

BIOTIC COUPLINGS ON SHALLOW WATER SOFT BOTTOMS—EXAMPLES FROM THE NORTHERN BALTIC SEA

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ABSTRACT Biotic couplings in brackish shallow water systems have been studied extensively in the northern Baltic Sea. The non-tidal Baltic is characterised by steep horizontal and vertical, local and basin-wide environmental gradients (salinity, temperature, oxygen, exposure, sediment quality, archipelago systems) ranging from almost limnic, sheltered inner bays to brackish 'marine' conditions in the exposed open coastal zone. The species number of zoobenthos and fish is generally low, and most species live at the border of their physiological tolerance. Despite the physiological pressure on the organisms, biotic interactions (intra- and interspecific; within- and between trophic levels and functional groups) are significant in establishing the community organisation recorded in any local habitat at any given moment. Due to the salinity-stress, few epibenthic invertebrate predators occur in the Baltic, and benthivorous fish are important in the regulation of the infauna of the shallow (0–5 m) archipelago waters. Fish, however, mainly utilise these habitats in the summer season, whereas zoobenthos have a less marked seasonal variability in terms of biomass and species composition. As the number of key species is low, the ecosystem is highly vulnerable to unexpected catastrophic events, or man-made stress, such as eutrophication, but simultaneously the recovery potential of the biota is high.

INTRODUCTION

In biological and ecological investigations of any given area the classical way has been to describe the components of the ecosystem, and possibly to relate them in often assumed causal relationships. Most often the biota has been treated as one unit (or possibly pooled at trophic levels) to be compared with a range of abiotic parameters (hydrography and chemistry of the water body, sediment properties, currents etc.), and a tool commonly used for this today is some multivariate analysis (for reviews on the application of these methods in marine ecology, see e.g. Gray *et al.*, 1988, and Kautsky & van der Maarel, 1990). The couplings within and between the biotic components of the systems have only recently become the focus of investigation, as quantitative or statistically valid results have been hard to obtain. With the expansion of experimental research the means for explaining the function of the biota of any given system have also been largely enhanced (Woodin, 1974, 1976; Arntz & Rumohr, 1982; Connell, 1983a, b; Schoener, 1983; Commito & Ambrose, 1985a; Reise, 1985a, b; Zajac & Whitlatch, 1985; Bonsdorff *et al.*, 1986a; Elmgren *et al.*, 1986; Olafsson &

Persson, 1986; Wilson, 1986; Hall *et al.*, 1990; Hill *et al.*, 1990; Nelson & Bonsdorff, 1990; Sandberg & Bonsdorff, 1990; Aarnio *et al.*, 1991; Mattila *et al.*, 1990; Mattila, 1992).

In estuaries and brackish water seas the biota is often poor in species, and many of the keystone species are well known, as exemplified in a complex food-web analysis from the Ythan estuary (Hall & Raffaelli, 1991). Thus, the benthic ecosystem (including epibenthic invertebrates and benthivorous fish, and the couplings between trophic and functional levels) of, for example, the coastal areas of the Baltic Sea, is one of the best known benthic systems in terms of total species composition and the principal intra- and interspecific couplings (Ankar, 1977; Arntz, 1978; Leppäkoski & Bonsdorff, 1989; Kautsky & van der Maarel, 1990; Sandberg & Bonsdorff, 1990). In the northern Baltic Sea, in the area between central Sweden and southern Finland (Fig 1), salinity is about 4–7‰ *S*, and the system consists of a mixture of organisms of different origin, ranging from marine (e.g. cod and flounder among the benthivorous fish, and a few polychaetes, bivalves and crustaceans among the benthos; Arntz, 1978; Elmgren, 1984), to limnic (such as perch and ruffe among the benthos-feeding fish, and some oligochaetes, gastropods and insect larvae among the benthos; Blomqvist, 1984; Sandberg & Bonsdorff, 1990). Some limnic species, such as the predatory fish, perch (*Perca fluviatilis*), have adapted so well to the estuarine environment, that their larvae even survive better in this environment than in the original freshwater habitat (Ribi, 1992). The total number of species present is low (about 50 macrobenthic species and some 30 species of commonly occurring fish) compared with most “marine estuaries”, and some of the zoobenthic species occurring in the Baltic Sea and the Atlantic system differ markedly in their genetical composition (Väinölä & Varvio, 1989; Väinölä & Hvilson, 1991). Thus, the links between species and trophic levels can be described and monitored relatively easily, as taxonomy does not offer a major problem (Segerstråle, 1957; Jansson, 1972; Ankar, 1977; Arntz, 1978; Arndt, 1989; Leppäkoski & Bonsdorff, 1989). Also, the life cycles of most key species are well known, and the roles of the species can be separated during different stages of development (for instance juvenile flounder may feed on newly settled bivalves, and simultaneously be preyed upon by adult *Crangon crangon*, which in turn will be preyed upon by the adult flatfish, mainly consuming adult bivalves). A comprehensive review of the biota (including the macrophytes, zoobenthos and fish) of the different parts of the Baltic Sea is given by various authors in Voipio (1981).

In this paper, it is our attempt to briefly describe and discuss some of the ecological couplings on shallow (0–10 m) soft-bottoms of different characters (in relation to e.g. exposure, sediment type and spatial heterogeneity) in the archipelago of the northern Baltic Sea, with the emphasis on the Åland Islands located in the central northern Baltic at the junction between the Baltic Proper, the Gulf of Finland and the Bothnian Sea (Fig 1). The main focus will be on secondary trophic levels, i.e. not on primary production and the pelagic part of the ecosystem, and no attempt is made to cover the entire literature from the Baltic Sea, although comparisons to other areas are made. A brief history of Baltic marine ecological studies is found in Leppäkoski & Rönnerberg (1988), and Leppäkoski & Bonsdorff (1989).

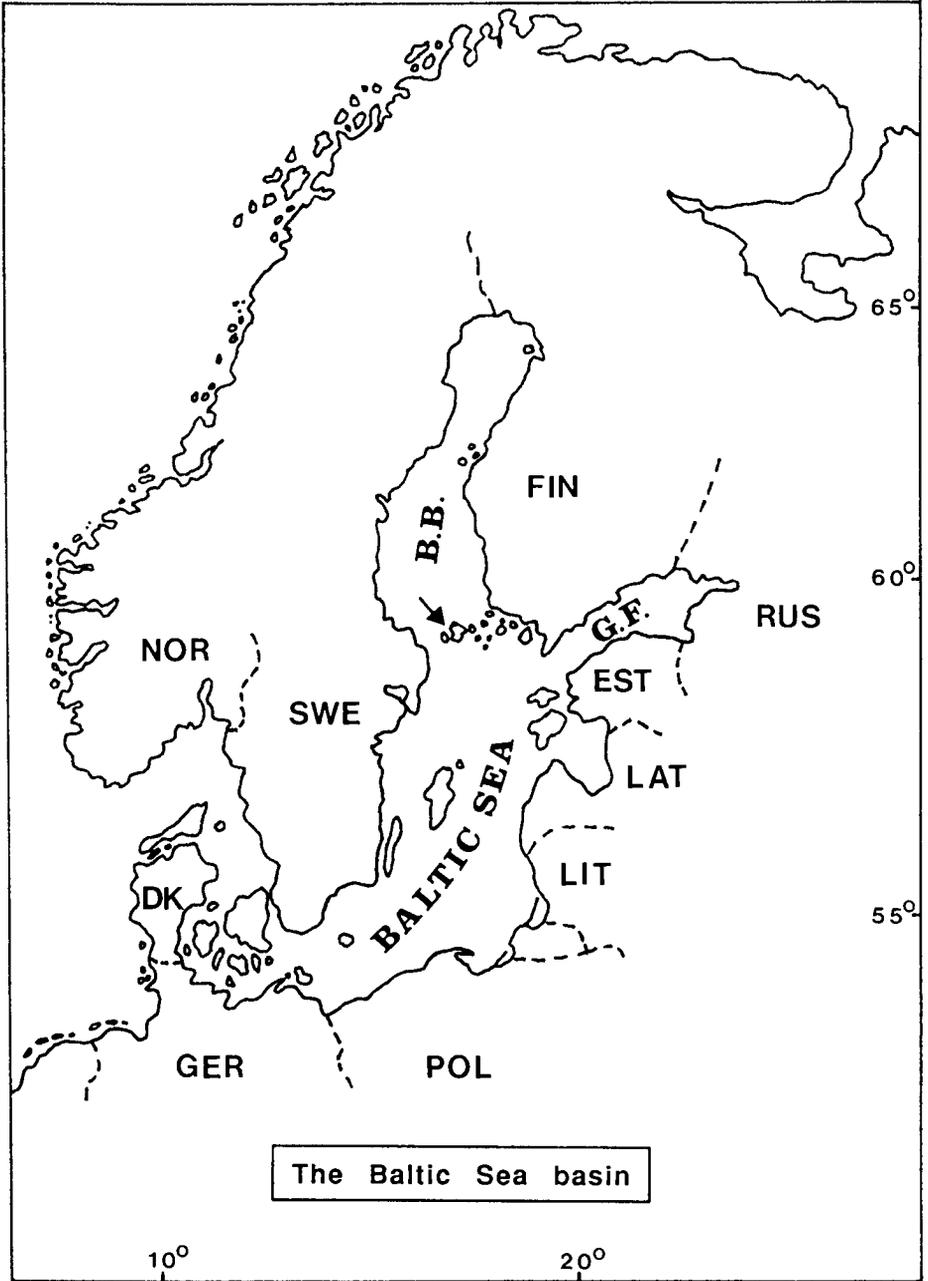


Fig 1.—The Baltic Sea including the Bothnian Bay (B. B.), the Gulf of Finland (G. F.), and the Åland archipelago (indicated by an arrow at 60°N : 20°E). The only present connection to the fully marine environment is through the shallow and narrow Danish sounds to the North Sea, from which any natural marine recruitment must take place.

THE BALTIC SEA

The Baltic Sea differs from the surrounding northern seas in that it is enclosed (connected to the North Sea only through the narrow and shallow Danish Sounds and the Öresund, with a sill depth of about 17 m), relatively shallow (max depth 459 m; average depth 52 m), and entirely brackish, with surface salinities ranging from $<1\text{‰}$ *S* in the far north and east (the innermost parts of the Bothnian Bay and the Gulf of Finland) to 10–12‰ *S* in the south (Kiel Bay in Germany and the Danish coastal waters). The water balance of the Baltic is driven mainly by the influx of fresh water from rivers and lakes, and by the Norwegian Current pushing marine water into the Baltic underneath the out-flowing Baltic Surface Current. Thus a range of marked horizontal gradients prevail over the entire Baltic Sea. The Baltic is characterised by steep vertical gradients, such as more or less permanent thermo- and haloclines causing periods of oxygen deficiency in the deeper water layers. This stratification contributes to the slow turnover of the waterbody, and also to the maintenance of the local physical and biological features of the different morphometric parts of the Baltic basin (Fig 1). The Baltic is practically non-tidal (although the annual amplitude in water level can be up to 1.5–2 m in the northern archipelago areas driven by air pressure and strong winds). Being low-saline, and for the northern parts sub-arctic, most of the coastal areas are ice covered for several months each year, adding to the ecological stress on the system. Furthermore, the littoral areas along the Finnish coasts and the Swedish coast of the Bothnian Bay change constantly due to the land-uplift after the last glaciation. This process raises the land from the sea at a rate of about 30–100 cm per 100 yr, constantly opening habitats for colonisation through several morphometric and ecological successional stages (Munsterhjelm, 1987; Lindholm, 1991). A detailed description of the entire Baltic basin and its sub-systems is given by Jansson (1972), Maggaard & Rheinheimer (1974), Voipio (1981) and Elmgren (1984).

In the northern Baltic archipelagoes the coastline is characterised by a vast mosaic of islands constantly changing with the land-uplift, creating an extensive archipelago including a great variety of habitats within the macro-habitat that consists of the open coast and sea. The Åland archipelago, as one example, consists of some 6000 islands and skerries, with a shoreline of thousands of kilometers in an area smaller than the island of Gotland in the central Baltic. This broken pattern of the coastline with more or less distinct zones of exposure (Häyrén, 1940, 1948; Jaatinen, 1960; Rönnberg, 1969) further adds to the spatial heterogeneity affecting vegetation, zoobenthos and fish over both local and regional scales (Blomqvist & Bonsdorff, 1986; Bonsdorff *et al.*, 1992).

As the entire sea is still in a process of ecological succession, including the process of land-uplift from the last glaciation some 10 000 yr ago, the ecosystem on an evolutionary scale is young and vulnerable, and has a low number of species within any trophic or functional level. Hence, the present ecological status of this changing environment can be regarded as a step in an ongoing community succession, and a number of species occurring in the Baltic today are considered as glacial relicts (Segerstråle, 1966, 1982; Järvekülg, 1973; Voipio, 1981). Examples of such species are the dominating epibenthic predatory isopod *Saduria* (syn. *Mesidotea*) *entomon* and several amphipods (including the numerically highly dominant *Monoporeia* (syn. *Pontoporeia*) *affinis*, mysid

shrimps (*Mysis relicta* and *M. mixta*), bivalves (*Astarte borealis*), a priapulid (*Halicryptus spinulosus*), and some fish species. One interesting component of the biota is the relatively large proportion of introduced species (e.g. the polychaete *Polydora redeki*, the molluscs *Mya arenaria* and *Potamopyrgus jenkinsi*, the crustaceans *Eriocheir sinensis* and *Corophium curvispinum* and some fish species, usually connected to aquaculture, and not able to maintain their populations), often competitive and ecologically dominant in their niches (Voipio, 1981; Elmgren, 1984; Leppäkoski, 1984, 1991). These facts partly explain the relatively large, local and basin-wide, effects at population and ecosystem level that any man-induced disturbance may have on the system (Leppäkoski & Bonsdorff, 1989).

The large drainage area of the Baltic Sea (about 1.7 million km²) inhabited by some 80 million people, compared with a water area of only about 390 000 km² (volume about 21 700 km³) and a slow water exchange (residence time about 20 yr), makes the entire basin vulnerable to human influence. At present, one major cause of gradual change of the entire Baltic Sea (and especially the shallow, inshore areas) is eutrophication (Cederwall & Elmgren, 1980, 1990; Anonymous, 1990; Bonsdorff *et al.*, 1991, 1992; Kautsky, 1991; Nehring & Matthäus, 1991). In coastal and inshore areas, the general trends have been increased primary productivity as a consequence of the enhanced nutrient levels throughout the Baltic (Grönlund & Leppänen, 1990; Anonymous, 1990; Nehring & Matthäus, 1991), and consequently increased standing stocks of zoobenthos and fish (Cederwall & Elmgren, 1980, 1990; Hansson & Rudstam, 1990; Bonsdorff *et al.*, 1991, 1992; Bonsdorff & Blomqvist, 1992).

A CONCEPTUAL MODEL OF INTERACTION— EXAMPLES FROM THE ÅLAND ARCHIPELAGO

Any field sampling of zoobenthos or fish will only produce a momentaneous picture of the system at that specific site (including the restrictions the methods used have, such as sediment penetration of the grab, sieve- and gill-net mesh size, etc.). By increasing the number of sampling occasions in time one can then obtain a succession of data that illustrates a pattern within the system, but still it does not explain the processes behind the possible changes seen. In the ecosystem studied here (zoobenthos and fish of shallow water bays of varying exposure in the Åland archipelago, northern Baltic Sea; about 60°N: 20°E) the conceptual model introduced to describe some of the main components behind the end-result, i.e. the faunal community, is summarised in Table I (references are to work done within one project to illustrate the specific levels described).

Within the specific area of interest in this case (a steep environmental gradient of about 30 km from the inner bays to the open coast) a number of topographical, physical and biological gradients occur, mainly governed by the geomorphology of the complex archipelago. To test for the ecological manifestation of the natural physical and hydrographical gradient, a multi-level approach, combining both field analysis and experiments, has been used to describe the biota of this specific system (Bonsdorff *et al.*, 1991, 1992; Backlund, 1992; Haldin, 1992; Lindholm & Bonsdorff, 1992; Wistbacka, 1992; Ådjers & Backlund, 1992):

TABLE I

Conceptual model describing the main component processes structuring the faunal communities of shallow soft-bottoms in the Åland archipelago, northern Baltic Sea.

| Factor | Main effect | Reference (examples) |
|-----------------------------------|---|---|
| Topography and habitat complexity | Physical boundaries, species composition | Blomqvist & Bonsdorff (1986); Bonsdorff (1989); Nelson & Bonsdorff (1990); Mattila (1992) |
| Hydrography | Physiological tolerance, species composition | Blomqvist (1984, 1986); Bonsdorff & Blomqvist (1989); Sandberg & Bonsdorff (1990) |
| Seasonality | Annual amplitude in community succession | Blomqvist (1984, 1986); Blomqvist & Bonsdorff (1986); Bonsdorff & Blomqvist (1989); Bonsdorff <i>et al.</i> (1990) |
| Biotic interactions | Momentaneous responses (population and community) | Bonsdorff <i>et al.</i> (1986a, 1990); Rönn <i>et al.</i> (1988); Mattila & Bonsdorff (1989); Sandberg & Bonsdorff (1990); Aarnio <i>et al.</i> (1991); Ejdung & Bonsdorff (1992) |
| Stochastic events | Species composition, community succession | Bonsdorff (1983, 1989, 1992); Bonsdorff & Österman (1985); Aarnio <i>et al.</i> (1991) |
| Man-made stress | Community composition | Blomqvist (1982, 1984); Bonsdorff (1980, 1983, 1989); Bonsdorff <i>et al.</i> (1986a, 1991) |

- (1) inner → middle → outer archipelago (as defined by Rönnerberg, 1969)
- (2) sheltered, vegetated (mainly *Phragmites australis*) muddy shores to exposed sandy and rocky shores (i.e. low to high natural physical disturbance)
- (3) heterogeneous shallow waters to homogeneous deeper bottoms (Sandberg & Bonsdorff, 1990)
- (4) high summer temperatures (up to 25°C) and regular winter-ice, to moderate summer temperatures (below 15°C) and irregular winter-ice (Bonsdorff & Blomqvist, 1989)
- (5) limnic or low-saline (1–3‰ S) to normal coastal conditions (5–7‰ S)
- (6) eutrophicated inshore waters and high organic contents in the sediment (5–10% loss on ignition) to background levels in nutrients and poor, sandy sediments (≈ 0.5% organics).

In order to understand the portions of the factors involved, a three-level strategy of analysing the community has been followed:

- (1) collection and analysis of empirical field data on hydrography and sediment properties (e.g. Blomqvist & Bonsdorff, 1986; Bonsdorff & Blomqvist, 1989; Bonsdorff *et al.*, 1991, 1992; Bonsdorff, 1992), on standing stock of vegetation, zoobenthos, fish and birds (Blomqvist, 1982, 1984, 1986; Blomqvist & Bonsdorff, 1986; Mattila & Bonsdorff, 1988; Bonsdorff & Blomqvist, 1989; Bonsdorff *et al.*, 1990, 1991; Aarnio & Bonsdorff, 1992; Bonsdorff, 1992; Haldin, 1992; Lindholm & Bonsdorff, 1992; Wistbacka, 1992), and on the food consumption of fish (Blomqvist, 1986; Mattila & Bonsdorff, 1988; Bonsdorff *et al.*, 1990),
- (2) experiments in the laboratory in order to establish and quantify effects of predation and disturbance at population level, and the mechanisms

behind them (Bonsdorff *et al.*, 1986b, Rönn *et al.*, 1988; Mattila & Bonsdorff, 1989; Sandberg & Bonsdorff, 1990; Nelson & Bonsdorff, 1990; Aarnio *et al.*, 1991; Aarnio & Bonsdorff, 1992; Ejdung & Bonsdorff, 1992; Mattila, 1992), and

- (3) field experiments on community establishment and early succession, predation and/or shelter from predation and physical disturbance to verify the mechanisms suggested by field results and laboratory tests (Blomqvist, 1982, 1984, 1986; Bonsdorff & Österman, 1985; Bonsdorff *et al.*, 1986a, b; Rönn *et al.*, 1988; Bonsdorff, 1989; Mattila & Bonsdorff, 1989; Sandberg & Bonsdorff, 1990; Aarnio *et al.*, 1991; Aarnio & Bonsdorff, 1992; Bonsdorff, 1992; Mattila, 1992).

With the framework given, the ecological characteristics of the specific environment created by the archipelago have been documented and some details characterised. Ecological analysis on comparable shallow soft-bottom systems have also been conducted in other archipelago- or inshore regions of the northern Baltic and surrounding areas (e.g. Lappalainen, 1973; Lappalainen & Kangas, 1975; Kautsky *et al.*, 1981; Meriläinen, 1988; Persson & Olafsson, 1986; Nellbring, 1988; Zander & Döring, 1989; Arndt, 1989; Kautsky & van der Maarel, 1990; Kautsky, 1991), thus providing us with a comprehensive view of both the structure and function of these specific ecosystems.

In connection with the soft-bottoms (both sandy and muddy), the northern Baltic archipelago is largely characterised by rocky shores, where the fauna is generally found in connection with macroscopic vegetation, which for the northern Baltic consists mainly of the uppermost *Cladophora*-belt and below that (to a depth of about 10 m) the *Fucus*-belt, totally dominated by the bladder wrack, *Fucus vesiculosus* (Jansson & Kautsky, 1977; Hällfors, *et al.*, 1984, 1987; Rönneberg, 1984; Kautsky & Kautsky, 1989; Kautsky & van der Maarel, 1990). Due partly to the ice winters with extensive ice-scraping of the rocky shores, and partly to the low salinity, the genuine rocky bottom fauna of the northern Baltic is primarily restricted to the blue mussel *Mytilus edulis* and the barnacle *Balanus improvisus* (Voipio, 1981; Laihonen & Furman, 1986), with numerous animals utilising the secondary habitat offered by the algae. Many fish species also use this habitat for spawning, food and shelter, and seasonal migrations play an important role for the dynamics of this specific community (Jansson *et al.*, 1985). The algal zones on the rocky bottoms, and also on the soft sediments, are among the most diverse systems to be found in the northern Baltic (Lappalainen, 1973; Lappalainen & Kangas, 1975; Lappalainen *et al.*, 1977; Blomqvist & Bonsdorff, 1986; Kautsky & van der Maarel, 1990; Plinski, 1990), and the functional interaction with the genuine soft-bottoms is important both in terms of cover and expanded habitat (Nelson & Bonsdorff, 1990; Mattila, 1992). Temporal changes in the vegetation will also be reflected in the fauna, adding to the variability of the system (Hällfors *et al.*, 1984; Kautsky & van der Maarel, 1990).

DYNAMICS OF THE ZOOBENTHIC COMMUNITIES

The zoobenthos of the shallow water soft-bottoms is relatively stable between annual seasons, although the species-turnover may be considerable (Blomqvist

& Bonsdorff, 1986; Bonsdorff & Blomqvist, 1989), whereas the fish community displays a significant variability in species composition, abundance and biomass over the year (Bonsdorff & Blomqvist, 1989; Bonsdorff *et al.*, 1990; Aarnio & Bonsdorff, 1992). The fish assemblage is primarily governed by temperature, whereas zoobenthos is more affected by oxygen, food availability, and salinity (Blomqvist, 1984; Bonsdorff *et al.*, 1990, 1991). Some important components of the zoobenthos, and their functional groups (based on feeding type, degree of mobility, and feeding habit; Pearson & Rosenberg, 1987) are presented in Table II.

TABLE II

Macrozoobenthos (meiofauna consists of juveniles of macrofauna and mainly nematodes, foraminiferans and harpacticoids) occurring on shallow (0–5 m) soft bottoms in the archipelagoes of the northern Baltic Sea, their ecological origin (freshwater = F, marine or brackish = M), functional group (feeding type: herbivore = H, suspension-feeder = F, surface detritivore = S, burrowing detritivore = B, carnivore = C; degree of mobility: mobile = M, semi-mobile = D, sessile = S; feeding habit: jawed = J, ciliary mechanism = C, tentaculate = T, other mechanism = X), bottom type preferred (gravel = G, sandy = S, muddy = M, vegetated = V, mixed = I), and region of main occurrence (inner archipelago = I, outer archipelago = O), ^(a) based on Bonsdorff, E. & Pearson, T. H. (in prep.). A functional group analysis of changing benthic community gradients of salinity and organic enrichment.

| Taxon, species | Ecological origin | Functional group ^(a) | Bottom type | Main occurrence |
|--------------------------------|-------------------|---------------------------------|-------------|-----------------|
| Mollusca | | | | |
| <i>Cardium glaucum</i> | M | FDX | S | I → O |
| <i>Macoma balthica</i> | M | F/SDX | M/S | I → O |
| <i>Mya arenaria</i> | M | FDX | S | O |
| <i>Mytilus edulis</i> | M | FDX | G | O |
| <i>Hydrobia</i> spp (2 spp) | M | SMX | M | I → O |
| <i>Potamopyrgus jenkinsi</i> | F | SMX | M | I |
| <i>Bithynia tentaculata</i> | F | SMX | V | I → O |
| <i>Theodoxus fluviatilis</i> | F | HMX | V | O |
| <i>Lymnea</i> spp (3–5 spp) | F | SMX | I | I |
| <i>Valvata</i> (sp) | F | SMX | V | I |
| <i>Physa fontinalis</i> | F | SMX | V | I |
| <i>Limapontia capitata</i> | M | H/SMX | M/V | I |
| <i>Embletonia pallida</i> | M | H/SMX | S/V | O |
| Crustacea | | | | |
| <i>Crangon crangon</i> | M | CMJ | S | O |
| <i>Palaemon adspersus</i> | M | CMJ | V | O |
| <i>Ostracoda</i> | M/F | SMX | I | I → O |
| <i>Monoporeia affinis</i> | F (M) | C/SMX | M | O |
| <i>Pontoporeia femorata</i> | M | C/SMX | M | O |
| <i>Bathyporeia pilosa</i> | M | C/SMX | S | O |
| <i>Leptocheirus pilosus</i> | M | FDX | M/S | I |
| <i>Gammarus</i> spp (4–6 spp) | M/F | FMX | V/I | I → O |
| <i>Corophium volutator</i> | M | SMX | M (S) | I (→ O) |
| <i>Saduria entomon</i> | M | C/SMJ | I (M, S) | I → O |
| <i>Asellus aquaticus</i> | F | HMX | V | I |
| <i>Idotea</i> spp (3 spp) | M | HMX | V | O |
| <i>Iaera albifrons</i> (coll.) | M | HMX | V | (I →) O |

TABLE II—Continued

| Taxon, species | Ecological origin | Functional group (°) | Bottom type | Main occurrence |
|----------------------------------|-------------------|----------------------|-------------|-----------------|
| <i>Praunus flexuosus</i> | M | CMX | S, G, V | O |
| <i>Neomysis integer</i> | M | CMX | S, G, V | O |
| <i>Mysis</i> spp (2 spp) | M/F | CMX | S, G, V | O |
| <i>Balanus improvisus</i> | M | FSX | G (stony) | I → O |
| Polychaeta | | | | |
| <i>Harmothoe sarsi</i> | M | CMJ | M (S) | O |
| <i>Nereis diversicolor</i> | M | C/SMJ | M (S) | I → O |
| <i>Polydora redeki</i> | M | S/FDT | M | I → O |
| <i>Pygospio elegans</i> | M | S/FDT | S | O |
| <i>Manayunkia aestuarina</i> | M | FDT | S (V) | O |
| <i>Fabricia sabella</i> | M | FDT | (S) V | O |
| <i>Fabriciolla balthica</i> | M | FDT | (S) V | O |
| Oligochaeta | | | | |
| Tubificoids (<i>et al.</i>) | M/F | S/BDX | I | I → O |
| <i>Stylaria lacustris</i> | F | HMX | V | I |
| Priapulida | | | | |
| <i>Halicryptus spinulosus</i> | M | CMJ | M (S) | O |
| Hirudinea | | | | |
| <i>Piscicola geometra</i> | F | PDX | (parasite) | I → O |
| Nemertinea | | | | |
| <i>Prostoma obscurum</i> | M | CMX | M | I (→) O |
| Turbellaria (spp) | M/F | CMX | I | I → O |
| Bryozoa | | | | |
| <i>Membranipora crustulenta</i> | M | FSX | (epi-) | I → O |
| Hydracarina | F | CMX | I | (I → O) |
| Diptera | | | | |
| <i>Chironomus plumosus</i> -type | (F) | BDX | M | I |
| Chironomidae (spp) | (F) | SDX | M, V | I → O |
| Tanypodinae (spp) | (F) | CDX | M, V | I → O |
| <i>Palpomyia</i> sp | (F) | CMX | M, V | I → O |
| (others) | (F) | S/CM/DX | V | I |
| Trichoptera | | | | |
| (a few families) | (F) | C/HM/DJ | V, M | I |
| Neuroptera | | | | |
| (a few families) | (F) | CMJ | V, M | I |
| Ephemeroptera | | | | |
| (a few families) | (F) | HMJ | V, M | I |
| Odonata | | | | |
| (a few families) | (F) | CMJ | V (M) | I |
| Coleoptera | | | | |
| (larvae + adults) | (F) | CMJ | I | I |

The benthic system is, however, extremely vulnerable to any unexpected or catastrophic event, regardless if it is natural (e.g. oxygen deficiency due to stagnation periods in the water column or drifting algal mats) or induced by man (e.g. eutrophication, oil spills or large-scale dredgings and other engineering works; see Leppäkoski & Bonsdorff, 1989). The recovery potential of the biota

after such events has proved to be high, though, and generally the community develops towards a mature system within one season in terms of species composition and abundance, whereas biomass may take years to recover (Bonsdorff, 1980, 1983, 1989; Bonsdorff & Österman, 1985; Bonsdorff *et al.*, 1986a). Generally, the species turnover (i.e. ratio of immigrating/emigrating species) is relatively large (up to 50%) in the early phases of community succession, whereas it plays a minor role in the mature community, and there reflects the natural dynamics of the equilibrium community (Bonsdorff, 1983, 1989), partly caused by the biotic interactions between species (or functional groups). In most cases of community establishment, the first species to arrive are the opportunists, which usually play a minor role, or are completely lacking in the mature marine system (Grassle & Grassle, 1974; Pearson & Rosenberg, 1978), but may contribute to a high rate of community change both structurally and functionally during succession (Arntz & Rumohr, 1982).

ZOOBENTHIC COMMUNITY ESTABLISHMENT AND SUCCESSION IN BALTIC COASTAL WATERS

In the northern Baltic areas, the total number of species available for establishing the new community is low, and thus the early phases of recovery are primarily governed by season and different occurring life-stages of the normally dominant fauna (an example of this is the bivalve *Macoma balthica*, which has an extreme peak in recruitment in early summer, and may initially dominate in terms of numbers although it will dominate in biomass later on; Bonsdorff, 1984; Bonsdorff & Blomqvist, 1989; Bonsdorff & Wenne, 1989). The amphipod *Corophium volutator* and other highly mobile infaunal species display some opportunistic characteristics in community establishment in the Baltic, but the low overall number of species present at any stage of community succession (usually 10–20 benthic species) will soon establish their internal dominance pattern more as a result of biotic interactions than new species being recruited (Bonsdorff, 1989). To some extent, however, the community establishment can be attributed more to season, distance to the recruiting community, and to the behavioural aspects of the species, than to an active competition for space or food (Menge & Sutherland, 1976, 1987; Gore, 1982; Zajac & Whitlatch, 1982a, b, 1991). Biotic tracers (such as chemical cues, prepared sediment properties etc) also seem to play an important role in the final recruitment phase of the individual settling juvenile, regardless of the method of transport to the recruitment-area (Woodin, 1991). It is noteworthy that the pattern of community succession in these species-poor low-saline systems follow the generalisations proposed for marine ecosystems by Pearson & Rosenberg (1978), and shown from a number of case studies from the northern Baltic Sea (Bonsdorff, 1980, 1983, 1989; Bonsdorff *et al.*, 1986a). In some cases, however, the predicted pattern may be altered by secondary disturbances to the environment caused by the initial stress-factor leading to a colonisation process. Such an example is reduced oxygen conditions in the near bottom water following dredging activities (Bonsdorff, 1983), where the zoobenthic community has to adapt to a situation of annual or repeated recovery after a short period of oxygen depletion in late summer after the main recruitment period for most benthic animals. Recovery from periodic oxygen depletion of large shallow areas in the

southern Baltic has followed similar trends to that described from the northern Baltic (Gosselck & Georgi, 1984).

The meiofauna-component of the zoobenthos generally recovers much faster than the macrofauna, which is attributed to high turnover ratios, and to passive transport of animals (Widbom, 1983; Bonsdorff & Österman, 1985; Aarnio *et al.*, 1991; Aarnio & Bonsdorff, 1992). In the case of the meiofauna, as well as for juvenile macrofauna, one major threat for the recruits (besides physical disturbance such as drifting algal mats or sediment reworking; Bonsdorff, 1992) is predation or interference either by conspecific adults (as shown for *Macoma balthica* and other bivalves by Bonsdorff *et al.*, 1986b, Olafsson, 1988 and André & Rosenberg, 1991 and for the predator *Saduria entomon* by Leonardsson, 1991; see also Woodin, 1976) or through interspecific interactions in the form of competition or predation (Aarnio *et al.*, 1991; Aarnio & Bonsdorff, 1992).

DYNAMICS OF SHALLOW WATER FISH COMMUNITIES

For the fish assemblages (Table III), the community succession follows an annual pattern, which is primarily set by temperature. Many nearshore shallow water habitats are completely devoid of fish during the winter season (Aneer & Nellbring, 1977; Blomqvist, 1984, 1986; Nellbring, 1985; Bonsdorff & Blomqvist, 1989), but as the ice breaks in the spring, high numbers of fish migrate into the area for shelter, spawning and feeding (Blomqvist, 1984, 1986; Mattila & Bonsdorff, 1988; Aarnio *et al.*, 1991). This pattern is true both for the innermost, densely vegetated areas, where freshwater fish species dominate (Bonsdorff *et al.*, 1990), and the outer, exposed sandy bottoms, where the fish community is dominated by gobies and juvenile flounder (Thorman, 1986; Wiederholm, 1987; Aarnio & Bonsdorff, 1992).

The standing stock of fish may consume up to 30% of the annual zoobenthic production, or roughly an equivalent of the momentaneous biomass of the benthos (Mattila & Bonsdorff, 1988; Bonsdorff *et al.*, 1990), and the predation effects have experimentally been shown to be important in regulating the success of individual benthic populations (Bonsdorff *et al.*, 1986b; Mattila & Bonsdorff, 1989). In the shallow archipelagoes where temperatures rise quickly in the spring, the metabolic rates of the fish also increase, thus further increasing the consumption of zoobenthos (Jobling, 1981; Mattila & Bonsdorff, 1988; Karås, 1990). In the northern Baltic nearshore archipelago waters, temperature rises rapidly in the spring, thus attracting fish to the area. Similarly in the fall, the shallow waters are cooled off earlier than the deeper waters, again driving the fish outwards (Neuman, 1977; Blomqvist, 1984, 1986; Wiederholm, 1987; Bonsdorff & Blomqvist, 1989). Some species, such as perch (*Perca fluviatilis*) seem relatively indifferent to temperature, whereas others are more strictly cold- or warm-water species (Neuman, 1979; Blomqvist, 1984), and only occur in the area during their optimal temperature range. In combination with other changes in the environment, such as eutrophication, differences in temperature become more important as well (Svärdson & Molin, 1981).

Fish in these shallow waters seem largely non-selective in terms of species consumed (Blomqvist, 1986; Mattila & Bonsdorff, 1988; Rask, 1989), but prey selection may change with season (Thorman & Wiederholm, 1983, 1984;

TABLE III

Fish species utilising the shallow water (0–5 m) archipelago areas of the northern Baltic Sea, their ecological origin (freshwater = F, and marine = M), mode of feeding (predatory = Pr, planktivorous = Pl, omnivorous = Om), and region of main occurrence (inner archipelago = I, middle archipelago = M, and outer archipelago = O). Note that most fish species utilising the shallow waters also consume benthos, and thus participate in the benthic interactions of these habitats (Blomqvist, 1982, 1984, 1986; Mattila & Bonsdorff, 1988; Bonsdorff & Blomqvist, 1989; Rask, 1989; Bonsdorff *et al.*, 1990; Koli, 1990; Wistbacka, 1992).

| Species | Origin | Feeding type | Occurrence |
|--|--------|------------------------|------------|
| Pike (<i>Esox lucius</i>) | F | Pr (fish) | I → O |
| Whitefish (<i>Coregonus lavaretus</i>) S. L. | F | Pr (plankton, benthos) | M → O |
| Perch (<i>Perca fluviatilis</i>) | F | Pr (benthos, fish) | I → O |
| Pikeperch (<i>Stizostedion lucioperca</i>) | F | Pr (fish) | I → M |
| Ruffe (<i>Gymnocephalus cernua</i>) | F | Pr (benthos) | I → M |
| Ide (<i>Leuciscus idus</i>) | F | Pr (benthos) | I → M |
| Roach (<i>Rutilus rutilus</i>) | F | Om | I → O |
| Rudd (<i>Scardinius erythrophthalmus</i>) | F | Om | I → M |
| White bream (<i>Blicca bjoerkna</i>) | F | Om | I → M |
| Bream (<i>Abramis brama</i>) | F | Om | I → M |
| Crucian carp (<i>Carassius carassius</i>) | F | Om | I |
| Bleak (<i>Alburnus alburnus</i>) | F | Pl | I → O |
| Cod (<i>Gadus morhua</i>) | M | Pr (benthos, fish) | O |
| Burbot (<i>Lota lota</i>) | F | Pr (fish, benthos) | I (→ O) |
| Minnow (<i>Phoxinus phoxinus</i>) | F | Pr (benthos) | M → O |
| Baltic herring (<i>Clupea harengus membras</i>) | M | Pl | M → O |
| Sprat (<i>Sprattus sprattus</i>) | M | Pl | O |
| Three-spined stickleback (<i>Gasterosteus aculeatus</i>) | F/M | PR (benthos, plankton) | M → O |
| Nine-spined stickleback (<i>Pungitius pungitius</i>) | F | Pr (benthos, plankton) | I → O |
| Fifteen-spined stickleback (<i>Spinachia spinachia</i>) | M | Pr (benthos, plankton) | M → O |
| Common goby (<i>Pomatoschistus microps</i>) | M | Pr (benthos) | I → M (O) |
| Sand goby (<i>P. minutus</i>) | M | Pr (benthos) | (I) M → O |
| Two-spotted goby (<i>Gobiusculus flavescens</i>) | M | Pr (benthos, plankton) | O |
| Black goby (<i>Gobius niger</i>) | M | Pr (benthos) | I → O |
| Eelpout (<i>Zoarces viviparus</i>) | M | Pr (benthos) | O |
| Bullhead (<i>Cottus gobio</i>) | F | Pr (benthos, roe) | M → O |
| Four-horned sculpin (<i>Myoxocephalus quadricornis</i>) | M | Pr (benthos) | O |
| Sea scorpion (<i>Ceratocottus bubalis</i>) | F | Pr (benthos) | O |
| Flounder (<i>Platichthys flesus</i>) | M | Pr (benthos) | O |
| Turbot (<i>Psetta maxima</i>) | M | Pr (benthos) | O |
| Deep-snouted pipefish (<i>Syngnathus typhle</i>) | M | Pl | M → O |
| Straight-nosed pipefish (<i>Nerophis ophidion</i>) | M | Pl | M → O |

Mattila & Bonsdorff, 1988; Nellbring, 1988; Aarnio & Bonsdorff, 1992), and with changed size of the fish (Aarnio & Bonsdorff, 1992; Mattila, 1992). Size selection within given prey populations (Leonardsson *et al.*, 1988) may ultimately participate in the structuring of the benthic community (Bonsdorff *et al.*, 1986b; Nellbring, 1988; Mattila, 1992). Many fish species are furthermore able to alter their feeding niche with changes in the environment (for example variations in water temperature, spatial heterogeneity etc.), or with altered competition for food (Magnhagen & Wiederholm, 1982; Bergman, 1987, 1988). If, on the other hand, the availability of food (i.e. the presence and abundance of zoobenthos) changes dramatically along a geographic gradient, this may regulate

the distribution of fish, especially in a situation of interspecific competition for food (Westin, 1970; Haahtela, 1975; Hansson, 1980). The benthic system may also affect the success of the fish, through altered conditions on soft-bottoms by accumulating drifting algae (Jansson *et al.*, 1985; Kääriä *et al.*, 1988; Rajasilta *et al.*, 1989), and the benthivorous fish may be affected in both behaviour and predation efficiency by their predators (e.g. gobies and cod; Magnhagen & Forsgren, 1991).

BIRDS AFFECTING THE SHALLOW WATER ECOSYSTEM

Waterfowl, waders, gulls and birds of prey use the archipelago both as a transitory area during their seasonal (spring and fall) migrations to and from their nesting grounds, and as actual nesting- and feeding grounds. Generally, densities are highest among the ducks and gulls, while waders are less common due to the fact that the area is non-tidal (Palmgren, 1936). Still, about 60 species can be recorded, almost half of which may actually breed in the area (Palmgren, 1936; Lindholm & Bonsdorff, 1992; Table IV). Their ecological importance for the shallow water ecosystem has been estimated for one restricted area in the inner archipelago (Bonsdorff *et al.*, 1990), and it was concluded that total food consumption by the birds (including vegetation) equals about 10% of the amount of food (mainly zoobenthos) consumed by benthivorous fish. The bird community changes dramatically with the seasons, however, and individual species redistribute after hatching their young (Kilpi *et al.*, 1990).

TABLE IV

Some dominant bird species affecting the shallow water ecosystem of the archipelagoes in the northern Baltic Sea (main feeding habit: bird of prey = Pr, piscivore = Pi, benthivore = Be, parasitic = Pa, and herbivore = He; and principal area of occurrence: inner archipelago = I, outer archipelago = O; mainly during migration = *).

| Species | Feeding type | Occurrence |
|------------------------------|--------------|------------|
| <i>Podiceps cristatus</i> | Pi/Be | I(→O) |
| <i>Cygnus olor</i> | He | I→O |
| <i>Anas crecca</i> | He/Be | I→O |
| <i>A. platyrhynchos</i> | He/Be | I |
| <i>A. clypeata</i> | He/Be | I |
| <i>Aythya ferina</i> | He | I |
| <i>A. fuligula</i> | Be/He | I→O |
| <i>Bucephala clangula</i> | Be | I→O |
| <i>Clangula hyemalis</i> * | Be | O |
| <i>Melanitta fusca</i> | Be/He | (I→)O |
| <i>M. nigra</i> * | Be | O |
| <i>Somateria molissima</i> | Be | O |
| <i>Mergus serrator</i> | Pi/Be | I→O |
| <i>M. merganser</i> | Pi/Be | I(→O) |
| <i>Haliaetus albicilla</i> | Pr/Pi | I→O |
| <i>Pandion haliaetus</i> | Pi | I→O |
| <i>Fulica atra</i> | He/Be | I |
| <i>Haematopus ostralegus</i> | Be | (I→)O |
| <i>Charadrius hiaticula</i> | Be | O |

TABLE IV—Continued

| Species | Feeding type | Occurrence |
|---------------------------------|--------------|------------|
| <i>Tringa totanus</i> | Be | I → O |
| <i>T. nebularia</i> | Be | O |
| <i>Actitis hypoleucos</i> | Be | I → O |
| <i>Arenaria interpres</i> | Be | O |
| <i>Stercorarius parasiticus</i> | Pa/Pr/Pi | O |
| <i>Larus marinus</i> | Pr/Pi/ (Be) | O |
| <i>L. argentatus</i> | Pi/ (Be/Pr) | I → O |
| <i>L. fuscus</i> | Pi/Be/ (Pr) | (I →) O |
| <i>L. canus</i> | Pi/Be | I → O |
| <i>L. ridibundus</i> | Be/Pi | I (→) O |
| <i>Hydroprogne caspia</i> | Pi | O |
| <i>Sterna hirundo</i> | Pi/ (Be) | I (→) O |
| <i>S. paradisea</i> | Pi/ (Be) | (I →) O |
| <i>Alca torda</i> | Pi/ (Be) | O |
| <i>Cephus grylle</i> | Pi | O |

BIOTIC COUPLINGS—EXPERIMENTAL EVIDENCE

Generally, zoobenthos is structured by the environment, but the functional manifestation of the community structure, and dynamic variability around the overall mean is likely to be modified by biotic couplings at many levels. Thus, epibenthic predators are considered important as regulators of the infaunal benthos through their mobility and ability to search for food (Reise, 1985a, b), although infaunal zoobenthos is known to be able to participate in the regulatory processes (Commito, 1982a, b; Ambrose, 1984, 1991; Commito & Ambrose, 1985b; Olafsson & Persson, 1986; Rönn *et al.*, 1988; Wilson, 1990). The biotic interactions recorded may be promotive or repressive, and when repressive the couplings may be both lethal (through direct predation, competition or physical disturbance of both the animal itself and its immediate environment) and sublethal, for example in the form of physical stress (disturbance, cropping or nipping), which will have a delayed effect at population- and community level (Connell, 1983a, b; Reise, 1985a, b; Wilson, 1991).

In most marine or estuarine shallow habitats epibenthic crustaceans, flatfish and cod (Pihl, 1982, 1985; Pihl & Rosenberg, 1984; Raffaelli *et al.*, 1989; Hall *et al.*, 1990) are the dominant predators, affecting both single populations and the entire infaunal zoobenthic community (Möller *et al.*, 1986). On tidal flats, birds will also contribute significantly to the community regulation (Reise, 1985a; Raffaelli & Milne, 1987). In the northern Baltic Sea epibenthic crustaceans are limited to a few species; the decapod *Crangon crangon* (Mattila *et al.*, 1990) and the isopod *Saduria entomon* being among the most important (Leonardsson, 1991; Sandberg & Bonsdorff, 1990; Aarnio *et al.*, 1991; Hill, 1991; Ejdung & Bonsdorff, 1992). *Crangon crangon* not only affects established macrofauna, but it may also regulate juvenile macrofauna and the meiobenthic community (Jensen & Jensen, 1985; Hedqvist-Johnson & André, 1991). The role of predation on meiofauna can be difficult to distinguish from other regulatory factors, as the turnover ratio is high, and most meiofaunal species occur in the uppermost layers of the sediment, affected also by, for example,

physical disturbance (Gee *et al.*, 1985; Palmer, 1988). Infaunal predation in the northern Baltic archipelagoes is important, as shown by Bonsdorff *et al.* (1986b), Elmgren *et al.* (1986), Rönn *et al.* (1988), Abrams *et al.* (1990), Hill *et al.* (1990), and Sandberg & Bonsdorff (1990). Tests in aquaria have shown, however, that predation may indeed be important also at meiofauna-level (Watzin, 1983; Olafsson & Moore, 1990; Aarnio *et al.*, 1991). Predation on the zoobenthos by fish seems quantitatively important (Pihl, 1982; Thorman & Wiederholm, 1983, 1984; Zander & Hagemann, 1987; Mattila & Bonsdorff, 1988, 1989), and several tests have shown the potential of the fish to regulate the densities of the prey populations in various environments (Mattila & Bonsdorff, 1989; Nelson & Bonsdorff, 1990; Aarnio *et al.*, 1991; Mattila, 1992). Recent studies indicate that biotic interactions in the shallow soft-bottom sediments may be more complicated than previously described, however (Kneib, 1991). Sublethal effects of disturbance and cropping or siphon nipping will affect the physiological condition of the animals, which in turn may affect the reproductive output. Similarly, mechanical disturbance (such as sediment reworking) may facilitate predation by making the prey more accessible to predation, and by activating the predators (Bonsdorff *et al.*, unpubl. obs.). Physical disturbances by drifting algae may also play an important part in structuring the infauna by reducing the success of settling larvae, reducing the oxygen conditions at the sediment surface, or by acting as cover for organisms (Sundbäck *et al.*, 1990; Raffaelli *et al.*, 1991; Bonsdorff, 1992). Other physical disturbances, such as decaying animals, may also affect the surrounding fauna, and thus a dead predator (such as amphipods or bivalves in relation to meiofauna) or competitor may still be a potential enemy for parts of the infauna (Olafsson & Elmgren, 1991; Olafsson, 1992).

CONCLUDING REMARKS

It is obvious that the shallow water soft-bottom benthos of the northern Baltic Sea is not just structured by the harsh environment, but indeed regulated by intricate, multi-level biotic couplings, affecting all functional groups, life-stages and size-classes of the biota. The seemingly poor ecosystems (low in species diversity) show complex webs of interactions that illustrate the need for profound knowledge of not just the key species in a community, but of all functional groups across trophic levels. In this respect the shallow, non-tidal, brackish-water environment of the northern Baltic Sea offers an excellent example of the relative diversity and importance of biotic interactions in the establishment, succession, and maintenance of dynamic benthic ecosystems, including benthic vegetation, benthic epi- and infauna, benthivorous fish, and birds. It also indicates how vulnerable to unexpected or man-made disturbances the system is, and that the extinction of one functional group may have effects on the entire ecosystem.

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