native species on various occasions; and the food of both native morepork and introduced little owl includes small birds, either native or introduced.

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RELATIONS BETWEEN SALMONIDAE AND THE NATIVE FRESHWATER FAUNA IN NEW ZEALAND

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The freshwaters of New Zealand provide an environment into which relatively few exotic species have penetrated, partly because the problems of survival during transportation are so difficult for a freshwater animal as to make accidental immigration very unlikely, and partly because the motives which may stimulate deliberate importation by man are so few in this case. So much remains to be done in the study of our freshwater fauna that a number of exotic species of the smaller invertebrates may exist unrecorded in this country, but the known freshwater fauna of non-native origin is limited to one snail and some dozen species of fish all deliberately introduced.

Most of the fish were introduced to provide sport, and it is not surprising that a large proportion of them belong to the Salmonidae since in its native Northern Hemisphere this family contains the majority of the most highly regarded game species. Of the species that were introduced, two have established themselves successfully over a large part of the country, and a third in a more restricted area. These are the brown and rainbow trouts (*Salmo trutta* and *S. gairdnerii*) and the quinnat salmon (*Oncorhynchus tschawytcha*) respectively. A few other species exist in small numbers in limited areas. For simplicity, I propose to limit consideration of the introduced freshwater fauna largely to these few highly successful species of Salmonidae; both because of their widespread abundance and because, on account of their popular esteem, they have been relatively intensively studied.

It should be realised that fresh waters

do not constitute an environment entirely isolated from those which surround it. Many animals of a variety of groups divide their time between freshwater and either land or air, either intermittently, or at set stages of their life history. It is therefore necessary to refer occasionally to events occurring outside the limits of the watery environment.

Since it is almost axiomatic that game fish should be carnivorous, it follows that one of the principal impacts of the Salmonidae on the native freshwater fauna is their predation on small native animals, both vertebrate and invertebrate. The converse is, of course, also true; that the native fauna may, by variations in its composition and abundance, play an important part in determining the density and structure of the introduced fish populations.

The principal food of the Salmonidae in almost all waters is derived from the invertebrate bottom fauna and from small fish. The degree to which the various species are eaten depends upon their abundance and upon the extent to which their habits and structure make them available to and eatable by the fish (Allen 1941). The latter may, in turn, be considerably affected by the size of the fish themselves; the larger the fish, the larger the animals which it eats, and the more easily are hard-shelled forms consumed. Among the invertebrates the principal groups eaten by stream-living Salmonidae in almost all countries are Chironomidae, Ephemeroptera, Trichoptera and Mollusca, the fish tending to advance through a sequence in this order as they increase in size. In lakes considerably greater diversity occurs. Small fish are mainly eaten by the larger salmonids, the particular species consumed varying according to the composition of the local fauna; in New Zealand the forms mainly eaten are bullies (*Gobiomorphus* and *Philypnodon* spp.) and smelts (*Retropinna* spp.).

The native invertebrate fauna of most of our rivers and streams is generally of about the same level of abundance as that of the north temperate region; for instance, there would commonly be between 100 and 1000 animals over about 3mm. in length for each square foot of stream bed. This fauna is clearly sufficiently abundant to support good trout populations in waters where conditions are otherwise suitable. Similarly many of our lakes contain numerous small native fish which provide good trout food; the large populations of fast-growing trout in many of the lakes of the Rotorua district are, for instance, enabled to develop by the abundant smelt stocks in these lakes.

While it is thus a simple matter to declare that New Zealand freshwaters now contain a native fauna of small animals which is generally sufficient to support strong populations of introduced salmonids, it is much less simple to determine what effect, if any, the salmonids have had upon the original fauna before the present position was reached. The difficulty arises partly from the almost complete lack of observations comparing the fauna of waters before and after the introduction of salmonids, partly from the scarcity at the present time of really comparable waters, some of which contain trout and some of which do not, and partly from the other environmental changes which have taken place simultaneously with the establishment of salmonids in New Zealand. These environmental changes include both physical changes like the increased instability and destruction of pools which often follow the clearing of catchment areas, and biological changes such as the introduction of insectivorous birds which may prey on the winged stages of insects with aquatic larvae.

Workers on various native aquatic animals have realised that the species they were interested in were subject to predation by trout and have suggested that this might threaten their survival. Generally however little evidence has been adduced as to the actual extent of the threat and one cannot avoid the feeling that sentiment has played an undue part in the formation of some of the opinions expressed. In 1915 a paper dealing with the freshwater crayfish (*Paranephrops* spp.) declared "It is evident that in common with other members of our native freshwater fauna, the crayfish are being destroyed by eels and the introduced fishes. Trout have been caught with partially digested crayfish in their stomachs, and it is probable that the restriction of crayfish to such places as cannot be inhabited by these fish is only a matter of time". Now, 45 years later, there are still lakes and rivers in which crayfish are abundant despite the presence of numerous trout, and there is little doubt that here, as in the northern hemisphere, trout and crayfish can exist side by side in a balanced relationship.

Among the mayflies there are some forms, particularly the various species of *Deleatidium*, which can maintain themselves in very large numbers despite the fact that they are freely eaten by trout. In the Horokiwi Stream, for instance, in 1940 they generally occurred at a density of 50 to 100 per sq. ft. despite the fact that they made up 60-90 per cent. of the food of trout in their first nine months. It has been suggested however that other mayflies, and particularly *Oniscigaster*, are more vulnerable to trout and that this may ultimately cause their extinction (Tillyard 1926). Some direct evidence regarding reduction in the numbers of *O. wakefieldi* is given by Hudson (1904), who quotes Hutton as saying "In 1874 the insect was common in the neighbourhood of Christchurch. I have lived there during the last 19 years without seeing a single specimen. Whether they have been killed off by the trout or by the sparrows I cannot say." Speaking of the related *O. distans*, Hudson himself seems more sure that the insect is destined for extinction than of the cause which will bring it about. He says of the nymph, "It is not very active, and owing to its large size, is easily seen and captured by means of the hand alone. Hence its speedy extinction by trout appears inevitable". However, when speaking of the imago, he writes, "Whilst thus resting it is no doubt often devoured by birds and the insect's early extinction through this cause alone would appear probable". Whatever their numbers may have been originally the mayflies of this genus are now far from common in New Zealand, although still widely dispersed. If the numbers have indeed diminished severely, introduced fish and birds may have been at least part of the cause, but physical changes may have played a part. The nymphs of this genus are active swimmers and also rest in exposed positions on the tops of stones. They are thus ill-adapted to withstand strong water-currents and normally live in sheltered pools and backwaters. Where, as has occurred in many places, man's activities have reduced the stability of river beds and diminished the amount of pools and other shelter, the extent of possible habitat for this genus has probably been drastically reduced. It is interesting that one of the few localities where it occurs regularly near Wellington is at the mouth of a tributary stream where in times of flood quiet conditions due to backing up from the parent river occur instead of the usual scouring.

An opportunity has arisen for studying the effects of the introduction of rainbow trout in L. Waingata in Northland. There is some evidence, for instance, that the freshwater crab, *Hymenosoma lacustris*, which was previously fairly common in the lake, may have diminished considerably in numbers since the introduction of trout.

Work has recently started on certain tributaries of the Wangaehu River which trout have been unable to reach because of the permanently toxic conditions in the main river. There is considerable variation in the bottom faunas among the troutless streams themselves, apparently due to environmental conditions, but a recent comparison of their faunas with that of another tributary with an abundant stock of rainbow trout supports the following general conclusions.

1. The stream containing trout has generally a greater number of individual animals to the square foot than the troutless streams.

2. In the stream with trout the proportion of the fauna made up of animals freely eaten by trout is at least as great as in the troutless streams.

3. The troutless streams apparently contain no species which do not commonly occur in streams containing trout.

Thus, here, at any rate, the introduction of trout seems to have made no substantial difference to the composition of the bottom fauna.

The general conclusion is therefore that the introduction of Salmonidae has probably not led to any great change in the fauna of New Zealand freshwaters, particularly where the bottom fauna is concerned. It is however possible that a few species have been adversely affected; these are likely to be forms which combine habits and appearance making them attractive to trout, with a low biological potential giving them little capacity to withstand increased predation. This conclusion might have been unexpected if New Zealand freshwaters had been originally without carnivorous fish, but in most of our waters the bottom fauna was in fact already subject to considerable predation from a fish population including, to varying extents in different localities, the smaller eels, the larger bullies and galaxiids, and the grayling (*Prototroctes oxyrhynchus*). The virtually complete disappearance of grayling between 1870 and 1925, from previous great abundance, is, incidentally, by far the most striking biological change which is known to have occurred in New Zealand waters. Since it has happened in some places where trout are still scarce or absent, and in others had begun before trout arrived, it does not seem that, whatever its cause was, it can be laid at the door of the salmonids.

The reverse relationship, predation on Salmonidae by native animals, may be more briefly considered. The two principal groups of predators are shags, particularly the black shag (*Phalacrocorax carbo*), and eels, especially the long-finned eel (*Anguilla dieffenbachi*). Although both species are undoubtedly predatory on trout to some extent, the existing trout populations were established in the face of this predation, and it seems unlikely that the native predators will seriously menace their continued survival.

Work in progress on the effect on trout populations of the removal of eels is still in an early stage, but results suggest that in some circumstances it may lead to a substantial increase in the numbers of trout. Areas in New Zealand which are permanently eel-less, as a result of natural barriers to the upstream migration, tend to have abundant trout stocks. The structure of the trout population in these circumstances may depend on the balance between food supply and spawning grounds. Where the feeding grounds are extensive in relation to the spawning areas, trout may be large as well as numerous, as in Lakes Taupo and Rotorua; but where there is abundant spawning ground in relation to the food supply the trout may only reach a small size; this appears to occur, for instance, in the upper Waihou River system. Whether the introduction of salmonids has affected the eel population of New Zealand is hard to determine. Although they have provided an additional source of food for the larger eels, over about 26in. in length, they may be competing to some extent with the smaller eels which feed mainly on the bottom fauna. Burnet (1959), however, has found that fluctuations in numbers of trout sufficient to affect their growth rate through intraspecific competition for food, have no measurable effect on the growth rate of small eels inhabiting the same waters. The introduction of trout has also led to some deliberate destruction of eels with the object of benefiting the trout stocks; it is doubtful, however, whether this has had any significant effect on eel populations except occasionally in very restricted areas. In any case, destruction of eels for this purpose may have merely replaced the taking of eels for food by Maoris in pre-European times. It is more likely that the numbers of eels have been reduced by the destruction of cover, since this is a very important factor controlling eel population (Burnet 1952).

The relationship between the shags and trout is complicated by the fact that, unlike eels, shags are able to move freely and rapidly between one body of water and another, and indeed between inland waters and the sea. Shags are also to some extent gregarious, and quite large bands of them sometimes descend on a particular length of river, fish it industriously for a time, and then depart elsewhere. Occurrences of this kind may have a considerable effect on the trout population of the water concerned, provided that other prey is not available. Where, however, other less active and presumably more easily caught fish are present, as for instance the goldfish in Lake Rotorua, very few trout seem to be eaten (Dickinson 1951). Shags probably have their greatest effect on trout in areas, such as parts of the South Island, where other species of fish are relatively scarce in the rivers. Destruction for the intended benefit of the trout has probably been more effective against shags than against eels, and in some areas few inland nesting sites are allowed to remain occupied for long. The coastal colonies, however, which are largely untouched, probably provide a reservoir from which the inland populations can be quickly rebuilt when control measures are relaxed.

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