Swimming activity of perch, *Perca fluviatilis*, in relation to temperature, day-length and consumption

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The swimming activity of a Baltic population of perch *Perca fluviatilis* was studied by gillnet fishing during a 13 year period in an experimental enclosure receiving cooling water from a nuclear power plant. A distinct seasonal rhythm was observed, correlated with temperature and day-length except for a peak during the spawning period in spring. The timing of the spring activity peak was not affected by the large differences in temperature between years and seemed to be more synchronized by day-length. Swimming activity was strongly related to consumption predicted by a bioenergetics model. The hypothesis that fish abundance may influence the cost of swimming through social interactions could not be supported by the studies, as growth rate remained unchanged although fish abundance increased considerably.

1. Introduction

The swimming activity of perch (*Perca fluviatilis* L.) and the closely related yellow perch (*Perca flavescens* Mitchill) has been the object for several field and laboratory studies. Both species are mainly day-active with activity maxima at dawn and dusk (Craig 1977, Eriksson 1978). Consequently, the duration of the diurnal activity period is correlated with day-length, while activity levels and swimming speed are more related to temperature (Hergenrader & Hasler 1967). Day-length and temperature effects thus combine to produce annual rhythms with high summer maxima and low winter activities in these species.

Fish swim for several reasons, e.g. foraging, escaping from predators, seasonal migrations, and social interactions. Kerr (1982) argued that loco-motor activity is dominated by food search seen over the whole year for actively foraging fishes, and that it is positively and linearly related to consumption. The observations of Adams *et al.* (1982) of parallel trends of active metabolism and consumption in largemouth bass (*Micropterus salmoides*), and of Boisclair and Leggett (1989a) on the actively foraging yellow perch, support Kerr's assumptions. However, by comparing growth rates of yellow perch in several lakes with different fish and food densities, Boisclair and Leggett (1989b) concluded that fish abundance as well may affect swimming activity positively through nonexploitive interactions. The influence of food availability was studied experimentally on juvenile brook trout (*Salvelinus fontinalis*) by Boisclair and Sirois (1993), who found that the activity rate decreased when food rations were restricted. High temperatures also increase the risk of energy deficits. The possibility for fish to save energy by re-
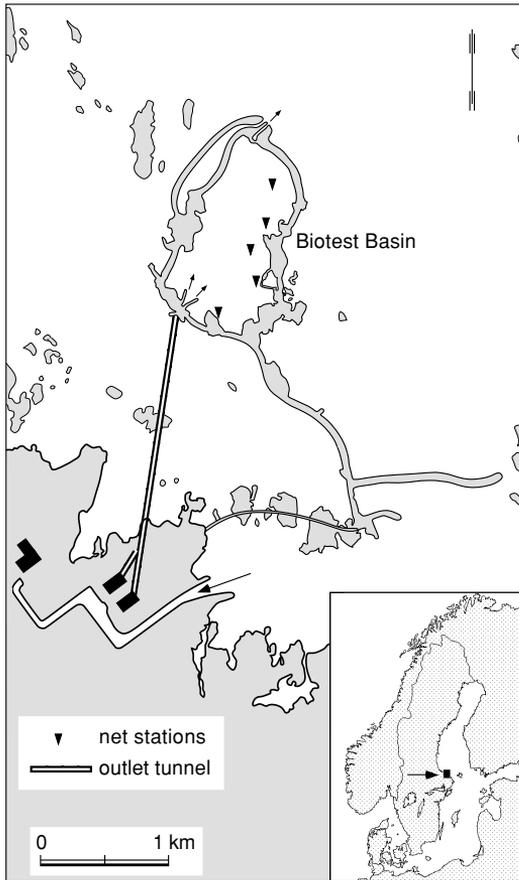
Fig. 1. The Biotest basin.

ducing swimming activity when temperature increases was investigated by Koch and Wieser (1983) for roach (*Rutilus rutilus L.)* and Mehner and Wieser (1994) for perch. They found evidence for such a reaction in roach, but the effect was hardly noticeable in perch.

One main reason for discussing locomotor activity of fish in recent years has been the difficulty to handle this factor in bioenergetics models, as it is not known how to achieve accurate estimates of the cost of swimming in terms of energy in free-living fish. Several workers in the field of bioenergetics have treated the costs for activity as a fixed multiple of the standard metabolism (e.g. Winberg 1956, Kitchell *et al.* 1977), lacking more accurate biological backgrounds for their assumptions. Kerr's (1982) hypothesis that swimming activity is linearly related to consumption may provide a more likely way towards a solution to the problem, but it needs further

validation on field populations and we are still faced with the problem of translating estimates of swimming activity to energy measures. Swimming activity may contribute only to a minor share of the total activity budget in sedentary predators like the pike *Esox lucius* (Diana 1983), but in more active feeders the cost of swimming is considered to be both large and variable (Boisclair & Leggett 1989a). Perch belongs to this second category, and a better understanding of locomotor activity will consequently facilitate a further development of predictive consumption models in this species.

The aims of this paper are to investigate how the swimming activity of fish, measured as catch per unit of effort (*CPUE*) in gill net fishing, is related to temperature, day-length, and consumption simulated by a bioenergetics model, and how these relations are influenced by variations in temperature, population density and food availability. The object selected for the study was a Baltic perch population living in an experimental enclosure big enough to harbour a complete coastal ecosystem.

2. The investigation area

The studies were made in an experimental system, the Biotest basin, at the Swedish coast of the S Gulf of Bothnia (Fig. 1). It receives cooling water from the Forsmark nuclear power plant. A series of islands have been joined by dikes, enclosing an area covering about 1 km² with an average depth of 2.5 m. Water pumped from a nearby bay at a rate of 90 m³/s is heated in the power plant about 10°C above ambient at full production before it runs through the Biotest basin. Fish larger than about 10 cm are prevented from entering or leaving the basin by 15 mm gratings at the outlet.

The constructions of the Biotest basin were finished in 1977. Heating started in spring 1980 when the first reactor began operating. When the second reactor reached full operation in the beginning of 1982, the period of maximum heating began. Heating effects are largest in winter, as the reactors are taken out of operation in summer for technical overhauls. Winter temperatures usually vary between 8 and 10°C, and summer temperatures only rarely exceed 25°C. Thermal stratification is very weak due to currents and the shallow water depths. The natural water temperature varies between 0 and 20°C

— conditions that existed in the Biotest basin before 1980 — and there is a 3–5 months period of ice cover. The salinity is rather stable around 5 ppt. Apart from the temperature increase, there were no other significant manipulations undertaken during the investigation period.

The community in the Biotest basin is monitored annually. As a consequence of the increased temperature, the fish community changed towards more warm-water adapted species, and roach (*Rutilus rutilus*) and perch have been dominating all through the study period (Sandström 1990).

3. Material and methods

Test fishing was conducted according to standardized guidelines (Thoresson 1993) at fortnightly intervals (with a few exceptions when weather conditions did not allow) throughout 1978–1990. Two 3-m high multi-mesh size gillnets consisting of five 7-m lengths with 16.5, 21.5, 25, 33.5, and 50 mm mesh bars were set at each of five locations. The nets were set between 2 and 4 p.m. and lifted between 8 and 10 a.m., the fishing thus covering the dusk-to-dawn period also in midwinter. To analyse possible bias in the seasonal distribution caused by the lack of daytime representation, additional samplings were made in 1984 to cover the whole 24-h period. Captured fish were recorded in 2.5-cm length classes. The smallest length class efficiently caught in these nets is 12.5–15.0 cm. Water temperature (0.1°C) was measured at each station when the nets were set and when they were lifted.

Catch per unit of effort (*CPUE*, the catch in one net during one fishing period) data were used to represent swimming activity, assuming a positive and linear relation. When constructing yearly activity distributions, the between-year differences in mean *CPUE* depending upon, for example, a trend in abundance due to improved recruitment, were compensated for by a standardization. The mean *CPUE* of the individual samplings were divided by the total mean for the actual year.

A minimum of 250 perch were randomly sampled from the annual gillnet catches during 1982–1994 for age and growth rate studies according to standardized routines (Thoresson 1993). Total annual growth was estimated by backcalculation after measuring the distance between annuli on the left opercular bone under a stereomicroscope. Growth rates were calculated for the 3rd, 4th and 5th growth seasons, representing the main part of the adult population.

A bioenergetics model was used to estimate consumption patterns in fish of different size (Karås & Thoresson 1992). This model is based on a previously reported model for yellow perch (Kitchell *et al*. 1977), which was adjusted by introducing day-length related feeding restrictions and seasonal variations in standard metabolic rate, thereby allowing more accurate predictions for juvenile Eurasian perch (Karås & Thoresson 1992). Data on day-length calculated on the basis of the latitude, temperature, and fish size were fed to the model. The weights of fish in different length classes were estimated from weight/length relations, assuming a condition factor (Fulton's index of condition) of 1.0.

The basic model in Karås and Thoresson describes changes in biomass as a function of consumption, respiration, egestion and excretion. From this model we have constructed a curve for the distribution over the year of the maximal consumption as a function of temperature, day-length and weight; the weight was kept constant. When estimating consumption by this model the costs for respiration and swimming activity are not incorporated. The consumption values were standardized by dividing the value for each fishing occasion by the total mean for the actual year.

Adult fish were sampled in the Biotest basin and in a nearby reference area, using multi-mesh size nets, to indicate spawning time by establishing gonadal state. The samplings were made in 1981–1982 and in 1984–1987, generally once a week during the spring and early summer period. Fish were classified as developing late, spawning and spent (stages V, VI and VII, according to Kesteven 1960). The spawning period was considered to have started when the first spawning and spent fish were observed in the samples, and to be ended when stage V fish no longer occurred.

Benthic fauna were sampled in 1976–1986 in May and September–October at five stations, using a grab covering 0.025 m². Ten samples per station were collected. In 1987 the monitoring routines were changed to cover also within-year variations. Samples were collected every second month at one station, selected to represent the soft bottom habitats after analysing the time series produced by the previous monitoring. A sieve of mesh size 0.6 mm was used to extract the animals, which were identified to species and counted under a stereomicroscope. Biomass data are available only from 1983. Perch of the size classes studied prefer crustaceans as food, according to analyses of many hundreds of perch stomachs from the Biotest basin (Karås 1987). Abundance data consequently were extracted for the most common crustacean species (*Gammarus* spp. and *Corophium volutator*).

4. Results

The analyses of activity patterns were based on a total catch of 28 862 perch. The seasonal distribution of the catches was basically similar before and after the start of the heating (Fig. 2). The levels were high in summer and low in late autumn and winter. In both periods, there was a simultaneous peak in spring. The main change after the start of the power plant was that a greater part of the annual catch was made in late autumn and winter, corresponding to the period when the temperature anomaly due to heating was most marked (Fig. 3).

Catches were always highest during the nighttime fishing, which included the dawn and dusk pe-
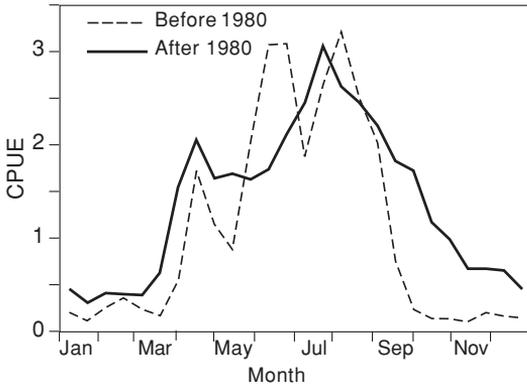
Fig. 2. Mean standardized total *CPUE* calculated for two-week periods under unheated and heated conditions. 1980, when the power plant started, is excluded.

Fig. 3. Average temperatures in the Biotest basin under unheated and heated conditions (1980, when the power plant started, is excluded).

riods, in the 1984 study. The average night-time share of the 24-h catches was about 70%. During the growth season (June–Sep.) the relation between day and night catches was rather stable, and about 75% of the catch was made during the night. There were, however, seasonal differences. Night-time catches during January–March were comparatively higher (about 85%) while they were lower in October–December (about 60%). Night-time catches thus underestimate total 24h activity most during the later part of the year.

The annual catch pattern roughly corresponded to the temperature and day-length curves (Fig. 4). A quadratic curvilinear model ($y = \beta_0 + \beta_1 T + \beta_2 T^2$) gave the best fit when mean standardized catches over all years distributed in two-week periods for the dominating size classes 12.6–22.5 cm (86% of the total catch) were related to the corresponding temperatures (Fig. 5a; $r^2 = 0.76$, $p < 0.001$). When comparing periods of similar temperatures, catches were higher in spring and summer than in autumn (Fig. 5a).

A period of high catches, deviating from the general temperature dependent pattern, was recorded in spring from the end of March to the beginning of
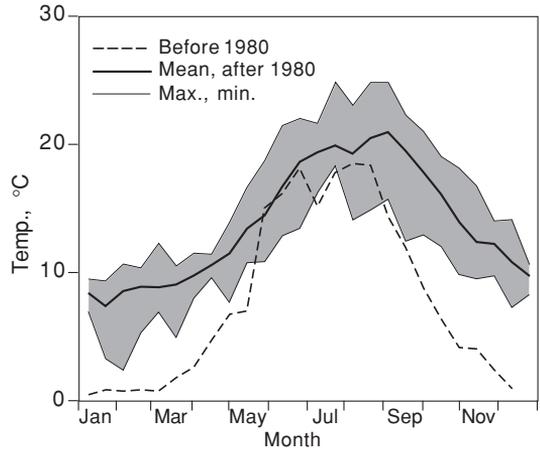
May (Figs. 4 and 5a; weeks 13–18). The pattern was consistent with catch maxima in April, except for two years when the anomaly was absent (Table 1). This spring peak appeared in temperatures varying between 1.5 and 11.4°C. To analyse the difference between the period before and after heating started, fish of the length classes 17.6–22.5 cm were selected as they were large enough to represent the sexually active part of the population also before 1980 (Sandström *et al.* 1995). The average difference in spring temperatures between the two periods was more than 5°C, but the catch maxima appeared during the same weeks (Fig. 5b and c). According to the observations of roe strings deposited on the spawning grounds by Karås (1987) and the analyses of the gonadal state of adult fish, the catch peak appeared during the spawning period. Perch spawning was generally very extended in the Biotest basin and the period of maximal spawning activity seemed to vary between years (Table 2). The sampling programme started in 1981, when heating already had begun, and conditions in the Biotest basin before

Table 1. The week when the highest total catch was recorded during the March–May period and the corresponding water temperature in the different years throughout 1978–1990. No catch maximum was recorded in 1979 and the fishing was incomplete in 1985.

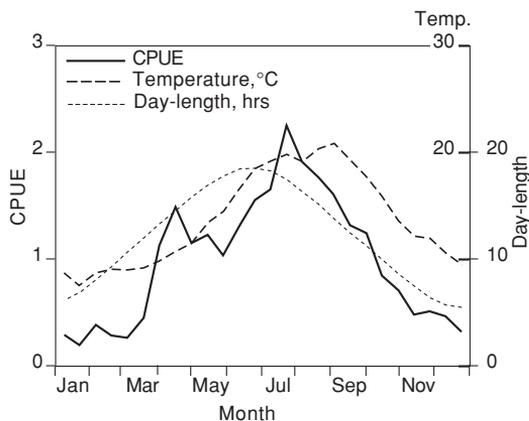| Year	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990
Week nr	15	–	15	15	15	14	15	–	14	17	14	17	17
T°C	4.8		1.5	11.0	9.9	8.9	11.0		10.2	10.5	11.2	11.4	10.6

Fig. 4. Mean standardized total *CPUE*, calculated for two-week periods under heated conditions (1981–1990), in relation to temperature and day-length.

1980 should be best illustrated by the studies made in the reference area in 1982 and 1984. Spawning was 2–4 weeks later in natural temperature, indicating that the temperature increase influenced the timing of spawning.

The analysis of the relation between catch and temperature was repeated with the spring peak period (weeks 13–18) excluded. The correlations were significant in all years for 17.6–22.5 cm fish as well as the 12.6–17.5 cm fish, which were not fully mature before 1980, except for the larger size class in 1982 (Table 3). A curvilinear function gave $r^2 = 0.91$ ($p < 0.001$) when calculated for the total material over all years. Significant regression as well occurred when catches (the spring peak period excluded) were related to day-length ($r^2 = 0.71$, $p < 0.001$).

Table 2. Beginning and end (week numbers) of the spawning period in the Biotest basin and the reference area, established by analyzing gonadal state of adult fish or by roe-string monitoring on the spawning grounds (from Karås 1987).

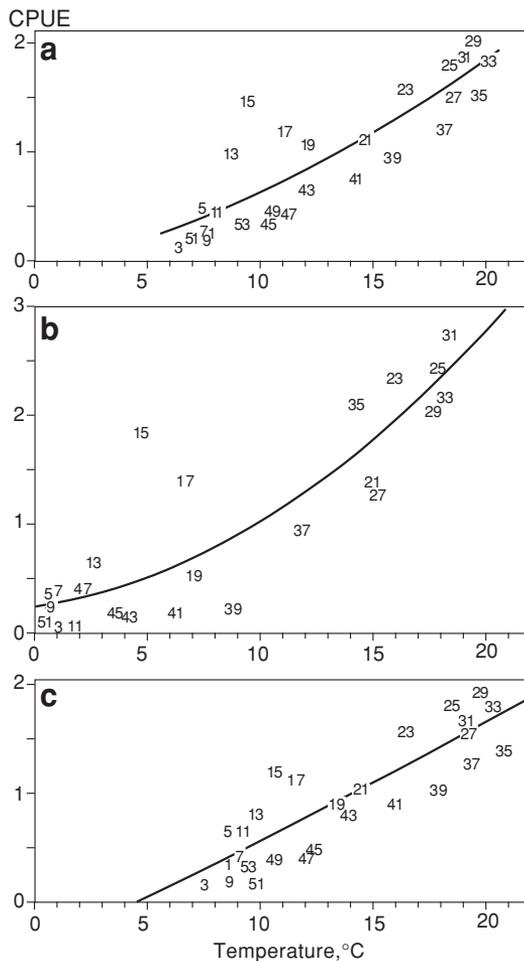| Year	Site	Method	Start	Stop
1981	Biotest basin	Adults	13	25
1982	Biotest basin	Adults	14	20
	Reference area	Adults	18	21
1984	Biotest basin	Roe strings	11	21
		Adults	15	20
	Reference area	Adults	17	22
1985	Biotest basin	Adults	15	23
1986	Biotest basin	Adults	12	18
1987	Biotest basin	Adults	12	25

Fig. 5. Mean standardized *CPUE* calculated for two-week periods in relation to corresponding mean temperatures. — a: 12.6–22.5 cm fish 1978–1990, — b: 17.6–22.5 cm fish 1978–1979, — c: 17.6–22.5 cm fish 1981–1990. 1 = week 1–2; 3 = week 3–4; 5 = week 5–6 etc.

Standardized *CPUE* data for 12.6–17.5 and 17.6–22.5 cm size classes were compared with the predicted annual consumption patterns for 15 and 20 cm (34 and 80 g) fish simulated by the model by Karås and Thoresson (1992). The relations were positive and statistically significant ($r^2 = 0.97$ and 0.94 respectively) for all years, the spawning periods excluded. Compared with the consumption curve estimated by the model, catches generally were lower in summer and higher during the rest of the year (Fig. 6a–d). The deviation between the two curves was smaller when the model was run without the reduction of winter metabolism introduced for ju-
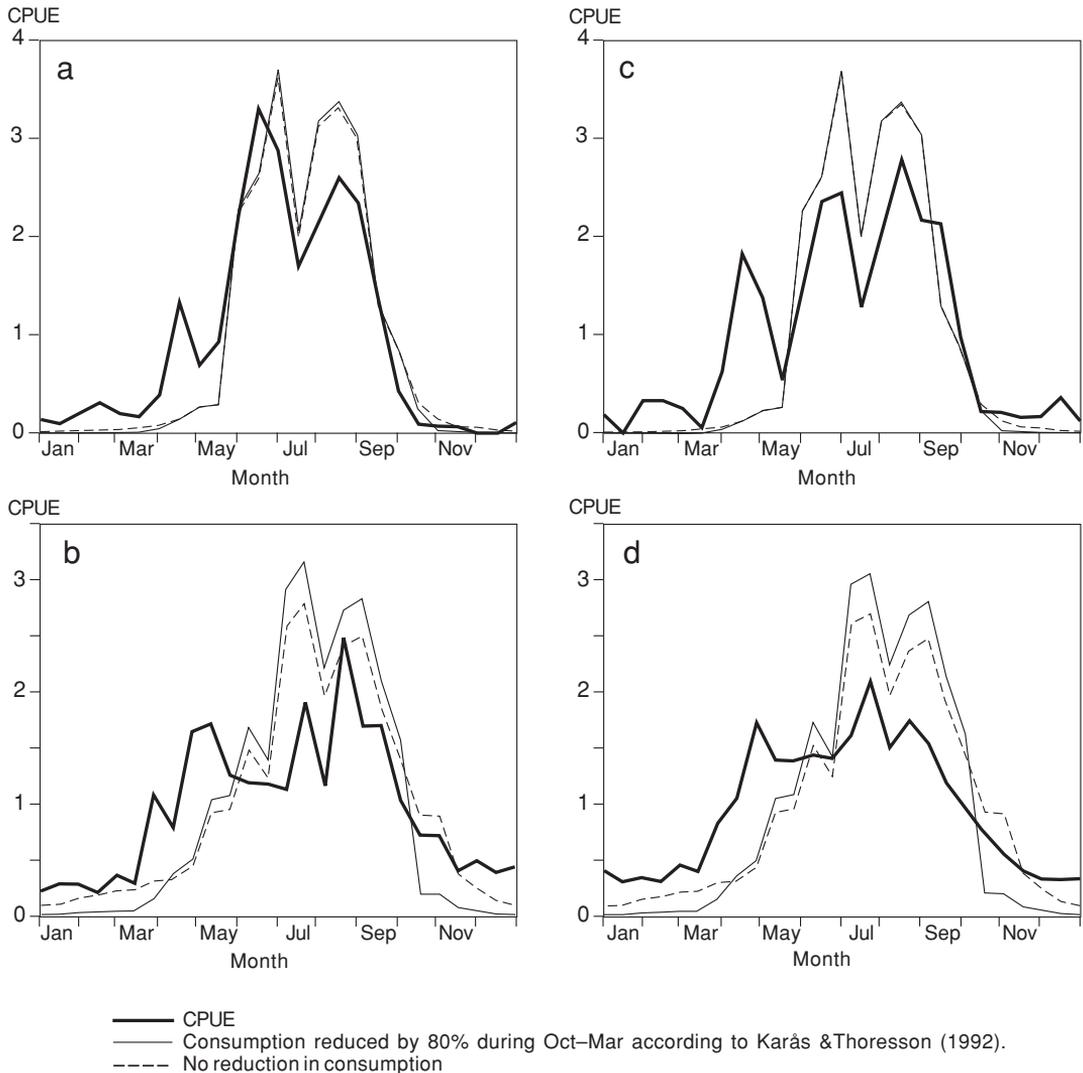
Fig. 6. Mean standardized *CPUE* in relation to consumption distributed over the year, calculated by the model of Karås and Thoresson (1992). Cpue and model curves are standardized analogously. — a: 12.6–17.5-cm fish in 1978–79. — b: 12.6–17.5-cm fish in 1987–90. — c: 17.6–22.5-cm fish in 1978–79. — d: 17.6–22.5-cm fish in 1987–90.

venile fish by Karås and Thoresson (1992), but it still remained. These differences increased under heated conditions (1978–79 compared to 1987–90, when heating was maximal), especially in autumn for the small-sized fish (Fig. 6a and b).

The mean annual growth of 3+, 4+ and 5+ perch, representing a major part of the population, varied little during the 1982–1990 period (Fig. 7). Growth was fastest in the younger fish (about 40 mm year^{-1} in 3+ compared to about 32 mm year^{-1} in 5+ fish). Statistically significant trends in annual length increase could not be detected (linear regression,

$F < 0.2$). There were no evident effects of fish abundance on annual length increase rate, when the growth data were compared with results from population studies reported by Sandström *et al.* 1995. *CPUE* increased during the study period while growth rates stayed at the same levels.

Abundances of benthic species at the selected sampling site increased after heating started, but during the following years the main prey for small sized perch, *C. volutator* and *Gammarus* spp., fluctuated strongly and often reached down to levels observed during the first years of the study period

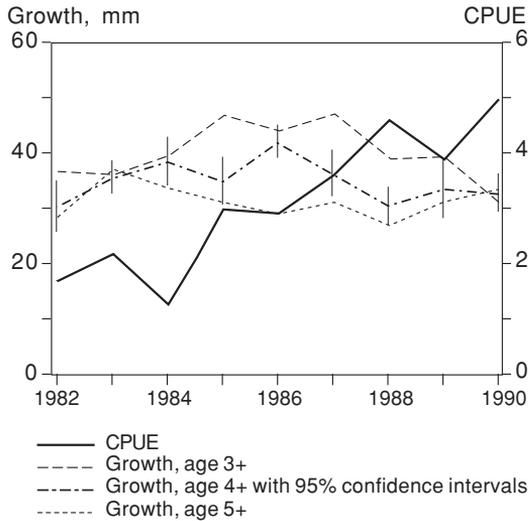Growth, mm   CPUE

Fig. 7. Standardized *CPUE* of perch in the Biotest basin (from Sandström *et al.* 1995) and annual growth for age 3+ to age 5+.

(Fig. 8). Changes between samplings were often large and indicated a considerable lack of stability also on a time scale of weeks.

5. Discussion

An annual activity rhythm with a maximum in summer and a minimum in winter and a spring peak in April was demonstrated for the perch population under study. The amount of activity,

expressed as *CPUE*, was correlated to both temperature and day-length. Although temperature effects seemed to be most important to produce a seasonal activity rhythm, the influence of day-length was clearly visible. Temperature and day-length were not in phase, as the temperature rhythm lagged behind the light curve. Swimming activity, measured as *CPUE* in the sampling pro-gramme, consequently was lower in autumn when compared to spring and summer in identical temperatures. Parts of this difference, however, should be an effect of the lower share of 24-h activity recorded during night-time fishing in autumn.

The annual rhythm as well as the temperature dependence remained mainly unchanged when the heating started, corresponding to the observations by Neuman (1979) in another heated effluent. The only year lacking a significant temperature correla-tion in the Biotest basin was 1982, when the catch pattern was disturbed by an extremely high adult mortality (Sandström *et al.* 1995). The spring peak occurred roughly the same time in all years in spite of big temperature differences, which indicates that its position was not affected by the temperature level. As the spring increase in temperature and day-length in most years occurred almost simultaneously, the temperature change may have triggered this superactivity. Sandström (1983), however, found that the swimming capacity in perch increased in March–May in constant light and temperature and that there was an endogenous background to the annual swim-

Table 3. Statistics of the relationships between standardized *CPUE* (the spring peak periods excluded) and temperature during the period 1978–1990.

Year	12.6–17.5 cm			17.6–22.5 cm		
	F	*P*	*r*²	*F*	*P*	*r*²
1978	54.0	< 0.001	0.75	34.2	< 0.001	0.66
1979	61.5	< 0.001	0.75	105.7	< 0.001	0.84
1980	32.0	< 0.001	0.63	94.6	< 0.001	0.83
1981	57.4	< 0.001	0.75	37.4	< 0.001	0.66
1982	12.6	< 0.010	0.38	0.0	> 0.050	0.00
1983	29.2	< 0.001	0.58	14.9	< 0.001	0.41
1984	36.2	< 0.001	0.64	21.8	< 0.001	0.52
1985	26.5	< 0.001	0.61	13.7	< 0.010	0.45
1986	36.3	< 0.001	0.68	74.1	< 0.001	0.81
1987	18.2	< 0.001	0.48	40.1	< 0.001	0.67
1988	42.3	< 0.001	0.73	110.7	< 0.001	0.87
1989	40.5	< 0.001	0.70	12.3	< 0.010	0.42
1990	65.7	< 0.001	0.79	5.40	< 0.050	0.24

Ind/m²

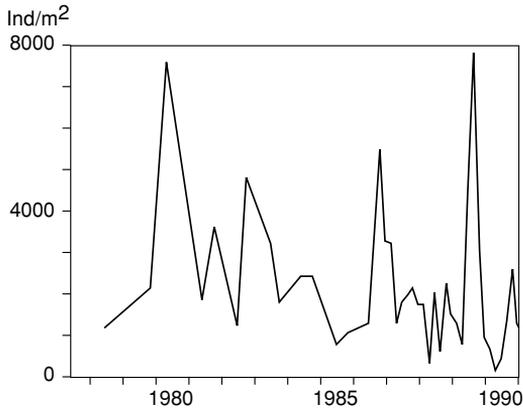

Fig. 8. Pooled abundances (numbers per m²) of *Gammarus* spp. and *Corophium volutator* on a benthic macrofauna monitoring station in the Biotest basin. Samplings were made in May and September–October in 1976–1986, and once every second month in 1976–1990.

ming activity rhythm. That the spring peak should be synchronized by day-length rather than by temperature thus seems more likely.

Superactivity during the spawning period has been documented in the laboratory (Eriksson 1978) as well as in the field (Neuman 1979). The increased swimming activity in spring observed in the Biotest basin also seemed to be related to spawning, as it occurred during the spawning period. This period, however, was very extended and seemed to be sensitive to between-years variations when compared to the activity peak, which was much more consistent in time and less extended in length. Consequently, swimming activity and the actual spawning may be triggered by different environmental cues. It is also obvious that reproduction brakes the apparently simple relation between activity and temperature and day-length existing during most of the annual cycle.

There was a high and consistent correlation between catch data from the Biotest basin and the annual consumption pattern simulated by the Karås and Thoresson (1992) model, in fact higher than the correlation with either temperature or day-length. This indicates a strong connection between swimming activity and consumption and supports Kerr's (1982) assumption that foraging explains most of the locomotor activity. The high correlation would be unlikely if it only constituted a minor part. However, the catch levels differed less between seasons than the model predicted. If we assume that the catches mirror the annual consumption pattern correctly, the model is overestimating the consumption in the summer and/or underestimating it during the rest of the year. Karås and Thoresson (1992), testing their model on growth data from perch from the Biotest basin, found evidence for a rather strong limitation of consumption during summer. If this is considered as the only deviation, and the curves are adjusted so that summer levels correspond, the difference would be unreasonably big during autumn and winter (Fig. 6). In the model of Karås and Thoresson (1992), consumption is reduced with 80% in October–March in addition to the restrictions caused by low temperatures and short day-lengths. This reduction was based on growth studies of juveniles. Our catch data, however, mainly provide information on adults. Sexual maturation has profound effects on, e.g., metabolic activity. In spring-spawning fish, like perch, the adults must support a growing gonad during autumn and winter. This is made possible by a dramatic change in hormonal climate, affecting physiology and likely also consumption rates.

Before the heating started, small fish (12.6–17.5 cm) seemed to be less active in autumn and spring than larger fish (17.6–22.5 cm), thus following the model more closely. This difference disappeared when heating started. Temperature, however, affects sexual maturation. In these Baltic waters most perch in the smaller size class (80–90% of the females) are juvenile under natural conditions, while a majority have reached maturity in the heated basin (Sandström *et al.* 1995). The main reason for the high catches in autumn and winter compared with the model may thus be that mature fish have large energetic commitments to reproduction during this season, forcing them to keep up consumption and hence their locomotor activity which is not necessary for the juveniles.

Boisclair and Leggett (1989b) conclude in their study on growth and consumption in yellow perch that locomotor activity costs account for a large and variable fraction of the total energy budget, and that swimming in an individual is related to social interactions and thus depends upon total fish density. Data from the Biotest basin were used in a further test of this hypothesis. Recruitment was improved in the studied perch population (Karås 1987) after 1980 and the long-term gillnet monitoring during 1978–1990 (Sandström *et al.* 1995) suggests a continuous and approximately linear nearly 10-fold increase in perch

abundance. Other species also became more numerous, and the total *CPUE* increased from about 20 fish to about 150 at the end of the period (Sandström 1990). These data, however, should be interpreted with some caution, as the initial temperature increase affected swimming activity and hence also *CPUE* data to an unknown extent. After 1980 there were no trends in temperature conditions, and the results present a more unbiased estimate of the population development.

There was a marked peak in benthic fauna abundances some years after the heating started, and the total biomass decreased from a maximum of about 100 g m^{-2} in 1985–87 down to 10–20 g m^{-2} in 1990 (Sandström 1990). Most of this biomass maximum was related to a strong development of the gastropod populations, species not eaten by perch (Karås 1987). Abundances of the major prey species, *Gammarus* spp. and *C. volutator*, indicated no trend in food abundance, and they fluctuated strongly and irregularly. Small fish could be alternative prey during periods of low benthic fauna production. Perch of the size groups studied, however, only consume small amounts of fish (Karås 1987), and the annual monitoring suggests a decrease of suitable prey fish like young cyprinids (Luksiene & Sandström 1994), sticklebacks and gobies (Sandström 1990). Consequently, the abundances of perch and other fish of similar size increased very much during the studied 13 year period, while there was no evident trend in prey abundances. A significantly increased allocation to swimming activity caused by the increased social interactions resulting from the higher abundances thus would produce a negative trend in perch growth rate (Boisclair & Leggett 1989b). As growth rates did not significantly decrease over time, strong density dependent variations in swimming activity seem less likely. Our results consequently differ from the observations made in Canadian lakes by Boisclair and Leggett (1989b).

There were no indications that swimming activity levels in relation to temperature decreased as temperature increased, as was suggested by Koch and Wieser (1983) and Mehner and Wieser (1994), and a saving of energy during shorter periods of high temperatures by allocating less to locomotion seemed unlikely from our data. On the contrary, the concave shape of the relation between standardized *CPUE* and temperature rather indicates that superactivity may be induced at the highest temperatures experienced during the studies.

As a conclusion this study demonstrated a strong seasonal pattern in swimming activity in perch. A well defined spring peak period could be identified, with strong coupling to day-length as it appeared during the same weeks although water temperature differed very much between years. Within the limits studied, fish size had little effects on the results, and when deviations appeared they could be explained by the influence of sexual maturation. The assumption that swimming during most parts of the year is linearly related to feeding could not be contradicted, and apart from the spawning period social interactions seemed to be of minor importance as a source of variations of the activity levels.

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