Low-temperature-driven early spawning migration of a temperate marine fish

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Summary

1. It is often assumed that the timing of annual migrations of marine fish to spawning grounds occurs with very little change over time. However, it is unclear how much migration is influenced by climate change in marine species that spawn at sea but spend most time in estuarine conditions, especially as thermal regimes in estuaries may differ significantly from those in the open sea.
2. Migration phenology was studied in a population of flounder, *Platichthys flesus* (L.) off south-west England using high-temporal resolution trawling data over a 13-year period.
3. Flounder migrated from their estuarine habitat to spawning grounds at sea some 1 – 2 months earlier in years that were up to 2°C cooler. Flounder arrived on the spawning grounds over a shorter time period (2 – 6 days) when colder than normal conditions prevailed in the estuary, compared to warmer years (12 – 15 days). This suggests they were responding to low temperatures by exhibiting a more synchronous, population-level early migration.
4. The timing of migration was earlier when the largest differences in temperatures between near-estuary and offshore environments occurred, differences that were related significantly to cold, negative phases of the North Atlantic Oscillation (NAO).
5. Flounder migration phenology appears to be driven to a large extent by short-term, climate-induced changes in the thermal resources of their overwintering habitat. This suggests climate fluctuations characterising the NAO may have significant effects on the timing of the peak abundance of fish populations generally, which, in turn, may have implications for fisheries management.

Key-words: climate change; weather; behaviour; migration; phenology; fish

Introduction

Climate change has had a clear impact on the annual timing of life-history events of animals and plants (Bradley *et al.* 1999; Walther *et al.* 2002). Analyses of long-term phenological patterns have shown climatic warming accounts for earlier dates of migration to breeding sites for amphibians and birds, earlier egg-laying in birds, and early flowering of plants (Crick *et al.* 1997; Forchhammer, Post & Stenseth 1998;

McCleery & Perrins 1998; Crick & Sparks 1999; Inouye *et al.* 2000; Both & Visser 2001; Post *et al.* 2001; Forchhammer *et al.* 2002). Because sea temperatures have risen in many regions over the past two decades, and recent predictions indicate a 0.5 to 4.0^{o}C increase in North Atlantic sea-surface temperatures over the next century (Hulme *et al.* 2002), it is possible that the timing and location of peak abundance of fish and cephalopods may be altered (Sims *et al.* 2001).

For aquatic ectotherms in particular, seasonal rises in temperature can act as an important cue in the timing of migration (Verwey 1949; Sims *et al.* 2001) and for synchronising reproduction with the seasonal increase in abundance of food (Cushing 1982; Cushing 1990). The different responses of species to climate change are important to understand because they will have important consequences for trophic dynamics and fisheries yields of the ecosystem (Murawski 1993). Nonetheless, phenological changes in the migration of marine fish as a consequence of climatic variation are poorly understood, mainly due to the obvious difficulties of direct observation.

There is evidence that higher sea-surface temperatures in spring contribute to earlier movements of migratory marine fish species to spawning grounds (Ware & Tanasichuk 1989; Carscadden, Nakashima & Frank 1997). Some fishes may have temperature-dependent gonadal development (Ware & Tanasichuk 1989) and so become ready to spawn, and hence migrate, earlier in warmer years. Other studies with weakly migratory species such as sole, *Solea solea* (L.), however, indicate no relationship between the timing of spawning and seasonal increases in temperature (Horwood 1993). But what has not been determined is how temperature influences the phenology of migration in marine species that occupy estuarine habitats and which return to sea each year to spawn. Climate warming or cooling may affect these species' migration patterns unpredictably because the magnitude and variance of temperatures in estuaries may differ significantly from those in the open sea.

To investigate the role of interannual temperature changes on spawning migration in a marine fish that lives for much of its life in reduced salinity, we investigated the migration phenology of flounder, *Platichthys flesus* (L.). This flatfish is a marine species that inhabits shallow inshore areas, including brackish and freshwater environments. Its range in the north-east Atlantic extends from southern Norway and the Baltic (~60°N) to Morocco, including the Mediterranean (~30°N), with subspecies present in both the Adriatic Sea and Black Sea (Galleguillos & Ward 1982). *P. flesus* has a wide salinity and thermal tolerance and is the only species of flatfish to be found in freshwater in Europe (Wheeler 1969). In this study we use high-temporal resolution trawl data collected off Plymouth, south-west U.K., to determine whether the timing of migration in *P. flesus* is dependent on temperature.

Materials and methods

SURVEY DATA

Mature flounder leave the Tamar estuary in Plymouth for their spawning grounds at sea in February and afterwards disperse back to local rivers and estuaries (Dando & Ling 1980). The spawning migration of mature flounder was studied using trawl data collected by the Marine Biological Association (MBA) research vessel RV 'Sarsia' over a 13-year period between 1953 and 1965. The high-temporal resolution dataset comprises counts of individual *P. flesus* captured during each of 1,084 trawls (mean duration of 2.40 h $\pm$ 0.64 S.D.; mean time between trawls 3.7 d $\pm$ 10.2 S.D., median 1.0 d, with 90% of all trawls less than 7 days apart). The hauls were taken with a

standard 'Granton' otter trawl with Vigneron-Dahl gear (headline length 8.9m; 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 areas off Plymouth were sampled (*n*, number of trawls), comprising two groups: (a) the inshore stations, Looe Grounds (latitude $50^o16'$ N, longitude $04^o24'$ W), *n* = 476, and the Middle Grounds, L4 ($50^o15.5'$ N, $04^o13'$ W), *n* = 229; (b) the deeper water grounds, Eddystone (inner) Channel Grounds ($50^o08.5'$ N, $04^o15'$ W), *n* = 109, and the Eddystone (outer) Channel Grounds ($50^o02'$ N, $04^o20'$ W), *n* = 293 (Fig. 1). A previous tagging study showed that flounder aggregating in these areas included mature, spawning individuals from the Tamar estuary (Dando & Ling 1980).

DATA ANALYSIS

The number of trawls in each of two years sampled (1954-55 and 1961-62) was less than 40, hence these years were discarded from the analysis, except for overall abundance estimates. The mean number of trawls per year was 100.7 ($\pm$ 37.3 SD; median 88.5) for the remaining 10 years in the dataset. The number of individual *P. flesus* captured per hour of trawl (or catch per unit effort, CPUE) was calculated for each trawl and transformed using the function $\log_{10} (x+1)$ to homogenise variances. The day of peak CPUE of flounder on the spawning grounds was estimated by determining the day number on which a catch of flounder was made, and which also corresponded to the day when 50% of the cumulative sum of the annual total mean abundance occurred. The CPUE of flounder on the spawning grounds was generally described by a normal distribution (Fig. 2), such that the day when 50% cumulative CPUE occurred was a reasonable proxy for the day of peak abundance.

We compared the estimated day of peak CPUE, or abundance, in each year with the annual mean sea-bottom temperature measured off Plymouth. Mean monthly temperatures for 12 months (October to September) in each year were used to obtain a mean annual temperature. Temperature data in stratified water 15 miles off Plymouth (International Council for the Exploration of the Sea (ICES) station E1, $50^o02'$ N, $04^o22'$ W) were available in the MBA long-term database (Southward 1960; Maddock & Swann 1977). We compared the annual mean temperatures on the sea bottom at station E1 with the annual mean near-surface temperatures recorded in Plymouth Sound (into which the Tamar and Plym rivers flow; Fig. 1). The mean monthly temperature for January was also compared. The mean monthly temperatures for Plymouth Sound were derived from data provided by G.H. Ivory and Partners and then by the City Medical Officer for Health, as detailed in Cooper (1958) and Southward (1960). The temperatures were measured three times a week on Plymouth waterfront, from 1941 to 1955 below the MBA Laboratory (Plymouth Hoe), and later from the outer pier at Millbay Docks, approximately 1.2 km to the west. They are here taken as a proxy indication of conditions in the Tamar, for which there is no consistent time series.

To determine if winter temperature differences between the inshore and open sea environments played a role in flounder migration phenology, the timing of peak abundance in each year was compared with the mean monthly temperature differential for February between E1 and Plymouth Sound. Similarly, the difference in days between the day in each year when flounder were first caught, and the day when 50% of the total mean annual abundance occurred, was compared with the annual mean bottom temperature at E1. We also compared the E1 – Plymouth Sound February temperature differential with the mean North Atlantic Oscillation (NAO) index over

five months (December–April) (Jones, Jonsson & Wheeler 1997) in the same year, and that also encompassed the period of flounder migration.

Results

TRAWL CATCHES

In the 12 years between 1953-54 and 1964-65 a total of 2,784 *P. flesus* were caught in 102 individual trawls out of a total of 1,084. Most of the trawl catches containing one or more *P. flesus* occurred at the inshore locations: Looe Grounds ($n = 71$) and Middle Grounds (L4) ($n = 29$). Over this period, flounder were caught between 28 January and 26 April (Table 1). The number of days between the first and last catches in each year varied between 1 and 72 days, with a mean of 28.1 days ($\pm$ 19.8 SD; median 23.0; $n = 10$). These results show that in broad terms the timing of migration and aggregation of flounder at sea was very regular, occurring in the late winter to early spring of each year studied (Fig. 3), and lasting, on average, for about one month.

MIGRATION PHENOLOGY

There was a significant positive relationship between the day of peak abundance and the mean annual sea-bottom temperature at station E1 ($r^2 = 0.47$, $P = 0.03$). This indicates that flounder migrate to the spawning grounds earlier in cold years (Julian day 28-58; temperature, 10.2–11.1^{o}C) compared to warmer years (Julian day 68-88; temperature, 11.3–12.2^{o}C) (Fig. 4a). The day of peak abundance was negatively related to an increased difference in February mean temperatures between station E1 and Plymouth Sound, indicating that migration occurred earlier when there was a maximal difference in temperature between the estuary and offshore (Fig. 4b). Furthermore, there was a significant negative relationship between the February temperature differential (E1 – Sound) and the winter mean NAO index showing that when the NAO index was more positive there was less difference between February temperatures at station E1 and in Plymouth Sound (Fig. 5). Interestingly, the duration in days between the first catch of flounder and when 50% of the cumulative annual mean abundance occurred, increased with greater mean annual temperature at E1 (Fig. 6).

TEMPERATURE TRENDS

The northern half of the western English Channel is stratified from May to September (Harvey 1955; Pingree 1975; Pingree & Pennycuick 1975; Pingree, Maddock & Butler 1977; Pingree & Griffiths 1978), and station E1 is just within this stratified zone. Moving inshore from E1 towards the River Tamar, the thermal stratification becomes weaker, and surface temperatures lower. For example, in July, a surface to bottom temperature difference of 5°C or more at E1 is reduced to 3 to 4°C on the Eddystone Grounds and only 2°C at the L4 grounds (Southward 1984). The mean annual temperature in Plymouth Sound is higher than the bottom temperature at E1 in all years (Fig. 7a). In contrast, the winter temperatures at E1, for the then unstratified water column, are always higher than the values in Plymouth Sound, by about 2°C more in cold winters (Fig. 7b). Unpublished records for the Tamar Estuary show complex local variations in salinity and temperature. However, in winter, when the flounders are migrating, the upper estuary may be 2°C cooler than Plymouth Sound, with an upper layer of cold water of lowered salinity. This trend from E1 to the estuary is brought about by the greater influence of air temperature near the land (Fig.

7c). The air temperature at Plymouth in January-February can be 4 to 5°C below the sea temperature at E1 (Fig. 7c).

There was no significant relationship between annual mean temperature at E1 and year (linear regression, $P = 0.33$) indicating that there was no underlying positive or negative trend in bottom temperature in the period 1953-65. However, the smoothed annual surface means show that the period from 1921 to 1950 was one of increasing temperature (Southward 1960; Southward & Butler 1970; Southward, Butler & Pennycuick 1975). In the mid 1950s there was a short period of cooling, but the upward trend was resumed with a peak in 1959-60. After 1961 there was a cooling trend and the winters became colder. The very cold winter of 1962-63 was evident both at E1 and in Plymouth Sound (Fig. 7a-c) with January-February mean temperatures of 7.6^{o}C at the former and 5.4^{o}C at the latter (Fig. 8a,b). Comparison of mean monthly temperatures in 1959-60 (warm year) and 1962-63 (cold year) both show that summer temperatures in Plymouth Sound were higher than at E1, but during winter, temperatures offshore were warmer than in Plymouth Sound (Fig. 8a,b). The means for the two months, January and February 1963 were the lowest since the start of the series (Fig. 8a,b), related to the fact that the cold spell began earlier in the year than previous cold years.

Discussion

Mature flounder migrate from the Tamar and Plym rivers to the spawning grounds off Plymouth during February and March (Dando & Ling 1980). Although the exact spawning grounds to which these fish migrate were not specified in the latter study, flounder generally spawn in inshore areas of 20 – 40 m depth (Wheeler 1969). In the data analysed, flounder were caught regularly between late winter (February) and spring (April) in each year but not at any other time. All but four of the 2,784 *Platichthys flesus* captured during the 13-year period were caught north of 50° 13′ N, that is, in water < 55 m deep. Furthermore, the 705 trawls conducted on these relatively shallow, inshore grounds showed that flounder CPUE increased each year to a peak before subsequently declining. Despite undertaking 402 trawls on grounds to the south in deeper water (~70 m depth) over the study period, only four specimens were captured. Taken together with previous work, this indicates that the trawls captured flounder when they were on the inshore grounds where they spawn, rather than individuals caught incidentally moving through this area to grounds farther offshore.

MIGRATION PHENOLOGY

Fishes may migrate earlier in warm years compared to colder ones because they have temperature-dependent gonadal development, and/or so as to match indirectly their spawning time with seasonal peaks in productivity, that in turn may shift with climatic changes (Cushing 1969; Cushing, 1990). Some studies on migratory fish species provide support for the phenological change predicted for warmer years. Capelin, *Mallotus villosus* (Müller 1777), off Newfoundland were found to have an earlier spawning time when mean fish lengths were lower and sea surface temperatures were higher than average (Carscadden *et al.* 1997). Pacific herring, *Clupea pallasi* (Valenciennes 1847), spawned earlier when the water was warmer because the instantaneous rate of gonad growth depended on fish mass and daily sea temperature (Ware & Tanasichuk, 1989). In contrast however, Cushing (1969) found that the variability in spawning periods of Atlantic herring (*Clupea harengus* L.), plaice

(*Pleuronectes platessa* L.) and cod (*Gadus morhua* L.) was low, although there were indications that cod may adapt slowly to climatic change. More recently though, substantial variation in the timing of cod spawning has been reported (Lawson & Rose 2000).

The results of the present analysis show that the timing of flounder spawning migration was not fixed. Instead, the day of peak abundance of flounder occurred significantly earlier (by about 1 – 2 months) when sea temperatures were lower by up to 2°C. Furthermore, our data show that the time between the arrival of the first *P. flesus* at sea and the day when 50% of the total annual abundance occurred, was positively related to sea temperature. This suggests that more individuals started their migration at a similar time when it was colder, resulting in more arriving on the spawning ground over a shorter time period compared to warm years. By comparison, the time for migration in warm years was protracted. The question of why flounder migrated earlier, and why individuals did so at a similar time when it was colder, may be related to temperature variation in their estuarine habitats prior to migration.

The water temperature in Plymouth Sound and on the sea bottom at an offshore station (E1) showed similar trends over the 13-year period studied. However, the annual fluctuation in bottom temperature was not only smaller at E1, but was cooler in the summer and warmer in the winter compared to the near-estuary station in Plymouth Sound. Therefore, during winter (January and February) when flounder commence seaward migration, the temperature at the near-estuary station was between 1.0 and 2.0°C colder than in the open sea at E1. When the difference in temperature between station E1 and Plymouth Sound was greatest, the day of peak abundance was significantly earlier. This indicates that flounder responded to decreased availability of warmer thermal habitat in their estuarine environment by migrating.

During cold years, the need for flounder to move from lower than average temperatures to waters about 2°C warmer is most likely related to physiological requirements. The thermal environment can be quantified as an ecological resource because animals, and ectothermic fish in particular, are likely to select temperatures that more or less deliver physiologically optimal interactions (Tracy & Christian 1986; Wurtsbaugh & Neverman 1988; Wildhaber & Crowder 1990). The thermal niche of fishes has been defined as the preferred temperature ± 2°C on account of fish in laboratory gradient studies spending two-thirds of their time within 2°C of their preferred temperature (Magnuson & Destasio 1997). It has been shown that a large number of performance optima for individual species occur within this range (Magnuson, Crowder & Medvick 1979). In our study, it seems likely that flounder migrated earlier when it was much colder to remain within their thermal niche, such that normal rates of energy expenditure associated with activity and growth could be maintained. There may be a strong pressure for flounder to start migrating earlier in colder than average years to maintain higher gonadal growth rates prior to spawning. The need to avoid low temperatures outside the optimal range may therefore act as a trigger for migration in flounder.

RELATIONSHIP WITH CLIMATE

The magnitude of the differential between near estuarine and marine environments of this study was related to the state of the North Atlantic Oscillation (NAO). The NAO determines the speed and direction of the surface westerlies across the Atlantic (Hurrell 1995). In years with a high, positive NAO index an accentuated pressure difference between Iceland and the Azores occurs, with the 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 when winter temperature differential between the sea and Plymouth Sound was lower, flounder migrated later. The largest temperature differences were in years with very negative NAO indexes, and documented severe winter weather (Crisp 1964). These were the years when flounder migration occurred earlier. Taken together, our findings suggest flounder responded to short-term, climate-driven fluctuations in availability of thermal resources by population-level movements to warmer areas offshore when estuarine conditions were colder than usual. To our knowledge, this is the first report of weather-driven, low-temperature-induced early spawning migration in a temperate marine fish.

The effect of very low temperatures on marine fish has been well documented (Lumby & Atkinson 1929; Simpson 1953; Woodhead 1964a,b,c; Horwood & Millner 1998). The severe winters of 1929, 1947 and 1963 caused large mortalities of fish when temperatures reached as low as $3^{o}C$ in some areas (Crisp 1964; Cushing 1982). In early 1963 widespread deaths of fish occurred in the North Sea and English Channel, particularly among flatfish such as *S. solea*, *P. platessa* and dab *Limanda limanda* (L.) (Woodhead 1964a,b). These deaths were probably brought about by physiological stress, because, for example, sole lose the capacity for ionic regulation in temperatures below about $4^{o}C$ (Woodhead 1964b). In temperatures approaching $0^{o}C$, flounder have high levels of serum sodium indicative of ionoregulatory perturbation (Woodhead 1964b) Dead flounders were not reported to have been caught in trawls during the present study, however, only 2 flounders were captured on the spawning grounds in the year following the severely cold winter of 1962-63. This suggests that the very low temperatures may have caused mortality in a large number of mature flounder, resulting in few adults migrating the next year. Because the spawning stock biomass was reduced, it is likely that this had a strong density-independent effect on larval abundance.

Behavioural changes in spatial distribution are arguably as important as demographic changes for understanding population dynamics more clearly (Elliott 2002). Migration from winter quarters to breeding grounds constitutes a major part of the life histories of migratory animals (Forchhammer *et al.* 2002). Our results show that a temperate marine fish population responded to climate-driven temperature changes by commencing migration earlier when winter temperatures in their estuarine habitat were colder than normal. This implies that the selection of optimal thermal resources by fish, perhaps for optimal gonadal development, has a role to play in determining the timing of migration. Effective fisheries management relies on a knowledge of the spatio-temporal distribution of fish populations, so the phenological changes of 1 – 2 months in the timing of flounder annual migration are significant in this context. It appears that both climate and local temperature changes in the habitats of fish need to be considered in relation to migration because, as we have shown here, they can affect not only its timing, but also the extent of the population moving at any one time.

Acknowledgements

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Table 1. Summary of trawl data for the ten years included in the analysis.

Year	Trawls (n)	Flounder captured (n)	Duration of Captures	Day of peak abundance (Julian day)
1953-54	121	103	22 Mar – 13 Apr	90
1955-56	175	232	22 Feb – 3 Apr	60
1956-57	141	401	26 Feb – 2 Apr	71
1957-58	89	91	25 Mar – 8 Apr	84
1958-59	113	528	11 Mar – 6 Apr	76
1959-60	78	189	17 Mar – 11 Apr	90
1960-61	88	77	28 Feb – 21 Mar	75
1962-63	65	208	28 Jan – 26 Apr	32
1963-64	50	2	5 Feb	43
1964-65	87	578	4 Mar – 25 Mar	67

Fig. 1. Study area in the western English Channel off Plymouth. Numbered boxes refer to the trawling areas given in the text: 1, Looe Grounds; 2, Middle Grounds (L4); 3, Eddystone (inner) Channel Grounds; 4, Eddystone (outer) Channel Grounds. Circles indicate the positions of temperature sampling in Plymouth Sound (waterfront and Millbay Docks) (grey circle) and at the offshore station E1 (black circle).

Fig. 2. Example of the temporal change in the relative abundance (catch per unit effort, CPUE) of flounder caught on the spawning grounds in 1957-58. Polynomial regression equation: $y = 0.00005x^3 - 0.0122x^2 + 1.0452x - 27.858$; $r^2 = 0.47$.

Fig. 3. The relative abundance of flounder caught on the spawning grounds over the 13-year period studied. Each point represents the catch per unit effort (CPUE) of an individual trawl.

Fig. 4. Changes in flounder day of peak abundance in relation to (a) sea temperature and (b) the difference in water temperature between Plymouth Sound and E1. Linear regression equations: a, $y = 22.63x - 188.82$; b, $y = -29.41x + 105.86$.

Fig. 5. The relationship between the difference in water temperature of E1 and Plymouth Sound with the North Atlantic Oscillation (NAO). Linear regression equation: $y = -0.38x + 1.31$.

Fig. 6. The duration of flounder abundance increase on the spawning grounds is related to sea temperature. Linear regression equation: $y = 6.59x - 67.62$.

Fig. 7. The fluctuations in (a) mean annual temperature, (b) mean January temperature in Plymouth Sound and at E1 and (c) mean January-February air temperature and Plymouth Sound water temperature over the 13-year study period.

Fig. 8. Annual variations in mean monthly temperature in Plymouth Sound and at E1 in (a) 1959-60 and (b) 1962-63. Grey square on each panel represents the mean January-February temperature for E1 (top line of square) and Plymouth Sound (bottom line) for 88 years between 1898 and 1989.
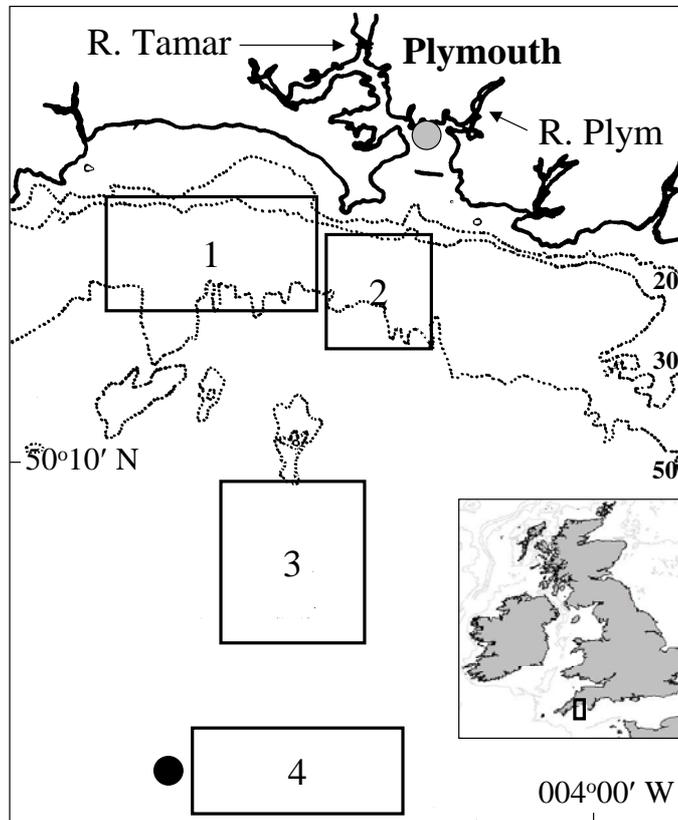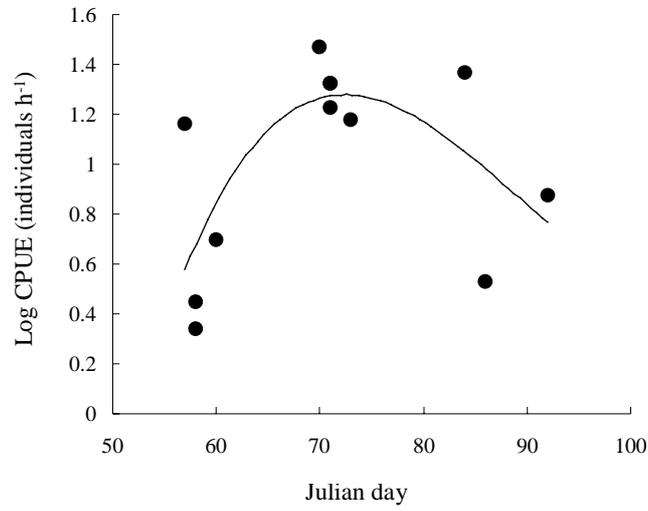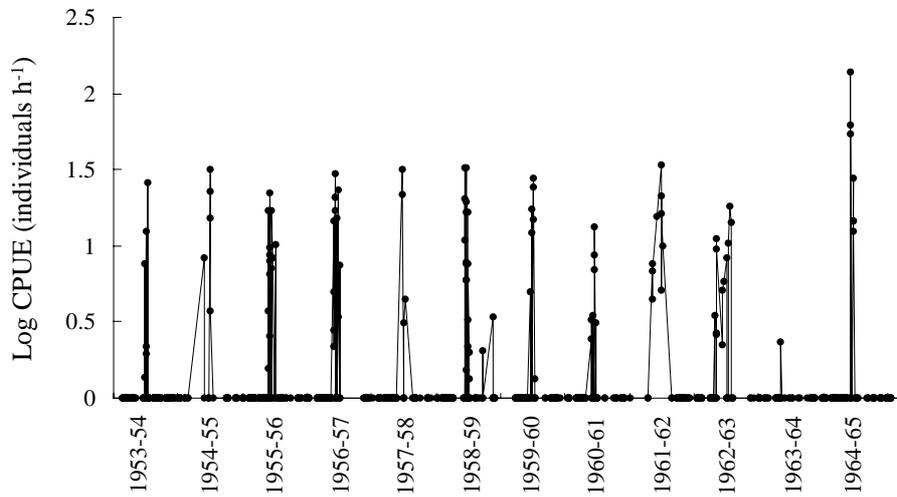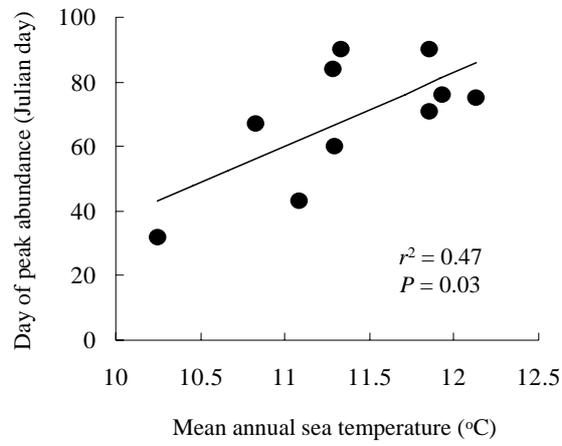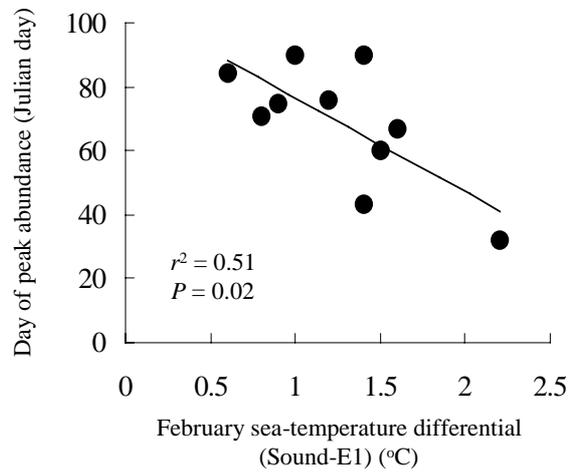
Figure 1

Figure 2

Figure 3

Figure 4

(a)

(b)

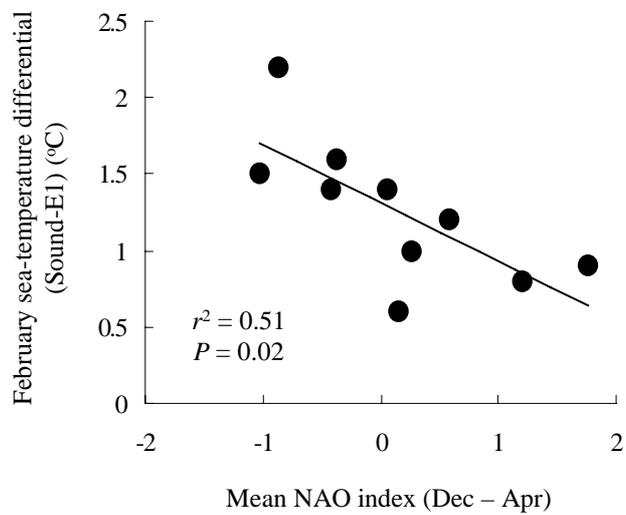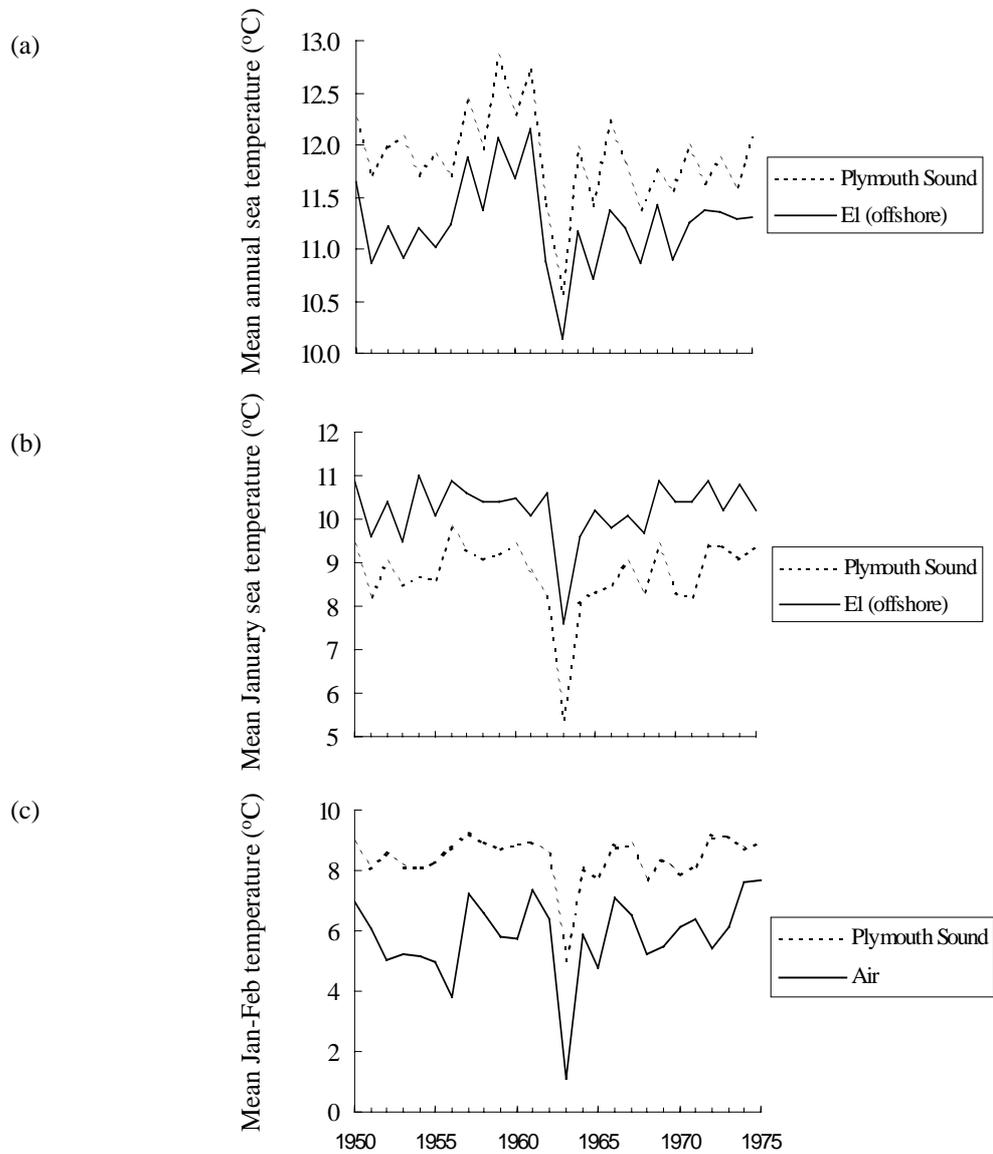

Figure 5

Figure 6

Figure 7

(a)

(b)

(c)

Figure 8

(a)

(b)

Mean monthly sea temperature (°C)

1959-60

1962-63

Jul   Sep   Nov   Jan   Mar   May

Plymouth Sound
E1 (offshore)