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Plankton effect on cod recruitment in the North Sea

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The Atlantic cod (*Gadus morhua* L.) has been overexploited in the North Sea since the late 1960s and great concern has been expressed about the decline in cod biomass and recruitment[1]. Here we show that, in addition to the effects of overfishing[1], fluctuations in plankton have resulted in long-term changes in cod recruitment in the North Sea (bottom-up control). Survival of larval cod is shown to depend on three key biological parameters of their prey: the mean size of prey, seasonal timing and abundance. We suggest a mechanism, involving the match/mismatch hypothesis[2], by which variability in temperature affects larval cod survival and conclude that rising temperature since the mid-1980s has modified the plankton ecosystem in a way that reduces the survival of young cod.

Fish stock biomass fluctuates in space and time, but the causes and mechanisms responsible for the observed variability remain poorly identified[3]. A number of studies have reported that temperature influences cod recruitment, although the relationships found were often weak for the North Sea[4]. Food quantity and quality are also essential because they influence the growth of fish larvae[2,5] and attempts have been made to establish relationships between changes in plankton (that is, availability of prey) and cod[6]. However, such studies, including the ICES/GLOBEC Cod and Climate Change programme[7], often focused on a limited number of biological parameters and no credible evidence has emerged[4,8].

Here we have simultaneously used six key biological parameters for the diet and growth of cod larvae and juveniles in the North Sea[5,9]. We considered the total calanoid copepod biomass as a quantitative indicator of food for larval cod, the mean size of calanoid copepods as a qualitative indicator of food, and the abundance (that is, mean number of individuals per sample) of the two dominant congeneric species, *Calanus finmarchicus* and *C. helgolandicus*, of the genus *Pseudocalanus* and of the taxonomic group euphausiids. These indicators were derived using data (46,777 samples) collected by the Continuous Plankton Recorder (CPR) survey[10]. We first examined long-term monthly changes (period 1958–1999) in the plankton ecosystem of the North Sea (including the Skagerrak), applying a standardized Principal Component Analysis (PCA, table years–months × indicators). The first principal component (Fig. 1, 33.71% of the total variability) revealed a clear distinction between the periods 1963–1983 and both of the periods 1984–1999 and 1958–1962. The period 1963–1983 was characterized by high abundance of prey for larval cod (positive anomalies in the biomass of calanoid copepods, in the abundance of *C. finmarchicus*, euphausiids and *Pseudocalanus* spp.) and a high mean size of calanoid copepods. In twelve of the 21 years from 1963 to 1983 cod recruitment (one-year-olds) in the North Sea was high, in parallel with positive anomalies in the plankton ecosystem (Fig. 1). Estimated recruitment during this period was
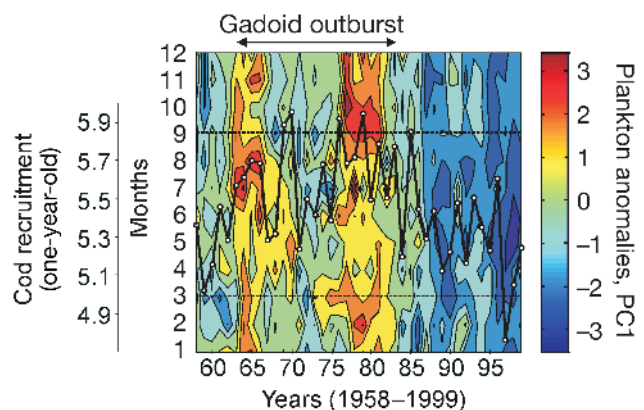

Figure 1 Long-term monthly changes (1958–1999) in the plankton index (as the first principal component, 33.78% of the total variability), resulting from analysis of the table years–months × biological indicators. The main variables related to this first principal component were, in order of importance, mean abundance (as mean number of individuals per CPR sample) of *C. finmarchicus* (normalized first eigenvector $C_m = 0.84$), euphausiids ($C_m = 0.72$), mean size of calanoid copepod ($C_m = 0.72$), *C. helgolandicus* ($C_m = -0.41$), calanoid copepod biomass ($C_m = 0.34$) and the genus *Pseudo-calanus* spp. ($C_m = 0.07$). A negative anomaly in the first principal component indicates a low value for all biological parameters with the exception of *C. helgolandicus* (opposite pattern) and *Pseudocalanus* spp. (no relationship). Cod recruitment (one-year-olds; in decimal logarithm) in the North Sea (curve in black) is superimposed with a lag of one year. The period of the 'gadoid outburst'[11] is indicated. Horizontal dashed lines indicate the period (March–September) of larval cod occurrence in the North Sea.

higher than at any time since 1921 (ref. 3) and the resultant high biomass of cod has been called the 'gadoid outburst'[11]. Cod recruitment decreased from the mid-1980s, coincident with unfavourable changes in the plankton ecosystem, compared to the earlier period 1963–1983.

To investigate further the relationships between plankton and cod recruitment, we performed a standardized PCA on the six plankton indicators for each month from March to September for the period 1958–1999 (42 table yr × 7 months–6 indicators). The 7-month period corresponded to the main period of larval/juvenile cod occurrence in the North Sea[2], a time when they experience high mortality[12], and the period of maximum changes in plankton (see Fig. 1). Long-term changes in cod recruitment (one-year-olds) significantly covaried positively with changes in plankton (as represented by the first principal component: PC1; 27.87% of the total variability) one year earlier (Fig. 2a, b). When the long-term variability was removed, the relationship between both variables was still highly significant (Fig. 2c). Because cod recruitment depends on the reproductive output of the spawning fish, we fitted a Ricker-type[13] stock-recruitment relationship for the years 1946–1999 and took the residuals from that relationship as an index of the survival in each year. This index of larval cod survival was also significantly positively correlated with the plankton index. The correlations indicate that changes in plankton affect survival of cod larvae/juveniles, resulting in bottom-up control. Our results explain the increase in recruitment and therefore cod biomass during the 'gadoid outburst' as a consequence of a plankton ecosystem that was highly favourable for the survival of larval/juvenile cod. This increase occurred despite the increase in fishing mortality during this period[3,14].

The match/mismatch hypothesis relates survival to the match between the time of larval occurrence and that of the production of their food[2]. The critical period for this match probably extends through the late-larval/early-juvenile stages and the prey must be of a suitable size[15–17]. Our results are consistent with this hypothesis and with a recent study that relates survival of larval haddock to the timing of the phytoplankton bloom[18]. For copepods, our results suggest that the link found with cod is primarily due to qualitative changes. Examination of variables contributing to the first principal component of plankton (see Fig. 2) showed that the relationship between PC1 and cod was mainly due to changes in the mean size of calanoid copepods (as indicated by the normalized eigenvectors, the mean contribution of this variable to the first principal component for the 7-month period was on average $C_{7m} = 46.24\%$). The mean size of calanoid copepods decreased by a factor of two after the beginning of the 1980s (Fig. 3a). The ratio between length of prey and cod, which is thought to remain constant throughout the larval and early juvenile stages (about 0.05 according to Munk's model[5]), was calculated for cod from 15 to 45 mm in length and for adult calanoid copepods in July. We found a mismatch between the size of prey and cod for fish larger than 30 mm after the mid-1980s (ratio less than 0.03 according to Munk's model[5], Fig. 3b). The diminution in the mean size of calanoid copepods is a probable consequence of major changes in the community structure of calanoid copepods recently detected in the northeast Atlantic and attributed to increasing temperature[19,20].

Changes in the abundance of *C. finmarchicus* ($C_{7m} = 44.89\%$) and *C. helgolandicus* ($C_{7m} = 23.04\%$) also contributed to PC1. *Calanus* (from eggs to adults) is an important prey for cod larvae/juveniles until July–August[5,9]. The progressive substitution of *C. finmarchicus* (Fig. 3c) by *C. helgolandicus* (Fig. 3d) has delayed the timing of occurrence of *Calanus* prey from spring to late summer at a time when larval/juvenile cod feed more on euphausiids and other fish larvae[9]. Although the total biomass of copepods ($C_{7m} = 3.61\%$) and the abundance of the genus *Pseudocalanus* ($C_{7m} = 0\%$) did not contribute to PC1, examination of their long-term monthly changes also shows a decrease after the beginning of the 1980s (Fig. 3e). A long-term decrease in euphausiids (Fig. 3f)
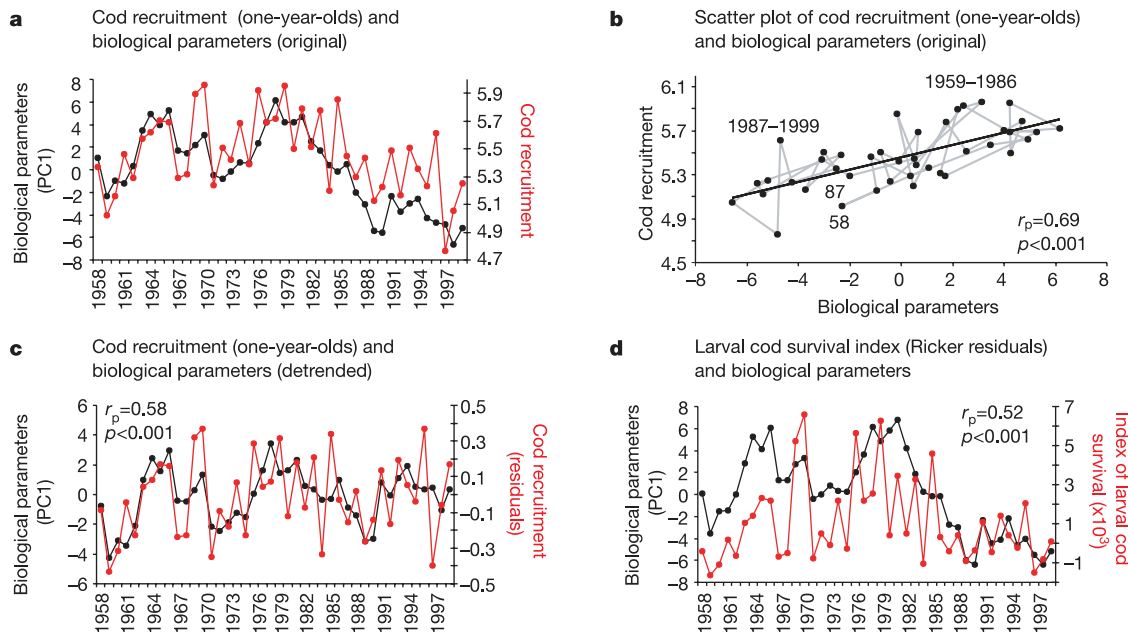

Figure 2 Relationships between plankton fluctuations and cod recruitment (one-year-olds) at lag one. **a**, Long-term changes (1958–1999) in the plankton index (as the first principal component, in black, explaining 27.87% of the total variability), resulting from analysis of the table years × months–indicators and long-term changes (1959–2000) in cod recruitment (in red, in decimal logarithm). **b**, Scatter plot of cod recruitment (at lag one) versus the plankton index. Key years and periods are indicated. **c**, Detrended plankton index (in black) and cod recruitment (in red, in decimal logarithm). **d**, Long-term changes in both the larval cod survival and plankton indices. The coefficient of linear correlation (r_p) and its associated probability (p) are indicated.

was significantly related to PC1 ($C_{7m} = 31.36\%$). Euphausiids also constitute an important part of the diet of cod larvae and juveniles[9]. In particular, euphausiids have a high-energy content and constitute an important source of vitamin A for fish such as cod, which cannot synthesize this vitamin[21]. Thus, all biological parameters, important for the diet and growth of larval/juvenile cod, contribute to explaining the long-term changes in cod recruitment. The major changes during the mid-1980s corroborate the hypothesis of a regime shift in the North Sea[22]. This switch radically changed the plankton environment of larval/juvenile cod. Since then, it has been unfavourable for the survival of young cod.

Plankton fluctuations (as PC1) are significantly correlated to sea surface temperature changes in the North Sea (original data: $r = -0.63$, $p < 0.001$; detrended data: $r = -0.58$, $p < 0.001$).

Temperature covaried less with cod recruitment (original data: $r = -0.56$, $p < 0.001$; detrended data: $r = -0.50$, $p < 0.001$). Increasing temperature may have had a doubly negative impact on cod survival in the North Sea. First, temperature increases cod metabolism and energetic cost[23]: thus, when food is limited, the optimal temperature for growth of cod decreases[24]. Second, increasing temperature reduces the number of prey available for larval/juvenile cod. The resultant diminution in growth may reduce survival (the hypotheses of size-specific survival[25] or growth-dependent mortality[26]) and lead to poor recruitment. Our results, therefore, provide evidence that unfavourable changes in the plankton ecosystem have exacerbated the impact of overfishing[1] in reducing recruitment of North Sea cod since the mid-1980s. Changes in the plankton ecosystem are also the probable cause of
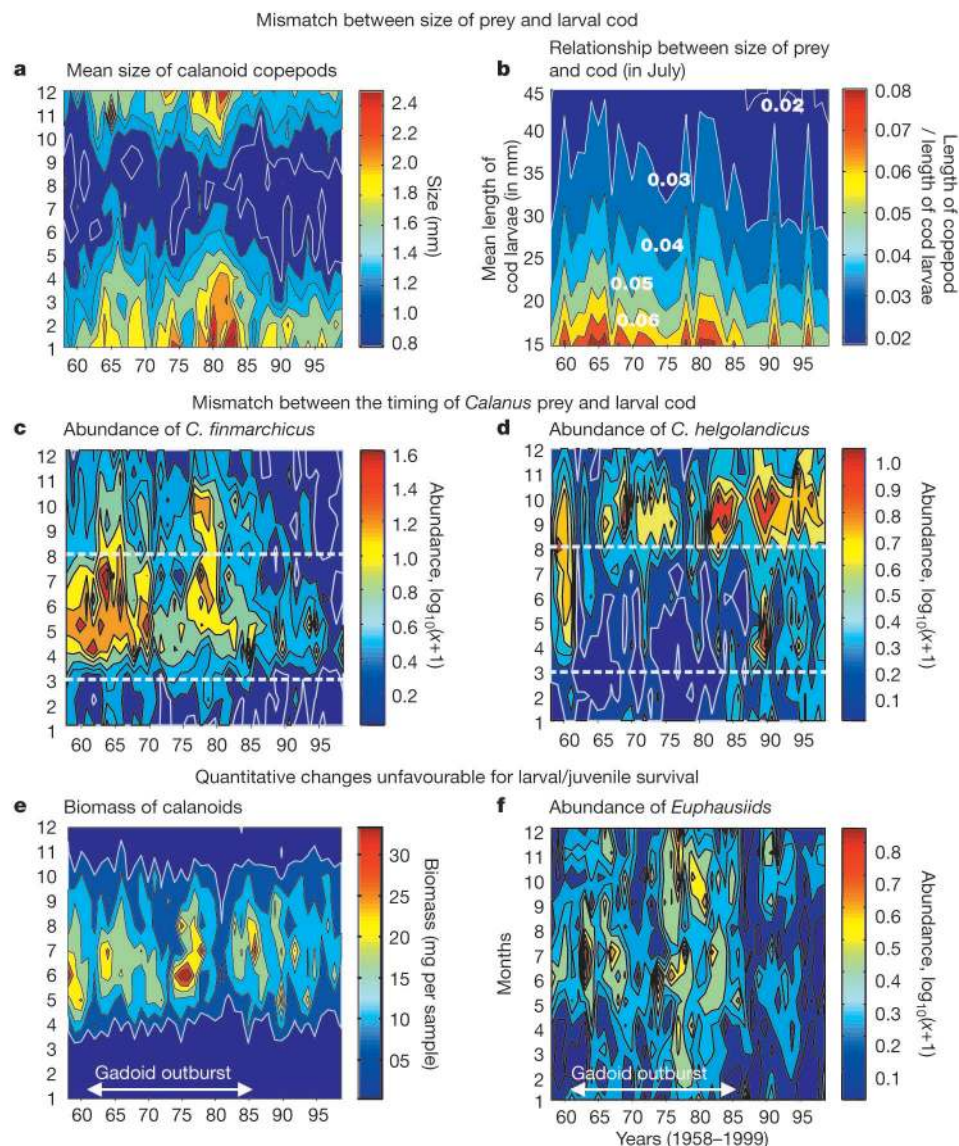

Figure 3 Plankton changes (1958–1999) and their consequences for larval/juvenile cod survival. **a**, Long-term monthly changes in the mean size of calanoid copepods (minimum size of female). **b**, Long-term changes in the ratio size of calanoid copepod:length of cod larvae. Larval cod (from 15 to 45 mm long) feed on adult *C. finmarchicus* in July[9] and according to Munk's model[5], the ratio should be close to 0.05, becoming highly unfavourable below 0.03 and above 0.08. **c**, Long-term monthly changes in the abundance (as mean number of individuals per CPR sample) of *C. finmarchicus*, showing a decrease after the mid-1980s. **d**, Long-term monthly changes in the abundance (as mean number of individuals per CPR sample) of *C. helgolandicus*. The period in which cod feeds on *Calanus* is indicated by the dashed grey horizontal lines. **e**, Long-term monthly changes in the total biomass of calanoid copepods. **f**, Long-term monthly changes in the abundance (as mean number of individuals per CPR sample) of euphausiids. The period of the 'gadoid outburst' is indicated.

the increased recruitment during the period 1963–1983, which resulted in the 'gadoid outburst'. ☐

Methods

Plankton data

Biological data used in this study were collected by the CPR survey. This is an upper-layer plankton monitoring programme that has been operated on a routine monthly basis in the North Atlantic and North Sea since 1946[10]. Sampling is carried out by a high-speed plankton recorder (about 20 km h^{-1}) that is towed behind merchant ships at monthly intervals on regular routes at a standard depth of approximately 6.5 m. One CPR sample corresponds to about 3 m^3 of sea water filtered[10].

Selection of plankton indicators

In the North Sea, cod spawn in March and eggs start to hatch a few weeks later[2]. From March to September, feeding of cod larvae/juveniles gradually progresses from mainly copepod eggs (April) to copepod and euphausiid nauplii (May), then a copepod-dominated diet until July and finally a progressive replacement of the copepod-based diet by euphausiids and other fish larvae from August[9]. Among copepods, *C. finmarchicus* is by far the dominant species eaten by larval cod, followed by *Pseudocalanus* spp[5]. Therefore, the abundance (number of individuals per CPR sample) of *Calanus finmarchicus*, its congeneric species *C. helgolandicus, Pseudocalanus* spp. and euphausiids was assessed in the North Sea (including the Skaggerak). The size composition of prey is also a crucial parameter[5]. The mean size of calanoid copepod (minimum size of female) per CPR sample was also calculated. We chose the minimum size of female because adult females, or copepodite stage V, represent the majority of copepods caught in the samples[27]. Total calanoid copepod biomass per CPR sample was used as a quantitative indicator of food for larval/juvenile cod and was estimated from the size of each calanoid copepod (a total of 108 calanoid species), their abundance and allometric relationships[28].

Cod data

Cod data on recruitment (one-year-olds) were derived from virtual population analysis[29]. Data for 1963–2000 are from ref. 14 and for 1958–1962 from ref. 3. These two sources overlap for the 31-yr period 1963–1993. The recruitment values taken from ref. 3 were adjusted using a linear regression analysis for the 31-yr period of overlap to produce a time series of recruitment from 1958.

Correlation analysis

The Pearson linear correlation was calculated between cod recruitment (one-year-olds) at lag one and the plankton index on original and detrended time series to take into account temporal autocorrelation. Series were detrended by the use of Singular Spectrum Analysis[30]. The method uses a principal component analysis performed on an autocovariance matrix (also called a Toeplitz matrix) to decompose a time series into a succession of signals of decreasing variance. The procedure is fully described in ref.20. The long-term trend of each time series was first assessed by using both the eigenvectors and the principal components representing the low-frequency variability. Then, the detrended time series were calculated by subtracting the original time series by their respective long-term trend.

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Visual control of action but not perception requires analytical processing of object shape

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The visual perception of object shape depends on 'holistic'[1–4] processing in which a given dimension cannot be perceptually isolated from the other dimensions of the object. The visual control of action (such as grasping an object), however, which is mediated by cortical areas that are largely independent of those mediating conscious perception[5–8], must take into account only the most action-relevant dimension of an object without being misled by other non-relevant object features. Here we report the results of two experiments showing that vision for perception and vision for action deal with objects in a fundamentally different manner. We tested participants' ability to make perceptual judgements of the width of different rectangular objects or to grasp them across their width, while in both cases ignoring length[9,10]. Participants could not ignore length when making perceptual judgements of width but they could completely ignore length when grasping the same objects. These results suggest that in situations in which the elementary dimensions of an object's