

Factors influencing the spatial distribution of zooplankton and fish in Loch Ness, UK

D. G. GEORGE AND I. J. WINFIELD

NERC Institute of Freshwater Ecology, The Windermere Laboratory, Far Sawrey, Ambleside, Cumbria LA22 0LP, UK

SUMMARY

1. The vertical and horizontal distribution of phytoplankton, zooplankton and fish in Loch Ness, Scotland, were monitored during one day-time and one night-time survey in July 1992. The vertical samples were collected at a site located at the northern end of the loch and the horizontal samples along a longitudinal transect.
2. The vertical distribution surveys demonstrated that the phytoplankton, the zooplankton and the fish were concentrated in the top 30 m of water above the seasonal thermocline. Within this layer, *Cyclops* stayed much closer to the surface than *Eudiaptomus* but both species moved towards the surface at night.
3. The most important factor influencing the horizontal distribution of the phytoplankton was the north–south gradient in productivity. The sub-catchments surrounding the north basin contain a greater proportion of arable land than those to the south and the concentrations of nitrate-nitrogen and phytoplankton chlorophyll increased systematically from south to north.
4. Zooplankton distribution patterns were influenced by wind-induced water movements and the dispersion of allochthonous material from the main inflows. The highest concentrations of *Cyclops* were recorded in the north, where there was more phytoplankton, and the highest concentrations of *Eudiaptomus* in the south, where there were higher concentrations of non-algal particulates.
5. There was no spatial correlation between total zooplankton and total fish abundance but the highest concentrations of small (1–5 cm) fish were recorded in the south where there was a large patch of *Eudiaptomus*. The number of *Eudiaptomus* at specific locations within this patch were, however, negatively correlated with the numbers of small fish. These results suggest that the fish were actively foraging within the patch and were depleting their zooplankton prey in the areas where they were most abundant.

Keywords: zooplankton, spatial distribution, *Salvelinus alpinus*, echo-sounding

Introduction

Zooplankton and fish have aggregated distributions that cover a range of spatial scales from metres to kilometres (Horwood & Cushing, 1978; George, 1981). Our ability to describe and understand the interac-

tions between these aggregations is, however, limited by the spatial resolution of our sampling techniques and the dynamic nature of the open-water environment. Many of the physical and biological factors that influence the spatial distribution of zooplankton in lakes are now quite well understood (George, 1976; George & Edwards, 1976) but similar studies on the spatial distribution of fish have been much more restricted. A major problem facing such fish distribution studies has been the limited availability of an appropriate quantitative sampling technique. Recent developments in echo-sounding technology have,

Correspondence: D. G. George, Institute of Freshwater Ecology, The Windermere Laboratory, Far Sawrey, Ambleside, Cumbria, LA22 0LP, UK. E-mail: g.george@ife.ac.uk

however, revolutionised the study of fish in lakes, and can now provide estimates of fish density on spatial scales that can be related to other limnological measurements. Although, for example, Frank & Leggett (1985), Rose & Leggett (1990) and the Geospace Group (1993) have demonstrated the application of such techniques in the marine environment, there have been few comparable studies in inland waters. A notable exception is a study of the spatial variation in temperature, oxygen, zooplankton and fish in Lake Kinneret, a large and eutrophic lake in Israel (Kalikhman, Walline & Gophen, 1992). This study showed that the zooplankton and the fish concentrated in frontal zones and suggested that high concentrations of fish could depress the local abundance of zooplankton.

This paper reports the first phase of a study designed to examine the factors influencing the spatial distribution of zooplankton and fish in Loch Ness, a large, oligotrophic lake in North-west Scotland. Loch Ness is a particularly appropriate location for such a study since it is morphometrically simple and supports a pelagic fish community of low diversity, which is not exploited by commercial fisheries.

Methods

Study site

Loch Ness is generally regarded as the largest freshwater lake in Britain since it has the greatest mean depth (132 m) and contains the largest volume of water ($7.45 \times 10^8 \text{ m}^3$). The loch is situated in a rock basin formed by the Great Glen Fault (latitude $57^\circ 15'$, longitude $4^\circ 30'$) and is morphometrically simple with steeply shelving sides (Fig. 1). Its hydrodynamic characteristics are primarily deter-

mined by the strong winds that blow along the glen and by the inflows from several large rivers. The loch typically becomes thermally stratified in late June (Laybourn-Parry *et al.*, 1994) but the seasonal thermocline is deep (30–60 m) and is frequently eroded by wind-mixing. The loch contains very low concentrations of nutrients but very high concentrations of coloured humic material leached from the catchment. The concentration of phytoplankton in the loch is consequently very low (Jones *et al.*, 1996) and has little effect on the vertical attenuation of light. The maximum concentration of phytoplankton chlorophyll is usually recorded in late summer and seldom exceeds $1.5 \mu\text{g L}^{-1}$. The summer phytoplankton is typically dominated by diatoms like *Asterionella formosa* Hass and *Tabellaria* with episodic growths of small flagellates such as *Cryptomonas* sp. and *Rhodomonas minuta* Skuja (Bailey-Watts & Duncan, 1981). A general description of the crustacean zooplankton found in the loch has been provided by Murray (1904) and Maitland, Smith & Dennis (1981). The zooplankton community is dominated by the copepods *Eudiaptomus gracilis* Lilljeborg and *Cyclops abyssorum* Sars with smaller numbers of the cladocerans *Bosmina coregoni* Baird and *Daphnia hyalina* Leydig. Most of the fish found in the open water are Arctic charr (*Salvelinus alpinus* L.) which are usually planktivorous even as adults (Bean, Winfield & Fletcher, 1996). Small numbers of Atlantic salmon (*Salmo salar* L.) also migrate through the loch and there are inshore populations of brown trout (*Salmo trutta* L.), three-spined stickleback (*Gasterosteus aculeatus* L.), eel (*Anguilla anguilla* L.) and pike (*Esox lucius* L.) (Maitland *et al.*, 1981). There are no commercial fisheries in the loch but the rivers flowing into the loch support valuable salmonid fisheries. Further information on the physical, che-

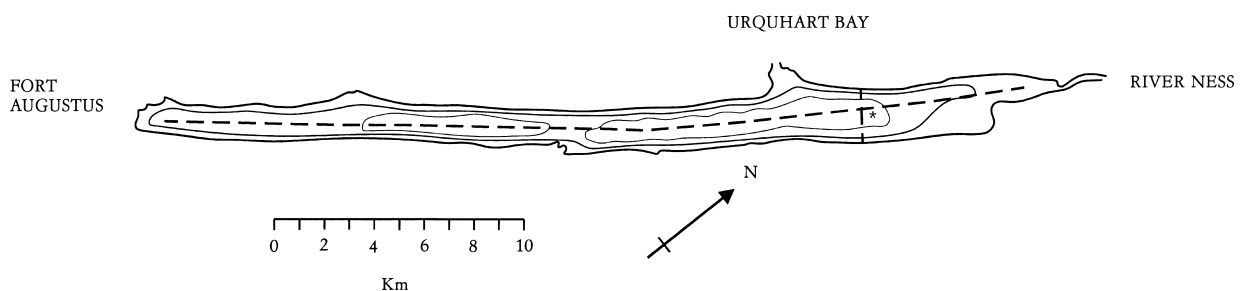


Fig. 1 Bathymetric map of Loch Ness showing the location of the fixed site (*) and the transverse and longitudinal sampling transects (---). Only the 100 and 200 m contours are shown.

mical and biological characteristics of the loch may be found in publications by Thorpe (1974); George & Jones (1987); Laybourn-Parry *et al.* (1994) and Jones *et al.* (1995).

Field methods

Vertical distribution. Diel changes in the vertical distribution of temperature, underwater-light, phytoplankton chlorophyll, zooplankton and fish were monitored at a fixed location near the northern end of the loch in July 1992. Sunset and sunrise were at 22.00 and 04.00 h GMT and six sets of samples were collected at 3–5 hourly intervals between 10.00 h GMT on 22 July and 07.30 h GMT on 23 July. Visibility was generally good with a fresh south-westerly wind decreasing in early evening and remaining calm during the night. Temperature and light measurements were recorded using a Windermere Profiler, a multi-parameter instrument developed at the Institute of Freshwater Ecology (Rouen, 1989). Samples of water for chlorophyll analysis were collected from successive 10 m intervals down to 100 m using a 5-L Friedinger bottle operated by a weighted messenger (Irish, 1980). Integrated zooplankton samples were collected over the same 10 m intervals using a messenger-operated closing net with a mouth area of 200 cm² and a mesh size of 180 µm. This net filtered ≈ 200 L of water per metre length of tow and was fine enough to retain all the cladocera and all but the smallest copepodite stages of *Cyclops* and *Eudiaptomus*. The water samples were taken to the shore at regular intervals for filtering and the zooplankton samples preserved in 70% methanol. Records of the vertical distribution of fish near the sampling site were obtained at the beginning of each sampling interval by echo sounding along a cross-loch transect. The average length of these transects was 1800 m and the boat travelled at an average speed of 4.5 knots (2.4 m s⁻¹). The echo sounder was a Simrad EY 200P single-beam instrument (Simrad, Horten, Norway) with a 200-kHz transducer of beam angle 7° recording with a 40 logR Time-Variied Gain (TVG) to analogue audio tape. The minimum target strength detectable by this system is –54 dB, which represents fish of ≈ 4 cm in length (Foot, 1987).

Horizontal distribution. Two synoptic surveys of the horizontal distribution of temperature, turbidity, phytoplankton chlorophyll, zooplankton and fish were conducted during the study by a team based

on the survey vessel 'm.v. Simrad'. In the first (day-time) survey, the vessel travelled north from Fort Augustus at an average speed of 6.4 knots. In the second (night-time) survey, the vessel travelled south along the same transect at an average speed of 6.5 knots. The day-time survey was completed between 13.00 and 17.40 h GMT on 22 July and was interrupted by a short stop in Urquhart Bay. The night-time survey was completed between 23.00 h GMT on 22 July and 02.00 h GMT on the 23 July without any deviations from the central transect. The sampling system used was very similar to that described by George (1976). Water was pumped on board by the ships' fire pump and then passed through a series of sensors before being filtered to remove the zooplankton. The inlet to the pump was located near the centre line of the ship at a depth of 3 m. The volume of water delivered was controlled by a valve, which was adjusted to produce a flow rate of 40 L min⁻¹. A Pitot tube in the hose leading to the plankton filters deflected representative samples of water (≈ 5% of the total flow) into collecting jars for chlorophyll extraction and chemical analysis. The horizontal variations in water temperature and turbidity were measured using a fast response thermistor and a dual-beam transmissometer (Partech Electronics, St. Austell, UK). Phytoplankton chlorophyll was measured by *in vivo* fluorescence using a Turner Model 10 fluorimeter (Turner Designs, CA) fitted with a red-sensitive photomultiplier, a blue lamp and a high-volume continuous flow attachment. The filters were a blue, narrow-peak excitation filter with a maximum transmission at 425 nm, and a red, sharp cut-off emission filter with a transmission maximum at 687 nm. Zooplankton samples were collected by filtering aliquots of water through two stainless-steel filter units (130 µm mesh). A two-way valve was used to deliver water to each unit in turn, one filter being washed when the other was collecting plankton. Since the concentration of zooplankton in the loch was very low, the filters were changed every 5 min (i.e. at ≈ 1 km intervals along the transect).

Records of the vertical and horizontal distribution of fish along the mid-loch transect were obtained during the day-time and the night-time surveys. The echo sounder was a Simrad EK 500 split-beam instrument fitted with a 38-kHz transducer with a beam width of 7° and was set to record target strength to audio tape through a 40 logR TVG. The target

strength threshold was set at -70 dB to record all targets greater than 1 cm in length.

Laboratory methods

The water samples for chlorophyll analysis were filtered on site using a hand-pump and a sintered glass funnel. Phytoplankton chlorophyll was extracted after filtration on GF/C filters using the aqueous methanol method described by Talling (1974). Subsamples of water for chemical analysis were transferred to glass bottles and stored in the cold before being analysed. Dissolved reactive phosphorus concentrations were measured using the solvent extraction method described by Stephens (1963) and nitrate-nitrogen concentrations by ion chromatography using a Dionex 2000i/SP automatic analyser (Dionex Corporation, CA). The echo sounding results from the cross-loch transects were analysed using the PC-based HADAS software system for echo counting (Walline, Pisanty & Lindem, 1992). This produces estimates of absolute densities and target strengths, the latter being derived using a modification of the algorithm of Craig & Forbes (1969). The echo sounding data from the horizontal distribution survey were analysed by echo counting using a less sophisticated software system on a Unix workstation at the Fisheries Research Department of Simrad in Horten, Norway. The numbers of echoes and their target strengths were extracted for successive 10 m layers and the results divided into 1 km sections that matched the zooplankton sampling interval. For both across-loch and along-loch transects, estimates of target strengths were converted to fish lengths using a rearrangement of the relationship recommended for physoclists by Foote (1987). The equation used was $TS = (20 \log L) - 67.4$, where TS is the target strength in dB and L is the fish length in cm. Results of the along-loch transect are presented for three arbitrarily chosen size groups: 'small' fish from 1 to 5 cm in length (TS from -60 to -54 dB), 'medium' fish from 5 to 10 cm in length (TS from -51 to -48 dB) and 'large' fish greater than 10 cm in length (TS greater than -45 dB). Results of the across-loch transects, which comprised too few echoes for a detailed size analysis, are presented only as total fish numbers.

Results

Vertical distribution

Since the numbers of zooplankton and fish sampled at any one time were low, the results from several zooplankton profiles and echo sounding transects were combined to form one day-time and one night-time series. The day-time plots (Fig. 2a) are the average of three samples taken at 11.00, 14.00 and 19.00 h GMT on 22 July. The night-time plots (Fig. 2b) are the average of two samples taken at 01.00 and 03.00 h GMT on 23 July. The echo-sounding plots include data from the top 50 m and cover the profundal section of the cross-loch transects. This procedure retains almost all fish echoes and avoids any acoustic complications with side and bottom echoes. The temperature and chlorophyll profiles in Fig. 2 (a and b) show that there was little diurnal change in the thermal and optical characteristics of the water column. A well defined thermocline was present at 35 m and most of the phytoplankton was concentrated in the top 50 m. Light attenuation measurements taken on 22 July showed that there was very little light below 10 m. The calculated extinction coefficient (Vollenweider, 1974) was 0.68 giving an estimated euphotic depth (1% light level) of only 9 m. The vertical distribution of the zooplankton and fish did, however, change over the same period. During the day (Fig. 2a), relatively large numbers of *Cyclops* were present in the top 10 m but the *Eudiaptomus* avoided this surface layer and concentrated at depths between 10 and 30 m. Most of the fish were also concentrated at depths between 10 and 30 m but numbers were low and the geometric mean density of fish recorded during the day was only 68 individuals ha^{-1} . During the night (Fig. 2b) many of the *Cyclops* moved towards the surface but most of the *Eudiaptomus* still avoided the surface and concentrated at depths between 10 and 20 m. Some of the fish also moved towards the surface at night but the number of fish echoes recorded in the top 10 m was too low for any meaningful comparison. In statistical terms, there was no significant change in the vertical distribution of fish over the 24-h period (contingency table analysis with data pooled into 2–20, 21–30 and 31–50 m layers to satisfy the test requirements, $\chi^2 = 1.69$, d.f. = 2, $P > 0.10$). The overall estimate of fish density during the night was ninety-one indivi-

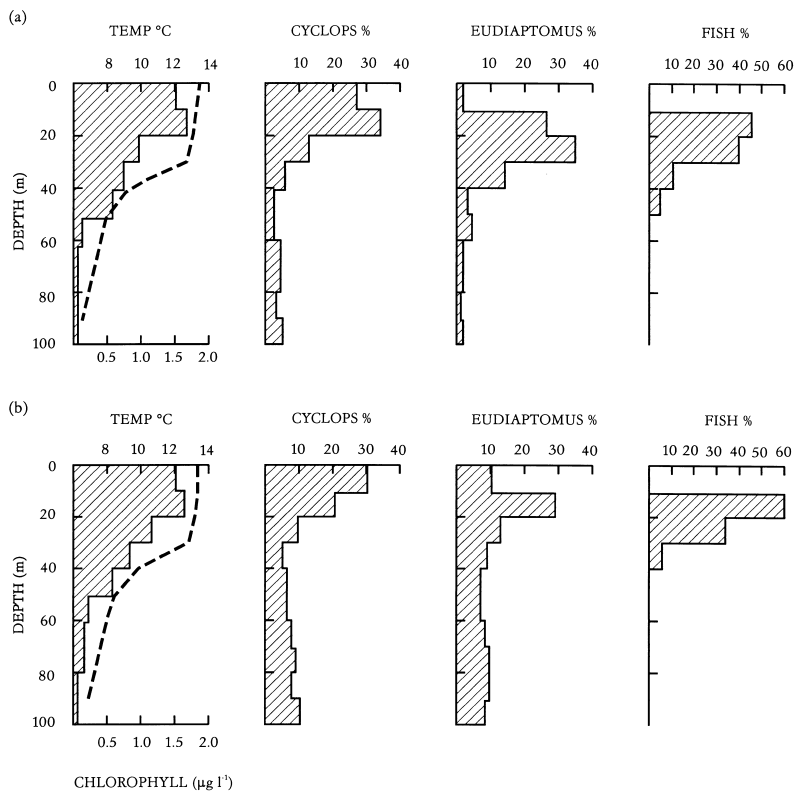


Fig. 2 The day-time (a) and night-time (b) vertical distribution of temperature, chlorophyll *a*, *Cyclops*, *Eudiaptomus* and fish echoes. The broken lines in the figure show the vertical distribution of phytoplankton chlorophyll.

duals ha^{-1} , an increase of 30% on the day-time estimate. Estimated target strengths ranged between -56 (the lower detection limit of the equipment) and -34 dB, representing fish of between 40 and 47 cm in length.

Factors influencing the horizontal distribution of the zooplankton

Wind-induced water movements. The microcrustacea that dominate the zooplankton are very weak swimmers so their spatial distribution is strongly influenced by wind-induced water movements. In a deep lake, like Loch Ness, the wind-induced circulation takes the form of a 'conveyor belt' running along the top of the seasonal thermocline (Fig. 3a). On 22 July, temperature profiles recorded at the two ends of the basin (Fig. 3b) showed that there was a very pronounced tilt in the seasonal thermocline. This tilt had been produced by the strong south-westerly winds that had been blowing for several days (inset to Fig. 3c) and was responsible for the persistent north-south gradient in surface temperature recorded during the day-time and night-time surveys (Fig. 3c).

The dispersion of allochthonous material from the major rivers. The five rivers that flow into Loch Ness drain mountainous subcatchments that periodically experience very heavy rain. The map in Fig. 4a shows the position of the five inflows and includes some simple measures of the topographic and hydrological characteristics of the four subcatchments. The upper values in the annotation boxes show the percentage discharge from each subcatchment and the lower values the mean slope of the subcatchment in metres per kilometer. Very little is known about the rate of erosion in these subcatchments, but microbial studies by Laybourn-Parry *et al.* (1994) suggest that large amounts of allochthonous material are periodically washed into the loch and serve as a carbon source for the bacterioplankton. In this study, we used the output from the Partech transmissometer and the Turner fluorimeter to estimate the concentration of 'non-algal' particulates at different points along the central transect. The concentration of non-algal particulates was assumed to be proportional to the residuals in a linear regression of turbidity vs. chlorophyll, where turbidity was used as the dependent variable. Fig. 4b shows the horizontal variation in non-algal turbidity

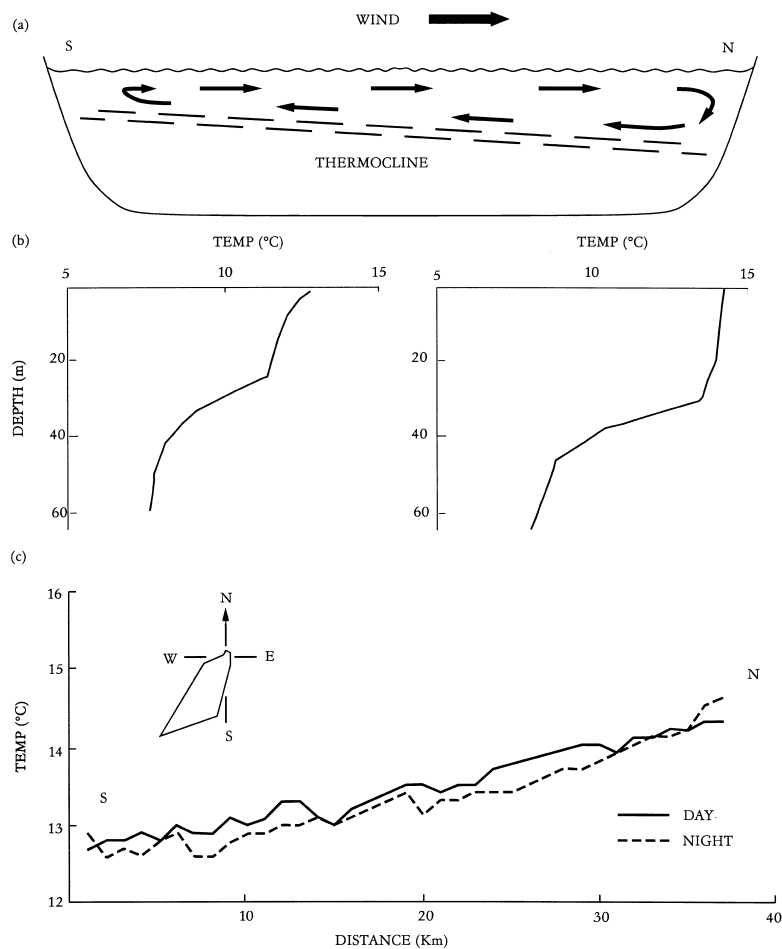


Fig. 3 (a) Schematic diagram showing the effect of the prevailing south-westerly wind on the circulation within the epilimnion and the depth of the thermocline. (b) The temperature profiles recorded at the southern and northern end of the loch on 22 July 1992. (c) The longitudinal gradients in near-surface temperature recorded during the daytime (—) and night-time (---) surveys. The inset wind rose shows the direction of the prevailing wind over the previous four days.

recorded during the uninterrupted night-time survey. The negative values in the plot show areas of water where the concentration of non-algal particulates was relatively low and the positive values areas where the concentration of non-algal particulates was relatively high. The highest concentration of non-algal particulates was recorded near Fort Augustus where the plume from the River Tarff enters the loch from the large southern catchment. Secondary maxima were associated with the discharge from the River Foyers and the Rivers Coiltie and Enrick in Urquhart bay. Relatively low concentrations of non-algal particulates were, however, recorded in the south basin where the River Moriston enters the loch after passing through two deep lochs in a neighbouring valley.

The north-south productivity gradient. The horizontal distribution of phytoplankton biomass in Loch Ness

is known to be influenced by local variations in the supply of nutrients (George & Jones, 1987). The subcatchments surrounding the northern end of the loch are much more productive than those to the south and include a much higher proportion of arable land (Fig. 5a). Fig. 5b shows the horizontal variation in the concentration of nitrate-nitrogen recorded along the central transect during the day-time cruise. We have used nitrate-nitrogen as a general measure of enrichment because the concentration of dissolved reactive phosphorus in the water samples was often below the limit of detection ($< 0.6 \mu\text{g L}^{-1}$). The plot shows that the concentration of nitrate-nitrogen was much higher in the northern basin where the main subcatchment contains 6.9% of arable land than in the south basin where there is no arable land in the main subcatchment. Fig. 5c shows the horizontal variation in phytoplankton chlorophyll recorded during the day-time and night-time sur-

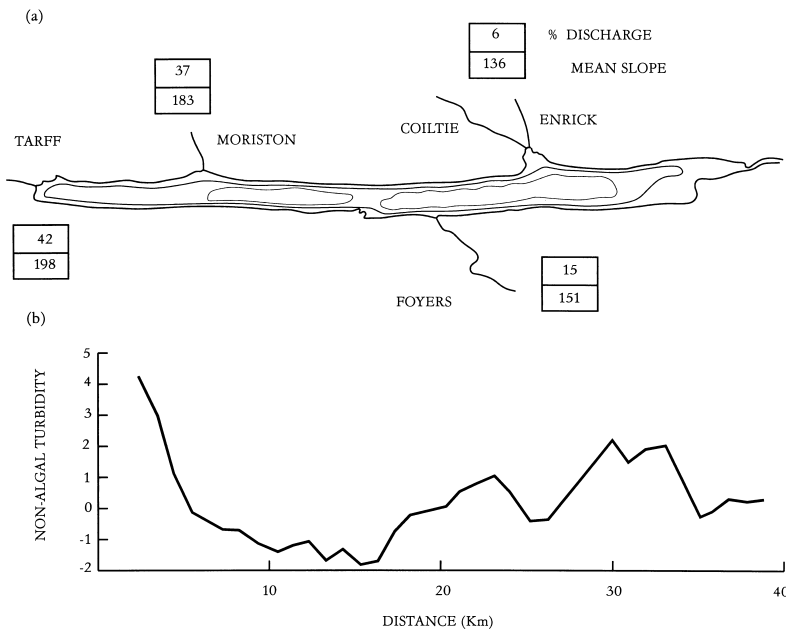


Fig. 4 (a) An outline map of Loch Ness showing the position of the major inflows. The annotations show the percentage discharge from each inflow and the mean slope of each subcatchment (after Maitland, 1981). (b) The horizontal variation in the concentration of nonalgal particulates recorded during the night-time survey of 22 July. Positive values of the index indicate high concentrations of non-algal particulates.

veys. The variation in the concentration of chlorophyll follows the same trend as the concentration of nitrate-nitrogen, with the highest concentrations being recorded just north of Urquhart bay.

The horizontal distribution of the zooplankton

Fig. 6 shows the day-time and night-time distributions of the two most abundant zooplankton species (*C. strenuus* and *E. gracilis*) along the centre-loch transect. The raw counts have been smoothed to highlight the general trend and the vertical scale adjusted to account for the diel change in vertical distribution. The highest numbers of *Cyclops* (Fig. 6a) were recorded at the northern end of the loch where they would have accumulated after being transported downwind by the near-surface flow. In contrast, the greatest number of *Eudiaptomus* (Fig. 6b), were recorded towards the south where they would have accumulated after being carried upwind by the deep return current. The number of *Cyclops* collected during the night was not very different from those collected during the day but there was a dramatic increase in the number of *Eudiaptomus* as the animals moved closer to the surface. The horizontal distribution patterns recorded in Fig. 6 are thus a direct consequence of the vertical distribution differences noted in Fig. 2. We do not know whether the behavioural differences recorded on 22 and 23 July are in any way typical but, on this occasion, they led

to the spatial separation of the *Cyclops* and *Eudiaptomus* concentrations at the opposite ends of the loch.

The horizontal distribution of the fish

Fig. 7 shows the day-time distributions of fish along the sampling transect. Over 6000 individual echoes were recorded in the top 50 m and were arbitrarily divided into the three size groups described in the methods section. Small fish (Fig. 7a) were much more abundant in the southern half of the loch, with an abrupt increase in abundance from 17 km southwards. Medium and large fish (Figs 7b and c) were less abundant and were concentrated even further to the south near the main inflow. For all size groups, the southern basin (taken as samples from 1 to 16 km) contained a significantly greater density of fish than the northern basin (taken as samples from 17 to 38 km). The calculated *t* statistics were: small fish, $t = 13.487$, d.f. = 29, $P < 0.001$, medium fish, $t = 4.464$, d.f. = 29, $P < 0.001$ and large fish, $t = 2.688$, d.f. = 29, $P < 0.05$. The night-time pattern of fish distribution (not shown) was very similar, but the number of echoes recorded in the top 50 m was almost an order of magnitude lower than those recorded during the day. This apparent reduction in abundance was probably due to the upward migration of targets into the narrower part of the acoustic beam. There were significant upward shifts in the number of echoes recorded for small and medium fish (con-

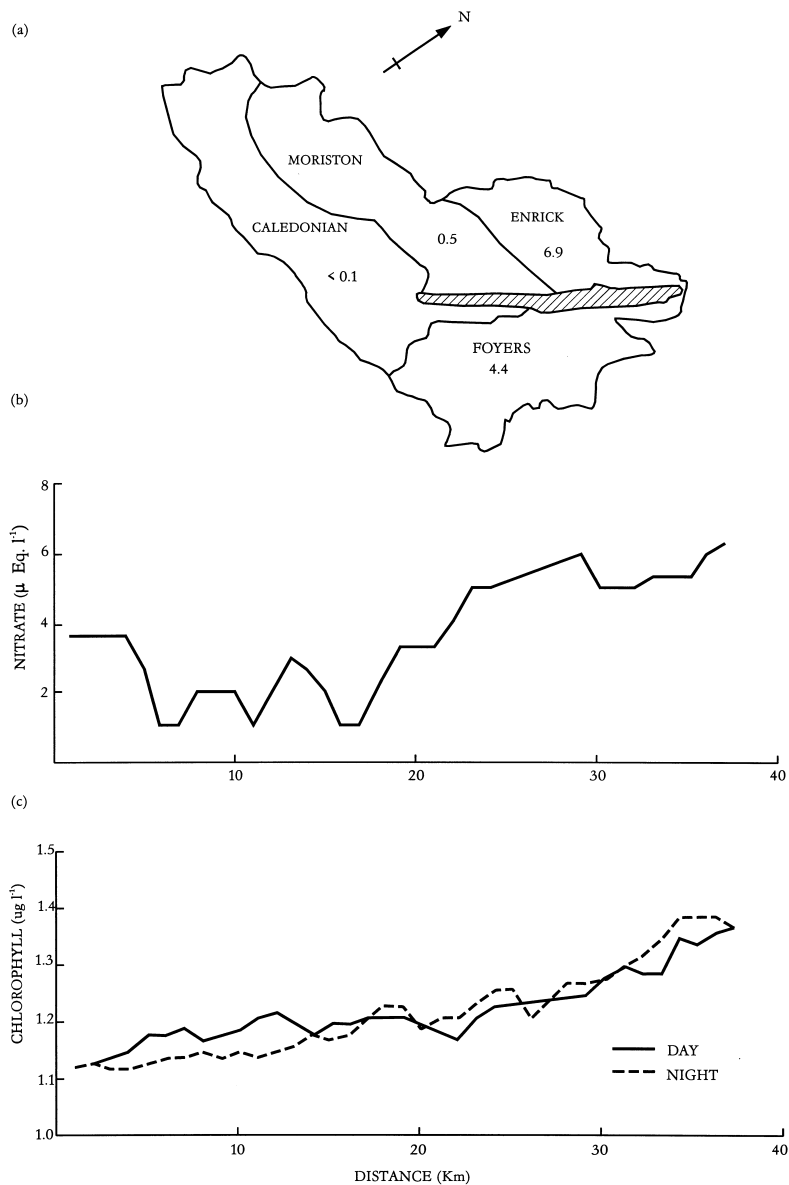


Fig. 5 (a) An outline map of the four subcatchments showing the relative proportion of arable land (after Maitland, 1981). (b) The horizontal variation in the concentration of nitrate-nitrogen recorded during the day-time survey. (c) The horizontal variation in the concentrations of chlorophyll *a* recorded during the day-time (—) and the night-time (---) surveys.

tingency table analysis: small fish, $\chi^2 = 187.399$, d.f. = 4, $P < 0.001$; medium fish, $\chi^2 = 21.721$, d.f. = 3, $P < 0.001$). No significant change was detected in the vertical distribution of the large fish ($\chi^2 = 4.426$, d.f. = 2, $P < 0.10$) but these fish were relatively rare, and no echoes were recorded from the top 10 m.

The spatial interactions between the fish and the zooplankton

There was no significant correlation between total fish echoes and the total number of zooplankton ($r = 0.09$, d.f. = 30, $P < 0.10$). However, significant negative

relationships did exist between particular size groups of fish and particular species of zooplankton. A comparison of Fig. 6 and Fig. 7 shows that *Cyclops* and all three size groups of fish were concentrated towards opposite ends of the loch (small fish, $r = -0.558$, d.f. = 30, $P < 0.001$; medium fish, $r = -0.619$, d.f. = 30, $P < 0.001$; large fish, $r = -0.552$, d.f. = 30, $P < 0.01$). There was no correlation between the general distribution of the fish and the concentration of *Eudiaptomus* (all $r \leq 0.297$, d.f. = 30, $P < 0.10$) but when data from the southern and northern basins were considered separately, there was a significant negative correlation between the number of small fish

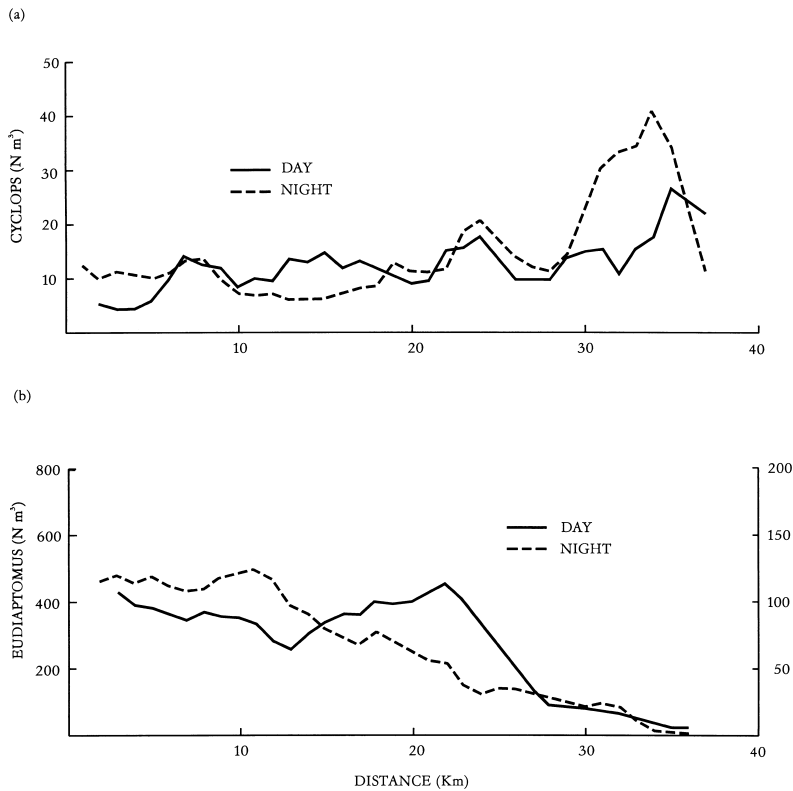


Fig. 6 (a) The horizontal variation in the numbers of *Cyclops* recorded during the daytime (—) and night-time (---) surveys. (b) The horizontal variation in the numbers of *Eudiaptomus* recorded during the day-time (—) and the night-time (---) surveys. The raw counts have been smoothed with a three-point running mean to highlight the general trend.

in the southern basin and the abundance of *Eudiaptomus* ($r = -0.70$, d.f. = 15, $P < 0.01$). The cross plots in Fig. 8a show the difference between the relative distribution of small fish and the numbers of *Eudiaptomus* in the northern and southern basins. There was no obvious relationship between the number of small fish and the number of *Eudiaptomus* in the northern basin but the number of small fish in the southern basin was negatively correlated with the number of *Eudiaptomus*. Fig. 8b shows the spatial relationship between the small fish and the number of *Eudiaptomus* in the southern basin. The small fish and the *Eudiaptomus* were both concentrated in this part of the loch but the numbers of *Eudiaptomus* collected at different locations within this large 'patch' were inversely related to the numbers of small fish.

Discussion

In most pelagic systems, the spatial variations that appear in the horizontal plane are closely correlated with those that develop in the vertical plane. Organisms that concentrate at different depths in the water column tend to be transported to different locations by water currents.

In Loch Ness, the most important factor influencing the vertical distribution of the phytoplankton is the rapid attenuation of light by dissolved humic compounds. Most of the zooplankton were also concentrated in the top 20–30 m where they tended to move towards the surface during the night. Similar 'nocturnal' migrations of zooplankton have recently been recorded in the loch by Shine, Martin & Majoram (1993a) who note that the filter-feeding *Eudiaptomus* remained deeper in the water column than the raptorial *Cyclops*. We suspect that the *Eudiaptomus* in Loch Ness remain in deep water in order to feed on the microorganisms associated with sedimenting organic matter. Relatively little is known about the sinking characteristics of these organic particles but Shine *et al.* (1993b), using a Marine Snow Camera, demonstrated that there was a pronounced increase in the number of small particles both above and within the thermocline. Our echo sounding results at the fixed station have to be interpreted with some caution since the volume of water sampled by the acoustic beam was relatively small. There is no doubt that most of the fish were concentrated in the top 30 m but the echo returns for the top 10 m were too sparse to monitor their diel movements in detail. The most

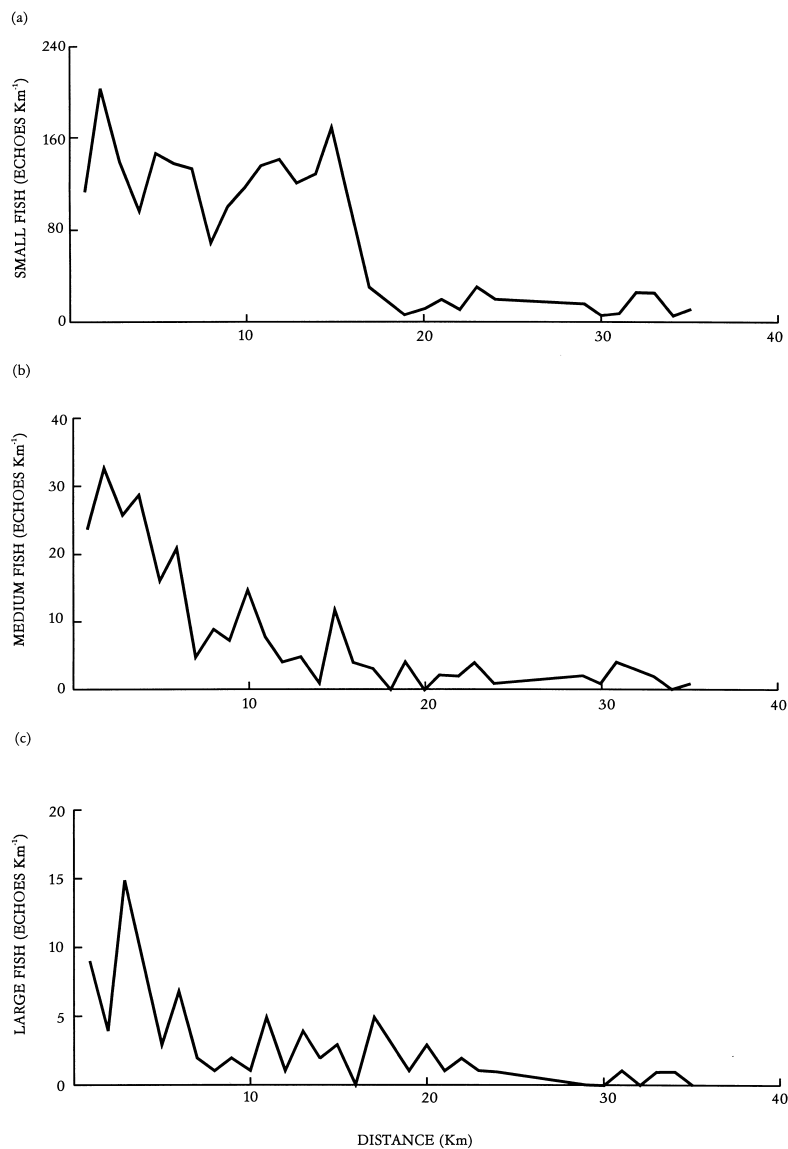


Fig. 7 The horizontal variation in the number of 'small' (1–5 cm), 'medium' (5–10 cm) and 'large' (> 10 cm) fish recorded during the day-time survey.

detailed echo sounding surveys reported to date are those of Shine *et al.* (1993) and Kubecka *et al.* (1993). They recorded similar near-surface accumulations of fish in the loch and showed that the number of echoes in the top 20 m increased during the night. Trawl surveys by Bean *et al.* (1996) have shown that 95% of the fish caught in the pelagic zone are Arctic charr (*S. alpinus*). Very little is known about the feeding behaviour of charr in Loch Ness but the species is known to feed extensively on planktonic crustacea. Maitland *et al.* (1984) and Shine & Martin (1988) found that the diet of the charr in the loch was dominated by cladocera but both these studies concentrated on adult fish and not the small size classes considered here. The vertical distribution of echoes at the fixed station

certainly suggests that the fish were foraging in water where they were able to use visual cues to locate their prey. Although the maximum density of zooplankton was recorded at a depth of 20–30 m, the highest concentration of fish were found at depths between 10 and 20 m. Physiological and behavioural studies by Ali, Klyne & Einarsson (1984) and Henderson & Northcote (1985) have shown that charr have a very high rod to cone ratio in their retinas and can feed selectively at very low light intensities. Northcote (1995) suggests that the visual irradiance threshold for Dolly Varden charr (*S. malma*) is 7.0×10^6 photons $m^{-2} s^{-1}$. If the charr in Loch Ness have the same irradiance threshold, their visual foraging range would effectively be restricted to the top 30 m.

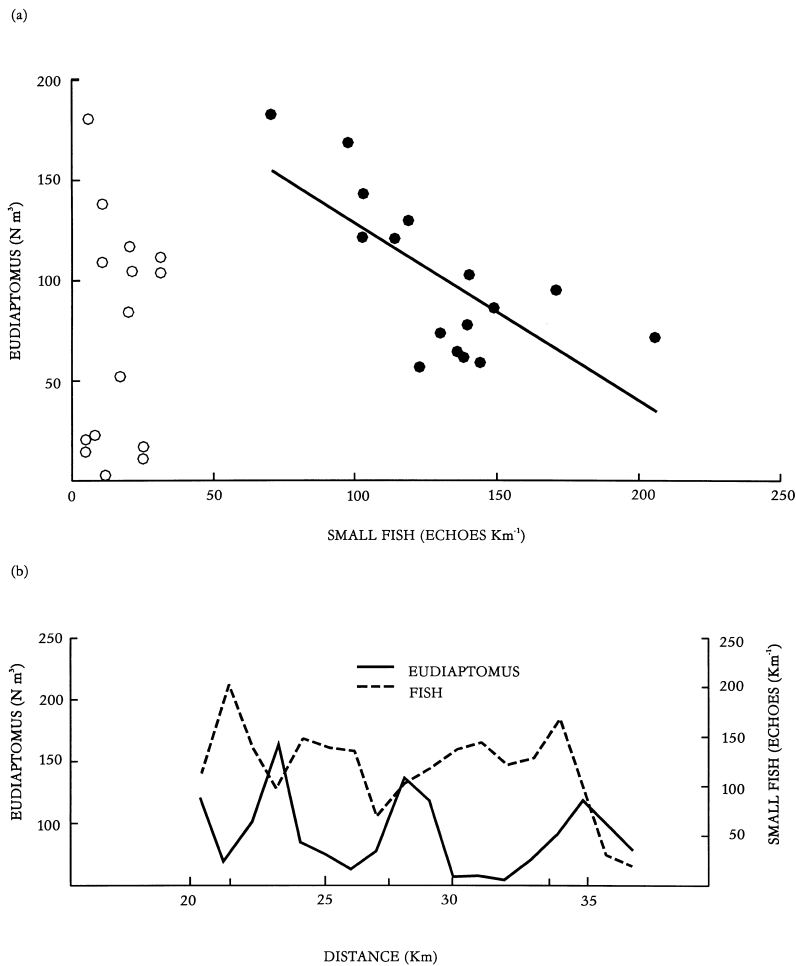


Fig. 8 (a) The relationship between the number of small fish and the number of *Eudiaptomus* in the northern (○) and southern (●) basins of Loch Ness. (b) The relative distribution of small fish and *Eudiaptomus* in the large 'patch' found in the south basin.

The most important factor influencing the horizontal distribution of phytoplankton in Loch Ness at the time of the survey was the north-south gradient in productivity. Most of the phytoplankton species present were non-motile and must therefore behave as passive contaminants of the physical flow. Similar 'nutrient driven' chlorophyll gradients were recorded by George & Jones (1987) but Jones *et al.* (1995) recorded phytoplankton gradients that change with the prevailing wind when motile flagellates were abundant. The horizontal distribution of zooplankton in Loch Ness is, however, strongly correlated with the direction of the prevailing wind. *Eudiaptomus*, the dominant filter feeder, appears to have evolved a vertical migration strategy that carries it away from phytoplankton concentrations found in the north towards the accumulation of non-algal particulates found in the south. The schematic diagram in Fig. 9 presents one possible explanation for the observed vertical and horizontal distribution

of *Eudiaptomus* in Loch Ness. This scheme envisages a wind-drift current moving towards the north with large quantities of sedimenting allochthonous material being carried towards the south by the deep return currents. The *Eudiaptomus*, concentrated at a depth of 20–30 m, would also be transported southward by the current and would therefore accumulate where the concentration of non-algal particulates was relatively high. This concentration of zooplankton towards the south appears to be a relatively persistent feature of the loch (A. Shine, personal communication) and is often associated with aggregations of foraging fish. Similar concentrations of fish were recorded in the south basin by Kubecka *et al.* (1993) and by Bean *et al.* (1996). In behavioural terms, aggregations of zooplankton and fish differ in one important respect. Zooplankton patches form when animals drifting passively downwind accumulate in areas of upwelling or downwelling water. Fish patches are the result of organised movements

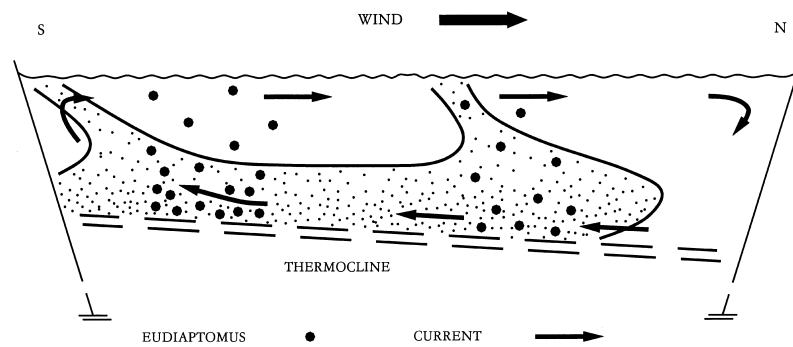


Fig. 9 Schematic diagram showing how the direction of the prevailing wind and the dispersion of non-algal particulates from the main inflows could influence the vertical and horizontal distribution of *Eudiatomus* in Loch Ness.

where the fish change their swimming behaviour when they encounter their selected prey. Little is known about the behavioural mechanisms used by pelagic fish to locate and remain in contact with their prey. Some species are thought to use olfactory cues (Westerberg, 1982) but others simply slow down to feed or increase their turning rate when they encounter high concentrations of prey (Horwood & Cushing, 1978). A variety of theoretical models have been developed to explain the foraging behaviour of animals in patchy environments (Charnov, 1976; Townsend & Winfield, 1985). Experimental tests of optimal patch use have also been performed on animals as diverse as great tits and net-spinning caddis (Krebs *et al.*, 1974; Townsend & Hildrew, 1980). Most suggest that the foragers never quite achieve the optimum performance predicted by the models, presumably because the animals find it difficult to decide when to move from a depleted patch to search for more prey. In the case of fish, no analyses of optimum patch use have hitherto been reported, but there is evidence that fish in large shoals are able to feed in a more efficient way (Pitcher & Magurran, 1983). The inverse relationship between the numbers of small fish and *Eudiatomus* in the south basin of Loch Ness suggests that the highest concentrations of fish within the patch were having an effect on prey density. Exactly how the fish were able to control their position within the patch remains to be demonstrated. The visual search radius of charr feeding at these depths would be severely restricted but they may be able to detect subtle changes in the quantity of food consumed. The fish-zooplankton interactions recorded in Loch Ness are, in many respects, very different to those reported by Kalikhman *et al.* (1992) in Lake Kinneret. The zooplankton patches in Loch Ness were large and sufficiently persistent for the fish to remain in

contact with the patches for several days or even weeks. The zooplankton patches in Kinneret were much smaller and concentrated on physical 'fronts' that were relatively ephemeral. In Loch Ness, the fish appear to have had a quantifiable effect on zooplankton numbers at a few locations in a large 'patch'. In Kinneret, predation by fish was more intense and reduced the number of zooplankton over a much wider area. The numbers of zooplankton and fish in the two lakes are, of course, very different. In Loch Ness, the maximum number of fish recorded in the zooplankton 'patch' was only 1000 individuals per hectare but numbers in Kinneret frequently exceeded 10 000 individuals per hectare.

Acknowledgments

We thank Elisar Baroudy, Janice Fletcher, Diane Hewitt and Piotr Krylov for help with fieldwork and Håvard Nes of Simrad for assisting with the initial analysis of the EK 500 data. Adrian Shine and colleagues from the Loch Ness and Morar Project, and Kaare Steel Groos and colleagues from Simrad provided generous logistical support for the vertical and horizontal distribution surveys, respectively. The final figures were drawn by Trevor Furnass and later edited by Yvonne Dickens. This study was supported by funding from Project Urquhart and a special grant from Scottish Natural Heritage.

References

- Ali M.A., Klyne M.A. & Einarsson G. (1984) Ecophysiological adaptations of the retina in the Arctic charr. *Biology of the Arctic Charr: Proceedings of the International Symposium on Arctic Charr*. (Ed. L. Johnson and B. Burns), pp. 251-261. University of Manitoba Press, Winnipeg.

- Bailey-Watts A.E. & Duncan P. (1981) The phytoplankton. *The Ecology of Scotland's Largest Lochs* (Ed. P.S. Maitland), pp. 91–118. Junk, The Hague.
- Bean C.W., Winfield I.J. & Fletcher J.M. (1996) Stock assessment of the Arctic charr (*Salvelinus alpinus*) population in Loch Ness, UK. *Stock Assessment in Inland Fisheries* (Ed. I.G. Cowx), pp. 206–223. Fishing News Books, Blackwell, Scientific Publications, Oxford.
- Charnov E.L. (1976) Optimal foraging: the marginal value theorem. *Theoretical Population Biology*, **9**, 129.
- Craig R.E. & Forbes S.T. (1969) Design of a sonar for fish counting. *Fiskeridirektoratets Skrifter*, **15**, 210–219.
- Foote K.G. (1987) Fish target strengths for use in echo integrator surveys. *Journal of the Acoustical Society of America*, **82**, 981–987.
- Frank K.T. & Leggett W.C. (1985) Reciprocal oscillations in densities of larval fish and potential predators: a reflection of present or past predation? *Canadian Journal of Fisheries and Aquatic Sciences*, **42**, 1841–1849.
- George D.G. (1976) A pumping system for collecting horizontal plankton samples and recording continuously sampling depth, water temperature, turbidity and in vivo chlorophyll. *Freshwater Biology*, **6**, 413–419.
- George D.G. (1981) Zooplankton patchiness. *Annual Report of the Freshwater Biological Association*, **49**, 32–43.
- George D.G. & Edwards R.W. (1976) The effect of wind on the distribution of chlorophyll *a* and crustacean plankton in a shallow eutrophic reservoir. *Journal of Applied Ecology*, **13**, 667–690.
- George D.G. & Jones D.H. (1987) Catchment effects on the horizontal distribution of nutrients in five of Scotland's largest freshwater lochs. *Journal of Ecology*, **75**, 43–59.
- Geospace Group (1993) The spatial organization of aquatic populations as observed using hydroacoustic methods. *Aquatic Living Resources*, **6**, 171–174.
- Henderson M.A. & Northcote T.G. (1985) Visual prey detection and foraging in sympatric cutthroat trout (*Salmo clarki clarki*) and Dolly varden (*Salvelinus malma*). *Canadian Journal of Fisheries and Aquatic Sciences*, **42**, 875–790.
- Horwood J.W. & Cushing D.H. (1978) Spatial distributions and ecology of pelagic fish. *Spatial Pattern in Plankton Communities. NATO Conference Series, IV Marine Sciences* (Ed. J.H. Steele), pp. 355–383. Plenum, New York.
- Irish A.E. (1980) A modified one-metre Friedinger sampler: a description and some selected results. *Freshwater Biology*, **10**, 135–139.
- Jones R.I., Fulcher A.S., Jayakody J., Laybourn-Parry J., Shine A.J., Walton M.C. & Young J.M. (1995) The horizontal distribution of plankton in a deep, oligotrophic lake – Loch Ness, Scotland, *Freshwater Biology*, **33**, 161–170.
- Jones R.I., Young J.M., Hartley A.M. & Bailey-Watts A.E. (1996) Light limitation of phytoplankton development in an oligotrophic lake – Loch Ness, Scotland, *Freshwater Biology*, **35**, 533–543.
- Kalikhman I., Walline P. & Gophen M. (1992) Simultaneous patterns of temperature, oxygen, zooplankton and fish distribution in Lake Kinneret, Israel. *Freshwater Biology*, **28**, 337–347.
- Krebs J.R., Ryan J.C. & Charnov E.L. (1974) Hunting by expectation or optimal foraging? A study of patch use by chickadees. *Animal Behaviour*, **22**, 953.
- Kubecka J., Duncan A. & Butterworth A.J. (1993) Large and small organisms detected in the open waters of Loch Ness by dual-beam acoustics. *The Scottish Naturalist*, **105**, 175–193.
- Laybourn-Parry J., Walton M., Young J., Jones R.I. & Shine A. (1994) Protozooplankton and bacterioplankton in a large oligotrophic lake – Loch Ness, Scotland. *Journal of Plankton Research*, **16**, 1655–1670.
- Maitland P.S. (1981) Introduction and catchment analysis. *The Ecology of Scotland's Largest Lochs* (Ed. P.S. Maitland), pp. 1–27. Junk, The Hague.
- Maitland P.S., Greer R.B., Campbell R.N. & Friend G.F. (1984) The status and biology of the Arctic charr *Salvelinus alpinus* L. in Scotland. *Biology of the Arctic Charr: Proceedings of the International Symposium on Arctic Charr* (Ed. L. Johnson and B. Burns), pp. 193–215. University of Manitoba Press, Winnipeg.
- Maitland P.S., Smith B.D. & Dennis G.M. (1981) The crustacean zooplankton. *The Ecology of Scotland's Largest Lochs* (Ed. P.S. Maitland), pp. 135–154. Junk, The Hague.
- Murray J. (1904) Biology of Loch Ness, *Geographical Journal*, **18**, 343–345.
- Northcote T.G. (1995) Confessions from a four decade affair with Dolly Varden: a synthesis and critique of experimental tests for interactive segregation between Dolly Varden char (*Salvelinus malma*) and Cutthroat Trout (*Onchyrhynchus clarki*) in British Columbia. *Nordic Journal of Freshwater Research*, **71**, 49–67.
- Pitcher T.J. & Magurran A.E. (1983) Shoal size, patch profitability and information exchange in foraging goldfish. *Animal Behaviour*, **31**, 546.
- Rose G.A. & Leggett W.C. (1990) The importance of scale to predator-prey correlations: an example of Atlantic fishes. *Ecology*, **71**, 33–43.
- Rouen M.A. (1989) The design and development of the 'Windermere Profiler'. *Annual Report of the Freshwater Biological Association*, **57**, 93–106.
- Shine A.J. & Martin D.S. (1988) Loch Ness habitats

- observed by sonar and underwater television. *The Scottish Naturalist*, 111–199.
- Shine A.J., Martin D.S. & Marjoram R.S. (1993a) Spatial distribution and diurnal migrations of the pelagic fish and zooplankton in Loch Ness. *The Scottish Naturalist*, **105**, 195–235.
- Shine A.J., Martin D.S., Bennett S. & Marjoram R.S. (1993b) Allochthonous organic inputs as an explanation of spatial biomass gradients observed in the pelagic and profundal zones of Loch Ness. *The Scottish Naturalist*, **105**, 257–269.
- Stephens K. (1963) Determination of low phosphate concentrations in lake and marine waters. *Limnology and Oceanography*, **8**, 361–362.
- Talling J.F. (1974) Photosynthetic pigments. General outline of spectrophotometric methods: specific procedures. *A Manual on Methods for Measuring Primary Production in Aquatic Environments*, 2nd edn (Ed. R.A. Vollenweider), pp. 22–26. International Biological Programme Handbook, 12, Blackwell Science, Oxford.
- Thorpe S.A. (1974) Turbulence and mixing in a Scottish Loch. *Philosophical Transactions of the Royal Society (Series A)*, **286**, 125–181.
- Townsend C.R. & Hildrew A.G. (1980) Foraging in a patchy environment by a predatory net-spinning caddis larva: a test of optimal foraging theory. *Oecologia*, **47**, 219.
- Townsend C.R. & Winfield I.J. (1985) The application of optimum foraging theory to feeding behaviour in fish. *Fish Energetics: New Perspectives* (Eds P. Tytler and P. Calow), pp. 67–98. Croom Helm, London.
- Vollenweider R.A. (1974) *A Manual on Methods for Measuring Primary Production in Aquatic Environments*. International Biological Programme Handbook 12, Oxford, Blackwell.
- Walline P.D., Pisanty S. & Lindem T. (1992) Acoustic assessment of the number of pelagic fish in Lake Kinneret, Israel. *Hydrobiologia*, **231**, 153–163.
- Westerberg H. (1982) The orientation of fish and the vertical stratification at fine- and micro-structure scales. *Mechanisms of Migration in Fish* (Eds J.D. Mc Cleave G.P. Arnold, J.J. Dodson and W.H. Neill), NATO Conference Series IV, 14, Plenum.

(Manuscript accepted 3 September 1999)

This document is a scanned copy of a printed document. No warranty is given about the accuracy of the copy. Users should refer to the original published version of the material.