Long-term annual and monthly changes in mysids and caridean decapods in a macrotidal estuarine environment in relation to climate change and pollution

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Short title: Annual and monthly changes in mysids and caridean decapods of a macrotidal estuarine environment

Abstract

A 26-year time series of monthly samples from the water intake of a power station has been used to analyse the trends exhibited by number of species, total abundance, and composition of the mysids and caridean decapods in the inner Bristol Channel. During this period, annual water temperatures, salinities and the North Atlantic Oscillation Index (NAOI) in winter did not change significantly, whereas annual NAOI declined. Annual mean monthly values for the number of species and total abundance both increased over the 26 years, but these changes were not correlated with any of the measured physico-chemical/climatic factors. As previous studies demonstrated that, during a similar period, metal concentrations in the Severn Estuary and Bristol Channel (into which that estuary discharges) declined and water quality increased, it is proposed that the above changes are due to an improved environment. The fauna was dominated by the mysids *Mesopodopsis slabberi* and *Schistomysis spiritus*, which collectively contributed 94% to total abundance. Both species, which were represented by juveniles, males, non-brooding females and brooding females, underwent statistically-indistinguishable patterns of change in abundance over the 26 years. When analysis was based on the abundances of the various species, the overall species composition differed significantly among years and changed serially with year. When abundances were converted to percentage compositions, this pattern of seriation broke down, demonstrating that changes in abundance and not percentage composition were responsible for the seriation. As with the number and abundance of species, changes in composition over the 26 years were not related to any of the physico-chemical/climatic factors tested. Species composition changed monthly in a pronounced cyclical manner throughout the year, due to statistically different time-staggered changes in the abundance of each species. This cyclicity was related most strongly to salinity.

Keywords: Cyclicity; estuary; micronekton; salinity; temperature

Introduction

Estuaries are among the most productive of all marine environments and thus provide a rich source of food for a range of fauna (Schelske and Odum, 1961; Bianchi, 2006; Tweedley et al., 2016b). These systems frequently receive, however, large amounts of contaminants from industrial, agricultural and urban activities along their shores and catchments and are subjected to the effects of climate change (Statham, 2012; Robins et al., 2016; Hallett et al., 2017). There is, therefore a need to have reliable methods for detecting and monitoring anthropogenic effects, including those associated with increases in water temperature. As crustaceans, such as mysids, are very sensitive to chemical contaminants and environmental perturbations, they are particularly useful for detecting degradation and remediation (Warwick and Clarke, 1993; Roast et al., 1998; Tweedley et al., 2012; 2016a). Since species of zooplankton and micronekton have short life cycles and vary markedly in abundance among and within years, their use as indicators should ideally be based on long-term annual data that also embrace variations that occur throughout the year (David et al., 2005; Hays et al., 2005).

The macrotidal estuaries of northern Europe, such as the Severn, Thames, Humber and Gironde estuaries, contain exceptionally high levels of suspended solids that are produced by the frictional stress on the seabed that occurs as a result of strong tidal movements (Kirby et al., 2004; Tweedley et al., 2016b). As the combination of extreme tidal action and funnel-shaped topography results in strong vertical mixing, salinity remains homogeneous throughout the water column (Uncles, 1984). Since the high turbidity restricts light penetration, planktonic primary production is low (Kirby and Parker, 1983; Joint, 1984; David et al., 2005). Consequently, the main primary inputs to the food web are detritus and dissolved organic material, most of which is of terrestrial origin (Heip et al., 1995). The main primary consumers in the water column are almost exclusively crustaceans, i.e. mysids, caridean decapods, copepods and euphausiids, with mysids particularly abundant in the Severn Estuary (Williams and Collins, 1986; Bamber and Henderson, 1994).

The Severn Estuary, in south-west England, is the second largest estuary in the United Kingdom, covering an area of 557 km^2, of which 100 km^2 is intertidal (Langston et al., 2003; Langston et al., 2010a). It opens into the wide Bristol Channel, whose innermost southern region is now included within the Severn Estuary Special Area of Conservation (http://jncc.defra.gov.uk/protectedsites/sacselection/sac.asp?EUCode=UK0013030). The Severn Estuary and Bristol Channel together constitute the largest estuarine environment in the United Kingdom, with an area of 4,800 km^2 and a catchment that drains nearly one sixth of the land area of England and Wales (Collins and Williams, 1981). The tidal range is the second highest in the world, with mean high water spring tides of 13.3 m at Avonmouth in the estuary and of 11.8 m at Hinkley Point in Bridgwater Bay in the inner region of the Bristol Channel (http://www.ntslf.org/tides/hilo). Although the Severn Estuary and inner Bristol Channel used to receive large amounts of contaminants, of which metals were of particular concern, total contaminant input has declined over recent decades due to a regional reduction in industrial activity and the implementation of environmental legislation (Duquesne et al., 2006; Jonas and Millward, 2010). The collation of data from four studies undertaken in different years has shown that this has been reflected in a reduction in the concentrations of heavy metals in the sediment and of the prevalence of reduced oxygen concentrations (Jonas and Millward, 2010).

The records of the UK Meteorological Office Hadley Centre (via the British Atmospheric Data Centre) demonstrate that the annual mean sea surface temperatures (SSTs) in the Bristol Channel underwent an overall increase of ~1.3°C between 1905 and 2002 (Genner et al., 2004). While the annual means of the monthly water temperatures recorded *in* *situ* at Hinkley Point increased between 1986 and 1989, they subsequently remained relatively constant until 2010 (Henderson et al., 2011b).

As strong tidal currents often make it difficult to use traditional methods to sample effectively the fauna of estuaries with very large tidal ranges, samples collected from the large volume of water in the cooling intakes at nuclear power stations have sometimes been employed for this purpose (Claridge et al., 1986; Marshall and Elliott, 1998; Power et al., 2000). The use of this method at Oldbury in the Severn Estuary and Hinkley Point in the Bristol Channel has provided a very effective standardised technique for obtaining medium or longer term quantitative samples of fish and also occasionally of crustaceans (e.g. Potter et al., 1986; Henderson and Bird, 2010). The resultant data indicate that, at Hinkley Point between the early 1980s and late 2000s, the abundance and number of species of fish increased, with the abundance of several of the most numerous fish and macro-crustacean species undergoing rapid exponential increases or decreases (Genner et al., 2004; Henderson et al., 2006; Henderson, 2007; Henderson and Bird, 2010). While, for some species, such changes were associated with water temperature, salinity and the North Atlantic Oscillation Index (NAOI), no such correlations were found with many other species (Henderson et al., 2011b). When the biotic variables increased in the absence of such correlations, it is possible that this was due to an improvement in water quality (Henderson and Bird, 2010). Although the annual mean numbers of species of these fish and macro-crustaceans did not undergo a long-term increase, the prevalence of several of these species increased during the study period. On the basis of multivariate analyses, the species composition of fish underwent two abrupt changes during that period, the first linked to changes in the NAO and the second to increases in water temperature (Henderson, 2007; Henderson et al., 2011b). On the other hand, the macro-crustaceans did not begin to form a distinct group until the 2000s (Henderson et al., 2011b).

The NAOI, which is a measure of the sea level pressure gradient between Iceland and Gibraltar (Jones et al., 1997), has also been implicated in changes in the composition and abundance of fishes in the Thames Estuary, UK (Attrill and Power, 2002) and in Narragansett Bay, USA (Collie et al., 2008). As this oscillation has its strongest influence in winter, exploration of its relationship with biotic variables has sometimes focused on the winter values for its index (Osborn, 2011; Hughes et al., 2017).

The species composition of fishes in the Severn Estuary undergoes pronounced cyclical changes during the year, reflecting, in particular, the sequential immigration and emigration of marine estuarine-opportunist species (Claridge et al., 1986; Potter et al., 1986), a trend paralleled in the Elbe and Scheldt estuaries (Thiel and Potter, 2001; Maes et al., 2005). The abundance of each of the five common mysid species at Hinkley Point in the Bristol Channel, which belong to a group that constitute key prey for the young of many fish and crustacean species and are an important link in food chains (Elliott et al., 2002), also peaks at varying times of the year (Bamber and Henderson, 1994). The spatial distribution of zooplankton along the highly turbid Charente Estuary in France was related, in particular, to salinity (Modéran et al., 2010), as with several mysid species in the Westerschelde Estuary in the Netherlands (Rappé et al., 2011). The temporal variations in the zooplankton community of the Charente Estuary were more closely related, however, to water temperature than to salinity (Modéran et al., 2010).

The first aim of this study was to explore whether the annual means for monthly water temperatures and salinities at Hinkley Point in the Bristol Channel and the NAOI and winter NAOI showed an overall increase or decrease between 1988 and 2013. The trends exhibited by the number of species and total abundance of mysids and caridean decapods were then analysed to determine whether they changed over the same period and, if so, whether they were related to one or more of the above abiotic variables. Any changes in the biotic variables were considered in the context of the reductions that have occurred, since the 1970s, in the concentrations of contaminants and the prevalence of reduced oxygen concentrations. Data were next used to test whether the species composition of the mysid and caridean decapod community changed in a serial manner over the 26 years and, if so, whether it was related to any of the above abiotic variables. The hypothesis was tested that the species composition changed cyclically during the year, in relation to the pronounced cyclical changes that occur in water temperature and/or salinity, reflecting different patterns of sequential monthly changes by individual species and/or groups of species.

Materials and methods

Sampling

Samples were collected from the cooling-water intake at Hinkley "B" power station in Bridgwater Bay in the inner Bristol Channel, the latter term retained in this paper as Hinkley Point has normally been referred to as located in this region rather than the outer Severn Estuary (http://jncc.defra.gov.uk/protectedsites/sacselection/sac.asp?EUCode=UK0013030). The entrance of the 3.45 m diameter intake pipe is located 640 m from the shore, with water pumped from depths ranging from 8 to 18 m, depending on the state of the tide. Four centrifugal pumps deliver a constant flow of 7.5 m^3 s^{-1} through separate rotating metal screens (10 mm square mesh). Full details of intake configuration and sampling method are given in Henderson and Seaby (1994; 1999).

Mysids and caridean decapods were sampled monthly between January 1988 and December 2013, except in the few months when sampling was prevented due to power station maintenance. Samples were collected midway between spring and neap tides, commencing at high water, by placing a plankton net (150 µm mesh) in the intake forebay of the power station for 1 h. Although catch rates at power stations with an intake in clear water tend to be greater at night (Whitehouse, 1986), this does not apply to Hinkley Point because very little light penetrates the turbid water at this location at any time of the day (Henderson and Holmes, 1991). Each sample was immediately fixed in 4% formalin in seawater. Water temperature and salinity at the time of sampling were recorded to the nearest 0.1 °C and 0.1, respectively. Note that the temperatures recorded between 1981 and 2002 at Hinkley Point, where the current study of mysids and caridean decapods was undertaken, were highly correlated with the SSTs recorded for those years in the Bristol Channel by the UK Meteorological Office Hadley Centre, via the British Atmospheric Data Centre (Genner et al., 2004). Monthly values of NAOI were extracted from https://crudata.uea.ac.uk/~timo/datapages/naoi.htm.

In the laboratory, each sample was washed through a 500 μm mesh stainless steel sieve with tap water and the retained mysids and caridean decapods identified to species, using a dissecting microscope, and the number of each recorded.

Univariate analyses of annual environmental and biotic variables

For each year between 1988 and 2013, the mean of the monthly values in each year (subsequently referred to as 'annual mean value') and its 95% confidence limits were calculated for water temperature, salinity and NAOI and for the numbers of species and the total abundance of mysids and caridean decapods (no. h^{-1}). The mean of the NAOI for just the winter months of each year, i.e. December to February, was also calculated, with the value for a given year represented by the January and February of that year and the December of the previous year. Pairwise Pearson's correlations coefficients were calculated for the relationship between the resultant annual means for each of the above environmental and biotic variables across the 26 years to determine the extent and direction of linear association of these variables over that period. When significant, the regression equation relating the dependent and independent variables was determined. Preliminary analyses demonstrated that the relationship between the total abundance of mysids and caridean decapods and year was described better by using a log-linear than linear relationship.

Multivariate analyses of annual biotic variables

All multivariate analyses employed PRIMER v7 (Clarke and Gorley, 2015). The abundance of each mysid and caridean decapod species in each monthly sample of each year was square-root transformed to down-weight the effect of taxa with consistently high abundances (Clarke and Warwick, 2001). These data were used to produce a Bray-Curtis resemblance matrix, which was subjected to two-way Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson et al., 2008) to determine whether species composition differed among years (26 levels; 1988-2013) and months (12 levels). As there was no replication within a month, the year × month interaction term was employed as the residual, thus providing a sound and conservative basis for assessing the statistical significance of the two main effects. The null hypothesis that there were no significant faunal differences among years or months was rejected if the significance level (P) was < 0.05.

To investigate the year effect, the square-root transformed abundance of each species in each month of each year was averaged to provide a single value for each species in each of the 26 years. These data were used to produce a Bray-Curtis resemblance matrix, which was subjected to hierarchical agglomerative cluster analysis to produce a dendrogram. The same matrix was then used to construct a non-metric Multidimensional Scaling (nMDS) ordination plot (Clarke, 1993). A bubble, whose size represents the annual mean abundance for the given year, was then superimposed on the point for each year.

To remove the influence of differences in overall abundances among years, the average of the monthly abundances of each species in each year was standardised, i.e. converted to a percentage contribution and square-root transformed (Clarke and Warwick, 2001). As above, these data were used to construct a Bray-Curtis resemblance matrix, which was subjected to cluster analysis and nMDS ordination. Segmented bubbles of proportional sizes, representing the square-root transformed percentage contributions of the three most abundant species, which contributed 97% to the total number of individuals (see Results), were overlaid on the nMDS plot.

The RELATE procedure (Clarke and Gorley, 2015) was used to determine whether species composition progressed in a serial manner with year, when the average abundance of each species in each year was (i) square-root transformed and (ii) standardised and square-root transformed.

A shade plot was developed to detect visually whether the abundances of any of the full suite of species changed over the 26 years. The shade plot was constructed from the square-root transformed average of the monthly abundance of each species in each year. The depth of shading, ranging from grey through to black, represents increasing values for the transformed abundance of that species, while a white space indicates that the species was not collected in that year (Clarke et al., 2014; Valesini et al., 2014). The order of species on the *y* axis of the plot is arranged according to the results of a cluster analysis produced from a Bray-Curtis resemblance matrix, derived from the above square-root transformed abundances.

The pattern of change in the abundances of individual species across the 26 years was also examined using coherent species curves (Somerfield and Clarke, 2013). This procedure employs a cluster analysis of species similarities, derived from a Bray-Curtis resemblance matrix constructed from square-root transformed data, to identify species or groups of species, whose patterns of abundance across the samples are indistinguishable and differ statistically ($P < 0.05$) from that of other species or groups of species (Veale et al., 2014).

The BEST test (Clarke et al., 2008) was used to determine whether the species composition was related to water temperature, salinity, NAOI and winter NAOI, either singly or in combination. As these latter two variables use a subset of the same data, i.e. NAOI values for particular months, they are not independent and thus combinations including both of these variables were excluded from the analyses. Prior to using this routine, draftsman plots (Clarke and Gorley, 2015) of the values for each pair of the four environmental variables showed that the data for none of these variables were skewed and those of no pair were highly correlated (all $r < 0.95$). The environmental data were then normalised so that all variables were on a common scale. The null hypothesis for the BEST test, that the pattern of rank orders of similarity between the faunal resemblance matrix and environmental data was not related, was rejected if the significance level P was < 0.05. The value for the test statistic (ρ) reflects the strength of the correlation between the composition of the fauna and the environmental data, with ρ values ranging from ~ 0 (little correlation) to ~ 1 (near-perfect correlation).

Multivariate analyses of monthly compositions

The square-root transformed abundance of each species in each corresponding month in each of the 26 years was averaged, thereby producing a single value for each species in each month. These data were used to construct a Bray-Curtis resemblance matrix, which was subjected to nMDS ordination, with lines drawn between the points for each successive month in the resultant nMDS ordination plot. RELATE was employed to determine whether species composition progressed in a cyclical manner. Bubbles, whose sizes in each calendar month represent the average salinity and water temperature, the two variables most closely correlated individually with composition, were then superimposed on the points for each month in their respective plots. Coherent species curves were constructed to identify which groups of species, if any, exhibited a similar pattern of abundance across months.

Following the approach for the annual data, the mean monthly values for water temperature and salinity were subjected to BEST to determine whether the species composition throughout the year was related to any one or a combination of those environmental variables. Draftsman's plots indicated that the data for none of the variables were skewed and consequently did not require transformation prior to normalisation and subjection to BEST.

Results

Annual trends in environmental and biotic variables

Annual mean water temperatures between 1988 and 2013 ranged only from 12.5 to 14.5 °C and showed no conspicuous tendency to increase or decline over those years (Fig. 1a), which is consistent with the results of Pearson's correlation analysis ($r = -0.058$, $P = 0.777$). Although annual mean salinities fluctuated to a greater degree across the 26 years, with values ranging from 22.5 to 29.5, they also did not obviously tend to increase or decrease (Fig. 1b), again supported by the results of correlation analysis ($r = -0.312$, $P = 0.120$). In contrast to temperature and salinity, NAOI exhibited a marginally significant decline between 1988 and 2013 (Fig. 1c), when using values for the whole year ($r = -0.401$, $P = 0.042$), but not when employing only those for the winter months ($r = -0.337$, $P = 0.093$).

Although the mean monthly numbers of species oscillated among years, they still clearly tended to increase between 1988 and 2013 (Fig. 2a), with that trend significant ($r = 0.724$, $P = 0.001$). Mean monthly total abundance varied markedly, ranging from <100 no. h^{-1} in 1988 to 1999 to as high as ~600 no. h^{-1} in 2002 and 1,250 no. h^{-1} in 2007 (Fig. 2b), but with an overall tendency for the natural logarithm of abundance to increase with time ($r = 0.604$, $P = 0.001$).

The annual mean number and total abundance of mysids and caridean decapods across the 26 years were not correlated significantly with water temperature, salinity, annual NAOI or winter NAOI (Table 1). The relationships in each case remained non-significant when abundance was log transformed.

Multivariate analyses of the crustacean community

Three families, representing nine genera and ten species, were recorded in the samples (Table 2). The fauna was dominated by the Mysidae, which contributed >99% to the total number of individuals, with *Mesopodopsis slabberi* and *Schistomysis spiritus* contributing 54.5 and 39.1%, respectively, to that overall total. As the carapace lengths of *M. slabberi* and *S. spiritus* ranged from 0.6 to 3.3 mm (S. Plenty, unpublished data), the maximum closely approximating that recorded for the individuals of these species retained when using a larger (10 mm) mesh on the intake screens of the same power station (Bamber and Henderson, 1994). While juveniles, males, non-brooding females and brooding females of *M. slabberi* and *S. spiritus* were sampled in certain periods, both species were present in very low numbers or absent in other months (see later).

On the basis of PERMANOVA, species composition differed significantly among years and months (Appendix 1). However, the contribution of 80.2% by month to the total mean squares far exceeds the 12.8% by year.

Two main clusters and one outlier (2007) are present on the dendrogram derived from square-root transformed abundances for the 10 species recorded between 1988 and 2013 (Fig. 3a). The first cluster represents mainly years in the early part of this period, while the second comprises two groups, the first containing many of the years between 1995 and 1999 and 2009 to 2013 and the second many of those between 2000 and 2010. These trends are essentially present in the MDS ordination plot, derived using the same resemblance matrix, with most years prior to 2001 lying to the left of those of later years (Fig. 3b). Furthermore, the sizes of the bubbles, which represent the total abundance, show a marked tendency to increase from left to right on the plot. RELATE demonstrated that species composition followed a weak, but significant linear sequence (seriation) over the 26 years ($\rho = 0.275$, $P = 0.002$).

In contrast to the trend for the compositions of sequential years to form relatively substantial groups when the abundances were square-root transformed and subjected to cluster analysis (Fig. 3a), this was not the case when the dendrogram was derived after standardisation and transformation of the abundances (Fig. 3c). Furthermore, while the sample for 2007 was a distinct outlier on the dendrogram constructed from non-standardised data, it is similar to those for 2006, 2002 and 1997. There was no consistent trend in this latter dendrogram for the points representing the compositions to progress in a sequential direction with year across the nMDS ordination plot (Fig. 3d). There was a shift, however, from left to right with year when the percentage contributions of the three most abundant species were superimposed on the nMDS plot in Fig. 3d. RELATE demonstrated that, following this analysis, the pattern of differences in species composition was not significantly related to the sequence of 26 years ($\rho = 0.110$, $P = 0.075$).

The shade plot emphasises that the mysid species *Mesopodopsis slabberi* and *Schistomysis spiritus* overwhelmingly dominated the mysids and caridean decapods, with their abundances increasing after the year 2000 (Fig 4). These two species, together with *Gastrosaccus spinifer* and *Crangon crangon,* were recorded in each of the 26 years and another three species (*Neomysis integer*, *Schistomysis kervillei* and *Praunus flexuosus*) in >80% of the years. Among the three least abundant species, *Pasiphaea sivado* and *Anchialina* *agilis,* were recorded as early as 1989 and in four of the next eight years and in five and two of the last five years, respectively (Fig. 4). *Paramysis arenosa* was recorded in only five years and in only one month in four of those years.

Coherent species curves demonstrate that the patterns of change in the relative annual abundances of the ten species formed seven groups, of which five contained a single species (Fig. 5). In the first group, the patterns of abundance of the two dominant species, *M. slabberi* and *S. spiritus,* together with the far less abundant *C. crangon,* were statistically indistinguishable across the 26 years. For example, the abundances of each of these species peaked sharply in 2002 and 2007 (Fig. 5a). In the second group, the relative abundances of the other two mysids, *S. kervillei* and *N. integer*, were low between 1988 and 1995 and high in 2002 and 2008 and increased sequentially between 2011 and 2013 (Fig. 5b). The third most numerous species *G. spiritus* (Table 2) and *Praunus flexuosus* formed a discrete group, with the abundance of the former peaking in 1990, 1993, 2000 and 2013 and the latter in 1993, 2001, 2010 and 2013 (Fig. 5c, 5d). As the remaining three species were never abundant in any year and absent in at least 50% of years, caution must be exercised in drawing conclusions from the annual abundances of these species.

The results of BEST showed that the trends exhibited by the rank order of resemblance of annual species compositions among the 26 years was not significantly correlated with the annual mean value for either temperature, salinity, NAOI or winter NAOI or with any combination of those variables ($P > 0.05$).

Monthly trends in environmental and biotic variables

Mean monthly salinities increased sequentially from a minimum of 24 in February to 29 in September and October and then decreased to 26 in December (Fig. 6a). Mean monthly water temperatures increased from a minimum of 7 °C in January and February to a maximum of ~20 °C in July and August and then declined to 8 °C in December (Fig. 6b).

The monthly points on the nMDS ordination plot, derived from the square-root transformed abundances of the ten species, progressed in a well-defined circular manner, emphasising that species composition underwent a very pronounced cyclical change throughout the year (Fig. 7a). This conspicuous trend was confirmed by the RELATE test for cyclicity ($\rho = 0.535$, $P = 0.001$). The sequential changes in composition closely tracked the trends exhibited by both salinity and water temperature (Fig. 7b,c). The BEST test demonstrated, however, that the changes in composition were related most closely to salinity ($\rho = 0.845$, $P = 0.001$) and that, while also related to water temperature ($\rho = 0.603$), a combination of the data for these two variables did not improve the correlation ($\rho = 0.794$).

Coherent species curves demonstrate that the pattern of abundance of each of the ten species throughout the year was significantly different. This reflects a sequential shift in the month(s) when the abundance of each species peaked. For example, the abundance of *Schistomysis kervillei* peaked in January, *P. flexuous* and *N. integer* in February, *G. spinifer* in April/May, *C. crangon* in June and July, *M. slabberi* in August, *S. spiritus* in October and November and *Anchialina agilis* in October to December (Fig. 8). Although the abundance of each species tended to peak at a particular time of the year, the duration of the period over which the different species were abundant varied.

Discussion

Annual trends in environmental variables

This study demonstrated that annual mean water temperatures at Hinkley Point in the Bristol Channel did not change significantly between 1988 and 2013, the duration of the current study of mysids and caridean decapods at that location. This parallels the lack of a trend in the SSTs, extracted from the records of the UK Meteorological Office Hadley Centre for the Bristol Channel over the same time period, with Pearson's correlation $r = 0.020$, $P = 0.923$ (https://www.webeaver.com/down?rid=6b9f7f1a378482330a004eafab9d68a1&sid=72610). Although there is indisputable evidence from the Hadley data that, over a much longer period of 1905 to 2002, the SSTs in the Bristol Channel increased markedly (Genner et al., 2004), the lack of an increase in temperatures between 1988 and 2013 demonstrates that there has been a levelling of this trend in recent years. As with annual mean temperatures, neither the minimum nor maximum annual temperatures at Hinkley Point exhibited a significant linear change between 1988 and 2013.

Although temperature and salinity at Hinkley Point did not undergo an overall change between 1988 and 2013, such a change was exhibited by annual NAOI but not by winter NAOI, which underwent far greater intra-annual variations.

Annual trends in biotic variables

In contrast to the lack of a significant change in water temperature, salinity and winter NAOI between 1988 and 2013, the annual mean monthly number of species and total abundance of mysids and caridean decapods both increased significantly over those 26 years. The abundance of mysids in the turbid environment of the Gironde Estuary did not change, however, over a similar period (David et al., 2005). In the inner Bristol Channel, *Mesopodopsis slabberi* and *Schistomysis spiritus*, which together contributed 93.6% to the total number of mysids and caridean decapods, exhibited statistically indistinguishable trends in abundance between 1998 and 2013. These trends were thus largely responsible for the significant and positive relationship between overall abundance and year. Although no additional species appeared in any month during the last 17 of the 26 years sampled, rare species tended to occur more frequently in the monthly samples from later years. This feature, together with the tendency for the number of months in which moderately common species were present in a year to increase, accounts for the increase in annual mean number of species with time. This parallels the situation recorded by Henderson et al. (2011b) for macrocrustaceans and fish at Hinkley Point during a similar period.

The lack of a relationship between the abundance of mysids and caridean decapods at Hinkley Point in the inner Bristol Channel and NAOI contrasts with the positive relationship found by Attrill and Power (2002) to exist between the abundance of the juveniles of marine fish species in the Thames Estuary and this index (Attrill and Power, 2002). As negative and positive NAOs result in colder and warmer SSTs than average, respectively, the NAO influences the extent of the differential between marine and estuarine water temperatures. Attrill and Power (2002) thus proposed that such differences in water temperatures allow the juveniles of marine fish species to facultatively exploit their most appropriate thermal habitats. The absence of a relationship between the total abundance of mysids and caridean decapods and NAOI could therefore reflect the waters of the inner Bristol Channel consistently representing a far more marine environment than the Thames Estuary and consequently with temperatures that differ less markedly from those of oceanic waters.

The lack of a significant relationship between both the number of species and total abundance and the water temperature, salinity and annual and winter NAOI strongly suggests that these two biotic variables are responding to other factors, such as changes in the concentrations of contaminants. Although data for such concentrations in the Severn Estuary and inner Bristol Channel are only available for some years, those data still demonstrate that, in the period between the years preceding the current study and the mid 2000s, there was a decline into this estuarine environment, of the input of metals, such as Hg, Pb, Cu and Zn, thereby accounting for the reduction in the concentration of such metals in the suspended matter and water column (Jonas and Millward, 2010). It is thus proposed that the overall increases in the annual mean of both the number of species and total abundance of mysids and caridean decapods during the present study reflect, in part, a response to the beneficial environmental effects of the introduction of stricter pollution controls, namely the Environmental Pollution Act (1990) and Integrated Pollution Prevention Control Directive (1996), and to closures of major industries (Langston et al., 2010b; Henderson et al., 2011a). These benefits include an improvement in overall sediment and water quality, including increased oxygen concentrations, and a reduction in the accumulated burdens in estuarine bio-indicator species in this previously heavily-polluted, estuarine environment (Duquesne et al., 2006; Jonas and Millward, 2010; Langston et al., 2010b).

While the annual mean number of both the species and total abundance of mysids and caridean decapods were always greater in the later than earlier years of the study, the mean abundances tended to level off in the recent years, recognising that the highly elevated value for 2007 was clearly an outlier. The levelling of annual mean abundances during more recent years suggests that the influence of the legislative pollution controls introduced in the 1990s had taken effect.

In the context of metal contamination, mysids have been shown to move away from areas containing Cd, when oxygen concentrations were low (Roast et al., 2002). Furthermore, the abundance of *M. slabberi* increased over the study period, during which Pb, to which this mysid is particularly susceptible (Sardo et al., 2005), declined markedly in concentration (Duquesne et al., 2006; Jonas and Millward, 2010). Since the intakes of power stations extract large numbers of mysids from their surrounding environment, it is also possible that the closure of several power stations during the period of this study may have contributed to the increase in the abundance of several crustacean and fish species in the inner Bristol Channel (Henderson et al., 2011a).

Phytoplankton concentrations in the North Sea and the Atlantic Ocean increased in the 1980s (Reid et al., 1998). However, as the inner Bristol Channel and Severn Estuary are exceptionally turbid, phytoplankton concentrations in this estuarine environment are very low (Kirby and Parker, 1983; Joint, 1984). Furthermore, in turbid estuaries, mysids feed predominantly on detritus and members of the detrital-microbial loop (Henderson et al., 1992; Vilas et al., 2008). Consequently, it seems unlikely that any changes in phytoplankton concentrations would have been sufficient to exert a marked influence on the abundances of the mysid and caridean decapod species in the inner Bristol Channel.

The serial change in species composition between 1988 and 2013, based on square-root transformed species abundances, was significant, but the correlation with a linear sequence was not particularly strong. Furthermore, this linear sequence was determined by increases in overall abundance rather than species composition alone, since it broke down after conversion of the abundances to percentages. The differences between using non-standardised and standardised data are visually clear from both the dendrograms and nMDS ordination plots, with the samples for sequential years tending to progress from left to right in the former but not in the latter (Fig. 3).

Cyclical inter-annual changes in biotic and environmental variables

The peaks in abundances of the main fish species in the Severn and other northern European estuaries form a time-staggered sequence throughout the year which, through the use of multivariate procedures, have been shown to result in species composition changing in a well-defined cyclical manner during the year (Potter et al., 1986; Thiel and Potter, 2001; Maes et al., 2005). Although the abundances of the main species of crustaceans at Hinkley Point and of zooplankton indicator species in the Clarente Estuary had previously been demonstrated to peak at more or less sequentially different times (Bamber and Henderson, 1994; Henderson and Bird, 2010; Modéran et al., 2010), the extent to which these trends were reflected in cyclical changes in composition was not explored.

The use of coherent species curves in the present study proved particularly useful as it revealed that, unlike the trends with annual data (see above), the monthly patterns of abundance of each species during the year at Hinkley Point were statistically unique. The pronounced tendency for the abundances of each species to peak in different month(s) would reduce any potential for inter-specific competition for food and/or spatial resources. The nMDS ordination plots illustrate that the time-staggered changes in the monthly abundances of the ten species of mysids and caridean decapods at Hinkley Point led to pronounced cyclical changes in composition throughout the year. For the first time for any estuarine invertebrate fauna, the validity of this cyclical trend was confirmed by the use of RELATE, with the high ρ and probability values demonstrating statistically that the sequential circular change in the composition of the mysid and caridean decapod fauna at Hinkley Point is very well defined. Although this cyclicity was strongly related to salinity, and to a lesser extent temperature, the combination of these two variables did not improve the relationship beyond employing salinity on its own.

Since the cyclicity in community composition was strongly related to salinity and driven by the two overwhelmingly dominant species, *S. spritus* and *M. slabberi*, the salinity ‘preferences’ of these species will be important in determining this pattern. It is therefore relevant that a detailed study of mysid distributions in the Bristol Channel and Severn Estuary showed that, in those waters, *S. spiritus* was most abundant in salinities ranging from 27 to 34 (Williams and Collins, 1984), and that the current study in the inner Bristol Channel demonstrate that this species was particularly abundant between July and November when salinities were greatest. This species also occurs at the upper end of salinities in the Mondego and Westerschelde estuaries elsewhere in Europe (Azeiteiro and Marques, 1999; Rappé et al., 2011). *Mesopodopsis slabberi* peaked in abundance in the inner Bristol Channel in August and September, when salinities were at their maxima (see also Collins and Williams, 1982), and was absent in January and February when salinities were lowest. It was most abundant, however, in far lower salinities in the Mondego, Guadalquivir and Westerschelde (Azeiteiro and Marques, 1999; Vilas et a., 2009; Rappé et al., 2011) and has been recorded from salinities ranging from 1.3 to 43 (Wittmann, 1992). These pronounced differences emphasise that this species is highly euryhaline and readily able to adapt to marked variations in salinity regime.

Other less abundant species, such as *N. integer*, that occur in the winter months also contributed to this cyclicity, since the correlation with perfect cyclicity is improved from a ρ of 0.44, when including the two overwhelmingly dominant species, to 0.53 when data for all ten species were incorporated. The results of Modéran et al. (2010), derived from data for samples collected along the length of the Clarente Estuary, pointed to salinity influencing the spatial distribution of the zooplankton whereas temperature played a greater role in regulating temporal variations.

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List of Figures

Fig. 1. Mean monthly values and 95% confidence limits for (a) water temperature and (b) salinity at Hinkley Point in the inner Bristol Channel and (c) the North Atlantic Oscillation Index (NAOI) are shown for each year between 1988 and 2013. Corresponding values for NAOI in the winter months of a year (i.e. December of the previous year and January and February of the current year) are given in (d).

Fig. 2. Mean monthly values and 95% confidence limits for (a) number of species and (b) total abundance of mysids and caridean decapods at Hinkley Point in each year between 1988 and 2013.

Fig. 3. Cluster dendrograms and nMDS ordination plots, constructed from resemblance matrices using the annual mean abundances of each species in each year between 1988 and 2013. (a) and (b) were constructed using square-root transformed abundances, while (c) and (d) employed standardised and square-root transformed abundances. Points for each year are overlaid with (b) bubbles showing the mean abundances of individuals in that year, and (d) with segmented bubbles showing the percentage contributions of the three most abundant species in that year.

Fig. 4. Shade plot showing the mean of the square-root transformed abundance h^{-1} of each species at Hinkley Point in each year between 1988 and 2013. White space indicates that a species was not collected in that year, while depth of shading from light grey to black denotes the relative abundance of a species.

Fig. 5. Coherent species curves showing mean square-root transformed monthly abundance h^{-1} of each species at Hinkley Point in each year between 1988 and 2013. Species with the same statistical pattern of abundance over time are shown on the same plot.

Fig. 6. Mean monthly values and 95% confidence limits for (a) salinity and (b) water temperature at Hinkley Point between 1988 and 2013.

Fig. 7. nMDS plots constructed from the mean abundance of each species at Hinkley Point in each corresponding month between 1988 and 2013 are shown in (c), (d) and (e). Points in (d) and (e) are overlaid with bubbles of proportionate sizes representing salinity and water temperature, respectively.

Fig. 8. Mean monthly abundances and 95% confidence limits for the ten mysids and caridean decapods recorded at Hinkley Point between 1988 and 2013.

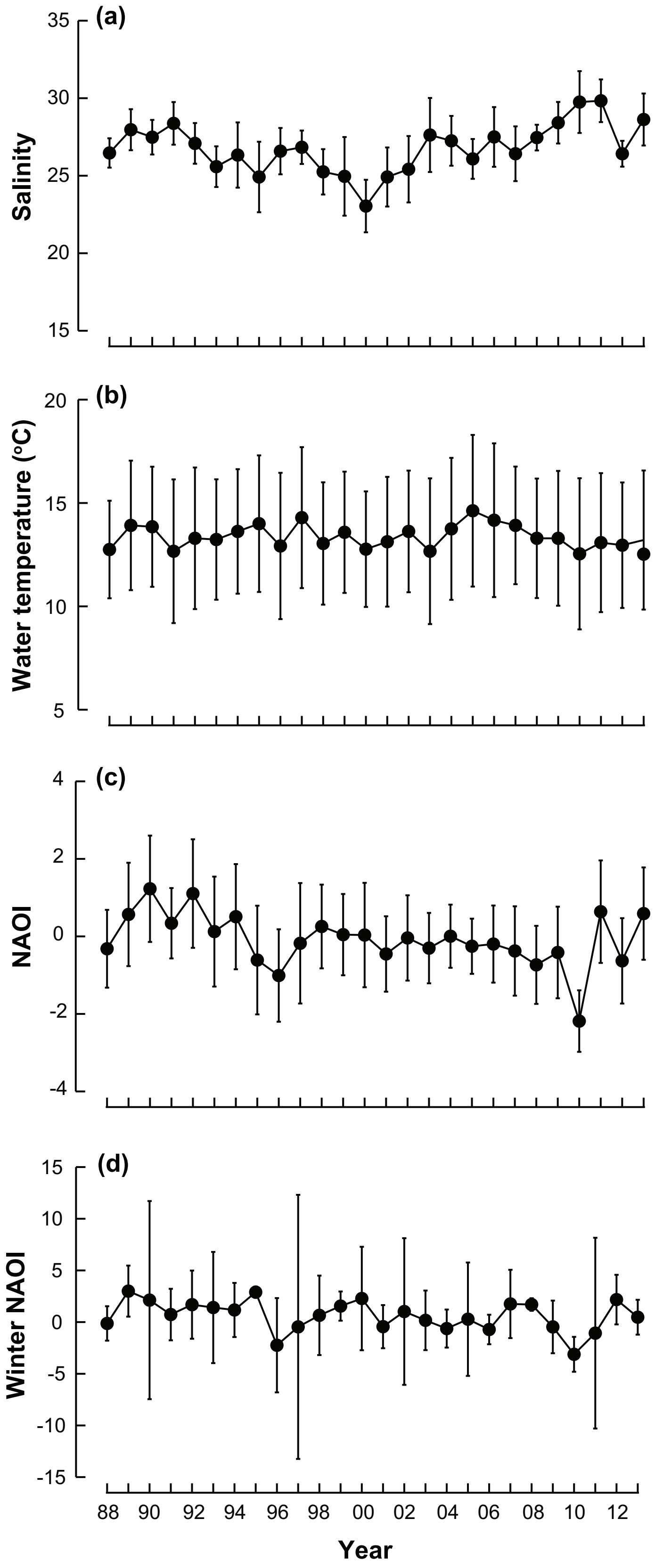

(a)
Salinity
35
30
25
20
15
(b)
Water temperature (°C)
20
15
10
5
(c)
NAOI
4
2
0
-2
-4
(d)
Winter NAOI
15
10
5
0
-5
-10
-15
88
90
92
94
96
98
00
02
04
06
08
10
12
Year

Fig. 1

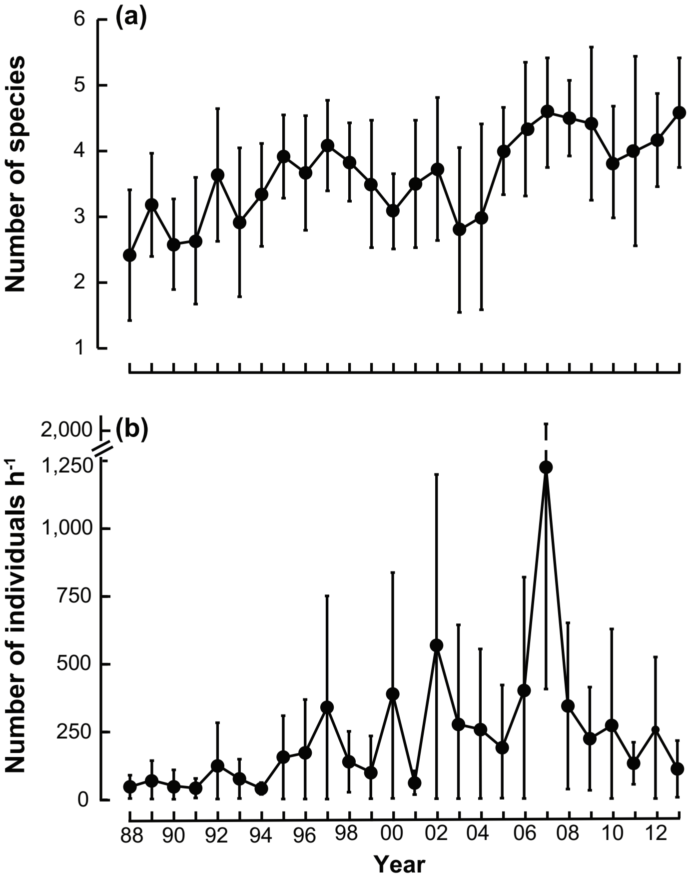
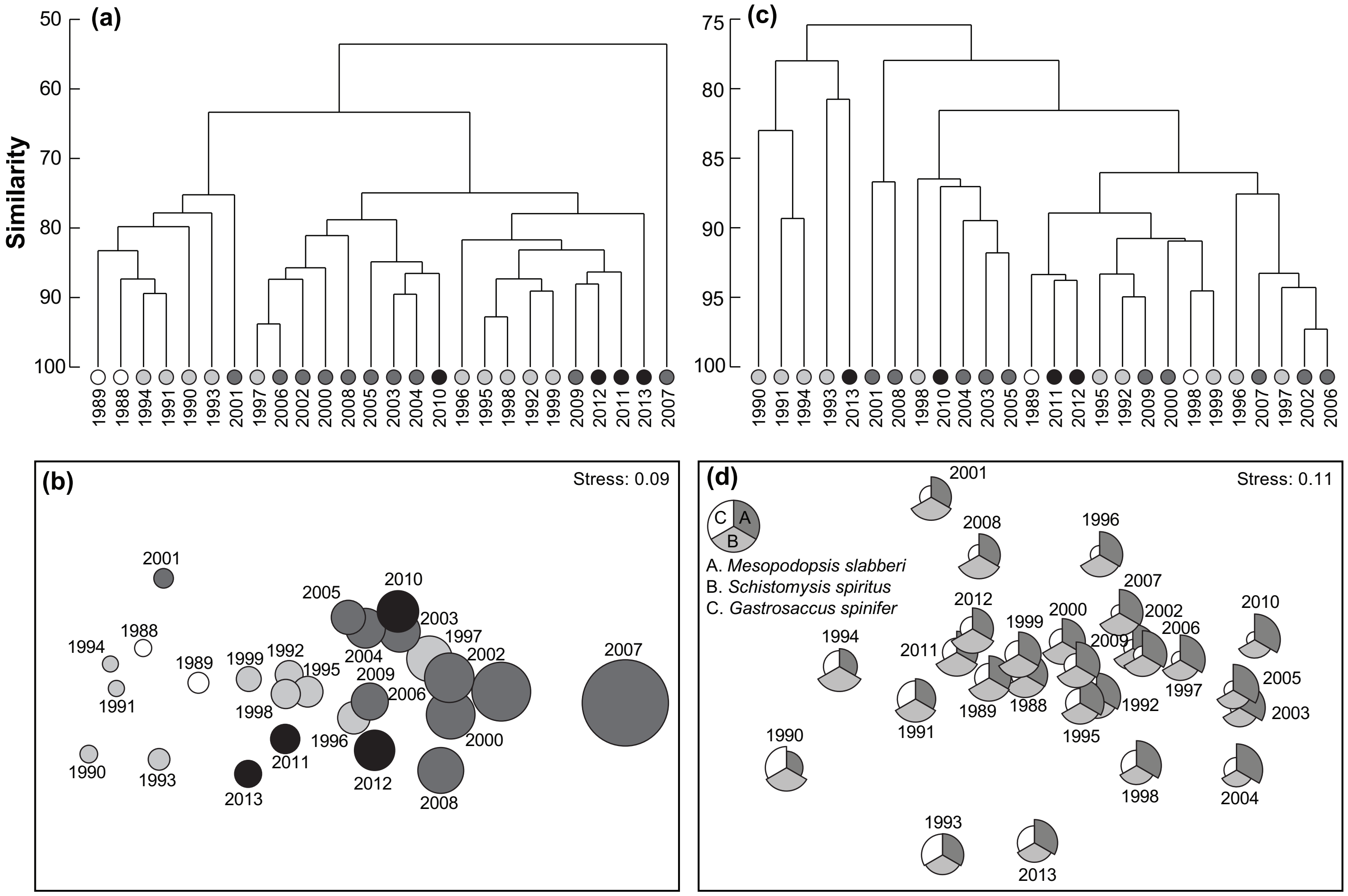

(a)
Number of species
1
2
3
4
5
6
(b)
Number of individuals h-1
0
250
500
750
1,000
1,250
2,000
88
90
92
94
96
98
00
02
04
06
08
10
12
Year

Fig. 2


(a)
Similarity
50
60
70
80
90
100
1989 1988 1994 1991 1990 1993 2001 1997 2006 2002 2000 2008 2005 2003 2004 2010 1996 1995 1998 1992 1999 2009 2012 2011 2013 2007
(b)
Stress: 0.09
2001
1988
1994
1991
1989
1999
1992
1995
1998
2005
2010
2003
2004
1997
2002
2009
2006
2007
1990
1993
2011
2013
1996
2012
2000
2008
(c)
75
80
85
90
95
100
1990 1991 1994 1993 2013 2001 2008 1998 2010 2004 2003 2005 1989 2011 2012 1995 1992 2009 2000 1998 1999 1996 2007 1997 2002 2006
(d)
Stress: 0.11
C
A
B
A. *Mesopodopsis slabberi*
B. *Schistomysis spiritus*
C. *Gastrosaccus spinifer*
2001
2008
1996
2007
2012
2002
2010
1994
1999
2000
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2011
1997
2005
1989
1988
1992
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1991
1995
1990
1998
2004
1993
2013

Fig. 3.

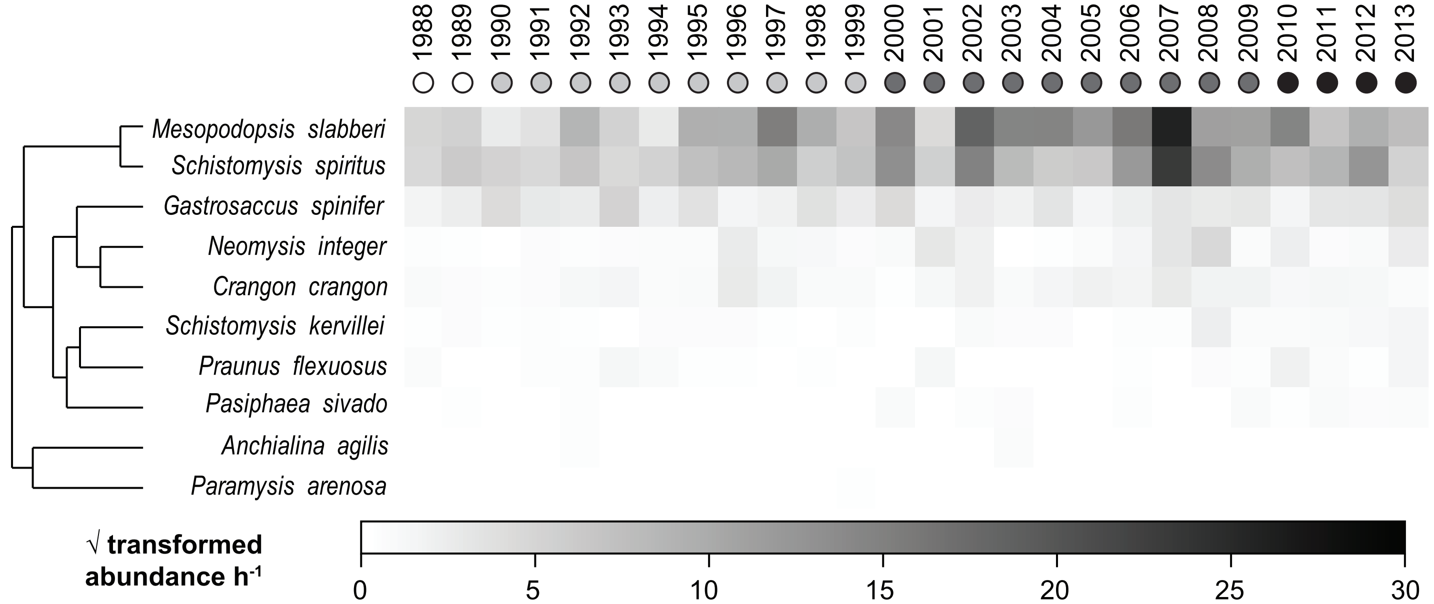
1988
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
Mesopodopsis slabberi
Schistomysis spiritus
Gastrosaccus spinifer
Neomysis integer
Crangon crangon
Schistomysis kervillei
Praunus flexuosus
Pasiphaea sivado
Anchialina agilis
Paramysis arenosa
√ transformed abundance h^{-1}
0
5
10
15
20
25
30

Fig. 4.

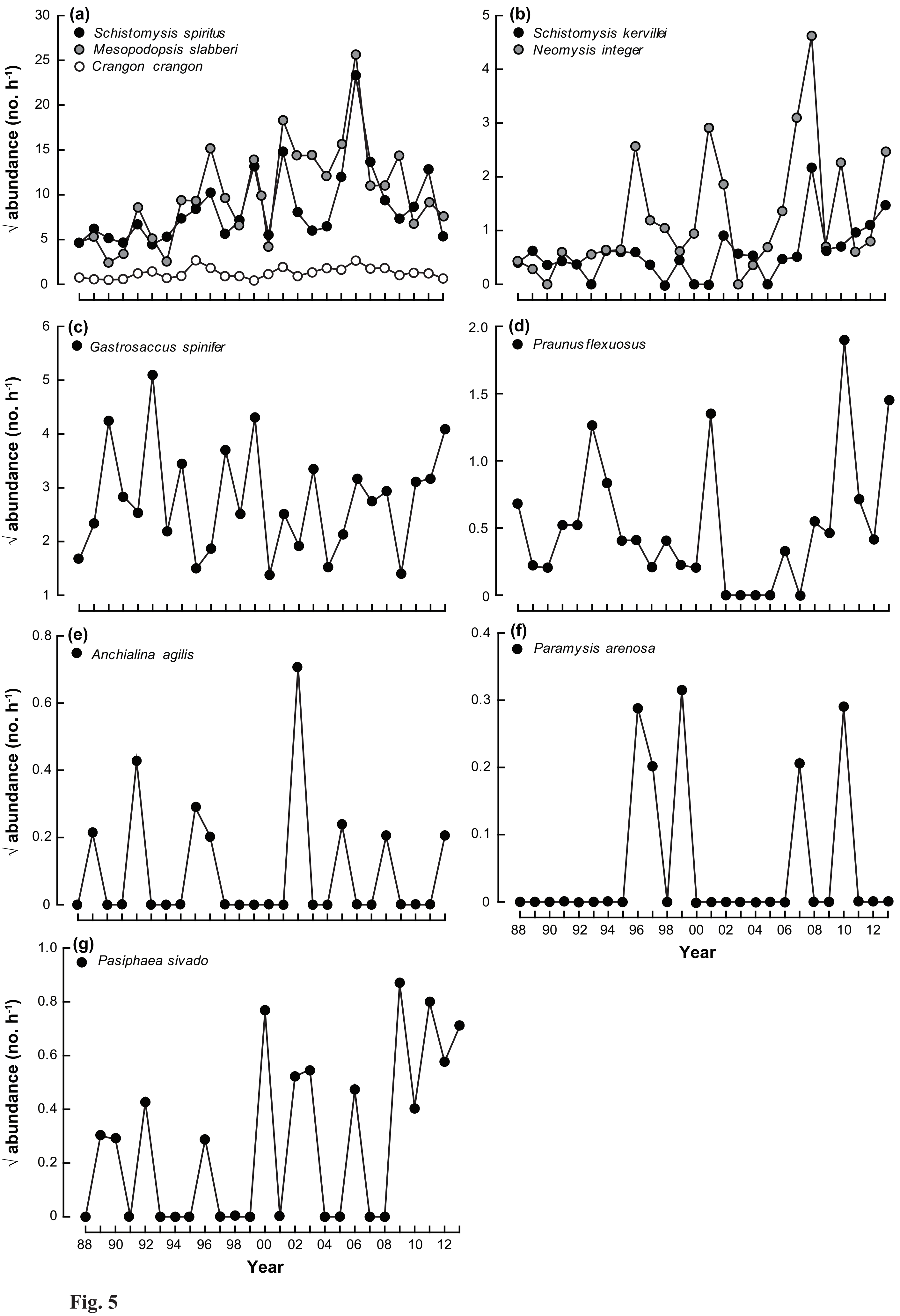
(a)
Schistomysis spiritus
Mesopodopsis slabberi
Crangon crangon
(b)
Schistomysis kervillei
Neomysis integer
(c)
Gastrosaccus spinifer
(d)
Praunus flexuosus
(e)
Anchialina agilis
(f)
Paramysis arenosa
(g)
Pasiphaea sivado
√ abundance (no. h-1)
30
25
20
15
10
5
0
4
3
2
1
6
2.0
1.5
1.0
0.5
0.8
0.6
0.4
0.2
0.3
0.1
88
90
92
94
96
98
00
02
04
06
08
10
12
Year

Fig. 5

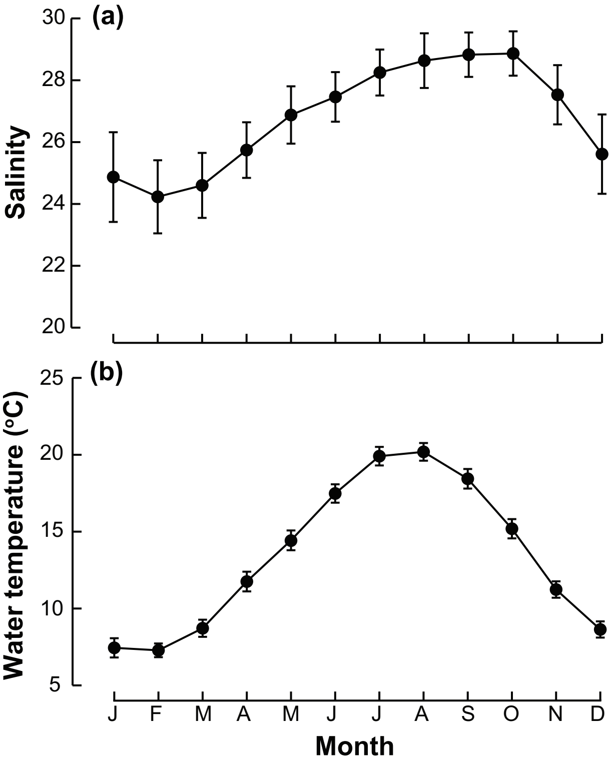
(a)
30
28
26
24
22
20
Salinity
(b)
25
20
15
10
5
Water temperature (°C)
J
F
M
A
M
J
J
A
S
O
N
D
Month

Fig. 6

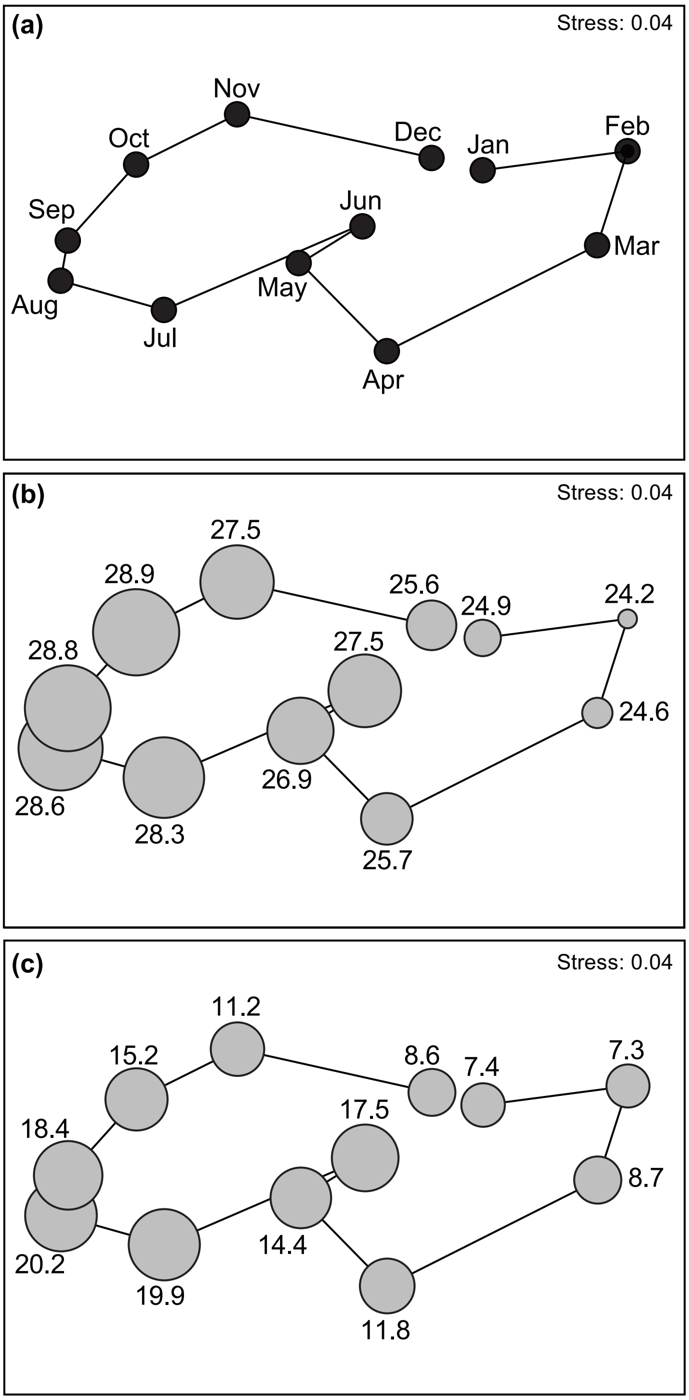
(a)
Stress: 0.04
Nov
Oct
Dec
Jan
Feb
Sep
Jun
Mar
May
Aug
Jul
Apr
(b)
Stress: 0.04
27.5
28.9
25.6
24.9
24.2
28.8
27.5
24.6
26.9
28.6
28.3
25.7
(c)
Stress: 0.04
11.2
15.2
8.6
7.4
7.3
18.4
17.5
8.7
14.4
20.2
19.9
11.8

Fig. 7.

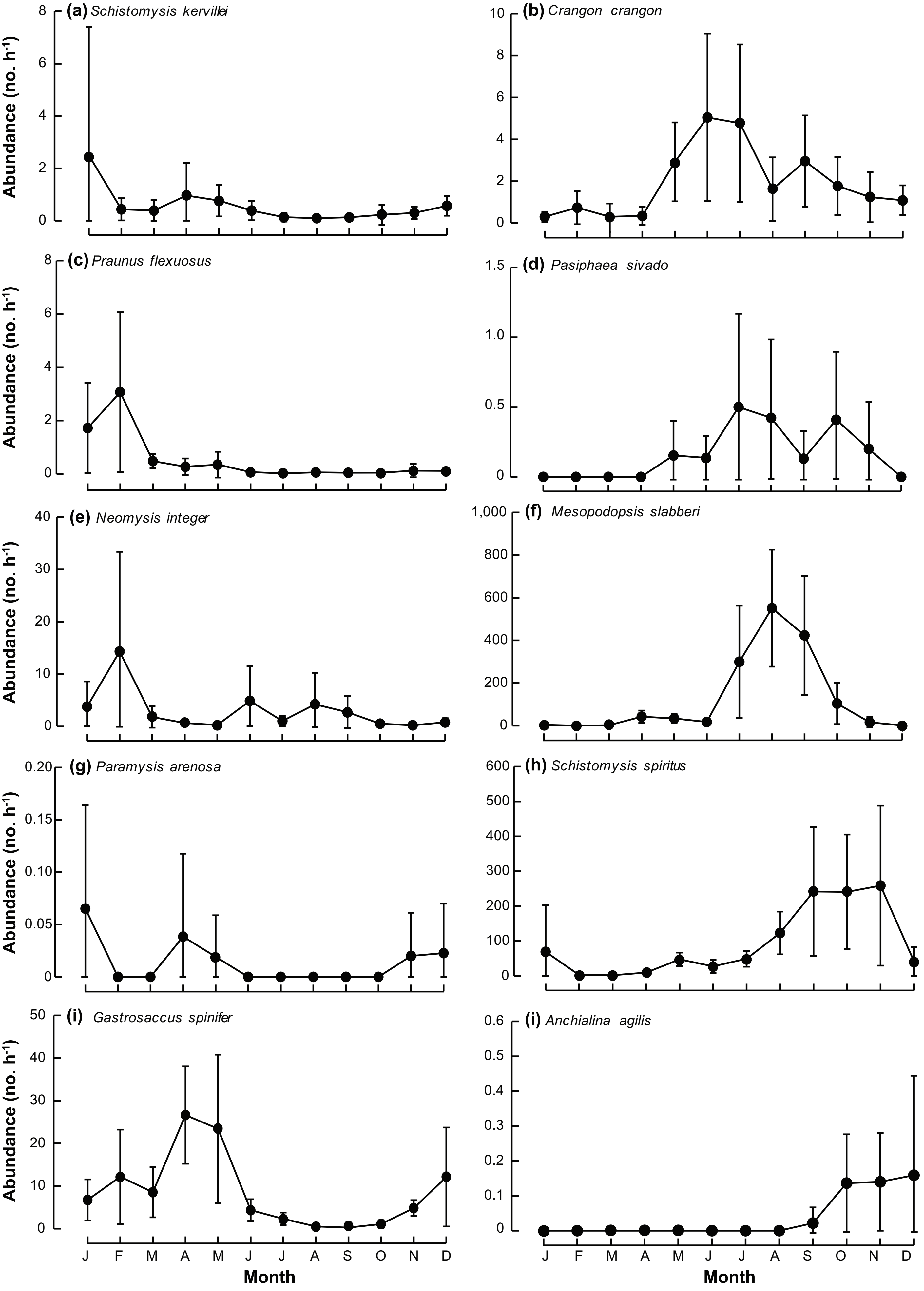
(a) Schistomysis kervillei
(b) Crangon crangon
(c) Praunus flexuosus
(d) Pasiphaea sivado
(e) Neomysis integer
(f) Mesopodopsis slabberi
(g) Paramysis arenosa
(h) Schistomysis spiritus
(i) Gastrosaccus spinifer
(i) Anchialina agilis
Abundance (no. h-1)
0
2
4
6
8
10
1.5
1.0
0.5
20
30
40
50
200
400
600
800
1,000
0.05
0.10
0.15
0.20
100
300
500
0.1
0.2
0.3
0.4
0.6
J
F
M
A
M
J
J
A
S
O
N
D
Month

Fig. 8.

Table 1. Pearson's correlation coefficients (*r*) and significance levels (*P*) for the relationships at Hinkley Point between both number of species and total abundance of mysids and caridean decapods and the water temperature, salinity, NAOI and winter NAOI for the years between 1988 and 2013.

	r	***P***
Number of species *vs*		
Water temp	0.303	0.066
Salinity	0.164	0.211
NAOI	-0.290	0.076
Winter NAOI	-0.115	0.288
Total abundance *vs*		
Water temp	0.228	0.132
Salinity	-0.106	0.303
NAOI	-0.560	0.392
Winter NAOI	0.056	0.392

Table 2. Mean abundance h^{-1} ($\bar{x}$) and percentage contribution (%) and cumulative percentage contribution (C%) of each mysid and caridean decapod species in samples from Hinkley Point between 1988 and 2013.

Family	**Species**	$\bar{x}$	**%**	**C%**
Mysidae	*Mesopodopsis slabberi*	129.25	54.52	54.52
Mysidae	*Schistomysis spiritus*	92.58	39.05	93.57
Mysidae	*Gastrosaccus spinifer*	8.90	3.76	97.33
Mysidae	*Neomysis integer*	2.95	1.24	98.57
Crangonidae	*Crangon crangon*	1.93	0.82	99.39
Mysidae	*Schistomysis kervillei*	0.65	0.27	99.66
Mysidae	*Praunus flexuosus*	0.57	0.24	99.90
Pasiphaeidae	*Pasiphaea sivado*	0.17	0.07	99.97
Mysidae	*Anchialina agilis*	0.05	0.02	99.99
Mysidae	*Paramysis arenosa*	0.02	0.01	100.00

Appendix 1. Mean squares (MS), percentage contributions of MS to total MS (%MS), Pseudo-*F*, significance levels (*P*) for the two-factor PERMANOVA tests on the Bray-Curtis similarity matrices constructed from the monthly abundances of mysids and caridean decapods at Hinkley Point between 1988 and 2013. *d.f.* = degrees of freedom.

Source	***d.f.***	**MS**	**%MS**	**Pseudo-*F***	***P***
Year	25	2,938	12.76	1.80	0.001
Month	11	18,459	80.17	11.33	0.001
Residual	249	1,629	7.07		