

The Effects of Recent Eutrophication on Freshwater Fish Communities and Fishery on the Northern Coast of the Gulf of Finland, Baltic Sea

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Academic Dissertation

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Abstract

The main objectives of this study were to examine the effects of coastal eutrophication on fish communities, and on local recreational fishery and commercial pikeperch fishery on the northern coast of the Gulf of Finland. The study focused on freshwater species, as they live their entire life cycle in the most eutrophied areas, i.e., the archipelago and inner bays. Freshwater species are important for the very popular recreational fishery, forming the bulk of the annual total catch. Certain freshwater species, such as pikeperch, are also important for the small-scale commercial fishery. The main study methods used were gill net surveys, a mailed questionnaire and an analysis of the log-book data of commercial fishery.

The most prominent recent change observed in coastal fish communities was the increased abundance of cyprinids in archipelago areas. Roach, in particular, is currently highly abundant, even in the outer archipelago along the entire northern coast of the Gulf of Finland. The basic reason for the rise in the overall abundance of cyprinids in the archipelagos is improved reproduction success: the reproduction areas are located in the innermost archipelago and inner bays, where slow eutrophication is the most likely change favouring cyprinids. As the state of the inner areas is mostly determined by local factors, national measures to reduce eutrophication play a key role in the future development of coastal fish communities.

The observed freshwater fish biomasses were higher in the less eutrophic western archipelago areas than in the more eutrophic eastern parts of the gulf. This finding was in contrast to general theories of temperate lakes. The most common freshwater species, perch and roach mainly use the intermediate and outer archipelago as feeding grounds. Since their feeding is closely confined to littoral areas, the rise in eutrophy eastwards curtails the food supply in the littoral zone of the archipelago and thus has adverse effects on the abundance of these species, perch in particular. A contributory effect is the decreasing west-east salinity gradient in the Gulf of Finland.

The most concrete eutrophy-related problem in recreational fishery in the Gulf of Finland is the fouling of fishing gear. The clearest change observed in freshwater fish communities — the increase in cyprinids in the archipelago zone — increases the proportion of less valuable species in the coastal fishery catch, but this is a less marked problem in both recreational and commercial fishery. The commercial fishery in the Gulf of Finland focuses less on freshwater species, of which pikeperch is the most important target species, than on sprat, Baltic herring and salmon. The recent coastal eutrophication may have favoured pikeperch, but this study demonstrates that commercial catches of this species are also dependent on other factors, such as temperature-related year class strength, the status of other commercially exploited fish stocks and the firsthand price of fish.

Original articles and author's contribution

- I** Lappalainen, A., Shurukhin, A., Alekseev, G. and Rinne, J. 2000. Coastal fish communities along the northern coast of the Gulf of Finland, Baltic Sea: responses to salinity and eutrophication. *International Review of Hydrobiology* 85: 687–696.
- II** Lappalainen, A. and Pesonen, L. 2000. Changes in fish community structure after cessation of waste water discharge in a coastal bay area west of Helsinki, northern Baltic Sea. *Archive of Fishery and Marine Research* 48: 226–241.
- III** Lappalainen, A., Rask, M., Koponen, H. and Vesala, S. 2001. Relative abundance, diet and growth of perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) at Tvärminne, northern Baltic Sea, in 1975 and 1997: responses to eutrophication? *Boreal Environment Research* 6: 107–118.
- IV** Lappalainen, A. and Pönni, J. 2000. Eutrophication and recreational fishing on the Finnish coast of the Gulf of Finland: a mail survey. *Fisheries Management and Ecology* 7: 323–335.
- V** Lappalainen, A., Söderkultalahti, P. and Wiik, T. 2002. Changes in the commercial fishery for pikeperch (*Stizostedion lucioperca*) on the Finnish coast from 1980 to 1999 — Consequences of environmental and economic factors. *Archive of Fishery and Marine Research* 49: 199–212.

Author's contribution

Articles I, II, IV and V were planned by the author. Article III was planned jointly by the author and Dr. Martti Rask. All articles were written by the author.

Introduction

Marine eutrophication and the Baltic Sea

Eutrophication, defined as the anthropogenic addition of nutrients that cause excessive growth of algae and higher plants followed by changes in other trophic levels, is a common phenomenon in freshwater ecosystems. It has, however, also been recognized as one of the major threats facing marine ecosystems on a global scale (Nixon 1990). A key issue and prerequisite for the control of marine eutrophication is assessment of its effects on ecosystems and the use of natural resources. In this respect, fish and fishery have an important role, as fish are something familiar to the 'general public' and fishery usually has high economic value for coastal countries.

Marine eutrophication is a well-known phenomenon in isolated sea areas, which have a slow rate of exchange of water in relation to volume, and also in shallow estuaries with a high riverine nutrient load. Another factor generally promoting the primary responses of ecosystems to nutrient enrichment is low tidal energy (Cloern 2001). The Baltic Sea is both semi-enclosed and nontidal, and since the early 1900s, total nitrogen and phosphorus loads on the Baltic Sea have increased by factors of about 4 and 8, respectively, as a consequence of human activities (Larsson et al. 1985). Hence, the Baltic Sea is one of the most severely affected sea areas in the world, and eutrophication poses a major threat to its ecosystems (e.g. Cederwall and Elmgren 1990). Examples of other semi-enclosed European seas showing the effects of anthropogenic eutrophication, for instance, as abnormal phytoplankton blooms in summer, are the Black Sea and the Mediterranean Aegean Sea (Kideys 1994, Moncheva et al. 2001). In larger seas and oceans, eutrophication is a more or less local phenomenon usually restricted to estuaries. The Dutch Wadden Sea is a striking example of a European estuary where the increased anthropogenic nutrition load caused an over tenfold increase in annual primary production between the 1950s and 1980s, followed by a clear increase in the macrozoobenthos biomass (De Jonge et al. 1996).

The Baltic Sea is a young sea area, as the last

glacial ice sheet withdrew only approximately ten thousand years ago. It is neither an ocean nor a lake, but a large (422 000 km²) and shallow (mean depth 60 m) brackish-water basin with a narrow and shallow connection to the North Sea via the Danish straits permitting the entrance of occasional inflows of saline water. The surface water salinity varies between 1‰ and 6‰ in northern areas, such as the Gulf of Finland, and usually between 8‰ and 12‰ in southern areas. The location of the Baltic Sea in northern high latitudes and the low salinity of the sea greatly affect the structure and function of its ecosystem (Hällfors et al. 1981). Many marine and limnic species live at the margin of their salinity tolerance and thus under excess stress in the Baltic Sea. The number of species adapted to these conditions is lower than in fresh or marine waters, and it has often been suggested that species-poor systems generally have a lower capacity for coping with disturbances in the environment than have high diversity systems (see Johnson et al. 1996). As a result, Baltic Sea ecosystems are relatively sensitive to various human impacts.

Eutrophication of the Gulf of Finland

The Gulf of Finland is one of the most heavily eutrophied areas in the Baltic Sea, the nutrient input being 3 to 5 times as high as in the Baltic Sea on average (Pitkänen 1994). The bulk of the nutrient load enters the eastern gulf via the River Neva, the Russian city of St. Petersburg being the main source of anthropogenic nutrients (Kiirikki et al. 2001). The symptoms of eutrophication are, thus, most severe in the eastern parts of the gulf (Kauppila et al. 1995). However, the nutrient load from Finland has a clear local influence on the northern coast of the gulf, especially in inner areas where there is only limited mixing with the open sea (Pitkänen 1994) and the nutrient concentrations are generally higher than in the open sea.

Regular water quality monitoring started in the Gulf of Finland in the 1970s. During that decade, the rate of eutrophication of the Gulf of Finland accelerated, as is well illustrated by the rise in nutrient concentrations and in vernal phytoplankton production at the entrance to the

gulf (Grönlund and Leppänen 1990). At the same time, the state of some heavily polluted areas of the northern Gulf of Finland started to improve due to water protection measures aimed at reducing point-source loading (see II). The decline of bladder wrack (*Fucus vesiculosus*) along the southern coast of Finland in the late 1970s and early 1980s (Kangas et al. 1982) was a distinctive phenomenon attributed to coastal eutrophication. During the 1980s, the total surface area of Finnish coastal waters defined as eutrophied increased further (Kauppila and Lepistö 2001). In the 1990s, the external nutrient input from Finnish territory to the Gulf of Finland was somewhat lower than in the 1980s (Kauppila et al. 2001) as was also the load via the River Neva (Pitkänen et al. 2001), but still the harmful effects did not diminish. Phosphorus concentrations began to increase heavily in the Gulf of Finland in the mid-1990s due to the acceleration of internal loading, especially in the eastern parts of the gulf (Pitkänen et al. 2001), and vast algal blooms were common in the late 1990s.

In addition to ongoing eutrophication, there have been variations in salinity and temperatures during the last 20–30 years. The main factors controlling salinity are the occasional inflow of high salinity water through the Danish straits and freshwater runoff to the Baltic Sea. Ultimately, both the pulses and the runoff are controlled by climatic factors in the Atlantic (Hänninen et al. 2000). Major inflows occurred in 1975–1976 and again in 1993, but the deep-water salinity in the Gulf of Finland was still generally lower during the 1990s than it had been earlier, especially in the 1970s (see Alenius et al. 1998). No trends were observed in surface water temperatures in summers in 1970–2000, e.g. at a monitoring station in the westernmost Gulf of Finland (P. Alenius, pers. com.), but the winters were mild, especially during the 1990s. During that decade, the duration of ice periods in the Gulf of Finland was much shorter than on the long-term average (Seinä et al. 1996, Seinä et al. 2001). Climate change models predict an increase in both temperature and precipitation in northern Europe (Déqué et al. 1998), which, if realised, will have an effect on future temperature and salinity conditions and nutrient enrichment in the Baltic Sea area.

Changes in fish communities in the Baltic Sea

The total fish catches of the Baltic Sea, which are dominated by pelagic marine species, have risen tenfold since the early 1900s. This rise is mainly due to intensified open sea fishing, but general eutrophication and increased production in the epilimnion may also have contributed (Hansson and Rudstam 1990). Changes in species composition, attributed to coastal eutrophication, have been reported from many coastal areas, and the observations relevant to the Gulf of Finland are here shortly reviewed using a classification into marine, migratory and freshwater species.

Marine species

Baltic herring (*Clupea harengus membras*) is the economically most important marine species in the Gulf of Finland. High mortality of eggs has been reported in some eutrophied archipelago areas of the Swedish coast (Aneer 1985) and in the Archipelago Sea, west of the Gulf of Finland (Rajasilta et al. 1989). The potential consequences for the population level are, however, unknown. The decline in the proportion of the larger zooplankton preferred by herring in the northern Baltic Sea due to a slight decrease in salinity has been suggested as a reason for the recent fall in herring growth (Flinkman et al. 1998). Flounder (*Platichthys flesus*) is a common species in the western Gulf of Finland, salinity being the most important factor determining its range. After a period of high abundance in the early 1980s due to strong year-classes (Jarre-Teichmann et al. 2000), cod (*Gadus morhua*) has been practically absent from the Gulf of Finland. The main spawning grounds of cod and also of sprat (*Sprattus sprattus*) are located in the southern Baltic Sea, and the recruitment of stocks is largely determined by conditions in those grounds. Cod is probably the species most adversely affected by the general eutrophication of the Baltic Sea. The frequency of anoxic condition in the spawning areas has increased partly due to eutrophication (Hansson and Rudstam 1990), although other factors such as changes in salinity and high fishing pressure have also affected cod stocks (Plikshs et al. 1993,

MacKenzie et al. 2000). Eelpout (*Zoarces viviparus*) has suffered from reproduction failures in the Gulf of Riga, possibly due to increasing pollution (Ojaveer 1997). There are also other marine species in the Gulf of Finland, mainly small and valueless for fisheries, but these species and their environmental requirements have been poorly studied.

Migratory species

The stocks of the important migratory species, e.g. salmon (*Salmo salar*), brown trout (*Salmo trutta*) and migratory whitefish (*Coregonus lavaretus*), were severely affected by the damming and pollution of most of the spawning rivers in the first half of the 20th century. There is no evidence that the eutrophication of coastal waters itself had any major effects on these stocks, which are now mainly dependent on stocking programmes. At present, reared fish account for 80–90% of Finnish salmon and brown trout catches, and for 65% of the migratory whitefish catch in the Baltic Sea (Anon. 1999). Wild salmon stocks are further threatened by the M-74 syndrome (Bengtsson et al. 1999). On the other hand, the smolt production of wild salmon in the large salmon rivers increased in the late 1990s due to tightened regulation of salmon fishery in the Baltic Sea (Anon. 2002).

Freshwater species

The effects of coastal water eutrophication on fish stocks are most clearly seen in freshwater species that live permanently and spawn near the coast and in the archipelago zone. The sea area close to Helsinki City has been one of the most highly eutrophied areas on the Finnish coast of the Gulf of Finland, especially during the 1960s and 1970s, when wastewater discharges into adjacent bay areas reached their maximum. Anttila (1973) reported that local burbot (*Lota lota*) and pike (*Esox lucius*) populations decreased or disappeared and that others, notably roach (*Rutilus rutilus*), ruffe (*Gymnocephalus cernuus*) and white bream (*Abramis bjoerkna*) populations, increased. Pikeperch (*Sander lucioperca*) and

bream (*Abramis brama*) populations withstood the wastewater discharges rather well. Paavilainen et al. (1985) carried out test fishing in the eastern Gulf of Finland and found the highest proportions of cyprinids and ruffe in the most heavily polluted areas. Hansson (1987) reported similar results from the Swedish side of the Gulf of Bothnia, and Bonsdorff et al. (1997) from the Archipelago Sea. Increased abundance of bleak (*Alburnus alburnus*) and pikeperch have been reported from the eutrophied Gulf of Riga during recent decades (Ojaveer 1997). The growth in commercial catches of pikeperch in some coastal areas of the Baltic Sea has been attributed to coastal eutrophication (Lehtonen 1985, Winkler 1991). In addition to these 'large' freshwater species, the coastal areas are inhabited by small species such as sticklebacks (*Gasterosteus aculeatus*, *Pungitius pungitius*) and minnow (*Phoxinus phoxinus*). Rajasilta et al. (1999) reported that the abundance of these species has declined during recent decades in the middle Archipelago Sea, one probable reason being eutrophication and consequent changes in the littoral zone.

Eutrophication and fish communities in lakes; general trends

In lakes, the increase in total catches and in cyprinid populations together with the decrease in percids and salmonids caused by strong eutrophication is a well documented phenomenon (e.g. Colby et al. 1972, Svärdsön and Molin 1981, Persson et al. 1991). The basic theories for these changes in temperate lakes are well defined (see Moss 1980). Organic matter depositing from the increased phytoplankton crops promotes oxygen consumption in the hypolimnion, causing even anaerobic conditions. A deoxygenated hypolimnion excludes some fish groups, such as coregonids and salmonids, as they are intolerant of the higher temperatures in the epilimnion. Fish tolerant of higher temperatures and lower oxygen concentrations may increase in production. These species, such as cyprinids and percids, usually spawn in relatively shallow water during the spring and summer, and thus also their eggs are less threatened by poor oxygen conditions. In extreme cases, usually in

shallow lakes, dense algal growth out-competes the original aquatic plant beds. This means a loss of living habitats for young fish and a loss of spawning habitats for species that attach their eggs to aquatic plants. The abundance of large invertebrates living on plants, such as snails and insect nymphs, is also much curtailed, reducing the amount of suitable food for many larger fish. Such extreme conditions may be less favourable for cyprinids, too (Moss 1980).

Persson (1983) and Diehl (1988) have studied the differences between the feeding strategies of perch and roach. They suggest that changes in the physical environment induced by lake eutrophication (decrease in submerged vegetation, increase in turbidity) could affect the competitive interactions of these species, and favour cyprinids to perch. Cyprinids are able to feed efficiently at low light intensities and even in darkness, whereas perch are visual hunters dependent on vision (Diehl 1988). Stenson (1979) showed that roach feed on smaller zooplankton than do perch when the species live sympatrically. He argued that this should imply a competitive advantage for roach when there is a shortage of resources, and zooplankton communities are dominated by small forms. The success of cyprinids under high nutrition conditions is usually related to their ability to consume plant material, too (e.g. Persson 1983).

Fishery in the northern Gulf of Finland

Fishing is an important leisure activity in Finland. The most recent estimates based on an extensive survey suggest that 193 000 Finns went fishing at least once in the Gulf of Finland in 1998 (Anon. 2000a). The most important species caught was perch, with an estimated total catch of 1278 tonnes. Other important species caught, with estimated annual catches of between 400 and 900 tonnes, were pike, roach, pikeperch and herring. The most commonly used fishing gears were the gill net and spinning rod (Anon. 2000a); the bulk of the catch was taken with gill nets.

The total number of commercial fishermen living on the Finnish coast of the Gulf of Finland was 431 in 1999 (Anon. 2000b). The majority of them were part-time fishermen, as only 197

of them earned more than 30% of their annual income from fishery. The main species caught were sprat and herring, the total catch of these species from the Gulf of Finland being 10 905 and 6706 tonnes, respectively. However, only 90 tonnes of this was taken by coastal fishery (trapnet, gill net), the bulk being taken by trawlers in the open sea. Other important species for commercial fishery were pikeperch (153 tonnes), salmon (136 tonnes) and perch (92 tonnes) (Anon. 2000b). No data on commercial and non-commercial fishery are available from the Russian side of the gulf, but fishing for freshwater species has been insignificant there due to the lack of suitable boats and gear (A. Shurukhin, pers. com.).

Eutrophication has other effects on fisheries besides changes in fish communities and catches. Observations of off-flavours or off-odours in fish have been common in some of the most polluted areas in the Gulf of Finland (Anttila 1973, Paavilainen et al. 1985, Persson 1985). Fouling of fishing gears of recreational fishermen has been reported from eastern parts of the Gulf (Paavilainen et al. 1985). The extensive sliming or fouling of gears has later been shown to be a more or less common occurrence in recreational fishery in all Finnish coastal waters (Lappalainen and Hildén 1993).

Aims and research strategies

The main objectives of this thesis were to study the effects of recent (last 20–30 years) coastal eutrophication on (1) fish communities, and on (2) recreational fishery and commercial pikeperch fishery off the northern coast of the Gulf of Finland. The findings from the Gulf of Finland were also compared with results from other coastal areas and eutrophied lakes.

The study focused on the 'large' freshwater species that are the dominant fish species in the archipelagos along the entire coast of the gulf (I–III). They also form the basis of the recreational fishery catch (IV) and some of them, such as perch and pikeperch, are important for commercial fishery, too. Studies on the effects of coastal eutrophication usually have a biological orientation; here the problem was also studied from the recreational fisherman's point of view,

using methods common in the social sciences.

Documentation of the effects of eutrophication in archipelago waters, which more or less act as direct recipients of the nutrient load, is meagre. There is no long time series available of freshwater fish communities in the Baltic Sea. A fish monitoring programme, 'Baltic Reference Areas' (see Ådjers et al. 2000), was set up in the late 1980s–early 1990s, but none of the six monitoring areas is situated in the Gulf of Finland. The 'common tragedy' is that the need for monitoring data and time series does not become urgent until an environmental change or accident has occurred. This has been the case with the eutrophication of Finnish coastal waters, too, and only episodic old fishery data have been available. All coastal areas of the Gulf of Finland are now eutrophied to some degree, which means that proper reference areas for recent eutrophication are lacking. Due to these limitations, a BACI (Before/After and Control/Impact) sampling design (Stewart-Oaten et al. 1986) could not be achieved in this study, and three compensatory and less effective approaches were applied instead. First, the west-east gradient in the eutrophy of the Gulf of Finland was utilized in two papers (I and IV). Second, old data from the 1970s were available from two localities, and these areas were re-sampled in the late 1990s (II and III). Third, a unique time series of the log-book data of small-scale commercial fishery was used (V).

Material and methods

Study area

The Gulf of Finland is an elongated estuarine sea in the northeastern part of the Baltic Sea. There are some quite deep areas — over 60 m — in the central parts of the gulf, but the northern coast — the current study area — is generally shallow. A special morphological feature of this northern coast is that it is highly indented and the number of bays is high. Furthermore, thousands of small islands form an archipelago zone outside the coastline (see Fig. 1). The archipelago waters of the Gulf of Finland freeze over every winter, the duration of the ice cover being around 4 months in the east and 2 to 4 months in the west. As

much as 67% of the total annual river runoff is discharged into the eastern end of the gulf from the River Neva (Alenius et al. 1998). As a consequence, the salinity of surface waters shows a clear gradient, being > 6‰ in the west and < 1‰ in the east. The summertime concentrations of chlorophyll *a* are generally 3 to 5 mg m⁻³ in the open gulf, and mostly 5 to 10 mg m⁻³ or higher in the more eutrophied areas (Kauppila and Lepistö 2001). The semi-enclosed small bays are generally less haline and more eutrophic than the archipelago zone and the open sea.

In this study, a major part of the field work was carried out in the Hanko and Helsinki regions (I, II, III, IV). A third important area was the Kotka region (I, IV), and finally there were two areas on the Russian side of the gulf (I) (Fig. 2). The catch data and statistics for small-scale commercial fishery (V) were collected from the entire Finnish Baltic Sea coast.

Methods for collecting fish community data

Gill net test-fishing was used as a basic method for collecting data on temporal and regional differences in local coastal fish communities and the growth and food of fish. Gill net sampling is practically the only effective method available for catching benthic warm-water species, like most of the freshwater species on the Finnish coast, on the rugged and stony bottoms common in shallow archipelago areas. The mesh sizes used were similar on each sampling occasion (12, 15, 20, 25, 30, 35, 45 and 60 mm, bar length). In the 1970s (II, III), the sampling was done with gill net series (8 × 30 m × 1.8 m), and in the 1990s (I, II, III) with multimesh gill nets (48 m × 1.8 m) at the same locations as in the 1970s (II, III). The catching efficiencies per gill net surface area of net series and multimesh gill nets are not equal (Kurkilahti and Rask 1996). Thus, in article III, the statistical testing between old and new data was based on the ratios of certain species to total catch. In article II, a special formula was used to make the catch per unit efforts (CPUEs) of sampling with multimesh gill nets and gill net series comparable and to allow the use of factor analysis.

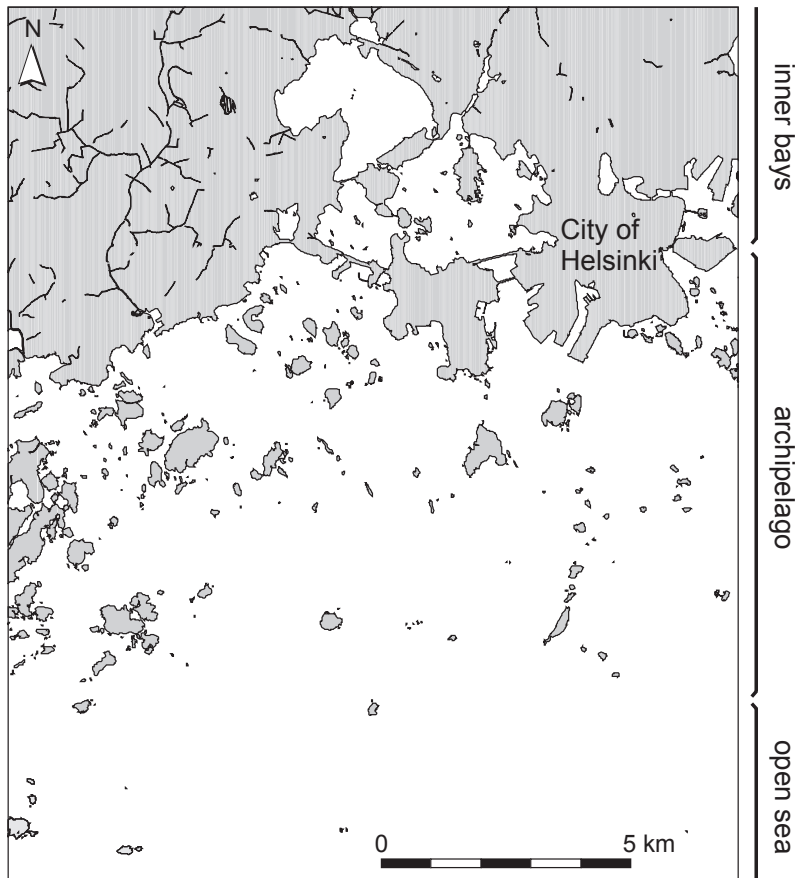


Fig. 1. An example of the bays-archipelago-open sea zone system on the northern coast of the Gulf of Finland.

Gill nets do not provide unbiased samples of local fish communities. Young and small individuals, which can constitute a high proportion of the total number of individuals and also of the biomass of fish populations, are underrepresented or totally excluded. Small mesh sizes — here < 12 mm — have usually been omitted from the sampling set, as their relative effectiveness for catching small fish tends to be low, one major reason being that the twine thicknesses used in industrially manufactured gill nets are too high for very small fish. Gill net series and multimesh gill nets are also selective for fish in the size-classes normally caught with mesh sizes between the minimum and maximum (here 12–60 mm) used. The bias is largest for small size-classes (Kurkilahti 1999) as the selectivity curves are narrower for small than for large fish. The small size-classes contribute a relatively smaller proportion to the biomass of the whole population than do the larger size classes. Bias

caused by the selectivity is therefore a less serious problem for CPUEs in terms of biomass, as used here, than for CPUEs in terms of number of individuals caught (Kurkilahti 1999). There are also differences in the catchability of individual species owing to differences in the shape or behaviour of the species. Furthermore, experiments conducted recently in some eutrophied lakes (M. Olin, pers. com.) have shown that test-fishing gill nets can become 'saturated' if a large amount of fish have been caught.

On the whole, CPUE data collected by gill nets do not provide absolute estimates of fish biomasses or densities of fish populations, and there is no simple linear relationship between the CPUEs and actual fish abundance. If, however, the limitations of the sampling method are taken into account in the interpretation of results, the CPUE data collected by standard gill nets are useful when the primary issue is the relative differences between areas or changes in time in

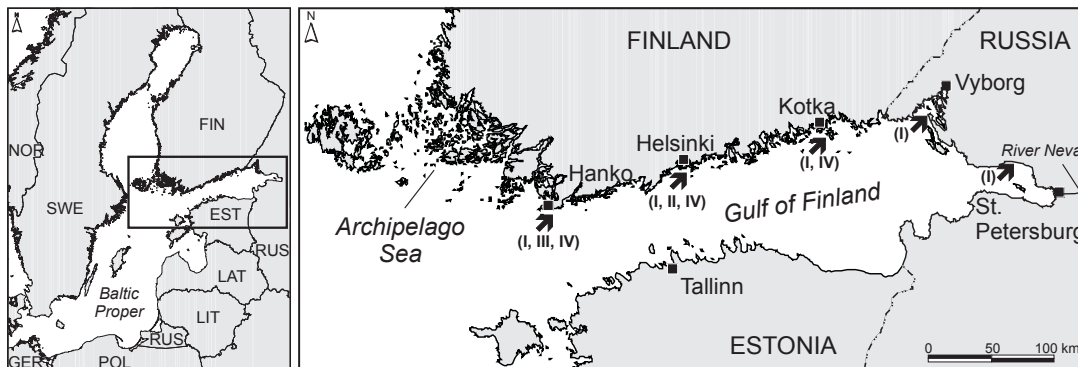


Fig. 2. Location of study areas. The Roman numerals in parentheses refer to the articles (I–IV).

a certain area. This is supported by the results of Peltonen et al. (1999a), who compared different methods for estimating roach and smelt (*Osmerus eperlanus*) abundances in Lake Vesijärvi, southern Finland. They showed that the gill net CPUE estimates of roach were consistent with the results of virtual population analysis (VPA) and hydroacoustics during an 8-year-long study period when roach stocks declined sharply. A further advantage of the gill net sampling method is that it provides practical information about how fish communities appear for ordinary fishermen using gill nets.

Methods for collecting fishery data

The effects of eutrophication on recreational fishery were studied with the aid of a questionnaire mailed to over 1500 persons fishing in the study areas in year 1993 (IV). The persons were selected by random sampling from local fishing fee registers. After two follow-up mailings, the response rate was over 80%. The four-page questionnaire contained questions on both quantitative and qualitative variables concerning respondents' actual fishing activities and other subjects related to fishing opportunities, such as water quality and the fishing licence system.

The log-book data collected by Finnish fisheries authorities were used to study recent changes in commercial pikeperch fishery (V). All commercial fishermen operating in the Finnish coastal area are obliged to report their catches, efforts and fishing areas to fishing authorities. This obligation, which formerly was based on

Finnish legislation, has since 1995 been based on EU regulations, too. The bulk of the commercial pikeperch catch is taken by small-scale coastal fishermen, using vessels < 10 m long or fishing on the ice in winter. The fishermen submit catch reports monthly in a log-book designed specifically for small-scale fishery. The data have been collected and processed in the same manner since 1980, offering a 20-year time series for the study of changes in commercial fishery.

Results and discussion

This section presents the main findings (1–6) of the thesis. Each finding is followed by a short discussion reviewing the original results. These are then examined in greater detail and compared with results found in the literature. The 'general discussion' at the end of this section looks briefly at the main findings of studies from sea areas outside the Baltic Sea, and finally draws short conclusions relevant to this study.

1. Roach is currently highly abundant in the intermediate and outer archipelagos along the entire northern coast of the Gulf of Finland. Clear evidence exists of an increase in roach abundance over the last decades.

Roach is a freshwater species that also lives in brackish waters with sufficient low salinity. In the northern Baltic Sea, roach is commonly found in productive bays and inner archipelago areas (Neuman 1982, Hansson 1984, II). Accord-

ing to the results of article I, in the late 1990s roach was also highly abundant in the intermediate and outer archipelagos along the entire northern coast of the Gulf of Finland, being the most abundant species in test-fishing catches in four out of five study areas in late summer. The mean catch per unit efforts (CPUEs) of roach in the intermediate and outer archipelago areas (1.0–2.7 kg/multimesh gill net/day) (I) were at the same level as in the bay areas west of Helsinki (1.3–2.2 kg) (II).

Peltonen et al. (1999ab) used similar multimesh gill nets in Enonselkä, a eutrophied basin of Lake Vesijärvi, southern Finland. In shallow waters the height of the nets was 1.8 m and the nets were set on the bottom in the same manner as in articles I, II and III. In deeper (> 4 m) waters they used 3-m-high nets set on the bottom, and in the deepest (> 10 m) waters one 3-m-high net was set on the bottom, one in mid-water and one at the surface. Roach catches from the deepest areas (> 10 m) were generally somewhat smaller than those from shallower areas (J. Ruuhijärvi, pers. com). Still, the results from Lake Vesijärvi are roughly comparable to those from the coastal area (I and II). During the first 3 years, 1989–1991, of food web management by the mass removal of fish, the CPUEs of roach in Lake Vesijärvi were between 1.8 and 2.6 kg/multimesh gill net/day; later, in 1992–1996 they were around 1 kg (Peltonen et al. 1999b). Thus, in Lake Vesijärvi the CPUEs were at the same level as those obtained in the Gulf of Finland, i.e. 1.0–2.7 kg (I, II, III).

The results from the Gulf of Finland and adjacent sea areas suggests that roach stocks have extended from inner areas to the outer archipelago during the last decades. The Helsinki region was among the first areas to be affected by a heavy municipal wastewater load in the northern Gulf of Finland, and the impact of the waste waters reached a peak in the late 1960s and early 1970s (II). Halme and Hurme (1952) conducted test-fishing by seine and collected fishery data from commercial fishermen in the Helsinki region in the early 1950s. They reported that roach was common in bays and the inner archipelago but did not occur in the outer archipelago of Helsinki. Later, in the early 1970s, Anttila (1973) found that roach was also common in the outer

waters of Helsinki, as it was also in the late 1990s (II). Similarly, the results of article III suggest that roach stocks in the Tvärminne archipelago, a less eutrophied area in the westernmost Gulf of Finland, increased and extended to the outer archipelago between 1975 and the late 1990s. Similar observations of a recent increase in roach abundance have been made in other Baltic coastal areas, some 50 and 150 km west of the western Gulf of Finland, and these changes are attributed to coastal eutrophication. In a monitoring area in the southern Archipelago Sea, an increase in roach abundance was observed during the 1990s (Ådjers et al. 2000), and in the Åland archipelago in 1985–1995 (Bonsdorff et al. 1997).

In both the 1970s and late 1990s, roach fed mainly on blue mussels (*Mytilus edulis*) in the Tvärminne archipelago (Rask 1989, III). The blue mussel populations in the Tvärminne area have, however diminished, and the proportion of larger mussels in the population has decreased since the late 1970s (Öst and Kilpi 1997). This finding, together with the observed decline in growth of roach at Tvärminne (III), indicates that an improvement in food supply cannot be the reason for the increase in roach abundance in the Tvärminne archipelago; a more likely reason is the improved reproduction of roach in the inner archipelago and bays, which is where the reproduction areas of the species are located. In temperate lakes, eutrophication often leads to cyprinid dominance (Persson et al. 1991). A similar mechanism may well operate in inner coastal areas, suggesting that the ongoing slow eutrophication contributes to the reproduction of roach there. The occurrence of several warm summers and the slight decrease in salinity during the 1990s (see III) may also have contributed to the increase in roach reproduction and abundance, as roach is a typical freshwater species favouring relatively warm conditions. The greater abundance of roach and intensified competition for food in inner areas force older roach to expand their feeding grounds towards outer areas, a pattern that leads to the high abundance of roach in the outer archipelago, too. The state of the inner reproduction areas is mostly determined by local factors. National measures to reduce eutrophication thus play a key role in the future development of coastal fish communities.

2. Extremely eutrophic conditions in coastal bays are more favorable for bream and white bream than roach.

The wastewater load in the bay area west of Helsinki reached maximum levels during the late 1960s to early 1970s. During that time, the innermost basin was probably the most polluted area on the Finnish coast of the Gulf of Finland. The results of article II revealed that white bream, and also bream, benefit from extremely eutrophic conditions, as they were particularly common at the most eutrophic site in the early 1970s. White bream was then the dominant species, constituting up to 43% of the biomass of test-fishing catches, followed by roach, 18%, and bream, 11%. This tendency agrees with results from temperate lakes (Svärdson and Molin 1981, Olin et al. 2002) showing that white bream and bream benefit from eutrophication more than roach does. The highest proportion of white bream among the test-fishing catches was only 26% in the 36 mesotrophic and eutrophic lakes studied by Olin et al. (2002).

Sandström and Karås (2002) studied the abundance of young-of-the-year (YOY) freshwater species in a gradient of eutrophication on the Swedish coast of the Baltic Sea. They found positive trends in YOY abundance of cyprinids with increasing eutrophy, and further that the abundance of YOY roach and bream (white bream and bream combined) behaved similarly in relation to eutrophication. The coastal areas — including the bays studied in article II — are ‘open’ areas allowing fish to migrate. Thus, feeding conditions may have a marked effect on the composition of older fish large enough to be caught by the multimesh gill nets used. The feeding adaptations of these cyprinids have been the subject of several studies (Lammens et al. 1987, Diehl 1988, Specziár et al. 1997), indicating that roach is more dependent on littoral habitats and light than are the other two species. Thus, a likely reason for the relatively high abundance of white bream and bream under these extremely eutrophic conditions is their better ability to utilize the food resources in locations, where turbidity is high and the bottom is heavily affected (II).

The water quality in the bays west of Helsinki has improved notably since the 1979s

and no effluents from the wastewater treatment plants have been discharged into the bays since 1986. In the late 1990s, catches of white bream and bream were only half of the level they were in the early 1970s, indicating a clear decrease in the relative abundance of these two species. Concurrently, white bream and bream have become more abundant in other coastal areas, such as Tvärminne in the western Gulf of Finland. These species were caught there only occasionally in the mid-1970s (II, III), but in the late 1990s, white bream in particular has been among the most common species in test-fishing catches (I, II, III). There has been no local point-source contamination in the Tvärminne region, but the effects of the ongoing general coastal eutrophication (Pitkänen et al. 2001) are apparent there, too, for instance, as elevated nutrient concentrations and intensified productivity in the pelagic system, for which some monitoring data is available (see III). The reverse changes in the abundance of white bream and bream, a decrease with decreasing eutrophy in Helsinki and an increase with increasing eutrophy at Tvärminne, suggest that the observed changes are not caused by far-reaching changes (e.g. climate) but rather are locally driven.

3. Recovery of the fish community structure in a once extremely polluted coastal bay area, west of Helsinki was slow despite a clear improvement in water quality.

The decline in white bream and bream abundance (see previous section) and partial increase in the abundance and species number of other cyprinids were the only clear changes in species relations in the bays west of Helsinki after the distinct improvement in water quality during the 1980s and 1990s (II). The general fish community structure remained much the same, less valuable species — ruffe and cyprinids — still accounting for about 80% of the fish sampled, whereas the corresponding proportion was 60% in the reference area (II).

A similar slow or insignificant recovery of fish communities has often been reported in eutrophied lakes after decline or cessation of the external load, e.g. from agriculture. In lakes, the

water quality, too, has tended to remain poor, due at least in part to internal loading, and fish stocks can be crucial in delaying the recovery of lakes (Jeppesen et al. 1990). An excess of nutrients, phosphorus in particular, has commonly led to blooming of blue-green algae. Manipulation of fish stocks has become a widely accepted method to restore eutrophic lakes (Perrow et al. 1997, Horppila et al. 1998). The goals of these lake restoration projects are usually to establish clear water and to stabilize the lake system (Perrow et al. 1997). In the case of the bays west of Helsinki, however, the water quality improved notably after the cessation of municipal discharges into the area (II), and blooming of blue-green algae has not been common, probably due to the relatively high inorganic N:P ratio in these bays. Such conditions do not favour N_2 -fixing blue-green algae species, the most common 'blooming species' in the Gulf of Finland (Kaupila et al. 2001).

The rapid improvement in water quality in the bays could be explained by at least two factors: (1) The load on the bays in the late 1960s and early 1970s was enormous, much higher than in eutrophied lakes. Thus, the bays west of Helsinki served merely as an extension of the ineffective local wastewater treatment plants, and the water quality was very much dependent on the instantaneous input of nutrients and other pollutants. (2) There is considerable water exchange between the bays and outer areas, caused mainly by the normal fluctuations in sea water level (even ± 1 m of the mean) induced by winds and changes in air pressure. Due to this water exchange, the salinities of the water column in the bays west of Helsinki are at almost the same level (3–6‰) as in the outer archipelago (5–6‰), as the freshwater river runoff into these bays is relatively low. The pulses of 'new water' to the eutrophic bays have a cleaning effect on the water quality of these shallow bays. Hence, the oxygen concentrations are generally high (Pesonen 1998, 1999) and conditions for an internal phosphorus load due to anoxia do not exist.

There are many reasons for the slow rate of recovery of fish communities in the bays west of Helsinki despite the improved water quality. The area was still eutrophic in the late 1990s, a state

that according to Sandstöm and Karås (2002), should favour reproduction of cyprinids and ruffe, the main species in test-fishing catches. The bay area is not enclosed, and fish migrations may balance out differences between the two periods compared. There are actually no data on the reproduction success of fish in the bays in the 1960s, but it is possible that the local fish community structure would have been quite different then if the area had been enclosed and received no external compensation for potential losses in reproduction. The general eutrophication of the surrounding areas and indeed the entire Gulf of Finland (Pitkänen et al. 2001) may also have masked any positive changes in the bay area (II). Fish migrations may, accordingly, lower the value of fish communities as an indicator of water quality changes in coastal areas. In addition, the results of article I suggested that the present high fishing pressure in the Helsinki region might have had an effect on local fish communities, as the proportion of predaceous fish in test fishing catches was lower in this region than in areas where fishing pressure is lower. The low proportion of large predatory fish may further have an indirect impact on local fish communities via the food-web.

4. Increased primary production does not lead to high (adult) fish biomasses in the archipelago zone.

A widely held conception is that, in lakes, eutrophication and the subsequent rise in primary production lead to increased fish production and biomasses (Colby et al. 1972, Leach et al. 1977, Lee et al. 1991) and that a shift commonly occurs from dominance of percids in medium productive lakes to dominance of cyprinids in highly productive ones (Leach et al. 1977, Persson et al. 1991). Svårdson and Molin (1981), for example, reported clear increases in the total catch and catch of cyprinids in a temperate lake undergoing slow eutrophication. Furthermore, comparisons between lakes have tended to show higher catches, especially of cyprinids, in eutrophic than in mesotrophic lakes (Olin et al. 2002). Thus, an increasing west-to-east trend in

the CPUEs of all species summed (totCPUE), and especially those of roach, was expected in the archipelago areas of the Gulf of Finland, too. However, the totCPUEs were clearly lower in the more eutrophic eastern parts of the gulf than in the west, and no trend was found in the CPUEs of roach (Table 1, I). The disappearance of marine species, flounder in particular, and the decline of perch were the main reasons for the diminishing total catches of freshwater species from west to east (I). The same patterns were found some years earlier (Table 1), when annual catches and fishing efforts of recreational fishermen were surveyed by mailed questionnaire in the same three areas in the Finnish side of the gulf (Lappalainen and Pönni 1996).

The sampling areas of article I were in the archipelago zone, an area with an increasing west-east eutrophic gradient, although a less clear one than in the open sea. The reproduction areas of freshwater species are, however, located in the innermost archipelago and inner bays, which are generally more eutrophic than the outer archipelago (e.g. Pitkänen et al. 2001). There are no general survey data on fish reproduction in the Gulf of Finland, but the innermost areas are probably equally eutrophic along the entire northern coast of the Gulf of Finland. This may tend to balance out large-scale differences in the reproduction potential of freshwater species between east and west. In the coastal area, juvenile and adult fish can later spread out effectively from their reproduction areas to the archi-

pelago zone (seen as similar CPUEs in the bay area (II) and the archipelago zone (I)) and could potentially migrate there in an east-west direction, too. Thus, it is supposed that fish biomasses (or CPUEs here) reflect merely the quality of each area as a feeding ground for fish, and this is the likely explanation for the observed 'reverse' trend in the archipelago areas.

The food available in the littoral zone is important for both roach and perch, which are the two most common freshwater species in the archipelago of the Gulf of Finland (I). Roach (adult) feeds mostly on littoral mussels and snails (Rask 1989, III) in the archipelago and perch feeds mostly on littoral crustaceans before the predaceous stage (Koli et al. 1988, III). On coastal soft bottoms, a certain increase in eutrophy can lead to an increase in benthic macrofauna as shown by Hänninen and Vuorinen (2001) in the Archipelago Sea, west of the Gulf of Finland; in the littoral, however, the situation may be different. In the Gulf of Finland, the total production and supply of suitable littoral food for the above and many other freshwater species are most likely better in the less eutrophic archipelago areas in the west than in the east. Due to higher turbidity, the productive layer is much narrower in the east than in the west, as is well illustrated by the Secchi-depths measured, 5–8 m in the westernmost gulf and less than 2 m in the east (I). An important consequence is that the productive littoral zone — also the bladder wrack belt where it exists — is then narrower in

Table 1. Secchi depths (I) and mean CPUEs for all species and cyprinids in the study areas based on multimesh gill net survey (I) and survey of recreational fishery (Lappalainen and Pönni 1996). Superscripts indicate whether statistically significant ($\alpha = 0.05$) differences between areas exist in the multimesh gill net survey (equal letter = no difference between areas).

	Hanko	Helsinki	Kotka	Vyborg	St. Petersburg
Secchi depth (m, summer 1998)	5–8	4–6	4–6	2	1.8
Gill net survey (1998)					
totCPUE (kg/gill net)	5.5 ^a	4.8 ^{ab}	4.0 ^b	2.9 ^c	2.9 ^c
CPUE of cyprinids	1.7 ^a	3.0 ^b	1.8 ^a	1.6 ^a	1.9 ^a
Recreational fishery (1994)					
totCPUE (kg/10 gill net)	12.3	6.6	5.5		
CPUE of cyprinids	1.1	1.3	1.0		

the east than in the west, restricting the surface area its quality. The bladder wrack belt is important — especially for perch — as this is a key habitat for most macro-crustaceans in the Baltic Sea, providing them with both food and shelter (e.g. Kautsky et al. 1992). The total absence of bladder wrack from the easternmost part of the Gulf of Finland is due to low salinity, as the alga needs 4‰ salinity to thrive in the long term (Luther 1981). However, eutrophication has affected the occurrence of bladder wrack in the Gulf of Finland in other ways, too, for instance, by promoting the growth of epiphytic algae (Kangas et al. 1982) and by raising the lower limit of the bladder wrack belt. Blue mussel is the dominant species in the diet of roach in the western Gulf of Finland (III). The range of this species, which inhabits hard littoral and sublittoral bottoms, is determined in the Gulf of Finland by salinity and extends to the central parts of the gulf (Westerbom et al. 2002). Hence, both the increasing eutrophy and the decreasing salinity are reducing the diversity of the littoral habitat eastwards, and thus probably affecting the supply of suitable food for roach and perch.

The CPUE values of article I can be roughly compared with values reported from lakes. In Enonselkä of Lake Vesijärvi, the combined CPUEs of roach and perch were 3.2 kg in 1989, when the mass removal of fish started (Peltonen et al. 1999b). The fishing methods had some differences, but the values were similar to those obtained on the Finnish side of the Gulf of Finland (2.9–3.7 kg) (I). In the easternmost Gulf of Finland, the summed CPUEs for perch and roach (1.6–1.9 kg) were clearly lower than those reported from Lake Vesijärvi. In 1998 and 1999, a total of 36 small (0.08–26 km²) mesotrophic and eutrophic lakes in southern Finland were surveyed by gill nets (Olin et al. 2002) according to ‘Nordic standards’ (Kurkilahti and Rask 1999). The methods differs from those used here (I, II, III). After a very rough correction based directly on the surface areas of the different net types, the totCPUEs of these lakes corresponded to values of between 1.0 and 8.6 kg. Thus, it can be concluded that the totCPUEs from the coastal studies (I, II, III) are of the same magnitude as those reported from lakes, and higher CPUEs can be found, at least in some eutrophic lakes.

5. The general deterioration in water quality was well perceived by the recreational fishermen. The most conspicuous eutrophy-related problem was fouling of fishing gear.

The results of article IV indicate that only 2–14% of recreational fishermen in three study areas rated the water quality of their fishing area as excellent (in a pristine state). In one area out of three, the water quality was most commonly rated as good, but in the other two areas it was usually rated only as passable. The results are well in line with an earlier and more robust nationwide survey, in which 55% of recreational fishermen fishing in the Gulf of Finland rated the water quality as excellent or good (Lappalainen and Hildén 1993). Catch is only one dimension of motives in recreational fishery. Non-catch related aspects, such as natural beauty, water quality, number of other fishermen etc., are also important factors for ‘good fishing’ (Quinn 1992, Spencer and Spangler 1992). Hence, the fishermen’s common perceptions of the deterioration of their fishing waters in the Gulf of Finland may have some direct adverse effects on their fishing experiences.

The most tangible problem caused by eutrophication to the recreational fishery in the Gulf of Finland was fouling of fishing gear, particularly gill nets (IV). This problem was experienced in the previous year by 67–86% of all fishermen in the three study areas. Observations of off-flavours or off-odours in fish caught, as well as the high abundance of less-desired species in the catch, were much less common, experienced by 5–22% of the fishermen. Fouling of gear is a common problem also in certain commercial fisheries, e.g. in the whitefish fishery of the Bothnian Sea. Fouling of gear is a typical phenomenon in coastal waters. In Finnish lakes, the three above problems, fouling of gear, high amount of unwanted species in catch and off-flavours or off-odours, occur more equally, estimated to be common problems in 13%, 11% and 4% of Finnish lakes, respectively (Tammi et al. 1999).

In the coastal area, the fouling of gear is largely caused by drifting macroalgae and to a lesser extent also by microalgae attaching to the mesh. Both types of fouling occur in coastal waters ‘naturally’ and would not be fully avoid-

able even if the coastal water were in a pristine state. The potential for fouling of gear has, however, been exacerbated by recent coastal eutrophication. Pelagic production has increased, as is seen in high summer chlorophyll-*a* values near cities where the nutrient load has been high (Kauppila and Lepistö 2001). An even more important factor is the escalating production of fast-growing filamentous algae on hard bottoms of the archipelago zone (Kiirikki 1996, Bäck et al. 2001), leading to accumulations of detached macroalgae drifting in large mats on the bottoms, notably in the Gulf of Finland (Lehvo and Bäck 2001) and in the south-eastern Archipelago Sea (Vahteri et al. 2000). The data for article IV were collected in 1994 during an invasion of the predaceous cladoceran (*Cercopagis pengoi*) in the Gulf of Finland (Ojaveer et al. 2000, Antsulevich and Välipakka 2000). This large alien cladoceran tends to attach to fishing gears, and mass occurrences of it during warm summers may also cause additional sliming of gears.

6. Commercial catches of pikeperch on the Finnish coast were higher during the 1990s than in the 1980s. Coastal eutrophication is one potential reason, but there are other — and more important — reasons explaining the recent increase in catch level.

The annual commercial catch of pikeperch was 74–241 tonnes in the first half of the 1980s. Since then the variation between years has been high, but a general increase from the 1980s to the late 1990s has been observed. The peak occurred in 1997, when the annual catch was 748 tonnes (V). This high figure was attributed to the coexistence of two strong year classes in the catch of that year. In 1998 and 1999, the annual catches were 491 and 438 tonnes, respectively (V) and in 2000 450 tonnes (Anon. 2001a), with approximately one third of the catch being taken in the Gulf of Finland. The increase in the commercial fishery of pikeperch has generally been attributed to eutrophication and the resulting indirect beneficial effects on pikeperch stocks. However, the results of article V suggest that other factors, such as the collapse of cod stocks and the relative increase in the firsthand price of

pikeperch, have promoted interest in pikeperch fishery and thus led to an increase in fishing effort and total catches of commercial fishery during the 20-year study period. Pikeperch is currently a highly valued species in Finland, and demand far exceeds the production of commercial fishery for the market. In 2000, for example, 241 tonnes of fresh filleted fish were imported into Finland from Estonia (Anon. 2001b), and this was mostly pikeperch (A. Vihervuori, pers. com.). To convert this figure to correspond to the fresh weight of fish, it should be multiplied by a factor of approximately two. This means that the original amount of fish needed to replace for the imported amount of filleted pikeperch would be equal to the entire Finnish commercial catch in recent years.

Pikeperch is an important target species for recreational fishery, too (IV). According to rough estimates, the total pikeperch catches of recreational fishery in the coastal area are higher, by even 2–3 times, than those of commercial fishery (Anon. 1998, Anon. 2000a). The CPUEs, calculated from commercial catch statistics, did not reveal any alarming trends in either the Gulf of Finland or the Archipelago Sea (V), although the fishing pressure on pikeperch is presumably high. In contrast, in Estonia, pikeperch stocks collapsed during the 1990s due to newly opened fishery and subsequent overfishing (Ojaveer 1999). This was clearly seen in the CPUEs of commercial fishery (Ojaveer et al. 1999).

General discussion

In sea areas outside the Baltic Sea, reports on the effects of eutrophication on fish focus on bottom-water anoxia and hypoxia problems, e.g. in Chesapeake Bay in Virginia (Breitbug et al. 2001), the northwestern Gulf of Mexico (Craig et al. 2001) and the Kattegat-Skagerrak area on the Swedish west coast (Baden et al. 1990, Pihl et al. 1995). The most severely affected species are demersal, and the indirect effects of low oxygen concentrations, such as energetic costs and habitat loss, have usually been more important than direct mortality due to lack of oxygen (Craig et al. 2001), although fish kills, too, have been observed (e.g. Pihl et al. 1995). Large

anoxic areas also exist in the Black Sea, but there a decrease in stocks of the pelagic anchovy (*Engraulis encrasicolus*) is the clearest change attributed to eutrophication (Kideys 1994). In more recent years, however, introduction of a new lobate ctenophore (*Mnemiopsis*) and overfishing have transformed the entire Black Sea ecosystem even more dramatically (Kideys 1994, Daskalov 2002).

Extensive anoxic bottom areas also occur in deep parts of the central Baltic Sea. Such conditions have a negative impact on the reproduction of cod (Plikshs et al. 1993). Due to drifting algal mats, local, temporary anoxic conditions prevail in the Baltic archipelago areas, too (e.g. Norkko and Bonsdorff 1996, Vahteri et al. 2000). Large anoxic areas are not, however, common in the archipelago areas, as the waters tend to be shallow, usually less than 10–20 m, and thus above the permanent halocline, which in the central Gulf of Finland is at a depth of about 60 m (Alenius et al. 1998). Freshwater fish species, which were the focus of this study, are usually dominant in the coastal archipelago areas of the Baltic Sea. Hence, it was not surprising that the changes observed in the archipelago fish communities here were similar to those reported from temperate lakes undergoing eutrophication (see Introduction). The only clear difference was that the abundance of freshwater fish biomasses was higher in the less eutrophic western archipelago than in the more eutrophic eastern parts of the gulf, a finding that was in contrast to trends observed in temperate lakes.

Among the typical signs of ecosystem response to stress are loss of diversity and a tendency to favour opportunistic species (Regier and Cowell 1972, Rapport et al. 1985). The increased richness of freshwater fish species documented in the Helsinki region after the clear improvement in water quality (II) is inversely in line with the notion of stress and diversity. At Tvärminne, no clear change in species richness was found from the 1970s to 1990s, suggesting that the stress caused by slow eutrophication was not strong enough there to markedly affect the species richness of freshwater fish. The two most common freshwater species in the archipelago, roach and perch, are both food generalists. Roach have, however, some opportunistic features lack-

ing in perch, such as the capability to use shelled molluscs and plant material as food and to feed in low light intensities or even in darkness (Diehl 1988). Thus, the increased abundance of roach due to eutrophication is consistent with the idea that environmental stress favours opportunistic species.

The increased dominance of filamentous algae observed in many estuaries and coastal bays worldwide during the 1970s and 1980s has been attributed mainly to increased nutrient discharges into the sea (e.g. Buttermore 1977, Lowthion et al. 1985, Sfriso et al. 1987, Pihl et al. 1995). However, there are no reports outside the northern Baltic Sea of fouling of fishing gear due to macroalgae. The most likely reason is that nowhere else are bottom gill nets used so commonly as they are used on the Finnish and Swedish coasts, where natural conditions as well as fishery legislation allow also the numerous recreational fishermen to use gill nets.

To conclude, the changes observed in coastal freshwater fish communities in the Gulf of Finland were highly similar to those widely reported from temperate lakes, the most prominent recent change in the coastal fish communities of the northern Gulf of Finland being the increased abundance of cyprinids in the archipelago areas. The most marked change in the coastal environment, offering an explanation for the changes observed in fish communities, is the recent eutrophication, although other factors, such as fishery and changes in salinity and possibly in climate, too, may also have some effect. In the recreational fishery in the Gulf of Finland, the most tangible problem caused by eutrophication is the heavy fouling of fishing gear. The commercial fishery in the Gulf of Finland is less focused on freshwater fish, as pikeperch is the only freshwater species among the most important target species. The recent coastal eutrophication may have favoured pikeperch, but this study shows that the commercial catches of this species are dependent on economic as well as environmental factors.

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References

- Alenius, P., Myrberg, K. and Nekrasov, A. 1998. The physical oceanography of the Gulf of Finland: a review. *Boreal Env. Res.* 3: 97–125.
- Aneer, G. 1985. Some speculations about the Baltic herring (*Clupea harengus membras*) in connection with eutrophication of the Baltic Sea. *Can. J. Fish. Aquat. Sci.* 42: 83–90.
- Anon. 1998. Recreational Fisheries in 1997. SVT-Official Statistics of Finland. *Environment* 1998: 15, 71 pp.
- Anon. 1999. Finnish Game and Fisheries Research Institute, Fisheries Biology and Management Research Unit. Kala- ja riistaraportteja 140b, 34 pp.
- Anon. 2000a. Recreational Fishing 1998. SVT-Official Statistics of Finland. *Agriculture, Forestry and Fishery* 2000: 1. 27 pp.
- Anon. 2000b. Professional Marine Fishery 1999. SVT-Official Statistics of Finland. *Agriculture, Forestry and Fishery* 2000: 7. 39 pp.
- Anon. 2001a. Professional Marine Fishery 2000. SVT-Official Statistics of Finland. *Agriculture, Forestry and Fishery* 2001: 46. 39 pp.
- Anon. 2001b. Foreign trade in fish 2000. SVT-Official Statistics of Finland. *Agriculture, Forestry and Fishery* 2001: 48. 28 pp.
- Anon. 2002. Report of the Baltic salmon and trout assessment working group. ICES CM 2002/ACFM: 13, 216 pp.
- Antsulevich, A. and Välipakka, P. 2000. *Cercopagis pengoi* — New important food object of the Baltic herring in the Gulf of Finland. *Internat. Rev. Hydrobiol.* 85: 609–619.
- Anttila, R. 1973. Effect of sewage on the fish fauna in the Helsinki area. *Oikos Suppl.* 15: 226–229.
- Baden, S.P., Loo, L.-O., Pihl, L. and Rosenberg, R. 1990. Effects of eutrophication on benthic communities including fish: Swedish west coast. *Ambio* 19: 113–122.
- Bengtsson, B.-E., Hill, C., Bergman, Å., Brandt, I., Johansson, N., Magnhagen, C., Södergren, A. and Thulin, J. 1999. Reproductive disturbances in Baltic Fish: a synopsis of the FiRe Project. *Ambio* 28: 2–8.
- Bonsdorff, E., Blomqvist, E.M., Mattila, J. and Norkko, A. 1997. Long-term changes and coastal eutrophication. Examples from the Åland Islands and the Archipelago Sea, northern Baltic Sea. *Oceanol. Acta* 20: 319–329.
- Breitburg, D.L., Pihl, L. and Kolesar, S.E. 2001. Effects of low dissolved oxygen on the behaviour, ecology and harvest of fishes: A comparison of the Chesapeake Bay and Baltic-Kattegat systems. *Coastal Estuarine Stud.* 58: 241–267.
- Buttermore, R.E. 1977. Eutrophication of an impounded estuarine lagoon. *Mar. Pollut. Bull.* 8: 13–15.
- Bäck, S., Lehvo, A., Rissanen, J. and Kangas, P. 2001. Changes in phytobenthos. In P. Kauppila and S. Bäck (eds.), *The state of Finnish coastal waters in the 1990s. The Finnish Environment* 472: 71–78.
- Cederwall, H. and Elmgren, R. 1990. Biological effects of eutrophication in the Baltic Sea, particularly the coastal zone. *Ambio* 19: 109–112.
- Cloern, J.E. 2001. Our evolving conceptual model of the coastal eutrophication problem. *Mar. Ecol. Prog. Ser.* 210: 223–253.
- Colby, P.J., Spangler, G.R., Hurley, D.A. and McCombie, A.M. 1972. Effects of eutrophication on salmonid communities of oligotrophic lakes. *J. Fish. Res. Board Can.* 29: 975–983.
- Craig, J.K., Crowder, L.B., Gray, C.D., McDaniel, C.J., Henwood, T.A. and Hanifen, J.G. 2001. Ecological effects of hypoxia on fish, sea turtles, and marine mammals in the northwestern Gulf of Mexico. *Coastal Estuarine Stud.* 58: 269–291.
- Daskalov, G.M. 2002. Overfishing drives a trophic cascade in the Black Sea. *Mar. Ecol. Prog. Ser.* 225: 53–63.
- Déqué, M., Marquet, P. and Jones, R.G. 1998. Simulation of climate change over Europe using a global variable resolution general circulation model. *Clim. Dyn.* 14: 173–189.
- De Jonge, V.N., Bakker, J.F. and Van Stralen, M. 1996. Recent changes in the contributions of River Rhine and North Sea to the eutrophication of the western Dutch Wadden Sea. *Neth. J. Aquat. Ecol.* 30: 27–39.
- Diehl, S. 1988. Foraging efficiency of three freshwater fishes: effects of structural complexity and light. *Oikos* 53: 207–214.
- Flinkman, J., Aro, E., Vuorinen, I. and Viitasalo, M. 1998. Changes in northern Baltic zooplankton and herring nutrition from 1980s to 1990s: top-down and bottom-up processes at work. *Mar. Ecol. Prog. Ser.* 165: 127–136.
- Grönlund, L. and Leppänen, J.-M. 1990. Long term changes

- in the nutrient reserves and pelagic production in the western Gulf of Finland. *Finnish Marine Research* 257: 15–27.
- Halme, E. and Hurme, S. 1952. Tutkimuksia Helsingin rannikkoalueen kalavesistä, kaloista ja kalastusoloista. Helsingin kaupungin julkaisuja 3. 157 pp. (in Finnish).
- Hansson, S. 1984. Competition as a factor regulating the geographical distribution of fish species in a Baltic archipelago: a neutral model analysis. *J. Biogeogr.* 11: 367–381.
- Hansson, S. 1987. Effects of pulp and paper mill effluents on coastal fish communities in the Gulf of Bothnia, Baltic Sea. *Ambio* 16: 344–348.
- Hansson, S. and Rudstam, L.G. 1990. Eutrophication and the Baltic fish communities. *Ambio* 19: 123–125.
- Horppila, J., Peltonen, H., Malinen, T., Luokkanen, E. and Kairesalo, T. 1998. Top-down or bottom-up effects by fish: issues of concern in biomanipulation of lakes. *Restor. Ecol.* 6: 20–28.
- Hällfors, G., Niemi, Å., Ackerfors, H., Lassif, J. and Lepäkoski, E. 1981. Biological oceanography. In P. Voipio (ed.), *The Baltic Sea*. Elsevier Scientific Publishing Company, Amsterdam. p. 219–274.
- Hänninen, J., Vuorinen, I. and Hjelt, P. 2000. Climatic factors in the Atlantic control the oceanographic and ecological changes in the Baltic Sea. *Limnol. Oceanogr.* 45: 703–710.
- Hänninen, J. and Vuorinen, I. 2001. Macrozoobenthos structure in relation to environmental changes in the Archipelago Sea, northern Baltic Sea. *Boreal Env. Res.* 6: 93–105.
- Jarre-Teichmann, A., Wieland, K., MacKenzie, B.R., Hinrichsen, H.-H., Plikshs, M. and Aro, E. 2000. Stock-recruitment relationships for cod (*Gadus morhua* L.) in the central Baltic Sea incorporating environmental variability. *Arch. Fish. Mar. Res.* 48(2): 97–123.
- Jeppesen, E., Jensen, J.P., Kristensen, P., Sondergaard, M., Mortensen, E., Sorkjaer, O. and Olrik, K. 1990. Fish manipulation as a lake restoration tool in shallow, eutrophic, temperate lakes 2: threshold levels, long-term stability and conclusions. *Hydrobiologia* 200/201: 219–227.
- Johnson, K.H., Vogt, K.A., Clark, H.J., Schmitz, O.J. and Vogt, D.J. 1996. Biodiversity and the productivity and stability of ecosystems. *Trends Ecol. Evol.* 11: 372–377.
- Kangas, P., Autio, H., Hällfors, G., Luther, H., Niemi, Å. and Salemaa, H. 1982. A general model of the decline of *Fucus vesiculosus* at Tvärminne, south coast of Finland in 1977–81. *Acta Bot. Fennica* 118. 27 pp.
- Kauppila, P., Hällfors, G., Kangas, P., Kokkonen, P. and Basova, S. 1995. Late summer phytoplankton species composition and biomasses in the eastern Gulf of Finland. *Ophelia* 42: 179–191.
- Kauppila, O. and Lepistö, L. 2001. Changes in phytoplankton. In P. Kauppila and S. Bäck (eds.), *The state of Finnish coastal waters in the 1990s*. The Finnish Environment 472: 61–70.
- Kauppila, P., Korhonen, M., Pitkänen, H., Kenttämies, K., Rekolainen, S and Kotilainen, P. 2001. Loading of pollutants. In P. Kauppila and S. Bäck (eds.), *The state of Finnish coastal waters in the 1990s*. The Finnish Environment 472: 15–29.
- Kautsky, H., Kautsky, L., Kautsky, N., Kautsky, U. and Lindblad, C. 1992. Studies on the *Fucus vesiculosus* community in the Baltic Sea. *Acta Phytogeogr. Suec.* 78: 33–48.
- Kideys, A.E. 1994. Recent dramatic changes in the Black Sea ecosystem: The reason for the sharp decline in Turkish anchovy fisheries. *J. Mar. Syst.* 5: 171–181.
- Kiirikki, M. 1996. Dynamics of macroalgal vegetation in the northern Baltic Sea — evaluating the effects of weather and eutrophication. W.&A. de Nottbeck Foundation Sci. Rep. 12: 1–15.
- Kiirikki, M., Inkala, A., Kuosa, H., Pitkänen, H., Kuusisto, M. and Sarkkula, J. 2001. Evaluating the effects of nutrient load reductions on the biomass of toxic nitrogen-fixing cyanobacteria in the Gulf of Finland, Baltic Sea. *Boreal Env. Res.* 6: 131–146.
- Koli, L., Rask, M., Viljanen, M. and Aro, E. 1988. The diet of perch, *Perca fluviatilis* L., at Tvärminne, northern Baltic Sea, and a comparison with two lakes. *Aqua Fenn.* 18: 185–191.
- Kurkilahti, M. and Rask, M. 1996. A comparative study of the usefulness and catchability of multimesh gill nets and gill net series in sampling of perch (*Perca fluviatilis* L.) and roach (*Rutilus rutilus* L.). *Fish. Res.* 27: 243–260.
- Kurkilahti, M. 1999. Nordic multimesh gillnet — robust gear for sampling fish populations. Ph.D. thesis. Finnish Game and Fisheries Research Institute, Helsinki. 27 pp + appendices.
- Lappalainen, A. and Hildén, M. 1993. Recreational fishing and environmental impacts in the Archipelago Sea and the Finnish part of the Gulf of Bothnia. *Aqua Fenn.* 23: 29–37.
- Lappalainen, A. and Pönni, J. 1996. The Gulf of Finland in the fisherman's eyes — Pollution and recreational fishery in the Gulf of Finland. Finnish Game and Fisheries Research Institute, Helsinki. Kalatutkimuksia 107. 44 pp. (In Finnish with English summary).
- Lammens, E.H.R.R., Geursen, J. and Mac Gillavry, P.J. 1987. Diet shifts, feeding efficiency and coexistence of bream (*Abramis brama*), roach (*Rutilus rutilus*) and white bream (*Blicca bjoerkna*) in hypertrophic lakes. *Proc. 5th Congr. Europ. Ichthyol., Stockholm 1985*, p. 153–162.
- Larsson, U., Elmgren, R. and Wulff, F. 1985. Eutrophication and the Baltic Sea: Causes and consequences. *Ambio* 14: 9–14.
- Leach, J.H., Johnsson, M.G., Kelso, J.R.M., Hartmann, J., Nümann, W. and Entz, B. 1977. Responses of percid fishes and their habitat to eutrophication. *J. Fish. Res. Board Can.* 34: 1964–1971.
- Lee, G.F., Jones, P.E. and Jones, R.A. 1991. Effects of eutrophication on fisheries. *Rev. Aquat. Sci.* 5: 287–305.
- Lehtonen, H. 1985. Changes in commercially important freshwater fish stocks in the Gulf of Finland during recent decades. *Finnish Fish. Res.* 6: 61–70.
- Lehvo, A. and Bäck, S. 2001. Survey on macroalgal mats on southeastern Baltic coast of Finland. *Aquat. Conserv.* 11: 11–18.
- Lowthion, D., Soulsby, P.G. and Houston, M.C.M. 1985.

- Investigation of a eutrophic tidal basin: Part 1 — Factors affecting distribution and biomass of macroalgae. *Marine Environ. Res.* 15: 263–284.
- Luther, H. 1981. Occurrence and ecological requirements of *Fucus vesiculosus* in semienclosed inlets of the Archipelago Sea, SW Finland. *Ann. Bot. Fenn.* 18: 187–200.
- MacKenzie, B.R., Hinrichsen, H.H., Plikshs, M., Wieland, K. and Zezera, A.S. 2000. Quantifying environmental heterogeneity: habitat size necessary for successful development of cod, *Gadus morhua*, eggs in the Baltic Sea. *Mar. Ecol. Prog. Ser.* 193: 143–156.
- Moncheva, S., Gotsis-Skretas, O., Pagou, K. and Krastev, A. 2001. Phytoplankton blooms in Black Sea and Mediterranean coastal ecosystems subjected to anthropogenic eutrophication: Similarities and differences. *Estuar. Coast. Shelf Sci.* 53: 281–295.
- Moss, B. 1980. Ecology of fresh waters. Man and medium. Blackwell Scientific Publications, Oxford. 332 pp.
- Neuman, E. 1982. Species composition and seasonal migrations of the coastal fish fauna in the southern Bothnian Sea. In K. Müller (ed.), *Coastal Research in the Gulf of Bothnia*. Dr. W. Junk Publishers, The Hague. p. 317–351.
- Nixon, S.W. 1990. Marine eutrophication: A growing international problem. *Ambio* 19: 101.
- Norkko, A. and Bonsdorff, E. 1996. Rapid zoobenthic community responses to accumulations of drifting algae. *Mar. Ecol. Prog. Ser.* 131: 143–157.
- Ojaveer, H. 1997. Composition and dynamics of fish stocks in the Gulf of Riga ecosystem. Ph.D. thesis. University of Tartu. *Dissertationes Biologicae Universitatis Tartuensis* 31. 33 pp. + appendices.
- Ojaveer, H. 1999. Exploitation of biological resources of the Baltic Sea by Estonia in 1928–1995. *Limnologica* 29: 224–226.
- Ojaveer, H., Järv, L. and Erm, V. 1999. Some tendencies in Estonian coastal fisheries in the mid 1990s. In: *Freshwater fish and herring populations in the coastal lagoons. Environment and fisheries: Proceedings of Symposium — Gdynia, Poland, 6–7 May 1998*. Sea Fisheries Institute, Gdynia. p. 174–184.
- Ojaveer, H., Simm, M., Lankov, A. and Lumberg, A. 2000. Consequences of invasion of a predatory cladoceran. *ICES C.M. 2000/U*: 16, 12 pp.
- Olin, M., Rask, M., Ruuhijärvi, J., Kurkilahti, M., Ala-Opas, P. and Ylönen, O. 2002. Fish community structure in mesotrophic and eutrophic lakes of southern Finland: the relative abundances of percids and cyprinids along a trophic gradient. *J. Fish Biol.* 60 (in press).
- Paavilainen, K., Langi, A. and Tana, J. 1985. Effect of pulp and paper mill effluents on a fishery in the Gulf of Finland. *Finnish Fish. Res.* 6: 81–91.
- Peltonen, H., Ruuhijärvi, J., Malinen, T. and Horppila, J. 1999a. Estimation of roach (*Rutilus rutilus* (L.)) and smelt (*Osmerus eperlanus* (L.)) stocks with virtual population analysis, hydroacoustics and gillnet CPUE. *Fish. Res.* 44: 25–36.
- Peltonen, H., Ruuhijärvi, J., Malinen, T., Horppila, J., Olin, M. and Keto, J. 1999b. The effects of food-web management on fish assemblage dynamics in a north temperate lake. *J. Fish Biol.* 55: 54–67.
- Perrow, M.R., Meijer, M.-L., Dawidiwicz, P. and Coops, H. 1997. Biomanipulation in shallow lakes: state of the art. *Hydrobiologia* 342/343: 355–365.
- Persson, L. 1983. Effects of intra- and interspecific competition on dynamics and structure of a perch *Perca fluviatilis* and a roach *Rutilus rutilus* population. *Oikos* 41: 197–207.
- Persson, L., Diehl, S., Johansson, L., Andersson, G. and Hamrin, S. 1991. Shifts in fish communities along the productivity gradient in temperate lakes — patterns and the importance of size-structured interactions. *J. Fish Biol.* 38: 281–293.
- Persson, P.-E. 1985. Off-flavours in fish from the Gulf of Finland. *Finnish Fish. Res.* 6: 112–117.
- Pesonen, L. 1998. Kemiallinen, fysikaalinen ja hygieeninen tarkkailu. In L. Pesonen (ed.), *Helsingin ja Espoon merialueiden velvoitetarkkailu vuonna 1997*. Helsingin kaupungin ympäristökeskuksen monisteita 4/98, p. 15–48. (in Finnish).
- Pesonen, L. 1999. Meriveden kemiallinen, fysikaalinen ja hygieeninen laatu. In L. Pesonen (ed.), *Helsingin ja Espoon merialueiden velvoitetarkkailu vuonna 1998*. Helsingin kaupungin ympäristökeskuksen monisteita 5/99, p. 17–51. (in Finnish).
- Pihl, L., Isaksson, I., Wennhage, H. and Moksnes, P.-O. 1995. Recent increase of filamentous algae in shallow Swedish bays: effects on the community structure of epibenthic fauna and fish. *Neth. J. Aquat. Ecol.* 29: 349–358.
- Pitkänen, H. 1994. Eutrophication of the Finnish coastal waters: Origin, fate and effects of riverine nutrient fluxes. *Publ. Water Environ. Res. Inst.* 18: 1–45.
- Pitkänen, H., Kauppila, P. and Laine, Y. 2001. Nutrients. In P. Kauppila and S. Bäck (eds.), *The state of Finnish coastal waters in the 1990s*. The Finnish Environment 472: 37–60.
- Plikshs, M., Kalejs, M. and Grauman, G. 1993. The influence of environmental conditions and spawning stock size on the year-class strength of the eastern Baltic cod. *ICES C.M. 1993/J*: 22, 13 pp.
- Quinn S. P. 1992. Angler perspectives on walleye management. *N. Am. J. Fish. Manage.* 12: 367–378.
- Rajasilta, M., Eklund, J., Kääriä, J. and Ranta-aho, K. 1989. The deposition and mortality of the eggs of the Baltic herring, *Clupea harengus membras*, L., on different substrates in the south-west archipelago of Finland. *J. Fish Biol.* 34: 417–427.
- Rajasilta, M., Mankki, J., Ranta-aho, K. and Vuorinen, I. 1999. Littoral fish communities in the Archipelago Sea, SW Finland: a preliminary study of changes over 20 years. *Hydrobiologia* 393: 253–260.
- Rapport, D.J., Regier, H.A. and Hutchinson, T.C. 1985. Ecosystem behavior under stress. *Am. Nat.* 125: 617–640.
- Rask, M. 1989. A note on the diet of roach, *Rutilus rutilus* L., and other cyprinids at Tvärminne, northern Baltic Sea. *Aqua Fenn.* 19: 19–27.
- Regier, H.A. and Cowell, E.B. 1972. Application of ecosystem theory: succession, diversity, stability, stress and conservation. *Biol. Conserv.* 4: 83–88.
- Sandström, A. and Karås, P. 2002. Effects of eutrophication

- on young-of-the-year freshwater fish communities in coastal areas of the Baltic. *Env. Biol. Fish.* 63: 89–101.
- Seinä, A., Grönvall, H., Kalliosaari, S. and Vainio, J. 1996. Ice seasons 1991–1995 along the Finnish coast. *Meri* 27: 3–13.
- Seinä, A., Grönvall, H., Kalliosaari, S. and Vainio, J. 2001. Ice seasons 1996–2000 in Finnish sea areas. *Meri* 43: 3–28.
- Sfriso, A., Marcomini, A. and Pavoni, B. 1987. Relationships between macroalgae biomass and nutrient concentrations in a hypereutrophic area of the Venice lagoon. *Marine Environ. Res.* 22: 297–312.
- Specziár, A., Tölg, L. and Bíró, P. 1997. Feeding strategy and growth of cyprinids in the littoral zone of Lake Balaton. *J. Fish Biol.* 51: 1109–1124.
- Spencer P. D. and Spangler G. R. 1992. Effect that providing fishing information has on angler expectations and satisfaction. *N. Am. J. Fish. Manage.* 12: 379–385.
- Stenson, J.A.E. 1979. Predator–prey relations between fish and invertebrate prey in some forest lakes. *Rep. Inst. Freshwat. Res. Drottningholm* 58: 166–183.
- Stewart-Oaten, A., Murdoch, W.W. and Parker, K.R. 1986. Environmental impact assessment: ‘pseudoreplication’ in time? *Ecology* 67: 929–940.
- Svärdson, G. and Molin, G. 1981. The impact of eutrophication and climate on a warmwater fish community. *Rep. Inst. Freshw. Res., Drottningholm* 59: 142–151.
- Tammi, J., Lappalainen, A., Mannio, J., Rask, M. and Vuorenmaa, J. 1999. Effects of eutrophication on fish and fisheries in Finnish lakes: a survey based on random sampling. *Fish. Manage. Ecol.* 6: 173–186.
- Vahteri, P., Mäkinen, A., Salovius, S. and Vuorinen, I. 2000. Are drifting algal mats conquering the bottom of the Archipelago Sea, SW Finland? *Ambio* 29: 338–343.
- Westerbom, M., Kilpi, M. and Mustonen, O. 2002. Blue mussels, *Mytilus edulis*, at the edge of the range: population structure, growth and biomass along a salinity gradient in the north-eastern Baltic Sea. *Mar. Biol.* 140: 991–999.
- Winkler, H. M. 1991. Changes of structure and stock in exploited fish communities in estuaries of the southern Baltic coast (Mecklenburg-Vorpommern, Germany). *Int. Rev. Gesamten Hydrobiol.* 76: 413–422.
- Ådjers, K., Lappalainen, A., Saat, T. and Sandström, O. 2000. Coastal fish monitoring in Baltic reference areas 1999. *Kala- ja riistaraportteja nro 190*. 11 pp.
- Öst, M. and Kilpi, M. 1997. A recent change in size distribution of blue mussels (*Mytilus edulis*) in the western part of the Gulf of Finland. *Ann. Zool. Fennici* 34: 31–36.

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