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#### Competing interests statement

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## Climatic influence on a marine fish assemblage

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Understanding the fluctuations in marine fish stocks is important for the management of fisheries, and attempts have been made to demonstrate links with oceanographic and climatic variability<sup>1–3</sup>, including the North Atlantic Oscillation (NAO)<sup>4,5</sup>. The NAO has been correlated with a range of long-term ecological measures<sup>6,7</sup>, including certain fish stocks<sup>8,9</sup>. Such environmental influences are most likely to affect susceptible juveniles<sup>10</sup> during estuarine residency, as estuaries are critical juvenile nursery or over-wintering habitats<sup>11</sup>. Here we show that, during a 16-year period, climatic forcing (by means of the NAO) is consistently the most important parameter explaining variation in assemblage composition, abundance and growth of juvenile marine fish during estuarine residency. A possible mechanism for the effect of the NAO is a temperature differential between estuarine and marine waters that allows fish to facultatively exploit optimal thermal habitats. The connection has potentially important implications for the size and numbers of individuals recruited to the fishery, for understanding and predicting the composition of juvenile fish stocks using estuaries, and for the appropriate conservation of estuarine systems in relation to fish stocks.

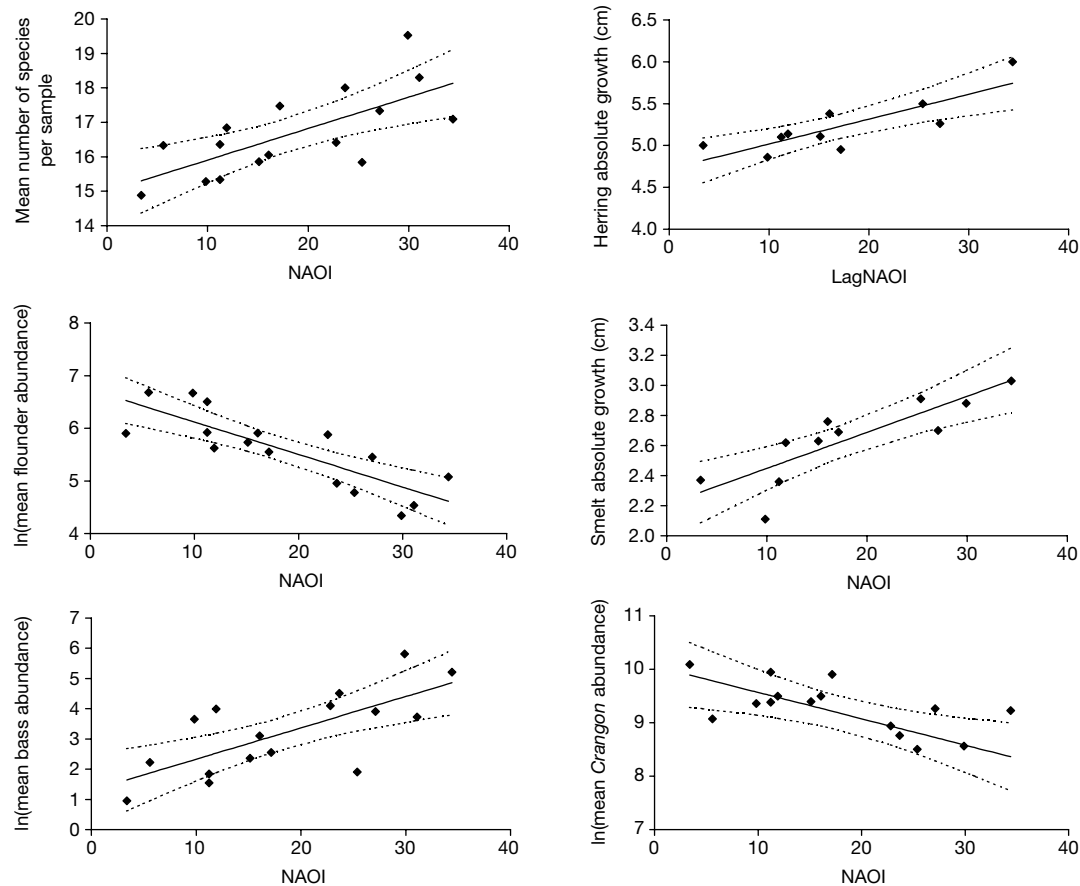
Over the past century, the principal issue in fishery science has arguably been understanding recruitment variability<sup>12,13</sup>, either as a tool for predicting future success of a fishery or as a method for explaining variation in fish stocks. Traditionally, investigations

correlating fish abundance and growth to environmental variables have focussed on the role of marine temperatures for commercially important species such as cod (*Gadus morhua*)<sup>3,14</sup>. Similarly, stock recruitment levels have been associated with variations in marine temperature during the first years of life<sup>9,15</sup>. In the North Atlantic, sea surface temperature (SST) has been related to the dominant signal of climatic variability<sup>16</sup>, the NAO, which has a potentially influential role in determining stock recruitment levels<sup>3,8</sup>. However, many commercially important marine fish spend critical juvenile stages in estuarine nursery grounds<sup>11</sup>, which may act as thermal buffers against more severe open-sea conditions, and therefore are not affected directly by marine conditions.

To investigate the potential impact of climatic variation on juvenile fish stages, we have analysed one of the most comprehensive long-term data sets available for estuarine fish communities, the 16-year data set compiled from the Thames estuary, UK. This has been used previously to model intra-annual responses of fish and invertebrate populations to physico-chemical trends<sup>17–19</sup>. As the fish assemblage is primarily composed of juvenile marine species using the estuary as a nursery<sup>20</sup>, we have collated the data by year to facilitate the investigation of interannual relationships between environmental variables and fluctuations in fish assemblage composition, abundance and juvenile growth. The environmental variables included measurements of estuarine water quality, freshwater flow, North Sea SST, and climatic variation as defined by the North Atlantic Oscillation Index (NAOI). The species selected *a priori* for population analysis included all commercially important marine groups (flatfish (*Solea solea*, *Platichthys flesus*, *Pleuronectes platessa*, *Limanda limanda*), gadoids (*Merlangius merlangus*, *Trisopterus luscus*, *T. minutus*), clupeids (*Clupea harengus*, *Sprattus sprattus*) and bass (*Dicentrarchus labrax*)), the dominant estuarine fish species (gobies (*Pomatoschistus* spp.), eel (*Anguilla anguilla*), smelt (*Osmerus eperlaunus*), pogge (*Agonus cataphractus*) and Nilsson's pipefish (*Syngnathus rostellatus*)), and invertebrates important either as prey or as predators<sup>18</sup> (brown shrimp (*Crangon crangon*) and gelatinous species (*Pleurobrachia pileus*, *Aurelia aurita*)). Where possible, growth during estuarine residency was examined in relation to the NAOI, as were standard summary measures (for example, diversity, evenness) of assemblage composition.

From a total of 50 possible relationships between biological measures and the NAOI, significant relationships were apparent in 24 cases (Fig. 1 and Table 1; see also Supplementary Information). All fish assemblage measures demonstrated significant relationships with NAOI, and when compared with other environmental data NAOI was always the best predictor (highest  $r^2$  value) of assemblage variation. Similarly, where significant relationships between fish population or growth measures and environmental variables were apparent, NAOI or NAOI that was lagged by 1 year best explained the variation in all but two cases (Gobiidae abundance and bass average size). Nonsignificant ( $P > 0.05$ ) or statistically inadequate regression models (autocorrelation, non-normal residuals) relating abundance to time suggested that temporal trends in the data did not account for observed correlations with the NAOI. Growth and abundance were not significantly correlated ( $P > 0.05$ ), suggesting that density dependence was not a factor in mediating observed correlations between NAOI and growth. Of the invertebrates, two species demonstrated significant abundance relationships: *Aurelia* and *Crangon*. Table 1 presents the statistically significant relationships with NAOI, which explained up to 54% of the variation over 16 years in assemblage measures, 69% of fish abundance, 76% of fish growth and 46% of invertebrate abundance.

To control further for possible temporal or density-dependent effects on correlations with the NAOI, partial correlation coefficients for abundance and growth data and the NAOI that controlled for temporal trends and abundance, were computed. These supported the regression results (Table 2; see also Supplementary



**Figure 1** Examples of relationships between NAOI and fish assemblage, population and growth measures. For all cases, NAOI was either the only variable significantly related with the dependent variable or had the highest  $r^2$  value. Regression details are in Table 1.

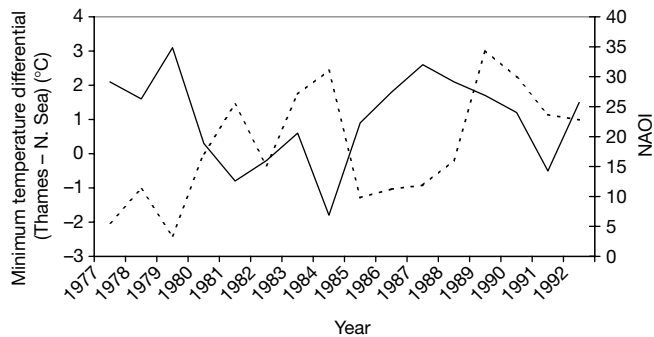
Solid line, model; dashed line, 95% confidence intervals; filled symbols, data points; LagNAOI, NAOI with a lag period of one year.

**Table 1** Statistically acceptable linear regressions for association between NAOI or LagNAOI and biological measures

Parameter	<i>n</i>	<i>x</i>	Regression equation	$r^2$	<i>P</i>
Fish assemblage measures					
Mean species number per sample	16	NAOI	$y = 14.99 + 0.091x$	<u>0.493</u>	0.002
Mean Shannon–Wiener index	16	NAOI	$y = 1.287 + 0.013x$	<u>0.541</u>	0.001
Mean Pielou's evenness index	16	NAOI	$y = 0.478 + 0.004x$	<u>0.493</u>	0.002
Mean Berger–Parker dominance index	16	NAOI	$y = 0.581 - 0.005x$	<u>0.371</u>	0.012
Number of rare fish species year <sup>-1</sup>	16	NAOI	$y = 5.533 + 0.262x$	0.308	0.026
ln(total marine fish abundance)	16	NAOI	$y = 10.77 - 0.016x$	0.319	0.023
ln(total marine fish abundance)	16	LagNAOI	$y = 10.79 - 0.016x$	0.357	0.015
Fish population measures					
ln(mean flatfish abundance)	16	NAOI	$y = 6.801 - 0.062x$	<u>0.685</u>	<0.001
ln(mean flounder abundance)	16	NAOI	$y = 6.745 - 0.062x$	<u>0.667</u>	<0.001
ln(mean bass abundance)	16	NAOI	$y = 1.294 + 0.104x$	<u>0.510</u>	0.002
ln(mean Gobiidae abundance)	16	NAOI	$y = 9.397 - 0.030x$	0.328	0.020
ln(mean pipefish abundance)*	16	NAOI	$y = 1.677 + 0.068x$	0.341	0.018
Fish growth measures (cm)					
Bass average age-0 size	13	NAOI	$y = 5.915 + 0.082x$	<u>0.630</u>	0.018
Bass absolute growth*	13	NAOI	$y = 0.176 + 0.069x$	<u>0.513</u>	0.006
Dab average age-0 size	10	NAOI	$y = 4.721 + 0.030x$	<u>0.684</u>	0.003
Dab entry size	10	NAOI	$y = 3.966 + 0.040x$	<u>0.652</u>	0.005
Herring absolute growth	12	LagNAOI	$y = 0.780 + 0.021x$	<u>0.578</u>	0.004
Sprat absolute growth	14	LagNAOI	$y = 0.381 + 0.021x$	<u>0.755</u>	0.001
Smelt average age-0 size	11	NAOI	$y = 6.057 + 0.093x$	<u>0.646</u>	0.003
Smelt absolute growth	11	NAOI	$y = 2.208 + 0.024x$	<u>0.702</u>	0.001
Whiting absolute growth	13	NAOI	$y = 2.153 + 0.071x$	0.430	0.015
Invertebrate measures					
Total <i>Aurelia</i> abundance*	16	LagNAOI	$y = 1702 - 57.24x$	0.275	0.037
ln(mean <i>Crangon</i> abundance)	16	NAOI	$y = 10.063 - 0.049x$	<u>0.402</u>	0.008
ln(mean <i>Crangon</i> abundance)	16	LagNAOI	$y = 10.004 - 0.046x$	<u>0.352</u>	0.015

Total abundance (*Aurelia* only) is the number of individuals caught per year; mean abundance is the mean number of individuals caught per sample (500 million litres of filtered water). Regression *P*-values are provided; all slope *P*-values are <0.05. For growth measures,  $n < 16$  owing to inadequate sample sizes ( $n < 25$ ) for growth calculations. Underlined values indicate models that remain statistically significant after Bonferroni inequality adjustment; *x*, NAOI or LagNAOI; LagNAOI, NAOI with a lag period of 1 year. Dab, *L. limanda*; flounder, *P. flesus*; whiting, *M. merlangus*.

\* Relationship not significant when data de-trended (Table 2).



**Figure 2** Differential in minimum recorded water temperatures (°C) between the Thames estuary and southern North Sea (solid line), together with NAOI (dashed line) for the period 1977–92. Temperature differential demonstrates a significant negative linear relationship with NAOI ( $r^2 = 0.318$ ,  $P = 0.023$ ).

Information), adding eight additional significant relationships and removing only three from those reported in Table 1. Our results suggest, therefore, that climatic variability has a principal controlling influence on the structure of the Thames fish assemblage, the growth of many resident juveniles, and the abundance of many of the dominant fish species using the estuary as a nursery area. Although the ecological effects of the NAO have been demonstrated on the abundance and growth of single species within a community<sup>7</sup>, or on limited community measures<sup>21</sup>, this study demonstrates relationships for the NAO at multiple levels of biological organization and for a wide range of species occupying a similar habitat.

All significant parameters of fish growth were positively correlated with NAOI. High NAOI values generally correspond to warm, wet and stormy winters in the northeast Atlantic<sup>5</sup>. As temperature strongly influences juvenile growth<sup>10</sup>, temperature has been assumed to be the causative mechanism underlying the influence of the NAO on growth<sup>7</sup>. However, in all cases, regressions with the

NAOI explained higher proportions of the variation in growth than either estuarine water temperatures or North Sea SST alone. Furthermore, the growth of the main species of Clupeidae was related to NAOI with a one-year lag, rather than climatic conditions during the winter of estuarine residency. This suggests that principal climate-mediated environmental influences determine growth during the earliest marine larval stage of these species, either directly or by influencing feeding conditions for the parent stock<sup>22</sup>. Accordingly, our study suggests that climate-influenced hydrographical and meteorological factors, in addition to temperature, are important in determining juvenile fish growth in estuaries. Consistently strong relationships were also apparent between measures of the assemblage composition and the NAOI, with the index alone explaining nearly 50% of the variability in the number of fish species caught per sample. Diversity increases during wet, warm winters (high NAOI), which is partly explained by the significant increase in the number of rare species (abundance less than 0.1% of total catches) sampled during high NAOI years. Most of the additional species were predominantly those with a southern distribution<sup>23</sup> (for example, gurnards, anchovy, wrasse, weever). The appearance of unusual species or the extension of species' ranges have been used as indicators of climate change<sup>24</sup>, but the appearance of warm-water southern species may simply reflect long-term climatic cycles<sup>1</sup>.

Most of the fish species investigated (9 out of 15) demonstrated a significant relationship between population abundance and the NAOI. The specific responses of fish populations to climatic variation can be categorized into three groups: a negative relationship with the NAOI (flatfish species, northern species<sup>23</sup>; for example, herring (*C. harengus*)), a positive relationship with NAOI (southern species<sup>23</sup>; for example, bass, sprat (*S. sprattus*)), or no significant relationship (for example, all gadoids, dover sole (*S. solea*), estuarine species). As the primary use of estuaries by marine fish is as a nursery ground, the results suggest that estuarine usage, and therefore the relative importance of estuaries, is dependent on climate for many species. Increases in the population size of southern species, such as bass, during warm, high NAOI years is consistent with an opportunistic use of available thermal habitat. In

**Table 2** Partial correlation coefficients measuring the association between NAOI or LagNAOI and biological measures

Parameter	n	x	r	Significance
Fish population measures				
ln(mean herring abundance)	16	LagNAOI	-0.599	* (additional relationship)
ln(mean sprat abundance)	16	NAOI	0.644	** (additional relationship)
ln(mean flatfish abundance)	16	NAOI	-0.782	**
ln(mean flounder abundance)	16	NAOI	-0.771	**
ln(mean plaice abundance)	16	NAOI	-0.596	* (additional relationship)
ln(mean Gobiidae abundance)	16	NAOI	-0.648	**
ln(mean sand goby abundance)	16	NAOI	-0.673	** (additional relationship)
ln(mean eel abundance)	16	NAOI	-0.563	* (additional relationship)
ln(mean bass abundance)	16	NAOI	0.568	*
Fish growth measures (cm)				
Whiting absolute growth	13	NAOI	0.715	**
Herring absolute growth	12	LagNAOI	0.677	**
Sprat absolute growth	14	LagNAOI	0.942	**
Dab average age-0 size	10	NAOI	0.826	**
Dab entry size	10	NAOI	0.927	**
Flounder average age-0 size	13	NAOI	0.678	** (additional relationship)
Plaice average age-0 size	10	NAOI	0.762	** (additional relationship)
Sole average age-0 size	13	NAOI	0.650	** (additional relationship)
Bass average age-0 size	13	NAOI	0.611	*
Smelt average age-0 size	11	NAOI	0.850	**
Smelt absolute growth	11	NAOI	0.838	**
Invertebrate measures				
ln(mean <i>Crangon</i> abundance)	16	NAOI	-0.636	**
ln(mean <i>Crangon</i> abundance)	16	LagNAOI	-0.574	*

Data were adjusted for trends (abundance data) or abundance (growth data) before statistical analysis. A single asterisk indicates significance at the 0.05 level; a double asterisk at the 0.01 level. Relationships additional to those presented in Table 1 are indicated. LagNAOI, NAOI with a lag period of 1 year. Plaice, *P. platessa*; sand goby, *P. minutus*.

contrast, several common fish species have lowest abundances during such years, and highest abundances during cold, low NAOI years. Analysis of water temperature data reveals that minimum and average winter temperatures are higher in the estuary than in the North Sea during low NAOI years, and vice versa (Fig. 2). Climatic conditions during years of low NAOI therefore result in estuarine areas becoming comparatively thermally favourable as nursery grounds, with higher numbers of fish using estuaries. This climate-driven pattern suggests a facultative rather than obligate use of the estuary by many juvenile fish<sup>25</sup>, and highlights the importance of estuaries in providing recruits for certain fisheries (for example, herring, flatfish) during years of low NAOI. This mechanism is supported by the results for fish species that spend most of the year in estuaries (such as smelt, pipefish, pogge), and so would not be influenced by any temperature differential. The abundance of these species did not show any strong relationship with NAOI. De-trending of the data resulted in a greater number of significant population results than for regression alone (Tables 1 and 2). Significant correlations with de-trended series are thought to indicate a rapid response to the NAO<sup>7</sup>. The Thames data, therefore, provide strong evidence for the facultative use of estuarine environments in response to climate-induced temperature differentials, and a plausible mechanism through which the NAO can influence the status of marine fish populations.

Recruitment of fish from estuaries can strongly drive marine population dynamics<sup>26</sup>, partly owing to their biological importance as nursery areas for many commercial fish species. Our results suggest that juvenile estuarine fish populations are strongly affected by climatic variability, as influenced by the NAO, in ways that may affect estuarine production potential through changes in either growth or abundance. In particular, the facultative use of estuaries implies that estuaries are important ecological buffers for many species in years of low NAOI. Therefore, estuaries are potentially critical for dampening climate-induced stock fluctuations. Knowledge of this role is important for sustainable management of fisheries, particularly during stock recovery<sup>27</sup>, and highlights the importance of targeting conservation resources into estuaries to preserve the ecological buffering capacity of estuaries for commercially important or endangered estuarine-dependent fish stocks. □

## Methods

### Sampling methodology

Fish were sampled approximately every two weeks over a 16-year (1977–92) period from West Thurrock Power Station, north bank of the Thames estuary, UK<sup>20</sup>. All species retained over a 4-h period at low spring tide were identified, counted, and individuals of commercially important species were measured<sup>17</sup>. We standardized abundance data to 500,000 m<sup>3</sup> of filtered water<sup>20</sup>. Data for estuarine environmental parameters (temperature, freshwater flow, salinity, dissolved oxygen, suspended solids, pH, nitrogen) coincident to biota samples were obtained from Environment Agency databases<sup>18</sup>. Southwest North Sea SST data were obtained from the German Federal Maritime and Hydrographic Agency (Bundesamt für Seeschifffahrt und Hydrographie). Winter NAOI data<sup>4</sup> (the difference between the normalized mean winter (December–February) surface-pressure anomaly for Ponta Delgadas (Azores) and that for Akureyri (Iceland)) were provided by the Department of Fisheries and Oceans, Canada. To investigate annual trends, the yearly mean values for sample diversity indices, fish abundance and the abundance of individual species were calculated, together with the total number of fish caught per year.

### Statistical analysis

Length–frequency data for individual sample dates were used to compute estuarine entry and exit sizes and absolute growth (cm) for the period of estuarine residency<sup>10</sup>. Length–frequency data for individual sample dates were used to compute estuarine entry and exit sizes and absolute growth (cm) for all juvenile fish less than one year old (age-0) for the period of estuarine residency. Mean values for estuarine environmental parameters (annual) and North Sea SST (monthly and annual) were also computed. Abundance data series were assessed for temporal trends before further use in statistical analysis using linear trend regressions. Insignificant slope coefficients (18 out of 22) or statistically inadequate regression models (4 out of 22) provided no compelling evidence of temporal trends in the data. Growth data were assessed for correlation with abundance before further use in statistical analysis using linear regression. We found no association between

growth and abundance. Biological data were regressed against NAOI values to assess the pervasiveness and significance of large-scale climate processes as influences on estuarine biota. Estimated regression model residuals were tested for statistical adequacy following standard practices including tests for normal, independent and homoscedastic residuals, all applied at the  $\alpha = 0.05$  level of significance. Adjusted significance levels for each regression were computed using the Bonferroni inequality to test the joint significance of all NAOI regressions<sup>7</sup> under the assumption that the joint probability of all results holding simultaneously was at least 0.90 ( $\alpha = 0.10$ ), and where  $\alpha$  was chosen to minimize corresponding type II error. Partial correlation coefficients for abundance and NAOI data that controlled for temporal trend (year), and growth and NAOI data that controlled for species abundance, were computed to verify regression results. We tested coefficients for significance using a two-tailed Student's *t*-test.

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