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The role of climate in determining the temporal variation in abundance, recruitment and growth of sole *Solea solea* in the Bristol Channel

P.A. Henderson* and R.M. Seaby

Pisces Conservation Ltd, IRC House, The Square, Pennington, Lymington, Hampshire, SO41 8GN, UK.
*E-mail: Peter@irchouse.demon.co.uk

Using a 24-year time series of monthly samples, the factors correlated with long-term variation in the abundance and growth of sole, *Solea solea*, in Bridgwater Bay in the Bristol Channel, England are identified. This bay offers shallow estuarine habitat used by sole as a nursery area. Sole first enter the bay in July when 2–3 months old and after a residence of 4–5 months, the majority migrate offshore at the beginning of winter to return the following April. By three years of age most have left the bay never to return although occasional large fish up to 480 mm in length are caught. Sole were found to be highly seasonal in their growth and only increased in length during the months of May to August inclusive. In recent years, there has been an approximately exponential increase in sole abundance that is highly positively correlated with seawater temperature during the early part of the season. The average length of fish in September, at the end of their first growing season, showed significant between year variation, ranging from 65.3 mm in 1989 to 79.8 mm in 2003. This variation was positively correlated with the North Atlantic Oscillation (NAO) winter index for the winter prior to their birth. Between year recruitment variation is correlated with both water temperature and the rate of growth. High temperatures allow faster development and a positive NAO index increases productivity and offers more food. Both of these positive influences act to reduce mortality resulting in stronger year-classes. No relationships between sole and other fish and macro-crustaceans living in the nursery were identified.

INTRODUCTION

Sole, *Solea solea* (L.), are one of the most abundant and commercially important fish in southern North Sea and north-east Atlantic coastal waters. Sole within this region are divided into a number of stocks that use different spawning and nursery grounds. The sole of Bridgwater Bay, which are the subject of this investigation, are part of Bristol Channel stock. Horwood (1993) concluded 'the sole of the Bristol Channel can be regarded as a valid population for studies of dynamic population demography and for management purposes'. This conclusion was based on the existence of distinct local spawning and nursery grounds, together with the observed fidelity to the region of tagged adults. While much is known about the biology of sole, the factors that determine the between year variation in recruitment remain obscure. The available data indicate that recruitment is determined before the end of the first year of life and that water temperature plays an important role (Rijnsdorp et al., 1992; Wegner et al., 2003). However, the pattern of recruitment has been found to differ between populations (Rijnsdorp et al., 1992) and has resulted in some widely different conclusions. For example, Henderson & Holmes (1991) and Henderson & Seaby (1994) demonstrated that year-class abundance in the Bristol Channel was positively correlated with spring sea temperatures while Rijnsdorf et al. (1992) noted that 0-group abundance in the southern North Sea was negatively correlated with the March seawater temperature. These results seem both contradictory and counter intuitive as it would be anticipated that the southern North Sea population, situated in the region with colder winter water at the northern extreme of the sole geographical distribution, would be the most temperature limited and thus respond positively to an increase in temperature.

Since this contradictory response in temperature was first noted, a further ten years of study of juvenile sole recruitment in the Bristol Channel has been completed. Over this recent period there has been a great increase in sole abundance, which has given an enhanced opportunity to study the inter-annual variation in growth and abundance. There has also been a growing body of evidence that the North Atlantic Oscillation (NAO) influences marine productivity and the abundance and growth of estuarine fish (Attrill & Power, 2002; Beaugrand & Reid, 2003). In this study the following questions are considered. (1) Does the abundance–temperature correlation noted by Henderson & Seaby (1994) still hold given a longer time period? (2) To what extent does temperature affect growth and is there appreciable between-year variation in size at the end of the first growing season? (3) Do other climatic and physical features such as sunlight, river flow, salinity, wind strength or the NAO influence either growth or recruitment? (4) Can between year variations in growth be related to variations in survival and abundance? (5) Is the abundance of sole correlated with the abundance of other fish and crustaceans such as *Crangon crangon* (L.)?

(6) Is there any evidence for density-dependent regulation during the juvenile period?

For plaice, *Pleuronectes platessa* L., predation by the crustaceans *C. crangon* and *Carcinus maenus* (L.) have been identified as key factors in regulation of density within the nursery areas (Van der Veer, 1986; Van der Veer & Bergman, 1987; Van der Veer et al., 1990). Sole might be predated like plaice by *Crangon crangon*, which is by far the most abundant crustacean at Hinkley Point. By addressing these questions it was hoped that a hypothesis could be presented as to how recruitment in the Bristol Channel is determined and this could in turn suggest possible explanations for the contradictory role of temperature in the southern North Sea and Bristol Channel.

A description of the Bridgwater Bay study area is given in Henderson & Holmes (1991) and references cited therein.

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 bank 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 sole were sampled from water varying in depth from about 8 to 18 m. A full description of the intake configuration and sampling methodology are given in Henderson & Holmes (1991) and Henderson & Seaby (1994). Methodology has not changed over the 24 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 & Holmes (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-h 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 the 24-y period, is 3.24×10^5 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. Since 1992 the standard length (SL) of all captured fish have been recorded to the nearest mm; prior to this date fish were measured between 1984 and 1990. Fish were assigned to age group following inspection of the length–frequency relationship. Data on the length at age of sole in the Bristol Channel derived from otolith annuli were presented by Claridge & Potter (1987) and their results gave confidence that the clear bi- or tri-modality in the length–frequency distributions were related to age-class. All fish were assumed to be born in April as in this region spawning is concentrated in March and April (Horwood, 1993) and young fish are first captured in plankton nets in the Bristol Channel in April and May (Russell, 1980).

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 and little light below 50 cm depth. The fish, 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. The efficiency of the sampling method is discussed in Henderson & Holmes (1991). The filter screens have a solid square mesh of 10 mm and start to retain sole >25 mm SL, 100% retention is expected at SL >40 mm. Brown shrimp, *C. crangon*, with a carapace length >11 mm are retained by the filters, smaller individuals are retained with reduced efficiency (Henderson & Holmes, 1987).

Water temperature and salinity were measured monthly using a mercury thermometer and refractometer respectively and were recorded monthly 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 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) was 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 sole, 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 lst principal component was obtained from the web site www.pml.ac.uk/gulfstream/inetdat.htm.

Statistical analyses were undertaken using SigmaStat software for non-parametric tests, Pearson correlation and linear regression. A growth curve allowing for seasonal variation in growth was derived. Because there is zero or apparently negative growth for five to six months of each year the commonly used seasonally adjusted von Bertalanffy growth equation (Cloern & Nichols, 1978) was unsuitable necessitating the derivation of a more generalized equation. As in the case of the standard von Bertalanffy equation, the rate of change of length was assumed to be described by the equation:

$$\frac{dL}{dt} = k(L_\infty - L(t)), \qquad (1)$$

where L is length, L_∞ is the maximum asymptotic length, t is time. If k is a seasonally varying growth rate that can be described by a Fourier series rather than a constant, then a good fit to the data could be obtained using only 2 terms of the Fourier series:

$$k = a_0 + a_1 \cos(t) + b_1 \sin(t) + a_2 \cos(2t) + b_2 \sin(2t). \qquad (2)$$

Substituting eqn 2 into eqn 1 and integrating gave after some rearrangement the growth equation:

$$L(t) = L_\infty(1 - \exp(\tfrac{1}{2}(-2b_1b_2 - 2a_0t + b_2\cos(2t) - 2a_1\sin(t)) + \cos(t)(b_1 - a_2\sin(t)))) \quad (3)$$

In this equation t is measured in radians so that 2π radians was equivalent to 1 year. The parameters in this growth equation were estimated by non-linear regression using CurveExpert 1.3, which uses the Levenberg–Marquardt method to solve the regression equations.

RESULTS

Long-term changes in sole abundance

The annual catch at Hinkley Point for the years 1981 to 2003 is shown in Figure 1. A clear and accelerating upward trend in abundance commenced in about 1987. The sharp increase in abundance observed in 2002–2003 continued into 2004 with relatively high rates of capture over the first six months, however no appreciable 0-group ingress had occurred by mid-September giving a total catch for the months January to September inclusive of only 132.

Age structure and growth

A growth curve allowing for seasonal variation in growth for sole at Hinkley Point averaged over all years and for both sexes is plotted in Figure 2. The equation parameters, obtained by non-linear regression were: $L_\infty=213$, $a_0=0.0618$, $a_1=0.0366$, $a_2=-0.058$, $b_1=0.0957$, $b_2=0.0554$. No significance should be attached to the estimate of L_∞ as the curve has only been fitted to juveniles and is the average for both sexes. Only individuals up to 3 years of age are frequently caught and about 95% of all the sole caught were juveniles less than 20 months old. Growth is highly seasonal and only occurs between May and August. The small changes in length observed during the winter months are probably related to age (size) specific migration as the mean length initially declines then increases back to the average observed the previous autumn.

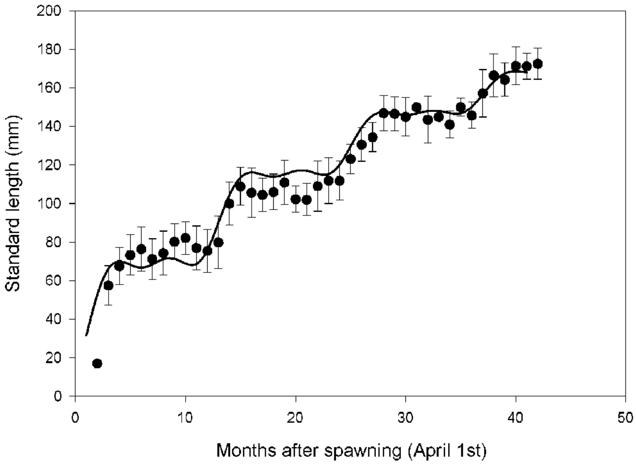

Figure 2. The average growth curve of sole in Bridgwater Bay for the first 42 months of life. It is assumed that the eggs were spawned on 1 April. The plot shows the mean standard length for each month of life together with the standard deviation of the lengths. The curve was fitted using non-linear regression.

Seasonal patterns of abundance

Figure 3 shows the average number of individuals caught per sample between the second and twentieth months of life for the years 1992 to 1999. A clear seasonal pattern of movement is observed. The 0-group first arrives in July although an occasional individual has been captured in June. At this time the smallest individuals are only 20–25 mm SL. Abundance increases rapidly and reaches a maximum in September. While some of this increase in catch may be related to improved retention on the 1-cm mesh as the fish grow, there can be no doubt that it is primarily linked to the arrival of new recruits as plankton nets deployed within the intake which would

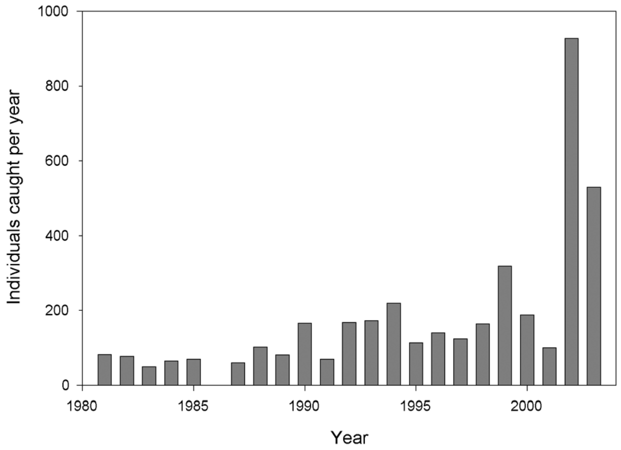

Figure 1. The annual abundance of sole at Hinkley Point for the years 1981 to 2003. Each year is the sum of individuals caught in 12 monthly samples. 1986 is missing because only seven samples were collected.

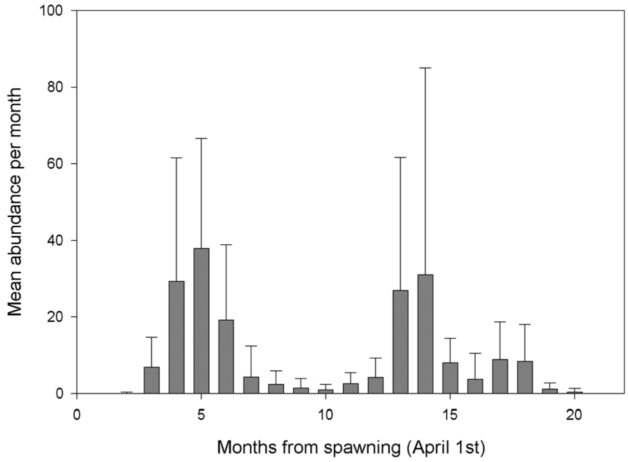

Figure 3. The pattern of seasonal abundance of 0 and 1 group sole in Bridgwater Bay. Average monthly catches for the years 1992 to 2003 are plotted. The error bars are the standard deviations of the monthly catches.

Table 1. *Standard length (mm) statistics for 0-group sole for the months of September to November combined for all years from 1987 to 2003.*

Year	Number of animals measured	Mean	Standard deviation	Median
1987	7	66.4	12.2	60.0
1988	20	66.5	10.0	61.0
1989	12	65.3	11.9	60.5
1992	43	73.1	10.1	71.0
1993	64	76.2	8.8	76.5
1994	62	73.8	9.3	72.0
1995	35	76.6	11.1	77.0
1996	55	68.5	10.8	66.0
1997	22	72.9	9.3	70.0
1998	41	68.6	10.9	66.0
1999	62	79.6	8.2	80.0
2000	52	78.4	10.7	78.5
2001	33	69.3	12.5	67.0
2002	218	74.3	10.9	73.0
2003	47	79.8	7.9	78.0

detect fish that would pass through the sampling mesh do not catch small sole.

During the winter fewer 0-group are caught although they start to return in March and reach a second maximum in abundance as 1-group in June before again moving away.

Between year variation in 0-group growth

Table 1 gives the mean, standard deviation and median standard length of 0-group sole in the months of September to November combined for each of the 15 years for which length data exist. September is at the end of their first growing season (see Figure 1). Length was not normally distributed and a Kruskal–Wallis test showed the differences in median length to be statistically significant ($H=94.4$, $df=14$, $P<0.001$). Dunn's multiple comparison procedure was used to compare pairs of years and showed that the differences between 1989 and both 2003 and 1999 were statistically significant at the 5% level.

Best subsets regression was used to screen physical environmental variables describing salinity, water temperature, river flow, wind speed and direction, position of the Gulf Stream and the NAO. This showed that only the variables describing the NAO and the position of the northern wall of the Gulf Stream were significantly correlated to sole 0-group length in September. Stepwise regression indicated that the only significant predictor of first year sole length was the NAO winter index for the previous winter (Pearson correlation between the NAOWI and sole length: $R=0.596$, $P<0.02$, $N=15$). As shown in Figure 4A, a linear regression model with NAOWI as the independent variable was found to be a good predictor of first year sole length (adjusted $R^2=0.306$, $F=7.177$, $P<0.02$, normality test passed $P>0.05$, constant variance test passed $P>0.6$) and the addition of further variables added no appreciable improvement to the prediction.

Table 2. *The total captures of sole in August and September in the year of their birth (0-group) at Hinkley Point Power Station intakes. Each record is for a 6-h standard sample of 3.24×10^5 m^3. Data prior to 1985 are not included as complete length data were unavailable so fish could not be allocated to age-class.*

Year	August	September	Total
1985	29	1	30
1986	2	0	2
1987	0	7	7
1988	30	16	46
1989	0	5	5
1992	28	43	71
1993	8	41	49
1994	15	46	61
1995	19	23	42
1996	15	24	39
1997	0	6	6
1998	5	20	25
1999	84	53	137
2000	13	37	50
2001	6	8	14
2002	67	117	184
2003	91	37	128

Between year variation in sole recruitment

By August or September of the year of birth the abundance of 0-group sole in the Bridgwater Bay nursery has reached the annual maximum and the relative size of the year-class is established. Table 2 gives the total captures of 0-group sole in the months of August and September for the 15 years for which age-grouping was possible.

Best subsets regression was used to identify physical variables that were potentially influencing abundance as for the investigation of length above. The only variable found to be a good predictor was spring water temperature (average for April and May) and the plot of the spring temperature against sole 0-group abundance is shown in Figure 4B (Pearson correlation $R=0.558$, $P<0.02$, $N=17$). While the correlation is significant, a simple linear regression model with spring temperature as the independent variable must be treated with caution as these data failed a constant variance test ($P<0.005$). A linear regression model of spring water temperature and log sole abundance was significant and passed all diagnostic tests (adjusted $R^2=0.352$, $F=9.676$, $P<0.01$, $df=16$, normality test passed $P>0.2$, constant variance test passed, $P>0.9$). The NAO indices lagged by one year were also tested as potential predictors of sole abundance. No significant relationships were observed.

The relationship between abundance and growth

Figure 4C shows the relationship between 0-group abundance (recruitment) and mean standard length at the end of the first growing season (growth). The positive correlation is statistically highly significant (Pearson correlation $R=0.888$, $P<10^{-5}$, $N=16$) and indicates that abundance and size are related. The NAO was insignificantly correlated with abundance ($R=0.101$) (Figure 4D).

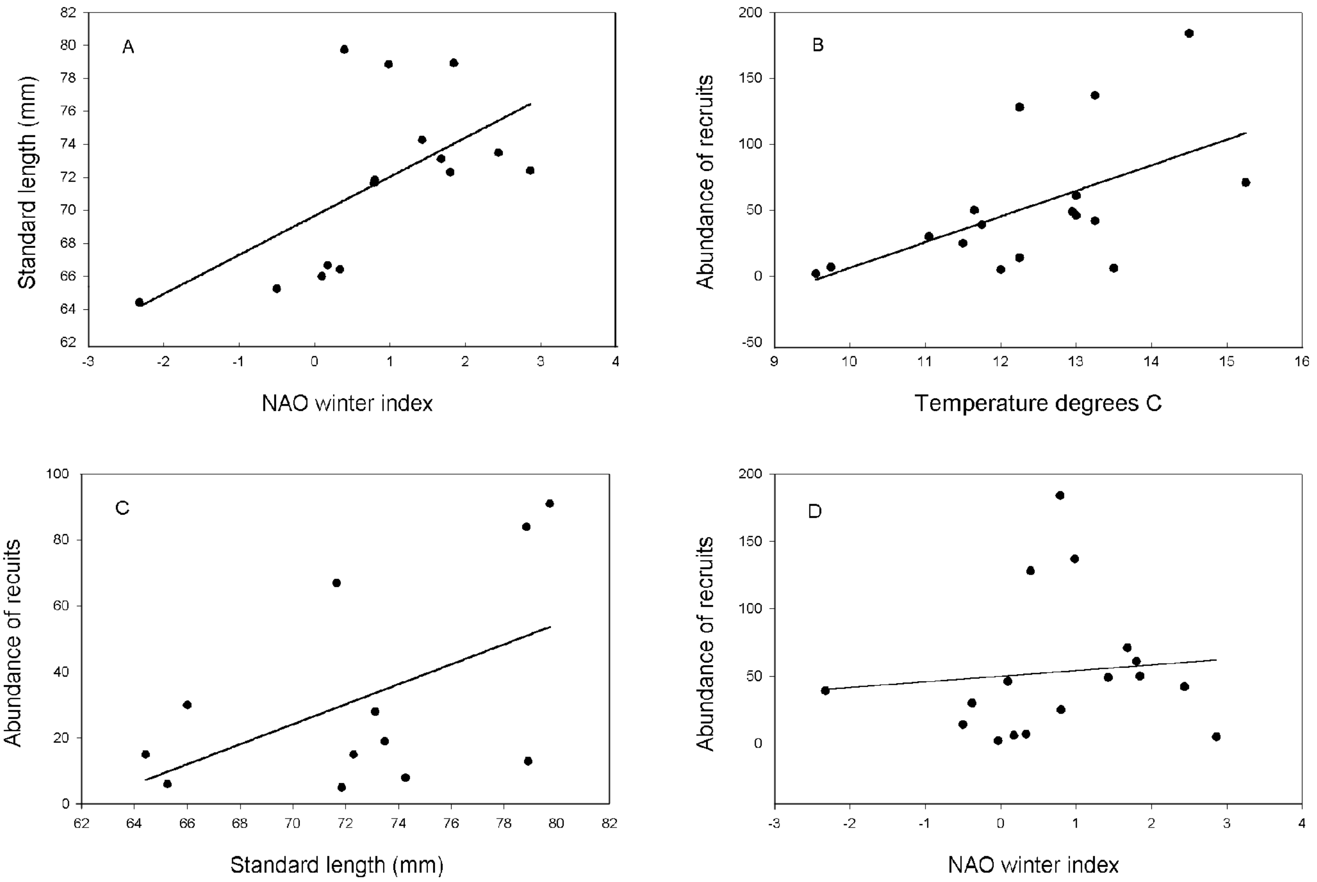

Figure 4. The relationship between the NAOWI, spring water temperature, 0-group sole length and 0-group sole abundance. The lines are fitted by linear regression. (A) The relationship between spring water temperature and abundance; (B) the relationship between standard length and abundance; (C) the relationship between the NAOWI and standard length; (D) the relationship between NAOWI and abundance.

The correlations between the variables for recruitment, growth, winter NAOI and spring surface-water temperature were investigated in more detail and an examination of alternative interaction pathways, using partial correlation coefficients, showed Figure 5 to be the most plausible causal network. Alternative causal models could be created which are consistent with these data. For example, it could be argued that increased abundance enhances growth. However, such a positive feedback seems unlikely, as sole are solitary hunters.

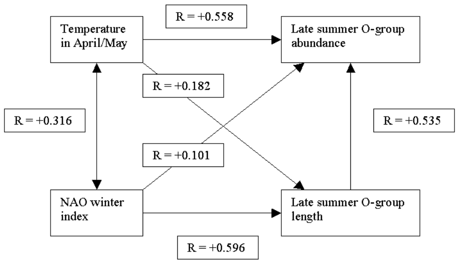

Figure 5. The pattern of correlation between physical variables and the abundance and growth of sole during their first year of life in the Bristol Channel. The factors are arranged to form the most likely causal model and the direction of the arrows shows the assumed direction of causality. The Pearson correlation coefficient, R, for each pair of variables is shown next to each line.

The abundance of sole in relation to other fish or crustaceans

A search for significant correlations between sole abundance and that of the other 95 species of fish and macrocrustacean regularly caught at Hinkley Point identified only two significant correlations: a positive correlation with bass *Dicentrarchus labrax* (L.) and a negative correlation with dab *Limanda limanda* (L.). Both of these species have been previously reported to show annual variations in abundance that are related to temperature (Henderson & Corps, 1997; Henderson, 1998) and it unlikely that the observed correlations are indicative of direct biological interactions as bass, dab and sole have completely different patterns of seasonal abundance within Bridgwater Bay. No correlation between the abundance of the common shrimp *Crangon crangon* and either the abundance or growth of 0-group sole was found. While common shrimp may be predating newly settled sole there is no evidence that they are a key factor in determining sole density. Between 1980 and 2002 shrimp abundance was notably stable with an annual catch rate at Hinkley Point of about 20,000 per year. In 2003 the abundance of common shrimp greatly increased to an annual catch of about 75,000. This great increase occurred in a year in which sole 0-group had their second highest abundance since 1981 and indicates that in the Bristol Channel common shrimp are not producing a detectable impact upon sole recruitment.

DISCUSSION

Bridgwater Bay is a nursery ground for sole. The small number of sole greater than three years old present in the bay is probably linked to the adults moving to deeper waters near the spawning grounds off the north Cornish coast (Horwood, 1993). Juvenile sole in the Bristol Channel show highly seasonal growth, which is limited to the months of May to August inclusive and mostly occurs during June and July. Since 1980 there has been an appreciable increase in sole abundance in the region, which had previously been correlated to the increase in surface-water temperatures (Henderson & Seaby, 1994). The previously identified spring temperature–sole abundance correlation is still holding following some of the warmest years since the study commenced. Given the additional ten years of data, which have extended the range of both the temperature and abundance observed, there can be no doubt that water temperature throughout the spring and summer affects abundance. The high correlation of September/October abundance with April/May average water temperature suggests that events during the spring at the time of spawning and the planktonic larval phase are particularly important to recruitment. The duration of the egg and larval stages are related to water temperature (Riley, 1974). For slower development to result in lower recruitment there must be increased mortality at lower temperatures. Two plausible reasons for such an increase are first that the early stages are likely to be highly susceptible to predation and the shorter the time spent as a small vulnerable egg or larva the better. Second, the early stages of fish have yet to develop an immune system and particularly when developing in sub-optimal conditions, may be afflicted by pathogens. At present we have insufficient knowledge about the role of pathogens in the mortality of early stages of fish to know if they are important, but the role of disease in determining juvenile survival in far better understood terrestrial animals, demonstrates the potential for disease to influence fish populations. The production of a large number of offspring by sexual reproduction is indicative of a reproductive strategy responding to high levels of disease early in life (Hamilton, 2002).

In the 1980s no sole were caught during the winter, however in recent, milder, winters they have been regularly caught. A seasonal pattern of low winter abundance was also reported by Claridge & Potter (1987) at Oldbury-on-Severn, suggesting that the sole leaving Bridgwater Bay are not moving up the estuary. It is probable that they move into warmer, deeper, more marine waters during the coldest winter months. This suggests that sole might cease to migrate if temperatures remained sufficiently high. These movements also serve to limit cannibalism, as the 1-group avoids Bridgwater Bay at the time of year when the 0-group is most abundant. We have found 1-group sole with 0-group sole in their guts, however the observed separation of the age-classes suggests that cannibalism is unlikely to be an appreciable cause of mortality.

Body size over the first season varied significantly between years. While size is only weakly positively correlated with temperature (Figure 5), juvenile sole body size is highly positively correlated with the NAO index for the winter months of December to March prior to the spawning season in May/April (NAOWI). This result supports the conclusions of Power & Attrill (2002) for the Thames Estuary. They found a positive correlation between the NAO index and sole growth, but found no significant relationship between the NAO index and abundance. Because the NAOWI is known to be positively correlated with the abundance of both phytoplankton and small copepods in the south-western region (Beaugrand & Reid, 2003) it seems likely that enhanced growth is related to food availability rather than increased temperature. Growth was also significantly correlated with the position of the north wall of the Gulf Stream, which is known to be correlated with the NAO. We have chosen to use the NAO index because it gave slightly higher correlation coefficients. It is possible that climatic variables influence the timing of spawning and that faster growth occurs in years when early spawning is successful. However, this seems unlikely as early spawning would be influenced by water temperature and we have found that body size is far better related to the NAOI than spring temperature.

The longest individual recorded during this study was 420 mm SL, which equates to a total length of about 483 mm and is above the previously published maximum length for Bristol Channel sole. Horwood (1993) concluded that sole above 500 mm total length (TL) should be regarded as 'exceptional'. Since the year 2000, sole with a TL greater than 450 mm have been regularly caught at Hinkley Point suggesting that adult growth and abundance are increasing.

No other physical or biological variables examined showed a significant correlation with either sole body size or abundance. Remarkably, only two significant correlations were detected with the 96 other species regularly recorded from Bridgwater Bay. These correlations are unlikely to be due to direct interactions as they occur with species with different patterns of seasonal occupancy, suggesting that they are independently responding to a general climatic variable such as temperature or the NAO.

There is also a high positive correlation between the length achieved by sole in their first year of life and their abundance, which is indicative of the need for a cohort to grow rapidly if they are to achieve higher than average survival rates. Taken together the observed pattern of correlations suggests that growth of juvenile sole is related to the general productivity of the sea in the year of birth and that rapid growth increases survival and cohort abundance. This is unsurprising as it is generally observed that fish survival rates increase with size. Around and just after the time of metamorphosis it is likely that sole are vulnerable to a wide range of predators including fish, crustaceans such as common shrimp, *Crangon crangon* and crabs and even older sole. Once they exceed a standard length of 60 mm there are far fewer predators present in the shallow waters of Bridgwater Bay to which they are vulnerable. In the case of some animals, such as common shrimp, the former predator becomes abundant prey for the growing sole.

Our results clearly show that recent warming, together with a positive NAOWI, has favoured the abundance of sole in Bridgwater Bay and probably the entire south-western region of Britain. While a positive NAO index is positively correlated with warmer seawater conditions the correlation is not great ($R=0.316$). It therefore seems that both temperature and NAO should be included in a predictive model. Using the NAOWI and spring temperature as variables, it is possible to construct a model that simulates the observed recruitment time series with pleasing fidelity.

Analysis of recruitment patterns in the North Sea shows that in this region recruitment is negatively correlated with winter seawater temperature (Rijnsdorp et al., 1992). This population, which is at the northern edge of the range, is responding to temperature in the opposite direction from its Bristol Channel neighbour. A possible explanation may be related to our observation that abundance is also correlated with body size. If growth were particularly fast after cold winters, possibly because of reduced competition for food, this might explain the difference. It is certainly the case that cold winters can harm and even kill North Sea sole (Horwood & Millner, 1998). Unfortunately, no data on the between year variation in 0-group length of sole for the North Sea were available to us. It seems likely that body size data may make an invaluable contribution for the interpretation of recruitment dynamics of sole and possibly other species. If our view that pathogens were important were true it might also be the case that cold winters reduced pathogen abundance in the North Sea and thus reduced competition and disease might follow colder than average winters. Again there is no supporting evidence for this conjecture but it deserves investigation. Reduced pathogens and disease towards the outer edge of the geographical range has frequently been assumed in terrestrial systems.

It is widely accepted that fish populations can be constrained by density-dependent interactions. This assumption is used in arguments to justify the view that fishing and other anthropogenic impacts, such as death on cooling water intakes will not produce a decline in population size. During the 1980s the sole population in Bridgwater Bay seemed remarkably stable and it seemed plausible then that the juveniles were under some degree of density-dependent control during their use of the mud bank nursery. Since 1987 sole abundance in Bridgwater Bay has increased almost ten fold and there is now no indication of any density-dependent limitation as in recent years population growth has been almost exponential. If there were some factor setting a carrying capacity during the 1980s this has evidently ceased operating or has moved to a far higher threshold allowing, for the present, almost unconstrained growth. The link between juvenile growth and the NAO suggests that general productivity sets a constraint on sole growth and survival rather than predation or competition on the nursery grounds. If the population in Bridgwater Bay continues to increase, some constraint on juvenile abundance may eventually come into play and will be a focus of further investigations.

Hallett et al., 2004, have questioned the use of large-scale climatic indices as causal explanations of ecological processes. Using a model for the Soay sheep population of St Kilda they argued that death was related to food competition coincident with bad weather. The superior ability of the NAOI when compared with local climatic variables to predict mortality was related to the inadequacy of local weather records to capture short-term events that lead to death. The NAOI was viewed as a 'catch all' variable for energetically challenging conditions rather than an adequate causal explanation; this required an understanding of density-dependent interactions acting together with brief spells of bad weather. In the case of Bristol Channel sole, we have no information on the actual causes of death but from the egg to the juvenile stage they are exposed to a wide variety of pathogens, predators and physical threats over a wide geographical area. It is the large scale over which the processes are occurring and the great changes in lifestyle over development that are likely to make large-scale climatic variables such as the NAO useful predictors of sole population dynamics. At present, the size of sole recruitment in the Bristol Channel seems to be controlled by climatic factors acting early in life and by the influence of the NAO on general ecosystem productivity.

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