

# Food webs and fish production in the North Sea

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## Abstract

*Pelagic primary production (growth of microscopic phytoplankton cells) forms the basis of marine food webs and, hence, ultimately limits the magnitude of fish production in the ocean. It is, however, only a minute fraction of the primary production that ends up as harvestable fish biomass. The magnitude of this fraction depends on the structure and functioning of the marine food web, which is ultimately governed by physical factors, particularly hydrodynamics. This paper briefly reviews recent major developments in our understanding of marine pelagic food web structure. On the basis of this modern view, it is discussed why the North Sea, in terms of fisheries, is among the most productive regions of the world oceans.*

## Introduction

Marine food webs are almost entirely based on the growth production of microscopic phytoplankton cells and contributions from the production of benthic algae and other sources are insignificant. Therefore, the magnitude of fish production in the ocean is ultimately limited by the magnitude of pelagic primary production. It is, however, only a small fraction of the pelagic primary production that is eventually channelled up the food web to end as harvestable fish biomass. The magnitude of marine fish yield corresponds to only about 1% or less of the pelagic primary production (e.g. Steele 1974). This fraction is variable, however, and the magnitude of fish production is therefore governed both by variation in the proportion of the primary production that ends as fish as well as variation in the magnitude of primary production. Thus, fish production depends on marine food web structure and functioning.

In this paper I shall examine the factors that govern pelagic primary production and food web structure and, hence, the magnitude of fish production in the ocean. In the spirit of this symposium, I shall focus on the North Sea, and I shall attempt to make explanations accessible to a non-expert audience. This presentation is to a large extent based on several previous reviews (Kiørboe 1991, 1993, 1996, 1998).

## Marine food web structure

J. H. Steele (from Aberdeen) excellently summarized the classical description of the pelagic food chain in his seminal book on the structure of the North Sea ecosystem (Steele 1974). According to this description, almost all phytoplankton production is consumed by zooplankton, particularly copepods, a group of mm-sized crustaceans. About one third of the phytoplankton consumed by copepods is expelled as large (~ 0.1 mm) faecal pellets that sediment rapidly to the sea floor. The organic material contained in the faecal pellets fuels the biological processes on the sea floor, including the production of demersal (bottom-living) fish. Another third of the consumed phytoplankton is transformed to copepod biomass and provides food for plankton-eating fish, such as herring and mackerel. And the last third is metabolized by the copepods. The classical description leaves room for additional trophic levels, such as arrow-worms and jellyfish feeding on copepods, and must be characterized as a food web rather than a food chain.

Steele (1974) attempted to construct a budget for the fate of the organic material produced by the phytoplankton in the North Sea. He found that about 1% of the pelagic primary production ended up as fish biomass that could be harvested. Based on knowledge of transfer efficiencies and on the assumed structure of the food web described above, he could make the budget fit exactly (but barely). That is, there was just sufficient pelagic primary production to account for the fish catches. However, the classical description has turned out to be far too simple and our understanding of pelagic food web structure and functioning has undergone major changes during the last 2-3 decades – in ways that make Steele's budget invalid. In this section I first discuss some of the concepts developed and discoveries made since Steele's book and then describe the present understanding of pelagic food web structure.

*New vs. regenerated production:* Because phytoplankton cells utilize light to combine inorganic carbon and mineral nutrients into organic compounds, primary production takes place only in the upper, illuminated part of the ocean (the 20-100 m deep *euphotic zone*). Vertical temperature stratification of the water column during the productive season limits vertical mixing and, hence, renewal of mineral nutrients from below the euphotic zone. Therefore, nutrients become exhausted in the euphotic zone, often to concentrations below the analytical detection level. Mineral nutrients are, however, to a large extent recycled within the euphotic zone; that is, phytoplankton cells are consumed by herbivores (e.g. zooplankton) that degrade the organic compounds to inorganic carbon and nutrients. These recycled nutrients may be used again for further primary production in the euphotic zone. Primary production based on recycled nutrients is termed *recycled production* (Dugdale & Goering 1967). It does not lead to net build-up of biomass in the euphotic zone and, thus, does not lead to formation of harvestable biomass. In contrast, mixing events caused by wind, currents or cooling of surface waters may inject new nutrients from below the euphotic zone, where nutrient concentrations are typically high. Primary production based on new nutrients is termed *new production*. New production may lead to net build-up of plankton biomass in the euphotic zone and to harvestable biomass. The source of mineral nutrients thus has implications for the fraction of primary production that is eventually channelled to fish. Therefore, the magnitude of fisheries depends on hydrodynamic processes.

*The significance of small primary producers.* Classical descriptions of phytoplankton communities were based on samples collected by plankton nets with a mesh size of 20  $\mu\text{m}$  or so. This, of course, led to emphasis on phytoplankton cells larger than that. However, improved sampling and microscopic techniques led to the discovery in the 70's and 80's that very small phytoplankton cells make up a large fraction of the phytoplankton biomass, and indeed dominate the phytoplankton community in vast areas of the ocean (Stockner 1988). Size fractionated primary production measurements revealed that cells less than a few microns in size normally make by far the most significant contribution to pelagic primary production. Cells of this small size are unavailable to copepods, which can only capture particles larger than about 5  $\mu\text{m}$  (e.g. Berggreen *et al.* 1988). Therefore, it is only a relatively small fraction of the primary production that is consumed by the copepods.



*Pelagic bacteria and dissolved organic matter.* The existence of free-living pelagic bacteria has long been recognized (Pomeroy 1970), but their concentration and activity were until recently assumed to be relatively low. The application of fluorescence microscopy, staining and radioactive labelling techniques (Fuhrman & Azam 1980, Hobbie *et al.* 1977) demonstrated, however, that bacteria are very abundant and grow rapidly in marine waters. Bacterial production may correspond to up to 50% of the primary production. Bacteria are heterotrophs; i.e. they feed on organic matter that must eventually stem from primary production, primarily dissolved organic matter. Thus, it seems that a large fraction of the pelagic primary production ends up in dissolved rather than particulate form, and is consumed by bacteria. Pelagic bacteria are small, typically less than 1  $\mu\text{m}$ , and are thus unavailable to copepods.

Even though bulk phytoplankton biomass varies dramatically seasonally and spatially in the ocean, microscopic counts of bacteria and small phytoplankton cells revealed that these appear to occur at remarkably constant concentrations (Malone 1980). Bacteria, for example, occur in concentrations varying only between  $10^4$  to about  $10^7$   $\text{ml}^{-1}$  (Azam *et al.* 1983).

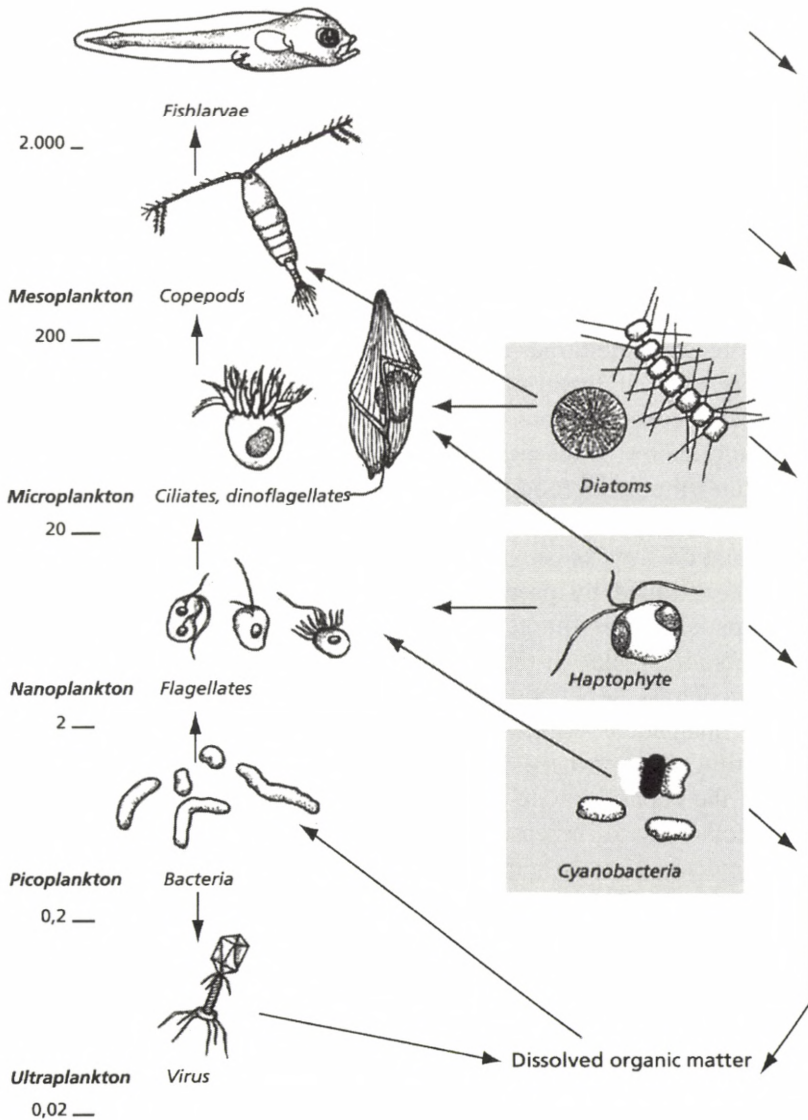
*The microbial loop.* From the above it appears that a significant fraction of the pelagic primary production is unavailable to copepods and, thus, is not channelled in the 'classical' food chain. What, then, is the fate of this significant production of small bacteria and phytoplankton? And what factors control the abundance of small cells and account for their remarkably constant concentrations in the pelagic environment? Fenchel (1984 and other papers) in a series of elegant papers demonstrated that small (2-10  $\mu\text{m}$ ) heterotrophic flagellates occur abundantly in the ocean and feed on and control the populations of bacteria and small phytoplankton cells. These flagellates are in turn preyed upon by

Fig. 1. The pelagic food web. The organisms are organized after size (largest at the top) and with autotrophs (phytoplankton) to the right and heterotrophs to the left. The fate of the primary production depends on the size of the primary producers. Production due to large phytoplankters (e.g. diatoms) are channelled in a relatively short, 'classical' grazing food chain to higher trophic levels (incl. fish), while production resulting from small cells (e.g. cyanobacteria) is channelled in a long microbial food web. Dissolved organic matter, leaking from all living organisms, is 'looped' back into the food web by bacteria. Most of the organic matter, which is processed by microorganisms, is 'burned' up before it reaches higher trophic levels. Modified from Fenchel (1988) and Nielsen & Hansen (1999). →

10-50  $\mu\text{m}$  large ciliates that may eventually be consumed by copepods and thus 'return' organic matter to the classical food web (Fig. 1). This 'shunt' in the pelagic food web became known as the *microbial loop*

**Size ( $\mu\text{m}$ )**

20.000 —



(Azam *et al.* 1983). Because of the inefficiency of energy transfer between trophic levels, and because of the large number of trophic steps in the microbial loop, most of the organic material processed in this loop is remineralized or 'burned up' by the involved organisms. Generally, about 90% or more of the organic material produced by small phytoplankton is degraded by pelagic microorganisms and, thus, unavailable for fish production. In contrast, primary production due to large cells is channelled in a short 'classical' grazing food chain (Fig. 1) and a much larger fraction of this production is potentially available for fish production.

*Why are there big phytoplankton cells in the ocean?* Small phytoplankton cells are in almost all respects superior to larger cells: they grow faster, they settle more slowly out of the euphotic zone, they harvest light more efficiently, and they take up nutrients faster and more efficiently, particularly at low ambient nutrient concentrations, than do large cells (Kiørboe 1993). Why, then, do not small phytoplankton cells always outcompete larger cells? Despite the dominance of small cells, there are, after all, larger phytoplankters in the ocean, although at highly variable concentrations. The existence of larger cells has not only academic interest since primary production resulting from large cells constitutes the main food for the copepods and, hence, nourishes the 'classical' food chain and supports fish production.

Population sizes of small phytoplankton cells and bacteria are efficiently controlled by predators while larger phytoplankton cells are not. This is because the generation times of bacteria and small phytoplankters are similar to the generation times of their flagellate predators. In contrast, copepods have generation times that are 1-several orders of magnitude longer than their large-sized phytoplankton prey populations. Thus, whenever or wherever new nutrients become available in the euphotic zone (see below), populations of both large and small cells start to increase. The small cells are rapidly caught up by their predators – and their populations controlled –, while the larger cells can continue their growth almost unexploited by their predators until all nutrients have been exploited. This is because the predator (copepod) population response is much delayed. Therefore, large-sized cells *bloom* whenever new nutrients become temporarily available. Injections of nutrients in the euphotic zone are due primarily to hydrographic events, such as mixing events caused by wind, tides or currents. Therefore, hydrodynamic processes govern the structure of the



pelagic food web, and the magnitude of fish production is related to the spatio-temporal frequency of such events. We shall return to this later.

*Feeding the sea floor.* According to the classical description of the pelagic food web, faecal pellets produced by copepods sink to the sea floor and provide the main input of organic matter here. However, observed fluxes of copepod faecal pellets to the sea floor are generally much less than would be expected from the abundance of copepods in the water column and their anticipated faecal production rate (e.g. Smetacek 1980). Apparently, faecal pellets are to a large extent remineralized (degraded) in the water column and before reaching the sea floor. This is both because of the rapid leakage of solute substances out of faecal pellets (Jumars *et al.* 1989), and because faecal pellets are captured and consumed by specialized copepods in the water column (González & Smetacek 1994). In effect, very few pellets reach the sea floor, even in relatively shallow regions.

How, then, does organic material reach the sea floor? Recall that there is no primary production of organic matter taking place at the sea floor (at least at depths exceeding 20-100 m), and benthic life depends entirely on organic matter supplied from above. Settling velocities of particles increase with the density difference between the particle and the ambient water, and with the square of the particle radius (Stokes' law). Phytoplankton cells do sink, but owing to their small size and almost neutral density, they do so only very slowly, about 1 m per day, or less. This is often far too little to account for the observed arrival rate of organic material at the bottom, which may require settling velocities orders of magnitude higher. Stokes' law implies that vertical material fluxes in the ocean must be due to relatively large particles.

Such particles were discovered in the ocean in the 50's by Japanese scientists (Suzuki & Kato 1953) and were named *marine snow*. Only within the last decade or so, however, have the occurrence, formation mechanisms and implications of these spectacular particles (Fig. 2) been studied in more detail (Alldredge & Silver 1988; Alldredge & Jackson 1995). Marine snow is mm-cm sized porous aggregates consisting of a wide variety of small primary particles. The aggregates are delicate and disintegrate easily into primary particles, for example when captured by plankton nets and other conventional sampling devices. This explains why marine snow was overlooked for so long. The primary particles of marine snow can be phytoplankton cells (live or

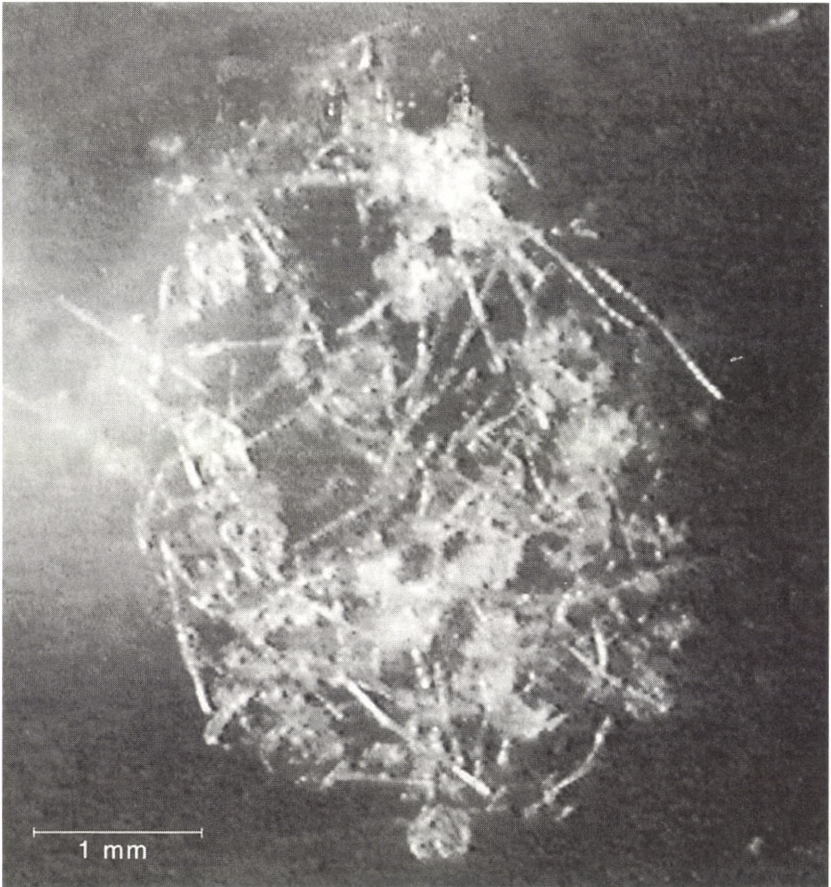


Fig. 2. *In situ* video micrograph of marine snow aggregate. This particular aggregate consists solely of diatoms cell chains (*Chaetoceros* sp), but aggregates can be composed of almost any type of particle that occurs in the water column.

dead) and other microorganisms, faecal pellets, dead animals or animal fragments, etc. Aggregates may be formed by a variety of mechanisms, of which an important one is *coagulation* (Jackson 1990, Kiørboe *et al.* 1990). This is a mechanism similar to the mechanism by which raindrops are formed from water particles in a turbulent cloud: differences in settling velocity between particles as well as turbulent water motion cause primary particles to collide. If the particles are 'sticky', they tend to adhere upon collision and to form subsequently larger and larger aggregates. With increasing size, the aggregates fall with increasing ve-



locity, and sinking rates sufficient to account for observed vertical particle fluxes will eventually result. Note that the aggregation process is strongly dependent on the size of primary particles. Collision frequency increases with the cube of particle radius! Therefore, aggregation and subsequent vertical flux is most important for relatively large particles, including large phytoplankton cells.

Marine snow aggregates appear to be ubiquitously present in the ocean, and often at high to extremely high concentrations. From observations of aggregate abundances, typically made by *in situ* photography or video, one would expect a constant rain of material to the sea floor. However, aggregation does not necessarily imply that the involved particles sink out of the euphotic zones. Aggregates are sites of elevated biological activity in that they house a rich flora and fauna. Some zooplankton organisms are specifically adapted to colonize and feed on aggregates, and aggregation may thus at times imply elevated mineralisation rates in the euphotic zone rather than sedimentation (Kiørboe *et al.* 1998). Nevertheless, marine snow aggregates are the main vehicles for vertical particle transport in the ocean (Fowler & Knauer 1986) and provide the direct or indirect supply of food for bottom dwelling organisms, including demersal fish.

*Hydrodynamic control of pelagic food web structure.* The pattern that emerges from the above is that pelagic food web structure depends on the size distribution of the phytoplankton. Primary production resulting from small cells is processed in a microbial food web, while large cells either sediment to the sea floor or are consumed by copepods. Thus, production owing to large cells – but not small ones – may eventually be channelled to fish production. The relative significance of large vs. small cells depends on hydrodynamic processes. Small cells occur in relatively constant concentrations owing to the density dependent predator control of their population sizes. Large cells, in contrast, vary substantially in population sizes. They bloom when and where nutrients become temporarily available, because in such dis-equilibrium situations their populations escape grazing control. Nutrients are injected into an otherwise nutrient-poor surface layer by vertical mixing processes. Too deep vertical mixing, however, implies that the phytoplankton become light limited. Therefore, blooms of large cells generally occur where or when mixed and stratified water masses meet. Only at such interfaces (in time or space) are the requirements for both light and nutrients satisfied. In the next section we shall examine examples of

how such spatio-temporal nutrient injections cause phytoplankton blooms, elevated production of copepods, gatherings of larval fish, and transport of organic matter to the sea floor. Eventually, it is the spatio-temporal frequency of such events that determine the magnitude of fish production in the ocean.

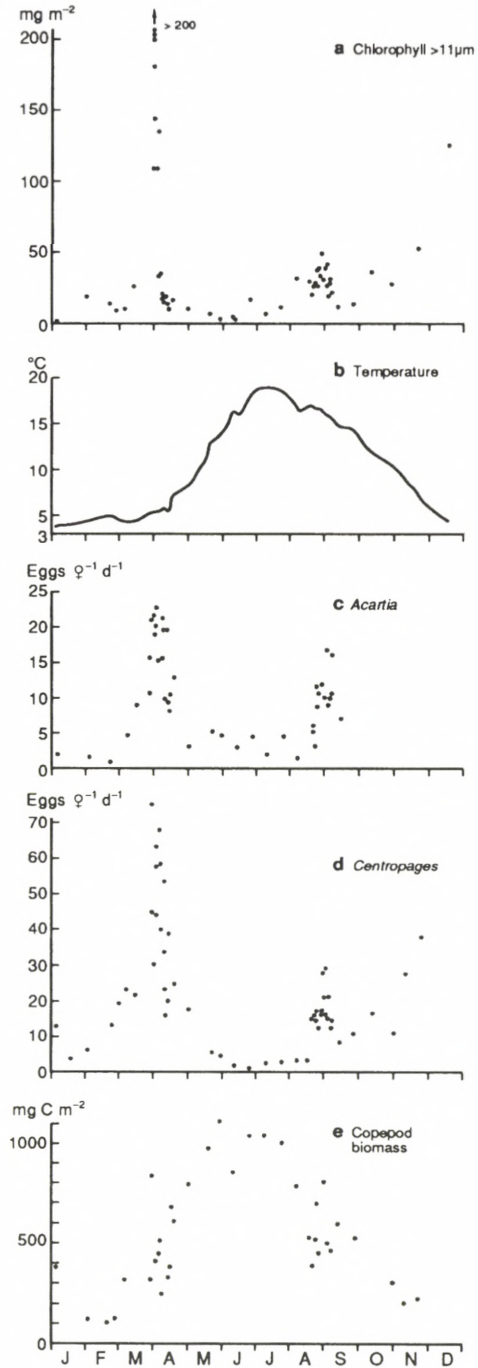
## Examples from the North Sea

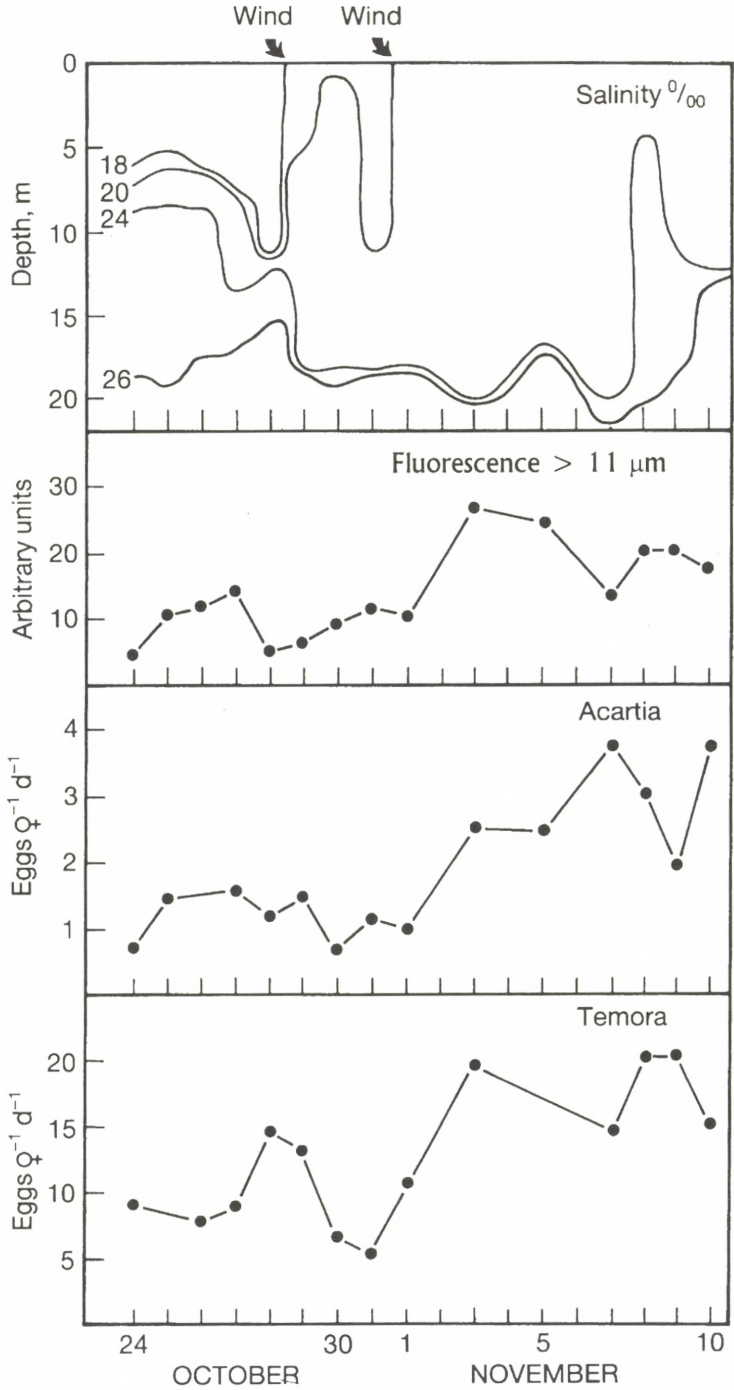
### *Seasonal changes*

During the winter the North Sea is vertically mixed and the concentration of inorganic nutrients is high throughout the water column because of insufficient light for primary production and, hence, nutrient uptake. With increasing solar radiation during the spring, the surface layer becomes heated, and the consequently lower density of the surface layer prevents it from being mixed with the cooler and denser deeper waters. Thus, residing phytoplankton populations are retained within the upper layer, experience a high and consistent light intensity, and owing to the plentiful supply of inorganic nutrients, their populations increase. This results in the spring phytoplankton bloom (Fig. 3 a). Although both large and small cells occur, the spring bloom is typically dominated in terms of biomass by large-sized diatoms. The spring bloom lasts only 1-2 weeks and ends when all inorganic nutrients have been exhausted. A major fraction of the phytoplankton may then combine into marine snow aggregates that settle to the sea floor (Smetacek 1985, Kiørboe *et al.* 1994). The copepods respond immediately to the elevated availability of phytoplankton food by producing eggs at high rates (Fig. 3 c,d), whereas the increase in copepod abundance is much delayed and reaches its highest annual value only several months later (Fig. 3 e). An additional peak in phytoplankton and copepod egg production occurs in the fall. This corresponds to the period where the vertical temperature stratification of the water column starts being eroded owing to reduced solar radiation and increased vertical mixing because of autumn storms (Fig. 3). This again leads to injection of new nutrients, and to a response in the pelagic food web. Thus, the sequence of events illustrated in Fig. 3 fits exactly into the generalized pattern described above. A significant fraction of the annual production of copepods is associated with these two seasonal events.



Fig. 3. Seasonal production events as recorded during an annual cycle in the North Sea area (Southern Kattegat). The biomass of large-sized phytoplankton, quantified as the concentration of chlorophyll retained on an 11-m filter (panel a) shows blooms in spring and autumn when vertical water column structure changes. These blooms are closely tracked by the productivity of copepods, quantified as rates of egg production (panels c,d), whereas the biomass of copepods (panel e) varies almost independently of phytoplankton concentration and rather follows variation in temperature (panel b). Data from Kiørboe & Nielsen (1994).







← Fig. 4. Effect of a wind event on vertical water column structure, biomass of large phytoplankters (quantified as fluorescence due to particles > 11 m), and egg production in two species of copepods (*Acartia tonsa* and *Temora longicornis*) in the southern Kattegat. Strong winds erode the water column stratification and result in an almost homogenous vertical salinity distribution (upper panel). This causes increased availability of nutrients in the upper layer and a subsequent bloom of large-sized phytoplankters and elevated productivity of copepods. Data from Kiørboe & Nielsen (1990).

### *Wind events*

Variation in vertical water column structure may occur at much shorter than seasonal time scales as a result of wind events. Strong winds may cause erosion of the temperature stratification, and subsequent surface heating may reestablish the water column structure. The wind-mixing event may bring inorganic nutrients from the bottom to the surface layer, and cause the larger-sized phytoplankters to bloom and subsequently cause elevated copepod production. Observations in the North Sea and elsewhere demonstrate this sequence of events (Fig. 4).

### *Tidal fronts*

In some shallow regions of the North Sea where tidal currents are strong, tidal mixing may locally overcome the vertical temperature stratification of the water column. Thus, while the deeper parts are stratified, the more shallow parts become tidally mixed. The transition zone between mixed and stratified water is called a tidal front. The position of the tidal front varies temporarily with variation in solar radiation, and with the intensity of tidal mixing, which varies with the neap-spring fortnightly tidal cycle. Thus, in the frontal region, the water column constantly changes between mixing and stratification. Mixing brings nutrients to the surface, and subsequent stratification retains phytoplankton in the illuminated surface layer. As expected from the above conceptual scheme, blooms of large sized phytoplankters often occur at tidal fronts, and the effect moves up the 'classical' food chain to both copepods and larval fish (Fig. 5). The effect is also manifest in a vertical flux of organic material to the sea floor, which results in elevated biomass of benthic invertebrates (Josefson & Conley, 1997). Tidal fronts occur abundantly in the North Sea (Pingree & Griffiths 1978) and may account for the very high fish yield in this area.

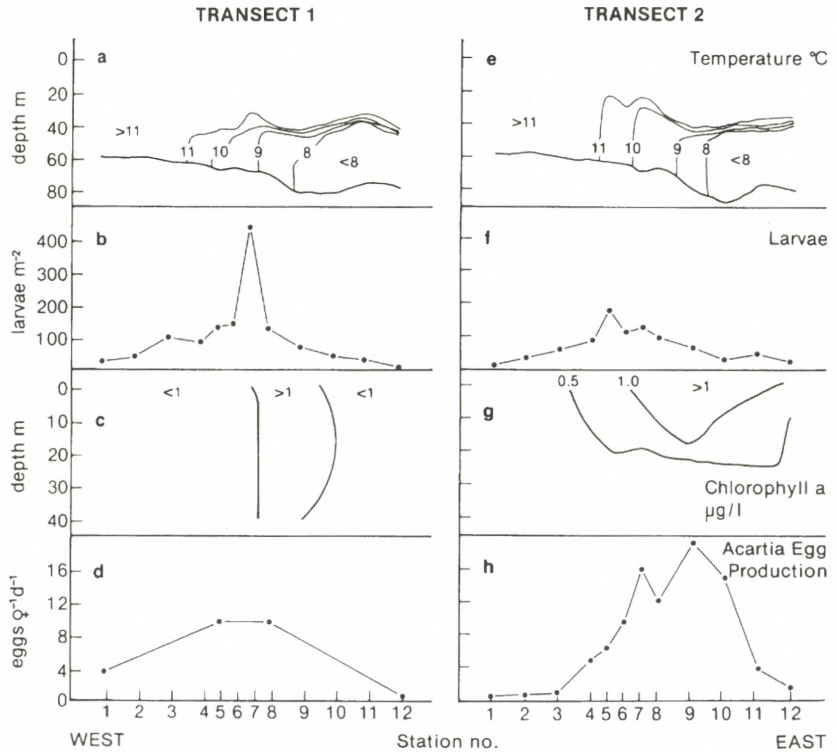


Fig. 5. Distribution of temperature (panels a,e) herring larvae (panels b,f), phytoplankton (panels c,g) and egg production of the copepod *Acartia tonsa* (panels d,h) across a tidal front in the North-western part of the North Sea. The frontal zone is the region between the entirely mixed water column (western part of the transect, where temperature is constant down to the bottom) and the stratified part (eastern part of the transect, where the temperature is higher at the surface than in bottom water). Data collected during two transects of the front. Data from Kiørboe *et al.* (1988).

### *Vertical discontinuities*

The vertical mixing that occurs on the shallow side of tidal fronts may impact phytoplankton production and pelagic food web structure in relatively large regions and beyond the immediate frontal area. Bo Pedersen (1994) described a mechanism whereby nutrients mixed into the surface layer may be transported along the layer separating the surface and the deep water (the pycnocline) over extended areas, and account for the frequent occurrence of sub-surface phytoplankton maxima asso-



ciated with the pycnocline (Fig. 6). Throughout the summer period, where the North Sea is vertically stratified owing to temperature differences, one often finds high concentrations of phytoplankton at the pycnocline, i.e., 15–25 m below the surface (called subsurface phytoplankton maxima). Such subsurface maxima may occur as a result of the accumulation of sinking phytoplankton at the density interface, or of a locally enhanced growth of phytoplankton. Direct measurements of growth rates suggest that the latter may often be the case in the North Sea (Richardson & Christoffersen 1991). This is most likely because of the local combination of sufficient light (from above) and sustained availability of nutrients. Vertical tidal mixing in the shallow region of a front generates water of intermediate density with a high nutrient concentration. This water flows horizontally into the vertically stratified region, exactly at the depth where the density matches that of the mixed water (Fig. 6). This way, nutrients are ‘pumped’ into the pycnocline. Pumping intensity varies on a fortnightly cycle, and thus causes a fortnightly cycle in the transport of nutrients for phytoplankton production. Because of the time variation in nutrient availability, grazing on large cells never comes into equilibrium with their production, hence the locally elevated concentration of big cells. The distribution of these sub-

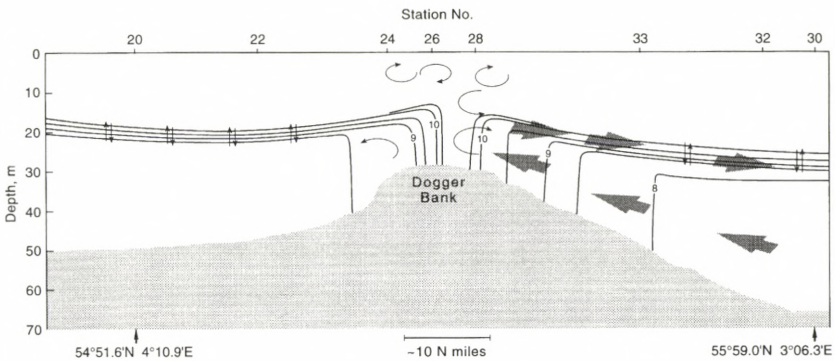


Fig. 6. Schematic of the tidal nutrient pump on Dogger Bank in the southern North Sea as described by Bo Pedersen (1994). Winds and tides cause mixing of the water column to the bottom of the centre of the bank. Water of intermediate density and nutrient content thus generated intrudes along the pycnocline away from the bank. This generates favorable growth conditions for phytoplankton at the pycnocline. Because tidal mixing intensity varies in a fortnightly cycle, this mechanism causes a pulsed supply of nutrients in the pycnocline. After Nielsen *et al.* (1993).

surface phytoplankton maxima in the North Sea fits nicely with those predicted from bottom topography, tidal energy, and hydrodynamic analyses (Bo Pedersen 1994). Our conceptual scheme above would suggest that these subsurface phytoplankton maxima would fuel a 'classical' grazing food chain and, thus, production at higher trophic levels. Recent studies in the North Sea confirm this (Richardson *et al.* 1998).

### *Other spatio-temporal oceanographic discontinuities*

There are several other processes that may cause injection of nutrients into the photic zone of the ocean. One well-known example is coastal upwelling. On a larger scale, this occurs on the east coasts of the continents, for example the Benguela current off South Africa, and off the Chilean east coast. These regions are extremely productive, both in terms of phytoplankton production, and in terms of fisheries. Coastal upwelling also occurs on a much smaller scale in, for example, the North Sea, although of much less significance here than elsewhere.

### *Fish production in the North Sea*

Fish production – or rather fisheries yield – on the continental shelves of the world's oceans varies between regions, mainly between 1-5 t per km<sup>2</sup> (FAO 1997). Upwelling regions may, however, experience significantly higher catches, e.g. about 25 t/km<sup>2</sup> in the Southeast Pacific off the South American coast. In our part of the world, the North Atlantic, peak fish landings correspond to 3-4 t/km<sup>2</sup> (FAO 1997). This average figure, however, covers relatively large local differences. Peak North Sea catches are about 3 x 10<sup>6</sup> t (ICES 1992) over an area of 0.5 x 10<sup>6</sup> km<sup>2</sup> (Steele 1974), corresponding to 6 t/km<sup>2</sup>, i.e. almost twice the average. At the other end of the range is the nearby Irish Sea, with annual catches of about 1 t/km<sup>2</sup> (Brander 1977). These differences are not the result of differences in fishing effort, because both numbers refer to the peak catches in the 70's. Subsequently, capture rates have declined in both areas, suggesting maximum efforts in both areas. What is the reason for the very productive fisheries in the North Sea?

The North Sea is rich on hydrographic 'discontinuities', i.e. regions or periods, where the water column structure varies spatially or temporally, and where inorganic nutrients become locally or temporarily available for new production. It is the availability of new nutrients and the spatio-temporal frequency of hydrographic discontinuities that eventually determine the magnitude of fish production in a particular area. These hydrographic 'structures' include the several tidal fronts in the western and



southern parts of the North Sea and coastal fronts in the eastern part. From a production point of view, the tidally driven nutrient pump described above also seems to be of importance in the North Sea. Richardson & Bo Pedersen (1998) estimated for the North Sea proper, that the spring bloom accounts for about 40% of the annual new primary production, frontal and coastal regions for another 40%, and the production in the subsurface phytoplankton populations for the remaining 20%. However, in the southern more shallow part of the North Sea, where a disproportionate fraction of the value of the fisheries is retrieved, the subsurface production may be relatively much more important. For the Dogger Bank area, for example, it has been demonstrated that the magnitude of the new production owing to this mechanism is more important than the spring phytoplankton production, and accounts for maybe 2/3 of the total annual new production (Richardson *et al*, 2000).

The total *new* production in the North Sea was estimated by Richardson and Bo Pedersen (1998) to be about 40 g organic carbon/m<sup>2</sup>/year. The *regenerated* production is presumably 2-5 times larger than this, making total primary production in the North Sea in the order of 150 g C/m<sup>2</sup>/year or more, which is largely consistent with measurements. However, it is only the 40 g of new production which leads to the building up of harvestable biomass. With the estimated fisheries yield converted to organic carbon, 6 t live weight/km<sup>2</sup>/year = ca. 3 g C/m<sup>2</sup>/year, it follows that corresponding to about 1% of the new production ends as harvestable fish biomass. This estimated efficiency is not very different from the efficiency estimated by Steele (1974) more than 25 years ago. However, it is arrived at in a very different manner, and it builds on a very different understanding of pelagic food web structure and functioning.

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