C H A P T E R

4

Marine biology

4.1. Introduction

The 1987 *QSR* described only the ecological effects attributable to human activities and their impact on the seabed and coastal flora, as well as on the plankton, fish stocks, seabirds, and mammals. The report did not provide a description of the biological components of the marine ecosystem.

The 1990 *QSR* focused on the effects of pollution on plankton populations in the North Sea and, in particular, on algal blooms. A seal disease epidemic that broke out in April 1988, with a significant impact on many harbour and grey seal populations, was also discussed in the report. In the wake of the epidemic, an extensive array of research projects was initiated that has led to greater knowledge about the status of seal colonies all around the North Sea.

This chapter describes the complexity of biological systems in the North Sea. General information on plankton, invertebrates, and vertebrates and their status in the North Sea is given first, followed by an assessment of recent changes. Interrelationships between communities are also discussed in order to present an overall description of the North Sea as an ecosystem.

4.2. General description of the marine biota

Plankton

Bacterioplankton

The importance of micro-organisms (principally bacteria, but also yeasts, fungi, and virus-like particles) in the marine food web has only been recognized and investigated during the last twenty years (Billen *et al.*, 1990). Some 60% of primary production (conversion of light energy into biologically usable energy via photosynthesis) may enter microbial food webs in which the main consumers of bacteria are microflagellates. Planktonic bacterial production in the open sea is related to primary production, and the abundance of bacteria increases, following phytoplankton blooms. Sea water contains around 10^9 bacteria per litre, which live mainly on organic matter produced by algal secretion, exudation, and lysis of cells. Bacteria remineralize organic matter to inorganic components.

Phytoplankton

Phytoplankton are microscopic, free-floating, usually single-celled, algae. These organisms are responsible for most of the primary production that occurs in the North Sea. Phytoplankton in the North Sea range in length from less than 0.001 mm up to 2 mm.

The size structure of the phytoplankton community is important in determining the efficiency of energy transfer through the food chain to the species of commercial interest. A population dominated by small cells (picocyanobacteria and flagellates) is highly productive, but the flux of energy to the next higher level is low. A population composed of larger cells (diatoms, dinoflagellates) is much more efficient in the transfer. Therefore, shifts in the population size structure will affect energy fluxes in the ecosystem in terms of their relative efficiency in transfer to species at higher trophic levels, including commercial species. Such shifts in populations can occur as a result of changes in nutrient inputs (total and relative quantities).

Most phytoplankton have very rapid maximum doubling times (of the order of < 1–3 days). When light and nutrient conditions are favourable, 'blooms' of these organisms can develop. Such blooms occur, for example, each spring in the North Sea.

There is a complex interaction between phytoplankton abundance and productivity and nutrient and light availability and the degree of mixing in the water column. The interaction plays a role in the geographic heterogeneity of phytoplankton distribution (Figure 4·1A), and presumably controls phytoplankton species succession in the North Sea. However, this interaction is not yet fully understood. Spatial and temporal heterogeneity in the abundance of larger (> 280 µm) phytoplankton in the North Sea can, for example, be demonstrated using data collected with the Continuous Plankton Recorder (CPR) (Box 4·1; Figures 4·1C and 4·1E).

There have been a number of examples of unusual or exceptional blooms of phytoplankton in the North Sea; given our present state of knowledge their occurrence is unpredictable. Here the term 'unusual algal blooms' refers to a large biomass production or to the occurrence of a species that has the potential for causing noxious effects. These blooms may or may not be blooms in the sense described above, but they are

Box 4·1. *The Continuous Plankton Recorder*

Continuous Plankton Recorders (CPR), which filter and trap plankton between two constantly winding lengths of 280 µm mesh silk, have been towed behind merchant ships at monthly intervals on regular routes across the North Sea since 1931. On average about 750 samples per year are analysed for the whole North Sea. They provide the only extensive and systematic information on community structure, spatial distribution, and seasonal and annual changes in plankton abundance. As such the surveys are of immense value in making it possible to distinguish between changes caused by local factors such as river outflow, and those caused by large-scale events such as weather patterns. For example, populations of most species of zooplankton (and large phytoplankton) in the North Sea declined between 1950 and 1980 and have since increased. The same trend can be observed in offshore parts of the North Sea and also in the open Atlantic from Iceland to the Bay of Biscay, therefore the cause of the decline was not local. It must be noted, however, that phytoplankton data from the survey need to be interpreted with care as most species pass through the coarse mesh of the silk. Since 1991 the survey has been operated by the Sir Alister Hardy Foundation for Ocean Science (named after the founder of the surveys).

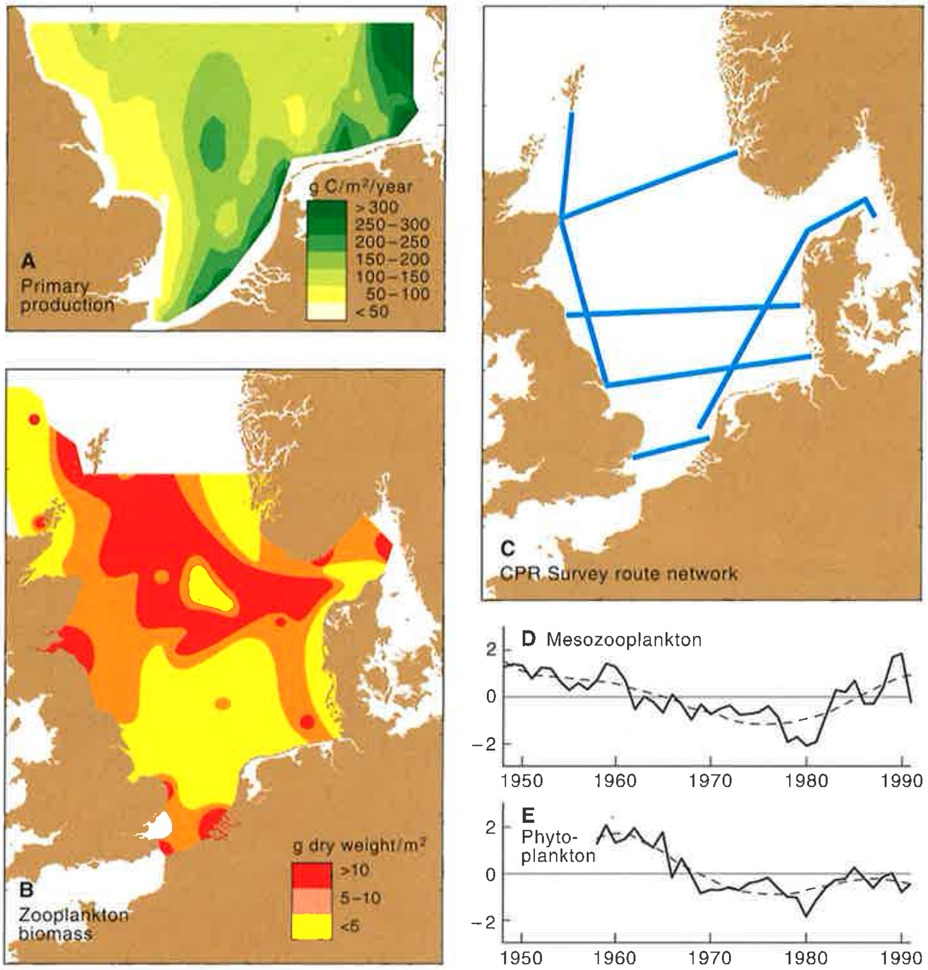

Figure 4·1. Plankton of the North Sea.
A: Annual primary production in the southern North Sea. Source: Joint and Pomeroy (1992).
B: Horizontal distribution pattern of zooplankton biomass in the North Sea, 2 May – 13 June 1986. Source: Krause and Martens (1990). Distribution of zooplankton biomass varies between seasons and between years, and the pattern shown represents only the period of sampling.
C: Present route network of the CPR Survey in the North Sea. Source: CPR Survey Team (1991).
D: Abundance of mesozooplankton in the North Sea, sampled by the CPR Survey, 1948–1991. Source: CPR Survey Team (1991). Data are standardized to zero mean and unit variance. The decline from 1950 to 1976 and subsequent increase occurred throughout most of the North Atlantic, as a result of large-scale (e.g., climatic) rather than local (e.g., eutrophication) effects.
E: Abundance of phytoplankton (>280 µm) in the North Sea, sampled by the CPR Survey, 1948–1991. Source: CPR Survey Team (1991). Data are standardized to zero mean and unit variance.

characterized by the presence of a phytoplankton species that arouses public concern. This concern can be caused by water discoloration (e.g., *Noctiluca* spp.), foam production (e.g., *Phaeocystis* spp.), fish or invertebrate mortality (e.g., *Chrysochromulina* spp., *Gyrodinium* spp.), or toxicity to humans (e.g., *Alexandrium* spp., *Dinophysis* spp.). Nutrient inputs from terrestrial sources may increase nutrient availability (and thus, increase the duration and intensity of blooms), but they do not necessarily initiate unusual blooms. Algal blooms, including unusual ones, are natural events that may or may not be associated with anthropogenic causes. For example, *Phaeocystis* spp. blooms have occurred in the North Sea for many years and can hardly be regarded as unusual. However, an increase in the dominance of *Phaeocystis* (cell numbers as well as duration of the bloom) between the mid-1970s and the late 1980s has been reported for the Marsdiep region (the westernmost Wadden Sea inlet). Levels of chlorophyll and primary production also increased over this period, but have decreased since then. These changes can be attributed to trends in eutrophication.

Zooplankton

Zooplankton are small animals living in the water column and transported mainly by water movement. They range in size from unicellular ciliates, flagellates, Radiolaria, and Foraminifera (microzooplankton < 0.2 mm) to krill, jellyfish, and fish larvae (macrozooplankton > 2 mm). The mesozooplankton (0.2–2 mm) are principally herbivorous copepods, which constitute 70–80% of zooplankton biomass in the North Sea and form the major link in the food chain between phytoplankton and fish larvae (Box 4·2).

Grazing by zooplankton is one of the major factors controlling phytoplankton populations. However, certain species of phytoplankton can repel grazers. For example, *Alexandrium tamarense* is regurgitated by copepods and it repels tintinnids (*Favella* spp.). Mesozooplankton graze on 40 to 100% of the phytoplankton production, but there are certain species of phytoplankton such as *Phaeocystis* spp. that are avoided (Davies *et al.*, 1992). The proportion of matter arising from primary production that settles to the seabed may thus be increased and the proportion remaining in the pelagic food web reduced.

Knowledge of the distribution of zooplankton throughout the North Sea is limited to a few extensive surveys (Figure 4·1B) and the Continuous Plankton Recorder surveys, which also show temporal trends in abundance (Figure 4·1D). Zooplankton abundance varies between areas owing to differences in production, predation, and transport. Most of the northern and central North Sea is dominated by oceanic species, particularly the copepod *Calanus finmarchicus*, whereas the southern North Sea and coastal areas are populated by neritic (open water) species (e.g., *Temora* spp., including high concentrations that have been reported in the Marsdiep area).

The eggs and larvae of most fish species are planktonic for a few months, and this period is critical in determining their year-class abundance. The growth and survival of fish during their planktonic stage depends on adequate feeding conditions, low levels of predation, and transport of larvae to suitable nursery areas.

Box 4·2. *Zooplankton*

Some species (Copepods, Euphausiids, and *Sagitta* spp.) remain as zooplankton throughout their life (holoplankton), whereas others have a zooplanktonic stage during their early life history (meroplankton). The latter group includes the eggs and larvae of most species of bony fish and also of a wide variety of the animals that live on the seabed and in the sediments. For example, sea urchins, starfish, molluscs, and polychaete worms all have a planktonic stage as do shrimps, crabs, hermit crabs, and lobsters.

In the North Sea these early life history stages are most abundant in the plankton during spring and summer, coinciding with the period of highest primary production. A general feature of this distributive planktonic stage is that large numbers of small eggs and larvae are produced, which grow rapidly but suffer very high mortality rates during their period in the plankton.

Box 4·3. *Categories of benthos and commercially important North Sea species*

Phytobenthos

Microphytobenthos: diatoms, flagellates, and other unicellular algae.

Macrophytobenthos: red, brown, and green algae, and sea grasses. The kelp *Laminaria hyperborea* is commercially used for alginate production.

Zoobenthos

Zoobenthos are divided into:

Epifauna: zoobenthos that live primarily on or above the sea bottom. Commercially important are lobsters (*Homarus gammarus*), spiny lobsters (*Palinurus vulgaris*), Norway lobsters (*Nephrops norvegicus*), brown crabs (*Cancer pagurus*), deepwater prawns (*Pandalus borealis*), shrimp (*Crangon crangon*), whelks (*Buccinum undatum* and *Neptunea antiqua*), periwinkles (*Littorina littorea*), scallops (*Pecten maximus*), queens (*Aequipecten opercularis*), oysters (*Ostrea edulis*), and the introduced Portuguese oyster (*Crassostrea angulata*), Pacific oyster (*Crassostrea gigas*), and blue mussels (*Mytilus edulis*). Oysters and blue mussels are cultivated on special beds or are grown on poles and ropes in sheltered areas.

Infauna: zoobenthos living within the sediment (polychaete worms, crustaceans, bivalves, gastropods, and members of many other animal groups). Commercially important are cockles (*Cerastoderma edule*) used as human food and lugworms (*Arenicola marina*) for bait.

Infauna are split into categories according to size:

Microfauna: animals smaller than 50 µm, including ciliates, flagellates, protozoans, bacteria, and fungi.

Meiofauna: Foraminifera, nematodes, crustaceans such as harpacticoid copepods, and members of many other animal groups that are so small they pass a 1 mm mesh. Many live in the interstices between sand grains.

Macrofauna: animals larger than 1 mm.

Benthos, including shellfish

General definition

The biota living near, on, or in the seabed are collectively called the benthos (Box 4·3). Bottom-dwelling and commercially important molluscs and crustaceans are called shellfish. A distinction is made between plants (phytobenthos) and animals (zoobenthos), which either live within the sediment (infauna) or move about on its surface (epifauna). Typical benthic fauna communities in the North Sea are shown in Figure 4·2. The infauna are split into categories according to size: macrobenthos/macrofauna (animals larger than 1 mm), meiobenthos/meiofauna (animals between 50 µm and 1 mm), and microbenthos/microfauna (animals smaller than 50 µm).

Both phytobenthos and zoobenthos are used in many monitoring programmes because they live permanently in or on a substrate and integrate the effects of the various environmental conditions.

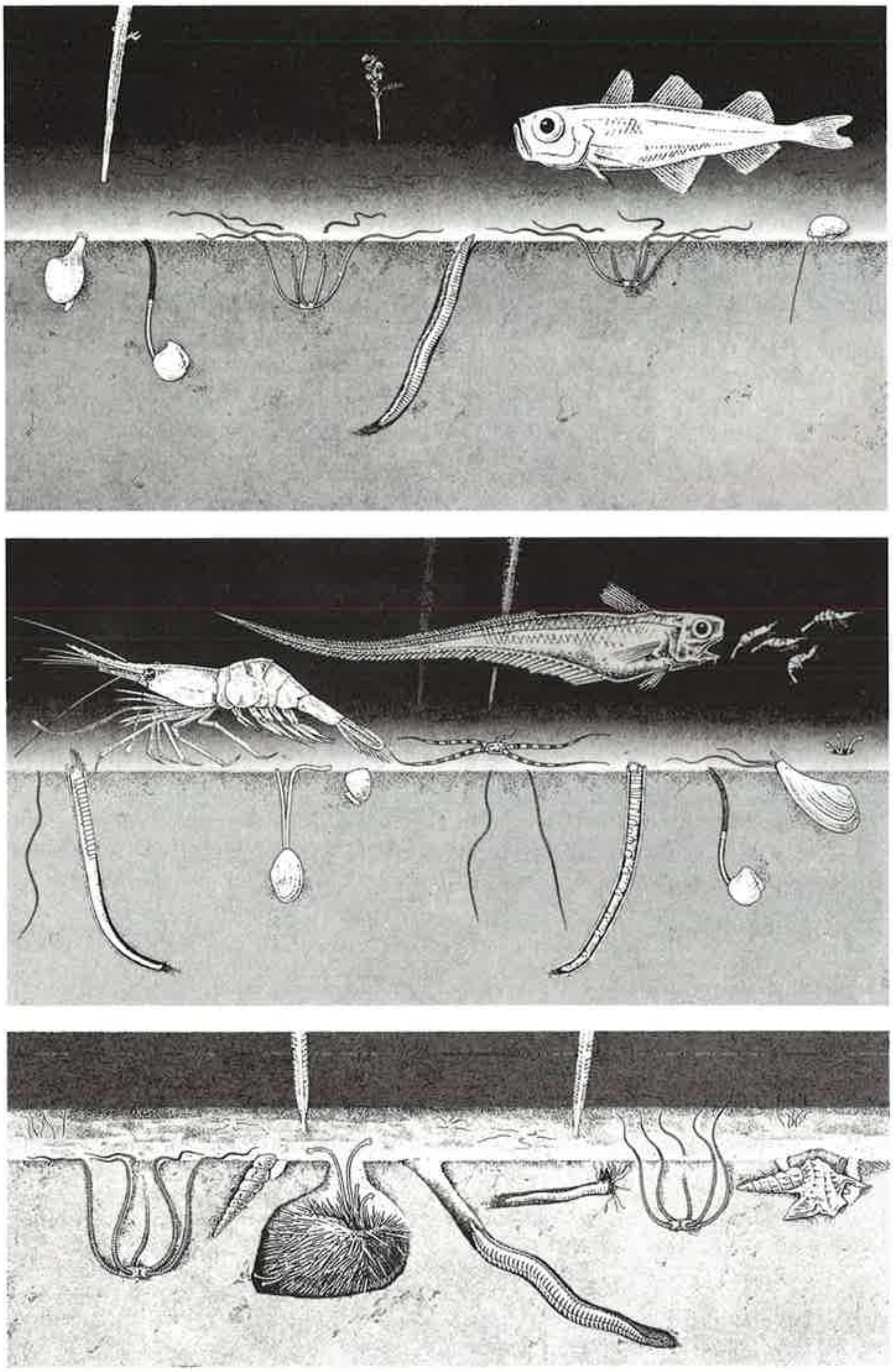

Figure 4·2. Conceptual views of the animal communities living on or in the bottom sediments of the North Sea.
Source: after Thorson (1979).

A: Deep Skagerrak, depth 400–700 m.
A silvery pout (*Gadiculus thori*) swims above the mud bottom, from which sea pens (*Kophobelemnon stelliferum*) rise. To the right, a tiny scallop (*Pecten vitreus*) is anchored by a byssus-thread to the mud. Infauna (from left to right): the clams *Cuspidaria obesa* and *Thyasira equalis*, the brittle star *Amphilepis norvegica*, and the polychaete *Orbinia norvegica*.

B: Skagerrak, depth 150–400 m.
A grenadier (*Coryphaenoides rupestris*) hunts for deepwater prawn (*Pandalus borealis*, enlarged specimen in left foreground). In the background, sea pens (*Funiculina quadrangularis*) rise from the sediment. On the surface of the mud there is a brittle star (*Ophiura sarsi*). Buried in the mud (from left to right): the clams *Abra nitida*, *Nucula tenuis*, *Thyasira equalis*, and *Nuculana pernula*; the polychaetes *Myriochele* spp. (very thin, thread-like tubes), *Melinna cristata*, and *Maldane sarsi*.

C: Skagerrak–Kattegat region, sandy mud bottom, depth 20–100 m.
A classic '*Amphiura* community'. Epifauna are represented by two sea pens (*Virgularia mirabilis*) anchored in the sediment. In the centre is the burrow of the polychaete *Nephtys ciliata*, a predator. Other animals feeding close to the sediment surface (from left to right): the brittle star *Amphiura chiajei*, the snail *Turritella communis*, the heart urchin *Brissopsis lyrifera*, the polychaete *Terebellides stroemi*, the brittle star *Amphiura filiformis*, and the snail *Aporrhais pespelecani*.

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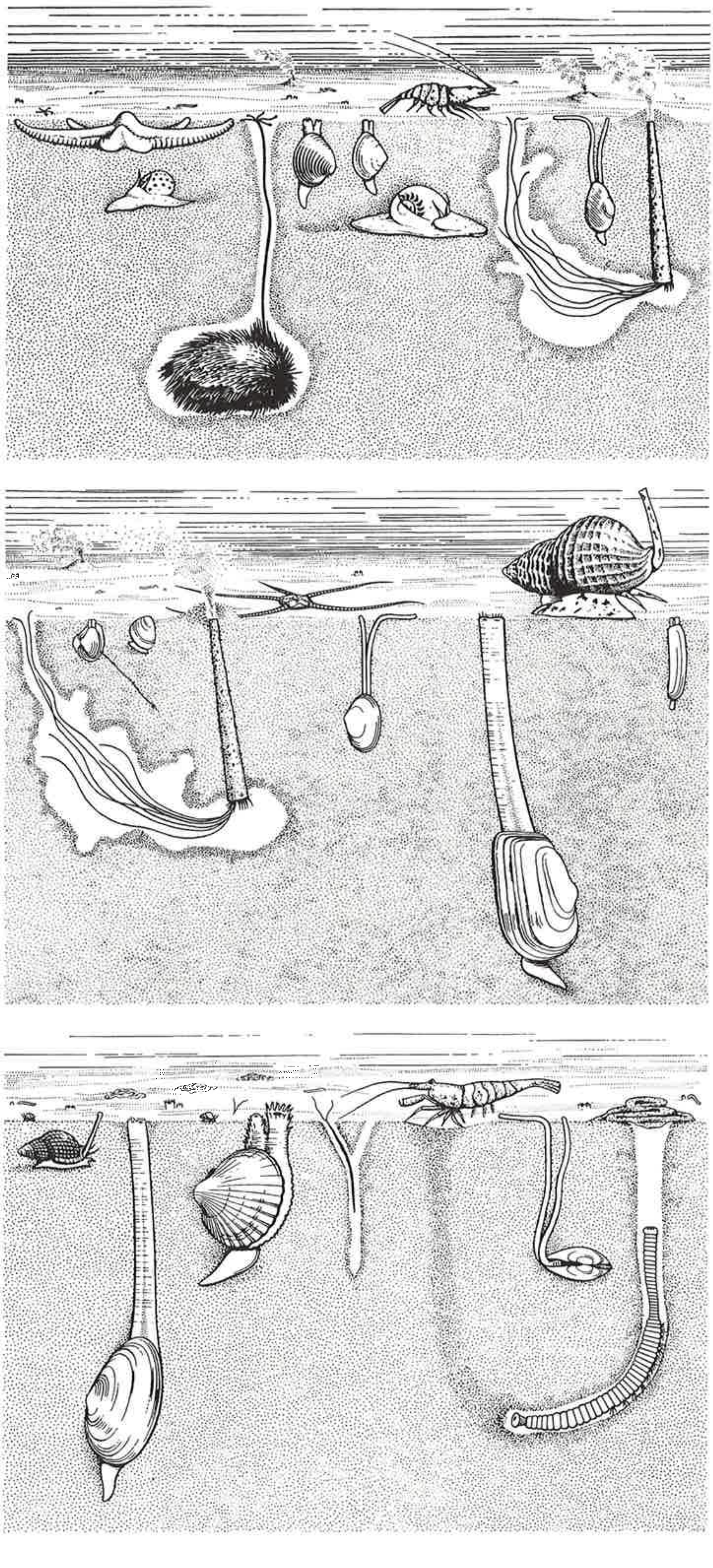


Figure 4·2 continued.

D: Skagerrak–Kattegat region, sandy bottom, depth 10–40 m.
A classic '*Venus* community'. Epifauna are represented by the shrimp *Leander adspersus*, searching for prey at the sediment surface. The sea star *Astropecten irregularis* preys on clams, as do the snails *Natica* spp. that move within the sand and, on contact, drill a hole through the clam shell. Clams are represented by (from left to right): *Venus striatula*, *Spisula subtruncata*, and (with two long siphons extending to the sediment surface) *Tellina fabula*. Buried deep in the sediment are the heart urchin *Echinocardium cordatum* and the polychaete *Pectinaria koreni*.

E: Near-shore sandy mud.
A classic '*Abra* community'. Epifauna are represented by the brittle star *Ophiura texturata* and the whelk *Buccinum undatum*. Four species of clams are abundant (from left to right): *Corbula gibba* (fastened by a byssus-thread to deeper sediment layers), *Nucula tenuis*, *Abra alba* (with its long ingestion siphon sampling particles from the sediment surface), and *Cultellus pellucidus*. Buried deep in the sediment is the clam *Mya truncata*. To the left, the polychaete *Pectinaria koreni* blows sediment particles through its conical tube into the water above, causing bioturbation.

F: Sandy bottom in shallow water or on tidal flats.
A classic '*Macoma* community'. Epifauna at the sediment surface are represented by minute snails, *Hydrobia ulvae*, and by the shrimp *Crangon vulgaris*. Below the sediment surface there is a predatory snail (*Nassarius reticulatus*). Buried in the sediment are (from left to right): the sand gaper clam *Mya arenaria*, the cockle *Cerastoderma edule*, the polychaete *Pygospio elegans*, the clam *Macoma balthica*, and the lugworm *Arenicola marina*, which feeds at depth from a sand column sunk into the sediment.

Sediment-dwelling bacteria and benthic animals play the major role in the decomposition of organic particles that originate from primary production in surface waters and settle on the sea bottom, or that are advected downslope from shallow to deep regions. Meiofauna mainly feed on sediment-dwelling bacteria and, at shallow depths, on microphytobenthos (benthic algae). Most macrofauna feed on organic particles and on bacteria in the sediment and at the sediment surface (deposit-feeding), or feed on suspended matter in the near-bottom water (filter-feeding). Other meiofauna and macrofauna species are predators. By burrowing in the sediment, ventilating burrows, and similar mechanical activities collectively called bioturbation, infauna animals facilitate the transport of oxygen down into the sediment. Areas of hard substrate near the coast are occupied by sessile and sedentary species that support mobile grazers, predators, and scavengers. Infauna and epifauna are the food of demersal fish, and meiofauna are an important food for certain species of flatfish. Some molluscan and crustacean epifauna are of commercial importance. Shellfish exploited for human consumption consist of two very dissimilar types of animals: a) crustaceans such as shrimps, crabs, and lobsters, and b) various groups of molluscs such as whelks (*Buccinum undatum*), bivalves (including cockles (*Cerastoderma edule*), mussels (*Mytilus* spp.), oysters (*Ostrea* spp.), and scallops (*Pecten* spp.)), and cephalopods such as squid (*Loligo* spp.) and cuttlefish (*Sepia officinalis*).

Benthic bacteria

The organic content of sediments is a reasonable predictor of benthic bacterial production and biomass. Benthic bacteria show great metabolic diversity, utilizing oxygen, nitrate, or sulphate as their reduction substrate. Their respiratory activity creates a chemical gradient within the sediment, with oxygen-utilizing forms found closest to the sediment/water interface and sulphate-utilizing forms at greater depths. Bacterial production is known to increase following the annual sedimentation of the spring phytoplankton bloom. There is also evidence that grazing of micro-organisms by benthic meiofauna enhances bacterial production and stimulates detrital decomposition, although the importance of this grazing to the micro-organisms is not well understood. Higher numbers of oil-degrading bacteria found in sediments in the central North Sea may be due to high oil concentrations.

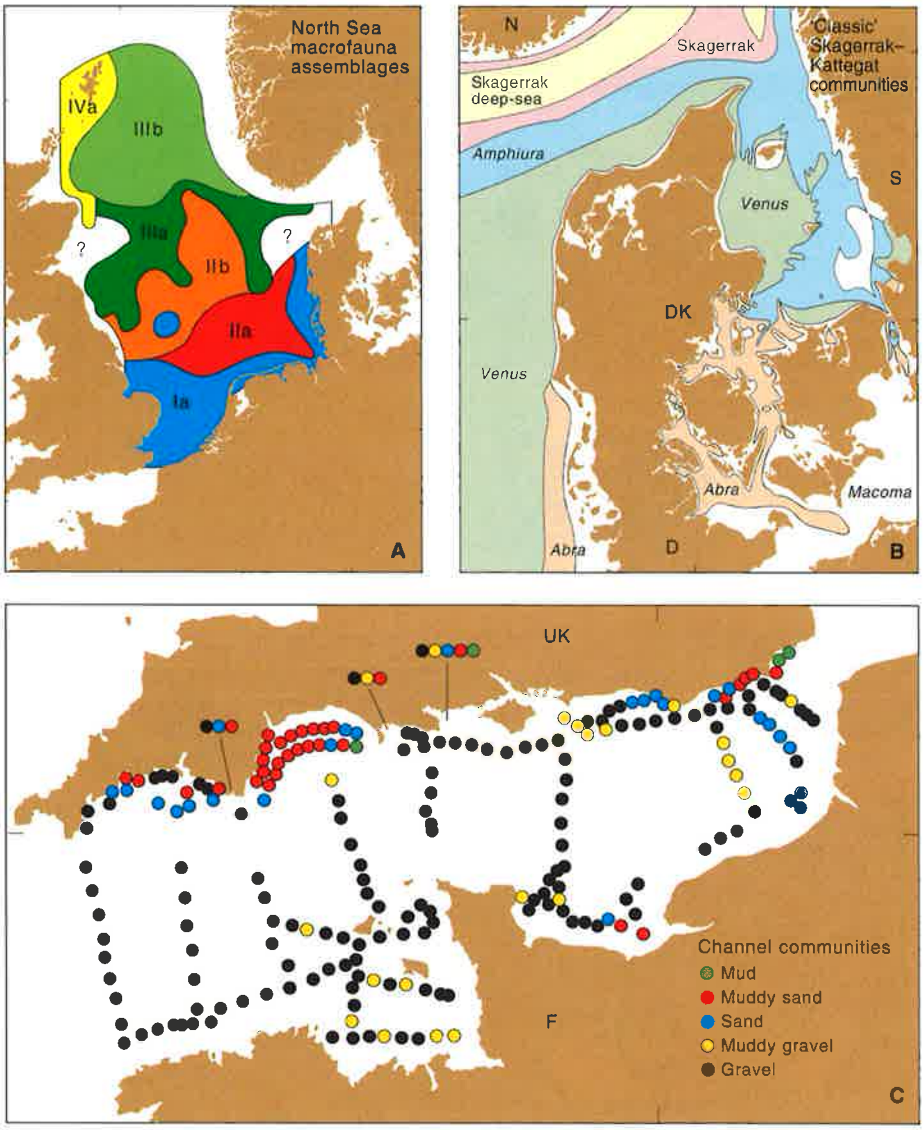


Figure 4·3. Benthos of the North Sea.

A: Distribution of some macrofauna assemblages in the North Sea. Source: Künitzer *et al.* (1992). Infauna assemblages of the subtidal North Sea, excluding the Channel, Skagerrak, and Kattegat:

A coastal assemblage in the southern North Sea and on the Dogger Bank at depths shallower than 30 m (group Ia, 52 stations, 27 ± 8 species per station, 805 ind./m^2, 9.5 g organic weight/m^2).

An offshore assemblage on fine sand at 40–70 m depth in the central North Sea (group IIb, 61 stations, 43 ± 10 species per station, 1093 ind./m^2, 7.6 g organic weight/m^2), and a similar offshore assemblage (group IIa, 40 stations, 44 ± 9 species per station, 1995 ind./m^2, 12.6 ± 7.5 g organic weight/m^2) in the southern North Sea, on muddy sand at 30–50 m depth.

An offshore assemblage occurring deeper than 100 m in the northern North Sea (group IIIb, 41 stations, 51 ± 13 species per station, 2863 ind./m^2, 3.5 g organic weight/m^2), and an offshore assemblage at 70 to 100 m water depth in the central North Sea (group IIIa, 46 stations, 54 ± 16 species per station, 1224 ind./m^2, 7.4 g organic weight/m^2).

A northwestern offshore assemblage in the region of the Orkney-Shetlands and off the Scottish coast (group IVa, 12 stations). The two northern North Sea assemblages IIIa and IVa have many indicator species in common that do not occur in the shallower areas of the southern North Sea.

B: Distribution of 'classic' communities in the Skagerrak-Kattegat area. Source: after Thorson (1979), and Petersen (1914).

C: Distribution of some macrofauna communities in the Channel. Source: Holme (1966). Few studies extend to the offshore areas of the Channel. The most detailed is that undertaken by Holme (1966), who sampled 311 stations by anchor dredge throughout the Channel. He identified five offshore animal communities:

- muds with the echiurid *Maxmulleria lankesteri* and the bivalve *Saxicavella jeffreysi*
- muddy sands with *Echinocardium cordatum*, *Amphiura filiformis*, and *Abra alba*
- sands with *Venus striatula*, *Echinocardium cordatum*, and *Acrocnida brachiata*
- muddy gravels with *Upogebia* sp., *Nucula nucleus*, and *Venus verrucosa*
- gravels with *Nucula hanleyi*, *Venerupis rhomboides*, etc. Often associated with beds of the brittle star *Ophiothrix fragilis* on harder ground

In shallow waters were found:

sands with *Arenicola marina*, *Nephtys* sp., *Tellina tenuis*, etc.
muds with *Macoma balthica*, *Cerastoderma edule*, *Nereis diversicolor*, etc.

Zoobenthos assemblages: distribution, biomass, and diversity

a) North Sea excluding the Channel, the Skagerrak, and the Kattegat

Large-scale subregional differences in the benthos of the North Sea have been demonstrated by modern studies following the pioneering work by C.G.J. Petersen, who estimated potential fish food in Danish waters in the beginning of the century (Petersen, 1914). In the spring of 1986 the International Council for the Exploration of the Sea (ICES) organized a comprehensive survey of the North Sea (excluding the Channel, the Skagerrak, and the Kattegat) (Künitzer *et al.*, 1992) covering the macrofauna, the meiofauna, and the epifauna. The survey did not cover inshore coastal areas of the North Sea or the Wadden Sea, but gave good coverage of the central and northern North Sea. The description that follows is based on results of the survey.

Macrofauna

The main patterns of macrobenthic species distributions showed that the bottom fauna of the North Sea consist of cosmopolitan species (northern elements) whose southern limit lies north of the Dogger Bank, and southern elements whose northern limit is the 100 m contour (see Figure 2·1). Northern and southern species mix in the central North Sea, and northern and southern assemblages overlap along the 70 m contour. It is possible that the separation of the macrobenthic infauna into northern and southern components along the 70 m contour is a result of the current pattern in the North Sea (see Chapter 2). Figure 4·3A shows assemblages of species representative of different areas of the North Sea. Assemblages resembling those of deep-sea areas occurred at depths greater than 200 m along the shelf edge of the North Sea (with deepwater corals of the genus *Lophelia*) and in the Norwegian Trench and the Skagerrak. The distribution of species also appeared to be determined by the sediment type. In a model using chlorophyll-*a* content and median grain size as predictors in addition to latitude, sediment characteristics accounted for most of the variance. In areas where macrobenthos assemblages were apparently determined by different water masses, the sediment may have been less important in structuring the assemblages. Total abundance showed a weak gradient with latitude. There was a tendency for density to increase towards the north. The average number of species per assemblage gradually increased with depth, ranging from fewer species in assemblages in water shallower than 30 m (group Ia) through median numbers of species in assemblages at 30–70 m depth (groups IIa and IIb) to the maximum recorded among assemblages in areas deeper than 70 m (groups IIIa and IIIb). Towards the Scottish coast (group IVa), the number of species decreased again. In northern areas, diversity (the number of species versus the number of individuals) was considerably higher than elsewhere. In addition to latitude, both depth and longitude (which are highly correlated in the North Sea, running along a slight southeast to northwest gradient) showed a correlation with increasing diversity. Other environmental variables that were measured had no clear influence on diversity.

Total biomass showed a clear and significant trend with latitude: at northern latitudes biomass decreased considerably. The main shift was not caused by one major taxonomic group overtaking another moving northwards. Rather, the same trends seemed to be operating within the different groups. Apart from latitude, sediment composition and chlorophyll-*a* content of the sediment also significantly influence both total biomass and the biomass of most separate groups. Biomass increased with silt contents between 0.1 and 1%, remained relatively uncorrelated for silt contents between 1 and 10%, and decreased with silt contents for very fine sediments (silt content > 10%). Mean weight per specimen also showed a very clear gradient with latitude. In areas to the north, with increasing depth, individual size became considerably smaller. The variation in mean biomass per assemblage was very high. Mean biomass was lowest in the northern North Sea (groups IIIb and IVa). The biomass increased towards the shallower southern North Sea and reached the highest values south of the Dogger Bank (groups Ia and IIa).

Meiofauna

At nearly all stations, nematodes were the dominant meiofauna group (Huys *et al.*, 1992). Densities ranged from 60 to 4200 ind./10 cm^2, with an average over all stations of 760 ind./10 cm^2. Nematodes became especially dominant at about 54°N, although there was no trend in their density with latitude. Only in the Southern Bight were copepods sometimes the dominant group. The fact that there is almost an order of magnitude of difference in diversity between the Southern Bight and the rest of the North Sea is linked with specific conditions in the area. It should be noted, however, that the nematode/copepod ratio varied considerably in the central and northern North Sea. Although this ratio is difficult to interpret, it suggests that nematodes and copepods are independently influenced by a complex suite of environmental parameters. Copepod density and diversity decreased with increasing latitude. The highest value was 181 ind./10 cm^2 in the Southern Bight against a minimum of 18 ind./10 cm^2 in the Norwegian Trench. Biomass decreased northwards until 57°N, but then increased again.

Epifauna (including shellfish)

Four assemblages can be distinguished in the northern North Sea, determined by depth and sediment characteristics. For example, Norway lobster (*Nephrops norvegicus*) and pandalid shrimps occur in deeper waters with appropriate sediments. Because of the greater influence of depth on epifaunal assemblages, the epifaunal communities appear to reflect hydrographic subdivisions of the North Sea. In summer, North Sea epifauna can be divided into two main clusters, one situated to the north and one to the south of the Dogger Bank. The epifauna on the Dogger Bank and in the central North Sea are dominated by filter-feeding species, in contrast to the scavenging or predating epibenthic species in the southern North Sea, which may reflect different ways in which energy is transferred through the benthic system. In winter the epifauna can be divided into a western cluster and an eastern cluster.

b) Kattegat and Skagerrak

In the Kattegat and Skagerrak (Figure 4·3B), the first quantitative investigations of marine soft-bottom benthos were made in the beginning of the century by Petersen. This work was later completed by mapping benthic communities in several parts of the area. Petersen's data were also reanalysed using modern multivariate techniques. The basic distribution of fauna is such that the shallower sandy-mud bottoms of the Kattegat are dominated by a typical '*Macoma* community', which grades into *Amphiura* spp. in deeper and more muddy sediments. In the Skagerrak, above 200 m, a typical '*Abra-Amphiura* community' prevails, with an average biomass of around 100 g Ash-Free Dry Weight (AFDW)/m^2. In the deeper basins (over 600 m in some places) typical dominant species are the polychaete *Spio* sp., *Chaetopterus variopedatus*, and the bivalve *Keliella*

Box 4·4. *Long-term changes in macrotidal estuaries*
The benthic animals living in macrotidal (tidal range up to 12 m in the Channel) estuaries are adapted to extreme temperatures, wave impact, sunlight, the tidal water regime, and the dilution of sea water by fresh water. Exposure to the atmosphere and the effect of tidal currents, storms, severe winters, and hot summers have been shown to operate as important regulating factors in the succession of the dominant species over time. Their distribution depends greatly on their capacity to control the osmotic pressure of body fluids (osmoregulation) and on sediment characteristics. Similar assemblages of animals are found in the various estuaries around the Channel in response to these two environmental parameters. Recent changes in the estuarine environment may be assessed by studying the relative size of the areas occupied by such assemblages for a specific type of sediment. From 1978 to 1990, the crustaceans *Eurydice pulchra* and *Haustorius arenarius* immigrated into several Channel estuaries together with marine sediment. At the same time, silting has been increasing on higher tidal levels where salt-marsh plants (*Spartina* spp.) have expanded. The result is continued shrinking of the true estuarine areas where the highest biomass of macrofauna (*Cerastoderma edule*, *Nereis diversicolor*) is currently found. It has also been shown that nutrient enrichment has indirectly facilitated the presence of opportunistic species such as *Pygospio elegans* which recolonized areas after benthos kills following anoxic conditions. The overall result of these successive changes is an impoverishment of the ecosystems.

sp., with other bivalves such as *Thyasira ferruginea*, *T. eumyaria*, *Yoldiella lucida*, and *Nucula turgida* also common. Below 200 m, biomass averages around 25 g AFDW/m^2. Because of the differences in bathymetry, there is little similarity between the fauna found respectively in the Skagerrak and the North Sea.

c) Channel

In the Channel (Figure 4·3C), infralittoral sands and their fauna extend down to approximately 20 m depth and are largely confined to a narrow band along the coast (Holme, 1966). A highly productive *Venus fasciata* community, dominated by molluscs, characterizes the coarse sands in the region between Normandy and Brittany, with mean biomass values reaching 51 g AFDW/m^2. In embayments off the coast of the United Kingdom and in French estuaries, muds down to 20 m depth are characterized by a *Macoma balthica* community, with very high densities of associated species reaching a biomass of 40 g AFDW/m^2 and more. Epifauna on the continuous coarse sediment deposits that extend from the Atlantic to the Strait of Dover show a correlation between the eastern limits of penetration of numerous species into the Channel and temperature gradients. In the reverse direction, there has been a penetration of species from the North Sea into the eastern Channel. The 70–80 m isobath marks a further division into coastal and open-sea fauna. In water deeper than 70 m, flats with gentle gradients are covered with species living on boulders or pebbles with developed epifauna on coarse, shelly sand. Very limited information is available on the meiofauna in the Channel.

d) Intertidal environments

Extensive shallow intertidal areas are found in estuaries (Box 4·4) and along rocky shores and sandy beaches. Soft bottoms also cover large areas of the Wadden Sea. As with the subtidal fauna, biomass increases with sediment fineness up to a certain point, reflecting the influence of physical and chemical factors and available organic matter. Fauna are poorer on exposed beaches than in sheltered areas such as the muddy Wadden Sea and sea-grass beds, which are rich in organic matter. For example, in the Dutch part of the Wadden Sea the biomass of intertidal fauna is highest in well-oxygenated muddy sands (42 g AFDW/m^2), lower in muds (18 g AFDW/m^2), and lowest in clean sands (13 g AFDW/m^2).

Commercial bivalves such as the cockle (*Cerastoderma edule*) and the blue mussel (*Mytilus edulis*) are found in intertidal or shallow subtidal areas. Scallops (*Pecten maximus*), crabs, lobsters, and crangonid shrimps are also found in inshore waters. The abundance of bivalves and shrimps varies greatly in relation to recruitment.

Distribution of phytobenthos

The distribution patterns of macroalgae also indicate that the North Sea is a transition area between the warm-temperate region in the southwest, and the cold-temperate region in the east and in the north. A number of salt-marsh plants reach their northern limit of distribution in the Firth of Forth and their eastern limit of distribution on the Dutch coast. During recent decades a number of species of plants have extended their range of distribution northwards and eastwards. For example, the Japanese weed *Sargassum muticum*, which was introduced to southern England in 1973, had reached the Norwegian part of the Skagerrak by 1986.

Superimposed on the effects of temperature and exposure mentioned above are local variations. Numbers of brown and red algae are reduced in the lower salinity waters of estuaries which appear to favour green algae such as *Cladophora* spp., *Enteromorpha* spp., and *Blidingia* spp. The type of bottom substrate (its mobility, hardness, and porosity) also influences the floristic composition of shores. For example, rapid erosion of chalk cliffs on the Kent coast prevents the long-term establishment of perennial algae. New artificial habitats, sea walls, embankments, and marinas have extended the local abundance and geographical range of a number of species. Some native macroalgal species are affected by competition with introduced species or are subjected to important fluctuations through episodic diseases of epidemic proportions. *Laminaria digitata*, *L. hyperborea*, *Ascophyllum nodosum*, *Fucus serratus*, and *Chondrus crispus* are harvested for commercial use. Deposits of calcareous algae (maerl) form a rare habitat with a rich associated fauna in the region between Normandy and Brittany, with more limited deposits in the Baie de Seine and Falmouth Bay.

Changes in North Sea benthos

a) Zoobenthos

Few long-term data sets on trends in the benthos of the open North Sea and the Channel existed in the late 1970s. Within the framework of the COST (Coopération Scientifique et Technique) 647 Programme of the European Economic Community, factors influencing variability in different geographical areas were investigated from the late 1970s onwards. Soft-substrate subtidal and intertidal systems have been the main subjects of collaborative studies (Souprayen *et al.*, 1992a and 1992b). Most of the time series are still too short to be of use, but interesting changes in benthos densities and biomass have been described.

The abundance and biomass of infauna have increased at most of the subtidal monitoring stations with muddy sands off the Northumberland coast (Austen *et al.*, 1991), on the Dogger Bank, and in the Southern Bight, the German Bight, the Skagerrak, and the Kattegat. For example, studies carried out in the 1970s and the 1980s showed a clear increase in biomass along the Swedish Skagerrak coast, in the open Kattegat, and in the Oslofjord. Stations first sampled in 1911–1912 were revisited in 1984. The ophiurid *Amphiura filiformis* had increased in numerical dominance at over 70% of the stations sampled. In general, ophiurids and annelids had increased in dominance, and the majority of species were found to be smaller in size than in earlier surveys.

In the western part of the Wadden Sea, biomass has doubled or tripled over the last 20 years. More than half of the species present contributed to this increase. Some significant changes in the composition of the macrozoobenthos were observed. The proportion of polychaetes increased at the expense of molluscs and crustaceans. Since about 1970, the polychaete *Heteromastus filiformis* has increased in abundance in several subtidal and intertidal sediments (in parts of the Wadden Sea and several estuaries of the Channel such as the Baie de Somme), where it has spread from its traditional muddy habitat to sandy sediments and established itself as a dominant species. In the northern part of the Danish Wadden Sea, an increase in macrozoobenthic biomass of dominant species was observed in the period 1980–1989. In the eastern Dutch Wadden Sea, which does not have a significant discharge of fresh water, no increase was found in macrozoobenthos.

Organic enrichment of muddy sediments, with high organic content, leads to an increase in macrobenthic biomass only up to a certain point. Sediments become anoxic when overloaded with organic matter, which then leads to the death of the benthos. In late summer of the years 1981–1983, 1986, and 1989, oxygen depletion was observed in the bottom water of some areas of the German Bight and off the Danish coast. Bottom fauna died and, in the following year, recolonization took place with pioneer species such as the polychaete *Spiophanes bombyx*. The oxygen deficits occurred after prolonged periods of water stratification when all oxygen in the water below the pycnocline had been used up by microbial and animal respiration without subsequent renewal by bottom currents.

Similar events have been reported from the southeastern Kattegat. Localized significant reductions of *Amphiura filiformis* were also related to hypoxia. Between 1983 and 1988 several dominant infauna species were wiped out. For instance, the trawl catches of Norway lobster (*Nephrops norvegicus*) fell from 10.8 kg/ha to nothing during the period 1984–1989.

In the intertidal area, anoxic conditions have also been reported. Small black areas have recently appeared on some sediment surfaces of intertidal flats in the German Wadden Sea, indicating the presence of anoxic conditions and causing the death of the interstitial fauna.

In order to assess the scale of the observed changes at some sites in the North Sea, data collected on benthos communities through the Monitoring Master Plan (MMP) of the North Sea in 1990–1991 were compared with data collected in 1986 by the ICES Benthos Ecology Working Group and fed into the same database. This preliminary comparison showed that the benthic assemblages seem in general to reflect natural variability within the North Sea, which should be taken into account when assessing anthropogenically induced changes in the North Sea. These changes may be different among the various assemblages. The general distribution of species and trends in biomass, diversity, and density may be explained by the following factors: current patterns and water masses, depth and stratification, surface productivity, sediment distribution and bottom shear stress, fisheries and other human impact, and the history of the North Sea. In other words, effects from anoxia appear to be localized and short-lived.

b) Phytobenthos

Several types of plants have apparently disappeared from stretches of the North Sea coast. Red macroalgae, for example, disappeared from the tidal creeks of the northern German Wadden Sea progressively up to the 1980s. On many North Sea coasts, eel grass (*Zostera marina*) was reduced drastically in the 1930s by the so-called wasting disease and was unable to recolonize the subtidal regions of the Wadden Sea. In the 1960s it also declined in other areas such as the Danish coast and the coast of Brittany. Together with the disappearance of the subtidal vegetation, the associated animals (snails, shrimps, pilefish) disappeared. In a review, Reise *et al.* (1989) summarize a number of possible causes for the changes in eel-grass distribution and abundance in the Wadden Sea. Some of the more recent declines have been linked to nutrient enrichment, which has led to decreased transparency and massive epiphytal growth. Reise *et al.* also suggest that declines in eel grass have coincided with a run of warm summers and mild winters. They conclude that the pattern of changes in distribution and abundance of eel grass is complex and that no definitive interpretation can be offered.

The toxic algal bloom of *Chrysochromulina polylepis* in the Skagerrak and Kattegat in May and June of 1988 resulted in direct drastic effects on both soft-bottom and hard-bottom organisms, from the surface down to at least 15 m. The most pronounced effects were observed in the hard-bottom habitats along the exposed coast, where for the first time macroalgae were observed to be affected by toxicity due to a phytoplankton bloom. Tissues of several red algae, but also brown and green algae, were bleached owing to inhibition of the chlorophylls. However, the effects appeared to be temporary (two to three months' duration).

Other types of phytobenthos, on the contrary, have increased dramatically in number in recent years. Prolific growth of the green algae *Ulva* spp. has occurred on a number of beaches on the north coast of Brittany (Piriou *et al.*, 1991) leaving algal deposits as high as 2 m at the strand line. These 'green tides' occur on sandy beaches with a gentle slope and large surface area, which have a slow turnover of water offshore and a large direct input of nitrogen. In the enclosed, shallow, mudflat-dominated Langstone Harbour on the English coast of the Channel, extensive growth of *Enteromorpha* spp. and *Ulva* spp. occurs. Accumulation of driftweed has been reported at a number of sites along the English coast of the Channel, which is believed to be caused by tidal current concentration. In the Wadden Sea, mass developments of green algae (including *Chaetomorpha* spp.) covering whole areas of tidal flats have occurred from May to September since 1989. In the Skagerrak, interesting successions of communities at fixed sites on coastal subtidal rocks regularly revisited since 1969 have been described by Lundälv *et al.* (1986). Filamentous red algae increased in 1971–1976, and at 5–10 m depth, a dense cover of the brown alga *Halidrys siliquosa* was shown to have declined in 1977, while mussels (*Mytilus edulis*) increased. In 1988 the common starfish (*Asterias rubens*) became abundant feeding on the dead mussels killed by *Chrysochromulina polylepis*. It has been suggested that an increase in phytoplankton density may have reduced the light penetration and water transparency in favour of the red algae. Large quantities have also been washed ashore in the Kattegat since the 1970s. The input of nutrients by man has been blamed (see Chapter 5), but recent studies have shown that some affected areas have recovered.

In other regions, no recent changes have been described in the macroalgal flora. At Helgoland, for instance, the dense *Laminaria hyperborea* forest and the deepest coralline crusts occupy the same levels in the 1990s (respectively, 4–8 m and 12–15 m) as they did in the 1960s.

Box 4·5. *Species alien to the North Sea*

Some alien benthic species and dates of introduction to the North Sea are:

- 1870 Marsh-grass (*Spartina anglica* syn. *townsendii*)
- 1887 Slipper limpet (*Crepidula fornicata*)
- 1890 Clam (*Petricola pholadiformis*)
- 1920 Chinese mitten crab (*Eriocheir sinensis*)
- 1937 Parasitic copepod (*Mytilicola intestinalis*)
- 1946 Barnacle (*Elminius modestus*)
- 1970 Pacific oyster (*Crassostrea gigas*)
- 1973 Japanese seaweed (*Sargassum muticum*) and kelp (*Undaria pinnatifida*)
- 1979 Razor shell (*Ensis directus*)
- 1981 Polychaete worm (*Marenzelleria viridis*)
- 1990 Algae (*Grateloupia doryphora* and *G. filicina*)

Alien species

In the course of the past century, various alien benthic species have found their way into the North Sea. A number of them are listed in Box 4·5. Some at least, for example *Crepidula fornicata*, cause problems and change the ecosystem.

Shipping creates another environmental risk: the spreading of exotic species by ballast water. This problem has been taken up as a subject of study by the International Maritime Organization (IMO). Most species of algae and fauna are killed either in transit or when the ballast water is discharged. Some, however, survive and can be a threat to native species.

Table 4·1. Twenty most abundant fish species in the North Sea in terms of biomass (thousands of tonnes), from analysis of survey records for the period 1977–1986. Source: Daan *et al.* (1990). The total estimated biomass of all species is ca. 12.3 million tonnes.

Demersal species	Biomass, 10^3 t	Pelagic species	Biomass, 10^3 t
Common dab (*Limanda limanda*)	2110	Herring (*Clupea harengus*)	1439
Haddock (*Melanogrammus aeglefinus*)	826	Sprat (*Sprattus sprattus*)	474
Cod (*Gadus morhua*)	670	Horse mackerel (*Trachurus trachurus*)	427
Whiting (*Merlangius merlangus*)	643	Mackerel (*Scomber scombrus*)	349
Saithe (*Pollachius virens*)	585		
Plaice (*Pleuronectes platessa*)	485	Not easily classified*	
Starry ray (*Raja radiata*)	308	Sandeels (mainly *Ammodytes marinus*)	1789
Long rough dab (*Hippoglossoides platessoides*)	227	Norway pout (*Trisopterus esmarkii*)	752
Grey gurnard (*Eutrigla gurnardus*)	206	Spurdog (*Squalus acanthias*)	175
Lemon sole (*Microstomus kitt*)	178	Blue whiting (*Micromesistius poutassou*)	84
Poor cod (*Trisopterus minutus*)	92		
Sole (*Solea solea*)	54		

* These species typically live within a few metres of the seabed but feed predominantly on organisms that live in the water column.

Box 4·6. *Fish classification*

The terms that are used to group or classify fish are often confusing since the classifications may be based on different criteria and may overlap with one another.

Scientifically, fishes, like other animals, are classified to Class, Order, Family, Genus, and Species. The two major classes are the Selachii (sharks, rays, and rabbit-fishes) and the Pisces or Ostichthyes (bony fishes). Representative examples of families with numerous species in the North Sea are Rajidae (rays) and Gadidae (cod fishes).

Fishes inhabiting the water column are called *pelagic fish*, while those living on or near the bottom are *demersal fish*. This classification is convenient, particularly in relation to the fisheries, as pelagic fish are mostly caught by gear like purse seines and drift nets, while demersal fish are most often taken in bottom trawls. Some species, however, are pelagic during the earliest stages of life and later become demersal. Others may shift seasonally, as they feed, for example, on plankton in the upper water layers in summer and on bottom organisms in winter.

The terms *flatfish* and *roundfish* originate from commercial use, particularly in the United Kingdom. Flatfish include many types of species such as turbot (*Psetta maxima*), plaice (*Pleuronectes platessa*), common dab (*Limanda limanda*), halibut (*Hippoglossus hippoglossus*), and sole (*Solea solea*). Roundfish, however, are generally understood to mean gadoids, i.e. fish belonging to the cod family: cod (*Gadus morhua*), whiting (*Merlangius merlangus*), pollack (*Pollachius pollachius*), saithe (*Pollachius virens*), haddock (*Melanogrammus aeglefinus*), etc.

By definition the term *whitefish* refers to the family Coregonidae, which are freshwater fish found in lakes of Northern Europe. In relation to the North Sea, however, the British meaning of whitefish is all commercially important marine fish, except salmon (*Salmo salar*), herring (*Clupea harengus*), and mackerel (*Scomber scombrus*).

Fish

A total of 224 species of fish have been recorded in the North Sea, ranging in size from 5 cm gobies (*Pomatoschistus* spp.) to the 10 m basking shark (*Cetorhinus maximus*). Most of the common species are those typical of shelf seas, although deepwater species are found along the northern shelf edge and in the deepwater channel of the Norwegian Trench and the Skagerrak.

The species of fish found in the North Sea differ widely in abundance, and it is estimated that fewer than 20 species make up over 95% of the total fish biomass. As in other areas, North Sea fish can be broadly classified into pelagic and demersal species, i.e., those that typically live in mid-water and those that live in association with the seabed, respectively (Box 4·6). Based on international surveys, the most abundant species in the North Sea are listed by category in Table 4·1. Many of these species are the object of commercial fisheries, but some that are not normally landed in large quantities, such as the common dab, may be equally abundant (Figure 4·4).

Within the North Sea different depth zones and bottom substrate types tend to have different assemblages of demersal fish species. Two assemblages typified by different relative abundances of saithe, haddock, cod, Norway pout, whiting, and blue whiting in northern and central areas give way to an assemblage typified by common dab, whiting, grey gurnard, plaice, cod, horse mackerel, and sandeels in southern and eastern areas (Figure 4·5).

The spawning grounds of fish that spawn their eggs in the water column (as most species do) are widely distributed over the North Sea. Fish whose eggs adhere to the substrate, e.g., sandeels (*Ammodytes marinus* and *Hyperoplus lanceolatus*) and herring (*Clupea harengus*), use spawning grounds that are more localized and that are determined by the availability of the appro-

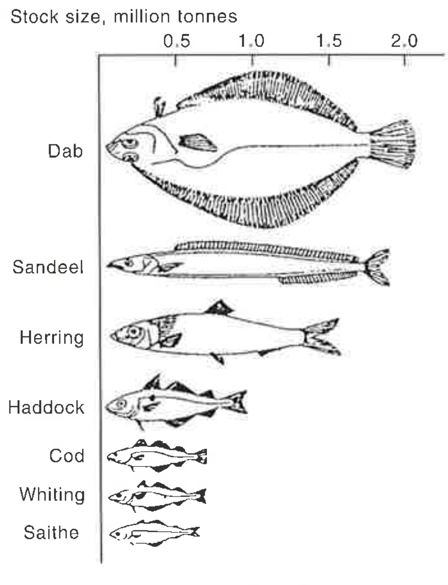


Figure 4·4. Estimates of the fish biomass of the North Sea. Source: Daan *et al.* (1990).

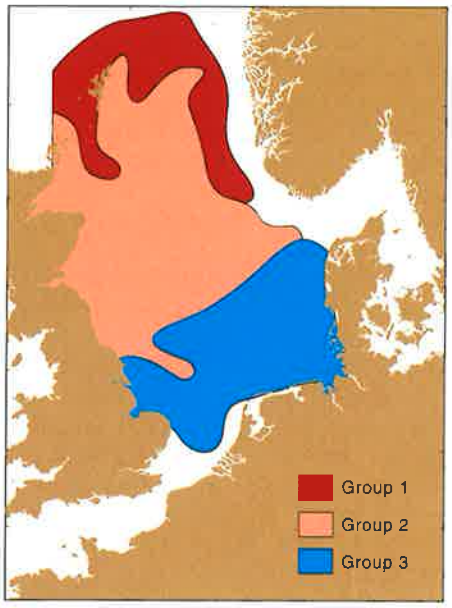
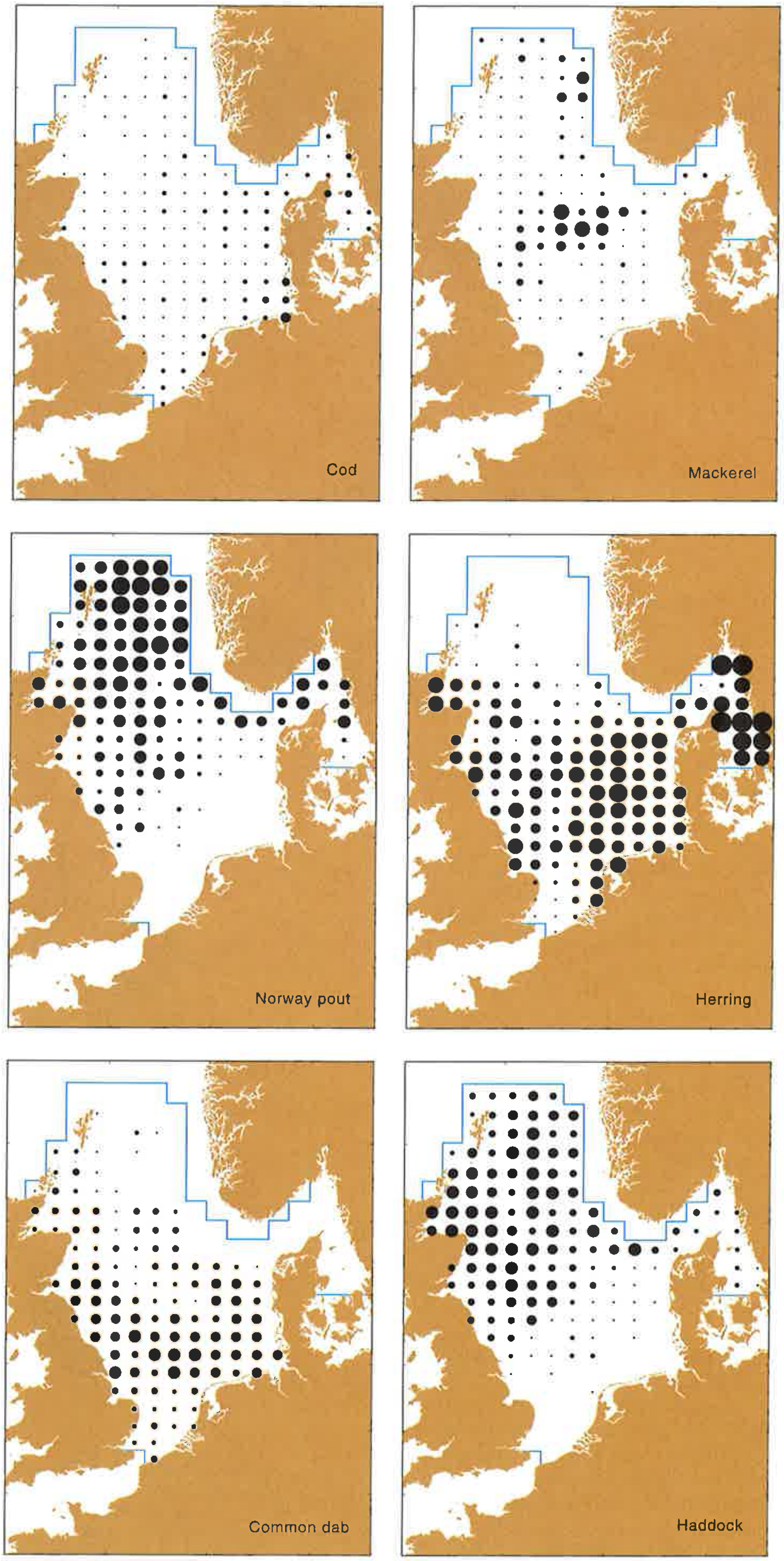


Figure 4·5. Typical North Sea fish assemblages, with species in order of abundance. Source: Daan *et al.* (1990). Refer to Table 4·1 for Latin names of species.

Group 1: Slope edge association: saithe (44%), haddock (12%), Norway pout (11%), whiting (9%), blue whiting (4%), cod (4%), other (16%).
Group 2: Central North Sea: haddock (42%), whiting (14%), cod (9%), Norway pout (5%), saithe (4%), other (26%).
Group 3: Southeastern North Sea: dab (22%), whiting (22%), grey gurnard (13%), plaice (6%), cod (6%), other (31%).

priate habitat. Herring, for example, require well-oxygenated gravel beds that are found in tidally energetic areas in the Channel, between the Orkneys and Shetlands, along the east coasts of Scotland and England, and off southern Norway.

The dispersal of fish larvae until their metamorphosis into small fish at an age of approximately 1–7 months after spawning, depending on species, is determined largely by the pattern of water circulation. As the small fish develop, however, they may concentrate in more localized nursery areas. The shallow coastal margin, especially in the southern North Sea, is an important nursery area for juveniles of many fish species while different areas are important for some other species. Figure 4·6 shows catch rates, indicative of geographical distribution, for six species of young fish in the North Sea.



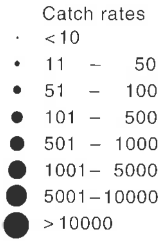


Figure 4·6. Catch rates of 1-group fish (<3 years old in the case of common dab) from the International Young Fish Survey in February, averaged over the years 1983–1987 (except mackerel: 1960–1987, and common dab: 1985). Catch rates are numbers per 10 h fishing for cod and mackerel, and numbers per hour for other species. Source: Daan *et al.* (1990).

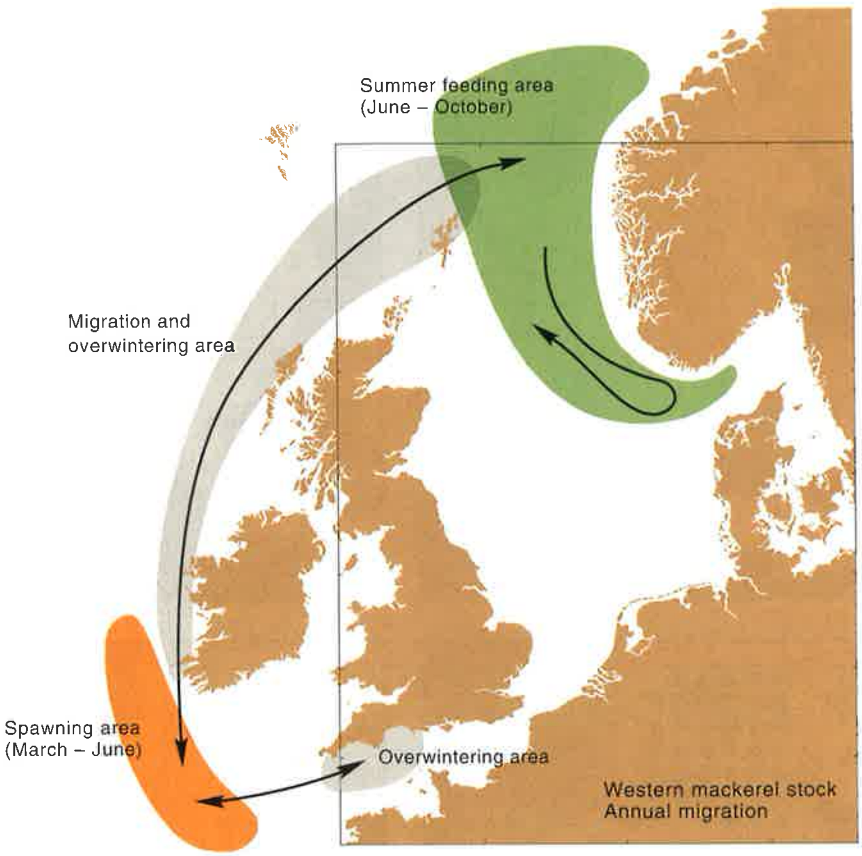


Figure 4·7. General pattern of the annual migration of the Western mackerel stock to the North Sea from spawning grounds along the continental slope. Source: ICES (1990).

Some fish species migrate between the North Sea and adjacent areas, notable examples being mackerel (*Scomber scombrus*) and horse mackerel (*Trachurus trachurus*), which migrate annually to the North Sea from spawning grounds along the continental slope to the west (Figure 4·7). In addition, herring migrate within the North Sea, while adult herring that spawn in the Baltic Sea migrate westwards as far as the eastern North Sea after spawning in spring, and then return in autumn.

Research is in progress to evaluate changes in the abundance of less common species in the North Sea. Studies of commercial fish landings at a port in the Netherlands indicate that catches of a number of species of fish have decreased over the last few decades. These include two species of dogfish (*Scyliorhinus canicula* and *Mustelus mustelus*), rays (Rajidae), conger eel (*Conger conger*), sturgeon (*Acipenser sturio*), and allis shad (*Alosa alosa*) (Bergmann *et al.*, 1991; de Vooys *et al.*, 1991). In addition, the greater weever (*Trachinus draco*) now appears to be locally extinct in the area close to the Dutch coast where the catches are made. Because these studies are dependent on an incentive scheme for reporting catches of rare fish and because fishing areas and practices may have changed, it is difficult to evaluate the extent to which decreases reflect a real decrease in abundance. The species concerned, moreover, are mainly species that are widely distributed in the North Sea and adjacent waters. It is therefore difficult to interpret the significance of, and reasons for, the observed changes.

A number of factors influence the abundance of fish stocks in the North Sea. Most of the demersal species exploited commercially in the North Sea are subject to fishing mortality rates that are among the highest recorded (ICES, 1993a). For cod and haddock, more than half the population present at the start of a year is caught during the same year. High fishing mortality combined with poor recruitment of young fish to the population has decreased some stocks to levels giving cause for considerable concern. The ICES Advisory Committee on Fishery Management has repeatedly advised a reduction in fishing effort on these stocks in the last few years (ICES, 1993a). In the case of herring, the stock was reduced to such a low level

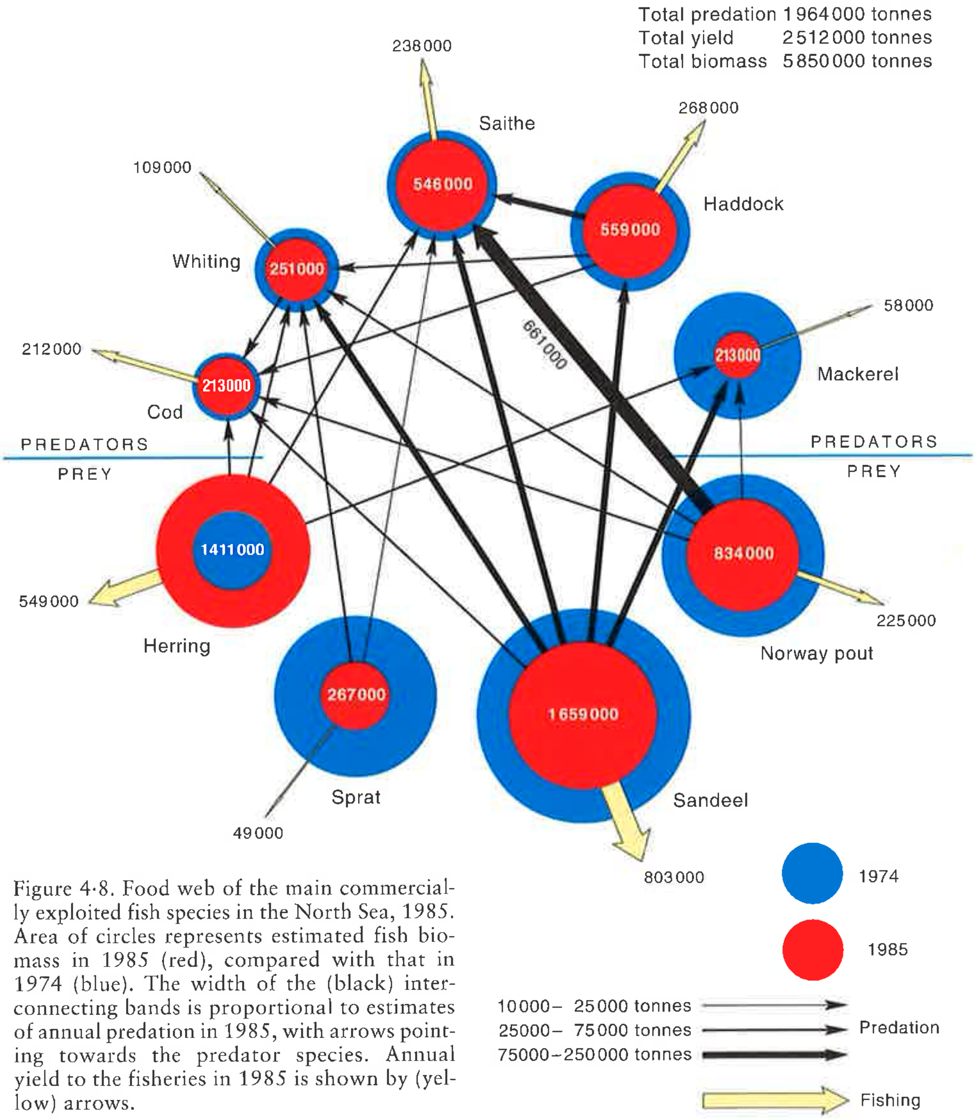


Figure 4·8. Food web of the main commercially exploited fish species in the North Sea, 1985. Area of circles represents estimated fish biomass in 1985 (red), compared with that in 1974 (blue). The width of the (black) interconnecting bands is proportional to estimates of annual predation in 1985, with arrows pointing towards the predator species. Annual yield to the fisheries in 1985 is shown by (yellow) arrows.

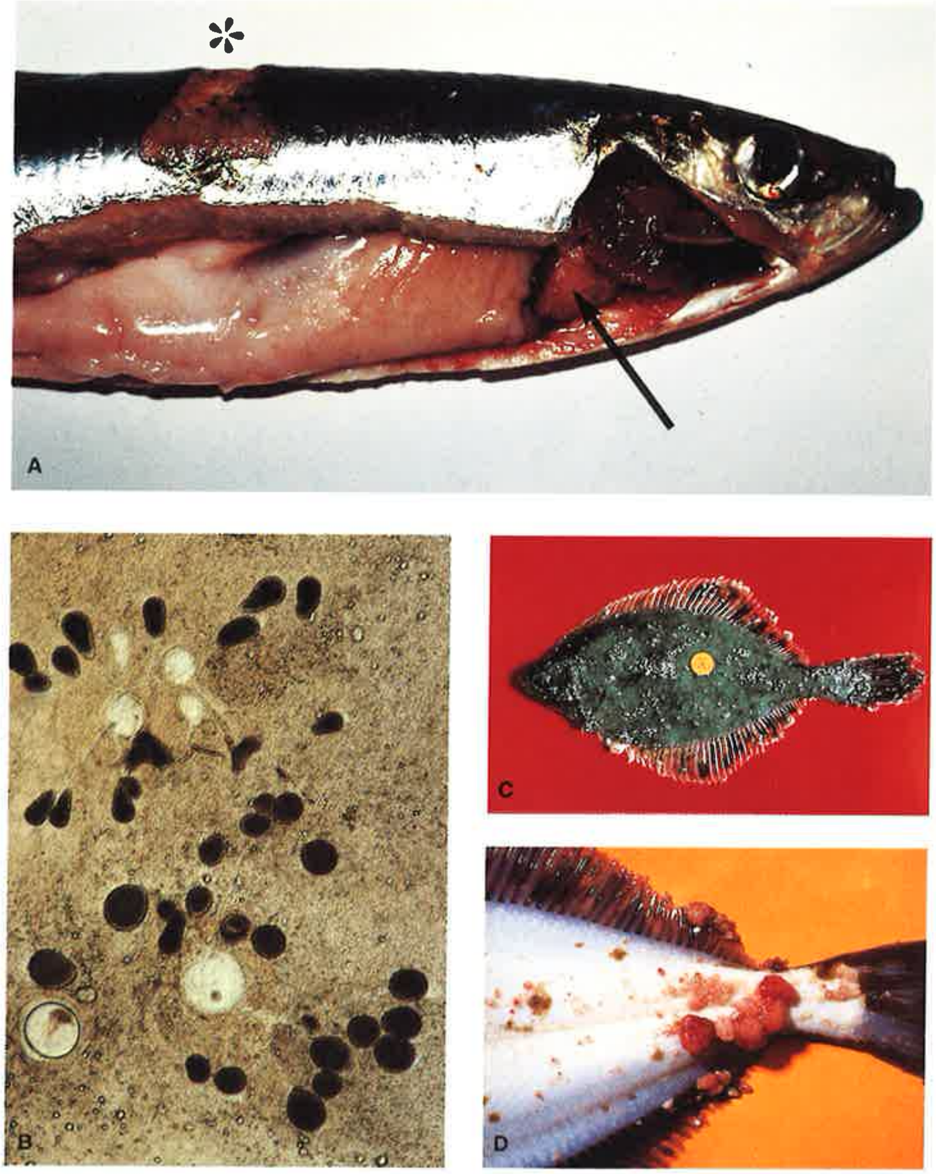


Figure 4·9. Examples of some fish diseases. Source: A and B, IMR, Lysekil, Sweden; C and D, Thalassa Picture Services.

A: Macroscopic signs of *Ichthyophonus hoferi* infection in herring: the arrow points to enlarged heart with white nodules; the asterisk shows a skin ulcer.

B: Hyphal (dark bodies) development of *Ichthyophonus hoferi* in the heart of herring as seen in a light microscope.

C and D: *Lymphocystis* in flounder.

that a closure of the herring fisheries was implemented from 1977 to 1982.

There is considerable variation in the annual recruitment of young fish to the stocks (recruitment means the number of fish that reach a particular age – for example, one year old – each year). The extent of this variation depends on the species concerned. In plaice, for example, recruitment is fairly stable from year to year, whereas for haddock the largest year classes can be 200 times larger than the smallest. This variation in recruitment is largely due to variation in survival during the first year or so of life and has a considerable impact on the size of stocks in any given year.

The causes of annual differences in survival are difficult to establish. However, it is likely that variation in mortality rates due to predation, and variation in the pattern of larval dispersal from the spawning grounds, both play an important role in the survival of the larvae and young fish. A link has been postulated between changes in recruitment to the herring and sprat stocks and in the migration pattern of mackerel on the one hand, and an environmental anomaly in the Northeast Atlantic during the mid-1970s on the other (Corten, 1986). Supporting evidence for such a link has recently been published showing a decrease in the inflow of Atlantic water to the North Sea at this time (Svendsen and Magnusson, 1992). Over the last half century there have been major changes in plankton communities in the North Sea that may also be implicated in the changes in fish stocks (CPR Survey Team, 1992).

In some cases, e.g., North Sea herring, a relationship has been suggested between recruitment and the size of the adult stock that produced those recruits (e.g., review by Bailey and Steele, 1992). As a result of the marked reduction in the spawning stock of North Sea mackerel (ICES, 1992), the production of eggs in 1986 is estimated to have been only 2% of that in the mid-1960s. Thus, it cannot be ruled out that the fisheries themselves have had a direct effect on recruitment through their effect on the spawning stock.

North Sea fish also interact with other marine organisms. One of the principal types of interaction is predation. Many top predators, including marine mammals and many species of seabirds, depend on fish, but by far the most important natural predators on fish are other fish (Figure 4·8). Fish are also subject to infection by diseases and parasites, and there are sporadic reports of mortalities caused by, for example, the fungus *Ichthyophonus* sp. (Figure 4·9) or the toxins associated with paralytic shellfish poisoning. However, occurrences of mass mortality due to such causes are normally local and transitory in nature.

Data from extensive trawling surveys and commercial catch information indicate that the average total fish biomass in the North Sea is around 12 million tonnes (Table 4·1). Estimates of the total annual production of fish (the quantity of new fish produced by growth and spawning each year) in the North Sea vary between five and ten million tonnes. Approximately three million tonnes are taken annually by the fishery, with natural factors (notably predation) accounting for the remaining losses.

Scientific investigations of fish in the North Sea have a history of about one hundred years. Serious concern about the fisheries, notably the North Sea fisheries for flatfish, was expressed during the last twenty years of the nineteenth century. Much of our present knowledge about fish is based on the commercially important stocks of flatfish (plaice and sole), roundfish (cod, haddock, whiting), pelagic fish (herring, mackerel, and sprat), and industrial fish (sandeel, Norway pout) species. Surveys carried out over the last twenty years, however, have provided information on the distribution and abundance of other less well-studied species. Studies of littoral and sublittoral fish communities have also been carried out on a more local basis.

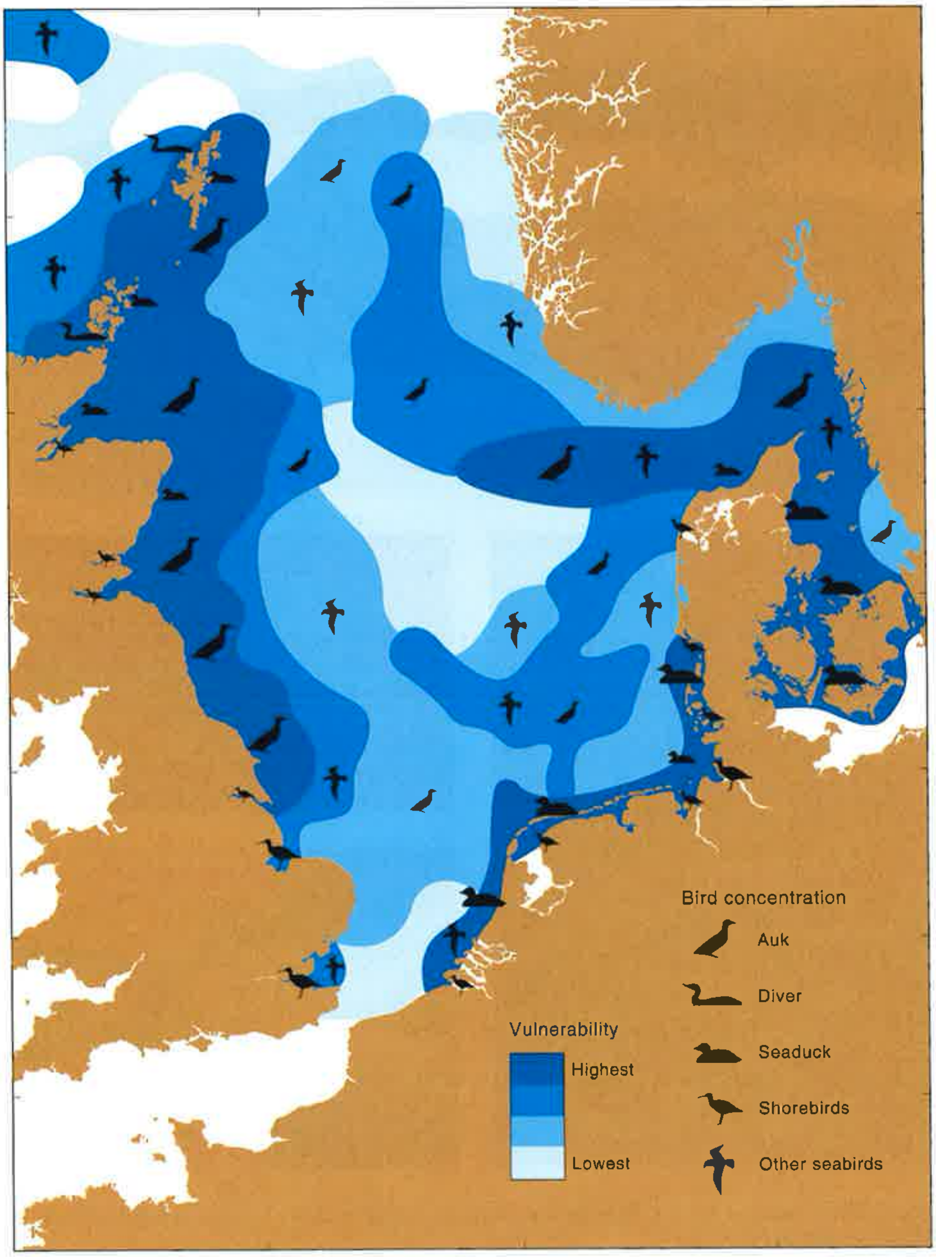


Figure 4·10. Vulnerability of bird populations in the North Sea to surface pollutants (mainly mineral oils) in August. The strength of the shading indicates the level of vulnerability, the bird silhouettes indicate the type of bird in the vulnerable concentration, and the size of the silhouette indicates the scale of importance of the bird concentration. Source: Carter *et al.* (1993).

Table 4·2. Numbers of common seabirds breeding in coastal areas of the North Sea. Source: Dunnet *et al.* (1990). Counts are of pairs, except for guillemot, puffin, and razorbill, which are counted singly.

Species	Number
Kittiwake (*Rissa tridactyla*)	420 000
Guillemot (*Uria aalge*)	680 000*
Fulmar (*Fulmarus glacialis*)	310 000
Herring gull (*Larus argentatus*)	250 000
Black-headed gull (*Larus ridibundus*)	140 000
Puffin (*Fratercula arctica*)	230 000*
Arctic tern (*Sterna paradisaea*)	77 000
Common gull (*Larus canus*)	76 000
Common tern (*Sterna hirundo*)	72 000
Lesser black-backed gull (*Larus fuscus*)	53 000
Gannet (*Morus bassanus*)	44 000
Razorbill (*Alca torda*)	73 000*

*number of individuals.

Birds

Some ten million seabirds are present in the North Sea at most times of the year. In summer more than four million seabirds of 28 species breed along the coasts of the North Sea. During autumn many species leave the area, but are replaced by visitors from northern and western waters. The bird migrations and seasonal shifts in distribution are pronounced. In broad terms, seabirds move southwards or towards the coasts in winter, and northwards and offshore again in summer.

In addition to the seabirds, many shorebirds, such as wading birds and ducks, feed on mud flats and sand flats or other intertidal areas along the coast. The southern shores have favourable conditions due to the large tidal amplitude and relatively mild climate, which prevent the mud flats from freezing for most of the winter. The Wadden Sea is of particular importance both for breeding bird populations and for migratory birds. Six to 12 million birds of more than 50 different species utilize the Wadden Sea at many times of the year. Coastal waters of the United Kingdom are also of importance as wintering and migratory staging areas for waterfowl, particularly when waters on the eastern shores of the North Sea freeze.

An offshore and an inshore group may be identified among the seabirds. The offshore group includes members of several families, most notably the fulmars, petrels, gannets, some gulls, and most auks. These birds breed on the coasts of the North Sea and the Channel, but frequently feed far offshore. Inshore birds include the seaducks, divers, cormorants, and terns. Some gull species and the black guillemot (*Cepphus grylle*) are also included in this group. These birds normally live within sight of land.

Many of the seabirds of the North Sea are present in numbers that represent substantial proportions of their world population, although none is endemic. The North Sea coasts support over 50% of the biogeographic populations of common terns (*Sterna hirundo*) and great skuas (*Catharacta skua*), and a further 12 species are present in numbers exceeding 10% of their biogeographic populations (Table 4·2).

Most seabirds are predators at or near the top of food chains. The majority eat fish both live and as discards and offal, some feed on benthos, and a few consume zooplankton. Few data exist on seabird diets in quantitative terms.

Seabirds are generally characterized by high annual survival rates (long lifespans), delayed maturity, and relatively low reproductive rates. This results in slow population changes and survival of adults even during periods of low abundance of suitable food (Figure 4·10).

Counts of bird populations breeding on United Kingdom coasts indicate an increase in number during recent decades (Figure 4·11), and in some cases,

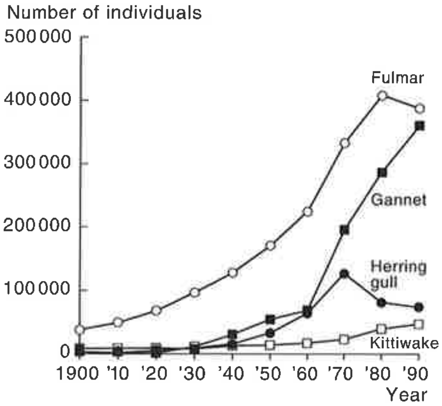


Figure 4·11. Changes over time in selected bird populations of the North Sea. Source: ICES (1994).

an expansion of range. Between 1969/1970 and 1985/1986 fulmar (*Fulmarus glacialis*), gannet (*Morus bassanus*), lesser black-backed gull (*Larus fuscus*), and guillemot (*Uria aalge*) increased by about 100%, while great skua and Arctic skua (*Stercorarius parasiticus*) increased by 150 and 220%, respectively. During the same period some species, e.g., roseate tern (*Sterna dougallii*), herring gull (*Larus argentatus*), and black-headed gull (*Larus ridibundus*), declined. In other areas, such as the Wadden Sea, the majority of the changes are increases.

Mammals

Estimated numbers of seals and harbour porpoises in the North Sea are shown in Table 4·3.

Seals

Two seal species breed along the coasts of the North Sea: the common or harbour seal (*Phoca vitulina*) and the grey seal (*Halichoerus grypus*) (Figure 4·12). Occasionally, stray ringed seals (*Phoca hispida*) and harp seals (*Phoca groenlandica*) are observed. In 1988, phocine distemper virus (PDV) led to major mortality among, mainly, harbour seals and, to a lesser extent, grey seals in the North Sea region (a total of approximately 16 000 seals), raising questions about the subsequent viability of the affected populations, and whether it would be possible to detect a relationship between the burden of contaminants, the health of stocks, and viral attack. Although there has been no conclusive evidence of an association between environmental contamination and the extent and severity of the epidemic, concern has been expressed that one may exist because evidence is accumulating from studies of other mammalian species about the potentially detrimental effects of organohalogens on reproduction and resistance to disease.

Although the harbour seal is one of the most widely distributed seal species in the world, the North Sea contains around 10% of the world population. The North Sea population of harbour seals is approximately 28 000. Broadly speaking, the harbour seal frequents estuaries and coasts where offshore banks and rocks are exposed at low tide. Diet, important in relation to transfers in the food chain, appears to vary according to the abundance of prey species. For example, an investigation in the Cromarty Firth, Scotland, illustrates that the seals switched from clupeids in 1988/1989 to gadoids and sandeels in 1989/1990, and shows a general increase in cephalopod prey from 1988 to 1991. Seasonal and yearly changes in the diet reflect changes in the local abundance of different fish species. Feeding sites also change. In the Wadden Sea area the harbour seal prefers flatfish species. The peak in pupping of the harbour seal usually occurs in late June, but may vary seasonally and geographically.

In the northern North Sea there is no evidence of population change in Norway or at Orkney, Scotland. In the Oslofjord, the area of Norway most affected by the 1988 disease outbreak, there were 102 harbour seals, including 26 pups, in 1991. At Shetland, the latest count (1991) is much lower than expected in relation to the previous count in 1984, but it is not clear if this

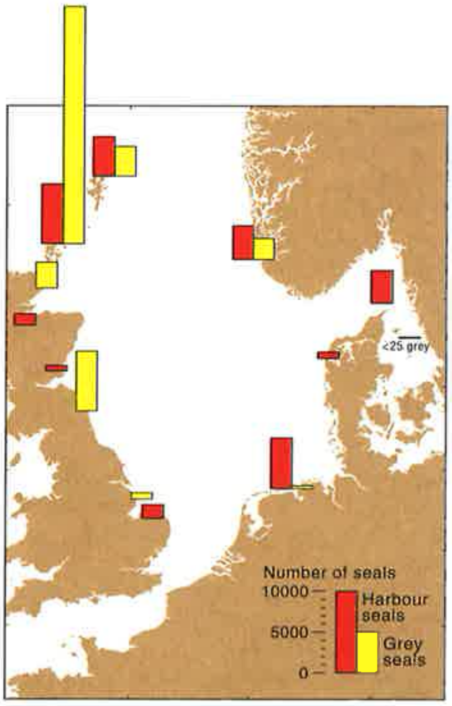


Figure 4·12. General distribution of the harbour seal (*Phoca vitulina*) and the grey seal (*Halichoerus grypus*) in the North Sea.

Table 4·3. Estimated numbers of seals and harbour porpoises in the North Sea in 1991. Source: ICES (1993b).

		Estimated number
Harbour seal (*Phoca vitulina*)		
Norway	Entire coastline	4 200
United Kingdom	Orkney/Shetland	12 000
	East Scotland	1 800
	East England	1 800
Wadden Sea		6 090
Danish Limfjord		750
Kattegat/Skagerrak		3 900
Grey seal (*Halichoerus grypus*)		
Norway	Entire coastline	4 200
United Kingdom	North Sea	43 600
Wadden Sea		250
Kattegat		< 25
Harbour porpoise (*Phocoena phocoena*)		
Northern North Sea		82 600

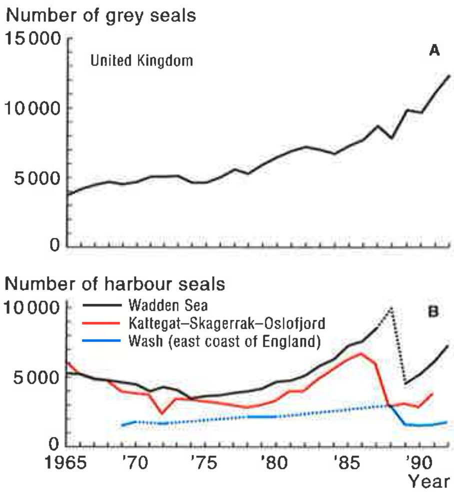


Figure 4·13. Long-term trends in seal populations.
A: Estimates of pup production for grey seal (*Halichoerus grypus*) breeding sites on the North Sea coast of the United Kingdom. Source of data: Sea Mammal Research Unit (UK).
B: Number of harbour seals (*Phoca vitulina*) in the North Sea, excluding Scotland and the west coast of Norway for which no detailed time series are available.

Table 4·4. Maximum numbers of harbour seals counted in the Wadden Sea area, 1987–1992. Source: Common Wadden Sea Secretariat.

Year	Denmark	Schleswig-Holstein	Nieder-sachsen	Netherlands	Total
1987	1400	3793	2245	1054	8492
1988*					
1989	870	1750	1400	535	4555
1990	1048	1974	1620	559	5201
1991	1097	2313	1924	750	6084
1992	1168	2861	2255	960	7244

*Data for 1988 are unreliable, owing to mortalities associated with the phocine distemper virus.

is due to a real decline or to a change in the haul-out (coming out of the water onto rocks or beaches) behaviour of the seals. For the rest of the North Sea, the population in 1991 was approximately 14 000 seals. At reference sites in eastern Scotland and eastern England the population was not affected by the epidemic. In contrast, the Wadden Sea harbour seal population was reduced from 10 000 before to 4000 individuals after the epidemic. From 1989 to 1992 the population recovered to some 7000 animals (Table 4·4). Seal numbers have also increased markedly in the Kattegat/Skagerrak, fulfilling recovery predictions made on the basis of changes in age structure following the 1988 disease outbreak. On balance, therefore, harbour seal populations have either not changed or have increased since 1988 (Figure 4·13B).

Grey seals have a more limited distribution than harbour seals. Approximately 40% of the world population breeds in European waters, mostly on remote islands around the coasts of the United Kingdom (Table 4·3). Grey seals produce their pups in autumn. The total number of pups born in colonies in the North Sea (particularly those at Orkney) has been increasing steadily for the last 20 years (Figure 4·13A). The total population of grey seals in the North Sea in 1991 was estimated at approximately 43 000. Radio-tracking has shown that adult grey seals regularly travel distances of 250 km between haul-out sites, and more than 50 km out to sea, apparently to feed. In the North Sea, the most prevalent food species of the grey seal are sandeels and larger gadoids, especially cod and, to a lesser extent, whiting.

Cetaceans

The harbour porpoise (*Phocoena phocoena*) is the most common cetacean species in coastal waters, particularly in the north and west. It feeds on a variety of fish and cephalopods. In some parts of the North Sea, there has been a decline in sightings in inshore waters. Population sizes and trends in the North Sea and the Kattegat/Skagerrak are largely unknown. However, analysis of sightings indicates that the harbour porpoise no longer frequently inhabits the Wadden Sea and the southern North Sea, but is still common in winter along the Danish, German, and northern Dutch North Sea coasts, in summer east of England, and throughout the year in the northern North Sea.

The white-beaked dolphin (*Lagenorhynchus albirostris*) is the most common cetacean species in the southern North Sea. It has been suggested that this species breeds off the Dutch coast in June and July, and migrates to waters of the United Kingdom to feed on herring and mackerel.

The bottlenose dolphin (*Tursiops truncatus*) has been recorded at low density throughout the North Sea. However, animals are observed year round at a number of sites, notably: the Moray Firth in Scotland; on the Cornish, Dorset, and Hampshire coasts of England; and at locations in Brittany and Normandy.

Other species of toothed whale that are sighted regularly in the North Sea include the long-finned pilot whale (*Globicephala melas*), the common dolphin (*Delphinus delphis*), the white-sided dolphin (*Lagenorhynchus acutus*), Risso's dolphin (*Grampus griseus*), and the killer whale (*Orcinus orca*). Of the baleen whales, only the minke whale (*Balaenoptera acutorostrata*) is sighted regularly in the North Sea.

Strandings of marine mammals are systematically recorded in several countries bordering the North Sea. Sighting and stranding records are helping to elucidate the current state of populations in the North Sea and their distribution and migration patterns. However, investigations are still in such an early stage that definite statements cannot yet be made about any species. Several collaborative projects are under way to determine the causes of death of stranded cetaceans as well as to build up a comprehensive picture of the health and biology of cetaceans in the North Sea.

4.3.

Interrelationships

Description of main communities

An essential aspect of protecting the living organisms and habitats of the North Sea is the identification of sites and species of importance for nature conservation. A structured approach is needed in order to describe the habitats and assemblages of species that are typical of any particular area. The concept of 'community' provides the basis for a structured description of marine sites and the changes they may undergo over time. The term 'community' applies to groups of animals and plants, particularly with respect to their biological relationship with a particular habitat. The habitat types in which specific communities develop may be separated according to their physical characteristics (such as substrate type, topography, and currents) and chemical characteristics (such as salinity, nutrients, and contaminants).

In general, the North Sea may be described as a region influenced by the land masses in its vicinity, with water depths of less than 200 m, in which there is interaction between the water column and the seabed. Coastal communities are complex but vulnerable as they are situated at the interface between terrestrial and marine ecosystems where human impact is the most intense. Humic substances and elements introduced with freshwater run-off from land are important for phytoplankton production. Their concentration is higher in shelf waters than in the open ocean. Organic detritus from the plankton in surface layers sinks to the sea bottom where it becomes the food of benthic bacteria and fauna and ultimately feeds demersal fish. The near-bottom water becomes enriched with mineralized compounds as a result of these processes, and in winter, when water stratification does not persist, it is recycled to the surface. In the zone from high-tide level to about 30 m water depth, the water column remains fully mixed all year round, and live plankton is transported continuously by turbulence from the surface layers to the bottom and back, coming within reach of the benthos. A wide variety of different benthic communities exists in this zone. Well-lit rocky bottoms are often covered by macroalgae, while poorly lit regions are dominated by sessile macrofauna. Owing to improvements in scuba-diving equipment over the last decade, greater knowledge has

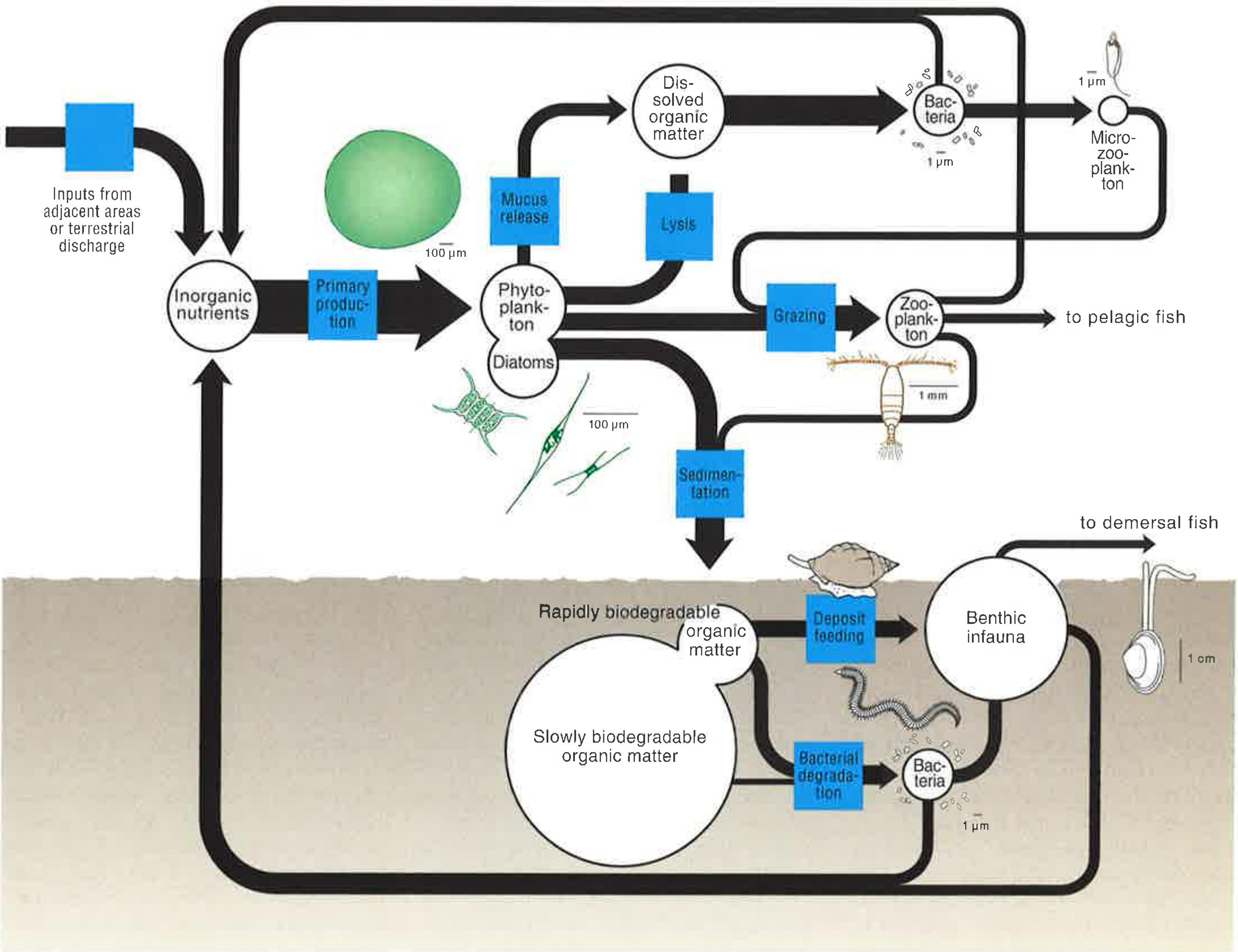


Figure 4·14. Major fluxes of nutrients through the lower trophic levels of a coastal ecosystem. Source: Fransz *et al.* (1991).
This simplified diagram of part of the food web gives an indication of the appearance and relative sizes of typical organisms (see scale bars), the biomasses of the components (size of circles), the pathways for transfer of nutrients between them, and the rates at which these transfers take place (width of arrows).

been gained about sublittoral hard-substrate communities dominated by kelps and the associated red algae. Gravel and sandy bottom communities occur wherever strong tidal currents prevail.

The boundary between terrestrial and marine ecosystems is inhabited by communities that are influenced by the sea only when very high tides or high onshore winds occur. Intertidal rocky-shore communities include a restricted variety of species, except on the lower shore, and show a marked zonation in relation to the degree of tidal immersion. Muddy and sandy intertidal sediments contain a variety of specialized organisms. Such communities develop extensively in the Wadden Sea, the Wash, and the Baie du Mont-Saint-Michel. These sites are of prime importance for wading birds, ducks, and other coastal species. Estuarine sites also provide shelter and food for spawning fish. Salt marshes are found in the upper reaches of sheltered intertidal areas. They display rich and often unique populations of marine plants and animals.

The various benthic communities have an important position in the food web which leads to exploitable production. Resting stages of many phytoplanktonic and zooplanktonic organisms overwinter on the seabed and repopulate the surface layers in the spring and summer. The processes of benthic–pelagic coupling are specific to the shelf sea environment and work together to make the North Sea very productive.

The North Sea as defined by the North Sea Task Force includes a small area of 'Oceanic Province' in the northwest, where waters are deeper than 1000 m. Organic detritus produced by phytoplankton and zooplankton in the surface layers of the oceanic province may be broken down in the water column, but otherwise sinks to the deep-sea bottom where mineralization by deep-sea bacteria and deep-sea fauna takes place. The resultant carbon dioxide, nutrients, and trace elements are then transported throughout the ocean in the deep-water circulation, and there is no direct recycling back to the surface of the North Sea.

Food chains/webs

The production of organic compounds from inorganic sea-water constituents is brought about by the photosynthetic activity of marine plants using energy derived from sunlight. These organic compounds are usually incorporated as plant tissue, which is of major importance as the primary source of food for animals. Most of the primary production in the North Sea is carried out by phytoplankton, although large marine algae growing in shallow water also play a part. Food-web pathways in a generalized North Sea coastal ecosystem are shown in Figure 4·14. It should be noted, however, that the flow of energy to the highest trophic levels can be more or less efficient within the food chains depending largely on the composition of the plankton community present.

In the deeper offshore areas of the North Sea, macroalgae become less important, and here it is almost exclusively phytoplankton photosynthesis that fuels the food chain. In general, phytoplankton production is not as high in the open North Sea as in the coastal zone. There are, however, a number of recent reports that suggest that the Dogger Bank area and its surroundings may exhibit higher primary production and more efficient energy transfer within the food chain than other regions of the open North Sea (Heip *et al.*, 1992), possibly owing to the particular hydrographic features that are dominant in this area. The special circumstances around the Dogger Bank may influence local contaminant distributions. Transfer of energy within the water column takes place through consumption of phytoplankton by zooplankton and, in turn, planktivorous fish by carnivorous fish. In addition, bacteria that are dependent on organic matter are consumed by small flagellates, which are eaten by microzooplankton, which are then eaten by larger zooplankton. Defecation and death at all stages in the planktonic food web supply organic detritus to bottom feeders. This organic matter is utilized by bacteria, microfauna, meiofauna, and then macrofauna. Deposit feeders in turn are consumed by predatory worms in the sediment and by predators/scavengers amongst bottom-feeding fish and by mobile epifaunal species, including crabs, bivalve molluscs, and starfish (Subregion 7b). Large stocks of pelagic copepods develop only in the northern North Sea, where they consume the summer production of phytoplankton; this may explain the low biomass of infauna in the northern North Sea.

The most prominent feature of the energy pathway in coastal waters is the close coupling of benthic and pelagic systems, and yet in the past these two systems have largely been studied separately. The general pathway in benthic systems, derived from case studies in the Channel, underlines the importance of allochthonous (originating from land or other sources) organic matter as a food supply to the benthos. A large proportion of the energy input is consumed by the bacteria which itself constitutes an important food source for meiofauna. The total demand of benthic consumers is significantly lower than the supply of energy. Even if a part of this surplus (the fraction of input energy not used by the food web) is buried, the major fraction may be exported to adjacent sea areas. Pelagic food-web dynamics in coastal areas indicate the role of the microbial grazers (protozoans, microzooplankton, bacteria) as the major link between planktonic primary production and mesozooplankton. Studies in the well-mixed waters of the western Channel suggest that regenerated production accounts for about 70% of annual production. This proportion is much higher than that in several other coastal ecosystems and may be an indicator of the importance of the microbial loop in Subregion 9.

Identical paths of energy transfer are present in the intertidal and shallow ecosystems. In the benthic food web, energy is transferred along the following pathway: microphytobenthos – bacteria – meiobenthos – macrozoobenthos – flatfish/birds – harbour seal. In the pelagic food web the pathway comprises phytoplankton – zooplankton – pelagic fish – fish-eating birds. In both the pelagic and benthic systems a microbial web is present in which organic matter is mineralized or transformed from organic matter into particulate organic matter by bacteria. It appears that the role of the so-called microbial food web is much more important than was assumed earlier (Billen *et al.*, 1990). Energy flow through the ecosystems of the Wadden Sea is highly dependent on the characteristics of the different parts of the sea that can be distinguished geomorphologically (intertidal:subtidal ratio) or hydrographically (degree of exchange with the North Sea; amount of input of fresh water and nutrients). In such coastal areas and estuaries, shrimps are of major importance as food for fishes, especially gadoids and flatfish. Conversely, adult shrimps and crabs are important predators of recently settled flatfish (1 to 2 cm). Shrimps are therefore keystone species in inshore and estuarine food webs. Suspension-feeding bivalves can very effectively crop phytoplankton from the water column (equivalent to the entire volume of a large marine bay being pumped over the gills of its cockle and mussel population every three or four days). They adapt quickly to increased nutrient loads and are thus a buffer against eutrophication. Many of the important shellfish species are exploited by nearshore fisheries that, especially in bivalve fisheries, may compete with predators such as eider ducks, common scoters, and oystercatchers.

The great significance of euphausiids makes the food web in the Norwegian Trench different from those of the shallow North Sea plateau. Euphausiids and caridean shrimps are prominent food sources of the gadoids. Only cod and haddock depend strongly on shrimps and other epibenthic crustacea and other benthos. Hence the most abundant fish species are primarily supported by a predominantly pelagic food chain where energy and matter flow from phytoplankton through euphausiids to fish.

Production

The minimum light intensity for photosynthesis is about 1% of the irradiation at the sea surface. Such intensity occurs down to 30 m water depth in the clear waters of the central North Sea, but no deeper than 10–15 m in the less transparent coastal waters of the southern North Sea. As most of the North Sea benthos lies deeper, phytobenthos (macroalgae, sea grasses, and microphytobenthos) contributes only little to the primary production of the North Sea.

Primary production in the sea is mainly carried out by photosynthetic phytoplankton. Estimates of the production at all levels of the marine food chain are imprecise because of difficulties with methods and definitions, and because of variability between areas and seasons. There have been no surveys to estimate primary production for the whole North Sea over an annual cycle, although the area south of 55°30'N was covered recently. The average annual primary production of the North Sea is probably in the range 150–250 g C/m^2 per year. In coastal areas the annual production can reach values of 400 g C/m^2 per year (Cadée, 1992). However, the phytoplankton biomass and production off the north-east coast of England are clearly much less than in central regions of the North Sea, but the reasons are not known.

The average annual production of copepods in the North Sea is 5–20 g C/m^2 per year, macrobenthos production is about 2.4 g C/m^2 per year, and fish production about 1.8 g C/m^2 per year. Direct production measurements of North Sea meiofauna do not exist, but indirect information based on respiration, body weight, and life history can be used to estimate an energy consumption of about 10 g C/m^2 per year. Benthic mineralization is important compared with mineralization in the pelagic compartment. Recent measurements show that benthic bacterial production in the surface layer of North Sea sediments is at about the same level as benthic community respiration. Therefore bacterial carbon demand must exceed total carbon input into the sediment, and internal recycling is essential. The contribution of meio- and macrofauna respiration to community carbon mineralization is probably relatively small, although macrofaunal bioturbation enhances bacterial production.

Of the total fish production, roughly one third is consumed by fish, one third is lost to other predators, disease, etc., and the remaining third is caught by fisheries (Daan *et al.*, 1990). Recent average annual landings of fish from the North Sea, Skagerrak, Kattegat, and Channel have been just over three million tonnes, plus a quarter of a million tonnes of invertebrates. This may be compared with average fish landings for the whole Northeast Atlantic of 9.4 million tonnes plus invertebrate landings of half a million tonnes. The total landings per unit area are among the highest for North Atlantic shelf areas.

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