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THE FISH OF SLAPTON LEY

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ABSTRACT

A 25-year data set, commencing in 1970, on the roach, rudd, perch and to a lesser extent pike populations in Slapton Ley is reviewed. Particular emphasis is placed on the changes in the composition of the fish community and in the biology of individual species that can be related to the increasing eutrophication of the lake over the same period. Eutrophication promoted expansion of the roach population and so reversed the historical dominance of rudd. This inter-specific competition between fish fry led also to a reduction in the perch population and, indirectly, to a high density population of smaller pike. The roach population expansion was checked by the effects of the pathogenic tapeworm *Ligula intestinalis*, which allowed a temporary expansion of rudd, but the decline in *Ligula* levels swung the balance in favour of roach again. A decline in numbers of all species was associated with hypereutrophication of the lake, but ice cover over the winter of 1984–85 caused winterkill and the virtual disappearance of all fish species from the lake. Recovery was slow but from 1990 to date the same sequence of changes in the composition of the fish community has been repeated. Rudd initially dominated, but declined as the roach population expanded again until checked by the re-appearance of *Ligula* at higher levels.

The biology of individual fish species varied in relation to the changes. Roach displayed the most rapid and adaptive response: population expansion led to intra-specific competition and reduced individual growth rates, but these improved as the population size declined in response to *Ligula* and hypereutrophication. This cycle was repeated after the crash. Growth rates of rudd and perch did not respond in an adaptive manner and remained relatively unchanged throughout the whole period. All species exhibited common characteristics of high mortality rates, poor survivorship and a short life span and roach additionally showed extreme variation in year class strengths and very high growth rates. Roach are the key species in the community as their rapid response to eutrophication and other changes had direct and indirect effects on all the other species: the two critical events in their recent history were the series of strong year classes that started the sequence of changes in the early 1970s and the winterkill that terminated them. The post-crash cycle was shorter, but confirmed the interpretations of the earlier cycle.

Gaps in the data set and lack of explanations for some changes are discussed, together with the possible relationships between fish and plankton changes and in particular whether fish responded to such changes or were responsible for them. The value of long-term data sets as a basis for prediction, management and detection of global warming is considered critically.

INTRODUCTION

Slapton is 'A Fortunate Place' (Stanes, 1983) in many, and sometimes unexpected, ways. In the context of the fish and fishery of Slapton Ley, we are particularly fortunate in that there exist reasonable historical records of the fishery, that scientific research into the fish commenced at a time when eutrophication was accelerating and continued through the period of hypereutrophication and that over the same period (1970 to present) there is such an excellent record of the changes in the catchment, the input streams and the lake sediments. This has meant that not only is there a long-term data set on the fish extending over one of the most critical periods of the lake's history and evolution but also that it is possible to relate the changes in the fishery directly and causally to the changes in the catchment and in the lake itself. The fish have not only responded to the changes but may well have influenced some of them.

The fishery in the Slapton Ley is, and always has been, a coarse fishery. The dominant and most important species are, and have been, pike (*Esox lucius* L.), perch (*Perca fluviatilis* L.), roach (*Rutilus rutilus* (L.)), rudd (*Scardinius erythrophthalmus* (L.)) and eel (*Anguilla anguilla* (L.)), although their relative abundances have changed throughout the lake's history. A few brown trout (*Salmo trutta* L.) may move into the lake from the River Gara in summer, but they are not permanent residents and make no contribution to the fishery. Trash fish, including three-spined stickleback (*Gasterosteus aculeatus* (L.)), are resident in parts of the Ley whilst bullhead (*Cottus gobio* L.) and stone loach (*Noemacheilus barbatulus* (L.)) may also move in temporarily from the streams but the fishery interest has always focused on the dominant species and especially on the pike.

The history of the fishery was reviewed by Bregazzi, Burrough & Kennedy (1982). Its early composition is not known for certain, but, apart from the suggestion that pike were introduced in the 14th century, all the dominant species appear to have been present throughout the recorded period. There is clear evidence that the fishery was regarded as a valuable economic resource from the thirteenth to the twentieth century inclusive. The majority of historical records come from the 19th century, when angling interests focused on pike. There is clear evidence that perch, rudd and roach were present at that time and, twentieth century rumours notwithstanding, the Ley was identified as the only site in Devon for roach. Pike were numerous and of good size (up to 30 lb weight) and rudd were large (up to 2 lb weight), numerous and far commoner that roach in the late 19th century, and into the early 20th. Information is sparse for the immediate pre-war years, as records from the Royal Sands Hotel were destroyed or lost. As far as can be ascertained, both before and after the war angling interest still focused on pike and rudd were far commoner than roach. The latter species was still present but uncommon, although there must be a strong suspicion that it was not always distinguished from rudd by anglers. The fishery was thus still essentially a natural, unmanaged one.

The modern history of the fishery began for all intents and purposes in 1970, when scientific studies commenced with the investigation of perch by Craig (1974a,b; 1975). In response to anglers' complaints of declining size and quantity of fish and reports of roach in catches, a research programme into the biology of roach, rudd, perch and pike commenced in 1973 (Bregazzi & Kennedy, 1980, 1982; Burrough, 1978; Burrough & Kennedy, 1979; Burrough, Bregazzi & Kennedy, 1979; Kennedy & Burrough, 1981). This intense period of activity terminated in 1977, when focus shifted to regular monitoring of roach and perch and their parasites. Studies on roach were intensified again between 1982 and 1984 (Wyatt, 1988; Wyatt & Kennedy, 1988, 1989), and during the recovery period from the population crash of 1985. Scientific effort, determined by funding and personnel, has thus been concentrated into short periods, with monitoring of some species only in between them. There are no data on eels, but there are good data on all other species from the early to mid-1970s. Thereafter there are data on roach, and to a lesser extent on perch and rudd, but nothing on pike. Research activity has now increased again, thanks to the generous support of the Whitley Wildlife Conservation Trust, and it is intended to provide information on all species, comparable to that from

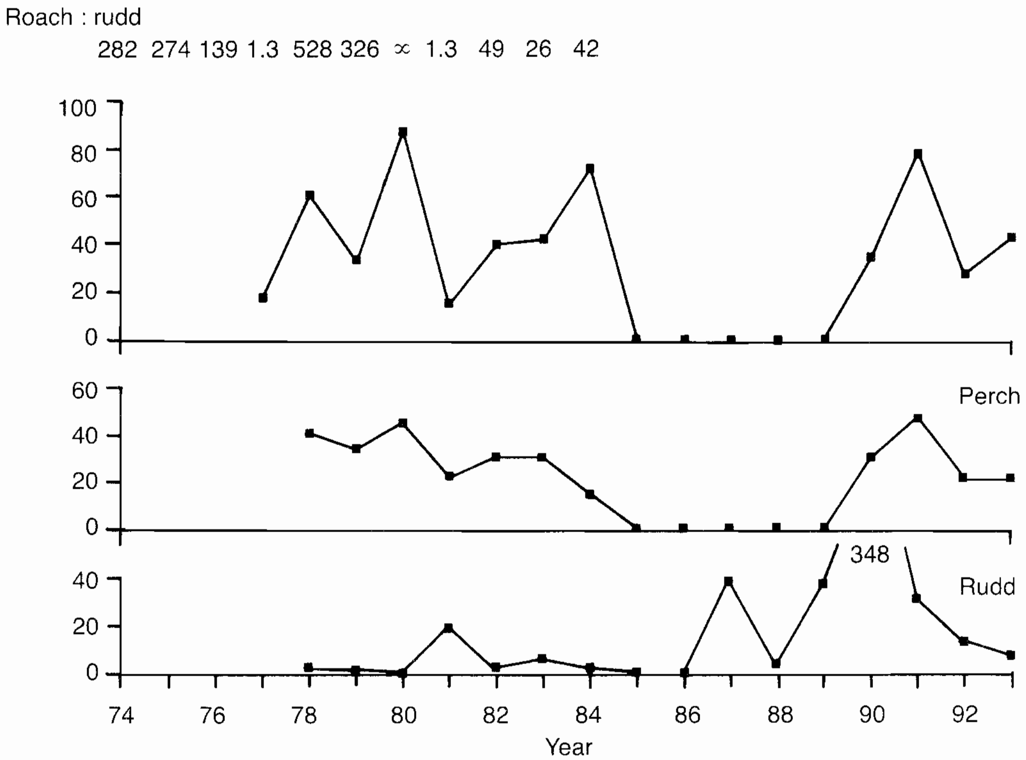

Fig. 1.
Changes in the abundance of roach, perch and rudd in Slapton Ley, and in the roach : rudd ratio. Since fish abundance could not be determined directly, an index of catch per unit effort has been used and data are expressed as numbers of each species caught per standard day's fishing. The roach : rudd ratio is based on the total numbers of each species caught throughout the year. Data from Burrough (1978), Burrough *et al.* (1979), Wyatt (1988) and unpublished.

the 1970s, in the late 1990s. Nevertheless, the 25 year data set with all its imperfections does provide an insight into the changes that have taken place in the fishery and does permit these to be related to the changes in the catchment land use and in water chemistry that have been documented over the same period. Only the main outlines and patterns of changes in the fishery will be summarised here : for further details and details of methodology reference can be made to the publications cited above and to Kennedy (1985) and Kennedy, Wyatt & Starr (1994).

Changes in the Composition of the Fishery

When the current scientific programme commenced, it soon became evident that a number of significant changes in the fishery had recently occurred and were still occurring. All four dominant species were still present but:-

- Pike were present at high density and biomass, but the population comprised large numbers of small fish and large pike were very scarce (Bregazzi & Kennedy, 1980),
- The perch population was declining in numbers (Burrough *et al.*, 1979) and
- The roach population had expanded from the late 1960s onwards such that roach were now commoner than rudd (Fig. 1 and Burrough *et al.* (1979)).

These changes are believed to be inter-connected. The increasing rate of eutrophication of the Ley over this period, due to changes in the land use in the catchment and resulting in increased sedimentation in the lake and rising levels of Nitrogen and Phosphorus (Burt *et al.*, 1988; Johnes & O'Sullivan, 1989; Heathwaite, Burt and Trudgill, 1990; Heathwaite, 1994; O'Sullivan, 1994), had favoured the expansion of the roach population. Such a link between dominance of a fishery by roach and eutrophication has been reported from a number of lakes (Svardson, 1976). The expansion of the roach population was at the expense of that of rudd, since the two species compete and to the detriment of the latter (Burrough *et al.*, 1979), and roach had replaced rudd as the dominant species. It was considered that inter-specific competition was taking place between the plankton feeding younger stages of roach, rudd and perch, and that therefore the expansion in numbers of roach was also responsible for the decline in the perch population (Burrough *et al.*, 1979). It has also been suggested, somewhat more tentatively, that the decline in the numbers of large pike may also be causally related to the presence of large numbers of small roach (Bregazzi & Kennedy, 1980) since pike may require large prey fish to increase substantially in weight.

In 1973, the larval stage of the tapeworm *Ligula intestinalis* was found for the first time in roach, having probably been introduced to the Ley by great crested grebes (*Podiceps cristatus* L.) attracted there by the abundance of roach (Kennedy & Burrough, 1981). *Ligula* uses planktonic copepods as its first intermediate host, roach (and other fish species) as its second intermediate host and matures in aquatic birds. It is highly pathogenic to roach, as it both sterilises its host fish and makes it more susceptible to predation by birds. Within two years of its arrival, almost 30% of the roach were infected (Fig. 2) and this not only checked the expansion of the roach population but actually caused it to decline (Burrough & Kennedy, 1979; Kennedy & Burrough, 1981). Relief from competitive pressure allowed the rudd population to expand again until by 1977 the two species were co-equal in numbers (Fig. 1). The subsequent decline in the infection levels of *Ligula*, related to an increasingly narrow window for transmission of the parasite from copepods to young fish (Wyatt & Kennedy, 1988, 1989), allowed the roach population to increase and dominate again in the late 1970s (Fig. 1). In the early 1980s it is believed that roach, rudd and perch were declining in numbers, but occasional failures of the roach population to produce a new generation of fry, as in 1980 (Fig. 2), allowed the rudd population to increase again, as in 1981 (Fig. 1).

In the late autumn of 1984, the situation in respect of the fishery appeared normal, with roach still dominant, although catches of perch were lower than usual (Fig. 1). When fishing commenced in spring 1985 no fish were caught, and this failure to catch anything other than the occasional fish continued throughout the year. It became increasingly clear that there had been a catastrophic decline of roach, rudd and perch populations over the winter of 1984–85 to a level at which they were undetectable in the samples. The lake had frozen over in this winter for the first time in 22 years and by this time had been triggered by the severe drought of 1976 into its hypereutrophic

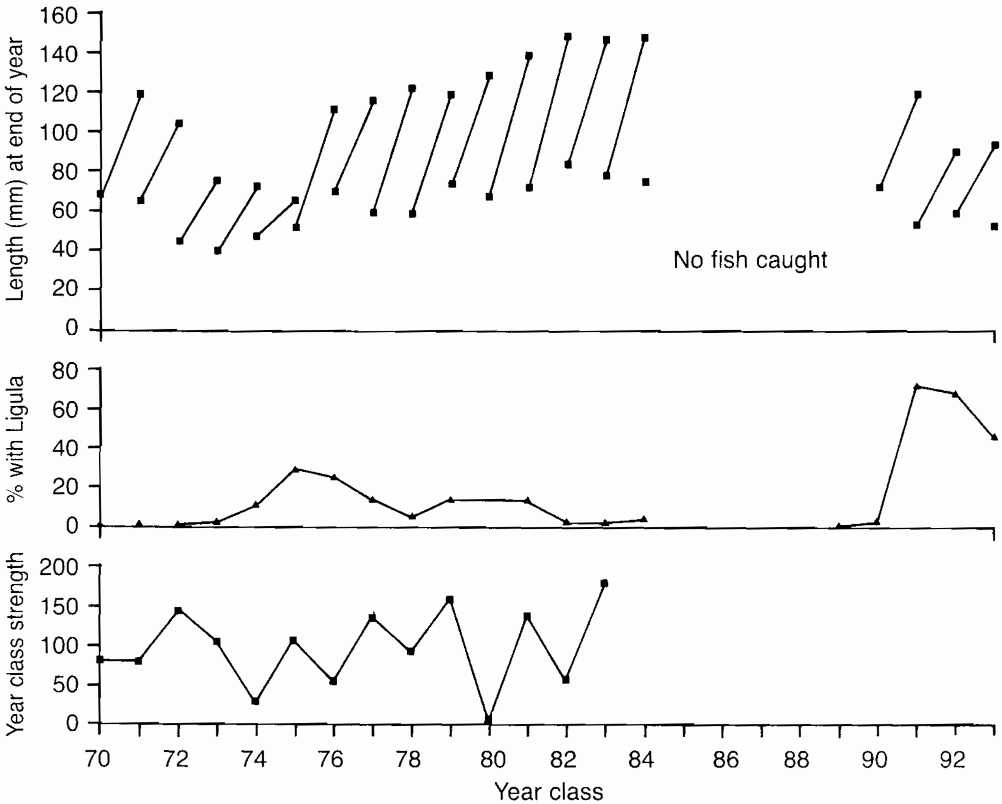

FIG. 2.

Changes in the growth, year class strength and prevalence of the parasite *Ligula intestinalis* in roach in Slapton Ley. Changes in the individual growth rate of roach are expressed as the mean length of fish of each year class at the end of their first and second years of life. Levels of *Ligula* are expressed as the % of fish up to and including 2 years old that are infected with the parasite. Changes in year class strengths are relative to a standard value of 100, but cannot yet be calculated for the post crash years. Data from Burrough (1978), Burrough & Kennedy (1979), Kennedy & Burrough (1981), Wyatt (1988), Kennedy *et al.*, (1994).

state (O'Sullivan, 1994). It is believed that, in the absence of any other credible and supported explanation such as increased levels of toxins or other forms of organic or inorganic pollution, the death of the fish was due to winter-kill (Kennedy *et al.*, 1994). This is a well-documented and common phenomenon in North America and Scandinavia, where winter ice-cover on shallow eutrophic/hypereutrophic lakes can lead to severe oxygen depletion in the water and so to the death of the fish. This explanation is entirely consistent with the then state of the Lower Ley, and must be viewed as a catastrophic event in the history of the lake. A nucleus of the fish populations survived in the Upper Ley around the mouth of the River Gara, from which re-colonisation of the Lower Ley could take place. Re-colonisation was in fact very slow (Figs. 1 & 2), perhaps retarded by a further cold winter in 1985–86. Rudd were first detected in numbers in 1987, but roach and perch did not recover until 1990 (Fig. 1).

This catastrophic event, in effect, provided a natural experiment on the fishery of the Ley. By virtually eliminating the fish populations, it provided a unique opportunity to study the interactions between the species as they re-colonised a barren habitat. The most interesting feature of the recovery is that not only did rudd recover first, but they dominated the fish populations until 1990 (Fig. 1) as they had done in the late 1960s when the roach population was small. As the roach population recovered and expanded, the roach : rudd ratio has improved in favour of roach although this species has not yet reached the levels of dominance characteristic of the early 1970s (Fig. 1). It would thus appear that the absence/decline of roach removed the competitive pressure from rudd, as happened also in 1977 and 1981, and allowed the latter species to dominate again. Thus, the whole cycle of dominance changes of the early 1970s is being repeated, but apparently over a much shorter time scale. Currently, all three species are again present in the Lower Ley, and at population levels comparable to those in the early 1980s (Fig. 1). A few pike were caught over the period of the crash in the Lower Ley, but were emaciated and in poor condition: they can now be caught in former numbers and condition.

POPULATION BIOLOGY OF INDIVIDUAL FISH SPECIES

Roach

In 1970, when scientific investigations commenced, growth rate of individual roach was quite good (Fig. 3) and comparable to that in several other British waters (Burrough & Kennedy, 1979). A few fish aged 5–9 were caught and the predicted maximum length that roach could attain in the lake was 258 mm. Thereafter, as population density of the roach increased and was reinforced by strong year classes in 1972 and 1973 (Fig. 2), the growth rate declined to a point at which intra-specific competition became very powerful and the population was composed of small, stunted fish (Figs. 2 & 3). Individual growth rates of fish in the 1973 and 1974 year classes were amongst the poorest recorded for any British waters and the maximum length that roach could attain was estimated at 157 mm. In 1975 and 1976 the infection with *Ligula* reached its highest levels and the resultant parasite induced host mortality reduced the population size of the roach. This reduced intra-specific competition and stunting and allowed individual growth rates to improve (Burrough & Kennedy, 1979) until in 1977 growth rate was comparable to that of 1970 (Fig. 2).

As the roach growth rate improved, fish spent a shorter period feeding on plankton and so the transmission rate of *Ligula* from copepod to roach declined (Wyatt & Kennedy, 1988, 1989) and prevalence of *Ligula* fell (Fig. 2). Roach growth rates continued to improve until by 1983 the individual growth rate was one of the highest (Fig. 3) ever recorded in British waters (Wyatt, 1988) and the predicted maximum size attainable had risen to 425 mm. The population, however, also exhibited low survivorship (rate of 0.223 in 1984 compared to 0.345 in 1975), extreme variations in year class strength and a tendency for year classes to alternate in strength (Fig. 2). Because of this poor survivorship, the roach spawning population in the early 1980s consisted predominantly of 2 year old fish (Wyatt, 1988). The size of the spawning stock was small and dependent on the strengths of the year classes that it contained. Thus, the occurrence of a poor year class in the population would set up an autonomous cycle of poor recruitment to the year class two years later, and a good year class would similarly produce a good year class two years later. This limited the population density of roach, simultaneously permitting the very high growth rates of individual fish and promoting the further decline of *Ligula* (Wyatt, 1988; Wyatt & Kennedy, 1988,1989).

The winterkill in 1985 virtually eliminated the roach population in the lake, and no data could be obtained until the recovery in 1990. Growth rates of this year class were similar to those observed in 1970 (Figs. 2 & 3). By 1991 catch indices suggested the roach population size had increased to a level comparable to those of the early 1980s and late 1970s and the reduction in growth rate (Fig. 2) suggests the onset of stunting again. This rapid expansion in the roach population size had, however, been accompanied by the re-appearance of *Ligula* which attained record levels of prevalence, 70%, in 1991, (Fig. 2). In 1992 roach catches fell (Fig. 1), presumably due to *Ligula* induced mortality of fish, and by 1993 *Ligula* had started to decline and roach growth and population size to increase. Thus, the whole cycle of *Ligula*-roach interactions has been repeated in the 1990s but over a much shorter time scale, reflecting the much higher prevalence and abundance of *Ligula*.

Little is known about the changes, if any, in other aspects of the population biology of roach. In the early 1970s a seasonal cycle in condition was evident: it declined through autumn and winter and increased shortly before spawning in May, after which it declined again. Gonads showed a comparable seasonal cycle in development and fecundity was related to the size of the fish (Burrough, 1978). Spawning was believed to take place in Ireland Bay and near the channel. Feeding activity declined over winter in all size classes: young fish fed predominantly on plankton but as they increased in size algae and detritus formed a greater part of their diet.

The roach population in Slapton Ley exhibits a peculiar combination of features, including the ability of fish to grow very rapidly, high population mortality rates, poor survivorship, early maturation, a short life span and an alternation of good and bad year classes. It is these features, together with the impact of *Ligula*, that have enabled the population to respond so rapidly and adaptively to the changes that have taken place in the lake and the fishery. Some of these features are also apparent in roach populations in other lakes of high productivity undergoing eutrophication (Townsend & Perrow, 1989) but the explanation for others remains to be found.

Perch

In contrast to the situation with roach, the growth rate of individual perch has changed relatively little and that very slowly over the period of the investigation (Fig. 3). Indeed, it is surprising that the steep decline in the size of the perch population (Burrough *et al.*, 1979) was not accompanied by adaptive responses in individual growth rate, age of maturation or fecundity such as were evident in roach. Between 1970 and 1974 perch trap catches fell from a peak of 700 to *ca* 200, yet individual growth rates remained remarkably similar (Fig. 3). A further decline in catch index and so population size up to 1984 produced only a slight increase in growth rate : in 1970, perch attained a length of almost 60 mm at the end of their first year and this had increased to only 75 mm in 1983 (Kennedy *et al.*, 1994). Perch were also slow to recover from the winterkill, and density appears to be settling at a lower level than before the crash (Fig. 1) whilst growth rate of younger, but not older, fish was higher in the 1990 year class (Fig. 3).

Throughout the period, there has been no pronounced variation in year class strengths, there being only minor and inconsistent differences from year to year and no domination of the population by a single year class (Craig, 1974b; Bregazzi & Kennedy, 1982). Mortality rates and survivorship have also shown little change. Small fish fed predominantly on plankton and chironomids whilst larger fish took a greater variety of food types including fish. Fecundity was low compared to other localities, but estimates of Bregazzi agree with those of Craig. Perch migrate into the Higher Ley for spawning in April, and later parents and progeny return to the Lower Ley.

There has, in fact, been very little change in the biology of perch in the lake despite eutrophication, changes in the fish community and changes in the density of perch. Slapton perch are not only unlike Slapton roach in this respect but also unlike perch in Windermere, which responded adaptively to density and other changes in a manner similar to the roach in Slapton and similarly showed large fluctuations in year class strength (Le Cren, 1958; Le Cren, Kipling & McCormack, 1977).

Rudd

Changes in rudd biology are much harder to interpret with any degree of certainty. This species has never proved easy to sample: in several years very few have ever been caught and in all years they tend to be far more abundant in catches in autumn only. The catch index can thus only be regarded as indicative of general trends (Fig. 1). Changes in rudd population densities are clearly linked causally and inversely with those in roach and from being the dominant species up to and including the 1960s they became the rarest in the early 1970s. Numbers subsequently increased only when roach densities were reduced by Ligula or other factors including the crash, from which they made the most rapid recovery (Fig. 1). Roach : rudd hybrids have been found in the lake at times when one or the other species was overwhelmingly dominant, but at other times they are rare (Burrough, 1978).

The biology of rudd has only been studied intensively between 1970 and 1975 by Burrough (1978). He reported only minor annual fluctuations in year class strength, though these seem to have become more extreme between 1978 and 1983 (Wyatt, unpublished). Individual growth rates are much slower than those of roach and appear to have been remarkably constant over the whole period of change (Fig. 3). both before and after the crash, Rudd mature at an earlier age in Slapton Ley than is usual elsewhere, but fecundity and growth rates are comparable to other British waters. Rudd spawn later than roach, in late June or early July, but their spawning site is unknown. Young fish feed on plankton, but as they grow larger switch to feeding on insects, or failing which, plants and detritus.

Pike

The biology of pike in the lake has been studied in detail only between 1974 and 1977 (Bregazzi & Kennedy, 1980), as their attraction to anglers inhibited further research. Individual growth rates were average when compared with those in other British waters, with females growing faster than males and reaching a length of 827 mm at age 8. There were no patterns to the variations in year class strengths, though 1973 was a particularly poor year. Maximum condition was attained in February, just prior to spawning. The population density was very high, with an estimate of 950 fish over 450mm long in 1977, indicating that this population has one of the highest biomasses per surface area of lake ever recorded. The survivorship rate of 0.59 was higher than that of any other species in the lake but comparable to values recorded for pike in other British waters.

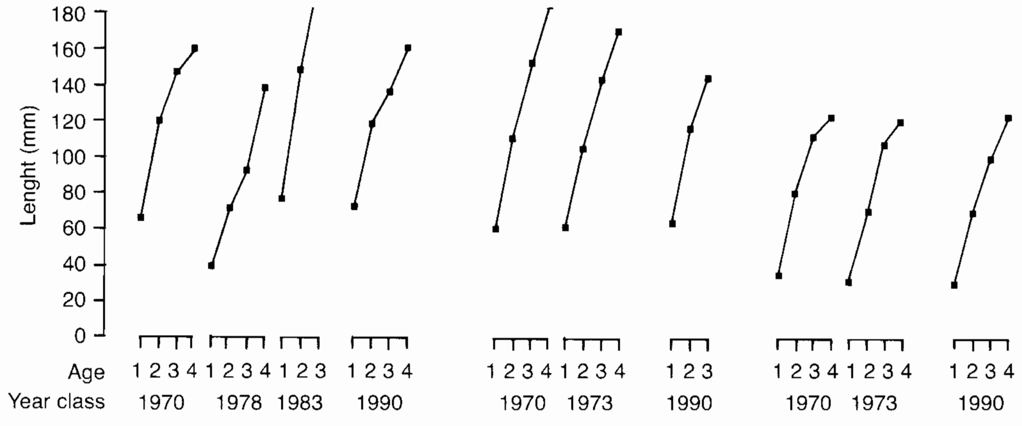

FIG. 3.
The growth of roach, perch and rudd of selected year classes in Slapton Ley. 1970 was selected as representative of the period before the massive expansion of the roach population and 1973 as representative of the period of that expansion. 1990 was the first year after the population crash for which data were available. Sources of data as for Fig. 2.

Most pike, however, did not attain either great age or great size. Immature pike fed mainly on invertebrates, but larger ones preferred roach, rather than perch as in Windermere (Kipling & Frost, 1970). Pike spawned in March, migrating to sites in the Higher Ley and to the Torcross end of the Lower Ley. Outside the breeding season they appeared to move freely throughout the lake. Such evidence as there is suggested that in the past there had been more larger pike in the Ley, whereas in the 1970s there was a preponderance of relatively small fish. The status of the population in the 1970s was believed to be a reflection of overcrowding and the changes in size and number of their prey fish. They were the only species to be caught regularly, albeit in small numbers, during the period of the fish crash, but it has not proved possible to investigate their biology in recent years.

Other species

None of the other species in the Ley has been studied scientifically. For a short period a licence was granted for eel fishing, but this proved to be economically inviable (though it was viable enough for a subsequent poaching fishery). The recent appearance of a pathogenic nematode in the swimbladder of eels has stimulated renewed interest in the eels of the Ley since conditions there are similar to those in some continental European lakes in which *Anguillicola crassus* has caused heavy eel mortalities.

DISCUSSION AND COMMENTS

Although the fishery has been monitored over 25 years, both records and coverage are incomplete. This largely reflects resources: intensive research could only be undertaken when funding was available, and at other times information was reduced to that obtainable from a monitoring programme directed selectively at roach and perch and their parasites. This has left several gaps in the picture that has emerged. Nothing is known about eels, and very little about pike before and after 1974–1977. The data obtained on individual growth rates of roach and perch and on catch indices of roach, rudd and perch have been invaluable and a high priority for the future is the obtention of data on the biology of all species to permit of a comparison between the recovery period of the 1990s and the pre-crash periods.

Long-term studies, however, seldom if ever start as such and so are never planned as such. Studies on the fish of Slapton Ley were no exception, as the scientific investigations in the early 1970s were designed with management of the fishery as their goal and were only funded for three years. The long-term programme grew out of this. The unfortunate consequence of such a development is that it only becomes clear in retrospect what else should have been done. In the case of the Slapton fishery, it has become increasingly evident that the investigations on the fish should have been accompanied by long-term studies on the plankton, both phyto- and zoo-plankton. Even in the mid 1970s it was clear that data on the quality and quantity of plankton would have been invaluable in interpreting the nature of the competition between the three species of fish at the fry stage. With the benefit of hindsight, it is also clear that knowledge of the plankton would have assisted interpretation of the rise and fall of the *Ligula* epidemics in roach. Eutrophication of the Ley has been accompanied by changes in the macroflora and the plankton (O'Sullivan, 1994), but the extent to which the fish and their parasites have responded to such changes or been responsible for such changes is far from clear. As O'Sullivan has pointed out, recent major changes in the flora of the Ley are related to eutrophication, but may also be related to variations in numbers of fish of each species and to their impact on the grazing of benthic and planktonic algae by zooplankton. There has always been a suspicion that part of the reason for the limitation of *Ligula* levels in 1975 and its subsequent decline was changes in the quality and quantity of copepods associated with eutrophication. It is similarly very tempting to explain the much more rapid rise in the level of *Ligula* in the 1990s in terms of a greater abundance of plankton as a consequence of the lack of fish feeding upon it between 1985 and 1989. Changes in fish predation on plankton may thus have influenced the biology of the fish species themselves, the levels of *Ligula* infection and the balance between plankton and macrophytes in the lake. In the absence of studies on the plankton, such possibilities must remain speculations but if one were now to design the whole programme anew and with greater resources concomitant studies on plankton would have to have a very high priority.

Retrospection also permits the identification of the critical periods in the history of the fishery, though these were never evident at the time. Two such periods can be identified in Slapton Ley. The first of these was 1970–1973, the time at which the roach population was undergoing its greatest expansion. There is some indication (Kennedy, 1985) that the alternation of good and bad year classes of roach was also a feature in the late 1960s. If true, the key events were those that broke this pattern and resulted in the series of good year classes from 1970–1973. It is not known what they were or how they were related to eutrophication, but it is clear that they set in motion a series of changes in the composition of the fish community that were only terminated by the population crash of 1984–85. This was the second critical period: it would have been highly desirable to investigate its causality at the time it was happening, but by its nature it was not even recognisable as such until long after it had happened. It is nevertheless important to recognise that critical, and in the one case catastrophic, events do take place and can have such dramatic effects on a fishery even if their causality cannot be investigated as thoroughly as is desirable.

Nevertheless, and despite these gaps in information, a 25-year data set with all its limitations is still invaluable. It has shown us how closely changes in the populations of some fish species are related to changes in the catchment; it has shown us how complex, dynamic and unpredictable these inter-related changes can be; and it has shown us that the changes in the fishery of one lake are by no means typical of changes in other lakes. In the case of Slapton Ley, we are particularly fortunate also in that the winterkill effectively eliminated the existing fish populations in the lake and enabled a new natural experiment to start in the course of which we could test conclusions based on investigations before the crash.

It is clear that eutrophication of the lake, itself resulting from changes in the catchment, has been the major determinant of the changes in the fish populations, both directly and indirectly. Even though the exact mechanisms of its effects are not known, it is evident that eutrophication promoted the expansion of the roach population at the expense of the populations of rudd and perch and this in turn affected that of pike. The increased productivity of the lake and its fish in turn attracted the great crested grebes to nest there, and their introduction of *Ligula* was to affect the whole balance of the fishery for the next decade. Eutrophication was a direct cause of the winterkill, and the current rather different balance of fish species may reflect the recent reduction in eutrophication rate.

The dynamic and unstable nature of the fishery was apparent from very early on in the investigation. Roach were clearly more responsive to changes and in an adaptive manner than any of the other species, but changes in the roach population had major effects on the size, if not the biology, of the populations of rudd, perch and pike. The repeat of the population cycles in the same sequence after the crash of 1985 confirmed the interpretation of the earlier, 1970s cycle. An expansion of the roach population led again to stunting and the build up of *Ligula*: a decline in the roach population released rudd from competition and allowed their populations to expand again. Perch once more showed little response to these changes.

The studies of the fish in Slapton Ley have also indicated the dangers of extrapolation of conclusions from one lake to another. In Windermere, the only other British lake from which there is a long-term fishery data set, pike feed on perch, not roach as in Slapton Ley, and the perch there behave more like roach in Slapton Ley in that they show great variations in year class strength, with a single year class dominating for several years, and perch growth responds adaptively to changes in population density (Kipling & Frost, 1970; Le Cren *et al.,* 1977), The fish species in Slapton Ley, however, show several features in common that are absent from fish in Windermere: all four species exhibit early maturation, have a short life span and a low survivorship rate. It is not yet understood why this should be so, and until it is, it will not be possible to explain why the same fish species behave so differently in the two lakes.

Two further points of wide relevance emerge from the Slapton fishery study. The fish species in Slapton Ley clearly persist in a dynamic, non-equilibrial state, yet this is a natural unmanaged fishery. They have responded rapidly and dramatically to past changes in the catchment, and would appear to be capable of responding just as rapidly to any future and as yet unpredictable changes. It would be a very confident person who would attempt to predict the future changes in the fishery or who would attempt to manage it ! Finally, there is great interest at present in long-term data sets in the belief that they may provide a background against which any changes due to global warming can be detected. It would be an equally confident person who would attempt to detect any impact of global warming against the pattern of changes in the Slapton fishery

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