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Understanding the spatial dynamics of predators and their prey is one of the most important goals in aquatic ecology. We studied spatial and temporal onshore–offshore distribution patterns in young of the year (YOY) Eurasian perch (Perca fluviatilis) and crustacean zooplankton (Daphnia hyalina, Cyclops prealpinus) along a transect in Lake Annecy (France). Our study represents a first attempt at coupling hydroacoustic fish survey and high frequency zooplankton recording to assess simultaneously the large-scale distribution patterns of YOY fish and their zooplankton prey over a diel cycle (day, dusk and night sampling). We hypothesized that the spatial distribution of zooplankton could be shaped by both anti-predator behaviour (horizontal and vertical migrations) and predation losses. Fish biomass, size structure and diet were assessed from split-beam echosounding and net trawling samples, whereas crustacean abundances were estimated with a small modified Longhurst–Hardy continuous plankton recorder. We evaluated the diel changes in the spatial distribution patterns of fish and zooplankton and determined the overlap between their distributions. Fish biomass was dominated by YOY perch in upper warmer layers and salmonids (Coregonus lavaretus and Salvelinus alpinus) in the colder and oxygenated deep layers. YOY perch were aggregated in dense schools in the epilimnion during the day and dispersed at night. Fish biomass was distributed along a strong increasing onshore–offshore gradient at night, whereas crustacean prey showed a decreasing gradient. This onshore–offshore negative gradient in crustacean distribution, expressed on a shorter scale during the day, shifted toward the surface waters at night. A distinct kinetic of diel vertical migration (DVM) patterns was exhibited by daphnid and cyclopoid populations and resulted in distinct vulnerability to perch predation. Spatio-temporal distribution of crustaceans in Lake Annecy during the diel cycle study was probably shaped both by predation loss to YOY perch and by anti-predator behaviour (DVM, DHM) by zooplankton. The implications for fine-scale studies of fish-zooplankton interactions are discussed.

INTRODUCTION

The spatial distribution of crustacean zooplankton in lacustrine environments is affected by multiple physico-chemical and biological processes, the nature and the relative importance of which vary among ecosystems and at different spatial and temporal scales (Lampert, 1993; Angeli *et al.*, 1995a; Pinel-Alloul, 1995). Fish predation has been cited as one of the most important factors influencing zooplankton community structure (Brooks and Dodson, 1965) and distribution over space and time (Urabe, 1990). To counteract fish predation, zooplankton have developed avoidance strategies, such as diurnal horizontal migration (DHM) in weedy littoral zones (Davies,

1985) and diel vertical migration (DVM) in deep and cold waters (Gabriel and Thomas, 1988; Lampert, 1993; Ringelberg, 1993) as well as in the sediment (De Stasio, 1993).

The relative importance of zooplankton DHM and DVM as predator avoidance strategies can be evaluated by simultaneously surveying the distribution of zooplankton and fish on both horizontal and vertical scales within lakes. Indeed, in the pelagic zone of lakes, horizontal and vertical scales are interdependent as zooplankton and fish can move within both. Relationships, in lakes, between predators and prey on horizontal and vertical scales can thus lead to spatial and temporal distribution patterns of high complexity (Franke, 1987).

Given the difficulty of coupling fish and zooplankton sampling [e.g. (Post and McQueen, 1988; Rudstam *et al.*, 1993; Stockwell and Rand, 1993; Scheuerell, 1996; Hülsmann *et al.*, 1999)], there are still only a few studies that evaluate simultaneously the spatio-temporal distributions of both zooplankton and fish. In most studies, vertical and horizontal distribution patterns were confounded by using discrete and coarse sampling designs based on only a few series of vertical hauls for zooplankton and catches with gill nets and/or seines for fish. Moreover, most studies were carried out on small scales and at few stations within a lake. Such sampling designs cope poorly with the discrimination and coupling of DHM and DVM patterns of fish and their zooplankton prey.

In this paper, we provide a more complex description of the diel patterns of the vertical and horizontal distributions of prey (crustacean zooplankton) and predators [young of year (YOY) Eurasian perch *Perca fluviatilis*] in a deep sub-alpine lake (Lake Annecy) along an onshore–offshore transect. We hypothesized that the spatial distribution of zooplankton could be shaped by both antipredator behaviour (horizontal and vertical migrations) and predation. Horizontal and vertical distributions of cladocerans, copepods and size classes of fish were explored in late June at different periods of a diel cycle (afternoon, twilight dusk and early night), using simultaneous acoustic sampling of fish distribution and continuous horizontal recording of zooplankton for the first time. The main objectives of this study were to assess: (i) the degree to which the onshore–offshore spring distribution of YOY perch is related to the horizontal and vertical distributions of pelagic crustaceans (daphnids and cyclopoids) during late spring; (ii) the variations in fish and crustacean distribution patterns at different periods during a diel cycle; and (iii) the relationships between prey and predator distributions, which account for the spatial structure.

METHOD

Study site and lake conditions

Lake Annecy (maximum depth 65 m, length 13.7 km, width 3.1 km) is a monomictic sub-alpine lake of glacial origin, situated at an elevation of 446 m in the Northern French Alps (45°50′N, 6°40′E) (Figure 1). The lake is divided into two geographic units of similar mean depth (41.5 m), covering a total area of 24.5 km^2 for a receiving catchment of 278 km^2. It is considered to be oligo-mesotrophic [total phosphorus 6–10 µg l^{-1} (Balvay *et al.*, 1997)].

Marked changes during the last two decades have been discribed in both the zooplankton and the fish communities in Lake Annecy (Balvay *et al.*, 1997; Carahnac, 1999; Gerdeaux *et al.*, 1999). With the drastic decrease of calanoid copepods, the mesozooplankton is actually mainly represented by *Cyclops prealpinus*, *Daphnia hyalina* and, in some years, by *Bosmina* spp. The large invertebrate predators (*Chaoborus flavicans*, *Leptodora kindtii* and *Bytotrephes longimanus*) remain in low densities. In contrast with the other large sub-alpine lakes of the region, Lake Annecy is distinct in having a very good salmonid production (Carahnac, 1999) and a high fish stock. This latter, before the reproduction of perch, is mainly represented by whitefish (*Coregonus lavaretus*), the dominant species, Artic char (*Salvelinus alpinus*) and, to a lesser extent, by lake trout (*Salmo trutta lacustris*).

Sampling was carried out at the new moon, in the third week of June 1996 in the Sevrier area of Lake Annecy (France). Climatic conditions were stable during the second and third weeks of June, with a clear sky, mean daily air temperatures of between 19 and 23°C and mean wind speeds from 1.9 to 3.4 m s^{-1}. Extensive observations, tightly coupling fish echosounding and zooplankton samplings, were undertaken on June 18–20, with vertical patterns of temperature, oxygen and chlorophyll *a* assessed using a multiparameter probe (ME, Standard-ECO-probe Version II, Series 52), at six stations distributed from onshore (10 m depth) to offshore (60 m depth) along the Sevrier transect (Figure 1). Secchi depth transparency was measured, but irradiance could not be assessed owing to equipment failure. However, as algal biomass is always weak in Lake Annecy and similar among years (Balvay *et al.*, 1997), we have inferred light variation patterns at dusk from records made on June 17–18, 2000 (very clear sky as on June 17–19, 1996, similar values and profiles of fluorescence) (see Figure 4). Isolumes of light intensity were deducted from the percentage of underwater light extinction (23% m^{-1}) obtained on June 17–18, 2000 from vertical profiles at a station 30 m deep, offshore of Sevrier. Ephemerides for
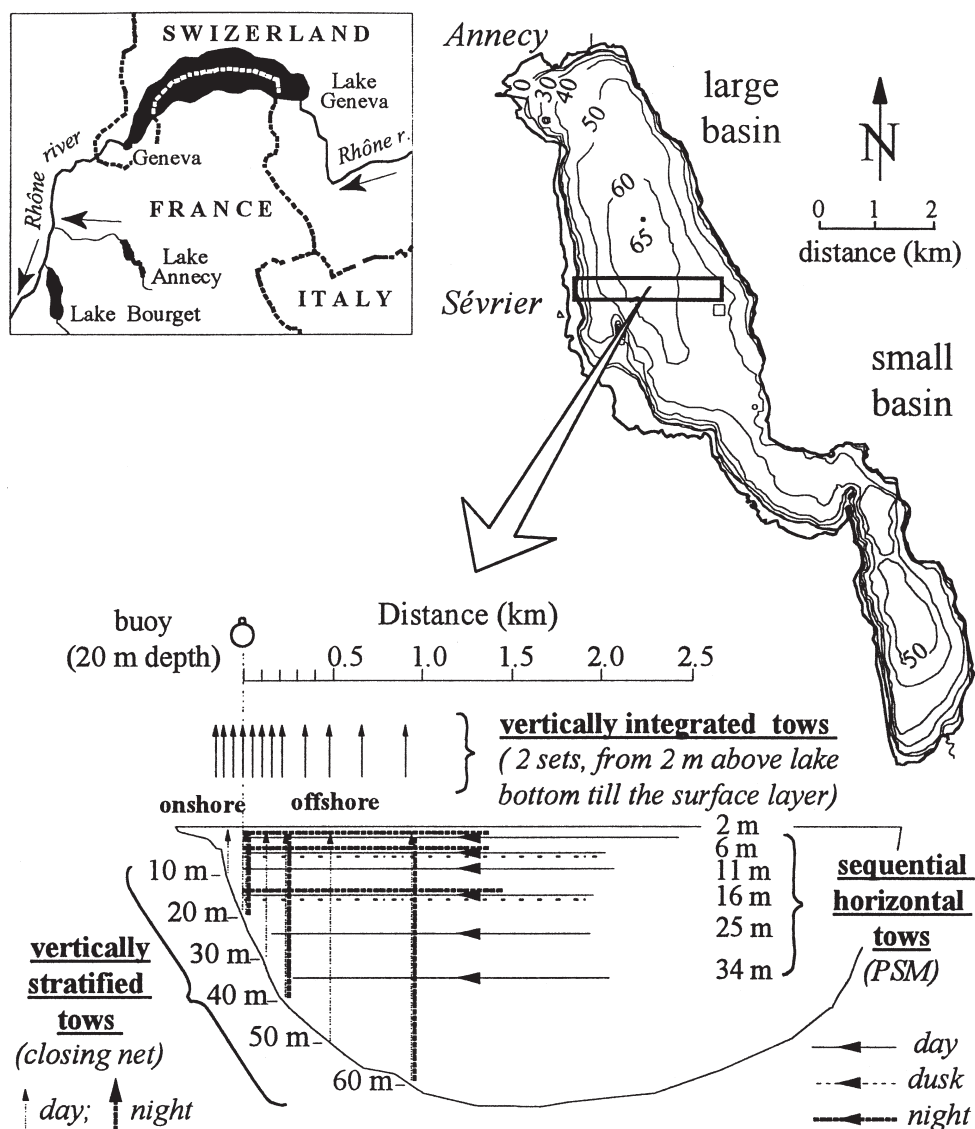
Fig. 1. Bathymetric map of Lake Annecy, with sampling locations for both physico-chemistry and zooplankton small-scale (a to f) and large-scale (2 to 34 m) surveys.

Annecy city were obtained from the 'Bureau des longitudes' (http://www.bdl.fr/), and light extinction data were collected with a LI-COR underwater quantum sensors (LI-192SA) connected to a LI-1400 data logger. As light intensities are often reported in photometric units in the literature, we have considered the rough equivalence between 1 lux and 0.0195 μE m^{-2} s^{-1} (Briggs, 1989).

Zooplankton continuous recording

Several complementary sampling devices were used to determine large- and fine-scale distributions of crustaceans. Zooplankton horizontal distribution was assessed with sequential tows using a multiple-serial

Plankton Sampling Mechanism (PSM, Figure 2a). Zooplankton horizontal sampling was tightly coupled with the acoustic survey of fish biomass. The PSM custom-made device is a light (28 kg) prototype of the oceanographic CPR (Continuous Plankton Recorder) or LHPR [Longhurst–Hardy Plankton Recorder (Longhurst *et al.*, 1966)]. The prototype used in this study (Figure 2b) was 2.22 m long with a frame diameter of 0.46 m, a mouth area of 0.024 m^2, and a net bag 1.17 m long with a 0.51 m long filter (200-μm-mesh size). The principle of this filtering system is simple: as zooplankton are collected, they are immobilized and stored between two rolls of gauze (200-μm-mesh size) rolled up at regular intervals in a
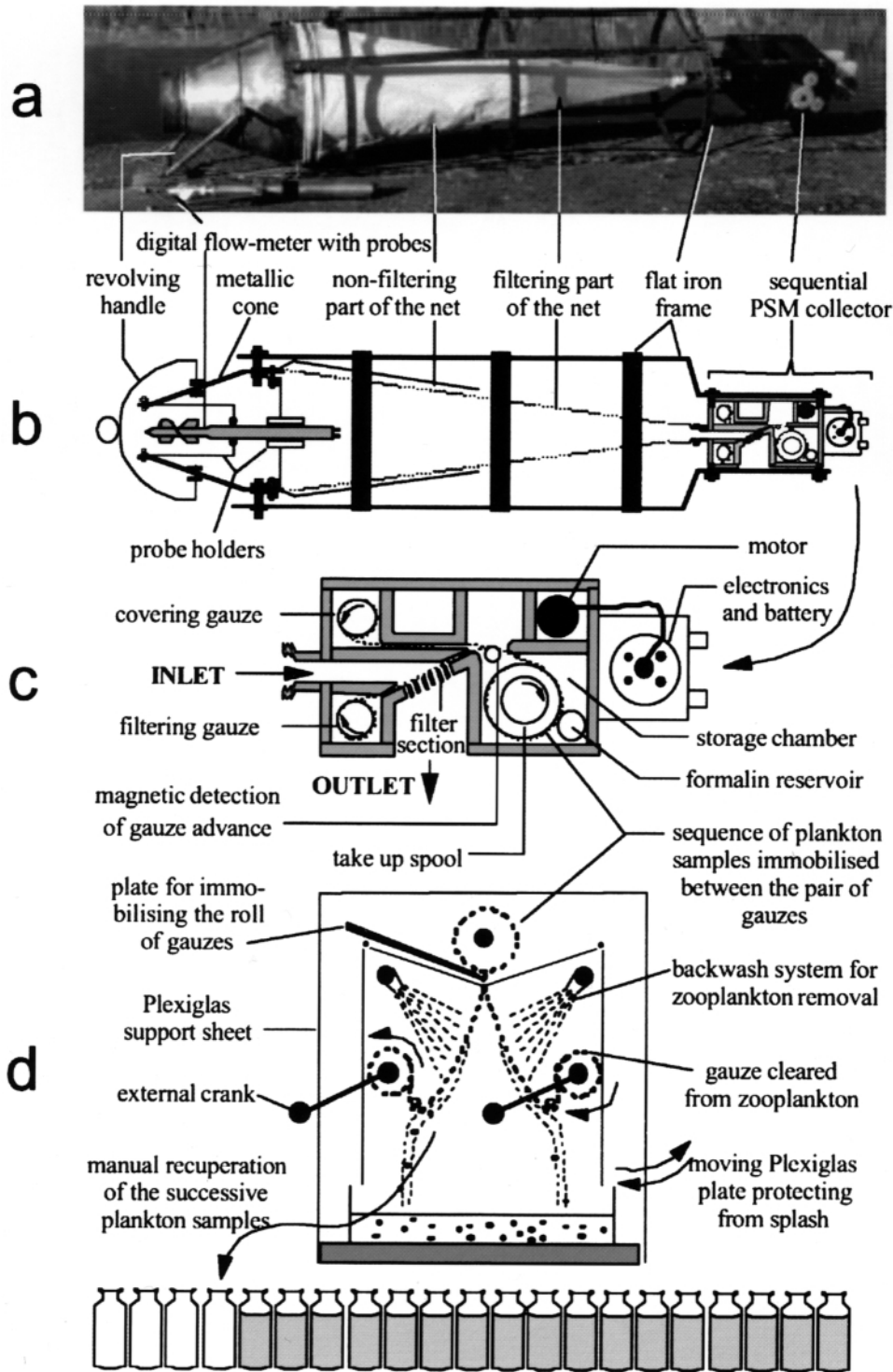
Fig. 2. Illustration of the continuous plankton recorder: (**a**) photography; (**b**) general characteristics; (**c**) Plankton Sampling Mechanism (PSM); (**d**) zooplankton extractor.

storage compartment (Figure 2c). Sampling frequency and gap between each zooplankton sample are controlled by the gauze advance, which is turned on by water contact and programmed by an electronic card. This PSM device provides sample series along large-scale distances and, with a maximal spatial resolution of a few

tenths of metres, it is adapted for the detection of horizontal aggregations of zooplankton. A digital flow meter, turned on by water contact (Valport U.K.: self recording model number 104-1, see Figures 2a to 2b) and equipped with a temperature and a pressure probe, was fixed in the mouth of the net for *a posteriori* estimation of the volume of water filtered per sample, water temperature and sampling depth. For better control of the digital flow meter, and a rapid stabilization of the PSM at the chosen sampling depth, a 17 kg depressor was fixed under the mouth of the PSM via a 2.5 m cable.

A pre-sampling was carried out at day and night on June 17, 1996; this allowed a rough detection of the distribution patterns of zooplankton and fish communities. On this basis, diurnal horizontal patterns of zooplankton distribution were assessed by continuous recording with the PSM, repeated along the Sevrier onshore–offshore transect at six successive discrete depths of 2, 6, 11, 16, 25 and 34 m (Figure 1). This extensive exploration was carried out on June 18 and lasted from 13:30 h to 18:00 h. To detect diel patterns in large-scale zooplankton distribution, the horizontal sequential tows were repeated at two depths (6 m and 16 m) during the short dusk period (from 21:30 h to 22:30 h) and at three depths (2 m, 6 m and 16 m) in the early night (23:00 h to 0:45 h) on June 18–19. All sampling depths were chosen because of their relative plankton densities assessed the previous day and night. Given the time (2–6 min) required for the device to reach a fixed sampling depth and to stabilize, the tows were always started offshore in the pelagic area, at a station 60 m deep, and carried out in the direction of a buoy anchored onshore at 20 m depth (Figure 1). The sampled distances varied between 1.8 and 2.52 km during the day, and between 1.32 and 1.44 km at dusk and night. By cruising at a constant speed of 3 knots, and by setting the PSM mechanism to obtain a segmentation of the zooplankton tows at 39 second intervals (corresponding to a spatial resolution of 60 m), each tow enabled the collection of between 21 and 42 zooplankton samples. After each transect, the pair of gauzes, with the animals sandwiched in between, were individually placed in a tight bag and preserved with formaldehyde solution (4% final concentration).

In the laboratory, the pair of gauzes was unrolled. Each section corresponding to a horizontal integration of 60 m was spatially identified, according to its position on the gauzes. The zooplankton were removed with a specially designed extractor (Figure 2d). For this operation, the free extremities of the gauzes were first introduced into the slot opened at the basis of the upper compartment. Then, the wires were placed below this splash protector, separating the pair of gauzes and enabling the zooplankton to be back-washed and retained in the lower compartment.

Because few zooplankton were collected at the shallower depth explored during the day, sequential samples of this series were pooled in sets of three samples for further analysis. In all samples, daphnid and cyclopoid copepod densities were estimated either from the entire samples or from sub-samples (10–50%), depending upon animal density.

Small-scale vertical distribution of zooplankton was assessed with discrete sampling using a closable plankton net (23 cm mouth aperture, 64-μm-mesh size) over six stations distributed along the transect from 10 m to 60 m depth (Figure 1) and repeated at the different periods of the diel cycle, as for the horizontal zooplankton recording (see before). To assess areal mesozooplankton biomass (deducted from the ash free dry weight of the sestonic fraction >200 μm) and composition, complementary sampling also included repeated series of vertically integrated tows (mesh size 200 μm) at 12 stations distributed along the studied transect.

Fish hydroacoustic surveys

The hydroacoustic estimates of fish biomass and size spectrum were made with a Simrad EY500 split beam digital sounder. The EY500 has a frequency of 70 kHz and a pulse duration of 0.6 milliseconds. The echosounder was equipped with a circular transducer (total beam angle of 11° at –3 dB) generating five pings per second and was utilized with two TVG (Time Varied Gain) amplification functions: $[2\alpha R + 20\log(R)]$ and $[2\alpha R + 40\log(R)]$, where α is the sound attenuation coefficient in freshwater and R is the distance in m between the target and the transducer. According to the TVG function selected, a calculation of the biomass $[2\alpha R + 20\log(R)]$ or the size distribution of the echoes $[2\alpha R + 40\log(R)]$ can be computed (MacLennan and Simmonds, 1992). The transducer was mounted on a pipe fixed to the side of the boat and submerged 0.5 m under the water surface.

The system was calibrated by insonifying a copper sphere (TS = –39.2 dB), as defined by the EY500 sounder manual (Simrad, 1994) and recommended by Foote *et al.* (Foote *et al.*, 1987). The discrimination of single fish targets was set at a threshold of –70 dB, using the tracking menu options of the EY500 with the default settings. Data processing was carried out in the laboratory using the EP500 software (Simrad, 1994). The results obtained were reported in dB for the target strength distribution and for the acoustic biomass calculation (Area back-scattering coefficient term Sa by Simrad) in m^{-2} ha^{-1}.

To relate fish and zooplankton distributions, the echosounding survey was performed simultaneously with the sequential PSM tows, three times during the diel cycle (at afternoon, twilight dusk and early night). Boat speed was maintained as constant as possible: $1.4 (\pm 0.1)$ m sec^{-1}.

The echointegration sequences were set to cover the same distances (spatial scale of 60 m) as each PSM sampling. Fish and zooplankton spatio-temporal distributions were compared by considering fish biomass detected in strata 5 m thick and centred on the depth of each PSM trawl taken at 2, 6 and 11 m, or in strata 10 m thick for tows made in the deeper zones (16, 25 and 34 m; Figure 1).

Following these simultaneous night time surveys of zooplankton and fish distributions, trawling was conducted at 1.5 and 4 m depths with an ichtyoplankton net (1.5 m of cone diameter and 1 mm mesh aperture) to identify the tiny epilimnetic acoustic targets. The collected fish were identified and measured. Then, sub-samples of individuals representative of the fish size range were used for gut content examination (20 fish from the first trawl, 15 from the second trawl). All organisms found in the digestive tracts were identified and counted.

Statistical analysis

The horizontal distributions of daphnids, cyclopoids and fish were first described by density maps at different depths and distances to shore. To reduce asymmetry and to increase the linearity of the product–moment correlation analyses (Legendre and Troussellier, 1988), a $\log_{10}(x + 1)$ transformation was applied to the variables. Normality of density values of zooplankton and biomass estimates of targeted fish was verified using Kolmogorov–Smirnov tests. Normalization tests and transformations were performed using SPSS 4.0 (Nie et al., 1984).

To detect spatial structures in fish and zooplankton distributions, spatial correlograms were computed for each sampling depth and period. Moran's index (Moran, 1950) was used as a spatial autocorrelation coefficient because it behaves mainly like Pearson's correlation coefficient and is sensitive to extreme values (Legendre and Fortin, 1989).

Standard correlational methods are inefficient at resolving spatial phenomena in studies of predator–prey distribution [e.g. (Ord, 1979)]. So, for each of the explorations made along the offshore–onshore transects in the epi- and metalimnion (at 6 and 16 m depths), Mantel tests (Mantel, 1967; Legendre and Fortin, 1989) were performed to determine the spatial association between daphnids, cyclopoids and fish. Similarity matrices were computed using Gower's asymmetric coefficient for the zooplankton and fish variables. Partial Mantel tests (Smouse et al., 1986; Legendre and Fortin 1989) were performed to determine if the observed correlations between organisms were spurious, resulting from the fact that daphnids, cyclopoids and fish follow a common or an opposed spatial structure as a result of some unknown factor(s). Partial Mantel tests are fully explained in

Legendre and Fortin (Legendre and Fortin, 1989). All statistics were performed using the R progiciel package (Legendre and Vaudor, 1991) for Macintosh computers.

RESULTS

Water stratification and light conditions

On the 3rd week of June 1996, Lake Annecy had been sharply stratified for several weeks, with its strongest temperature gradient between 7.5 m and 10 m (Figure 3). Epilimnetic temperatures ranged from 21.5 to 18°C. As often happens in this lake (Balvay et al., 1997), phytoplankton presented a metalimnetic peak (chlorophyll a 5.1 ± 0.25 µg l^{-1} at around 15 m depth) a few metres below the oxygen maximum (14 ± 0.3 mg l^{-1} at 12–13 m depth). The entire water column was well oxygenated, with more than 9.5 mg l^{-1} O$_2$ down to lake bottom (Figure 3).

The Secchi depth ranged from 4 to 4.6 m, suggesting that the euphotic layer extended down to 10–12 m. The relative light variation (RLV) threshold of –0.06 mn^{-1} [reported by (Ringelberg, 1991) for obtaining positive phototactic responses (i.e. an upward migration) of Daphnia], is likely to be met first at a time of 19:27 h (RLV > |0.06|; Figure 4) when the sun is hidden by a mountain ridge that represents the catchment watershed. This period of light variation is short-lived and the signal is soon reversed. This threshold is again exceeded after 21:10 h (Figure 4), during a longer period starting a quarter of an hour before 'theoretical' sunset (21:27 h) (by 'theoretical' we mean that
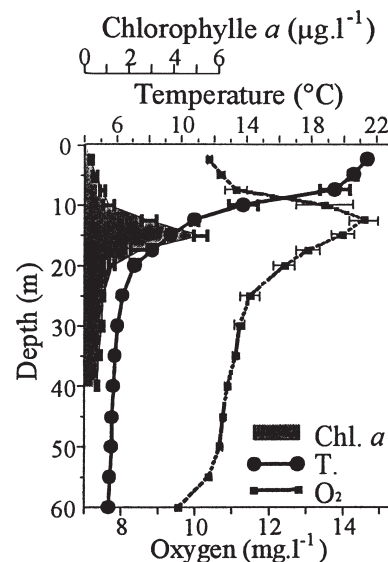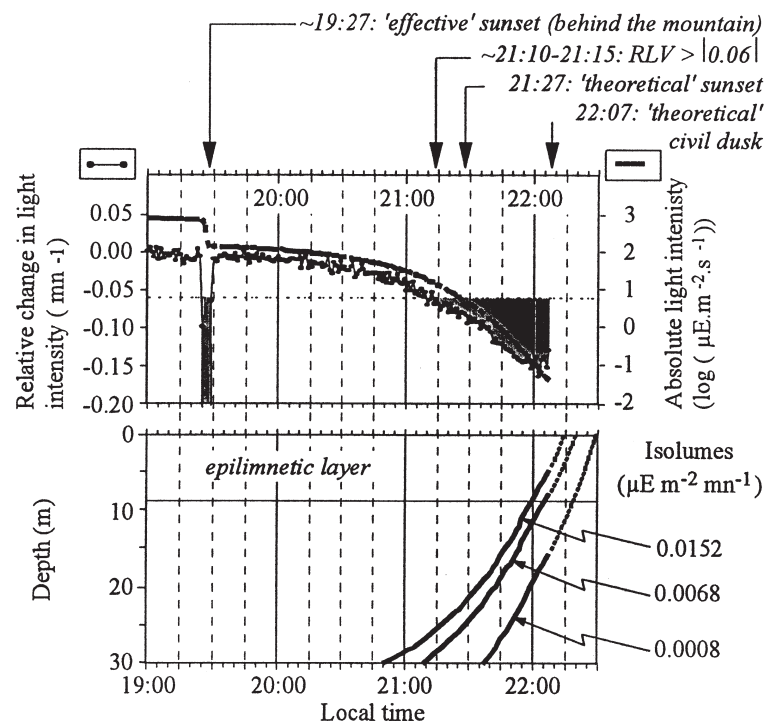

Fig. 3. Vertical profiles of temperature, oxygen and chlorophyll fluorescence in Lake Annecy, June 18, 1996. Standard deviations are presented with mean for every 5 m depth.

Fig. 4. Timing of light variations recorded on June 17–18, 2000 under ambient conditions close to those prevailing on June 17–18, 1996 (very clear sky, similar values and profiles of fluorescence). Thick, dotted curve, absolute light variations; solid circles, relative light variations (RLV); dashed area, absolute values of RLV exceeding the threshold reported by Ringelberg (Ringelberg, 1991) for obtaining a phototactic response of *Daphnia hyalina*; thick oblique lines, isopleths of light intensities expressed in µE m^{-2} s^{-1}. Theoretical sunset and civil dusk are respective moments when the sun should be at the horizon, then 6° below, if there where no relief.

ephemerides provided by 'the Bureau des longitudes' are not corrected for local relief; thus, sunset corresponds to the time when the sun would be at the horizon if there were no relief). Moreover, the isolumes deducted from civil dusk (the time at which the sun should be 6° below the horizon if there were no relief) to around 23:00 h, cover the range of light intensities at which Flik *et al.* (Flik *et al.*, 1997) observed a shift from 90% to 10% in the efficiency of prey attacks by YOY perch in *in vitro* experiments.

Diel and spatial distributions of fish and crustaceans

Diurnal surveys revealed a marked opposition between fish and zooplankton distributions on both vertical and horizontal axes. Overall, most (85 ± 8%) of the fish biomass detected was concentrated in the upper 10–12 m and presented greater values offshore (400–2000 m) than onshore (10–400 m), especially at night (Figure 5). The autocorrelograms (Figure 6) reveal that fish did not present a significant horizontal spatial structure over the range of distance classes (60–1200 m) and depths (6–34 m) during daytime (Figure 6a) and at dusk at 6 m and 16 m (Figure 6b), but were strongly spatially structured at night in the epilimnion at 6 m (Figure 6c).

By contrast, daphnids and cyclopoids exhibited a very strong diel vertical migration pattern. They were extremely scarce in the epilimnion (0–10 m) and concentrated in the metalimnion (10–20 m) and hypolimnion (>20 m) during daytime, whereas they were highly aggregated in the epi- and metalimnion (0–20 m) at night (Figure 5). Moreover, zooplankton exhibited a marked decreasing onshore–offshore gradient in the metalimnion and hypolimnion during the day, and in the epilimnion at night, which opposed that of the fish. According to the autocorrelograms (Figure 6), this onshore–offshore negative gradient in crustacean abundances extended over the entire transect in the metalimnion during daytime (Figure 6a). The same decreasing trend was also detected in the upper part of the hypolimnion (at 25 m depth), but there this pattern only persisted a short distance (<240 m; Figure 6a), at least in the case of daphnids.

Distribution patterns observed at dusk are better documented for the vertical axis, at least for the offshore region, than for the horizontal axis (Figure 5). Although there were only two PSM trawls made at dusk, the pattern at 6 m revealed slightly greater zooplankton densities in this upper layer than during daytime, and the inverse at 16 m, suggesting an upward migration (Figure 5). In contrast to
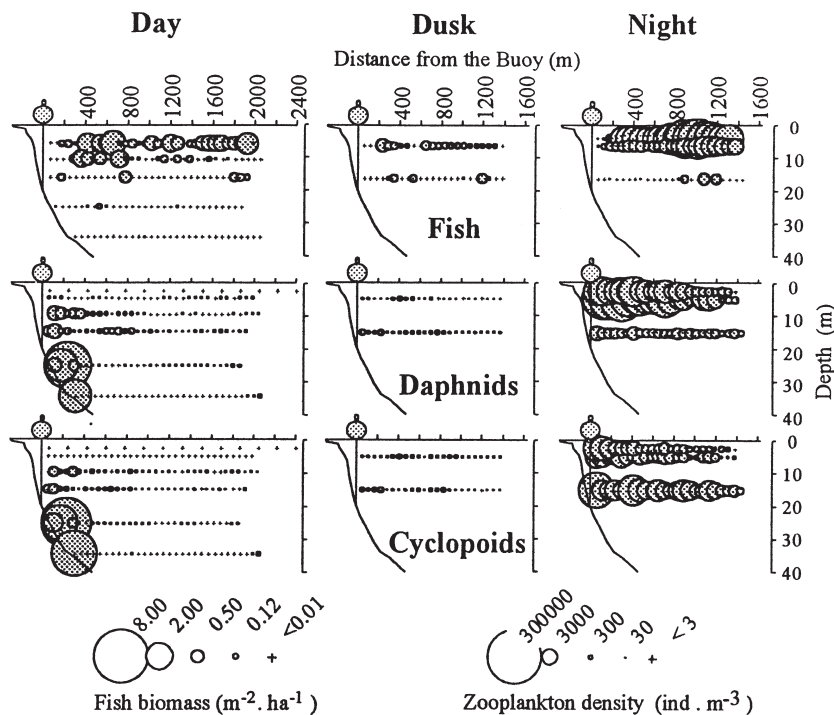
Fig. 5. Horizontal and vertical distribution of fish, daphnids and cyclopoid during the day, dusk and night periods in Lake Annecy, June 18–19, 1996.

daytime, the epilimnetic dusk distribution of daphnids and cyclopoids was then structured and presented a significant decreasing onshore–offshore gradient (Figure 6b). The three further explorations conducted at night with the PSM (from respectively 21:10 h at 16 m depth, 23:30 h at 6 m depth and 0:30 h at 2 m depth), showed that the negative onshore–offshore gradient was reinforced at night (Figure 5) and extended to mid-lake (Figure 6c). The biomass of fish then showed a significant correlogram, indicating an opposite increasing trend from onshore to offshore in the epilimnion, which did not extend in the metalimnion (Figure 6c).

Spatial variations in fish echograms and size spectrum.

The increasing onshore–offshore gradient of fish biomass detected in the epilimnion at night on June 18 (Figures 5 and 7b) was observed on both sides of the lake (Figure 7a) during each of the consecutive nights of this campaign. It was also observed over a wider region (about 10 km²) during the pre-sampling campaign. The main difference between the diurnal and nocturnal onshore–offshore distribution of fish in the epilimnion was that, during daytime, epilimnetic fish were cruising in small schools (Figure 7c). These tight and numerous

aggregations dispersed at dusk. The first signs of this phenomenon, which developed fast, were detected around of 21:45–21:50 h (i.e. some 20 min after 'theoretical' sunset and just before civil dusk: see Figure 4). The vertical distribution of fish biomass presented a strong discontinuity at a depth of 5–6 m at night (Figure 5) to around 8.5 m depth at dusk (that is at the upper limit of the thermocline), after the beginning of the dispersal of the schools (Figure 7c). Once schools were broken at night (allowing a better estimation of the total area backscattered) epilimnetic echoes represented $85 \pm 8\%$ of the detected biomass (Figure 7b). All those distributions are representative of echoes observed at greater scales a few consecutive days and nights before and after the extensive surveys coupled with the PSM tows.

In the upper 10 m, fish were cruising in such tight schools during the day that only a few individuals per diurnal transect could be discriminated as individual echoes by the algorithm of data treatment (Figure 8a). In contrast, single echoes were common from 10 m depth to near the lake bottom. There, more than one hundred individual targets were discriminated per diurnal transect, allowing evaluation of their size spectrum. The diurnal scattergram (Figure 8a) suggests a vertical distribution in two large patches, one extending below 40 m
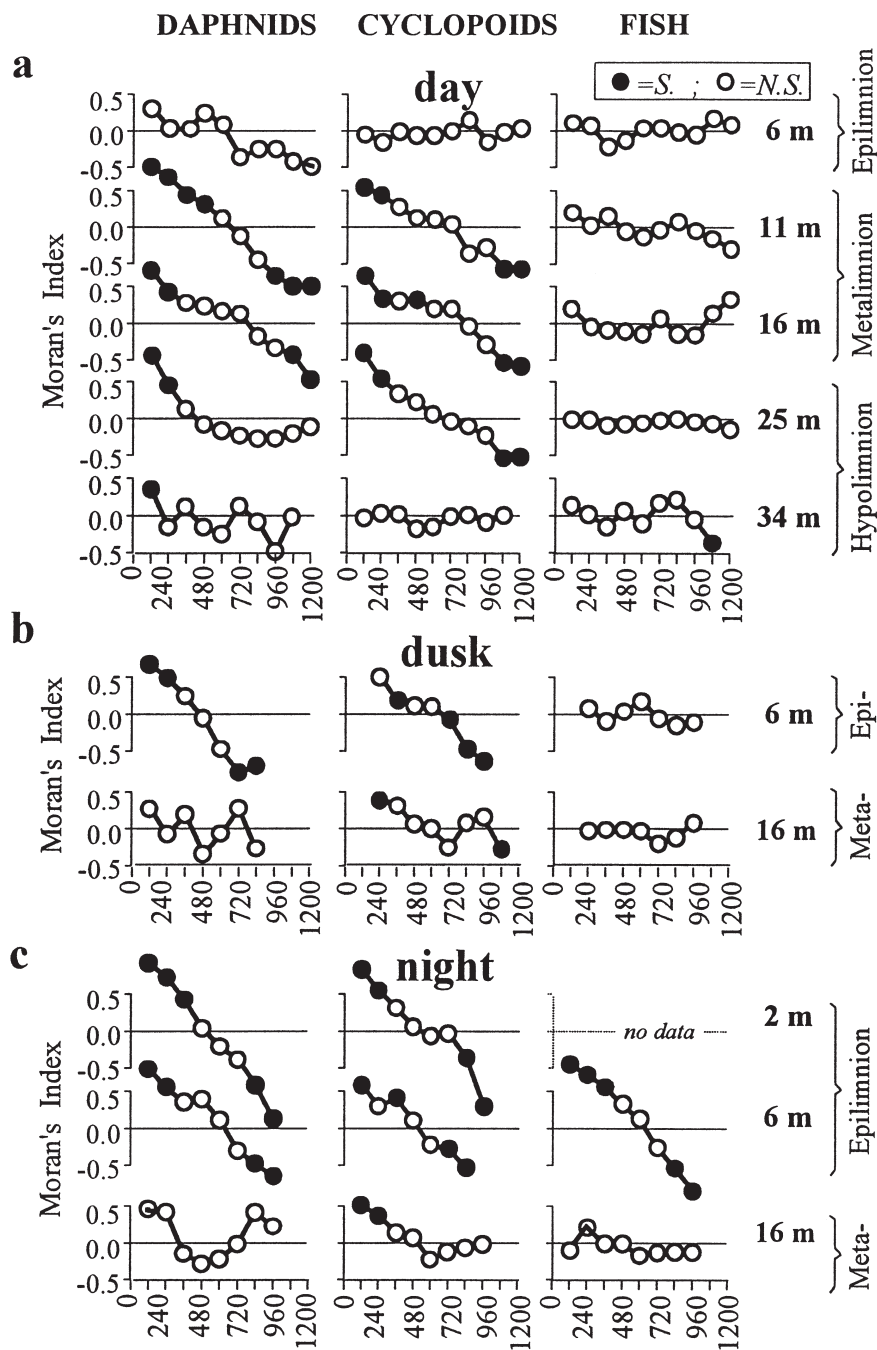
Fig. 6. Spatial correlograms obtained for the daphnids, cyclopoid copepods and fish distribution during the day (**a**), dusk (**b**) and night (**c**) periods in Lake Annecy, June 18–19, 1996. ●, represent significant autocorrelation, whereas ○, indicate no significant autocorrelation.

and the other one through the upper part of the hypolimnion. The size spectrum of these targets ranged from –48 dB to –30 dB and presented a weak mode between –38 dB and –34 dB (Figure 8b). School dispersal at night led to a maximization of the occupation of space in the upper part of the epilimnion (Figures 7c).

Targets discriminated as single fish were widely spread in the water column at night (Figure 8c); they also presented a more variable size and a wider spectrum (Figure 8d). These two characteristics seem to be related to a nocturnal, upward migration of the fish that was very clearly observable in the case of large benthic fish. Below 10 m,
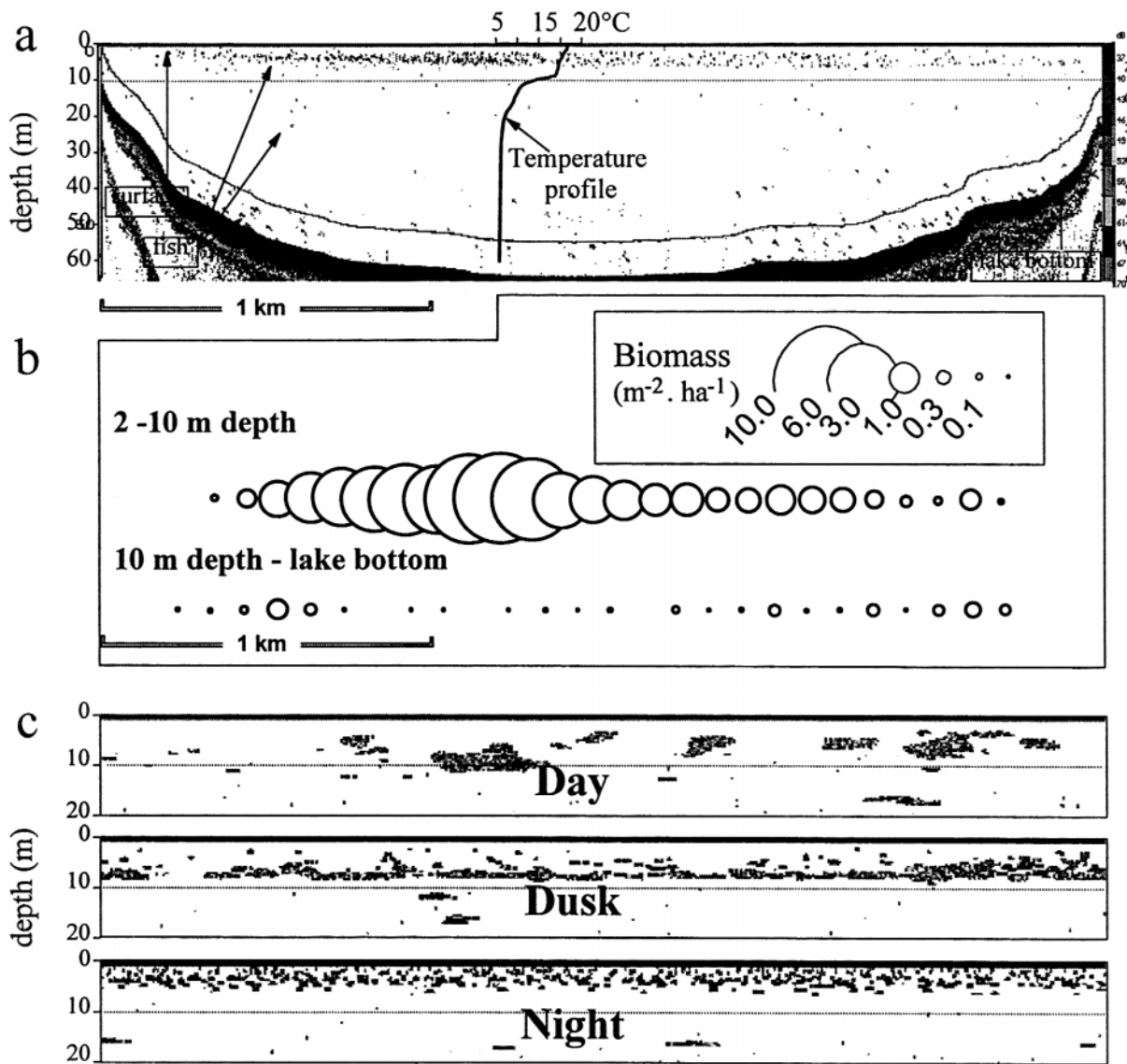
Fig. 7. Distribution of fish along a transect in Lake Annecy on June 18–19. (**a**) Nocturnal echogram recorded from the western to the eastern shore; (**b**) global areal acoustic biomass detected respectively above and below 10 m depth; (**c**) offshore echograms showing the day-to-night changes in fish aggregation and vertical distribution in the top 20 m.

this nocturnal size spectrum was somewhat flattened than during daytime. In contrast, above 10 m it presented a very distinct mode at –58 dB (Figure 8d).

Species composition, size and diet of the dominant size-classes of fish echoes

Nocturnal trawls carried out on June 19 at 1.5 and 4 m depths (from respectively 22:50 h to 23:03 h, then 23:06 h to 23:18 h), enabled echoes of –58 dB (main mode) to be identified as YOY perch (29 ± 5 mm). In fact, perch were the only species caught. Their size distribution in the two samples ranged from 21 to 42 mm. Based on an

examination of a large sample of YOY perch captured in 1997 during the same period as in 1996, the vast majority of specimens had achieved the juvenile period of development [*sensu* (Zedivá *et al.*, 2000)], with <5% not possessing one or more of the essential characters of that period (e.g. complete scale cover, complete bifurcation of fin rays). Given their narrow size spectrum and the strong contribution of small echoes to acoustic back-scattering (Figures 7a, 8c,d), YOY perch seem to dominate strongly the fish biomass of epilimnetic offshore waters in June. Given this dominance and the vertical distribution of small echoes, one may tentatively convert the total

DAY   **NIGHT**

Distribution
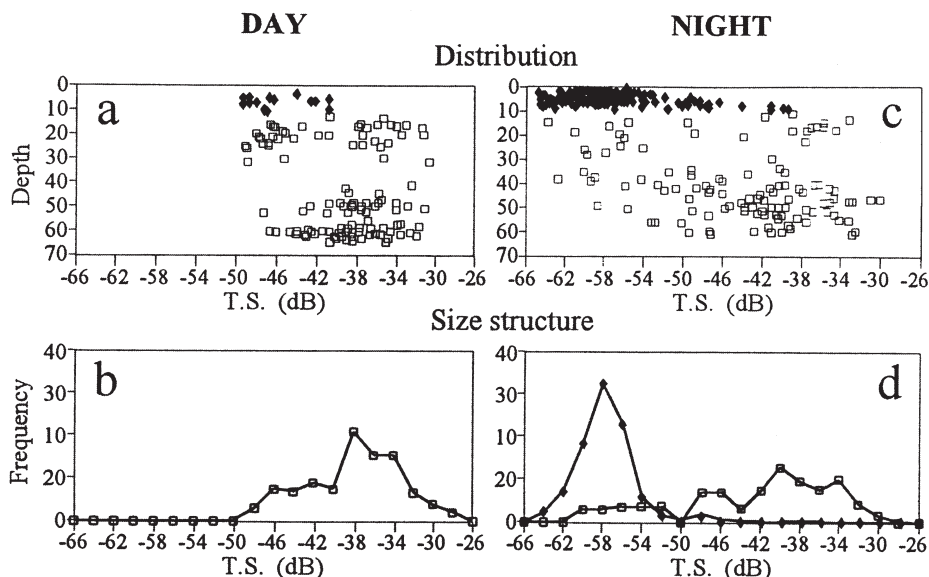
Size structure

Fig. 8. Day and night depth distribution (**a**) and size structure (**c, d**) of the acoustic targets detected during the explorations made with the PSM in Lake Annecy, June 19–20, 1996. Echoes from 0–10 m depth (△)and from 10 m to lake bottom (□). Areas without filled symbols in (**a**) and (**b**) strictly means no fish apart from a shoal (and not necessarily no fish at all).

surface back-scattered per surface unit in the upper 11 m into a rough order of perch abundance or fresh weight (Table I). On the basis of the formulae proposed in the literature (see legend of Table I) and assuming that the acoustic biomass was represented by fish having the same modal size (29 mm) and weight (0.25 g) as the captured perch, a mean density of 24–51 YOY perch m^{-2} (60–130 kg ha^{-1}) can be estimated for the offshore region (depth >20 m) and twice as much in the mid-lake region of the biomass peak (see Figure 7b).

The analysis of the digestive tracts of the perch collected 120 and 140 min, respectively, after 'theoretical' sunset, revealed that daphnids and cyclopoids were the main food items. With a mean number per gut of 67 ± 22 cyclopoids and 9 ± 7 daphnids in fish from the first tow and 43 ± 25 cyclopoids and 6 ± 4 daphnids in fish from the second tow, cyclopoids represented 88% of the ingested prey. In the gut of fish captured 140 min after 'theoretical' sunset, cyclopoids as well as daphnids were on average 20% less numerous. Given that fish presented the same modal size in both samples and that prey appeared more digested in the second one, this decrease seems more related with the speed of gut evacuation than with sampling depth or fish size. Indeed, epilimnetic temperature was very mild, and this percentage decrease within 20 min (53% h^{-1}) is consistent with the very fast rates of full gut evacuation (1–2 h) reported for YOY fish, including yellow perch *Perca flavescens* (Mills *et al.*, 1984), a closely related congener of Eurasian perch. It is difficult to compare this

diet with the composition of zooplankton in the environment. Indeed, the contents of fresh guts probably reflect twilight migrations of both plankton and fish. However, if we refer to the stratified samples collected offshore just before the first catch, in which the cyclopoid-to-daphnid ratio shifted from 80% in the 2.5–5 m layer to 97% in the upper 2.5 m, gut contents appear to reflect prey availability. With respect to fish size, no trends, could be detected in the size or composition of prey which ranged greatly in size.

Spatio-temporal coupling between distributions of daphnids and copepods

The spatial relationships between daphnid and cyclopoid distributions, quantified by simple and partial Mantel tests for the three sampling periods and two depths (6 and 16 m), varied with both time and depth (Table II). During the day, the correlation between daphnid and cyclopoid abundances in the epilimnion (6 m depth) was significant but weak ($r = 0.31$ $P < 0.001$; Table IIa), increasing at dusk ($r = 0.55$; Table IIb), and becoming strong at night ($r = 0.93$; Table IIc). For both taxa, autocorrelation with space was either non-significant or weak during the day ($r = 0.22$; Table IIa) but increased at dusk ($r = 0.31$–0.42; Table IIb) and night ($r = 0.62$–0.63; Table IIc). Indeed, simple correlations between daphnid and cyclopoid abundances did not change during the day (–S = 0.30; Table IIa) when removing the effect of space, but decreased significantly (–S = 0.49 and 0.89; $P < 0.001$) at dusk and night (Tables

Table I: Mean areal density and biomass assessed for zooplankton (whole water column) and YOY perch (upper 11 m) in Lake Annecy on June 17–20, 1996

	Zooplankton			YOY perch	
Depth of stations	Biomass fraction >200 μm (g m^{-2} FW)	Density (ind. m^{-2})	Cyclopoids (%)	Density (ind. m^{-2})	Biomass (FW g m^{-2})
5 m	0.4	2000	62	–	–
10 m	2.1	130 000	76	2*–4**	<1*–1**
20–65 m	23.0	660 000	29	24*–51**	6*–13**
				(Max. 48–103**)*	*(Max. 12*–26**)*

Conversion of ash-free dry weight (DW) to fresh weight (FW), assumes a DW : FW ratio of 1:10. The rough conversion of acoustic records to perch density and biomass, using the formulae of *(Foote, 1991), *(Guillard, unpublished data) and **(Imbrock *et al.*, 1996), assumes that all acoustic targets in the layer dominated by perch presented the same modal size (29 mm) and weight (0.25 g) as the captured perch.

IIb,c) suggesting a common spatial structuring. A similar decrease in correlations between daphnids and cyclopoids, after removing the effect of space, was also observed in the metalimnion (16 m depth samples). But there, the relationships between taxa were almost of similar strengths ($r = 0.66$–0.70) regardless of the diel period considered (Tables IId–f).

Spatio-temporal coupling between onshore-offshore distributions of fish and crustaceans

As expected from the maps (Figure 5), during day and dusk, the horizontal spatial structure of the daphnids and cyclopoids in the epi- (6 m) and metalimnion (16 m) was not significantly correlated with that of fish (Table IIa, b, d and e). Most crustaceans were below 20 m (Figure 5), thus interactions with juvenile perch were limited. In contrast, at night, when crustaceans and fish presented opposite onshore–offshore distribution patterns, correlations between fish and crustaceans distributions in the epilimnion ($r = 0.25$ for daphnids; $r = 0.29$ for cyclopoids) were positive and significant, although weak (Table IIc). However, once spatial effect was removed this correlation was no longer significant for cyclopoids whereas for daphnids the correlation became negative and stronger ($–S = –0.40$ $P = 0.001$) as could be suspected from the maps (Figure 5). Thus, partial Mantel tests suggest that the horizontal distribution of cyclopoids is partly explained by a factor, or factors, not retained in the study and that that of daphnids is partly explained by one or more of the factors not considered in this study as well as by the distribution of epilimnetic fish. In other words, partial Mantel tests suggest a nocturnal avoidance by daphnids of the regions of high fish density. No significant relationships were observed between crustaceans and fish in the metalimnion at any diel periods, whereas autocorrelation with space also increased during the night, as seen in the epilimnion (Table IId–f).

Coupling in fish vertical distribution and crustacean DVM

The timing of DVM is only partly documented with the series of stratified tows made in June 1996 (Figure 9). This series was completed later at almost the same period of the year and under same ambient conditions (June 22, 1997). The combination of both series on Figure 9 helps in understanding the dusk DVM phenology and its implications. The strong avoidance of the epilimnion (upper 7.5 m) detected in the afternoon (14:00–16:00 h) by both cyclopoids and daphnids, was still observed for daphnids but no longer for cyclopoids at 'theoretical' sunset. At that time, only a small percentage of the sub-population of daphnids collected in the upper 20 m was found in the epilimnion compared to >50% in the case of cyclopoids. Similarly, the maximal upward movement of cyclopoids was detected some 30–45 min after 'theoretical' sunset, but some 75–90 min later for daphnids. According to underwater light records made in June 2000 (Figure 4) and to the light requirement of perch for efficient prey capture (Flik *et al.*, 1997), in Lake Annecy the dense colonization of the surface layer by daphnids should only be developed once perch are likely to have sharply reduced (or stopped) feeding. The apparent result is a weaker and shorter dusk overlap between daphnid and perch vertical distribution than between perch and the dominant cyclopoid prey found in their gut after dusk. This phenology also suggests

Table II: Simple (upper right) and partial (lower left) Mantel statistics for the diurnal, twilight and nocturnal sampling of daphnids (D), cyclopoids (C) and fish (F) at 6 and 16 m depth in Lake Annecy, June 18–19, 1996

	6 m depth (epilimnion)				16 m depth (metalimnion)			
	Daphn.	Cyclop.	Fish	Space	Daphn.	Cyclop.	Fish	Space
Day (a)					**Day (d)**			
Daphn.	–	**0.31**	NS	**0.22**	–	**0.66**	NS	**0.38**
Cyclop.	**–F: 0.31** **–S: 0.30**	–	NS	NS	**–F: 0.69** **–S: 0.59**	–	NS	**0.49**
Fish	–C: NS –S: NS	–D: NS –S: NS	–	NS	–C: NS –S: NS	–D: 0.31 –S: NS	–	NS
Space	**–C: 0.21** **–F: 0.22**	–D: NS –F: NS	–D: NS –C: NS	–	–C: NS **–F: 0.40**	**–D: 0.34** **–F: 0.48**	–D: NS –C: NS	–
Dusk (b)					**Dusk (e)**			
Daphn.	–	**0.55**	NS	**0.42**	–	**0.66**	NS	**0.25**
Cyclop.	**–F: 0.54** **–S: 0.49**	–	NS	**0.31**	**–F: 0.67** **–S: 0.64**	–	**NS**	**0.25**
Fish	–C: NS –S: NS	–D: NS –S: NS	–	NS	–C: NS –S: NS	–D: NS –S: NS	–	NS
Space	**–C: 0.32** **–F: 0.47**	–D: NS **–F: 0.34**	–D: NS –C: NS	–	–C: NS **–F: 0.26**	–D: NS **–F:0.25**	–D: NS –C: NS	–
Night (c)					**Night (f)**			
Daphn.	–	**0.93**	0.25	**0.63**	–	**0.70**	NS	**0.33**
Cyclop.	**–F: 0.93** **–S: 0.89**	–	0.29	**0.62**	**–F: 0.70** **–S: 0.65**	–	NS	**0.51**
Fish	–C: NS **–S: –0.40**	–D: NS –S: NS	–	**0.74**	–C: NS **–S: 0.41**	–D: NS	–	NS
Space	**–C: 0.18** **–F: 0.67**	–D: NS **–F: 0.62**	**–D: 0.77** **–C: 0.75**	–	–C: NS **–F: 0.33**	–D: NS **–F: 0.51**	–D: NS –C: NS	–

Daphn., daphnids; Cyclop, cyclopoides.
Only significant values have been reported (values in bold, *P* <0.001).
Mantel tests are significant here at the Bonferroni-corrected probability level of 0.05/600 = 0.008; and partial Mantel tests at the Bonferroni-corrected probability level of 0.05/12 = 0.004; only significant values have been reported. Values in bold have a *P* <0.001. NS, tests not significant; negative values are underlined. –C, –D, –F, –S indicate the removal of, respectively, the effect of copepods, daphnids, fish, or space.

that the dusk period, during which YOY perch of Lake Annecy can meet a large amount of daphnids in the warmer waters before being too strongly light-limited to feed, is shorter than 1 h (at least by new moon).

A second difference between taxa was also recorded for the early 'midnight sinking' period, detected around 23:30 h, that is more than 2 h before astronomical midnight (01:42 h local time). This downward trend of the population seems to occur soon after full night for both taxa, but is more pronounced in the case of cyclopoids.

DISCUSSION

Vertical and horizontal distribution of fish biomass

Obviously, our study in late June, and further investigations in summer (Gerdeaux *et al.*, 1999) indicate that YOY perch are more densely represented in the pelagic zone of Lake Annecy at day and night times, in contrast to daphnids and cyclopoids which deserted the epilimnion during the day.
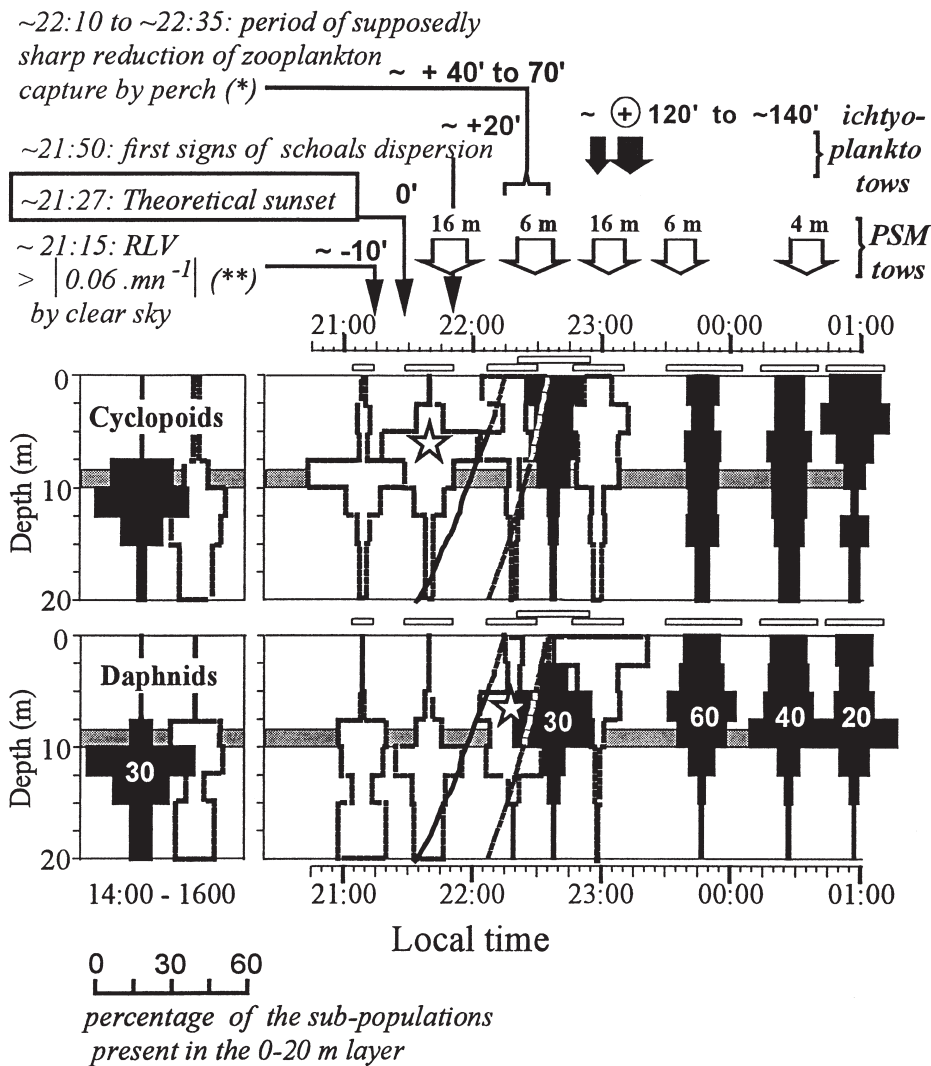
Fig. 9. Percentage distribution of daphnids and cyclopoids at depths in Lake Annecy in late June and tentative evaluation of the timing of their respective DVM. Solid histograms indicate part of the stratified tows made at different stations of the transect on June 19, 1996; open histograms represent similar tows made on June 22, 1997 at a station 60 m deep; white numbers are local depth of lake bottom. Small horizontal bars represent sampling duration of stratified tows; large black arrows indicate duration of ichthyoplankton tows; large white arrows show duration of sequential PSM tows, with indication of sampling depth. The horizontal shaded bars show the layer of sharper thermal decrease (~19°C to ~13°C). Oblique curves represent the supposed spatio-temporal window of sharp reduction of perch feeding (see legend of Figure 4). RVL, relative light variations recorded on June 17, 2000 under very clear sky (as on late June 1996); *According to both the experiences of Flik et al. (Flik et al., 1997) and to the local timing of light variations at this date on sunny days (Figure 4). (**)Minimal signal reported for obtaining a phototactic response (vertical movement) of D. hyalina (Ringelberg, 1991).

Most of the fish biomass detected in late June in Lake Annecy, in the upper 10 m, was mainly represented by YOY perch and these young were mainly staying in the upper warmer layer at temperature varying between 15 and 22°C. This behaviour is consistent with that reported in other studies (Post and McQueen, 1988; Flik et al., 1997). Indeed, with a physiological optimum of 25°C (Craig, 1987), these juveniles require relatively high temperatures (Houde, 1989; Imbrock et al., 1996), which enhance foraging ability in terms of distance attack reactions, swimming speed and capture rate (Bergman, 1987). Moreover, the genus *Perca*, with an ocular structure favouring more visual acuity than visual sensitivity [absence of a reflective *tapetum lucidum* (Craig, 1987)], also have high light requirements to detect the prey (Bergman, 1988; Flik et al., 1997) that can be met in the clear upper layers of lakes.

In June, YOY perch reached a modal size of 29 mm. At this size, Eurasian perch, like its American congener, is already very motile and more likely to return to shallow regions during daytime (Treasurer, 1988; Post and

McQueen, 1988). In the small mesotrophic lake Maarsseveen, schools of YOY perch are also encountered in the pelagic zone during the day in late June, but in this lake part of the population is also present onshore in large schools (Flik *et al.*, 1997). Ontogenetic habitat shift of perch, though rather considered as size-dependent (Post and Prankevicius 1987 in Urho, 1996), may vary with habitats and has been reported for very small sizes [10 mm (Urho, 1996)] as well as for larger ones [40 mm in Lake Constance (Wang and Eckmann, 1994)] than those found in Lake Annecy (modal size 29 mm). Between-lake discrepancies in fish distribution seem to be explained by the amount of offshore predators and the ratio of planktonic to benthic resources (Treasurer, 1988; Wang and Eckmann, 1994). Early return to the littoral zone is rather reported when there is a large amount of benthic prey (Urho, 1996). In Lake Annecy, benthic prey are abundant (Gerdeaux *et al.*, 1999) but macrophyte refuge areas are limited to a few places on the western shore and are absent on the steep eastern shore. A large population of salmonids and poor development of refuge areas could explain the extended colonization of the pelagic zone by YOY perch in Lake Annecy during summer.

At night, a marked onshore–offshore gradient of fish biomass was always observed. Hartmann (Hartmann, 1984) also reported increasing yields of perch from the western to eastern sides of Lake Constance, but the gradient was limited to the littoral zone. All other authors mention a nocturnal, contagious distribution of the juveniles in the offshore zone rather than a regular gradient, but between-lake differences of horizontal distribution patterns could also be a result of lake size (Post and McQueen, 1998) and probably, as observed in Lake Geneva (C. Gillet, personal communication), of community structure and cohort strength.

The vertical distribution of fish biomass in Lake Annecy is species-specific. The diurnal echograms (Figure 8) revealed two spatially segregated hypolimnetic assemblages that, given the composition of the fish community, could correspond to whitefish (possibly those closer to the metalimnion) and Arctic char, respectively. This hypolimnetic distribution is typical of these salmonids in alpine lakes (Juget *et al.*, 1995; Ptak and Appenzeller, 1998), where the species distribution in the water column is controlled by the lake thermal structure (Brandt *et al.*, 1981; Goyke and Brandt, 1993). Oxygenation (>9 mg l^{-1}, Figure 3) in the hypolimnetic waters of Lake Annecy also allows for such vertical segregation. This vertical structure tended to shade off at night when salmonids were probably searching for pelagic prey. Although, most of the year, benthic invertebrates represent a significant part of the diet of Arctic char and whitefish in Lake Annecy, daphnids make up a larger contribution in June–July

(Gerdeaux *et al.*, 1999). In Lake Annecy, adult fish are dominated by whitefish and Artic char, both of which in this lake consume large amount of daphnids in June and July (Gerdeaux *et al.*, 1999). Being both competitors and predators of perch juveniles these salmonids may shape the spatial behaviour of young perch as well as that of daphnids.

Spatio-temporal distribution of zooplankton

As we hypothesized, both of the dominant potential zooplankton prey presented a decreasing onshore–offshore gradient in late June. During the day, this decrease was only detectable in the metalimnion and part of the hypolimnion, where the stronger variations of abundance only concerned a short segment of the sub-littoral region (Figure 5). This gradient progressively shifted towards the surface during the dusk and night periods and extended then more regularly to the mid-lake region. The twilight ascent, was more clearly observed with the stratified tows made in June 1997 (Figure 9). Though only providing a rough picture of the twilight phenology, these complementary samples underline that, despite the fact that daphnids and cyclopoids exhibited similar patterns of horizontal and vertical distributions during the daytime, the upward movement at dusk developed faster for cyclopoids than for daphnids. A distinct spatial compartment between the two taxa was also detected for the 'midnight sinking' phase of the DVM, which in the case of copepods concerned a wider strata but led to a more even vertical distribution than for daphnids (Figure 9). These phenomena are a classic characteristic of diel vertical migrations by zooplankton as observed for either of these taxa in deep lakes of moderate [e.g. (Geller, 1986, Taleb *et al.*, 1993; Angeli *et al.*, 1995b)] or high elevation (Gliwicz, 1986). The more peculiar phenomena observed in Lake Annecy were: first, this distinct kinetic of DVM in daphnids and cyclopoids, and second, the extension to the mid-lake region of the strong horizontal gradient previously mainly expressed in the deeper waters of the sub-littoral region. This development suggests some oblique or horizontal movement of the plankters. DHM have been reported for a few taxa in freshwaters, including the midge larva *Chaoborus* (Franke, 1987), *Daphnia hyalina* (Davies, 1985; Kvam and Kleiven, 1995) and the calanoid copepod *Diaptomus sanguineus* (De Stasio, 1993). The factors regulating these short-term horizontal migrations are largely unknown, but Siebeck (Siebeck, 1969) described a mechanism by which plankton crustaceans migrate in a horizontal plane coincident with the symmetry plane of the angular light distribution. He found that, in the littoral zone, the direction was determined mainly by the elevation of the horizon. Such a factor could play a greater role in basins such as that of Lake

Annecy, surrounded next to the shore by high relief mountains. But, the diel horizontal migration of plankton may also be a response to chemical cues released by their predators, as suggested for instance by the behaviour of *Daphnia longispina* in the presence of its predator *Chaoborus flavicans* (Kvam and Kleiven, 1995). Plankton can also detect chemical cues released by vertebrate predators, and in response to these cues, alter their sensitivity to light and the amplitude of their DVM, as suggested for *Daphnia* (Flik *et al.*, 1997), *Chaoborus* larva (Dawidowicz *et al.*, 1990) and for the copepod *Diaptomus sanguineus* (De Stasio, 1993). Though no relevant information was available on the individual behaviour of copepods during the twilight periods, their population behaviour reported over several months for *Eudiaptomus gracilis* in Lake Maarsseveen (Ringelberg *et al.*, 1991) strongly indicates that, like daphnids, copepods also react to both light cues and fish exudates. The strong analogies observed in Lake Annecy between the large-scale distribution of daphnids and cyclopoids could thus be partly shaped by the spatial gradients of fish biomass, supposedly resulting in gradients of both predation and fish exudates.

When horizontal variations of plankton concern more than a few tens of metres, the question remains as to how can they develop within only a few hours. Of the different hypotheses that can be proposed, none is fully satisfying, underlining the need to better integrate large-scale processes in the study of DVM. One possible explanation would be the presence of dense swarms next to the bottom and more frequent in the sub-littoral region. This possibility is suggested by the concentrations of crustaceans observed onshore in the PSM tows made at 34 m, close to the bottom (Figure 5). Another hypothesis involves 'plankton navigation' [first proposed by (Hardy and Gunther, 1935)], whereby the organisms take advantage of horizontal currents of various speeds and directions during their upward and downward movements. DVM necessarily interferes with hydrodynamic processes, but it remains unclear how advection, currents, or even seiches could lead to diel cyclic patterns of distribution. In the present study, the areal zooplankton densities we recorded with the integrated tows (partly reported in Table I) indicate that diurnal zooplankton abundance remained in the same order of magnitude in the studied region. As observed with the PSM survey, the steeper horizontal increase (three orders of magnitude) was noted between stations 10 and 20–25 m deep, after which offshore variations of abundances were much weaker (less than one order of magnitude). A significant part of the horizontal variations recorded at discrete depths could thus also largely result from the temporal evolution of the vertical distribution patterns along the transect.

Although extensive migrations have been recorded in oceans for a long time (Nybakken, 1988), our study provides the first large-scale record (1–2.5 km) of such vertical movements in a large lake. Bast and Seitz and Taleb *et al.* have studied the DVM of several lacustrine species in relation to their horizontal distribution (Bast and Seitz, 1993; Taleb *et al.*, 1993). They detected DVM for most species, with some differences of migration amplitudes relative to the sampling stations, but no apparent horizontal gradient. Although these works were carried out at smaller scale (i.e. lake size: 0.1 and 0.6 km²) and with low spatial resolution (less than five stations), they clearly showed that differences in zooplankton abundances at different sampling locations could be important, especially if several species are considered. Our results also revealed very strong horizontal and vertical variations of the abundances of daphnids and cyclopoids during the night, thus underlining the need to consider both horizontal and vertical axes in the study of ecological processes. The use of the Plankton Sampling Mechanism (PSM) or advanced technologies developed to study zooplankton heterogeneity [for a brief review see (Pinel-Alloul, 1995)] are thus essential to determine horizontal and vertical zooplankton distributions at large scales and within short periods.

Spatio-temporal interactions between fish and zooplankton

As hypothesized, fish biomass and zooplankton abundance presented an opposite distribution during the diel cycle. Moreover, given the high light requirement of perch juveniles for prey capture (Flik *et al.*, 1997) and the timing of light variations in Lake Annecy in late June, the foraging activity of these planktivores, which presented a high contribution to fish biomass, should already start to drastically decline in the epilimnion around civil dusk (22:07 h). The spatial segregation between zooplankton and fish, as well as the preliminary information obtained on the timing of daphnids and cyclopoids DVM and light variations over this lake, suggest avoidance behaviour by prey to their main epilimnetic vertebrate predators. The strong day-to-night differences in the zooplankton densities in the surface (variations up to more than three orders of magnitude) reinforce the hypothesis that zooplankton adapt their vertical distribution to minimize the predators' effects.

Predation is now widely recognized as the major reason (adaptive significance) for DVM (Ringelberg, 1999). Nevertheless, it seems difficult to explain why zooplankton concentrated as deep as they did during the day, especially in the sub-littoral region, when most vertebrate predators were detected in the epilimnion and mainly in more offshore regions. There was no peak of chlorophyll *a* under

15 m depth, which could explain local zooplankton aggregations in the deepest sub-littoral waters. However, the depth where denser zooplankton densities were recorded could be related with that occupied during day time by the other planktivorous species (whitefish, especially). This later is often met in larger abundance in the sub-littoral regions (Guillard, 1991) and, in June–July, its diet in Lake Annecy was mainly composed of cladocerans (Gerdeaux *et al.*, 1999). If, as supposed, plankton responses to the presence of fish depend on the concentration of fish exudates, the vertical structure of the fish community could be potentially responsible for such a vertical repartition of zooplankton.

Two potential factors may shape the observed opposite horizontal onshore–offshore distribution of fish and zooplankton. The first one is that, given the highest density of perch juveniles in the offshore area, the zooplankton would be more vulnerable to predation in this region and, therefore, onshore migration would provide a refuge. Some studies indicate that DVM in many zooplankton species can be induced by kairomones exuded by predators (Pijanowska, 1993; Van Gool and Ringelberg, 1998). If more fish biomass or higher concentrations of fish exudates are present, the strength of zooplankton migration must increase (Ringelberg *et al.*, 1997), at least when, as demonstrated for daphnids, these exudates exceed a critical level (Loose, 1993; Ringelberg *et al.*, 1997). Thus, the occurrence of an opposite pattern detected for the horizontal distribution of predators and prey could suggest that the high fish biomass in the offshore region has induced an horizontal movement of prey. Moreover, in early summer, fish biomass was strongly represented by YOY perch, indicating that such a spatial structure is maintained during the pelagic phase of larval and juvenile fish stages. Post and McQueen (Post and McQueen, 1988) also observed opposite distributions between zooplankton and perch juveniles in Lake St George (Ontario). They also found that when perch juveniles were staying offshore during both day and night, the highest densities of cyclopoids occurred onshore. This relationship evolved in time and, once juveniles moved into the littoral zone during the day, the densities of cyclopoids increased offshore. Such horizontal movements of zooplankton, have already been suggested as a behavioural antipredator defence, (Davies, 1985; Bast and Seitz, 1993; Taleb *et al.*, 1993).

Another explanation is that the high number of planktivorous fish might be responsible for low local density of their prey. A few articles have mentioned that the perch juveniles would have a strong contribution to the midsummer decline and that it could lead to a consumption of up to 80% of the zooplankton production (Rand *et al.*, 1995; Post *et al.*, 1997). In contrast, many papers rather suggested that predation was not the unique factor which contributes to the zooplankton midsummer decline, considering food limitation and invertebrate predation as two important key processes (Wu and Culver, 1994; Boersma *et al.*, 1996; Menher *et al.*, 1998, Menher and Thiel, 1999). Post (Post, 1990) and Houde (Houde, 1989) showed that young fish larvae could have daily consumption rates exceeding their own biomass. The interactions between larval fish and their zooplankton prey can be pivotal in determining larval growth, survival, recruitment, food web structure and seasonal successions (Houde, 1987; Post and Rudstam, 1992). However, in late June, YOY perch were already mainly represented by juveniles [i.e. by individuals with lower food requirements (Karås and Neuman, 1981; Karås, 1990, 1992)]. Daily consumption rates of 16%, exceptionally up to 30%, have been reported for juvenile Eurasian perch (Spanovskaya and Grygorash, 1977). For a temperature of 20°C, i.e. close to that recorded in June in the diurnal mixed layer of Lake Annecy, a daily consumption rate of 16% is also predicted for juveniles of this species by the bioenergetic model developed by Karås (Karås, 1992). On this basis, given the amount of zooplankton >200 μm and YOY perch deducted from the tows and acoustic records (Table I), if perch were likely to feed limitlessly in Lake Annecy, at this density they could consume offshore an average of 3–6% per day of the whole sestonic mass available and some 7–15% in the mid-lake region. Given a minimum generation time of a few weeks, for both daphnids and copepods, one may suppose that YOY perch could have (at least locally) a significant impact on zooplankton density within a few days. Thus, the inverse diel distribution patterns between zooplankton and fish could be potentially shaped by both antipredator behaviour (vertical and horizontal migrations) and spatially structured predation losses.

Implications for field studies on fish–zooplankton interactions and conclusions

Our study, although limited to a short-term diel cycle, pointed out the need to consider both horizontal and vertical scales and combine fish echosounding and continuous plankton sampling when studying interactions in zooplankton and fish distributions, especially in large lakes [see also (Bast and Seitz, 1993; Taleb *et al.*, 1993)]. Large aggregations of zooplankton detected in deep waters, combined with the aggregated distributions of fish juveniles, are the results of predator–prey interactions, and suggest that standard sampling designs are likely to miss detection of the spatio-temporal relationships observed in this study. Coupling high-frequency sampling of fish biomass and size by echosounding and

continuous zooplankton sampling with the PSM allows us to detect phenomena that can happen at large spatial and short temporal scales. Such sampling technologies (hydroacoustic, L-P plankton sampler) are important to advance our understanding of predator–prey interactions in lakes.

Although multiple driving forces (physico-chemical and biological factors) can explain the DVM and DHM, the observed spatial distribution of zooplankton in Lake Annecy during the diel study period was very likely shaped both by predation losses by perch juveniles and by antipredator behaviour by zooplankton. Thus, in this subalpine lake, predation affects the spatio-temporal distribution of zooplankton. However, as this study was only carried out on a diel cycle, future works should be addressed to define better the temporal evolution of the dynamic of the predator–prey relationships in such aquatic systems. Since juvenile perch are visual predators, it would also be valuable to determine accurately the critical diel temporal window of their impact on zooplankton. The twilight period could be particularly important in the spatial restructuring for food searching for both fish and zooplankton. In this perspective, future work should consider light measurements to obtain a good estimation of the critical temporal window of the zooplankton migration. Light attenuation plays a key role as a biological clock in the spatio-temporal dispersion and migration of both zooplankton and fish, as well as on biotic interactions.

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