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Long-term and short-term fluctuations in the numbers and catches of Arctic charr, *Salvelinus alpinus* (L.), in Windermere (northwest England)

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Keywords : Arctic charr, Windermere Lake, anglers'catches, gill-net catches, echo sounding.

All English populations of Arctic charr are found in the Lake District (northwest England). There are at least four races of charr in Windermere, the largest natural lake in England, with the north and south basins of the lake each containing two distinct races that spawn in autumn and spring respectively. Three methods have been used to estimate levels of the charr stocks ; namely gill-netting each November (1939-1991) for autumn spawners in the north basin, anglers' catches from both basins (1966-1991), echo-survey data from both basins (July 1989 - December 1991). An increase in gill-net catches from 1945 to 1965 was associated with a cull of larger pike, *Esox lucius* L. ; since 1965, catches have fluctuated around a high mean level. There was good, if not excellent, agreement between the anglers' catches and the gill-net catches. The ratio of anglers' catches in the north and south basins showed that catches have been relatively low in the south basin since 1984. Although there has also been an increase in brown trout, *Salmo trutta* L., taken by the charr anglers since 1984 in the south basin, this increase was not responsible for the lower charr catches. When estimates of fish densities with an echo sounder were restricted to fish > 20 cm and depths down to 20 m, this being roughly the stock available to charr anglers, there was good agreement between monthly estimates and anglers' catches, especially in the north basin. The echo-sounder data confirmed the higher numbers in the north basin, and lower numbers in winter in both basins. The three different methods therefore provided comparable data on the fluctuations in levels of charr stocks in Windermere. Possible reasons for these fluctuations are discussed briefly.

Fluctuations historique et récente des nombres et prises d'omble chevalier, *Salvelinus alpinus* (L.), dans le lac Windermere (nord-ouest de l'Angleterre)

Mots clés : Omble chevalier, Lac Windermere, prise par pêcheur, prise au filet, écho-sondage.

Toutes les populations anglaises d'omble chevalier sont situées dans la région des lacs, au nord-ouest de l'Angleterre. Il existe au moins quatre races d'omble chevalier à Windermere, le plus grand lac naturel d'Angleterre. Les bassins nord et sud du lac contiennent deux races distinctes : l'une fraye en automne, l'autre au printemps. Trois méthodes ont été utilisées pour évaluer les stocks d'omble chevalier, principalement par capture au filet chaque mois de novembre (1939-1991) pour les géniteurs d'automne dans le bassin nord, par prises des pêcheurs des bassins nord et sud (1966-1991) et par écho-sondage des bassins nord et sud (juillet 1989 - décembre 1991). Une augmentation dans les prises au filet de 1945 à 1965 est liée à l'élimination des grands brochets, *Esox lucius* L. ; depuis 1965, les prises ont fluctué autour d'un niveau moyen élevé. Un très bon rapport est trouvé entre les prises des pêcheurs et les captures au filet. Les rapports des prises des pêcheurs dans les deux bassins montrent la diminution des prises dans le bassin sud, depuis 1984. Bien qu'il y ait eu une augmentation de truites, *Salmo trutta* L., dans les prises des pêcheurs depuis 1984 dans le bassin sud, cette augmentation n'était pas responsable de la baisse des captures d'omble. Lorsque l'évaluation des densités de poisson par écho-sondage s'est limitée aux poissons d'une taille supérieure à 20 cm et se trouvant entre 1 et 20 mètres de profondeur, ce qui représente le stock disponible pour les pêcheurs d'omble, il existe une bonne relation entre les évaluations mensuelles et les prises des pêcheurs, surtout dans le bassin nord. Les données de l'écho-sondage confirment les chiffres élevés dans le bassin nord et les chiffres plus faibles en hiver dans les deux bassins. Ainsi, les trois méthodes utilisées fournissent des données comparables pour les fluctuations des niveaux des stocks d'omble chevalier à Windermere. Les raisons de ces fluctuations sont brièvement discutées.

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1. Introduction

The Arctic charr, *Salvelinus alpinus* (L.), is a holarctic species that is frequently anadromous in northern latitudes higher than 65°N. At lower latitudes, this species forms numerous land-locked populations, usually found at high altitudes. In the British Isles, there are several populations in Ireland and Scotland, only five recorded in Wales, and all the English populations are found in eight lakes in northwest England (Maitland & Lyle 1991). There are at least four races of charr in Windermere, the largest natural lake in England, with the north and south basins of the lake each containing two races that spawn in spring and autumn respectively (Frost 1965, Child 1984, Partington & Mills 1988). Most charr in the lake are autumn spawners with spring spawners representing 4-6 % of the adult population (Mills 1989, Mills & Hurley 1990). Rough estimates of the adult charr in the lake are 132,000 autumn spawners and 8,000 spring spawners with a total biomass of 30 - 35 Mg (tonnes) (Mills & Hurley 1990).

Windermere is divided by shallows and islands (Fig. 1) into a north basin (area 8.1 km^2, mean depth 25.1 m, maximum depth 64 m) and a south basin (area 6.7 km^2, mean depth 16.8 m, maximum depth 42 m). At an altitude of only 39.3 m, Windermere is one of the few lowland lakes with a substantial population of charr. The lake is situated in a National Park and is therefore a focus for tourism and recreation. Since 1945, regular measurements from both basins have shown that the lake has become nutrient enriched (Lund 1972, Sutcliffe et al. 1982, Heaney et al. 1988, Talling & Heaney 1988). The increasing concentration of NO_3-N may be due to a large increase in the use of nitrogenous fertilizers with subsequent winter fluctuations conditioned by climatic factors, including temperature. Large increases in winter concentrations of PO_4-P, especially in the south basin, are probably due to increases in sewage-borne phosphorus discharged to the lake (see also Mills et al. 1990). Associated with this increasing enrichment, there has been an increase in hypolimnetic deoxygenation during summer and autumn in the south basin, first recorded in 1981. Complete anoxia has not occurred in the north basin because it is less productive, deeper, and its ratio of epilimnetic to hypolimnetic volume is lower than that of the south basin (Heaney 1987).

Although nutrient enrichment is not directly harmful to charr, the associated anoxia will restrict the water space available to the fish. This space will be reduced further in hot summers when surface temperatures may be higher than the preferred values for this species. It is therefore important that levels of charr stocks in the lake are monitored so that suitable measures may be taken to ensure the survival of this species in Windermere. Evidence from other European lakes indicates that increasing enrichment can lead to a reduction and eventual extinction of charr populations (Mills et al. 1990).

In marked contrast to stream salmonids that can be sampled by electrofishing, it is not possible to obtain absolute estimates of charr numbers in lakes. Three methods have been used in Windermere to obtain relative estimates of the levels of charr stocks. The chief objective of this investigation is to compare data obtained by these different methods. If results are similar, then conclusions on the short-term and long-term fluctuations in stock levels can be drawn with greater confidence.

2. Methods

Since 1939, gill nets with a 32 mm (bar) mesh have been used each November to catch autumn spawning charr in the north basin of Windermere. The results are expressed as catch-per-unit-effort (CPUE) which is the mean catch per gill-net day. The original monitoring site was just south of Low Wray Bay (1939-1973) but was moved south to North Thompson Holme (1975-1991) because of interference with the gill nets (see sites in Fig. 1).

Charr were last netted commercially in Windermere in 1921, but they are still caught by fishermen using plumb lines (for detailed account of methods, see Kipling 1984). Fish are caught down to a depth of 15-20 m depending upon the rowing speed of the angler's boat and the minimum size limit for charr is 203 mm (equivalent to 8 inches). Anglers catch-per-unit-effort (CPUE) data are expressed as mean catch per boat per hour. Data are now available from 1966-1991 for angler A and from 1975-1991 for angler B.

The third and final method was echo sounding, using a Simrad EY-M echo sounder. This equipment has been used extensively to estimate the density of pelagic fish communities dominated by coregonids,

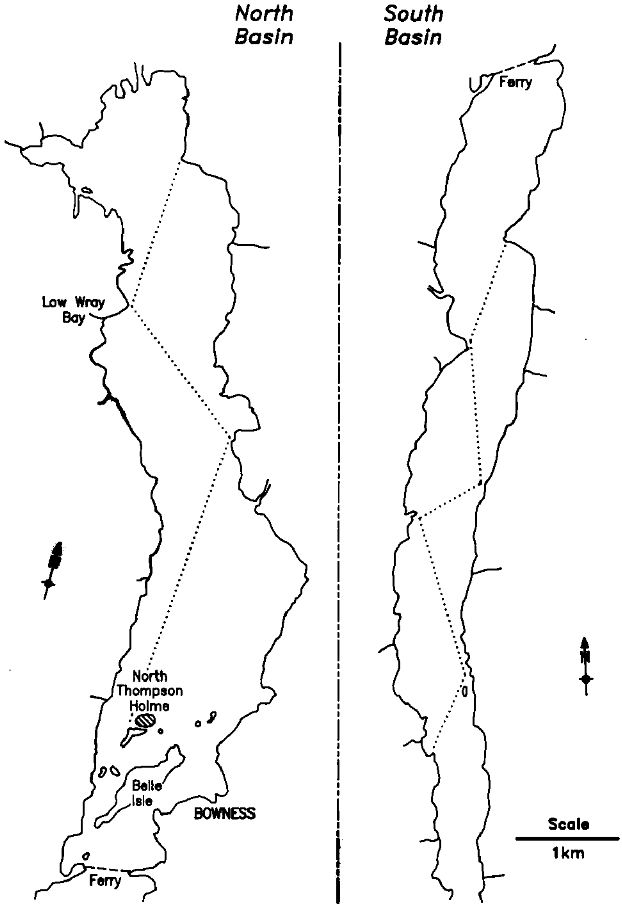

Fig. 1. Map of the north and south basins of Windermere showing echo-survey transects (broken line) and sites for annual gill-net catches of spawning charr in November (north basin only) ; a site south of Low Wray Bay was used from 1939-1973 and a site north of North Thompson Holme was used from 1975 to the present.

Fig. 1. Cartes des bassins nord et sud de Windermere indiquant les transects parcourus pour l'écho-sondage (en pointillés) et les sites des prises annuelles au filet des géniteurs d'omble chevalier en novembre (bassin nord seulement) ; l'omblière sud de Low Wray Bay a été suivie de 1939 à 1973 et l'omblière de North Thompson Holme de 1975 jusqu'à aujourd'hui.

osmerids and cyprinids in Scandinavia (e.g. Lindem 1982, Lindem & Sandlund 1984, Brabrand 1986, Jurvelius et al. 1987, Bjerkend et al. 1991). Few echo sounding studies have been performed on charr (Brabrand 1991). The Windermere surveys were made along fixed transects (broken lines in Fig. 1). Surveys of both basins in daylight were performed once every two weeks throughout most of the year and every week during the spawning season. Data from July 1989 to December 1991 are used in the present investigation. Night surveys have also been made each month from October 1990. A survey was postponed on some occasions because of dangerous weather or the absence of the boat during its annual maintenance (the echo-sounder is mounted on the hull of the boat). A Hydro-Acoustic-Data-Acquisition-System (HADAS) provided quantitative information about the fish in the water column by transforming and processing the received echo. Results are expressed as mean density of fish per hectare.

3. Results

3.1. Gill netting and anglers' catches

Gill-net catches of autumn spawning charr in the north basin showed a general upward trend from 1945 to about 1965 (Fig. 2a). This increase was associated with a cull of larger pike, *Esox lucius* L., and the reduction of the biomass of this major predator by about 65 % could be responsible for the increase in charr numbers (Kipling 1984). Since

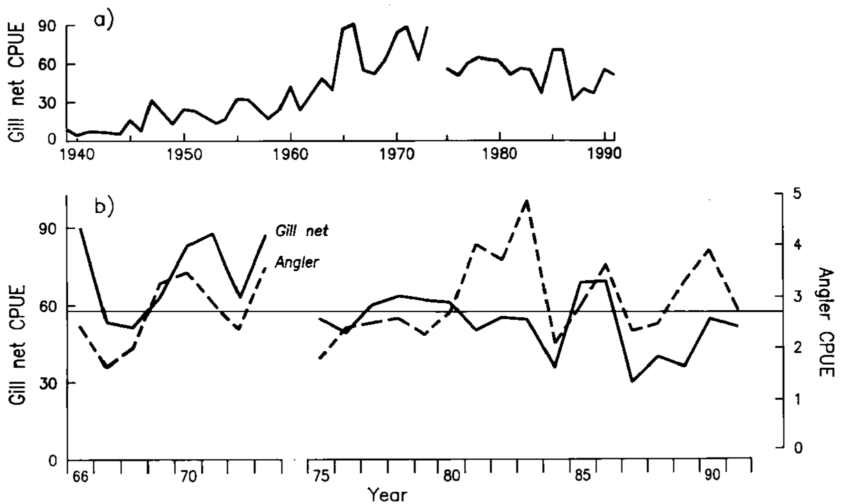

Fig. 2 (a) Gill-net catch-per-unit-effort (CPUE) for charr at Windermere north basin spawning sites from 1939-1991. CPUE is the mean catch per gill-net day in November near Low Wray Bay (1939-1973) and North Thompson Holme (1975-1991) spawning sites. (b) Gill-net CPUE (solid line) and angler CPUE (broken line) from 1966 to 1991. Angler CPUE is the mean catch per boat per hour. The scales for gill-net and angler CPUE have been arranged so that the overall means for each coincide.

Fig. 2. (a) Unités d'effort de pêche au filet sur les omblières du bassin nord de Windermere de 1939 à 1991. L'unité d'effort de pêche correspond à la prise moyenne par jour de pêche au filet en novembre sur l'omblière de Low Wray Bay (1939-1973) et North Thompson Holme (1975-1991). (b) Unités d'effort de pêche par filet (trait continu) et par pêcheur (tirets) de 1966 à 1991. L'unité d'effort de pêche par pêcheur correspond à la prise moyenne par bateau et par heure. Les échelles de l'unité d'effort de pêche des filets et des pêcheurs sont ajustées pour que les moyennes coïncident.

1965, gill-net catches of charr have fluctuated considerably with no obvious discrepancy caused by a change of site from 1973 to 1975 (break in series in Fig. 2a).

Gill-net and angler's catches (CPUE for whole lake) generally followed a similar pattern (Fig. 2b), but there was a marked discrepancy about 1980 when the relative catches crossed (note that both sets of catches were scaled so that their overall means coincided ; means indicated by horizontal line on Fig. 2b). There was a positive relationship between the two sets of catches when the periods 1966-1980 and 1981-1991 were treated separately (angler A in Fig. 3). A similar relationship was not obtained for a second angler, probably because fewer data points were available (angler B in Fig. 3). This explanation was supported by the strong positive relationship between catches by the two anglers even though the CPUE for angler B was generally lower than that for angler A (Fig. 3). It was therefore concluded that there was good, if not excellent, agreement between the anglers' catches and the gill-net catches.

As the anglers' catches generally reflected changes in charr abundance, they could be used to compare population changes in the two basins of the lake. A simple, but useful, index of these changes was provided by the ratio of mean catch in the south basin to mean catch in the north basin. Values of one angler's catches from 1966 to the present showed that, prior to 1983, catches were similar in both basins or were higher in the south basin (angler A in Fig. 4). The marked decrease in the ratio for the next five years indicated the relative decline in south basin catches from 1984 to 1988. The ratio of catches for a second angler over a shorter period (1975 to 1988) followed a similar pattern (angler B in Fig. 4). There was a clear improvement in 1989 with similar catches in both basins (ratio ≃ 1) for both anglers, — but a decline in 1990 and 1991 to earlier values indicated that the 1989 improvement was temporary, not permanent.

Charr fishermen on Windermere have expressed the general, but subjective, view that more brown trout, *Salmo trutta* L., have been taken on charr tackle in recent years. Records were obtained from the two anglers and these confirmed an increase in the percentage of trout taken in the catches, especially in the south basin (Fig. 5). It is notable that the latter increase commenced in 1984, the same year which marked the onset of changes in the ratio of catches in the north and south basins of Windermere (cf. Fig. 4). The change in the latter ratio could have been due to the increased proportion of trout in the catches, but a comparison of the ratio for total catches (charr + trout) in both basins revealed little change in the temporal pattern from that obtained for charr alone. Further comparison of the two ratios revealed few differences but the presence of trout slightly increased the ratio in a few years (e.g. 1988, 1990, 1991 in Fig. 6). However, the general conclusion must be that the increases in the catches of trout in the south basin were not responsible for the lower catches of charr relative to those of the north basin.

Monthly catches were compared for both anglers in the fishing season (March/April to September) in 1989, 1990, 1991. These years were chosen for more detailed examination because the anglers' catches could also be compared with fish density estimated by the echo sounder (Fig. 7). Apart from one large catch by angler B in April 1991, brown trout were rarely taken by both anglers in the north basin. They were, however, frequently taken in the catches in the south basin, especially in spring and early summer. These comparisons also show that in most months, catches were lower in the south basin than in the north basin. Comparisons with the results from the echo sounder are made in the next section.

3.2. Echo sounding

The echo sounder provides estimates of the total number of fish present in the open water of the lake but cannot identify the species. Shoaling fish recognized with the echo sounder were undoubtedly perch, *Perca fluviatilis* L., and these fish could be easily deleted from the records. Pike, *Esox lucius*, were probably rare in the open water of the lake. It was impossible to separate charr from pelagic brown trout and the echo sounder therefore provided estimates of the total number of pelagic salmonids (charr + trout) in the north and south basins of Windermere. As mentioned earlier, the methods used by anglers to catch charr take fish at water depths about 1 m to no more than 20 m, and charr taken from the lake have a fork length greater than about 20 cm. For these reasons, the results from the echo sounder were filtered to leave those from water depths down to 20 m and fish longer than 20 cm. The final estimates of fish density were therefore

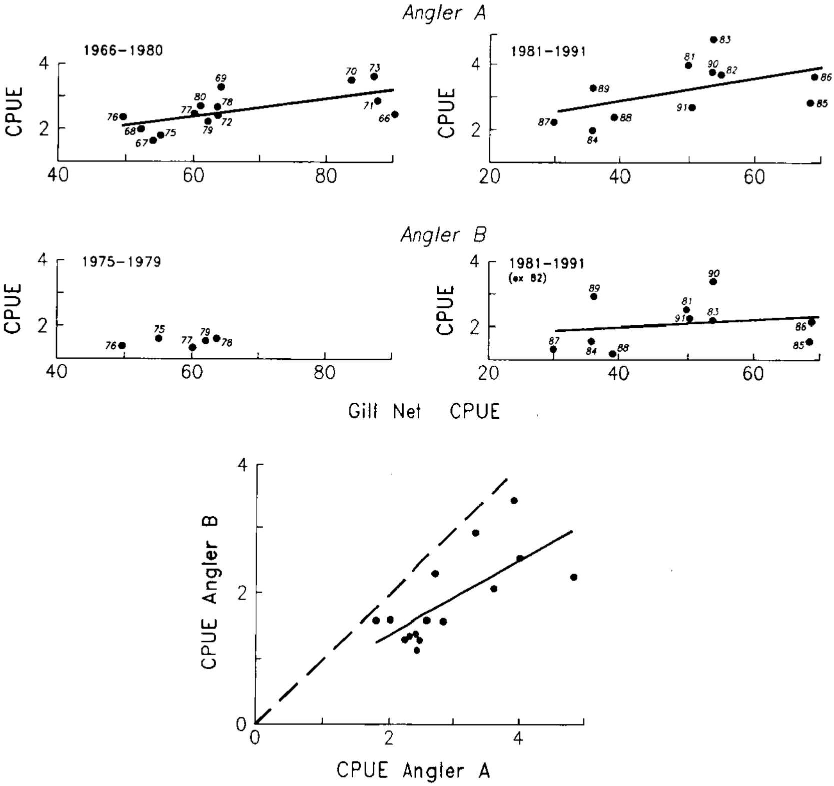

Fig. 3. **Relationship between angler catch-per-unit-effort** (CPUE) and gill-net CPUE for the periods **1966-1980 and 1981-1991 for angler** A, and for the periods 1975-1979 and 1981-1991 (excluding 1982) for angler B, together with the relationship between CPUE for angler A and B (angler CPUE is the mean catch per boat per hour, gill-net CPUE is the mean catch per gill-net day). Regression lines for angler A (1966-1980) : Angler CPUE = 0.791 + 0.027 (gill-net CPUE), r = 0.66 ; for angler A (1981-1991) : Angler CPUE = 1.666 + 0.032 (gill-net CPUE), r = 0.50 ; for angler B (1981-1991) : Angler CPUE = 1.607 + 0.011 (gill-net CPUE), r = 0.20 ; for both anglers : CPUE angler B = 0.268 + 0.559 (CPUE angler A), r = 0.70.

Fig. 3. Relation entre l'unité d'effort de pêche par filets maillants et par pêcheurs pour les périodes 1966-1980 et 1981-1991 pour le pêcheur A, et pour les périodes 1975-1979 et 1981-1991 (1982 exclu) pour le pêcheur B ; relation entre unité d'effort de pêche pour les pêcheurs A et B (l'unité d'effort de pêche pour les pêcheurs est la prise moyenne/bateau/heure et pour les filets, l'unité d'effort de pêche est la prise moyenne par jour de pêche). Droites de régression pour pêcheur A (1966-1980) : unité d'effort de pêche du pêcheur = 0.791 + 0.027 (unité d'effort de pêche des filets), r = 0.66 ; pour pêcheur A (1981-1991) : unité d'effort de pêche du pêcheur = 1.666 + 0.032 (unité d'effort de pêche des filets), r = 0.50 ; pour pêcheur B (1981-1991) : unité d'effort de pêche du pêcheur = 1.607 + 0.011 (unité d'effort de pêche des filets), r = 0.20 ; pour pêcheurs A et B, unité d'effort de pêche du pêcheur B = 0.268 + 0.559 (unité d'effort de pêche du pêcheur A), r = 0.70.

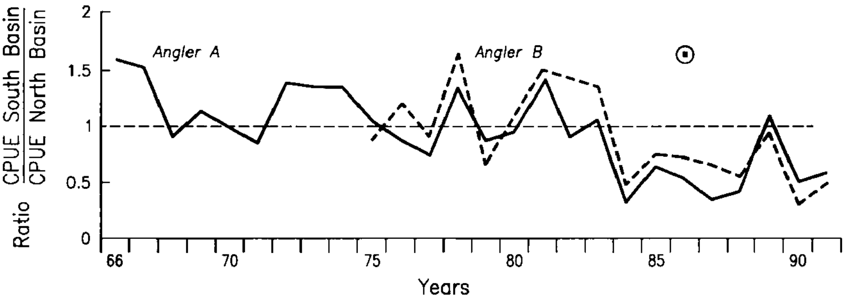

Fig. 4. Ratio of angler CPUE for south basin to north basin for angler A (solid line) from 1966 to 1991 and angler B (broken line) from 1975 to 1991. (Note : the high encircled value for angler B in 1986 was due to the inclusion of one exceptionally high catch in the south basin ; when this was excluded from the analysis the estimated ratio was very similar to adjacent values).

Fig. 4. Rapport de l'unité d'effort de pêche du bassin sud au bassin nord pour le pêcheur A (trait continu) de 1966 à 1991 et pour le pêcheur B (tirets) de 1975 à 1991. (Note : la valeur encerclée pour le pêcheur B en 1986 est due à l'inclusion d'une prise exceptionnelle dans le bassin sud ; quand cette valeur était exclue de l'analyse, le rapport estimé était semblable aux valeurs adjacentes).

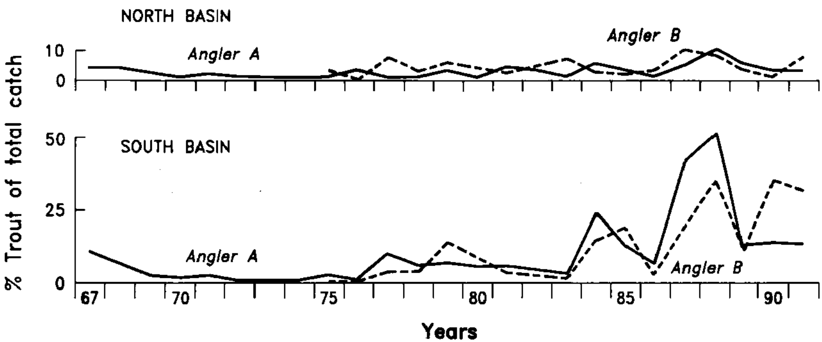

Fig. 5. Percentage of brown trout taken in the north and south basins in annual catches by anglers A and B.

Fig. 5. Pourcentages de truites des prises annuelles des pêcheurs pour les bassins nord et sud.

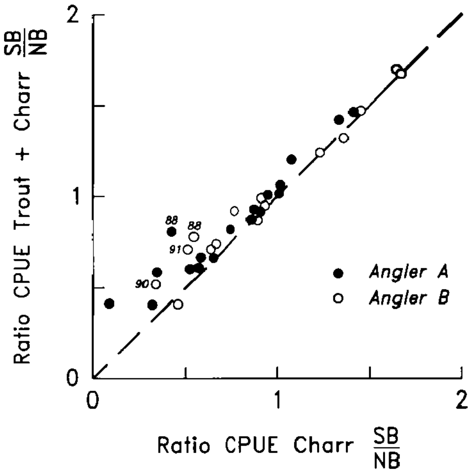

Fig. 6. Comparison between ratios (south basin : north basin = SB/NB) of CPUE for anglers A and B using total catch (charr + trout) and charr only.

Fig. 6. Comparaison entre les rapports (bassins sud : nord = SB/NB) de l'unité d'effort de pêche pour les pêcheurs A et B, à partir de la prise totale (omble + truite) et de la prise seule d'omble.

for those fish that should, in theory, be available to the angler (Fig. 7).

The results confirmed the earlier conclusion from the anglers' catches that the density of fish was consistently higher in the north basin. In the north basin, there was also a similar pattern in the fluctuations in fish density and anglers' catches, e.g. a late summer peak (August), especially in 1989, 1990. Similarities were less evident for the lower numbers in the south basin, but more fish were usually available in months in which anglers fished. Estimates of fish density at night were usually higher than the corresponding estimates during the day but there were three exceptions in which the reverse was true (October 1990, September, October 1991).

These comparisons are generally encouraging because they show that the results obtained with the echo sounder are generally comparable to angler's catches. The echo sounder data not only confirmed the higher numbers in the north basin but also demonstrated lower numbers in winter in both basins (Fig. 7). It is therefore concluded that the three different methods provided comparable data on the fluctuations in levels of charr stocks in Windermere.

4. Discussion

Nutrient enrichment is not directly harmful to charr and has indeed been used to increase productivity for charr in some extremely oligotrophic lakes in Scandinavia (Milbrink & Holmgren 1984). However, in many lakes, any short-term benefits to charr from increasing enrichment are soon outweighed by lower concentrations of oxygen, siltation of spawning grounds and increased competition from other fish, especially cyprinids. Examples include Lake Neuchatel where charr became extinct in 1970

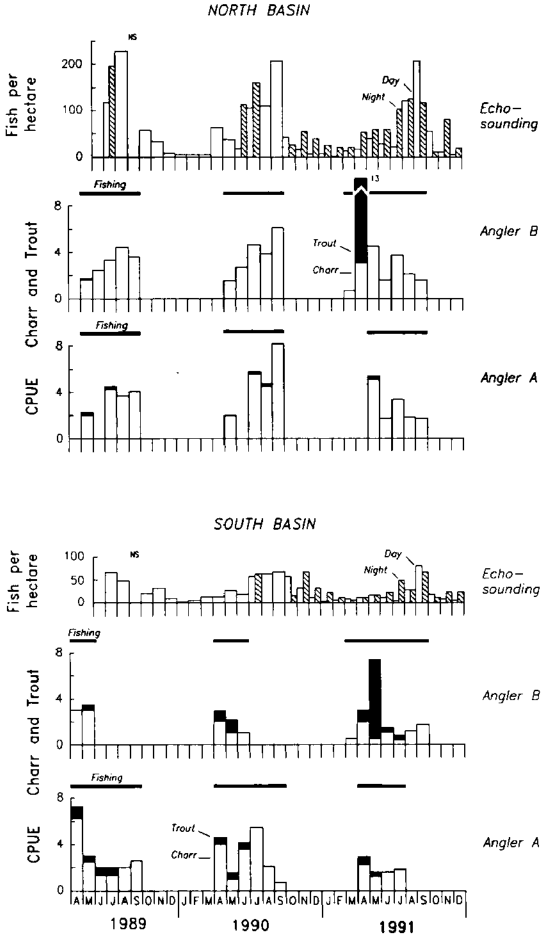

Fig. 7. Comparisons of monthly CPUE for charr (open columns) and trout (black portion of columns) taken in north and south basins by anglers A and B ; estimates of fish density from echo-sounding are also provided.

Fig. 7. Comparaison de l'unité d'effort de pêche mensuelle entre les ombles (colonnes blanches) et les truites (partie noire des colonnes) prises dans les bassins nord et sud par les pêcheurs A et B ; l'estimation de la densité de poisson par écho-sondage est aussi présentée.

(Pedroli 1983), Lake Constance where the charr population is maintained only by continual restocking (Hartmann 1984), and Lake Zug where catches of charr have fallen by 98 % (Ruhlé 1984). Other, more local factors may be responsible for the extinction of a charr population. For example, charr were once present in Ullswater in the English Lake District, but have been absent for at least 50 years. The most probable reason for their disappearance was pollution of their spawning grounds by suspended solids and lead from mine workings.

Although there is no evidence to suggest that Windermere charr are endangered, the loss of other charr populations throughout Europe provides an obvious reason for monitoring the levels of charr stocks in both basins of the lake. The three different methods of gill-netting, angling and echo sounding have been shown in this investigation to provide comparable data on the fluctuations in levels of charr stocks. This similarity increases confidence in the conclusions drawn from one or more of the sampling methods.

The long-term records for gill-net catches are essential for the assessment of the relevance of short-term change. For example, low gill-net catches were obtained in the north basin in 1987, 1988, and 1989, but the higher catch in 1990 demonstrates that there has been no permanent decline in catches. The 1990 value is similar to values obtained in the early 1980's (Fig. 2).

The ratio of anglers' catches in the north and south basins of the lake clearly identifies the persistently lower catches in the south basin from 1984 to 1988, and demonstrates that the improvement in 1989 was temporary, not permanent (Fig. 4). Such comparisons highlight the need for long-term records. It is remarkable that the start of lower catches of charr in the south basin coincided with an increase in trout catches taken on charr tackle (Fig. 5). Replacement of charr by trout would have been an obvious reason for the lower charr catches but further analyses showed that this was not the case (Fig. 6).

The increase in brown trout in the anglers' catches from 1984 to the present has been most marked in the south basin (Fig. 5). An explanation for this increase has yet to be found, but there could have been a general increase in trout density in the south basin and/or a shift in the habitat frequented by the trout. Trout have been thought traditionally to inhabit the shallow littoral regions of the lake but if the shore areas become unsuitable for some unknown reason, then the fish would move to the open water to join the pelagic charr. Fishermen on Windermere have expressed the subjective view that brown trout are now sparse in the littoral region of the lake. There are also energetics reasons why brown trout should move into cooler water so that their conversion of food into growth is more efficient (Elliott 1979, 1981). Such speculations indicate a need for further research to determine why brown trout appear to have become more numerous in the open water of the south basin, but not the north basin, in recent years.

The echo-sounding technique provides, for the first time, estimates of fish density in the open water of the lake. Previous methods all used nets or traps, and usually provided an index of abundance, most frequently of spawning adults. Such methods cannot provide estimates of absolute numbers. Echo-sounding overcomes this problem and provides frequent estimates of fish density at different depths as well as the size frequency distribution of the fish in the water column. The chief disadvantage of this method is that it cannot separate charr from pelagic brown trout in Windermere. A similar problem exists in other studies of pelagic fish stocks in lakes (see references in Brabrand 1991, Brandt et al. 1991).

In spite of this problem, the results from the echo sounder are encouraging. Comparisons with the anglers' catches produced no major problems in interpretation (Fig. 7). The echo-sounding data showed that fish densities in the open water of the north basin were usually markedly higher than those in the south basin, that few fish were present outside the fishing season at depths usually fished by the anglers, and that fish densities at night were usually higher than those recorded in the day.

It can be inferred from the angler's catches that most of these pelagic fish are charr, especially in the north basin (Fig. 7). The seasonal, and even daily, fluctuations in the fish densities recorded by the echo sounder indicate that the behavioural movements of the charr must be extensive. The causes of such movements are as yet unknown but could be related to fluctuations in the food supply or environmental factors such as temperature and oxygen. These two latter factors would be limiting in the south basin of Windermere in years in which deoxygenation occurs at water depths below 20 m and water temperatures near the surface exceed 16°C (Mills et al. 1990). It is clearly important to establish the tolerance limits for different life-stages of charr to both temperature and oxygen. Experiments have almost been completed to provide such values.

This investigation has shown that by combining results from three different sampling methods, it is possible to describe quantitatively the long-term and short-term fluctuations in the density of charr in Windermere. Such a quantitative description is only a first step in investigating the ecology of charr in Windermere. Several important aspects must be examined as soon as possible, and these include information on the temperature and oxygen tolerance limits of the charr, an explanation for the increasing numbers of pelagic brown trout in the south basin of the lake, and a detailed analysis of the diel and seasonal movements of different size groups of charr throughout the lake. Work is proceeding to answer all these problems.

Acknowledgements

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