Fisheries Research Bulletin No. 2 (New Series)

Galaxias maculatus (Jenyns), the New Zealand Whitebait

By R. M. McDowall

Fisheries Research Division

New Zealand Marine Department

Galaxias maculatus (Jenyns),
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National Publicity Studios Photo.

Frontispiece: Whitebait fishing on the Awarua River, south Westland. Registered fishermen are transferring freshly caught whitebait from net to live box for storage.

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FOREWORD

Ever since the European settlement of New Zealand there has been a keen and developing interest in the whitebait fishery, both commercially and recreationally. Nevertheless, surprisingly little information has been published on either the fish or the fisheries.

This study is the first comprehensive account of the New Zealand whitebait. The author has shown that though whitebait are principally the juveniles of *Galaxias maculatus,* other species contribute to the catch.

With the exception of the marine stage in the life cycle, about which very little is known, the biology and ecology of *G. maculatus* have been described in detail.

Considerable concern has been expressed about the possible effect on the stocks of intensive fishing and of agricultural and industrial development in the river catchments. This study shows that the populations are subject to considerable natural fluctuations irrespective of these factors. It also provides some of that fundamental information which is essential for the understanding and effective management of the fisheries.

G. D. Waugh,
Director, Fisheries Research Division.

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INTRODUCTION

Galaxias maculatus (Jenyns) (fig. 1) is a small migratory freshwater fish common in most New Zealand lowland streams and known also from the Australian mainland, Tasmania, South America, and the Falkland Islands.

Scott (1962) gave the distribution of *G. maculatus* in Australia as "coastal streams of South Australia, Victoria, New South Wales, southern Queensland, and Tasmania". In New Zealand it is present throughout the coastal regions of both the North and South Islands. Moreland (1957) recorded it from the Chatham Islands, but it is not known from the Subantarctic islands of New Zealand, where *G. brevipinnis* Günther is present. The distribution in South America is not well documented, but Regan (1905) gave the range as follows: Tierra del Fuego, Patagonia, Chile, and the Falkland Islands. In Chile it is found north of Valparaiso.

In New Zealand, where *G. maculatus* has considerable commercial importance, the juvenile stage is known as whitebait. This name is also used to refer to the adult fish, but the adult is more generally known by the Maori name inanga. Best (1929) listed about 30 Maori names, but inanga appears to be the only name now in common usage. In the older literature (for example, Hector, 1872) and in some more recent works (for example, Phillipps, 1940; Graham, 1956) the name minnow has been used, but this has been rightly criticised by Stokell (1955) because of the confusion arising with the quite different Cyprinidae. Other names, applied mostly by the early settlers, were "Maori trout", "native trout", "rock trout" (Graham, 1956), and "cowfish" (Gibson, 1903; Phillipps, 1924b; Graham, 1956). In Australia common names include "jolly-tail", "eel gudgeon" (McCulloch, 1915), "native trout", and "pulangi" (Scott, 1962).

After hatching on the banks of stream estuaries the larvae are carried into the sea with the outgoing tide and are thought to live there for about six months. At about 50 mm L.C.F. (length to caudal fork) the juvenile fishes migrate back into the coastal rivers, where they grow and mature. During this migration the young *G. maculatus* are netted, with the juveniles of other species of *Galaxias,* and make up the bulk of the New Zealand whitebait catch. The New Zealand whitebait fishery dates back to pre-European times, and since the settlement of New Zealand in the middle of last century the fishery has been continued commercially and as a recreation. In 1965 the commercial catch amounted to 2,416 cwt and was valued at $232,856.

The earliest publications about New Zealand whitebait (for example, Powell, 1869) discussed the identity of the young migratory whitebait and were usually concerned with whether the whitebait was the juvenile of some other fish or a distinct species. Satisfied that the whitebait was the young stage of *G. maculatus,* the inanga of the Maori, later writers examined the life history of the fish. Although details of the breeding of *G. maculatus* were first published in 1904 (McKenzie), this report was little known, probably because of the rather obscure journal in which it appeared. Phillipps (1924b) further described the breeding of *G. maculatus.*

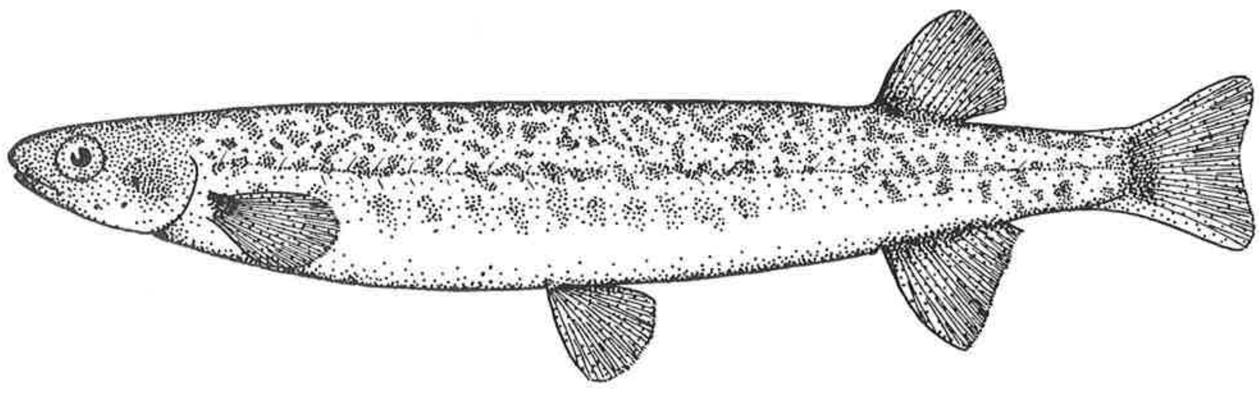


Fig. 1. *Galaxias maculatus* (Jenyns), adult 95 mm L.C.F.

The present study is an attempt to obtain a general understanding of the life history and ecology of *G. maculatus* as a primary basis for management of the whitebait fishery. At an early stage of the study the discovery that the fishery involved not one but five species of *Galaxias* resulted in a temporary diversion of activity from the general biology of *G. maculatus* to an examination of the composition of the commercial fishery. This work, which has been described elsewhere (McDowall, 1964, 1965b, and 1966), showed that in the more important whitebait area (the west coast of the South Island) a substantial proportion of the catch is contributed by species other than *G. maculatus*. Consequently an examination of the biology of these other species, particularly *G. brevipinnis*, becomes necessary, but it is not dealt with in this bulletin.

Public concern about the condition of the whitebait fishery began to grow during the 1920s, and at the end of that decade Captain L. Hayes was appointed by the New Zealand Marine Department to investigate the whitebait life history. Hayes's work was never completed or fully published, although sections of it were published by the Marine Department (see Hefford, 1931a, 1931b, and 1932). A few of Hayes's notes remain, in manuscript form, on Marine Department files and are referred to in later sections.

In the early 1930s McKenzie studied the embryology of the whitebait and the anatomy of the migratory juvenile; in a second study she described the anatomy of the adult of *G. maculatus* (McKenzie, 1933 and 1935). A further study of the whitebait was carried out by Benzie (1961), who compared the life histories of *G. maculatus* and *G. vulgaris* Stokell. Unfortunately, none of these studies has been published.

"Whitebait" fisheries occur in several countries besides New Zealand. Tasmania has a whitebait fishery based primarily on the anadromous adult of *Lovettia seali* (Johnston), but *G. truttaceus* Valenciennes, *G. maculatus, G. weedoni* Johnston, *Retropinna tasmanica* McCulloch, and other species are also recorded in the catch (Blackburn, 1950; Lynch, 1965). Graham (1956) reported that whitebait fisheries in Britain utilised "young Sprats, mixed with the young of Shad, Herrings, Sticklebacks, Gobies and Shrimps" and in Japan the young of "Seaperch". Chinese and Japanese whitebait fisheries also utilise the young of peculiar neotenic fishes of the family Salangidae (Okada, 1960). Lynch (1965) referred to whitebait fisheries in Holland and the Atlantic coast of the U.S.A. In the Philippines (Manacop, 1954) several species of goby are the basis of a fishery involving migratory juvenile fishes. All that these whitebait fisheries have in common is the utilisation of small transparent fishes, some of which are juveniles but others of which are adults.

In the present study it has been found that despite earlier assertions (for example, Hector, 1903) the New Zealand whitebait catch does not comprise only *G. maculatus.* Other species of *Galaxias,* besides species of *Retropinna, Stokellia* (f. Retropinnidae), *Philypnodon, Gobiomorphus* (f. Eleotridae), and *Anguilla* (f. Anguillidae), are also caught, sometimes in substantial quantities (McDowall, 1965b). In addition fishermen commonly report whitebait in the sea around New Zealand. Although some of these reports may be genuine ones of the river-running whitebait shoaling in the sea before their upstream migration, there are no published cases of *G. maculatus* or other species of *Galaxias* identified from the sea around New Zealand and no *Galaxias* has been seen in the sea by the author.* Most of these reports seem to concern the young of clupeoid fishes, usually the anchovy *Engraulis australis* (Shaw). In North Auckland there is a substantial localised fishery for juvenile *E. australis,* which also occurs in Auckland Harbour, where it is known as Devonport whitebait. In the Chatham Islands a whitebait fishery in one of the brackish lagoons involves the young of *Retropinna retropinna* (Richardson). Juvenile stages of *Retropinna* very like whitebait have been collected from the sea on the mainland coast of New Zealand. *Grahamichthys radiatus* (Valenciennes) (f. Eleotridae) is also sometimes mistaken for whitebait.

Recent studies (McDowall, 1964, 1965b, and 1966) have shown that five species of *Galaxias* occur in the whitebait catch. These are *G. maculatus, G. argenteus* (Gmelin), *G. fasciatus* Gray, *G. postvectis* Clarke, and *G. brevipinnis.* Migratory smelts, *Retropinna osmeroides* Hector, *R. retropinna,* and *Stokellia anisodon* (Stokell), are frequent constituents of the catch. In addition three eleotrids are caught with the whitebait as they migrate upstream. These are *Gobiomorphus basalis* (Gray), *G. huttoni* (Ogilby), and *Philypnodon hubbsi* Stokell. The elvers of *Anguilla dieffenbachi* Gray and *A. australis schmidti* Phillipps are also caught.

* Recently (Mr A. Baker, pers. comm.) *G. maculatus* whitebait were collected from the Marlborough Sounds.

In most parts of New Zealand the five species of *Galaxias* are the only fish of commercial importance, although in the Waikato River and some Thames rivers *Retropinna* species are commercially significant.

It was found (McDowall, 1965b) that the relative abundance of the *Galaxias* species in the catch varied with locality and time of year. *Galaxias maculatus* was nearly always the most important species and made up 85 percent of 36,089 *Galaxias* whitebait examined. On the west coast of the South Island the whitebait of the other species were found to be important. *Galaxias brevipinnis* was more abundant early in the season, declining later, and the kokopu species (*G. argenteus, G. postvectis,* and *G. fasciatus*), although never abundant, increased toward the end of the fishing season.

In New Zealand fisheries, such as those for the snapper (*Chrysophrys auratus* Forster) and tarakihi (*Cheilodactylus macropterus* Forster) or the trout fisheries, protective practices have been adopted to maintain population densities by limiting the size of the fishes taken. These practices are designed to ensure that the population is protected as far as is necessary for it to maintain itself, and surplus population is harvested. Such protective practices cannot be implemented in the *G. maculatus* fishery, because the juvenile is harvested, and the only way to protect the fishery is to allow for sufficient escapement. In determining the necessary escapement, consideration has to be given to the size of the juvenile population being harvested each year, the distribution of this population along the coasts of New Zealand, the mortality and fecundity of the fishes which are allowed to escape during the harvesting period, and the subsequent mortality of the larvae and juveniles between hatching and the next fishing season.

At present none of these variables is understood, and the present study has elucidated some information on only one of them—adult fecundity. Regulations up to the present have been largely designed to reduce the exploitation of the fishery by imposing restrictions on fishing practices and have had as a basis, immediately preceding trends in the productivity of the fishery.

However, the realisation that the regulations are governing the exploitation of five species should have some effect on conservation practices, especially since it appears that the composition of the catch varies through the season (McDowall, 1965b).

Efforts to protect the habitat of the maturing *G. maculatus* and its breeding habitat and prohibition on the capture of the adult for food have probably also been beneficial in conserving stocks. Protection of this nature should be extended to the other species involved in the fishery so that where possible the adult habitat, the spawning grounds (these are at present largely unknown), and the adult fish themselves are protected.

Although this study attempts to provide much of the background information on the biology of *G. maculatus,* it must be regarded as a beginning. The major task of the future is a concentrated study of specific aspects of the biology of the species, of which breeding biology and factors affecting the juvenile migration are probably the most significant and relevant.

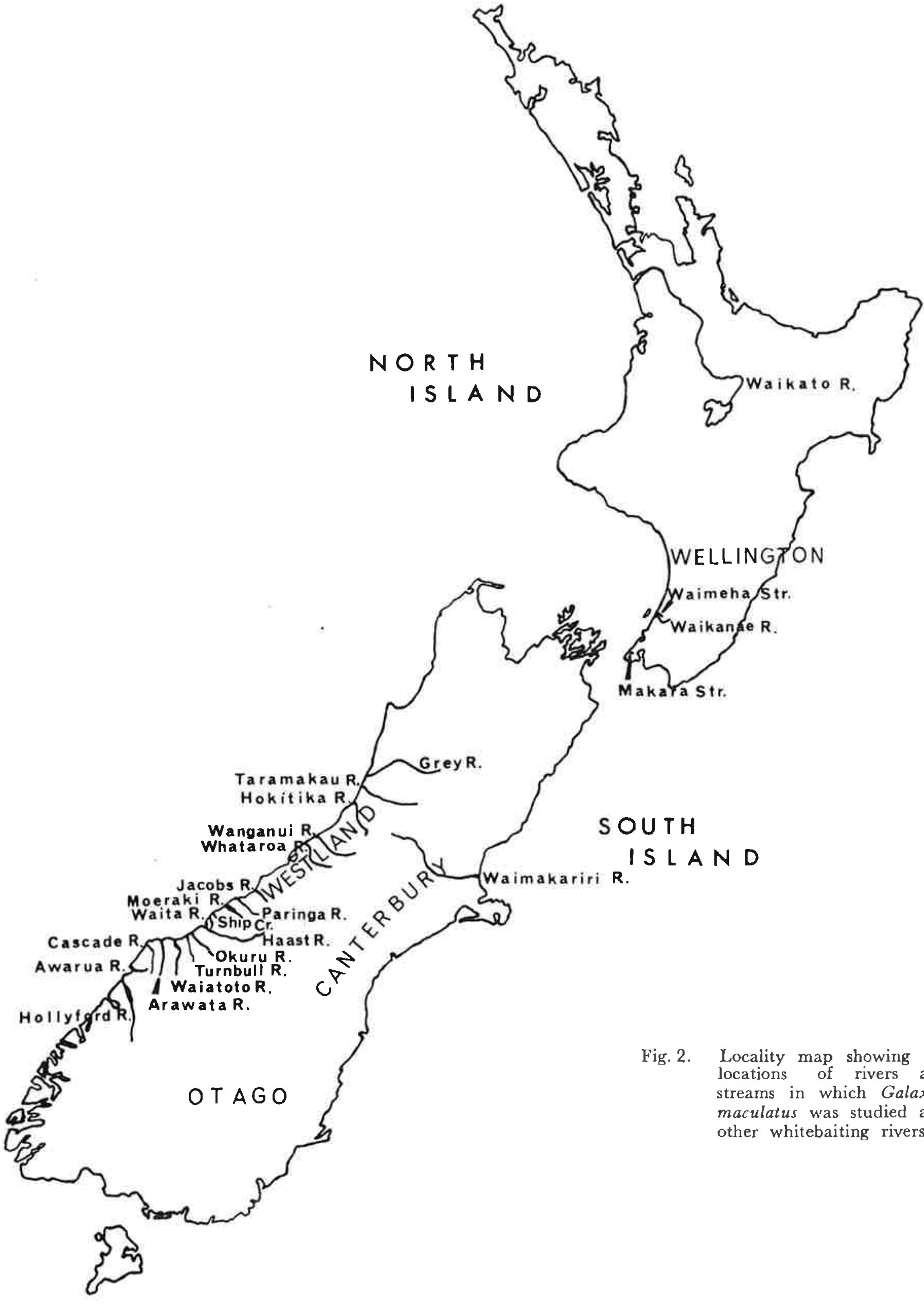


Fig. 2. Locality map showing the locations of rivers and streams in which *Galaxias maculatus* was studied and other whitebaiting rivers.

MATERIALS AND METHODS

SAMPLE AREAS AND SPECIES COLLECTED

Samples of *G. maculatus* and its habitat associates were collected from a wide range of localities (fig. 2.) A concentrated study of the population in the Waikanae River was begun in July 1963. A series of monthly samples taken as near as practicable to the beginning of each month was collected from three stations in the Waikanae River from September 1963 until November 1964. In general an attempt was made to collect 200 or more *G. maculatus* from each station, but sometimes river conditions or low fish numbers in the station areas prevented this and samples were smaller. Sample sizes ranged from 42 to 602 and averaged 286, a total of 12,896 *G. maculatus* being collected from the river. Sample stations were spread over the range of *G. maculatus* in the Waikanae River and occasional visits were paid to localities further upstream than the limit of *G. maculatus*.

The downstream limit for river resident *G. maculatus* in substantial numbers was found to be the upper estuary, where one of the monthly series of samples was obtained. The sample was collected several hundred yards upstream from the Otaihanga Boating Club hall, on the banks of the estuary. At the time of the sampling, the river there was relatively broad and shallow with a gravel bed and had several backwaters and small lagoons from which the bulk of the fish in the estuary sample was obtained.

The second sample station was about $1\frac{3}{4}$ miles upstream from the river estuary and was accessible from the end of Greenaway Road, on the north side of the river. At this station the river was much narrower than at the estuary and comprised a succession of swift riffles and deeper runs with few real pools. The river bed was usually coarse gravel, with finer gravel and sand in the slower-flowing water. *Galaxias maculatus* samples were usually taken from the quieter waters of the runs and from marginal cover and backwaters. A small creek joined the river from the north side at this station and shoals of *G. maculatus* were often collected from this tributary where it crossed the flood bed of the main river.

The upstream limit of *G. maculatus* in the Waikanae River during the period of study was fixed by a weir across the river just below the main highway bridge, about $3\frac{1}{2}$ miles upstream. Despite several thorough searches, only one *G. maculatus* was found to have passed the weir. The weir sample was obtained from a large rocky pool which formed below the weir and in the pools and backwaters nearby. The river was braided there and consisted of a series of swift riffles with a few more placid runs but no real pools. *Galaxias maculatus* was caught from marginal rock or vegetation cover and in backwaters. Large shoals of *G. maculatus* usually gathered in the pool below the weir. For part of the sampling period there was a series of large holes and muddy shallows on the south side of the river, formed by draglines and bulldozers removing gravel from the river. From February until June separate samples were collected from these backwaters, in which *G. maculatus* was very abundant.

During sampling, specimens of *Gobiomorphus basalis, Salmo trutta* Linnaeus, and both species of *Anguilla* were collected for stomach analysis, and samples of the other fish species in the river were also collected (table 1).

Additional fish collections were made from the Makara Stream, just west of Wellington, over the

Table 1: Occurrence of Fish Species at Localities in Waikanae River Sampled during Study

	Estuary	Greenaway Road	Weir	Above Weir
Geotria australis	X	X	X	X
Galaxias maculatus ..	X-x	X-x	X-x	Xp
Galaxias argenteus ..		X	X	
Galaxias fasciatus ..	x	x	x	X
Galaxias postvectis ..	x	Xp-x	x	X
Galaxias brevipinnis ..	x	x	x	X
Galaxias divergens ..				X
Retropinna retropinna ..	X-x	X-x	X	X
Retropinna osmeroides ..	X-x	X-x	X	X
Salmo trutta		X	X	X
Salmo gairdneri		Xp		
Anguilla australis schmidti ..	X-x	X-x	X-x	X-x
Anguilla dieffenbachi ..	X-x	X-x	X-x	X-x
Rhombosolea retiaria ..	X	X	X	
*Rhombosolea leporina** ..	X			
Gobiomorphus huttoni ..	X-x	X-x	X-x	X
Gobiomorphus basalis ..	X-x	X-x	X-x	X
Gobiomorphus gobioides ..	Xp			
Philypnodon hubbsi ..	X-x	X-x	X	
Tripterygion spp.* ..	X			
*Aldrichetta forsteri** ..	X			
*Geniagnus monopterygius** ..	X			
Cheimarrichthys fosteri ..	X-x	X	X	X

X Adults and resident juveniles.
x Migratory juveniles.
p Presence indicated by a single record.
* Primarily a marine species.

whole of the range of *Galaxias maculatus* in the stream. *Galaxias maculatus* occurred in the lower 5 miles of the stream; other species present were *G. argenteus, G. fasciatus, Gobiomorphus huttoni,* both species of *Anguilla,* and *S. trutta.* Several samples were also taken from the Waimeha Stream, about ½ mile north of the Waikanae River. Samples were taken from the lower reaches where *Galaxias maculatus,* the two species of *Anguilla, Gobiomorphus huttoni, G. basalis, Rhombosolea retiaria* Hutton, and *Geniagnus monopterygius* (Bloch and Schneider) were present.

In the 1963 whitebait fishing season samples of migratory whitebait were collected from the Awarua River by Mr E. R. Midgley. In the 1964 season an extensive whitebait sampling programme was carried out to collect whitebait samples from as many of the whitebaiting rivers as possible. With the assistance of Marine Department fisheries inspectors and fisheries laboratory staff, more than 380 samples were collected, mainly from the west coast of the South Island, Otago, Canterbury, and Wellington areas. In four West Coast* rivers (the Taramakau, Hokitika, Wanganui, and Moeraki) and the Waikato River frequent periodic samples were collected by fishermen working on the rivers. Apart from *Galaxias maculatus,* these samples contained the other four species of *Galaxias* with marine whitebait, *Gobiomorphus huttoni, G. basalis, Philypnodon hubbsi, Anguilla australis schmidti, A. dieffenbachi, Retropinna retropinna, R. osmeroides,* and *Stokellia anisodon.* Some of the Canterbury samples also contained *Philypnodon breviceps* Stokell, *Gobiomorphus gobioides* (Valenciennes), and *Cheimarrichthys fosteri* Haast, but these are unlikely to have been migrating with the whitebait.

SAMPLING METHODS

In the Waikanae River sampling programme electro-fishing techniques were used extensively. The equipment consisted of a portable "pack set" machine powered by two 6-volt motor-cycle batteries with a "wand" type positive electrode and a drag earth. This was workable in all waters except those of high salinity. Salinity sometimes became limiting in the estuary after a particularly high tide, but at low tide little trouble was experienced with high salinities. The gear was most effective in capturing fish in confined waters and from cover of all types, but was less useful for sampling shoals of fast-moving fishes which were able to disperse from the effective field of the electrode before they were paralysed. However, techniques were developed to overcome this problem. Either shoals were driven into confined areas by the electric field, or the electrode was introduced quietly near a shoal before the power was applied. Samples were thus frequently obtained by use of only the electric fishing gear.

Supplementary use was made of a short 5-ft-long "one-man seine" net constructed of fine "Ulstron" mosquito netting strung between two bamboo poles. A length of light chain was used to weigh down the lower edge of the net. When it was used in conjunction with the field of the electric fishing machine or independently, this net was very effective for catching shoals of *Galaxias maculatus.* The electric fishing equipment was also used for collection from other local rivers. In the larger whitebait sampling programme most samples were obtained from whitebait fishermen fishing on the banks of the rivers. Only where this failed to produce adequate samples was use made of the one-man seine net for collection of migratory whitebait. Because *G. maculatus* whitebait migrate in shoals, the electric fishing machine was unsuitable for this sampling programme.

METHODS OF PRESERVATION

When being collected in the field, fish were generally carried in a plastic bucket containing water and a narcotic, usually chlorbutol. Thus the fish were narcotised as soon as they were caught, which minimised distortion through asphyxiation. Where practicable, specimens were also fixed in the field. They were laid in shallow plastic trays, just covered with 10 percent formalin, and left until firm. The usual practice was to fix one sample while the next was being collected. When fixation in the field was not possible and had to be carried out during travelling, the fish were packed carefully into jars and formalin was poured in so that when the sealed jars were placed on their sides the fish were just covered with fixative. Most fish thus handled remained straight until fixed. Subsequently the jars were topped up with more formalin. The specimens were held for four to five days in 10 percent formalin, washed for a similar period in several changes of water, and stored in 40 percent iso-propyl alcohol.

* West Coast means the west coast of the South Island.

METHODS OF MEASUREMENT

Fish measurements were made according to the methods suggested by Hubbs and Lagler (1947). The most usual length measurement was length to caudal fork (from tip of snout to angle of caudal fork). For microscopic measurement an eye piece micrometer was used in a stereo-microscope.

GONAD STUDIES

For examining approach to maturity of *G. maculatus* in the Waikanae River, fish were sexed by gonad examination, and fish able to be sexed were placed in one of four arbitrary groupings based on gonad development: (1) **quiescent,** gonads a slender usually colourless thread; (2) **developing,** gonads beginning to swell; (3) **maturing,** gonads showing considerable growth but smaller than when mature; (4) **mature,** gonads more or less fully developed, eggs at about maximum size and in some fish ripe, testes creamy white and turgid. In both sexes mature gonads almost filled the abdomen.

Eggs were counted by fractional weight methods, although in small fishes, the whole egg complement was counted.

EXAMINATION FOR FOOD AND PARASITES

Food and parasite analyses were made together. The entire gut was removed from the fish and the stomach severed from the intestine. For reasons discussed in a previous study (McDowall, 1965a) food items were simply enumerated; owing to the time available it was not possible to carry out gravimetric or volumetric analyses of the food. In comparison with the food organisms found in the gut of *Gobiomorphus huttoni* the food of *Galaxias maculatus* was found to be in very poor condition. The reasons for this are not clear, but may relate to more rapid digestion in *G. maculatus.* Identification of food items in the stomach of *G. maculatus* was difficult because of this and except for a very small number of organisms identification in the intestine was almost impossible.

Parasites in the stomach and intestine of the fish examined were listed and the sites of infection noted.

To assess predation on *G. maculatus* by other fish species the guts of the fish of several species were collected. Analyses of these were confined to the stomach region.

MIGRATION AND EARLY FRESHWATER GROWTH

PERIOD OF MIGRATION

The whitebait run in the North Island usually begins in July and in northern areas of the South Island in August (New Zealand Marine Department, 1932–47). In the southern areas of the South Island, from the Whataroa River to the Cascade River and including many of the more productive whitebait rivers, the run usually starts in September (fig. 3).

Investigations by the writer in the Waikanae River showed that whitebait were migrating from the sea at all times of the year. There were fresh-run whitebait in every sample taken from the Waikanae estuary between September 1963 and November 1964. Using the same divisions of the Waikanae River samples as those used to illustrate size changes, the writer calculated the proportion of the more recently run fish as a percentage of the total sample for each locality each month (fig. 4). Young fish were uncommon in the estuary samples during March to June, more plentiful in July, and abundant from August to February. The period of few juveniles was longer in the Greenaway Road samples, extending from February to July. Numbers increased rapidly during July and August and remained high until December, declining during January to low again in February. At the weir there were no young fish from March to August and numbers there increased more slowly during subsequent months than in the localities closer to the sea. High proportions were present from September to December in the 1963 samples. In 1964 the rise in juvenile frequencies did not begin at the weir until after the collection of the September sample.

Despite the apparently large proportions of recently run whitebait in the samples taken during January and February, the numbers of whitebait running during these months were probably lower than these percentages indicate. From January to April and sometimes much later the adult *G. maculatus* are known to migrate downstream to the tidal estuaries to breed and there is at present no evidence to suggest that significant numbers survive breeding and migrate back upstream. Length-frequency histograms from 45 Waikanae River samples did not indicate that the population contained more than one age group or that there was at any time a major migration of adults from the sea. However, the few very large fish were probably two or three years old. Burnet (1965) found that most *G. maculatus* breed during their first autumn in fresh water, but a few do not breed until the second autumn and some fish delay breeding until the third autumn. All the fish observed by Burnet were maiden spawners. Apparently because of high breeding mortality, there is a marked depletion of the adult stocks during the breeding period, and the proportion of juveniles thus rises without any increase in abundance. The reduction of the adult population and the migration of some whitebait into the river mean that the juveniles are a high proportion of the population during January and February.

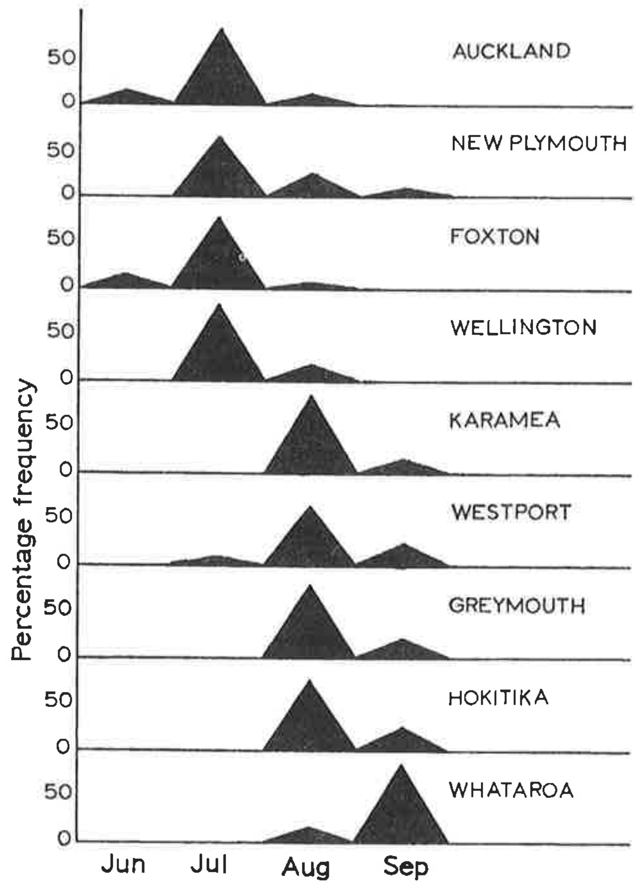


Fig. 3. Regional frequency of the start of the whitebait run during the fishing season. (Information extracted from New Zealand Marine Department's Annual Reports, 1932–47.)

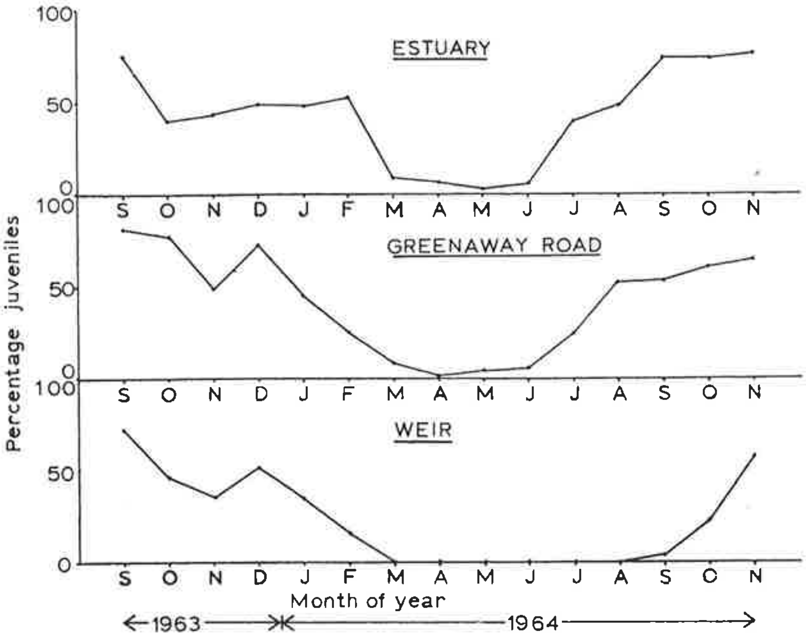


Fig. 4 Proportion of recently run juvenile *G. maculatus* in Waikanae River samples, September 1963 to November 1964.

Thus the main period of whitebait migration is usually mid August to early November, but whitebait migrate at all times of the year and occasional "runs" occur during the month or six weeks before and after the main migration period.

The whitebait fishing season is in late winter and spring, August to November in the North Island and September to November in the South Island. This limitation of the fishing season allows the utilisation of the most intense period of migration, but still permits some escapement before and after the season. Presumably the opening of the season one month later in the south is intended to take into account the later migration there than in the north.

PIGMENTATION OF FRESH-RUN WHITEBAIT

When whitebait first enter fresh water they are transparent, being pigmented with xanthophores and melanophores. The xanthophores occur as two mid-dorsal rows along the trunk and a scattering in the dorsum of the head. The melanophores are present as well defined mid-lateral and ventral lines with a scattering along the dorsum of the trunk. Melanophores are also present on the dorsum of the head, mostly behind the eyes, around the mouth, and on the posterior and ventral margins of the operculum (fig. 5). There are deeper-set melanophore areas along the vertebral column and the upper surface of the abdominal cavity. These are visible in freshly captured specimens, but become partly obscured after fixation.

DEVELOPMENT OF ADULT PIGMENTATION

Pigmentation begins to intensify in the young *G. maculatus* soon after they enter fresh water. Initially a peppering of very small melanophores develops over the surface of the trunk, being more concentrated dorsally and extending laterally to about the mid-lateral melanophore series of the fresh-run juvenile. Below this the melanophores are concentrated along the myotomes of the trunk. As the pigmentation intensifies, it becomes broken up into a rather variable mottled pattern. A guanine layer develops in the lining of the abdominal cavity and on the inner surface of the latero-ventral operculum. Because the body wall is translucent and there is no epithelial pigmentation in these areas, the guanine layer is easily seen in fresh specimens.

SIZE OF MIGRATORY WHITEBAIT

The L.C.F. of 8,722 fresh-run whitebait measured varied from 37 to 62 mm (mean 52.5 mm). Whitebait on the west coast of the South Island were distinctly larger than those from other areas (table 2).

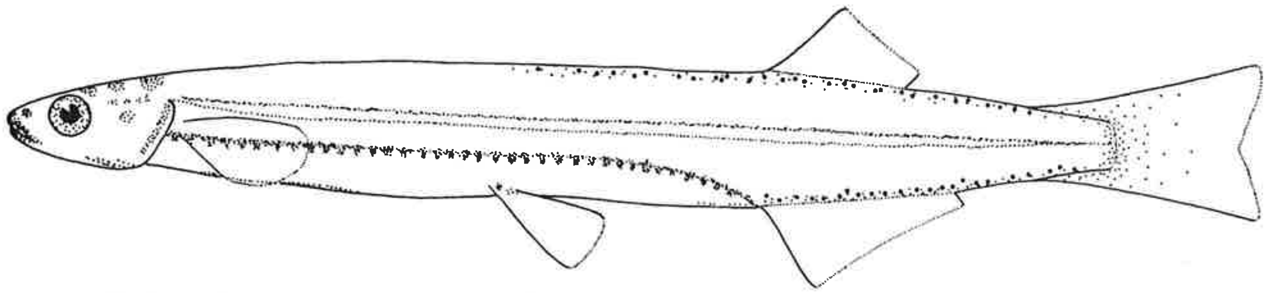


Fig. 5. *Galaxias maculatus* whitebait, 56 mm L.C.F., showing deep-seated and superficial pigmentation.

Table 2: Size of Migratory Whitebait

		No. of Fish Measured	Mean L.C.F. mm
North Island east coast	..	136	48.9
North Island west coast	..	1,687	51.1
South Island east coast	..	1,436	51.3
South Island west coast	..	5,463	53.4
Total	..	8,722	Mean 52.5

When a series of samples caught during October 1964 from New Zealand west coast rivers was arranged in north-south order, differences between North Island and South Island samples were noted. Although no statistical test was made, it appeared that fish from the north were smaller than those from the south (fig. 6). Whitebait from the west coast of the North Island were about the same size as those from the east coast of the South Island and the few fish obtained from rivers on the east coast of the North Island were smaller than those collected elsewhere (table 2).

Seasonal Size Variation

Samples were collected every three days from the Awarua River during the 1963 whitebait fishing season and at short intervals from the Taramakau, Wanganui (west coast of the South Island), and Moeraki Rivers in the 1964 season. The mean L.C.F. of Awarua River samples increased irregularly from the beginning of sampling (early September) until early October, and thereafter there was a distinct decline until sampling ceased in mid November (fig. 7). In the Moeraki River samples (fig. 7) there was a slight decline in average size from mid October onward, but in the Taramakau River (fig. 7) and Wanganui River samples there were no obvious trends. In all three 1964 series there were large fluctuations in the average size of the whitebait from sample to sample.

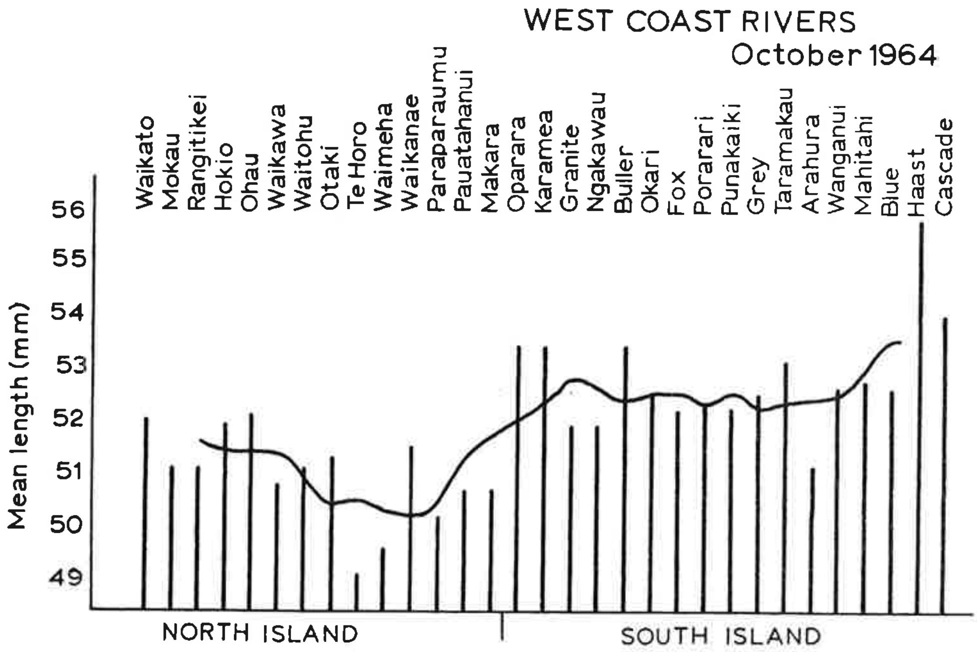


Fig. 6. Variation in mean L.C.F. of whitebait caught in rivers along the west coast of New Zealand, October 1964.

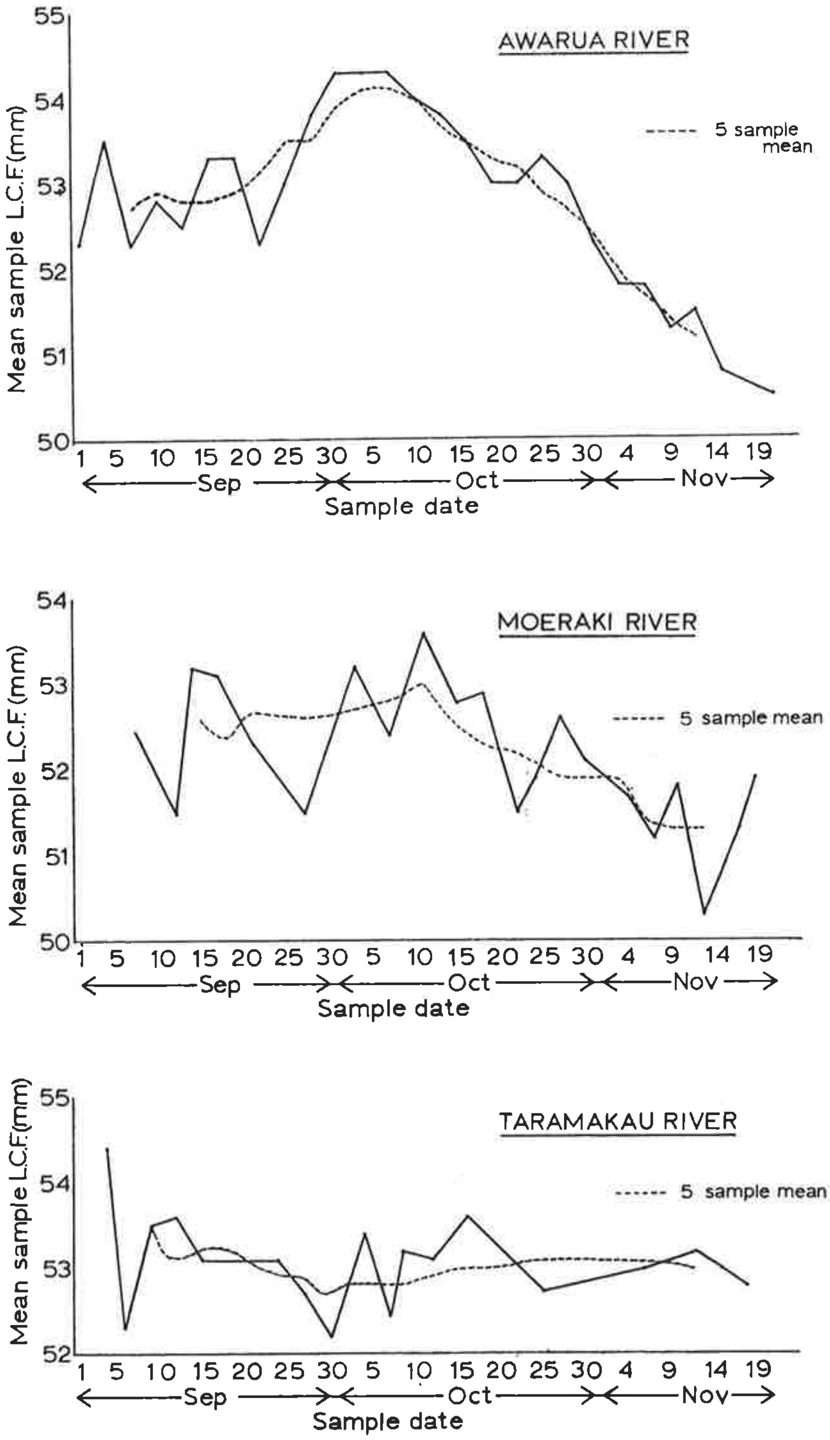


Fig. 7. Seasonal changes in sample mean L.C.F. of whitebait from selected rivers on the west coast of the South Island in the 1963 (Awarua River) and 1964 (Moeraki and Taramakau Rivers) fishing seasons.

The monthly Waikanae River samples were also examined to determine any change in the size of the juveniles migrating from the sea. The fish in these samples were divided into two groups—those which had adult pigmentation and those which were either fresh run or had the initial covering of melanophores which is present in fish that have only recently entered fresh water from the sea—and the average length of these was determined for each sample and station. In the samples from all three stations there was a peak fish size for recently arrived juveniles during the main period of the whitebait migration, with a rise to this peak beforehand and a decline afterward (fig. 8). There appears to be a period of maximal whitebait size during the period of most intense migration, with the size considerably lower during the period between annual peak migrations. The regularity of the rise and fall of the mean whitebait size suggests that this is a well defined pattern of change, although it may be more complex than the Awarua River and Waikanae River samples indicate.

AGE AT MIGRATION

Opinions have differed over the age of the migratory whitebait. Until recently the usual view has been that the spring migration is the product of the previous autumn's breeding. Stokell (1955) questioned this view on the grounds that the growth of whitebait in the sea was far too great for such a short period. He favoured the view that whitebait spent 18 or even 30 months in the sea before the upstream migration.

The larvae and juveniles of *G. maculatus* have not been recorded from the sea and nothing is known of their growth during the marine existence except their total growth at that time. Woods (1963) recorded *G. maculatus* breeding at one year, indicating agreement with the attribution of a marine life of about six months, and Benzie (1961) from a comparison of the life histories of *G. maculatus* and *G. vulgaris* concluded that there was nothing to indicate a marine period for the juvenile *G. maculatus* greater than the interval between the autumn breeding and the subsequent spring migration. The writer considers that the duration of the marine larval and juvenile stages of *G. maculatus* is about six months.

FACTORS AFFECTING THE WHITEBAIT MIGRATION

At present there are few objective data on factors affecting the whitebait migration. Opinion among the whitebait fishermen is that the best whitebait runs are near high tide each day and that the higher the tide the better the run tends to be. Thus the best runs are often near the spring high tides. Large runs also sometimes occur at or after floods and it seems that high water volume in a river estuary, whether it is caused by high tides or high river levels, may encourage migration.

It is not certain whether whitebait migrate at night. The fishing regulations prohibit whitebait fishing between dusk and dawn, and although most fishermen are adamant that whitebait do not migrate at night, cases of whitebaiters caught fishing at night are not uncommon. If there is no night migration, it seems unlikely that night fishing would be worth while.

The failure of any of the whitebait species to migrate in commercially significant quantities into rivers like the Waiho, Karangarua, and Cook, which are very cold, murky, snow-fed rivers, suggests that temperature probably influences the migration. Evidence that temperature is a controlling factor may also be deduced from the differences in the composition of the whitebait catches in different rivers. Analysis of whitebait samples from many rivers has shown that in the colder rivers *G. maculatus* is replaced to varying degrees by *G. brevipinnis*. The fact that the main migration appears to begin earlier in the north than in the south also indicates that temperature is involved in the timing of the whitebait run (McDowall, 1965b).

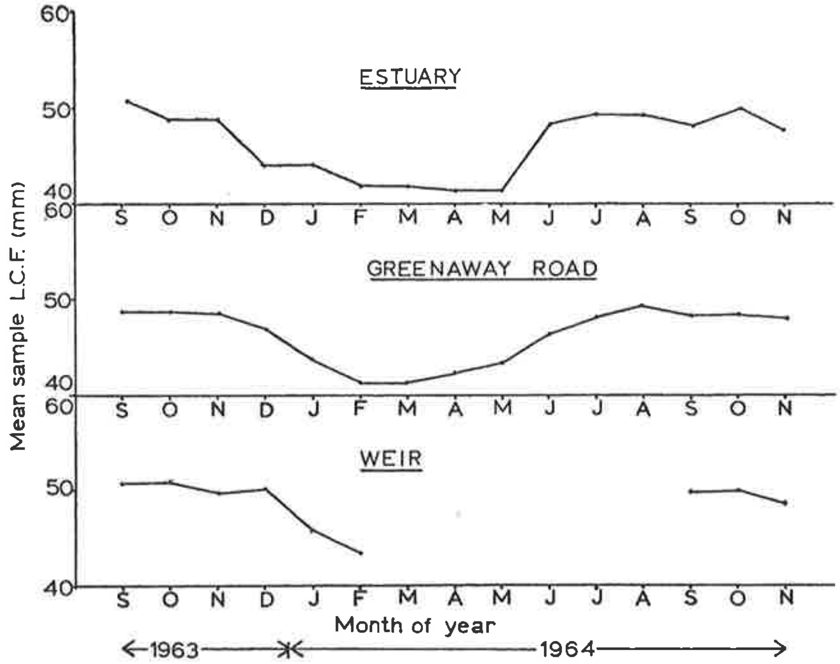
GROWTH PATTERN AFTER MIGRATION

During the monthly sampling of *G. maculatus* from the Waikanae River some of the fresh-run fish were larger than those in which trunk pigmentation indicated a longer freshwater life. Samples taken on 9 July 1963 and 2 July 1964 showed this clearly. The fish in these samples were sorted into two groups—fresh-run juveniles and pigmented fish (adults and juveniles). In the 1963 sample, the fresh-run juveniles measured between 45 and 55 mm L.C.F., and the pigmented fishes occurred in two separate length categories—40–50 mm and 55–90 mm L.C.F. The fresh-run juveniles were thus larger than some of the pigmented (older) fish, but were smaller than others (fig. 9B).

A length-frequency histogram of the Waikanae sample of 2 July 1964 showed a relationship between the fresh-run whitebait and the river population similar to that of the 1963 sample (fig. 9A). Although the pigmented fishes were not completely divisible into two size groups, there were two distinct modes for them, with the mode for the fresh-run fishes lying between. Again the fresh-run fishes were longer than many of the pigmented juveniles.

This relationship appeared most clearly at the beginning of the rise of the whitebait population in the river. Before this the population of *G. maculatus* in the river was low, comprising those fish which failed to reach sexual maturity in the first autumn in fresh water, a few which survived

Fig. 8. Seasonal change in sample mean L.C.F. for recently run juveniles in the Waikanae River, September 1963 to November 1964.



breeding, and those which had entered the river as whitebait during the autumn and winter of that year. The length-frequency distribution of the May and June samples showed an even distribution of sizes, with no marked mode for small fish. The population began to increase as the whitebait migration gathered momentum in early July, and with this there was a rapid increase in the proportion of small fish. The July samples in 1963 and 1964 showed that the fresh-run fish were migrating from the sea at between 45 and 56 mm L.C.F., but there were fish in the samples much smaller than this. These length-frequency histograms pose two questions: First, why are there fish in the population smaller than those known to be the most recent migrants from the sea and therefore presumably younger than those already in the river? and, second, why is the distribution for the pigmented fish bimodal?

These questions are adequately answered by the hypothesis that the fresh-run whitebait shrink during their early freshwater life. On the basis of this hypothesis, the smaller pigmented fish can be derived from the fresh-run fish by shrinkage. The bimodality of the length-frequency distribution of the pigmented fish can be attributed to recent increase in the number of small fish in the population, some of which have shrunk, but because substantial whitebait migrations have only recently begun, few of the fish have begun to grow after having undergone shrinkage.

Shrinkage in recently run whitebait was observed in the Awarua River by Mr E. R. Midgley, who reported (pers. comm.) that there was noticeable shrinkage of whitebait held in live boxes after capture. Although it adequately explains the length-frequency distribution in the samples, trunk shrinkage is a fairly unusual phenomenon in fish growth-pattern studies, especially in fish which, like *G. maculatus,* undergo little visible metamorphosis. Shrinkage reported in the early growth of fishes usually occurs along with a fairly striking metamorphosis, an extreme example of which is the metamorphosis of the anguillid leptocephalus. Such a metamorphosis does not occur in *G. maculatus,* and it was thought that a further investigation of growth in *G. maculatus* should be made.

If shrinkage was occurring, it would probably not be equal in all parts of the head and trunk and there would thus be changes in the proportions of various body parts and such changes would be revealed by measurement analysis.

Benzie (1961) found that there were marked differences in the S.L./H.L. (standard length/head length) ratio for *G. maculatus* of different sizes. The ratio for 1,096 fresh-run whitebait was reported by Benzie to be 5.3–8.0, mean 6.9, and for 372 adults 4.3–6.4, mean 5.35. Thus a reduction

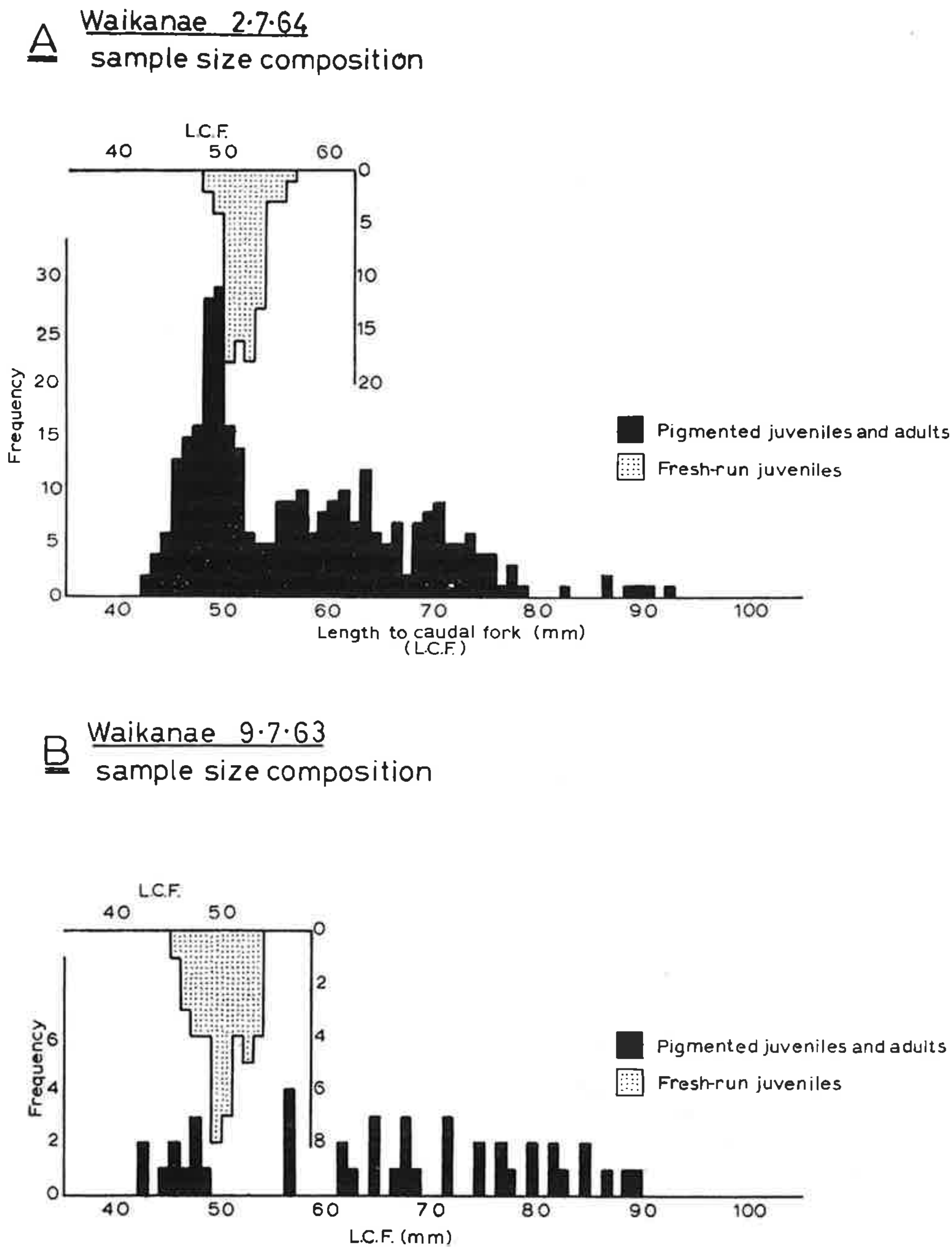


Fig. 9. Length - frequency distribution of fish in samples from the Waikanae River.

in the S.L./H.L. ratio was observed as the fish grew longer. She concluded that the fish undergo a rapid change in proportions as they enter fresh water and that adult proportions are reached by pigmented fish at 55 mm S.L.

Examination of Waikanae River samples showed, as Benzie had found, that with growth there is a distinct change in the proportional length of the head. The head length and length to caudal fork of 1,770 *G. maculatus* between 40 mm and 152 mm L.C.F. were measured; the size distribution for these specimens is given in fig. 10. A large proportion of the fish was between 40 mm and 60 mm L.C.F., because this is the size range at which the change in proportions occurred.

The L.C.F./H.L. ratio range for fish up to 60 mm L.C.F. was 4.7–8.1, but for fish over 60 mm the range was 4.9–6.3. The juvenile range therefore completely encloses the range for larger fish. The slight extension of the juvenile range to values lower than the adult range, from 4.9 to 4.7, is regarded as due to the much greater number of measurements

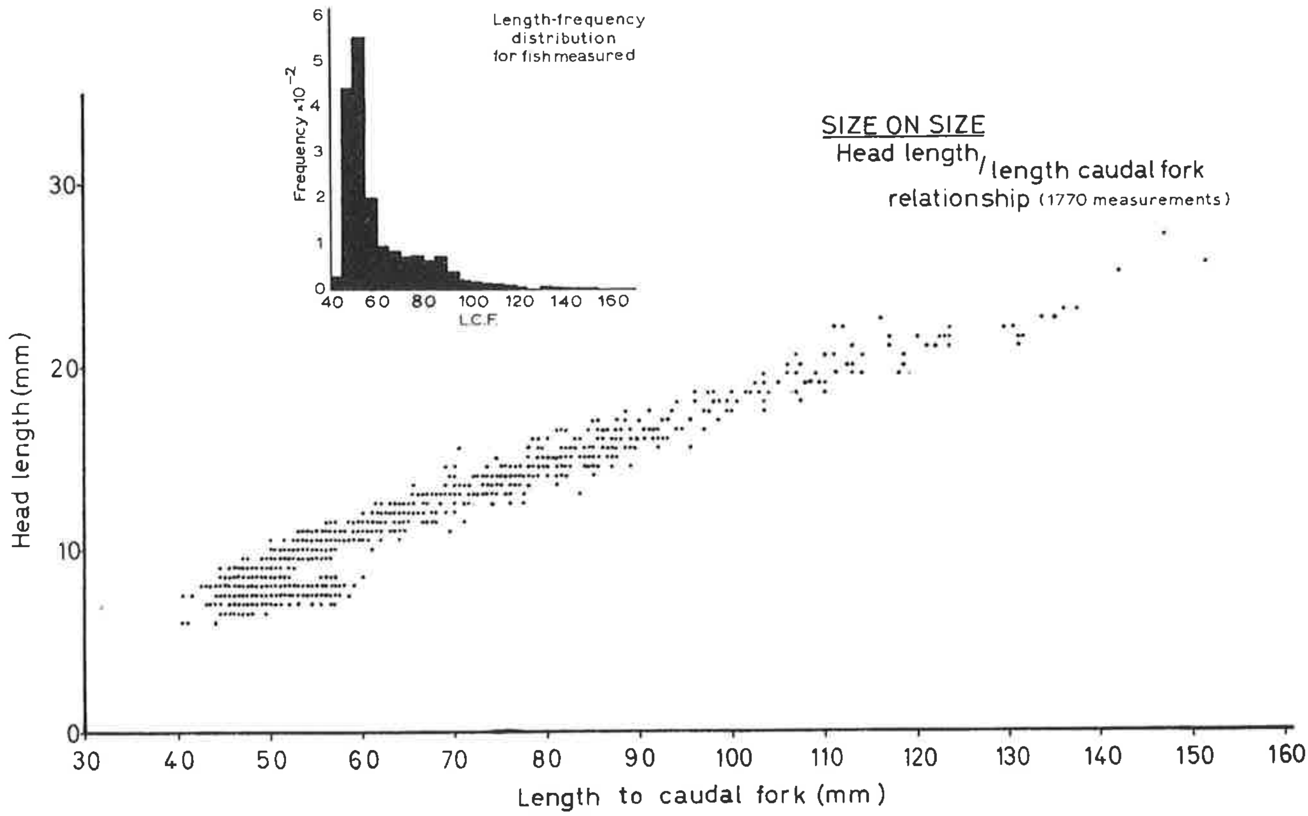


Fig. 10. L.C.F./H.L. plot for *G. maculatus* proportional growth changes.

of juveniles and is probably of no consequence. The increase in range of the small fish above the observed limits for the larger fish, from 6.3 to 8.1, is considerable and highly significant.

A plot of L.C.F./H.L. produces a distribution of unusual shape (fig. 10). In the lower size ranges the L.C.F/H.L. distribution is cleft, with the arms of the cleft diverging with increasing L.C.F. The upper arm of the distribution continues through the whole L.C.F. range, but the lower arm fails at 59 mm L.C.F. This size coincides with the maximum length of the fresh-run whitebait measured. A series of length-frequency polygons (fig. 11) shows the cleft in the distribution developing from 53 mm L.C.F., and becoming complete at 55 mm, and the two halves of the distribution diverging until the lower arm fails at 59 mm L.C.F.

The graph of the L.C.F./H.L. ratio against L.C.F. also has an unusual form. The distribution is L shaped (fig. 12). The upwardly directed arm, for L.C.F./H.L. ratios above 6.0, has a regression equation of $y = 0.39x - 12.8$, where y is L.C.F./H.L. and x is L.C.F. The arm of the distribution has positive gradient and thus slopes away from the L.C.F. axis.

These observations support the earlier hypothesis that whitebait shrink during their early freshwater life and they show that the shrinkage is in the trunk of the fish. The apparent divergence of the L.C.F/H.L. distribution is thus a convergence. The whitebait whose L.C.F./H.L. ratios lie in the lower arm of the distribution shrink and as they do so their ratios approach the values in the main axis of the distribution. The positive gradient of the upper arm of the ratio-on-size plot (fig. 12) also indicates that shrinkage is taking place.

Parr (1960) graphed measurements published by Ahlstrom and Counts (1958) for the early growth of *Vinciguerria lucetia* (Garman) (f. Gonostomatidae). Ahlstrom and Counts, defining the metamorphosis of *V. lucetia,* stated that "marked changes occur in body proportions and body structures without any marked increase in standard length. The length may not increase at all, or it may even diminish". Parr showed that the distribution of the S.L./H.L. ratio in *V. lucetia* has a cleft distribution similar to that of *G. maculatus* and attributed it to trunk shrinkage. Ahlstrom and Counts considered that the shrinkage resulted from compression of the narrow unossified

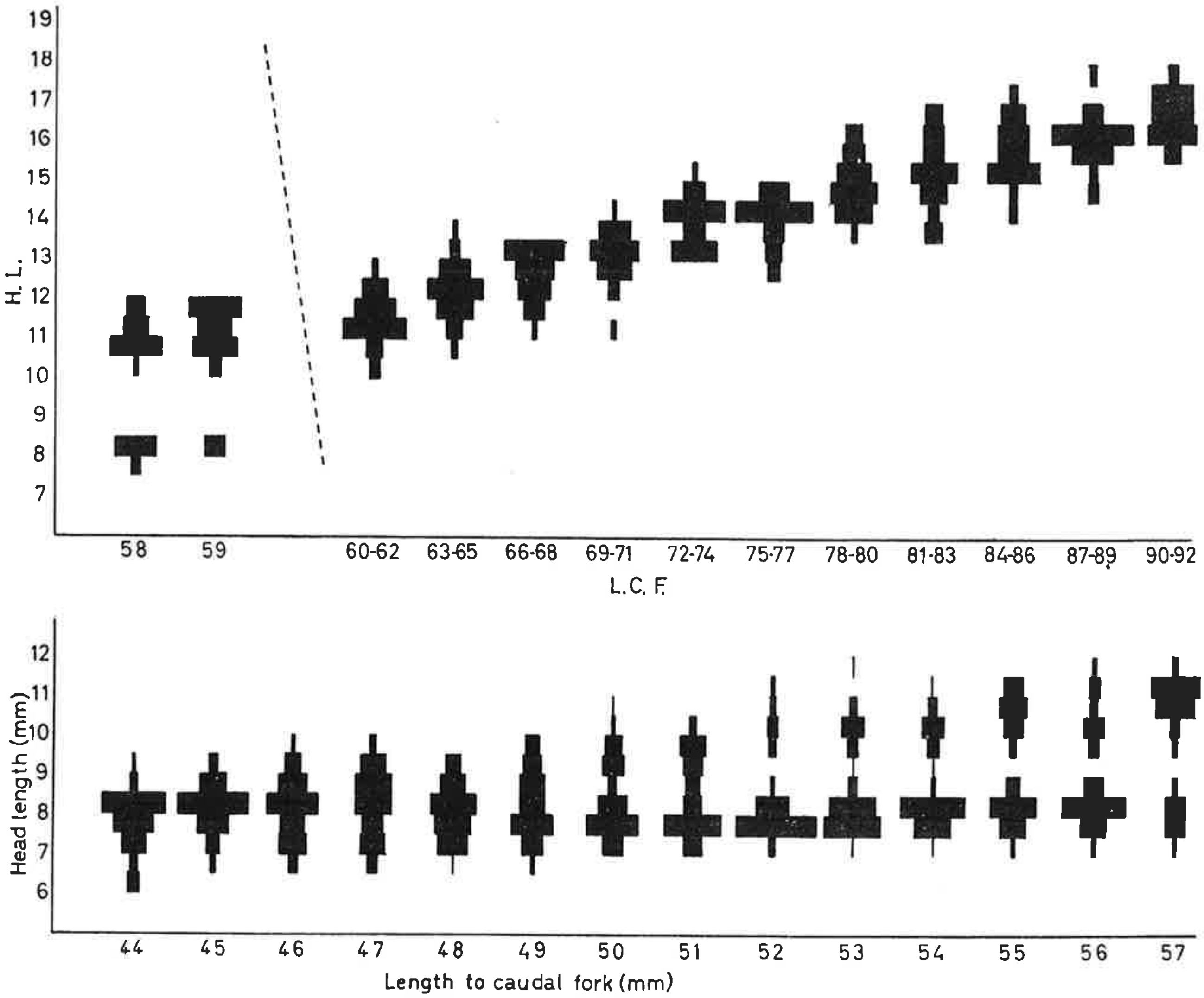


Fig. 11. L.C.F./H.L. plot of length-frequency polygons for small length intervals for *G. maculatus*.

spaces between the centra of the vertebral column. The mechanical aspects of the shrinkage of *G. maculatus* have not been studied.

Further investigation was made of the growth pattern of *G. maculatus*. A distinct change in the relative length of the pre-dorsal dimension also occurred (fig. 13). The L.C.F./pre-dorsal length ratio became smaller as the young fish grew and became stable in the adult. This indicated that the pre-dorsal length was becoming relatively larger with the growth of the fish. Plots of the L.C.F./pectoral base-pelvic base length and L.C.F./pelvic base-anal base length ratios indicated that uniform shrinkage was occurring along the trunk (fig. 13). The change in the relative pre-dorsal length must be attributed to the relatively larger head contained within the pre-dorsal dimension as the trunk shrank. Above the size at which these changes were taking place, about 60 mm L.C.F., growth of longitudinal dimensions was found to be isometric in all characters examined.

METAMORPHIC CHANGES IN THE GUT OF *G. MACULATUS*

During the early period of "growth" of *G. maculatus* in fresh water there is a change in the shape of the gut. In the fresh-run whitebait the gut is a straight tube with a minor swelling in the region which later becomes the stomach (fig. 14A). At the anterior end of this region there is a small dorsal diverticulum from the end of which the pneumatic duct of the air bladder opens. After the fish has been in fresh water for several days

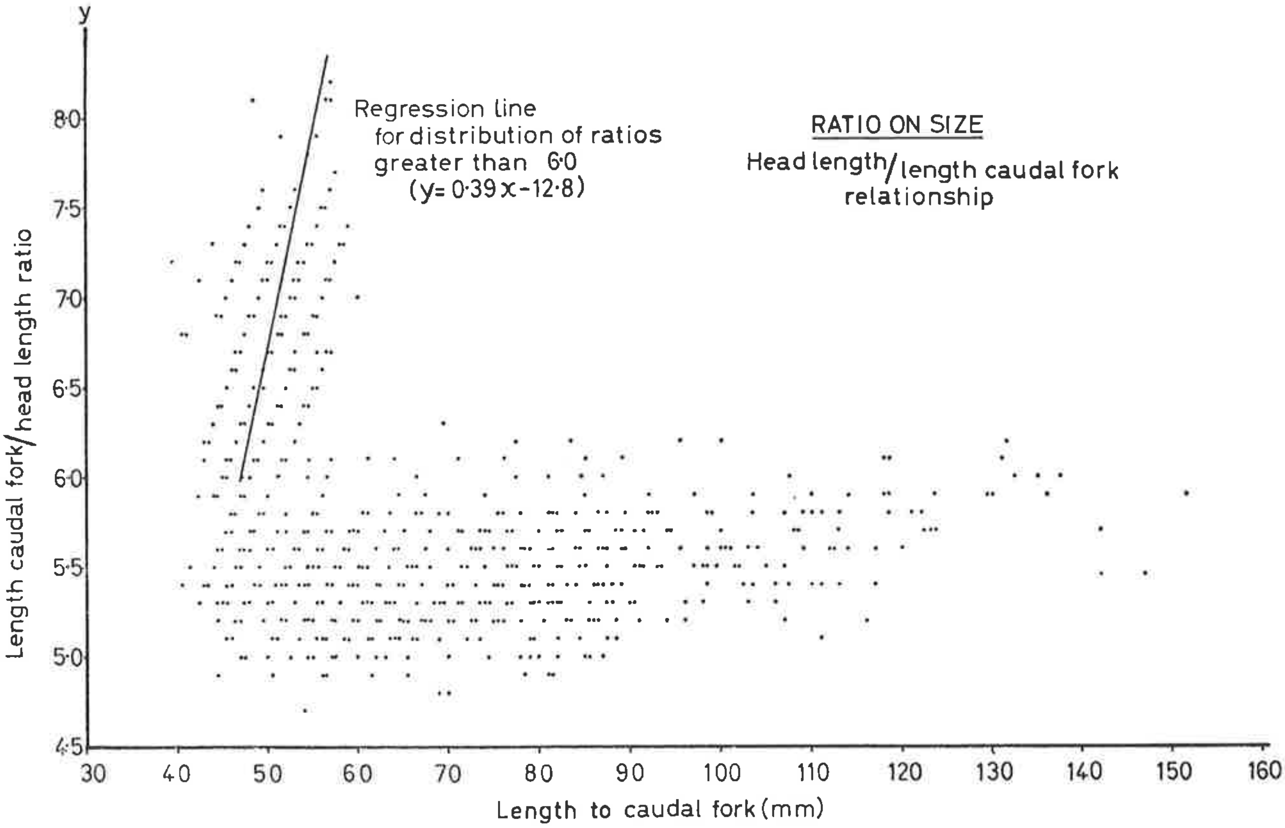


Fig. 12. L.C.F./H.L. ratio on L.C.F. plot for changes in proportional head length in *G. maculatus*.

(fig. 14B) the stomach begins to swell and it expands to incorporate this diverticulum in the stomach lumen. The pneumatic duct opens from the postero-dorsal margin of the formative stomach (fig. 14C).

Scott (1938) commented on the young of *G. maculatus* having "a pit or furrow, indicating the point of absorption of the yolk sac, and, just internal to, and dorsad of, this depression a bright red spot, formed by a subspherical vascular plexus, conspicuously visible through the transparent abdominal wall". The red spot which Scott described is in the ventral abdomen about midway between the pectoral fin base and the vent. The red colouration develops in the first few days after whitebait leave the sea and the structure is the spleen. It is bright red and easily seen in unpigmented whitebait. No trace of a yolk sac or its vestige has been seen by the author in any migratory whitebait in New Zealand. It seems unlikely that such a structure would remain after a life of six months, for much of which the young whitebait must have been feeding actively.

DISCUSSION

The regional differences in the size of the migratory whitebait suggest that there is not free mixing of the whitebait stocks in the seas around New Zealand. This is further supported by regional differences in the composition of the whitebait catch observed previously (McDowall, 1965b) and is illustrated well by a comparison of the whitebait catches of the east and west coasts of the South Island. East coast whitebait catches are predominantly *G. maculatus* and the whitebait are shorter than those taken on the west coast, where the catches often contain relatively low proportions of *G. maculatus*. If the whitebait stocks were being freely mixed in the sea, it would be expected that the cold, snow-fed rivers on both coasts would receive a high proportion of *G. brevipinnis,* but this was not found to be so. *Galaxias brevipinnis* was not common in the whitebait caught on the east coast of the South Island. Further, mixing of the stocks would eliminate the regional size differences which occurred. Blackburn (1950) con-

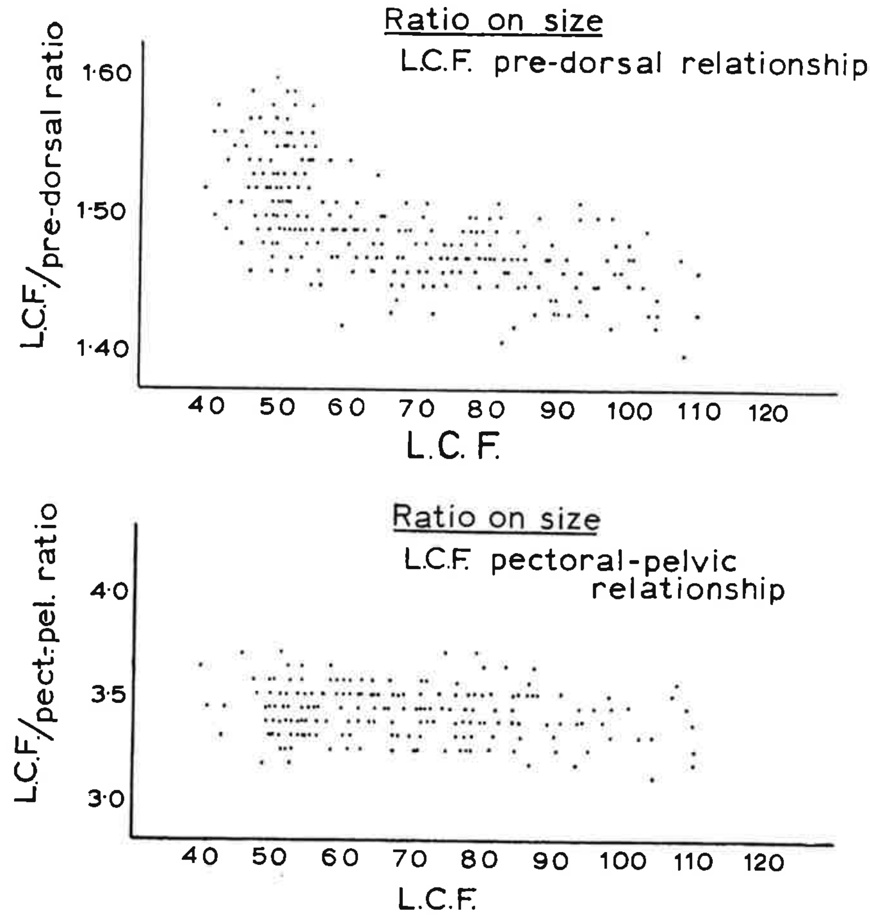


Fig. 13. Proportional growth changes in pre-dorsal and pectoral base-pelvic base dimensions.

cluded that in the whitebait fishery for *Lovettia seali* in Tasmania the northern and southern fishing areas had different populations.

The significant changes in the relative head length of *G. maculatus* are interesting in that there are no extensive changes in the appearance of the fish. Suttkus (1956) described growth changes in the Gulf menhaden, *Brevoortia patronus,* in which there are "profound changes in the body shape during the development and transformation of larval to young stages". Twenty different body proportions were found to alter significantly during the early life. Ahlstrom and Counts (1958) described distinct growth changes in the body proportions of *Vinciguerria lucetia* in its early growth, and the marked changes in the body proportions of anguillid leptocephali at metamorphosis are well known.

The primitive isospondylid fish families Elopidae and Albulidae have several species with leptocephalus-like juveniles in which there is substantial alteration in body proportions and as much as 50 percent shrinkage in the metamorphosis from leptocephalus to juvenile (Gehringer, 1958 and 1959; Rasquin, 1955). The larva has the typical leaf-like form of the anguillid leptocephalus, which becomes altered during the shrinkage period. In complete contrast the metamorphic shrinkage in *G. maculatus* is not of great proportions and is accompanied by no obvious changes in the general body form.

Very little is known of the early larval life of *G. maculatus.* The freshly hatched juveniles were, however, hatched and reared for several months, probably with greatly retarded growth (see "Breeding Biology: Development and Hatching", p. 39), and the form of the early juvenile is not leptocephaloid; the trunk of the larva is rounded and shows no deepening characteristic of leptocephali. Nevertheless, the transparent, probably pelagic, juveniles, which undergo a metamorphic shrinkage, are comparable with the primitive isospondylous and apodal metamorphosis. The migratory whitebait is very similar to the "stage III" larva of *Albula vulpes* (Linnaeus) illustrated by Rasquin (1955). Rasquin considered that much

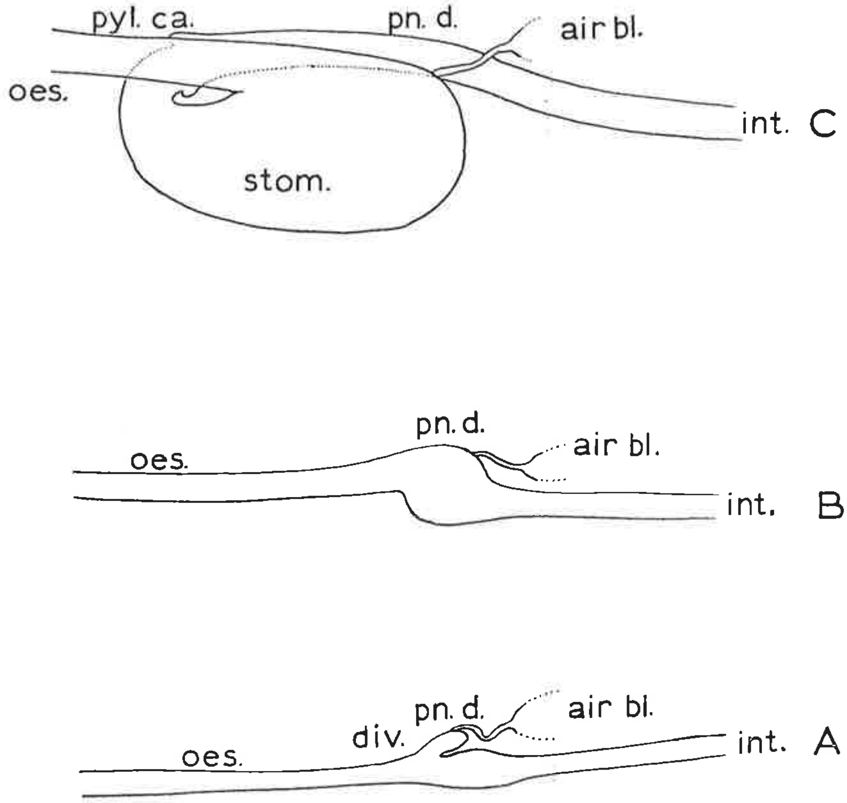


Fig. 14. Metamorphic changes in gut. A: Fresh-run whitebait. B: Pigmenting juvenile after 9 days in fresh water. C: Adult. (a.bl., air bladder; int., intestine; oes., oesophagus; pn.d., pneumatic duct; pyl. ca., pyloric caeca; stom., stomach; div., diverticulum.)

of the bulk of the leptocephalus of *A. vulpes* and eels is due to gelatinous material which is resorbed or otherwise removed during metamorphosis. The parts of the metamorphosis of *G. maculatus* which are known, the stages subsequent to migration, do not suggest substantial resorption of body substance. Since *G. maculatus* juveniles have not been examined before entry to fresh water, a greater marine metamorphosis may take place, the final stages of which are discussed here. However, study of the larvae in the laboratory and evidence from other Galaxiidae whose juveniles are known offer no support for the existence of a more leptocephalus-like larva and a more substantial metamorphosis.

BREEDING BIOLOGY

INTRODUCTION

The breeding of *G. maculatus* was undescribed until McKenzie (1904) reported his observations of the breeding of fish on the banks of the Rangitikei River. Phillipps (1924b) subsequently published an account of the breeding of *G. maculatus* in the Hokitika River. Hayes (see Hefford, 1931a, 1931b, and 1932) studied the breeding biology of *G. maculatus* for several seasons and described the events associated with the breeding of the fish, listing the localities where and months when breeding was observed to occur. More recently Benzie (1961) compared the breeding and life history of *G. maculatus* and *G. vulgaris*, and Burnet (1965) described his observations on the spawning migrations of *G. maculatus*. Despite these studies, much of the breeding biology is not well known and nothing is known of the marine phase of the life history. In this section the data in these reports are combined with information acquired during the present study.

SIZE AND LONGEVITY

The largest specimen of *G. maculatus* caught during the study was 142 mm L.C.F. As is usual with large specimens of *G. maculatus*, this was a female. The largest male observed was 116 mm L.C.F. Stokell (1949) recorded *G. maculatus* up to 6 in. (152 mm) and Clarke (1899) "barely 7 inches" (about 175 mm). Mr A. M. R. Burnet (pers. comm.) has taken *G. maculatus* up to 169 mm L.C.F. *Galaxias maculatus* does not commonly grow more than 125 mm, and examples over 110 mm are large. In samples containing about 15,500 fish, only 49 (0.3 percent) were 110 mm or larger and only five of these (0.03 percent) were over 125 mm. These large examples probably comprise two groups of fish—survivors of previous spawnings and maiden fish two or three years old (see "Breeding Biology: Fate of the Spent Fish", p. 41).

Of the 49 fish 110 mm or larger, 42 (86 percent) were females and all the fish over 120 mm were females. Greater length in the female could be due to various factors. The female may grow more rapidly than the male and a greater number of females may either delay breeding until the second or third season or survive an earlier spawning to breed again.

Little difference was found between the average lengths of the fishes of each sex in the Waikanae River samples. One sex was usually only a little larger than the other, and the average male was larger than the average female in about as many samples as those in which the average female was larger. From this it may be inferred that the growth rate of the sexes is similar and the larger maximal size and greater number of large fish among the females must be ascribed to longer survival either with or without breeding during earlier life. Burnet (1965) suggested that more of the fish which delayed spawning moved further upstream than first-year spawners. This agrees with the writer's observations that more of the large fish are females and that the females tend to be found in the upstream range of the species.

Attempts to determine the ages and thus growth rates of individual fishes were not successful. The otoliths of about 100 *G. maculatus* were examined for growth rings, but ageing of the fish was not accomplished. Neither spawning nor winter growth checks were identifiable in the otoliths, although many of them had various rings present. This is not surprising when it is considered that *G. maculatus* may be breeding from September until June, is migrating from the sea into fresh water throughout the year, and may breed in its first, second, or third year, and that a small percentage of fish may survive breeding. Because the breeding season and migratory period are so prolonged, a winter growth check may occur in fish which had left the sea in the previous spring and which enter their first winter in fresh water at about 15 months, while other fish may have just entered fresh water for their first winter (autumn migrants) and would be about six to seven months old. The physiological adjustment necessary in the movement from salt to fresh water may produce a growth check (see "Migration and Early Freshwater Growth: Growth Pattern after Migration", p. 20), and ring formation in the otolith. Not only is the beginning of the life of the whitebait possible in most months of the year because of the long breeding season, but for survivors of breeding, any otolith ring formed as a result of breeding could be developed during any month from September to June. Thus a winter ring may form in the otolith of fishes whose ages may differ by nine months or more, a ring may be formed as a result of the salt water-freshwater migration at any month of the year, and in the few spawning survivors a spawning ring may develop at any month from September to June. There would thus be no relationship between the times of formation of such rings, and the ageing of *G. maculatus* from otoliths, if possible, would therefore be very complex. For similar reasons the determination of age-length relationship by length-frequencies was not accomplished.

The only information available on the age-growth relationship of *G. maculatus* was published by Burnet (1965), who found from controlled growth experiments that first-year spawners were about 73 mm long, second-year spawners were 120 mm, and the few fish which delayed spawning until their third year were about 140 mm long.

AGE AND SIZE AT MATURITY

Galaxias maculatus usually matures during its first summer in fresh water and breeds in the following autumn. The juvenile probably has a marine life of about six months, so that the adult breeds at an age of about one year, and the life cycle is basically an annual one. The large size of some fish in the population indicates, as discussed above, that not all the fish are one year old at breeding; some are two or more years of age.

Burnet (1965) found that when *Galaxias* whitebait were transferred upstream above a trap the great majority migrated downstream in their first autumn, although about 3 percent delayed their migration until the second autumn and a few did not reach maturity until the third year. Thus most *G. maculatus* appear to breed at one year, a few at two years, and occasional fish at three years of age. Evidence of breeding survival shows that a few may breed more than once.

The smallest ripe female found during the study was 57 mm L.C.F. and the smallest ripe male 54 mm L.C.F. The presence of a female 56 mm long in one of the samples, which had already spawned and was recovering, indicated that smaller females may breed. As *G. maculatus* usually migrates from the sea at between 40 and 55 mm, it appears that in some fish there is very little increase in length before the gonads ripen. Length-frequencies of breeding shoals (fig. 15) show that most of the breeding fish are between 60 mm and 90 mm L.C.F. Average lengths of each sex in breeding shoals from the Waimeha Stream, Makara Stream, and Ship Creek (south Westland) were 74.2 mm, 73.4 mm, and 76.3 mm for males and 78.7 mm, 73.7 mm, and 91.4 mm L.C.F. for females respectively. The Ship Creek sample contained many very large females and was a sample of rather unusual size distribution.

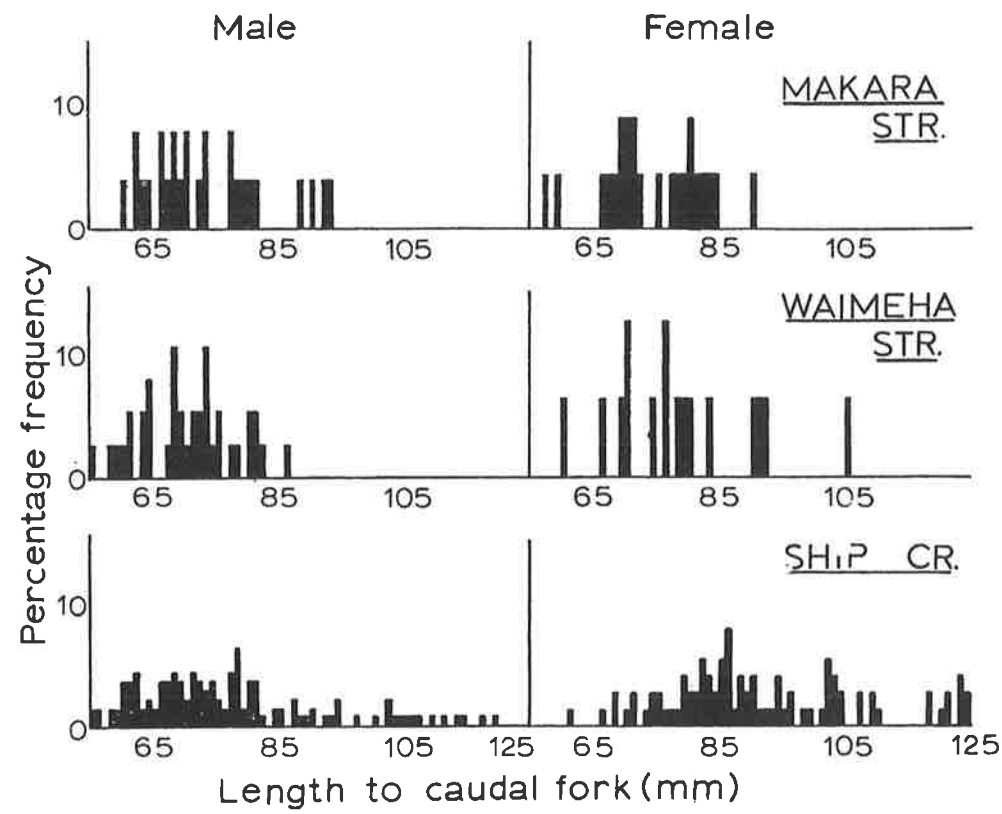


Fig. 15. Size distribution in breeding shoals of *G. maculatus*.

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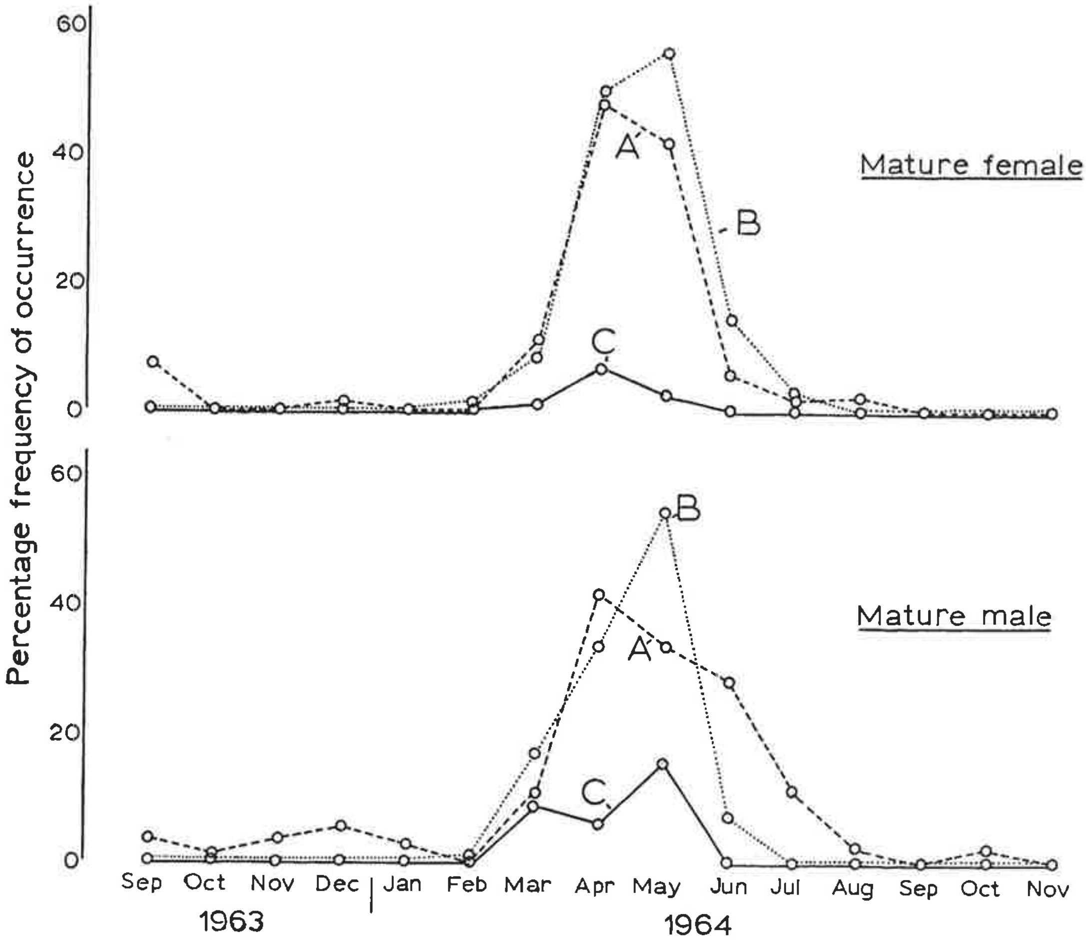


Fig. 16. Proportion of fish with mature gonads in monthly samples from the Waikanae River. A: Estuary. B: Greenaway Road. C: Weir.

SEX RATIO

The sex ratio of *G. maculatus* samples collected varied from 0.2 : 1.0 (male : female) to 5.0 : 1.0. In the Waikanae River samples there was a great preponderance of males in the estuary; this was less marked in the Greenaway Road samples, and in the weir samples there were more females than males. Mean sex ratios for the 15 monthly samples from each station in the Waikanae River were as follows: Estuary 2.0 : 1.0, Greenaway Road 1.3 : 1.0, weir 0.4 : 1.0 (male : female).

In the estuary samples the proportion of mature males rose abruptly in March, reached a peak in April, and declined steadily to a low and constant level from August onward. The proportion of females with mature ovaries was high during March, April, May, and June; that is, over a period similar to that in which there were high proportions of mature males (fig. 16). Breeding of *G. maculatus,* although it has been recorded from September until July, is thought to occur mainly during autumn and early winter. The sharp rise in the proportion of males in the estuary population may be related to breeding and associated migrations and mortality (fig. 17).

Sex ratios were obtained from the three samples from breeding shoals. The sample from the Makara Stream consisted of 49 fish with a sex ratio of 1.1 : 1.0. A sample from Ship Creek consisting of 226 fish had a ratio of 1.6 : 1.0, and a sample from the Waimeha Stream of 52 fish had a ratio of 2.7 : 1.0. These few observations suggest that the sex ratio in breeding shoals is variable. It probably depends on the size of the downstream migration, which builds up the proportion of females in a male-dominant estuarine population.

GONADS

The gonads of *G. maculatus* are similar to those of other salmonoid fishes.

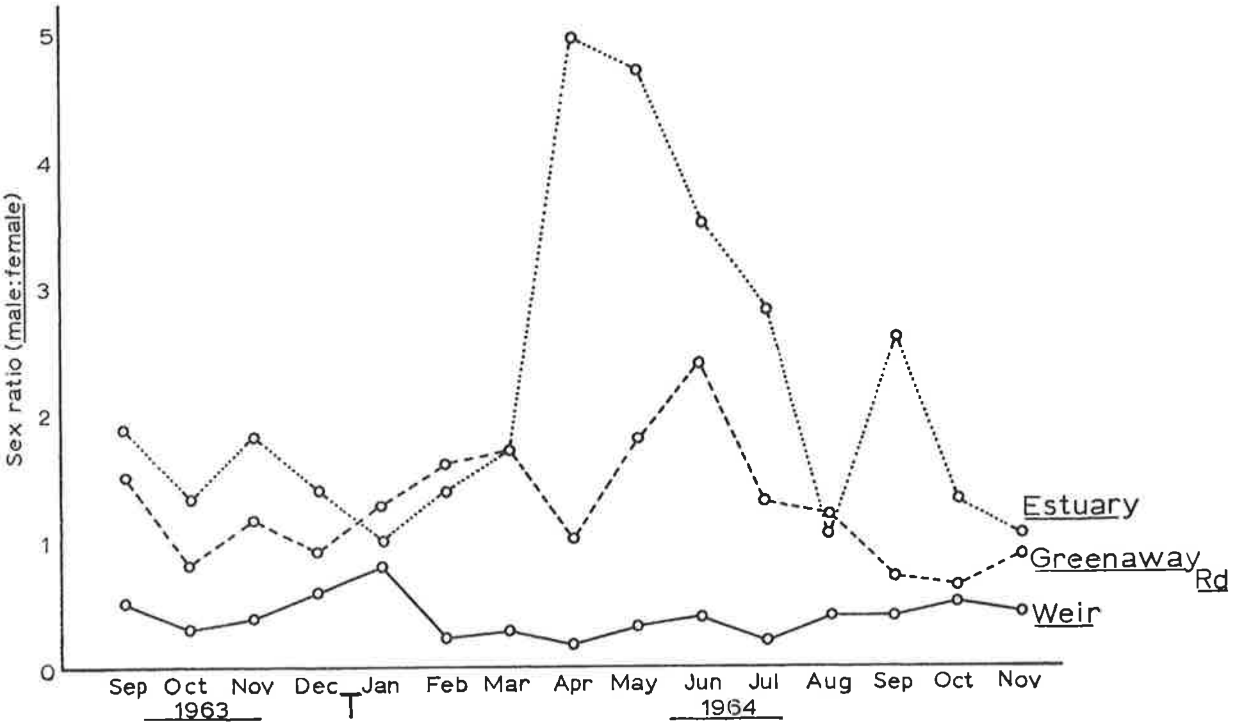


Fig. 17. Monthly variations in sex ratio of samples of *G. maculatus* from the Waikanae River, September 1963 to November 1964, from three stations.

Testes

The paired testes develop in juveniles as fine whitish thread-like bands along the upper abdomen below the air bladder. They extend from the vent to forward of the pelvic fin bases. As the fish grow, the testes extend further anteriorly and expand, so that the intestine becomes displaced dorsally to lie against the air bladder between the medio-dorsal edges of the paired testes. The testes are initially translucent, but become opaque and eventually a milky white. The ripe testes are creamy white and soft, almost filling the abdomen. The right testis is commonly longer than the left.

The urinogenital pore opens on a bilobed papilla lying in the urinogenital sinus situated immediately behind the vent. The vasa deferentia pass from the testes, through the posterior wall of the abdomen, and open at each side of the base of the papilla.

In the ripe male a tubercle develops from the anterior border of the vent and overgrows the vent and sometimes the urinogenital papilla and sinus. It is unpigmented and of a soft fleshy texture (fig. 18). Neither the immature male nor the female has it. No similar structure has been seen in the ripe males of *G. fasciatus* and *G. brevipinnis,* and its significance is not understood.

Quiescent testes in adult fish may be recognised by their amber colour, firm texture, and toughness. It is not known whether fish with such testes include breeding survivors or are entirely delayed breeders.

Ovaries

The paired ovaries appear similar to the testes in juvenile fishes and are in the same position in the abdomen. As they mature the ovaries enlarge greatly. The oocytes appear to be produced from

Fig. 18. Lateral aspects of anal and urinogenital apertures in mature *G. maculatus.* (an., anus; pr.a., pre-anal; ur.p., urinogenital papilla; ur.s., urinogenital sinus.)

a germinal epithelium along the medio-dorsal surface of the ovary. The eggs are released freely into the abdomen. Hoar (1957) described such ovaries, which are found throughout the salmonoid fishes, as gymnoarian.

At maturity the ovaries fill the abdomen from the stomach to the vent. The genital pore lies between the lobes of the urinogenital papilla in the urinogenital sinus and penetrates the posterior abdominal wall from the abdominal cavity into the sinus, immediately above the vent.

The ovaries are whitish throughout development and are opaque until they ripen, when they become a pale straw colour. In the maturation of the ovaries of *G. maculatus* all the eggs appear to be at a similar stage of development and they probably ripen and are spawned together or during a short period (fig. 19).

SEASONAL MATURATION OF GONADS

The fish in samples from the three Waikanae River stations were measured and sexed and their gonads graded into four categories based on the degree of development: **quiescent,** juvenile condition or quiescent gonads of adults; **developing,** showing enlargement over juvenile condition; **maturing,** ovaries enlarged and eggs visible to the naked eye in the female, testes full and rounded in the male; **mature,** ovaries fully developed and mature or ripe, testes creamy white and soft.

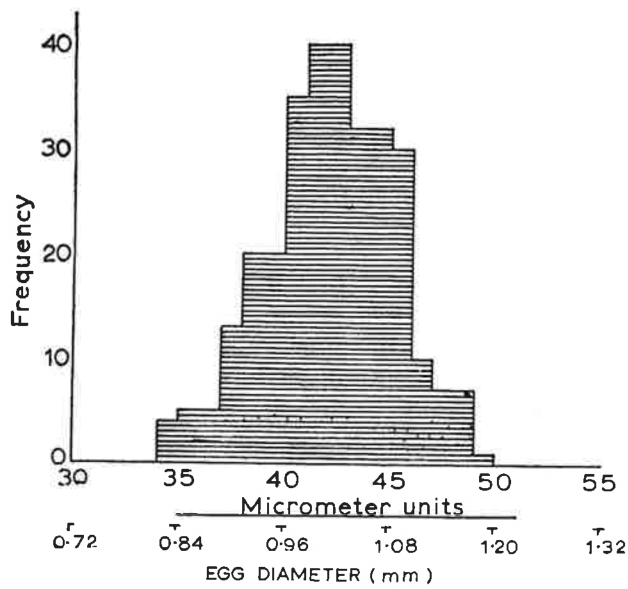


Fig. 19. Typical diameter-frequency distribution for ripe eggs from *G. maculatus*. Example from a female 84 mm L.C.F.; 300 eggs measured.

The gonads of *G. maculatus* mature mostly in late summer and autumn. Fig. 20 and 21 show the percentage of fish with quiescent gonads; this diminishes sharply in February and remains low until April before rising again. The frequency of occurrence of quiescent, developing, maturing, and mature gonads was determined for each sex for each of the 15 monthly samples. Most fish matured during March, April, and May at all three main sample areas, and many more fish matured at the estuary and Greenaway Road stations than at the weir. From January to June 1964 there were large gravel dredging holes at the side of the river about 200 yd below the weir. These holes varied from 12 to 30 in. deep in most places, had a sand and mud bottom, and had little or no water flow. They were inhabited by large shoals of *G. maculatus.* Separate samples were collected from these holes and it was found (fig. 22) that the proportion of fish with gonad growth was much higher there than in the river nearby. This difference could be due to one of two factors: either the habitat occupied by the fish affects gonad maturation, the slow-flowing or still water encouraging maturation and swifter water discouraging it, or the fish maturing move away from swift to more placid waters as maturation begins. No evidence was obtained to indicate that either of these hypotheses is correct to the exclusion of the other.

Comparison of the proportions of the samples in each developmental stage shows each rising to a peak in succession in order of degree of development. In the estuary the proportion of developing males rose sharply from February to April; there was a similar change in females, a rapid rise for developing females between January and February and for maturing and ripening females from February to April. At Greenaway Road the same successive maturation of the gonads was observed. Because few fish at the weir showed growth of the gonads, the change there is not as clear, but a rise in the proportion of developing gonads is evident for both sexes before an increase in the proportion of other gonad development categories.

Examination of the estuary and Greenaway Road samples showed that the fish which matured early in autumn tended to be large. The data for fig. 23 were derived by grouping the fish in the maturing and ripening categories and determining their mean length in each month. Mean fish size declined for each sex at both sample localities during the early period of maturation and was minimal when the greatest number of fish reached

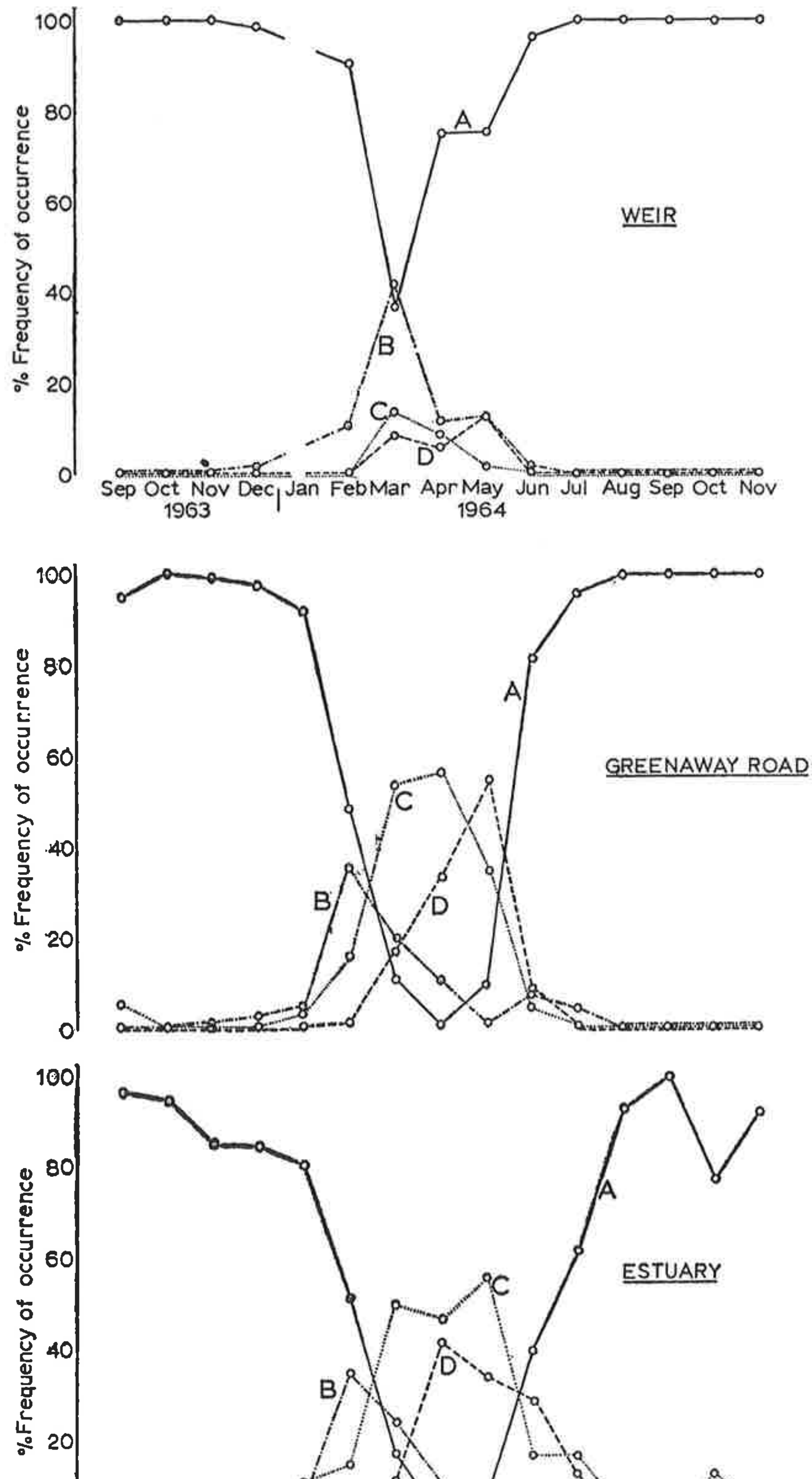


Fig. 20. Gonad maturation in males from the Waikanae River samples. A: Quiescent. B: Developing. C: Maturing. D: Mature.

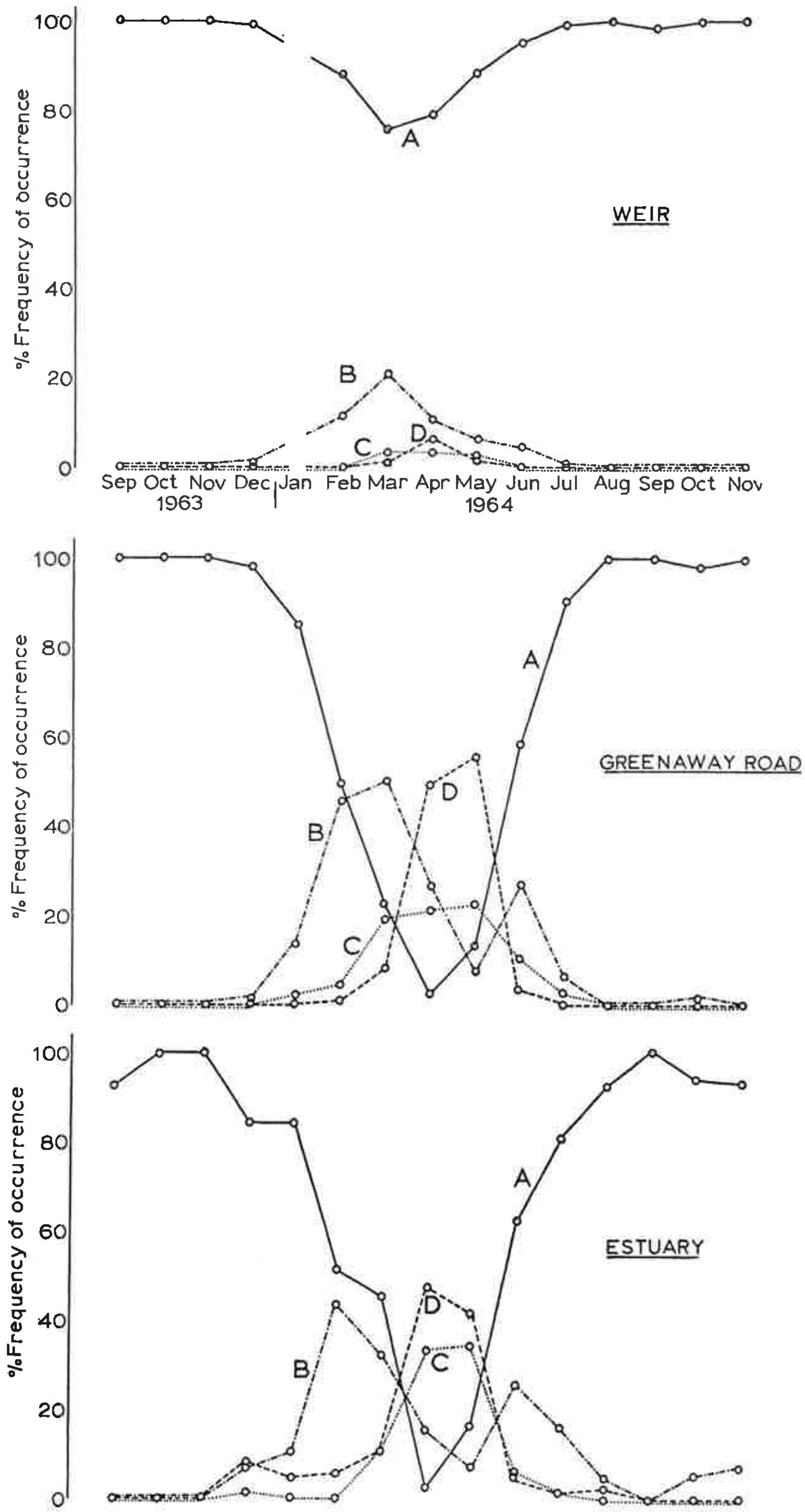
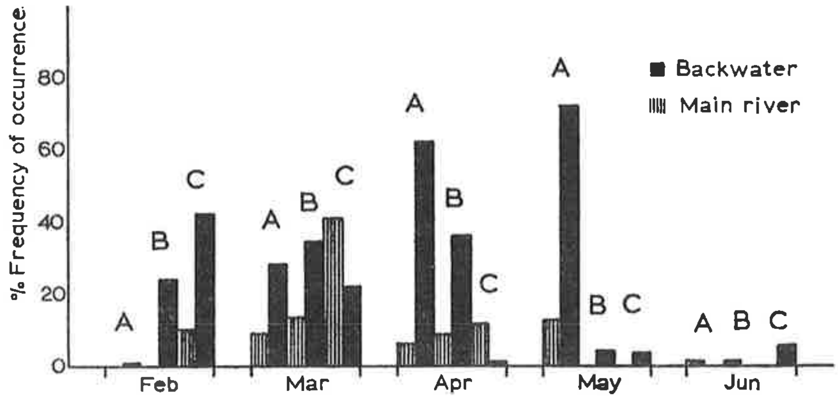


Fig. 21. Gonad maturation in females from Waikanae River samples. A: Quiescent. B: Developing. C: Maturing. D: Mature.

Fig. 22. Maturation of fish in backwaters at the weir station. A: Mature B: Maturing. C: Developing.



maturity. The early spawners were probably delayed spawners from the previous autumn and the adults of whitebait which migrated too late to mature and spawn in the immediately following autumn, but which had not spawned in the intervening period. Burnet (1965) also suggested that fishes spawning in their second year in fresh water migrate a little earlier.

When the differences in the sex ratios at the estuary and Greenaway Road are taken into account it appears that the "centre" of male maturation is further downstream than that for female maturation.

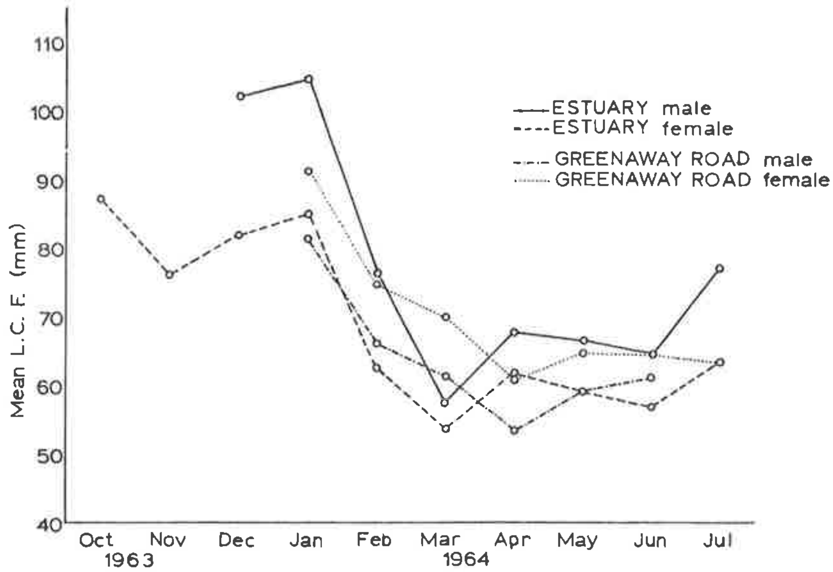
THE EGGS OF *G. MACULATUS*

The unspawned eggs of *G. maculatus* are roughly spherical and about 1 mm in diameter. They contain numerous small, almost colourless oil globules and the chorion appears to have very fine pitting over the whole surface. In mass the eggs are a pale straw colour, but individual eggs have no obvious pigmentation.

The eggs develop in humid air, presumably in the presence of plenty of oxygen. That they are practically colourless and appear to be lacking in carotenoids may be associated with Nikolsky's (1963) suggestion that there is a direct relationship between the amount of respiratory carotenoid pigment and the favourability of the oxygen supply. He pointed out that eggs developing under poor oxygen conditions tend to have more intense colouration because of the presence of these yellow-red carotenoids.

The spawned but unfertilised egg of *G. maculatus* is spherical and slightly sticky and measures between 0.9 and 1.4 mm in diameter. There are numerous oil globules in the yolk mass and the chorion has a finely pitted appearance. The sizes of spawned eggs in turf varied considerably. Egg diameter measurements made from 15 fish between

Fig. 23. Variation in size of fish with mature gonads, October 1963 to July 1964, in Waikanae River samples.



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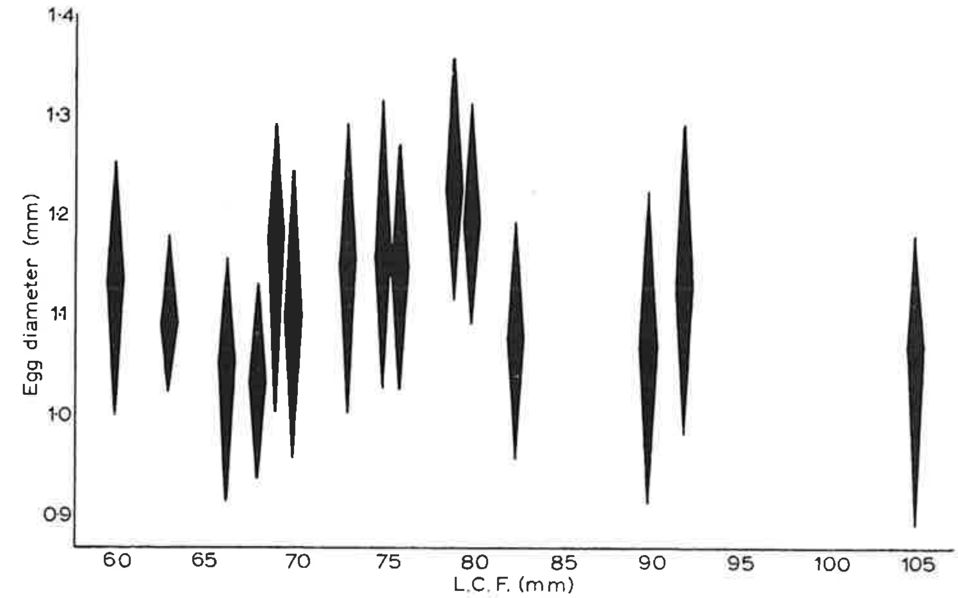


Fig. 24. Relationship between ova size and fish size in mature *G. maculatus* from the Waikanae River.

60 and 105 mm L.C.F. to determine if there was any relationship between egg size and fish size showed that there was none (fig. 24). The ratio of mean egg diameter to L.C.F. similarly showed that there is no connection between these two variables.

After spawning and fertilisation a small perivitelline space forms and the eggs retain their spherical shape. When samples of developing whitebait eggs were sorted from the turf, those eggs in which there was no perivitelline space (that is, unfertilised eggs) were covered in debris from the grasses and soil; small pieces of rotting fibrous matter and soil and sand particles were adhering to them. Developing eggs had no such covering. Whereas the fertilised eggs had lost their stickiness after spawning, the unfertilised ones had apparently retained it and had become covered with rubbish from the substrate. This loss of stickiness may be related in some way to fertilisation and the formation of the perivitelline space. Nikolsky (1963) reported that the eggs of *Osmerus eperlanus* Linnaeus undergo changes in stickiness, so that the early development occurs with the eggs attached to a substrate and the later development with the eggs freely floating. Lagler, Bardach, and Miller (1962) stated that in some fishes "adhesiveness can be due temporarily to the process of water hardening". The apparent loss of stickiness in the eggs of *G. maculatus* may result from a similar cause. Non-adhesive fertilised eggs would tend to drop down among the bases of the stream bank vegetation, where their chances of development in the more humid atmosphere would presumably be greater.

FECUNDITY

The fecundity of 275 *G. maculatus* females measuring between 43 and 135 mm L.C.F was determined. Egg number varied from 175 to 13,500. Although there was a fairly good relationship between egg number and fish size (fig. 25), variation was considerable, especially among the larger fish. Fish from three localities were used for fecundity determinations. One hundred and sixty counts were taken from Waikanae River fish, 44 from Makara Stream fish, and 71 from Ship Creek fish. There were marked differences in the fecundity of fish from the three localities. *Galaxias maculatus* from the Waikanae River had fewer eggs than those from the Makara Stream, which themselves had fewer than those from Ship Creek. The high fecundity of the fish from Ship Creek was noticeable from their deep and laterally distended abdomens.

The differences in fecundity appear to be related to the types of stream from which the fish were taken. The Waikanae River is a fairly swift shingle river with numerous rapids and shallow runs and few deep, quiet pools. There is little suitable habitat for *G. maculatus*. The Makara Stream is smaller with deep, long, quiet pools and runs and plentiful aquatic vegetation; it is subject to fairly severe pollution from farm effluents in several areas, but *G. maculatus* is fairly resistant to pollution and is abundant in the pools and runs of the stream, especially in the more lowland reaches. Ship Creek is a small sand-bedded stream draining large areas of lowland bush swamp. *Galaxias maculatus* appeared to be very abundant in these bush

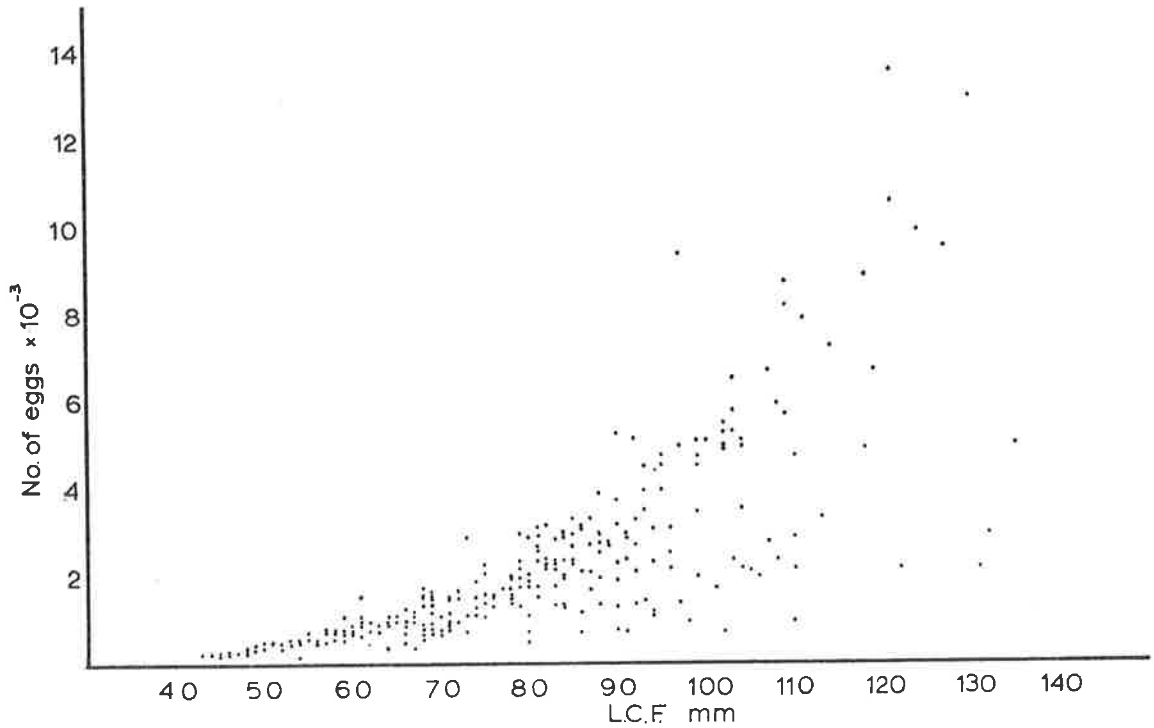


Fig. 25. Fecundity of *G. maculatus*.

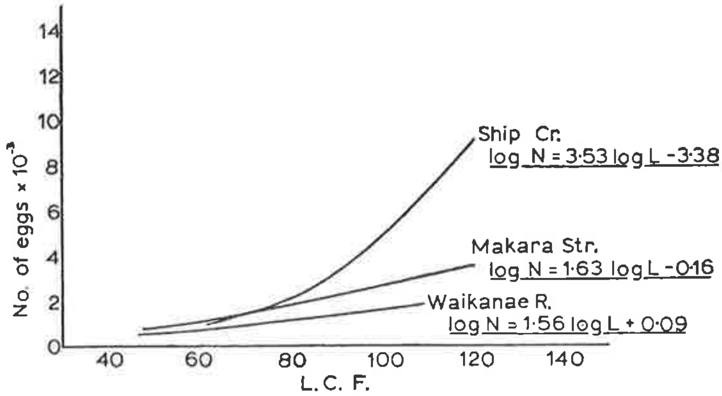
swamps, in which the water was so brown that the fish could not be seen unless they were right at the surface. From the high fecundity and large size of the fish living in them, bush streams such as Ship Creek, draining lowland forests, appear to be ideal habitats for *G. maculatus*. The faster-flowing, less stable gravel rivers like the Waikanae are less productive and appear less suitable. The differences in the fecundity of the fish from the three river systems are compared in regression equations for each (fig. 26); these differences are considerable.

BREEDING SEASON

Hayes's notes (unpublished) recorded *G. maculatus* breeding from October until May and reported ripe fish of both sexes during September. Graham (1956) noted instances of *G. maculatus* breeding during September in the Bay of Plenty. The author has found recently deposited ova as late as June. Thus *G. maculatus* has been recorded breeding from September until June, a breeding period of about 10 months.

Judging from the proportion of maturing fish in the population, the main period of breeding in the Waikanae River was during March, April, and May in 1964, but this was not confirmed from observations of breeding shoals or egg deposits on the river bank. The breeding localities were located in the Waikanae River only in June of that year.

Fig. 26. Variation in fecundity in population samples from Ship Creek, the Makara Stream, and the Waikanae River, with regression equations for the samples from each locality.



Burnet (1965) found that most downstream migrations of *G. maculatus* in the south branch of the Waimakariri River were in February and March and extended into April and May, which indicated that the fish were breeding in the estuary during these months.

BREEDING MIGRATIONS

Although *G. maculatus* may commonly reside in estuarine waters, it is best regarded as a lowland dwelling species. Population densities were lower in the estuaries than in areas further upstream unaffected by tidal changes. Thus for breeding purposes *G. maculatus* migrates downstream into the estuaries. Burnet (1965) recorded the downstream migrations of *G. maculatus* and showed that there is a close relationship between migration and the lunar-tidal cycle. He found that the downstream movement was at either the full moon or the subsequent spring tides. The work of Hayes (see Hefford, 1931a, 1931b, and 1932) has shown that spawning occurs after spring tides.

Tidal and lunar influences are known for a number of fishes, but these are generally marine fishes (for example, *Leuresthes tenuis* (Ayres), the Californian grunion), in which there is a contact between the fishes and the changing tidal movements. Spawning *G. maculatus* live mostly in small creeks and streams, some of which are many miles from any tidal influence. Nevertheless these fish are apparently able to respond to the changes in the lunar and tidal cycles and arrive in the river estuaries at the correct part of the tidal cycle. All the breeding shoals observed by the author were in estuarine waters at about the spring tide period.

The fish certainly migrate downstream during daylight hours, as this was observed by bridge builders on Ship Creek, but there are no records of the breeding migration at night. Fish in the Ship Creek breeding shoal had empty stomachs and intestines with the stomach reduced to a small thick-walled pouch.

SPAWNING HABITAT

Galaxias maculatus spawns in tidal estuaries, either in salty or fresh water, but usually in areas affected by upstream tidal push. Hayes (unpublished notes) recorded spawning grounds about 12 miles up the Waikato River, where the water may be entirely fresh. There is some doubt about the need for tidal effect. Stokell (1949) suggested that *G. maculatus* might spawn in the Selwyn River and contended that the lower reaches of the river were not tidal because the river discharged into Lake Ellesmere. McKenzie (1933) also reported that *G. maculatus* breeds on the banks of Lake Wairarapa at flood periods.

Further evidence that *G. maculatus* does not demand tidal changes to induce spawning is found in the presence of landlocked derivatives of *G. maculatus* in a number of coastal lakes in the North Auckland area. There are thriving populations of these fishes in lakes which are isolated from the sea and not affected by tides. The fish populations must have been derived from typical sea-going *G. maculatus* and yet have survived and bred in the lakes and continue to do so, although isolated from any tidal fluctuations of water level.

Hayes (unpublished notes) described the usual breeding habitat of *G. maculatus* as follows:

> "Spawning beds will be found on the banks of the tidal portion of the river where the ground is covered at high water time of the highest or nearly the highest of the spring tides, and is left uncovered even at high water when the spring tides 'take off'. The places chosen by the parent fish must be accessible and must afford cover for the spawn. The type of bank most usually selected and regularly used by the spawning shoals are the low-lying rush and grass covered portions over which the spring tides creep for a distance of anything up to four to eight yards, exceptionally up to 20 yards. Fairly long, thickly growing grasses and rushes or similar vegetation is usually chosen."

The spawning habitat of *G. maculatus* was observed only twice in the present study, once in the Waikanae River and again in the nearby Waimeha Stream. At both streams *G. maculatus* had bred among the thick pasture grasses and other stream bank vegetation on the edge and top of quite steep stream banks. Main components of the vegetation at the Waikanae River site were fescue (*Festuca* sp.), cocksfoot (*Dactylis* sp.), and small amounts of clover (*Trifolium* sp.). At the Waimeha Stream spawning site eggs were also laid in a parsnip-like weed, *Apium nodiflorum*. McKenzie (1933) found spawning to be most frequent among *Juncus acutifolius*.

The eggs were found to lie deep within the vegetation, between the bases of the leaves and stems and among the fibrous roots of the plants. Greatest numbers of eggs were at the very bases of the clumps of grass, which had to be broken apart piece by piece to expose them. The eggs could not reach these positions by being deposited there by the fish, but they must have been washed down by the water as the tide fell. This suggests that eggs may not retain their stickiness for long after spawning, and the eggs in the turf clumps examined did not adhere to the vegetation, but were lying freely among the stems and leaves of the plants.

Hayes (see Hefford, 1931a) reported that spawning takes place at a high tide after the highest of the spring tides at each lunar period, so that the deposited eggs would not be covered by the water again until the next spring tide period. Observations in the Waikanae River and Waimeha Stream showed that not all the eggs are placed above, or remain above, normal high water levels. Some eggs were found on the banks of the Waimeha Stream in a position in which they were covered and uncovered repeatedly during the daily changes in the tide for much of the lunar cycle.

Turf Fauna

By far the most abundant macro-organism in the turf with the eggs was the aquatic gastropod *Potamopyrgus*. Millipedes (Diplopoda), terrestrial Amphipoda, small earthworms (Oligochaeta), a few caddis pupae (Trichoptera), beetles (Coleoptera), and spiders (Arachnida) also occurred. These organisms were not observed to prey on the whitebait eggs; nor was there any indication, from ruptured eggs, of predation.

SPAWNING BEHAVIOUR

Hayes (unpublished notes) described his observations of the breeding of *G. maculatus* as follows:

> "Under favourable conditions, the schools of inanga ready to spawn may be seen cruising about near the water's edge at about the time of the high water. As soon as it has reached its highest level but not before, and usually some minutes or possibly as much as an hour after high water, the fish make their way among the herbage, swimming or wriggling in the inch or two of water covering the ground. The eggs are deposited on the ground around the bases of the stems of the grass, and at the same time are fertilised by the milt extruded by the males. Sometimes a slight spattering sound may be heard, caused by the movement of the fish, and if spawning is taking place to any considerable extent, the water which drains off as the tide goes down may be seen to be milky-white from the presence of the milt."

Hayes reported that spawning may continue for about three-quarters of an hour. This milkiness of the water associated with breeding of *G. maculatus* was known to fishermen on the West Coast. Gibson (1903) recorded that *G. maculatus* was known as cowfish, and Phillipps (1924b) has explained that this name is due to the milt from the male at spawning, which makes the water cloudy.

Although breeding was not observed by the writer, the behaviour of shoals of ripe fish was observed in the Makara Stream, Waimeha Stream, and Waikanae River. The three observations were made at about the time of spring tide, usually with the tide rising at the time of observation. In all three streams the shoals were moving quickly and apparently with purpose, their movement being best described as streaming. They kept together much more closely than is usual in feeding shoals of *G. maculatus* moving together in a compact mass. The movements of the fish in the shoals appeared to be highly co-ordinated as they moved upstream and downstream, the fish giving the impression that they were searching along the bank. They "explored" indentations in the bank and places where the rising water covered the bank vegetation.

These shoals may be very large indeed. A very rough estimate of the size of a shoal in Ship Creek was that it was 40 to 50 ft long and 8 to 15 in. wide; the fish, swimming head to tail, were three or four deep in the shoal. These shoals differ markedly in size, structure, and behaviour from the small loose aggregations of fish which typify the feeding shoals.

DEVELOPMENT AND HATCHING

The eggs of *G. maculatus* develop among the vegetation on the banks of the rivers, where they are deposited at the high spring tides. It appears that usually they are not immersed in water between deposition and hatching, although this is not always so.

Hatching is stimulated by immersion in water. Hayes (see Hefford, 1931a) found that hatching may occur within a few minutes of immersion, but trials in the present study showed that only some of the eggs will hatch soon after being covered with water. In one trial eggs began to hatch when immersed and continued to do so for 17 days afterward, and some eggs hatched on all but three of these days. This indicates that in natural river bank conditions the eggs may not hatch at the first spring tide which re-covers them. A turf sample from the Waimeha Stream showed this to be so. The eggs in this turf belonged to two different spawnings; some of the eggs were just beginning to develop, with the primitive streak just forming, but others were fully developed and began to hatch when placed in water. The fully developed eggs made up 42 percent of the 509 eggs removed from this piece of turf. The tide must have covered the older group of eggs when the younger ones were spawned among them, and yet the older ones did not hatch. As Hayes found, *G. maculatus* eggs will hatch in fresh or salt water or any mixture of the two.

The eggs of *G. maculatus* have considerable ability to survive without immersion in water. Eggs presumed to have been spawned on the banks of the Waimeha Stream about 11 or 12 June were kept in the original turf in a plastic bag until 10 August, when they were placed in salt water. Nine eggs had hatched within 40 minutes, and hatching of other eggs continued for three days, when 35 had hatched and the remaining 23 were dead. The larvae which hatched were extremely lively and swam actively.

Thus *G. maculatus* eggs may be spawned at one spring tide and the larvae hatch on the next or successive spring tides. Under unusual conditions eggs can apparently survive for at least two months and still hatch.

At hatching, the larvae measure between 6.0 and 8.1 mm (mean from 75 measurements, 7.1 mm). The mouth is then well developed and the jaws are moving, the pectoral fins are present, and the median fin-fold encompasses the body from the yolk sac ventrally, around the caudal region, and for about two-thirds the distance along the dorsum of the trunk toward the head. The fin-fold is not interrupted for the vent, which opens latero-ventrally on the left side. The alimentary canal is a long straight tube, extending well back along the ventral trunk.

The size of the yolk sac at hatching varies considerably. In some larvae the yolk sac is very prominent and almost as deep as the trunk, but in others it has almost disappeared. These variations may be correlated with development time. Melanophores occur along the ventral surface of the yolk sac and alimentary canal, those below the canal having spider-like proliferations around the canal. Melanophores also occur along the ventral and dorsal borders of the caudal peduncle, and some larvae have xanthophores along the dorsal trunk. If not present at hatching, they soon develop.

Attempts were made to feed the larvae with infusoria, with negative result. After about two weeks without food the larvae readily took newly hatched nauplii of the brine shrimp, *Artemia salina,* on which they were reared from late June to early October. After about three and a half months the survivors had grown to about 15 mm (fig. 27). Their growth rate appears to have been much slower than presumed natural growth rates in the sea, where they are thought to reach about 50 mm in six months, but a two-week starvation period after hatching must be taken into account. Eventually all the larvae succumbed to the effects of pollution in the tanks resulting from the use of old brine shrimp cultures in which heavy mortality was occurring. There is, however, considerable promise in the use of brine shrimps for rearing whitebait larvae if the water

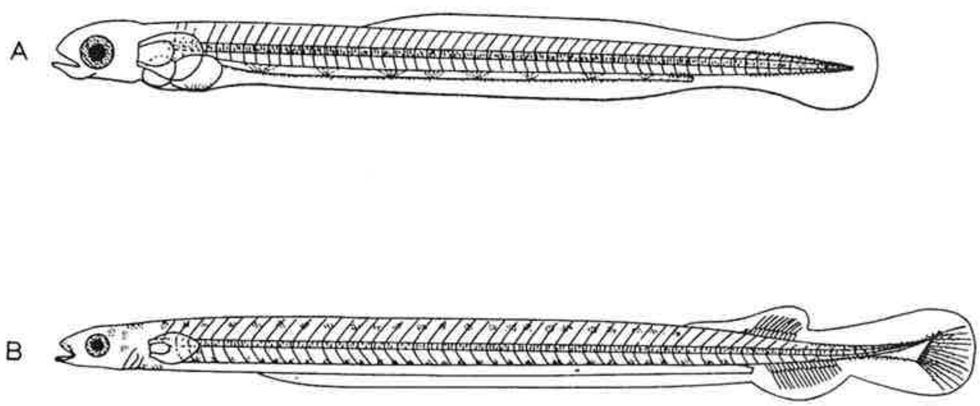


Fig. 27. Whitebait larvae reared artificially from naturally fertilised river bank ova. A: At hatching, 7 mm total length. B: At 109 days, 15 mm total length.

can be kept pure. Transferring the larvae periodically to fresh tanks of sea water would eliminate this trouble.

The fin-fold of the tank-reared larva 15 mm long had retreated both dorsally and ventrally and the rudiments of the unpaired fins were evident. The yolk sac had disappeared and there was further development of pigmentation.

On hatching on the river bank the larvae must be washed out to sea with the ebbing tide. From the free-swimming behaviour of the larvae in small tanks it appears that they are probably pelagic. They were not observed to form true shoals or even aggregations. Their readiness to eat brine shrimps indicates that they are predatory.

FATE OF THE SPENT FISH

The fate of the spent fish has not been determined directly. Clarke (1899) reported that *G. maculatus* "periodically descends to the sea in January, February, and March, where it spawns, returning in March, April, and May". From the examination of many thousands of *G. maculatus* only a little evidence was obtained of breeding survival. Only five females were found in which the presence of ripe, unspawned eggs and recovering ovaries indicated that they had bred and survived. These fish generally showed external characters similar to those of unrecovered, spent trout; they were long and shallow bodied with a prominent head and thin caudal peduncle and were in generally poor, emaciated condition. Such fish usually had a few ripe eggs clustered around the vent or extending along the latero-ventral margins of the recovering ovary, with a further series of eggs beginning to develop more anteriorly along the medio-dorsal edge of the ovary (fig. 28). The numbers of unspawned eggs varied from 19 to 340 and the state of rejuvenation of the ovary was from early stages to fully mature. Other fish with similar external characteristics were examined and in none of them was there firm evidence of breeding survival; nearly all were females.

No upstream migration of adult *G. maculatus* from the sea as Clarke (1899) described has been observed by the writer, and later workers have given no support for Clarke's comments. There was no evidence from numbers and length-frequencies in the Waikanae River samples to suggest that adults had migrated into the river in significant numbers at any time. It is concluded from present evidence that *G. maculatus* does not usually survive breeding, although a few fish may do so.

DISCUSSION

Some aspects of the spawning of *G. maculatus* appear to be similar to spawning of the Pacific surf smelt *Hypomesus pretiosus* (Girard) and the grunion *Leuresthes tenuis*. Both these fishes are marine, but, like *G. maculatus,* they have tide-controlled spawning habits and deposit their eggs above mean high-water mark. The spawning cycle of *L. tenuis* is similar to that of *G. maculatus,* as it is correlated with the lunar cycle, and the fish spawn just after the highest of the spring tides, mostly on the full moon (Clark, 1925). *Hypomesus pretiosus* has less specifically controlled spawning, which takes place when flood tides are above a certain level (Loosanoff, 1937). These two Californian fishes differ from *G. maculatus* by laying their eggs in the sand surfaces of beaches devoid of vegetation. However, it was found that *H. pretiosus* chose beach areas shaded from the sunshine by trees growing above the beach. The

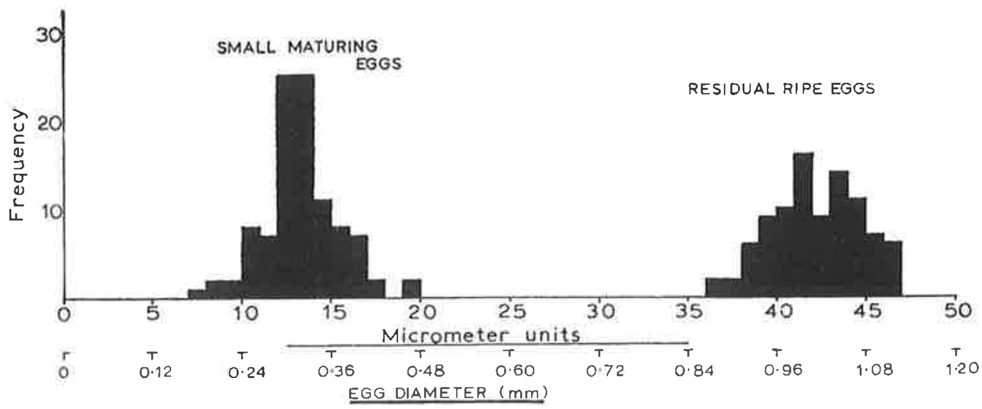


Fig. 28. Size distribution of eggs in a female with residual ripe eggs; measurement of 75 ripe eggs and 100 small eggs from a female 92 mm L.C.F.

eggs of *H. pretiosus,* like those of *G. maculatus,* hatch only when they are covered with water, which generally happens at the spring tides after spawning. The surf stirs up the beach sand and releases the fully developed eggs, which then hatch. Grunion eggs hatch similarly.

The failure of spawning salmonoid fishes to feed is well known; for example, Loosanoff (1937) found that *H. pretiosus* did not feed "much" while spawning, and Blackburn (1950) found that only 8.4 percent of 1,200 *Lovettia seali* examined during the spawning run had been feeding. In this respect *G. maculatus* is typical of the group.

Differences in fecundity, such as were observed in three populations of *G. maculatus,* are related by Nikolsky (1963) to differences in the food availability. He suggested that with other factors constant, reduced population will lead to increased food supplies and as a result higher fecundity. In the earlier comparisons here of the fecundity of the three populations, the complicating factor of altered river conditions must also be taken into account, although one of the more significant effects of the altered river may be changes in food availability. Food does not have to become limiting to reduce the fish's viability, but reduction in food supply may have considerable effect simply by increasing the effort necessary to obtain food.

The failure of spent fish to rejuvenate is not uncommon in salmonoid fishes. The Tasmanian whitebait *Lovettia seali* has an annual life cycle in which only very few fish live for more than one year. Blackburn (1950) did not indicate whether two-year fish were breeding survivors or delayed breeders. The Japanese salmonoid *Plecoglossus altivelis* Temminck and Schlegel also has an annual life cycle, with most adults dying after breeding, and *Salangichthys microdon* Bleeker (f. Salangidae, Japan) also has a similar life history pattern (Okada, 1960). The better known life cycles of the Pacific salmons (*Onchorhynchus*), although including longer maturing life, end in almost total loss of the adult population after spawning. *Hypomesus pretiosus* is an osmerid in which the life cycle is annual and leads to high adult mortality (Loosanoff, 1937). As in *G. maculatus,* there are a few two-year-old maiden spawners.

Although many of the characteristics of the breeding cycle of *G. maculatus* are distinctive, others have marked salmonoid similarities and can be seen in members of the Salmonidae, Osmeridae, or others of the smaller salmonoid families.

PREDATION

Several authors have referred to the importance of *G. maculatus* as a trout food. Hope (1928) expressed the opinion that whitebait formed the staple diet of trout for most of the year and he attributed a decline in the trout fishery in Canterbury to a decline in the whitebait. Phillips (1929) considered that whitebait and elvers should be allowed unobstructed entry into the rivers to provide food for the trout recovering from spawning and suggested that a restriction on the period of whitebait fishing should be imposed with this in mind. Spackman (1892) also attributed the rapid expansion of the trout stocks in New Zealand to the abundance of whitebait and smelts (*Retropinna* spp.) in New Zealand waters. None of these authors presented data to show that whitebait are important as trout food. Arthur (1884) found whitebait in the stomachs of trout from a size of ½ lb upward, but did not indicate their abundance. Stokell (1928) recorded only one adult whitebait from the stomachs of 69 trout from Canterbury, and Allen (1951) found that none of 91 trout two years of age or older that were examined contained *G. maculatus*.

Williams (1945) listed the stomach contents of 34 trout caught in Otago. These were mostly small trout, less than 2 lb, but Williams found 133 inanga in 14 of 34 stomach analyses listed. Two fish (weighing 2 lb 14 oz and 1 lb 10 oz respectively) contained 20 whitebait each, another (weighing 1 lb 8 oz) contained 18 whitebait, and a fourth trout (of 1 lb 2 oz) had 16 whitebait.

Butcher (1945) reported that rainbow trout (*Salmo gairdneri*) take *G. maculatus* as food in Lake Bullen Merri, Victoria, Australia, and that *G. maculatus* also occurred in the food of the English perch, *Perca fluviatilis*.

Eels (*Anguilla australis schmidti* and *A. dieffenbachi*) were recorded by Cairns (1942) as preying on *G. maculatus*. He found that inanga were poorly represented in the food of eels up to 40 cm long living in gravel streams, but were important to eels of this size living in lake areas. Inanga also made up part of the food of larger eels, which ate trout as well as "*Galaxias* (adult whitebait), *Gobiomorphus* (bully), *Retropinna* (smelt), carp, eels, and lamprey". The diet of the larger eels was found to be similar in the upstream and tidal waters.

Whitebait fishermen have suggested (pers. comm.) that large trout and eels lurk in the tidal areas of rivers during the spring migration of whitebait and eat large quantities of them. Fishermen on the Grey River considered that during the autumn spawning season of the adult whitebait the white-faced heron (*Notophoyx* sp.) preyed heavily on the inanga as they came over the tidal flats to spawn.

Fordham (1964) examined the food of the black-backed gull, *Larus dominicanus*. Although freshwater and estuarine fishes, for example, *Anguilla* spp., *Aldrichetta forsteri*, and *Tripterygion* sp., were found in the food of the gull, *G. maculatus* was not recorded.

Falla and Stokell (1945) investigated the food of the black shag, *Phalacrocorax carbo*, but although birds were obtained from coastal lakes and rivers, whitebait were not recorded in their food. Williams (1945) examined the stomachs of 2,883 shags over 23 years and although he found trout, kokopu, bullies, eels, lamprey, flounders, mullet, and other fishes, he recorded no inanga in the shags.

Manikiam (1963) examined the stomachs of about 200 yellow-eyed mullet (*Aldrichetta forsteri*), but found no evidence that they are fish predators, although this species has been regarded at times as a serious whitebait predator. *Galaxias maculatus* was not found in the food of 615 *Gobiomorphus huttoni* examined, most of which came from the Makara Stream and Waikanae River (McDowall, 1965a).

In the present study the stomach contents of 30 *Salmo trutta*, 33 *Anguilla* spp., and 34 *Gobiomorphus basalis* were analysed. Most of the *S. trutta* and *Anguilla* were caught in the Waikanae River and Makara Stream when the *Galaxias maculatus* samples were being collected. Some of the *Gobiomorphus basalis* were also collected in this way; further trout were collected from south Westland lakes and rivers and most of the *Gobiomorphus basalis* came from the Awarua River, south Westland.

Sixteen *Galaxias maculatus*, mostly recently run whitebait, were found in the stomachs of 10 of 30 *S. trutta* examined. The maximum number of whitebait taken from any fish was four and there was only one in most trout. A single

Gobiomorphus basalis occurred in one trout stomach and two small *Cheimarrichthys fosteri* in another. Allen (1951) found only five trout containing fish and these were all about two years old or older and at least 20 cm long. Seven of the 10 trout in the present study which contained whitebait were less than 20 cm, one being only 13 cm. The trout containing the two *C. fosteri* was 17 cm long. Other components of the food of the trout examined were: Insecta—Trichoptera (Sericostomatidae, Leptoceridae, Rhyacophilidae), Ephemeroptera (*Deleatidium-Zephlebia, Ameletus*). Diptera (Chironomidae), Coleoptera (Elmidae*, terrestrial beetles), Hemiptera (*Scolypopa australis*); Crustacea—Decapoda (*Paratya curvirostris*); Mollusca—Gastropoda (*Potamopyrgus*).

Only one of the 33 eels examined had eaten *G. maculatus;* this eel was 40.5 cm long and contained a single specimen. Other fish taken by the eels examined included trout (*S. trutta,* one example) and eels (*Anguilla* spp., two examples); two other eels contained a total of three unidentifiable fish. Invertebrates in eel stomachs were: Insecta—mostly Trichoptera (Sericostomatidae, Rhyacophilidae), with sundry other forms (terrestrial Coleoptera, Diptera, Orthoptera, Dermaptera); Crustacea—Decapoda (*Paranephrops planifrons*); Mollusca—Gastropoda (*Potamopyrgus*).

Fourteen of the 34 *Gobiomorphus basalis* whose stomach contents were examined contained a total of 28 *Galaxias maculatus.* These *Gobiomorphus basalis* were mostly large, the ones containing whitebait averaging 100 mm in length, and the smallest bully containing whitebait was 76 mm long. All the bullies which had eaten whitebait were from the Awarua River, south Westland, and were caught when chasing migrating whitebait upstream. Other components of the food of *Gobiomorphus basalis* were: Insecta—Trichoptera (Sericostomatidae, Rhyacophilidae), Ephemeroptera (*Deleatidium-Zephlebia*), Diptera (Chironomidae), Coleoptera (Elmidae); Crustacea—Decapoda (Amphipoda, *Paratya curvirostris*); Mollusca—Gastropoda (*Potamopyrgus*). One large *Gobiomorphus basalis* had eaten a smaller one.

Apart from *S. trutta, Anguilla,* and larger *G. basalis,* most of the habitat associates of *Galaxias maculatus* are too small to prey on it and can be disregarded as significant predators on the species. The role of these large species is not fully clear, but it appears to be less important than the comments of Hope (1928) and Phillips (1929) would suggest.

* Mr J. G. Penniket, Canterbury Museum, Christchurch, comments: Elmidae are the aquatic beetles commonly referred to in New Zealand as parnids. Most of them are certainly Elmidae; a few, if not Elmidae, are certainly closely related to them.

FOOD STUDIES

INTRODUCTION

Little attention has been paid in the past to the food of *G. maculatus*. Phillipps (1924b and 1926), Stokell (1955), and Hayes (see Hefford, 1932) all commented briefly on the food of *G. maculatus*. Phillipps found *Potamopyrgus* (Mollusca), copepods and other crustaceans, algae, minute flies, and beetles in *G. maculatus*, and Stokell reported that the food of the migratory juveniles consisted of insect larvae, small crustaceans, water snails, and the young of fishes. Hayes's examination showed that the food of *G. maculatus* consisted primarily of ostracods, cladocerans, and copepods. In Australia Butcher (1945) found Coleoptera, Hemiptera, Diptera, Mollusca, and Crustacea to be the main foods, with Diptera making up nearly a half of the total food and Mollusca second in importance (16 percent).

The purposes of the present food study are varied. Questions on which it was envisaged that information would be obtained included how differences in habitat affect food composition and feeding intensity and how stream modification by man's activities may have affected feeding. Changes in food and feeding intensity with growth, seasonal changes, and migratory and breeding patterns were also examined. A further objective was to gain information on the niche occupied by *G. maculatus*. Such information contributes to an effort to determine the feeding interactions of the native freshwater fish fauna as a whole and its relationship to the introduced Salmonidae. Finally the food study formed a basis for parasitology and parasite ecology as far as these are affected by, and related to, feeding.

In the present study the stomachs of 1,916 *G. maculatus* were examined. Most of these (1,796) came from the Waikanae River, but specimens from the Waimeha Stream (57), Makara Stream (30), and other localities (33) were also examined.

The food study in the Waikanae River population was designed to cover the range of sizes captured and the period of capture from each of the three stations. An effort was made to examine five fish of each sex from each station each month over a series of six size categories. This would have resulted in the examination of the stomachs of 2,160 *G. maculatus*. Because there were insufficient fishes in some size categories, samples taken in corresponding months of 1963 and 1964 had to be bulked, and even so the total number of fishes examined in most months was below the figure set. Nevertheless a fairly good coverage of these categories was obtained.

GENERAL DIET

Galaxias maculatus was found to have carnivorous feeding habits and to eat a wide variety of aquatic and terrestrial organisms. As such it belongs to the euryphagous feeding group of Nikolsky (1963) and is best described as a generalised carnivore. The division of the food into aquatic and terrestrial components is fairly obvious at most points, the only doubtful cases being the very few imagines, of Trichoptera, Plecoptera, and Ephemeroptera, all of which were listed as aquatics, and the more substantial category of adult Diptera, some of which were probably of aquatic derivation (Chironomidae, Simuliidae, and perhaps Culicidae), although others may have been terrestrial. These flies were arbitrarily designated terrestrial. Most of the food types thus distinguished were aquatics, nearly 98 percent of the total food belonging to this grouping, with only 2.2 percent terrestrial. A total of 43,365 food organisms were listed from the 1,796 fish examined from the Waikanae River, an average of about 24 per fish; about 12 percent of the fish (223) had empty stomachs. In addition all of the fresh-run whitebait of *G. maculatus* examined and ripe fish in samples from breeding shoals had empty stomachs.

A division of the food organisms into major categories is given in table 3. Many of the food organisms were identified more precisely than is given in this table, but these identifications are discussed in subsequent sections where appropriate.

Despite great diversity of food types, 81.7 percent of the food consisted of three categories: Chironomidae larvae and pupae 21.6 percent, Copepoda 39.4 percent, and the gastropod mollusc *Potamopyrgus* 20.7 percent. Although these three groups were consistently important in the food analysis, data showed that their proportions varied widely with season, fish size, and fish habitat. The relative abundance of other food types was low, always less than 5 percent of the total food and usually less than 2 percent.

Table 3: Numbers of Food Organisms Taken from the Stomachs of 1,796 *G. maculatus* and their Percentages of the Total

Table 3A: Aquatic Food Types

		No.	Percentage of Total
Ph. Chordata			
Cl. Pisces			
O. Isospondyli, F. Galaxiidae		2	..
O. Percomorphi, F. Eleotridae		4	0.01
Unidentified fish eggs		1,235	2.85
Ph. Arthropoda			
Cl. Insecta			
O. Ephemeroptera,	F. Siphlonuridae	12	0.03
	F. Leptophlebiidae	394	0.91
	Others	4	0.01
O. Plecoptera,	F. Eustheniidae	14	0.03
	F. Gripopterygidae	228	0.53
	Others	2	..
O. Coleoptera,	F. Elmidae	898	2.07
	F. Dytiscidae	3	..
O. Neuroptera,	F. Corydalidae	3	..
O. Diptera,	F. Tipulidae	3	..
	F. Culicidae	2	..
	F. Chironomidae	9,362	21.59
	F. Tabanidae	4	0.01
	F. Simuliidae	5	0.01
O. Trichoptera,	F. Sericostomatidae	1,743	4.02
	F. Rhyacophilidae, F. Leptoceridae, F. Hydropsychidae	403	0.93
	F. Hydroptilidae	328	0.76
	Others	5	0.01
O. Hemiptera,	F. Corixidae	1	..
Cl. Arachnida			
S.O. Hydracarina		44	0.10
Cl. Crustacea			
S. Cl. Branchiopoda			
O. Diplostraca,	S. O. Cladocera	367	0.85
S. Cl. Ostracoda		170	0.39
S. Cl. Copepoda		17,051	39.32
S. Cl. Malacostraca			
O. Peracarida,	S. O. Mysidacea	1	..
	S. O. Isopoda	22	0.05
	S. O. Amphipoda	877	2.02
O. Eucarida,	S. O. Decapoda	7	0.02
Unidentified Crustacea		13	0.03
Ph. Mollusca			
Cl. Gastropoda			
O. Prosobranchiata,	F. Hydrobiidae	8,962	20.67
	F. Thiaridae	1	..
O. Pulmonata,	F. Lymnaeidae	6	0.02
	F. Ancylidae	1	..
Cl. Lamellibranchiata			
O. Eulamellibranchiata,	F. Sphaeriidae	23	0.05
Ph. Annelida			
Cl. Polychaeta		1	..
Cl. Oligochaeta		195	0.45
Total		42,396	97.74

Table 3B: Terrestrial Foods

		No.	Percentage of Total
Ph. Arthropoda			
Cl. Insecta			
O. Collembola		64	0.15
O. Orthoptera		3	0.01
O. Hemiptera		252	0.58
O. Coleoptera,	F. Melolonthidae	38	0.09
	Others	287	0.66
O. Dermaptera		1	..
O. Hymenoptera		54	0.13
O. Diptera		157	0.36
O. Lepidoptera		8	0.02
Cl. Myriapoda			
S. Cl. Chilopoda		1	..
S. Cl. Diplopoda		42	0.10
Cl. Arachnida			
O. Araneida		43	0.10
Cl. Crustacea			
S. Cl. Malacostraca			
O. Peracarida,	S. O. Isopoda	1	..
	S. O. Amphipoda	1	..
Ph. Mollusca			
Cl. Gastropoda			
O. Pulmonata		1	..
Ph. Annelida			
Cl. Oligochaeta		16	0.04
Total		969	2.24
		42,396	97.74
Total		43,365	99.98

Although most of the food items of *G. maculatus* were small, and some, for example, the Copepoda, were minute, the fish ate some food organisms of considerable bulk. Quite frequently a single food organism completely filled the distended stomach. The most common example was the terrestrial hemipteran *Scolypopa australis,* which was taken by fish of all sizes despite its bulk. Fish, lepidopteran caterpillars, some of the beetles and earthworms, and the aquatic crustacean *Paratya curvirostris* were other food items of considerable size eaten.

The initial analysis of the food types has been confined to the Waikanae River population, and the food of fish from other localities is discussed only in comparison with that of Waikanae River fish.

Aquatic Food Organisms

Few fish were found in *G. maculatus* stomachs. Four small eleotrids, probably either *Gobiomorphus huttoni* or *G. basalis,* were in two *Galaxias maculatus,* and two migratory juvenile *G. maculatus* occurred in one large adult. In addition many fish eggs were eaten by *G. maculatus,* mostly by fish caught from the estuary, although a few were in fish from the Greenaway Road and weir stations. Some of the eggs were identifiable as those of *G. maculatus* or *Gobiomorphus* spp.

Aquatic insects in the stomachs examined were diverse. Most of the Ephemeroptera (total 394) belonged to the *Deleatidium-Zephlebia* group, and although they constituted only 0.9 percent of the total food, they were in 9.7 percent of the fish examined. A few specimens of the genera *Ameletus* and *Coloburiscus* and four unidentified ephemeropteran imagines were found.

Like the Ephemeroptera, most of the Plecoptera belonged to a single group. Apart from two *Stenoperla* (f. Eustheniidae) and two unidentified plecopteran imagines, all the Plecoptera belonged to the family Gripopterygidae. These made up 0.5 percent of the total diet and were in 5.2 percent of the fish examined.

All the aquatic Coleoptera apart from three Dytiscidae were larvae and beetles of the family Elmidae. These were not further identified. Elmidae made up 2.1 percent of the food, there being 670 larvae and 228 beetles in 6.0 percent and 2.1 percent respectively of the fish examined.

Neuroptera were rare, there being only one larva of *Archichauliodes* in each of three fish.

Diptera made up a large proportion of the diet of *G. maculatus*. Culicidae (two larvae) and Simuliidae (five) occurred, although they were not important foods, but Chironomidae were very abundant, contributing 21.6 percent of the food and occurring in 36.4 percent of the fish examined. Although there were fewer Chironomidae in the food of *G. maculatus* than Copepoda and slightly more than *Potamopyrgus,* they were the most widely occurring food type.

A number of groups of caddis larvae (Trichoptera) were important in the food of *G. maculatus*. These included Rhyacophilidae (*Hydrobiosis*), Leptoceridae (*Triplectides*), Hydroptilidae (*Oxyethira*), and Sericostomatidae (*Olinga, Pycnocentria, Pycnocentrodes,* and *Helicopsyche*). Identification of some of the caddises was difficult, particularly the caseless forms and cased forms that had become removed from their cases, since the case is usually the most easily identified structure. The three families Hydropsychidae (caseless), Rhyacophilidae (caseless), and Leptoceridae (cased, but cases not found in food of *G. maculatus*) are grouped in table 3A because of the difficulty of separating the larvae in the absence of adequate larval descriptions. A few *Pycnocentria* and *Pycnocentrodes* removed from their cases are likely to have been included in this category. *Pycnocentria* and *Pycnocentrodes* are small to medium-sized sandy-cased caddises and were the most abundant of the Trichoptera, 1,607 examples contributing 3.7 percent of the food and occurring in 16.4 percent of the fish examined. The other common caddis was the tiny *Oxyethira,* which made up only 0.8 percent of the food and was found in 4.6 percent of the fish. *Olinga,* a large horny-cased form, was present in a few fish (56 examples) and 80 *Helicopsyche,* a small, spiral-cased form, were listed.

Hemiptera were represented by only one aquatic form, a corixid.

An interesting, although very minor, component of the food of *G. maculatus* was a number of water mites (Hydracarina). Forty-four of these minute arachnids were found in whitebait stomachs.

Several groups of crustaceans contributed to the diet of *G. maculatus.* Small Cladocera occurred in 83 fish (4.6 percent) and made up 0.9 percent of the food; Ostracoda were another minor component, the 170 examples counted in Waikanae River fish contributing 0.4 percent of the food.

Minute Copepoda were the most abundant food of *G. maculatus*; 17,051 examples (39.4 percent of the food) occurred in 29.1 percent of the fish. Because of their minute size, soft texture, and therefore rapid digestion and also because of the tedium of counting such large numbers of small animals, these figures probably underestimate the proportion of Copepoda in the food.

One mysid was found in the food of *G. maculatus.* This was probably an estuarine form which is carried into the lower reaches of some rivers with rising tides (McDowall, 1965b). Aquatic Isopoda were not common, there being only 22 specimens.

Amphipoda were one of the more important subsidiary food types, and the 877 examples were 2.12 percent of the food and were present in 7.7 percent of the fish. Decapoda taken by *G. maculatus* included one *Paranephrops planifrons,* identified solely by the presence of a pair of chelae (which suggested that the animal itself probably escaped) and six *Paratya curvirostris.*

The third most abundant food was the common, small freshwater and estuarine mollusc *Potamopyrgus.* There were 8,962 of these (20.7 percent of the food) and they were present in 30.3 percent of the fish. Other Mollusca were rare. One specimen of the estuarine gastropod *Melanopsis trifasciatus* and one *Latia neritoides,* several small Lymnaeidae, and 23 of the small bivalve *Pisidium* were present.

Terrestrial Food Types

In addition to the more abundant aquatic invertebrates a diverse assemblage of terrestrial forms was found in the food of *G. maculatus*. These are more interesting in the variation of types than in the size of their contribution to the food of the fish. As indicated in table 3B these included Collembola, grasshoppers and wetas (Orthoptera), an earwig (Dermaptera), ants and wasps of varied types (Hymenoptera), and a moth and several caterpillars (Lepidoptera); spiders (Araneida) were quite common, and a few terrestrial crustaceans (Amphipoda and Isopoda), a small slug (Gastropoda), one centipede (Chilopoda), and a number of millipedes (Diplopoda) and earthworms (Oligochaeta) were also eaten.

In addition to these less common terrestrial forms three categories were almost as abundant as many of the secondarily important aquatic forms. Dipteran imagines occurred 157 times, these being mostly small gnat-like flies. A total of 325 terrestrial beetles of a great variety were present; 38 of these were cockchafers (f. Melolonthidae), with *Pyronota,* a grass grub, among them.

An unusual and strangely abundant item of the food was a small hemipteran *Scolypopa australis,* an introduced plant bug. The 252 of these contributed 0.6 percent of the food. This is a relatively large food organism for *G. maculatus* and was a more important member of the diet than its frequency suggests. *Scolypopa australis* occurred in 6.3 percent of the fish.

Galaxias maculatus readily eats terrestrial invertebrates falling on to the surface of the water and must take some from the surface and not as they fall through the water, because spiders and other invertebrates of low density would float at the surface; this happening was confirmed by observations of *G. maculatus* rising to the surface to feed on floating objects. Butcher (1945) recorded that the food of *G. maculatus* in Australia consisted of 13.3 percent terrestrial forms, a much greater proportion of the food than in the New Zealand fish examined. The quantity of terrestrial food in the diet of *G. maculatus* is probably limited largely by the availability of that food and perhaps by the abundance of stream invertebrates as alternative food sources. As the Waikanae River is fast flowing and its banks have little vegetative cover overhanging them, surface food for fish in the river is limited. Reduction in bank and catchment cover since the bush was cleared has probably led to stream flooding and aggradation and the present gravel-filled flood bed. The river consequently flows rapidly over the built-up flood bed, and pools are fewer and smaller. Fewer terrestrial invertebrates are therefore likely to fall into the river because of the reduced cover, and those that do are probably less easily seen and taken by *G. maculatus* because of the rapid, turbulent flow. Offsetting this is a substantial stream-bottom invertebrate fauna in the Waikanae River which supports a large and diverse native fish population. *Galaxias maculatus* appears able to utilise this food source, although fish fecundity may decline through deteriorated river conditions.

Butcher (1945) has reported that many of the trout lakes and streams in Australia are in bush country, so that they have marginal flora which harbours large numbers of insects. He suggested that, in particular, Hymenoptera and Coleoptera are important to trout as year-round food sources. Butcher noted that in the three Australian States which have developed trout fisheries terrestrial foods were of considerable importance to the trout. He also quoted several authorities who stated that surface feeding was important to trout in Australia (for example, McKeown, 1934a and 1934b), but that this was not so in New Zealand (Phillips, 1929; Percival, 1932). Allen (1951) studied the trout population of the Horokiwi Stream*, which flows for part of its course through bush, but found that only about 5 percent of the total food was of terrestrial origin and that only 11 percent of the terrestrial food organisms had aquatic stages. This is also largely true for *G. maculatus* in New Zealand. The terrestrial component of the food is small and nearly all the organisms involved are of truly terrestrial origin. Imagines of aquatic invertebrates like Plecoptera, Ephemeroptera, and Trichoptera totalled only 11 specimens; in addition, many of the organisms in the category "adult Diptera" may also have had the same origin—imagines of Chironomidae, Simuliidae, and other partially aquatic families. The differences between the size of the terrestrial components of the food of these fishes in Australia and New Zealand could be due either to greater numbers of terrestrial forms in the Australian rivers compared with those in New Zealand or to the presence of a more prolific stream bottom fauna in New Zealand streams compared with that in Australia, or to both causes.

* Now designated as the Horokiri Stream by the New Zealand Geographic Board.

The prolific bottom faunas characteristic of many New Zealand streams may provide adequate food and lead to a difference in the feeding habits. Such a change has occurred to the brown trout, *S. trutta,* in some parts of New Zealand. Although it is largely a surface feeder in its native Europe, in some New Zealand localities it has become a ground feeder.

By the use of the classification of Nikolsky (1963) the food types can be divided into three categories of abundance, the dividing lines between which are variable.

1. **Basic food:** "that which the fish usually consumes, comprising the main part of the gut contents"; foods high in abundance and in frequency of occurrence; in *G. maculatus* Copepoda, Chironomidae, and *Potamopyrgus.*

2. **Secondary food:** "frequently found in the guts of the fishes but in smaller amount"; foods lower in abundance, but relatively high in frequency of occurrence; in *G. maculatus* foods such as fish eggs, Leptophlebiidae, Gripopterygidae, Elmidae, Sericostomatidae, Hydroptilidae, Cladocera, Amphipoda, terrestrial Hemiptera, and Coleoptera.

3. **Incidental foods:** "only rarely enters the guts of fishes"; low in both abundance and frequency of occurrence; forms such as Siphlonuridae, Eustheniidae, Ostracoda, and terrestrials like Diplopoda and Collembola.

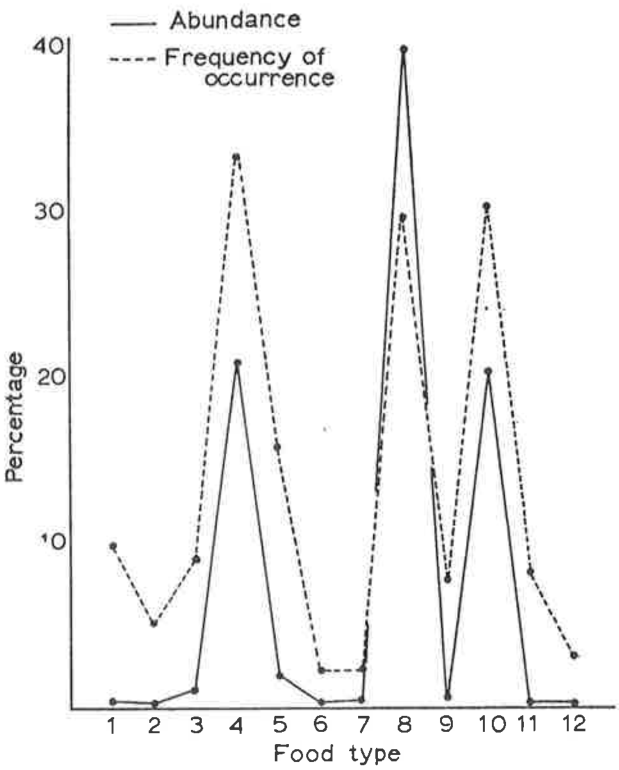


Fig. 29. Comparison of abundance and frequency of occurrence of major food types. 1. *Deleatidium-Zephlebia*; 2. Gripopterygidae; 3. Elmidae; 4. Chironomidae; 5. *Oxyethira*; 6. *Pycnocentria-Pycnocentrodes*; 7. Cladocera; 8. Copepoda; 9. Amphipoda; 10. *Potamopyrgus*; 11. terrestrial Coleoptera; 12. *Scolypopa.*

The dividing line between groups one and two for Waikanae River *G. maculatus* is clearly defined when the total food listing is examined, but between groups two and three the division is more arbitrary. Food types in group two were selected subjectively from a knowledge of their importance in the food, and subsequent examination of their frequencies showed them to be the food types making up more than 0.5 percent of the total food.

Finer analysis of the food on a seasonal and locality basis revealed that what is a basic food in one situation may become a secondary food in another and vice versa. Such apparent inconsistencies do not, however, negate the value of these groupings, but indicate that they should not be applied too rigidly.

Frequency of occurrence data (fig. 29 and table 4), as so often happens, boosted fairly considerably the importance of the widespread but not intensively utilised food types. This was particularly so in the *Pycnocentria-Pycnocentrodes* group and also in Amphipoda, *Deleatidium-Zephlebia,* Elmidae, and terrestrial Coleoptera. These are probably forms which occurred at low densities but in widespread localities and seasons in the habitat of *G. maculatus* or occurred abundantly but at the periphery of the usual habitat occupied by the fish. The significance of Copepoda, in contrast with the other two "basic foods", increased in frequency of occurrence analysis, which shows that it is even more widespread than it is abundant. Chironomidae and *Potamopyrgus* appeared to be less widespread in the samples of *G. maculatus* than they were abundant in the total food of the fish examined.

To what extent the food of *G. maculatus* is an expression of the relative abundances of the invertebrates in the Waikanae River is not clear, as bottom sampling was outside the scope of the present study. Phillips (1931) listed the results of analyses of the bottom fauna of the Waikanae River just above the railway bridge in conditions described as "areas with gravel and boulder bottom, heavily

Table 4: Occurrence of Major Food Types

	Total Abundance	Frequency of Occurrence	Percentage of Frequency	Mean Frequency	Maximum Frequency
Deleatidium-Zephlebia	394	175	9.7	2.3	21
Gripopterygidae	228	93	5.2	2.5	16
Elmid larvae	672	107	7.7	6.3	62
Chironomidae..	9,362	654	36.4	14.3	293
Oxyethira	328	82	4.6	4.0	36
Pycnocentria-Pycnocentrodes	1,607	294	16.4	5.5	73
Cladocera	367	83	4.6	4.4	60
Copepoda	17,051	523	29.1	32.8	1,175
Amphipoda	877	138	7.7	6.4	140
Potamopyrgus	8,962	523	30.3	17.1	544
Terrestrial Coleoptera	287	146	8.6	2.0	15
Scolypopa australis	252	114	6.3	2.2	18

bushed banks, pools". Apart from the lack of bush, this remains a fair description of the locality at present. Phillips found Diptera to be the most frequent invertebrate, with high frequency of Siphlonuridae, Leptophlebiidae, and various Trichoptera, including *Pycnocentria.* A further table listed the organisms from rapids at the same locality and gave much lower frequency for Diptera, but emphasised the other groups mentioned above.

The weir sample of *G. maculatus* was taken from similar stream conditions, just a few hundred yards below this railway bridge, and the food of the fish expressed similar proportions. Diptera were numerous and various caddises and mayfly larvae abundant. The tiny Copepoda, not recorded by Phillips but occurring in the food of *G. maculatus* from the weir, may well have escaped collection by Phillips.

The broad spectrum of food types utilised by *G. maculatus* is shown in fig. 30. Up to 12 different food types occurred in a fish and the proportion of fish with four to six food types was relatively high. Despite diversity of food types per fish, many of the food types were taken in large numbers by individual fish (table 4), particularly the basic food types. In one fish there were 1,175 Copepoda and in another 616; 38 percent of the fish containing Copepoda had 10 or more present. *Potamopyrgus* also reached a high maximum for a relatively bulky food organism, the greatest number being 544, and 38.6 percent of fish had 10 or more present. Chironomidae reached a maximum of 293, with 26.7 percent of fish having 10 or more present. Thus at least a quarter of the fish containing the three basic foods had 10 or more of the same organisms.

Among the secondary food types high maximum frequency was also recorded (for example, Amphipoda 140, *Pycnocentria-Pycnocentrodes* 73, elmid larvae 62, and Cladocera 83), although the maxima were much lower than those of the basic foods. Between about 10 and 17 percent of the fish had 10 or more of these food organisms. Even unlikely foods such as terrestrial beetles (maximum 15), *Scolypopa* (18), and ants (10) occurred in substantial numbers in some fishes. These frequencies suggest that *G. maculatus* is an intensive feeder with diverse food tastes.

Subdivision of the data on the number of food types per fish into the six size categories used showed that there was little increase in the diversity of food types consumed with growth (table 5).

Some very large total numbers of food organisms eaten by fish were recorded. For a predatory, not planktonic, feeder, figures such as 1,381, 547, 745, and 658 organisms per fish are very high. The median, disregarding fish with no food in their

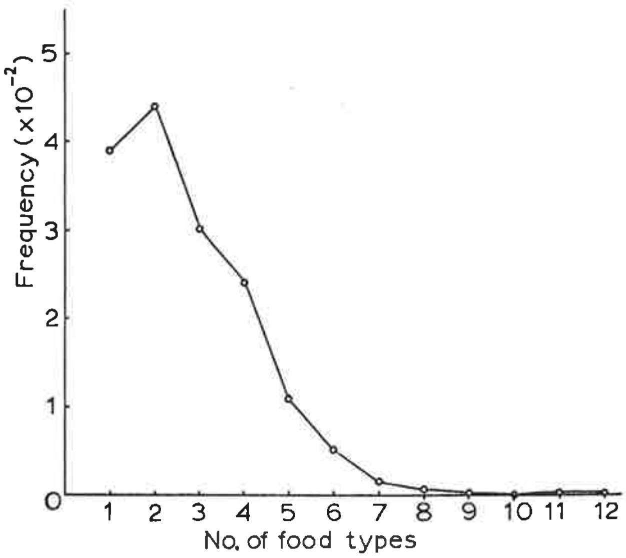


Fig. 30. Frequency distribution of the number of different food types per fish.

Table 5: Number of Organism Types Recorded per Fish in Six Fish-size Categories

No. of Org. Types	40–49 mm		50–59 mm		60–69 mm		70–79 mm		80–89 mm		90 mm—	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
1	75	26.1	88	26.9	74	24.3	58	23.3	59	26.6	38	27.5
2	89	31.0	101	30.9	76	23.9	71	27.3	61	27.4	39	28.3
3	60	20.9	63	20.6	61	20.0	46	17.9	43	19.4	25	18.1
4	44	15.3	48	14.7	50	16.4	45	17.5	31	14.0	13	9.4
5	17	5.9	19	5.8	23	7.5	21	8.4	14	6.3	17	12.3
6	7	2.4	6	1.6	16	5.2	9	3.5	10	4.5	3	3.3
7	1	0.3	2	0.6	4	1.3	7	2.7	2	0.9	2	1.5
8	1	0.3	0	..	1	0.3	3	1.2	2	0.9	0	..
9	0	..	0	..	1	0.3	0	..	0	..	0	..
10	0	..	0	..	0	..	0	..	0	..	0	..
11	0	..	0	..	0	..	0	..	0	..	1	0.7
12	0	..	0	..	0	..	0	..	1	0.7	0	..

stomachs, was 10 organisms per fish and the mean was 24. The total numbers, maximum frequency, mean frequency, and frequency of occurrence for 12 of the more important food types are listed in table 4.

Observations indicated that *G. maculatus* does much of its feeding in a loose shoal. Shoals in small pools in the Makara Stream were composed of fish of all sizes. In times of fright a particular shoal would form a compact, highly co-ordinated group. After a time such a shoal was observed to break up into feeding groups varying in size from two or three fish to a half or two-thirds of the original shoal. These groups moved very quietly about the pool, one or several fish occasionally rising gently to "test" some object at the surface or dropping obliquely to the stream bed to pick up some organism there. The composition of these feeding groups changed constantly, some fish leaving to forage on their own while other solitary fishes joined the group.

Observations of feeding in captivity suggested that feeding responses are largely visual, the fish usually responding to the wriggling or jerking movements of the food organisms introduced to the aquaria.

Galaxias maculatus shows no particular modification for carnivorous feeding. It does not have the highly developed canine teeth of some New Zealand Galaxiidae, for example, *G. brevipinnis.* The well developed teeth on the entopterygoids and tongue of *G. maculatus* may constitute the chief grasping and holding structures. The rather short gill rakers are typical of predatory fishes, and the terminal mouth provides adaptability for feeding on the surface, in mid-water, or at the bottom.

Table 6: Diet of *G. maculatus* at Various Localities

	Waimeha		Makara		Oparara		Others		Total No.
	No.	%	No.	%	No.	%	No.	%	
Deleatidium	5	0.6	5	0.7	..	..	1	0.5	11
Elmidae	5	0.6	5	0.7	..	..	..	..	10
Culicidae	2	0.3	..	..	3	0.3	..	..	5
Chironomidae	203	25.8	90	11.8	65	6.8	147	67.0	505
Simuliidae	5	0.6	1	0.1	..	..	1	0.5	7
Pycnocentria	18	2.3	..	..	..	..	..	..	18
Rhyacophilidae	6	0.8	..	..	..	..	..	..	6
Oxyethira	97	12.4	100	13.1	..	..	1	0.5	198
Hydracarina	..	..	..	..	4	0.4	..	..	4
Cladocera	..	..	2	0.3	863	90.5	..	..	865
Ostracoda	30	3.8	231	30.2	..	..	11	5.0	272
Amphipoda	354	45.0	13	1.7	..	..	4	1.8	371
Copepoda	12	1.5	..	..	22	2.3	6	2.7	40
Paratya	..	..	..	..	..	..	1	0.5	1
Potamopyrgus..	15	1.9	317	41.5	..	..	16	7.3	348
Other gastropods	..	..	1	0.1	..	..	19	8.7	20
Pisidium	1	0.1	..	..	..	..	..	..	1
Oligochaeta..	..	..	1	0.1	..	..	3	1.4	4
Scolypopa	21	2.7	1	0.1	..	..	..	..	22
Other terrestrials	12	1.5	..	..	..	..	10	4.6	22
Total organisms	786		767		957		220		2,730
No. of fish		57		30		6		27	120

FOOD OF *G. MACULATUS* AT DIFFERENT LOCALITIES

Stomach analyses of fish from various river systems indicated that the food of *G. maculatus* varies in its composition from locality to locality. Table 6 lists the results of stomach analyses of fish from the Waimeha and Makara Streams and a swamp at Oparara, on the West Coast, and the bulked results from a variety of widely separated localities. The stomach contents of the fish vary according to changes in the habitat characteristics of the localities from which the samples were obtained.

The Waimeha Stream, apparently deriving its water through the ground from the Waikanae River system, is an extremely stable, gently flowing stream, suffering from few floods and having a deep, sand-bottomed channel with prolific plant growth. It has hardly any rapids and gravel runs in its lower reaches. The food of the fish from this stream is remarkable for its very high content of Amphipoda and, compared with that of the Waikanae River samples, *Oxyethira*. *Scolypopa australis* is again quite prominent. The great abundance of Amphipoda and also probably of *Oxyethira* is almost certainly related to the gently flowing, weedy habitat.

The Makara Stream also differs from the Waikanae River in the habitat conditions it offers to *G. maculatus*, although they are much more diverse than those in the Waikanae. The Makara Stream is much less stable than the Waimeha, flooding quickly and severely at times, and is also more swiftly flowing than the Waimeha throughout most of its length, with boulder rapids and gravelly runs at frequent intervals. In these respects it is similar to the Waikanae River, but it is a much less mature watercourse. Whereas the bed of the Waikanae is largely graded gravels to rounded stones, that of the Makara consists mostly of angular boulders and gravel chips. *Galaxias maculatus* penetrates most of the Makara Stream, although the greatest population densities are in the lowland reaches. The samples for the present investigation came from various small pools in the lower ½ to ¾ mile of the stream. These were mostly relatively deep pools, the beds of which were strewn with large algae-covered boulders. *Potamopyrgus*, which browses on the rocks of the stream in very great numbers, formed a prominent part of the diet. High numbers of Ostracoda may relate to this rocky stream substrate. Chironomidae, as always, were an important, if not dominant, component of the food.

A small sample of six fish taken from a swamp at Oparara, on the West Coast, is listed separately in table 6 only to show how completely the diet of *G. maculatus* may change in different localities. Here, their diet was almost exclusively tiny Cladocera, a presumably abundant and easily available food in this locality. In the fourth grouping of table 6, samples from several localities have been bulked and show a broad spectrum of food types. Chironomidae made up the bulk of the food of these fishes.

Several differences between the Waikanae River results and those for other localities are worth noting. There are almost no Copepoda in these samples, and the rapid-water, rocky-stream invertebrates—Ephemeroptera, Trichoptera (like Rhyacophilidae and Sericostomatidae), and Plecoptera—made up only a very small proportion of the food. The stream conditions in the Waikanae River force the population to inhabit more rapidly flowing, rocky conditions than in streams like the Waimeha and Makara, and as a result the proportion of rocky stream invertebrates in the food of the Waikanae fishes is higher than in those from the Waimeha and Makara.

Taken together, these results show that *G. maculatus* is a predatory carnivore which has varied food habits, feeds successfully on the stream bottom, in mid-water, or at the surface, and is able to ingest organisms varying in size from minute crustaceans to bulky terrestrial or aquatic insects and crustaceans and small fish.

Perhaps the most persistent characteristic of the food is the presence, in considerable proportions, of Chironomidae, probably the most abundant and widespread food utilised by *G. maculatus*.

Variation of diet and adaptability to available food seem characteristics of generalised carnivores like *G. maculatus*. The food of such fishes thus becomes an expression of the foods available in a particular locality.

Hopkins (1965) recorded the food of *Philypnodon breviceps* and *Salmo trutta* from two different, but adjacent, tributary streams and found substantial differences for both species at each locality; for example, Leptophlebiidae (that is, *Deleatidium*) composed 49.5 percent of the diet of *S. trutta* at one station and 8.4 percent at the second and for *P. breviceps* adults it composed

73.0 percent at one station and 46.5 percent at the other. Chironomidae varied similarly; for *S. trutta* it constituted 36.5 percent and 84.5 percent and for *P. breviceps* 5.1 percent and 22.8 percent. Other, less important, food types also varied widely. McDowall (1965a) found large differences in the diet of *Gobiomorphus huttoni* in the Makara Stream. These appeared to be related to differences in the habitats of the various localities which resulted in the presence of different invertebrate faunas. Most of these fish thus appear to prey on whatever invertebrates abound in the area inhabited, and *G. maculatus* is a typical example.

Cannibalism is a minor factor in the feeding relationships of *G. maculatus* with its habitat associates. Only one example was found in which a fish had taken a smaller member of the species. Of the fairly large number of fish eggs eaten some were those of *G. maculatus*. Since much of the breeding habitat of *G. maculatus* is in stream bank vegetation above the normal tidal levels in the stream estuaries, egg predation is unlikely to be a factor of much significance. The hatching larvae are washed from the estuaries into the sea on hatching or soon after and so there is no interaction between the adults of the population and the year's hatch until the young fish migrate back into fresh water at a length of about 50 mm. At this stage they are probably too large and active for the larger adults to prey on them significantly.

VARIATION IN DIET WITH GROWTH

To ascertain whether there was any change in food related to growth, the samples were divided into six arbitrary length groups: up to 49 mm, 50–59 mm, 60–69 mm, 70–79 mm, 80–89 mm, and 90 mm and larger. Fig. 31 illustrates the distribution among the size categories of the 12 major food types. In this figure areas are proportional to abundance of each food type at each size. These data indicate that there are some important changes in diet with growth. In particular there is a rise in several food types—Elmidae (food type No. 3) from 0.6 to 3.5 percent through increasingly large size categories, *Pycnocentria-Pycnocentrodes* (No. 6) 1.4 to 6.0 percent, Amphipoda (No. 9) 0.7 to 8.5 percent, and terrestrial Coleoptera (No. 11) 0.3 to 2.6 percent. Cladocera (No. 7) showed reduction in numbers with growth. *Deleatidium-Zephlebia* (No. 1) and Gripopterygidae (No. 2) both declined considerably through the first five size categories, but re-emerged as important foods in the 90 mm-and-larger group. Although stable from the up-to-49 mm group to the 70–79 mm group, Copepoda (No. 8) declined sharply in the larger sizes.

Maximum feeding intensity was exhibited by fish in the middle sizes. Mean numbers of food organisms per fish in the six size categories were: up to 49 mm, 15.9; 50–59 mm, 18.9; 60–69 mm, 26.4; 70–79 mm, 30.5; 80–89 mm, 25.8; 90 mm and larger, 20.9. These figures show that feeding activity is greatest when the fish approach maturity in their first year; the lower figures in the largest fish are indicative of spent adult survivors and fish with delayed maturity, which appear to be less intensive feeders (fig. 32).

Throughout the size groups, the three basic food types were the main components, although the order of their prominence became reversed—from Copepoda, Chironomidae, and *Potamopyrgus* to *Potamopyrgus*, Chironomidae, and Copepoda.

LOCALITY FREQUENCIES OF MAJOR FOOD TYPES

The food of fish taken from the three Waikanae River sample stations differed in the proportions of some food types. Table 7 and fig. 33 record the number of organisms of each type per fish in the series of samples from each station. Estuarine samples had many more organisms per fish than samples taken further upstream. This difference correlates with the much higher numbers of Copepoda and *Potamopyrgus* in the estuarine fishes. These two food types, which made up 90.3 percent of the food of the fishes in the estuary, became reduced to comparatively negligible proportions in the sample areas further upstream. Amphipoda reached highest numbers in the estuary and showed a corresponding decline in the upstream localities. Terrestrial Coleoptera were also most abundant in the estuary, but this may merely be an expression of the locality in the estuary where the greatest number of *G. maculatus* were collected—a small deep backwater heavily overgrown with river bank grasses and willows, the probable source of the beetles. This difference thus has little ecological significance regarding the habitat changes of *G. maculatus* in the three stations.

At Greenaway Road very marked reduction in Copepoda, *Potamopyrgus*, and Amphipoda is partially compensated for by increased numbers

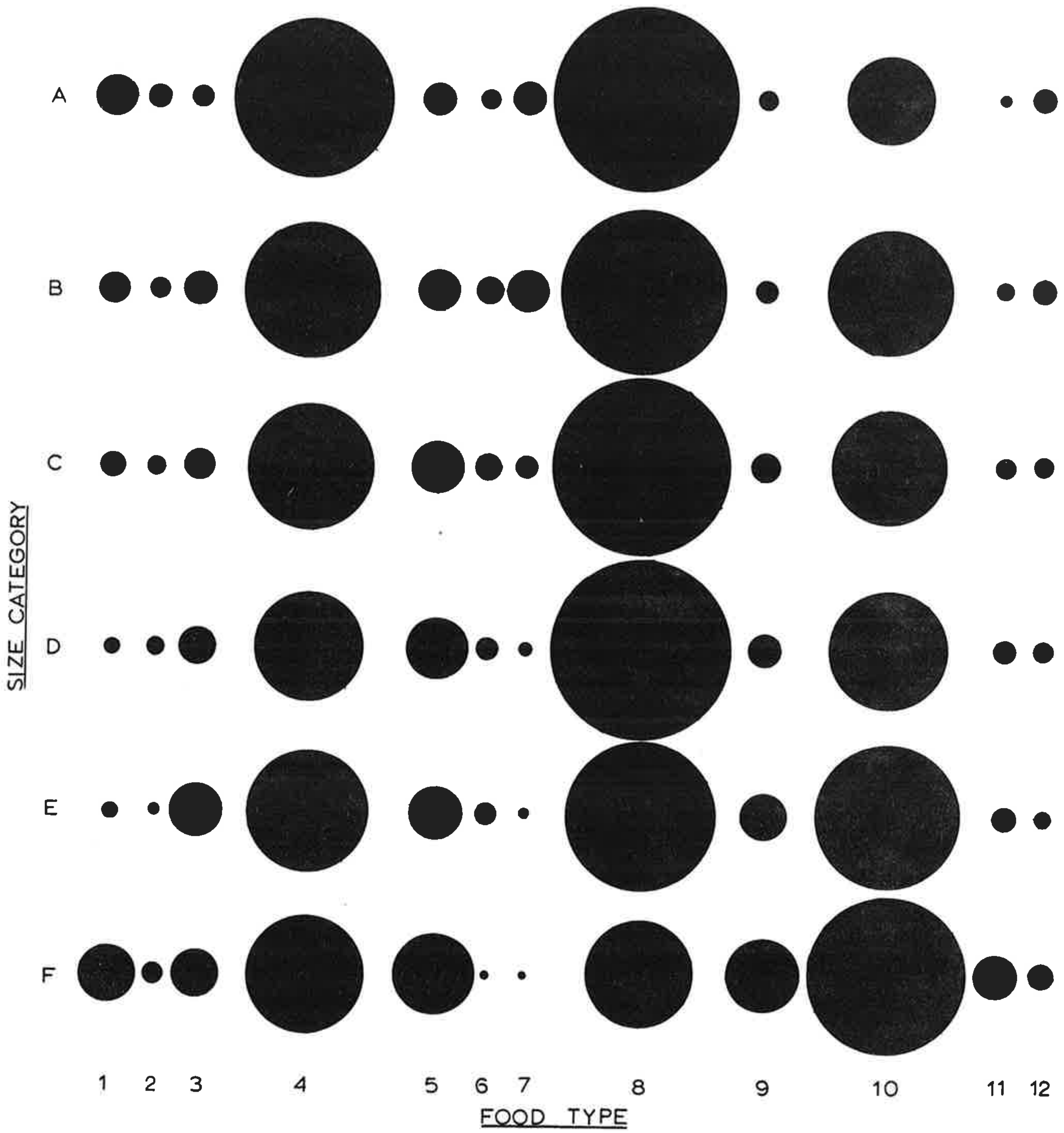


Fig. 31. Changes in diet with growth. Food types: 1. *Deleatidium-Zephlebia*; 2. Gripopterygidae; 3. Elmidae; 4. Chironomidae; 5. *Oxyethira*; 6. *Pycnocentria-Pycnocentrodes*; 7. Cladocera; 8. Copepoda; 9. Amphipoda; 10. *Potamopyrgus;* 11. terrestrial Coleoptera; 12. *Scolypopa.* Size categories: A, up to 49 mm L.C.F.; B, 50–59 mm; C, 60–69 mm; D, 70–79 mm; E, 80–89 mm; F, 90 mm and greater. The area of the circle is proportional to the abundance of each food type in each size category.

of Chironomidae and also a general rise in secondary food types like *Deleatidium-Zephlebia,* Gripopterygidae, Elmidae, Cladocera, and *Scolypopa.* Some of these increases are small, but *Scolypopa* and Cladocera showed increases of similar proportions to the reduction in *Potamopyrgus,* Copepoda, and Amphipoda. Greenaway Road fish had substantially fewer food organisms per fish than those from the estuary.

Reduction in the number of food organisms may be related to the less suitable river conditions at Greenaway Road. Subjective observations suggest that quantitatively this change is less significant than simple numbers indicate, since an increase in the larger animals like *Scolypopa,* Elmidae, and Chironomidae compensates for the lower numbers of the very tiny Copepoda.

Food organism numbers per fish at the weir station were only half those at Greenaway Road. Chironomidae remained the most important food type, although their frequency became much lower. Additional increases in the numbers of *Deleatidium* and Gripopterygidae were substantial, but there was also a reduction in other food types—Elmidae and *Pycnocentria-Pycnocentrodes.*

Changes in the type of food consumed appear to be related to differences in availability of the food types at each locality and also the type of habitat which *G. maculatus* occupied at each. Estuarine food types must be those able to withstand daily changes in salinities brought about by penetration of sea water into the sample area at each high tide. Salinity in the estuarine sampling area became strong enough to prevent satisfactory operation of the electric fishing equipment, which is fairly tolerant of low salinities. Thus Copepoda, *Potamopyrgus,* and Amphipoda appear to be abundant and available to *G. maculatus* in the localities it inhabited in the estuary; conversely, Chironomidae, Elmidae, Cladocera, *Deleatidium-Zephlebia,* and Gripopterygidae are apparently restricted to less saline waters. *Scolypopa* was more plentiful in Greenaway Road fish than in those from other areas, although this is unlikely to relate to estuarine salinities or other stream conditions, but rather to the presence of suitable food plants for the bugs near the river at Greenaway Road.

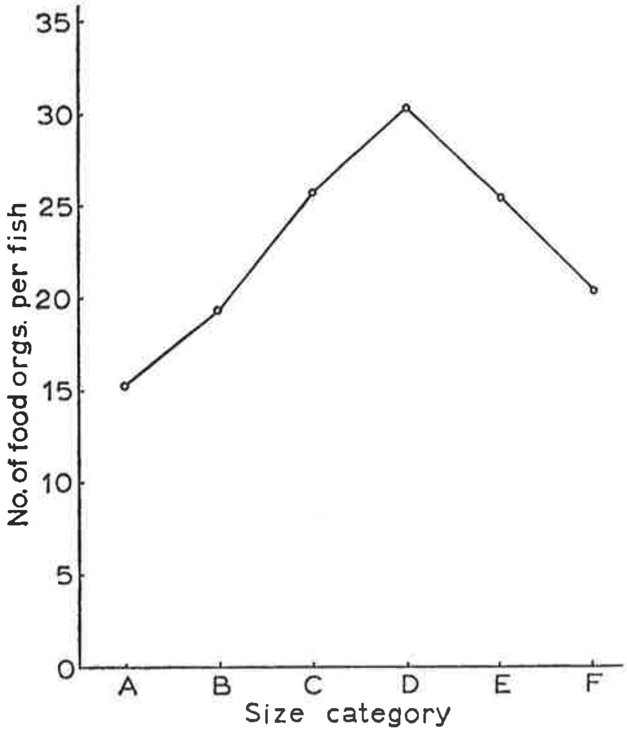


Fig. 32. Changes in feeding intensity with growth. Size categories: A, up to 49 mm L.C.F.; B, 50–59 mm; C, 60–69 mm; D, 70–79 mm; E, 80–89 mm; F, 90 mm and greater.

The increases in *Deleatidium* and Gripopterygidae in the upstream stations indicate the in-

Table 7: Variation in Food at Waikanae River Sample Localities

	Estuary No./fish*	%	Greenaway No./fish	%	Weir No./fish	%
Deleatidium-Zephlebia	0.18	0.42	0.22	1.34	0.27	3.02
Gripopterygidae	0.09	0.21	0.11	0.67	0.21	2.35
Elmidae	0.35	0.82	0.94	6.74	0.20	1.61
Chironomidae	1.72	4.04	9.68	60.04	5.07	56.78
Oxyethira	0.16	0.38	0.18	1.10	0.22	2.46
Pycnocentria-Pycnocentrodes	0.24	0.56	1.77	10.81	0.74	8.29
Cladocera	0.05	0.12	0.26	2.49	0.33	3.70
Copepoda	25.00	59.74	1.32	8.07	1.50	17.70
Amphipoda	1.38	3.24	0.03	0.18	0.07	0.78
Potamopyrgus	13.00	30.55	1.37	8.37	0.25	2.80
Terrestrial Coleoptera	0.27	0.63	0.17	1.04	0.04	0.45
Scolypopa australis	0.07	0.16	0.32	1.96	0.03	0.34
Total	42.51		16.37		8.93	

* Figures give mean number of organisms of each type per fish in each sample area.

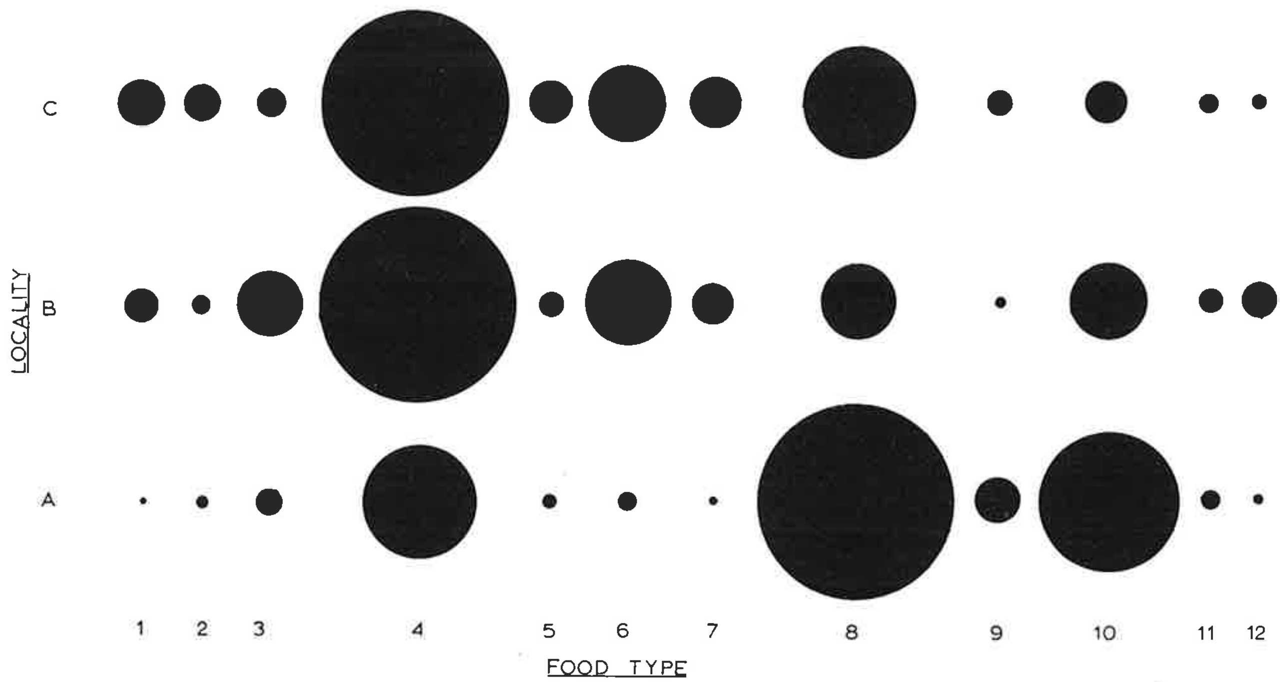


Fig. 33. Changes in food with locality. A: Estuary. B: Greenaway Road. C: Weir. Food types: 1. *Deleatidium-Zephlebia*; 2. Gripopterygidae; 3. Elmidae; 4. Chironomidae; 5. *Oxyethira*; 6. *Pycnocentria-Pycnocentrodes*; 7. Cladocera; 8. Copepoda; 9. Amphipoda; 10. *Potamopyrgus;* 11. terrestrial Coleoptera; 12. *Scolypopa.* The area of the circle is proportional to the abundance of each food type in each station.

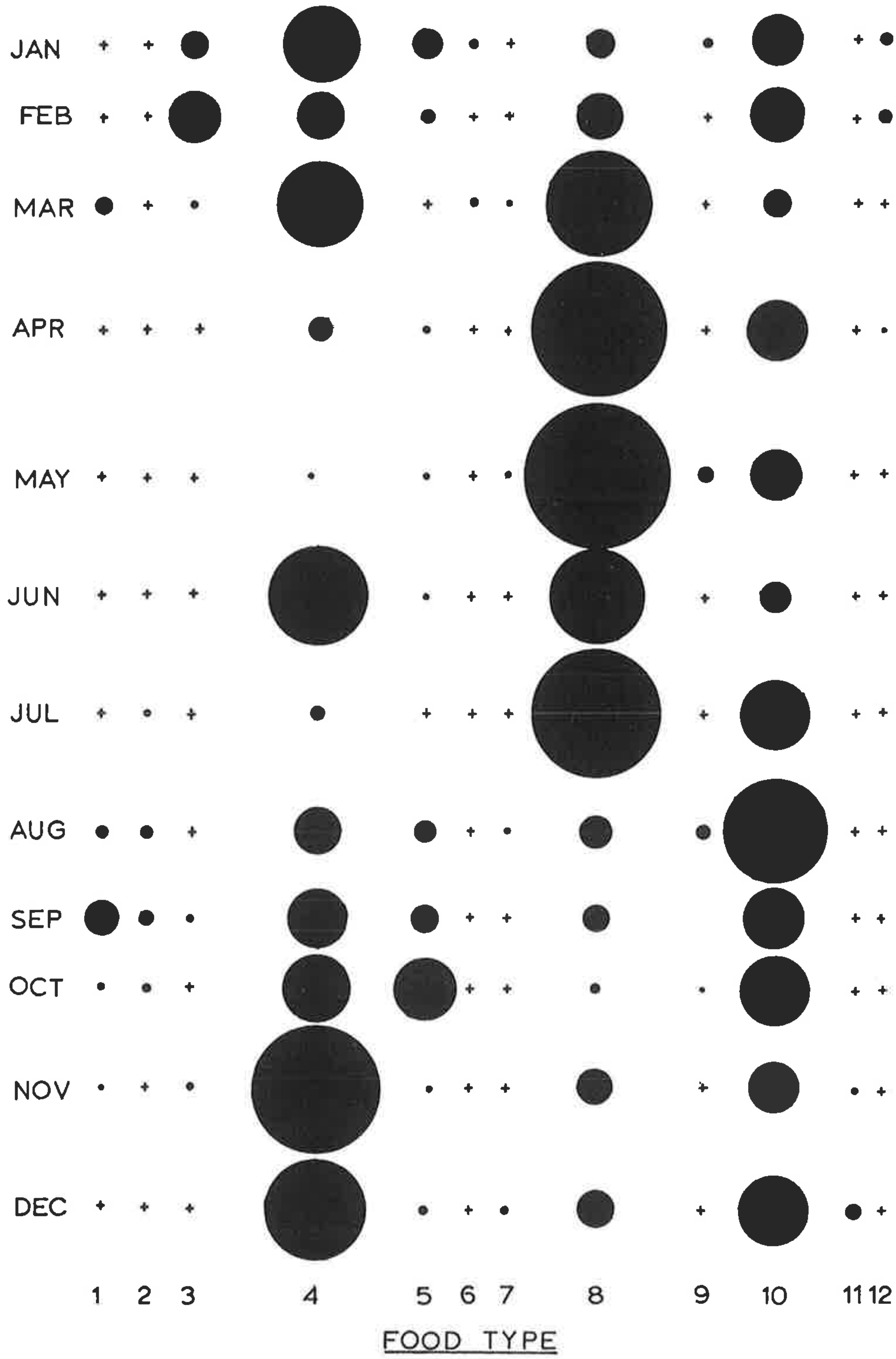
creasingly rocky habitats which characterise the three stations and also the relatively more rocky habitat type occupied by *G. maculatus* in each area. This change in habitat type partly explains the greater utilisation of rocky stream invertebrates in the upstream habitats.

SEASONAL CHANGES IN FOOD

Examination of seasonal abundance of the various food types showed that some of the foods varied seasonally. Various food types which were very small contributors to the total food of *G. maculatus* in the Waikanae River attained prominence in the food for short periods, for example, *Deleatidium-Zephlebia* in early spring (August–September, see fig. 34), Elmidae for two months in early summer, and *Oxyethira* in early spring and summer. The two more abundant terrestrial food types, Coleoptera and *Scolypopa,* as expected, were most frequent in spring and summer. The basic food types also fluctuated in numbers. Apart from inconsistent high abundance in June, there were few Chironomidae in the April to July period. At this time Copepoda attained greatest prominence. They were much less abundant in spring and early summer. Although numbers of *Potamopyrgus* fluctuated, the changes were irregular.

Allen (1951) found that Chironomidae were more abundant in the bottom fauna of the Horokiwi Stream during mid winter, yet apart from the abundance during June, these were most frequent in the food of *G. maculatus* in early spring and summer. These facts may not be as contradictory as they seem. Allen also found that Chironomidae are most abundant "on the flats", defined as "water of slight to moderate current and generally smooth flow, but of less depth than in pools". During collection of *G. maculatus* from the upstream localities where Chironomidae were mostly utilised by *G. maculatus* it was found that in winter, apart from a general reduction in abundance after the previous autumn's breeding mortality, *G. maculatus* altered its habitat and behaviour. For most of the year *G. maculatus* was found to shoal in the slower-flowing waters and probably fed there almost exclusively. In winter the fish appeared to become more solitary and more secretive and occupied cover at the edges of the fast-water habitat. They were taken even from the habitat types common for *Gobiomorphus huttoni,* the heads and tails of rapids. As there is less likely to be abundance of Chironomidae there, they appear less frequently in the food during winter.

Fig. 34. Seasonal changes in composition of food. Food types: 1. *Deleatidium-Zephlebia*; 2. Gripopterygidae; 3. Elmidae; 4. Chironomidae; 5. *Oxyethira*; 6. *Pycnocentria - Pycnocentrodes*; 7. Cladocera; 8. Copepoda; 9. Amphipoda; 10. *Potamopyrgus*; 11. terrestrial Coleoptera; 12. *Scolypopa*. The area of the circle is proportional to the abundance of each food type in each month. The cross indicates that the food category is present, but in very low abundance.



Feeding activity appeared to become reduced during winter, although the mean number of organisms fluctuated (fig. 35). Peak feeding activity was recorded during autumn. This is interesting, as this is the period when *Galaxias maculatus* breeds, and examination of fish from breeding shoals showed that they had not been feeding. Feeding of the ripe adults is thus probably intense during the pre-breeding period, but stops before the breeding migration. It is possible that feeding intensity is related to water temperatures, but unfortunately suitable temperature recording equipment was not available to allow such comparisons to be made.

DISCUSSION

Chironomidae appear to be a consistently important food for stream bottom invertebrate feeding fish throughout the world. Phillips (1929) states that "Johannson, writing of the genus *Chironomus,* quotes Garnon as saying, 'Probably no other one genus of insect constitutes as important an item in the food of as large a number of fishes'." Food studies of New Zealand fishes have revealed that Chironomidae are a very important fish food. Phillips (1929) found the food of fingerling trout to be 80 percent culicid and chironomid larvae, and of 26 bullies (unnamed species) he listed 356 Chironomidae among a total of 468 food organisms. Figures quoted by Cairns (1942) from Stokell (1928 and 1936), Hudson (1904), and Phillips (1929) suggest that Diptera are relatively minor components of the food of trout, but Phillipps (1924a) stated that in trout "dipterous larvae and cicadas were the most commonly found". Hopkins (1965) recorded figures of 36.5 percent and 84.5 percent of the food for young *Salmo trutta* from two localities.

Allen (1951) found that the forage ratios of Chironomidae and Simuliidae are very high for young trout, but that they later fall rapidly. Percival (1932) stated that "small *Galaxias brevipinnis* up to 3 in., *G. attenuatus* of 2½ in., taken in fresh water, and *Gobiomorphus gobioides* up to 1 in." had fed entirely on midge larvae. The study of Hopkins (1965), that of McDowall (1965a), and the present study have shown that these are important foods for some species of *Gobiomorphus, Philypnodon,* and *Galaxias.* Hopkins found that Chironomidae had constituted 73.0 percent and 63.1 percent respectively of the food organisms eaten by first-year *P. breviceps* at two stations

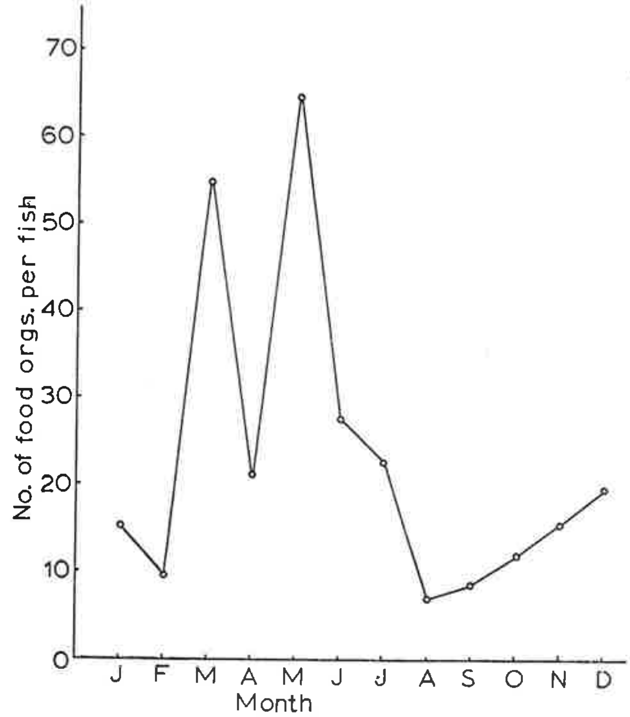


Fig. 35. Seasonal changes in feeding intensity.

and 5.1 percent and 22.8 percent respectively of the food organisms eaten there by adults. McDowall (1965a) ascertained that Diptera, largely Chironomidae, made up 53.2 percent of the food of *Gobiomorphus huttoni* and that the importance of Diptera decreased from about 70 percent of the food intake in small fish to less than 30 percent in larger adults.

Butcher (1945) studied the food of several species of Australian freshwater fishes and found Diptera in 33.4 percent of *Salmo trutta* examined, 42.8 percent of *S. gairdneri,* 45.2 percent of *Macquaria australasica,* only 4 percent of *Perca fluviatilis,* and 33.3 percent of *Gadopsis marmoratus,* which emphasises again the importance of Diptera in the food of freshwater fishes.

The food of *G. maculatus* shows some agreement with the food chain for "food relations in inland waters of New Zealand" constructed by Percival (1932). Percival envisaged juvenile trout, *Galaxias,* and *Gobiomorphus* feeding primarily on Chironomidae and *Deleatidium,* but the adults diversifying to feed also on Trichoptera, Ephemeroptera, Elmidae, and *Potamopyrgus,* and the trout feeding on Crustacea like *Paratya, Paranephrops,* and Amphipoda and on larger stream insects like *Archichauliodes* and *Stenoperla.*

Such a food chain is substantially in accord with food studies made since Percival's paper, although the importance of Crustacea like Copepoda, Cladocera, and Ostracoda has become more apparent in studies on both Galaxiidae and Eleotridae. Differences in the food of *Galaxias* in juvenile and adult stages suggested by Percival are not applicable to *G. maculatus* and probably also not to other Galaxiidae with migratory juveniles. No diversification in the food types consumed by *G. maculatus* was evident between the size at which they migrate into fresh water and adulthood. However, in other migratory Galaxiidae greater total growth may lead to more significant changes with growth, and diversification of the diet is more likely.

PARASITOLOGY

INTRODUCTION

During the food study parasites were commonly found in the guts of the fishes. The parasites were removed and the number and infection site of each parasite recorded.

Parasitology is probably one of the most neglected fields of study in the New Zealand freshwater fish fauna. Stokell (1936) examined the nematode parasites of trout (*Salmo trutta*) in Lake Ellesmere and recorded *Hedruris spinigera* Baylis in their stomachs and also in a variety of marine and estuarine fishes, for example, *Galaxias maculatus, Retropinna retropinna, Anguilla dieffenbachi,* and *Aldrichetta forsteri.* Stokell concluded from examination of the food in the two most frequently infested fishes, *R. retropinna* and *A. forsteri,* that the most probable intermediate host for *H. spinigera* was *Tenagomysis novaezealandiae,* an estuarine mysid. Stokell also found that fish which had moved out of the estuarine regions of the rivers running into Lake Ellesmere lost their infections within about three months of leaving the estuaries. Fish that were considered never to have entered Lake Ellesmere estuaries were shown to be free of parasites. The other nematode discussed at length by Stokell was the intermediate stage of a bird-infesting *Eustrongylides* sp. which encysts in a coil in the abdomens of some fishes. In Lake Ellesmere Stokell found it in *S. trutta, Gobiomorphus gobioides, Galaxias maculatus,* and *Rhombosolea retiaria.* The primary hosts of this nematode were listed as *Phalacrocorax carbo,* the black shag, *Phalacrocorax punctatus,* the spotted shag, and *Botaurus poecitophilus,* the brown bittern. Stokell suggested that occurrence of *Eustrongylides* in trout is associated with a lake existence. Another nematode listed by Stokell for trout and *Gobiomorphus gobioides* was a species of *Contracaecum* which has the adult stage in shags and *Podiceps cristatus,* the crested grebe.

Between 1939 and 1951 Macfarlane described the life histories of three trematodes from New Zealand freshwater fishes. These included *Coitocaecum anaspidis* Hickman, which infests *Gobiomorphus gobioides, S. trutta, Galaxias brevipinnis, G. maculatus,* and small *Anguilla* spp. Macfarlane (1939) showed that infection occurs from amphipods (*Paracalliope fluviatilis*), through the gastropod *Potamopyrgus,* to the fishes. *Telogaster opisthorchis* Macfarlane was shown (Macfarlane, 1945) to infect *Potamopyrgus,* then *Gobiomorphus* spp., *Philypnodon* spp., *Galaxias maculatus, G. brevipinnis,* and *S. trutta* as an integumentary and muscular encysting metacercaria, and *Anguilla* spp. as an adult. *Stegodexamene anguillae* Macfarlane has a similar life cycle (Macfarlane, 1951); the first intermediate host was shown to be *Potamopyrgus,* the cercaria encysts in *Gobiomorphus gobioides* and *Galaxias brevipinnis,* and the adult infects *Anguilla* spp.

Manter (1954) further examined trematodes from some New Zealand fishes and described *Dematrema minutum* Manter from *G. maculatus* and suggested that it probably had a marine origin.

These studies summarise the work on parasites of New Zealand freshwater fishes. In Australia Johnston and Mawson (1940, 1944, and 1947) have listed further nematodes from Galaxiidae. The parasites found in the present study, excluding Trematoda, have been examined by Dr Dominic L. DeGiusti, Wayne State University, Detroit, U.S.A.

PARASITES FROM *G. MACULATUS*

Trematoda. Few Trematoda were found in the gut of *G. maculatus*; on occasions a few small adult trematodes were present in the anterior region of the intestine. Examples of these were identified by Mr M. J. Howell, Victoria University of Wellington, as *Dematrema minutum.* Manter (1954) listed this species as a gall bladder parasite.

Metacercarial cysts were common in the skin, muscles, liver, and gonads of *G. maculatus,* but these were not dealt with in the present study.

Cestoda. A small unidentified cestode was found in the lower intestine of *G. maculatus.* Previously, no Cestoda have been recorded from New Zealand freshwater fishes. It was found in 2.1 percent of the fish examined from the Waikanae River, with a mean frequency of 1.2 per fish. The maximum number in a Waikanae *G. maculatus* was three, a few fish had two, but most had only one. No evidence was obtained to indicate intermediate hosts for this parasite. Cestodes were a little more numerous in the estuary fishes than in Greenaway Road and weir ones, and show progressive upstream reduction in frequency of occurrence, although mean abundance per fish, always low, did not vary (fig. 36).

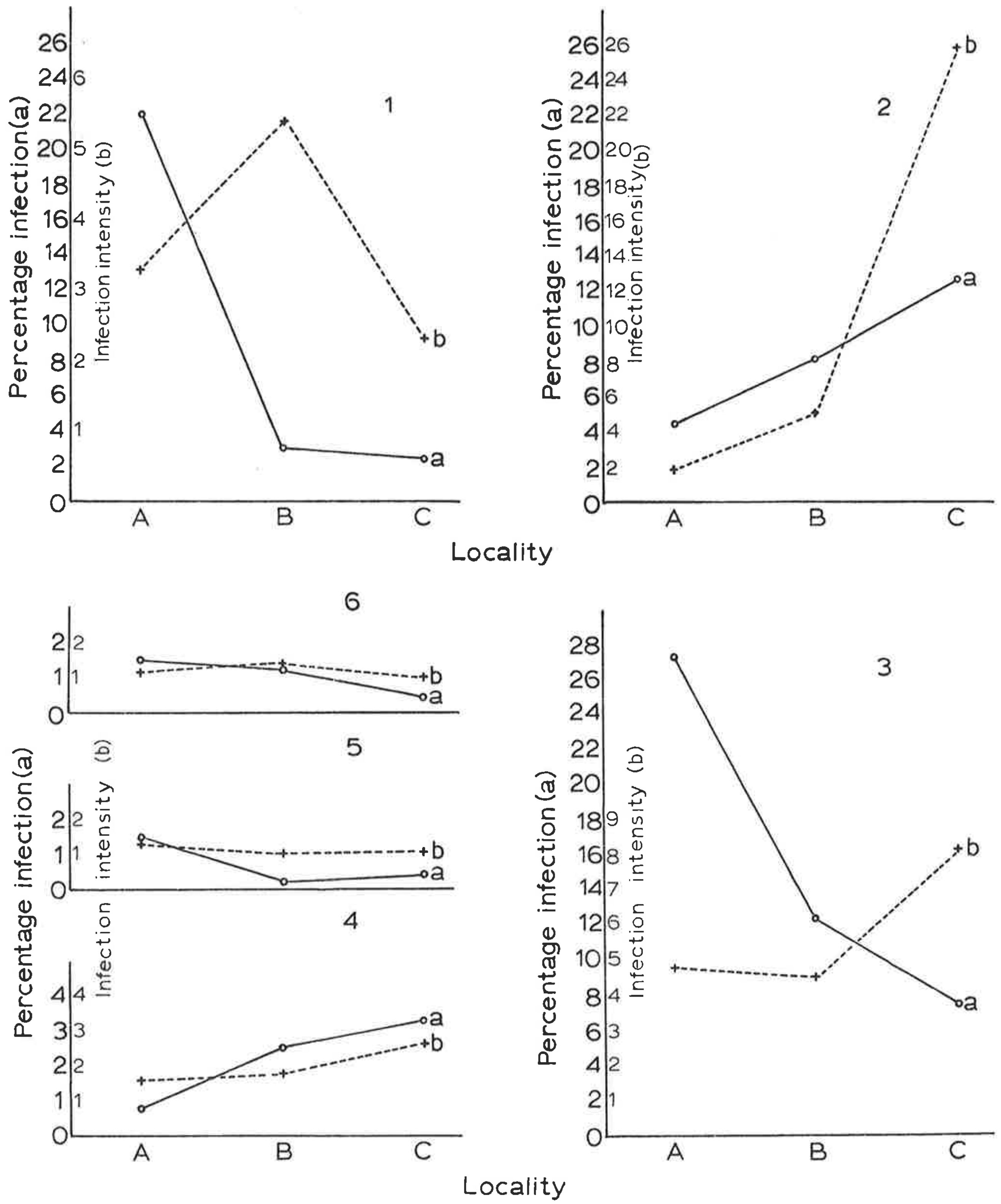


Fig. 36. Differences in percentage of fish infected and infection intensity (parasites per fish) from three Waikanae River sample stations. 1. *Hedruris spinigera*; 2. filiform nematodes *Dorylaimus* and *Aphelenchus*; 3. Acanthocephala; 4. ascarid nematode; 5. *Eustrongylides*; 6. Cestoda. A: Estuary. B: Greenaway Road. C: Weir.

Frequency of infection was low in small fishes (0.6 percent in the up to 49 mm length group) and rose to a peak (3.2 percent) in the maturing first-year spawning group (about 70–79 mm), falling away in larger fish (fig. 37). The percentage of infection in the larger fishes fell in nearly all parasite groups at either 70–79 mm or 80–89 mm and may be related to either changes in food with growth or the reduction in feeding activity known to occur in the bigger fishes (see "Food Studies", p. 45).

Cestoda were also recorded from fish in the Waimeha Stream, one example containing 31 cestodes in addition to a nematode and 48 acanthocephalans.

Nematoda. Five types of nematode were found in *G. maculatus*. Most were in the stomach, but in fishes heavily infested a few were in the anterior intestine. Two of the nematode types, *Hedruris spinigera* and two rhabditoid species, *Dorylaimus* sp. and *Aphelenchus* sp., were much more abundant than others. *Hedruris spinigera* occurred with the female firmly attached to the stomach wall by a hooked bursa and the longer, thinner male coiled round the female and not attached to the stomach wall. In some fish more than one male nematode was attached to a single female. *Hedruris spinigera* occurred in 166 fish (9.4 percent of the fish examined), the average number in each fish infected being 3.4 (total 569 parasites). The modal frequency, 1, was much lower than the mean, and maximum abundance in Waikanae River fishes was 57; a fish caught in the Waimeha Stream had a higher total of 63 *H. spinigera*.

Data showed (fig. 36) that infection was much more frequent in estuarine fish (21.9 percent of fish) than Greenaway Road (3.0 percent) or weir (2.4 percent) fish, although the infection intensity (parasites per fish) rose markedly for Greenaway Road fish. These data support Stokell's opinion (1936) that infection with *H. spinigera* is restricted to estuarine and marine fishes. However, his suggestion that the mysid *Tenagomysis novaezealandiae* is the intermediate host has received no support from the food-parasite study of *G. maculatus*. Only one mysid was found in the food of nearly 2,000 *G. maculatus* examined for food, 600 of which were from the Waikanae River estuarine waters. It is improbable that *T. novaezealandiae* is an important source of infection of *H. spinigera* in *G. maculatus*. The most prominent differences in food between estuarine and upstream fishes in the Waikanae River were the numbers of *Potamopyrgus*, Copepoda, and Amphipoda (fig. 33). Stokell (1936) found that "young smelts", *Retropinna retropinna*, which had fed "exclusively on copepods" were free from infection with *H. spinigera*. Additions to the diet in the adult smelt with which Stokell related presence of infection included *Tenagomysis*, *Paracalliope fluviatilis* (Amphipoda), and small Diptera. Adult mullet, *Aldrichetta forsteri*, the other fish which Stokell found to be consistently infected, consumed *Paracalliope*, *Tenagomysis*, and *Potamopyrgus*.

Data from fish caught in the Waimeha Stream were not consistent with those from the Waikanae River, as greatest infection was not found in the estuarine samples. Four of 48 fish examined from the estuary were infected with *H. spinigera*, and 26 nematodes were present in the four fish; eight of nine fish examined from further upstream in the Waimeha were infected and contained 105 nematodes. Fish from the Waimeha Stream contained many more Amphipoda than those from the Waikanae River. None of the fish from the Waimeha estuary contained Amphipoda, and the high numbers of Amphipoda in the Waimeha Stream fishes (see table 6) is completely attributable to nine fish taken upstream, which contained 354 Amphipoda (39 per fish). There is thus an apparent correlation between presence of Amphipoda and presence of *H. spinigera* in fish in the Waimeha Stream, and this relationship is independent of estuarine existence. It is known that the intermediate host of an acanthocephalan found in *G. maculatus* occurs in these Amphipoda, and *H. spinigera* and the acanthocephalan were more frequently found together in a fish than any other pair of parasites. Of 164 fish carrying *H. spinigera* 64 were also infested with Acanthocephala. Twelve Waimeha Stream fish contained *H. spinigera* and 11 of these also had Acanthocephala.

The only prominent food types in both *Retropinna retropinna* and *Aldrichetta forsteri*, in which it was reported (Stokell, 1936) that infection with *H. spinigera* was common, were *Tenagomysis* and *Paracalliope*. *Tenagomysis* has already been ruled out as a source of infection for *G. maculatus* in the Waikanae River, which suggests that although Stokell failed to find larval stages of *H. spinigera* in 100 *Paracalliope* examined, the amphipod may be the source of infection. Two observations point to an amphipod like *Paracalliope* as an intermediate host for *H. spinigera*. First, Acanthocephala, which also have their larval stage in these amphipods, and *H. spinigera* often occurred together in *G. maculatus*. In addition, infection with *H. spinigera* in areas where amphipods are important components of the food was high and much lower where amphipods are less important.

Infection with *H. spinigera* increased with growth to maxima in the 80–89 mm and 90 mm-and-larger sizes (fig. 37), although heaviest infections in individuals were recorded in the 70–79 mm group. Amphipoda (fig. 31) also increased steadily in the food with growth. As suggested earlier, reduction in the intensity of infection in older fishes may be related to lower feeding activity in the largest fishes. Seasonal changes in numbers of *G. maculatus* infected and the infection intensity (fig. 38) did not appear to relate to changes in other factors, but were irregular. Greatest number of fish were infected from late autumn to early winter and in spring.

Dorylaimus and *Aphelenchus* are tiny filiform nematodes which exist freely in the stomach of *G. maculatus*. They occurred in 144 *G. maculatus* examined from the Waikanae River (8.2 percent of fish examined) at an average rate of 14.3 per fish (total, 2,052). These rhabditoid nematodes were not found in fish from other water bodies. Contrasting with *H. spinigera,* they were more abundant in fish upstream from the estuary than in estuarine fishes and increased steadily from an "infection" rate of about 4.5 percent (estuary) to 8.5 percent (Greenaway Road) and 12.5 percent (weir). Infection intensity per fish also increased from one station to the next (1.9, 5.0, and 25.9), that of the weir samples rising sharply. These changes correlate with increasingly rocky habitat in the three sample areas. Dr DeGiusti stated (pers. comm.) that he is certain that these nematodes are not parasitic, but are free living and were taken as food by the fish. The only datum tending to conflict with this view is that they were found to be restricted to the stomach and did not occur in the intestine despite the large numbers in some fish. It seems likely that if they had been taken as food, they would also occur in the intestine even if only in a partially digested state. If they had been taken as food, they represent a much smaller food type than others represented in the diet of *G. maculatus*.

Abundance of these nematodes in *G. maculatus*, as can be inferred from a mean abundance of 14.3, sometimes reaches high figures; examples of high infections are 251, 233, 190, and 161 per fish. Even so, the modal frequency lay in the two per fish group and was only just above the one per fish grouping; that is, nearly one half of the infected fish had only one nematode present. The number of fish infected declined with growth (fig. 37), although the intensity of infection of individual fishes rose to a peak of 32.9 per fish in the 80–89 mm size category. It is difficult to reconcile these changes with observed alterations in food at different sizes.

Seasonally, infection rates and intensities of rhabditoid nematodes were much higher during summer (fig. 38), rising irregularly in spring and dropping almost to nil in early autumn. Whether this cycle relates to a seasonal change in the life cycle of the nematode which is in turn related to the migratory-breeding cycle of *G. maculatus* is of course unknown at present, but the rise in abundance during spring, when *G. maculatus* population numbers in fresh water are building up as the whitebait migrate upstream, and the complete drop in parasite numbers after summer, when *G. maculatus* breeds and dies, is interesting.

An ascarid nematode occurred in only 38 fish (2.2 percent) at an average rate of 2.2 per fish. The intermediate host of this nematode is known from observations of Chironomidae larvae partially digested in the stomachs of *G. maculatus,* in which the nematode was present, coiled up within the soft body of the insect larva. There is also good correlation between occurrence of this parasite at the three stations and the occurrence of Chironomidae in the food of the fishes at these localities, both infection rates and infection intensities rising with upstream progression (fig. 36). No significant changes in abundance were evident with growth (fig. 37) and this is in agreement with no great changes in the numbers of Chironomidae in the food of *G. maculatus* with growth. Seasonally, fluctuations in parasite numbers showed no clear pattern (fig. 38).

A rare parasite in *G. maculatus* is a species of *Eustrongylides,* probably the one recorded by Stokell (1936); three of these were present in two fish from the Waikanae River and seven in a fish from the Awarua River, south Westland. This parasite usually encysts on the outer stomach wall; *G. maculatus* and some other fishes are intermediate

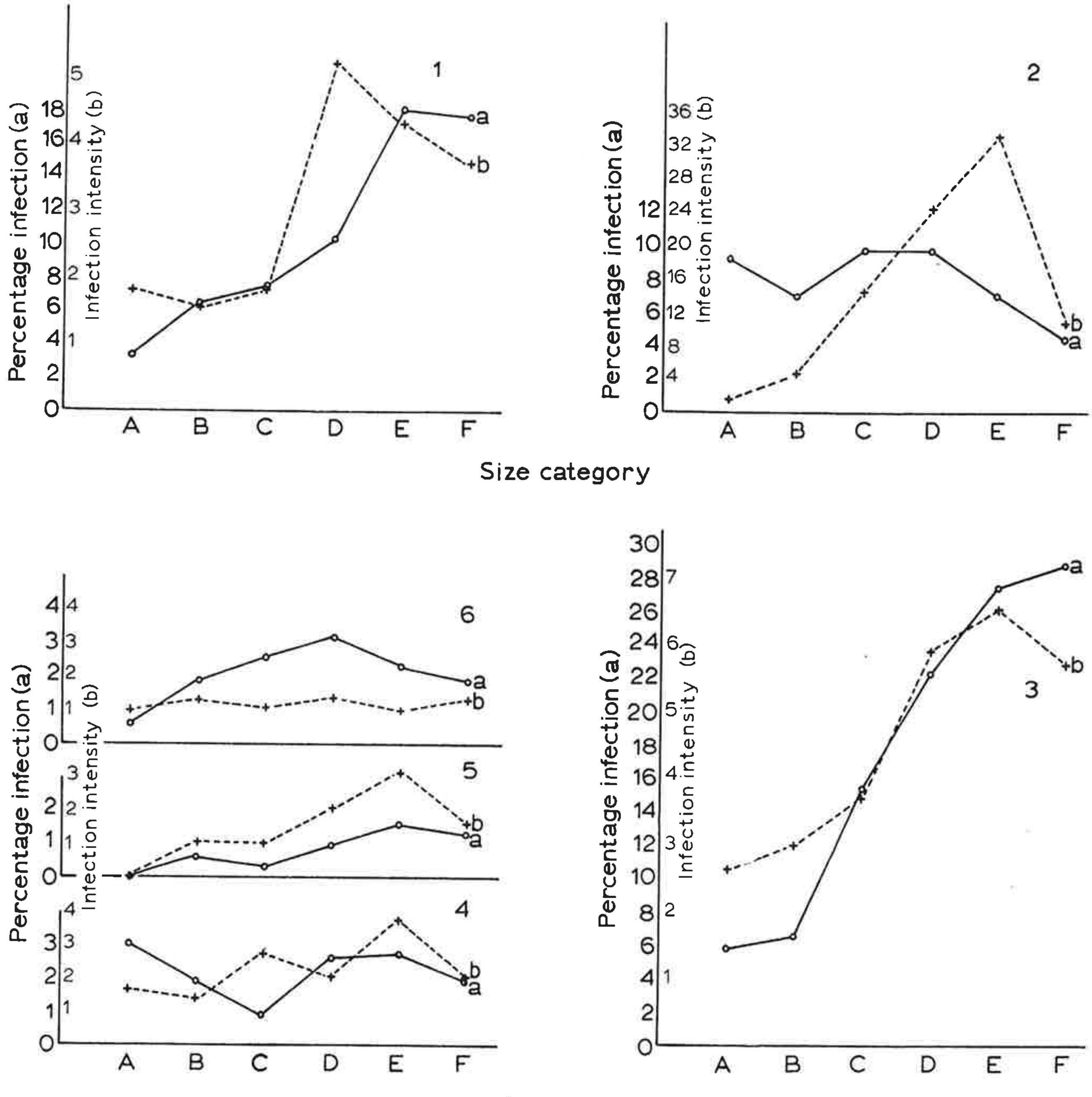


Fig. 37. Variations in parasite infections with growth. 1. *Hedruris spinigera*; 2. filiform nematodes *Dorylaimus* and *Aphelenchus*; 3. Acanthocephala; 4. ascarid nematode; 5. *Eustrongylides*; 6. Cestoda. Size categories: A, up to 49 mm L.C.F.; B, 50–59 mm; C, 60–69 mm; D, 70–79 mm; E, 80–89 mm; F, 90 mm and greater.

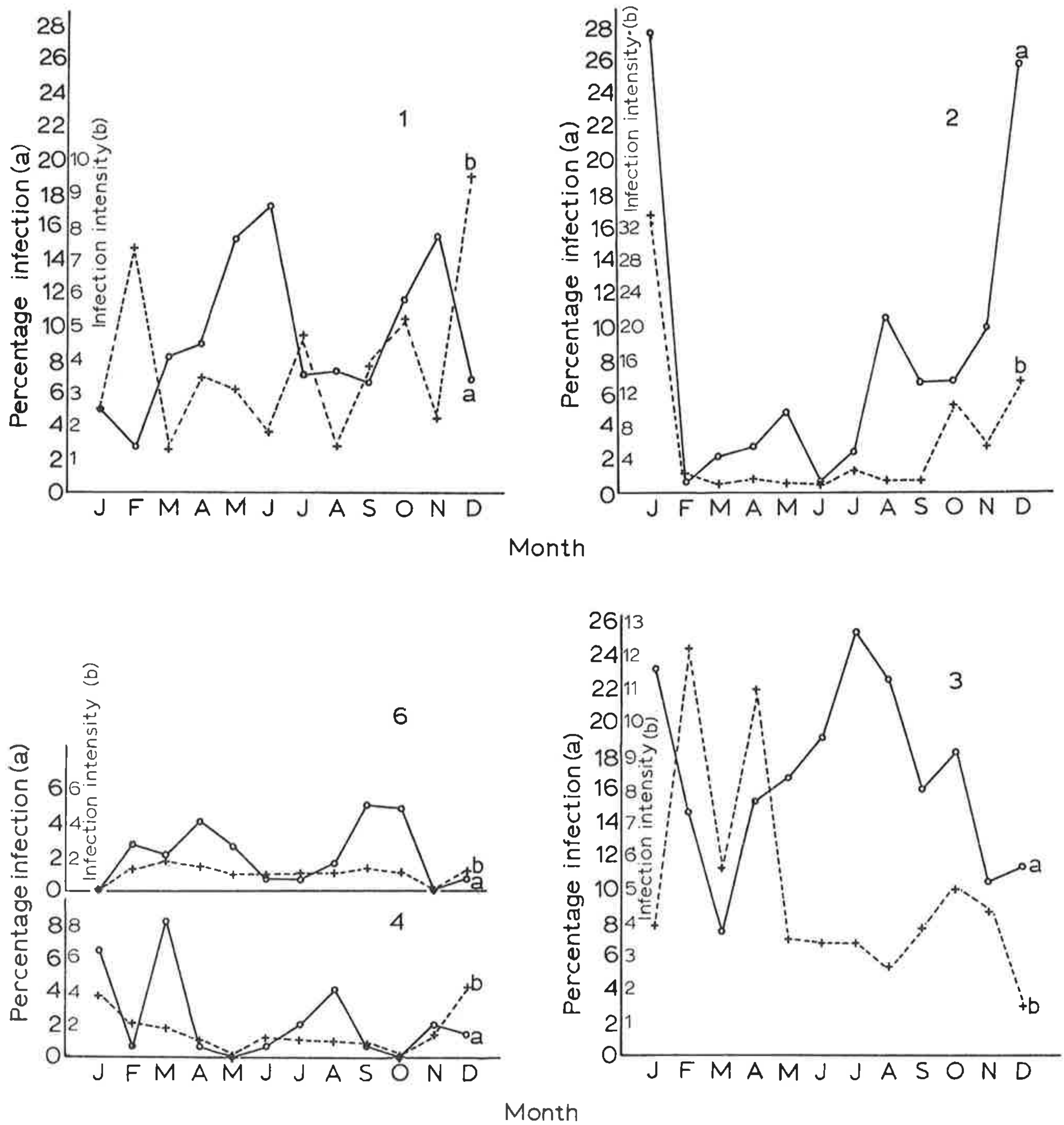


Fig. 38. Seasonal changes in infection. 1. *Hedruris spinigera*; 2. filiform nematodes *Dorylaimus* and *Aphelenchus*; 3. Acanthocephala; 4. ascarid nematode; 6. Cestoda.

hosts. The low frequency of the parasite is in accord with Stokell's finding that it is prevalent only in lake areas.

A spiruroid nematode was found in *G. maculatus*, 24 examples occurring in 12 fish. It existed freely in the stomach. It was most abundant in estuarine fishes, decreasing upstream, and was more frequent in fish of greater size, although these data are based on too few occurrences to have much significance.

Acanthocephala. Sometimes very large numbers of Acanthocephala (f. Echinorhynchidae) occurred in *G. maculatus*, mostly in the lower intestine, but occasionally in the stomach and beyond. Those in the stomach are probably released from their amphipod intermediate host during digestion.

Acanthocephala occurred in 282 of the *G. maculatus* examined from the Waikanae River (16.0 percent), being the most widely occurring parasite. Average abundance was 5.1 per fish, a somewhat lower figure than that of the rhabditoid nematodes. Modal frequency of occurrence was two, the mode lying midway through the two per fish category. Peak frequencies were 86, 66, 56, and 40 per fish. For a somewhat bulky parasite, 1 cm and more long and almost 1 mm in diameter, the numbers of acanthocephalans in the gut were high. Acanthocephala were more frequent parasites in the fish from the Waimeha Stream, which corresponds with the importance of Amphipoda in the food of the fish there. Nineteen of 47 *G. maculatus* examined from the Waimeha estuary contained Acanthocephala, the greatest number being 71 and the average 17 per fish. The nine fish taken further upstream, in which extremely high frequencies of amphipods were recorded, were all infected with Acanthocephala, the highest number being 233 and the average 127 per fish. The guts of these fishes were simply packed with Acanthocephala to the point at which the canal appeared to be blocked by them.

DISCUSSION

The parasite load in some fishes was high. Large numbers of *H. spinigera* and Acanthocephala infected many fishes, and both *H. spinigera* and the acanthocephalans often occurred together. One fish, 86 mm L.C.F., had 233 Acanthocephala and 19 *H. spinigera,* and another, 91 mm, had 66 Acanthocephala and 63 *H. spinigera*. Another fish, only 70 mm long, contained 31 cestodes, one nematode (*H. spinigera*), and 48 Acanthocephala. Only 14 fish carried more than two types of parasite, although two were commonly present.

The effect of these parasites on the condition of the fish was not examined objectively, but general observations did not indicate that fishes with very large numbers of parasites were in poor condition and the fish were certainly not emaciated. In general, fish which were in poor condition were usually not feeding intensively and had few or no gut parasites. However, reduced fecundity, suggested earlier to be due to stream conditions, may be partly caused by parasite load.

Examination of 35 fresh-run whitebait from the Waikanae River showed them to be free of gut parasites, which indicates that the young fish probably enter the stream without parasites or lose them during the transition from salt to fresh water and also that most of the parasites in the adults must have their origin in fresh water. Analyses of fish from breeding shoals showed that there are generally no parasites in the guts of breeding fishes.

SUMMARY

Galaxias maculatus is the major component of an important seasonal fishery in New Zealand. The fishery dates from pre-European times and was rapidly developed at the end of the last century after the colonisation of New Zealand. As a result of early overexploitation, land development and its consequent damaging effects on river conditions, and other effects following land development the fishery quickly declined. Restrictive fishing regulations, aimed at conservation of the existing stocks and prevention of fishing malpractices, were therefore introduced and have been altered periodically and locally as circumstances demanded. Since reasonably good records have been kept, from the 1930s, the fishery has fluctuated widely from season to season, but it is difficult to find any long-term decline. At present the fishery is mostly on the west coast of the South Island, the more productive and less fluctuating rivers being in the less developed far south (see Appendices 1, 2, and 3).

Apart from *G. maculatus* (the species of major importance to the fishery), *G. brevipinnis, G. fasciatus, G. postvectis,* and *G. argenteus* are of commercial importance, and migratory stages of *Retropinna* spp., *Anguilla* spp., *Gobiomorphus* spp., and *Philypnodon* sp. are taken in the catches.

At migration into fresh water *Galaxias maculatus* is about 50 mm long and is transparent. It undergoes a metamorphosis involving trunk shrinkage, development of pigmentation, and the formation of a pouch-like stomach. The size of the migratory whitebait varies with locality, those taken on the west coast of the South Island being larger than those from other areas. Size also varies seasonally, the whitebait being largest at the peak migration period, which is usually between August and November, although the fishes migrate throughout the year. The numbers migrating begin to increase earlier in the north than in the south. The age of the migratory juveniles appears to be about six months.

Galaxias maculatus grows to about 180 mm and probably has a maximum longevity of about three years. More of the larger fish are females than males. Age-growth data were not obtained from otolith or length-frequency studies. *Galaxias maculatus* matures during its first summer in fresh water and breeds in the subsequent autumn, but a few maiden spawners may be two or three years old. In the Waikanae River the sex ratio varied with distance from the sea, the females penetrating further upstream than the males.

The reproductive organs are typical for salmonoid fishes, except that the ripe male has a peculiar, small, fleshy tubercle which overgrows the anus and urinogenital sinus. The gonads usually mature between February and May, and larger fish mature earlier in the breeding period.

The egg of *G. maculatus* is small, about 1 mm in diameter, and spherical with numerous oil globules, but it is almost colourless. It is sticky on extrusion, but loses its stickiness after fertilisation. The eggs are deposited among stream bank grasses at high spring tides and this loss of stickiness may have important implications in facilitating the washing of the eggs down among the bases of the grass clumps as the tide falls.

Fecundity varied widely, from 175 to 13,500 eggs, and differences in fecundity were related to habitat differences in three populations examined. Breeding has been recorded from September until June, but is most prominent in March to May.

Downstream breeding migrations occur before spring tides. Spawning takes place in the tidal estuaries, typically on flat grassy banks exposed at all times of the tidal cycle except the high spring tides. Thick vegetation, usually grass, is generally necessary for spawning. The eggs usually develop within two weeks and hatch at the next spring tide cycle, but they may take longer to develop in the colder months and may still hatch after about two months without immersion in water.

Little is known of the life history of *G. maculatus* from hatching to migration. Spent fish probably die, although evidence suggests that a few, mostly females, may survive, perhaps to spawn again.

Galaxias maculatus is probably a source of food for several large predatory fishes, although there is little evidence to suggest that predation is heavy enough to affect the whitebait stocks. Predators include *Salmo trutta, Anguilla* spp., and *Gobiomorphus basalis*.

Galaxias maculatus is a carnivore, feeding on a wide range of stream bottom invertebrates with a small proportion of surface forms. Its feeding habits result in its classification as a euryphagous carnivore. Nevertheless the three most important foods,

Chironomidae, Copepoda, and a small gastropod, *Potamopyrgus,* contributed more than 80 percent of the total food of examples examined from the Waikanae River. Foods varied widely in importance with locality, the locally abundant foods apparently being utilised. Variations in diet with season and with growth were also evident. Chironomidae appeared in almost all situations to be a food of major importance.

Several parasites were found in the gut of *G. maculatus* during the food study. These comprised five nematodes, one acanthocephalan, and a cestode; a trematode which usually infests the bile duct was also present in the guts of some fish. In some of these parasites infection was related to feeding habits and a part of the parasite life cycle could thus be constructed.

Parasitic infection varied with locality, season, and fish size. The parasite load was often high. Examination of freshly run whitebait showed them to be free of gut parasites, so that all those present in the adult were of river or estuarine origin.

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Finally, thanks are due to all those fishermen who gave parts of their whitebait catches with friendly willingness.

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APPENDIX 1: THE WHITEBAIT FISHERY

WHITEBAIT AND THE MAORI

Galaxias maculatus was well known to the Maori, both as the adult and as the migratory juvenile, before European settlement of New Zealand. Best (1929) listed many Maori names for the various stages of the life history of the fish, including names for the juvenile, the adult, and the adult "going to sea to breed".

From the accounts of Hutton (1872), Hector (1872), Best (1929), Phillipps (1940), and Firth (1959) it appears that Maori terminology did not distinguish between the whitebait stages of *G. maculatus* and those of other species of *Galaxias,* including the lake species (*G. koaro* Phillipps and *G. lynx* Hutton). There also appears to have been some confusion about the adults of some of these species. Hutton (1872) recorded inanga from Lake Taupo, and Best (1929) figured Maoris fishing for inanga from a canoe in Lake Taupo. Phillipps (1940) also recorded inanga from South Island lakes. The confusion is not reduced by the specific names these authors used.

THE EARLY WHITEBAIT FISHERY

The whitebait fishery was probably well known to the pakeha from the beginnings of European settlement of New Zealand. The first record of whitebait as a commercially important species appears to be that of Hector (1872), whose opinion was that the New Zealand whitebait was a "very poor substitute for the little herring that is so well known at Greenwich by that name". Phillipps (1940) reported a remark attributed to a Mr A. J. Rutherford that he had seen cartloads of whitebait coming from the Hutt River in 1880. Hector (1883) listed *G. maculatus* as one of the chief food fishes on the New Zealand market, and Reid (1886) wrote that the "whitebait was sold from August to November by the pint, peck or bushel". Reid recorded that whitebaiting was a livelihood for the Chinese on the West Coast. According to Clarke (1899), the Chinese dried the whitebait and exported it to China, obtaining 35c to 50c a pound for the dried fish from the exporter. Clarke described the whitebait in the West Coast rivers as follows: "The extent of the shoals . . . in the South Island west coast rivers at times was incredible; often I have seen the surface of the Chinamen's gardens . . . for several acres each in extent, covered some inches in depth with these fry, used as top-dressing manure. This was when an expressly heavy run occurred. . . ." Clarke also indicated that whitebait was being canned at that time.

Graham (1956) described the taking of whitebait as they ascended the rivers on the West Coast before 1900, when a bucketful could be caught in a few minutes and was worth 5c to 10c. "They were fed to the fowls and ducks until the eggs had a fishy taste. I can remember my father using whitebait as garden manure. The supply exceeded the demand." Such was the former abundance of whitebait in New Zealand. Graham recorded how a single fisherman in 1928 caught 1,100 lb of whitebait in a day and packed it by horse to the nearest township.

Even in the beginning of the whitebait fishery the records of prodigious quantities of whitebait being caught came mostly from the West Coast, where the main fishery still is.

THE DECLINE IN THE FISHERY

Despite the enormous quantities of whitebait caught up to the end of the nineteenth century, there was even then an awareness of the need to conserve stocks. The first person whose comments on this need were published appears to have been Clarke (1899): "This wholesale destruction for manure purposes . . . was of late years stopped by preventing the use of the long shingle abutments with the set nets at intervals. . . . One hopes that the supply will last, and be properly fostered to allow sufficient to be left for annual reproduction."

The quantities of whitebait taken each year were not recorded until 1928 and it is not possible to determine when a recognisable decline in the whitebait catch began. The New Zealand Marine Department (1928) stated that "depletion has been almost universal" and referred to the "benefits to be derived from a limited fishing season". Hope (1928) stressed the need for some change in the fishing. He related the decline in the catch to increased demands of a rising population leading to heavily reduced escapement and expressed the view that the "whitebait fishery . . . is a valuable national asset, but under the present system of fishing the whitebait is in extreme danger of extermination". A year or two later the work on the whitebait life history was started by Captain L. Hayes for the Marine Department (see Hefford, 1931a, 1931b, and 1932).

Hefford (1937) in reviewing the New Zealand fishing industry considered that the whitebait runs of that time were small compared with those of former years. That the numbers of whitebait had declined is clear from the comments of many authors. Phillipps (1940) compared the previously mentioned remark of Mr A. J. Rutherford, who had seen cartloads of whitebait coming from the Hutt River in 1880, with the situation there in 1940, when there were "seldom enough whitebait to entice the local fishermen to catch them". Little whitebaiting appears to be done in the Hutt River at present.

Stokell (1955) expressed concern for the future of the whitebait fishery, saying: "These amounts [recent catches] are small compared with those taken in the early days of colonization when the fish were retailed for a few pence per quart . . . while the fish appears to be in no danger of extermination the protection of its habitat in certain localities would be in the interests of the fishing industry."

There can be little doubt that in comparison with those of last century, whitebait runs today over most of the country are much smaller, but it is hard to determine just what changes have taken place in the fishery. It is fairly clear that in the North Island, at least, there has been very heavy, long-term depletion of the whitebait stocks. Even though runs of whitebait are sometimes still good, they are sporadic, vary from river to river, and cannot be relied on season by season. A comment from a large Auckland fish buyer indicates that the decline has continued until recently in the Waikato River: "Our handling of whitebait in recent years has been only a fraction of that just after World War II or even during the war and in the years before it. During these periods we would frequently receive a complete lorry load from the Waikato River several nights a week. Now only occasionally do we get more than a few 4-gallon tins."

The situation is the same over most of the South Island, but on the West Coast a fishery of considerable value remains and this supplies much of the New Zealand demand for whitebait. The changes that have occurred in this fishery are not clear. In the Westport-Greymouth area there has no doubt been a substantial decline since the end of last century, but on the West Coast generally the situation is confused by a marked southward movement of fishing intensity and opening up of the southern areas by new roads and by air transport. Rivers in the south, the Hollyford, Cascade, Awarua, and probably some of those in the Haast area, the Waita, Haast, Okuru, Turnbull, Waiatoto, and Arawata Rivers, are probably still close to their original condition. Land development and subsequent river changes affecting the whitebait have probably been fairly small and until recently the fishing pressure has not been high.

The quantity of the annual catch of whitebait has been published for every year since 1927, although in the earlier years the information was probably not wholly reliable (New Zealand Marine Department, 1928–65). There is no evidence from the published figures to indicate that there has been a permanent decline in the catch of the West Coast whitebait fishery since these records were begun. The largest catch on record for the West Coast was taken as recently as 1955 (6,343 cwt), and although there was a decline in the ensuing seven years up to 1962, the 1963 and 1964 catches showed a marked improvement (fig. 39). There appears to be no reason to take a more serious view of the latest decline than of the other declines leading to periods of low yield during the 35 years for which catches are shown in fig. 39. The catch in 1950 was only 676 cwt, in 1942 it was only 245 cwt, and between 1933 and 1939 it fluctuated between 600 and 2,000 cwt. These must be regarded as poor years in comparison with the period 1944–49, when the average yield was about 4,500 cwt, and 1953–56, when it was over 4,000 cwt per year.

There seems little reason to conclude that the recent poor years are anything more than a normal irregular fluctuation of the fishery which cannot at present be explained. Although the general feeling among whitebait fishermen is that the fishery is not what it used to be, catch figures do not indicate that any long-term decline is discernible between 1930 and 1964. The probable reason for complaints that catches are lower than they used to be is that fishing pressure has been increased, with the result that many more fishermen are catching less fish each.

The decline in catch since the beginning of the century or even before has almost certainly been greater in the north of the West Coast than

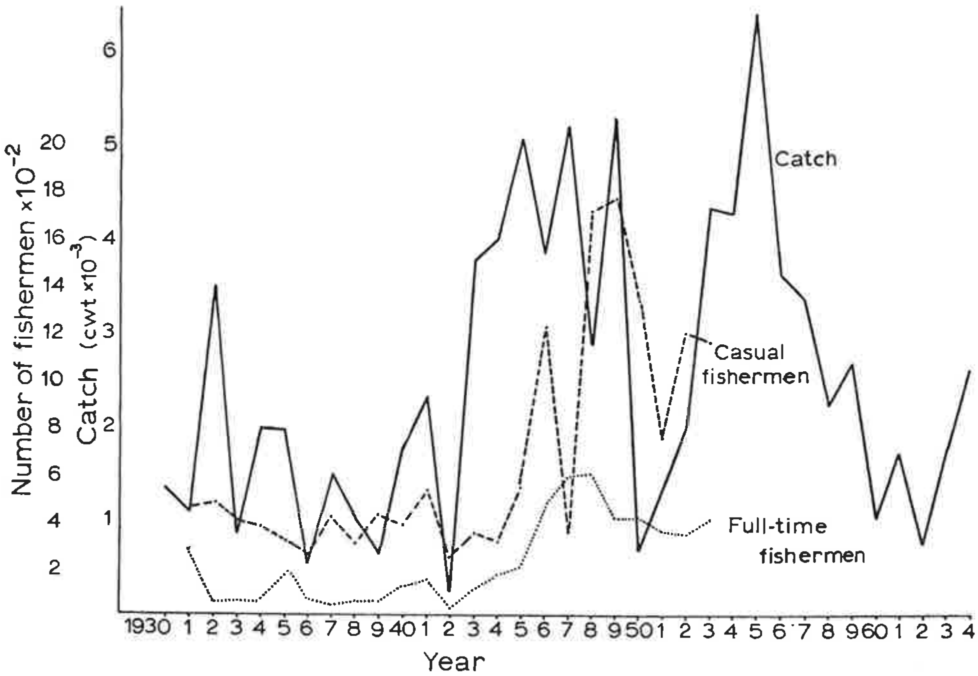

Fig. 39. Records of whitebait catch and fishing effort on the west coast of the South Island, 1930–64 (data from the Marine Department's Annual Reports).

in the south, since the fishery in the little modified southern rivers remains highly productive. This is also suggested by the much greater fluctuations occurring in the northern rivers, particularly in the Hokitika and Whataroa regions, where there have been good catches occasionally, but where the variation from year to year has been considerable. Fluctuations in the southern rivers have been less extreme than in the north, and the total catch in the south has never dropped as low as that in the north. Moreover in the northern regions the fluctuations have often been related in different areas, especially in the Hokitika and Whataroa districts (fig. 40). Such parallel fluctuations do not seem to have occurred in the Okuru and Awarua areas, where the patterns of change were found to be largely independent of those of other regions. This finding agrees with suggested reasons for the decline in the fishery. Whereas in the north the catch is affected by prevailing weather conditions leading to floods or droughts during either the juvenile migration or the adult spawning period, in the south the rivers are more stable and less likely to flood and the fluctuations are more likely to be the product of intrinsic changes in the population dynamics. Externally imposed changes in the habitat (for example, by man) are probably less important in the rivers in the south than in those of the north.

The numbers of whitebait fishermen, both casual and full-time, for the years between 1931 and 1953 are given by the New Zealand Marine Department (1932–54). These numbers show fishing intensity to be fairly stable from the beginning of records until 1944, when there was a substantial increase (fig. 39). More recently there are no figures available for comparison, but the number of full-time commercial fishermen has been kept fairly steady by limitation of the number of registrations. Although the number of registered fishermen in 1963 (424) was practically the same as that 25 years ago, the number of amateurs has probably increased considerably, as better roads have made the rivers more accessible to them.

Numerous reasons for the decline in the whitebait fishery this century have been suggested. Hayes (see Hefford, 1931b and 1932) mentioned the danger from the trampling of stock, the annihilation of possible spawning grounds through grazing, the occurrence of deciduous trees, which make the ground beneath them unsuitable for the herbage necessary to give cover to the spawn, the effect of willows on the banks of streams, swamp drainage, and use of chemical weedkillers. Stokell (1955) considered that a major influence had been drainage of swamps and lowland streams. Other likely causes are changes in rivers through land development and overgrazing of

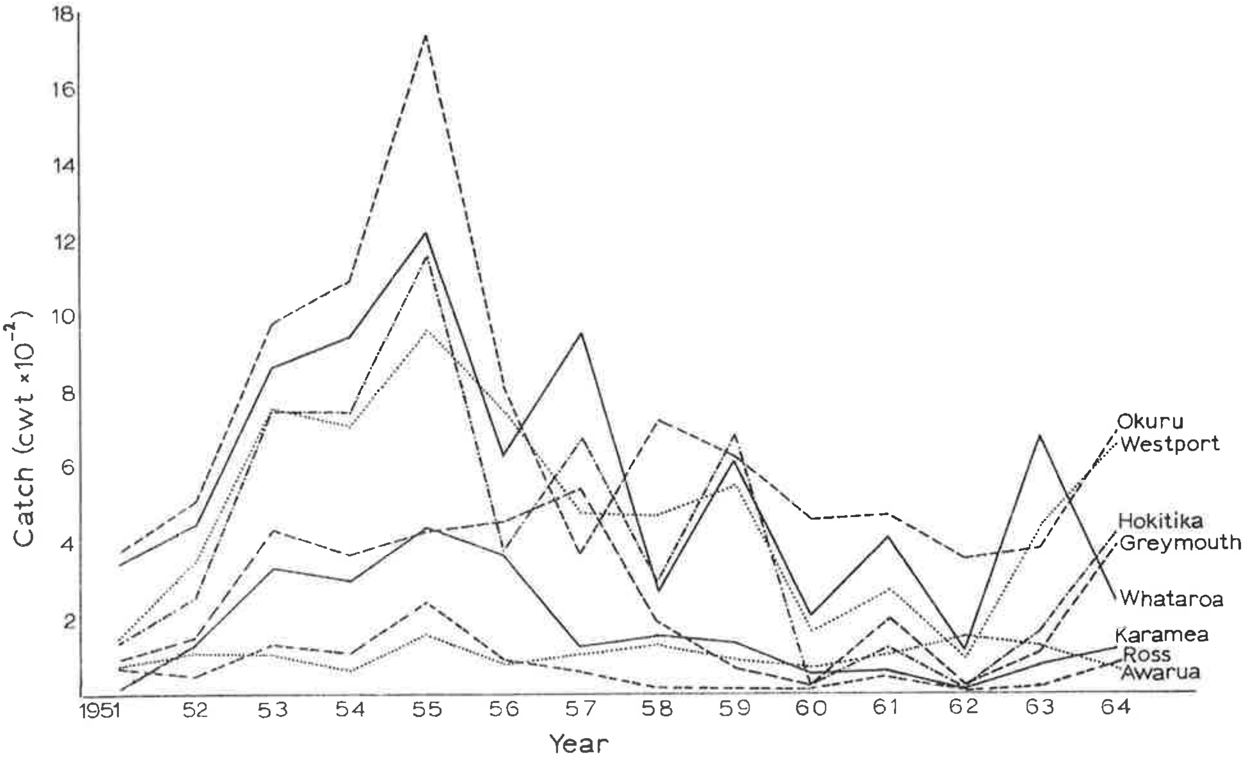

Fig. 40. Regional returns for whitebait catch on the west coast of the South Island, 1951–64, as recorded in the Marine Department's Annual Reports.

pasture land, which has caused flooding, chemical pollution from use of fertilisers, and man's wasteful exploitation of whitebait in the early days of the fishery.

THE PRESENT FISHERY

Although good fisheries formerly existed in many New Zealand rivers, few rivers outside the West Coast now produce sufficient whitebait to satisfy even local demands. Whitebait from the West Coast fishery is therefore sold throughout New Zealand. Because the West Coast is at present an economically depressed area and because of the considerable demand for whitebait in other parts of New Zealand, the whitebait fishery there is of economic importance to the area.

There is great variation in the productivity of the rivers on the West Coast. Rivers which are stable and more slow flowing tend to have higher production than other rivers, and snow- and glacier-fed rivers, which are usually murky and cold, are almost invariably poor whitebait rivers. Those in the south, because they have not been affected so much by logging, land development, and pollution, are generally more productive than northern rivers. Catch records indicate that the most productive rivers are the Hokitika, Jacobs, Wanganui, Paringa, Moeraki, Waita, Turnbull, Waiatoto, Hollyford, Awarua, and Cascade. Of these the Waiatoto and Cascade are probably the best whitebait rivers. All these rivers except the Jacobs, Hokitika, Wanganui, and Paringa have until recently been inaccessible by road. There is still no road access to the Awarua, Hollyford, and Cascade. This inaccessibility has protected the rivers and their fisheries and explains why they have maintained high production while the more northern rivers are probably much less prolific than in the early days of settlement of the West Coast.

After a decline from a peak catch in 1955 to the low figure of 1962 the whitebait fishery appears to be recovering, as the catches in the 1963 and 1964 seasons were substantially bigger. The catch for 1964 was almost four times that of 1962.

A clause in the 1964 whitebait regulations stipulated that registered fishermen must supply monthly returns of their daily whitebait catches to their local fisheries inspectors. These returns enabled the size of the catch from each river to be gauged for the first time, although the returns may not be very accurate. However, a good number of them appear to be authentic records of individual fishermen's catches for the season. They show little or no distinction between days on which no fish were caught and on which no fishing was done; so it has been possible to deal only with days on which a catch is recorded. The returns provided the quantities of whitebait caught on 8,620 fisherman-days for about 20 of the West Coast registration rivers. The average catch from these records was 16.5 lb per day, the maximum catch for any one day being 840 lb and for any month 3,372 lb.

In fig. 41 the frequency of occurrence of a series of weight categories shows that on a very high proportion of fisherman-days (61 percent) the total catch was 5 lb or less and that on a further considerable number of days (13 percent) it was between 6 and 10 lb. Thus, despite very high catches on some days in a few rivers, the daily catch was generally low. This was more true in some rivers than others; those from which high catches were recorded on individual days were the rivers from which high average daily catches were also recorded. In fig. 42 the distribution of daily catches for given weight categories is shown for selected rivers. The data indicate that those rivers for which occasionally very high catches were recorded are also the rivers on which there is sustained yield throughout the season, but that in other rivers the catch was consistently poor. The maximum catch figure for one day's fishing, cited above, was recorded from the Haast River. Other instances of high catch were 733 and 621 lb on the Waiatoto River, 360 lb on the Hokitika River, 320 lb on the Wanganui River, 510 and 400 lb on the Haast River, and 320 lb on the Paringa River.

The highest catches for consecutive days were recorded from the Waiatoto River. One fisherman caught 621, 362, 733, 331, and 189 lb (total 2,236 lb) on consecutive days; another 523, 354, and 433 lb (total 1,310 lb); and a third 381, 200, and 247 lb (total 828 lb). Similar results were recorded from the Haast River (105, 295, 104, and 200, total 704 lb); the Paringa River (140, 320, 130, 130, and 210, total 930 lb), the Awarua River (180, 240, 140, and 200, total 760 lb), and the Wanganui River (120, 100, 320, 120, and 160, total 820 lb). Unfortunately the catches of eight fishermen on the Cascade River were grouped together in one return; so no analysis of the catch per fisherman on a daily basis is possible. However, in October their catch totalled 26,440 lb, an average of 3,305 lb per fisherman for the month.

Most of the whitebait fishing rivers on the West Coast are now accessible by road. This eases the access of buyers to the fishermen and reduces the difficulties of transporting the catch to the market.

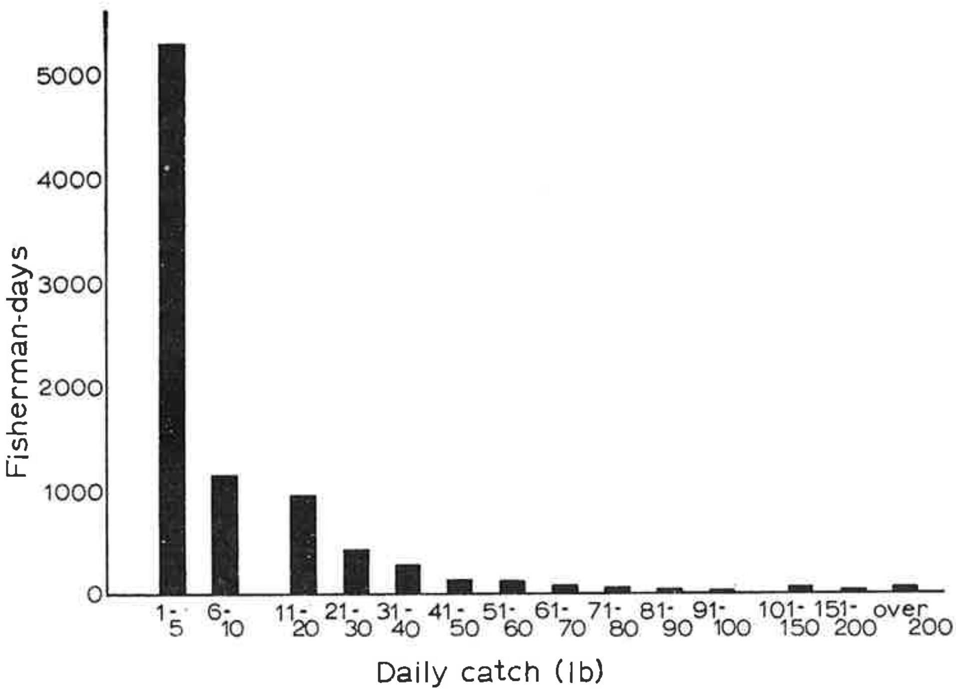

Fig. 41. Frequency distribution of catch per fisherman per day on the west coast of the South Island for the 1964 fishing season.

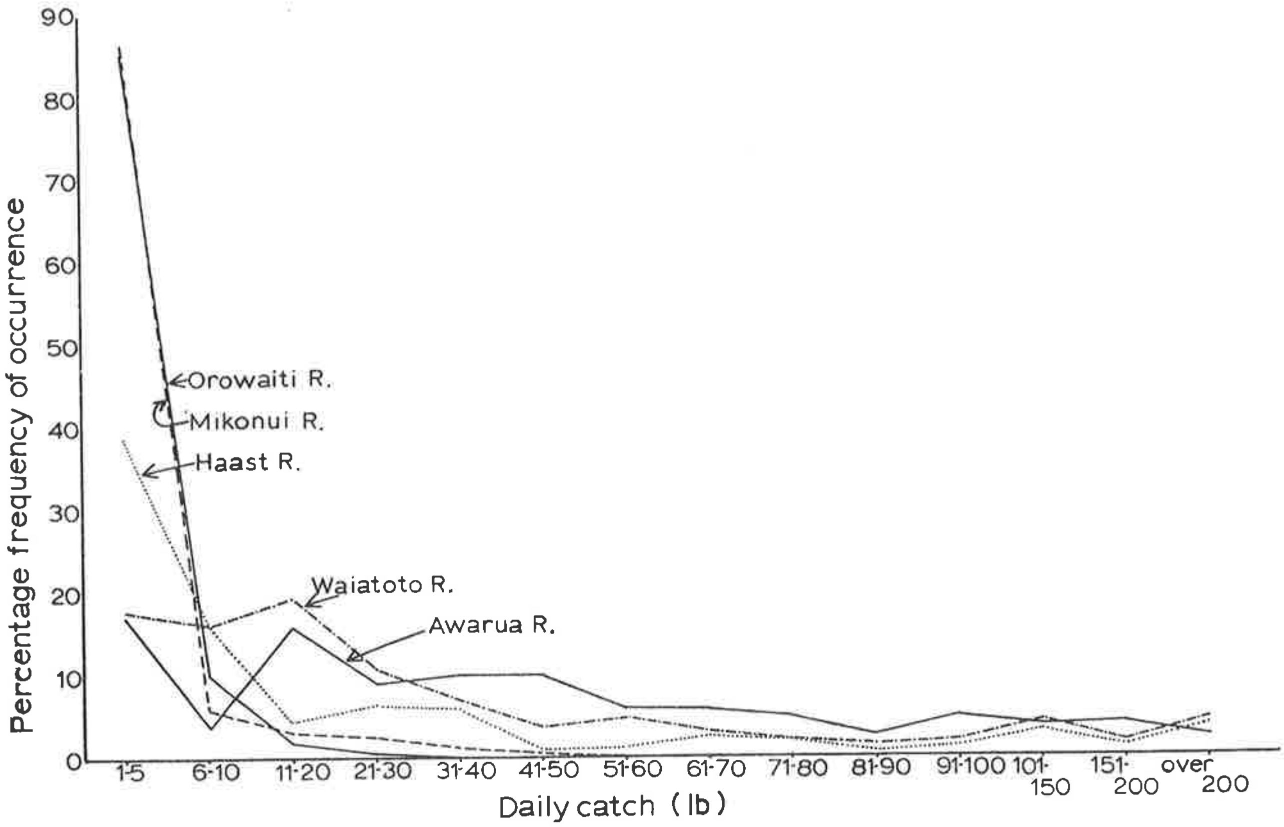

Fig. 42. Frequency distribution of catch per fisherman per day for selected rivers for the 1964 fishing season.

Whereas formerly the whitebait catches had to be stored at the fishing site for some days and then packed out by horse, nowadays much of the catch can be loaded on to transport close to the river soon after it is caught. Of the more northern rivers the Whataroa and Paringa Rivers still have rather difficult access and in the far south the Awarua, Hollyford, and Cascade have no road access at all. The three southern rivers are reached by wheeled aircraft, which land on the beaches or primitive landing strips, or by amphibious aircraft, which land on inland lakes.

The main market at present is for fresh whitebait, but in the past, partly because of the isolation of the rivers, large quantities of whitebait were canned. One firm began canning on the West Coast in 1891 and had several canneries close to the fishing rivers at Okuru, Bruce Bay, and Westport; today only one is operating. This firm canned 87 tons of whitebait in 1910 and 80 tons in 1943, so that until quite recently there have been adequate supplies for large-scale canning. Considerable quantities of canned whitebait have been exported, the maximum being 128 tons in 1946, valued at $109,500 (New Zealand Marine Department, 1947). The development of large-scale frozen food businesses has probably reduced the demand for canned whitebait. Several large frozen food companies employ buyers on the West Coast during the fishing season and they move from river to river buying the catch from the fishermen. Fish retailers also buy up whitebait in excess of their immediate requirements and hold it in freezers, releasing it from time to time during the off-season.

Information from an Auckland cannery which processes whitebait from the Waikato River indicated that most of the canned whitebait they exported was sent to Australia, with small quantities in only one year going to Canada. Whitebait continues to be canned and in 1965 whitebait exports totalled $10,456.

WHITEBAIT PRICES

The mean price per hundredweight of whitebait for each year between 1930 and 1965 was calculated from production figures of the New

Table 8: Whitebait Prices 1930–65 (1930–50 New Zealand Catch, 1951–65 West Coast Only)

Year			Catch cwt	Value $	$ per cwt	5-Year Mean $ per cwt	Consumer Index	Adjusted prices $ per cwt	5-Year Mean $ per cwt
1930	..	..	1,420	24,102	17.0	..	518	33.0	..
1931	..	..	2,941	65,430	22.2	..	479	44.6	..
1932	..	..	4,748	43,240	9.2	14.6	443	21.0	31.4
1933	..	..	2,118	21,986	10.4	14.2	420	24.8	31.6
1934	..	..	3,241	43,888	13.6	13.4	427	31.2	30.4
1935	..	..	3,251	48,534	15.0	16.0	442	34.0	35.4
1936	..	..	1,888	35,242	18.6	17.2	456	40.8	36.8
1937	..	..	3,111	69,686	22.4	18.2	488	45.8	37.8
1938	..	..	3,053	50,408	16.6	18.4	503	32.4	36.8
1939	..	..	1,837	34,290	18.6	16.8	523	36.2	32.6
1940	..	..	3,982	62,642	15.8	21.0	547	29.2	38.4
1941	..	..	4,826	53,650	11.2	21.0	567	19.6	37.2
1942	..	..	1,206	51,968	43.0	20.4	586	73.6	35.8
1943	..	..	5,002	84,022	16.8	21.6	599	27.6	37.2
1944	..	..	6,172	92,168	15.0	123.8	510	29.2	40.6
1945	..	..	8,698	194,836	22.4	19.8	618	36.4	32.8
1946	..	..	6,578	147,348	22.4	23.0	623	36.0	36.8
1947	..	..	7,056	158,054	22.4	30.2	643	35.0	45.6
1948	..	..	4,517	147,710	32.8	35.8	694	47.0	51.6
1949	..	..	7,899	408,538	51.8	40.2	706	74.0	55.2
1950	..	..	1,962	97,074	49.4	45.8	745	66.4	59.6
1951	..	..	1,301	58,320	44.8	49.4	828	54.0	61.0
1952	..	..	1,998	100,686	50.4	51.0	892	56.8	58.6
1953	..	..	4,338	218,630	50.4	56.0	933	54.0	59.8
1954	..	..	4,305	259,296	60.2	62.2	976	61.4	63.8
1955	..	..	6,343	467,680	73.8	65.8	1,000	73.2	65.4
1956	..	..	3,587	273,866	76.4	73.8	1,035	74.0	70.8
1957	..	..	3,312	227,730	68.8	78.2	1,057	65.0	73.0
1958	..	..	2,266	203,034	89.6	79.0	1,104	80.8	71.8
1959	..	..	2,766	227,180	82.2	79.6	1,146	71.6	70.4
1960	..	..	1,011	79,262	78.4	89.2	1,154	67.6	76.8
1961	..	..	1,695	132,888	78.4	96.6	1,175	66.8	81.2
1962	..	..	753	88,552	117.6	100.8	1,206	97.4	83.0
1963	..	..	2,011	255,262	127.0	104.4	1,230	103.2	85.4
1964	..	..	2,822	289,726	102.6	..	1,273	80.6	..
1965	..	..	2,416	232,856	96.4	..	1,316	79.4	

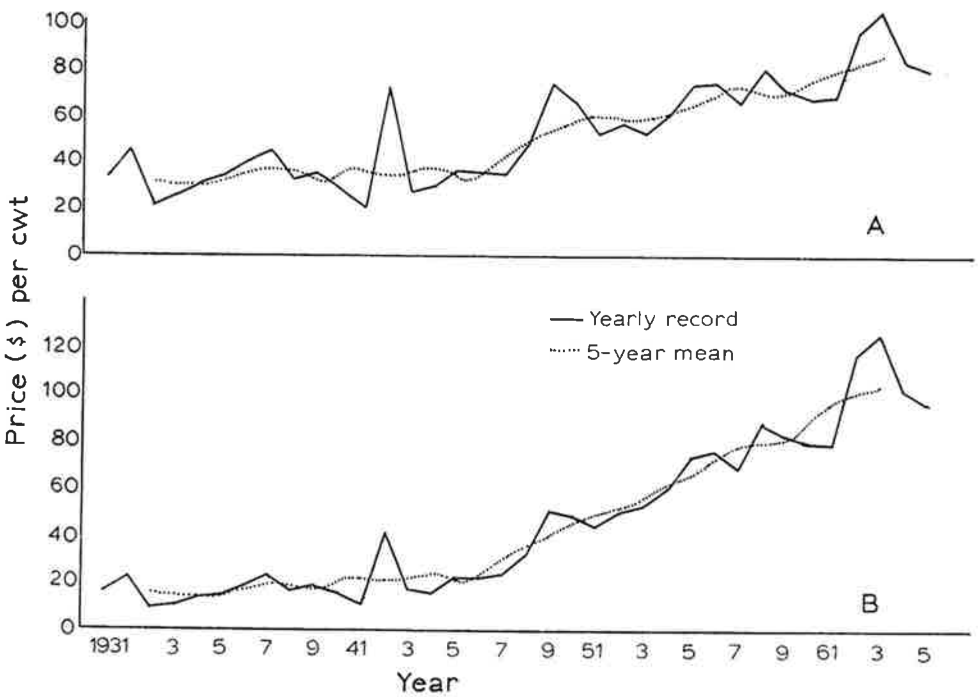

Fig. 43. Whitebait prices: A, as modified by the consumer price index; B, as recorded in the Marine Department's Annual Reports.

Zealand Marine Department (1931–66) (table 8). Up to 1950 these figures were taken from the whole of the New Zealand fishery, but from 1951 onward, the published figures included only prices and quantities of the marketed catches from rivers on the West Coast. Whether restriction of catch records to the West Coast fishery had any effect on the average whitebait prices published cannot be determined.

Apart from a year of high prices in 1942, prices from 1930 to 1947 were fairly stable at between about $9 and $22 per hundredweight (about 8c to 20c per pound). From 1948 there was a marked rise in price, from about $22 per hundredweight in 1947 to a peak of $127 in 1963. The price dropped in the 1964 season to $102 per hundredweight and in the 1965 season to $96.

The reasons for the high price in 1942 are not obvious. The catch that year was low, perhaps because of reduced manpower during the war, which affected both the number of fishermen and the ability to obtain complete records. Apart from recent years, there seems to be little relationship between price and catch for the year. A poor catch in 1939 brought little increase in price and there was a particularly good catch in 1946, but the price continued to rise. In 1949 a good catch was coupled with a 30 percent price increase. Despite low catches in 1960 and 1961, the price dropped, but then rose very sharply in the very poor year of 1962. There was a further rise in 1963, although the catch was better. In 1964 an oversupply of the market in Christchurch caused a reduction in price.

To determine whether the price of whitebait has risen in proportion to the cost of living in New Zealand, whitebait prices for the years 1930-65 have been compared with the New Zealand consumer price index (fig. 43). The price index is based on 1955. The cost of whitebait has risen more rapidly than the cost of living and is now more of a luxury than ever. The five-yearly means for whitebait prices indicate a persistent rise in the price of the fish. Whitebait currently sells in New Zealand shops at between $1.60 and $1.80 per pound, usually in $\frac{1}{4}$ or $\frac{1}{3}$ lb punnets.

APPENDIX 2: WHITEBAIT FISHING REGULATIONS

The first legislation affecting whitebait appears to have been approved in 1894, when the use of "openings in banks of streams or dams constructed therein" was prohibited. This probably refers to the method initiated by the Maoris of cutting a diversion channel up which whitebait were diverted and then captured. At this time also the mouth size of the whitebait net was limited to 8 sq. ft.

The next significant change in legislation affecting whitebait fishing was the prohibition (1896) of "jiggers". A jigger was a cord set in the water toward mid stream of the whitebait net to which small pieces of shiny metal were attached. The current moved the metal strips, which frightened the fish toward the net. In 1896 some seasonal limitation was also introduced for Westland fishermen. Except between 15 September and 24 October, when a net size of 7 sq. ft. was permitted, the maximum net size was limited to 5 sq. ft.

From these beginnings a series of complicated and largely local whitebait regulations gradually evolved. They concentrated mainly on limiting the fishing season, net size, spacing of nets, use of wings or shingle banks to divert the whitebait, and numerous other similar provisions. Early in the history of the whitebait fishing regulations (1911) the uniqueness of the Westland whitebait fishery was recognised, and special regulations were gazetted for fishing there. These applied to the type of fishing now allowed only by registered fishermen, who are permitted to use several nets and long fishing stands.

The New Zealand Marine Department (1928) stated that a questionnaire was sent to acclimatisation societies in 1927 requesting comments on the need to institute a closed season for whitebait fishing, but the questionnaire was not discussed further in the reports. In the early 1930s repeated reference was made by the Marine Department to the decline in the whitebait fishery, and at the beginning of this period Captain L. Hayes began his investigation of the biology and life history of *Galaxias maculatus*. About this time an effort was also made to bring all the earlier legislation together in a comprehensive set of whitebait regulations. Before finally drafting the regulations the then Chief Inspector of Fisheries, Mr A. E. Hefford, held a meeting with fishermen in Hokitika. The fishermen made proposals on the draft regulations, but on the whole they approved most of them and the regulations were gazetted as the Whitebait Fishing Regulations 1932 with few changes from the original draft. After the 1932 regulations there were minor changes, apparently related to local differences in fishing methods which had been prohibited by the more comprehensive provisions of 1932.

In 1947 the whitebait regulations were again rewritten and were gazetted as the Whitebait Fishing Regulations 1947. These introduced changes in the duration of the fishing season, closed some waters to fishing, prohibited the use of mechanical power when fishing, required fishermen to be in constant attendance at their nets, and made a number of smaller but similar changes.

A further set of regulations was issued in 1951, but these made few changes; they remained in force until 1964.

In response to demands from fishermen and others and to the recommendations of the Select Committee on the New Zealand fishing industry, the Whitebait Fishing Regulations 1964 were directed at increasing the escapement of juvenile whitebait during the fishing season to allow a buildup of the adult breeding stocks. As the main commercial fishery is on the West Coast, the changes were directed mainly at the registered fishermen working there.

The 1964 regulations limited the stands of registered fishermen to one-third the width of the river and restricted the fishermen's activities to tidal waters. The number of set nets permitted was limited to six, with a further reduction enforceable under the regulations by fisheries inspectors wherever they thought it desirable. The rivers on which registrations were allowed were defined for the first time to prevent spread of registrations within the West Coast area. In addition, several small streams in the registration area were closed to all fishermen, and the rivers of Fiordland between St Anne Point and Puysegur Point were also closed.

In general the whitebait fishing regulations are directed at preventing further depletion of whitebait stocks while at the same time making the fishing as equitable as possible for the fishermen. Beginning as a means of preventing malpractices in localised areas, the regulations have become more general in their application and few of the clauses now have only localised importance.

At present fishermen may be divided into two distinct groups—registered fishermen in Westland and amateur fishermen in all parts of New Zealand, including Westland. The season for all fishermen is 1 August to 30 November in the North Island and 1 September to 30 November in the South Island. Other general provisions include restriction of fishing to between sunrise and sunset, a requirement that the fishermen are not to leave the proximity of the net, a prohibition on modifying the stream bed or banks, and the prohibition on the use of jiggers and similar devices to turn the whitebait into the net.

The more important regulations applying to registered fishermen are: Use of six or fewer nets on a stand not more than one-third the distance across the river, with vertical mesh screens on the stand; and the requirements that the registered stand must be used at least four days a week through the season, must be situated in the tidal reaches of the river, and must be at least 2 chains from another stand and 1 chain from the "confluence of any river, stream, or estuary with another river, stream, or estuary".

Amateur fishermen are allowed only one net with a maximum circumference at the mouth of not more than 15 ft; fishermen must be at least 10 yd apart and may use a flat, portable screen up to 10 ft long in streams more than 20 ft wide. In some areas the construction of small stands or jetties for whitebait fishing is allowed. There are no restrictions in the regulations on the sale of whitebait by either amateur or registered fishermen.

APPENDIX 3: WHITEBAIT FISHING METHODS

Within the limitations of the existing fishing regulations whitebait fishermen use several fishing methods. Fishermen in the non-registration areas (that is, those outside the area between the Taramakau River and Cascade Point on the West Coast) and amateurs within this area generally use set nets or scoop nets.

Set nets usually have rectangular frames of light steel and are covered with gauze, either galvanised iron or nylon. They are usually simple, without a false front to form a trap. Set nets are placed at or near the edge of the water and are lifted and emptied each time a shoal of whitebait is seen to enter the net. A few fishermen build a trap into the net to hold the fish more effectively, but trap nets are not commonly used by amateurs. Few amateurs seem to take advantage of the allowance of the 10 ft screens used with the ordinary net.

In the Southland area nets are of different construction. They consist of a series of wire hoops over which a long fabric netting cone is fitted. The apex of the cone is anchored to the bank and the net drawn out along the edge of the river. As the hoops are not rigidly fixed to each other, the net can be collapsed into a small bundle for easy transport.

Scoop nets are usually smaller than set nets. They generally consist of an oval hoop up to about 5 ft long fastened to the end of a long pole. A cone net about 6 to 8 ft long is attached to the hoop, which is commonly made of supplejack (an indigenous vine, *Rhipogonum scandens*), wood slats, twisted wire, or, more recently, aluminium alloy. The pole is usually wooden or aluminium. Net fabrics, formerly cotton or hessian, are now nearly all made of synthetic fibres because of their much greater durability and strength. Scoop fishermen watch for moving shoals of whitebait and scoop them out as they move upstream. Both set and scoop nets are usually used with the net opening facing downstream, opposite to the direction of movement of the fish.

Registered fishermen on the West Coast use various fishing methods. Up to six nets may be used and gauze screens are allowed between the nets to extend fishing coverage to one-third the distance across the river. In the more northern areas of the West Coast full use is made of these provisions, and large stands or "trenches" are constructed. These consist of rows of stakes driven into the stream bed to support narrow "catwalks" many of which extend many yards across tidal river flats. Wire mesh screens are placed on the downstream side of the stakes, and gaps are left at intervals for the placement of nets. The nets are usually box-shaped structures with wooden frames covered with wire gauze.

In the southern areas of the West Coast the rivers are deeper and few fishermen use more than one net. A solidly constructed stand, usually with a spacious wooden decking, is built at the edge of the river and usually extends out over the water only 6 to 10 ft. The downstream side of the stand is covered with wire gauze screens.

The nets used by these fishermen are very large, having a mouth 3 to 3½ ft square, and are commonly 4 to 5 ft deep. One or, more usually, two traps are built into the net, the outer trap having an opening about 2 ft square and the inner 4 to 6 in. square. The whitebait, migrating upstream, move against the stream flow and find their way into the inner trap chamber, which holds many pounds of whitebait. Once in the trap the fish continue to swim against the flow of water passing through the net, and few leave the trap.

The fisherman removes the catch from the net by lifting the net from the water and opening a small trapdoor about 6 in. square in one of the bottom corners of the net. The fish are allowed to "flow" from the net into some large receptacle. The nets usually have wooden frames and are covered with wire gauze. As they seldom rest on the river bed, but are suspended so that the top of the net is just out of the water, a length of hessian is attached to the lower edge of the front of the net to drape on to the river bed and prevent the whitebait from swimming under the net. Because of their large size, these nets are heavy, especially when filled with fish, and are difficult to lift from the water. South Westland fishermen lift their nets with a block and tackle attached to a long pole reaching out over the water.

In some areas where transport of whitebait from the river is difficult and aeroplanes are used the whitebait are held in large mesh-covered boxes in the river and are kept alive for several days until sufficient quantity is obtained to warrant a flight. The time whitebait can be held in live boxes is limited, as they lose their fresh blue-green colour and become darker after a few days. They are then less acceptable at the markets.

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