

## Impacts of fisheries on plankton community structure

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There has been much debate on the extent to which resource availability (bottom-up) versus predation pressure from fish (top-down) modulates the dynamics of plankton in marine systems. Physico/chemical bottom-up forcing has been considered to be the main mechanism structuring marine ecosystems, although some field observations and empirical correlations support top-down modulation. Models have indicated possible feedback loops to the plankton and other studies have interpreted a grazing impact from long-term changes in fish stocks. In freshwater systems, evidence for top-down forcing by fish and trophic cascading is well documented. First, evidence for equivalent top-down effects in the marine environment is presented, with an overview of relevant publications. In the second part, time series, averaged for the North Sea (when possible from 1948 to 1997), of fish catch, recruitment, and spawning stock biomass are related to the abundance of species or larger groupings of zooplankton and phytoplankton from the Continuous Plankton Recorder survey and selected environmental parameters. Preliminary analysis suggests that there is strong interaction between different fish species and the plankton and that the fishery, through top-down control, may at times be an important contributor to changes in the North Sea ecosystem.

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### Introduction

The extent to which shifts in ecosystem structure may be caused by resource limitation – “bottom-up” factors – against predation – “top-down” mediation – has been a subject of intense debate in ecology over the last few decades. In the bottom-up hypothesis, each trophic level is resource limited (e.g., nutrients, light, food); in the top-down hypothesis, the top predators are food limited and lower trophic levels may be resource or predation controlled. In the marine environment, top-down control has been favoured as the dominant mediatrix (Steele, 1998) in view of the lack of convincing evidence, on an ecosystem scale, for alternative forcing. The considerable literature on eutrophication as well as the precision with which phytoplankton biomass and production can be modelled globally using new data from satellites and a limited set of environmental variables (Longhurst, 1998) tends to support bottom-up mediation. Against this background, views on the issue have

tended to become polarized and have not fully recognized that both forcing systems are likely to operate in varying proportions (e.g., Roff *et al.*, 1988) in different time/space scenarios.

As an extension of the top-down theory, limnologists have developed the trophic cascade hypothesis (Carpenter and Kitchell, 1993). In this hypothesis, predatory effects on numbers/biomass and composition of fish and plankton may cascade down trophic levels to govern levels and composition of phytoplankton and nutrients at the base. By using both ecosystem manipulations and cross-sectional correlations (Carpenter *et al.*, 1991, 1996), about 50% of the variance of primary production could be explained by cascades. Part of the nutrient pool used by phytoplankton is derived from recycling by excretion from the zooplankton. The rates of excretion are size dependent, with larger zooplankton excreting less per unit mass than smaller individuals. Rates of primary production may thus depend on size-selective predation higher up the food web. The

cascading theory has been widely applied, with varying degrees of success, as a management tool in the bio-manipulation of lakes to reduce phytoplankton abundance and improve water clarity (Hansson *et al.*, 1998; Persson, 1999).

We first review evidence for top-down control and trophic cascades in marine pelagic ecosystems. The second part includes a comparative analysis of long-term (49 years when possible) time series of plankton, fishery, and environmental data from the North Sea to identify patterns of change at the population level that may be attributable to top-down mediation.

### Top-down control in marine pelagic systems

Verity and Smetacek (1996) drew attention to the traditional focus that has been placed on bottom-up structuring of marine planktonic ecosystems and reviewed evidence to support the complementary view that top-down trophic effects may be equally important. Predatory impacts are expected because many zooplankton groups are morphologically adapted to predatory avoidance. The authors examined a range of reasons why top-down control is not more evident in the marine pelagial. They considered that key taxa with distinct life histories, morphologies, and behaviour that may not easily fit into traditional trophic categories, are likely to play an important role and that physical processes at a range of scales may dampen evidence of top-down effects. Changes in community structure and interactions within trophic levels, rather than strict trophic divisions, may also be important in modulating top-down effects (see McCann *et al.*, 1998). With two exceptions, all observations of top-down effects recorded by Verity and Smetacek (1996) were from small enclosures or were interpretations of patterns seen at single sites, and few provided evidence to support any cascade across three or more trophic levels. Three-quarters of the cascades noted were initiated by gelatinous zooplankton predators. The most convincing field example was a ctenophore-zooplankton-phytoplankton cascade in Narragansett Bay, USA (Deason and Smayda, 1982). Only one of the examples started with fish and that one was based on an experimental enclosure using sticklebacks. They concluded that "adult fish in the oceans are seldom likely to control the abundance of their prey". Steele (1998) affirmed that he knew of no case where the large changes seen in marine fish stocks had affected their food supplies.

In contrast, trophodynamic calculations by Rudstam *et al.* (1994) for the Baltic ecosystem suggest that top-down control on the zooplankton is intense and yet no correlations were found with measured changes in fish abundance. However, their estimates of zooplanktivory in the Baltic only varied by a factor of two compared with the order-of-magnitude changes that have been

observed in lakes. They concluded that with such low predation rates other factors such as changes in inter-annual primary productivity or nutrient inputs could override any effects from the fish.

Perhaps the clearest example of top-down control and possible trophic cascading from fish has been described from the Barents Sea (Skjoldal and Rey, 1989; Dalpadado and Skjoldal, 1996). An alternation between periods when herring (*Clupea harengus*) are abundant and stocks of capelin (*Mallotus villosus*) low and vice versa has been observed from the mid-1960s to the present. Herring stocks declined dramatically at the end of the 1960s and a fishery on capelin started. As the herring stocks recovered they fed on capelin larvae, leading to poor capelin recruitment which, combined with heavy fishing and possible environmental changes, led to a stock collapse. When capelin stocks were low, larger zooplankton groups such as euphausiids and hyperiids increased to up to ten times their former abundance owing to a release of predation pressure. Cod, living in the colder waters of the system closer to the bottom and further to the north, were also affected. Capelin are their preferred diet; in the mid-1980s when capelin stocks first collapsed and herring stocks were low, the cod switched to euphausiids and hyperiids. This inferior diet led to a drastic reduction in cod growth. A trophic cascade may also form part of the above changes as an alternation between *Phaeocystis* and diatoms, which is reflected in changing levels of nitrogen and silica and high/low periods of diatom sedimentation.

A further example of a possible cascade was described by Shiimoto *et al.* (1997) from the North Pacific. From 1989 onwards, chlorophyll *a* concentrations and the abundance of pink salmon (*Oncorhynchus gorbuscha*) showed similar year-to-year patterns (mean summer values) which were inverse to a measure of macrozooplankton biomass.

In a study of seasonal variability of phytoplankton and copepods from the Continuous Plankton Recorder (CPR) survey, Colebrook (1979) demonstrated that the rapid spring increase of phytoplankton over most of the northern North Atlantic is underexploited by grazers. The factors controlling the seasonal phytoplankton cycle are primarily physical (Longhurst, 1998), but Colebrook's analysis showed that a strong grazing impact from copepods occurs only in the summer and autumn months. This view is supported by the observation by Longhurst and Williams (1992) at Weather Station India that algal growth becomes unchecked once *Calanus finmarchicus* initiates its diapausal vertical migration.

In a subsequent paper, Colebrook (1982) drew attention to the unexpected similarity seen in the long-wavelength variability in both zooplankton and phytoplankton time series. If zooplankton abundance

was determined by grazing or if both phytoplankton and zooplankton numbers were forced by common environmental factors, zooplankton should show greater persistence at high wavelengths in spectral analyses. This was not the case, and he concluded that the abundance of phytoplankton is influenced by the zooplankton through some feedback mechanism, which he suggested (Colebrook, 1986) was probably nutrient recycling. In associated work, Colebrook (1978) estimated that approximately half the variance of interannual changes in North Sea plankton could be attributed to density-independent, environmental forcing by regional climate. Part of the remaining variance may be attributable to predatory effects from fish, as suggested by Reid (1984), who noted the similarity between the trends in CPR plankton and the stocks and yields of North Sea fish. A modelling study by Steele and Frost (1977) examined trophic interactions in the North Sea. They suggested that long-term changes in the plankton might be a function of predation by fish and that changes in predation pattern could be transferred both up and down the food web.

## North Sea plankton-fish relationships

### Materials and methods

Annual time series of abundance of plankton and fish as well as of hydroclimatic indices were compiled for as long a period as possible between 1948 and 1997. Plankton data were derived from the CPR survey (Warner and Hays, 1994; Table 1) and averaged for the North Sea (ICES Area IV). A total of 45 463 CPR samples, on average, equally spread throughout each month of the year, were used. Zooplankton biomass was calculated by converting counts for the taxa listed to dry weight with measurements (unpublished) from a seasonal survey of zooplankton off Plymouth. Data on total catch, recruitment, and spawning stock biomass for a variety of fish species (Table 2; the unit stocks extend sometimes beyond the borders of the North Sea proper; Latin names are also given) were derived from the ICES stock-assessment database. The environmental variables included: the North Atlantic Oscillation index (NAO; Hurrell, 1995), Gulf Stream Index (GSI; Taylor, 1995, annual sea surface salinity (SSS), and sea surface temperature (SST; winter, spring, summer, autumn, and annual).

Correlation analyses were completed on these data ( $67 \times 67$  matrix) and repeated with lags of plus and minus one to four years. It was recognized that the data are auto-correlated as they contain persistence from year to year. Some of the variables in the matrix are not likely to be functionally related and therefore may be redundant, although absence of a correlation is not evidence for a lack of ecological interaction. An unknown

Table 1. List of plankton parameters derived from the CPR survey that were used in correlation analyses (\* indicates species that were included in the estimate of zooplankton biomass).

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Phytoplankton colour <sup>2</sup>
Diatoms <sup>3</sup>
Ceratia <sup>3</sup>
<i>Podon</i> spp.
<i>Evadne</i> spp.
<i>Calanus finmarchicus</i> *
<i>Calanus helgolandicus</i> *
<i>Calanus</i> (V, VI)
<i>Para-Pseudocalanus</i> *
<i>Temora longicornis</i> *
<i>Acartia</i> spp.*
<i>Centropages typicus</i> *
<i>Oithona</i> spp.*
Total copepods
Copepod nauplii
Gammarids
Hyperiid*
Euphausiid*
Decapods*
Chaetognatha eyecount*
<i>Clione</i> spp.
<i>Limacina retroversa</i> *
Echinoderm larvae*
Larvacea*
<i>Metridia lucens</i> *
Fish larvae

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<sup>2</sup>See Reid *et al.* (1998).

<sup>3</sup>See Reid (1975).

Table 2. Unit fish stocks for which time series of catches and, (marked with asterix) recruitment and spawning stock biomass (derived from virtual population analysis) were included in correlation analyses.

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Sub-area IV dab <i>Limanda limanda</i>
Sub-area IV plaice* <i>Pleuronectes platessa</i>
Sub-area IV sole* <i>Solea solea</i>
Sub-area IV, III saithe* <i>Pollachius virens</i>
Sub-area IV, III, VIId (east) cod* <i>Gadus morhua</i>
Sub-area IV, III haddock* <i>Melanogrammus aeglefinus</i>
Sub-area IV, IIIId whiting* <i>Merlangius merlangius</i>
Sub-area IV Norway pout* <i>Trisopterus esmarkii</i>
Sub-area IV, IIIId sandeel* <i>Ammodytes</i> spp.
Sub-area IV sprat <i>Sprattus sprattus</i>
Sub-area IV, III, VIId herring* <i>Clupea harengus</i>
Sub-area IV mackerel <i>Scomber scombrus</i>
Sub-area IV horse mackerel <i>Trachurus trachurus</i>

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number of the correlations are likely to be fortuitous. Only correlations that were significant at the 1% level were considered and were used as an initial exploratory tool to establish possible ecological relationships and in particular to look at lagged effects, which would not have been possible if the data had been treated to remove auto-correlation.

## Results

Here we examine relationships between CPR and fisheries data for the North Sea, comparing 23 zooplankton taxa, 3 phytoplankton categories, and 13 fish species over a long time period. More than 130 correlations at the 1% level of significance were found between plankton entities and fish entities at zero lag. The pattern of correlations found between plankton and fish catch and/or SSB distinguished the gadoids as a group with mostly negative relationships to small copepods and other taxa, phytoplankton colour, and GSI; in contrast *C. finmarchicus* and euphausiids were positively related. Herring and sole were distinguished as a separate group, especially in the plankton-SSB correlations with mostly positive correlations. Sprat and mackerel also showed similarities in their patterns of mostly negative correlations, but with a different set of species than for the gadoids. Only a few correlations (e.g., between whiting and GSI) were found between fish recruitment and other variables at zero lag. Whiting and sandeel catch were negatively and positively, respectively, correlated with the NAO index. There were few other fish/environment correlations. Thirty-one correlations were found between the plankton and environmental data, ten of which were with *C. helgolandicus* and *Centropages typicus*. Both species were correlated with the NAO and different seasonal temperatures. Spring and winter temperatures were positively correlated with the NAO (Reid and Planque, 1999). Eight zooplankton taxa were correlated with salinity.

Lagging the data plus or minus by a further year progressively reduced the number of significant correlations, but in many cases increased the significance or produced new relationships. Here, we primarily consider relationships with the plankton at zero or negative (behind the other entities) lag.

Because of space constraints, graphs are only presented for a limited number of time series. The patterns of change seen in the zooplankton range from a downward trend in *Oithona* (Fig. 1a) to an upward trend in *Acartia* (Fig. 1b) to an ellipsoidal curve in echinoderm larvae (Fig. 1c) to a stepwise increase to a new higher level in *Podon* (Fig. 1d). Zooplankton biomass (Fig. 1e) reflects the dominant downward trend seen in most species and declined by 30% over the period 1948 to 1997; a pronounced minimum occurred between 1978 and 1982. The downward trend was comparable to that seen in the first principal component for the Atlantic and North Sea (Reid and Planque, 1999); taxa with this pattern showed tendencies to be positively correlated with temperature (Fig. 1g), salinity (Fig. 1h) and the GSI. It is a pattern of change seen in many taxa, and the minimum was evident in graphs for 17 taxa. In contrast, euphausiids, *C. finmarchicus* (Fig. 1j), and total *Calanus* (Fig. 2b) showed patterns that tended to be negatively

correlated with the above group of species, showed increased levels of abundance at the time of the minimum, and were positively associated with the NAO (Fig. 2j) and winter temperature. *C. finmarchicus* and *C. helgolandicus* are strongly inversely related (Fig. 1j). Phytoplankton colour (Fig. 1f) showed an increasing trend and a pronounced stepwise increase from the mid-1980s onwards (Reid et al., 1998). *Ceratium* spp. showed peaks in abundance centred on 1960 and 1988, whereas diatoms generally decreased over the period and were correlated with total *Calanus* (Fig. 1i). Higher temperature, a sequence of higher salinity years, and increased phytoplankton colour after 1988 coincided with the highest values of the NAO index seen in the 20th century (Reid and Planque, 1999). The GSI reached its maximum value of the time series in 1995.

Some of the changes that have taken place in fish are summarized in Fig. 2. Herring catches, together with mackerel catches, peaked in 1967, declined to a minimum between 1977 and 1982, and returned to a new higher level from 1985 with another reduction in the last two years of the time series. Herring catches (best with a one-year lag) are correlated with total copepods (Fig. 2d). The pronounced reduction in the catch from 1977 to 1982 was caused by the introduction of a ban on herring fishing.

On the basis of catch statistics, small industrial species (sprat, sandeel, and Norway pout) appear to have replaced herring and mackerel as the dominant herbivores from 1975 onwards. Sprat were inversely correlated with *Limacina* spp. (Fig. 2a) and chaetognaths. Gadoid catches increased to a peak in 1967 and 1968 since when they have declined. *C. finmarchicus* showed a minimum at the time of the peak gadoid catches (Fig. 2c). Horse mackerel catches showed a progressive increase throughout the time series and were inversely correlated with total copepods (Fig. 2b).

The time series for recruitment and SSB are much shorter than the catch statistics, of variable length, and in the case of the mackerel, incomplete after 1984. Spawning stock biomass for many species showed a downward trend with a stepwise increase to a higher level in 1977 followed by a return to higher levels. The spawning stocks of sandeels and Norway pout have shown considerable variability around a mean of approximately 5.9 and  $5.3 \times 10^6$  t respectively. Whiting SSB was correlated with euphausiids (Fig. 2e). The graphs for recruitment showed great interannual variability, with an overall declining trend for a number of stocks (e.g., Norway pout, haddock, saithe, whiting) and exceptionally low recruitment in 1997 for these species. Sole recruitment was correlated with spring temperature (Fig. 2f) and saithe recruitment with zooplankton biomass (Fig. 2h). Cod dropped to a new low level from 1987 and was inversely correlated with *C. helgolandicus*

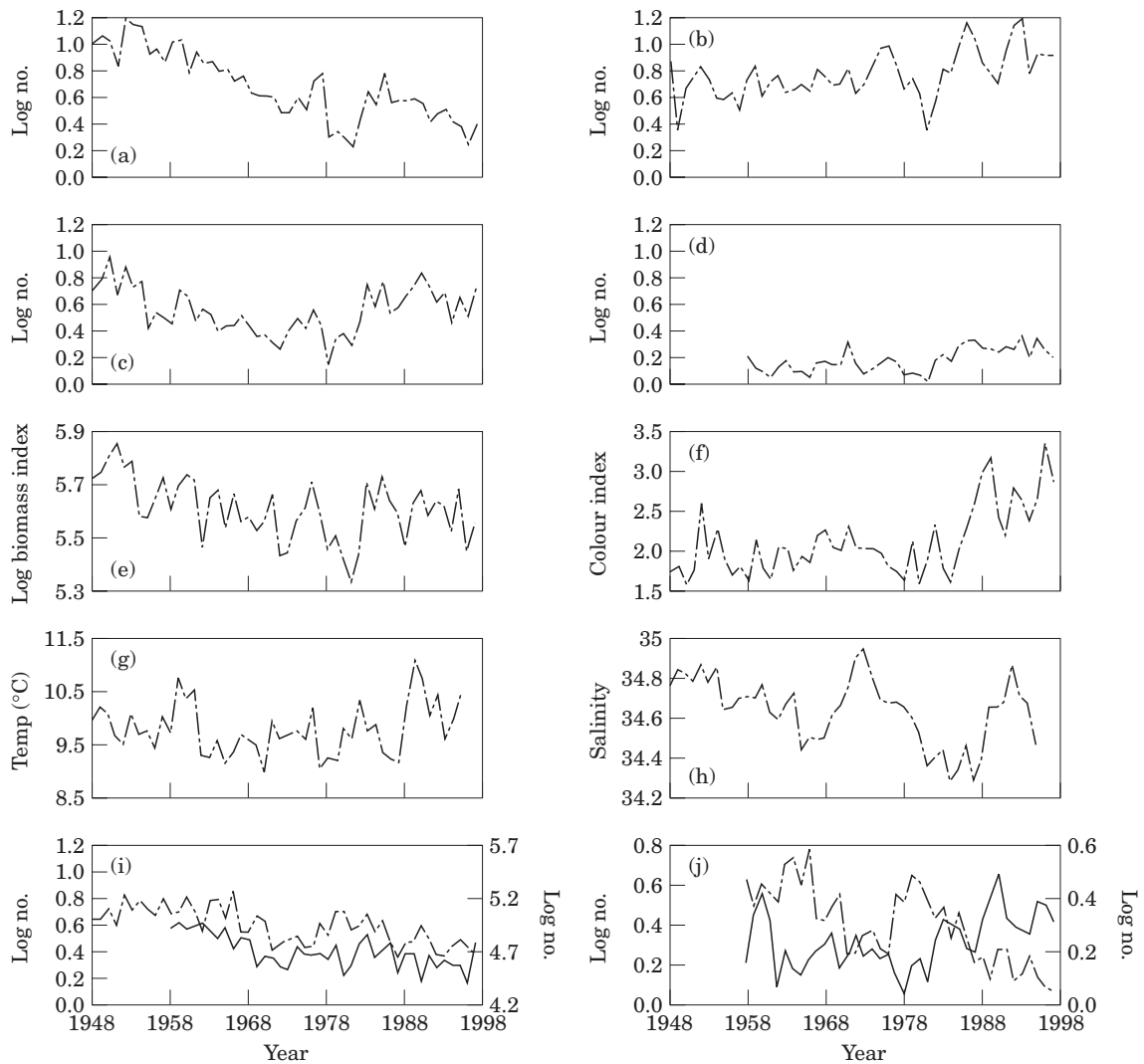


Figure 1. Selected time series data averaged for the North Sea (all logs are to the base 10): a: *Oithona* spp.; b: *Acartia* spp.; c: echinoderm larvae; d: *Podon* spp.; e: zooplankton biomass; f: phytoplankton colour; g: annual sea surface temperature; h: annual sea surface salinity; i: total *Calanus* spp. (dotted; left scale), diatoms (solid; right scale); j: *Calanus finmarchicus* (dotted; left scale), *Calanus helgolandicus* (solid line; right scale).

(Fig. 2g). After a minimum in the mid-1970s, herring recruitment improved to a new higher level from 1982 onwards and was correlated with total copepods (Fig. 2i).

The zooplankton time series can be divided into five periods of differing length within which individual years show broadly similar patterns of abundance and composition. Generalized levels of abundance for these periods are shown in Table 3 for fish, zooplankton predators, small and large herbivores, and phytoplankton colour. Diatoms and *Ceratium* spp. are not included as data were only available from 1958 onwards. In the first two periods, up to 1962, high abundance of herring

and zooplankton carnivores coincided with high numbers of zooplankton herbivores and with lower phytoplankton levels, suggesting no top-down control by herring, but a possible impact on the phytoplankton. From ~1963 to 1977, with possibly increased predation from mackerel (and gadoid larvae), the carnivorous and herbivorous zooplankton and phytoplankton declined. There is no suggestion of a size-selective effect on the herbivores, except possibly between 1971 and 1976 on *C. finmarchicus* when the gadoid catches were at a peak. The period 1978 to 1982 provides the strongest evidence for top-down control, with a major reduction in the majority of zooplankton taxa at a time when small

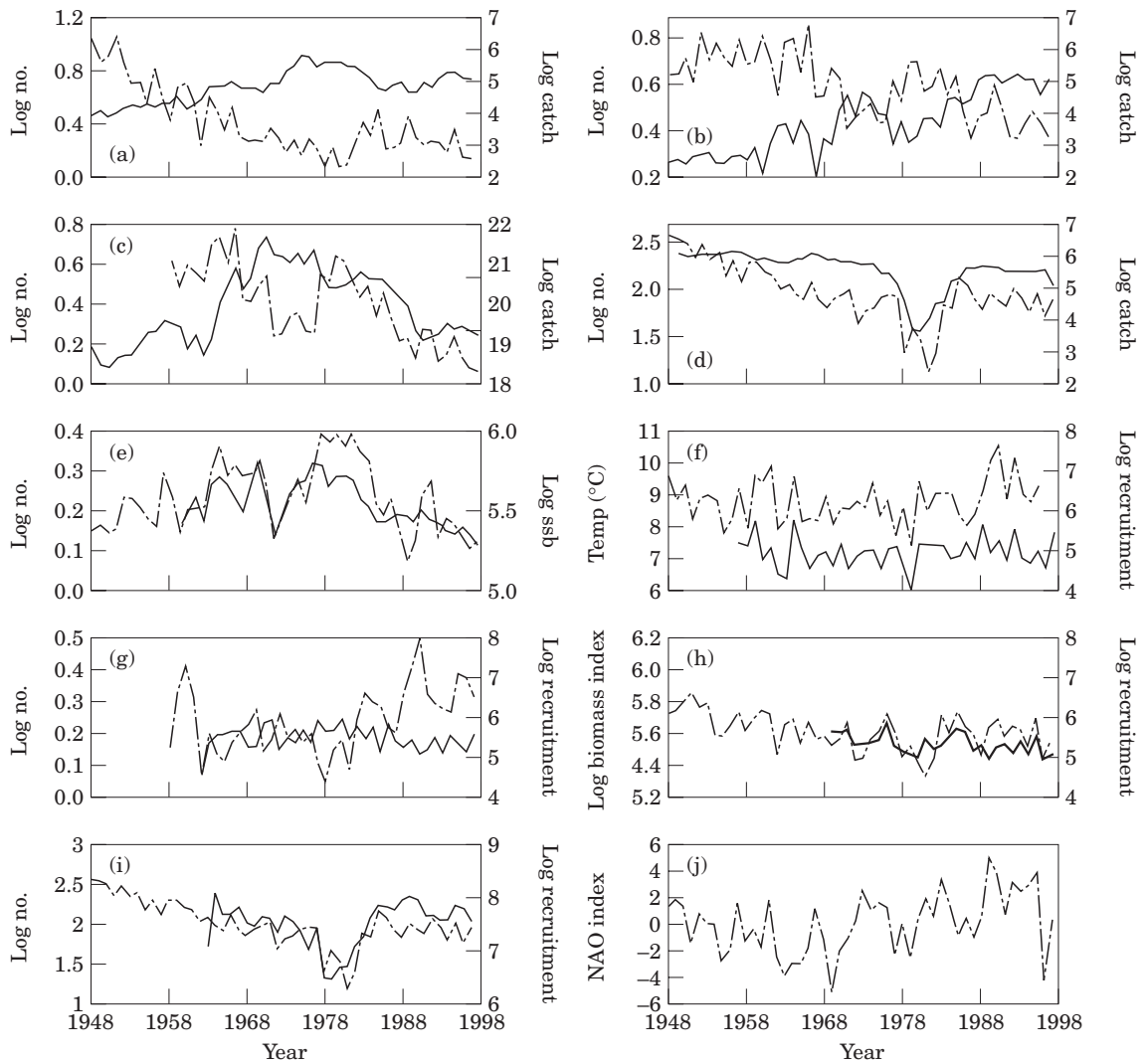


Figure 2. Selected time series data averaged for the North Sea (dotted lines – left scale, solid lines – right scale; all logs are to the base 10): a: *Limacina* spp. (dotted), sprat catch (solid); b: total *Calanus* (dotted), horse mackerel catch (solid); c: *Calanus finmarchicus* (dotted), gadoid catch (solid); d: total copepods (dotted), herring catch lagged one year forward (solid); e: euphausiids (dotted), whiting SSB (solid); f: spring sea surface temperature (dotted), sole recruitment (solid); g: *Calanus helgolandicus* (dotted), cod recruitment (solid); h: zooplankton biomass (dotted), saithe recruitment lagged two years forward (solid); i: total copepods (dotted), herring recruitment lagged three years forward (solid); j: NAO index (updated from Hurrell, 1995, by pers. comm.).

pelagic industrial species were at a maximum and herring and mackerel at a minimum. These small fish may preferentially eat smaller species of zooplankton, possibly explaining the increases in euphausiids and larger copepods seen at that time. The changes do not, however, appear to be reflected in a trophic cascade as phytoplankton colour, diatoms, and *Ceratium* spp. were generally at a low level. As herring and mackerel recovered from 1983 onwards, zooplankton other than large copepods also increased with phytoplankton, and horse mackerel showing especially high values from 1988 onwards.

## Discussion

There are few convincing examples of top-down modulation and trophic cascading at the population level in marine planktonic systems. Cascading across more than two trophic levels has rarely been demonstrated, and most of the reported examples were initiated by gelatinous zooplankton predators. The only clear example of top-down and size-selective predation by fish on zooplankton populations, with possible cascading effects, is described from the Barents Sea, a relatively simple Arctic ecosystem with reduced planktonic and

Table 3. Categorisation (high +++, medium ++, and low +) of fish catch (HER: herring; MAK: mackerel; SMP: small pelagic species; HMK: horse mackerel) and plankton abundance (CHA: Chaetognatha; OIK: *Oikopleura*; EUP: euphausiids; LIM: *Limacina*; SCO: small copepods; LCO: large copepods; COL: phytoplankton colour) during five periods between 1948 and 1997.

Period	HER	MAK	SMP	HMK	CHA	OIK	EUP	LIM	SCO	LCO	COL
1948–1953	+++	++	+	+	+++	+++	+	+++	+++	++	++
1954–1962	+++	++	++	++	+++	++	+	++	+++	+++	+
1963–1977	++	+++	+++	+++	++	+	++	++	++	++	+
1978–1982	+	+	+++	++	+	+	+++	+	+	++	+
1983–1997	++	++	++	+++	++	++	+	++	++	+	+++

fish biodiversity. Thus as ecosystem complexity increases, environmental factors may be more dominant and top-down effects less easy to distinguish.

Koslow (1983) investigated whether size-selective predation by fish and trophic cascading, as seen in freshwater lakes, was likely to occur in the North Sea. He included only one pelagic fish (herring) and four grouped zooplankton and two phytoplankton categories from CPR data in his calculations. The model predictions suggested that top-down control should be present. However, when this model output was compared with data on herring SSB (1950–1976) and CPR plankton (1948–1980), the correlations, in most cases, were opposite in sign to the field data. He concluded that North Sea zooplankton is food limited (rather than predation limited) and that this may have been a consequence of differences in scale between small lakes and the North Sea. He also suggested that it was unlikely that herring and mackerel were substantially replaced by other pelagic species. The evidence from the North Sea presented here suggests that top-down effects were only clearly evident (1978–1982) when the system was severely stressed by overexploitation of the key planktivore – the herring. Samples taken monthly as vertical profiles at a single site off Northumberland, England, UK, confirm the alternation between total copepods and euphausiids seen in CPR samples at this time (Roff *et al.*, 1988). These authors, using a completely different sampling system, provide a valuable confirmation of the representativeness of the CPR sampling system as a measure of monthly and long-term plankton variability in the North Sea. Although they attributed the decline in copepods to increased grazing pressure from euphausiids, the true story is likely also to involve size-selective predation by changes in the levels and composition of pelagic fish.

Carpenter *et al.* (1998) showed that the magnitude of cascading effects appears to increase in eutrophic lakes. There is evidence for increasing effects of eutrophication in the marine environment, and cascading effects may also be more evident in such polluted systems.

The unexpectedly large number of correlations observed between plankton and fishery statistics suggests close interaction between different components and similar forcing of long-term change. The results also indicate that CPR and other plankton data have potential as environmental input to improved models for fishery management. However, the relationships obtained are static ones and not based on rates (e.g., prey growth rates versus predator consumption rates). While many rate processes are still poorly known, there is considerable scope for use of CPR data in ecosystem models to increase understanding of processes governing top-down and cascading effects.

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