

Discrete and continuous change in the fish community of the Bristol Channel in response to climate change

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Using a 25-year time series of monthly samples, it is shown that the fish community of Bridgwater Bay in the outer Severn estuary is rapidly responding to changes in seawater temperature, salinity and the North Atlantic Oscillation (NAO). The number of fish caught each year has followed an increasing trend, which could be related to increased temperature and decreased salinity. In contrast to this smooth change, there have been two discrete transitions in fish community structure around 1986 and 1993. The first of these step changes, which altered the relative abundance of the dominant species, was linked to a change in the NAO. The second, which was caused by a change in the set of occasional visitor species, was linked to an increase in average seawater temperature. A marked increase in population variability for many fish in recent years is linked to increased seawater temperature. Generally, the position of the southern geographical limit of a species is a good indicator of their individual responses to higher temperatures. The effects of future climate change are discussed. A 2 °C increase in inshore seawater temperature is predicted to increase total species richness of fish in Bridgwater Bay by 10%, although most of this gain will be warm water tourists. Predicting future communities requires consideration of combined changes in temperature, the NAOI and salinity. While the system can change to a warmer water community, there is likely to be increased short-term community instability during periods with unfavourable combinations of the key environmental variables. Such a destabilization was observed in 2002 when the abundance of many species suddenly increased then declined. A different combination of NAO, high temperature and salinity may, in the future, produce a considerable less favourable combination resulting in recruitment collapse for many species.

INTRODUCTION

Recent predictions of increasing global temperatures have focused attention on predicting the resulting changes to both marine and terrestrial ecosystems. Models predict British average annual temperature increases from the 1990 level of between 2 and 3.5 °C by 2080 (Intergovernmental Panel on Climate Change, 2002) and there are strong indications that this will lead to appreciable changes in the British inshore flora and fauna. The influence of climate on marine fish has long been recognized, and the effects of climate change on temperate estuarine fish was reviewed by Roessig et al. (2004). Southward et al. (1995) described transitions between warm and cold-water demersal fish assemblages off Plymouth. In the 1920s, there was a warm water assemblage, which switched to a cold-water assemblage by the 1950s before reversing to warm water species in the 1970s. More recently, a progressive northern expansion of warmer water fish in North Atlantic waters has occurred (Quero, 1998; Swaby & Potts, 1999; Stebbing et al., 2002).

There have been few long-term studies of the quantitative effect of physical conditions and seawater temperature in particular on temperate estuarine fish assemblages. A notable exception was the recent study by Attrill & Power (2002) on the fish community of the Thames estuary, which reported significant changes in abundance and growth correlated with the North Atlantic Oscillation Index

(NAOI). The importance of both seawater temperature and the NAOI was shown by Beaugrand & Reid (2003) in a study of the plankton of the north-east North Atlantic where large changes in both the phytoplankton and zooplankton assemblages occurred during the 1980s. They also presented data to show that changes in the plankton could be associated with the decline in salmon, *Salmo salar*, in south-west British rivers. Similarly, Henderson & Seaby (2005) found sole, *Solea solea*, abundance and growth in the Bristol Channel was correlated with seawater temperature and the NAOI. In the North Atlantic, the NAOI is correlated with surface seawater temperature (Bjerknes, 1964) and with precipitation and storminess (Rodwell et al., 1999). These observations show that the NAOI is a key synoptic variable for predicting the abundance of marine life in south-west British waters and the study of climate change cannot consider temperature in isolation from changes in the NAOI, precipitation, salinity and wind.

Numerous autecological studies of temperature on fish have been undertaken. Within the Bristol Channel the significant role of seawater temperature in determining growth and/or abundance has been identified for bass, *Dicentrarchus labrax* (Henderson & Corps, 1997), sea snail, *Liparis liparis* (Henderson & Seaby, 1999), dab, *Limanda limanda* (Henderson & Seaby, 1994) and sole, *Solea solea* (Henderson & Seaby, 2005). However, given the potential complexity of community-level interactions, it is inappropriate to

extrapolate from a small number of single species studies to predict the response of an entire assemblage comprising at least 81 fish species as is found in Bridgwater Bay. Further, to the west and south live many more species that might invade if conditions were to change appropriately. Therefore, as argued by Davis et al. (1995), a multi-species approach must be taken to assess the likely magnitude of the change in species abundance under climate change. Further, as we have no reliable body of theory, the only available approach is the analysis of long-term datasets collected for entire fish communities over periods of change. This study analyses such a data set and considers the way in which the community responds. In particular, the tendency of the estuarine fish assemblage to change smoothly or discretely and suddenly is investigated.

The 25-year time series of fish and crustacean abundance for Bridgwater Bay used in the present study offers an unusual opportunity to study the effects of seawater warming and other climatic influences on a temperate fish community. Not only has the sampling method and intensity of sampling allowed all the common fish, pelagic, proximo-benthic and benthic to be studied contemporaneously, but, fortuitously, the study was undertaken over a period of exceptional climatic change. The study commenced in 1981 when winters were considerably colder than at present and followed the community through large changes in NAOI and salinity.

The Bridgwater Bay study site lies within the Bristol Channel, in the outer zone of the Severn estuary. This is the largest estuarine system in the British Isles and unlike many other British estuaries, such as the Thames or Mersey, the fish community has not been seriously disrupted by pollution. The region holds a characteristic estuarine ichthyofauna dominated by juvenile fish. The common species within this fauna are the same as they were in the 1880s (Day, 1890) and 1930s (Lloyd, 1941). This study follows the climatic response of a well-established and historically stable fauna that until recently has changed little since the 1880s. The depth of knowledge of past conditions together with a 25-year time series of monthly quantitative samples gives an exceptional opportunity to quantify the influence of recent climate change and predict the future.

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 (51°14'14.05"N 3° 8'49.71"W). The offshore cooling water intakes are in front of a rocky promontory within Bridgwater Bay, to the east are the 40 km² Stert mud flats. Depending upon the tide, the fish were sampled from a depth varying between 8 and 18 m. The power station intake is a 3.45 m diameter pipe situated 640 m offshore rising vertically up to the seabed. Water is pumped into the station using four centrifugal pumps each delivering a constant 7.5 m³ s⁻¹. Each pump is an independent unit with its own drum screen filtering system. This filtering system is designed to stop debris passing through the condenser tubes and acts as a trap for fish and other marine life. On each sampling visit the fish and crustaceans were collected from two of these filter screens.

The filter screens have a solid square mesh of 10 mm and experimental observation has shown that they will retain all flatfish of standard length (SL) >25 mm and round fish with a standard length greater than approximately 60 mm (Turnpenny, 1981). Smaller fish are retained with reduced efficiency and their rate of capture might not reflect their abundance in the environment. Gobies as small as 20 mm SL are frequently retained.

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). Regular monthly quantitative sampling commenced in January 1981. 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. Sampling methodology and the total volume of water sampled per month has not varied over the entire sampling period.

The power station intakes at Hinkley B Nuclear Power Station 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 fish, pelagic or benthic, move towards the intake in the tidal stream, often as they retreat from the inter-tidal zone where they feed, they are unable to see or otherwise detect the intake until they are too close to make an escape. The efficiency of the sampling method is discussed in Henderson & Holmes (1991). A description of the Bridgwater Bay study area is given in Henderson & Holmes (1991) and references cited therein. 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.

Water temperature and salinity were measured monthly about one hour before low water using a mercury thermometer and refractometer respectively. Flow measured at the Bewdley on the River Severn (from the Environmental Agency <http://www.nwl.ac.uk/ih/nrfa/webdata/054001/g.html>) was used as a measure of freshwater flow into the estuary and records of sunshine, air temperature, wind speed and wind direction for Bristol were obtained from the UK Meteorological Office. The average monthly rainfall for England and Wales (Jones & Conway, 1997) was obtained from the Hadley Centre (http://www.metoffice.com/research/hadleycentre/CR_data/Monthly/HadEWP_act.txt). The NAOI, calculated as the difference between the normalized sea level pressure over Gibraltar and south-west Iceland (Jones et al., 1997) were acquired from <http://www.cru.uea.ac.uk/cru/data/nao.htm>. The annual position of the Gulf Stream north wall as expressed as the 1st Principal

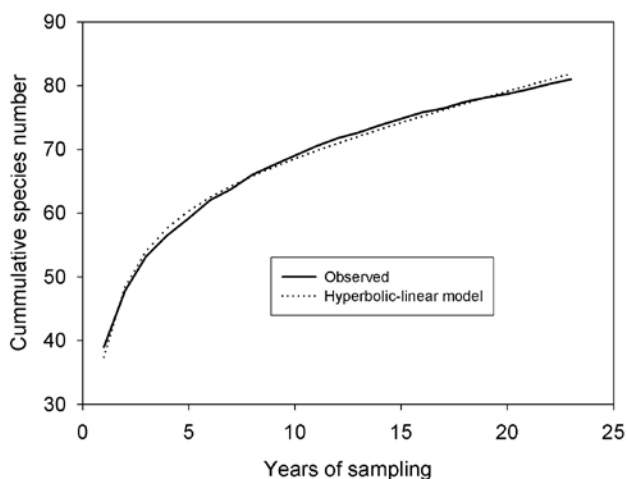


Figure 1. The rate of fish species accumulation from monthly sampling at Hinkley Point Nuclear Power Station in Bridgwater Bay, Somerset. Sample order effects have been removed by undertaking 20 randomizations of sample order and plotting the average species number. The dotted line is a hyperbolic linear model fitted by non-linear regression.

component was obtained from the web site www.pml.ac.uk/gulfstream/inetdat.htm.

Non-parametric statistical tests, Pearson correlation and linear regression were undertaken using SigmaStat (Systat Software Inc.). Regression and correlation were used to determine the environmental variables that were the best predictors for species richness and abundance. The CAP III (Pisces Conservation Ltd) was used for multivariate statistical and community analysis. Principal components analysis (PCA) used a variance–covariance matrix derived from square root transformed abundance data to study the change in the community of dominant fish species between years. The PCA was only applied to data for the 16 common species as the method is seriously distorted if the data array holds large number of zero values. These 16 species, recorded in every year of sampling (see Appendix 1), contributed more than 95% to both the total number of individuals and biomass caught. Non-metric multidimensional scaling (nMDS) using the Sørensen distance measure was used to study changes in the entire community of 81 fish. This method was selected as it used presence–absence data and therefore the analysis would give equal weight to all species. Analysis of similarity (ANOSIM, Clarke, 1993) was used to test if the groups identified from PCA and from climatic considerations were statistically significant and the Similarity Percentages (SIMPER, Clarke & Warwick, 1993) to identify species that contributed the most to the observed dissimilarity between groups.

The ECOM II software package (Pisces Conservation Ltd) was used for Canonical correspondence analysis (CCA) to identify those environmental variables most influential in determining community composition and to create an ordination of species along environmental gradients. The species abundance data was log transformed before CCA. Monte Carlo randomization methods determined if the observed relationships between the species and independent physical variables were statistically significant. Diversity

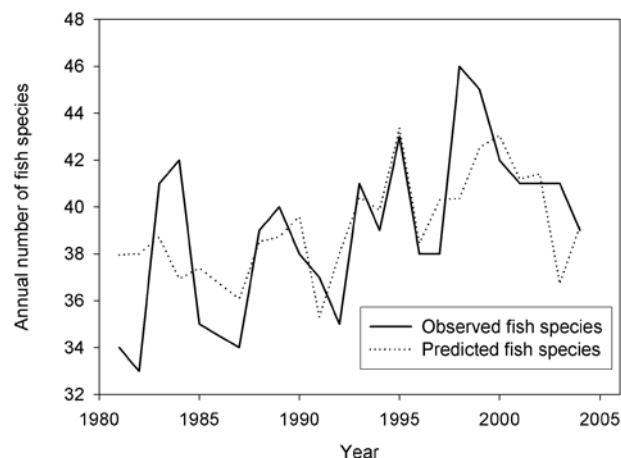


Figure 2. The observed and predicted number of species of fish recorded annually from 12 monthly samples from Bridgwater Bay. The samples were collected from the intake screens of Hinkley Point Nuclear Power Station. Predicted values were calculated from observed average salinity, S , and temperature, T , data using the equation $N=51.094-1.343S+1.794T$.

indices, species richness and averaged species accumulation curves were estimated using Species Richness and Diversity v. 3 (Pisces Conservation Ltd) using methods described in Southwood & Henderson (2000).

The number of resident and occasional visitor fish (termed tourists by Southwood et al., 2005) was estimated using a hyperbolic-linear model described by the equation:

$$S(n) = \left[\frac{S_r n}{k_1 + n} \right] + k_2 n \quad (1)$$

where $S(n)$ is the number of species recorded after n samples, S_r is the total number of resident species, k_1 is a constant that determines the rate of acquisition of resident species with sampling effort and k_2 is a constant that describes the rate of acquisition of tourist (non-resident) species. The hyperbolic-linear model was fitted using the Levenberg–Marquardt non-linear regression method.

RESULTS

Species richness and change

A list of the fish species, giving common and scientific names, that have been captured at Hinkley Point between 1981 and 2005 together with abundance and summarizing frequency data are given in Appendix 1. Species richness estimators gave a total species number ranging from 87 to 103 for the sum of both resident and tourist species (Chao quantitative=87; 2nd order Jackknife=103; Bootstrap=86.8).

The species acquisition curve smoothed by randomizing sample order shows a rapid de-acceleration in the rate of capture of new species with increasing sampling effort followed by an extended period with an almost linear increase (Figure 1). The hyperbolic-linear model produced an almost perfect fit to the observed curve ($R=0.998$) and gave estimates for the resident fish population (S_r) of 65 and a rate of acquisition of tourists (k_2) of 0.83 per year of monthly sampling.

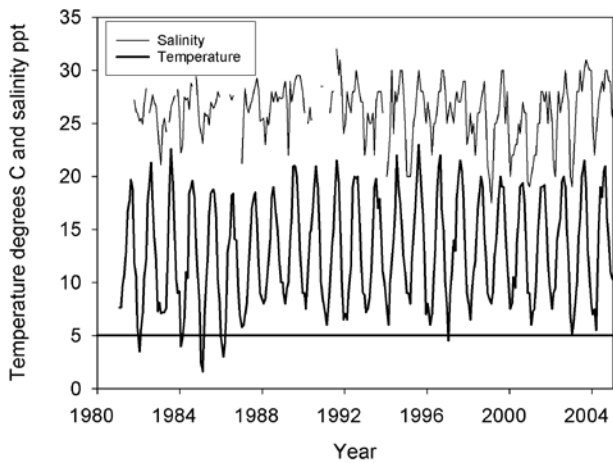


Figure 3. Temperature and salinity at Hinkley Point between 1981 and 2005.

The annual number of fish species caught (N) showed an increasing trend from a minimum of 33 in 1982 to a maximum of 46 in 1998 (Figure 2) which could be explained by changes in the environment. Multiple linear regression gave the equation:

$$N = 51.094 - 1.343S + 1.794T \quad (2)$$

where S, salinity (ppt) and T, water temperature (°C) are annual averages. The regression gave a significant fit to the data ($F=6.28$, $df=22$, $P=0.008$, adjusted $R^2=0.324$). A variance inflation factor of 1.0 indicated that the independent variables showed low multicollinearity. The predicted number of fish species captured per annum using eqn 2 is plotted on Figure 2.

No α diversity index of annual catch showed any temporal trend. Given the observed increase in the number of species recorded through time this can only occur if the equitability decreased.

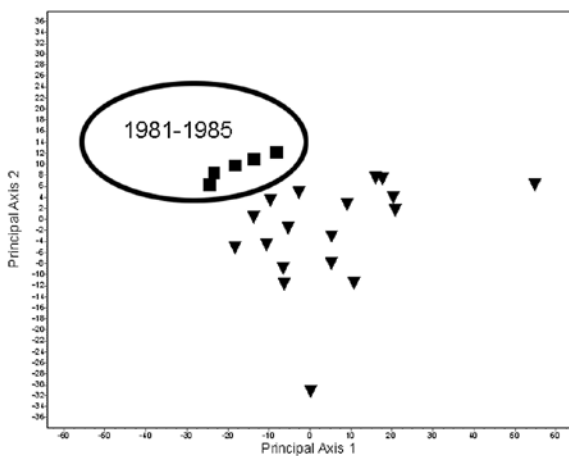


Figure 4. The ordination produced by principal components analysis of annual fish abundance data at Hinkley Point for the years 1981 to 2004 inclusive. The year 1986 is excluded because only seven months were sampled. Squares represent years between 1981 and 1985.

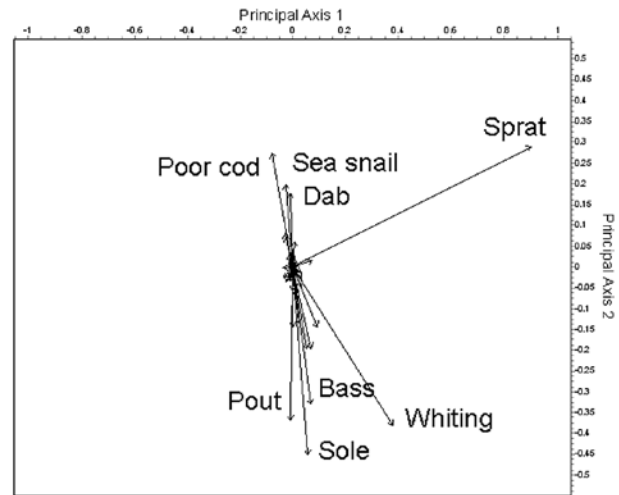


Figure 5. The direction of the Eigenvectors representing the most abundant species within the space defined by the two largest principle axes generated by a principal components analysis of annual fish abundance data at Hinkley Point for the years 1981 to 2004 inclusive.

Temporal changes in temperature and salinity

Figure 3 shows the temporal variation in salinity and seawater temperature in Bridgwater Bay between January 1981 and August 2005. Maximum summer temperatures have varied between years but show no trend. The maximum temperature recorded was 23°C in July 2005. Winter temperatures have increased since 1987/1988. The 5°C line marked on Figure 3 shows that temperatures below 5°C occurred regularly in the early 1980s with a minimum of only 1.6°C in February 1985. Since 1986, a winter minimum below 5°C was only recorded in 1997. The winter of 1982/1983 seems to be an exception to the series of low winter temperatures in the early 1980s. While the minimum for this winter was only 7.2°C, it was still unusually cold, as the temperature remained below 8.5°C for five months, a remarkably extended period of winter temperature.

Salinity has ranged between 17.5 and 32 parts per thousand (ppt). Salinity varies with freshwater inputs and shows both seasonal variation and long-term trend. Between 1991 and 2000 average salinity declined and since 2000 it has increased. Seasonal variability in salinity has increased between the 1980s and 2000s.

Changes in community structure

A PCA ordination of annual abundance data for the permanently resident fish species is plotted in Figure 4. This plot used coordinates generated for the two largest Eigenvalues, which represented 62% of the total variability within the data set. It is unusual for such a high proportion of the total variability with a species abundance data set to be explained in only two dimensions and indicates a high level of correlation in species abundance and allows the between year relationships to be summarized in two axes. In Figure 4, the years between 1981 and 1985 form a discrete group on the periphery of the scatter of points. An analysis of similarity (ANOSIM Clarke, 1993) between a first group comprising

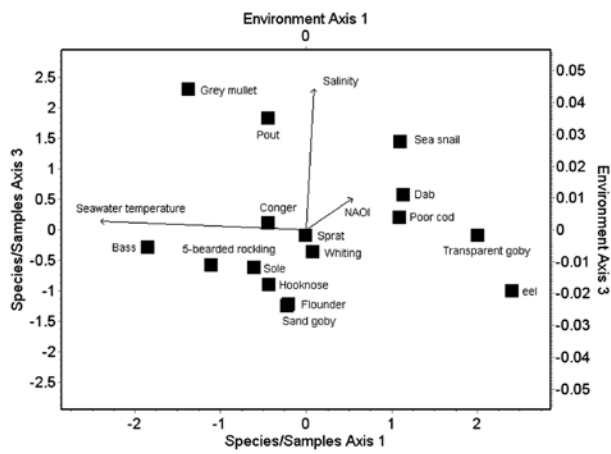


Figure 6. Ordination biplot of fish species and environmental variables generated by Canonical correspondence analysis. The data were collected at Hinkley Point between 1981 and 2004 inclusive. The calculations were undertaken using the 16 fish species always present.

the years 1981 to 1985 inclusive and a second holding all subsequent years up to 2004, demonstrated that the fauna in the early years was significantly more similar than would be expected by random chance (Test statistic, $R=0.4$, $P=0.02$, 1000 randomizations).

The direction of the eight largest Eigenvectors within the space defined by the two largest principle axes are labelled in Figure 5 and shows that the years between 1981 and 1985 were characterised by relatively large numbers of sea snail, dab and poor cod, *Trisopterus minutus*, and low numbers of pout, *Trisopterus luscus*, bass, *Dicentrarchus labrax*, sole, *Solea solea* and whiting, *Merlangius merlangius*. Axis 1 principally represents sprat abundance, so that years to the right of the plot in Figure 4 are years in which sprat were most abundant. The abundance of sprat and all other common fish were uncorrelated.

An examination of the ordination of the total fish community using nMDS found that years pre and post 1993 occupied distinct regions of the ordination space, indicating

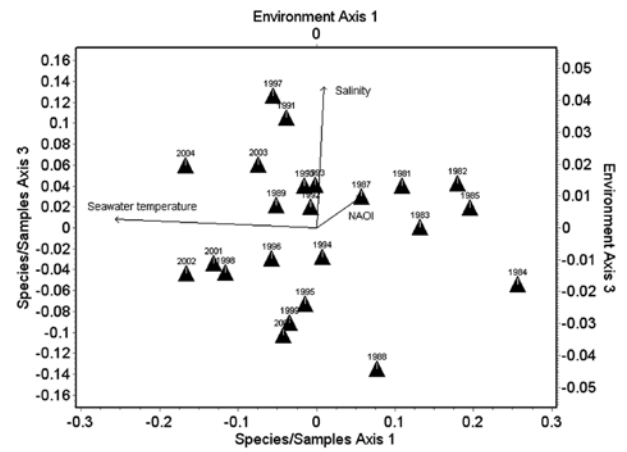


Figure 7. Ordination biplot of years of sampling and environmental variables generated by Canonical Correspondence Analysis. The calculations were undertaken using the 16 fish species always present.

a marked change in the total fish species complement after 1993. A direct comparison of 11 years pre and post 1993 shows a small increase in the total species recorded from 69 to 74 out of a total complement of 81. More significant than the change in total species richness is the marked change in the frequency of occurrence of many species. The annual frequency of occurrence of all fish species pre and post 1993 is given in Appendix 1.

Constrained ordination of the permanent residents

Canonical correspondence analysis (CCA) was undertaken using the 16 fish species captured in all 23 years with complete monthly sampling (see Appendix 1). The less abundant species were not included as sampling may not have been of sufficient intensity to allow reliable statistical analysis. Initially, stepwise CCA was undertaken to identify environmental variables that could explain a statistically significant proportion of the observed between year variation. This procedure resulted in the retention of

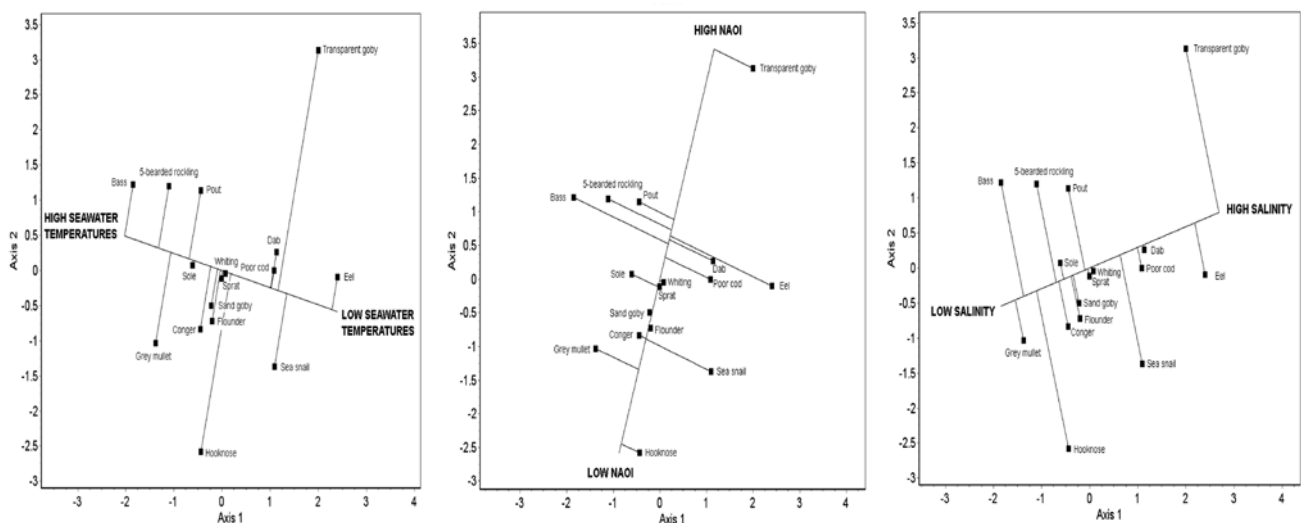


Figure 8. The inferred ranking of common fish species to the environmental variables, seawater temperature, NAOI and salinity at Hinkley Point. Results obtained by Canonical correspondence analysis.

Table 1. Southern limit of the range of species common in Bridgewater Bay, Bristol Channel. Information derived from distribution maps on Wheeler (1969). The species are arranged in their order along the temperature vector generated by CCA.

Species	Southern limit of range
Bass	Senegal N. Africa, Canary Islands
5 bearded rocking	Lisbon, Portugal
Thin-lipped grey mullet	Mediterranean N. Africa
Pout	North Africa to Canary Islands.
Sole	Senegal N. Africa
Conger	Senegal N. Africa
Whiting	Portugal rare in Mediterranean
Flounder	Mediterranean N. Africa
Sand goby	North Mediterranean
Sprat	N. African Mediterranean
Hooknose	North France
Dab	North France
Poor cod	Northern Spain (subspecies in Western Mediterranean)
Transparent goby	North Mediterranean
Sea snail	Southern England
Eel	North Africa

only three environmental variables; annual average seawater temperature, annual average salinity and annual average NAOI. A test for multi-collinearity between these three variables gave variance inflation factors of between 1.03 and 1.1, indicating that each was varying independently of the others. A CCA using these three variables was then subjected to a Monte Carlo randomization test to ensure that the observed relationships could not have been generated by random chance. The probability that the Eigenvalues for axes 1, 2 and 3 were generated by random chance was estimated as 0.0529, 0.1778 and 0.011 respectively. This indicated that at just over the 5% significance level, axes 1 and 3 were explaining more of the total variability than would be expected by random chance. Axis 2 was clearly not significant.

The CCA biplots for species and years in relation to the environmental variables are plotted in Figure 6 and Figure 7 respectively. Grey mullet and pout are associated with years of higher than average salinity, sea snail, dab, poor cod, transparent goby and eel were most abundant in years with lower than average seawater temperatures and a higher than average NAOI. Bass was highly responsive to increased seawater temperature. Figure 7 shows that years from 1981 to 1987 formed a group characterized by lower seawater temperatures and high NAOI.

The ordination of the species along each of the environmental axes is shown in Figure 8A–C. The position of species along the vector representing each environmental variable was found by projecting orthogonal lines from the species positions on to the vector. These points of intersection show the relative response of each species to the environmental variables. Figure 8A shows a response to temperature which generally mirrors the known southern limit of geographical distribution (Table 1) with species favouring warmer, more southerly waters increasing in

warmer years. Two notable exceptions were the eel and transparent goby. Figure 8B shows that hooknose and transparent goby were particularly responsive to the NAOI with high values favouring transparent goby and low values hooknose. It is also notable that Figure 8C indicates that transparent goby and eel were most abundant in years of high average salinity and bass and grey mullet preferred low salinity years. The totality of these trends suggests that the anomalous temperature response of eel and transparent goby is because these species are responding strongly to changes in salinity. As higher than average salinities tend to occur in warmer than average drought years the response to salinity also results in increased abundance in warmer years. Additionally, analysis of eel dynamics is problematical as the species has experienced a dramatic long-term decline in abundance in the Bristol Channel that is almost certainly linked to factors such as habitat damage, parasite introduction and over-fishing which are not included within this analysis. Both bass and grey mullet juveniles favour estuarine waters.

DISCUSSION

The present study demonstrates that the properties of large ecosystems can respond in both a continuous and discrete manner to climate change and that the future extent of this change could be large. Changes in estuarine systems are particularly important, as they are nurseries for coastal fish including many of the key commercial species of temperate waters. Two discrete changes in the fish community of the Bristol Channel have been identified. The first was the change in the relative abundance of the permanent members of the community in the late 1980s (see Figures 4 & 5). This abrupt event coincides with changes in the plankton of the north-east Atlantic. Reid et al. (1998) reported that in both the North Sea and the Atlantic Ocean between 52° and 58°N there was an increase in phytoplankton abundance inferred from chlorophyll concentration between 1948 and 1995 with 'evidence for a stepwise increase after the mid-1980s'. It is notable that the observed change in the Bristol Channel fish community occurred contemporaneously with this 'regime shift' (Beaugrand, 2004) in the plankton. Many of these fish initially live as planktonic larvae in the open sea, suggesting that events in early life may be influencing estuarine relative abundance. While the mechanism through which control operates are conjectural, the observed temporal coincidence indicates bottom up control of the abundance of common fish in the Bristol Channel.

Beaugrand & Reid (2003) argue that changes in the phytoplankton are linked to large-scale changes in ocean productivity caused by climatic variables such as the NAO and surface seawater temperature. This suggests that the correlations reported here between temperature, the NAO and the abundance of individual fish species is a product of a causal chain in which physical conditions change phytoplankton productivity, which then alters the zooplankton community, which in turn affects larval fish abundance. Beaugrand et al. (2003) concluded that such a causal chain is a determinant of cod recruitment in the North Sea. An increase in primary production may also, in part, explain the increasing fish and crustacean abundance

observed in Bridgwater Bay over the last 25 years (Henderson et al., 2006). The possibility that the NAO is acting on fish via changes in the plankton is supported by the observation that the species showing the greatest response to changes in the NAO is the transparent goby, *Aphia minuta* (see Figure 8B). This tiny, short-lived, fish always remains a member of the plankton and would be expected to respond markedly to any changes in the plankton.

Temperature influences young fish directly by changing their rate of development, which in turn may reduce mortality. For example, Henderson et al. (2004) in a study of sole, *Solea solea*, recruitment in the Bristol Channel argued for independent roles for the NAO and temperature. While changes in the NAO altered the rate of growth, presumably by changing ecosystem productivity, changes in temperature acted directly upon larval sole to reduce mortality, possibly by reducing the duration of the highly vulnerable early stages. Generally, changes in abundance and frequency of occurrence relating to temperature follow patterns that would be predicted from the known geographical distribution and temperature preference of individual species. This suggests that the local dynamics of many fish species are not tightly coupled, but partially determined by large scale physical variables.

A second discrete change, affecting the total species assemblage, occurred in the early 1990s. This marks a sudden alteration in the set of tourist species. After 1993, these predominately possess distributions centred to the south of the Bristol Channel and northern cold-water species disappear. This change correlates with seawater temperature rather than the NAO and productivity. There are other reports of sudden changes in fish presence or abundance in British waters in the 1990s linked to sea temperature. For example, Beare et al. (2004) found that Scottish catches of the warm water pelagic species, anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*), increased suddenly after 1995.

In addition to these two discrete changes in community structure, there has also been a continuous increase in fish species richness in Bridgwater Bay correlated with increased average seawater temperature (Figure 3). The increase in richness results from a more frequent capture of warmer water species without a corresponding loss of members of the permanent community. Permanent members close to the southern edge of their range, such as dab, *Limanda limanda*, and sea snail, *Liparis liparis*, have become less abundant, but have not been lost, probably because they are able to avoid harm during periods with excessively warm water by moving deeper (Henderson & Seaby, 1999) or their upper thermal tolerance has not yet been exceeded. Spatial responses would probably be insufficient to support an increased species assemblage if competition for food intensified as those species avoiding warm shallow waters are leaving invertebrate rich feeding areas. However, increased species richness in the late 1980s and early 1990s coincided with a period of high phyto and zooplankton (Beaugrand & Reid, 2003) and macrocrustacean (Henderson et al., 2006) abundance, increasing the size of the prey resource. As this increased production has been linked to the unusually high NAOI over this period, this production may not be

maintained and competition for food may intensify. It is notable that both fish species richness and total fish numbers did return to lower levels in 2003/2004.

While species richness has increased, α diversity has shown no trend because almost all the additional species are tourists that occur in low numbers. It is unlikely that there are any fundamental principles leading to a stabilization of α diversity, rather the relative abundance of fish results in an overwhelming numerical dominance of two or three species making these indices insensitive to community change.

Total fish species number in Bridgwater Bay was found to decline with increasing salinity and salinity was also found to influence the distribution of individual species. It is well known that salinity influences the distribution of fish (e.g. Maes et al., 1998) so the observed responses may, in part, be produced by changes in distribution within the Bristol Channel rather than population size. Salinity was highly negatively correlated with river flow, so reduced salinity indicates greater allochthonous inputs from the land. Because the present study is restricted to a single area, it cannot distinguish between changes in distribution from any changes in abundance linked to riverine inputs and changing productivity. Further, the NAO is known to influence rainfall (Rodwell et al., 1999) which is directly correlated to river flow and therefore estuarine salinity.

Predicting the impact of climate change

Climate Change Scenarios for the United Kingdom, prepared by the Hadley Centre and the Tyndall Centre for Climate Change Research, includes the following predictions for the 2080s:

- Annual average air temperatures across the UK may rise by between 2°C (low) and 3.5°C (high).
- Warmer summers will become more frequent and very cold winters increasingly rare.
- Winters will become wetter, summers perhaps drier.
- The Gulf Stream may weaken, but probably not enough to cool the UK during this century.

Using eqn 2, a 2°C increase in average shallow water temperature, together with increased river flow resulting in a drop in salinity of 2 ppt would increase the average number of fish species caught in Bridgwater Bay by 6.3 per annum, a 10% increase. Changes in the behaviour of the Gulf Stream and NAO are unlikely to influence this estimate greatly, although a consistently low NAOI would reduce precipitation and thus raise salinity. A 2°C increase in average temperature would inevitably lead to a large change in relative abundance of the dominant fish in Bridgwater Bay. Bass, *Dicentrarchus labrax*, grey mullet species, five-bearded rockling, *Ciliata mustella*, pout, *Trisopterus luscus* and sole, *S. solea*, would increase, and dab, *L. limanda*, poor cod, *T. minutus*, and sea snail, *L. liparis*, would decline. Amongst subdominant species there would be an increase in species with ranges that extend further south, for example, conger eel, *Conger conger*. Present occasional visitors from the south such as red mullet, *Mullus surmuletus*, would probably become resident as the area is already acting as a summer nursery. There would also be a further increase in warm water tourists, which would represent most of the predicted increase in species richness.

The predicted climate change would greatly change seasonal movements. Many species of fish and some macrocrustaceans such as the common shrimp, *Crangon crangon*, leave Bridgwater Bay during summer months when shallow water temperatures exceed 20°C (Henderson et al., 2006). This retreat to cooler waters may be linked to species specific temperature preferences, but could also be influenced by the reduction in dissolved oxygen. An average increase in water temperature of 2°C would produce temperatures above 20°C from early July to the beginning of October. In 2005 and 2006, maximum temperatures $\geq 23^\circ\text{C}$ were recorded and temperatures remained above 20°C from June to September. These were the warmest summers since recording began in 1980. Equally dramatic changes would occur during the winter months when the minimum temperature would often remain above 8°C. Cold water loving winter migrants would reduce their period of occupancy, or in the case of sea snail, *L. liparis*, no longer visit the bay. Further, many species would continue to feed throughout the winter producing a dramatic change in seasonal production. These seasonal changes would be further increased if rainfall became more seasonal as seasonal variations in salinity would be greater. The salinity time series from 1980 to 2005 already shows a trend of increased seasonal variation in salinity.

A sudden change in community structure can be triggered by the NAO and possibly the position of the Gulf Stream, which are correlated, with a lag of about 18 months (Frankignoul et al., 2001). At present, the Bridgwater Bay data does not allow a clear separation of the effects of the NAO from temperature as the period from 1980 to 2000 was characterized by an increasing trend in both temperature and the NAOI. The NAO does influence temperature by changing the frequency of the westerly airstreams over Britain. The greatest impact of global warming will occur during swings in the NAO when high temperatures interact with sudden changes in planktonic productivity. This may produce a dramatic change in fish recruitment and growth in large estuaries such as the Bristol Channel. The ability of the Bristol Channel system to suddenly greatly increase ecological activity was demonstrated in 2002 (Henderson et al., 2006). An unfavourable combination of high temperature, low NAOI and high salinity would produce a dramatic collapse in recruitment and productivity.

While species richness and seasonal occupancy would be predicted to change considerably, and short-term instability greatly increases, there are no reasons to believe that temperature and rainfall change would produce a permanent catastrophic collapse in the community. This is because Atlantic estuaries from Portugal to Scotland form a continuum in terms of fish community structure and many fish may rapidly respond to climate change by altering their geographical range. A northerly range extension is the most frequently reported response to recent warming. However, increased population variability may reduce stability and could lead to local extinctions.

In conclusion, there have been marked changes in the fish community of the Bristol Channel over the last 25 years. Increased water temperatures have produced a steady increase in species richness as more southerly distributed fish enter the estuary in greater numbers. In the mid 1980s

there was an abrupt change in relative abundance of the permanent members of the community, which was likely caused by changes in the NAO and offshore plankton productivity. In the early 1990s, a second abrupt change in the total species assemblage occurred which could be related to temperature increase. Climate warming is predicted to continue the trend of increasing species number and the decline and loss of fish with the most northerly distributions. Seasonal variability will also increase as fish avoid warm inshore waters during the summer and continue feeding during the winter. Predicting future communities require consideration of changes in temperature, NAO and salinity. While a smooth transition to a warmer water community is possible, there is a risk of bursts of instability as unfavourable combinations of climatic and physical factors interact with fish recruitment processes.

To undertake this work more than a million animals have been identified and measured, an impossible task without the support of many other scientists including in particular Dr Richard Seaby and Mr Robin Somes. This paper has greatly benefited from the criticism of two referees.

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Appendix 1. Alphabetically arranged list of fish species caught at Hinkley Point, Bridgwater Bay, between 1981 and 2004 inclusive. Only 23 of the possible 24 years are included in the frequency calculations as 1986 was excluded because not all 12 months were sampled.

Latin name	Common name	Mean number captured per year	Total years observed maximum=23	Frequency pre-1993 maximum=11	Frequency post-1993 maximum=12
<i>Agonus cataphractus</i> (L.)	Hooknose	5.7	23	11	12
<i>Alosa fallax</i> (Lacepede)	Twaite shad	19.9	22	10	12
<i>Ammodytes tobianus</i> L.	Common sand eel	0.8	12	6	6
<i>Ammodytes marinus</i> Raitt	Raitt's sand eel	0.04	1	0	1
<i>Anguilla anguilla</i> (L.)	Eel	13.0	23	11	12
<i>Aphia minuta</i> (Risso)	Transparent goby	15.9	23	11	12
<i>Atherina boyeri</i> Risso	Sand smelt	0.9	10	3	7
<i>Balistes carolinensis</i> (Gmelin)	Trigger Fish	0.04	1	0	1
<i>Belone bellone</i> (L.)	Garfish	0.04	1	0	1
<i>Blennius gattorugine</i> L.	Tompot blenny	0.2	5	2	3
<i>Buglossidium luteum</i> (Risso)	Solenette	0.09	1	0	1
<i>Callionymus lyra</i> L.	Dragonet	2.8	19	7	12
<i>Centrolabrus exoletus</i> (L.)	Rock cook	0.09	1	1	0
<i>Ciliata mustela</i> (L.)	Five-bearded rockling	45.5	23	11	12
<i>Ciliata septentrionalis</i> (Collet)	Northern rockling	2.6	21	9	12
<i>Clupea harengus</i> L.	Herring	36.8	21	9	12

Appendix 1. (Continued).

<i>Conger conger</i> L.	Conger	10.6	23	11	12
<i>Crenilabrus melops</i> (L.)	Corkwing wrasse	0.09	2	0	2
<i>Crenimugil labrosus</i> (Risso)	Thick-lipped grey mullet	0.39	4	0	4
<i>Crystallogobius linearis</i> (von Duben)	Crystal goby	0.4	4	3	1
<i>Ctenolabrus rupestris</i> (L.)	Goldsinny	0.3	5	3	2
<i>Cyclopterus lumpus</i> L.	Lumpsucker	4.7	16	9	7
<i>Dicentrarchus labrax</i> (L.)	Bass	99.8	23	11	12
<i>Engraulis encrasicolus</i> (L.)	Anchovy	0.3	3	2	1
<i>Entelurus aequoreus</i> (L.)	Snake pipefish	2.9	21	11	10
<i>Eutrigla gurnardus</i> (L.)	Grey gurnard	7.6	20	8	12
<i>Gadus morhua</i> L.	Cod	41.3	22	10	12
<i>Gaidropsaurus vulgaris</i> (Cloquet)	Three-bearded rockling	0.2	3	2	1
<i>Gasterosteus aculeatus</i> L.	Three-spined stickleback	1.7	15	4	11
<i>Glyptocephalus cynoglossus</i>	Witch	0.04	1	1	0
<i>Gobius paganellus</i> L.	Rock goby	0.08	1	0	1
<i>Gobius niger</i> L.	Black goby	0.96	8	3	5
<i>Hyperoplus lanceolatus</i> (Lesauvage)	Greater sand eel	0.17	4	1	3
<i>Labrus bergylta</i> Ascanius	Ballan wrasse	0.65	6	2	4
<i>Labrus mixtus</i> L.	Cuckoo wrasse	0.13	3	2	1
<i>Lampetra fluviatilis</i> (L.)	River lamprey	0.3	6	2	4
<i>Limanda limanda</i> (L.)	Dab	59.3	23	11	12
<i>Liparis liparis</i> (L.)	Sea snail	104.8	23	11	12
<i>Liza auritus</i> (Risso)	Golden mullet	1.0	4	0	4
<i>Liza ramada</i> (Risso)	Thin-lipped grey mullet	47.4	23	11	12
<i>Lophius piscatorius</i> L.	Angler fish	0.74	6	4	2
<i>Maurolicus muelleri</i> (Gmelin)	Pearlsides	1.4	12	1	11
<i>Merlangius merlangus</i> (L.)	Whiting	1474.6	23	11	12
<i>Merluccius merluccius</i> (L.)	Hake	8.6	16	10	6
<i>Micromesistius poutassou</i>	Blue Whiting	2.6	6	1	5
<i>Microstomus kitt</i>	Lemon sole	0.09	2	1	1
<i>Molva molva</i> (L.)	Ling	0.1	3	2	1
<i>Mullus surmuletus</i> L.	Red mullet	4	11	4	7
<i>Nerophis lumbriciformis</i>	Worm pipefish	0.04	1	0	1
<i>Petromyzon marinus</i>	Marine lamprey	0.04	1	0	1
<i>Platichthys flesus</i> (L.)	Flounder	95.6	23	11	12
<i>Pleuronectes platessa</i> L.	Plaice	5.4	20	9	11
<i>Pollachius pollachius</i> (L.)	Pollack	4.0	21	10	11
<i>Pollachius virens</i> (L.)	Saithe	0.04	1	1	0
<i>Pomatoschistus microps</i> (Krøyer)	Common goby	1.7	8	4	4
<i>Pomatoschistus minutus</i> (Pallas)	Sand goby	307.2	23	11	12
<i>Pomatoschistus pictus</i> (Malm.)	Painted goby	0.7	9	1	8
<i>Psetta maxima</i> (L.)	Turbot	0.96	7	2	5
<i>Raja brachyura</i>	Blonde ray	0.04	1	1	0
<i>Raja clavata</i> L.	Thornback ray	2.6	19	9	10
<i>Raja microocellata</i>	Small eyed ray	0.087	2	1	1
<i>Raniceps raninus</i> (L.)	Tadpolefish	0.17	4	4	0
<i>Salmo salar</i> L.	Salmon	0.39	8	4	4
<i>Sardina pilchardus</i> (Walbaum)	Pilchard	0.22	2	1	1
<i>Scophthalmus rhombus</i> (L.)	Brill	0.78	7	5	2
<i>Scyliorhinus caniculus</i> (L.)	Lesser spotted dogfish	1.22	15	6	9
<i>Solea solea</i> L.	Sole	179.8	23	11	12
<i>Spinachia spinachia</i> (L.)	Fifteen-spined stickleback	0.2	5	2	3
<i>Spondylisoma cantharus</i> (L.)	Black sea bream	0.3	7	4	3
<i>Sprattus sprattus</i> (L.)	Sprat	1655.91	23	11	12
<i>Syngnathus acus</i> (L.)	Great pipefish	1.56522	9	1	8
<i>Syngnathus rostellatus</i> Nilsson	Nilsson's pipefish	2.52174	19	9	10
<i>Trachinus vipera</i> Cuvier	Lesser weever	0.0434783	1	0	1
<i>Trachurus trachurus</i> (L.)	Scad	0.478261	9	6	3
<i>Trigla lucerna</i> L.	Tub gurnard	1.34783	13	6	7
<i>Trigla lyra</i> L.	Piper	0.0869565	1	1	0
<i>Trisopterus esmarkii</i> (Nilsson)	Norway pout	9.73913	22	10	12
<i>Trisopterus luscus</i> (L.)	Pout	160.87	23	11	12
<i>Trisopterus minutus</i> (L.)	Poor cod	239.391	23	11	12
<i>Zeugopterus punctatus</i> (Bloch)	Topknot	0.0434783	1	0	1
<i>Zeus faber</i> L.	John Dory	0.0869565	2	2	0