

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

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22
23 **Short title:** Annual and monthly changes in mysids and caridean decapods of a macrotidal
24 estuarine environment

25 **Abstract**

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

49 **Keywords:** Cyclicity; estuary; micronekton; salinity; temperature

50 **Introduction**

51 Estuaries are among the most productive of all marine environments and thus provide
52 a rich source of food for a range of fauna (Schelske and Odum, 1961; Bianchi, 2006;
53 Tweedley et al., 2016b). These systems frequently receive, however, large amounts of
54 contaminants from industrial, agricultural and urban activities along their shores and
55 catchments and are subjected to the effects of climate change (Statham, 2012; Robins et al.,
56 2016; Hallett et al., 2017). There is, therefore a need to have reliable methods for detecting
57 and monitoring anthropogenic effects, including those associated with increases in water
58 temperature. As crustaceans, such as mysids, are very sensitive to chemical contaminants and
59 environmental perturbations, they are particularly useful for detecting degradation and
60 remediation (Warwick and Clarke, 1993; Roast et al., 1998; Tweedley et al., 2012; 2016a).
61 Since species of zooplankton and micronekton have short life cycles and vary markedly in
62 abundance among and within years, their use as indicators should ideally be based on long-
63 term annual data that also embrace variations that occur throughout the year (David et al.,
64 2005; Hays et al., 2005).

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

75 caridean decapods, copepods and euphausiids, with mysids particularly abundant in the
76 Severn Estuary (Williams and Collins, 1986; Bamber and Henderson, 1994).

77 The Severn Estuary, in south-west England, is the second largest estuary in the United
78 Kingdom, covering an area of 557 km², of which 100 km² is intertidal (Langston et al., 2003;
79 Langston et al., 2010a). It opens into the wide Bristol Channel, whose innermost southern
80 region is now included within the Severn Estuary Special Area of Conservation
81 (<http://jncc.defra.gov.uk/protectedsites/sacselection/sac.asp?EUCode=UK0013030>). The
82 Severn Estuary and Bristol Channel together constitute the largest estuarine environment in
83 the United Kingdom, with an area of 4,800 km² and a catchment that drains nearly one sixth
84 of the land area of England and Wales (Collins and Williams, 1981). The tidal range is the
85 second highest in the world, with mean high water spring tides of 13.3 m at Avonmouth in
86 the estuary and of 11.8 m at Hinkley Point in Bridgwater Bay in the inner region of the
87 Bristol Channel (<http://www.ntsif.org/tides/hilo>). Although the Severn Estuary and inner
88 Bristol Channel used to receive large amounts of contaminants, of which metals were of
89 particular concern, total contaminant input has declined over recent decades due to a regional
90 reduction in industrial activity and the implementation of environmental legislation
91 (Duquesne et al., 2006; Jonas and Millward, 2010). The collation of data from four studies
92 undertaken in different years has shown that this has been reflected in a reduction in the
93 concentrations of heavy metals in the sediment and of the prevalence of reduced oxygen
94 concentrations (Jonas and Millward, 2010).

95 The records of the UK Meteorological Office Hadley Centre (via the British
96 Atmospheric Data Centre) demonstrate that the annual mean sea surface temperatures (SSTs)
97 in the Bristol Channel underwent an overall increase of ~1.3°C between 1905 and 2002
98 (Genner et al., 2004). While the annual means of the monthly water temperatures recorded *in*

99 *situ* at Hinkley Point increased between 1986 and 1989, they subsequently remained
100 relatively constant until 2010 (Henderson et al., 2011b).

101 As strong tidal currents often make it difficult to use traditional methods to sample
102 effectively the fauna of estuaries with very large tidal ranges, samples collected from the
103 large volume of water in the cooling intakes at nuclear power stations have sometimes been
104 employed for this purpose (Claridge et al., 1986; Marshall and Elliott, 1998; Power et al.,
105 2000). The use of this method at Oldbury in the Severn Estuary and Hinkley Point in the
106 Bristol Channel has provided a very effective standardised technique for obtaining medium or
107 longer term quantitative samples of fish and also occasionally of crustaceans (e.g. Potter et
108 al., 1986; Henderson and Bird, 2010). The resultant data indicate that, at Hinkley Point
109 between the early 1980s and late 2000s, the abundance and number of species of fish
110 increased, with the abundance of several of the most numerous fish and macro-crustacean
111 species undergoing rapid exponential increases or decreases (Genner et al., 2004; Henderson
112 et al., 2006; Henderson, 2007; Henderson and Bird, 2010). While, for some species, such
113 changes were associated with water temperature, salinity and the North Atlantic Oscillation
114 Index (NAOI), no such correlations were found with many other species (Henderson et al.,
115 2011b). When the biotic variables increased in the absence of such correlations, it is possible
116 that this was due to an improvement in water quality (Henderson and Bird, 2010). Although
117 the annual mean numbers of species of these fish and macro-crustaceans did not undergo a
118 long-term increase, the prevalence of several of these species increased during the study
119 period. On the basis of multivariate analyses, the species composition of fish underwent two
120 abrupt changes during that period, the first linked to changes in the NAO and the second to
121 increases in water temperature (Henderson, 2007; Henderson et al., 2011b). On the other
122 hand, the macro-crustaceans did not begin to form a distinct group until the 2000s
123 (Henderson et al., 2011b).

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

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

143 The first aim of this study was to explore whether the annual means for monthly water
144 temperatures and salinities at Hinkley Point in the Bristol Channel and the NAOI and winter
145 NAOI showed an overall increase or decrease between 1988 and 2013. The trends exhibited
146 by the number of species and total abundance of mysids and caridean decapods were then
147 analysed to determine whether they changed over the same period and, if so, whether they
148 were related to one or more of the above abiotic variables. Any changes in the biotic

149 variables were considered in the context of the reductions that have occurred, since the 1970s,
150 in the concentrations of contaminants and the prevalence of reduced oxygen concentrations.
151 Data were next used to test whether the species composition of the mysid and caridean
152 decapod community changed in a serial manner over the 26 years and, if so, whether it was
153 related to any of the above abiotic variables. The hypothesis was tested that the species
154 composition changed cyclically during the year, in relation to the pronounced cyclical
155 changes that occur in water temperature and/or salinity, reflecting different patterns of
156 sequential monthly changes by individual species and/or groups of species.

157

158 ***Materials and methods***

159 *Sampling*

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

169 Mysids and caridean decapods were sampled monthly between January 1988 and
170 December 2013, except in the few months when sampling was prevented due to power
171 station maintenance. Samples were collected midway between spring and neap tides,
172 commencing at high water, by placing a plankton net (150 μm mesh) in the intake forebay of
173 the power station for 1 h. Although catch rates at power stations with an intake in clear water

174 tend to be greater at night (Whitehouse, 1986), this does not apply to Hinkley Point because
175 very little light penetrates the turbid water at this location at any time of the day (Henderson
176 and Holmes, 1991). Each sample was immediately fixed in 4% formalin in seawater. Water
177 temperature and salinity at the time of sampling were recorded to the nearest 0.1 °C and 0.1,
178 respectively. Note that the temperatures recorded between 1981 and 2002 at Hinkley Point,
179 where the current study of mysids and caridean decapods was undertaken, were highly
180 correlated with the SSTs recorded for those years in the Bristol Channel by the UK
181 Meteorological Office Hadley Centre, via the British Atmospheric Data Centre (Genner et al.,
182 2004). Monthly values of NAOI were extracted from
183 <https://crudata.uea.ac.uk/~timo/datapages/naoi.htm>.

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

187

188 *Univariate analyses of annual environmental and biotic variables*

189 For each year between 1988 and 2013, the mean of the monthly values in each year
190 (subsequently referred to as ‘annual mean value’) and its 95% confidence limits were
191 calculated for water temperature, salinity and NAOI and for the numbers of species and the
192 total abundance of mysids and caridean decapods (no. h⁻¹). The mean of the NAOI for just the
193 winter months of each year, i.e. December to February, was also calculated, with the value
194 for a given year represented by the January and February of that year and the December of
195 the previous year. Pairwise Pearson’s correlations coefficients were calculated for the
196 relationship between the resultant annual means for each of the above environmental and
197 biotic variables across the 26 years to determine the extent and direction of linear association
198 of these variables over that period. When significant, the regression equation relating the

199 dependent and independent variables was determined. Preliminary analyses demonstrated that
200 the relationship between the total abundance of mysids and caridean decapods and year was
201 described better by using a log-linear than linear relationship.

202

203 *Multivariate analyses of annual biotic variables*

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

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

222 To remove the influence of differences in overall abundances among years, the
223 average of the monthly abundances of each species in each year was standardised,

224 i.e. converted to a percentage contribution and square-root transformed (Clarke and Warwick,
225 2001). As above, these data were used to construct a Bray-Curtis resemblance matrix, which
226 was subjected to cluster analysis and nMDS ordination. Segmented bubbles of proportional
227 sizes, representing the square-root transformed percentage contributions of the three most
228 abundant species, which contributed 97% to the total number of individuals (see Results),
229 were overlaid on the nMDS plot.

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

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

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

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

263

264 *Multivariate analyses of monthly compositions*

265 The square-root transformed abundance of each species in each corresponding month
266 in each of the 26 years was averaged, thereby producing a single value for each species in
267 each month. These data were used to construct a Bray-Curtis resemblance matrix, which was
268 subjected to nMDS ordination, with lines drawn between the points for each successive
269 month in the resultant nMDS ordination plot. RELATE was employed to determine whether
270 species composition progressed in a cyclical manner. Bubbles, whose sizes in each calendar
271 month represent the average salinity and water temperature, the two variables most closely
272 correlated individually with composition, were then superimposed on the points for each

273 month in their respective plots. Coherent species curves were constructed to identify which
274 groups of species, if any, exhibited a similar pattern of abundance across months.

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

281

282 **Results**

283 *Annual trends in environmental and biotic variables*

284 Annual mean water temperatures between 1988 and 2013 ranged only from 12.5 to
285 14.5 °C and showed no conspicuous tendency to increase or decline over those years
286 (Fig. 1a), which is consistent with the results of Pearson's correlation analysis ($r = -0.058$,
287 $P = 0.777$). Although annual mean salinities fluctuated to a greater degree across the
288 26 years, with values ranging from 22.5 to 29.5, they also did not obviously tend to increase
289 or decrease (Fig. 1b), again supported by the results of correlation analysis ($r = -0.312$, $P =$
290 0.120). In contrast to temperature and salinity, NAOI exhibited a marginally significant
291 decline between 1988 and 2013 (Fig. 1c), when using values for the whole year ($r = -0.401$,
292 $P = 0.042$), but not when employing only those for the winter months ($r = -0.337$, $P =$
293 0.093).

294 Although the mean monthly numbers of species oscillated among years, they still
295 clearly tended to increase between 1988 and 2013 (Fig. 2a), with that trend significant
296 ($r = 0.724$, $P = 0.001$). Mean monthly total abundance varied markedly, ranging from <100
297 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),

298 but with an overall tendency for the natural logarithm of abundance to increase with time
299 ($r = 0.604$, $P = 0.001$).

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

304

305 ***Multivariate analyses of the crustacean community***

306 Three families, representing nine genera and ten species, were recorded in the samples
307 (Table 2). The fauna was dominated by the Mysidae, which contributed >99% to the total
308 number of individuals, with *Mesopodopsis slabberi* and *Schistomysis spiritus* contributing
309 54.5 and 39.1%, respectively, to that overall total. As the carapace lengths of *M. slabberi* and
310 *S. spiritus* ranged from 0.6 to 3.3 mm (S. Plenty, unpublished data), the maximum closely
311 approximating that recorded for the individuals of these species retained when using a larger
312 (10 mm) mesh on the intake screens of the same power station (Bamber and Henderson,
313 1994). While juveniles, males, non-brooding females and brooding females of *M. slabberi* and
314 *S. spiritus* were sampled in certain periods, both species were present in very low numbers or
315 absent in other months (see later).

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

319 Two main clusters and one outlier (2007) are present on the dendrogram derived from
320 square-root transformed abundances for the 10 species recorded between 1988 and 2013
321 (Fig. 3a). The first cluster represents mainly years in the early part of this period, while the
322 second comprises two groups, the first containing many of the years between 1995 and 1999

323 and 2009 to 2013 and the second many of those between 2000 and 2010. These trends are
324 essentially present in the MDS ordination plot, derived using the same resemblance matrix,
325 with most years prior to 2001 lying to the left of those of later years (Fig. 3b). Furthermore,
326 the sizes of the bubbles, which represent the total abundance, show a marked tendency to
327 increase from left to right on the plot. RELATE demonstrated that species composition
328 followed a weak, but significant linear sequence (seriation) over the 26 years ($\rho = 0.275$,
329 $P = 0.002$).

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

342 The shade plot emphasises that the mysid species *Mesopodopsis slabberi* and
343 *Schistomysis spiritus* overwhelmingly dominated the mysids and caridean decapods, with
344 their abundances increasing after the year 2000 (Fig 4). These two species, together with
345 *Gastrosaccus spinifer* and *Crangon crangon*, were recorded in each of the 26 years and
346 another three species (*Neomysis integer*, *Schistomysis kervillei* and *Praunus flexuosus*) in
347 >80% of the years. Among the three least abundant species, *Pasiphaea sivado* and *Anchialina*

348 *agilis*, were recorded as early as 1989 and in four of the next eight years and in five and two
349 of the last five years, respectively (Fig. 4). *Paramysis arenosa* was recorded in only five
350 years and in only one month in four of those years.

351 Coherent species curves demonstrate that the patterns of change in the relative annual
352 abundances of the ten species formed seven groups, of which five contained a single species
353 (Fig. 5). In the first group, the patterns of abundance of the two dominant species, *M. slabberi*
354 and *S. spiritus*, together with the far less abundant *C. crangon*, were statistically
355 indistinguishable across the 26 years. For example, the abundances of each of these species
356 peaked sharply in 2002 and 2007 (Fig. 5a). In the second group, the relative abundances of
357 the other two mysids, *S. kervillei* and *N. integer*, were low between 1988 and 1995 and high
358 in 2002 and 2008 and increased sequentially between 2011 and 2013 (Fig. 5b). The third
359 most numerous species *G. spiritus* (Table 2) and *Praunus flexuosus* formed a discrete group,
360 with the abundance of the former peaking in 1990, 1993, 2000 and 2013 and the latter in
361 1993, 2001, 2010 and 2013 (Fig. 5c, 5d). As the remaining three species were never abundant
362 in any year and absent in at least 50% of years, caution must be exercised in drawing
363 conclusions from the annual abundances of these species.

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

368

369 ***Monthly trends in environmental and biotic variables***

370 Mean monthly salinities increased sequentially from a minimum of 24 in February to
371 29 in September and October and then decreased to 26 in December (Fig. 6a). Mean monthly

372 water temperatures increased from a minimum of 7 °C in January and February to a
373 maximum of ~20 °C in July and August and then declined to 8 °C in December (Fig. 6b).

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

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

391

392 **Discussion**

393 *Annual trends in environmental variables*

394 This study demonstrated that annual mean water temperatures at Hinkley Point in the
395 Bristol Channel did not change significantly between 1988 and 2013, the duration of the
396 current study of mysids and caridean decapods at that location. This parallels the lack of a

397 trend in the SSTs, extracted from the records of the UK Meteorological Office Hadley Centre
398 for the Bristol Channel over the same time period, with Pearson's correlation
399 $r = 0.020$, $P = 0.923$

400 (<https://www.webeaver.com/down?rid=6b9f7f1a378482330a004eafab9d68a1&sid=72610>).

401 Although there is indisputable evidence from the Hadley data that, over a much longer period
402 of 1905 to 2002, the SSTs in the Bristol Channel increased markedly (Genner et al., 2004),
403 the lack of an increase in temperatures between 1988 and 2013 demonstrates that there has
404 been a levelling of this trend in recent years. As with annual mean temperatures, neither the
405 minimum nor maximum annual temperatures at Hinkley Point exhibited a significant linear
406 change between 1988 and 2013.

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

410

411 *Annual trends in biotic variables*

412 In contrast to the lack of a significant change in water temperature, salinity and winter
413 NAOI between 1988 and 2013, the annual mean monthly number of species and total
414 abundance of mysids and caridean decapods both increased significantly over those 26 years.
415 The abundance of mysids in the turbid environment of the Gironde Estuary did not change,
416 however, over a similar period (David et al., 2005). In the inner Bristol Channel,
417 *Mesopodopsis slabberi* and *Schistomysis spiritus*, which together contributed 93.6% to the
418 total number of mysids and caridean decapods, exhibited statistically indistinguishable trends
419 in abundance between 1998 and 2013. These trends were thus largely responsible for the
420 significant and positive relationship between overall abundance and year. Although no
421 additional species appeared in any month during the last 17 of the 26 years sampled, rare

422 species tended to occur more frequently in the monthly samples from later years. This
423 feature, together with the tendency for the number of months in which moderately common
424 species were present in a year to increase, accounts for the increase in annual mean number
425 of species with time. This parallels the situation recorded by Henderson et al. (2011b) for
426 macrocrustaceans and fish at Hinkley Point during a similar period.

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

439 The lack of a significant relationship between both the number of species and total
440 abundance and the water temperature, salinity and annual and winter NAOI strongly suggests
441 that these two biotic variables are responding to other factors, such as changes in the
442 concentrations of contaminants. Although data for such concentrations in the Severn Estuary
443 and inner Bristol Channel are only available for some years, those data still demonstrate that,
444 in the period between the years preceding the current study and the mid 2000s, there was a
445 decline into this estuarine environment, of the input of metals, such as Hg, Pb, Cu and Zn,
446 thereby accounting for the reduction in the concentration of such metals in the suspended

447 matter and water column (Jonas and Millward, 2010). It is thus proposed that the overall
448 increases in the annual mean of both the number of species and total abundance of mysids
449 and caridean decapods during the present study reflect, in part, a response to the beneficial
450 environmental effects of the introduction of stricter pollution controls, namely the
451 Environmental Pollution Act (1990) and Integrated Pollution Prevention Control Directive
452 (1996), and to closures of major industries (Langston et al., 2010b; Henderson et al., 2011a).
453 These benefits include an improvement in overall sediment and water quality, including
454 increased oxygen concentrations, and a reduction in the accumulated burdens in estuarine
455 bio-indicator species in this previously heavily-polluted, estuarine environment (Duquesne et
456 al., 2006; Jonas and Millward, 2010; Langston et al., 2010b).

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

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

472 Phytoplankton concentrations in the North Sea and the Atlantic Ocean increased in
473 the 1980s (Reid et al., 1998). However, as the inner Bristol Channel and Severn Estuary are
474 exceptionally turbid, phytoplankton concentrations in this estuarine environment are very low
475 (Kirby and Parker, 1983; Joint, 1984). Furthermore, in turbid estuaries, mysids feed
476 predominantly on detritus and members of the detrital-microbial loop (Henderson et al.,
477 1992; Vilas et al., 2008). Consequently, it seems unlikely that any changes in phytoplankton
478 concentrations would have been sufficient to exert a marked influence on the abundances of
479 the mysid and caridean decapod species in the inner Bristol Channel.

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

488

489 *Cyclical inter-annual changes in biotic and environmental variables*

490 The peaks in abundances of the main fish species in the Severn and other northern European
491 estuaries form a time-staggered sequence throughout the year which, through the use of
492 multivariate procedures, have been shown to result in species composition changing in a
493 well-defined cyclical manner during the year (Potter et al., 1986; Thiel and Potter, 2001;
494 Maes et al., 2005). Although the abundances of the main species of crustaceans at Hinkley
495 Point and of zooplankton indicator species in the Clarente Estuary had previously been
496 demonstrated to peak at more or less sequentially different times (Bamber and Henderson,

497 1994; Henderson and Bird, 2010; Modéran et al., 2010), the extent to which these trends were
498 reflected in cyclical changes in composition was not explored.

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

513 Since the cyclicity in community composition was strongly related to salinity and
514 driven by the two overwhelmingly dominant species, *S. spiritus* and *M. slabberi*, the salinity
515 ‘preferences’ of these species will be important in determining this pattern. It is therefore
516 relevant that a detailed study of mysid distributions in the Bristol Channel and Severn Estuary
517 showed that, in those waters, *S. spiritus* was most abundant in salinities ranging from 27 to 34
518 (Williams and Collins, 1984), and that the current study in the inner Bristol Channel
519 demonstrate that this species was particularly abundant between July and November when
520 salinities were greatest. This species also occurs at the upper end of salinities in the Mondego
521 and Westerschelde estuaries elsewhere in Europe (Azeiteiro and Marques, 1999; Rappé et al.,

522 2011). *Mesopodopsis slabberi* peaked in abundance in the inner Bristol Channel in August
523 and September, when salinities were at their maxima (see also Collins and Williams, 1982),
524 and was absent in January and February when salinities were lowest. It was most abundant,
525 however, in far lower salinities in the Mondego, Guadalquivir and Westerschelde (Azeiteiro
526 and Marques, 1999; Vilas et al., 2009; Rappé et al., 2011) and has been recorded from
527 salinities ranging from 1.3 to 43 (Wittmann, 1992). These pronounced differences emphasise
528 that this species is highly euryhaline and readily able to adapt to marked variations in salinity
529 regime.

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

537

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548

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733 **List of Figures**

734 **Fig. 1.** Mean monthly values and 95% confidence limits for (a) water temperature and (b)
735 salinity at Hinkley Point in the inner Bristol Channel and (c) the North Atlantic Oscillation
736 Index (NAOI) are shown for each year between 1988 and 2013. Corresponding values for
737 NAOI in the winter months of a year (i.e. December of the previous year and January and
738 February of the current year) are given in (d).
739

740 **Fig. 2.** Mean monthly values and 95% confidence limits for (a) number of species and (b)
741 total abundance of mysids and caridean decapods at Hinkley Point in each year between 1988
742 and 2013.
743

744 **Fig. 3.** Cluster dendrograms and nMDS ordination plots, constructed from resemblance
745 matrices using the annual mean abundances of each species in each year between 1988 and
746 2013. (a) and (b) were constructed using square-root transformed abundances, while (c) and
747 (d) employed standardised and square-root transformed abundances. Points for each year are
748 overlaid with (b) bubbles showing the mean abundances of individuals in that year, and (d)
749 with segmented bubbles showing the percentage contributions of the three most abundant
750 species in that year.
751

752 **Fig. 4.** Shade plot showing the mean of the square-root transformed abundance h^{-1} of each
753 species at Hinkley Point in each year between 1988 and 2013. White space indicates that a
754 species was not collected in that year, while depth of shading from light grey to black denotes
755 the relative abundance of a species.
756

757 **Fig. 5.** Coherent species curves showing mean square-root transformed monthly
758 abundance h^{-1} of each species at Hinkley Point in each year between 1988 and 2013. Species
759 with the same statistical pattern of abundance over time are shown on the same plot.
760

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

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

767

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

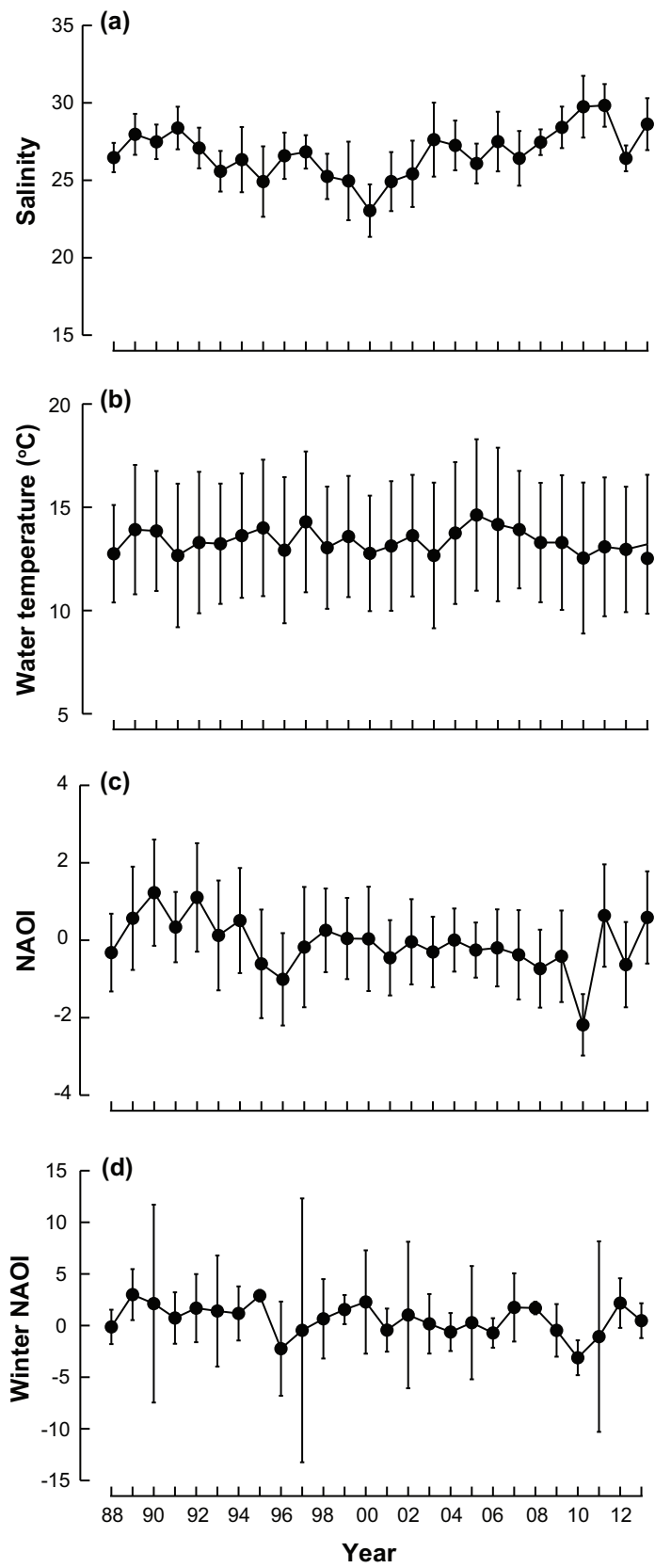


Fig. 1

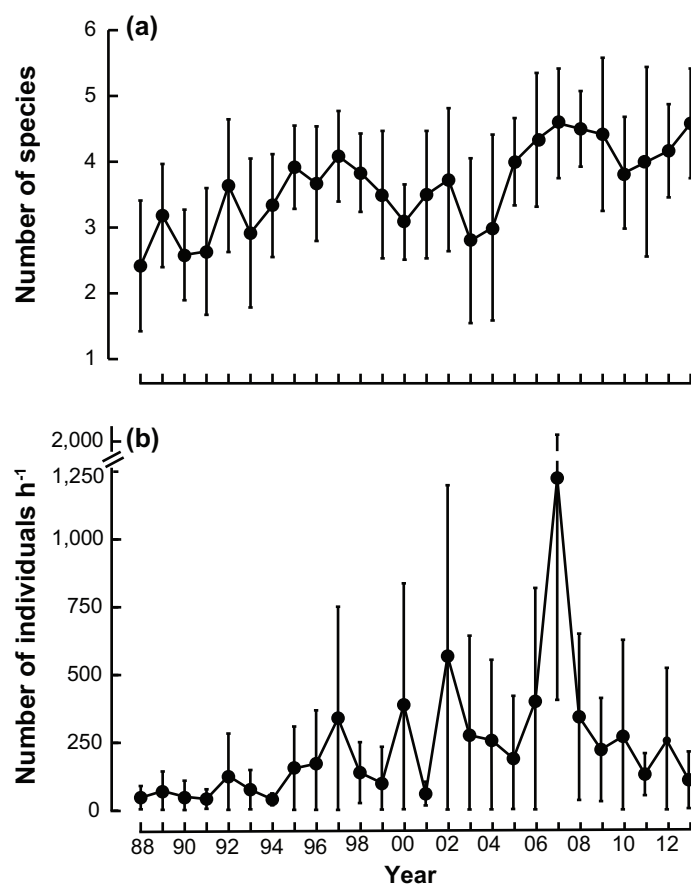


Fig. 2

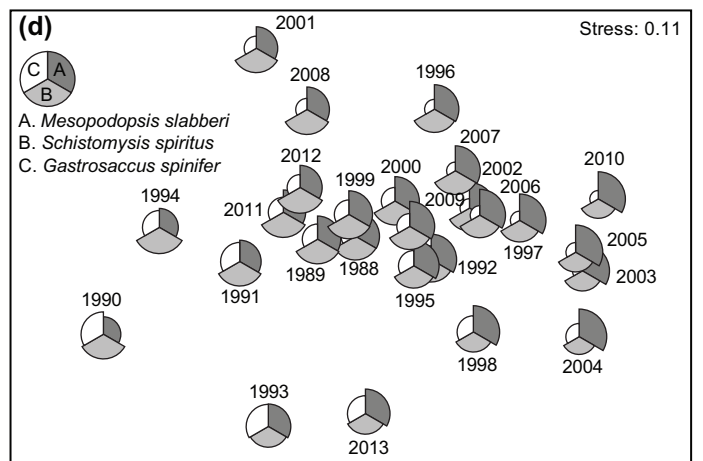
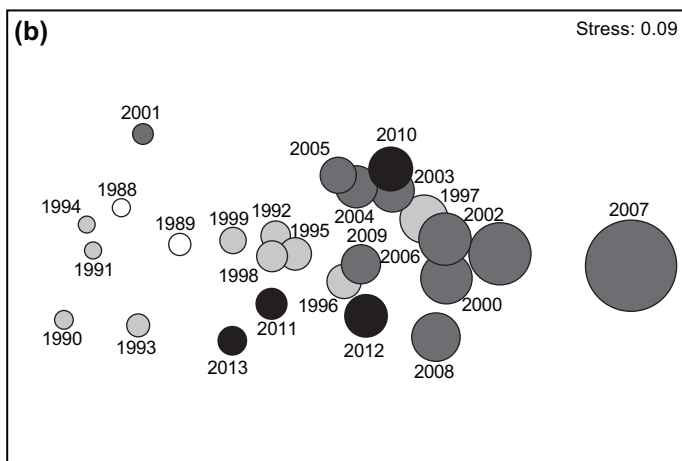
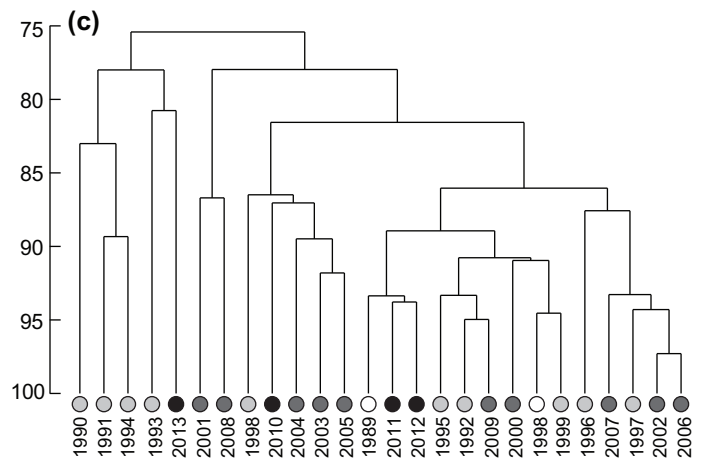
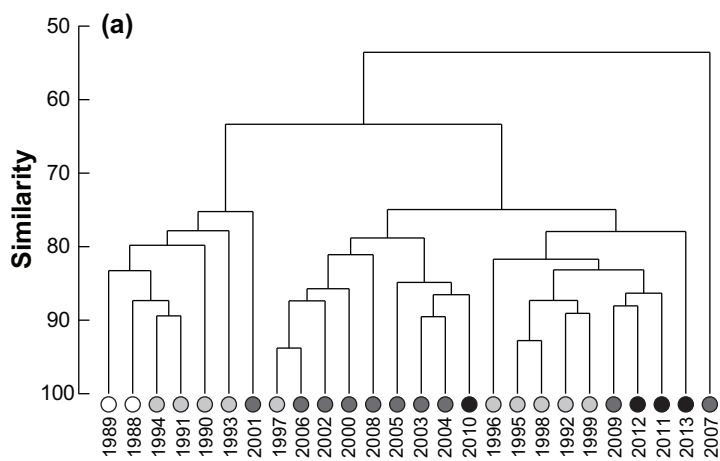


Fig. 3.

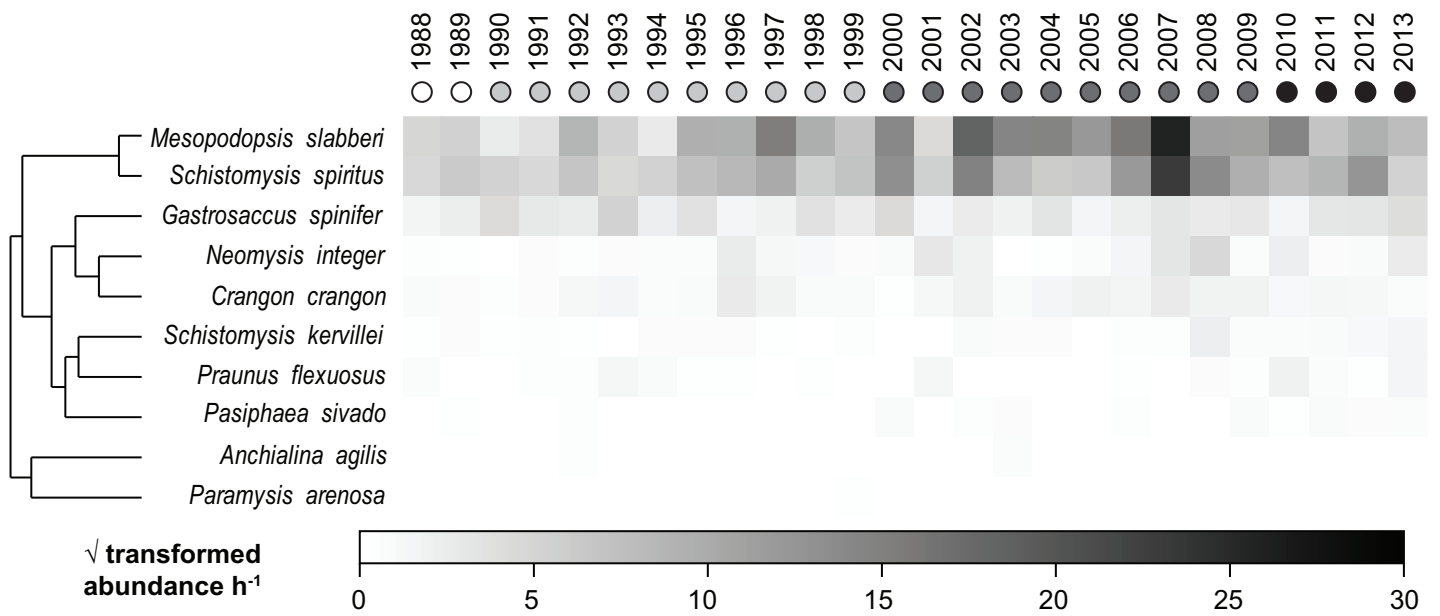


Fig. 4.

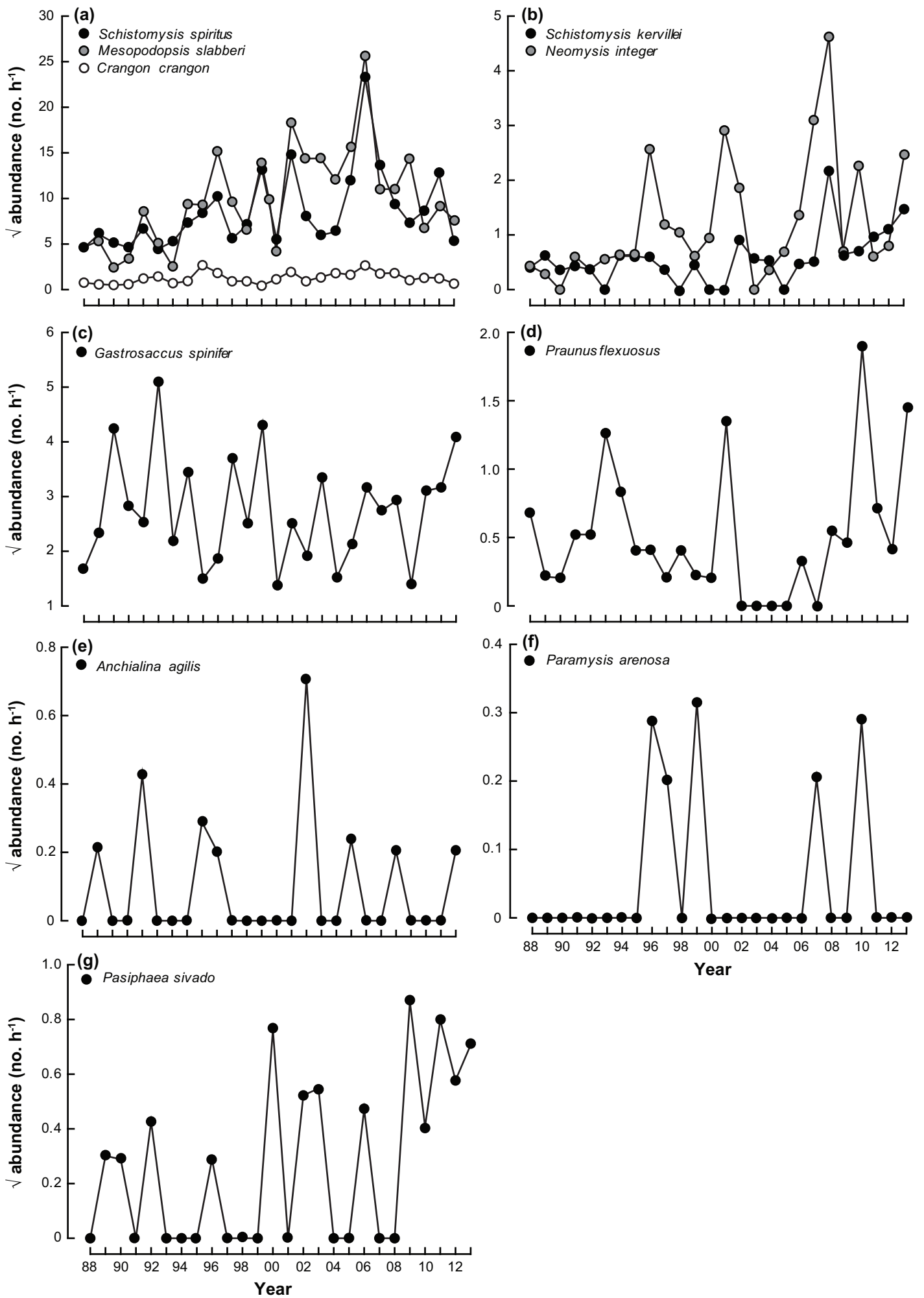


Fig. 5

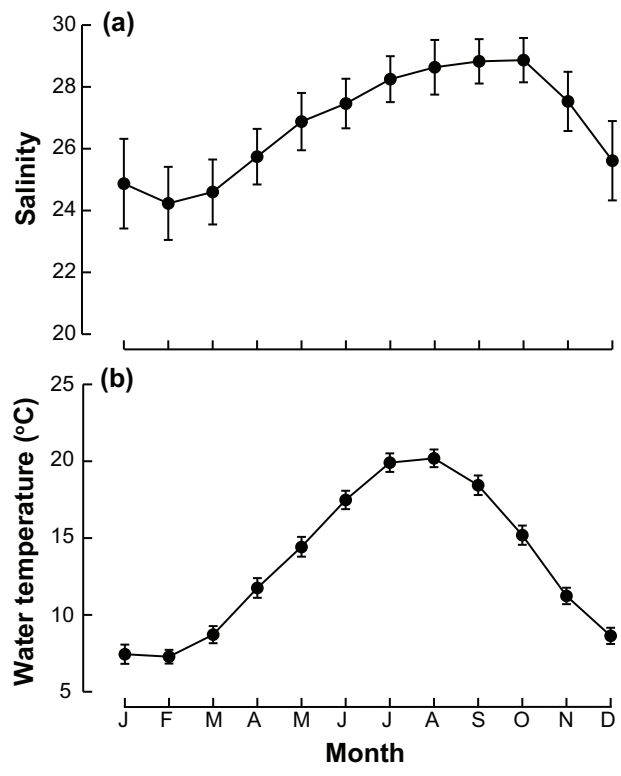


Fig. 6

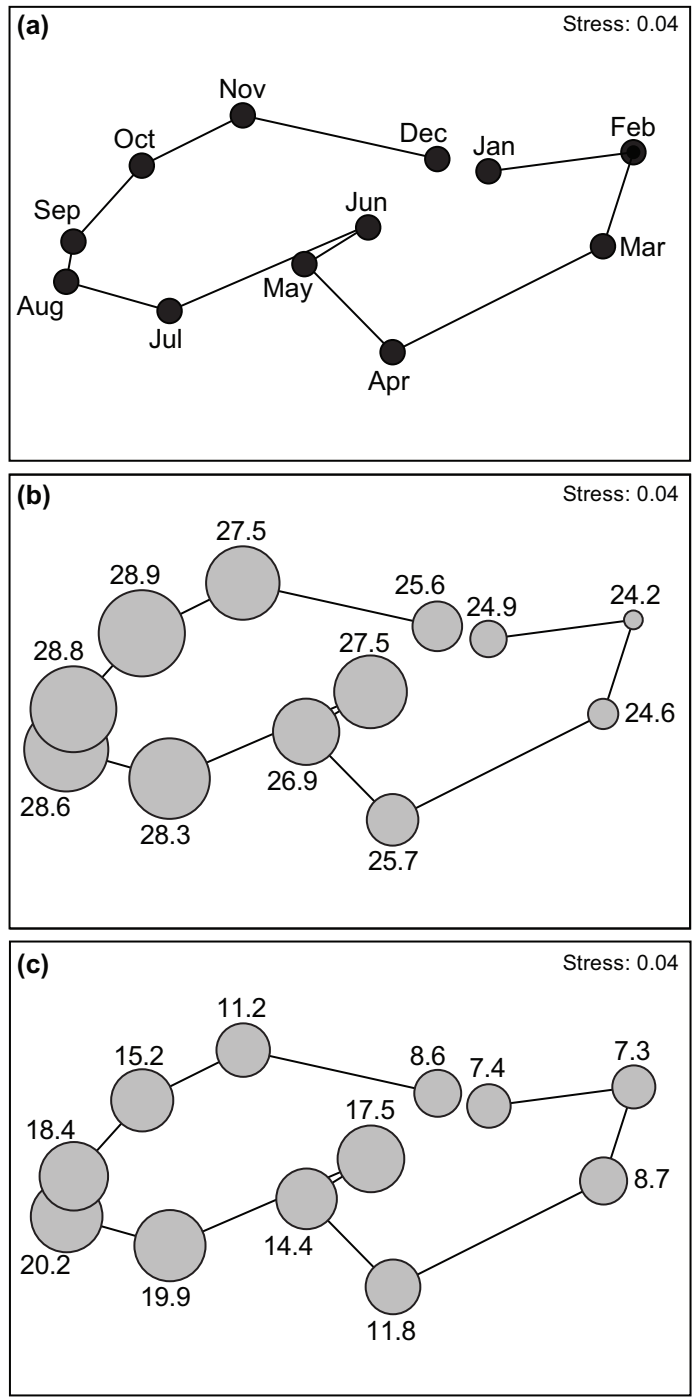


Fig. 7.

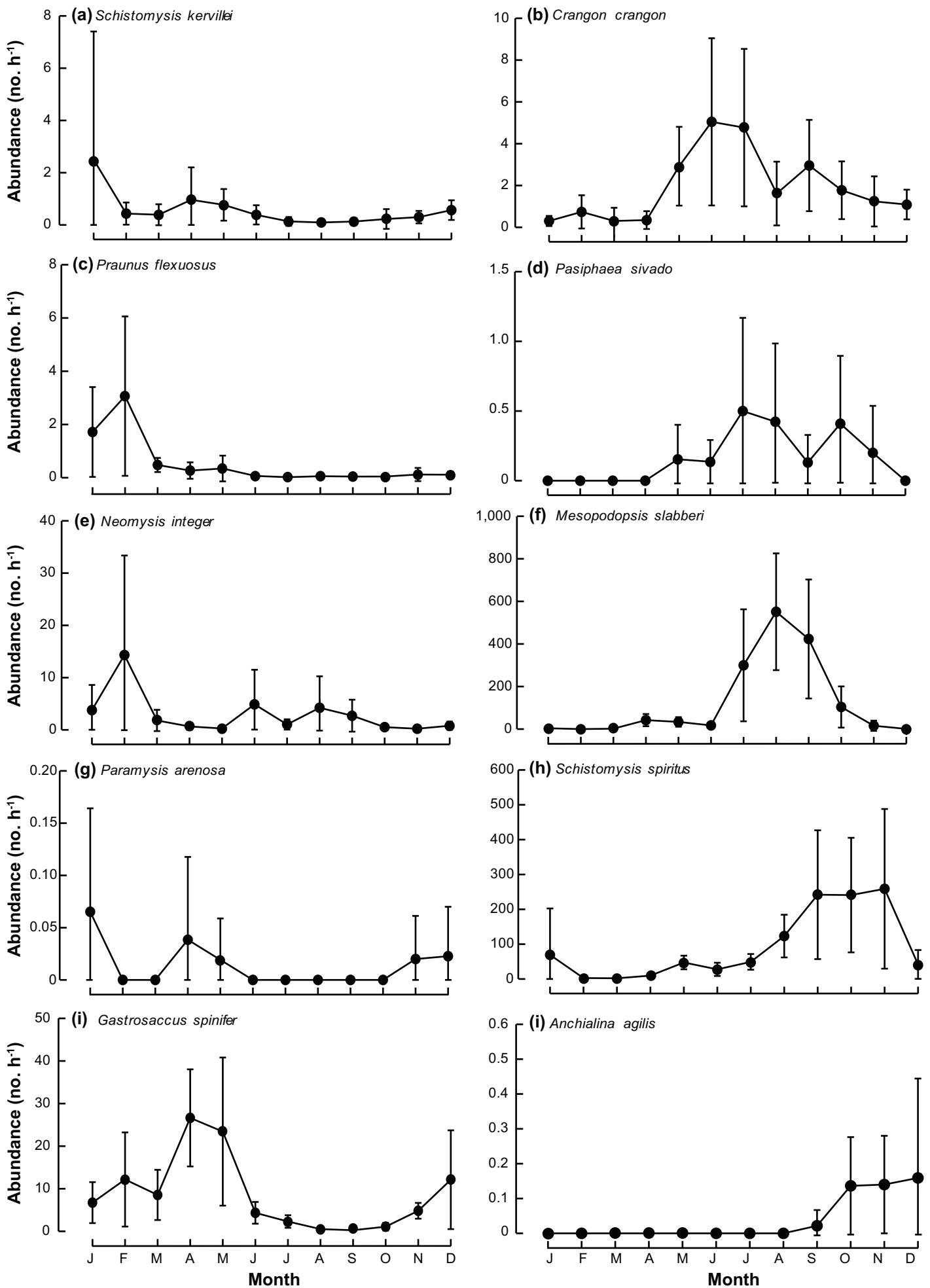


Fig. 8.

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	<i>Mesopodopsis slabberi</i>	129.25	54.52	54.52
Mysidae	<i>Schistomysis spiritus</i>	92.58	39.05	93.57
Mysidae	<i>Gastrosaccus spinifer</i>	8.90	3.76	97.33
Mysidae	<i>Neomysis integer</i>	2.95	1.24	98.57
Crangonidae	<i>Crangon crangon</i>	1.93	0.82	99.39
Mysidae	<i>Schistomysis kervillei</i>	0.65	0.27	99.66
Mysidae	<i>Praunus flexuosus</i>	0.57	0.24	99.90
Pasiphaeidae	<i>Pasiphaea sivado</i>	0.17	0.07	99.97
Mysidae	<i>Anchialina agilis</i>	0.05	0.02	99.99
Mysidae	<i>Paramysis arenosa</i>	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	<i>d.f.</i>	MS	%MS	Pseudo-<i>F</i>	<i>P</i>
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		

