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# A 25-year study of climatic and density-dependent population regulation of common shrimp *Crangon crangon* (Crustacea: Caridea) in the Bristol Channel

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The results of a 25-year study of the population dynamics of the common shrimp, *Crangon crangon*, in the Bristol Channel are presented. The population size varied seasonally, with maximum abundance occurring in early autumn at the completion of annual recruitment. The number of recruits changed greatly between years, and was positively correlated with both average water temperature from January to August, and river flow rate, and negatively correlated with the Winter North Atlantic Oscillation Index. A wide range of other physical and biotic variables was found to have no significant impact on *C. crangon* abundance. The positive relationship between temperature and *C. crangon* abundance observed for the Atlantic coast during this study is the opposite of that found for southern North Sea populations. Similar contradictory responses have been noted previously for flatfish such as sole, *Solea solea*. This suggests that global variables may act to produce different outcomes for Atlantic and North Sea populations of the same species. Over-winter mortality was found to vary with population size so that the adult *C. crangon* population in spring was found to be remarkably stable, and little influenced by temperature or other variables. The mortality rate increased with population size producing clear evidence of density-dependent control. It is suggested that this stability is linked to the constant limited availability of suitable habitat, with individuals unable to find shelter vulnerable to a range of predatory fish. Given the pivotal role of *C. crangon* within the northern European estuarine ecosystems, this stability may be a critical component for the overall stability of the system. A particular feature of this study was the exceptional recruitment observed in October 2002. This did not result in any subsequent increase in adult *C. crangon* numbers, possibly because there was a synchronous increase in a wide range of predators. While the adult population has remained stable and showed no temporal trend, there has been an increase in both the average magnitude and between year variability in recruitment, which can be related predominately to the recent increase in water temperature. The difficulty of predicting the response of this population to continued climate warming is discussed. If temperature continues to rise, the present power law describing the increase in recruitment with temperature must inevitably break down. If this were to occur, the future trajectory of the *C. crangon* population could not be predicted, and the continued stability of this ecosystem would no longer be assured.

## INTRODUCTION

Common or brown shrimp, *Crangon crangon* (L.), are amongst the most abundant macro-crustaceans in north-east Atlantic estuaries and shallow bays (Henderson & Holmes, 1987; Hamerlynck et al., 1993; Maes et al., 1998; Hostens, 2000) where they play a key trophic role, feeding upon polychaetes and other small animals, particularly meiofauna (Pihl & Rosenberg, 1982, 1984; Evans, 1984; Jensen & Jensen, 1985). In Dutch estuarine waters, Hamerlynck et al. (1993) found 80% of all epibenthic individuals captured to be *C. crangon*. It is in turn a favoured prey of a wide variety of fish and invertebrates including many of great commercial importance (Henderson et al., 1992); Singh & Bromley (1999) noted that in the central and southern North Sea the mean daily consumption of *C. crangon* for a whiting weighing 150 g was 0.1 g. Closely related decapod crustaceans fulfil the same key role in other geographical regions, for example, sand shrimp, *C. septemspinosa* Say, in North America.

*Crangon crangon* are the subject of a large commercial fishery in northern European waters (Temming & Damm, 2002). Within Britain, the fishery is centred on the Wash, Thames Basin, Bristol Channel, Morecambe Bay and the Solway Firth. Since the 1970s a series of studies has reported upon the population dynamics of *C. crangon* and the environmental variables that influenced their recruitment. These studies have tended to emphasize different environmental variables. In one of the earliest, Driver (1976) reported on a 30-year time series for Morecambe Bay and noted that the best predictors of *C. crangon* landings were salinity and landings in the previous year. In contrast, Boddeka (1968) showed a negative correlation between February seawater temperature and the October *C. crangon* catch off Holland. Attrill et al. (1999) analysed a 12-year time series from the intakes of West Thurrock Power Station in the Thames estuary and

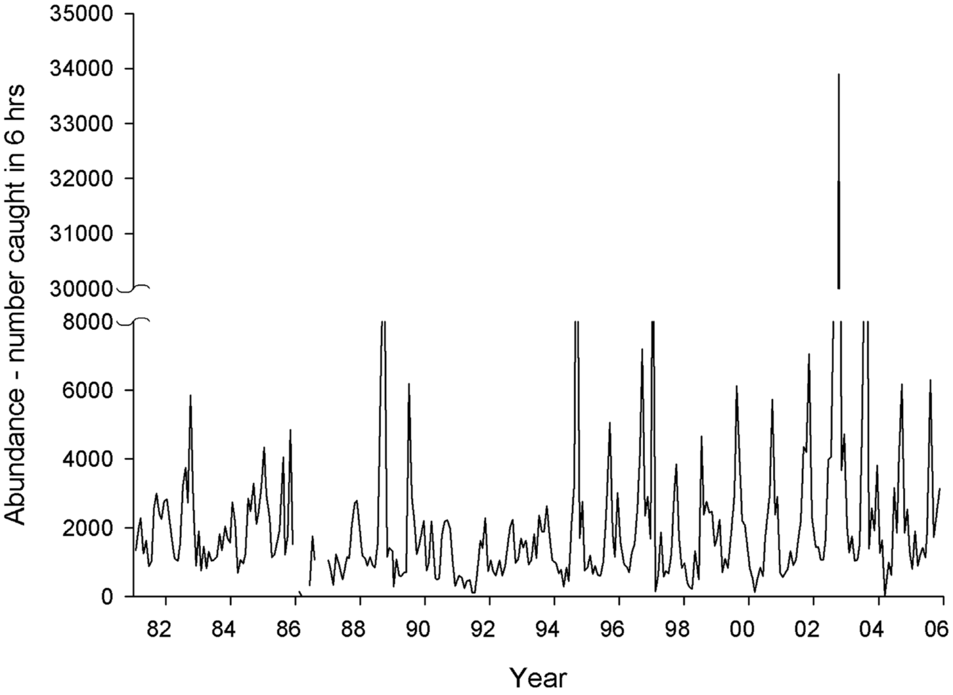

**Figure 1.** Monthly time series of common shrimp *Crangon crangon* abundance in Bridgwater Bay for the years 1981 to 2005. The abundance is the number of shrimps caught over six hours between high and low water by two of the cooling water pumps at Hinkley Point B Nuclear Power Station. The volume of water sampled each month was $3.24\times10^5$ m$^3$.

found that *C. crangon* abundance was correlated to dissolved oxygen concentration. Spaargaren (2000) reported on the 40-year time series collected by netting from a beach on the island of Texel, the Netherlands, and found that annual fluctuations could be explained by variation in salinity and temperature. Most recently, Siegel et al. (2005) report on a 30-year time series for the German Wadden Sea. They found that autumn abundance was negatively correlated to winter water temperature and the Winter North Atlantic Oscillation Index (WNAOI), and positively correlated with river run-off. However, they noted that it was difficult to explain why the response to the WNAOI was lagged by 18 months, given that the majority of *C. crangon* only live for one year. In addition to these large-scale factors, they also found that gadoid predators could influence local abundance. An important observation was that no factors were discovered that correlated with spring *C. crangon* abundance.

The present study of the *C. crangon* population within Bridgwater Bay in the Bristol Channel adds to our knowledge through the analysis of a data set specifically collected to study *C. crangon* population dynamics. In particular, monthly sampling has been undertaken which gives sufficient data to study mortality rates for each recruitment cohort and identify short-term movements in response to environmental conditions. The original motivation for the study in 1980 was concern about the decline in *C. crangon* abundance expressed by fixed-net shrimp fishermen after the opening of Hinkley Point Nuclear Power Station. The study was initiated because of an acknowledged lack of understanding of the factors determining *C. crangon* abundance.

Previous studies on *C. crangon* in the Bristol Channel undertaken in the 1930s by Lloyd & Yonge (1947), in the 1970s by Moore et al. (1979), and the 1980s by Henderson & Holmes (1987) described their growth, reproductive biology and seasonal movement, and presented estimates of the total population size. Together with the morphometric study undertaken by Henderson et al. (1990) the known information all points to the Bristol Channel and Severn estuary as holding a single, self-sustaining, population. Within the Bristol Channel, *C. crangon* can live for a number of years, reproducing first when about one year old. There are two peaks in reproductive activity, the first in January and the second in late spring (Henderson & Holmes, 1987). Newly metamorphosed *C. crangon* enter Bridgwater Bay during the summer and recruitment is complete by the autumn. Only a small proportion of the population survives to reach two or more years of age, resulting in a population with the population dynamics characteristic of a species that only lives for one year. This is similar to the situation found in the Rhone delta (Gelin et al., 2000).

**Table 1.** *Statistics comparing* Crangon crangon *abundance in Bridgwater Bay, Somerset for the 5 year periods 1981–1985 and 2000–2004. The abundance is expressed as the number of* C. crangon *captured over six hours in a constant volume of* $3.24\times10^5 m^3$. *The time series was adjusted to a standard tidal range.*

| Period | 1981–1985 | 2000–2004 |
|---|---|---|
| Number of observations | 61 | 60 |
| Mean | 2046 | 3026 |
| Variance | 1,125,291 | 20,372,735 |
| Minimum | 686 | 11 |
| Maximum | 5865 | 33,901 |

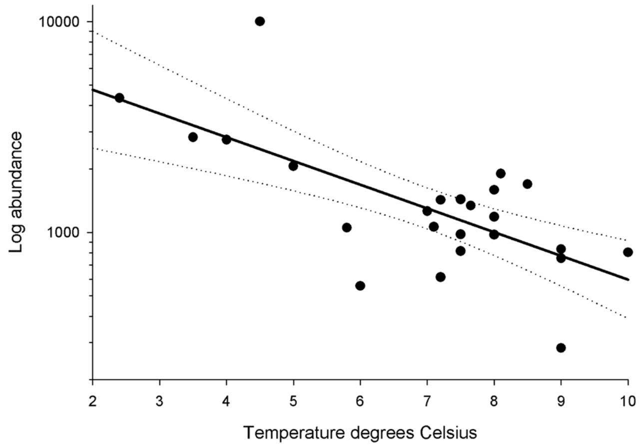

**Figure 2.** The relationship between *Crangon crangon* abundance and water temperature in January for the years 1981 to 2004 inclusive. The trend line is fitted by linear regression and the 95% confidence intervals are shown as dotted lines. No sample was available for January 1986.

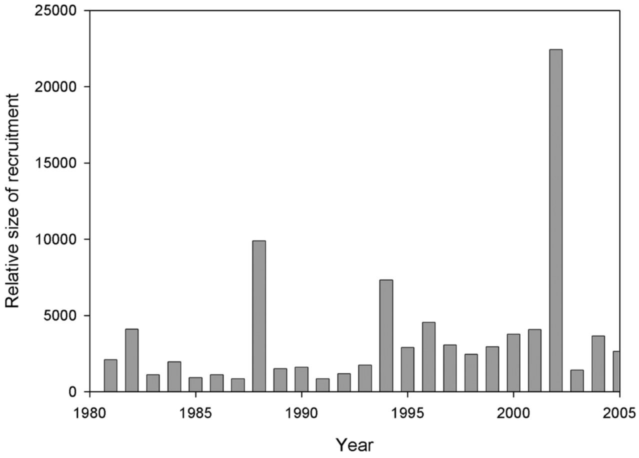

**Figure 3.** The relative size of *Crangon crangon* recruitment in Bridgwater Bay for the years 1981 to 2005. Recruitment is measured as the average of the total catch for the September and October samples.

**Table 2.** *Analysis of variance for the multiple regression model relating log recruitment to the North Atlantic Oscillation, average river flow and average seawater temperature.*

| | DF | SS | MS | F | *P* |
|---|---|---|---|---|---|
| Regression | 3 | 1.674 | 0.558 | 8.936 | <0.001 |
| Residual | 19 | 1.187 | 0.0625 | | |
| Total | 22 | 2.861 | 0.130 | | |

Over the last 25 years of our study there have been appreciable changes in climate and the biological community of Bridgwater Bay. These changes have broadened the research objectives to include an understanding of the potential effects of global warming. The present analysis addresses the role of both physical and biotic factors in determining the abundance of *C. crangon*. In particular, we wished to examine changes in population size and the extent to which the abundance of this key species is constrained within tight bounds. If climate variation can lead to appreciable changes in *C. crangon* abundance then global warming can be anticipated to produce great changes in British estuarine communities.

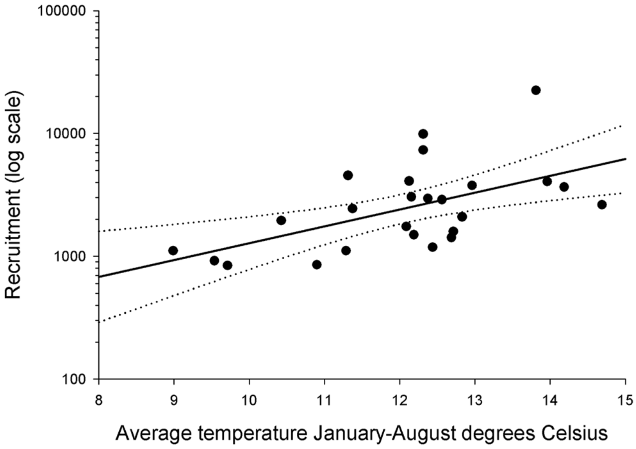

**Figure 4.** The influence of water temperature on *Crangon crangon* recruitment in Bridgwater Bay. Relative recruitment is the average abundance during September and October. Temperature is the average temperature from January to August for the same year as the recruitment. The line is fitted by linear regression; the dotted lines are the upper and lower 95% confidence intervals for the regression line.

## MATERIALS AND METHODS

Fish and crustacean samples were collected from the cooling water filter screens at Hinkley Point B Power Station, situated on the southern side of the Bristol Channel in Somerset, England. The water intakes are in front of a rocky promontory within Bridgwater Bay; to the east are the 40 $km^2$ Stert mud flats. The *Crangon crangon* were sampled from water varying in depth from about 8 to 18 m. A full description of the intake configuration and sampling methodology is given in Henderson & Holmes (1991) and Henderson & Seaby (1994). Methodology has not changed over the 25 years of study. The seasonal movement of fish and crustaceans within the Severn estuary is described by Claridge et al. (1986), Bamber & Henderson (1994), Henderson & Homes (1991) and Moore et al. (1979). Henderson et al. (1992) give an account of the trophic structure within Bridgwater Bay.

Quantitative sampling commenced in 1980 when 24 h surveys of the diurnal pattern of capture were undertaken in October and November. From these surveys it was concluded that samples collected during daylight were representative of the 24 hour catch (Henderson & Holmes, 1990), and monthly quantitative sampling commenced in January 1981. The total volume of water sampled per month, which has not varied over 25 years, is $3.24\times10^5$ $m^3$. To standardize for tidal influence, all sampling dates were chosen for tides halfway between springs and neaps, with sampling commencing at high water (normally about 1200 h). The fish and crustaceans were collected hourly from two filter screens for a 6-h period, identified to species, and the number of individuals recorded.

The power station intakes at Hinkley Point are an effective sampler because of their position at the edge of a large inter-tidal mudflat in an estuary, with extremely powerful tides resulting in suspended solid levels of up to 3 g $l^{-1}$, and little light below 50 cm depth. The crustaceans and fish,

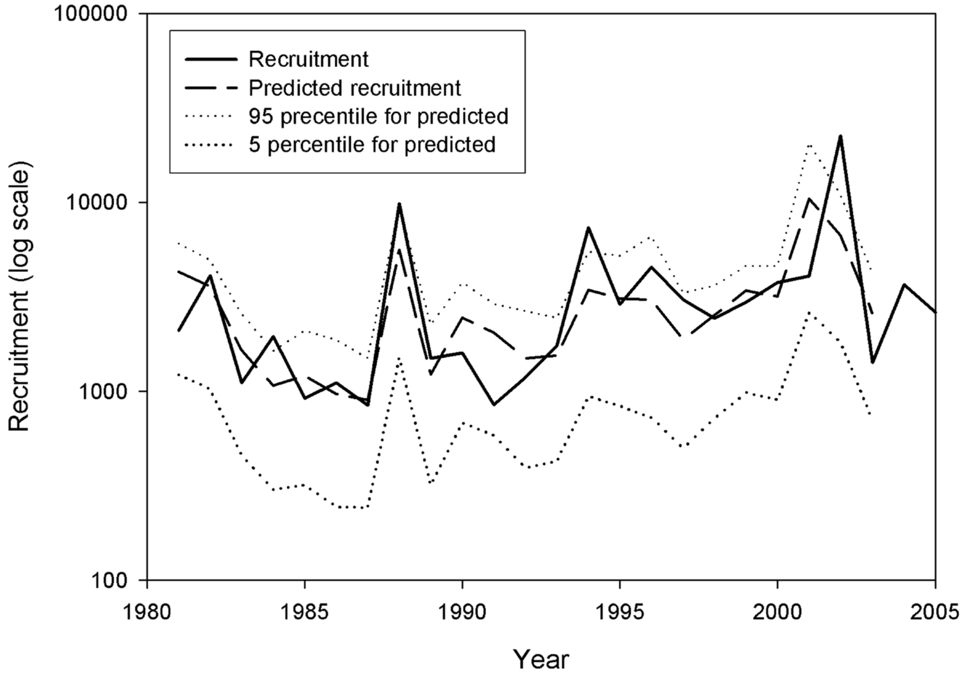

**Figure 5.** Comparison of the observed and predicted recruitment of shrimp, *Crangon crangon* in Bridgwater Bay. The observed values are the mean number sampled in September and October and the predicted were obtained from a multiple regression model with the Winter North Atlantic Oscillation Index, average seawater temperature and average river flow as the independent variables.

pelagic or benthic, are moved towards the intake in the tidal stream, often as they retreat from the inter-tidal zone where they feed. It is likely that they are often unable to see or otherwise detect the intake until they are too close to make an escape. Light is clearly important for avoidance, because at power station intakes situated in clear water, captures are higher at night (Whitehouse, 1986). The efficiency of the sampling method is discussed in Henderson & Holmes (1991). The filter screens have a solid square mesh of 10 mm and *C. crangon* with a carapace length >11 mm are fully retained by the filters, while smaller individuals are retained with reduced efficiency (Henderson & Holmes, 1987).

Water temperature and salinity were measured monthly using a mercury thermometer and refractometer respectively, approximately one hour before low water. Flow measured at the Saxon gauge station on the River Severn was used as a measure of freshwater flow into the estuary, and records of sunshine, air temperature, wind speed and wind direction were obtained from the UK Meteorological Office. The North Atlantic Oscillation (NAO) indices, calculated as the difference between the normalized sea level pressure over Gibraltar and the normalized sea level pressure over south-west Iceland (Jones et al., 1997), were acquired from http://www.cru.uea.ac.uk/cru/data/nao.htm. While indices for each month and the annual average of the monthly indices were tested for their influence upon *C. crangon*, it is well known that the NAO is particularly important in winter, and the NAO winter index (NAOWI) was calculated as the December to March average as suggested by Jones et al. (1997). The annual position of the Gulf Stream north wall, as expressed as the 1st Principal component, was obtained from the web site www.pml.ac.uk/gulfstream/inetdat.htm. Data on sunspot numbers were obtained from the SIDC web site at http://sidc.oma.be/index.php3.

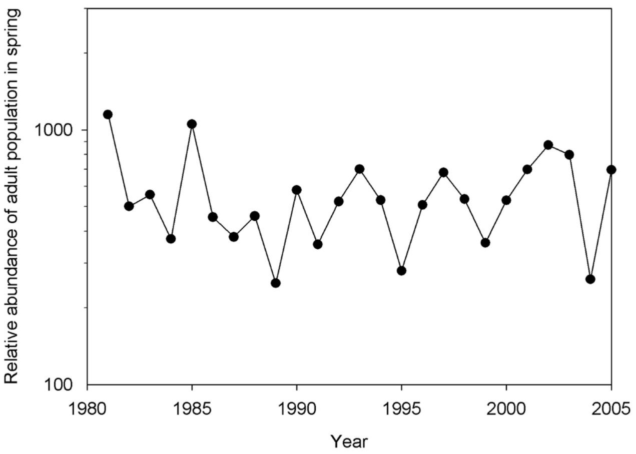

**Figure 6.** The temporal variation in abundance of adult *Crangon crangon* in Bridgwater Bay. Relative abundance was calculated as the average abundance over the months March to May inclusive.

It was not possible to always sample under the same tidal conditions, and the number of *C. crangon* captured was positively correlated with tidal height, because *C. crangon* retreat from the intertidal flats with the falling tide and concentrate in the vicinity of the intake. To allow for tidal differences, the predicted captures were calculated using a linear regression of *C. crangon* numbers, and tidal range and the tidally adjusted time series calculated as the difference between the observed and predicted series, with a constant added to give only positive values and a mean abundance approximately equal to that of the original series.

A search using forward and backward multiple linear regression was made for physical and biotic factors correlated with the strength of recruitment. Relative annual

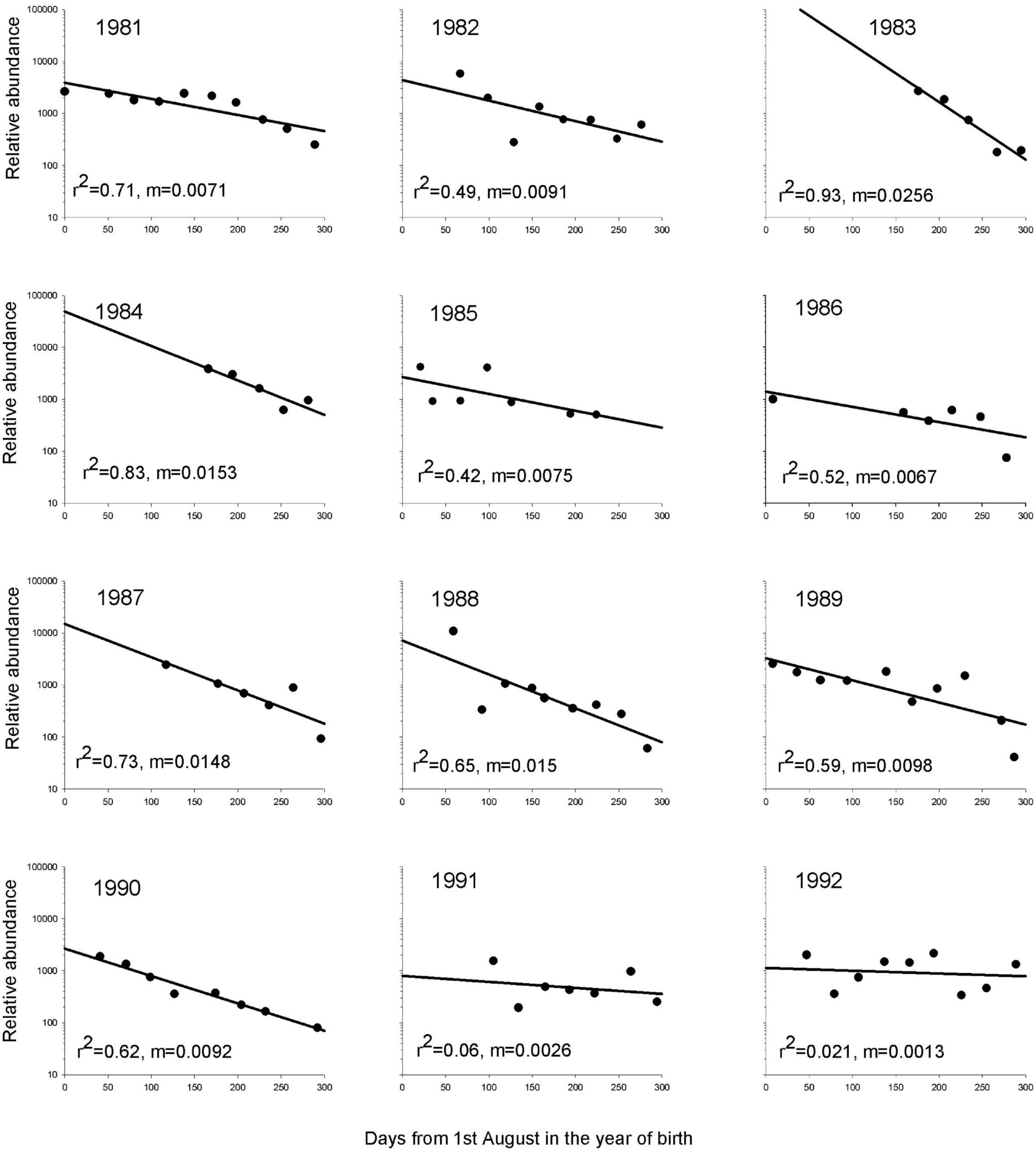

**Figure 7.** Curves showing the decline in abundance of shrimp, *Crangon crangon*, cohorts for the years 1981 to 1992 in Bridgwater Bay. The lines were fitted by regression analysis and each graph includes the coefficient of determination ($r^2$) and the gradient which is the instantaneous daily rate of mortality (m).

recruitment was measured as the average monthly catch for the months of September and October. The physical factors considered were the North Atlantic Oscillation annual average and winter indices, total rainfall, total river flow, average salinity, average seawater temperature, average annual sunspot number, average wind speed and total solar insolation. Biotic factors considered were the total annual abundance between January and August inclusive of: (1) the approximately 80 species of fish caught in the samples; (2) all predatory fish (mostly gadoids); (3) whiting, *Merlangius merlangus*; and (4) swimming crabs which were predominately *Liocarcinus holsatus*.

## RESULTS

### *Long-term trends in abundance*

The 25-year time series of monthly relative abundance of *Crangon crangon* in Bridgwater Bay is shown in Figure 1. There is a seasonal cycle of abundance, with annual maxima in late summer/early autumn, when annual recruitment was

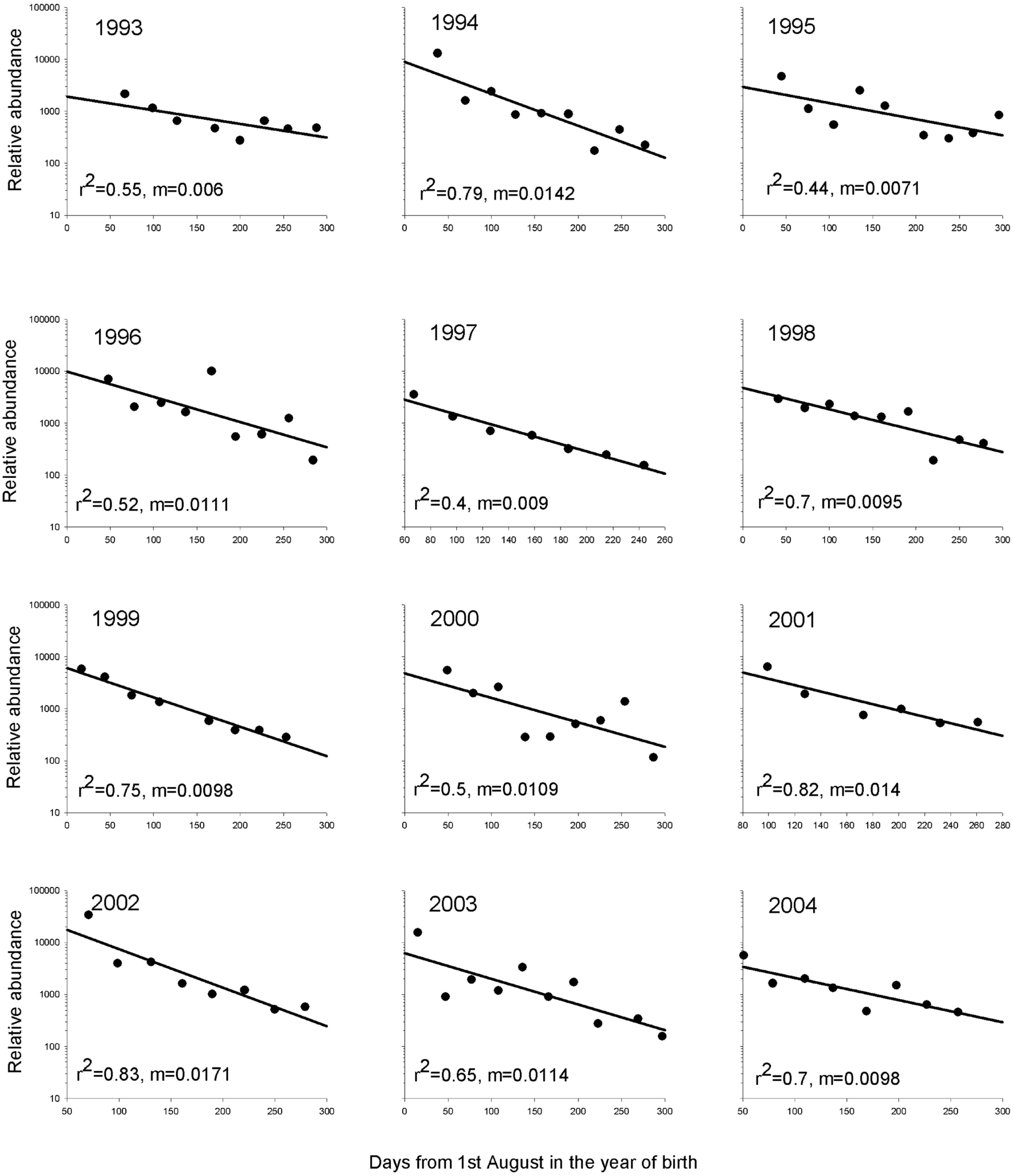

**Figure 8.** Curves showing the decline in abundance of shrimp, *Crangon crangon*, cohorts for the years 1993 to 2004 in Bridgwater Bay. The lines were fitted by regression analysis and each graph includes the coefficient of determination ($r^2$) and the gradient which is the instantaneous daily rate of mortality (m).

complete, and minima in May following losses over the winter months. The time series shows a gradual decline in mean abundance between 1981 and 1991 followed by an increase that has continued until 2005. More notable than the trend in abundance is the clear difference in the variability of the series. Since 1994 the series shows a much more pronounced seasonal pattern of abundance with generally higher maximum autumnal abundances. Table 1 compares abundance statistics for the two 5-year periods between 1981 and 1985 and 2000 and 2004. There has been an approximately 50% increase in mean abundance, but this is not statistically significant ($t=-0.170$, df=119, $P=0.866$) because the variance has increased from approximately $10^6$ to $20\times10^6$. Much of the increase in mean abundance and variance is related to a single exceptional burst in abundance in October 2002 (Figure 1).

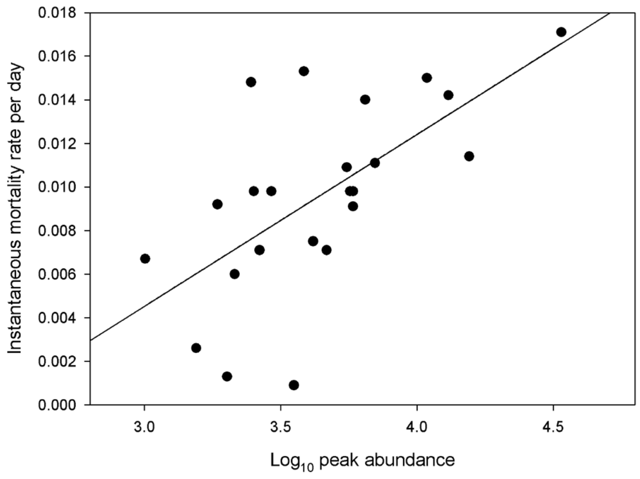

**Figure 9.** The variation in mortality rate with population size for shrimp, *Crangon crangon* in Bridgwater Bay. Population size is the peak number of recruits in autumn. Instantaneous mortality rate was calculated using regression analysis. The straight line was fitted by linear regression.

### *Outliers*

There have been six occasions when unseasonably extremely low or high catches have been recorded. The two lows were in August 1983 and 1995 when water temperatures were respectively 22.6 and 23°C. These are the only two sampling occasions in the last 25 years when the seawater temperature exceeded 22°C. Unusually high abundances were observed in four late summer-autumn samples, September 1988, September 1994, October 2002 and August 2003. These peaks in abundance reflect years with exceptionally good recruitment, which is discussed below. The peak abundance in January 1997 occurred when water temperature was only 4.5°C, and as shown in Figure 2, winter abundance tends to be higher at lower seawater temperatures ($r^2$=0.34).

### *Variation in annual recruitment*

The annual abundance of *C. crangon* reaches a maximum in September or October, and the average abundance over these months gives an index of the between-year variation in recruitment. As shown in Figure 3 there is considerable between-year variation, and recruitment in 2002 was about 25 times as large as that observed in 1985. There are also indications that recruitment has increased through time, as the average relative recruitment index for the years 1981–1993 was 2221 and from 1994 to 2004 it was 5322 captured in six hours.

Multiple regression analysis identified the following three factors as statistically significant predictors of log recruitment strength: (1) the Winter North Atlantic Oscillation Index (WNAOI) for the winter prior to recruitment; (2) average monthly River Severn flow for the months of September and October (F) in the year of recruitment; and (3) average seawater temperature (T) for the months of January to August in the year of recruitment. The regression equation shown below explained a high proportion of the total variability in annual recruitment (Table 2) with an adjusted coefficient of determination of 0.52.

$$\log_{10}(\text{Recruits}) = 0.587 - 0.127\text{WNAOI} + 0.000634\text{F} + 0.181\text{T}$$

where F is measured in millions of cubic metres per month and T in degrees centigrade.

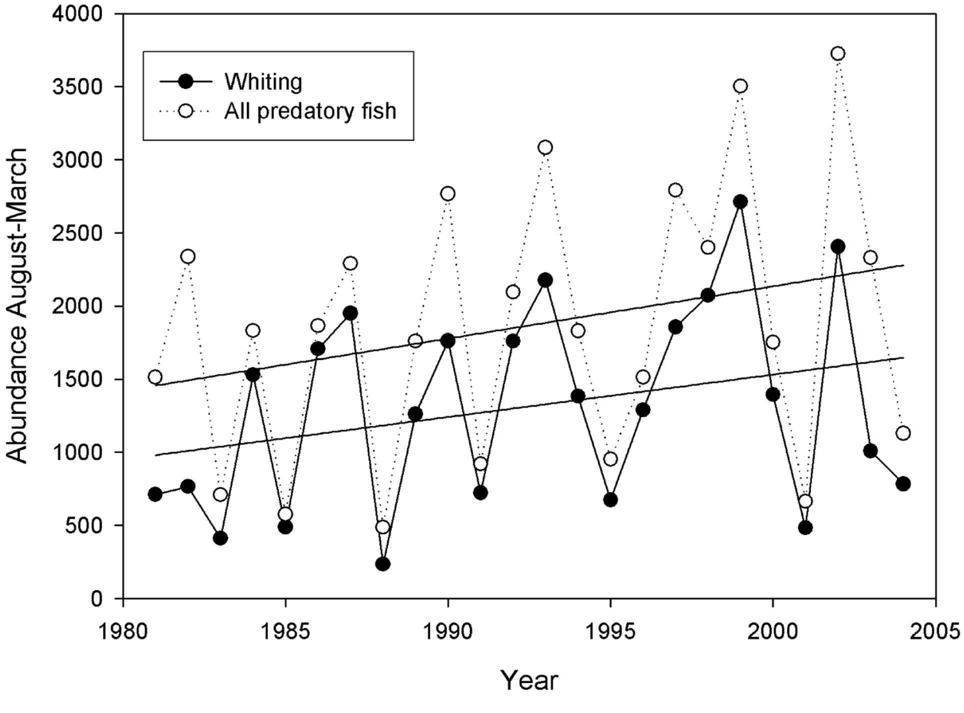

**Figure 10.** The variation in predatory fish abundance for Bridgwater Bay between 1981 and 2005. Abundance is expressed as the total catch between August and March, which is the period from peak *Crangon crangon* recruitment to the beginning of *C. crangon* reproduction. Separate lines are shown for whiting, *Merlangius merlangus*, and all predatory fish including whiting.

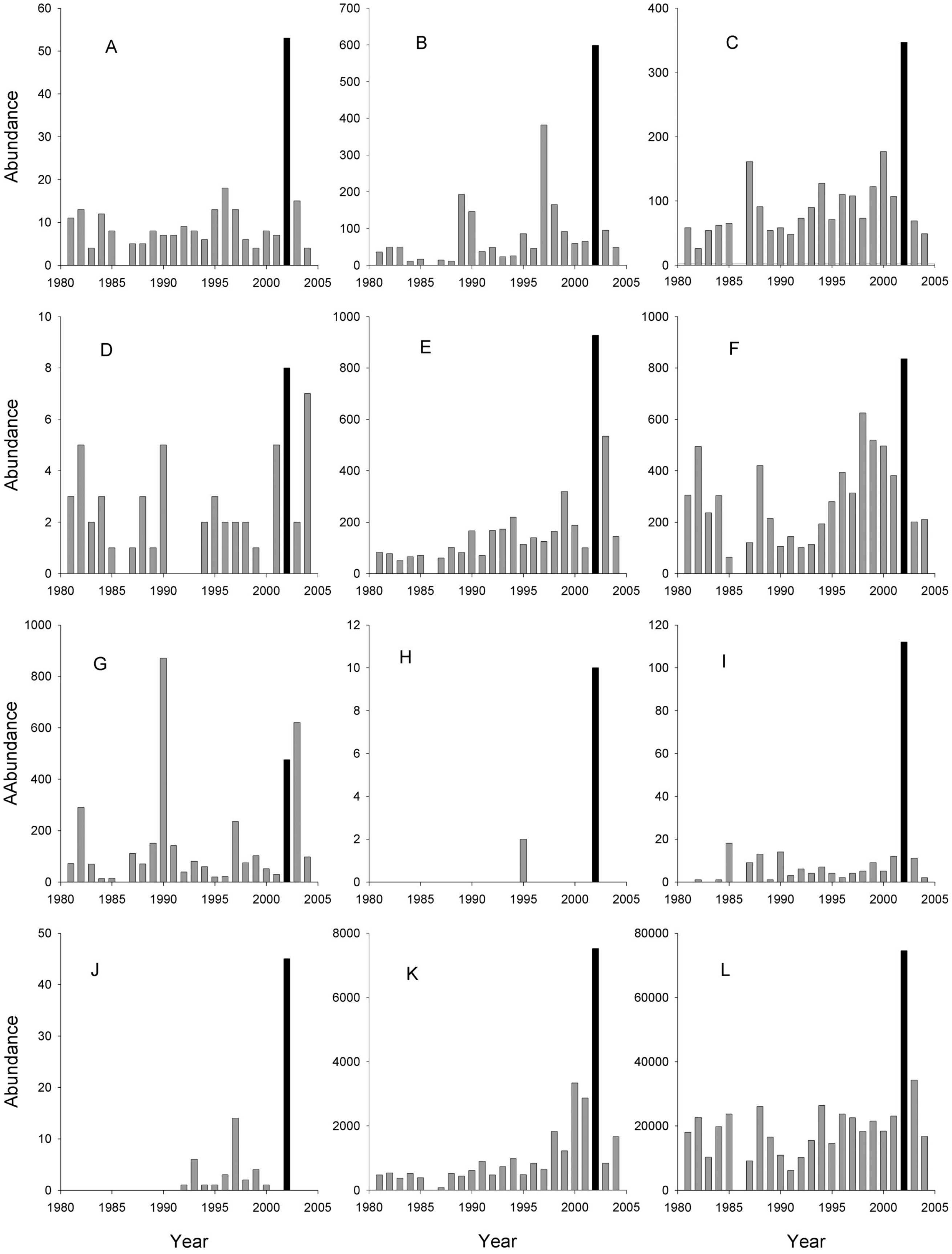

**Figure 11.** The pattern of annual abundance in fish and crustacean species that showed a marked peak in relative abundance in Bridgwater Bay in 2002. (A) *Conger conger*; (B) *Dicentrarchus labrax* (L.); (C) *Platichthys flesus* (L.); (D) *Syngnathus rostellatus* Nilsson; (E) *Solea solea* L.; (F) *Pomatoschistus minutus* (Pallas); (G) *Trisopterus luscus* (L.); (H) *Liocarcinus depurator*; (I) *Eupagurus bernhardus*; (J) *Pilumnus hirtellus*; (K) *Palaemon serratus*; (L) *Crangon crangon*. Data for 2002 are shown as a black bar.

Average seawater temperature showed the largest ($r^2$=0.60) and most significant ($P<0.001$) correlation with the logarithm of recruitment abundance (Figure 4). Figure 5 compares the observed and predicted recruitment through time. While the model clearly captures the general trend and level of the population it failed to predict the extraordinarily large recruitment observed in 2002.

### *Temporal variation in the adult population*

In the Bristol Channel *Crangon crangon* reproduces from January to July, with the highest proportion of female *C. crangon* (approximately 75% of the female population) carrying eggs in June (Henderson & Holmes, 1987). The average abundance between March and May inclusive gives the best estimate of the relative size of the reproducing population prior to the main reproductive effort. Abundance in July is a less reliable measure, as females with mature eggs leave Bridgwater Bay.

As shown in Figure 6, there is no significant trend in adult abundance. A comparison of Figure 3 and Figure 6 demonstrates that recruitment in the autumn is considerably more variable than adult abundance in the spring (recruitment varies between years by a factor of almost ×25 for recruits, compared with only ×4.4 for the adults).

### *Density-dependent control*

The general stability of the *C. crangon* abundance time series, together with the considerable reduction in temporal variability between autumn recruitment and the spring adult population, suggests density-dependent regulation. Bulmer's test for density-dependence (Bulmer, 1975) when applied to the time series of the total number caught per year, indicated that the time series was significantly different from a random walk (test statistic $R=-1.37\times10^{-14}$, which is less than the 5% significance value of R=1.055, N=24). This test is highly conservative, as density-dependence would be rejected if there had been any drift or trend in the data.

Using the monthly abundance estimates, the instantaneous mortality rate of the recruits over their first winter was calculated using linear regression with $\log_{10}$ abundance as the dependent and days since 1 August as the independent variable.

The fitted curves for recruitment for the years 1981 to 2004 are shown in Figures 7 & 8. In each case the abundance was plotted from the annual peak in recruitment in the autumn until May the following year. The actual month in which the peak occurred varied from year to year. The estimated instantaneous mortality rate, m, varied considerably between years ranging from a minimum of 0.0013 $d^{-1}$ in 1992 to a maximum of 0.0171 $d^{-1}$ in 2002. A mortality rate of 0.0256 $d^{-1}$ was estimated for the 1983 cohort, but this is unreliable as the peak in recruitment was not observed until January (typical peaks were in August or September) and it is likely that the peak reflected movement within the estuary rather than recruitment. The geometric mean mortality rate for all cohorts except 1983 was 0.008 $d^{-1}$.

The mortality rate, m, was positively correlated ($r$=0.67) with log *C. crangon* abundance (Figure 9) and could be approximately expressed by the equation,

$$\text{Mortality rate} = -0.0191 + 0.0079 \log(\text{peak abundance}),$$

where peak abundance is the maximum number of individuals captured over six hours during autumn sampling.

### *Predation and the abundance of other species*

While the observed over-winter loss rate for *Crangon crangon* may be related to both migration and mortality or a combination of the two, a strong candidate explanation for the observed density dependence is fish predation. Previous studies (Henderson et al., 1992) have established that many of the fish abundant in Bridgwater Bay, including whiting, *Merlangius merlangus*, pout, *Trisopterus luscus*, poor cod, *Trisopterus minutus*, five-bearded rockling *Ciliata mustela*, bass, *Dicentrarchus labrax* and sole, *Solea solea*, feed heavily on *C. crangon*. During the winter period, when *C. crangon* numbers decline, the gadoids, and whiting in particular, are highly abundant and appreciable mortality must be caused by fish predation. While winter seawater temperature clearly affects *C. crangon* movement into Bridgwater Bay, there is no evidence to suggest that the loss in abundance between September and May is primarily caused by migration. The observed winter decline in abundance is observed throughout the Bristol Channel and Severn estuary and there is no other region of estuarine or shallow water habitat of sufficient size or productivity capable of holding such a large population. If the loss is caused by predation or competition then an increase in predator/competitor abundance with *C. crangon* abundance might be observed. The trend of increased *C. crangon* recruitment (Figure 3) is reflected in an increase in predatory fish numbers between August and March (Figure 10). Over the period of study there has been a general tendency for biological activity to change with *C. crangon* abundance. For example, as shown in Figure 11, the massive eruption in *C. crangon* numbers observed in 2002 coincided with peaks in abundance of 12 other common species.

## DISCUSSION

For the past 25 years the adult population of *Crangon crangon* within Bridgwater Bay has been notably stable (see Figure 6). However, average *C. crangon* abundance has increased because recruitment has increased with average seawater temperature. This has resulted in a clear example of density-dependent control as the mortality rate of recruits over their first winter increases with recruitment. The most impressive example of the regulatory ability of the system was the response to the extraordinarily large recruitment in 2002 (see Figures 1 & 3). Recruitment in this year was more than twice as large as that observed in any year since 1980, yet by the following spring, numbers were close to those observed in other years. While the factors controlling *C. crangon* numbers cannot be definitively identified, it is clear that increased *C. crangon* abundance is associated with increased predator and competitor abundance. The tendency for whiting, the most abundant of the fish predators, to change in abundance with *C. crangon* has been previously noted (Henderson & Holmes, 1989).

In Bridgwater Bay, *Crangon crangon* migrates with the rising tide onto the intertidal flats, which is a normal behaviour for the species (Hartsuyker, 1966; Al-Adhub & Naylor, 1975). At low water, the population, which was dispersed over 40 km$^2$ of intertidal flats, becomes concentrated within the permanent water of the estuary. The predators of this species are also similarly confined and it must be a time of great vulnerability for *C. crangon* individuals that cannot find a place where they can burrow into the substrate. The striking stability of the adult population in spring suggests that a fixed physical constraint, possibly the amount of available habitat, is setting an upper limit on the adult population. It is unlikely that top-down control alone could produce such stability, as the abundance of predators has varied considerably through time (Figure 10), and there is no correspondence between the peaks and troughs in predator and *C. crangon* abundance. The need to utilize inter-tidal mud flats for feeding is probably essential, as the subtidal benthic community is greatly impoverished, because of substrate instability linked to the strong tidal streams. It may be the extent and productivity of these mud flats that constrains *C. crangon* abundance. However, if bottom-up control through food availability were acting we would need to assume that invertebrate productivity did not change with the rise in average temperature. As this seems unlikely, the availability of shelter, with predation taking those that are excluded, is the explanation that best fits the facts.

While the adult population has remained stable, recruitment as measured by abundance in September and October has increased with water temperature. Female *C. crangon* carry their eggs and move towards the mouth of the estuary to release their eggs; larvae are never found in plankton samples collected in Bridgwater Bay. The offshore movement of ovigerous females is a well-known behaviour of the species (Meyer-Waarden & Tiews, 1957; Tiews, 1970). This is almost certainly related to the availability of food, as the high sediment loadings in the Severn estuary and Bristol Channel greatly restrict the density of both phyto- and zooplankton (Joint & Pomroy, 1981). Boddeke et al. (1986) found in the southern North Sea that the settlement of postlarval *C. crangon* in late May–July was linked to the bloom in calanoid copepods, which are the major food of *C. crangon* of 10–20 mm in length. *Crangon crangon* do not enter Bridgwater Bay until they have metamorphosed into fully formed small *C. crangon* that have adopted a more benthic lifestyle (Henderson & Holmes, 1987). The size of recruitment is therefore determined by events outside Bridgwater Bay.

Recruitment in the autumn was found to be correlated to seawater temperature, the NAOWI and river flow. These variables are all known to affect the productivity and growth of estuarine animals. The NAOWI is known to be positively correlated with recent increased abundance of both phytoplankton and small copepods in the south-western region (Beaugrand & Reid, 2003) and the enhanced growth of sole in Bridgwater Bay is positively correlated to the NAOWI (Henderson & Seaby, 2005). River flow, and by implication the NAO, were also identified as key variables affecting production and sole growth in the Gulf of Lions (Salen-Picard et al., 2002). It is therefore surprising that *C. crangon* recruitment is *negatively* correlated with the NAOWI. It would appear that *C. crangon* recruitment is higher when copepods and fish do poorly. A negative correlation between *C. crangon* recruitment and the NAOWI was also found by Siegel et al. (2005) for the German Wadden Sea, but with an 18-month lag, which is difficult to explain given that most *C. crangon* only live for one year in their study area. It is also notable that, whereas Siegel et al. (2005) found a negative correlation between *C. crangon* recruitment and water temperature, we have found a positive correlation. To some extent, contradictory responses to temperature can be explained by differences in migration over the life cycle. Recruitment of the young is positively correlated with seawater temperature while winter abundance of adults shows a negative correlation. Thus, the perceived role of temperature will depend on the timing of sampling within the annual cycle. The strength of the present study is based on the use of a monthly sampling interval. There are indications that climatic variables do not act to produce the same trends in North Sea and Atlantic waters. Henderson & Seaby (2005) also noted a similar contradiction in the effect of temperature for sole.

The strong density-dependent control acting upon the *C. crangon* population is demonstrated by the remarkably stable adult population and the positive correlation between the instantaneous mortality rate over their first winter of life and the size of the population. In this study, the geometric mean mortality rate for all cohorts except 1983 was 0.008 d$^{-1}$, which is of a similar magnitude although higher than the rate of 0.006 d$^{-1}$ estimated by Henderson & Holmes (1987) over the entire life of a cohort. This would be expected as older and larger *C. crangon* are probably less prone to predation. A similar stability in adult population size was also noted by Siegel et al. (2005) for the German Wadden Sea.

The simple power law relationship between recruitment and seawater temperature reported here can only apply over a limited temperature range and we have no indication of the upper temperature at which it will break down. *Crangon crangon* can certainly live in warmer waters as its geographical range lies between 45° and 57°N (Tiews, 1970), and the Bristol Channel lies between 51 and 51.5°N. While higher spring temperatures increase larval development rates and probably result in reduced mortality, there must also be an increase in food availability if this is to be translated into higher recruitment. It is notable that the variability of the *C. crangon* population has increased with seawater warming. The temperature response observed in this study may reflect particular features within this geographical area and shrimp populations in other areas may respond differently to changes in temperature.

Using previous estimates of population size it is possible to estimate the recent increase in *C. crangon* standing crop. In June 1981 and November 1983 the population size on the Stert flats in Bridgwater Bay was estimated as $3\times10^6$ and $5\times10^7$ individuals respectively, suggesting a standing crop that varied between $10^6$ and $10^8$, with an average of around $10^7$ individuals (Henderson & Holmes, 1987). This represents a biomass of about $10^4$ kg wet weight, as the average *C. crangon* weighs approximately 1 g. The abundance in Bridgwater Bay in October 2002 was about 26 times that observed in the early 1980s, suggesting an increase in standing crop to about $3\times10^8$ individuals, weighing $2.6\times10^5$ kg. It is notable that this great increase had little impact on the stability of the system as measured by continuing species presence. However, the abundance of shrimp predators has increased. Over the last 25 years the total biomass and species richness of higher animals in the Bristol Channel has increased and this change must in part be supported by, and possibly caused by, the increase in *C. crangon* recruitment.

The present study demonstrates the difficulties in predicting the effects of climate warming on estuarine communities. If temperature were to fluctuate within the range experienced over the last 25 years a remarkably effective predictive model could be produced to describe the change in recruitment with temperature, the temperature-related winter migrations and the density-dependent control on adult numbers. However, recruitment presently increases as a power of the temperature and this relationship must break down if temperature continues to increase. It is notable that abundance is low when seawater temperature exceeds 22°C, indicating that *C. crangon* avoids the highest temperatures presently experienced. It is possible to envisage both stabilizing and catastrophic changes if temperature should increase further. The most benign possibility would be that *C. crangon* recruitment gradually decelerates with further temperature rises, as warm water species enter the system and compete for resources. The predators would respond by widening their feeding niches and the ecosystem would gently evolve to a higher diversity system more similar to that observed in Portuguese estuaries (Costa, 1988). The catastrophic scenario is that *C. crangon* recruitment will initially continue to increase with increasing temperature, until a point is reached at which recruitment fails. This might lead to a break down in the present density-dependent control as predation pressure intensifies, resulting in a further decline in *C. crangon* recruitment. If such lagged responses are important then the system may pass through a period of high instability before finding a new equilibrium. While further research is required before the effects of climate warming can be predicted, the response of *C. crangon* to temperature makes it clear that major changes will occur should temperatures continue to rise.

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