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Long-term changes and coastal eutrophication. Examples from the Åland Islands and the Archipelago Sea, northern Baltic Sea Baltic Sea Eutrophication Long-term changes Nutrient Zoobenthos

Mer Baltique Eutrophisation Changements à long terme Nutriment Zoobenthos

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ABSTRACT

The coastal and archipelago waters of the northern Baltic Sea are influenced by increasing eutrophication (significantly increasing temporal trends in nutrient availability). Increased nutrient levels and pelagic primary production have led to decreased transparency in the water body, increased plankton biomass, and increased amounts of filamentous algae. Large-scale and long-term (15-30 years) comparisons have shown that zoobenthic communities have changed significantly (altered species diversity, increased total abundance and increased biomass). The stress in the ecosystem is also illustrated at the population level (*Macoma balthica*). An increasing trend is shown for a near-shore fish community, where the increase in biomass has been linear over the past twenty years. Significant predictability of the regression has been shown for 1989-1994. Some areas show signs of community recovery, or changes attributable to natural variation, whereas other nearby areas may display opposite trends.

The paper illustrates: (a) overall long-term changes (abiotic: nutrients and turbidity; and biotic: primary production, zoobenthos and fish); (b) site- specific long-term dynamics (infaunal and fish communities); and (c) cases of alternating long-term recovery and deterioration (water quality, zoobenthos).

RÉSUMÉ

Changements à long terme dans les écosystèmes littoraux (Iles d'Åland et archipel du nord de la Mer Baltique.

Les eaux littorales de l'archipel du nord de la Mer Baltique sont soumises à une eutrophisation accélérée (augmentation significative des tendances temporelles dans la disponibilité de nutriments). L'accroissement de la production primaire pélagique a réduit la transparence de l'eau, augmenté la biomasse du plancton et la quantité d'algues filamenteuses.

Des comparaisons à grande échelle et à long terme (15 à 30 ans) révèlent une évolution significative des communautés zoobenthiques (modifications dans la diversité des espèces, augmentation de l'abondance totale et de la biomasse). Le degré de stress de l'écosystème est aussi marqué dans la population (*Macoma balthica*). Dans une communauté littorale de poissons, la croissance de la

biomasse a été linéaire pendant les vingt dernières années. Une prédicibilité significative de la régression est observée pour 1989-1994. Quelques régions présentent des signes de récupération des communautés, ou montrent des changements dûs à la variabilité naturelle, tandis que dans des régions voisines les tendances sont parfois opposées.

Ce travail illustre : a) les changements globaux à long terme (abiotiques: nutriments et turbidité; et biotiques: production primaire, zoobenthos et poissons), b) la dynamique locale à long terme (communautés de poissons et de zoobenthos), et c) l'alternance entre la récupération et la dégradation à long terme (qualité de l'eau, zoobenthos).

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INTRODUCTION

Temporal trends have been analysed for the Baltic Sea for several decades (Helcom, 1990, 1993, 1994). In particular, the hydrographic features of this isolated brackish-water sea have been documented in detail since the later part of the 19th century (Helcom, 1990). Biotic conditions, and also the nutrients regulating organic production, have been monitored continuously since the early 1960s, and for the open sea some apparent trends have been observed. Nutrient contents of the productive layer have increased significantly in the entire Baltic Sea (Wulff et al., 1994), whereas the zoobenthos of the open Baltic is primarily governed by the oxygen content of the bottom waters below the permanent halocline characterizing this sea (Andersin and Sandler, 1989; Leppäkoski and Bonsdorff, 1989; Helcom, 1990). For the coastal waters, most monitoring has been related to local effluents (industrial, municipal or riverine: Pitkänen, 1994), and focused on the areas close to the point sources, although large-scale processes may affect the ecosystem. Hence, Helcom (1993) listed the Åland archipelago and the Archipelago Sea (Fig. 1) as "environmental hot spots" (of a total of 132 hot spots in the entire catchment area) in the Baltic Sea, with eutrophication (excess nutrient loading), with aqua- and agriculture being the main sources. Only recently has the importance of an overall analysis of the coastal waters, and of the Finnish coasts of the vast Archipelago Sea in particular, been acknowledged (Helcom, 1991; Jumppanen and Mattila, 1994; Norkko and Bonsdorff, 1994).

The aims of this study were (a) to describe the present state of the coastal archipelago waters of SW Finland; (b) to analyse temporal (≥ 10 years) trends compared to both spatial variability and overall, long-term changes recorded for the open Baltic Sea; and (c) to compare site-specific patterns with general trends (hydrography, nutrients, and zoobenthos). All parameters studied were evaluated in relation to the assumed process of eutrophication in the Baltic Sea (Helcom, 1990, 1993; Pitkänen, 1994; Wulff *et al.*, 1994), which has been linked



Figure 1

Investigated area (the Åland Islands and the Archipelago Sea, SW Finland) in the northern Baltic Sea (59° 45′ -60° 45′ N, and 19° 30′ -23° 00′ E).

to changes at various trophic and functional levels in the coastal waters (pelagic primary production: Grönlund and Leppänen, 1990; zoobenthos: Cederwall and Elmgren, 1990; Bonsdorff *et al.*, 1991; fish: Hansson and Rudstam, 1990; ecosystem level: Jumppanen and Mattila, 1994).

MATERIALS AND METHODS

Area of investigation

The investigated area (Fig. 1) is the extensive archipelago that encompasses the Åland Islands and the Archipelago Sea on the SW coast of Finland, northern Baltic Sea (59° 45'-60° 45' N, and 19° 30'-23° 00' E), and covers approximately 15,100 km². The area is characterized by some 30,500 islands, forming a mosaic of more or less distinct zonation ranging from the innermost sheltered coastal zone to the open coastal areas. Average water depth is 23 m (with deep trenches >100 m), with a shoreline of over 20,000 km, emphasizing the importance of littoral, near-shore, shallow areas for the functioning of the ecosystem (Bonsdorff and Blomqvist, 1993). The sea is non-tidal, and characterized by a strong seasonality, including high summer temperatures (surface waters reach 18-20°C), and a more than 90% probability of annual ice cover during winter (Leppäkoski and Bonsdorff, 1989). Further, the land uplift after the last glaciation still prevails at 50-100 cm per 100 years, continuously forming new littoral areas. As a consequence of the profound changes in the Baltic aquatic environment over the past 10,000 years since the last glaciation, with rapid changes from limnic to fully marine to brackish conditions, few species have evolved in the area, and the continuous input of (often highly successful) non-indigenous species (Leppäkoski, 1984, 1992, 1994; Jansson, 1994) illustrates the ongoing succession (Fig. 2) characterized by high instability and large variability of both abiotic and biotic conditions (Pearson and Rosenberg, 1978; Menge and Sutherland, 1987). Due to the relatively high degree of isolation from the fully marine environment and as a consequence of the large riverine input of fresh water (Carlsson and Bergström, 1993; Pitkänen, 1994), the northern Baltic Sea is today characterized by low salinities (4-7), with a permanent halocline. Regular anoxic conditions occur in the bottom waters in the open sea (Andersin and Sandler, 1989). In the archipelago areas, however, no permanent halocline is found, but stratification due to rapid warming of the surface waters occurs annually. For more details on the Baltic Sea ecosystems and prevailing gradients, see Voipio (1981) and Leppäkoski and Bonsdorff (1989).

Data used

The long-term data on the pelagic parameters (hydrography, nutrients, pelagic primary production) are taken from Jumppanen and Mattila (1994) for the Archipelago Sea, and obtained from ongoing monitoring programmes for the Åland area. All parameters studied, sampling procedures and subsequent chemical and biological analyses are described in Helcom (1990, 1994), Jumppanen and Mattila



Figure 2

Conceptual model of successional dynamics in time or space, illustrating (a) the need to include the scaling problem in the analysis of large-scale or long-term patterns (dashed lines illustrating changes in amplitude and magnitude of community responses with increasing distance in time or space from an initial stress affecting succession); (b) the importance of alternative starting points (marked as open circles) for the successional pattern (solid lines following the Pearson and Rosenberg 1978-model of succession during organic enrichment of soft sediments); and (c) the increasing uncertainty and decreasing predictability of the ecosystem with increasing spatial and temporal scales and amplitudes of the investigated parameters.

(1994), and Nehring (1994). The basic nutrients (Tot-N and Tot-P) are given as $\mu g/l = mg/m^3$, primary production as phytoplankton biomass (g/m³) or primary production capacity (mg C/m³/d). For the littoral filamentous and benthic drifting algae, biomass is given as g dwt/m² (Mäkinen and Aulio, 1986).

For sediment characterization and zoobenthos, various methods have been used over time, but the comparisons made have only been with compatible data, based on three to five replicate samples per station (Van Veen or Ekman-Birge type grabs), with animals analysed to species level, and abundance values given as individuals per m^2 , and biomass as g wwt per m^2 (Dybern *et al.*, 1976; Leppäkoski, 1975; Bonsdorff and Blomqvist, 1992; Jumppanen and Mattila, 1994; Norkko and Bonsdorff, 1994). For the Baltic soft clam, *Macoma balthica* (L.), population structure was analysed in 1 mm size classes.

To determine long-term changes in a fish assemblage, a Finnish standard set of gill nets (eight individual nets covering mesh sizes of 12 to 75 mm knot-to-knot) was used for monthly sampling in the summer season (May-August) during the period 1975-1994. The data are presented as a mean summer standing stock (catch per effort; kg live wet weight) of the entire assemblage (Blomqvist, 1984; Bonsdorff and Blomqvist, 1992).

The numerical treatment of the data is descriptive, primarily based on linear regression for time series analysis, and t-tests and/or one-way Anova for the comparisons of means. Size-frequency distributions of *M. balthica* were compared with the Kolmogorov-Smirnov test.

RESULTS

The Åland archipelago

In the Åland archipelago, with few local sources of nutrient input, significant changes have occurred in the water body during the period 1984-1994 (Fig. 3). In this area, aquaculture (fish farming in net cages; primarily Oncorynchus mykiss) accounts for more than one third of the local total nitrogen input, and about 55% of the total phosphorus input to the marine environment. Turbidity in the water column has increased, and is recorded as a significant reduction in Secchi depth readings (winter values; no ice cover) from about 8 m in 1984 to 4.3 m in 1994 (Fig. 3). Simultaneously, the basic nutrient levels (winter values) in the productive layer (1-10 m) have increased, whereas the pool of available silica has decreased (p < 0.05). The N:P-ratio has also decreased significantly, a fact which in combination with the changes in nutrient and silica levels indicates both structural and functional changes in the pelagic ecosystem, *i.e.* increased frequency and magnitude of coastal blooms of cyanobacteria as surplus phosphorus is available, and nitrogen and silica become limiting. Phosphorus is the main determinant in the system, with significant positive correlations to both the N:Pratio ($r^2 = 0.58$; p < 0.01) and Secchi depth/transparency $(r^2 = 0.73; p < 0.02)$. Simultaneously, a non-significant



Figure 3

Long-term (1984-1994) trends (winter values) in transparency (Secchi depth; m), oxygen saturation (%; bottom water), nutrients (Tot-P, Tot-N and Si of the productive layer, 1-10 m; µg/l), and the N:P- ratio at Marhällan, Åland Islands, northern Baltic Sea.

decreasing trend is seen in the minimum oxygen saturation at 80 m depth (Fig. 3).

The changes observed in the water body are reflected in the zoobenthos in the form of altered community composition and increased productivity. For the entire outer archipelago zone (20-30 m depth; $4.8 \pm 0.3\%$ organic content of the sediment), the total abundance and biomass have increased significantly between 1976 and 1994 (summer values, pooled information for the entire area; Fig. 4), whereas the number of species has not changed. In 1976-1978, 23 macrozoobenthic species were recorded vs. 22 in 1993-1994. During the intervening period, however, 40% of the total species composition had changed, indicating functional disturbances as well, with a shift from suspension feeders to deposit feeders (Bonsdorff and Blomqvist, 1993). This structural change was caused by a loss of five benthic crustacean species (found in the 1970s but not in the 1990s), and a gain of four species, two of which were polychaetes new to the benthic infauna of the northern Baltic Sea (Polydora redeki and Marenzelleria viridis: Bonsdorff, 1981; Jansson, 1994; Leppäkoski, 1994; Norkko and Bonsdorff, 1994). These overall temporal trends are based on information from numerous stations, and individual stations may differ from the general pattern. One such locality (25 m) in the vicinity of Mariehamn, Åland Islands has been studied since 1972 (Fig. 5), and a significant increase in species numbers and abundance values, but not in biomass, were found 1972-1994. This is due mainly to a large variability between samples in the biomass (occasional batches of Mytilus edulis found attached to gravel or other hard objects), and to the dominance of one species; Macoma balthica. The increase in abundance correlates positively to the increase in species numbers (p < 0.01), whereas biomass is so dominated by the bivalves M. balthica and M. edulis that no correlation with the community composition is recorded. Biomass, on the



Åland Islands 1976-94: S, A, B (20-30 m)





Community changes in soft-bottom zoobenthos (10 stations with ≤ 5 replicates each per station and year; 20-30 m depth; summer values) in the outer Åland archipelago 1976 (dark)-1994 (diagonally lined). #spp = mean number of macrozoobenthic species per sample, $A (\times 100) =$ mean total abundance/ m^2 , B ($\times 10$) = mean total biomass (g wwt)/ m^2 . Error bars = 1 standard error of the mean.







Long-term development of macrozoobenthos at one station (Mariehamn, Åland Island; 25 m; single bars represent summer mean values for samples taken May-August) during 1972-1994. #spp, $A (\times 100)$ and $B (\times 10)$ as in Fig. 4. r^2 and p-values for the linear regression for the entire period.

other hand, correlates strongly with abundance (p < 0.05). The structure of the *M. balthica*-population (Fig. 6) has remained stable since the 1970s (no significant changes in size-frequency distribution; Kolmogorov-Smornov test), with successful annual recruitment ($47.0 \pm 5.2 \% \le 2$ mm), and a low mean individual weight (72.5 ± 3.2 mg wwt/ind). Simultaneously, however, both total abundance and biomass of *M. balthica* have increased significantly (Anova; p < 0.05) over time.

The fish assemblage of an inshore area has also displayed a significant (p < 0.001; $r^2 = 0.62$) linear increase in biomass during 1975-1994 (Fig. 7). The period 1975-1988 was used to estimate the rate of biomass increase (Bonsdorff and Blomqvist, 1992), and a prediction was made for the following years. Assuming a continuous linear increase, the subsequent catches (1989-1994) followed the prediction with an error of 3-13% of the expected catch (Fig. 7). During the period investigated, the species composition has remained stable, although dominance patterns have changed (Blomqvist, 1984, 1986). Roach (Rutilus rutilus L.) has increased from <15% to about 45% of the total biomass, illustrating the ongoing eutrophication. Hence, a gradual shift towards an increasing proportion of omnivores also affects the trophic status of the fish community (Bonsdorff and Blomqvist, 1993).



Figure 6

Population dynamics of the Baltic soft clam (Macoma balthica) at station Mariehamn (Åland Islands) in 1979-1994 presented as relative size-frequency distribution (%: 1 mm classes). Numbers presented are total abundance (ind) and biomass (g wwt)/ m^2 , and mean individual weight (mg wwt) for the population at the time of sampling.

The Archipelago Sea

The basic features of the present state of the Archipelago Sea (nutrients and primary production) are summarized in Table 1. The overall nutrient levels (Tot-N, Tot-P) are high, indicating large-scale eutrophication. The increase over time (pooled areal data from the 1960s to the 1990s) is significant (p < 0.01) for both major nutrients in spite of local reduction in the inner parts of the archipelago (Fig. 8), where municipal waste waters have been treated effectively since the late 1960s (Jumppanen and Mattila, 1994). The reduction in nutrient loading in the inner archipelago has been counteracted in the outer archipelago (open coastal zone), where nutrient levels have risen significantly (p < 0.01) during the same period (Fig. 8), mainly through extensive fish farming (Jumppanen and Mattila, 1994). Thus the natural situation with a gradient



Long-term changes in fish-biomass (Åland Isl.); 1975-94

Figure 7

Long-term (1975-1994) development of the standing stock of an inshore fish community in the Åland archipelago. Values are given as catch- per-effort (summer averages; kg) for the total assemblage. The linear equation (p < 0.001) is for the entire period, and open dots indicate predicted values 1989-1994.

of decreasing nutrient levels from the inner bays towards the open sea no longer exists, but rather a more or less uniform distribution of nutrients throughout the system (Fig. 8; Table 1). The increase in nutrient levels has resulted in a significant decrease in transparency (p < 0.01) in the inner part of the archipelago (Fig. 9), as well as in the outer regions (Jumppanen and Mattila, 1994). The increase in nutrient levels is also reflected in the pelagic primary production, measured as both planktonic biomass (Table 1) and primary production capacity (Fig. 10; Table 1). Pelagic primary production capacity has increased throughout the archipelago, and average levels have doubled in 15 years (Fig. 10). Simultaneously, the amounts of annual filamentous algae on hard substrates have increased significantly (p < 0.05) during the same period (Table 1). The average nutrient levels in the Archipelago Sea are at a noticeably higher level than in the Åland area (Figs. 3, 8;

Table 1

Table 1), illustrating the importance of local nutrient input through riverine inflow (Jumppanen and Mattila, 1994; Pitkänen, 1994). Transparency has decreased more rapidly in the Åland area, however, and average Secchi-depth is similar (about 4 m) throughout the investigated archipelago areas, indicating similar pelagic primary production levels.



Figure 8

Development of nutrient levels (Tot-N, Tot-P; g/l) in the productive layer (1-10 m; single winter measurements) in the open outer archipelago zone (Kumlinge; outer Archipelago Sea) and the inner archipelago zone (Airisto Sound; central Archipelago Sea) 1965-1993.

The zoobenthos in the Archipelago Sea has not been studied comprehensively over the entire area, and studies have focused on the inner bays affected by both eutrophication and pollution since the 1950s (Leppäkoski, 1975; Bonsdorff

Parameter	Level (1990s)	Status/trend	Ecological effects
Oxygen resource (min.) ⁽¹⁾ Bottom water (mg/l)	5-6	Decreasing	Effets on zoobenthos
Nutrients (winter)			
Tot-N (mg/m ³)	670 ± 135	Increasing	Induces eutrophication
Tot-P (mg/m^3)	31 ± 1.7	Increasing	Induces eutrophication
Transparency ⁽²⁾ (average; m)	4.0 ± 0.3	Decreasing	Reduces light penetration Reduces depth distribution of macroalgae
Primary production (plankton) ⁽³⁾			
Biomass (g/m ³)	1600 ± 325	Increasing	Increases turbidity and O ₂ -consumption
Capacity (mg C/m ³ /d)	530 ± 95	Increasing	Increases O ₂ -consumption
Filamentous algae ⁽⁴⁾			
$(g dwt/m^2)$	263 ± 108	Increasing	Altered energy pathways \rightarrow drift algal mats \rightarrow increased O ₂ -consumption \rightarrow effects on zoobenthos

Some general trends based on the pelagic and littoral zones in the Turku area, Archipelago Sea, SW Finland 1966-94 (based on Jumppanen and Mattila, 1994, and references therein).

(1) Central Airisto Sound; late summer.

(2) Summer average.

⁽¹⁾ Comparisons of pooled data (average values for the productive season): late 1960s, mid-1970s, late 1980s.

(4) Attached rocky shore annual algae (late 1980s).



Figure 9

Long-term development of transparency (Secchi depth in mean of the open water period; m) in the inner archipelago zone (Airisto Sound; central Archipelago Sea) 1965-1993.



Figure 10

Pelagic primary production capacity (mg C/m³/d; summer means) in the outer (Korpo) and central (Rymättylä) parts of the Archipelago Sea, 1976-1990.

et al., 1986; Jumppanen and Mattila, 1994). Thus, overall long-term changes reflect levels of pollution rather than increasing eutrophication (Fig. 11). Temporal changes illuminate successive phases of recovery after a depletion of the fauna in the early 1960s (Jumppanen and Mattila, 1994), which was most severe outside the Turku harbour area (Fig. 12). In this inshore area, sediment quality was





Overall long-term changes in macrozoobenthos (summer values) in the inner parts of the Airisto Sound off Turku (Archipelago Sea; 13 stations, mean depth = 18.6 m) 1970-1991. #spp, A (\times 100) and B (\times 10) as in Fig. 4. Error bars = 1 sd of the mean. damaged (Leppäkoski, 1975), and the fauna was almost eliminated. Through reduced input of pollutants, a gradual recovery has been observed, with an initial overshoot in all community parameters (species, abundance and biomass) gradually stabilizing at intermediate levels.



Figure 12

Long-term (1960-1991; summer values) development of macrozoobenthos at two stations (3 m and 21 m) in the Turku area (innermost Archipelago Sea) after local pollution in the 1950s. #spp, A (\times 100) and B (\times 10) as in Fig. 4. 0 = dead bottoms.

Another example of recovery is illustrated in Fig. 13, where the succession after cessation (1975) of effluent emission from a fish treatment factory is shown. This local point source of organic enrichment (i.e. eutrophication) was estimated at 3,000 person equivalents (BOD7, Tot-P), and resulted in anoxia and 80 ha dead bottoms below 20 m 1972-1976 (Leppäkoski et al., 1983; Bonsdorff et al., 1986). All community parameters showed rapid, significant (p < 0.05) recovery after the cessation of the point source pollution, but for the period 1980-1988 no significant changes were noted (Fig. 13). This is partly due to the high levels of organic matter in the sediment (>10% in 1977), reflected in the population dynamics of Macoma balthica (Fig. 14). After an initial recruitment in 1976-1977 (40.7% < 2 mm clams), the population structure changed significantly over time, with mean individual wet weight increasing from 51.1 in 1977 to 663.6 g wwt/ind in 1986. As the population grew senile (no recruitment), the organic content of the sediment was gradually reduced from > 10%to 3-4% in 1986-1988. At that time, the density was also very low (450 ind/m²), and only then could a successful recruitment occur, with more than half of the population being newly recruited ($\leq 2 \text{ mm size}$) in 1988 (Fig. 13). M. balthica constituted 75-95% of the total biomass in the recovery-period 1977-1988. Thus local conditions may significantly affect the quality of the biota.

DISCUSSION

Increased nutrient levels affect coastal pelagic systems

During recent decades (from about 1970), basic nutrient levels have risen in the open Baltic basin as a consequence





Long-term development (1972-1988; summer values) of macrozoobenthos at a locality affected by strong local organic enrichment 1971-1975 (Nagu: central Archipelago Sea). #spp, A (×100) and B (×10) as in Fig. 4. 0 = dead bottoms due to anoxic conditions (r^2 and p-values for the linear regression are for the entire investigated period).

of increased runoff from land, increased input with inflowing marine water, and through air deposition (Helcom, 1990; Nehring and Matthäus, 1991; Carlsson and Bergström, 1993; Nchring, 1994; Pitkänen, 1994; Wulff et al., 1994). This increase has, in general, not been directly coupled with structural or functional changes in the macro-scale ecosystem, possibly because such changes are hard to detect in a system largely governed by semi-permanent stratification and anoxia in the water mass below the halocline, causing mortality among the zoobenthos (Andersin and Sandler, 1989, 1991; Leppäkoski and Bonsdorff, 1989). In recent years, however, the pelagic ecosystem has undergone functional changes, which have been detected in the productive surface layers (Grönlund and Leppänen, 1990; Kivi et al., 1993), and on other trophic levels (Aneer, 1985; Hansson and Rudstam, 1990; Helcom, 1990; Norkko and Bonsdorff, 1994).

The coastal waters are primarily non-stratified (by salinity) and directly affected by local sources of nutrient loading. Some clear effects of eutrophication have been demonstrated in these systems in the central and northern Baltic Sea (Mäkinen and Aulio, 1986; Cederwall and Elmgren, 1990; Bonsdorff *et al.*, 1991, 1992; Helcom, 1991; Bonsdorff and Blomqvist, 1992; Jumppanen and Mattila, 1994). Consequently, Larsson *et al.* (1985),



Figure 14

Population dynamics of the Baltic soft clam (Macoma balthica) at station Nagu (central Archipelago Sea) in 1977-1988 presented as relative size-frequency distribution (%; 1 mm classes). Numbers presented are total abundance (ind) and biomass (g wwt)/m², and mean individual weight (mg wwt) for the population at the sampling occasions.

Rosenberg (1985) and Elmgren (1989) raised concern about the health and future of coastal ecosystems under continued increasing nutrient loading. The data presented here (Figs. 3, 8*a*, and Table 1) for the SW Finnish archipelago waters, covering over 15,000 km², clearly demonstrate the magnitude of the problem. In this topographically highly complex system, dominated by shallow areas important as spawning- and nursery grounds with complex biotic interactions (Leppäkoski and Bonsdorff, 1989; Bonsdorff and Blomqvist, 1993), nutrient levels (Tot-N, Tot-P) have increased significantly throughout the system. Exceptions are areas closest to municipal waste water treatment plants, where local recovery has been documented (Fig. 8). In recent years (1980s), these changes have been stronger in the outer archipelago and the Åland area, where levels remained low (close to background) until the early 1980s (Fig. 3), as the inner Archipelago Sca was affected by local eutrophication already in the 1960s (Jumppanen and Mattila, 1994). The natural differences in the pelagic ecosystem between the inner archipelago areas and the open sea are gradually being resolved, with the productive water layer becoming more turbid, and the primary production capacity increasing (Fig. 10). The balance between nutrients has also changed, with altered N:P-ratios and decreased Si-reserves in the winter/spring as prominent features (Grönlund and Leppänen, 1990; Jumppanen and Mattila, 1994; Wulff et al., 1994). Against this background, it is somewhat surprising that the longterm changes observed in zooplankton have been mainly attributed to hydrographical parameters, such as salinity (Viitasalo et al., 1990; Viitasalo, 1992). This is possibly explained by the life-history strategies of the dominating zooplankton species (Viitasalo, 1992, 1994), and by the lack of studies on zooplankton in direct relation to nutrients and eutrophication. In general, marine eutrophication in the Baltic has shifted from local to regional scales.

Organic enrichment increases benthic production

Increasing amounts of energy are being transferred through the littoral macroscopic primary producers (Mäkinen and Aulio, 1986). As the filamentous algae increase, organic material is transported to the benthic subsystem in increasing amounts, which can be registered as drifting algal mats on soft bottoms (Bonsdorff, 1992). Sedimentation rates also increase as a consequence of increased primary production (Jumppanen and Mattila, 1994). With increasing organic enrichment of the sediment, the zoobenthic communities respond in terms both of impoverished species composition and diversity (Pearson and Rosenberg, 1978; Bonsdorff et al., 1991, 1992), and increasing productivity (Pearson and Rosenberg, 1978, 1987; Cederwall and Elmgren, 1990; Bonsdorff et al., 1991, 1992). This is also the case with the zoobenthic system of the archipelago areas of the northern Baltic Sea (Fig. 4). Hence, the entire energy transfer pathways may be altered under "stress" in terms of, for example, eutrophication (Menge and Sutherland, 1987; Pearson and Rosenberg, 1987; Elmgren, 1989). In situations where eutrophication leads to periodic hypoxia or anoxia, sediment properties change and nutrients are released back to the water column (Sundby et al., 1992), and biotic interactions within the zoobenthos are disturbed (Menge and Sutherland, 1987; Bonsdorff and Blomqvist, 1993). This type of local anoxia in combination with the anoxic conditions of the deeper parts of the Baltic Sea (Andersin and Sandler, 1989), emphasizes the ecological importance of the archipelago waters in maintaining both biodiversity and production. In analysing long-term trends, where changes are induced over time at various rates in different locations, site-specific patterns are important (Figs. 5, 12, 13), and although larger sampling areas (or longer time scales including alternating stages of successional maturity during e.g. organic enrichment: Pearson and Rosenberg, 1978) increase variability and decrease predictability (Fig. 2), community analysis based on large areal coverage is valuable when interpreting trends (Leppäkoski, 1975; Cederwall and Elmgren, 1990; Andersin and Sandler, 1991; Bonsdorff et al., 1992). As the biota of the Baltic Sea is constantly changing, and a significant proportion of the species are non-indigenous (Leppäkoski, 1984, 1992, 1994; Jansson, 1994), functional aspects may change according to the success of an immigrant. In the present case, several species have established themselves in the area studied during the past decades (Jansson, 1994; Leppäkoski, 1994), possibly counteracting some of the effects of community degradation through increased eutrophication. Given all the parameters studied (nutrients, primary production and zoobenthos), the rate of change at ecosystem level in the archipelago waters fits well with descriptive models proposed for marine systems under the influence of eutrophication (Monitor, 1988; Dederen, 1992; Gray, 1992).

The state of the zoobenthos is also reflected at species level, and in a system with few species present at any given time (Leppäkoski and Bonsdorff, 1989; Bonsdorff and Blomqvist, 1993), population analysis of dominant, long-lived species such as the bivalve *Macoma balthica* can reveal much about the state of the environment (Figs. 6, 14). In cases of strong organic enrichment, recruitment may fail (Pearson and Rosenberg, 1978), leading to senile (non-reproductive) populations: and as *M. balthica* is the dominating component of zoobenthic biomass in the northern Baltic coastal waters (Jumppanen and Mattila, 1994; Norkko and Bonsdorff, 1994), weakened populations of this (or other important) species may have severe effects at ecosystem level (Rosenberg and Loo, 1988; Loo and Rosenberg, 1989).

Fish respond to eutrophication

The fish community studied here (Fig. 7) clearly demonstrates that the increased productivity in the pelagic and benthic systems is reflected also in the fish biomass. Both planktivorous and benthic feeders are known to benefit initially from increased food supply (Aneer, 1985; Hansson, 1985; Mattila and Bonsdorff, 1988; Hansson and Rudstam, 1990), as shown also for zoobenthos (Pearson and Rosenberg, 1987). As the water column becomes increasingly turbid and/or benthic vegetation increasingly dense, cyprinid fish will benefit, as they are omnivorous, and able to utilize any increased food supply (Persson et al., 1988; Hansson and Rudstam, 1990). In the present case, roach (Rutilus rutilus) has gained in importance, which may be a consequence of both increased food supply and altered predator regulation (Persson et al., 1988). Some general effects of eutrophication on the Baltic fish communities are discussed by Hansson (1985) and Hansson and Rudstam (1990), and an example of selective effects in various archipelago zones is given by Kääriä et al. (1988). It seems evident that the long-term changes recorded in the pelagic nutrient supply will have spin-off effects throughout the shallow-water food webs as demonstrated here and also discussed by Bonsdorff and Blomqvist (1993).

Concluding remarks

(a) Nutrient enrichment in the coastal waters of the Åland Islands and the Archipelago Sea has been significant during the past 10-30 years, dissolving the natural differences in trophic status between sheltered archipelago waters and open waters;

(b) The increase in nutrients has altered the pelagic ecosystem, as reflected in higher primary production capacity and reduced transparency;

(c) The increase in primary production is also reflected in the growth and production of filamentous, annual macroalgae, and subsequent problems with drifting algal mats;

(d) The zoobenthic communities of large areas have undergone both structural and functional changes, linked to an increased food supply and periodic oxygen deficiency even in shallow areas. This underlines the importance of

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(e) The increased productivity in both the water column and the sediment can be reflected in the fish assemblages, indicating cascading trophic effects throughout northern Baltic archipelago and coastal ecosystems.

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