LIMNETIC CRUSTACEANS IN ESTHWAITE WATER AND ADJACENT LAKES

W. J. P. SMYLY

The word 'limnetic' refers to a community of organisms, mostly microscopic in size, which live in the open water of lakes and ponds. In this community, the crustaceans are represented by two groups, Copepoda and Cladocera. These animals feed on other planktonic organisms and are themselves eaten by both fish and invertebrate predators.

Research on zooplankton in the Windermere laboratory over the last twenty years has centred mainly on discovering and quantifying the factors which regulate population abundance. The problem has been tackled (1) by comparing events in different lakes, (2) by laboratory experiments and (3) by field experiments, e.g. in enclosures such as the Lund tubes.

Evidence about annual changes in Esthwaite Water comes from two main sources. Goulden (1964) studied the abundance of cladoceran remains in the bottom sediments and found evidence that cladoceran populations change little over hundreds of years, and changes that do occur appear to be slow gradual shifts in relative abundance of two species within the same genus, probably in response to changing environmental conditions. Recent work begun in 1956 (Smyly 1972) provides evidence of more rapid cyclical changes which may temporarily reverse some more general trend. Trends in mean annual abundance of the two species of cyclopoid copepod in this lake show (Fig. 1) that the dominant species, *Mesocyclops leuckarti* (Claus), has been declining in abundance, while the

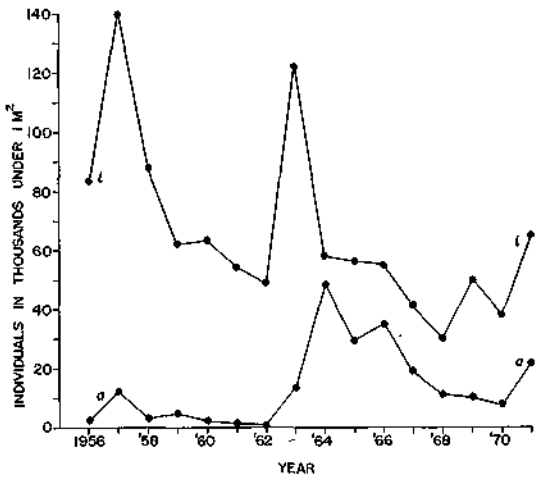

FIG. 1. Mean annual totals of *Cyclops abyssorum*, (a), and *Mesocyclops leuckarti*, (l), in Esthwaite Water from 1956 to 1971.

scarcer of the two species, *Cyclops abyssorum* Sars, began in 1963 a recovery which persisted subsequently for two or three years, before declining again. Because *C. abyssorum* is found mostly in deep cold lakes in the world at large and also in most lakes of the English Lake District, and *M. leuckarti* tends to be found in the less deep and less cold lakes both here and elsewhere, Smyly (1968) suggested that *C. abyssorum* was an indigenous species and *M. leuckarti* an invader from the south penetrating northwards with amelioration of climate. Recent work however provides little evidence to support the hypothesis that *M. leuckarti* is a successful competitor in process of replacing *C. abyssorum*. On the contrary, under certain conditions, *C. abyssorum* seems well-adapted to maintain a superiority, e.g. in Rydal Water, and to recover lost ground, as in Esthwaite Water. We seem to have here a delicate balance between two adaptable species with similarities in life-cycle but also differences, e.g. in body-size, periodicity and vertical distribution, all strategies for successful coexistence. The question has to be asked therefore why they co-occur in only three out of eighteen lakes. One possible explanation lies in the carnivorous habits of the copepodid instars of both species. Two advantages are gained by switching from a herbivorous to a carnivorous diet: more efficient conversion of energy from food to body-tissue is possible, and the opportunity arises to prey on herbivorous instars of the slower-growing species. Success could be associated with water-temperature and its influence on growth-rate, cooler water favouring *C. abyssorum* and warmer water favouring *M. leuckarti*. According to this hypothesis, short-term fluctuations are to be expected, while in the long run one species should predominate and eventually exclude the other.

One feature common to almost all limnetic crustaceans is the possession of a resting stage. In several species a resting stage is obligatory, i.e. the resting stage is essential to the continued existence of that species; in others it is facultative, i.e. the species can produce a resting stage if necessary but does not always do so, or may regularly produce a resting stage but not be dependent on it. *Daphnia* for example produces resting eggs in spring and early winter in Esthwaite Water but is present all through the year, whereas in Grasmere it disappears from the limnetic zone from late December to early May, when it reappears as small individuals hatched from resting eggs laid in the previous year. The two species which have been most thoroughly studied, *Cyclops abyssorum* and *Mesocyclops leuckarti*, also have resting stages but these are in the final copepodid instars, chiefly stage V. *M. leuckarti* leaves the limnetic zone altogether in winter and spends from October to February dormant in the bottom sediments. *C. abyssorum* never completely deserts the limnetic zone, and in some lakes has a resting stage in the bottom sediments from August to February. Most such lakes are less than 20 m deep but one, Thirlmere, is much deeper (42 m). This exception rules out a direct correlation between a

resting stage in this species and some factor shared by all the shallower lakes. At the present time, we do not know how dormancy in copepods is initiated, and not much about how it is maintained and finally ended. Low temperatures seem essential for maintenance though there comes a time beyond which dormancy cannot be prolonged. We also know that if it is ended prematurely, for example by a rise in temperature, dormancy cannot be restored by a return to low temperatures.

Quantitative field sampling estimates the number of individuals present at a given time. This amount, the standing stock, is easily measured and often used to describe changes in seasonal abundance. It can however be misleading, because a low standing stock can arise as well from a high recruitment rate linked with a high mortality rate as from low recruitment linked to low mortality. To find out how much is actually produced, we have to examine separately the causes of increase from those of decrease. Research is currently in progress on both aspects. Smyly (1970, 1973) found that the growth-rate of cyclopoid copepods is affected by both amount and kind of food, and clutch-size is affected by food, age and body-size.

It is sometimes assumed that animals invariably lay eggs up to the limits of their capacity: this was not true of the limnetic copepod *Cyclops abyssorum* in Buttermere, where clutch-size was limited by food to about half of the maximal number of eggs possible. The volume of the thoracic region, in which the ovaries lie, was calculated from measurements of length, width and breadth of many adult females. The volume of the egg was calculated from the diameter of the egg, allowance being made for swelling of the egg after extrusion from the ovary, and estimates were made of clutch-size. Then total yolk volume was calculated and this volume was expressed as a percentage of the thoracic volume. This percentage lay mostly between 14% and 17%, occasionally as high as 20%, in Esthwaite Water, a productive lake, but never exceeded 8% in Buttermere, an unproductive lake. If these calculations were correct, the animals in Buttermere were laying only about half the number of eggs which the size of their thorax would allow. They could have laid more but smaller eggs, but measurements showed that the eggs were all similar in size, regardless of seasons or lake of origin. To test both the accuracy of the calculations and the deduction that clutch-sizes of Buttermere females could be doubled, experiments were made by feeding these females artificially on a diet of newly hatched brine-shrimp nauplii, an outstandingly good food for adult cyclopoid copepods (Smyly 1970). On this diet, adult females from Buttermere increased their mean clutch-size from 12·6 to 29·8 eggs per clutch, and the total yolk volume expressed as a percentage of thoracic volume increased from 6% in the lake to 14% in the laboratory.

Results from lake samples show that stocks and fecundity are often poorly correlated. Size of stock often seems to depend more on survival of young after hatching than on numbers of eggs laid. Predation intensity varies directly with prey density, and increased fecundity may be offset by increased predation. Lack of food through competition with other species is another cause of mortality. In populations of cyclopoid copepods it is difficult, however, to separate the effects of mortality caused by food-limited competition from those caused by predation, because additional food not only enhances directly the chances of survival of young stages but simultaneously reduces cannibalism by providing an alternative source of food. Competition is better studied between non-predatory species, especially under experimental conditions. Laboratory experiments are however often unsatisfactory; field experiments, using artificially manipulated populations in enclosures, offer an attractive alternative possibility. Observations over four years in Blelham Tarn show that, in enclosures holding 18 000 m^3 of water, population densities of *Daphnia hyalina* were essentially similar inside and outside the enclosures in each year, despite the very small numbers of fish during the first two years and of predatory larvae of the midge *Chaoborus* throughout the period. In contrast, the calanoid copepod *Diaptomus gracilis* has been more abundant inside than outside the enclosures in all four years. There was little annual variation in clutch-size of either *Daphnia* or *Diaptomus,* so it seems that adults of both species found as much food inside the enclosures as outside. The implication is that rate of survival after hatching was higher for *Diaptomus* than for *Daphnia* inside the enclosures. Further experiments are planned to try and elucidate the reasons for these differences.

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References

Goulden, C. E. (1964). The history of the cladoceran fauna of Esthwaite Water (England) and its limnological significance. *Arch. Hydrobiol.* **60,** 1–52.

Smyly, W. J. P. (1968). Observations on the planktonic and profundal Crustacea of the lakes of the English Lake District. *J. Anim. Ecol.* **37,** 693–708.

Smyly, W. J. P. (1970). Observations on rate of development, longevity and fecundity of *Acanthocyclops viridis* (Jurine) (Copepoda, Cyclopoida) in relation to type of prey. *Crustaceana,* **18,** 21–36.

Smyly, W. J. P. (1972). The crustacean zooplankton, past and present, in Esthwaite Water. *Verh. int. Verein. theor. angew. Limnol.* **18,** 320–26.

Smyly, W. J. P. (1973). Clutch-size in the freshwater cyclopoid copepod, *Cyclops strenuus abyssorum* Sars in relation to thoracic volume and food. *J. nat. Hist.* **7,** 545-49.