Habitat shifts of perch larvae as survival strategy

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Perch (*Perca fluviatilis* L.) spawn in lakes, rivers and estuaries and even in the brackish water of the Baltic Sea. In the outer archipelago of the Baltic the selection of unexposed spawning sites can be explained by the genetic component in larval dispersal and the return to inshore waters. The larvae were found to be active, at least in initiating the dispersal. Nevertheless, currents probably aid in the dispersal process. Although the shift back inshore has been documented in all lakes studied, it was here noted to be a gradual process. The timing of the return to littoral areas varies somewhat from one lake to another, and it may also depend on the size and trophic state of the lake. Perch thus appears to be adapted to variable environments. It is suggested that the shift may be a sensitive period in the formation of year-class strength, since the 0+ perch are then more exposed to predator pressure. The dispersal strategies of roach and perch larvae differed, and only after perch returned to the littoral did the distribution area of 0+ perch overlap with that of 0+ roach.

1. Introduction

According to most authors the year-class strength is established during the first year of a fish's life. The decisive period, however, is still not known exactly. The distribution of early stages may also be important (Iles & Sinclair 1982, Urho *et al*. 1990), especially the distribution as related to predator and prey species and to species competing for the same resources. During their early development, perch use the whole lake area, selecting, however, different habitats at different times. Perch (*Perca fluviatilis* L.) larvae are known to move out into the pelagic area and after some time return to shallow-water areas (Whiteside *et al*. 1985, Post & McQueen 1988, Treasurer 1988, Wang & Eckmann 1994). There is lack of agreement, however, as to

when and why these changes take place. Previous hypotheses were based on data often collected from only a few inshore and offshore stations or on samples taken only at certain depths. These shortcomings were not always recognised when the hypotheses were formulated. Observations made on the habitat shifts of two closely related species (perch and yellow perch) manifest very similar, but still not quite identical, patterns. This does not mean that the species behave differently; rather that several different surroundings are involved. A number of papers have been published on the subject of habitat changes in lakes, but data on rivers, estuaries and sea areas are scarce.

Here I present data on habitat shifts in the early life history of perch in a small lake and review earlier publications. By comparing different lar-
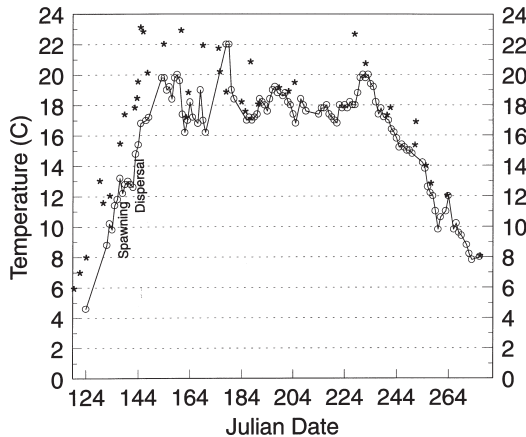
Fig. 1. Surface water temperature in Lake Saarlampi in summer 1979. Measured at 6 a.m. (open circles) and later in the day (asterisk).

val surroundings (different lake types, estuary and coastal sea area) and larvae I shall try to establish why and when perch larvae change their habitat, and whether these changes are based on inherited traits or whether they depend on the food or predator situation. I assume that these shifts are key issues in population dynamics. The manner in which the shifts are associated with feeding, predation and other interactions is discussed in an attempt to answer the following questions: When does the offshore translocation of perch larvae take place and why? When does the inshore migration take place and why? Could spawning-place selection affect the distribution of perch larvae? How could these shifts affect the year-class strength?

2. Material and methods

The main source of material is an oligotrophic headwater lake, Saarlampi (13 ha), in southern Finland. The lake has a maximum depth of 12 m. The area less than 2 m deep is called the littoral zone, since the vegetation, mainly yellow water lily (*Nuphar luteum*) and bur reed (*Sparganium friesii*), does not reach much deeper than that. The most extensive vegetation areas (water lily) are at the northern and southern shallow ends of the lake. Areas with *Phragmites communis*, *Carex rostrata*, *C. lasiocarpa*, *Potentilla palustris* and *Equisetum fluviatile* extend for only a few metres offshore.

Samples were taken with Bagenal (1974) buoyant nets (1-m² opening, 0.8×1.0-mm mesh size net). Nets were lifted 100 times per week from May to July in 1979. After each setting, the nets remained on the bottom for 20 to 30 (min.

10, max. 45) minutes before rising to the surface. The perch and roach (*Rutilus rutilus* (L.)) larvae and juveniles caught were preserved in 10% formalin and counted. After fixation, their total length (*TL*) was measured to the nearest 0.1 mm. The developmental stage was also determined. Other species reproducing in the lake were pike (*Esox lucius* L.) and burbot (*Lota lota* (L.)), but the larvae and juveniles were caught only with a hand net.

For random sampling the lake area was divided into 20 × 20-m squares. The squares located in water < 2 m deep were subdivided into four squares (about 40% of the total lake area). The buoyant net sampling consisted of 669 lifts, 77% of which were in the littoral area. The abundance of perch larvae was estimated only four times within a month of hatching; the estimates were made separately for pelagic and littoral areas. The material did not allow reliable estimates later than that since the probability of hitting a perch school with the buoyant nets set at random was probably already too low by the end of June.

The egg strands of perch spawn were counted from a boat, since the secchi disc reading was 3 to 4 m, and as most of the strands occurred at a depth of < 1 m. The water temperature was measured daily between 5 and 7 am at the surface (20 cm), 10 m from the shoreline where the water depth was 1 m and again during the daytime sampling (Fig. 1).

Data from the literature were gathered and analysed in the discussion together with the results for Saarlampi and scattered observations and unpublished data from several studies (Hudd *et al.* 1984, Hudd *et al.* 1987, Urho & Ahvonen 1990, Urho *et al.* 1990, Karås & Hudd 1993, Kjellman *et al.* 1996).

3. Results

3.1. Spawning sites of perch

In Saarlampi, perch spawned between 16 and 24 May (peak 17–19 May) near the shoreline on branches of *Potentilla* and *Carex* around the whole lake, although some areas were more favoured than others (Fig. 2a). Altogether 160 egg strands were counted. The last new egg strands were recorded on 24 May, when the first perch larvae were also caught. Roach spawned at the same time as or a few days earlier than perch.

3.2. Larvae community surrounding 0+ perch

The first burbot larvae were caught in Saarlampi, in holes in the ice on 22 April, when the buoyant nets were tested in the pelagic area. After ice break-up in the first week of May, feeding burbot larvae were observed daily and were caught with
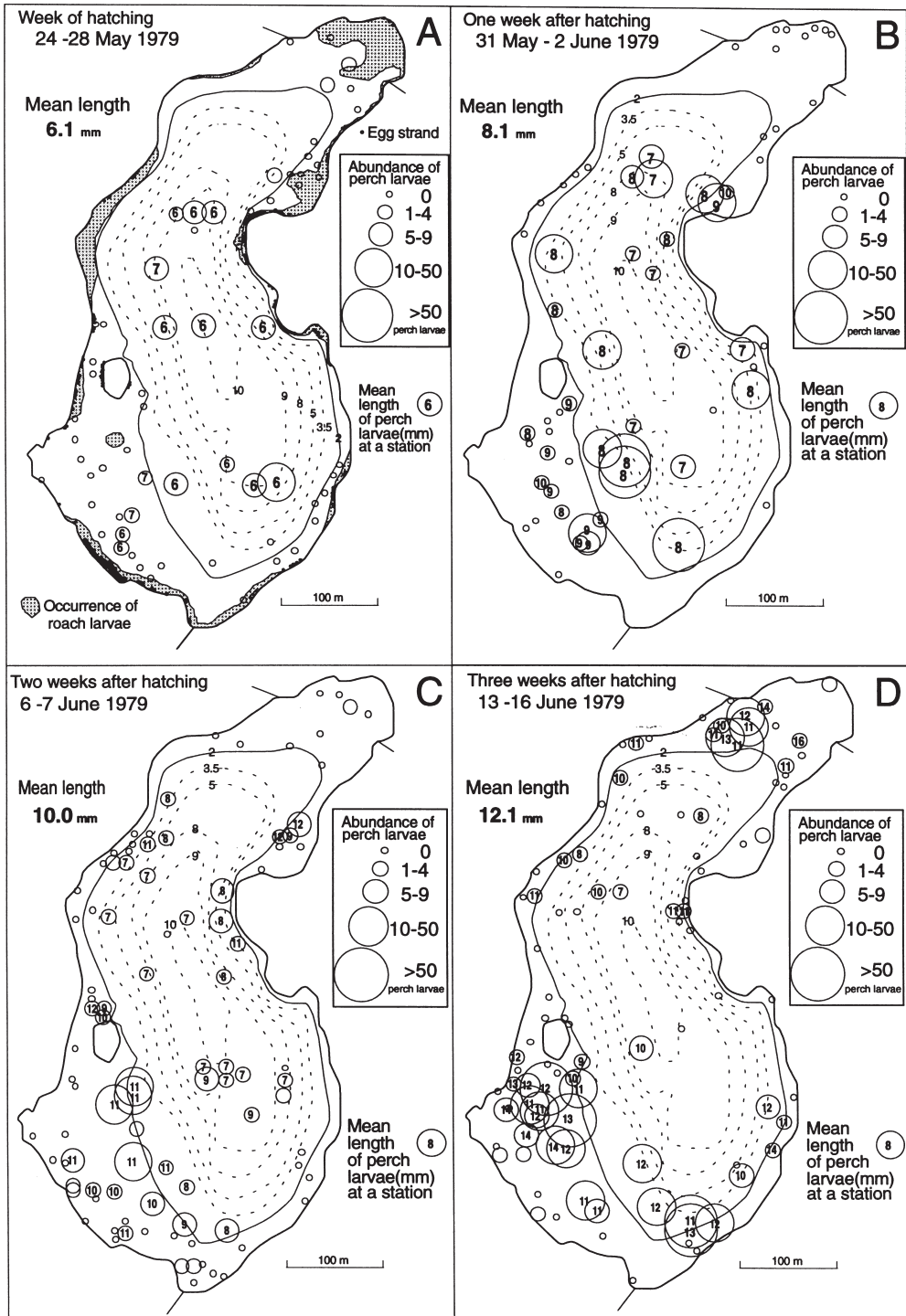
Fig. 2. Distribution of egg strands found (16–24 May) black dots, distribution and abundance of perch larvae (24–28 May) circles with numbers (numbers refer to mean size of perch larvae at that station), and distribution of roach larvae (24 May–16 June) filled area in Lake Saarlampi in 1979 (A). Distribution, abundance and mean length of perch larvae one week (B), two weeks (C), and three weeks (D) after hatching.

a hand net in very shallow water (0.1–0.5 m) near the shoreline. At the end of May, after the development of barbels and ventral fins, most of the 0+ burbot gradually adopted a demersal lifestyle, only a few burbot larvae with a total length (*TL*) of about 12 mm still being observed in the water column among plants near the shoreline.

Pike larvae hatched in the middle of May. After using their yolk while still hanging on plants, pike larvae with some gas in the swim bladder were caught among the vegetation at the same time as the first roach and perch larvae hatched (24 May). By the end of May, the pike larvae had attained a length of 15 to 23 mm and already had teeth even though they were still living among plants. A week later (6 June) a pike with a length of 30 mm was caught in the vegetation area. Pike measuring 50 to 150 mm were also observed further from the shoreline, but still close to vegetation.

Roach spawned in the middle of May, and on 24 May the yolk sac larvae were observed hanging on the plants. Two days later almost all the roach larvae caught had gas in the swim bladder, although the majority still had some yolk left. Most of the roach larvae caught the next day had started feeding. By the last day of May, the mean length of roach larvae was 8.5 mm and the flexion stage was just beginning. By the middle of June, rays had appeared in most of the fins of roach larvae, which now measured 10 to 16 mm (mean 14 mm). It was at this time that a perch (17.2 mm *TL*) was observed swimming along with roach (13 to 16 mm *TL*). By the end of June roach larvae roughly five weeks old (22 mm *TL*) had lost the larval fin fold and received the full count of fin rays, thus becoming scaled juveniles.

Roach larvae, like burbot and pike larvae, remained in the littoral area, mostly among plants. 0+ roach were not once observed in the pelagic area before the end of June. Roach larvae were caught in shallow water (depth < 2 m) around almost the whole lake (Fig. 2a). At the yolk sac stage, most of the roach larvae were near the spawning sites; exceptionally, two individuals out of a total of 2 000 were caught 50 m from the shoreline, at a spot where the water was 2.5 m deep. By the beginning of June the abundance of roach larvae (8.5 mm *TL*) in the littoral area was 1.7 indiv./m² according to an estimate made with the aid of 71 buoyant nets. Later, the formation of bigger schools of roach impaired

the reliability of the abundance estimates. For instance, on 15 June, 958 roach larvae from a school were caught with one buoyant net lift (1 m²). From June to July, schools of 0+ roach were surveyed in the littoral area and although they were seen to prefer certain sites/habitats, more detailed analysis was not done. Later, roach juveniles extended their feeding area, since schools were found above the 3- to 4-m contour, too.

3.3. 0+ perch shift to the pelagial area

Most of the perch larvae hatched in near-shore spawning sites in the week beginning 24 May. During the next four days, the yolk sac larvae of perch were mainly caught in the pelagic area (Fig. 2a). The total length was between 4.8 and 7.2 mm. Most hauls in the littoral area were empty. The pigmentation of perch larvae was much weaker than that of roach larvae. On 27 and 28 May half of the perch larvae still had some yolk left and 90% had started feeding, although the majority had a small amount of the oil globule left. On the latter day, the swim bladder of one-fifth of the larvae had started to fill. By early June almost all the larvae had some gas in the swim bladder, and a few had even reached the flexion stage. More advanced larvae were caught in the littoral, not the pelagic, area.

3.4. 0+ perch move back to the littoral area

The perch larvae gradually moved shorewards, and it was not long before they were found in aggregations near the vegetation edge (Fig. 2b and c). The shift started when the larvae had attained a mean size of as little as 8 mm and some gas had appeared in the swim bladder. During the shift, unpaired fins also developed. The biggest larvae reached the flexion stage and were at the 10-mm size one week after the mass hatching. Almost all stations where the mean size of larvae exceeded 8 mm were located in the littoral area; those where the mean size was less than 8 mm were in the pelagic area (Fig. 2b). However, less than 4 per cent of the perch larvae were caught in the littoral area, as the abundance was much higher in the pelagic (26.3 larvae/m²) than in the littoral (1.4 larvae/m²) area.

The following week (6–7 June), two-week-old larvae had a mean size of 10 mm. Larvae smaller than that still occupied the area deeper than 2 m; bigger larvae were in the area with a maximum depth of 3.5 m (Fig. 2c). The mean abundance estimates for the littoral and pelagic areas were equal (only 2.0 larvae/m²), but due to its smaller extent the littoral area had fewer larvae. The highest abundance of perch (max. 38 larvae/m²) was caught between the 2- to 3.5-m contours. Many of the lifts in the very shallow areas were empty, but those in the pelagic area generally yielded one to four larvae each, the majority at the flexion stage. Many of the larvae in or near the littoral area had already developed buds of pelvic fins.

Three weeks after hatching (13–16 June) the mean size of larvae caught was 12.1 mm (Fig. 2d). The mean abundance in the pelagic area was 6.7 and in the littoral 11.7 indiv./m². Strikingly high larval concentrations of up to 393 perch larvae/m² were found in a sample taken near vegetation. In that particular sample, the length of perch ranged from 9 to 19 mm. Several lifts yielded more than 50 larvae in the littoral area, and there were fewer empty lifts; some perch were even caught in water < 1 m deep. There were several empty hauls in the pelagic area, and the larvae were also smaller (maximum length 12.5 mm) than in the littoral area (Fig. 2d). The mean size of perch was thus much bigger in the littoral area, and the biggest individuals should actually be called juveniles.

Later in the summer, the number of perch schools had declined so much that the probability of hitting one with the random sampling procedure was extremely small and mostly solitary perch larvae were caught. By triggering the buoyant net with a string when a school appeared above it we could, however, still catch bigger samples at certain sites commonly frequented by schools. Although perch were occasionally observed in schools with roach, they mostly formed their own schools. Later in the summer and autumn, perch schools were encountered outside the littoral area, too.

4. Discussion

4.1. Shift to the pelagial serves dispersal

Back at the beginning of this century, Nordqvist (1914) claimed that perch larvae must seek open water soon after hatching, as he had found larvae measuring as little as 7–8 mm in the pelagic area. Many other workers have since noticed the same, which is aptly termed the 'pelagic or planktonic phase' (Noble 1968, Coles 1981). The beginning and end of the phase seem to vary, as do the definitions of pelagic, or open-water, areas. Moreover, the sampling effort put into pelagic and littoral areas is not usually reported. In Lake Saarlampi, the abundance of perch larvae was much higher in the pelagic area only a few days after hatching, when the larvae still had yolk left (mean size of 6.1 mm). An immediate shift by European perch to the pelagial after hatching is consistent with findings of Nordqvist (1914), Alm (1917), Kuznetsov (1970), Treasurer (1988) and Wang and Eckmann (1994). There may, however, be a slight difference between perch and yellow perch, since Ward and Robinson (1974) found that the shift took place soon after hatching, at about 8 mm *TL*, but not before the water temperature reached 15°C (Whiteside *et al.* 1985). According to Post and McQueen (1988), yellow perch larvae remained in the littoral zone until the yolk sac was absorbed, approximately 1–2 weeks, and then migrated to the pelagic zone for 4–8 weeks.

An interesting question is: How do the larvae shift and why? It has been suggested that they are carried out by currents (Houde 1969ab, Nellen & Schnack 1974, Konobeyeva *et al.* 1980, Coles 1981, Wang & Eckmann 1994). The distribution of larvae in the Rybinsk Reservoir is determined by wind currents and the contour of the bottom, but there is no clear link between the water-mass movement and the distribution of young fish (Konobeyeva *et al.* 1980). The results from Saarlampi do not support merely passive translocation; the very rapid shift to the pelagic area in that lake can be explained only by the short distance and larval swimming activity, since there were no strong winds or noticeable currents. Some daytime warming took place during the days of hatching (Fig. 1); the aid of convectional currents cannot therefore be totally ignored. The yolk sac larvae in an aquarium seek light. They soon swim at an angle of 45° and disperse actively in surface waters. Whether dispersal is totally a random process or not cannot be judged with present knowledge. I agree that currents and the wind may often help larvae to disperse, since they cannot resist very strong currents,

but they must swim actively, too. According to Houde (1969ab), perch larvae under 9.5 mm could sustain velocities of < 3.0 cm/sec only.

If the translocation of perch larvae were totally dependent on currents, all other larvae, e.g. roach, would also end up in the pelagic area. This did not happen in Saarlampi, although it seems that roach larvae cannot resist stronger currents than perch larvae (Houde 1969ab, Mutsin'sh 1979). Roach larvae hatched a few days before perch and remained in the littoral area throughout (Fig. 2a). There is a slight difference in posthatching development and behaviour between roach and perch larvae; roach larvae hang on plants for few days and thereafter fill the swimbladder, whereas perch start to swim immediately without filling the swimbladder first. The difference in swimming behaviour may partly explain the dispersal tactics of the species. Likewise burbot larvae, which dispersed earlier at the yolk sac stage and ended up in the littoral, also occurred in the spawning sites of perch and remained there while perch larvae moved out. It would thus seem indisputable that perch larvae have to swim actively to reach the pelagic zone. By moving directly into the pelagic area, perch larvae also may avoid predation by most invertebrates; this cannot, however, be the reason for the shift, since individual larvae have no experience of predation. Nevertheless, predation pressure may be the ultimate reason for habitat shift through natural selection. As the shift into the pelagial seems to be a universal form of behaviour it must be basically genetic.

4.2. Importance of spawning site selection

Most investigators report that perch spawn in shallow water (usually < 3 m), although egg-masses are known to deposit at depths of 4 to 14 m in some deeper lakes (e.g. Guma'a 1978a, Perrone *et al.* 1983, Newsome & Aalto 1987). Perch accept a wide variety of substrates on which to deposit spawn, which they generally drape or wind round the chosen object in order to hold it clear of the lake bed (Thorpe 1977, Jones 1982, Treasurer 1983). Perch are, however, known to exhibit demic behaviour, too (Aalto & Newsome 1990).

In lakes, except where acidic waters enter directly into near-shore spawning sites and thus expose eggs to critical water quality, the spawning site is probably not so important as it is in rivers and by the sea. In the Gulf of Finland, spawning sites become more rare offshore, and in the outer archipelago most egg strands are deposited in unexposed areas. This is consistent with the spawning site records for the Gulf of Bothnia (Karås & Hudd 1993). On the basis of a temperature-based recruitment model, Karås (1996) concludes that the recruitment production of perch is restricted in exposed archipelago areas as the water is too cold. Reproduction includes spawning, larval and juvenile production as well as shifts between the areas. Sixty years ago Hjort (1926) already hypothesised that some larvae might end up in unsuitable areas. If the shift of perch larvae into the pelagic area is basically genetic and used for dispersal, as concluded in the previous section, the selection of spawning sites in the coastal area may be crucial for later larval survival. If spawning were to take place in a site facing the open sea in the outer archipelago, dispersing larvae would probably be lost in an area which is too cold for perch recruitment. This is probably the reason why perch in the outer archipelago tend to prefer unexposed spawning areas resembling a small lake.

4.3 When 0+ perch return to the littoral area

Migration back to the littoral seems to be common to all perch populations (Table 1), and to take place gradually when the fish have reached a length of 8 to 40 mm. The timing of the near shore migration of young-of-the-year perch is related to size (Post & Prankevicius 1987). There are apparently considerable differences between different lakes and probably between years, too. Due to the insufficiency of data in the literature it is very difficult to judge what proportion of the difference in timing is due to the sampling method and what proportion to interpretation of the results e.g. whether the commencement or completion of the shift or the first or last individuals to move were reported. Another reason for the variation lies in the different definitions of inshore and littoral areas. In Saarlampi, the littoral (depth < 2 m) comprised 40% of the total surface area. In some lakes, the corresponding proportion may be only a few per cent. In big lakes, shifts should also take longer than in small ones. In Saarlampi, the whole shift back to the littoral took place rather fast, and within 3 weeks the abundance of 0+ perch in the littoral

area was already higher than that in the pelagial. The distance from the deepest point of the lake to the littoral area ranges from 50 to 200 m only. One week after hatching, larval abundance was highest above the 3- to 5-m contour and 3 weeks later above the 1- to 3-m contour. The later inshore shift of yellow perch in the small Lake St. George could be due to better feeding conditions in the offshore area (Post & McQueen 1988). In the large meso-eutrophic Lake Constance, the shift is not completed until perch are more than 30 to 40 mm long (Wang & Eckmann 1994).

An important observation is that some individuals change habitat faster than others. As in Lake Opinion (Amundrud *et al*. 1974), the biggest larvae caught in the pelagic area of Lake Saarlampi measured 10–11 mm, even though the mean larval size was 12 mm, and at the same time perch larvae measuring 9 to 19 mm were caught in the littoral area. The larval size difference between littoral and pelagic areas cannot be explained by gear avoidance.

4.4 Reasons for the shift to the littoral

4.4.1. The better growth conditions hypothesis

Temperature, food and predation has been postulated as reasons for the shifts; convincing evidence,

however, seems to be hard to find. Referring to the findings of Nordqvist (1914) and Alm (1917), Schneider (1923) suggested that inshore migration is a response to the warmer near-shore water. In spring and summer, the very near-shore waters are often warmer than even pelagic surface waters, but the situation varies depending on the wind. In general, perch larvae prefer lower optimum temperatures than juveniles (McCormack 1976), but temperature preferences may also change during the larval period. Post and McQueen (1988) and Gliwicz and Jachner (1992) reported dial migration of 0+ perch between littoral and pelagial areas, but found no association with temperature. Diurnal migrations could neither be confirmed nor explained in the present study. Better temperature conditions may, at least in some cases, partly explain why 0+ perch stay in the littoral area but not why the larvae begin to move inshore in the first place.

A higher growth rate is achieved at higher temperatures but also at higher prey densities (Kudrinskaya 1970). 0+ perch seem to be slightly bigger in inshore areas (Coles 1981, Wang & Eckmann 1994). In Lake Saarlampi, the larvae approaching the littoral area were bigger than those further offshore. The size difference also increased, as larvae grew much faster, on average, in the littoral area than in the pelagial, even though the abundance increased in the littoral.

Table 1. Summary of literature findings on perch larval return to littoral area.

Commenced	Completed	Lake	Area (ha)	Type	Reference
Perca fluviatilis					
8–9 mm		Stråken	Small	Olig.	Nordqvist 1914
(Offshore, not longer than 11 mm)		Opinicon	Small	Eutr.	Amundrud *et al*. 1974
7 mm	12 mm	Saarlampi	13	Olig.	This study
	19 mm	Llyn Tegid			Coles 1981
	17–20 mm	Loch Kinord	82		
		Loch Davan	42	Olig-M	Treasurer 1988
10 mm		Rimov Reservoir	210		Matena 1995a
9–11 mm	30 mm	Rimov Reservoir	210		Matena 1995b
12–15 mm		Bay in a reservoir			Kuznetsov 1970
8–20 mm					Nellen & Schnack 1974
16 mm		Windermere	1 480		Guma'a 1978
15–20 mm		Yxtasjö		Eutr.	Alm 1922,1952
	30/40 mm	Constance	5 390	Eutr.	Wang & Eckmann 1994
Perca flavescens					
	17–25 mm	St. George	10.4		Post & McQueen 1988
14–25 mm		Itasca	436		Whiteside *et al*. 1985
	Pigm. juv.	West Blue	160	Olig-M	Kelso & Ward 1977

The shallow and warm vegetated inlets of the Kyrönjoki estuary resemble small lakes, and perch larvae disperse over the whole area. The larvae do not have to move altogether from the inlet centre to the nearshore edges, since overgrowing vegetation soon provides suitable feeding conditions and protection against predators throughout the inlets. Larvae and 0+ juveniles are, however, bigger in near-shore areas, except when they start to migrate seawards. Juveniles are also bigger in denser vegetation than in open water areas of the vegetation zone at the end of July (Kjellman *et al*. 1996).

There are several reports that the decline in prey abundance in open water coincides with the time of the inshore migration (Whiteside *et al*. 1985, Treasurer 1988, Wang & Eckmann 1994). Estimates on zooplankton in Lake St. George do not, however, support this hypothesis (Post & McQueen 1988). Overall, the usability of prey abundance data may be questioned since young perch or other fish species may already have reduced the density of some prey species (see e.g. Mills & Forney 1981, Whiteside 1988, Treasurer 1992, Wu & Culver 1992). In smaller, oligotrophic lakes with a relatively large littoral area, 0+ perch seem to return to the littoral at the end of the larval period, whereas in larger and perhaps in eutrophic lakes the shift probably takes place later, often not until the juvenile stage (Table 1). This finding is in agreement with the feeding theory, which, in expanded form, may also explain the gradual shoreward shift with large individual variation. It is even possible that by searching for higher food densities in the pelagial, 0+ perch sooner or later end up in the littoral area.

The results of this study show that the distribution of perch and roach larvae differs almost completely at the time that the number of 0+ fish is most abundant. During the juvenile period, nevertheless, the distribution overlaps, as perch return to the littoral area, and this takes place earlier in waterbodies with a proportionally large littoral area. There are indications that roach and perch have some competitive interactions in the juvenile period (Persson 1986), which may affect their growth (Persson 1987). Predators may also reverse the outcome of competitive interactions between prey species (Persson 1991).

4.4.2. The predation hypothesis

The size differences in young perch between open-water and littoral areas cannot be explained by better feeding conditions alone. In addition to the more active shoreward shift of larger individuals, there are some indications that smaller larvae may be eaten by predators (Brandt *et al*. 1987, Post & Prankevicius 1987, Urho 1994).

In the pelagic area, perch larvae are probably less vulnerable to predation owing to their scarce pigmentation, a feature that is typical of other pelagic larvae, too (Urho 1990). The characteristic melanophores bordering myotoms in perch larvae are less intense in turbid than in clear-water lakes (Urho 1994, 1996), possibly as an adaptation to turbid (eutrophic) waters. In clear-water lakes, the pigmentation becomes more pronounced as the larvae develop, thus increasing the pressure to seek shelter among vegetation. Pigmented juveniles are more susceptible to predation in the offshore habitat (Kelso & Ward 1977).

The abundances of predator fish in pelagic and littoral areas are difficult to quantify, especially as the fish have a diurnal migration pattern. Walleye, zander and perch may induce predation pressure on larval and juvenile perch in the open water area (Menshutkin *et al*. 1968), although there is more evidence of predation during the transition from offshore to inshore waters (Ward & Robinson 1974, Noble 1975, Wang & Eckmann 1994). There are several potential predators, e.g. pike, and at certain times of the day, roach and perch, in the littoral area. Even young-of-the-year pike are known to eat perch larvae that have returned to the vegetation area, but the amount consumed in Saarlampi was probably not very high. In Lake Windermere the predation of 0+ pike on 0+ perch is significant (Treasurer *et al*. 1992). Adult roach eagerly eat small larvae, but most likely cannot easily catch juveniles. Perch, in contrast, are known to eat juveniles as well. Cannibalism was noted when early juveniles began to migrate inshore (Wang & Eckmann 1994). Fish predators or predation was not quantified in Saarlampi. Buoyant net catches were, however, checked for *Argulus foliaceus*, a free swimming fish lice found to occur almost only in the littoral area (Fig. 3). Thus, perch larvae and juveniles be-

came more susceptible to *Argulus* after their return to the littoral area. *Argulus* causes fin damage to adults but often leads to the death of juveniles (Urho 1995). Young-of-the-year perch that move back to the littoral area very soon have to face a higher predation pressure earlier. In a laboratory experiment, the move from the open water into a structurally highly complex part of an aquarium was due to the presence of predators (Persson 1991). There is no evidence in the wild of predators or parasites chasing young perch from the pelagial to the littoral. Thus, the return of 0+ perch to the littoral must basically have a genetic background but be influenced by environmental variables.

Schooling is in general regarded as a defensive mechanism against predation. The results of this study confirm that, before entering the vegetation area, perch form larger aggregations prior to school formation. Elsewhere, too, perch have been observed to form aggregations on the eighth day after hatching, only three days before schooling (Il'ina 1973). Schools of juvenile perch and also mixed schools with roach were seen rather early in the littoral zone of Saarlampi. Kuznetsov (1970) reported mixed schools with roach and other cyprinids, too. According to Alm (1922), perch schools often occur at slightly greater depths than cyprinid schools, that is, 1 m closer to the bottom. Jachner (1991) found that at night-time in July and August 0+ perch occupied the pelagic 4–7-m layer between roach and smelt, although some mixing also took place (Gliwicz & Jachner 1992). In lakes, 20–25-mm-long perch form schools in mid-water at a depth of 1.5 m (Disler & Smirnov 1977). The schools cruise in the littoral zone searching for food, although they are observed at certain sites more often than at others. The juveniles have to strike a balance between feeding and avoiding predators (Urho 1994). Schools of perch juveniles may therefore also leave the littoral and confuse the picture of migration patterns.

In the inner coastal archipelago area of the Baltic Sea, schools of 0+ juvenile perch may sometimes be collected further offshore during the day, and 0+ roach may sometimes occur in the pelagic area of some lakes (Bohl 1980, Matena 1995a). To establish whether these observations are exceptions or adaptations to changes in the environment (prey or predator situation) requires further study.
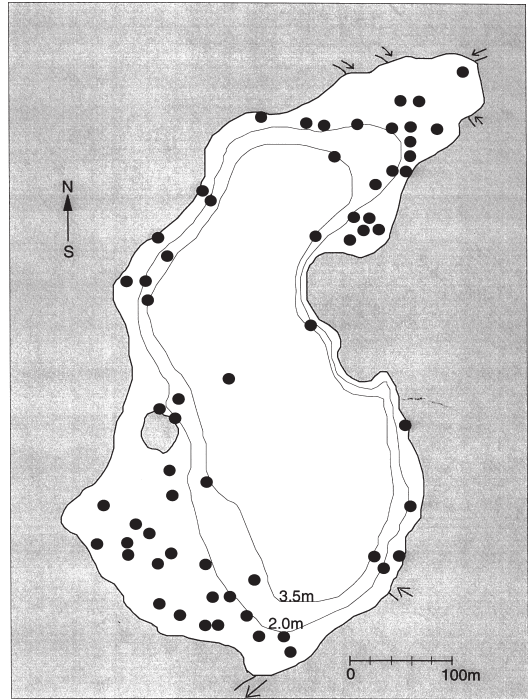

Fig. 3. Distribution of free swimming fish lice, *Argulus foliaceus*, caught during larval sampling in Lake Saarlampi in summer 1979.

At the end of the summer and in autumn juvenile perch move offshore in lakes and downstream in river and estuaries due to changes in environmental conditions, e.g. food availability, and thus once again become more exposed to predation (Guma'a 1978b, Coles 1981, Treasurer 1988, Urho *et al*. 1990, Wang & Eckmann 1994).

4.5. Larval habitat changes and their contribution to year class strength

The variation in the strength of perch year-classes correlates best with summer temperatures during the first year (Neuman 1976, Böhling *et al*. 1991, Lehtonen & Lappalainen 1995). It has been suggested that temperature affects larval survival either directly (Clady 1976) or secondarily through food availability and growth rate (Karås 1987). According to Karås, there is no indication that the variation is due to food availability. A limited growth rate due to lower temperatures may, how-

ever, induce higher mortality, especially during the first winter. During the first summer after dispersal, 0+ perch seem to change place, most probably to find food even at the risk of predation. Mikheev (1992) concludes that the survival of fish larvae in the pelagic environment is mainly influenced by food limitation, whereas in a boundary environment predation may be a more important constraint. It has previously been postulated that predation may affect the year-class strength (Alm 1952, Smyly 1952, LeCren 1962, Forney 1971, LeCren *et al*. 1977, Nielsen 1980, Wang & Eckmann 1994). During the shoreward shift of 0+ perch, the predation risk is obvious, and the effects possibly depend on the timing of the shift. More data are also needed to provide insight into the predation on perch juveniles at the time of the offshore (Wang & Eckmann 1994) or seaward migration (Urho *et al*. 1990).

Direct mortality of perch larvae occurs if the temperature drops below 10–12°C (Karås 1987). This may be critical to larvae in outer coastal areas, where the main and more secure reproduction of perch takes place only in unexposed warmer areas; there is a risk of uncontrolled dispersal into a cold environment in more exposed areas. Larval drift or later migration from the main spawning areas may, however, provide an opportunity for a bigger year-class in some exceptional years when the temperature is high enough in sea areas around the spawning ground. The partly sheltered areas with only a few egg strands could possibly also act as potential reserve areas. Accordingly, good year-classes should be much rarer among outer-archipelago than inshore populations. This hypothesis, too, needs to be tested with more data analyses, although there is an indication that the year-class strength in offshore populations and in environmentally disturbed populations may differ from the general trend (Böhling *et al*. 1991). As a whole, year-class strength is influenced by several variables, the effect of which is exposed by larval habitat changes.

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