Freshwater Biology (2002) **47**, 2370–2379

Activity and food choice of piscivorous perch (*Perca fluviatilis*) in a eutrophic shallow lake: a radio-telemetry study

LENE JACOBSEN, SØREN BERG, MADS BROBERG, NIELS JEPSEN and CHRISTIAN SKOV
Danish Institute for Fisheries Research, Department of Inland Fisheries, Vejlsøvej, Silkeborg, Denmark

SUMMARY

1. Radio transmitters were implanted in large perch (27–37 cm) in a shallow lake in Denmark. Between 6 and 13 perch were tracked every 3 h for 24-h periods twice (summer) or once a month (winter) from August 1997 to July 1998. Activity levels were recorded as minimum distance moved per hour.
2. No significant differences in activity levels of individual fish were observed.
3. Highest activities were observed at daytime with peaks at dawn and dusk or midday. This diel pattern was most pronounced from October to April, whereas diel variations were less in the summer months, with no peaks occurring in midsummer. The general lack of activity at night supports the idea that perch is a visually oriented forager.
4. There was no significant relationship between daytime activity during the year and temperature or day length, but nighttime activity was correlated with temperature. In contrast with previous findings, activity levels varied little seasonally, except for high activity levels that occurred concomitantly with high temperatures in August. Instead, we found a significant relationship between the total distances moved per day and temperature, indicating that perch moved at the same average speed in the wintertime, but did so for shorter periods than in summer because of shorter day lengths.
5. Diet of the tagged perch shifted from fish dominance between August and January to invertebrates from February to June. There was no correlation between the diet shift and activity levels, indicating that feeding on invertebrate requires similar activity levels as predation on fish.
6. The results of this telemetry study throughout a year suggest that perch are more active during the winter than previously inferred from gill-net catches. This observation underscores the importance of perch as a predator of 0+ planktivorous fish in lakes and has potential implications for pelagic food web structure and lake management by biomanipulation.

Keywords: fish activity, fish behaviour, food choice, perch, telemetry

Introduction

Perch is a common fish species in European lakes (Thorpe, 1977), occurring, for example, in >95% of all Danish lakes, where it often accounts for a substantial part of the fish number and biomass (Jensen *et al.*, 1997). The diel and seasonal activity of perch (*Perca fluviatilis* L.) has been the subject of several studies. In general, the species has been found to be active during the day, with activity peaks during dusk, dawn and at midday (Craig, 1977; Alabaster & Stott, 1978; Eriksson, 1978; Mackay & Craig, 1983; Rask, 1986; Huusko, Vuorimies & Sutela, 1996), depending on time of the year. Seasonal activity has been found to

Correspondence: Lene Jacobsen, Danish Institute for Fisheries Research, Department of Inland Fisheries, Vejlsøvej 39, 8600 Silkeborg, Denmark. E-mail: lj@dfu.min.dk

show a maximum in summer and a minimum in winter (Craig, 1977; Eriksson, 1978; Neuman, Thoresson & Sandström, 1996). Some authors have correlated activity with temperature (Eriksson, 1978; Huusko *et al*., 1996) or light (Craig, 1977; Alabaster & Stott, 1978).

The diet of perch is variable, comprising zooplankton, benthic invertebrates and fish. Perch often undergoes one or two ontogenetic diet shifts during its development (Johanneson & Persson, 1986), but it has not been possible to set straight rules for the size or age at which these shifts occur. For example, specimens larger than *c*. 15 cm may feed on either fish or benthic invertebrates (Craig, 1978; Persson, 1983; Berg *et al*., 1994). As a piscivore, perch generally preys on the 0+ age group of fish, caused by gape limitation (Holcik, 1977; Benndorf, 1990). Large perch is an active hunter seeking its prey, both fish and invertebrates, in open water rather than in vegetated areas (Craig, 1978).

Perch can, together with other piscivores such as pike (*Esox lucius* L.), be an important factor in controlling the density of 0+ fish during summer (Berg, Jeppesen & Søndergaard, 1997). Perch is an effective piscivore in clear-water lakes and less effective under turbid conditions. Boisclair & Rasmussen (1996) found a negative correlation between perch growth and total fish density across lakes of varying trophic state, indicating that under turbid conditions, perch is unable to exploit a high density of prey fish effectively. In accordance with this observation, perch populations in Danish lakes have been found to be negatively affected by eutrophication, with both reduced total perch biomass and average body weight as indicators of reduced growth (Jeppesen *et al*., 2000). Thus, the establishment or sustenance of a perch population that effectively preys on 0+ cyprinids, might be an important component of successful lake management. However, because of the complex activity patterns and ontogenetic diet shifts of perch, the successful use of the species in lake management requires precise knowledge on activity patterns and feeding behaviour (Berg *et al*., 1997).

Most previous studies on perch activity have been based on catches in gill-nets, other types of fishing gear, or laboratory experiments (e.g. Craig, 1977; Sandström, 1983; Rask, 1986). Radio-telemetry is an alternative technique, which has become widespread during the last 20 years (Nielsen, 1992). Radio-telemetry overcomes some of the disadvantages of most fishing gears and makes it possible, in particular, to follow the behaviour and activity of individual fish for extended periods, including periods when fish are inactive or habitats are inaccessible for fishing (Jepsen *et al*., 2001). Mackay & Craig (1983) used radio-telemetry on eight perch to describe the diel activity pattern of the species in summer, but no data are available for a whole annual cycle.

The aim of this study was to elucidate the behaviour and activity levels of large perch as potential fish predators on a diel basis throughout a whole year. Activity was related to food choice and environmental factors. The study was conducted in a lake with high water transparency and a predator-dominated fish community. Perch is known to show high growth rate and form a large part of the fish biomass in this lake. Thus, the results were expected to reflect the behaviour of a well-established, dominating perch population.

Methods

Study area

Lake Ring is a shallow, eutrophic lake situated in Mid-Jutland, Denmark (Berg *et al*., 1994). The lake covers 22.5 ha, has a mean depth of 2.9 m and a maximum depth of 5.0 m. Before 1987, mean summer Secchi depth was constant at 1.0 m. During 1988 and 1989, Secchi depth increased to almost 3.0 m and has been fluctuating between 1.5 and 3.0 m since. In spite of the high water transparency recorded in the last 10 years, the phosphorus level in the lake is high (mean summer total phosphorus concentration of 290 µg P L^{-1} in 1997), indicating that algal growth is nitrogen-limited (870 µg N L^{-1} in 1997). The fish population is dominated by the potentially piscivorous species perch, pike and eel (*Anguilla anguilla* L.). Minor populations of roach (*Rutilus rutilus* L.), burbot (*Lota lota* L.) and whitefish (*Coregonus lavaretus* L.) are present. The fish fry found in the lake during summer is almost exclusively perch (Berg *et al*., 1994). During summer, *c*. 20% of the lake area is covered with macrophytes, mainly *Potamogeton pectinatus* L. Reed belts consisting of *Phragmites australis* eL Trin. ex. Steud and *Typha* sp. are present along the shores. Several peaks of very high densities of zooplankton occur regularly during summer.

Radio transmitter implantation

In June 1997, 11 large perch (27–37 cm, 341–847 g) were caught in Lake Ring using gill-nets (mesh size: 46 mm) set for a maximum of 1.5 h. The perch were gently cut out of the gill-nets, to avoid damage to the fish. The perch were brought to the shore and anaesthetised in a 5-mg L^{-1} solution of Methomidate (Marinil™, Wildlife Laboratories Inc., Fort Collins, CO, U.S.A.) until the opercular rate became slow and irregular (5–6 min^{-1}). The radio-transmitter was inserted in the body cavity through a 10–12 mm incision anterior to the pelvic girdle. The antenna was run through a small hole from the body cavity, pierced with a blunt needle. The incision was closed with two separate sutures. Finally, body length and weight of the perch were measured. The duration of the operation was between 3 and 5 min. Immediately after tagging, the fish were released back into the lake in a shallow sandy area. Here the perch were observed until they regained consciousness and swam off.

Transmitters used were cylindrical ATS model 10–28 (10 × 30 mm, weight 7.3 g, battery life >180 days, pulse rate 30 per min, exterior antenna). Weight of the transmitter was between 0.9 and 2.3% of the body weight of the perch. Only three fish had a transmitter/body weight relation exceeding 2%, which is the limit generally recommended (Winter, 1983). Frequencies ranged from 142.010 to 142.339 MHz; transmitters were tuned to be at least 0.01 MHz apart. New perch were tagged when transmitters ran out of power or if one of the radio-tagged perch was caught by anglers or found dead. As a result, a total of 29 perch was marked during the study period and between 6 and 13 perch were monitored during all tracking periods.

Tracking

During the period August 1997 to July 1998, all radio-tagged perch were monitored by positioning each of them every 3 h over a 24-h period once (winter) or twice a month (summer). Radio-tracking was carried out from a boat using a handheld antenna. Perch were positioned by locating the boat over or very close to the fish and then logging and storing the position in a Differential Global Positioning System (DGPS) navigator (Trimble Pathfinder® TDC1, Trimble Navigation Ltd., Sunnyvale, CA, USA, accuracy: ±5 m). From the nine positions during a 24-h period, eight distances were measured for each fish on digital maps using the Pathfinder Office® (Trimble Navigation Ltd.) and MapInfo® (Mapinfo Corporation, Troy, NY, USA) computer programs. These were used to calculate the minimum distance moved in the 3-h tracking period for each fish. Distance moved during one tracking interval was converted to *minimum distance per hour* (*minimum activity*). This conversion was chosen because the fish are unlikely to swim in a straight line between two tracking points and because the period between two trackings of the same fish were not exactly 3 h.

Water temperature was measured once during each 24-h period. The 24-h period was always identified with the starting date and the individual fish with the last three digits in the frequency of the implanted transmitter (e.g. '049' for the perch with the transmitter at the frequency 142.049 MHz).

Food choice

Large perch were caught for stomach analysis at monthly intervals, with the exception of December 1997 and March 1998. If possible, all samples were taken during a 24-h tracking period. On each date, 10–26 large perch were caught in 46-mm mesh-size gill-nets set for 1–3 h during daylight hours. The perch were gently cut out of the nets and their stomach contents were pumped out and preserved in 70% ethanol. Subsequently, the perch were released back into the lake.

In the laboratory, the prey items in each stomach were determined to species or group. For invertebrates, all specimens of the same species or group were weighed together as wet weight and corrected for loss of weight when preserved in alcohol according to Wiederholm & Eriksson (1977). For fish prey, the degree of digestion was determined according to Fickling & Lee (1981) and for partly digested fish the original length of the fish was determined based on measures of three abdominal vertebrae (Wise, 1980). Fresh weight was calculated from length using the length–weight relation of prey fish caught by electrofishing (perch fry; $n = 40$; total length: 63–85 mm). Fresh weight of stomach contents, weight of or number of prey fish in the stomachs was used to compare diet with activity levels throughout the year.

Statistics

Differences in diel mean minimum activity levels between individual fish during all trackings in 6 months were evaluated with a Kruskal–Wallis test (Siegel & Castellan, 1988). Differences in activity of the radio-tagged perch among four time periods of the day during the whole year were tested by Kruskal–Wallis tests followed by pair-wise comparisons (Mann–Whitney *U*-tests). *P*-values were corrected by the Dunn–Sîdák method (Sokal & Rohlf, 1995). The dependence of mean minimum activity of perch during day and night time with temperature, day length and diet changes were tested by linear regression analyses, as was the total distance moved during daytime and nighttime. All statistics were computed in Statgraphics plus 4.1® (Manugistics, Inc., Rockville, MD, USA).

Results

A total of 16 successful 24-h tracking periods were carried out between 7 August 1997 and 16 July 1998 (Fig. 2, Table 1). There were minor gaps in the data-set for a few of these 16 periods, because of difficulties with equipment or bad weather conditions; eight tracking periods were rejected from data analysis, because these problems resulted in insufficient data. A total of 977 distances between tracking points was recorded.

Activity of individual fish

The longest distance recorded between two tracking points was 694 m in 2.5 h, approximately three-fourths of the total length of the lake, whereas another fish moved hardly at all (7 m) during the same tracking interval. Movements <10 m between two trackings were most frequently recorded during night.

For nine individual fish that were tracked for at least 6 months during the experiment, mean minimum activity for all trackings (all dates, days and nights) are shown in Fig. 1. There appeared to be individual differences in activity levels recorded

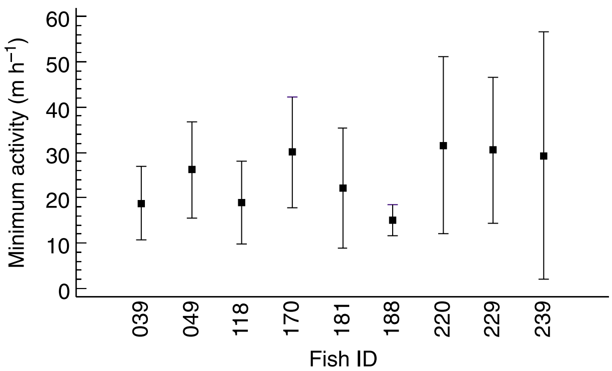

Fig. 1 Mean individual minimum activity of nine radio-tagged perch during 5–10 tracking periods over 24 h. Fish ID or 'name' on the *x*-axis refers to the frequency of the transmitter in the fish. Vertical bars indicate 95%-confidence limits.

Table 1 Results of Kruskal–Wallis tests showing differences in activity of radio-tagged perch between four different periods of the day

Date	07/08 1997	13/08	03/09	01/10	29/10	10/11	26/11 1997	21/01 1998	18/02	18/03	15/04	29/04	14/05	27/05	16/06	16/07 1998
Number of fish	8 (7)	8	9 (8)	9 (3)	9 (8)	9 (8)	9	8	6	6	6	13 (12)	6	10	7	7 (6)
P-value of Kruskal–Wallis test	0.004	0.07	0.55	0.74	0.001	0.001	0.014	0.005	0.002	0.005	0.014	0.24	0.012	0.1	0.89	0.23
Pair-wise comparisons																
Midnight versus dawn	ns*	ns	ns	ns	–	ns*	0.000	0.024	0.03	ns*	–	ns	ns*	ns	ns	ns
Midnight versus midday	0.012	ns	ns	ns	0.018	ns	ns	0.018	0.048	ns*	ns	ns	ns*	ns	ns	ns
Midnight versus midday	0.018	ns	ns	ns	0.000	0.006	ns	ns	0.030	0.030	0.003	ns	ns*	ns	ns	ns
Midday versus dawn	ns	ns	ns	ns	–	0.018	0.204	ns	ns	ns	–	ns	ns	ns	ns	ns
Midday versus dusk	ns	ns	ns	ns	ns	0.006	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Dawn versus dusk	ns	ns	ns	ns	–	ns	ns	ns	ns	ns	–	ns	ns	ns	ns	ns

P-values of the pair-wise comparisons, shown in the lower part of the table, are corrected according to the Dunn–Sidak method. Dash indicates missing data. Numbers in parentheses means that lower fish numbers were available for some periods of the day.
ns, not significant. ns*, significant before correction.

between these nine fish, which were not related to length of the fish or any other grouping criterion. These differences were not significant, however (Kruskal–Wallis test, KW = 7.9, $P = 0.44$) (Fig. 1). For the least and most active individuals, the mean minimum activity was 15.1 m h^{-1} (fish no. 188) and 31.5 m h^{-1} (fish no. 220), respectively.

Diel activity patterns

Distance moved also varied between different times of the day (Fig. 2). The most consistent result was lower activity during night (defined as the tracking period 23–02) compared with midday (11–14) and dusk and dawn (varying tracking-periods during the year according to day length) (Table 1). On eight dates, there was no significant diel variation, but on the rest of the dates, almost all significant results were found in the comparison of midnight to one or more of the other three periods of the day (Table 1). This result was almost exclusively seen during the winter (29 October to 15 April) when nights are longer than days. Very little significant diel variation was found during the summer (Table 1). On one occasion (14 May), there was a significant difference in diel activity, but the pair-wise comparisons did not retain sufficient power to detect the in-between differences, although they also indicated lower activities during the midnight period. Even when no significant difference was found, the lowest activity was almost always recorded around midnight during all 24-h periods (Fig. 2).

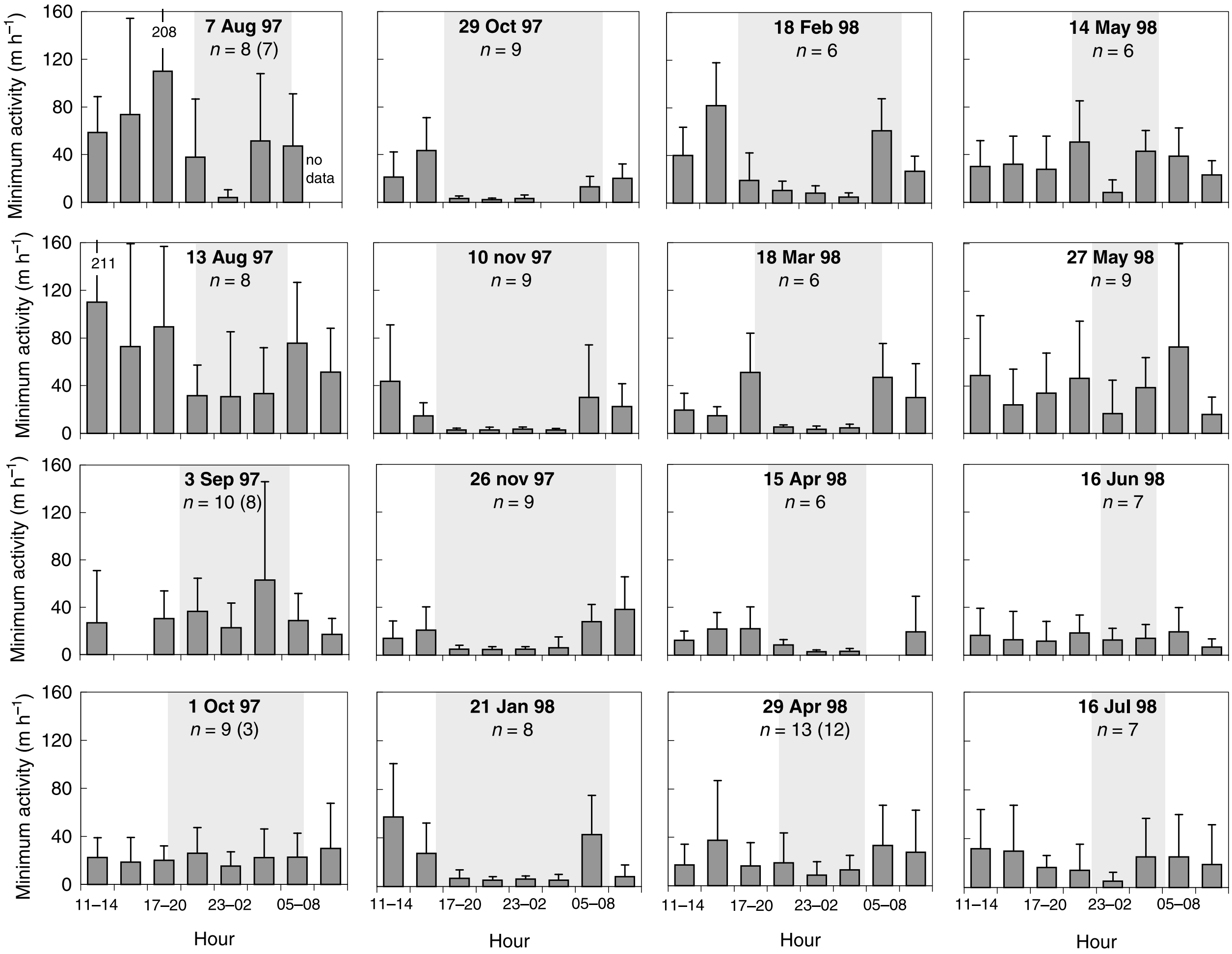

Fig. 2 Minimum activity of radio-tagged perch in Lake Ring during 16 tracking periods over 24 h from August 1997 to July 1998. Bars indicate the mean distance moved by the perch per hour during 3-h tracking periods. No data are available when bars are missing. Vertical bars indicate standard deviations and the shaded areas indicate the period from sunset to sunrise.

Activity peaks were often seen at dusk and dawn compared with midday (Fig. 2); however, none of these peaks were significant (Table 1). The activity recorded at midday appeared to be higher than at dusk and dawn on a few dates (Fig. 2), although this difference was only significant on 10 November. There was no significant difference between activity at dusk and dawn.

Seasonal activity patterns

Very high temperatures and high mean minimum activities per hour were recorded in August 1997 during both day and night (Fig. 3a). Activity levels were reduced when temperature decreased in September, but in both September and October, night activity was still as high as the activity during the day.

An activity peak was found in February 1998 following a rise in temperature from 1.8 °C on 21 January to 5.6 °C on 18 February. Apart from this increase, there appeared to be no seasonal trend in the mean minimum daytime or nighttime activity during the rest of the investigation period (Fig. 3a). No significant relationship was detected between the minimum activity per hour during the day and temperature ($r^2 = 0.18$, $P = 0.10$) or day length ($r^2 = 0.01$, $P = 0.66$). However, night minimum activity showed a significant positive relationship with temperature ($r^2 = 0.33$, $P < 0.05$), although not with day length ($r^2 = 0.08$). When calculating the total minimum distance recorded during all day and night trackings, respectively (Fig. 3b), we found a significant relationship between temperature and the total minimum distance moved during daytime ($r^2 = 0.48$, $P < 0.01$). There was no significant relationship of total minimum distance moved during daytime with day length ($r^2 = 0.21$, $P = 0.07$), nor of total minimum distance moved during the night with day length or temperature ($r^2 < 0.09$).

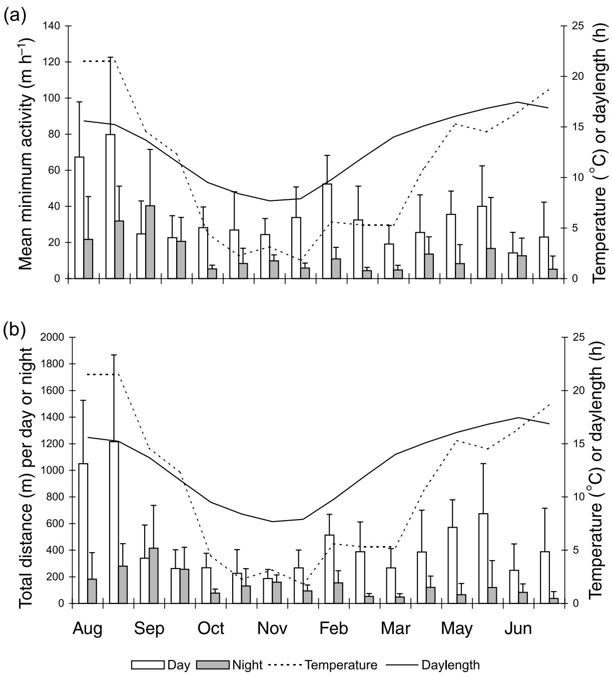

Fig. 3 Mean activity per hour (a) of and total distance moved (b) by large radio-tagged perch in Lake Ring during 16 tracking periods over 24 h from August 1997 to July 1998. All bars represent the mean of 6–13 individual perch. Vertical bars indicate standard deviations. Day length and water temperature are also shown.

Food choice of large perch

A total of 186 stomachs of large perch (25.5–37.5 cm) were analysed. Only eight (4.3%) were empty. The perch fed on both fish and invertebrates (Fig. 4). The dominant invertebrate prey and prey item by number were Chironominae larvae and pupae, with a mean of 104 per stomach. More than 99% of the fish prey eaten were 0+ perch. Fish were found to dominate the stomach contents by weight from August to January. From February to June, invertebrates were the dominating prey item. In July, fish prey reappeared in the stomachs (Fig. 4).

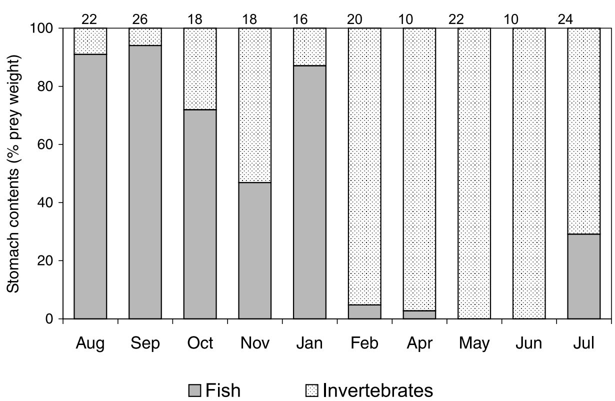

Fig. 4 Proportions of fish and invertebrates in the diet of large (25.5–37.5 cm) perch from Lake Ring between August 1997 and July 1998. Figures at the top of bars indicate the number of fish analysed at each date.

No significant relationship was found between day or night mean activity per hour or total activity (distance moved per day) (Fig. 3) and the wet weight of stomach contents, or the weight or number of prey fish in the stomachs.

Discussion

The main premise for using radio-telemetry is that the tagging does not affect the behaviour and growth of the animal (Jepsen, 1999). In the present study, almost all fish recovered from the tagging after 10 min or less and behaved normally at the following tracking session, usually more than a week later. Fish caught by anglers or during sampling of perch for stomach analysis showed the incisions to be healed up. In the perch examined, we found the transmitter in the body cavity incorporated in fat tissues. Recaptured tagged fish showed normal growth. One tagged fish showed an increase in weight from 787 to 1100 g, when caught by an angler 22 months after release. Another recaptured perch (no. 239 in Fig. 1) increased its weight from 358 to 862 g in 13 months. The flushed stomachs of five tagged perch contained both fish and invertebrates, as those of untagged fish, and two of the perch that were released into the lake again, acted normally on subsequent tracking sessions. Based on these observations, we conclude that the radio-tagging of large perch had little or no permanent effect on fish behaviour and growth after a short recovery period lasting <1 week.

Activity levels obtained by telemetry using 3-h tracking intervals reflect the minimum activity level during the period. Direct measurement of speed cannot be made, as the fish do not move in a straight line between two tracking points. The apparent activity level can also be restricted by lake size, a 900-m distance at most in the present study. In smaller lakes, perch can cross the entire lake and change direction when reaching the other side during a 3-h period (Mackay & Craig, 1983). To overcome this problem, Mackay & Craig (1983) tracked the fish more frequently (i.e. at 30-min intervals) during high-activity periods. The maximum mean activity found in this way was 33 m h^{-1} in June and 8 m h^{-1} in August. These activity levels are comparable with the maximum activity found in the present study in June and July (18 and 32 m h^{-1}) and lower than the highest activity level found in August (110 m h^{-1}). Furthermore, we found that 94% of the 977 recorded distances between two tracking points were <300-m long and all mean distances were below 120 m h^{-1} (Fig. 2). Thus, it is unlikely that the size of Lake Ring seriously affected our estimates of diel activity levels recorded every 3 h, as has been found in previous studies (Craig, 1977; Rask, 1986). The finding of no significant variation in activity level between the individual perch suggests that data from the individual fish can be used to draw conclusions on the whole population of large perch in the lake. However, the variation in activity of individual fish should be borne in mind, when making inference from telemetry results.

The lack of correlation between fish activity and length might be because of the intended rather small length variation of the tagged perch (27–37 cm). A correlation between distance moved and body length has been observed for pikeperch (*Stizostedion lucioperca* (L.)) (Jepsen, Koed & Økland, 1999), although the range of lengths in those fish were not larger than in the present study (62–74 cm for females, 55–64 cm for males). During operations and recaptures of the perch in the present investigation, it was not possible to determine the sex of the fish. However, a size-dependent difference in activity within each sex is unlikely, as there was no grouping of the individual activity levels. The diel activity rhythm of perch generally confirms previous studies (Craig, 1977; Alabaster & Stott, 1978; Eriksson, 1978; Mackay & Craig, 1983). As found by Craig (1977), we observed that the difference in day and night activity with noticeable peaks at dusk and dawn is most pronounced in fall, winter and early spring (October–April). Craig (1977) also observed the lack of difference in diel activity at midsummer (June and July), although Mackay & Craig (1983) found a diel activity rhythm in June in a single radio-tracked perch. The general lack of activity peaks in summer might be related to the rather few dark hours at midsummer at the present latitudes (54–58°N); from 5 May to 7 August the sun never exceeds 6° below the horizon. Craig (1977) suggested that light intensity is optimal for perch only during dawn and dusk, and light intensities both below and above this value reduce activity. Our results do not support this conclusion, as significant differences between dusk–dawn and midday were found on only one date, where maximum activity occurred at midday. Tendencies towards higher activities during dawn and dusk were only seen during winter. A reason for activity rhythms could be diel changes in food. Perch might be feeding whenever food is available during daylight hours.

Night activity in September and the almost invariant diel activity differences in October have no clear explanations, but show the large variation in diel activity pattern during the summer. Some night activity in summer has also been observed by Mackay & Craig (1983). The generally very low night activity on almost all tracking-occasions nevertheless confirms the contention that perch is a visual hunter (Bergman, 1988; Diehl, 1988). This conclusion of course is based on the assumption that swimming activity mainly represents feeding activity (Kerr, 1982).

The annual activity rhythm shows some variation to the commonly observed activity pattern in relation to temperature regimes. The minimum activity level during the daytime fluctuated over the year, but was not related to changes in temperature, except that high temperatures in August 1997 coincided with a very high activity during both day and night. This result contrasts with findings by Craig (1977), Neuman *et al*. (1996), Sandström (1983) and Eriksson (1978), who reported temperature- and daylength-dependent activity with variable relative importance of the two factors. Nevertheless, daytime activity correlated with nighttime activity, which again followed temperatures, so activity showed some associations with the temperature regime. Perch has been found to prefer temperatures of around 21 °C (Thorpe, 1977) and is therefore expected to be most active in summer. However, the rather low activity in summer [June and July, in the present study; Neuman (1979)] indicates that activity level can be determined by other factors than temperature.

The decrease in activity in spring might be as a result of spawning, given that perch normally spawn in late April in Denmark. Gathering in spawning areas will not include any migration in a smaller lake such as Lake Ring, hence swimming activity is probably reduced during spawning. In contrast, high activity may occur during the spawning period in coastal areas because of extended migratory behaviour (Neuman *et al*., 1996).

The significant relationship of temperature with total distance moved during daytime but not with the mean activity (minimum distance per hour) indicates that perch cover shorter distances in the wintertime because they spend fewer hours swimming. Perch thus appear to be able to meet their food requirements in a shorter time in the wintertime. This assumption seems reasonable because food requirements are lowest at low temperatures (Karås & Thoresson, 1992) and gastric evacuation rates increase as temperature decreases (Persson, 1979). A rise in activity at dusk may reflect the need to fill the stomach before a dark period of up to 17 h.

There was no direct link between diet shifts and activity levels. Although the diet of perch showed a remarkable shift from almost exclusively fish from August to January to benthic invertebrates from February to June, no corresponding shift in activity levels was observed. Preying on fish therefore does not appear to lead to an overall increase in swimming activity compared with feeding on benthic invertebrates. This finding may be related to the greater energy intake per food item when feeding on fish, so that more time is spent feeding when the diet consists of invertebrates. Another explanation for the lack of correlation between food choice and activity might be that the activity of perch is only in part associated with feeding, although this hypothesis is counter to explanations of the movements of actively hunting predators in general.

Some of the differences observed in the present study compared with previous ones may be the result of different methods. As the first radio-telemetry approach to follow perch movement throughout a year, the present study overcomes some of the methodological shortcomings of previous studies. We were able to radio-track perch in all habitats, whereas perch moving into the reeds along the shore at night time or to deep waters in the wintertime might not be caught in gill-nets. It is possible that observed low activities during winter based on gill-net catches are the result of perch being able to avoid the nets during periods of high water transparency (Neuman, 1979). In the present investigation we also found that catching perch for stomach analysis was very difficult during winter, although we observed normal activity during simultaneous tracking sessions. Moreover, radio-telemetry allowed us to follow the same fish during most tracking sessions during the year, and to follow the fish even during inactive periods. This strengthens our results, which should hence show a more accurate picture of perch movement than activities derived from gill-net catches or laboratory experiments under unnatural conditions.

Differences in perch activity found in our investigations compared with previous studies could also be explained by the size of fish. The fish in our study was larger (27–37 cm) than in most other published studies where perch were ≤22 cm (Eriksson, 1978; Alabaster & Stott, 1978; Sandström, 1983; Neuman *et al.*, 1996). It may be therefore that larger perch show more variable activity patterns independent of temperature than smaller perch, including higher activity at low temperatures. This idea has been previously stated by Neuman (1979), who compared perch <15 cm and >15 cm.

In conclusion, we showed that large perch are mainly active during daytime with some individual variation. This pattern was clearest in the winter, whereas diel activity patterns varied less in the summer. Overall activity levels were not significantly lower in winter, nor clearly correlated with temperature, indicating that perch also forages actively in the wintertime, especially on the 0+ year-class fish. This behaviour might be an important structuring feature of piscivorous perch, because fish prey, such as 0+ roach, might be easier to catch in winter because of reduced activity or passive winter shoaling (Jepsen & Berg, 2002). Thus, wintertime foraging improves the potential of large perch to reduce the stock of planktivorous fish in clear-water lakes with subsequent effects on pelagic food web structure in the following spring and summer. In addition, the high daytime activity throughout the year may induce behavioural changes of the 0+ fish because of a high predation risk (e.g. Werner *et al.*, 1983). The 0+ fish seek refuge at daytime and are mainly active at night (Johnson & Müller, 1978; Jacobsen & Berg, 1998), which reduces the grazing pressure on zooplankton. Thus, the results of radio-tracking large perch provided new insight in perch behaviour, revealing the potential of the species to act as a fish predator throughout the year in clear-water lakes. Using telemetry in turbid lakes will be a future objective to be able to compare the role of this piscivore and its predatory abilities under different environmental conditions, which would have implications for lake restoration and management.

Acknowledgments

We gratefully acknowledge the support of the technical staff at the Department of Inland Fisheries, especially Morten Carøe, during tracking sessions and for computer-processing GPS-positions. We also thank two anonymous referees for valuable comments on the manuscript. The Danish Angling Licence Funds financed this work.

References

Alabaster J.S. & Stott B. (1978) Swimming activity of perch, *Perca fluviatilis* L. *Journal of Fish Biology*, **12**, 587–591.

Benndorf J. (1990) Conditions for effective biomanipulation: conclusions derived from whole-lake experiments in Europe. *Hydrobiologia*, **200/201**, 187–203.

Berg S., Jeppesen E. & Søndergaard M. (1997) Pike (*Esox lucius* L.) stocking as a biomanipulation tool 1. Effects on the fish population in lake Lyng, Denmark. *Hydrobiologia*, **342/343**, 311–318.

Berg S., Jeppesen E., Søndergaard M. & Mortensen E. (1994) Environmental effects of introducing whitefish (*Coregonus lavaretus* L.) in lake Ring. *Hydrobiologia*, **275/276**, 71–79.

Bergman E. (1988) Foraging abilities and niche breadths of two percids, *Perca fluviatilis* and *Gymnocephalus cernua*, under different environmental conditions. *Journal of Animal Ecology*, **57**, 443–453.

Boisclair D. & Rasmussen J.B. (1996) Empirical analysis of the influence of environmental variables associated with lake eutrophication on perch growth, consumption, and activity. *Annales Zoologici Fennici*, **33**, 507–515.

Craig J.F. (1977) Seasonal changes in the day and night activity of adult perch, *Perca fluviatilis* L. *Journal of Fish Biology*, **11**, 161–166.

Craig J.F. (1978) A study of the food and feeding of perch, *Perca fluviatilis* L., in Windermere. *Freshwater Biology*, **8**, 59–68.

Diehl S. (1988) Foraging efficiency of three freshwater fishes: effects of structural complexity and light. *Oikos*, **53**, 207–214.

Eriksson L.-O. (1978) A laboratory study of diel and annual activity rhythms and vertical distribution in the perch, *Perca fluviatilis*, at the arctic circle. *Environmental Biology of Fishes*, **3**, 301–307.

Fickling N.J. & Lee R.L.G. (1981) Further aids to the reconstruction of digested prey lengths. *Fisheries Management*, **12**, 107–110.

Holcik J. (1977) Changes in fish community of Klicava Reservoir with particular reference to Eurasian perch (*Perca fluviatilis*), 1957–72. *Journal of the Fisheries Research Board of Canada*, **34**, 1734–1747.

Huusko A., Vuorimies O. & Sutela T. (1996) Temperature- and light-mediated predation by perch on vendace larvae. *Journal of Fish Biology*, **49**, 441–457.

Jacobsen L. & Berg S. (1998) Diel variation in habitat use by planktivores in field enclosure experiments: the effects of submerged macrophytes and predation. *Journal of Fish Biology*, **53**, 1207–1219.

Jensen J.P., Søndergaard M., Jeppesen E., Lauridsen T.L. & Sortkjær L. (1997) *Ferske Vandområder, Søer. Vandmiljøplanens Overvågningsprogram* (*Freshwater Areas, Lakes. Water Environment Monitoring Programme*). National Environmental Research Institute, Ministry of Environmemt and Energy, Copenhagen.

Jeppesen E., Jensen J.P., Søndergaard M., Lauridsen T.L. & Landkildehus F. (2000) Trophic structure, species richness and biodiversity in Danish lake: changes along a phosphorus gradient. *Freshwater Biology*, **45**, 201–218.

Jepsen N. (1999) *Behaviour of Lake Piscivores and Their Predation on Migrating Smolts*. PhD Dissertation, Aalborg University, Aalborg.

Jepsen N. & Berg S. The use of winter refuges by roach tagged with miniature radio transmitters. *Hydrobiologia*, (in press).

Jepsen N., Beck S., Skov C. & Koed A. (2001) Behaviour of pike (*Esox lucius* L.) >50 cm in a turbid reservoir and in a clearwater lake. *Ecology of Freshwater Fish*, **10**, 26–34.

Jepsen N., Koed A. & Økland F. (1999) The movements of pikeperch in a shallow reservoir. *Journal of Fish Biology*, **54**, 1083–1093.

Johanneson L. & Persson L. (1986) The fish community of temperate eutrophic lakes. In: *Carbon Dynamics of Eutrophic, Temperate Lakes: the Structure and Functions of the Pelagic Environment* (Eds B. Reimann & M. Søndergaard), pp. 237–266. Elsevier, Amsterdam.

Johnson T. & Müller K. (1978) Different phase position of activity in juvenile and adult perch. *Naturwissenschaften*, **65**, 392–393.

Karås P. & Thoresson G. (1992) An application of a bioenergetics model to Eurasian perch (*Perca fluviatilis* L.). *Journal of Fish Biology*, **41**, 217–230.

Kerr S.R. (1982) Estimating the energy budgets of actively predatory fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, **39**, 371–379.

Mackay W.C. & Craig J.F. (1983) A comparison of four systems for studying the activity of pike, *Esox lucius* (L.), perch, *Perca fluviatilis* (L.) and *P. flavescens* (Mitchill). In: *Proceedings of the Fourth International Conference of Wildlife Biotelemetry* (Ed. Pincock, D.G.), pp. 22–30. Applied Microelectronics Institute and Technical University of Nova Scotia, Halifax.

Neuman E. (1979) Activity of perch, *Perca fluviatilis* L. and roach, *Rutilus rutilus* (L.), in a Baltic Bay, with special reference to temperature. *Institute of Freshwater Research, Drottningholm, Report*, **58**, 107–125.

Neuman E., Thoresson G. & Sandström O. (1996) Swimming activity of perch, *Perca fluviatilis*, in relation to temperature, day-length and consumption. *Annales Zoologici Fennici*, **33**, 669–678.

Nielsen L.A. (1992) Methods of marking fish and shellfish. *American Fisheries Society Special Publications*, **23**, 1–208.

Persson L. (1979) The effect of temperature and different food organisms on the rate of gastric evacuation in perch (*Perca fluviatilis*). *Freshwater Biology*, **9**, 99–104.

Persson L. (1983) Food consumption and competition between age classes in a perch *Perca fluviatilis* population in a shallow lake. *Oikos*, **40**, 197–207.

Rask M. (1986) The diet and diel feeding activity of perch, *Perca fluviatilis* L., in a small lake in southern Finland. *Annales Zoologici Fennici*, **23**, 49–56.

Sandström O. (1983) Seasonal variations in the swimming performance of perch (*Perca fluviatilis* L.) measured with the rotatory-flow technique. *Canadian Journal of Zoology*, **61**, 1475–1480.

Siegel S. & Castellan N.J. Jr (1988) *Nonparametric Statistics for the Behavioural Sciences*. McGraw-Hill Book Co, New York.

Sokal R.R. & Rohlf F.J. (1995) *Biometry*. W.H. Freeman Co, New York.

Thorpe J. (1977) Synopsis of biological data on the perch, *Perca fluviatilis*, L. & *Perca flavescens*, Mitchell 1814. *FAO Fisheries Synopsis (Rome)*, **113**, 138 pp.

Werner E.E., Gilliam J.F., Hall D.J. & Mittelbach G.G. (1983) An experimental test of the effects of predation risk on habitat use in fish. *Ecology*, **64**, 1540–1548.

Wiederholm T. & Eriksson L. (1977) Effect of alcohol-preservation on the weight of some benthic invertebrates. *Zoon*, **5**, 29–31.

Winter J.D. (1983) Underwater biotelemetry. In: *Fisheries Techniques* (Eds L.A. Nielsen & D.L. Johnson), pp. 371–395. American Fisheries Society, Bethesda.

Wise M.H. (1980) The use of fish vertebrae in scats for estimating prey size of otters and mink. *Journal of Zoology (London)*, **192**, 25–31.

(Manuscript accepted 1 August 2002)