BOREAL ENVIRONMENT RESEARCH 6: 107–118 ISSN 1239-6095
Helsinki 28 June 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?

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Lappalainen, A., Rask, M., Koponen, H. & 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 Env. Res.* 6: 107–108. ISSN 1239-6095

The coastal waters of the northern Baltic Sea have been undergoing a progressive process of eutrophication in recent decades. Gill net samples were taken in the Tvärminne area (SW Finland) to assess the effects of coastal eutrophication on the stocks of two common species, perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*). The relative abundance, diet and growth of perch were rather similar in 1975 and in 1997. However, the higher abundance of roach catches in the outer archipelago and their slower growth rate indicate that roach stocks have increased during the last 20 years. Perch feed mainly on macro-crustaceans and fish, whereas roach feed mainly on molluscs. In 1997, *Saduria entomon* was absent from the diet of perch, and the contribution of *Mytilus edulis* and *Cerastoderma glaucum*, two important components in the diet of roach, had decreased, possibly reflecting changes in local benthic communities. The most pronounced change, however, was the increase in local roach stocks, which was attributed to coastal eutrophication.

Introduction

Perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) are freshwater species widely distributed throughout Europe. These species are adapted to various types of habitat, from freshwater ponds smaller than 0.01 km^2 to large brackish water areas such as the Baltic Sea coast. Interspecific food competition is common between the species in lakes, a higher trophic status favouring roach to perch (e.g. Persson 1983a). In the Tvärminne area, at the entrance to the Gulf of Finland (Rask 1989), and also in other shallow coastal areas of the northern Baltic Sea (e.g. Hansson 1984, Neuman and Karås 1988, Mattila and Bonsdorff 1988), perch and roach are the most common freshwater species. Perch is the main target of recreational fishery in Finnish coastal areas, with an annual catch approaching 2000 tonnes (Anon. 1998).

Important properties explaining the good adaptation of the two species to various habitats are that both are food generalists and they have no special requirements for spawning areas. Perch can feed on zooplankton throughout its life span or turn to zoobenthos and further to fish. Roach, for its part, is able to feed on detritus and plant material as well as on zooplankton and zoobenthos (Persson 1983b, Mattila and Bonsdorff 1988). Koli *et al*. (1988) showed that crustaceans and fish were the most important food for perch in the Tvärminne area in 1975. Rask (1989) reported that the most important food items for roach in the same area were the mussels *Mutilus edulis*, *Cerastoderma glaucum*, *Macoma balthica* and snails *Hydrobia* ssp., and suggested that the dominance of animal food in the diet of roach is an indication of favourable feeding conditions. Hansson (1984) and Mattila and Bonsdorff (1988) both reported higher proportions of insects in the diet of perch and higher proportions of plant material in the diet of roach in more sheltered study areas in the northern Baltic Sea.

Since 1975 some gradual changes have taken place in the Tvärminne region, as well as in other coastal areas of the northern Baltic Sea. The whole sea has been undergoing a steady process of eutrophication over the last decades (Cederwall and Elmgren 1990). The Gulf of Finland is one of the most heavily eutrophicated areas in the Baltic Sea and vast algal blooms have become common in recent years (Rantajärvi 1998). The local nutrition load in the Tvärminne region, near the western entrance to the Gulf of Finland, has been lower than in eastern coastal areas of the gulf, where most of the land-based load is discharged (Pitkänen *et al.* 1987). Nevertheless, the Tvärminne region is a well-known upwelling region, and the importance of wind-driven upwelling (Haapala 1994) as a source of nutrients is probably greater there than further east, where local anthropogenic nutrient sources may dominate (Kiirikki 1996a). In the early 1990s, nutrient concentrations and productivity in the pelagic system in the area were higher than the levels observed in the 1970s (Grönlund and Leppänen 1992). Symptoms of large-scale eutrophication in the Tvärminne area are also seen in the macroalgal vegetation, for example, in the regular spring mass occurrence of epiphytic algae *Pilayella littoralis* (Kiirikki 1996a). The decline in bladder wrack (*Fucus vesiculosus*) in the Tvärminne region and in many other coastal regions of the Baltic Sea during the late 1970s and early 1980s has also been attributed to increased nutrient concentrations and the resulting changes in ecosystems (e.g. Kangas *et al*. 1982, Kautsky 1991).

In addition to ongoing eutrophication, there have been variations in salinity during the last 20 years. The main factors controlling the salinity of the Baltic proper are the occasional inflow of high salinity water through the Danish straits and freshwater runoff to the Baltic Sea. Both the pulses and the runoff are ultimately 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 northern Baltic Sea was still lower in the late 1990s than it had been in the early 1980s (e.g. Laine *et al*. 1997). Along with the decline in salinity, the biomass proportion of the larger zooplankton preferred by herring (*Clupea harengus*) has decreased in the northern Baltic Sea (Flinkman *et al*. 1998), partly explaining the recent decline in herring growth. Due to favourable conditions in the Baltic proper, the year classes of cod (*Gadus morhua*) were unusually strong in 1976, 1979 and 1980. Baltic cod stocks

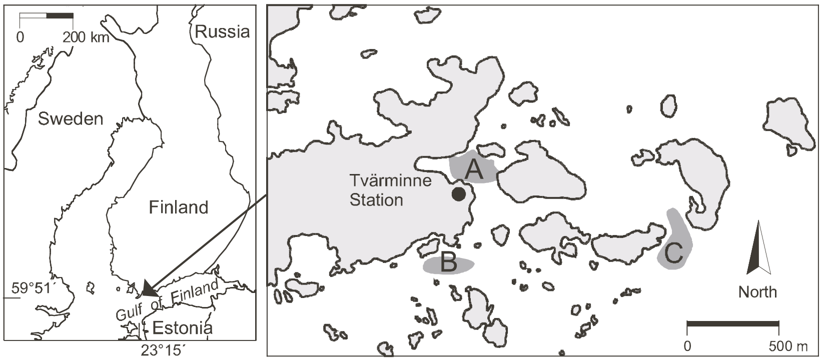

Fig. 1. The study area and the sampling sites (A–C).

then expanded dramatically, and commercial catches of cod in Finnish coastal areas reached a maximum in 1983 and 1984, being then many times larger than the total catches of other predatory species occurring in coastal areas (Anon. 1993). Cod stocks diminished during the late 1980s and practically no cod at all were caught off the Finnish coast during the 1990s.

Due to the general scarcity of comparable historical data, little information is available on the potential effects of eutrophication on freshwater fish communities in the Baltic Sea. Anttila (1973), Hansson (1987) and Bonsdorff *et al*. (1997a) reported high abundances of cyprinids in other, more polluted areas of the northern Baltic, and Anttila (1973) reported a decrease in pike (*Esox lucius*), burbot (*Lota lota*) and ide (*Leuciscus idus*) populations. The increase in commercial catches of pikeperch (*Stizostedion lucioperca*) in some coastal areas of the Baltic has been attributed to eutrophication (Lehtonen 1985, Winkler 1991). In temperate lake ecosystems, eutrophication often leads to cyprinid dominance (e.g. Persson *et al*. 1991). The responses might be similar in the Baltic coastal area (Hansson and Rudstam 1990), but the differences in hydrological features and the presence of marine organisms can make the situation more complicated than in lakes.

The main aim of the present study was to establish whether the widespread coastal eutrophication affects local perch and roach stocks in the Tvärminne area. To this end, we compared the relative abundance, diet and growth of perch and roach between 1975 and 1997. Although the samples were collected in single years, the data on the relative abundances of fish taken by multimesh gill nets and also those on their growth give combined information on the circumstances prevailing during several years before sampling.

Material and methods

Test fishings were carried out at three sampling sites (Fig. 1) at Tvärminne, in the western Gulf of Finland, in 1975 and in 1997. Site A is a shallow (< 5m) bay with a fine and soft mineral substratum and abundant macrophytic vegetation, including *Fucus vesiculosus*, *Phragmites communis*, *Potamogeton perfoliatus* and *Ranunculus baudotii*. Site B, a 2–7 m deep strait area, has a hard mineral bottom with *Fucus* in the littoral and *Zostera maritima* in the deeper parts. The outermost site, C, is more exposed to high winds. It is 5 to 12 m in depth and has a hard, mostly sandy bottom; *Fucus* was abundant in the shallow parts of this site. The surface water salinity of the Tvärminne area varies between 5‰ and 7‰ (Fig. 2). The total concentrations of phosphorus, measured at Längden sampling station in outer archipelago of Tvärminne, are generally higher than the levels in the early 1970s and the peaks of the spring phytoplankton blooms have become more intensified in the early 1980s (Fig. 2). The surface water temperature varied between 3 and 21 °C during May–October in 1975 and 1997 (Fig. 3).

All sampling sites were sampled in May–early June, July, August and October (Table 1). In 1975, a gill net series with nine combined nets was used. Each net was 30 m long and 1.8 m high. In each series the mesh sizes were 12, 15,

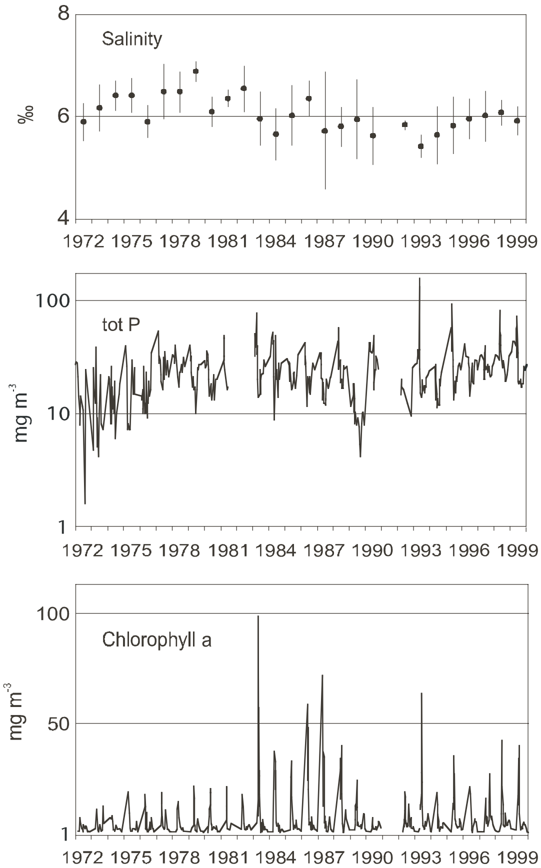

Fig. 2. Annual mean (±SD) salinities, total concentrations of phosphorus (logarithmic scale) and chlorophyll a concentrations of surface water at Längden sampling station, outer archipelago of Tvärminne, in 1972–1999 (Finnish Institute of Marine Research, Finnish Environment Institute and Uusimaa Regional Environment Centre, unpubl. data).

20, 25, 30, 35, 45, 60 and 75 mm (bar length) and the catch of each series was treated as a single

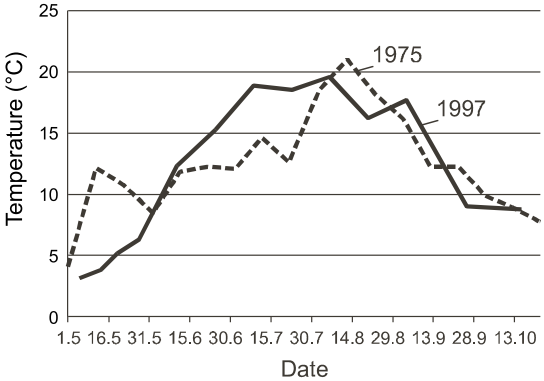

Fig. 3. Water temperature at 5 m depth at Längden in 1975 and 1997 (Finnish Institute of Marine Research and Uusimaa Regional Environment Centre, unpubl. data).

sample. In 1997, multimesh gill nets were used and the catch from one multimesh gill net was treated as a single sample. Each net consists of panels 6 m long and 1.8 m high, with mesh sizes of 12, 15, 20, 25, 30, 35, 45 and 60 mm. As the mesh size of 75 mm was not included in the multimesh gill nets used in 1997, the 1975 catches taken with that mesh size were excluded from the study. Nets were set on the bottom during the late afternoon and hauled up the next morning. The catching efficiencies per gill net surface area of the gill net series and the multimesh gill nets are not equal (Kurkilahti and Rask 1996), and thus the abundance of each species in 1975 and 1997 are presented in relative terms rather than as absolute catch per unit effort (CPUE). An estimator of the ratio ($r = y/x$) for the catch of certain species (y) to total catch (x) was used in the statistical tests. The denominator (x) is also a random variable and contributes to the total vari-

Table 1. Number of test fishing efforts (independent observations) in the study area in 1975 and 1997.

	1975*				1997**			
Site	May–June	July	August	October	May–June	July	August	October
A	1	2	2	2	6	6	6	6
B	2	2	2	2	6	6	6	6
C	2	2	2	2	6	6	6	6

* In 1975 samples were taken with a series of nine gill nets (each 1.8 × 30 m), mesh sizes 12, 15, 20, 25, 30, 35, 45, 60 and 75 mm (bar length).
** In 1997 samples were taken with multimesh gill nets (1.8 × 48 m), mesh sizes similar to those in 1975, except that 75 mm was not included.

ance of the ratio estimator, implying that the variance estimation is nonlinear (Cochran 1977, Lehtonen and Pahkinen 1996). The ratio procedure of SUDAAN 7.10 software (Shah *et al.* 1996) used a linearization method to approximate the variance of the ratio estimators. Thereafter, the same procedure was applied in *t*-tests to compare the ratios between the years. Each of the four sampling periods within the years was treated as a separate stratum, as the SUDAAN software can take into account the sample design parameters in the analysis. In addition, absolute CPUE values for roach were calculated, and an analysis of variance was carried out to compare the means between sites within years.

Samples for food and growth analyses were collected from the gill net catches during all periods and from each of the three sampling sites. The samples were then pooled because the earlier results (Koli *et al*. 1988, Rask 1989) did not show any large differences between sampling sites or periods. In 1975, a total of 1010 perch and 372 roach were collected for food and growth analyses; in 1997, 400 perch and 400 roach were collected. The stomachs of perch and the digestive tracts of roach were removed and preserved in 4%–10% formaldehyde (in 1975) or 70% ethanol (in 1997). Food items were identified and counted under a dissecting microscope. For perch, the importance of different food categories was estimated with a volumetric points method (Windell 1971) and, for each food category, the percentages of fullness points were calculated. Since cyprinids lack a distinct stomach, quantitative estimation based on fullness points is difficult for roach. The diets of roach were therefore characterized mainly by the frequency of occurrence of each food item (found or not found), and the association between frequency of occurrences and year was with the Chi-square test (2 × 2 tables). The number of individual food items was also counted. To take into account the dietary transition of perch during its life span, the fish were divided into different length groups before comparison with the earlier results of Koli *et al.* (1988). This was not done for roach as the diet of roach of different size was almost uniform in 1975 (Rask 1989).

The age of perch was determined from the opercular bones and that of roach from the scales. The age and growth of the samples taken in 1975 were determined during the late 1970s and the original data were no longer available. Back calculation of growth was done according to the formula of Fraser and Lee (roach) and Monastyrsky (perch) (*see* Bagenal and Tesch 1978). The differences in the growth of roach between 1975 and 1997 could be compared by a *t*-test as the mean, SD and n of the back calculated lengths of roach for 1975 were reported by Rask (1989). A logarithmic growth model ($W = aL^b$) for the relation of weight (g) to length (mm) of roach was fitted using combined data of both years.

Results

Relative abundance of species

The relative abundance of perch was, in general, much the same in 1997 as in 1975, although the proportion of perch was a little lower (p = 0.021) in the innermost sites and higher (p = 0.013) in the outermost site, C, in 1997 than in 1975 (Table 2). The relative abundances of roach in the innermost sites were similar in 1997 and 1975. However, in the outermost site, C, the proportion of roach was much higher (p < 0.001) in 1997 than in 1975, roach being the most abundant species in the catch in 1997 (Table 2). This same change is seen in the CPUE values for roach (Table 3), the mean CPUE for roach at site C in 1997 having reached the same level as at sites A and B. In both 1975 and 1997, the proportion of roach at site C was highest in October, being 16% in 1975 and 64% in 1997. During that time, the water temperature had already decreased to 8–9 °C in both years (Fig. 3), indicating that the high abundance of roach at the outermost site C in 1997 can not be explained by different temperature conditions between 1975 and 1997. Cod was occasionally a common species at site C in 1975, but no cod were caught at sites A and B, nor at any sites in 1997. In 1975, the bulk (76%) of the total catch of cod at site C was taken in October. Cod was not included in Table 2, because its extraordinarily high occurrence, due to favourable circumstances in the southern Baltic, would have masked the proportions of the local species.

Table 2. Proportion (% of weight) of the most common species in the total catch from the sampling sites in May–September 1975 and 1997. Sites A and B were combined as the catches were similar. Only the species with a proportion > 5% in a sampling site are shown in the table. Differences between years were tested with the ratios *t*-test.

	Sites A and B			Site C		
Species	1975	1997	*p*-value	1975	1997	*p*-value
Perch (*Perca fluviatilis*)	41	31	0.021*	12	26	0.013*
Pikeperch (*Stizostedion lucioperca*)	0	2	–	2	6	0.029*
Ruffe (*Gymnocephalus cernuus*)	3	4	0.156	14	12	0.514
Pike (*Esox lucius*)	13	4	0.097	3	0	–
Roach (*Rutilus rutilus*)	30	33	0.619	7	36	0.000***
Bream (*Abramis brama*)	2	5	0.019*	0	1	–
White bream (*Blicca bjoerkna*)	1	11	0.000***	2	4	0.282
Flounder (*Platichthys flesus*)	2	1	0.436	47	9	0.000***
Other species	7	9	–	13	6	–
Total weight (kg)	259	403		138[x)]	150	

[x)] Cod catches (total 90 kg) not included

Diet composition of perch and roach

Mysidacea, Amphipoda and fish were the main food items for smaller perch, 12–20 cm in total length (Table 4). Isopoda and Chironomidae were also prominent, and fish were important for large perch. The proportion of Mysidacea was approximately twice as high in samples taken in 1997 as in those taken in 1975. On the other hand, the proportions of Amphipoda in 1997 were only half of those in 1975.

Larger perch, > 20 cm, fed mainly on fish, especially in 1997. In both 1975 and 1997, Gobiidae accounted for approximately half of the fish diet of perch, other important species being herring and three-spined stickleback (*Gasterosteus aculeatus*). In 1975, a large Isopoda, *Saduria entomon*, accounted for 26% of the fullness points of larger perch but in 1997 no Isopoda were found. Slightly lower proportions of Amphipoda in 1997 than in 1975 could also be seen in the diet of larger perch. The proportion of empty stomachs of smaller perch, < 20 cm, was higher in 1997 than in 1975, but among larger perch, > 20 cm, the proportions were equal. The diet of perch between years could not be compared statistically, as the primary data for 1975 were not available.

Judging by both occurrence frequency and number of food items, molluscs clearly dominated the diet of roach. In 1997, the total proportion of molluscs was > 85% (Table 5). The most numerous species were *Hydrobia* spp. and *Mytilus edulis*, both of which were more frequently found in the guts of roach in 1975 than in 1997. The same is true for *Cerastoderma glaucum* and *Theodoxus fluviatilis*. The proportion of empty guts was higher in 1997 than in 1975. *Balanus improvisus* was the only item found more frequently in 1997 than in 1975.

Table 3. Average catch per unit efforts (CPUE) for roach in 1975 and 1997. The statistical differences in the averages between sites are indicated with superscripts, different letters indicating significant differences (analysis of variance, $\alpha = 0.05$). Number of observations are given in parentheses.

Year	Site A	Site B	Site C
1975 (kg/gill net series/day)	4.3^{ab} (7)	5.9^{a} (8)	1.2^{b} (8)
1997 (kg/multimesh gill net/day)	2.7^{a} (24)	2.8^{a} (24)	2.3^{a} (24)

Growth of perch and roach

Male perch grew similarly in samples taken in 1975 and 1997 (Fig. 4). The growth of females

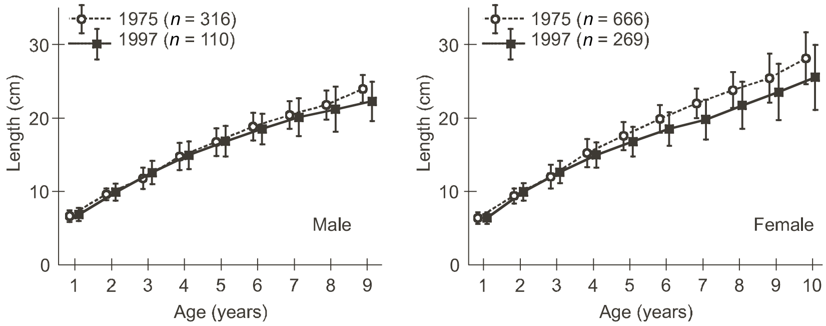

Fig. 4. Back calculated length at age (mean and SD) of perch at Tvärminne in 1975 (Koli *et al.* 1985) and in 1997.

during the 5–6 first years of life was also similar in the early 1970s and 1990s. The mean lengths of older females in 1975 appeared to be somewhat greater than in 1997, indicating faster growth of older females in the early 1970s. Statistical comparison between years could not be done as the original growth data on perch for 1975 were not available. The mean, SD and total number of samples were available, but the number of observations in each age group was unknown.

A preliminary comparison of back-calculated growth data of roach taken in 1975 (Rask 1989) and 1997 revealed a difference of almost 20 mm in the mean growth during the first year between these two years. Most probably this was not a true difference, but was caused by an inexperienced scale-reader systematically defining the first annulus as a juvenile ring in 1975. We later checked the first year growth of roach in Tvärminne using also the cleithrum, and the results confirmed our data for the 1997 samples. Thus, one year was added to ages in the length-at-age data for 1975. After this correction, the growth of roach during the first years of life appears to have been similar in the 1975 and 1997 samples (Table 6). The growth of older roach was still faster in the early 1970s than in the 1990s. The difference in mean length increased with age at least until 9–10 years. Based on the logarithmic growth model ($W = aL^b$, where $a = 1.253 \times 10^{-6}$ and $b = 3.40$), the weight of older roach (> 7 years) in 1975 was nearly twice as high as in 1997.

Table 4. Composition of diet (% of total amount of fullness points) of perch in Tvärminne in 1975 and 1997. Perch divided into four size classes.

Food item	12.0–15.9 cm		16.0–19.9 cm		20.0–23.9 cm		24.0–27.9 cm	
	1975	1997	1975	1997	1975	1997	1975	1997
Polychaeta	0.5	6.7	1.5	4.0	0.3	7.9	–	–
Mysidacea	23.1	37.0	13.3	35.1	9.4	17.5	1.7	1.2
Isopoda	3.3	11.5	6.2	9.0	26.6	–	26.0	–
Amphipoda	32.1	12.7	29.7	15.5	12.3	9.9	15.7	2.0
Decapoda	2.3	–	3.4	0.7	4.9	1.8	3.3	–
Chironomidae	11.3	9.6	6.5	6.4	1.9	0.2	–	2.9
Odonata	0.2	–	0.6	–	1.0	0.9	2.3	–
Trichoptera	2.4	3.0	2.1	3.4	0.6	–	–	–
Mollusca	0.4	–	1.3	0.7	2.3	–	1.3	–
Fish	18.3	19.0	26.1	22.8	33.0	61.8	40.0	93.9
Other	6.1	0.5	9.3	2.4	7.8	–	9.7	–
n	329	128	271	109	149	76	54	30
Empty (%)	8.8	34.4	19.6	33.0	36.9	34.2	37.0	40.0

Discussion

Perch

According to our gill net sampling, perch, together with roach, is the most common freshwater species in shallow areas of the archipelago at Tvärminne. The relative abundance of perch was at the same level in both 1975 and 1997, suggesting that no major changes had occurred in that species. This observation is supported by the growth data, as no major changes were detected between the years although the larger perch (> 20 cm) seemed to grow a little faster in the 1970s than in the 1990s. The growth of perch at Tvärminne has been at the same level as reported from other Baltic coastal areas (e.g. Koli *et al*. 1985, Hansson 1985). Neuman (1982)

Table 5. Composition of diet of roach in Tvärminne. Frequency of occurrence and abundance of food items in 1975 and 1997. Associations between frequencies of occurrence and year were with the Chi-square test.

	Frequency of occurrence (%)			Ind./100 roach	
Food item	1975	1997	*p*-value	1975	1997
Gastropoda					
Hydrobia ssp.	38.4	19.1	< 0.001***	655	189
Theodoxus fluviatilis	14.8	5.8	< 0.001***	33	7
Bithynia tentaculata	8.1	6.0	0.273	26	17
Potamopyrgus jenkinsi	3.2	2.5	0.557	5	9
Lymnea peregra	< 1.0	2.8	0.016*	< 1	3
Bivalvia					
Mytilus edulis	38.7	21.2	< 0.001***	119	61
Cerastoderma glaucum	30.6	7.6	< 0.001***	74	10
Macoma balthica	12.6	8.3	0.050	26	15
Mya arenaria	< 1.0	< 1.0	0.948	1	1
Crustacea					
Amphipoda	2.2	1.5	0.508	3	2
Isopoda	1.9	1.0	0.308	2	1
Ostracoda	2.2	< 1.0	0.104	12	1
Balanus improvisus	< 1.0	8.6	< 0.001***	1	12
Insecta					
Chironomidae	7.0	3.0	0.011*	18	8
Trichoptera	1.3	< 1.0	0.422	1	1
Number of diet analyses	372	397		371	397
Empty stomachs (%)	24.0	48.4			

Table 6. Back calculated length (mm) at age for roach in Tvärminne 1975 and 1997. Differences in means between years compared with the *t*-test.

		Length at age of									
Year		1	2	3	4	5	6	7	8	9	10
1975	Mean	?	66	92	115	135	161	182	203	224	239
	SD	?	6	9	12	14	14	16	16	17	15
	n	?	100	100	89	75	67	53	40	36	26
1997	Mean	48	68	87	105	122	140	157	173	187	202
	SD	5	9	11	13	15	17	19	20	21	24
	n	383	383	380	352	312	275	244	212	179	139
t-value			–1.72 ns	4.29***	6.63***	6.71***	9.51***	9.04***	9.01***	9.97***	5.99***

reported that the activity and catchability of perch correlated positively with water temperature, but that relationship was less clear for roach. The division of sampling into four periods may have reduced the effects of actual weather conditions on the results. The year-class strength of perch is positively correlated with temperature (Koli *et al*. 1985, Böhling *et al*. 1991), but with multimesh gill nets, which catch several year classes, this variation tends to be balanced out in our results.

Overall, crustaceans were the main macroinvertebrate food category for perch > 10 cm in our study area, as also reported by Koli *et al*. (1988), whereas insects are relatively more important in lakes (e.g. Koli *et al*. 1988). Koli *et al*. (1988) found zooplankton, mainly copepoda, only in the diet of perch < 8 cm at Tvärminne. *Fucus vesiculosus* is a keystone species along the Baltic coast (Kautsky *et al*. 1992), and forms a belt at a depth of 2–5 m in the littoral zone of the Tvärminne area (Kiirikki 1996b). The *Fucus* belt and the hydrolittoral belt of filamentous algae (Hällfors *et al*. 1975) offer food and shelter for numerous macrocrustaceans. The lower proportion of Amphipods, mainly *Gammarus ssp*, in the diet of perch, may be connected to eutrophication and the decline of *Fucus* in the late 1970s and early 1980s (Kangas *et al*. 1982). The absence of *Saduria entomon* from the diet of perch in 1997 suggests that local densities of this species on shallow bottoms were higher in 1975 than in 1997. However, the situation was the reverse on the deep bottoms off Tvärminne. From late 1960 to 1976, the sub-halocline bottoms (> 70 m) at the entrance to the Gulf of Finland were devoid of benthic macrofauna due to stagnation and poor oxygen conditions (Laine *et al*. 1997). The 1975–1976 and 1993–1994 inflows of North Sea water into the Baltic Sea improved the oxygen conditions and led to a recovery of macrofauna on the deep bottoms. In the first half of the 1990s, *Saduria* frequently occurred in samples taken from deep areas (Laine *et al*. 1997).

Roach

In 1975, roach was abundant only in the innermost study sites. In 1997, however, roach was the most abundant species in all three sites, suggesting that abundance of roach has increased during the last 20 years. Catches of roach in the Tvärminne area in the late 1990s were at the same level as in other similar archipelago areas in the more eutrophicated central and eastern areas of the Gulf of Finland (Lappalainen *et al*. 2000). On the other hand, CPUEs for roach and other cyprinids were still low in the late 1990s in the Brunskär archipelago, one of the least eutrophicated areas of the northern Baltic Sea, 80 km northwest of Tvärminne (Ådjers *et al*. 1998). There, catches of roach, however, slowly increased during the 1990s.

Eutrophication often leads to cyprinids dominance, at least in temperate lake ecosystems (e.g. Persson *et al*. 1991); observations of increased cyprinid catches have also been made in other, more polluted coastal areas of the northern Baltic Sea (e.g. Anttila 1973, Hansson 1987, Bonsdorff *et al*. 1997a). Thus, we suggest that eutrophication is the main reason for the increase in roach populations in the Tvärminne area. Presumably, eutrophication has promoted the survival and production of juvenile roach in the inner bays by increasing the supply of suitable habitats or zooplankton food. The grater abundance of roach and increased competition for food in the innermost areas have forced older roach to expand their feeding area into the more exposed, outer areas.

According to Rask (1989), the diet of white bream (*Blicca bjoerkna*) was similar to that of roach. The observed increase in the relative abundance of white bream might therefore intensify the competition for food between those two cyprinid species in the Tvärminne area. On the whole, the lower growth rate of roach in the 1990s than in the early 1970s, together with the high proportion of empty stomachs in 1997, suggests that the feeding conditions of roach have deteriorated. This could simply be the result of an increase in the number of mollusc feeding fish, but some other environmental factors affecting important prey stocks may also have contributed.

Rask (1989) described the diet of roach in Tvärminne in 1975 also in terms of biomass composition by roughly multiplying the number of individual food items counted in the whole material by the mean ash free dry weight (AFDW) of different prey types. In 1975, *Mytilus edulis* and *Cerastoderma glaucum* accounted for 60% of the total AFDW of the diet of roach, and *Hydrobia* spp. for 15%. In 1997, the frequency of occurrence and the abundance of these important species in the diet were only half, or less than half, of those in 1975. As the sampling methods in 1975 and 1997 were similar and the growth rate of roach has also decreased, it is evident that the amount of these prey items available for roach has decreased. Unfortunately, no time series of mollusc densities have been collected in Tvärminne or nearby areas to confirm our observations. According to a classification by Leppäkoski (1975), *Hydrobia* spp. and *Cerastoderma glaucum* are regressive species sensitive to deteriorating water quality, whereas *Macoma balthica* benefits from slight pollution. Kautsky (1981) has described the Baltic *Mytilus edulis* populations as stable and extremely dense, living near the carrying capacity of the area with regard to food and space availability. However, Öst and Kilpi (1997) reported that the mean size of *Mytilus edulis* in the Tvärminne area has decreased in recent decades, and suggest that greater selective predation by a diving duck, *Somateria mollissima*, may have locally contributed to this change. Thus, it is possible that intensified fish predation also can affect mollusc populations, in particular species such as *Mytilus*, which lives near its lower salinity tolerance limit in the Tvärminne area and thus can hardly grow large enough to avoid fish predation.

Relationships between perch and roach

Our results suggest that there were no major changes between the early 1970s and 1990s in the living conditions of perch, but that roach stocks increased. Hence the roach/perch ratio was higher in 1997 than in 1975, reflecting a trend commonly noted in temperate lake ecosystems undergoing eutrophication (e.g. Persson *et al*. 1991). The ongoing eutrophication of the coastal areas would appear to have favoured early stages of roach in the nearby inner bays, which are typical reproduction and nursery areas of roach. Persson (1983a) and Diehl (1988) have suggested that changes in the physical environment induced by lake eutrophication (decrease in submerged vegetation, increase in turbidity) could affect the competitive interactions that favour cyprinids to perch, as the feeding strategies are different. Cyprinids are also able to feed efficiently at low light intensities and even in darkness, whereas perch are visual hunters dependent on vision (Diehl 1988).

After the juvenile stage, perch is strictly carnivorous and an adept predator of relatively large and mobile prey but it expends more energy per capture whereas roach is omnivorous and has a feeding strategy that minimizes energy costs (Persson 1983a). Roach is adapted to utilizing molluscs, as it can crush the food mechanically with the pharyngeal teeth. Persson (1983a) reported a clear decrease in perch biomass and number as the roach stocks increased in an eutrophic lake with high competition between these species. In the Tvärminne area, the proportion of perch in the outermost site was even a little higher in 1997 than in 1975, even though the proportion of roach had increased heavily. Thus, in our study, the scarcity of similarities in the food of perch and roach suggests that there might not be any serious food competition between age classes > 3 years of these species. Contrary to roach, however, the proportion of flounder (*Platichthys flesus*) was considerably lower in 1997 than in 1975. Flounder also feeds mainly on molluscs (Ojaveer *et al*. 1981), and it is possible that there is competition between roach and flounder.

Acknowledgements: We are grateful to Christer Karppinen and Pekka Ahlfors for assistance in the field work. We thank Sture Hansson, Mikael Kilpi, Lauri Koli, Johanna Mattila, Erik Neuman and Olof Sandström for improvements to the manuscript. We also thank the Tvärminne Zoological station for putting the facilities of the station at our disposal during our field work.

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Received 29 August 2000, accepted 8 May 2001