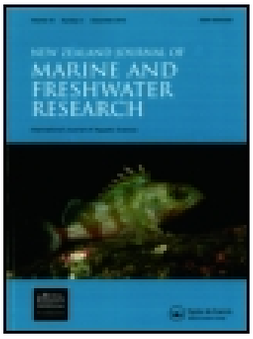

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VARIATION AND TAXONOMIC CHANGES IN THE FAMILY RETROPINNIDAE (SALMONOIDEA)

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SUMMARY

The family Retropinnidae contains one monotypic genus, *Stokellia,* in New Zealand, and nine nominal species of *Retropinna*: five in New Zealand, three in Australia, and one on Chatham Island. Four Chatham Island populations contain much of the recorded range of variation for the family for head length in standard length ratios, numbers of dorsal and anal rays, and numbers of scale rows. These characters are analysed for 29 populations incorporating five nominal species from New Zealand and Chatham Island. When interrelated these characters are shown to be linked (loosely) and high values are typical of coastal populations. When related to latitude their values increase to the south. The reverse trend is found with increase in altitude. Decrease in salinity depresses the values. Area of the lake habitat has little effect.

Observations suggest that size of fish and numbers of teeth vary predictably. Thus all observed variation is related to environmental conditions. The four nominal lake species are submerged in *Retropinna retropinna* (Richardson), the type species of the genus, which is considered to be highly adaptable rather than highly variable. *R. osmeroides* Hector is recognised as distinct from *R. retropinna* on one character and on sympatric distribution. Records of Australian and Tasmanian species suggest that *R. victoriae* Stokell differs fundamentally from all other species but that *R. semoni* Weber and *R. tasmanica* McCulloch do not differ greatly from *R. retropinna.* Similar environmentally correlated variation is suggested to relate some diadromous species of *Galaxias* and their lacustrine isolates.

INTRODUCTION

The small family Retropinnidae is a Southern Hemisphere counterpart of the Northern osmeroid fishes. It is confined to land masses bordering the Tasman Sea and adjacent coastal waters and occurs on Chatham Island, which lies 500 miles east of New Zealand. Its closest affinities are with the family Aplochitonidae which has a similar distribution but, unlike the Retropinnidae, is also represented in southern South America. Two genera are described for New Zealand. *Retropinna* Gill, 1862, has one largely marine, coastal species, *R. osmeroides* Hector, 1870, one diadromous species, *R. retropinna* (Richardson, 1845, after Stokell, 1941)), and four lacustrine forms† in New Zealand.

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† "Form" is used here to denote that the specific status of these fish is in question, and in anticipation of taxonomic changes. *R. retropinna* is the first described species of the family so the use of this name is not in question.

These lacustrine forms are *R. obtusirostris* Stokell, 1941, *R. lacustris* Stokell, 1943, *R. chathamensis* Stokell, 1949, and *R. abbreviata* McDowall, 1965. The other genus *Stokellia* Whitley, 1955, is monotypic with *S. anisodon* (Stokell, 1941) which is confined to coastal and estuarine waters of southern and south-eastern New Zealand.

In his original description of *R. anisodon*, Stokell (1941) suggested that this species could warrant generic or subgeneric distinction from *Retropinna*, and Whitley (1955) referred *R. anisodon* to a new genus, *Stokellia* (Fig. 1a). McMillan (1961) did not recognise this generic change but it has been recognised by Woods (1963) and by McDowall (1965). Stokell based his opinion of the distinctness of *S. anisodon* on the structure of the jaws and the high number of scale rows (Table 1). These characters do not overlap with species of *Retropinna*. Large vomerine teeth are diagnostic for *R. osmeroides* (Fig. 1b). All other described forms are of similar structure to *R. retropinna*, as recognised by Stokell (1941). New Zealand forms which have been described as being distinct at the species level from *R. retropinna* will be shown to differ only in highly variable characters.

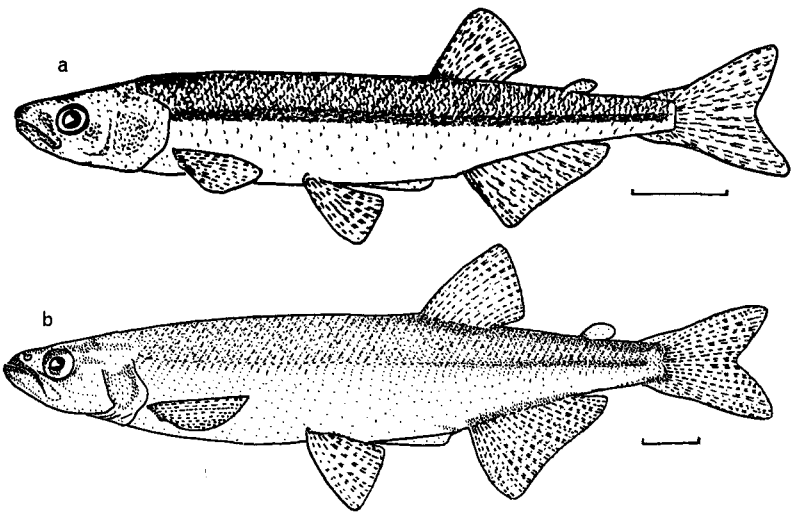


FIG. 1—(a) *Stokellia anisodon*. Female. Rakaia River mouth, Canterbury. Lat. 44°S. (b) *Retropinna osmeroides*. Male. Horokiwi Stream mouth, Wellington. Lat. 41°S. (Scale interval 10 mm.)

The habitats of these forms and of *R. retropinna* (after Stokell) range from warm mangrove estuaries to small southern lakes at an altitude above 2,000 ft and to a supersaline lagoon on an oceanic island. No two populations of *Retropinna* have been found with the same range and with similar frequencies for observed characters. This is well known although nowhere is it explicitly stated, except perhaps

when Stokell (1941, p. 366) could not define the limits of variation in the vertebral number of *R. retropinna*, and used the range of 59 to 61 which he observed in material from the type locality (coastal waters and river mouths of the Auckland Province). Populations which were otherwise similar, including some from inland lakes, he then considered to be local races. Subsequently he defined one of these as a distinct species (*R. lacustris*, 1943) and later suggested that several new estuarine forms and a lacustrine form from Canterbury (Lakes Marion and Howard) needed to be similarly distinguished (1955, p. 15; 1966, p. 139).

Table 1, which is compiled from published accounts, summarises the present taxonomy of the family. Personal records of four populations of *Retropinna* from Chatham Island are included for comparison. The ranges observed for these are almost as great as the combined ranges for the family. Only one species can be clearly distinguished from the remainder by use of the data for the 10 described species in this table; this is *S. anisodon*, which has distinctive scale counts.

Stokell (1941, p. 365) was aware of the range of variation for some characters. He gave a range of 45 to 62 vertebrae for species and unidentified populations which otherwise agree closely with *R. retropinna* from the type locality. Using group averages, he noted an association of high number of teeth with a large size of fish. In describing *R. lacustris* and *R. chathamensis* he used material from only one population of each and the new species to which he alluded remain undescribed. McDowall (1965) described *R. abbreviata* n.sp from a North Island lake, stating that "a detailed examination showed that the Lake Omapere smelt is distinct from all previously described species".

McMillan (1961) described the pronounced sexual dimorphism present in *S. anisodon* and found the differences to be similar to those in many osmeroid fishes. Following this, Woods (1963, p. 17) made the generalisation that in *R. retropinna* "as for all types of New Zealand smelts, the males at maturity have tubercles standing out from their scales . . . and the fins are larger than those of the females". To this may be added that nuptial tubercles are present on all fin rays of males; these are best seen in the dorsal and anal fins. McMillan found that Stokell's description of *S. anisodon* had been based on male specimens only, from a Southland river mouth, and that by not recognising sexual dimorphism he had (191, p. 372) apparently mistakenly suggested a new form, from a Canterbury river mouth, which could have been the female of *S. anisodon*.

The widely accepted system given by Hubbs and Lagler (1947) for measuring and enumerating the various parts and structures of fishes is followed in this account, except in the vertebral count where the hypural plate is not counted (in conformity with the general practice in New Zealand and elsewhere). No such system has been consistently applied to New Zealand freshwater fishes and the following points are

TABLE 1—Summary of variable characters recorded for all described species of Retropinnidae and for a collection from Chatham Island from two brackish lakes and two estuarine localities. McC = McCulloch 1920–23; McD = McDowall 1965; S = Stokell 1941, 1943, 1949; C = coastal; E = estuarine; L = lacustrine

Species (some nominal)	Principal rays		Vertebrae	Scale rows	Head length ratio	Max. obs. S.L., mm	No. rows vomerine teeth	Author	Habitat
	Dorsal	Anal							
R. semoni	8–10	12–18	50	50–54	4.0–4.7	55	x2	McC	E & L
R. victoriae	8	15–17	45–49	57	4.0–4.3	49	x1	S	?
R. tasmanica	9–10	15–19	—	70–74	5.0	67	x1–2	McC	E
R. abbreviata	8–9	15–17	50–52	50–53	(3.4–3.8)*	49	x1	McD	L
R. lacustris	9–12	16–17	52–54	56–59	4.1–4.3	60	x1	S	L
R. chathamensis	8–9	14–16	54–57	55–59	4.2–4.8	90	x2	S	L
R. retropinna	10–12	16–19	59–61	59	4.6–4.9	95	x1	S	E
R. obtusirostris	10–11	17–18	56–57	60	4.1–4.6	67	x1	S	L
R. osmeroides	11	18–20	60–63	65	4.4–4.6	134	x1	S	C & E
S. anisodon	10–11	18–20	59–62	100	4.7–5.0	75	x1	S	C & E
Chatham Islands	9–12	14–20	—	50–64	(3.7–4.8)*	92	x1–2	—	L

* Obtained by using the maximum head length measurement; Stokell used a lesser measurement.

made so that present data can be compared with figures recorded by other authors:

Head length is measured from the tip of the snout to the posterior extremity of the opercular membrane.

Standard length is the distance between the tip of the snout and the hypural joint. When combined, these two measurements give the lowest possible head in standard length ratio, as used by McDowall, whereas Stokell has until recently (1966a) used a lesser head length which gives a significantly higher ratio. McCulloch (1920–23) probably used a similar low head length reading.

Principal ray counts are used below for the dorsal and anal fins. This count is used when branched soft-rays (segmented and paired) are preceded by unbranched soft-rays, the most anterior of which are rudimentary, and when spines (unbranched, unsegmented, and unpaired) are absent. The principal ray count gives the number of branched rays (the last ray being double from the base) plus the largest anterior unbranched ray. Stokell records all unbranched rays as spines (Roman numerals) but McDowall (1965) includes these with the branched ray count except for the smallest ray at the anal, but not at the dorsal, origin. This he sometimes designates as a spine, thus illogically differentiating between rays which are structurally identical but of different sizes. Even very small leading rays which require to be dissected out may show a paired structure. Dorsal and anal ray counts of D.ii,8; A.iii,14 (Stokell) = D.10; A.i,16 (McDowall) = D.9; A.15 (principal ray count).

THE RETROPINNA COMPLEX

This account is based on an analysis of variable characters for 29 New Zealand samples, including four Chatham Island samples, of *Retropinna*. All specimens are uniform or have overlapping variation for key taxonomic characters. They all possess short premaxillaries; most specimens in most samples have teeth on the maxillaries, and the teeth on the head of the vomer are about the same size as these. Thus they are distinct from *Stokellia anisodon* in which the premaxillaries bear all the teeth for the upper jaw and exclude the maxillaries from the gape, and from *R. osmeroides* in which the vomerine teeth are conspicuously enlarged. All other species were classified as a subgroup with *R. retropinna* by Stokell (1941). The three more recently described species clearly belong to this assemblage which is here termed the *retropinna complex*.

The type locality of *R. retropinna* is represented in Table 2 and relevant figures by three samples (Nos. 2, 3, and 4) from freshwater streams communicating with the sea in North Auckland. The locations of all samples analysed here are indicated in Fig. 2 and the sample reference numbers employed there are used, where relevant, in subsequent figures and tables. Fig. 3b depicts a specimen of *R. retropinna* as generally recognised. Three nominal lake species are

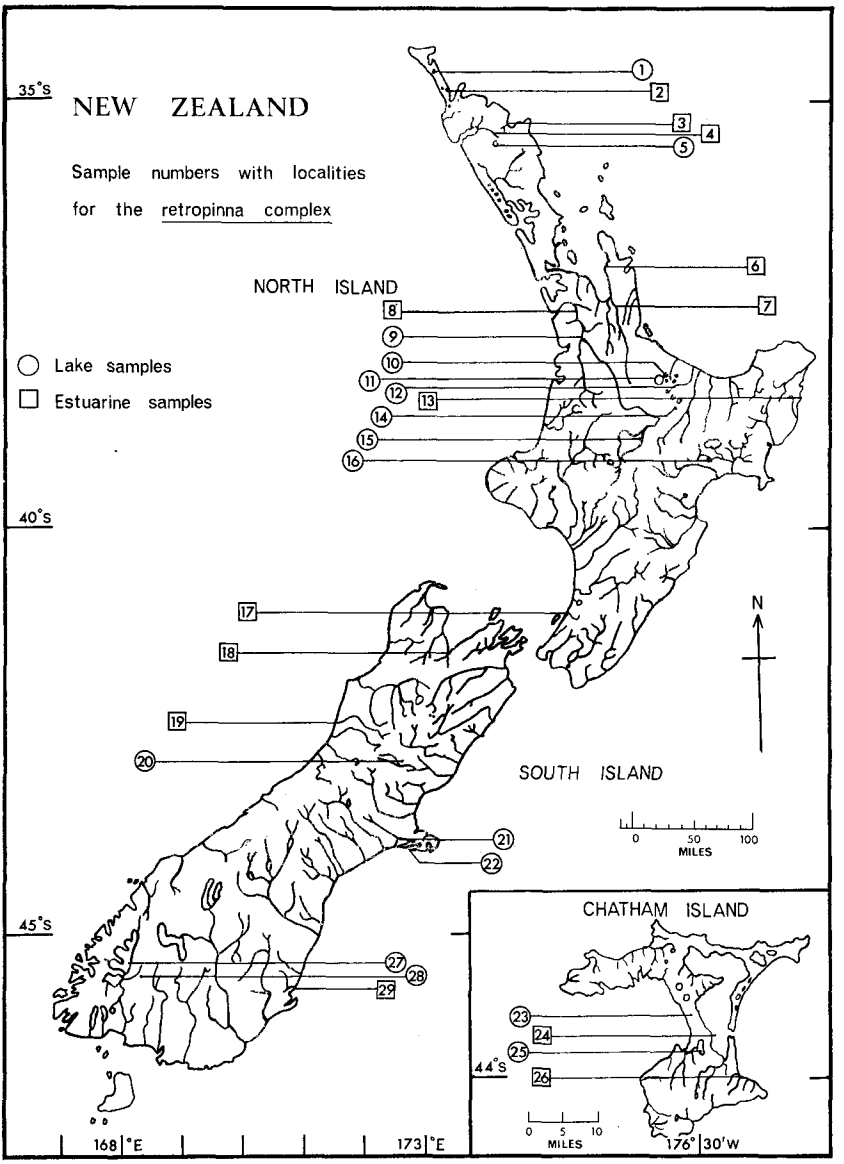


FIG. 2—New Zealand and Chatham Island showing the localities of all lake and estuarine samples. Sample numbers are as in Table 2 where the names of each are given.

represented by samples 5, 11 (and 10), and 23 (Figs 3c, 3d, and 4b) from their type localities, Lake Omapere, the Ohau Channel between Lake Rotorua and Lake Rotoiti, and a small lake near Henga, Chatham Island, respectively. The nominal form, *R. obtusirostris,* from a lake near Lake Te Anau (Fig. 3e), and forms from Lake Marion (sample No. 18), and Lake Ellesmere (No. 21), which Stokell (1955, 1966b) discussed as new species are analysed below as part of the *retropinna complex.*

CHATHAM ISLAND *Retropinna*

Chatham Island has numerous small shallow lakes which are low-lying and a large lagoon (Te Whanga) which may at times be supersaline when evaporation from its 70 square mile surface exceeds freshwater inflow. That its salinity has not varied greatly from that of normal sea water in very recent geological time is inferred by the author from the presence of distinctive characters in a species of *Gobiomorphus* (Eleotridae) from tributaries of Te Whanga Lagoon. This species shows very little variation throughout its New Zealand-wide range and appears to be stenohaline (marine) at the larval stage. Skrzynski (1967) has recorded the habitats available to freshwater fishes and a checklist of known species for Chatham Island. All of these, excluding *R. chathamensis,* occur on the New Zealand mainland and are known to have a marine stage in their life-histories (for *Galaxias* see Woods, 1968).

By permission of the Marine Department, which I gratefully acknowledge, I can report on samples of Chatham Island *Retropinna* obtained by Mr Skrzynski in October 1966. Mr Skrzynski noted marked superficial dissimilarities between specimens from the Lake Huro outflow stream (No. 25, Fig. 4b) and others from the Te Whanga Lagoon and its tributaries (No. 24, Fig. 4a) and from the mouth of a stream near Owenga (No. 26). An older Chatham Island sample (No. 23) collected by Major G. F. Hutton from a small land-locked lake near the Kairakau school near Henga (?L. Marakapia), is used below with these.

The frequencies of variants for four characters of four Chatham Island samples are included in Table 2. Each sample is seen to have a dissimilar assemblage of characters and each appears to represent a distinct population. But a dichotomy is evident between the lake samples and the lagoon and estuarine samples. The lake fish tend to have fewer dorsal and anal fin rays, fewer scales, and lower head in standard length ratios, than the estuarine fish. Also, for the Lake Marakapia sample, eight fish have a double row of vomerine teeth, two have a single row, and two have an intermediate tooth arrangement. The two largest Lake Huro fish have these teeth in two rows, but the 18 remaining fish, juveniles, have either a single row, or one row and a few additional teeth. The holotype of *R. chathamensis* (Canterbury Museum Fish Catalogue No. 67, 78 mm S.L.) has been inspected and has the following characters: 9 dorsal, 16 anal, 57 scales

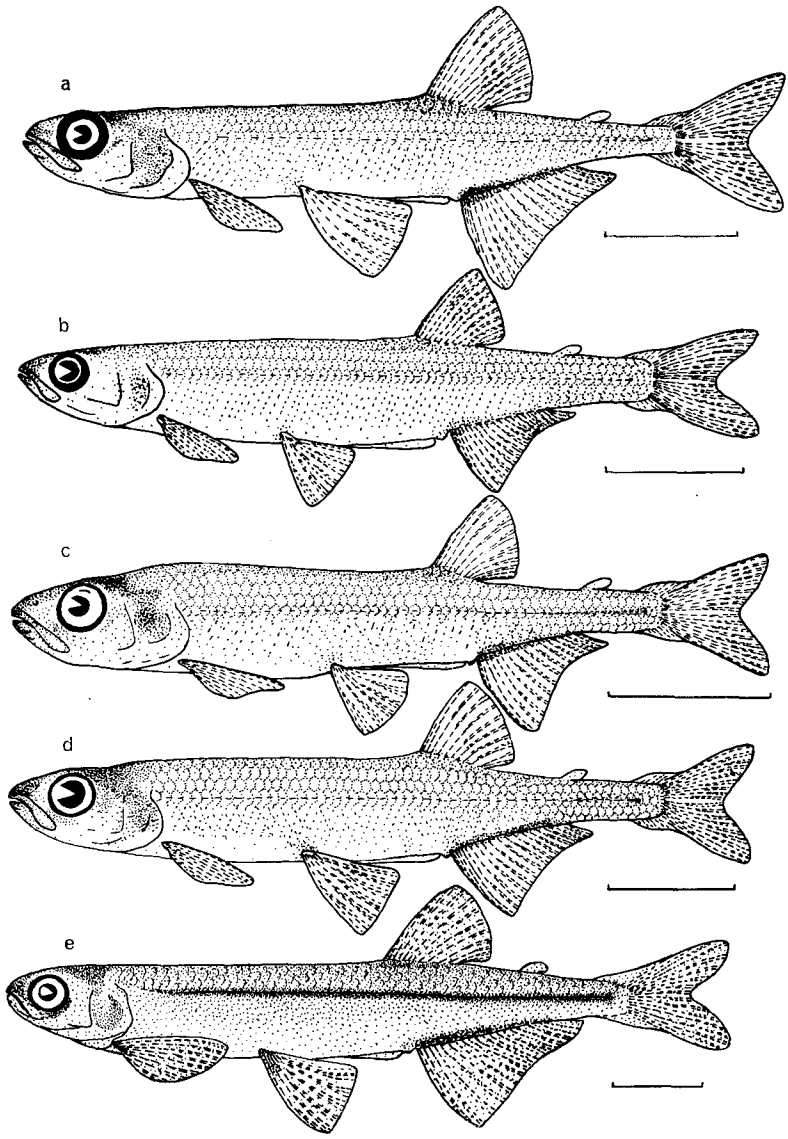


FIG. 3—*Retropinna retropinna complex* from New Zealand. (a) Male. Lake Wahakari. Sample No. 1. (b) Stream at Opua. Sample No. 3. Type area for *R. retropinna*. (c) Lake Omapere. Sample No. 5. Holotype of *R. abbreviata*. (d) Ohau Channel, Lake Rotorua. Between samples Nos 11 and 12. Holotype of *R. lacustris*. (e) Male. Small lake near Lake Te Anau. Paratype of *R. obtusirostris*. (Scale interval 10 mm.)

TABLE 2—Numbers of specimens observed for various characters from each of 29 population samples of the *retropinna complex*

REF.NO.	LOCALITY	HEAD IN S.L. RATIO																	DORSAL RAYS					ANAL RAYS							NO. LONG. SCALE ROWS															
		3							4							4															4		5					5					6					6
		4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	8	9	10	11	12	14	15	16	17	18	19	20	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5
1	LAKE WAHAKARI			1	3	3	1	1									1	1	4	3				4	3	1	1							1	1	1	2	2	0	2						
2	TRIB. HOUHORA HBR.						1	4	1	3									8	1				1	3	4	1						1	2	3	2	0	1								
3	STM. OPUA							2	2	3	4	2							9	4				2	4	6	1							2	4	2	2	1	2							
4	HOKIANGA HBR.					1	3	5	7	1	2	1						1	8	11					3	9	8											3	6	7	4					
5	LAKE OMAPERE	3	4	8	6	3											3	19	2				2	8	11	3				2	3	6	7	6												
6	STM. COROMANDEL							2	1	2	3	2							4	5	1		1	0	3	4	2											2	1	3	3	1				
7	WAIHOU RIVER TRIB.						2	5	1	2									1	7	2				3	5	2									2	0	2	4	2						
8	WAIKATO R.						2	6	4	0	1								7	5	1			1	8	3	1									2	3	2	1	2	2	1				
9	LAKE KARAPIRO							1	3	4	1	1						8	2				2	1	7							1	1	5	2	1										
10	LAKE ROTOITI						1	4	2	2							1	5	3					1	2	5	1				2	2	3	2												
11	LAKE ROTORUA						1	6	3	7	1	2						9	11					4	13	3						5	8	4	1	1	1									
12	LAKE OKATAINA					3	2	2	1								1	4	3						5	3				1	0	2	1	5	1	1									
13	STM. TOKOMARU							1	4	2	1								6	2					4	4												1	0	1	0	1	4	0	1	
14	LAKE NGAPOURI						1	5	4	1							3	7						4	6					1	0	2	2	2	2	1										
15	LAKE TAUPO				1	2	3	8	4	1	1						1	12	7					2	12	6					1	2	4	5	3	2	1	0	2								
16	PUTERE LAKES			1	3	3	5	3	2	1							1	14	3					7	7	4				1	5	5	4	1	2												
17	WAIKANAE R.									2	2	2	3	1					5	4	1			1	4	4	1																	1	1	3	5	
18	WAIROA R.							1	1	1	0	2							3	2	1			1	1	2	1	1																				5
19	KARAMEA R.										1	2	0	1	0	1			2	3					2	2	1																			2	3	
20	LAKE MARION												3	1	1		3	1	1				2	2	1								2	0	1	1	1										
21	LAKE ELLESMERE					1	1	1	7	4	5	2						10	8	2				2	10	2	1								1	4	6	4	1	2							
22	LAKE FORSYTH					2	3	3	2	4	3	3						11	9					3	15	2					2	1	2	5	4	2	2	2								
23	LAKE MARAKAPIA					1	2	1	2	4	2							5	7						7	5							1	1	2	2	4	1	0	1						
24	WHANGA LAGOON										3	6	6	3	2					7	13			1	4	10	5											1	3	4	5	5	1	1		
25	LAKE HURO				1	0	1	4	8	5	1								14	6		1	1	13	5						1	1	1	2	7	4	2	2							
26	OWENGA STM.									2	4	5	2	3	2	2			4	14	2			1	7	8	3	1						2	1	1	3	3	4	2	3	0	1			
27	LAKE TE ANAU												2	1	1	1		2	2	1					3	2												1	1	2	1						
28	LAKE THOMAS								1	2	4	1	2					7	2	1		10												4	2	2	1	1									
29	WAITATI R.								1	0	1	1	2	0	1				1	4					2	2	1																		1	1	3	

in the lateral line, a head in standard length ratio of 4.3, two complete rows of teeth on the head of the vomer, and 56 vertebrae (radiograph). Thus the Lake Marakapia and Lake Huro samples are satisfactorily identified with the type of *R. chathamensis*. The remaining two samples of estuarine fish do not conform closely to this form as described. In addition to the shorter head and higher fin ray and scale counts they typically have only one row of teeth on the vomer. The Te Whanga Lagoon sample has three specimens with two rows, three with one row plus one incomplete row, and one with two rows plus one incomplete row; the remainder (13 fish) have only one row. Only one deviant was found amongst 20 Owenga stream specimens; this fish has an incomplete second row. During this investigation no specimen of *Retropinna* from New Zealand has been observed with other than a single row of vomerine teeth. This is as found by Stokell (1949, p. 205) who pointed out that *R. semoni* and *R. tasmanica* are described as having these teeth biserial. Stokell (1955, p. 18) states that the affinities of the (lacustrine) Chatham Island *Retropinna* lie with Australian species rather than with New Zealand ones. No character other than the double rows of vomerine teeth is known which would support this view. The considerable variation for this character between population samples from Chatham Island requires that its significance be re-evaluated (*see* following).

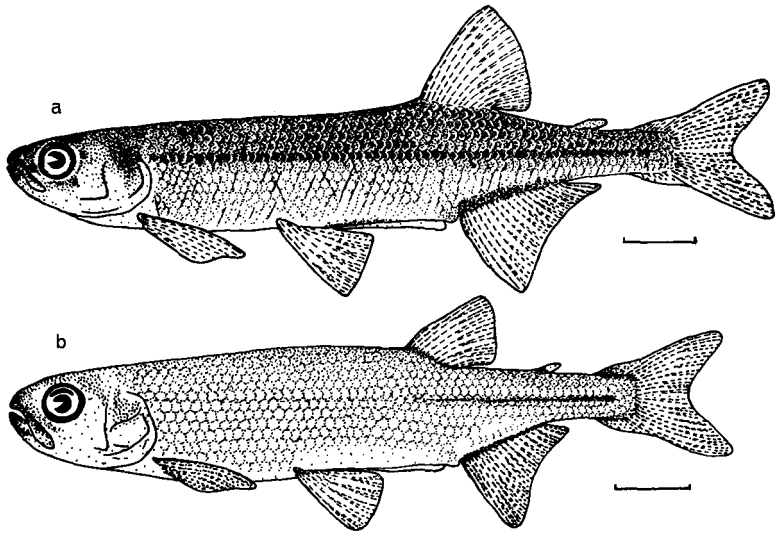


FIG. 4—*Retropinna retropinna complex* from Chatham Island. (a) Male. Te Whanga Lagoon. Sample No. 24. (b) Female. Lake Huro outflow. Sample No. 25. (Scale interval 10 mm.) Large fins are characteristic of males.

Stokell nowhere records examining estuarine smelts from Chatham Island and the taxonomic status of these fish has not been investigated. The lake and estuarine Chatham Island fish differ greatly for several characters (as above) yet only one of the extremes of these (two rows of vomerine teeth) would distinguish them from New Zealand fish. The questions raised by these observations are placed in a wider context and discussed in the following section.

VARIATION WITHIN THE RETROPINNA COMPLEX

Little variation exists within the Retropinnidae for the number of branchiostegal, ventral, or caudal rays, but other meristic characters show considerable variation between individuals within samples, and between samples for the *retropinna complex*. These are the number of dorsal and anal rays, the number of scales in the lateral line, and the number of vertebrae. The latter is not tabled, as its value is very similar to the scale count in all observed populations of the *retropinna complex* (except *R. victoriae*); the vertebral number is not known for *R. tasmanica* (Table 1).

The head length is very variable with respect to the body length, and, to a less extent, the positions of the dorsal, anal, and ventral fins vary. Sample averages show a large head length tends to be associated with a more posterior insertion of the dorsal and ventral fins. Allometric growth was not detected for head length in four large samples which contained a wide range of sizes. Thus the head in standard length ratio is directly comparable for different samples irrespective of the size of the specimens in the samples.

Most available samples were collected during the summer months and several, including lacustrine and estuarine Chatham Island samples, contained ripe fish. All published records on breeding are of spawning (or maximum spawning activity) in the warmer months. It is assumed that there is no important difference in breeding season between any of the populations recorded below. A further assumption is that all species require lake, lagoon, marine, or other non-flowing water conditions at the larval stage. Thus any sample taken in running water is assumed to have come from standing water. No entirely fluviatile populations are known to the author but McCulloch (1922–23, p. 48) assumes that "specimens living in western New South Wales cannot get so far down as the sea to breed . . .". Estuarine *R. retropinna* is known to move considerable distances into rivers. In March 1962, two specimens of *R. retropinna* with estuarine characters appropriate to the latitude of the river mouth were taken by the author from a small shoal (all forms shoal for much of the year) in the Wanganui River above Taumarunui, 160 miles from the sea by river, and at about 600 ft above sea level. This is a unique record for this century, but the Inanga, which Mair (1880) reported to be common in the Upper Whanganui (Wanganui) River, may have been this species.

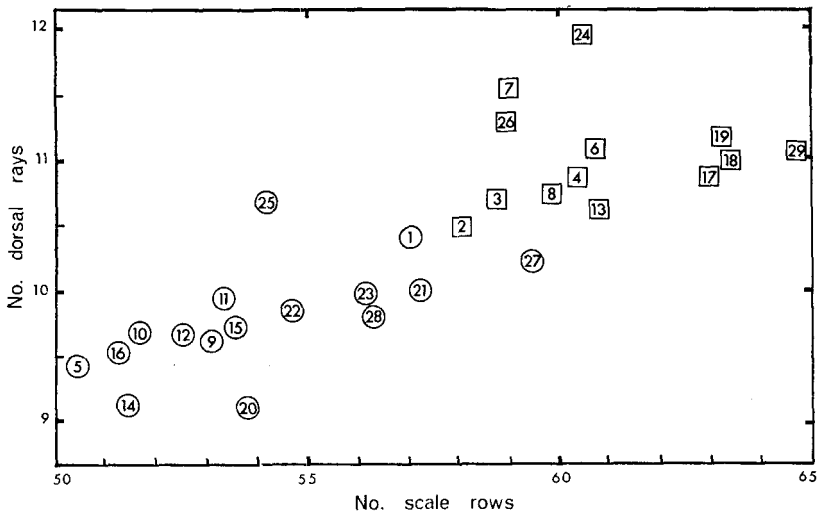
McCulloch (*op. cit.*, p. 52) tabled all fin rays counts for 37 specimens of *R. semoni* from seven localities and showed that those from Queensland have generally fewer anal rays than others from further south. Stokell (1941, p. 364) discussed the relationships between latitude and vertebral number, following Jordan (1919), Huntsman (1919), and Hubbs (1922, 1926). He found a weak irregular gradient of increasing vertebral number towards higher latitudes for New Zealand coastal *Retropinna*, and a decrease from coastal to lacustrine populations. He considered that the variation which he had observed could not be interpreted in terms of temperature gradients and must be regarded, in at least some populations, as being influenced by "other than external causes". Hubbs (1926) described a mechanism for understanding population variation in vertebral number and other characters. He showed that fish in cool, saline conditions have a protracted period of development and tend to be larger, with smaller heads and eyes, and to have more vertebrae and fin rays than related fish living in "accelerating conditions". Warmer, less saline conditions cause increases in the rate of overall growth, and to a less extent, in the rates of development and differentiation of metameric structures. Development is completed at a smaller size and is terminated more abruptly and before a high number of elements have formed. Accelerated development can also lead to the retention of the more juvenile features of some characters and of body proportions.

Temperature is generally acknowledged to be the prime factor involved (Hubbs 1922). D'Ancona (1937, *in* Bertin 1956, p. 46) recorded trends, as given by Hubbs (1926), between Mediterranean fishes and related species in the North Sea and the North Atlantic. Taning (1952) investigated the effects of temperature on meristic characters in *Salmo*. His experiments showed that temperature acts at an early stage to determine the number of vertebrae and fin rays; that the vertebral number is determined before the number of ray elements; and that there is a minimum temperature below which the trends are reversed. Hubbs (1926, p. 60) found that increase in salinity has similar effects to decrease in temperature.

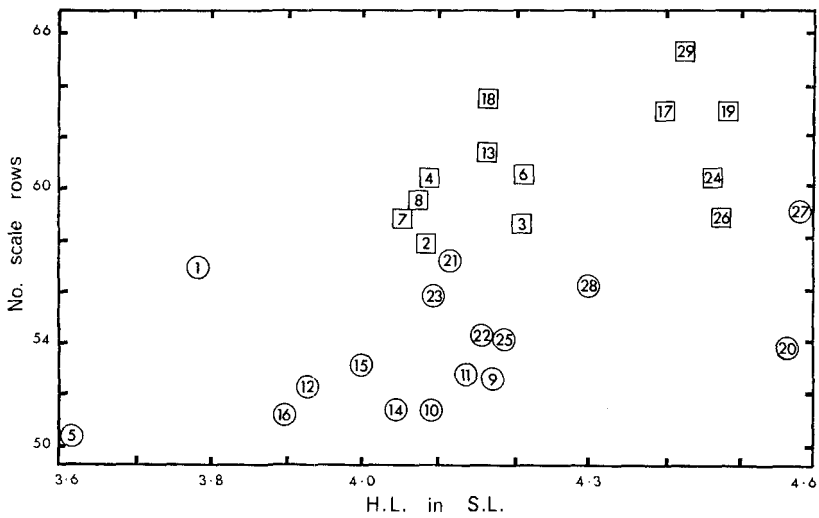
The *retropinna complex* is ideally suited for analyses based on Hubb's (1926) hypothesis. Anatomically similar forms, some marine or coastal, and others lacustrine (to altitudes exceeding 2,000 ft), range through about 20 degrees of latitude. In New Zealand the observed range (*see* Table 2) is from 34°40′S (Lake Wahakari, No. 1) to 45°30′S (Lake Thomas, No. 29), and coastal forms probably occur on Stewart Island (47°S). *R. semoni* ranges northwards in Australia to southern Queensland (27°S).

Table 2 presents the observed frequencies of variants of four characters for each of 29 population samples of the *retropinna complex*. These data have been plotted graphically to relate the mean values of each character, for individual samples, against the mean sample values of the other characters (6 plots) (Figs 5–7). Similarly, for each character the mean values of each sample have been plotted against

Fig. 5

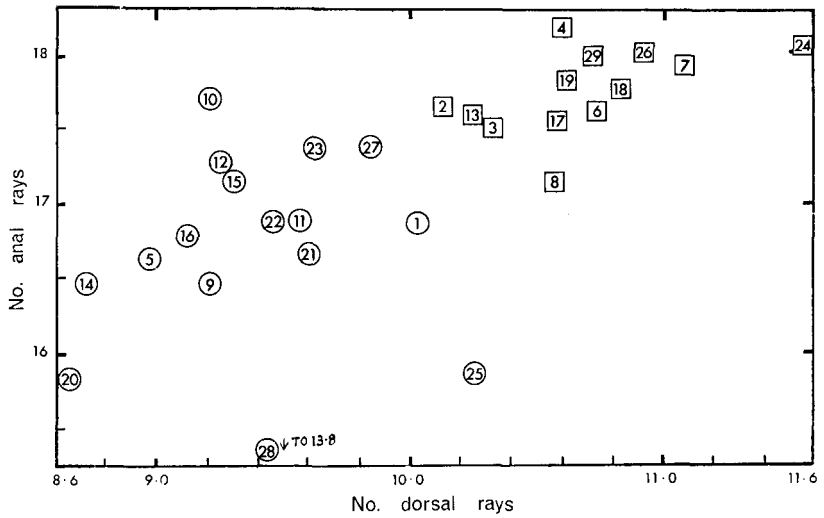


2. Fig. 6

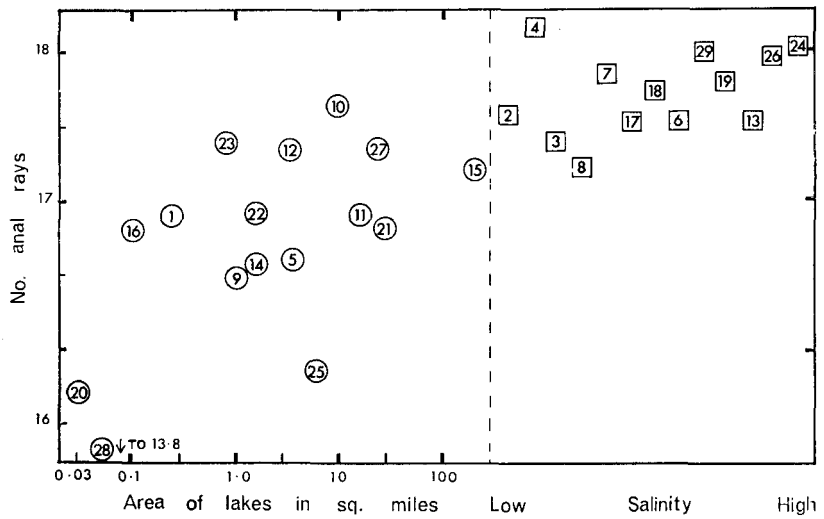


FIGS 5–12—*Retropinna retropinna complex*. Inter-relationships of fin ray numbers and head in standard length values, using sample means, and relationships of these with latitude, salinity, altitude. and area of lake surfaces using mean values of 29 population samples. Sample numbers are as for Fig. 2 and Table 2. Lake and estuarine samples are indicated by circles and squares respectively.

Fig. 7



2. Fig. 8



(1) latitude, (2) salinity or altitude, and (3) salinity or area of lake (12 plots) (Figs 8–12).

The main features of the graphs in Figs 5, 6, and 7, and of the other three in this series (not figured) are: 1. Estuarine samples tend to aggregate at the higher values. 2. The lake samples show a wider

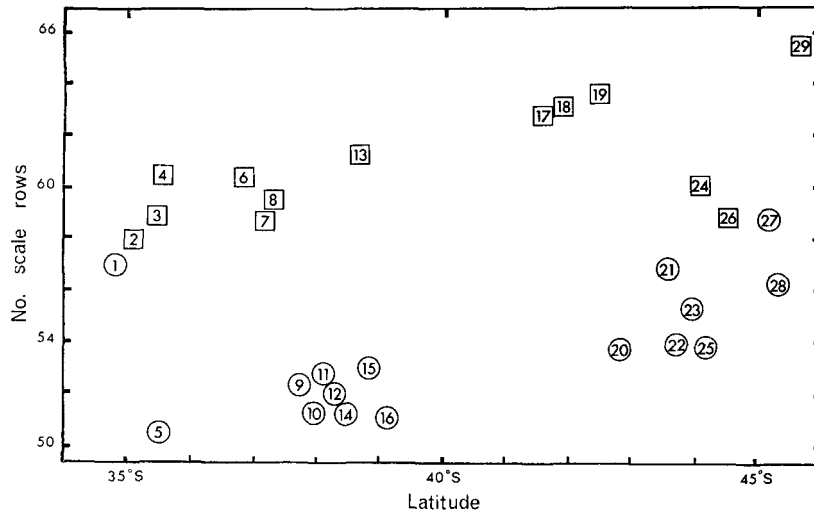
scatter, at lower values. 3. Four samples (Nos 21, 22, 23, 25) from brackish lakes or lagoons close to sea level lie at intermediate values. Thus the lacustrine, brackish water, and estuarine samples form a continuous series along a positive axis for each pair of characters. This suggests that there is a similar relationship between these four characters in all populations and that saline conditions have a retarding effect leading to a shorter head length and an increase in the numbers of meristic characters, and that freshwater conditions produce the opposite effects. However, the scatter of points is wide in all the graphs, particularly for the head in standard length ratio against the number of anal rays. The samples which deviate most from a mean line on any graph are investigated here following an analysis of the relationships between observed character values and environmental conditions.

Latitude. With increase in latitude there is a tendency for the number of scale rows to increase. In lake samples this increase is from about 50 to about 56 scale rows, with estuarine samples increasing from about 58 to 65 (Fig. 9). The value of the head in standard length ratio increases similarly from about 3.8 to about 4.3 in lacustrine samples, with esturane samples approximately 0.2 units higher (Fig. 10). The mean dorsal ray count increases by about one ray from about nine for lake fish, and 10 for estuarine fish (not figured). No relationship is apparent for the anal ray count.

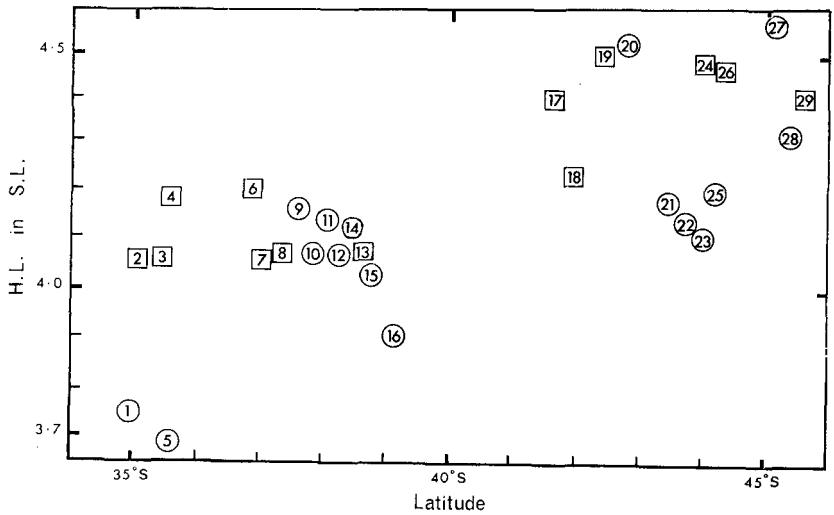
Since temperature decreases with increase in latitude the above observations are readily interpreted in terms of a transition from accelerating to retarding thermal growth-conditions. Minor climatic effects cause local fluctuations in temperature which will certainly account for some of the variation observed between samples at similar latitudes. Likewise, individual variation within samples must partly be accounted for by temperature differences related to the prolonged spawning season of these lake fish. Jolly (1963) records a spawning season of nine months in Lake Rotorua at temperatures ranging from 52° to 77°F, and of seven months in Lake Taupo at 59° to 72°F; eggs were most numerous in late spring and early summer and were most commonly found near stream mouths. The very high values for the head in standard length ratios for samples Nos 20 and 27 (Lake Marion and Lake Te Anau) may be due to local factors. One such factor could be the very low temperature of inflowing water since these lakes are closely surrounded by mountains of altitudes from 5,000 to 6,000 ft.

Salinity. As recorded earlier the differences in meristic counts between estuarine and lacustrine samples are attributed to the retarding effects of highly saline as compared to freshwater conditions. The sequence into which the estuarine samples have been placed with regard to salinity (*see* above) is highly subjective and no scale is given. The desired data are the salinities in which the larvae are living at decisive periods of their development. However, the sequence of localities from inferred high to low salinities tends towards a positive correlation with the number of anal rays (Fig. 8), the number of scale rows

Fig. 9



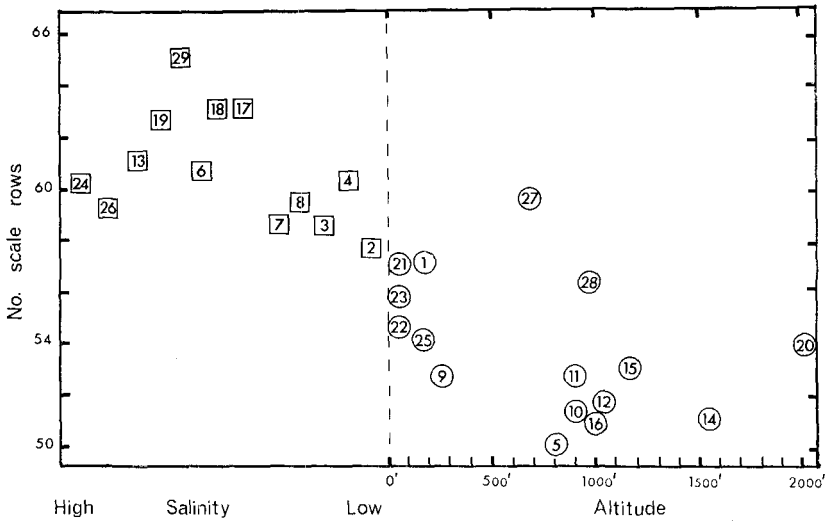
2. Fig. 10



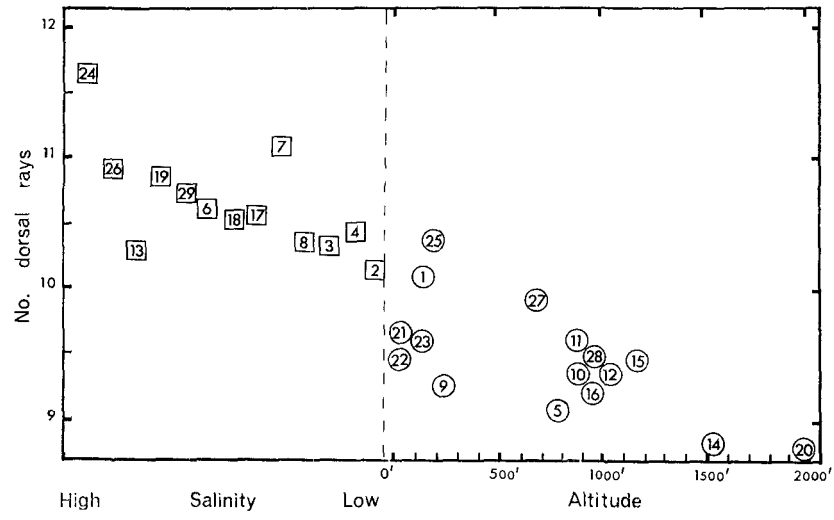
(Fig. 11), and the number of dorsal rays (Fig. 12). The graph (not figured) which related salinity, as above, and sample values for the head in standard length ratio has a similar but less clear trend. Overall, the tendency shown is for the more saline waters to produce fish with higher meristic counts and smaller heads than those of the less saline waters.

Altitude. Temperature decreases predictably with increase in altitude. Increasing altitude, therefore, could be expected to produce an increase in the number of meristic elements similar to that observed above for increasing latitude. However, the opposite effect has been found for *Retropinna.* The plots of number of scale rows (Fig. 11), and of numbers of dorsal rays (Fig. 12), against altitude, showed negative

Fig. 11



2. Fig. 12



correlations and a scatter of points no greater than for the plot which relates these two characters (Fig. 5). The negative correlation for the number of anal rays and altitude is not so clear and no relation is apparent between the head in standard length ratios and altitude (not figured).

A reversal in the expected relationships of number of dorsal or anal rays to temperature gradients, owing to latitude and altitude, is recorded by Hubbs (1926, p. 66) in five species, all of different genera, of American cyprinodonts and minnows. He concludes that, "in all these cases the exceptional variational trend seems to involve only the one fin, not the number of vertebrae, or other characters. No explanation of such cases can be offered now". Subsequent work (Hubbs 1940, p. 199) has shown that these reverse trends are a general feature of the middle American viviparous cyprinodonts and are due to genetic differences between populations of the same species. A similar slight negative correlation between the anal ray count and altitude may exist in lake populations of the *retropinna complex.*

The present case differs in that it is the effect of one environmental factor, altitude, on at least two characters (numbers of scale rows and dorsal rays) which shows a reversal of the usual trend while these same characters show the usual relationship with other environmental factors. Necessary field data and experimental results are not available to help in understanding how two opposed trends can both operate on at least two characters which, if temperature (heat) is the operative influence, should have synergic effects. One explanation which could account for these observed effects is that populations at high altitudes may breed during a short period which coincides with peak temperatures. This could be regulated either directly, for example, by the development of a thermocline, or indirectly, through seasonal abundance of food organisms. Alternatively a genetic cline with altitude could be opposing the general effects of temperature differences with latitude. That two environmental factors, each producing opposing results in terms of temperature, can affect the same character is shown by Lindsey (1953) who, in a detailed study of the North American redside shiner, finds a positive correlation between mean anal ray counts and both increasing temperature and increasing latitude.

The most relevant conclusion in the present instance is that the mechanism, whatever it may be, has a similar influence on all the lake populations.

Area. Many fishes and other animals do not grow to their normal size if space is limited, or if they are overcrowded. These two features cannot be distinguished for *Retropinna* in this study. Size of fish is not used as a character in this account, except very broadly, since in these shoaling fishes no sample can be expected to reflect the typical size of fish in a population.

Rupp and Redmund (1966) show that the mean size and rate of development of *Osmerus mordax* may be greatly altered by transferring fish from one lake to another. Jolly (1963, fig. 1) reared a Lake

Rotorua specimen of *Retropinna* in a pond until it was 40% longer than any specimen which she had observed from this lake, or from Lake Taupo. McDowall (1965), on the basis of one collection of *Retropinna* from Lake Omapere, stated that this is the shortest form of *Retropinna*. Of 26 fish taken in this lake by the author, 16 were longer than any found by McDowall. How large might Lake Omapere smelt grow if transferred to Lake Huro? (Figs. 3c and 4b.) With the present material it can be stated with certainty only that *Retropinna* from Chaham Island and from coastal localities grow larger than mainland lake populations. The fish in Lake Omapere show the most "accelerated" features of any sample and could be expected to remain small (another feature of accelerated development), but several other samples, including those from the inland South Island lakes with "retarded" characters are of smaller fish still. However, the largest New Zealand lacustrine specimen known to the author (Fig. 3e) is from a South Island lake.

The mean number of anal rays in each lacustrine sample has been plotted against the surface area of the lake (Fig. 8). The trend is not marked, but if anything, it is for fewer anal rays to develop in fish in the smaller lakes. No relationship exists between lake area and the number of dorsal rays, scale rows, or the head in standard length ratio. The area of each body of water is therefore unimportant for these characters.

Atypical characters. In Table 3 the samples which deviate most appreciably from the general scatter of points for any graph, whether figured or not, are recorded. The table shows the character involved, and whether it is unusually high or unusually low with respect to another character or environmental feature. The last column refers to any feature in which this character conforms to other samples.

Table 3 shows that five of the 14 characters, in 10 samples, which deviate most on the various graphs, conform with a majority of other samples when related to latitude. With some duplication, five cases conform when related to altitude and one when related to salinity. The low anal counts of the Lake Huro (No. 25) and Lake Thomas (No. 28) samples cannot be accounted for by an environmental factor on present evidence, but in both these cases a neighbouring lake population has normal anal ray counts. The dorsal ray count of sample No. 7 is higher, and the number of scale rows of sample No. 26 is lower than could be expected.

DISCUSSION

The observed relations between the effects of accelerating and retarding environmental factors and meristic characters are presented in Table 4. Differences in salinity and latitude, despite the opposing influence of altitude, allow the best interpretation of variation. The effects of altitude, although not understood, have a marked influence on lake samples, but the area of lake surface is unimportant. The

TABLE 3—Characters which deviate most appreciably from observed relationships in the *retropinna complex* and environmental features or other characters with which these conform

Sample No.	Deviant Character	Deviates with respect to: (*Low*)—relative value—(*High*)		Conforms with respect to:
1	Dorsal		Latitude; H.L.R.*	Altitude; Scales
	Scales		Latitude; H.L.R.	Altitude
7	Dorsal		Latitude; H.L.R.; Salinity	Anal
10	Anal		Altitude; Area; Dorsal; Scales	Latitude; H.L.R.
13	Dorsal	Salinity		Latitude; Scales; H.L.R.
20	Dorsal	Latitude; H.L.R.		Altitude
	Anal	H.L.R.; Scales		Altitude; Area; Dorsal; ?Latitude
	Scales	H.L.R.		Latitude
24	Dorsal		Scales	Salinity
25	Dorsal		Scales	Latitude; Altitude
	Anal	Area; H.L.R.; Scales; Dorsal		?Latitude
26	Scales	Latitude; Salinity		—
27	Scales		Altitude	Latitude; H.L.R.
28	Anal	Area; H.L.R.; Scales; Dorsal		—

* Head length in standard length ratio.
"Dorsal", "Anal", and "Scales" refer to mean sample values of ray counts and number of scale rows.

mean sample values of any character will be in a balanced relation involving each of these factors and other influences.

Present results relate all lacustrine forms of *Retropinna* and estuarine *R. retropinna* and no meaningful divisions can be made between observed populations for the characters recorded above. Samples from low-lying lake populations on Chatham Island are very similar to the brackish Lake Ellesmere and Lake Forsyth samples, and fish from South Island lake samples are more similar to North Island coastal fish than to North Island lake fish. The coastal and lacustrine populations from Chatham Island (Nos 23–26) differ widely for the characters analysed above. However, these differences can be attributed to the environmental conditions of each population, and variation follows the same patterns as in the mainland forms.

TABLE 4—Causative conditions for protracted and accelerated rates of development, and the effects produced in the *retropinna complex*. (Items not tested other than by observation are in parenthesis.)

Protracted Development	Accelerated Development
Causative Conditions	
High salinity	Reduced salinity
High latitude	Lower latitude
Low altitude	Greater altitude
(Large body of water)	(Smaller body of water)
(Limited heat)	(More heat)
Effects Produced	
More scale rows	Fewer scale rows
More fin elements	Fewer fin elements
Smaller head	Larger head
More vertebrae	Fewer vertebrae
(Smaller eyes)	(Larger eyes)
(Larger size)	(Smaller size)

No osteological differences are known which distinguish any population of the *retropinna complex* but the numbers of teeth on the head of the vomer vary according to the geographical location of the specimen. A double row characterises the nominal *R. chathamensis* and also *R. semoni* and *R. tasmanica,* whereas in all populations of the *retropinna complex* in New Zealand there is a single row. As observed above, the lagoon and coastal populations of *R. chathamensis* typically have only one row and occasional deviants have one additional row, rarely more. It is considered significant that a double row occurs more often in the large lacustrine Chatham Island fish which have relatively large heads, and only occasionally in the large lagoon and coastal fish which have relatively small heads. This is seen to parallel the loss or reduction in number of maxillary teeth in South Island lacustrine populations where specimens have relatively small heads. *R. obtusirostris* is described as usually lacking maxillary teeth and as having uniserial teeth in the lower jaw. *R. lacustris* is described as variable for the number and disposition of teeth. *R. retropinna* (after Stokell) is larger and usually has maxillary teeth while the lower jaw has biserial teeth anteriorly. As recorded above, Stokell (1941) found, in group averages, a tendency for larger fish to have more teeth. These observations have been confirmed during this study and it is considered that they are applicable to the New Zealand and Chatham Island fish as a whole, and that variation in the number and disposition of teeth is an unsound taxonomic character within this group. The double row of vomerine teeth in lake specimens of the nominal *R. chathamensis* is considered to be a local phenotypic expression related to a general capacity. The occurrence of the same character in Australian species is assumed to have a similar basis and does not imply a specially close affinity with Chatham Island fish.

Some small genetic differences are assumed to be present between all more or less isolated populations of any animal species. The results of this study, however, suggest that none of the characters which distinguish observed populations of the *retropinna complex* need to be interpreted as being attributable to major genetic differences. The evidence given above does not preclude genetically based speciational changes related to the environment. Nongenetic differences induced by retarding or accelerating environmental factors may become fixed by genetic modifications. This requires that the nongenetic characters produce a well adapted phenotype in a stable environment, such that the characters need not usefully be labile. For a new species to be formed a period of time is then required sufficient to allow genetic modifications to accumulate.

This process has not gone far in the *retropinna complex* in New Zealand. Marine wandering undoubtedly links all diadromous populations and these are readily accepted as being of one species. Lake samples bear an approximately constant relationship to diadromous samples at any given latitude, allowing for fluctuations due to other environmental factors. This is interpreted as indicating that no major differences exist in any sample and that speciation has not been completed in any lake. If speciation had occurred, two species could co-exist in one locality, but no lake in New Zealand is known to contain more than one form of *Retropinna*. This suggests that the invasion of lakes is recent and incomplete.

It is probable that most lakes have been entered independently, and repeatedly, by *Retropinna* from coastal stock, and that this is still occurring. Chatham Island populations are probably assimilating such a large number of New Zealand immigrants that expression of local genotypic variation is limited. Skrzynski (1967, p. 94) gives evidence that Lake Huro and other small lakes near Henga are probably of very recent origin. Some may be less than 200 years old.

Speciation has occurred in *Retropinna; R. osmeroides* is distinct from all observed populations of the *retropinna complex* in its large vomerine teeth and its large size. It is the number, rather than the size, of these teeth that increases with the size of the fish in the *retropinna complex*. Otherwise the size, small head, and high number of vertebrae, scale rows, and fin rays of *R. osmeroides* are at values which would be expected for a largely marine-living member of the *retropinna complex*. It is principally the circumstances of wide, largely overlapping coastal distributions (sympatry) of *R. osmeroides* and coastal populations of the *retropinna complex* which proves the specific identity of the former.

The main conclusion reached in this study is that the coastal and lacustrine populations of the *retropinna complex* in New Zealand and Chatham Island are of one species. Variation has been demonstrated to be largely related to environment; otherwise no differences are known which can be used to distinguish any population or groups of populations. The 29 populations which have been analysed are considered

to belong to one species, *R. retropinna* Richardson, which should be considered to be highly adaptable rather than very variable. Variation, as demonstrated, is a specific property common to all component populations, and it relates them.

No distinguishing features which would warrant taxonomic (subspecific) distinction for any local populations are known. While a case could be presented for recognising *R. retropinna* from Chatham Island as a subspecies it is felt that a more detailed study of variation in the arrangement of vomerine teeth and in the size of fish is desirable first, particularly for Chatham Island populations and Australian forms.

The concept of local races is useful here and does not involve nomenclatural distinctions. Following Wilson and Brown (1953) it is suggested that, where necessary, geographic groups of populations be referred to by colloquial names, as follows:

Common smelt for diadromous populations from New Zealand and Chatham Island (*R. retropinna* of Stokell, 1941; Woods, 1963);

North Island lake smelt for *R. lacustris* and *R. abbreviata*, etc.;

South Island lake smelt for *R. obtusirostris*, etc.;

Chatham Island lake smelt for *R. chathamensis*.

"Smelt" refers to, and may be replaced by, "*R. retropinna*" and the family may be called the "southern smelts".

Australian and Tasmanian *Retropinna* have been included in the *retropinna complex* and require to be distinguished from the comprehensive species of *R. retropinna*. The recorded disparity between the number of vertebrae and scale rows in *R. victoriae* (Table 1) is unique in Retropinna (but occurs in *Stokellia* at different values) and would appear to be sufficient evidence of a major difference in organisation from *R. retropinna* to validate this species if confirmed on further samples. *R. semoni* and *R. tasmanica* are isolated geographically, unlike the nominal forms in New Zealand, and comparison is difficult. Also the number of vertebrae of *R. tasmanica* is unknown to the author. The characters of *R. tasmanica* indicate protracted development and of *R. semoni*, accelerated development, relative to New Zealand forms. Jolly (1967, pp. 331, 337) confirms that *R. semoni* has both diadromous and lacustrine populations, as for *R. retropinna*, and shows that ova of both species have similar rates of development. It is suggested that the recorded differences between *R. semoni* and *R. tasmanica* do not constitute important distinctions, and these species do not differ appreciably from *R. retropinna* as described below.

The author at first considered the *Retropinna* population at Lake Wahakari to be a new species. All observed specimens have large heads, relatively high dorsal ray and scale row counts, and extremely large eyes (Fig. 3a). The large head is found to be normal, taking into account the low latitude of this locality (No. 1), and large eyes (Hubbs 1926) are to be expected as an associated character. The numbers of dorsal rays and scale rows are higher than would be

expected at this latitude, but the opposed influence of altitude places these characters in a predictable relationship with other populations of the *retropinna complex*.

Stokell (1955, p. 12) suggests that "the marine and estuarine species of Retropinnidae appear to have evolved from freshwater ones". McDowall, in his description of *R. abbreviata* (1965, p. 91) suggests that this fish, *R. lacustris*, and *R. obtusirostris* "appear to have differentiated from *R. retropinna* in the geographic isolation resulting from restriction to freshwater". Stokell supports his arguments with the evidence that all species spawn in freshwater, including marine species (*R. osmeroides* and *S. anisodon*) that enter freshwater only to spawn, and suggests that this shows that freshwater is the ancestral habitat. McDowall does not support his statement.

The conclusion following from the taxonomy of *Retropinna* adopted here is that there are no entirely freshwater-living species (?*R. victoriae*) and that freshwaters are being colonised by *R. retropinna* in New Zealand and *R. semoni* in Australia. The problem of the origin of spawning in freshwater will be discussed elsewhere as the same situation has been found to occur in the New Zealand Eleotridae and in some species of *Galaxias*.

McDowall (1967, p. 9) used his interpretation of the relationships of *R. abreviata* and *R. lacustris* with coastal *R. retropinna* to support his recognition of two new species of *Galaxias* as lacustrine isolates of the diadromous species *G. maculatus attenuatus*. These isolates have larger heads and eyes, fewer vertebrae, and lower ray counts for most of the fins than *G. m. attenuatus*, and thus bear a similar relationship to *G. m. attenuatus* as do lacustrine to diadromous populations of *R. retropinna*. McDowall records meristic characters for these *Galaxias* and suggests that the "distinctions may not be simply a case of temperature related differences". His evidence for this, and for naming two new species among these isolates, is that the number of gill-rakers is greater, whereas the numbers of vertebrae, etc., are fewer in both lacustrine forms, and that for one or two body proportions *G. m. attenuatus* is somewhat intermediate between the lacustrine forms. The significance of these features requires to be investigated further.

McDowall (1967, p. 9) suggests that the diadromous species *Galaxias brevipinnis* is the parent species of *G. lynx* from South Island alpine lakes and of *G. koaro* from lakes in the central North Island plateau, New Zealand. He states that "further study may well suggest that *G. lynx* and *G. koaro* are conspecific". This will probably be confirmed since these three species are similar in most respects and *G. brevipinnis* has the pattern of the smaller head, more vertebrae, and more rays in each fin, as found in *R. retropinna*.

The concept of speciational changes related to the environment will prove to be a rewarding field when applied to the Galaxiidae. For New Zealand freshwater fishes, such changes are probably seen in their earliest stages and simplest form in the Retropinnidae.

DESCRIPTION

Richardson (1845), in the original description of *R. retropinna*, records that the mandible projects conspicuously and figures a specimen in which the mouth is open and the lower jaw protruding. This fact is noted by McCulloch (1920–23, p. 49) who figures two specimens with equal jaws and records that, "In other specimens the mandible projects well beyond the upper jaw as described and figured by Richardson." He records that a specimen which he received from the British Museum as "Cotype of *R. richardsonii*" (= cotype of *R. retropinna*, see following) has sub-equal jaws, and he figures this specimen with equal jaws. Stokell (1941, p. 370) records that *R. osmeroides* may show a moderate projection of the lower jaw and as McCulloch did not distinguish this species from *R. retropinna* he may have used material of *R. osmeroides* (Fig. 1b). No specimen of *R. retropinna* has been observed which agrees with the original description in this character.

There would appear to be a serious discrepancy between the original description of *R. retropinna* and all specimens subsequently referred to it (excluding *R. osmeroides*), and the position has not been resolved. The present author suggests that Richardson's specimens, all juveniles, may have been preserved with open mouths, as figured by him. In this condition, because of the form of suspension in the lower jaw, it does appear to project conspicuously in *R. retropinna*.

Retropinna retropinna (Richardson)

Figs 3 and 4

Argentina retropinna Richardson, 1845, p. 121, Pl. lii, figs 1–3.
Retropinna Richardsonii Gill, 1862, p. 14.
Retropinna richardsonii Guenther, 1866, p. 171.
Richardsonia retropinna Kner, 1865–1867, p. 318.
Retropinna Richardsonii Hector, 1870, p. 133, Pl. xviii, fig. 3; Hutton, 1872, p. 58 (partim); Hector (*In* Hutton, 1872), p. 126.
Retropinna Richardsonii var *elongata* Klunzinger, 1879, p. 413, Pl. 53.
Retropinna retropinna Waite, 1907, p. 10; McCulloch, 1920–23, p. 47, figs 1 and 2; Phillipps, 1940, p. 53, fig. 32; Stokell, 1941, p. 361, Pl. LV, figs 1 and 4; Pl. LVI, fig. 2.
Retropinna obtusirostris Stokell, 1941, p. 367, Pl. LVII.
Retropinna lacustris Stokell, 1943, p. 172.
Retropinna chathamensis Stokell, 1949, p. 205, Pl. XLIII.
Retropinna sp. Stokell, 1955, p. 15, Pl. V, 1.
Retropinna abbreviata McDowall, 1965, p. 89; figured.

B.5–6; D.8–12; A.13–20; V.6; P.10–11; C.18–19 (principal rays). Vertebrae 49–66 (excluding hypural).

Head 3.4–4.8 in standard length; body moderately slender to elongate; caudal peduncle narrow. Jaws equal or nearly so with mouth closed; mouth moderately oblique to steeply inclined; premaxillary underlies anterior third, to half, of maxillary; maxillary dilated posteriad,

reaching to the pupil. Eye moderate to very large, 4.2–3.1 in head length. Pectorals low set; ventrals mid-abdominal, inserted at 0.41–0.52 of S.L.; dorsal rearward, inserted at 0.62–0.70 of S.L., its base just anterior to, or up to 0.6 of it overlapping the anal base; anal base long, 1.5–1.9 of dorsal base; adipose fin above or just behind anal insertion; caudal deeply forked.

Teeth generally small and variable in number in adults; those on vomer somewhat larger but not protruding below profile of gape; lingual teeth longest, curved; hyoid teeth small. Teeth typically present and uniserial on premaxillary, maxillary (may be absent), mandible (may be biserial), head of vomer (parallel to premaxillaries, from 3–15 teeth in 1 (typical) to 2+ rows), palatine (may be biserial), and lingual (towards lateral margins, may have smaller median teeth). Endopterygoid with 1 to several rows, hyoid teeth dense.

Scales moderate, delicate, cycloid; 48–67 rows from upper angle of opecular opening to hypural joint; 8–13 between anal and dorsal origins; isthmus, breast, and fin bases naked. No true lateral line. Abdominal keel extends from pectoral base to anus, progressively enlarging from behind ventrals.

Maximum size varies with habitat; usually least in lakes, from about 50 mm L.C.F.; greatest in estuaries and brackish waters, 101 mm L.C.F. observed.

Habitats marine, estuarine, and fluviatile or lacustrine throughout New Zealand and Chatham Island. Breeding period spans several months, maximum activity in shoals in early summer, ova small, usually deposited near flowing water. Males develop nuptial tubercles along fin rays and on scales; fins larger in males.

Dark pigment around mouth, on occiput, fin bases, and in a thin lateral strip which increases posteriad to hypural joint. Dorsal surface lightly to moderately pigmented. General surface, in life, pale, with a highly reflecting lateral band, which may appear blue to purple depending on incident light.

Types. The British Museum has 11 Cotypes; four specimens, Registered No. 1855.9.19.885–6, no locality, ex Haslar Collection, labelled *R. richardsonii* (probably by Guenther, after Gill, 1862) measuring 49, 45, 45, and 44 mm S.L.; and seven specimens, unregistered, from New Zealand, ex Haslar Collection, measuring 56, 55, 55, 53, 53, 50, and 48 mm S.L.

R. retropinna differs from *R. osmeroides* in the size of the vomerine teeth which are not greatly enlarged; in having equal or almost equal jaws; in smaller maximum size; and in being less marine in habit. It differs from *Stokellia anisodon* in having the premaxillary short and fewer number of scales; from *R. victoriae* in the number of vertebrae and of scales in the lateral line; and from *R. tasmanica* and *R. semoni* in exclusive distribution.

Variation. *R. retropinna* exhibits wide geographic variation in many characters. Fish from northern lake populations tend to have larger heads and eyes and fewer serial elements than those from estuarine or southern lake populations. Lacustrine fish tend to be smaller than estuarine specimens.

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