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The dynamics of a population of roach (*Rutilus rutilus* (L.)) in a shallow lake: is there a 2-year cycle in recruitment?

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Abstract

Recruitment success of roach varied dramatically between 1978 and 1985 in Alderfen Broad, a small lake in eastern England. All size classes of roach feed to a significant extent upon zooplankton, but the underyearling fish have the greatest effects upon the abundance, species composition and mean size of zooplankton. During years of good recruitment (1979, 1981, 1983 and 1985) when the 0 + age group was abundant, they showed poor growth as a result of the depression of their prey populations. Older fish also tended to grow poorly in these years and may have been less fecund the following year. In years of poor recruitment (1980, 1982 and 1984), with the release of the depressive effect upon the zooplankton exerted by underyearling fish, the older size classes tended to grow well with higher fecundity the following season, giving rise to good recruitment of underyearling fish, even when the number of spawners was low. The evidence indicates that there is a 2-year cycle of roach recruitment in Alderfen and this will be described.

Introduction

The interactions between zooplankton and zooplanktivorous fish are of critical importance in determining not only microcrustacean abundance and species composition (Hrbacek *et al.*, 1961; Brooks & Dodson, 1965; Hall, 1970; Wells, 1970; Stenson, 1976; Hamrin, 1983; Mills & Forney, 1983) but also the diet, growth and survivorship of the fish (Kempe, 1962; Frank, 1970; Kuznetsov, 1972; Noble, 1975; Broughton *et al.*, 1977; Lemly & Dimmick, 1982). In particular, when the intensity of predation is sufficiently high the preferred prey classes become limiting and intraspecific competition, both within and between year classes, may be evident (Cryer *et al.*, 1986; Hamrin & Persson,1986).

Alderfen Broad is a small (4.7 ha), shallow (mean depth 0.8 m, maximum depth 1.3 m) lake in eastern England (National grid reference TG 354196). A previous paper described how recruitment success of roach (*Rutilus rutilus* (L.)), the lake's principal predator of pelagic zooplankton, varied dramatically between 1979 and 1982, with large populations of underyearling fish in 1979 and 1981 and small populations in 1980 and 1982 (Cryer *et al.*, 1986; Townsend, 1988; Townsend & Perrow, 1988). It was postulated that a two-year cycle of recruitment occurred as a result of abundant underyearling fish depressing cladoceran densities which, in turn, led to poor growth of adult fish and low fecundity the following year. However, this hypothesis rested on only four years' data and required further substantiation. In the present paper, we provide 8 years' information on recruitment and growth of roach and reassess the original hypothesis.

In the years prior to 1979 Alderfen Broad was devoid of macrophytes, being generally turbid with dense phytoplankton populations. Early in 1979 a nutrient-rich input, derived from agricultural runoff and septic tank overflow, was diverted from the lake. This had consequences for water chemistry and phytoplankton populations (Moss *et al.*, 1986) and macrophytes returned from 1981 to 1984, being particularly dense in 1982 but declining again thereafter. The fish community also changed from one that was cyprinid-dominated to a cyprinid-percid mixture. However, the general pattern of abundance and year class structure of the roach population has not altered substantially.

Methods

Underyearling roach are notoriously difficult to sample quantitatively. We used as an index of recruitment of underyearling fish (hatched in June) the abundance of the year class when it achieves 1 + status in the year following hatching. This was assessed as catch per unit effort (CPUE) of 1 + fish taken by electrofishing (using a pulsed D.C. unit -Weiss, 1977 from a 3-m fibreglass dinghy) of the entire perimeter of the lake each October. At this time of year roach are concentrated around the margins and are conveniently taken (Peirson, 1986). Each year between 1 and 4 perimeters surveys were performed, and CPUE was expressed as mean number of 1 + fish per perimeter survey. Information on the relative abundance of older year classes was obtained in the same way.

The fork-length of each roach (including underyearlings) was measured and a sample of the population was aged by scale-reading with a microfiche viewer. Estimates of size for each class of roach in October 1978 (not measured at the time) were derived from known lengths in May 1979 (Peirson, 1986), back-calculated to allow for the small amount of growth that occurs during the winter months. Instantaneous growth rates (G), October to October, were estimated from

$$G = \frac{\mathrm{Log_e}\, L_2 - \mathrm{Log_e}\, L_1}{t}$$

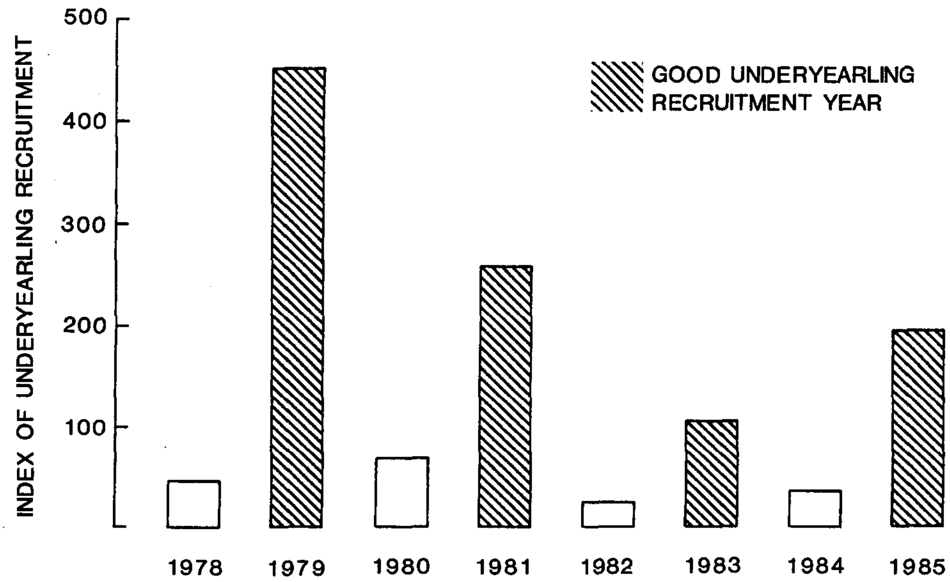

Fig. 1. Index of underyearling recruitment of roach in Alderfen Broad during a period of 8 years. The index is taken as the average catch-per-unit-effort (per complete electrofishing of the lake perimeter) of yearling fish in October of the year following hatching.

where L_1 = initial length
L_2 = final length
t = time lapsed, 1 year

Results

The index of underyearling recruitment shows convincing evidence of alternation of bad (even) and good (odd) years (Fig. 1) (the probability of this pattern occurring by chance is < 0.01, and the

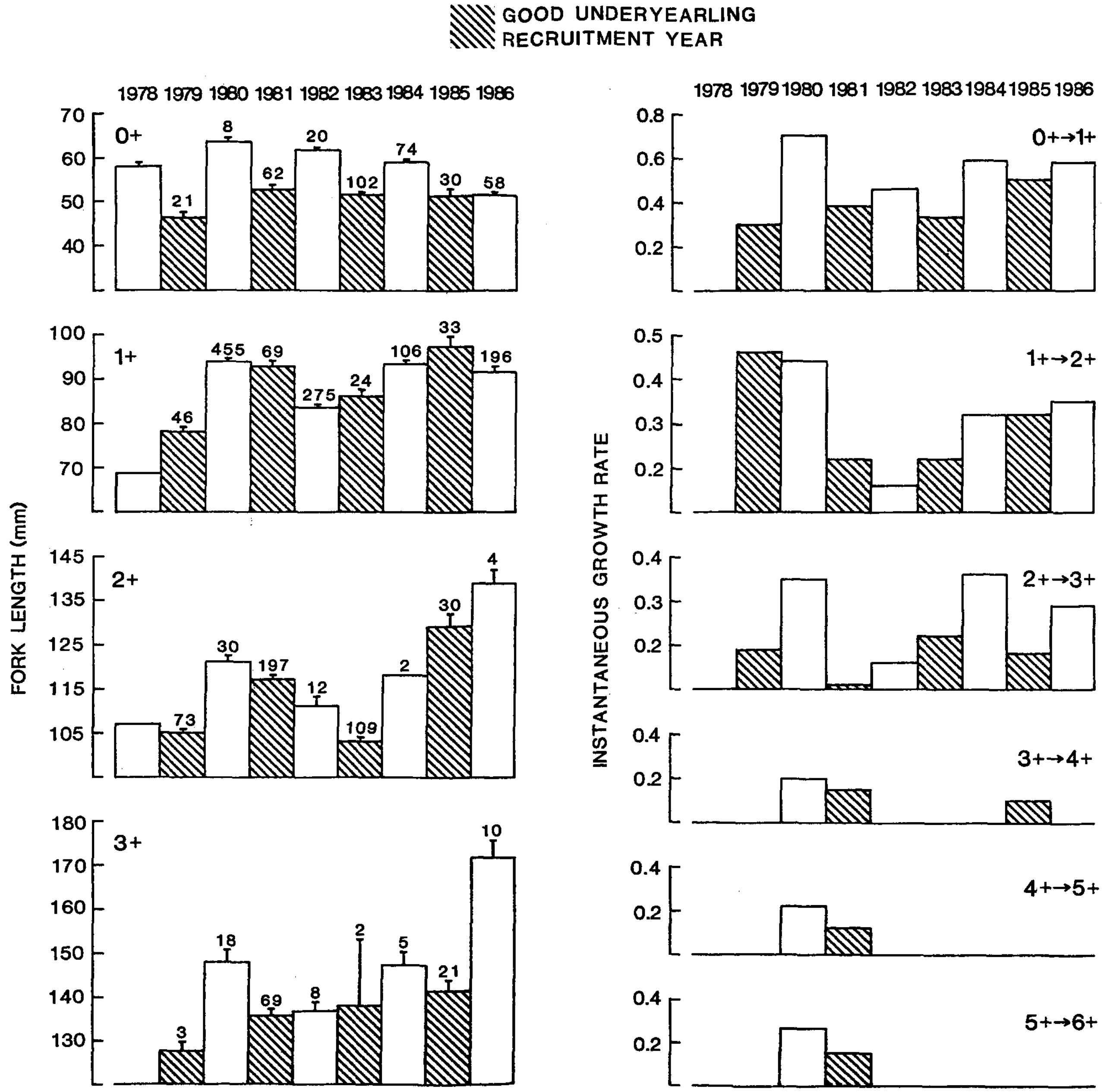

Fig. 2. Size and growth of the different age classes of roach in Alderfen Broad taken in October surveys (a) mean fork length (± S.E.) achieved in October (b) instantaneous growth rate estimated from October to October.

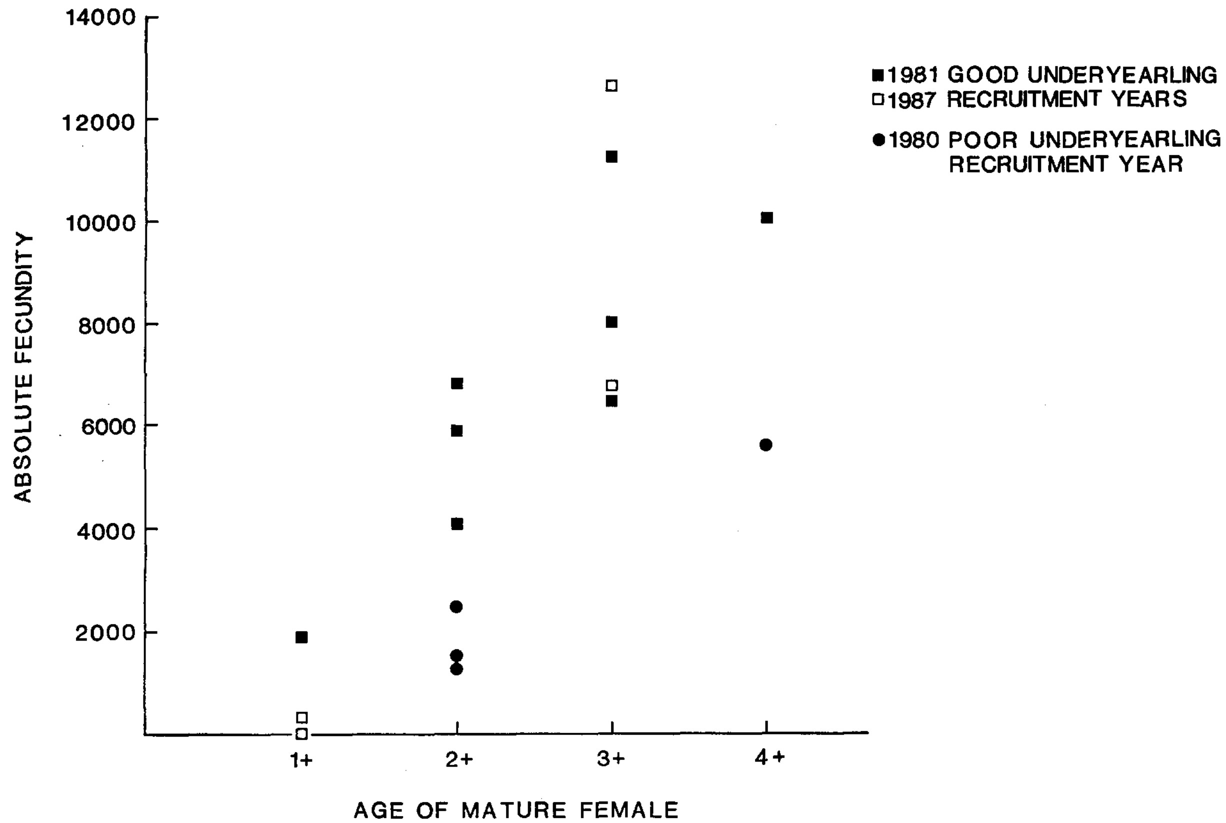

Fig. 3. Estimates of absolute fecundity of fish of a variety of age classes in three years. -1981, -1987, -1980. Note that 1981 and 1987 were years of good recruitment which followed years of good growth whereas 1980 was a year of poor recruitment which followed a year of poor growth.

pattern receives further substantiation from results for 2 + fish which also alternated in abundance and always achieved high numbers in years following high 1 + numbers.

The relative success of recruitment had a profound effect on the growth of underyearling fish. During good recruitment years the underyearlings grew more poorly through the summer and attained a smaller size in October than their counterparts in bad recruitment years (Fig. 2a).

To what extent is the alternating pattern of growth of underyearlings paralleled in the growth of older fish? The lengths achieved in october by 1 +, 2 + and 3 + do not show a clear pattern though there is an indication of consistently good growth in some of the years of poor underyearling recruitment and good underyearling growth (1980, 1984, 1986). When expressed as instantaneous growth rates a clearer pattern emerges (Fig. 2b), particularly for the 0 + → 1 +, 2 + → 3 + and the older classes (where few data are available because of the rarity of specimens). During the summer of 1982 (when most year classes grew less well than might have been expected) extremely dense beds of *Ceratophyllum demersum* developed and may well have reduced feeding efficiency of roach, which have been shown to forage less well in dense plant structure (Peirson *et al.*, 1985).

The suggestion of poorer growth of older fish in years of good recruitment could have important consequences for the condition and fecundity of the spawning population in the following year. Limited data from mature female roach in 1987 (expected to be a good recruitment year) and 1981 (a good recruitment year) do indicate higher absolute fecundities for a given age class than roach in 1980 (a poor recruitment year) (Fig. 3).

Discussion

In general, annual variation in the recruitment of freshwater fish may be predominantly under climatic control (Mills & Mann, 1985). However, feeding conditions in the period before spawning may also be influential (Lyagina, 1972; Kuznetsov & Khalitov, 1978), and Hamrin & Persson (1986) have shown how recruitment in a population of vendace, *Coregonus albula*, alternates because of competition for crustacean zooplankton between underyearling recruits and the spawning population (almost entirely 1 + fish).

In the case of roach, most studies have pointed to irregular recruitment with a few very strong year classes, which have coincided with highly favourable climatic conditions, separated by poorly represented or non-existent year classes (e.g. Mann, 1973; Goldspink, 1978; Linfield, 1980). Why in Alderfen Broad should there be such a regular alternation of roach recruitment success? Unlike vendace the spawning population of roach normally consists of a large number of age classes, up to 12 + (Papageorgiou, 1979; Spivak *et al.*, 1979), many of which have quite different diets to that of underyearlings. However, in Alderfen Broad roach older than 3 + are very rare (probably mainly as a result of intensive predation by pike, *Esox lucius*) and the spawning population consists primarily of 2 + and some 3 + fish (Peirson, 1986). The diets of these fish overlap significantly with underyearlings, all taking predominantly planktonic crustaceans (Cryer *et al.*, 1986). Thus, competition can occur between recruits and fish old enough to spawn the following year, in a manner analogous to that described for vendace (Hamrin & Persson, 1986).

The alternation of recruitment success is well matched with differences in zooplankton biomass and composition during the period 1979 to 1982 (Cryer *et al.*, 1986). During years when fry were abundant (1979 and 1981) the summer zooplankton was dominated by cyclopoid copepods and rotifers, which are infrequently taken by roach because of efficient escape responses and small size, respectively. The preferred prey items of roach, planktonic cladocerans (Winfield *et al.*, 1983), tended to decline in abundance abruptly as they entered the diet of underyearlings during the summer. In contrast, when fry were scarce in 1980 and 1982 the zooplankton was dominated by cladocerans which maintained a high standing crop throughout the summer. The poor feeding conditions in 1979 and 1981 has a depressive effect on growth of underyearling fish in comparison to 1980 and 1982. This trend of poor growth when underyearling density is high was also show in 1983 and 1985 (and 1977 – see Peirson, 1986), and we propose that this is a result of intraspecific competition for a preferred prey resource which becomes limiting in late summer (all age classes of roach show hardly any growth in winter).

Given the high dietary overlap of roach up to 3 + we might expect the growth of older fish to be influenced by competition with underyearlings in good recruitment years and this is seen in the annual variation in instantaneous growth rates (Fig. 2b). Since there is generally a positive relationship between growth and fecundity (Mackay & Mann, 1969; Nikolskii, 1969; Papageorgiou, 1979), a depression of growth rate in older roach during years of good recruitment and poor growth of underyearlings would be expected to lead to lowered fecundity the following year. Limited data from 1980, 1981 and 1987 support this contention (Fig. 3). The bulk of Alderfen's spawning population consists of young fish (with even some 1 + female fish attaining maturity, at least in good recruitment years) and so depression of fecundity may be expected to have a profound effect with few eggs being laid. The resulting low numbers of underyearling fish would not significantly depress cladoceran populations, growth of underyearlings and older fish would be good and recruitment the following year may be expected to be high.

During the years 1979–1985, there were major ecological changes which could have interrupted the postulated two year cycle. The return of macrophytes in 1982 not only affected the zooplankton community by increasing the importance of non-planktonic Cladocera, but also greatly increased the densities of macro-invertebrates which may have provided an alternative source of prey for older fish, thereby potentially reducing competition between year classes. Underyearling roach have also been shown to be less efficient foragers in structurally complex environments compared to open water (Winfield, 1986), and this could account for low growth rates of young fish in 1982. The onset of macrophyte growth also favoured an increase in the number of perch, and as these are zooplanktivorous in their first few months of life and highly efficient predators of zooplankton among macrophytes (Winfield, 1986), they represent a major potential competitor for zooplankton. Even though the potential influence of such factors is great, the 2-year cycle of roach recruitment has gone on uninterrupted.

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