CHANGES IN THE FAUNA OF THE STONY SUBSTRATUM OF LAKES IN THE ENGLISH LAKE DISTRICT*

T. T. MACAN

Stevney, Outgate, Ambleside, Cumbria, LA22 ONH, England

* Text of a contribution to the jubilee symposium of the Freshwater Biological Association, the proceedings of which were not published.

Keywords: Lakes, Littoral fauna, Eutrophication, Immigrants

Abstract

The population in the drainage basins of the various lakes varies according to the amount of land flat enough for human settlement. Where there is plenty, increased tourism, the replacement of the earth closet by the water closet and improved agricultural practices have enriched the lake involved. The consequent changes in the littoral fauna are described. The spread of foreign immigrants is discussed. No great changes with increasing enrichment in the future are predicted.

Introduction

The English Lake District, in the north of the country on the west side, is a dome exceeding 915 metres at three places, and about 48 kilometres in diameter. The Ice Age left behind fourteen lakes over 1.5 km long (Ramsbottom, 1976). Windermere, the largest, is 17 km long.

All are typical glacier lakes, narrow, relatively deep, and parallel-sided except where deltas intrude into the shoreline. The shallow water near the edge is generally floored by stones derived from the disintegration of rock or the erosion of moraines. Only in deeply indented bays, or more extensively in small lakes, are reeds or other rooted plants found in shallow water.

The late Professor Pearsall started to study these lakes in the second decade of the present century and he was one of a group of scientists who founded the Freshwater Biological Association in 1929. A laboratory was opened in 1931, and since then most aspects of the biology of the lakes have been studied. Macan (1970) has summarised the work.

Pearsall made some chemical analyses but concerned himself mainly with algae and rooted plants. He pointed out that the lakes could be arranged in a series from unproductive to productive, a concept which has influenced much subsequent work. The unproductive lakes lie in the mountains in valleys with steep sides and narrow floors. The rain falling on these valleys brings little in solution to the lake. The productive lakes lie near the periphery, where relief is more gentle and there is more soil from weathered rocks and moraines. Rain water seeping through the soil would bring more in solution to the lake even if man were not present but, in fact, man is to-day responsible for much of the differences among the lakes. In the valleys where the unproductive lakes lie, there is little room for farming or settlement; around the productive lakes there is plenty of room for both with resulting enrichment of the lakes from agricultural fertilizers and sewage.

There have been farms in the valleys for about one thousand years. Tourists and those who wished to live permanently in the picturesque surroundings were unknown before the middle of the eighteenth century; their numbers increased in the middle of the nineteenth when the railway came and again in the middle of the twentieth century as standards of living rose. There is no exact information about numbers to-day, as the censussed population is increased greatly by summer visitors, many of whom have come just for the day since the motorway was constructed. Not only has the population grown but the number changing from earth closets to water closets since the end of the war in 1945 has added significantly to

Hydrobiologia 72, 159-164 (1980). 0018-8158/80/0722-0159$01.20.

the enrichment of the lakes. Furthermore, camping has become much more popular since the war and most campsites are now connected to the sewage system. The subject is discussed by Lund (1972) who records that in Windermere the mean weekly concentration of phosphate phosphorus in December and January, when algae are taking it up least actively, fluctuated around 1 $\mu g\ l^{-1}$ between 1945 and 1963 and then rose steadily to reach 12 $\mu g\ l^{-1}$ in 1970.

Ennerdale is one of the least productive lakes and its fauna has probably been little influenced by man in recent centuries. Esthwaite and Windermere lie at the other extreme of the series. A comparison of the fauna of Ennerdale and Esthwaite reveals the changes that have been brought about by the increase in the human population outlined above. Changes that have taken place in Esthwaite and Windermere in recent decades have been observed by workers at the laboratory of the Freshwater Biological Association.

Methods

The invertebrates of the stony substratum were collected by means of a hand-net thrust under each stone as it was lifted from the bottom; specimens clinging to the stones were brushed off by hand if swilling did not dislodge them. Each collection lasted two minutes and five such collections, each 50 paces apart, constituted a station. This technique was first used by Moon (1957a).

Table 1. Fauna of the stony substratum in Ennerdale (En) and Esthwaite (Es). Numbers of the commoner species caught in 20 minutes in February.

		En.	Es.
Diura bicaudata	Plecoptera	18	0
Capnia bifrons	,,	3	0
Heptagenia lateralis	Ephemeroptera	10	0
Leuctra hippopus	Plecoptera	12	0
Chloroperla torrentium	,,	4	2
Nemoura avicularis	,,	1	1
Ecdyonurus dispar	Ephemeroptera	+	+
Lymnaea peregra	Mollusca	42	1
Erpobdella octoculata	Hirudinea	8	9
chironomid larvae	Diptera	12	47
Polycentropus flavomaculatus	Trichoptera	22	22
Gammarus pulex	Crustacea	+	145
Polycelis spp.	Platyhelminthes	0	253
Dugesia sp.	,,	0	37
Asellus aquaticus	Crustacea	0	57

+ indicates that the species was not taken in this collection but was recorded in other collections.

Comparison of Ennerdale and Esthwaite

There has been much collecting in both these lakes, and the data in Table 1 have been selected as typical samples representing the difference between them. There is, as expected, a big difference in total numbers. Qualitatively the Ephemeroptera and Plecoptera are well represented in Ennerdale but not in Esthwaite. Conversely, planarians and *Asellus* sp. abound in Esthwaite but have not been recorded from Ennerdale. The explanation put forward (Macan, 1977) is that the planarians and crustaceans which could inhabit Ennerdale do not do so because the small population which the food there would support cannot survive predation by the active carnivorous stonefly *Diura bicaudata.* A larger population is possible in more productive lakes and coexistence is observed. Planarians are slow movers which do not fare well when food is scarce, but when it is plentiful they can reproduce rapidly. *Diura* sp., favoured by its mobility when food is scarce, cannot, like planarians, take advantage of a rich food supply because it has a rigid life-history with one generation a year. Consequently, in the most productive lakes the planarians eliminate the predator which, in unproductive conditions, eliminates them. Other insects, notably Ephemeroptera and Plecoptera are eliminated too. The eggs of species in these groups are scattered singly and may well be eaten by a variety of animals, even herbivores. In contrast those animals which are successful when numbers per unit area are high make provision for protecting their eggs; they carry them till they hatch (Crustacea) or enclose them in relatively large tough cocoons (Hirudinea and Platyhelminthes) or in a mass of jelly (Mollusca, Trichoptera, Chironomidae).

The fauna of Windermere

The first study of the communities in Windermere was made by Moon (1934), unfortunately for present purposes, in a region where changes have been least. At the same time Allen (1935) investigated the diet of *Perca fluviatilis,* a fish abundant in the lake. In 1965 and 1966 Macan & Maudsley (1968, 1969) surveyed the stony substratum of much of the lake, and McCormack (1970) gathered further information about the food of *Perca.* In 1979 the writer revisited those parts of the lake where changes were likely to be most evident.

McCormack found many more *Asellus* inside *Perca* than Allen did. Evidently in the thirty-two years between the two investigations the numbers of *Asellus* had increased greatly.

Macan and Maudsley found in the south basin a community similar to that in Esthwaite. This community continued through the shallow region beset with islands which separates the two basins to the southern end of the northern one. It occurred again at the north end of the north basin but in between on the west side planarians and *Asellus* were scarce and the insects recorded from Ennerdale were found. This region, indicated on Fig. 1., includes that studied by Moon (1934).

The south basin is enriched by the sewage works serving Windermere Town and Bowness, now contiguous and the biggest tourist resort in the Lake District. The north of the north basin receives the effluent from Ambleside, another place that has developed considerably since the railway came to Windermere Town. In between the west side is thinly populated and the lake is at its broadest and deepest. Thus the two communities found in Windermere support the hypothesis based on the study of all the lakes that one replaces the other as the concentration of nutrients in the water rises.

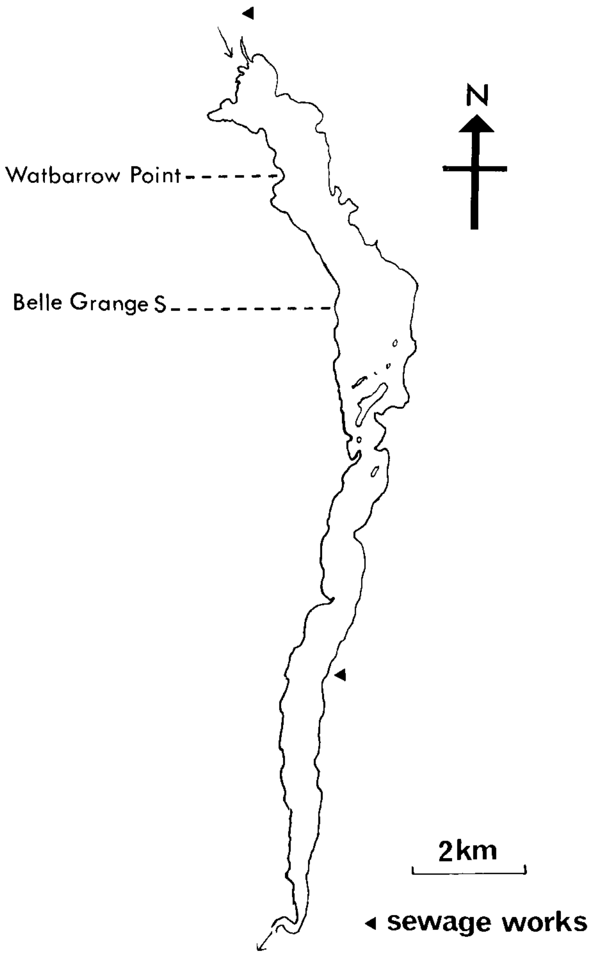

Fig. 1. Windermere showing the points between which the collections in table 2 were made and the positions of the sewage-purification plants.

If any changes associated with the continued enrichment of Windermere were to be detected in 1979, the likely place was the middle region of the north basin and, accordingly, a further set of collections was made here. The results are presented in Table 2. Except at the bottom of the table differences are not great, but it is noteworthy that all the insects, which are associated with less productive conditions, are scarcer in 1979. In contrast, all the species associated with productive conditions, indicated by absence from or scarcity in Ennerdale, have increased in numbers during the fourteen years which have elapsed between the two collections. The increase in the number of planarians and crustaceans has been large; it may be emphasized by consideration of the findings at one of the stations which was visited regularly on fourteen occasions between May 1965 and October 1966. The total captures in this 140 minutes of collecting were 3 *Polycelis* and 3 *Asellus;* in February 1979 20 minutes along the same stretch yielded 61 *Polycelis* and 15 *Asellus.*

From the 1965 survey it is concluded that qualitatively the fauna had not changed since Moon studied it in 1933 but since 1965 there have been distinct changes in the direction which might have been forecast.

Distribution of Asellus

An exact correspondence between the conditions in a lake that is changing and the fauna is not to be expected. First, a species for which conditions in a lake have become suitable must reach that lake. Having done so it must build up a population in the face of predation and competition. Both processes involve a certain element of chance and may take a long time. It is not, therefore, surprising to find that *Asellus* sp. was probably absent from Esthwaite in 1933 when Moon (1934) was finding it in Windermere, although Esthwaite is more productive than Windermere and in all likelihood always has been. In 1944, 1945 and 1950 a class of students found a few specimens of *Asellus* in the *Phragmites* at the north end of Esthwaite. The classes of 1942, 1947, 1948, 1949 and 1951 did not find any. In 1956 the supply department of the Freshwater Biologi-

Table 2. Windermere – the commoner species of the stony substratum between Watbarrow Point and Belle Grange South (Fig. 1).
Totals of 40 collections each lasting two minutes.
1965 (May) and 1979 (Feb., Mar., & Apr.)

		1965	1979	in Ennerdale
Ecdyonurus dispar	Ephem.	211	192	+
Heptagenia lateralis	,,	194	62	+
Centroptilum luteolum	,,	59	24	+
Diura bicaudata	Plecopt.	13	2	+
Chloroperla torrentium	,,	59	42	+
Capnia bifrons	,,	0	5	+
Nemoura avicularis	,,	3	2	+
Polycentropus flavomaculatus	Trichopt.	90	39	+
Agapetus fuscipes	,,	1360	643	
Lymnaea peregra	Moll.	33	10	+
Ancylus fluviatilis	,,	305	72	+
Erpobdella octoculata	Hirud.	10	7	+
Physa fontinalis	Moll.	3	56	
Planorbis contortus	,,	0	6	1
Gammarus pulex	Crust.	28	265	+
Crangonyx pseudogracilis	,,	21	39	
Asellus aquaticus	,,	11	74	
Polycelis spp.	Plat.	8	329	
Dugesia spp.	,,	3	13	
Dendrocoelum lacteum	,,	0	6	

Polycelis nigra and *P. tenuis* occur in Windermere. The species can be separated only when mature and then only after the compression of each individual. (P. felina is sometimes abundant near the mouths of streams, but this species is easily distinguishable on external characters).

Dugesia lugubris. 'Most of the earlier records of this species belong to D. polychroa' (Reynoldson, 1978). Collections in Windermere are insufficient to determine whether both species occur.

Capnia bifrons was not recorded in 1965 because most had emerged before May (Macan & Maudsley, 1968).

The numbers of *Ancylus* sp. and *Agapetus* sp. are unreliable as it is difficult to sweep every specimen off each stone or count them during the course of the collection. The remaining figures are strictly comparable.

cal Association reported that *Asellus* sp. was more abundant than usual. Thereafter Moon (1968) kept a close watch on the distribution of *Asellus aquaticus* in Esthwaite. Between 1957 and 1962 it spread from the bay at the inflow end of the lake down both sides to colonize the entire lake.

Between 1930 and 1949 Moon (1968) did not find *Asellus* in Ullswater. In 1963 specimens of *A. meridianus* were reported, and in 1964 Moon found this species to be abundant only in the vicinity of the inflow. There had been no extension of range in 1969 (Moon in litt.).

Moon (1957a) found that, whereas *A. aquaticus* was the commoner species in the central region of Windermere, *A. meridianus* was the commoner in the southern half of the south basin, in most of the north basin, and in deeper water everywhere. Now *A. meridianus* is scarce in all parts of Windermere. Its replacement by *A. aquaticus* has been noted in some other localities (Moon in litt., Williams, 1963, 1979).

In 45 collections Moon (1957b) found only *A. meridianus* in Bassenthwaite. In 1966 and 1967 Macan & Maudsley also found this species round most of the lake, but in addition they recorded *A. aquaticus* in a short stretch near the inflow. This stretch had lengthened only a little by 1978 (Moon in litt.).

Immigrants

The ramshorn snail, *Planorbis carinatus*, was recorded by Moon (1936) in Windermere but not by the earlier collectors and it may be a recent addition to the fauna.

Potamopyrgus jenkinsi, a small snail probably native to the Antipodes, and *Crangonyx pseudogracilis*, a small amphipod originating in North America, are two species which have reached Britain within the last hundred years and established themselves in many parts. Both are numerous in Windermere, without, as far as can be ascertained, having any effect on the rest of the community.

Potamopyrgus also occurs in Derwentwater and a few specimens were found in Ennerdale in 1978 near the mouth of a stream flowing past one of the few farms in the drainage area of that lake.

Crangonyx was first noticed in Windermere in 1960 and in the following year was found to be confined to the south basin and the island region. By 1965 it had colonized the whole lake. It was taken also in Ullswater in 1965 and in Bassenthwaite and Derwentwater in 1966. In 1972, the most recent year in which collections were made in Esthwaite, it was not found. Esthwaite is close to Windermere and flows into it, though, as *Crangonyx* does not occur in swift water, the connecting river is probably not a potential invasion route.

Neither of the two foreign species, nor *Planorbis carinatus* have found their way to Esthwaite, the lake colonized by *Asellus* only recently. Privately owned, it is one of the least accessible to the general public, and these observations support Moon's (1957b) contention that much transport of species from one piece of water to another is due to man, whether he be an aquarist, a creator of ornamental water, an angler, a naturalist or a boating enthusiast who transports his craft from one lake to another.

Prediction

Harman (1968a, b) records in some lakes in New York State that enrichment was followed by a great increase in the numbers of *Bithynia tentaculata*, an immigrant from the palaearctic region, and the disappearance of various species recorded by earlier collectors. He suggests that *Bithynia* was favoured by the enrichment and successful in competition with species already there by its ability both to graze and to feed by means of a ciliary mechanism. The unsuccessful species could only graze. In general observation of this kind are scarce and there has been no study of the benthic fauna of shallow water, where, as in Lake Washington, there has been a great and undesirable change in the phytoplankton.

Two comparatively recent and successful immigrants into Britain are the planarian *Dugesia tigrina* and the lamellibranch *Dreissena polymorpha*. *Dugesia tigrina* was abundant in the Lancaster Canal in 1974; *Crangonyx* was also abundant in this locality before it appeared in Windermere. *Dreissena* sp. was first recorded in Britain in 1824 and is now well-established in canals and navigable rivers, mainly in the midlands of England (Kerney & Morton, 1970). It occurs in many of the eutrophic Baltic lakes and was recorded for the first time in the Bodensee in 1966 (Walz, 1978) and the Grand Lac de Laffrey near Grenoble in 1957 (Degrange & Seassau, 1971). It can attach itself to rocks, a substratum with few colonists in fresh water, it feeds on plankton and detritus; it is itself food for various birds and fish, and, therefore, its establishment in a lake can have a big effect on the lake's economy. The Lake District, however, is probably not suitable for it on account of the low concentration of calcium.

Changes in Windermere are likely to continue in the direction indicated but nothing dramatic seems probable. The catchment area of Windermere is large and mostly unproductive, and the rainfall is heavy and irregular, which is likely to hinder the excessive development of any organism of the kind recorded in some other lakes.

Summary

The lakes of the English Lake District range from those naturally unproductive lying in narrow steep-sided valleys to those which, naturally more productive because they are in lower more weathered regions, are now enriched by agricultural fertilizers and sewage. In the unproductive lakes insects predominate, in the productive planarians and crustaceans. The change from one community to the other is explained in terms of reciprocal predation with the advantage changing as conditions become more productive. In one stretch of Windermere, a lake in which enrichment by sewage has increased fast recently, a transition from one community to the other has been observed during the last fourteen years (Table 2). Before it can take advantage of conditions which have become favourable in a lake, a species must reach it. A study of immigrant

species suggests that this overland transport is assisted unwittingly by various human activities. Drastic changes are not predicted; heavy irregular rainfall on extensively unproductive gathering grounds is not conducive to the attainment of pest proportions by species that proliferate to excess elsewhere.

Résumé

Dans le Lake District anglais les lacs varient entre ceux qui, en vallées étroites à côtés raides, sont naturellement peu productifs à ceux qui, plus productifs parce qu'ils se trouvent dans une région moins accidentée, sont actuellement enrichis par les engrais agricoles et les vidanges. Dans les lacs peu productifs on remarque surtout les insectes, dans les lacs plus productifs les planaires et les crustacés. On explique le changement de l'une communauté à l'autre en termes de prédation réciproque; l'équilibre change à mesure que le taux d'enrichissement augmente. Dans une des parties de Windermere, un lac où la concentration en phosphate et nitrate a monté pendant les décennies récentes, on a remarqué une diminution en nombres d'insectes et un accroissement en nombres de planaires et de crustacés pendant les derniers quatorze ans (Tableau 2). Avant qu'elle puisse coloniser un lac où les conditions sont devenues favorables, une espèce doit y arriver. Une étude des immigrants suggère que leur transport par voie terrestre est effectué par les hommes à leur insu en cours d'activités diverses. Des changements radicals de la faune des lacs ne sont pas prévus; la pluie copieuse qui tombent sur la région tendent a empêcher les pullulations extraordinaires.

Acknowledgement

My sincere thanks are due to Professor H. P. Moon who has supplied unpublished information and also commented on the typescript.

References

Allen, K. R. 1935. The food and migration of the perch (Perca fluviatilis) in Windermere. J. Anim. Ecol. 4: 264-273.

Degrange, C. & Seassau, M.-D. 1971. Une introduction accidentelle: Dreissena polymorpha (Pallas) 1771 (Mollusque Lamellibranche) au Grand Lac de Laffrey. Trav. Lab. Hydrobiol. Piscic. Grenoble, 62: 59-73.

Harman, W. N. 1968a. Interspecific competition between Bithynia and pleurocerids. Nautilus, 82: 72-73.

Harman, W. N. 1968b. Replacement of pleurocerids by Bithynia in polluted waters of central New York. Nautilus, 81: 77-83.

Kerney, M. P. & Morton, B. S. 1970. The distribution of Dreissena polymorpha (Pallas) in Britain. J. Conch. 27: 97-100.

Lund, J. W. G. 1972. Eutrophication. Proc. R. Soc. Lond. B. 180: 371-382.

Macan, T. T. 1970. Biological Studies of the English Lakes. London: Longman. xvi + 260.

Macan, T. T. 1977. The influence of predation on the composition of freshwater animal communities. Biol. Rev. 52: 45-70.

Macan, T. T. & Maudsley, R. 1968. The insects of the stony substratum of Windermere. Trans. Soc. Brit. Entom. 18: 1-18.

Macan, T. T. & Maudsley, R. 1969. Fauna of the stony substratum in lakes in the English Lake District. Ver. int. Verh. Limnol. 17: 173-180.

McCormack, J. C. 1970. Observations on the food of perch (Perca fluviatilis) in Windermere. J. Anim. Ecol. 39: 255-267.

Moon, H. P. 1934. An investigation of the littoral region of Windermere. J. Anim. Ecol. 3: 8-28.

Moon, H. P. 1936. The shallow littoral region of a bay at the north-west end of Windermere. Proc. Zool. Soc. Lond. 490-515.

Moon, H. P. 1957a. The distribution of Asellus in Windermere. J. Anim. Ecol. 26: 113-123.

Moon, H. P. 1957b. The distribution of Asellus in the English Lake District and adjoining areas. J. Anim. Ecol. 26: 403-409.

Moon, H. P. 1968. The colonization of Esthwaite Water and Ullswater, English Lake District, by Asellus (Crustacea, Isopoda). J. Anim. Ecol. 37: 405-415.

Ramsbottom, A. E. 1976. Depth charts of the Cumbrian lakes. Sci. publ. freshwat. Biol. Assoc. no. 33, 39 pp.

Reynoldson, T. B. 1978. A key to British species of freshwater triclads. Sci. Publ. Freshwat. Biol. Assoc. no. 23 (2nd ed.) 32 pp.

Walz, N. 1978. Die Produktion der Dreissena-population und deren Bedeutung im Stoffkreislauf des Bodensees. Arch. Hydrobiol. 82: 482-499.

Williams, W. D. 1963. The ecological relationships of isopod crustaceans Asellus aquaticus (L.) and A. meridianus Rac. Proc. zool. Soc. Lond. 140: 661-679.

Williams, W. D. 1979. The distribution of Asellus aquaticus and A. meridianus (Crustacea, Isopoda) in Britain. Freshwat. Biol., 9: 491-501.