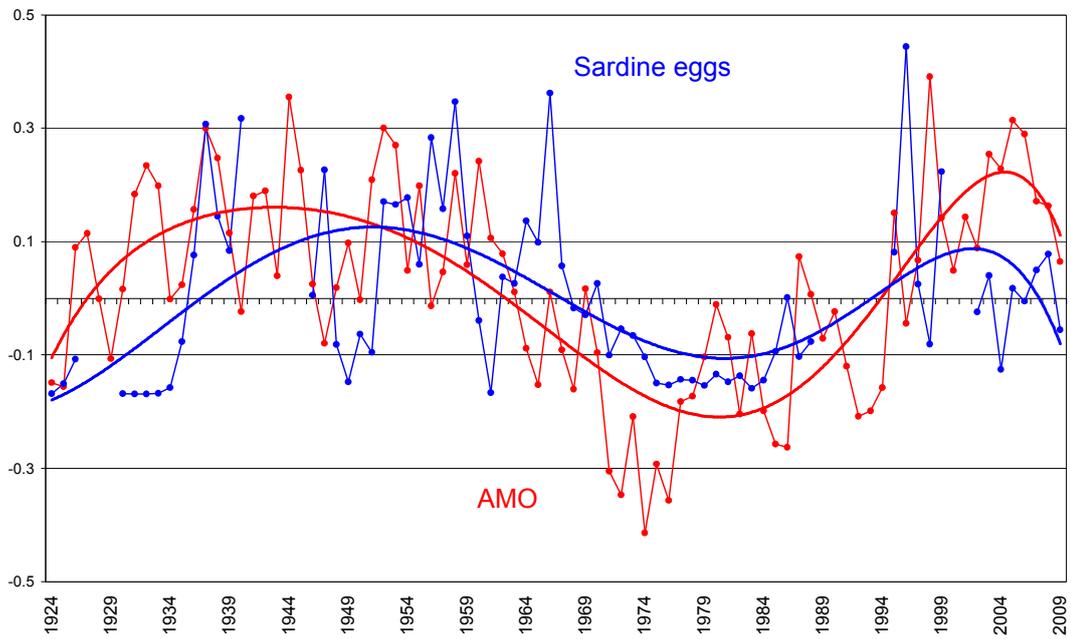


Fig. 22. AMO index and annual abundance of sardine eggs (re-based to common scale).

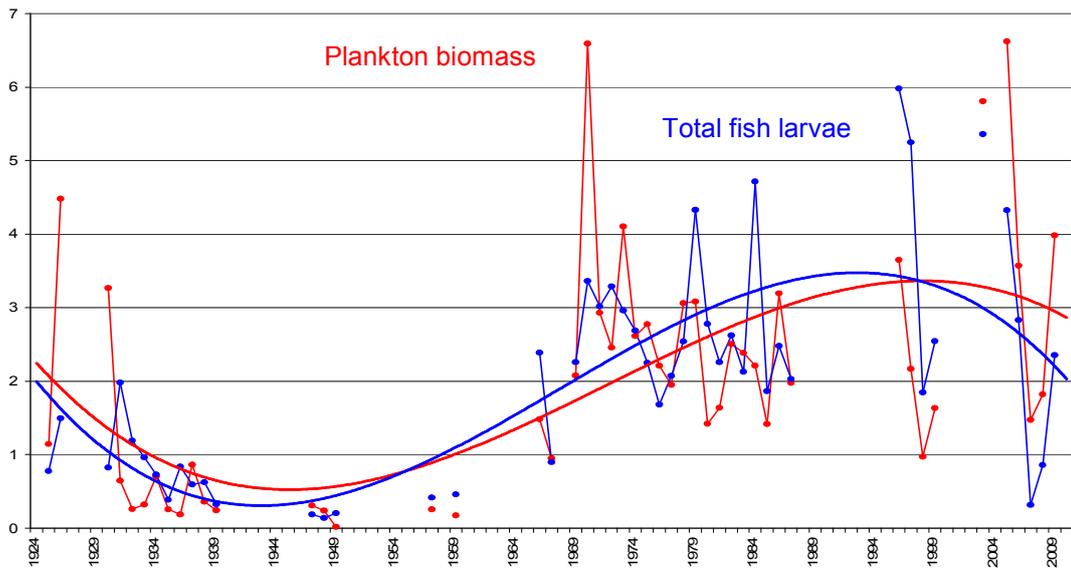


Fig. 23. Annual abundance of zooplankton biomass and total fish larvae (re-based to common scale).

Table 3. Correlation matrix. Relationships referred to in the text and significant at 1% and 5% levels are indicated by light and dark shading, respectively (with adjustment of  $\alpha$  level for multiple correlations, but without allowance for auto-correlation).

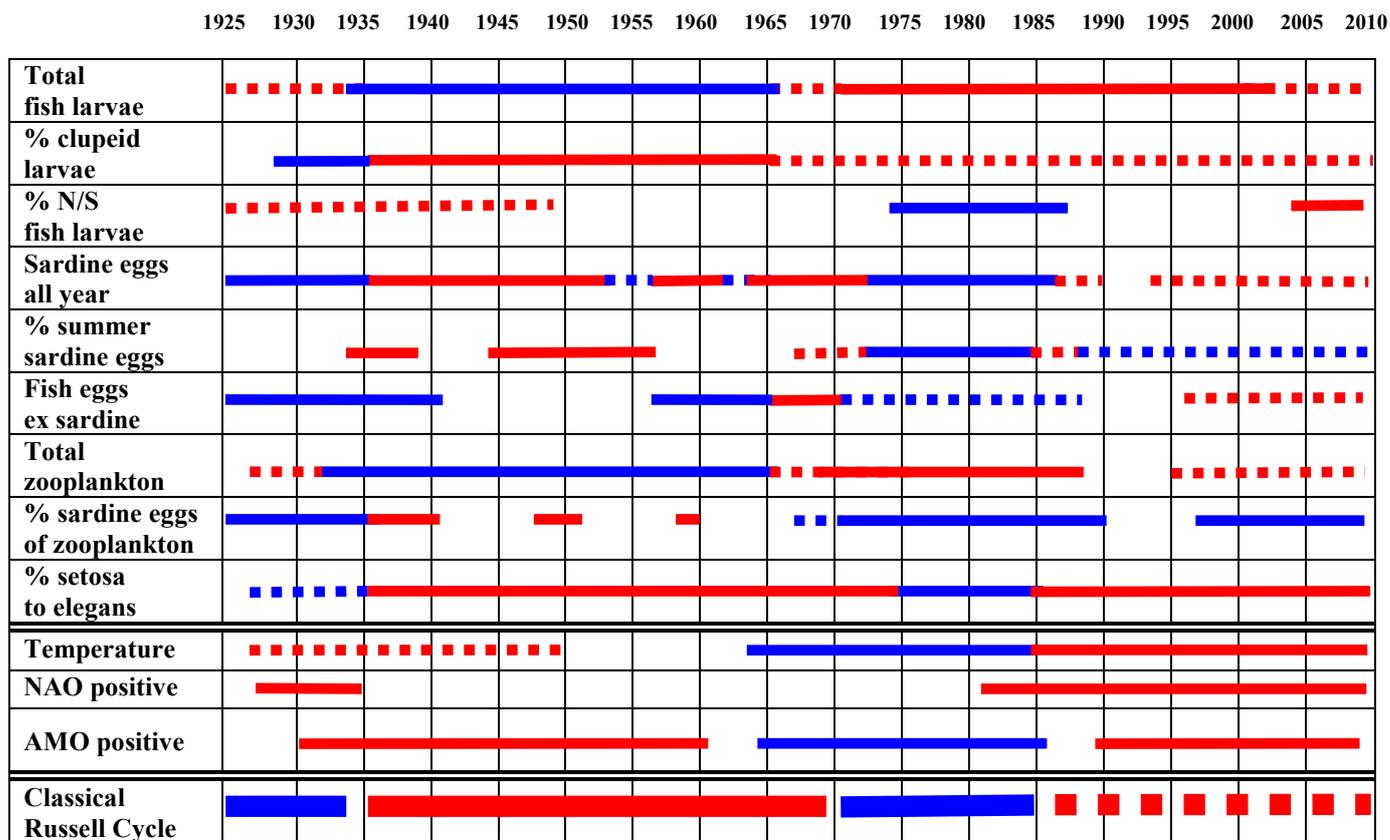
	Winter NAO	AMO	E1 temp	Total larvae	S larvae	N larvae	Fish eggs	Sard eggs all yr	Sard eggs Jan - Aug	Sard eggs Aug- Dec	Plankton vol	NW plankton	SW plankton	S. elegans	S. setosa	Calanus
Winter NAO	1.00															
AMO	-0.01	1.00														
E1 temp	0.38	0.32	1.00													
Total larvae	-0.41	-0.17	-0.05	1.00												
S larvae	-0.36	-0.14	-0.06	0.68	1.00											
N larvae	-0.33	-0.42	-0.29	0.44	0.39	1.00										
Fish eggs	-0.23	0.25	0.07	0.19	0.18	-0.23	1.00									
Sard eggs all year	-0.28	0.26	0.05	0.07	0.09	-0.22	0.89	1.00								
Sard eggs Jan-Aug	-0.17	0.35	0.02	-0.25	-0.26	-0.37	0.72	0.90	1.00							
Sard eggs Aug-Dec	-0.17	0.12	0.12	0.44	0.53	0.01	0.61	0.40	-0.08	1.00						
Plankton vol	-0.22	-0.14	-0.06	0.69	0.61	0.25	0.05	-0.05	-0.29	0.27	1.00					
NW plankton	0.05	-0.01	-0.05	0.01	0.11	-0.03	-0.19	-0.20	-0.28	0.04	0.23	1.00				
SW plankton	0.00	0.00	0.16	0.53	0.31	-0.06	0.05	-0.09	-0.28	0.27	0.78	0.43	1.00			
S. elegans	-0.02	-0.34	-0.33	0.18	0.16	0.32	-0.40	-0.41	-0.43	-0.13	0.28	0.70	0.25	1.00		
S. setosa	-0.23	0.16	0.06	0.55	0.29	0.11	0.30	0.10	-0.02	0.29	0.71	-0.12	0.64	-0.20	1.00	
Calanus	-0.11	-0.10	-0.05	0.43	0.38	0.00	-0.01	-0.09	-0.14	0.00	0.85	0.11	0.53	0.20	0.53	1.00

## Summary

Considering the correlations in Table 3 and observed trends in the updated data (summarised in Table 4):

1. The change from the 1930s to the 1970s (i.e. original Russell Cycle) is clearly evident. Furthermore, the calculation of settled plankton biovolume for the period 1930-1970 is in agreement with the illustrations of plankton samples in Russell *et al.* (1971).
2. For the results after the 1970s there was less coherence across the data and relatively high levels of plankton biomass and fish eggs and larvae were maintained. This argues against a simple cyclical process and indicates the 1930 levels of abundance were rather lower than the post-1970s i.e. a less symmetrical change 1930-1970 than originally interpreted in the Russell Cycle.
3. Referring to changes post the 1980s as being part of, or a continuation of, the Russell Cycle is not supported. There were several clearly contrary changes in the most recent period of warming compared with the 1930s-1960s *viz.* high plankton biomass (inc. *Calanus*) + dominance of autumn sardine in recent warming *c.f.* low biomass and spring/summer spawning 1930s-1960s.
4. Although certain groups showed a relationship with E1 temperature e.g. southern fish larvae post 2003, the more north-westerly character of plankton in the late 1970s to early 1990s, or the *Sagitta spp.* alternations, there was no consistent relationship with E1 temperature across the data.
5. The relationship in trend between the Atlantic Multidecadal Oscillation (AMO) and plankton biomass, total fish larvae and total sardine egg abundance is evidence for underlying hydro-climatic links; possibly with the AMO being the index most closely related to the original Russell Cycle.
6. The relationship between temperature and increased westerly weather (positive NAO) did not extend to include increased south-westerly plankton, as might be expected. In fact, a confounding relationship was observed between negative NAO and total fish larvae, although total fish larvae were related positively with south-westerly plankton.
7. The positive relationship between total fish larvae and plankton biomass supports the view that enhanced survival of fish larvae is due to better feeding conditions.
8. The high variance in this type of plankton sampling is noted (see Appendix).

Table 4. Summary of trends. Positive in red, negative in blue.



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## Appendix

### Methods

A comprehensive outline of the sampling off Plymouth and analysis methods is given in Southward *et al.* (2005) and papers referred to therein. Briefly, the routine plankton sampling was generally carried out several times a month at stations L5 and E1 (~10 and 20 miles off Plymouth, respectively; Fig. A1) using variants of the MBA Young Fish Trawl (YFT, essentially a coarse-meshed plankton net). The young fish taken in the net have a mean length of ~12 mm and include some post-larvae but are mainly late-stage larvae, and are all here referred to as larvae.

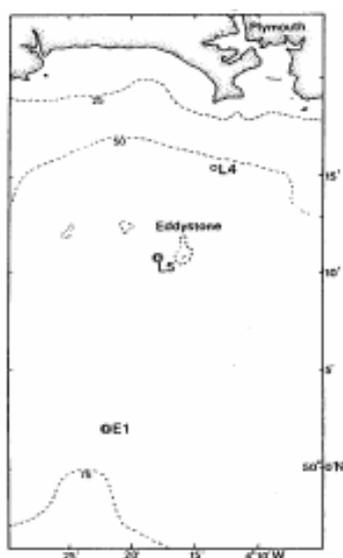
### Data limitations and data presentations

As with most plankton data, haul-to-haul variation, site selection, temporal changes and sampling methodology all affect the precision and accuracy of results. These and other specific factors in relation to the present data need to be considered as a caution to over-interpretation of the results:

- **Sampling site.** Historically, results have generally been monthly means from several samples taken each month, mostly at station L5 (Fig. A1) but also including a significant proportion at E1 and other local sites (although the combined results often being referred to in the literature as “L5”). In recent years fewer samples have been taken each month (potentially, higher variance) and in more equal numbers at L5 and E1 (the mean from these two stations being used for the post-2002 results), hence a possible bias towards E1.

However, comparison of annual means for the last few years at L5 and E1 did not show any striking bias e.g. typical comparison for total zooplankton or total fish larvae (Fig. A2). But significant differences were noted for *Calanus* and *S. elegans* (although lower numbers for both), which were present at around 23% and 33% higher numbers respectively, over the past 8 years at E1 compared with L5 (Fig. A2).

Fig. A1. Sampling sites.



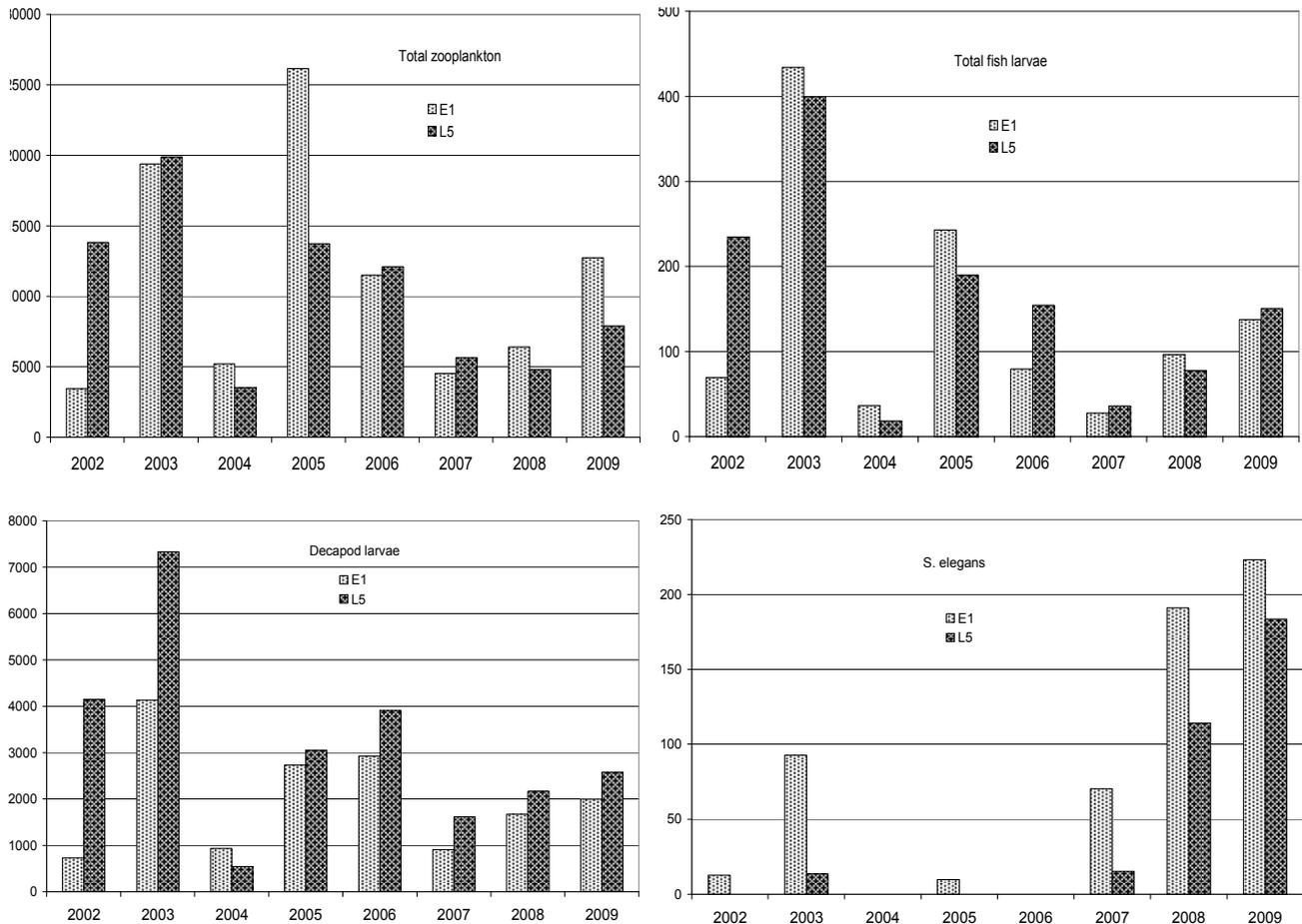


Fig. A2. Comparisons of annual means 2002-2009 at E1 and L5.

- **Precision and accuracy.** As for all plankton sampling, there is a high haul-to-haul variance in abundance estimates, typically 50-200% of the mean (Southward, 1970) and large temporal variations in a single month (monthly means being the basic data unit used for all present analyses) both within and between stations (Fig. A3).

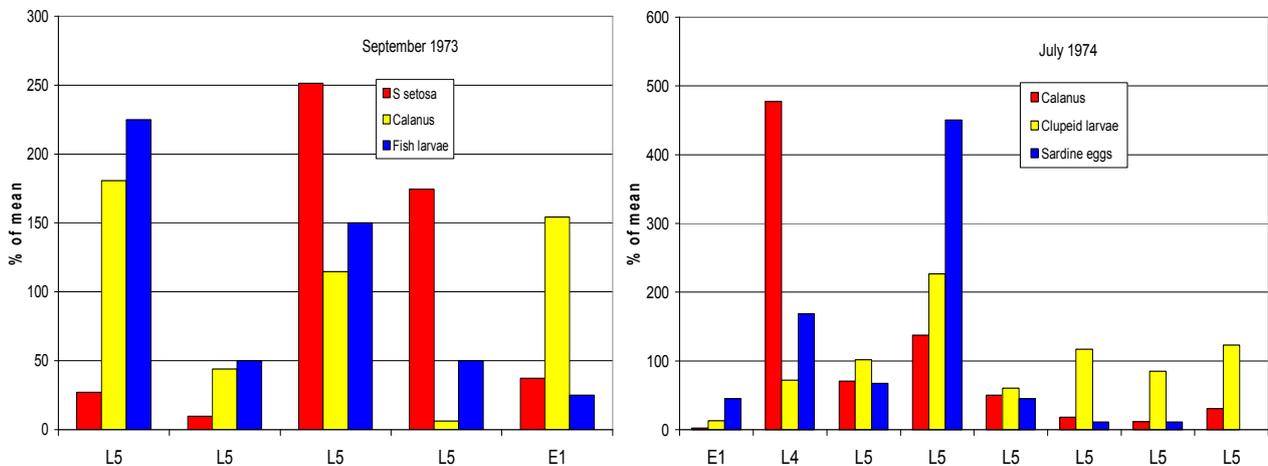


Fig. A3. Comparisons of sample results within and between stations for two individual months.

- **Variations in procedure.** Over the years there have been various changes in net dimensions, rigging arrangements, deployment routine, mesh type and aperture etc. of the YFT used off Plymouth. Standardisation of results (essentially to unit volume sampled) has mitigated these factors as far as possible, but there will doubtless be remaining bias (and perhaps some influence of varying analysis procedures).

The mesh type has changed over the years but has been consistently a relatively coarse mesh aperture (currently around 700  $\mu\text{m}$ ) designed primarily to sample fish post-larvae. It is also effective for (most) fish eggs and larger macro-zooplankton, with *Calanus* (probably near 100% *C. helgolandicus*) and decapod larvae dominating the crustacean catch (Fig. A4). Smaller zooplankton and early fish larvae are not sampled particularly efficiently so that results for these groups are not directly comparable with more usual plankton sampling with  $\sim 200\text{-}300\ \mu\text{m}$  mesh nets.

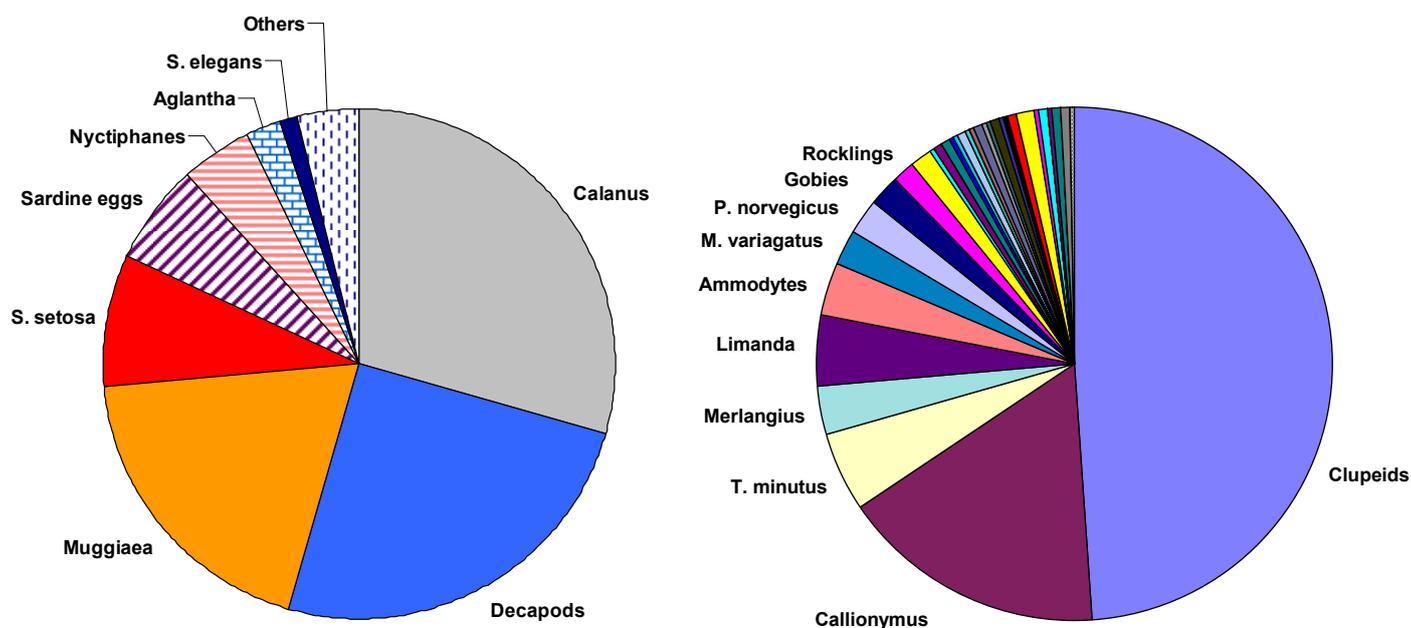


Fig. A4. Biomass (left) and fish larvae (right) composition from E1/L5 YFT sampling 1924-2009.

- Despite the problems of data reliability, some comparisons with other plankton sampling have been supportive e.g. Fig. A5 (and see Coombs *et al.* (2005) for L5 sardine eggs against Continuous Plankton Recorder (CPR) sardine eggs).

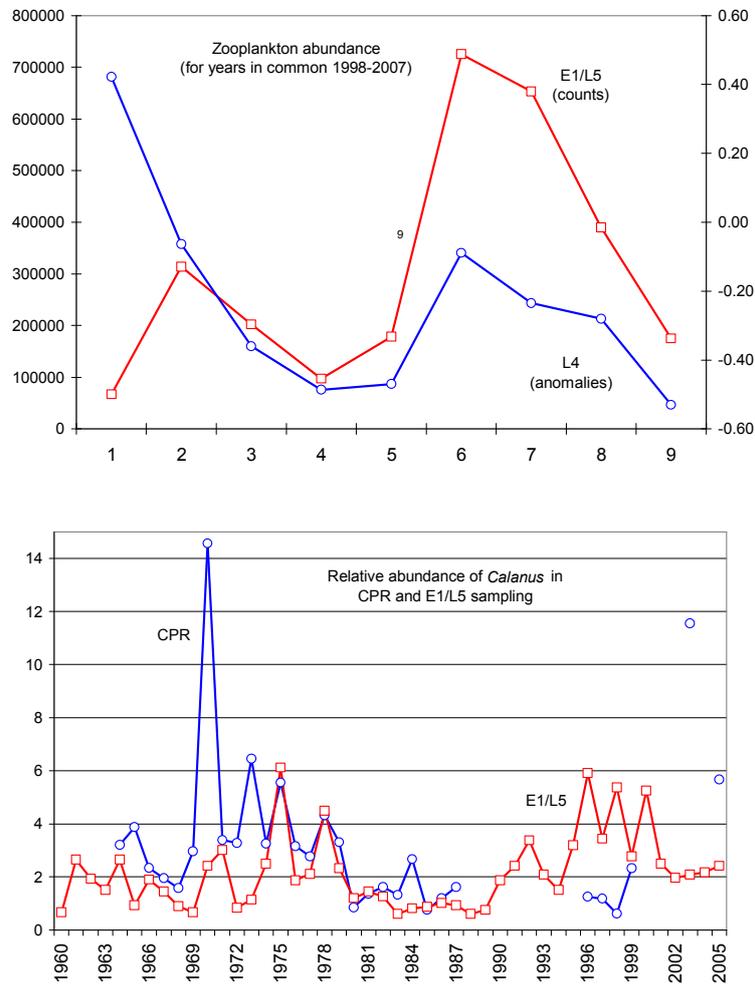


Fig. A5. Comparisons of E1/L5 sampling with L4 and CPR results.

- **Missing data.** Sampling gaps occur both for intermittent months and as blocks of several years. Also, for the samples taken, sometimes certain groups only were analysed, resulting in varying amounts of missing data for different groups (e.g. Fig A6).

Plotting annual abundance as the sum of the monthly means can give misleading results where only a few or even a single month was sampled for a particular year. The dataset for each species group was inspected and for those years where there were insufficient data to compute a reliable annual mean (generally set at the level where the months sampled equate to <50% of long-term annual mean production) those years were treated as un-sampled (i.e. allocated no annual abundance value). Where inspection of the plots of the modified datasets (i.e. excluding poorly sampled years) against the un-modified ones showed significant differences, then the edited data were used (see Fig. A7). Fitted polynomial curves (generally 5<sup>th</sup> order but lower where appropriate) were used to summarise long-term trends in the annual plots.

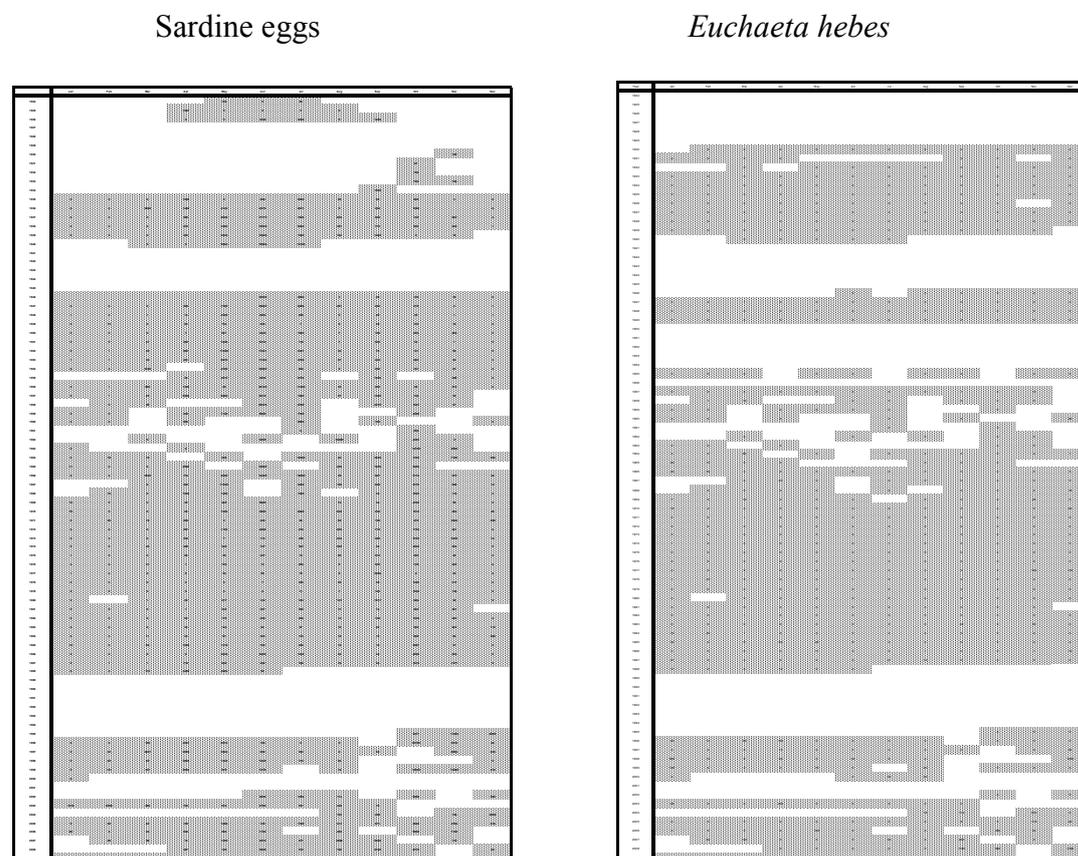


Fig. A6. Examples for two datasets (12 months x 85 years) showing months (shaded rectangles) for which data values are available (i.e. both sampling and analysis completed).

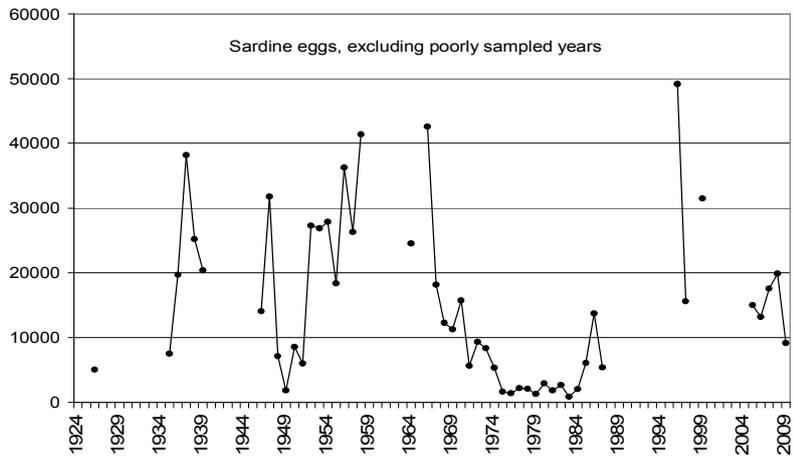
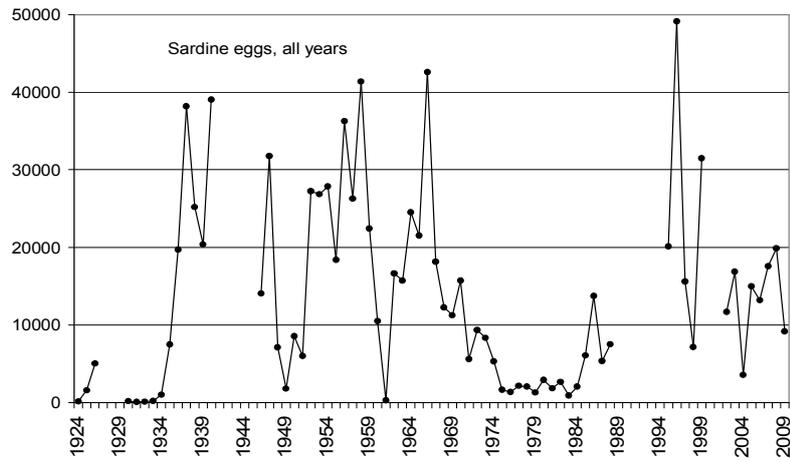


Fig. A7. Abundance of sardine eggs (as sum of monthly means) for all years (top plot) and excluding years with inadequate sampling (bottom plot).