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Timing of squid migration reflects North Atlantic climate variability

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The environmental and biotic conditions affecting fisheries for cephalopods are only partially understood. A problem central to this is how climate change may influence population movements by altering the availability of thermal resources. In this study we investigate the links between climate and sea-temperature changes and squid arrival time off southwestern England over a 20-year period. We show that veined squid (*Loligo forbesi*) migrate eastwards in the English Channel earlier when water in the preceding months is warmer, and that higher temperatures and early arrival correspond with warm (positive) phases of the North Atlantic oscillation (NAO). The timing of squid peak abundance advanced by 120–150 days in the warmest years ('early' years) compared with the coldest ('late' years). Furthermore, sea-bottom temperature was closely linked to the extent of squid movement. Temperature increases over the five months prior to and during the month of peak squid abundance did not differ between early and late years, indicating squid responded to temperature changes independently of time of year. We conclude that the temporal variation in peak abundance of squid seen off Plymouth represents temperature-dependent movement, which is in turn mediated by climatic changes associated with the NAO. Such climate-mediated movement may be a widespread characteristic of cephalopod populations worldwide, and may have implications for future fisheries management because global warming may alter both the timing and location of peak population abundance.

Keywords: phenology; sea temperature; North Atlantic oscillation; loliginid squid

1. INTRODUCTION

It seems likely that the present climate-warming scenario of the 1.4–5.8 °C rise in surface temperature over the next 100 years (Schneider 2001) will influence the timing and extent of animal movements and associated ecological processes. The possible large-scale ecological consequences of global warming have been emphasized recently using analyses of long-term data on phenological patterns of plants and animals (Post *et al.* 2001). Earlier dates of migration to breeding sites for both amphibians and birds have been ascribed to climatic warming, as have earlier egg-laying dates for birds and flowering time of plants (Beebee 1995; Crick *et al.* 1997; Forchhammer *et al.* 1998; McCleery & Perrins 1998; Crick & Sparks 1999; Post *et al.* 2001; Both & Visser 2001). However, by comparison the likely effects of climate change on the migration phenology of marine animals remain poorly understood, even though this may have important implications for fisheries management.

Squid are important members of marine food chains, not only as food items in the diet of fish, sea birds and marine mammals (Clarke 1996; Croxall & Prince 1996; Smale 1996), but also as predators on fish and crustaceans (Rodhouse & Nigmatullin 1996). Furthermore squid, together with cuttlefish and octopus, are now of major economic importance, making up just over 3% of the world's total capture production (FAO Yearbook 2000). Despite this, relatively little is known about the factors determining movement patterns and trends in abundance, although loliginid squid are known to be very responsive to temperature (Rathjen & Voss 1987; Waluda & Pierce 1998). Spatial shifts of fish such as tuna have been linked to warm-water displacements that occur during short-term climate fluctuations (Lehodey *et al.* 1997). However, the role of climate variability on squid migration phenology has not been established, even though climate-induced changes in distribution may affect capture fisheries by, for example, altering the location of peak abundance away from managed areas.

Given the lack of basic data for squid, the role of short- and long-term climate change on patterns of squid distribution will be difficult to predict because past and present responses have never before been determined. To shed light on the possible relationships between squid movements and temperature and climatic variables, in this paper we test the hypothesis that changes in sea temperature and climatic fluctuations of the North Atlantic oscillation (NAO) alter the phenology of migration in veined squid (*Loligo forbesi*). The results show for the first time, to our knowledge, that climate-mediated behavioural regulation occurs in cephalopods.

2. STUDY ANIMAL AND METHODS

The loliginid (myopsid) squid *L. forbesi*, known as the veined squid, inhabits subtropical and temperate waters over a broad geographical range in the eastern Atlantic. It is found in continental shelf waters in temperate regions and deeper in subtropical areas, generally between 60° and 20° N excluding the Baltic Sea (Roper *et al.* 1984). *L. forbesi* is known to carry out seasonal migrations off southwestern England and has an annual life cycle; they hatch in the western English Channel and migrate eastwards appearing in trawls off Plymouth around May (Holme 1974).

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After a few months of rapid growth in the English Channel and southern North Sea, including some summer spawning, they move back to the western approaches to spawn and die during the following December–January (Holme 1974).

(a) *Survey data*

We analysed catch data of *Loligo* from bottom trawls carried out by the Marine Biological Association's (MBA) research vessel, *RV Sarsia*, from 1953 to 1972 off Plymouth. This period included the end of a warm phase and onset of cold conditions, with parallel changes in the pelagic ecosystem (Southward 1980). *L. forbesi* was the dominant loliginid during this period (97.7% of individuals (Holme 1974)). The MBA dataset is particularly appropriate for studying squid seasonal movement and abundance patterns because it was collected before extensive commercial squid exploitation in British waters, is fishery independent and possesses very high temporal resolution: 1557 trawls, each of *ca.* 2 h duration (mean 143 min ± 38 s.d.) were undertaken over a 20-year period, a rate of about one experimental trawl every 4.5 days.

L. forbesi were taken by *RV Sarsia* using an otter trawl with Vigneron–Dahl gear (headline length 8.9 m; foot-rope length 27.4 m; bridle length 54.9 m). The cod-end had a mesh of 6.35 cm measured diagonally inside a stretched mesh. Four trawling stations off Plymouth were sampled (n, number of trawls): Looe Grounds (latitude 50°16′ N, longitude 04°24′ W), $n = 735$; Middle Grounds, L4 (50°15.5′ N, 04°13′ W), $n = 325$; Eddystone (inner) Channel Grounds (50°08.5′ N, 04°15′ W), $n = 111$; Eddystone (outer) Channel Grounds (50°02′ N, 04°20′ W), $n = 386$. The number of trawls carried out in each year varied, having a range of 28–160 (mean 83.7 trawls ± 32.7 s.d.; median 76.5). The majority of trawls were conducted between 06.00 and 21.00 (89.3%). Individual *L. forbesi* captured in each trawl were counted.

(b) *Data analysis*

Trawls from all four Plymouth stations were pooled for analysis because *L. forbesi* showed very similar trends in annual temporal abundance at each location. The number of squid captured per hour of trawl was log transformed using the function $\log_{10}(x + 1)$ individuals per hour of haul to standardize variances. A number was then assigned to each trawl according to when it occurred in relation to 1 April (day 1) in each year. For example, day 200 was 17 October. Day of peak abundance in each year (1 April to 31 March) was determined from models of fitted third-order polynomial regression to $\log_{10}(x + 1)$ individuals per hour of trawl haul versus the day of haul.

We compared the timing of peak abundance in each year with bottom temperature measured off Plymouth. Mean monthly temperatures for 12 months (April–March) prior to day 1 in each year were used to obtain a mean annual temperature. Temperature data were from MBA long-term bottom records in stratified water 15 miles off Plymouth (International Council for the Exploration of the Sea (ICES) station E1 50°02′ N, 04°22′ W) (Southward 1960; Southward & Butler 1972; Southward *et al.* 1995). We also compared the day of peak squid abundance in each year with the mean NAO index over the five months (December–April) (Jones *et al.* 1997) prior to, and including, 1 April (day 1) in each year. The relationship between annual mean E1 bottom temperature (January–December) and NAO index in the five months preceding May in each year was examined for a 40-year period (1947–1986) using the same data sources as given above.

3. RESULTS

Our results demonstrate that annual peak abundance of *L. forbesi* off Plymouth occurred significantly earlier when the sea was warmer in the preceding months (figure 1*a*; $n = 18$, $r^2 = 0.51$, $p < 0.001$). The difference in timing was as much as 150 days between early peak abundance (beginning of August) in warm years and late peaks (end of December) in cold years. The regression revealed that 51% of the interannual variability of *L. forbesi* day of peak abundance was explained by E1 bottom temperature. The day of peak abundance of squid showed a similar relationship with the NAO index, with early peaks occurring when the NAO was more positive (figure 1*b*; $n = 18$, $r^2 = 0.33$, $p < 0.02$). We also found a significant positive relationship between mean annual bottom temperature at station E1 from January to December between 1947 and 1986 and the NAO index in the five months (December–April) at the start of each of those years (figure 1*c*; $n = 40$, $r^2 = 0.31$, $p < 0.001$). Furthermore, increases in sea temperature over the five months prior to and during the month of peak squid abundance in each year varied little between years, irrespective of whether the peak in abundance occurred early or late (figure 2). In each year over a 20-year period, peak squid abundance occurred when the bottom water temperature was 13.0 °C (± 1.0 s.d.). Taken together, this indicates that veined squid responded to specific temperature changes independently of the time of year. In contrast, there was no relationship between annual abundance of *L. forbesi* and annual mean E1 bottom temperature in the months preceding 1 April ($n = 18$, $r^2 = 0.002$, $p > 0.50$).

4. DISCUSSION

The NAO index quantifies the alternation of the atmospheric mass between the North Atlantic region of subtropical high pressures centred on the Azores and the subpolar low pressures centred on Iceland, changes which determine the speed and direction of the surface westerlies across the Atlantic (Hurrell 1995; Fromentin & Planque 1996). In years with a high, positive NAO index an accentuated pressure difference between the Azores and Iceland occurs, with resultant strong wind circulation producing high temperatures in western Europe and low temperatures on the Canadian east coast (Fromentin & Planque 1996). Our results show that during positive phases of the NAO, warmer water (11.5–12.2 °C) occurred off Plymouth whereas colder water (10.0–11.5 °C) predominated during negative phases. This suggests that fluctuations in the NAO determine to a large extent the thermal regime in the western English Channel.

In this study, the day of the year when the highest number of *L. forbesi* individuals were present off Plymouth was used to indicate the timing and extent of the 'population' movement up-Channel along their known migration route (Holme 1974). The results of our study indicate that the day of peak abundance of veined squid was closely linked to changes in sea-bottom temperature that in turn appear to have been brought about by fluctuations in the NAO. When warmer temperatures coincided with

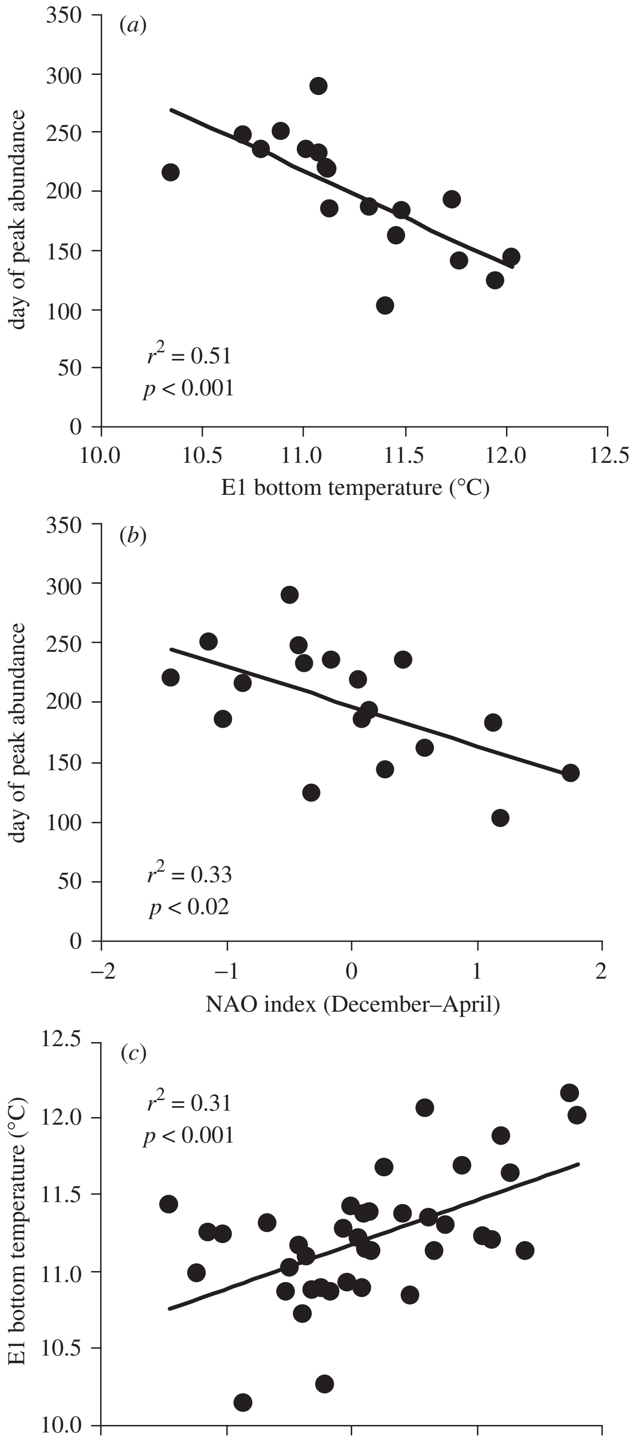

Figure 1. Relationships of (*a*) sea-bottom temperature at ICES station E1 and (*b*) NAO index to day of peak abundance of veined squid, *L. forbesi* off Plymouth over a 20-year period (1953–1972). (*c*) The relationship between bottom temperature and NAO over a 40-year period (1947–1986). Day of peak abundance, day 1 = 1 April.

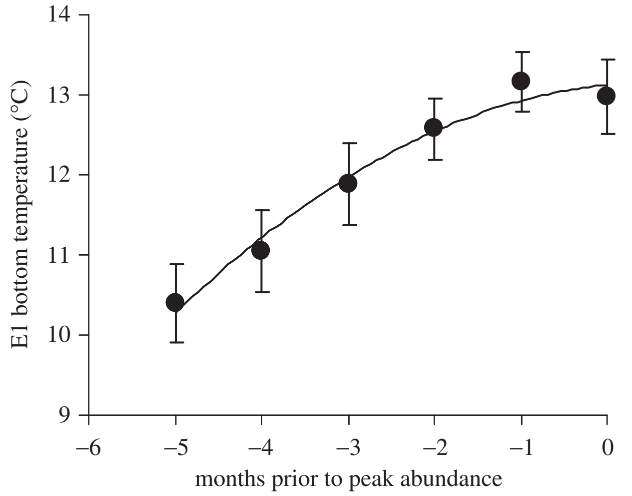

Figure 2. Mean monthly E1 bottom temperature during the five months prior to, and in the month of peak abundance over a 20-year period (1953–1972) ($n = 18$, $r^2 = 0.98$). Bars denote 95% confidence limits.

squid hatching time (December–January) in the western Channel and persisted during subsequent up-Channel migration, squid were found much earlier off Plymouth compared with years when cold water predominated over the same period. A maximal increase of 1.5 °C was observed to shift the day of peak abundance forward by about four months. For the first time, to our knowledge, this demonstrates that a squid species (*L. forbesi*) migrates earlier in years when water temperatures are generally higher, and that these changes in peak abundance phenology are in turn mediated by atmospheric fluctuations characterizing the NAO.

Links have been made between trends in seawater temperature and distribution for a number of squid species (Waluda & Pierce 1998). However, the causal relationships underlying such links have been difficult to establish (Waluda & Pierce 1998; Bellido *et al.* 2001). It is not known whether distribution results from habitat selection for specific thermal resources (via physiological tolerance or preference), access to temperature-dependent food resources, or whether effects on maturation and growth or migration are the dominant factors (Waluda & Pierce 1998). A probable relationship between seasonal temperatures, prevailing winds and the inshore arrival of long-finned squid (*L. pealei*) off New England has been suggested (Rathjen & Voss 1987), but hitherto, the role of the NAO on squid migration phenology has not been documented (Dawe *et al.* 2000). Our data do not support the idea that the timing of squid migration occurs independently of temporal changes in temperature. The present study shows that water temperature was closely linked to the extent of veined squid movement because increases in sea temperature over the five months prior to and during the month of peak abundance varied little between years irrespective of whether the peak occurred early or late. This suggests that water temperature and indirectly, climate fluctuations, play important roles in determining the extent of squid movements in any given year.

Enhanced rates of embryonic development and earlier emergence times of young squid in warm years may also occur. It would be expected that in years with warmer sea temperatures, development and growth would be faster and result in earlier appearance of young squid in trawls off Plymouth. However, because development times range from only 30 to 40 days (Holme 1974), this variation would be unlikely to be the main factor driving the much larger differences in timing of peak abundance observed in this study (maximum differences of about 120–150 days). Similarly, temperature-independent migration coupled with slower growth during cold conditions (which could maintain small size and reduce trawl catchability) cannot explain our findings either. This is because the cod-end mesh size used was small enough to capture squid of 10–11 cm (Holme 1974). Thus, for squid to appear off Plymouth at the same time in both 'warm' and 'cold' years regardless of water temperature, and to remain uncaught, suggests that in cold years they would have to maintain a body length less than *ca.* 10 cm. Because in cold years the day of peak abundance occurred around December, this suggests that squid would need to delay growth for about four months to avoid being captured in trawls. This seems unlikely given that *L. forbesi* off Plymouth are known to increase in length by about 2.5 cm per month (Holme 1974). We conclude therefore, that the temporal variation in peak abundance of squid seen off Plymouth represents temperature-dependent movement. Although we do not know the precise mechanism determining the timing of movements, our observations suggest that temperature may act as a proximate cue to ensure occupation of preferred thermal habitat and/or as a response to available trophic resources. In either of these scenarios, our data indicate that the extent of annual veined squid distribution as a result of migratory movements is related to temperature, and over longer temporal scales, climatic variables.

Fishery landings of loliginid squid can be predicted by temperature over large spatial scales (Serchuk & Rathjen 1974; Robin & Denis 1999). However, off Plymouth at a local scale, we found no relationship between annual abundance and sea temperature. This may be because over large geographical areas the direct effects of climate-induced thermal changes on cohort size may be more apparent. This may contrast with local scales, where the roles of density and resource-dependent ecological processes such as competition and predation, that in turn may be influenced by temperature effects on physiology and behaviour, e.g. dispersal (Davis *et al.* 1997; Post *et al.* 2001), may be more important to quantify. Nevertheless, even though these links between regional sea-temperature changes and squid cohort abundance remain to be determined, our analysis shows that in the northeastern Atlantic the timing and extent of *L. forbesi* migration is closely linked to sea-temperature changes mediated by the NAO. These findings may be a general characteristic of cephalopod populations worldwide. More importantly, the response of squid to global warming may result in changes in both the timing and location of annual peak abundance, responses which could act to shift exploited populations away from managed or protected zones.

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