

Chapter 14

Ecosystem function at low biodiversity – the Baltic example

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Abstract

For a marine area, the Baltic Sea has a uniquely low species diversity, due to its low salinity, recent geological origin and harsh climate. Its flora and fauna consist of a mixture of marine, freshwater and brackish-water species. The three major basins of the Baltic Sea, from south to north, have quite stable surface salinities of 6–8 psu in the Baltic proper, 5–6 psu in the Bothnian Sea and 2–4 psu in the Bothnian Bay.

A comparison of Steele's (1974) carbon flow model of the high diversity North Sea ecosystem, with Elmgren's (1984) carbon flow calculations for the Baltic Sea shows great similarity for the Baltic proper, and similar, but proportionally reduced, flows in the Bothnian Sea. Only the Bothnian Bay has a markedly different carbon flow pattern, due to a near-total absence of benthic filter-feeders. Only when a major functional group was lost, was there a drastic alteration of ecosystem function. The Baltic example suggests we should not claim without good proof that high biodiversity is needed to 'maintain ecosystem function'.

The possibility remains that low diversity may destabilise ecosystem function, even without the loss of major functional groups. With fewer species in each functional group, there is a greater risk that the loss or drastic reduction of a single species may affect ecosystem processes. Published data on ecosystem variability over time and on ecosystem resilience under experimental stress are not yet sufficient for testing this hypothesis in the Baltic Sea.

The Baltic also has fewer species of commercial interest than the North Sea, with a lower average value per unit of catch weight. The recent catastrophic decline in Baltic cod catches vividly illustrates the vulnerability of a fishery with few alternative target species.

14.1 Introduction

The discussion of biodiversity has to a large extent centred on areas of particularly high biodiversity, on threats to that biodiversity, and on efforts at protecting it. Yet it is often studies of simple systems that help us understand complex phenomena. Thus, to understand the causes and effects of biodiversity and its loss, it may be useful to also study areas of intermediate and low natural biodiversity.

The Baltic Sea is an area of exceedingly low natural biodiversity. In the following, we discuss mainly species diversity, but also touch upon genetic diversity and diversity at high taxon level. We first present the Baltic biota, and the causes of its poverty, and then discuss how its low biodiversity influences the way in which the Baltic ecosystem functions, as exemplified by an overview of its major carbon flows and its fisheries yield. Finally, we ask what light studies of the Baltic Sea ecosystem may throw on the general biodiversity debate.

14.2 Abiotic conditions in the Baltic Sea

The Baltic Sea (see map, Fig. 14.1(a)), excluding the Kattegat and the Danish Sounds, covers 373 000 km² and has a volume of 20 500 km³. It is a semi-enclosed sea, that is connected to the Kattegat, and indirectly to the North Sea, only through the narrow Danish straits. Some 500 km³ of seawater enters the Baltic each year through these straits, and about the same volume of freshwater reaches the Baltic each year from land, and as excess of precipitation over evaporation. The sum, roughly 1000 km³ of brackish water, leaves each year, giving a water residence time on the order of 20 years.

The Baltic may be viewed as a huge, atidal estuary, with the salinity of the surface waters varying from 10 psu in the Arkona Sea, just inside the Sound, to about 7 psu in the northern Baltic proper, 5–6 psu in the intermediate Bothnian Sea and only 2–4 psu in the northernmost basin, the Bothnian Bay. (psu is the practical salinity unit, based on seawater conductivity, and has approximately the same value as the older, weight-based unit ‰). The salinity of the surface water varies relatively little over time. During intermittent inflows of North Sea water the salinity of the bottom water in the Arkona Basin may reach over 20 psu (Voipio, 1981).

The inflowing seawater is denser than the brackish surface water of the Baltic, creating permanently stratified conditions in the Baltic proper.

In the main basin, a primary halocline is found at 60–80 m, and there are secondary ones at greater depths, where the bottom water is exchanged only intermittently, following large inflows of seawater of particularly high density. In recent decades, the deep, more saline waters of the Baltic proper have become largely devoid of oxygen, as a result of a combination of long periods without deep-water exchange and an increasing rate of oxygen consumption due to eutrophication (Elmgren, 1989).

14.3 Baltic biodiversity: Patterns and causes

It has long been known that the Baltic has fewer plant and animal species than fully marine areas. Lovén (1864) identified low salinity as the primary cause of this biological poverty. The effects of salinity on the Baltic biota were extensively reviewed by Remane & Schlieper (1971), who also described some of the proximate, physiological reasons why so many marine and freshwater species are excluded from the intermediate salinities of the Baltic Sea. Dahl (1956) discussed the main ultimate (evolutionary) cause of low biological diversity in brackish waters, i.e. that such waters depend on a delicate balance between the supply of seawater and freshwater, a balance unlikely to remain relatively constant long enough to allow a distinct, species-rich flora and fauna to evolve.

Pleistocene history has exacerbated the species poverty of the Baltic Sea. Glaciations forced the European brackish-water fauna through a series of long-distance migrations up and down the European coastline (Wolff, 1973), with a gradual loss of species as a result. Since the last glaciation, the Baltic has gone through several freshwater and marine stages (the freshwater Baltic Ice-Lake, the Yoldia Sea, the freshwater Ancylus Lake and the Littorina Sea). Each meant a drastic reorganisation of the biota. The last change from lake to sea occurred only about 7000 years ago, and the present brackish-water stage is only 2–3000 years old (Voipio, 1981).

The climate of the northern part of the Baltic Sea area is harsh. The Bothnian Bay is covered with a thick layer of ice for almost half the year, and in particularly cold years the entire Baltic Sea may be ice-covered. The severe climate is thought to exclude some brackish-water animals from the northern Baltic (Segerstråle, 1972). Scouring by ice prevents perennial plants from becoming established in shallow waters (Wallentinus, 1991).

The Baltic fauna and flora consist of a mixture of marine, brackish-

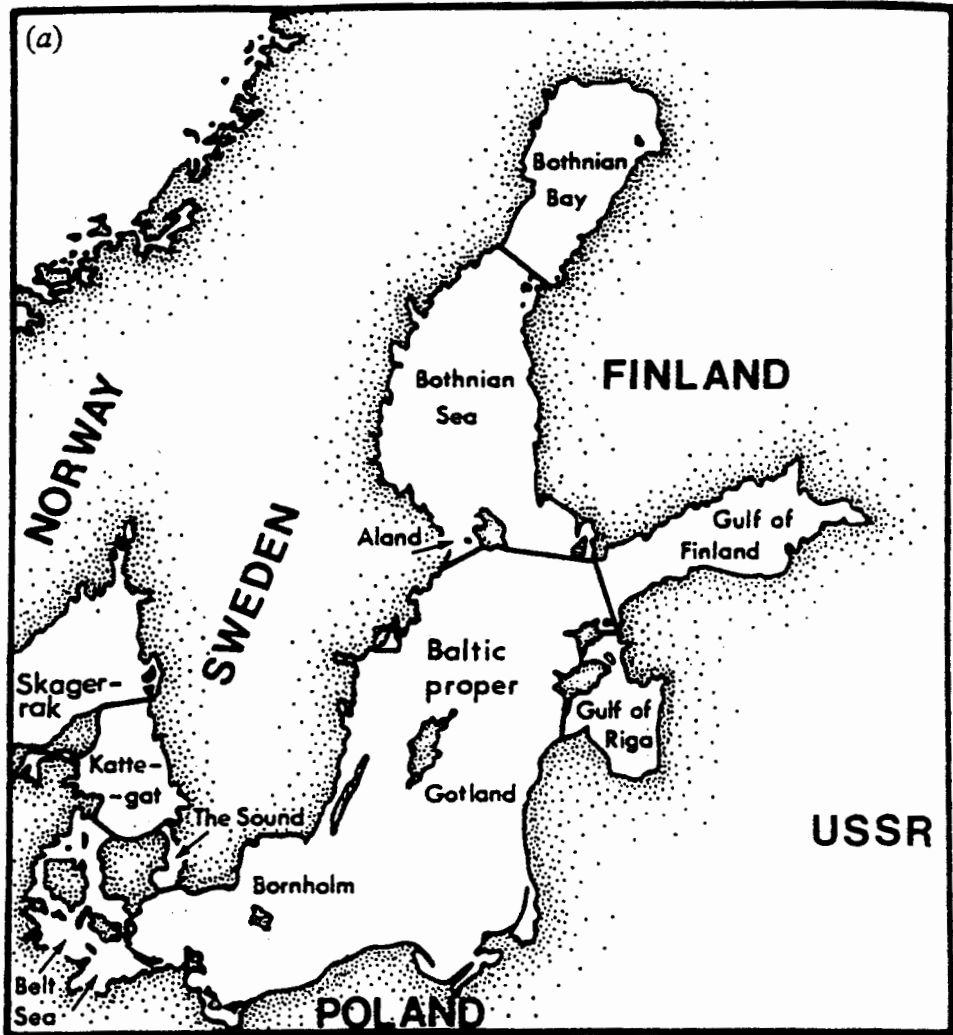
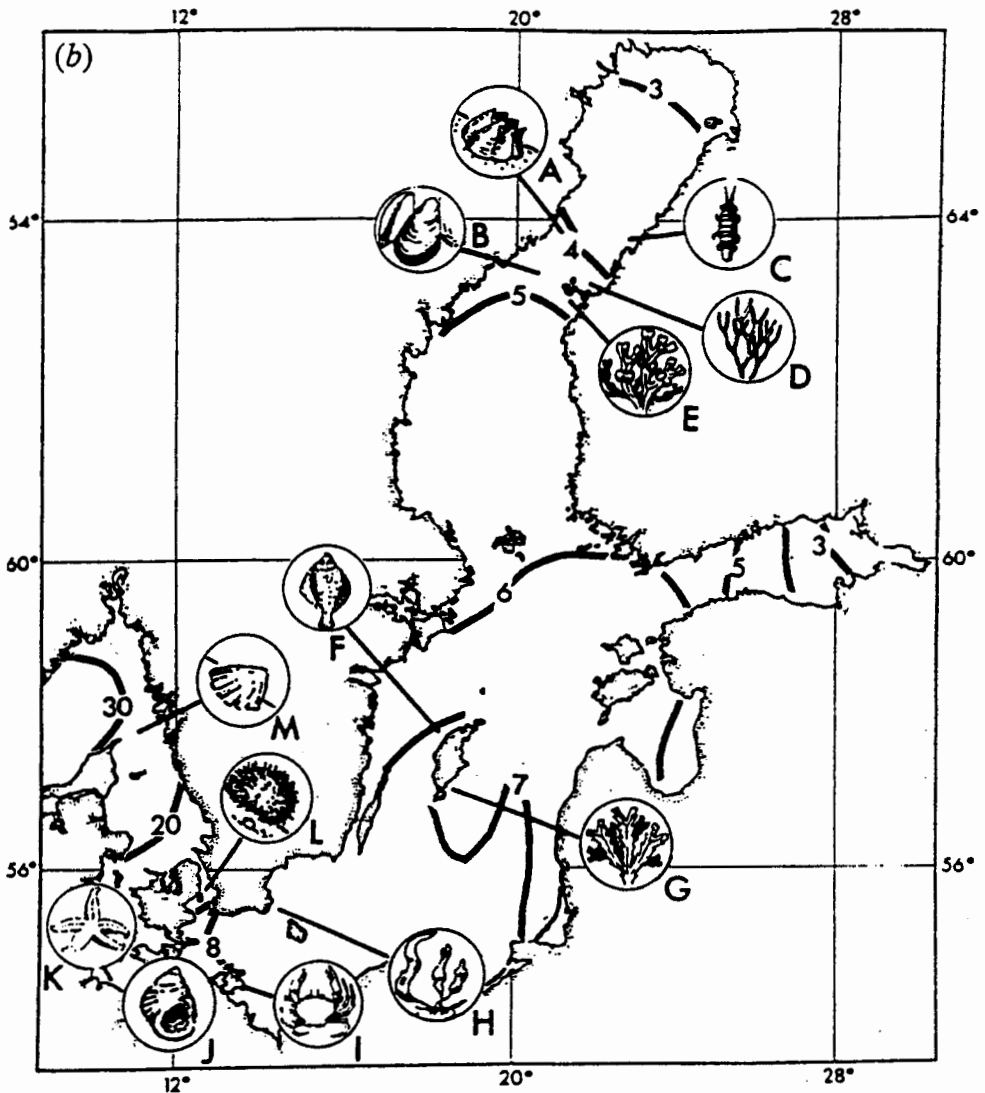


Fig. 14.1. The Baltic Sea, showing (a) major subdivisions and (b) isohalines of the surface water and distribution limits for some common marine species in the Baltic Sea: A, the bivalve *Macoma balthica*; B, the blue mussel, *Mytilus edulis*; C, the isopod *Idotea balthica* (Pallas); D, the red alga *Furcellaria lumbricalis* (Huds.) Lamour.; E, bladderwrack, *Fucus vesiculosus*; F, plaice, *Pleuronectes platessa*; G, serrated wrack, *Fucus serratus* L.; H, the kelp *Laminaria saccharina* (L.) Lamour., I, shore crab, *Carcinus maenas* L.; J, periwinkle, *Littorina littorea* (L.); K, starfish, *Asterias rubens* L.; L, sea urchin *Strongylocentrotus droebachiensis* Müller; M, limpet, *Patella vulgata* L. From Wallentinus (1991).

H. barnacle
Balanus improvisus

water and freshwater species (Segestråle, 1957; Wallentinus, 1991). Freshwater fish such as European perch, *Perca fluviatilis* L., can be caught in the same net as marine species such as cod, *Gadus morhua* L. (Fig. 14.2). The distribution of Baltic organisms reflects the north-south salinity gradient, with marine species gradually disappearing as one



moves from the Swedish west coast to the southern Baltic and then northwards to the Bothnian Bay (Fig. 14.1(b)). Major marine groups such as coralline algae, kelps, radiolarians, echinoderms and elasmobranchs are absent from most of the Baltic Sea.

Freshwater taxa, such as insects, show a reduction in the opposite direction, from north to south, and their diversity in the Bothnian Bay, at 2–4 psu, is already much lower than in lakes. A few species typical of brackish water are common at intermediate salinities (Segerstråle, 1957). The resulting species diversity is low in comparison with fully marine or freshwater areas, as is generally the case in estuarine and brackish waters (Remane, 1934). The low diversity is evident both within

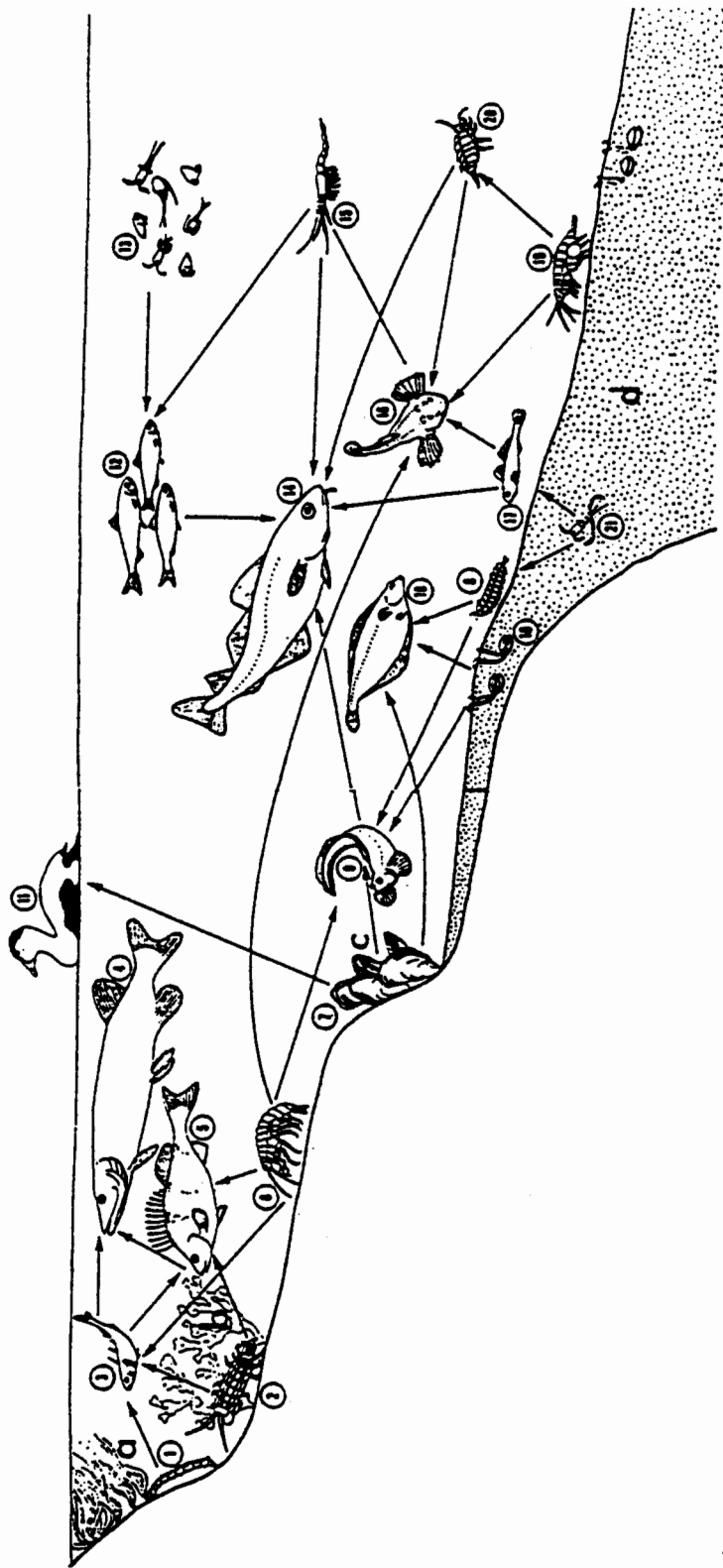


Fig. 14.2. Some fundamental food chains in the northern Baltic proper. 1, Chironomid larva; 2, Isopod; 3, Stickleback; 4, Pike; 5, Perch; 6, Amphipod; 7, Blue mussel; 8, Polynoid polychaete; 9, Viviparous blenny; 10, Baltic clam; 11, Eider duck; 12, Herring; 13, Plankton; 14, Cod; 15, Opossum shrimp; 16, Four horned sculpin; 17, Goby; 18, Flounder; 19, Amphipod; 20, Isopod, *Saduria*; 21, Meiofauna; a, *Cladophora* belt; b, *Fucus* belt; c, Blue mussel belt; d, Soft bottoms. From Jansson (1972).

and between habitats, with Baltic organisms generally having wider realised niches than is normal in fully marine areas (Remane & Schlieper, 1971). There is a tendency for the reduction in species richness to be more drastic for macroscopic organisms, compared to microscopic organisms such as phytoplankton (Bernes, 1994) and benthic meiofauna.

Some 240 taxa of phytoplankton have been recorded from the southern Baltic and the Baltic proper (Willén, 1995), which is as high as about 6% of the total marine species pool of the world (approximately 3500–4500 species: Sournia *et al.*, 1991). The phytoplankton diversity declines to about 160 taxa in the Bothnian Bay.

The zooplankton communities in the Baltic consist of less than about 50 species, most of which are smaller than 1 mm in size (Voipio, 1981). Subsets of about 10 species account for most of the biomass and production in the Baltic proper and the Bothnian Bay (Hernroth & Ackefors, 1979; Kankaala, 1987).

Of about 180 species of macroalgae found in the Kattegat, less than half enter the Baltic proper, and only about a dozen reach the Bothnian Bay (Wallentinus, 1991). In most of the Baltic, the only large, belt-forming species is bladderwrack, *Fucus vesiculosus* L., which extends as far north as the northern Bothnian Sea. Eelgrass, *Zostera marina* L., is not found north of the Baltic proper. The Baltic wrack-belts and eelgrass beds support a comparatively high diversity of macroscopic animals. In the Bothnian Bay, most macrophytes are either annual fresh-water phanerogams or stoneworts (Characeae).

The number of benthic macrofaunal species declines drastically from south to north in the Baltic, from about 1500 in the Skagerrak off the Swedish west coast, to about 150 in the Arkona area of the southern Baltic, 80 in the waters off Gotland and 50 in the northern Baltic proper (Voipio, 1981). On hard substrates in the Baltic proper, the filter-feeding blue mussel, *Mytilus edulis* L., forms large banks down to about 30 m depth, dominating the animal biomass (Kautsky, 1981). In the Bothnian Bay, where the salinity is as low as 2–4 psu, there are no mussels or other major filter feeders (Kautsky *et al.*, 1981; Elmgren *et al.*, 1984).

On soft-sediment bottoms, the species diversity of the benthic macrofauna is low. A single grab sample of 0.1 m², taken below the thermocline, normally contains about 6–7 species of macrobenthos in the northern Baltic proper, and only 1–2 in the Bothnian Bay (Elmgren *et al.*, 1984), whereas 40–50 species are commonly found in similar grab samples from the North Sea. The species diversity of the macrofauna on soft-sediment bottoms declines with depth in the Baltic proper (Ankar

& Elmgren, 1976), in contrast to the general pattern of an increase in diversity with depth in fully marine areas (Grassle & Maciolek, 1992). The diversity of meiofauna (animals less than 1 mm in size) is higher than that of the macrofauna, with up to 20 or more species in a few cubic centimetres of Baltic sediment (Elmgren, 1978, and unpublished results), but it is still lower than that in similar North Sea samples, where there may be more than 100 species of meiofauna.

The diversity of marine fishes decreases from 120 species in the North Sea to 69 in the Kiel Bay, 41 in the southern and central Baltic Sea, 20 in the Gulf of Bothnia and 6–10 in the Bothnian Bay (Voipio, 1981). Herring, *Clupea harengus* L. and sprat, *Sprattus sprattus* (L.), are found in the entire Baltic. Although cod can live in the Bothnian Bay, spawning is restricted to the deep, salty basins of the Baltic proper. Of the freshwater species, salmon, *Salmo salar* L., migrates from about 20 rivers along the whole coast to feed in the Baltic. The proportion of freshwater species is greatest in coastal areas, where perch and roach, *Rutilus rutilus* (L.), are common, and in the Bothnian Bay (Voipio, 1981).

14.4 Does the Baltic Sea have endemic species?

Beginning with Linnaeus, a number of plant and animal species were first described from the Baltic Sea, but the overwhelming majority were later also found in other areas. A few are still known only from the Baltic Sea area, but those are from little-studied or taxonomically difficult groups, and are likely to represent poor knowledge rather than true endemism (Elmgren, 1984).

There are, however, several instances where genetically differentiated populations, or even physiological races, seem to be found in the Baltic (Wallentinus, 1991). Examples include bladderwrack (Bäck *et al.*, 1992), cod (Mork *et al.*, 1985), the bivalve *Macoma balthica* (L.) (Väinölä & Varvio, 1989), and the blue mussel (Johannesson *et al.*, 1990). The blue mussels of the Baltic have also been proposed to belong to a separate brackish-water species, *Mytilus trossulus* Gould, with wide distribution in brackish areas (McDonald & Koehn, 1988). On the other hand, Baltic herring, which on phenotypic grounds was long thought to be a distinct subspecies, *Clupea harengus harengus*, shows little real genetic differentiation from the Atlantic herring *Clupea harengus* (Ryman *et al.*, 1984).

14.5 Species gained and lost

The species diversity of the Baltic has increased in recent times, due to the successful invasion of foreign species from distant waters, probably in all cases helped by man. At least 30 immigrant species have become established (Leppäkoski, 1991, 1994; Jansson, 1994).

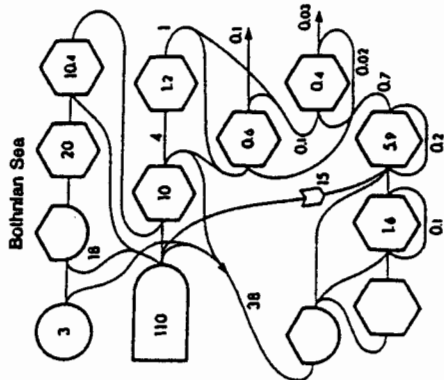
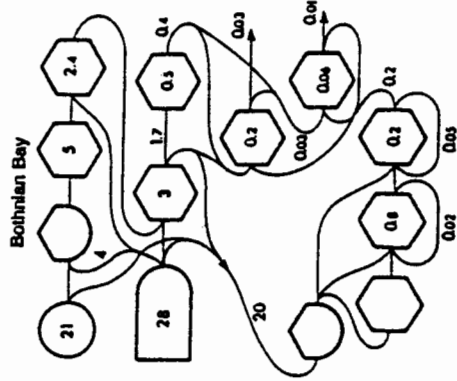
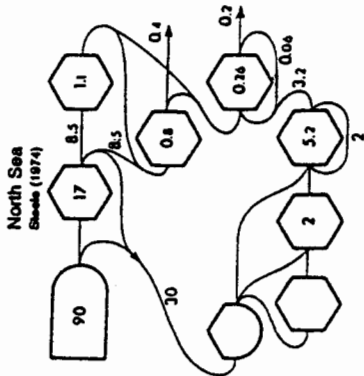
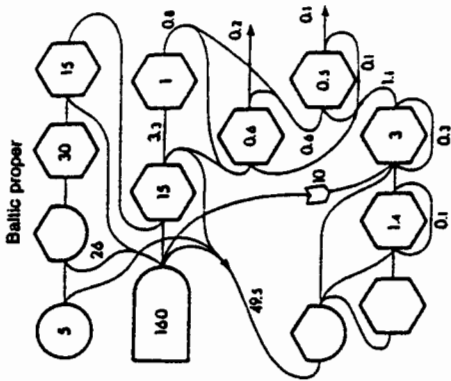
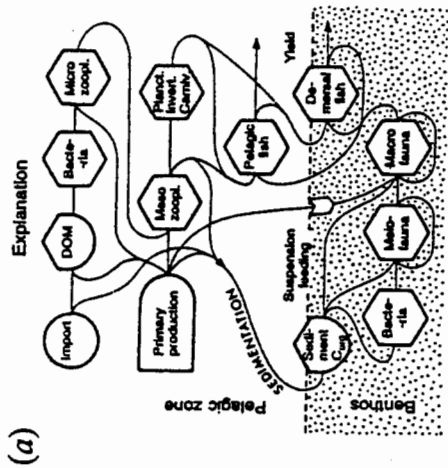
This influx may have started as far back as the Vikings (Petersen *et al.*, 1992) and some immigrants have become important community members. Examples include the bivalve *Mya arenaria* L., the barnacle *Balanus improvisus* Darw., and the New Zealand snail *Potamopyrgus jenkinsi* (Smith). Some freshwater species are important in marginal water bodies of very low salinity, for instance the aquarium weed *Elodea canadensis* Michx., the zebra mussel, *Dreissena polymorpha* (Pall.), the American crayfish, *Orconectes limosus* (Raf.), and the freshwater mysid *Hemimysis anomala* G.O. Sars, which now dominates the food of fishes in the Couronian lagoon in Lithuania. Some are typically found in polluted conditions, e.g. the polychaete *Polydora redeki* Horst., and the bryozoan *Victorella pavida* Kent.

Most of the immigrants are found in shallow water, and only a few have established themselves below the thermocline of the Baltic, e.g. the north American polychaete *Marenzelleria viridis* Verrill, which now dominates the benthos of the Vistula lagoon in Poland, and is spreading in the Baltic proper (Jansson, 1994).

Invasion by further new species is a real threat to the Baltic ecosystem as we know it today. There is a fear of large-scale changes should the filter-feeding zebra mussel, or its close relative the quagga mussel, *Dreissena bugensis* Andrusov, find its way to the Bothnian Bay, or should the American comb jelly, *Mnemiopsis leidyi* (A. Agassiz), spread via ballast water to the Baltic. In the Black Sea this comb jelly now occurs in enormous numbers and feeds on zooplankton and fish larvae (Mee, 1992). In contrast, few species have been totally lost to the Baltic ecosystem in historical times, but the sturgeon, *Acipenser sturio* L., may soon be gone (Witkowski, 1992).

14.6 Comparison of energy flows in the Baltic and North Seas

Elmgren (1984) summarised the patterns of energy flow in the Baltic Sea and its three main basins (the Baltic proper, the Bothnian Sea and the Bothnian Bay). Pelagic primary production is the main energy source, but riverine input of organic matter is almost as large in the oligotrophic



(b)

Fig. 14.3. (a) Carbon-flow diagrams for the North Sea and the Baltic proper. Explanation at left. Flows enter symbols at left, exit at right. (b) Carbon-flow diagrams for the Bothnian Sea and the Bothnian Bay. Notice loss of benthic suspension-feeding pathway and reduction of benthic macrofauna in the Bothnian Bay. For all diagrams the figures ($\text{gC/m}^2 \text{yr}^{-1}$) inside symbols are annual production, those outside are annual flows. Sources of dissolved organic matter (DOM) other than algal exudates are not shown. Figures for planktonic invertebrate carnivores in Baltic diagrams refer to mysids. From Elmgren (1984).

Bothnian Bay. Locally, in the coastal zone, benthic primary producers may also be important (Wallentinus, 1991). Primary production decreases along the salinity gradient from the Baltic proper to the Bothnian Bay, by a factor of about 4–6 (Elmgren, 1978).

There are four major routes for the organic carbon produced by phytoplankton: release of algal exudates that become available to bacteria; grazing by zooplankton; filter-feeding by zoobenthic animals such as mussels; and sedimentation to the benthic zone. Most of the carbon input is used up by the pelagic system, and the food chain based on algal exudates, pelagic bacteria and microzooplankton (e.g. ciliates) processes more carbon than that based on grazing of phytoplankton by larger zooplankton, even though the latter food chain leads more directly to pelagic fish.

Macrofauna account for most of the benthic biomass in the Baltic Sea, except in the Bothnian Bay, where meiofauna dominate the benthic biomass, in the absence of filter-feeding bivalves. Even though the Baltic is poor in species, biotic interactions can be quite complex (Ankar, 1977; Bonsdorff & Blomqvist, 1993). By aggregating species into functional groups, it is still possible to give an overview of carbon and energy flows.

Elmgren (1984) compared his estimated carbon flows for the three main basins of the Baltic Sea with Steele's (1974) model of carbon flows in the high-diversity North Sea ecosystem, and found striking similarity between the largest and southernmost Baltic basin, the Baltic proper and the North Sea (Fig. 14.3(a)). There were, however, also some differences, partly due to knowledge acquired since Steele formulated his model, and partly due to real differences between the systems. The North Sea model did not include the pelagic microheterotrophic food chain, which was insufficiently known in the 1970s. The Baltic calculations included not only open sea, but also coastal areas, where benthic suspension-feeders derive substantial amounts of energy from phytoplankton, a food chain link not included by Steele. Steele's estimate of phytoplankton primary production is a good deal lower than the estimate for the Baltic proper, but recent studies indicate that Steele's primary production estimate was too low (North Sea Task Force, 1993). In the North Sea, benthic invertebrate predators, such as echinoderms and large decapods, form a predation loop within the benthos, that is not present to the same degree in the Baltic.

Going north to the Bothnian Sea, there were still no principal differences in carbon flow from the North Sea model. The Bothnian Sea

carbon flow chart indicated that the production of most trophic groups had diminished in rough proportionality to the lower phytoplankton primary production in this basin (Fig. 14.3(b)). The importance of benthic fauna had, however, increased, since, unlike the Baltic proper, the Bothnian Sea lacks extensive areas with oxygen deficiency.

In contrast, the carbon flow chart for the Bothnian Bay showed a radical re-structuring of the ecosystem, due mainly to the lack of a whole functional group, the benthic filter-feeders (Fig. 14.3(b)). In the absence of filter-feeding bivalves (e.g. blue mussels), there is almost no direct utilisation of phytoplankton by benthic filter-feeders, and a much smaller proportion of the primary production is used by macrobenthos. This leads to lower macrobenthos biomass and a biomass dominance by meiobenthos.

The Baltic Sea example thus suggests that as long as major functional groups are present, a simple, low-diversity ecosystem may be functionally almost equivalent to a high-diversity ecosystem, in terms of flows of organic carbon. Only the near-total loss of a major functional group resulted in drastic alterations of ecosystem processes. The Baltic/North Sea comparison is, however, as rough as the model calculations on which it is based, calculations that to some extent have been superseded by new research, and which do not take into account dynamic changes with time, the effect of fisheries, the eutrophication of the Baltic, fluctuations in climate and other complicating factors.

14.7 Effects of low biodiversity on natural resource

The low diversity of fish species in the Baltic affects the fishery and its commercial value. Fewer species are landed commercially in the Baltic, compared to the west coast. The main commercial species in the Baltic are herring, sprat, cod, eel, *Anguilla anguilla* (L.), salmon and freshwater fish, such as vendace, *Coregonus albula* L.

On the west coast, many more species are fished. Commercially important species include flatfishes such as witch flounder, *Glyptocephalus cynoglossus* (L.), common sole, *Solea solea* (L.) and plaice, *Pleuronectes platessa* L.; gadoids such as saithe, *Pollachius virens* (L.) and haddock, *Melanogrammus aeglefinus* (L.); and mackerel, *Scomber scombus* L. There are also crustaceans of high commercial value: deepwater prawns, *Pandalus borealis* Krøyer, and Norway lobster, *Nephrops norvegicus* (L.).

The landed weight of the west-coast fishery in 1993 was about 38%

of the total Swedish catch of 336 kilotonnes, while that from the coasts off the Sound and the Baltic constituted about 12% (Anon., 1994). However, half of the Swedish fisheries yield was landed in Denmark, and consisted overwhelmingly of industrial fish (mostly herring and sprat) from the Baltic. This means that the actual yield of the Swedish fishery in the Sound and the Baltic in 1993 was larger than that of the west coast.

The greater diversity of the marine fish, crustaceans and molluscs on the Swedish west coast supports a fishery with almost double the value per unit catch. For instance, crustaceans and molluscs from the west coast, which constituted only 1% of the yield, accounted for 15% of the total commercial value of the Swedish fishery in 1993 (Anon., 1994). The recent catastrophic decline in Baltic cod stocks (Hammer *et al.*, 1993) illustrates the vulnerability of a fishery with few alternative target species.

14.8 Does high diversity stabilise ecosystem function?

There are two opposing views about the importance of species diversity for ecosystem function. The first view holds that species in areas of high diversity are highly specialised and often co-evolved (Jackson, 1994) and that each species is of importance for ecosystem function. Every loss of a species is thought to affect ecosystem function, making it in some way less effective (Ehrlich & Wilson, 1991). According to the second view, many of the species present in high-diversity ecosystems may be redundant, as they carry out the same function, and the loss of some species is unimportant for ecosystem processes (Lawton, 1991; Walker, 1992).

The Baltic example suggests that we should not claim without good proof that high biodiversity is needed to maintain ecosystem function, even if it may be a boon to fisheries. The simple Baltic ecosystem, with its mixed origin and short history, is clearly not a co-evolved unit (cf. Jackson, 1994), yet functions similarly to the more diverse and co-evolved North Sea ecosystem. There is no scientific consensus on the relationship between the diversity of species within an ecosystem and its 'stability' (Pimm, 1984), and theoretical studies have even suggested that ecosystems with more species and a greater complexity should be less stable (May, 1972).

Nevertheless, the possibility remains that lowered diversity may destabilise ecosystem function, even before the loss of major functional

groups. From an intuitive standpoint, one could expect that several species within each functional group will do a more reliable and less variable job than a single species. The risk of a single species being knocked out by a pathogen or an unusual climatic event must be larger than for a whole guild of species of similar function and different origins. Thus, we may perhaps expect more diverse systems to function in a less variable manner, given similar environmental variability, and to be more functionally resilient to perturbations (cf. Pimm, 1984).

For terrestrial ecosystems, both field studies and controlled experiments are now at hand in support of such a view. Experimental manipulations of species diversity in terrestrial ecosystems have shown that reducing species numbers affected ecosystem functions: species-poor ecosystems had a lower primary productivity, were more vulnerable to perturbation (drought) and took longer to recover (Naeem *et al.*, 1994; Tilman & Downing, 1994). The simple ecosystems of the Baltic Sea would seem to be well suited for similar experiments in the aquatic environment, but this potential has not yet been exploited.

Can we judge whether the simple Baltic ecosystem is more variable than the more diverse North Sea system? Both areas have long series of observations, but in most cases they are not compatible, and lack information on external forcing functions that govern the recorded variability. At least one study reports co-variation between Baltic and North Sea communities, and indicates large-scale climatic cycles as a cause (Gray & Christie, 1983). In the Bothnian Bay there are regular fluctuations in populations of the benthic amphipod *Monoporeia affinis* (Lindström) (Andersin *et al.*, 1978). However, there are also many reports of fluctuations in North Sea systems, e.g. the so-called Russell cycle in the abundance and species composition of zooplankton and pelagic fish in the English Channel, and changes in the relative abundances of plankton, fish and seabirds in the North Sea (Southward, 1980; Aebischer *et al.*, 1990; Steele, 1991). Published analyses of natural ecosystem variability over time do not allow us to conclude whether the ecosystem of the Baltic is more or less variable than that of the North Sea.

As the Baltic is one of the most polluted seas in the world (Fitzmaurice, 1993), it is natural to wonder whether its low biodiversity influences its sensitivity to anthropogenic perturbations. Jernelöv & Rosenberg (1976) advanced the theory that Baltic ecosystems should be less sensitive to such stress than more diverse ecosystems on the Swedish west coast. Their main argument was that many of the dominant species

in the Baltic are hardy, estuarine species that on the west coast are among the last to survive under polluted conditions. Elmgren (1984) countered by pointing out that at least some species in the Baltic, the so-called glacial-relict crustaceans, are in fact known to be quite sensitive to various pollutants. In addition, Tedengren & Kautsky (1986) argued that marine species in the Baltic are under greater osmotic stress than in the North Sea, due to the low salinity, and that this increases their susceptibility to other perturbations. Finally, as mentioned above, functional redundancy is low in the Baltic – loss or drastic reduction of a single species may mean the loss of a whole functional group, and thus greatly change ecosystem processes.

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