

Long-term changes in the meroplankton of the North Sea

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Data from the continuous plankton recorder (CPR) survey collected in the late-1940s to early-1960s indicated that the abundance of decapod larvae was low and the seasonal peak of abundance was late following cold winters. The phenological effect of temperature was shown to be consistent with relationships between both geographical and interannual patterns of variation. Analyses of CPR data collected from the 1940s to the present day reveal large-scale long-term changes in the abundance and phenology of the North Sea meroplankton. Echinoderm larvae, whose peak abundance has advanced by 47 days, show the greatest shift in timing. Echinoderm larvae have also increased in abundance to become the most abundant taxon in North Sea CPR samples. Genetic and morphological analyses of CPR samples show that the variations in echinoderm larvae are mainly attributable to an increasing abundance and earlier occurrence of the larvae of a resident species, *Echinocardium cordatum*, rather than a change in species composition. The remarkable scale of the changes in abundance and phenology of the meroplankton, which are greater than those seen in the holoplankton, has stimulated the development of further research into the causes and effects of these changes.

Keywords. Continuous Plankton Recorder, meroplankton, phenology, long-term change.

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Introduction

Analyses of long-term change in the zooplankton have usually concentrated on the holoplankton (e.g. Planque and Batten, 2000, Johns et al. 2001, Licandro et al., 2001, Lindley & Reid, 2002 and Beaugrand, 2003). However the plankton and the benthos are intimately linked (Reid and Edwards (2001), in particular by the production of pelagic life-cycle stages, the meroplankton, by the macrobenthos and by the partitioning of the available food resources.

The meroplankton show large-scale variations in abundance and timing of occurrence in response to temperature variation. Rees (1951, 1952) and Bodo et al. (1965) showed abundance of meroplankton was low and its timing was delayed in

western European waters following the cold winters of 1947 and 1963. Lindley et al. (1993) demonstrated that the decapod larvae occurred earlier than usual in the North Sea in 1989 which was, at that time, exceptionally warm. This advance in timing was consistent with the results of analysis by Lindley (1987) of the geographical variability in timing in relation to temperature (Figure 1). Edwards and Richardson (2004) also demonstrated larger phenological changes in response to temperature in the meroplankton than in holoplanktonic taxa, with echinoderm larvae showing the greatest advance of 47 days in the peak of their abundance between 1958 and 2002.

Increases in relative and absolute abundance in echinoderm larvae in the CPR survey in the North Sea were noted by Lindley et al. (1995) and Lindley and Batten (2002) (Data updated by Kirby and Lindley, 2005 shown in Figure 2). In some regions they became numerically dominant regularly in the samples. In addition to a change in abundance, the timing of occurrence of echinoderm larvae in the CPR samples has become significantly earlier, which is consistent with the results of Greve et al. (2001) who showed a strong negative correlation between temperature and the start of season for spatangoid echinoderms in the Helgoland Bight. The dominant species of echinoderm larvae in North Sea CPR samples is the spatangoid, *Echinocardium cordatum* (Kirby and Lindley 2005). Kirby and Lindley suggested that the changes in seasonal cycles and abundance were consistent with known effects of temperature on the reproductive biology of *E. cordatum*. Recently, the long-term changes have been analysed in greater detail by Kirby et al. (2007) who found that echinoderm larvae had become more abundant than copepods in the samples by 1998-2002. The changes in abundance and timing appear to be linked to a stepwise increase in temperature in 1987 resulting in higher temperatures, particularly during the early months of the year (January to May)

Here, we describe long-term changes in the abundance and phenology of the major components of the meroplankton in the CPR samples (echinoderm, decapod and bivalve larvae) as background to a more detailed study of the changes by Kirby et al. (submitted).

Methods.

The CPR (Figure 3) and the methods used in analysis of the samples are described by Batten et al. (2003a). The recorders are towed by ships-of-opportunity, usually merchant ships on their regular routes. As far as possible a tow is taken on each route in each calendar month. The recorders are towed at a depth of approximately 7 m. The sampling aperture is a 1.27 mm square opening at the front of the machine. The water is filtered through a band of silk gauze with mesh size ~ 270 μm . The gauze is wound on by a drive powered by an impeller and the gauze with the retained plankton is covered by a second gauze band, to create a plankton sandwich, and the whole is rolled into a storage tank where it is preserved with formalin.

On return of the CPRs to the laboratory, the gauze is divided into sections representing 10 nautical miles (18 km) of tow during which 3 m³ of water are filtered. The positions and times of the mid-point of each sample are calculated from data provided by the ship. Normally alternate samples are analysed. The method of analysis of samples is described by Batten et al. (2003a). Numbers of smaller zooplankton, including bivalve, echinoderm, cirripede and ectoproct (cyphonautes) larvae are estimated in an examination of a sub-sample of about 1/49 of the sample while total numbers in the sample of larger zooplankton, including decapods, are counted.

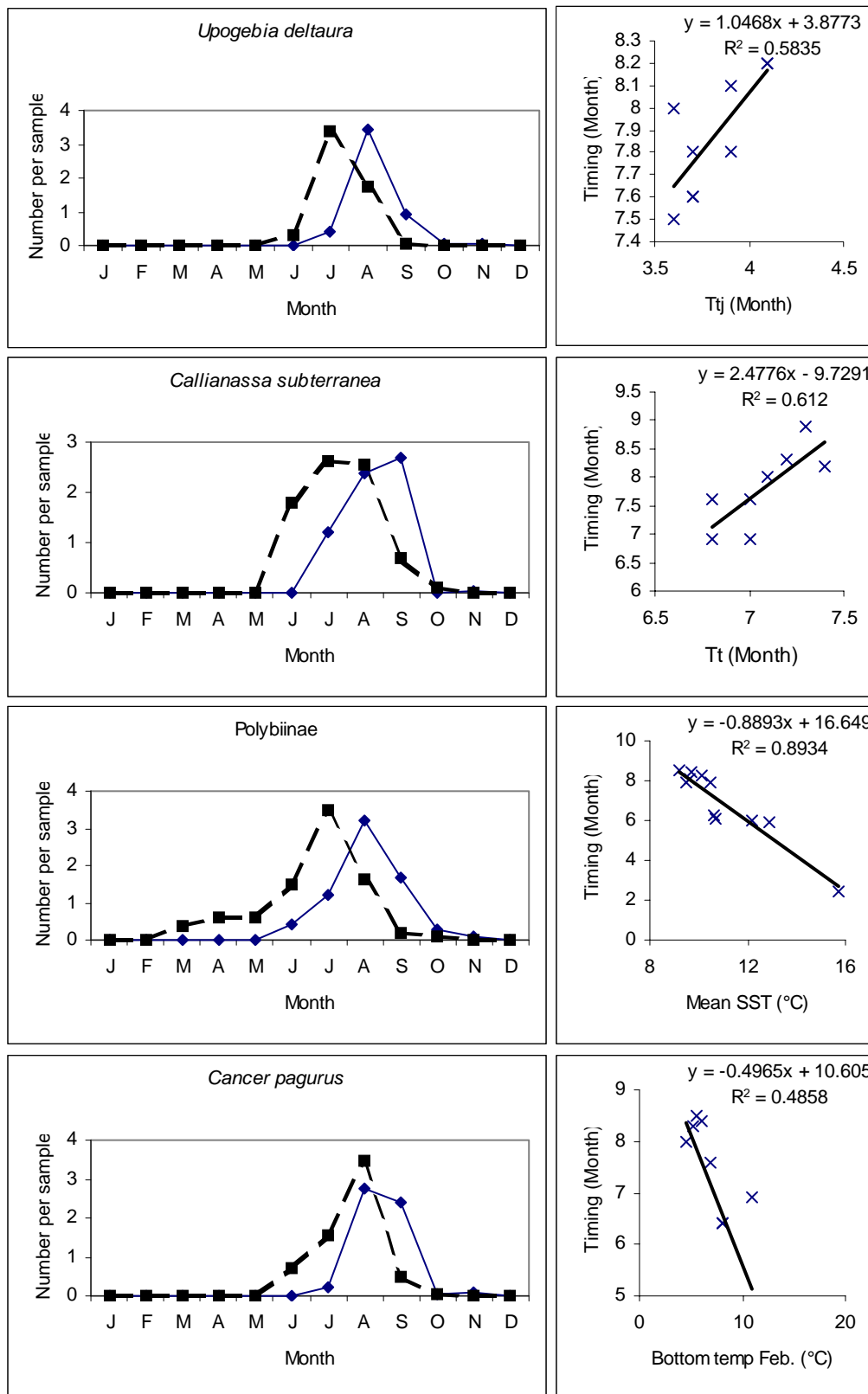


Figure 1 . Left. Mean numbers per sample per month of abundant decapod larvae in CPR sample in the North Sea in 1989 (squares and broken line) and between 1981-1983 (diamonds and continuous line) (after Lindley et al. 1993). Right. Geographical variations in the timing of the larvae in 1981-83 in relation to temperature, replotted and recalculated after Lindley (1987). T_{tj} is timing of the spring increase in temperature, and T_t is the timing of the peak of the seasonal cycle of temperature. Timing was calculated according to the methods of Colebrook and Robinson (1965).

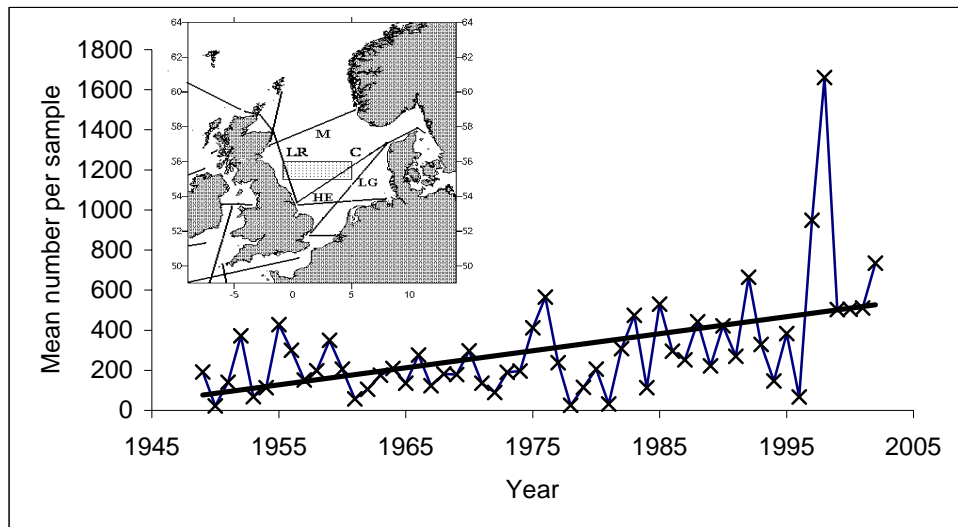


Figure 2. Echinoderm larvae. Mean numbers per CPR sample in the Dogger area (stippled rectangle on inset map) 1949-2002 from data presented by Kirby and Lindley (2005)

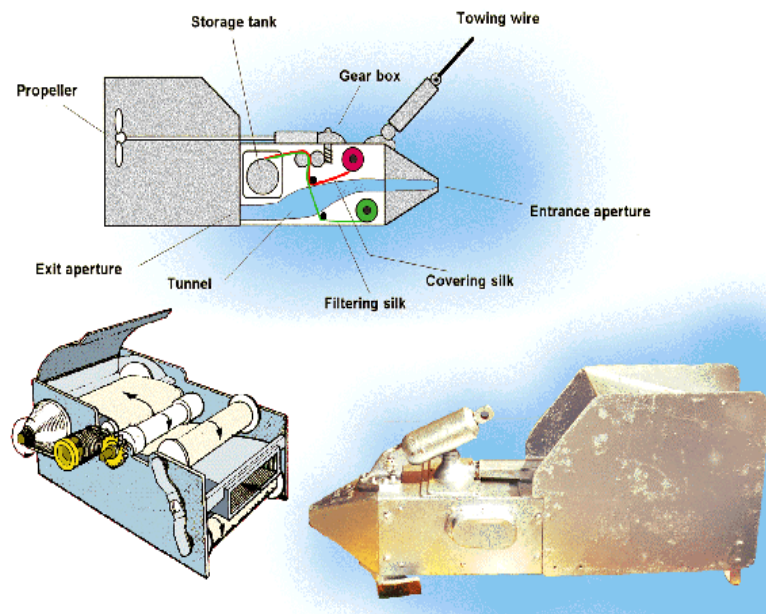


Figure 3. The Continuous Plankton Recorder. Cross-section (top), the internal mechanism (below left) and external appearance (below right)

Mean numbers per sample of echinoderm, decapod and bivalve larvae for the North Sea (51° - 61° N, 3° W- 11° E) have been calculated for the period 1958-2005 and the monthly mean numbers per sample were calculated for the decades 1958-67 to 1988-1997 and for the period 1998-2005.

Results

The annual mean numbers of echinoderm, bivalve and decapod larvae per sample for the 48-year period 1958-2005 are shown in Figure 4. Over the whole North Sea (as opposed to the restricted areas considered by Lindley et al. 1995, Lindley and Batten, 2002 and Kirby and Lindley 2005) the increase in abundance of echinoderms was not notable until the period from 1998 onwards. Bivalves, overall, declined in abundance with some of the lowest values in the years from 2000 onwards. Decapods increased in numbers, with values from 1990 onwards fairly consistently above the counts in earlier years. Low numbers of all three groups were recorded in 1978-1981.

The seasonal cycles of the three groups are shown in Figure 5. The echinoderms reached their peak of abundance in July in each of the three decades from 1958-1987, but in 1988-1997 the peak was in June and by 1998-2005 the much-elevated monthly maximum was in May. The bivalve larvae were most abundant in July throughout. From 1958 to 1987 the decapods reached maximum abundance in August but were much more abundant with a July peak in 1988-1997 and 1998-2005.

The cirripedes showed no obvious trends in abundance or timing, cyphonautes were more abundant early in the period but then showed little change while echinoderm post-larvae were more abundant after 1990 than in earlier years (data not shown).

Discussion

The changes in the abundance and phenology of the meroplankton appear to be related to temperature change. The increase in North Sea SST has been greatest in the winter and spring months but temperatures are now higher throughout the year (Kirby et al. 2007). Egg size and number in poikilotherms are phenotypically plastic traits that are known to respond to by temperature. Shearer (1996) and Fischer et al. (2003) have shown that higher temperatures during gametogenesis are usually associated with smaller eggs and larger clutch sizes. This relationship may contribute to latitudinal gradients in reproductive output as shown for decapod crustaceans by Lardies and Wehrmann (1997), Lardies and Castilla (2001), Brante et al. (2003) and Morley et al. 2006). In this way, increases in temperatures could influence reproductive output in a wide variety of organisms with similar life-history strategies.

Meroplankton abundance is also likely to be influenced by temperature during the planktonic phase. For example, higher temperatures will shorten larval development times thereby increasing larval survival (Mackie, 1984; Olson and Olson, 1989; Fenaux et al., 1994; Reitzel et al., 2004). The availability of phytoplankton food during the planktonic stage is also likely to affect larval abundance. Batten et al. (2003b) show that chlorophyll levels in the North Sea, indicated by the Phytoplankton Colour Index (a measure of phytoplankton chlorophyll derived from the CPR survey) have increased in the North Sea since the mid-1980s. Elevated levels of chlorophyll are now evident throughout the year (Edwards et al. 2001). Coincident changes in temperature and phytoplankton in the North Sea could therefore act in concert to increase larval abundance. However there is a contrast in the results presented here in between the increase in echinoderm and decapod larvae and the decline in numbers of bivalves in the samples.

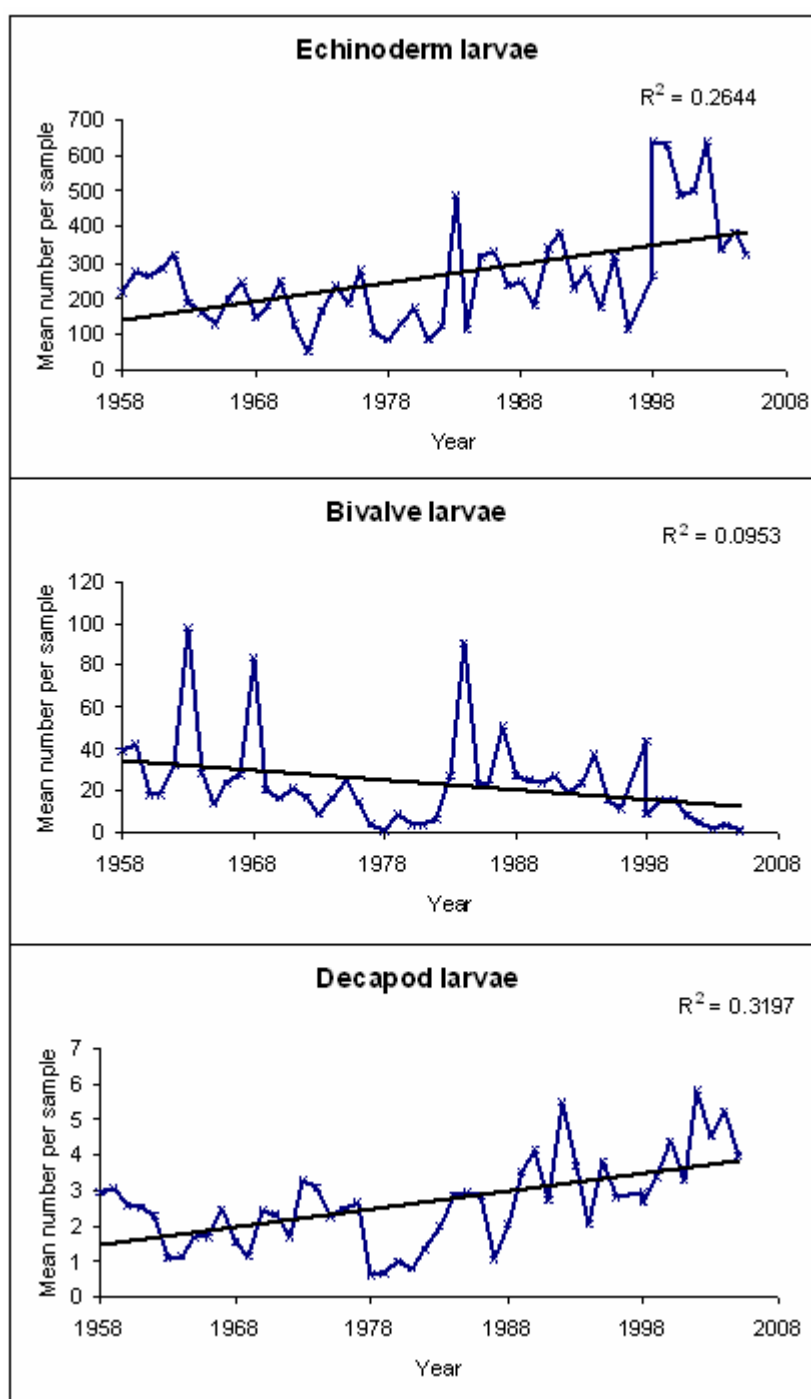


Figure 4. Variations in the mean numbers per sample (y-axis) of echinoderm, bivalve and decapod larvae in the North Sea 1958-2005.

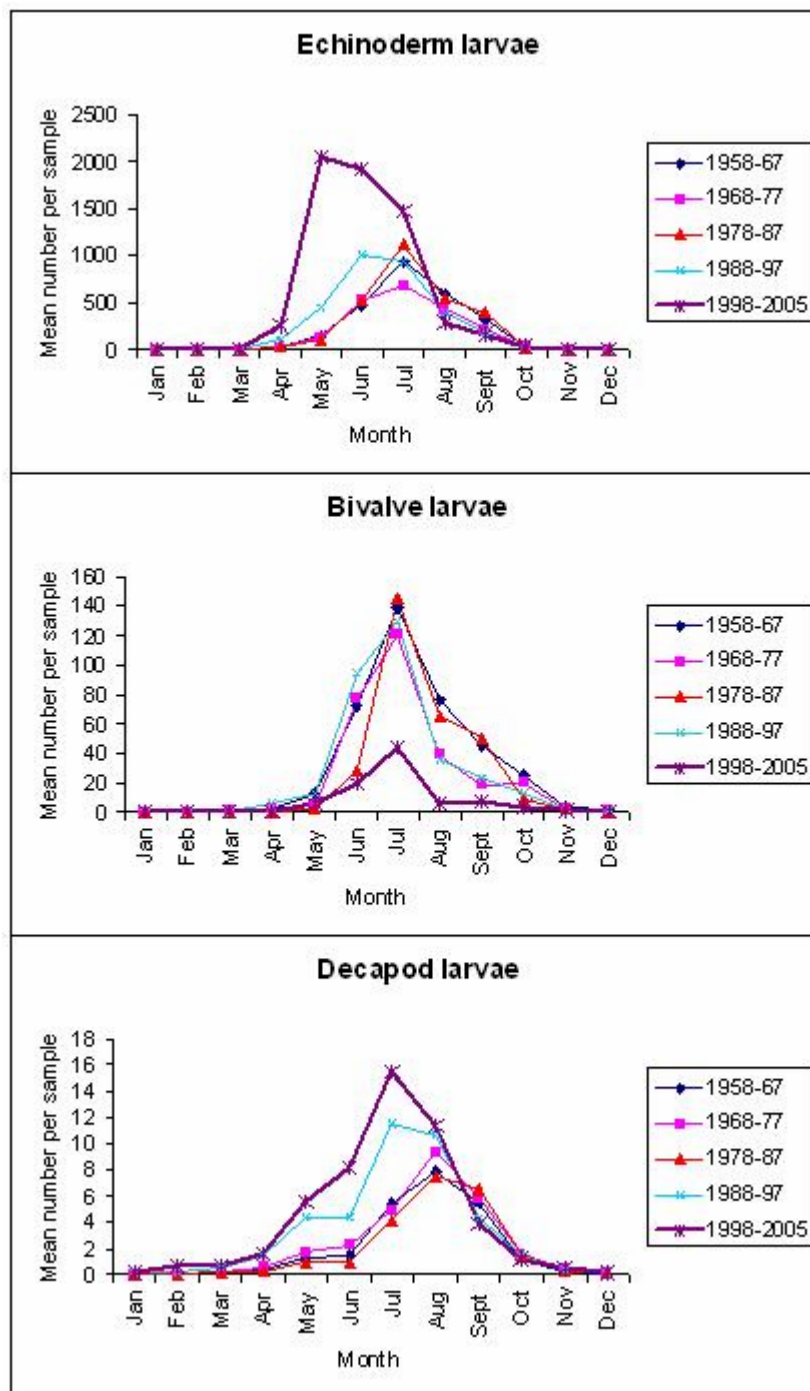


Figure 5. The seasonal cycles the mean numbers per sample (y-axis) of echinoderm, bivalve and decapod larvae in the decades between 1958 and 1997 and the period 1998-2007.

Climate change can alter aquatic ecosystems with considerable consequences for resource flow (Winder and Schindler 2004). Changes in merozooplankton abundance have implications for the trophodynamics of the spring and summer plankton. Changes in recruitment may impact benthic community ecology to intimately link the benthic and pelagic components of the ecosystem. In the North Sea the changes in the merozooplankton may indicate substantial changes in the nutrient

cycling and community ecology. The decline in bivalve larvae in contrast with the other taxa may be a consequence of community change within the benthos.

Our results present a background to extending the previous analysis of the interaction between echinoderm larvae, SST and chlorophyll (Kirby et al. 2007) to merozooplankton taxa from other phyla in order to determine whether changes in the North Sea plankton reflect a synchronous, community-wide response to hydroclimatic change, from the benthos to the pelagos (Kirby et al. submitted).

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References

- Batten, S.D., Clarke, R., Flinkman, J., Hays, G., John, E. John, A.W.G., Jonas, T.D., Lindley, J.A., Stevens, D. and Walne, A. 2003a. CPR sampling: the technical background, materials and methods, and issues of consistency and comparability. *Progress in Oceanography*, 58: 193-215.
- Batten, S.D., Walne, A.W., Edwards, M. and Groom, S. B. 2003b. Phytoplankton biomass from continuous plankton recorder data: an assessment of the phytoplankton colour index. *Journal of Plankton Research*, 25: 697-702.
- Beaugrand, G. 2003. Long-term changes in copepod abundance and diversity in the north-east Atlantic in relation to fluctuations in the hydroclimatic environment. *Fisheries Oceanography*, 12: 270-283.
- Bodo, F.C., Razouls, C. and Thiriot, A. 1965. Étude dynamique et variations saisonnières du plancton de la région de Roscoff. II. *Cahiers de Biologie Marine*, 6: 219-254.
- Brante, A., Fernández, M., Eckerle, L., Mark, F., Pörtner, H.-O. and Arntz, W. 2003. Reproductive investment in the crab *Cancer setosus* along a latitudinal cline: egg production, embryo losses and embryo ventilation. *Marine Ecology Progress Series*, 251: 221-232.
- Colebrook, J.M. and Robinson, G.A. 1965. Continuous plankton records: seasonal cycles of phytoplankton and copepods in the north-eastern Atlantic and the North Sea. *Bulletins of Marine Ecology*, 6: 123-139.
- Edwards, M., Reid, P.C. and Planque, B. 2001. Long-term and regional variability of phytoplankton biomass in the Northeast Atlantic (1960-1995). *ICES Journal of Marine Science*, 58: 39-49.
- Edwards, M. and Richardson, A. J. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature*, 430: 881-883.
- Fenaux, L., Strathmann, M. and Strathmann, R.R. 1994. Five tests of food-limited growth of larvae in coastal waters by comparisons of rates of development and form of echinoplutei. *Limnology and Oceanography*, 39: 84-98.
- Fischer, K., Brakefield, K.M. and Zwaan, B.J. 2003. Plasticity in butterfly egg size: why larger offspring at lower temperatures? *Ecology*, 84: 3138-3147.
- Greve, W., Lange, U., Reiners, F. and Nast, J. 2001. Predicting the seasonality of North Sea zooplankton. *Senckenbergiana martitima*, 31: 263-268.

- Johns, D.G., Edwards, M. and Batten, S.D. 2001. Arctic boreal plankton species in the North West Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences*, 58: 2121-2124.
- Kirby, R.R., Beaugrand, G. and Lindley, J.A. Submitted. Climate induced effects on the merozooplankton and the benthic-pelagic ecology of the North Sea.
- Kirby, R.R., Beaugrand, G., Lindley, J.A., Richardson, A.J., Edwards, M. & Reid, P.C. 2007 Climate effects and benthic-pelagic coupling in the North Sea. *Marine Ecology Progress Series*. 330: 31-38.
- Kirby, R.R. and Lindley J.A. 2005. Molecular analysis of Continuous Plankton Recorder samples, an examination of echinoderm larvae in the North Sea. *Journal of the Marine Biological Association of the United Kingdom*, 85: 451-460.
- Lardies, M.A. and Castilla, J.C. 2001. Latitudinal variation in the reproductive biology of the commensal crab *Pinnaxodes chilensis* (Decapoda: Pinnotheridae) along the Chilean coast. *Marine Biology*, 139: 1125-1133.
- Lardies, M.A. and Wehrtmann, I.S. 1997. Egg production in *Betaeus emarginatus* (H. Milne Edwards, 1837) (Decapoda: Alpheidae): fecundity, reproductive output and chemical composition of eggs. *Ophelia*, 46: 165-174.
- Licandro, P., Conversi, A., Ibañez, F. and Jossi, J. 2001. Time series analysis of interrupted long-term data set (1961-1991) of zooplankton abundance in Gulf of Maine (northern Atlantic, USA). *Oceanologica Acta*, 24: 453-466.
- Lindley, J.A., 1987. Continuous plankton records: the geographical distribution and seasonal cycles of decapod crustacean larvae and pelagic post-larvae in the north-eastern Atlantic Ocean and the North Sea. *Journal of the Marine Biological Association of the United Kingdom*, 67: 145-167.
- Lindley J.A. and Batten S.D. 2002. Long-term variability in the diversity of North Sea zooplankton. *Journal of the Marine Biological Association of the United Kingdom*, 82, 31-40.
- Lindley J.A., Gamble, J.C. and Hunt, H.G. 1995. A change in the zooplankton of the central North Sea (55°-58°N): a possible consequence of changes in the benthos. *Marine Ecology Progress Series*, 119: 299-303
- Lindley, J.A. and Reid, P.C. 2002. Variations in the abundance of *Centropages typicus* and *Calanus helgolandicus* in the North Sea: deviations from close relationships with temperature. *Marine Biology*, 141: 153-165.
- Lindley, J.A., Williams R. and Hunt, H.G. 1993. Anomalous seasonal cycles of decapod crustacean larvae in the North Sea in an exceptionally warm year. *Journal of Experimental Marine Biology and Ecology*, 172: 47-66.
- Mackie, G.L. 1984. Bivalves. *In* The Mollusca Vol 7, Reproduction pp. 351-418. Ed. by A. S. Tompa, N.H. Verdonk and J.A.M. van den Biggelaar Academic Press, Inc.
- Morley, S.A., Belchier, M., Dickson, J. and Mulvey, T. 2006. Reproductive strategies of sub-Antarctic lithodid crabs vary with habitat depth. *Polar Biology*, 29: 581-584.
- Olson, R.R. and Olson, M.H. 1989. Food limitation of planktotrophic marine invertebrate larvae: does it control recruitment success? *Annual Review of Ecology and Systematics*, 20: 225-247.
- Planque, B. and Batten, S.D. 2000. *Calanus finmarchicus* and the North Atlantic ecosystem: the year of *Calanus* in the context of interdecadal changes. *ICES Journal of Marine Science*, 57: 1528-1535.
- Rees, C.B. 1951. First report on the distribution of lamellibranch larvae in the North Sea. *Hull Bulletins of Marine Ecology*, 3: 105-134.
- Rees, C.B. 1952. Continuous plankton records: the decapod larvae in the North Sea 1947-1949. *Hull Bulletins of Marine Ecology*, 3: 105-134.

- Reid, P.C. and Edwards, M. 2001. Long-term changes in the pelagos, benthos and fisheries of the North Sea. *Senckenbergiana Maritima*, 31: 107-115.
- Reitzel, A R., Webb, J. and Arellano, S. 2004. Growth, development and condition of *Dendroaster excentricus* (Eschscholtz) larvae reared on natural and laboratory diets. *Journal of Plankton Research*, 26: 901-908.
- Richardson, A.J., Walne, A., Witt, M., Lindley, J.A., John, A.W.G. and Sims, D.W. 2006. Using Continuous Plankton Recorder Data. *Progress in Oceanography*, 68: 27-74.
- Shedder, M. 1996. Factors influencing egg size in the gammarid amphipod *Gammarus insensibilis*. *Marine Biology*, 124: 519-526.
- Winder, M. and Schindler, D.E. 2004. climate change uncouples trophic interactions in an aquatic ecosystem. *Ecology*, 85: 2100-2106.