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# An analysis of the meroplankton assemblages of Station L4 and the development and application of molecular techniques to aid taxonomic resolution.

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# Seasonal dynamics of meroplankton assemblages at station L4

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Zooplankton data from 20 years of weekly sampling were used to determine inter- and intra-annual patterns of meroplankton community change at Station L4, off the coast of Plymouth, UK. From these data, abundances were calculated for five groups; Cirripedia, Decapoda, Polychaeta, Echinodermata and Lamellibranchiata. This taxonomic level of analysis was chosen to minimize the potential effects of variation in taxonomic expertise over the 20-year period. Analyses showed that while there is some annual variability, it is seasonal variation that accounts for the major changes in the meroplanktonic community composition throughout the time series. Cirripedia are the most abundant meroplankton in March and April, followed by Echinodermata in August, and Lamellibranchiata in September and October. Abundance is low during the winter period. The average monthly contribution of the meroplankton community as a percentage of the total zooplankton abundance is highest in spring, when meroplankton (predominantly Cirripedia) can account for up to 42.5% of the total zooplankton community following spawning events linked to phytoplankton blooms. Little evidence was found for any major trends of change in the meroplankton community (at the taxonomic level examined here) at Station L4 over the 20-year period.

**KEYWORDS:** meroplankton; Western English Channel; inter-annual variability; seasonal variation; time series

## INTRODUCTION

Many marine invertebrate species have complicated and intricate life-cycles in which earlier stages often differ considerably from their adult counterparts in terms of morphology, diet, habitat and ecology (Pechenik, 1999; Pradillon *et al.*, 2007). Many marine invertebrates spend their juvenile and adult lives in the benthos, but release gametes or larvae into the water column. Their larvae are planktonic, growing and developing through one or more larval stages (Eckman, 1996) and allowing potential dispersal over hundreds or

thousands of miles (Thorson, 1950; Belgrano *et al.*, 1995; Livi *et al.*, 2006). Onset of a rapid and extensive metamorphosis is triggered by, in most cases, contact with certain physical or chemical cues that correspond with a favourable environment for juvenile development (Thorson, 1950; Giese and Pearse, 1974; Starr *et al.*, 1990; Young, 1995; Pechenik, 1999; Pradillon *et al.*, 2007). These planktonic larvae of marine benthic invertebrates comprise the majority of the *meroplankton*, which include a variety of taxa and forms such as the planktotrophic and lecithotrophic larvae of both

benthic and nektonic species, planktonic eggs and medusae (Marcus and Boero, 1998; Pechenik, 1999).

The success of meroplanktonic larvae is affected by numerous factors including adult fecundity and fertilization success, growth and larval stage duration, mortality, behaviour, dispersal (Bhaud, 2000) and settlement (Eckman, 1996). Larval mortality is also influenced by multiple factors, including predation, inter- and intra-specific competition for food or space, disease, parasites and various physiological stresses such as temperature and salinity (Eckman, 1996; Todd, 1998).

The nourishment of meroplanktonic larvae is directly dependent upon the existing plankton community and the release of larvae is often timed to correspond with phytoplankton blooms to maximize the exposure to an abundant food supply (Thorson, 1946). This synchronicity often leads to meroplanktonic larvae becoming the dominant members of the coastal zooplankton community during the reproductive season of benthic organisms (Thorson, 1946; Williams and Collins, 1986; Martin *et al.*, 1996). In the Bay of Blanes in the NW Mediterranean, for example, meroplanktonic larvae generally account for around 13% of the total zooplankton throughout the year, but at certain times they can contribute up to 60% of community biomass (Andreu and Duarte, 1996).

Meroplanktonic larvae have been an object of study in the Western English Channel at the sampling site in this study, Station L4, for the duration of a long-term time series. Station L4 is located 10 km southwest of the Plymouth breakwater in the UK, and has been sampled since the 1920s and a weekly zooplankton time series sampling programme began in 1988. Such long-term time series data can provide insights into short- and long-term patterns of abundance and community change in a given area, and so can be used to study long-term zooplankton dynamics (Pitois *et al.*, 2009). Long-term data sets also facilitate phenological studies such as those in the North Sea (Greve *et al.*, 2005) and of the Continuous Plankton Recorder (Edwards and Richardson, 2004) in the North-East Atlantic.

Various physical, chemical and biological data have been collected at Station L4 (Smyth *et al.*, in press), with zooplankton and phytoplankton species' composition being of particular note (Aiken *et al.*, 2004; Southward *et al.*, 2004; Eloire *et al.*, in press; Widdicombe *et al.*, in press). The depth is ~51 m and the water is totally mixed from September to March. A transitional period from mixing to stratification then occurs during the spring, before it becomes stratified during the summer months. The site is also subject to influence from estuarine outflow from Plymouth Sound (Southward *et al.*, 2004). Numerous phytoplankton blooms occur

during the spring and summer months (Southward *et al.*, 2004), that, along with a small autumn bloom (Boalch, 1987; Edwards and Richardson, 2004), provide a food source for planktotrophic larvae (Holligan and Harbour, 1977).

While numerous studies have focused on zooplankton dynamics at Station L4 (Irigoiien and Harris, 2003; López-Urrutia *et al.*, 2004; Bonnet *et al.*, 2007; Eloire *et al.*, in press; Widdicombe *et al.*, in press), very few have considered the dynamics of meroplanktonic larvae off Plymouth. There are many species-specific records in the Plymouth Marine Fauna (Marine Biological Association of the United Kingdom, 1957) primarily based on some earlier records, such as those of Lebour (Lebour, 1947) who reported presence/absence observations on a monthly basis. Due to the paucity of recent explicit meroplankton studies over the past 50 years, the aim of this investigation is to describe how the composition of the meroplankton community and its contribution, in terms of percentage composition, to total zooplankton varies on a seasonal and annual basis at Station L4.

## METHOD

Zooplankton samples were collected weekly (weather permitting) at Station L4 (50.25°N 04.217°W) from March 1988 to December 2007. No samples were collected in August 2000 and a total of 862 samples were collected over the 20 years. On each sampling date, two replicate vertical WP2 net hauls (mesh size = 200 µm, mouth aperture = 57 cm diameter) were taken from the seabed (51 m) to the surface and stored in 5% formalin. Owing to the large number of organisms in most samples, two sub-samples were taken from each haul. Distinct sub-samples for small and large organisms were necessary because the wide range of sizes and abundances of organisms present meant that one sub-sample size would not adequately sample all the sizes of those organisms present in a sample. For sub-sampling, each sample was made up to a known volume e.g. 500 mL, and split using an appropriate method. For smaller organisms, sub-samples were taken with a stempel pipette, while larger (and rare) organisms were counted in sub-samples taken using a Folsom splitter to separate the sample into a half, a quarter or an eighth depending on the richness of the original. Both hauls were analysed, the average numbers calculated and counts were converted to numbers per m<sup>3</sup> (John *et al.*, 2001). The full data set can be found at the Western Channel Observatory website [www.westernchannelobservatory.org.uk](http://www.westernchannelobservatory.org.uk).

Owing to the difficulties in larval identification and because different analysts, with varying abilities to discriminate larvae, have worked on the samples over the years, our analysis is restricted to variation in five different groups defined at a broad taxonomic level. These groups are: Decapoda; Cirripedia (including nauplii and cyprids); Echinodermata; Lamellibranchiata and Polychaeta. These groups provide an overall picture of the seasonal changes in the meroplankton assemblages at L4. They also occur in significant numbers as adults in the benthic community at the study site (Allen, 1899; Marine Biological Association of the United Kingdom, 1957; Holme, 1961; Personal observations) and so can be said to be representative of the existing local benthic ecosystem. Phytoplankton and physico-chemical measurements were also collected using methods described in Smyth *et al.* (in press), and Widdicombe *et al.* (in press). Average weekly sea surface temperatures °C (SST) were measured using a thermometer and bucket during the years 1988–1998, with the Plymouth Marine Laboratory CTD system during the years 1998–2002, and since 2002 using a SeaBird SBE19+ (Smyth *et al.*, in press).

The average seasonal cycles of the total zooplankton, total meroplankton, each meroplankton group and SST were examined using weekly averages, over the entire time series. Then, abundances of each group were determined for each month over the period 1988–2007. A monthly abundance anomaly for each month of the time series was obtained using the formula:

$$x'_{m,y} = \frac{x_{m,y} - \bar{x}_m}{\sigma(x_m)}$$

where  $m$  is the month ( $m$ : 1 = January, 2 = February, . . . , 12 = December) and  $y$  is the year,  $x'_{m,y}$  is the monthly anomaly for month  $m$  in the year  $y$ ;  $x_{m,y}$  is the monthly average abundance in month  $m$  in the year  $y$ ;  $\bar{x}_m$  is the average abundance and  $\sigma(x_m)$  is the standard deviation in month  $m$  over the entire time series. Thus, a positive anomaly means that the observed value was higher than the overall average for that month, and vice versa. Gaps occurred in January and February 1988, and August 2000. Prior to estimating annual anomalies by using monthly anomalies, the values for the missing months were interpolated using the overall average for that month over the entire time series. Annual anomalies were obtained by averaging the monthly anomalies for each year of the time series from 1988 to 2007.

Trends for the monthly anomalies were obtained by applying a type I linear model. Prior to testing the significance of the trend slope, a Durbin–Watson test was performed to detect autocorrelation in the residuals of

the regression analysis (MacKenzie and Köster, 2004). When autocorrelation was present, the effective number of degrees of freedom for significance tests was adjusted using the following formula:

$$n_{\text{eff}} \approx n_t \frac{1 - r_1}{1 + r_1}$$

where  $n_{\text{eff}}$  is the effective number of independent values,  $n_t$  is the total number of values and  $r_1$  is the lag-1 temporal autocorrelation coefficient (Quenouille, 1952; Hays *et al.*, 1993; Pyper and Peterman, 1998; Santer *et al.*, 2000). A Student's  $t$ -test was used to determine whether the slope of the linear model was significantly different from 0 (Table I).

Variation in community composition in the time series data was analysed using nonparametric multivariate analysis (Clarke, 1993). Data were converted to monthly within-year averages in order to discern any patterns that would not otherwise be evident among the 862 samples. The Bray–Curtis similarity resemblance coefficient (Clarke *et al.*, 2006) was calculated between every pair of monthly average values. Inter-sample resemblances were ordinated in 2D using non-metric multi-dimensional scaling (MDS).

## RESULTS

The average seasonal cycle of phytoplankton at Station L4 (Fig. 1) is characterized by a large increase in cell concentration that starts in March, and reaches its peak in May (the spring bloom), followed by a series of smaller peaks that occur throughout the summer months before a larger peak occurs in September. This peak corresponds with the autumn bloom which is smaller than the spring bloom. Cell abundance then continues to decrease throughout autumn and winter. The increase in cell concentration that occurs in March is concurrent with the onset of an increase in sea surface temperature. Anomaly analysis (Table I) shows that there was a slight, but significant ( $P < 0.0002$ ) increase in the average sea surface temperature over the duration of the time series.

The average percentage contribution of meroplanktonic larvae to the total zooplankton over the annual cycle varies throughout the year (Fig. 2) and averages 13%. The highest values occur in March where meroplankton may comprise 42.5% of the total zooplankton, with April showing the next largest contribution. The fraction comprising meroplankton increases again in July and August before decreasing in the autumn and winter.

Table I: Statistics of the total zooplankton, total meroplankton, each meroplankton group and the SST

Time series (1988–2007)	Average abundance ( $N\ m^{-3}$ )	SD ( $N\ m^{-3}$ )	Relative contribution (%)	Monthly anomalies			
				DW statistic	DW <i>P</i> -value	Trend <i>P</i> -value	Trend slope
Total zooplankton	3075.61	2138.65	–	2.06	0.68	0.542	–0.0006
Meroplankton	536.98	928.53	17.46	2.00	0.95	0.032	0.0020
Cirrropedia	300.67	881.00	9.78	2.01	0.97	0.007	0.0024
Decapoda	14.82	13.58	0.48	2.03	0.82	0.193	0.0012
Polychaeta	29.15	31.82	0.95	2.03	0.82	0.482	–0.0006
Echinodermata	76.30	232.18	2.48	2.01	0.95	0.644	0.0004
Lamellibranchiata	52.19	124.74	1.70	2.04	0.81	0.425	0.0007
SST	12.80	2.78	–	2.16	0.24	0.0002	0.0033

The average abundance, standard deviation and relative contribution of the meroplankton were estimated over the period 1988–2007. DW indicates results of the Durbin–Watson test. Trend *P*-value gives the significance of the slope (trend slope) of the regression analysis (highlighted in grey are the non-significant trends with *P*-value > 0.1).

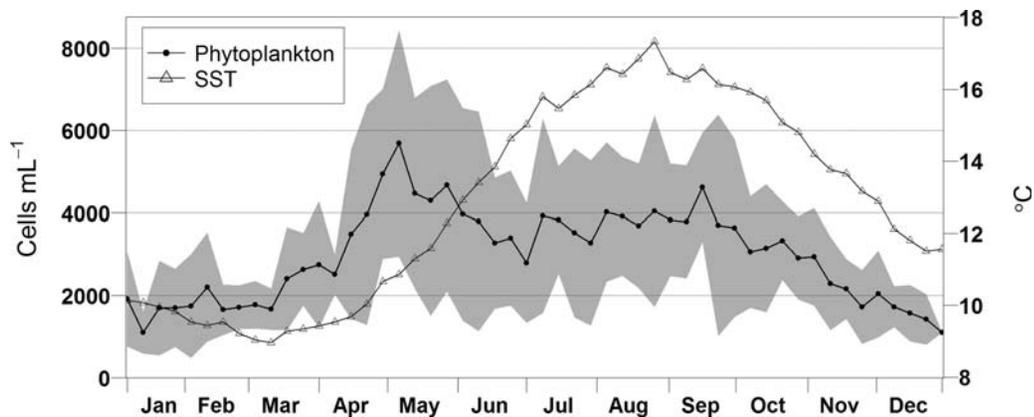


Fig. 1. Changes in weekly average abundance ( $Cells\ mL^{-1}$ ) of total phytoplankton over the annual cycle at Station L4. Solid line indicates the mean; gray band indicates  $\pm 1$  SD. Mean weekly sea surface temperature ( $^{\circ}C$ ) is also shown.

Plots of the raw abundance data over 20 years for the total zooplankton, total meroplankton and each of the five groups under study (Fig. 3) do not show strong inter-annual changes or trends and show that within-year variability is relatively large. Plotting monthly anomalies (Fig. 4) fails to clarify any seasonal or multi-annual patterns in the data.

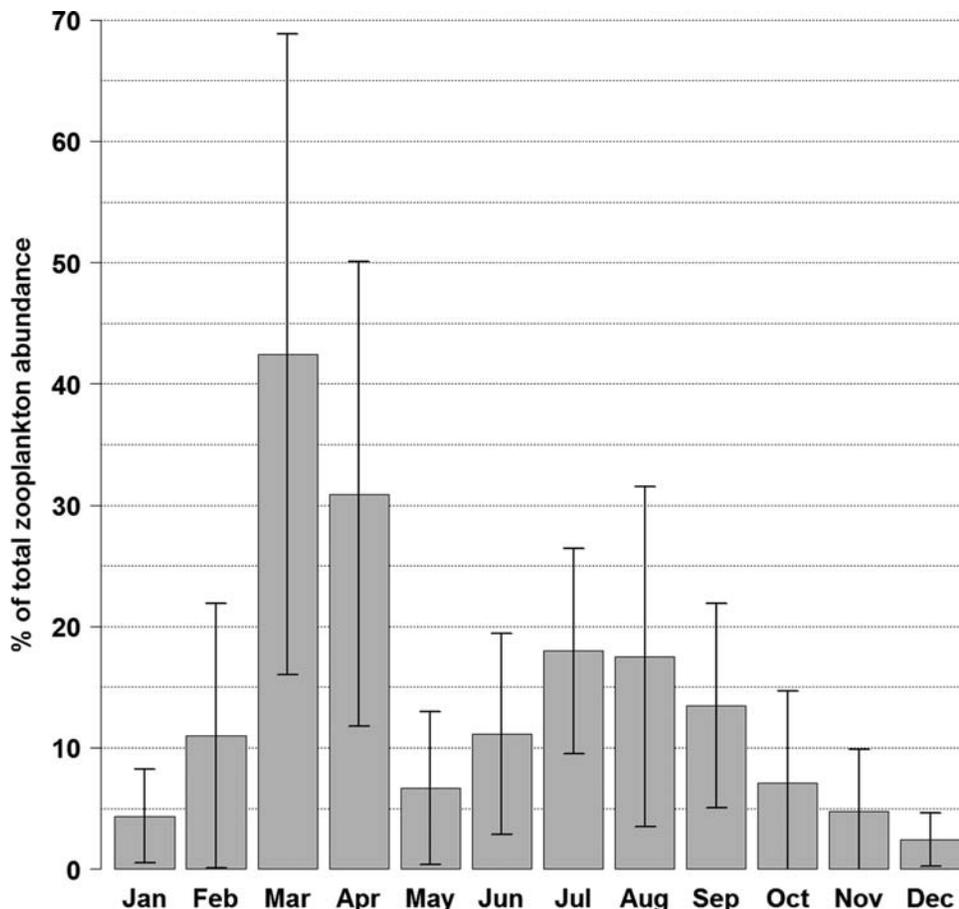
The general seasonal cycles of total zooplankton (Fig. 5A) and total meroplankton (Fig. 5B) are both characterized by large increases in abundance during March and April, which coincides with the onset of sea temperature increase. This is then followed by a steady decrease in total zooplankton for the rest of the year. For total meroplankton, there is a decrease in May followed by a slight increase during August and September before falling again during the autumn and winter months.

Anomaly analysis (Figs 4A and 6A) shows no significant variation ( $P = 0.542$ , Table I) in total zooplankton abundance over the time series. However, a significant ( $P = 0.032$ ) overall increase in abundance was seen in

total meroplankton (Figs 4B and 6B, Table I) over this period.

Cirrropedia larvae occur in relatively low numbers in the water column for most of the year. There is a massive increase in abundance in March and April (Fig. 5C) when sea-surface temperature begins to increase, corresponding to the spring phytoplankton bloom (Fig. 1), that can exceed  $15\ 000\ N\ m^{-3}$  ( $15\ 251\ N\ m^{-3}$  were recorded on 17 March 1997). This is the largest increase in abundance exhibited by any of the five groups examined in this study. The abundance of cirripede larvae then falls by the end of May and remains relatively low ( $< 100\ N\ m^{-3}$ ) for the rest of the year except for a slight increase during August and September (e.g.  $777.42\ N\ m^{-3}$  on 05 September 1988). Annual anomaly analysis (Fig. 6C, Table I) shows a significant increase in abundance ( $P < 0.007$ ) over the 20 years of the time series.

Decapod larvae are present in the plankton in every month in varying amounts (Fig. 5D). Numbers are



**Fig. 2.** The average monthly percent contribution of meroplanktonic larvae to the total zooplankton abundance at Station L4.

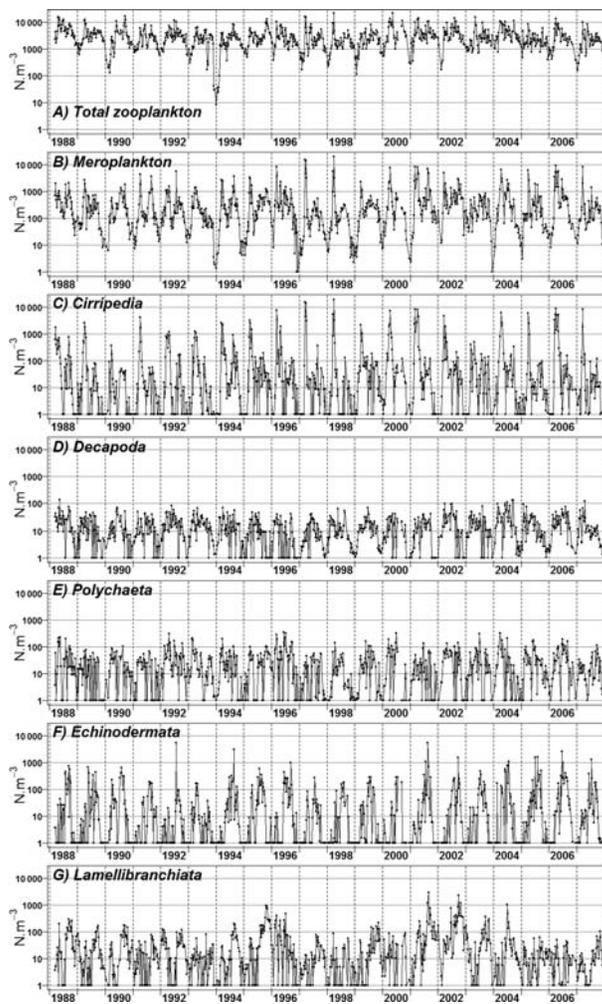
generally low, ranging from 0 to  $136.17 \text{ N m}^{-3}$ . Few larvae are found from November to January before abundance increases during spring. A major peak tends to occur at the end of March before abundances fall in April and become variable. The highest average abundances occur in June and at the start of July, before abundances fall quite dramatically into August. Continuing increases and decreases occur before abundances fall to low winter levels. The abundances of decapod larvae increase before SST reaches its lowest value at around  $9^\circ\text{C}$ , but only reach their highest numbers once the temperature has reached  $13\text{--}14^\circ\text{C}$ . The analysis of annual anomalies (Fig. 6D) shows no significant trend (Table I).

Polychaete larvae are found in the plankton in low numbers in January and February (Fig. 5E) before increasing in numbers and reaching a peak in late spring. Highest abundances occur in June and July (e.g.  $172 \text{ N m}^{-3}$  on 10 June 1996). The seasonal cycle of polychaete larvae at L4 is then characterized by a steady decrease towards the winter months reaching the lowest average abundance in December and January

(Fig. 5E). Abundance of polychaete larvae appears to increase before SST reaches its lowest value at around  $9^\circ\text{C}$ , but their highest levels occur once the temperature has reached  $13\text{--}14^\circ\text{C}$ . The overall trend in polychaete abundance over the last 20 years (Fig. 6E) is not significant (Table I).

Echinoderm larvae, including ophiopluteii, echinopluteii and auricularia, are found in low numbers during the winter and spring months before increasing as summer begins (Fig. 5F). The larvae are present in their highest numbers (as high as  $5546 \text{ N m}^{-3}$ ) in August and September before decreasing again through the autumn and winter months (Fig. 5F). The abundances of Echinodermata appear to increase when sea surface temperature is approaching its highest level at around  $17^\circ\text{C}$ . The annual anomaly analysis (Fig. 6F) shows no significant trend (Table I) over the 20 years of sampling.

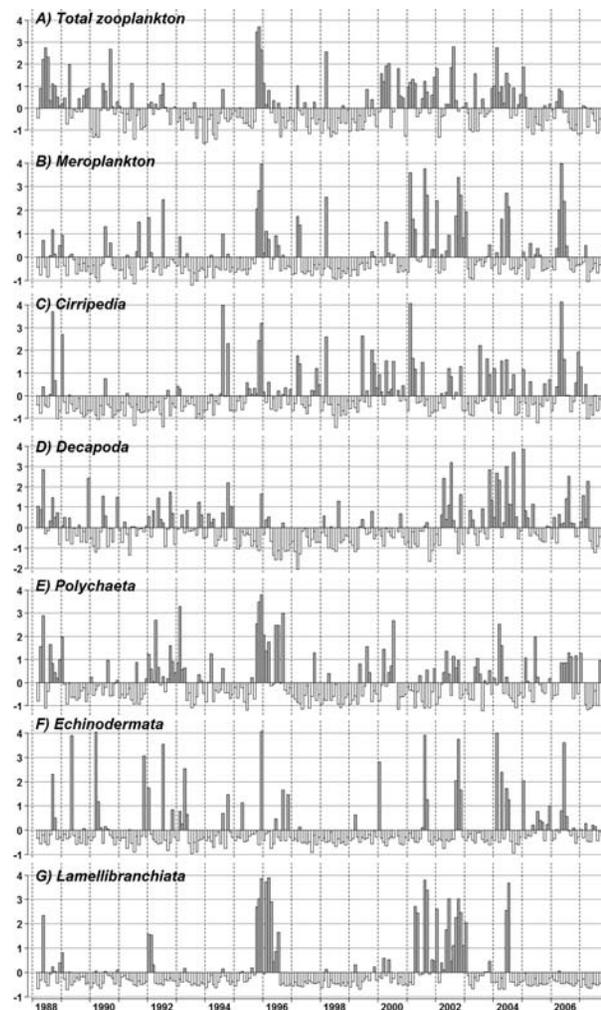
Lamellibranch larvae are present in the meroplankton throughout the year at L4 (Fig. 5G). They are found in low numbers from January to June before increasing during the summer months. During September and



**Fig. 3.** Plot of raw data showing the changes in abundance over the last 20 years for (A) total zooplankton, (B) total meroplankton, (C) Cirripedia, (D) Decapoda, (E) Polychaeta, (F) Echinodermata and (G) Lamellibranchiata at Station L4.

October, there is a very large peak in the numbers of larvae (up to  $2940 \text{ N m}^{-3}$ ), before numbers fall again during the winter. This large increase in the abundance of Lamellibranchiata appears to occur once sea surface temperature has reached its highest level at around  $17^\circ\text{C}$ . Changes in annual anomalies (Fig. 6G) show no significant trend (Table I).

The composition of the meroplankton community at Station L4, as visualized in MDS, changes throughout the year (Figs 7 and 8), and intra-annual changes in community composition are very much larger than inter-annual changes, as symbols representing the same month in different years tend to be grouped together in the ordination (Fig. 7). Three seasonal groupings may be seen. The winter months (October to February) are characterized by low overall abundances, leading to relatively high variability in inter-sample resemblances

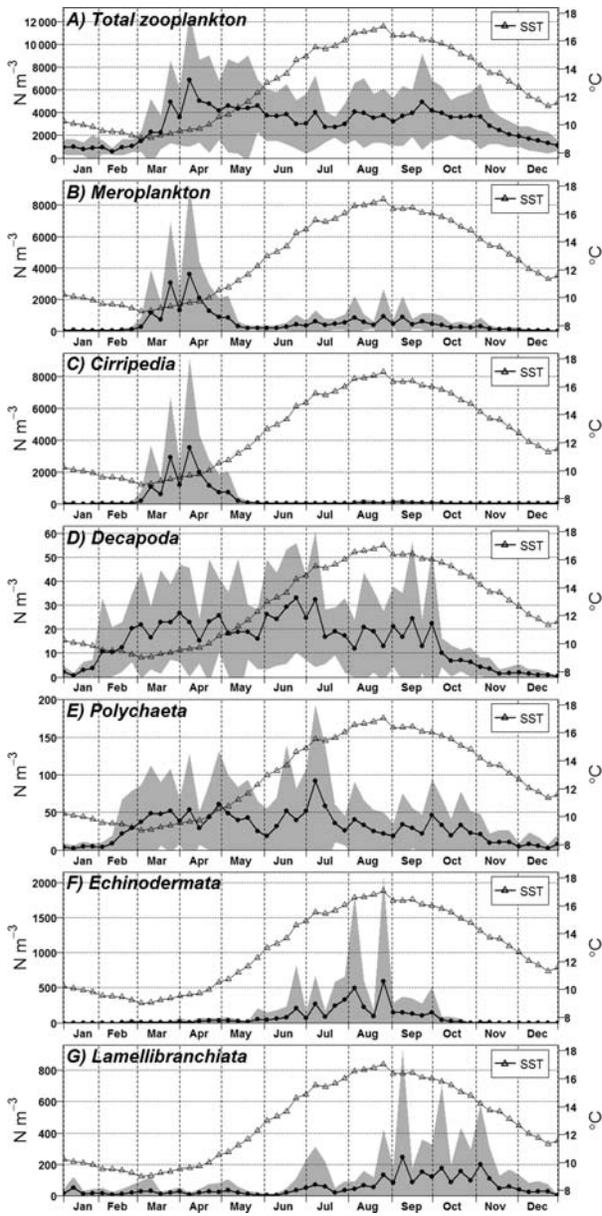


**Fig. 4.** The monthly anomalies in the data for (A) total zooplankton, (B) total meroplankton (C) Cirripedia, (D) Decapoda, (E) Polychaeta, (F) Echinodermata and (G) Lamellibranchiata at Station L4.

(Clarke *et al.*, 2006). The assemblage in spring (March and April) is dominated by Cirripedia (Fig. 8), but also contains relatively high numbers of polychaete and decapod larvae. Following the spring outburst, the community in June has sometimes almost returned to winter conditions owing to generally low abundances. The summer (May to September) shows an increasing trend in Lamellibranch and Echinoderm larvae and high numbers of Polychaeta and Decapoda. The reversion back to winter conditions tends to be abrupt, occurring between September and October.

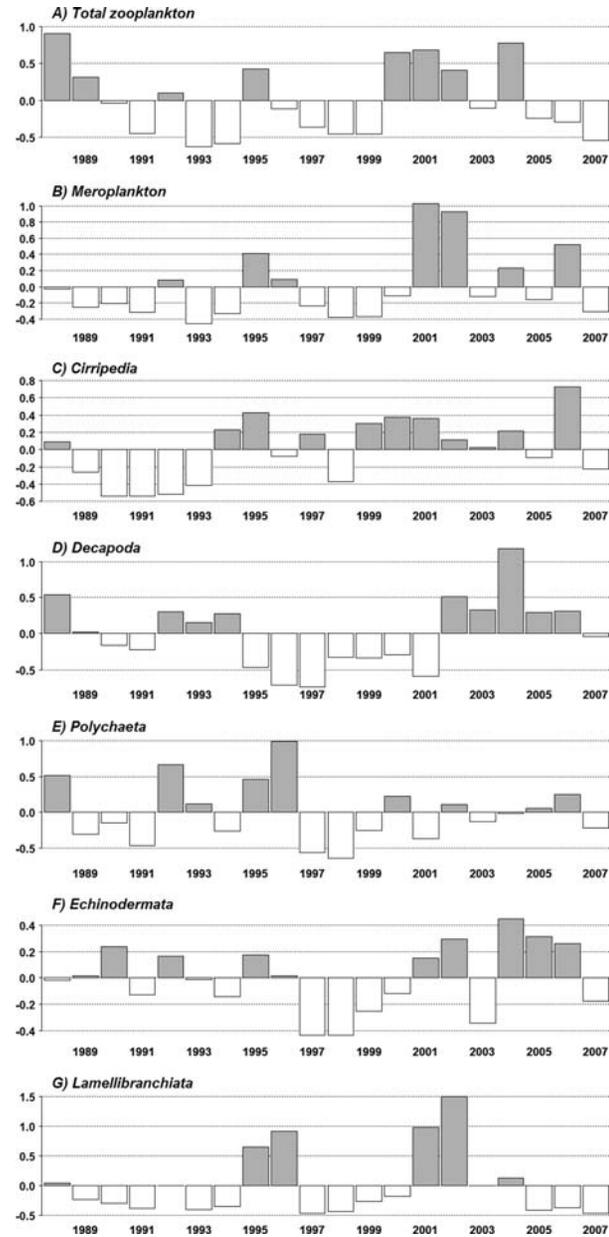
## DISCUSSION

The relationship between the spring phytoplankton bloom and the spawning of meroplanktonic larvae has



**Fig. 5.** Changes in the weekly average abundance  $N\ m^{-3}$  and the transition of meroplanktonic composition over the annual seasonal cycle for (A) total zooplankton, (B) total meroplankton, (C) Cirripedia, (D) Decapoda, (E) Polychaeta, (F) Echinodermata and (G) Lamellibranchiata at Station L4, calculated from 20 years data. Solid line indicates the mean; gray band indicates  $\pm 1$  SD. Mean weekly sea surface temperature ( $^{\circ}C$ ) is also shown.

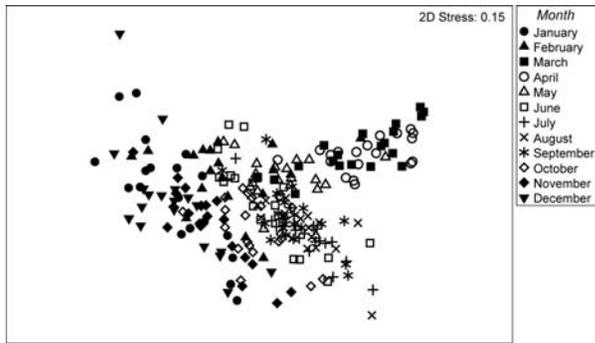
been studied extensively and examples of both direct and indirect induction of spawning in benthic species as a consequence of either blooms or those environmental conditions that trigger blooms have been reported. For example, certain species of barnacle and spider crab spawn upon direct contact with phytoplankton cells (Starr *et al.*, 1991; Starr *et al.*, 1993; Starr *et al.*, 1994; Andreu and Duarte, 1996) while the Green Sea urchin,



**Fig. 6.** The annual anomalies in the data for (A) total zooplankton (B) total meroplankton, (C) Cirripedia, (D) Decapoda, (E) Polychaeta, (F) Echinodermata and (G) Lamellibranchiata at Station L4 as calculated from the monthly anomalies in the data having removed the average abundances.

*Strongylocentrotus droebachiensis* (Müller), and the Blue mussel, *Mytilus edulis* (Linnaeus), both undergo spawning upon detection of a heat-stable metabolite released by certain phytoplankton species (Starr *et al.*, 1990; Starr *et al.*, 1992). It is this benthic–pelagic coupling that drives the patterns of meroplankton composition at Station L4.

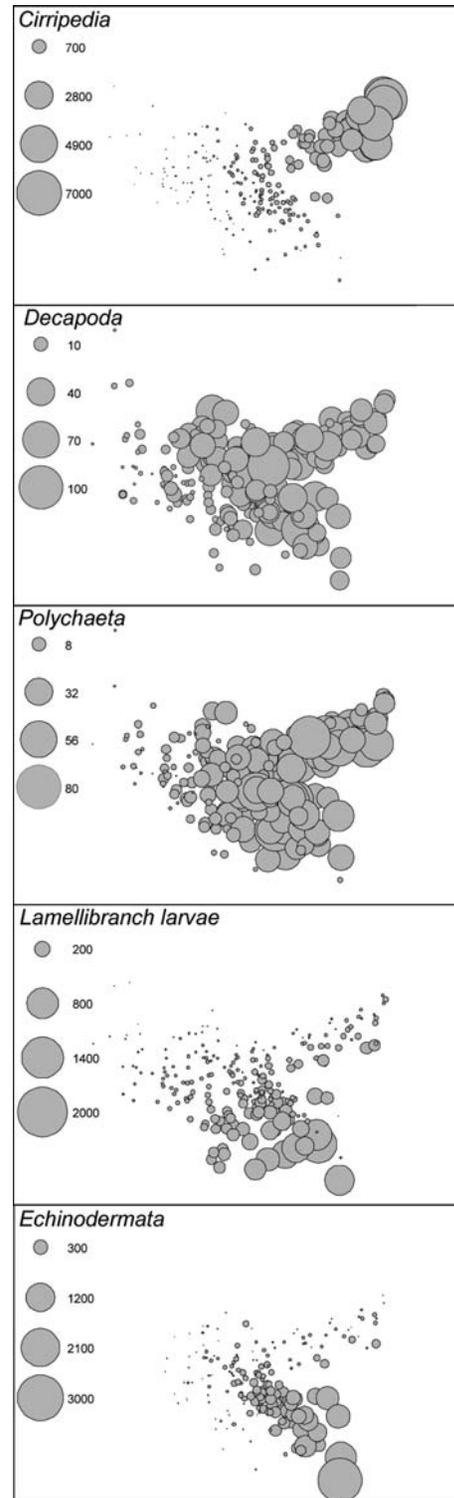
Historical data (Lebour, 1947) show that the larvae of the cirripede *Semibalanus balanoides* (Linnaeus), in



**Fig. 7.** Non-metric multi-dimensional scaling (MDS) ordination of Bray–Curtis similarities among monthly within-year average abundances of the five major meroplankton groups in the study.

particular, undergo their main settlement during March and April (Marine Biological Association of the United Kingdom, 1957). *Semibalanus balanoides* (Linnaeus) is one of those previously mentioned species that initiates spawning upon direct contact with phytoplankton cells (Starr *et al.*, 1991). It is known to store embryos in its mantle cavity until the presence of a food source is detected such as the diatom *Skeletonema costatum* (Gaston *et al.*, 1997) which contributes significantly to the spring bloom at Station L4 (Barnes, 1962). Thus, the timing of the massive release of cirripede larvae during this time period is probably determined by a response to the spring phytoplankton bloom that occurs every year at L4 (Boalch, 1987; Aiken *et al.*, 2004; Southward *et al.*, 2004) and has been observed for the past 20 years. The small but significant increase in cirripede abundance over the past 20 years is responsible for the significant increase seen in total meroplankton abundance over the same time period ( $P$ -value = 0.032) given that cirripede larvae occur in greater numbers than any other group.

Decapod larvae are not as abundant in the plankton community as cirripede larvae. Cirripede larvae are much smaller than decapod larvae and so it is likely that their much greater numbers reflect the lower relative per-individual energetic costs of producing smaller larvae (Thorson, 1946). Historical records from the early 20th century show that, while some decapod species bred throughout the year, many reproduced during the spring and summer (Lebour, 1928; Marine Biological Association of the United Kingdom, 1957) and so larvae are more common in the plankton in these months. Although not discriminated to species, the pattern observed at Station L4 over the last 20 years in this study suggests that the overall seasonal cycle has remained the same, and there is no evidence of a trend in changing abundance over this period.



**Fig. 8.** MDS ordinations of Bray–Curtis similarities among monthly within-year average abundances of the five major meroplankton groups (as in Fig. 7) overlaid with circles proportional in size to abundances of individual major meroplankton groups.

Historical records of the plankton in and around Plymouth Sound (Lebour, 1947; Marine Biological Association of the United Kingdom, 1957) show that polychaete larvae were found in the water column in their highest abundances in the spring and summer months. Timing varied between different polychaete species, but all tended to decrease during the autumn and winter period. The patterns observed in this study are similar. There is a wide range of reproductive strategies among the Polychaeta, and presumably among their larvae, with some polychaete larvae feeding upon other planktonic larvae (Thorson, 1946). Therefore, it may be that some polychaete species release their larvae in response to the available food source provided by other planktonic larvae that in turn are produced as a result of the spring bloom.

During the summer period, there are a number of peaks in echinoderm larval abundance, characterized by rapid increases and decreases. This suggests either that different species are spawning, or that species have different spawning periods and that the larvae themselves do not have a long residence time in the plankton. The historical data show that echinoderm larvae, particularly the ophiopluteii of *Ophiothrix fragilis* (Abildgaard), were common in the plankton in and around Plymouth Sound from July to September (Lebour, 1947). Increases in abundance of echinoderm larvae correlated to increasing sea surface temperatures have been reported from the North Sea (Kirby *et al.*, 2007; Kirby *et al.*, 2008), but although there has been an increase of 0.6°C per decade over the last 20 years at the study site (Smyth *et al.*, in press), there was no significant increasing trend in Echinoderm larval abundances over the same period.

The explosion in lamellibranch larval numbers is probably related to the autumn phytoplankton bloom which provides a readily available food source for the larvae. It may well be that this release occurs in the autumn rather than spring to avoid a higher level of predation by other meroplanktonic organisms that are produced during the spring months, but this has yet to be proven. This dramatic increase in the late summer is known from historical records (Lebour, 1938) with the larvae of *Lima hians* (Gmelin) showing the most pronounced change in abundance. This peak in abundance has occurred annually over the last 20 years at Station L4 and analyses of anomalies show no significant trend of change over the same period.

Variation in community composition throughout the year is a result of the different spawning triggers for the five groups. These groups vary in the time scales in which they appear in the water column and thus determine the observed changes in the composition of the

meroplankton community throughout the year. The seasonal cycles of the five groups examined at L4 exhibit low numbers followed by rapid increases during the spring and, in some cases, autumn months before declining towards the winter period. There is significant seasonal variation in the composition of meroplankton community at Station L4 over the year in terms of the five groups studied, with Cirripedia being the dominant member of the community in March and April and Lamellibranchiata being the dominant member in terms of abundance in September and October. Multivariate analysis shows that seasonal variation accounts for the majority of variability in community composition at the study site (Figs 7 and 8) rather than inter-annual variability, as the same months from each of the 20 years are clustered together on the MDS plot. Similar patterns of long-term variability have been shown in other studies where seasonal variation was more pronounced than inter-annual variation which, in terms of species richness and diversity, remained relatively constant despite a few species showing overall changes in abundance (Pitois *et al.*, 2009).

Cirripedia abundance appears to correspond with the spring bloom and thus the associated increase in sea surface temperature while lamellibranch and echinoderm larvae exhibit their highest numbers during the autumn bloom which is associated with the highest sea surface temperatures seen throughout the year. Decapod and polychaete larvae appear to have less correlation with sea surface temperature as their numbers start to increase as the temperature is still falling in February. However, the highest abundances in both of these groups occur when sea surface temperature is approaching its maximum. Previous studies have highlighted the correlation between timing of peak abundance and sea surface temperature for each of the groups in this study (Edwards and Richardson, 2004). It appears that the coupling between phytoplankton abundance and the release of meroplankton larvae is a driving force in the seasonal cycles of these organisms and, in turn, is linked to sea surface temperature.

Meroplanktonic larvae play an important role in coastal pelagic marine ecosystems. At certain times of the year, usually in conjunction with phytoplankton blooms, they comprise a large percentage of the total zooplankton community and can act as both planktonic predators and a food source for other planktonic predators such as fish (Beaugrand, 2005) and planktivorous zooplankton species thus having a major effect upon community composition. Given this important role that meroplankton play in marine ecosystems, it is important to understand the trends in abundance and seasonality in this group to estimate how these trends might change

in response to various environmental triggers. The availability of long-term data sets such as that from Station L4 allows us to study the temporal variability in the taxa recorded and provides a valuable insight into the long-term cycles in their life-histories. It is important to continue this time series in order to further understand changes that occur over a longer time period than 20 years and to allow us to monitor the effects of possible climate change and northward expansion of species distribution as is being observed elsewhere today (Greve *et al.*, 2005). Further work focusing on a higher level of taxonomic discrimination including the use of molecular methods, and examining the seasonal cycles of individual species or genera will allow a finer picture of annual and seasonal variation in the meroplankton to be generated.

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