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Variability in the spatio-temporal distribution of larval European whitefish (*Coregonus lavaretus* (L.)) in two Austrian lakes

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The spatial and temporal distributions of larval European whitefish (*Coregonus lavaretus*, species complex) were investigated in the years 1998 and 1999 in two Austrian lakes, Traunsee and Hallstättersee. The fish communities of both lakes are dominated by whitefish, but in addition to a normal-growing form Traunsee is also inhabited by a dwarf phenotype. Larval sampling was done weekly between January and June using a push net system. Whitefish larvae showed a preference for nearshore areas at both lakes. In Traunsee, the mean catch on the first sampling date was higher than those obtained during the following sampling dates in February for both years. A local minimum in temporal occurrence was observed in mid-February (1998) or early February (1999). Catches increased again during March before reaching a maximum in early April of both years. In Hallstättersee, the sampling started at the beginning of February with very few larvae caught. During the subsequent weeks the catches increased steadily until a single peak was reached in mid-March (1998) or late April (1999). This high within-lake variability in maximum larval occurrence between two successive years is the greatest ever reported. The degree of variation in spatial distribution of larvae observed between years was also novel.

Introduction

In many pre-alpine and alpine lakes of Central Europe, fish communities are dominated by the European whitefish (*Coregonus lavaretus*, species complex), which often forms an important component in the economy of commercial fisheries and has been exploited for centuries (e.g. Haempel 1930). From the perspectives of both fisheries and population dynamics it is necessary to pay special attention to larval abundance, because this life stage in general represents the most sensitive stage in the development of a population. The passage of individuals through several critical phases, e.g. hatching, first feeding and the initiation of swim-bladder function, with the variability of abiotic factors dominated by weather conditions, can exert substantial effects on their growth and mortality (Chambers & Trippel 1997).

In general, the spatial distribution patterns of larval coregonids vary widely in European lakes:

Whitefish larvae can be distributed heterogeneously over the whole lake (Ponton & Müller 1988), or their occurrence can be restricted primarily to the littoral zone (Wanzenböck & Jagsch 1998, Karjalainen *et al*. 2002), or they can change their distribution during ontogenetic development (Hudd *et al*. 1988, Sarvala *et al*.1988, 1994). One potential cause of the concentration of whitefish larvae close to the shore during the first weeks after hatching is proximity to the spawning grounds (Ponton & Müller 1988, Sarvala *et al*. 1994). Spawning sites located in shallow inshore areas are typical in European lakes, although spawning in offshore areas has also been reported (Eckmann 1991). River spawning coregonid populations are rather common in Scandinavian lakes (Skurdal *et al*. 1985, Naesje *et al*. 1986), but rarer in Middle and Western Europe. Rhulé and Kindle (1992) reported one such population in Lake Constance which ascends the inflowing Alpenrhein River to reach its spawning areas located 45 km upstream.

Central European lakes are often inhabited by different growth forms of whitefish (Kottelat 1997), with for example four to six forms reported for Lake Constance (Rhulé & Kindle 1992) and normal- and dwarf-growing forms reported for a number of Austrian lakes (Neresheimer & Ruttner 1928, Einsele 1955, Einsele & Hemsen 1959, Wanzenböck *et al*. 2002). Temporal occurrence of whitefish larvae is generally linked to spawning time. In Swiss lakes, slow-growing forms spawn in autumn and their offspring hatch in early winter, whereas normal-growing forms spawn in early winter with their offspring hatching in late winter or spring (Kirchhofer & Lindt-Kirchhofer 1998).

The objective of the present study was to investigate the inter annual variability in the spatial distribution and seasonal occurrence of whitefish larvae in two Austrian lakes, Traunsee and Hallstättersee. In both of these lakes, one part of the population ascends into the inflowing rivers for spawning (Traunsee: Neresheimer & Ruttner (1928), Wanzenböck *et al*. (2002), Hallstättersee: Lahnsteiner (2001), pers. obs.), whereas the other parts spawn nearshore within the lakes. However, the lakes differ in that Traunsee has both normal- and dwarf-growing forms, but Hallstättersee has only the former. In contrast to research on vendace (*Coregonus albula*), where annual variability in larval recruitment has been studied intensively (Karjalainen *et al*. 2000), the natural variability of whitefish larval occurrence patterns among lakes and between years is not very well known. The close geographical location of both lakes, the same post-glacial formation and a similar trophic status may lead to the assumption that similar spatio-temporal phenologies of whitefish larvae should be found. However, we hypothesised that in the two lakes different spatio-temporal larval distributions might be found because of the occurrence of different phenotypes.

Materials and methods

Study area

Traunsee and Hallstättersee are lakes situated in the Traun River drainage basin in the lake district Salzkammergut east of Salzburg, Austria (Fig. 1). Both are typical glacial, oligotrophic, pre-alpine lakes with rather low retention times due to the relatively large Traun River, which flushes them. They differ considerably in lake basin morphometry, but the shorelines of both lakes consist almost entirely of very steep slopes. The main limnological characteristics of Traunsee and Hallstättersee are shown in Table 1. Both lakes are dominated by whitefish, which serves as the main commercial target species. In addition to whitefish, the fish communities comprise mainly Arctic charr (*Salvelinus alpinus*), perch (*Perca fluviatilis*), pike (*Esox lucius*) and several cyprinid species. Altogether 19 fish species are present in Traunsee and 14 species in Hallstättersee (Gassner & Wanzenböck 1999). The ecological integrity of Traunsee is influenced by silt from grinded limestone together with highly alkaline pore waters emitted via industrial wastewater from a Sodawork and covers part of the lake bottom. However, no influence of this pollution on larval recruitment of whitefish was detected (Wanzenböck *et al*. 2002). In contrast to Traunsee, Hallstättersee is not influenced by any industrial tailings and is almost pristine.

Sampling techniques

To estimate the density of larval and juvenile fishes, a push net system modified after Wanzenböck *et al*. (1997) was used. The push net (mesh size 750 μm at the cylindrical front part, 650 μm at the conical rear part) had an overall length of 3 m, with a front opening consisting of a rectangular metal frame, 100 cm × 120 cm. A collecting bucket with a removable bottom was fixed at the rear end of the net and the whole construction mounted at the front of a boat. At the beginning of a haul, the net was lowered by means of a winch so that the upper rim of the metal frame was at the water surface. One haul lasted 6 minutes and the speed of the boat was 1.6 m s^{-1}, thus filtering 644 m^3 of water (± 4% according to flowmeter measurements).

At each lake 12 sampling sites were selected in order to cover different habitats and presumed spawning areas (Fig. 1). Nine sites were situated nearshore, but at both lakes two of these stations had a pelagic character because of steep underwater slopes (Traunsee: Stations 2 and 3, Hallstättersee: stations 4 and 9). At both lakes, three stations were situated offshore. The schedules of the sampling periods and the number of hauls are shown in Table 2. Note that in early 1999 the northern sampling sites (6, 7, 8 and 10) at Hallstättersee were covered with ice, which persisted until 15 March.

Upon capture, all fish larvae were preserved in 4% formaldehyde solution. In the laboratory, the larvae were separated from plankton and other organic matter. Larvae of all species caught

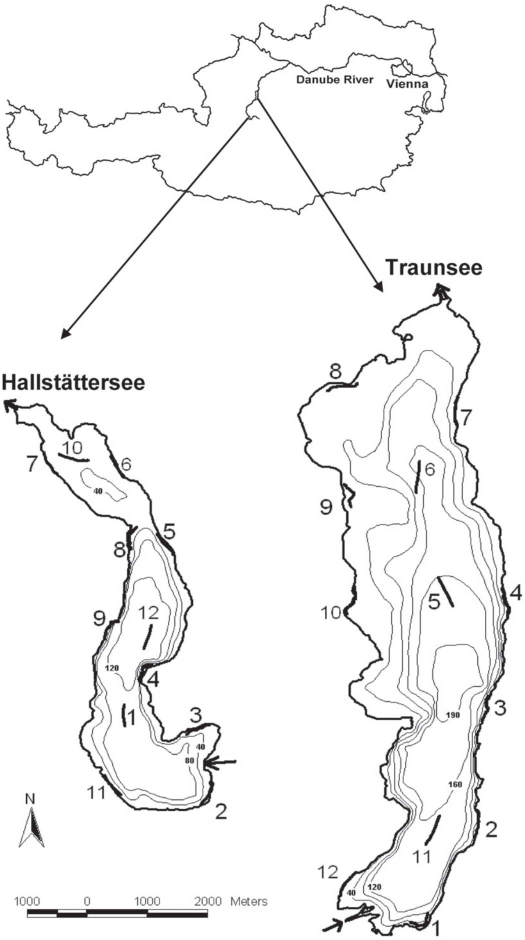

Fig. 1. Location of the study lakes and sampling sites (numbered thick lines) at Traunsee and Hallstättersee, Austria. Depths contours are given in 40-m increments.

Table 1. Limnological characteristics of Traunsee and Hallstättersee. Data from Schwarz and Jagsch (1998).

	Traunsee	Hallstättersee
Height above sea level (m)	423	508
Drainage area (km^2)	1422	646.5
Lake area (km^2)	24.35	8.55
Maximum depth (m)	191	125.2
Mean depth (m)	94.54	65.15
Volume (10^6 m^3)	2302	557
Outflow (m^3 s^{-1})	70	36
Theoretical retention time (years)	1.04	0.49
Mean total phosphorus content (mg m^{-3})	2	13
Oxygen level in the hypolimnia (mg l^{-1})	10.6	2.7
Average Secchi depth (m)	5.6	7
Trophic classification	oligotrophic	oligo–mesotrophic

were identified routinely on the basis of pigmentation and by counting myomeres (Kobiltskaja 1981, Spindler 1988, Urho 1996).

Statistical analyses

The catch per unit of effort (CPUE) for push net fishing was standardised to the number of larvae (ind. × 100 m^{-3}). As CPUE values were not normally distributed, the Mann-Whitney *U*-test was used to examine the data of 1998 and 1999 at each lake, as well as the data of both years between the lakes. A probability level of ≤ 0.05 was considered significant.

Table 2. Time schedule of larval sampling in Traunsee and Hallstättersee and number of hauls. In early 1999, the northern sampling sites (6, 7, 8 and 10) at Hallstättersee were covered with ice up to 15 March.

Year	Date	No. of hauls
Traunsee		
1998	28 January–29 May	214
1999	12 January–1 June	234
Hallstättersee		
1998	5 February–3 June	204
1999	4 February–2 June	165

Results

Although catches were dominated by 0+ whitefish, the young of several species were also recorded (Table 3).

In both study years, the mean abundance of whitefish larvae was significantly lower for Traunsee compared to Hallstättersee (Mann-Whitney *U*-test, 1998: $p \leq 0.001$, 1999: $p = 0.029$).

Differences in temporal distribution were also detected between years and/or lakes. Though the catches for the entire season were lower in Traunsee, larval catches at the beginning of the sampling period were higher compared to Hallstättersee in both years (Fig. 2). The mean catches on the first sampling date were higher than those obtained during the following sampling dates in February for both years. During February a local minimum in mean catches was observed, after which sample sizes increased through March until the maximum catch was reached on 9 April 1998 (2 ind. × 100 m^{-3}) and 8 April 1999 (7 ind. × 100 m^{-3}). During the second half of April and in May, the number of individuals decreased rapidly (Fig. 2). The temporal pattern of occurrence was basically similar in both years. At some single sampling sites (e.g. sites 5, 11) a bimodal pattern was apparent, whereas at others it was absent (Fig. 3).

Table 3. Mean CPUE values (number of individuals × 100 m^{-3}, of all sampling dates and sampling stations) for push net catches performed at Traunsee and Hallstättersee. Unless indicated otherwise, all fish were 0+.

Species	CPUE (ind. × 100 m^{-3})			
	1998		1999	
	Mean	SE	Mean	SE
Traunsee				
Coregonus sp.	0.942	0.146	2.535	0.259
Lota lota	0.007	0.003	0.007	0.004
Perca fluviatilis	0.056	0.014	0.030	0.011
Rutilus rutilus	0.000	0.000	0.041	0.010
Chalcalburnus chalcoides mento	0.001	0.001	0.000	0.000
Chalcalburnus chalcoides mento 1+	0.000	0.000	0.017	0.013
Esox lucius	0.000	0.000	0.003	0.001
Hallstättersee				
Coregonus sp.	1.533	0.690	3.810	0.187
Lota lota	0.154	0.089	0.301	0.034
Perca fluviatilis	0.502	0.738	0.902	0.216

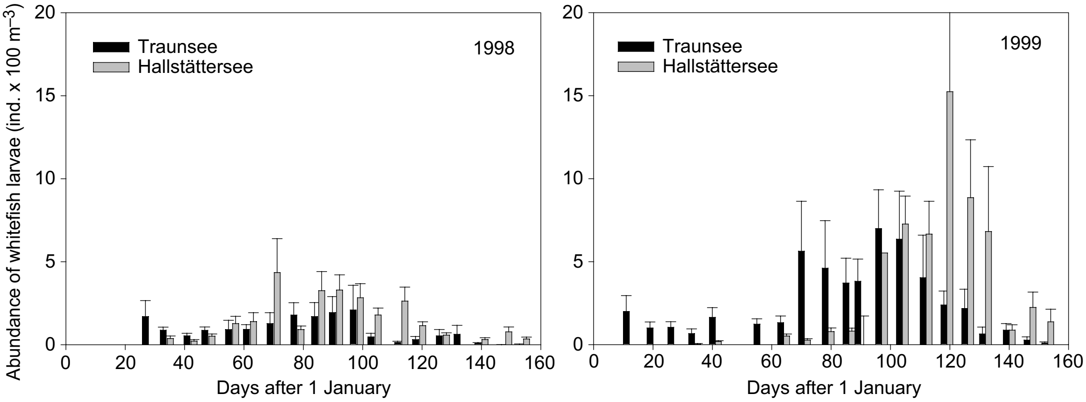

Fig. 2. Temporal variation of whitefish larvae abundance in Traunsee and Hallstättersee during 1998 and 1999. Date shown as means ±1 S.E. of the 12 sampling sites at each date.

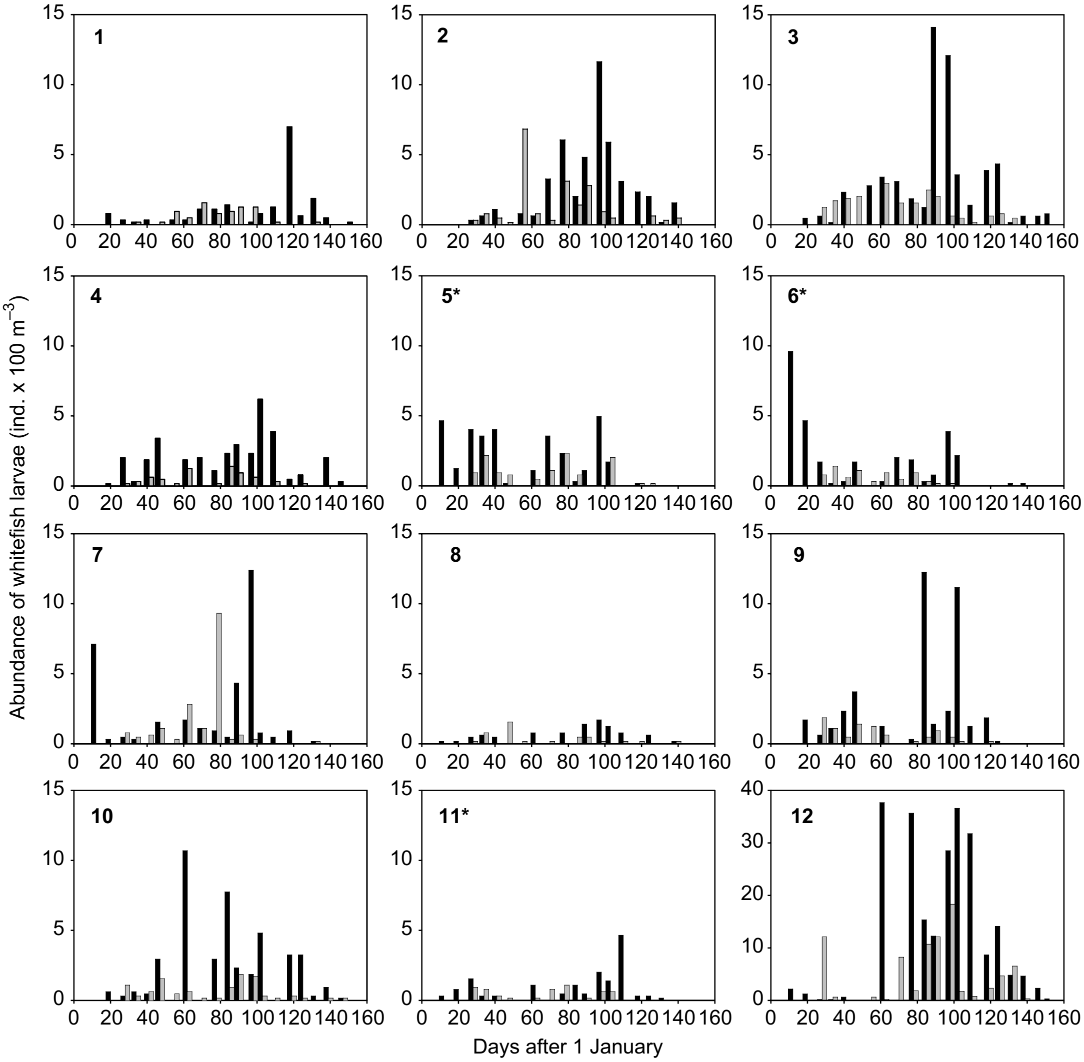

Fig. 3. Temporal variation of whitefish larvae at the 12 sampling sites at Traunsee in 1998 (grey bars), and 1999 (black bars). Offshore sites are marked with a star. Note the different scaling of the *y*-axis at Site 12.

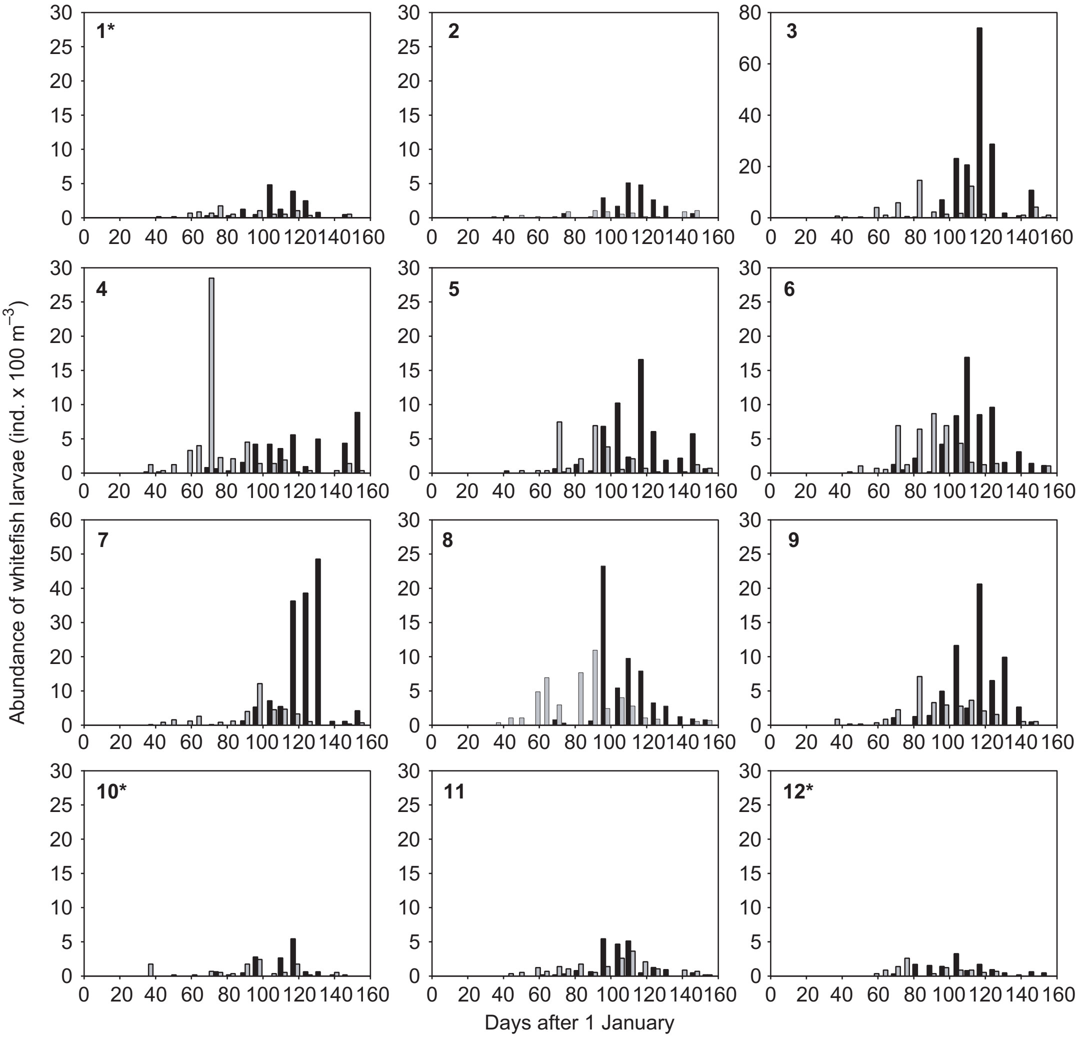

Fig. 4. Temporal variation of whitefish larvae at the 12 sampling sites at Hallstättersee in 1998 (grey bars), and 1999 (black bars). Offshore sampling sites are marked with a star. Note the different scaling of the *y*-axis at Sites 3 and 7.

The temporal occurrence of whitefish larvae in Hallstättersee followed a different pattern from that in Traunsee (Fig. 2). The first larvae occurred at the beginning of February at quite low densities, but their number increased steadily during February and March until a maximum was reached. Inter-annual variation in the date of the maximum catch was detected. In 1998 the highest density of larvae averaged over all sampling sites (4 ind. × 100 m^{-3}) was found on 12 March, and in 1999 (15 ind. × 100 m^{-3}) on 28 April. In Hallstättersee, a unimodal pattern of larval temporal distribution was obvious at all 12 sampling sites (Fig. 4). The maximum catches at all stations were taken between 18 and 31 March in 1998. In 1999, almost exactly one month later, maxima were obtained at all sites.

In Traunsee, the numbers of individuals caught at the offshore sites (sites 5 and 6) in January and early February 1999 were quite high in relation to the remaining sites (Fig. 3). In contrast, very few larvae were caught at offshore Site 1 and no larvae were caught at offshore Site 12 in early February 1999 in Hallstättersee (Fig. 4). Though larvae were found at the pelagic sampling sites early in the season in Traunsee, a preference for littoral sites was evident at both lakes for the entire season and this was statistically significant for each year when nearshore and offshore sites were compared (Mann-Whitney U-test, Traunsee 1998: $p = 0.008$, 1999: $p = 0.030$, Hallstättersee 1998: $p \leq 0.001$, 1999: $p = 0.003$). At the nearshore Site 12 in Traunsee an extraordinarily high density of larvae was found in both years, with averages of 4.50 larvae × 100 m^{-3} in 1998 and 12.48 larvae × 100 m^{-3} in 1999 (Fig. 5). The second rank was taken by Site 3 in both years, with following ranks occupied by different sites in each year. In Hallstättersee, only the second rank was consistently occupied by the same site (site 3), whereas rank one differed by year. In 1998, the highest number of larvae was caught at Site 4 (2.88 ind. × 100 m^{-3}), but in 1999 it was at Site 7 (16.07 ind. × 100 m^{-3}). The remaining ranks in both years did not show any consistent pattern at Hallstättersee. The offshore sites always occupied lower ranks at Traunsee with the sole exception of Site 5 in 1998, and even the very lowest ranks at Hallstättersee in 1999 (Fig. 5).

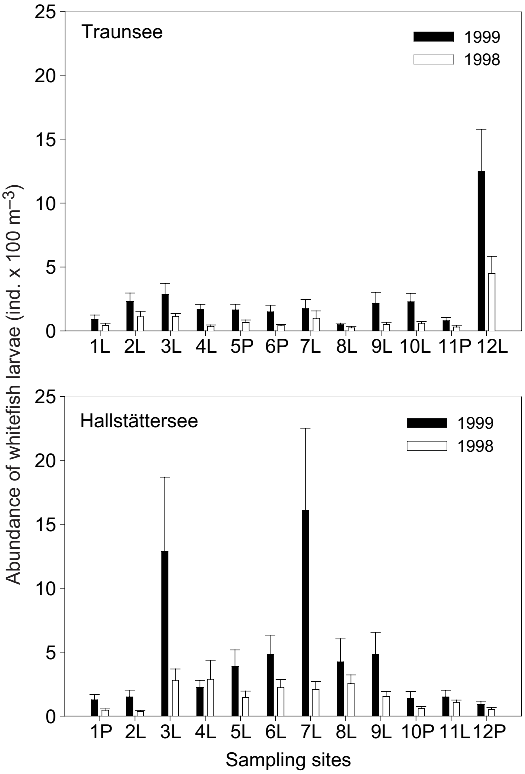

Fig. 5. Site variation of whitefish larvae at Traunsee and Hallstättersee in 1998 and 1999. The x-axis indicates sampling sites, with L site numbers indicating nearshore sites, while those marked with P indicating offshore sites. Data are shown as mean ± 1 S.E. of all dates at each site.

Discussion

The period with considerable catches of whitefish larvae was unexpectedly long at both Traunsee and Hallstättersee, particularly so for the former lake. In previous studies on spawning and reproduction of coregonids in these lakes, Einsele (1955) and Wanzenböck *et al.* (2002) suggested that larvae of the slow-growing form hatch earlier than those of the normal-growing form because of their extended spawning time. A direct relationship between larval hatching and spawning time of adults is made more likely by generally uniform water temperatures for the whole incubation period. Hassan (2000) caught mature individuals of the slow-growing form as early as 20 October, but spawning of the normal form is known to take place from the end of November to mid December in both lakes (Hamann 1954, Einsele 1955). In Traunsee, the earlier occurrence of larvae and the relatively high number of whitefish caught in mid-January is hypothesised to be a consequence of the presence of the slow-growing population, with the maximum catch in early April presumably consisting mainly of individuals belonging to the normal-growing population. In contrast to this capture pattern, the unimodal distribution in Hallstättersee corresponds with the occurrence of only a single growth form. Our results are in accordance with the findings of Kirchhofer and Lindt-Kirchhofer (1998) who reported for three Swiss lakes that slow-growing forms spawn in autumn and their offspring hatch in early winter, whereas fast-growing populations spawn in winter with the offspring hatching later. Further assessment of this hypothesis requires a genetic study.

At the start of our sampling campaigns, relatively high catches were obtained at offshore zones in Traunsee, but in Hallstättersee only a few or no larvae were caught in offshore sites. This difference was obvious for our first three sampling dates. In the subsequent course of our investigation at both lakes, whitefish larvae were predominantly caught at nearshore sampling stations. The appearance of larvae in nearshore zones could represent a relationship between the known spawning grounds and the occurrence of larval whitefish. Local commercial fishermen and former investigations reported littoral areas at Traunsee as preferred spawning sites of the whitefish (Wanzenböck *et al*. 2002). Recent studies with egg traps exposed in Traunsee confirmed areas at the east coast as preferred spawning sites, although no eggs could be found in traps exposed on the sediment in the middle of the lake (Wanzenböck *et al*. 2002). Surveys with a sled dredge did not record eggs at profundal offshore sites, but whitefish eggs were sampled with this method at nearshore areas (Lahnsteiner 2001). The results of these recent surveys suggest that larvae caught in the middle of Traunsee might be passively drifted from the Traun River, which serves as an additional important spawning site (Lahnsteiner 2001, Wanzenböck *et al*. 2002). The consistently highest larval abundance at Site 12 close to the mouth of the Traun River and the strong river currents which extend well into the north part of the lake (Eckel 1967) support this assumption. Alternatively, the relative proximity between the two offshore sampling sites and the traditionally known spawning sites of the slow-growing form at the west coast of Traunsee (Hamann 1954) might explain the observed pattern.

Similar observations have been reported in most other studies of distribution patterns of larval whitefish, i.e. that their occurrence can be restricted primarily to the littoral zone (Karjalainen & Viljanen 1994, Ventling-Schwank & Livingstone 1994, Karjalainen *et al*. 2002). Sarvala *et al*. (1994) concluded that the locations of spawning grounds, as well as prevailing water currents and predation avoidance, are responsible for the distribution patterns of early larval stages, rather than active migrations towards habitats with better food conditions.

At Traunsee, Site 12 situated at a southern bay exhibited the highest densities of larval whitefish. This area, covered by industrial sediments, is not a spawning ground and is effectively avoided by adult coregonids (Wanzenböck *et al*. 2002). Consequently, it is assumed that the accumulation of whitefish larvae in this area is caused by drift from the Traun River. The accumulation of larvae in the bay may also be influenced by surface water currents induced by south-west winds, the main wind direction at Traunsee (Kann 1959, Eckel 1967). The limited swimming ability of newly-hatched whitefish larvae was reported by Fabricius and Lindroth (1954) and active phototactic behavior causes them to occur close to the surface (Ventling-Schwank & Meng 1995), both features which could enhance their passive horizontal transport by surface water movements, caused mainly by winds.

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