AN INVESTIGATION OF THE GREENBACK FLOUNDER,

RHOMBOSOLEA TAPIRINA GUNTHER

by

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C O N T E N T S

I. INTRODUCTION

Apart from the work of Thomson and Anderton (1921), Finlay (1928), and Rapson (1940), little is known of the biology of southern hemisphere Heterosomata.

As it is usual for fishery investigations to be first directed towards commercially important species the relative minor importance of the flatfishes in most southern countries accounts for the small contributions made to the knowledge of this interesting group. The three papers referred to above, describe work done in New Zealand where flatfish form about ten per cent. of the landed weight of trawled scale fish or seven per cent. of the total catch of all species.

Although the annual catch of the commercial species of flounders and soles is less than one per cent. of the total scale fish catch of Australia, they are nevertheless economically important in the areas where they are caught due to the high market price they command.

The greenback flounder is the predominant flatfish of Victorian and Tasmanian waters and forms more than ninety per cent. of the whole Australian flatfish catch. The entire flounder fishery is limited to the operations of onshore fishermen and the numbers taken by either trawl or Danish seine are negligible.

This represents the first attempt to contribute to the biological knowledge of the species in Australia and it should be pointed out that its contents should be regarded as an introductory rather than a comprehensive account of the problems investigated. Throughout the work the writer has been conscious of the need for a far more extensive sampling programme than funds and facilities permitted but it is hoped that what is presented will form a useful guide to any future investigation of the greenback flounder.

II. SYSTEMATIC POSITION

Rhombosolea tapirina Gunther is one of four species of the genus *Rhombosolea* belonging to the subfamily Rhombosoleinae of the order Heterosomata. All four species are represented in New Zealand but *tapirina* is the only member occurring in Australian waters. The Rhombosoleinae were first described by Gunther (1862) who published descriptions of six species. This number was added to in subsequent years but it was not until 1926 that any attempt was made to elucidate the accumulated synonymy. This was ably undertaken by J. R. Norman during his taxonomic study of flatfishes collected during the cruises of F.I.S. "Endeavour". In his report (Norman 1926) he stated that he had not attempted to complete the synonymy for every species but had endeavoured to include all of the more important references of Australian ichthyologists. The four species of *Rhombosolea* recognized by Norman, namely *plebeia*, leporina, retiaria, and tapirina adequately describe the present known members of the genus.

The synonymy of R. tapirina is extensive and is given below with references.

Rhombosolea tapirina (part) Gunther, 1862, p. 459; Macleay, 1882, p. 130.

R. flesiodes Gunther, 1863, p. 117; Macleay, 1882, p. 131; Waite, 1906, p. 197; Stead, 1908, p. 104; McCulloch, 1921, p. 36; 1934, p. 36, pl. XIII; Waite, 1923, p. 181; Waite, 1927, p. 223; Lord & Scott, 1924, p. 47; Lord, 1927, p. 13.

Pleuronectes victoriae (Castelnau), 1872, p. 168.

Rhombosolea tapirina Hutton, 1873, p. 401; 1874, p. 106, pl. XIX, fig. 83c; 1876, p. 215; Boulenger, 1902, p. 188; Waite, 1909, p. 590; 1911, p. 204, pl. XXXVI; Phillips, 1921, p. 122; 1927, p. 29; Thomson & Anderton, 1921, p. 87; Lord & Scott, 1924, p. 47; Norman, 1926, p. 284; McCulloch, 1929, p. 282; Whitley, 1929, p. 66.

R. victoriae, Macleay, 1929, p. 132; Waite, 1921, p. 158.

R. monopus Woodward, 1902, p. 272; Stead, 1906, p. 181.

The existence of this synonymy can be attributed to the smallness of the early collections, which failed to indicate the wide variation of meristic characters. This will be considered in a following section on raciation within the species.

R. tapirina is vernacularly known as the Common, Southern, or Greenback Flounder, but as it is more widely known by the last mentioned name, it will be referred to as such throughout the paper.

III. DISTRIBUTION AND HABITAT

The geographical range of the greenback flounder is confined to the southern states of Australia, Tasmania, and the South Island of New Zealand. The latitudinal extent of its occurrence is from 34° S. to 48° S. whilst in terms of longitude its range is from 115° E. to 174° E. In Australia the western and northern limits are not known accurately and it is doubtful whether it occurs in Western Australia as there is but a single record from King George's Sound identified from a skin only, Gunther (1862). In New Zealand (South I.), Victoria, and Tasmania, it is common and in the latter two places is the most important commercial flatfish. It is found on almost all parts of the Tasmanian coastline often in association with the local "sole", Ammotretis rostratus Gunther.

The latitudinal range of the species is small in comparison with that of equatorial and northern hemisphere Heterosomata. The distribution of all members of the subfamily Rhombosoleinae is somewhat limited, and apart from the tropical subfamily Paralichthodinae it occupies the smallest geographical range of all the flatfishes.

The greenback flounder occurs mainly in estuaries and bays although it has been taken by trawlers down to a depth of nineteen fathoms. It may be regarded as an estuarine fish from the point of view of the commercial catch but as trawling in shallow water within the three mile limit is prohibited in Australian waters the extent of its occurrence there is not known. The limited amount of Danish seining done in shallow water around Tasmania has indicated that quantities of flounder were small, (Blackburn & Fairbridge 1946).

In New Zealand, Graham (1953) noted that R. tapirina was taken in seine nets in two to five fathoms in Otago Harbour but was less abundant outside the harbour, although taken down to nineteen fathoms off Wickliffe Bay. Graham observed that during the autumn this species was more common in the harbour, but most were outside the harbour where they presumably go after spawning. He also indicated that R. tapirina did not inhabit the very shallow waters of the harbour as did the sand flounder Rhombosolea plebeia (Richardson). In Australia however it is common in fairly shallow water throughout the year, especially in its young stages.

Although the greenback flounder is fairly evenly distributed within the limits of its range, certain areas possessing suitable environmental characteristics support large populations and consequently these localities are well fished. (See Fig. 1) Such an area is Pittwater, near Hobart, in southern Tasmania. This expanse of water about eleven miles in length varies in

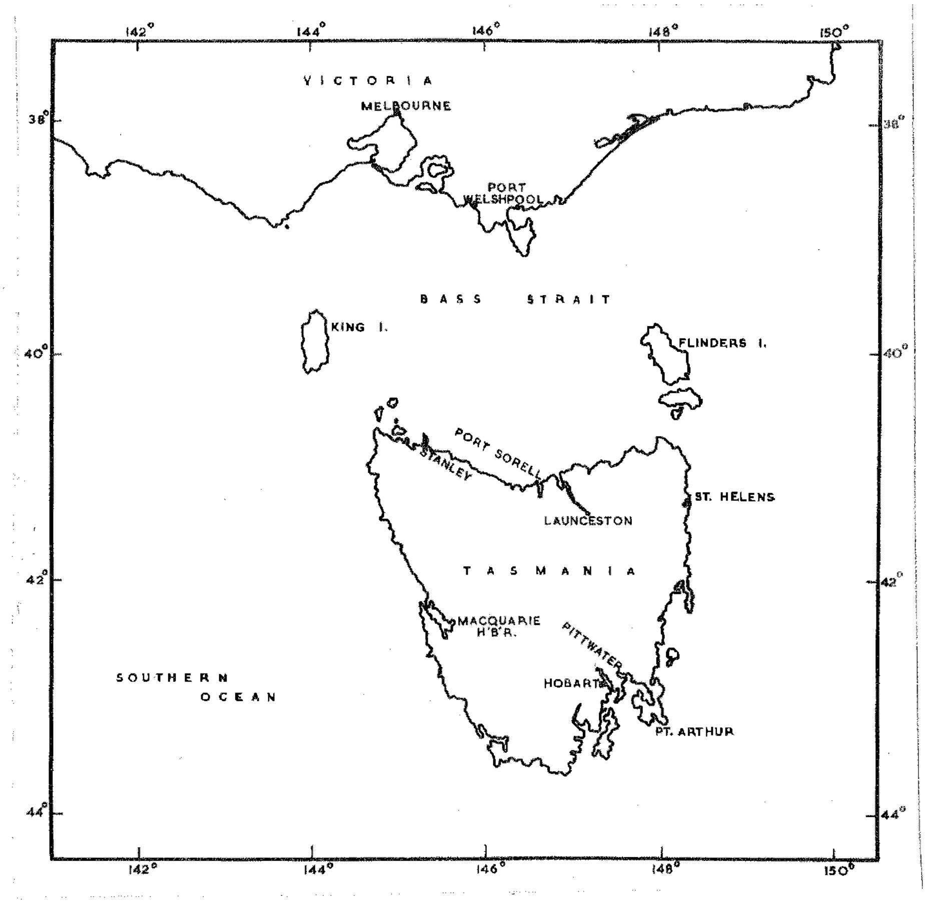

Fig. 1 Map of Victoria and Tasmania showing localities mentioned in the text.

breadth from one quarter of a mile to two miles. It is open to the sea through a channel about a quarter of a mile in width which permits a tidal fluctuation of three to four feet. The depth of water in Pittwater varies from thirty feet in the central channels to six feet or less on the flats which are partially uncovered at low water and form a large proportion of the total area. The flats are sandy and are covered in parts with beds of Zostera. Flounders prefer fine muddy sand to hard bottom as they spend most of the daylight hours lying covered by a fine layer of bottom material, and a soft bottom facilitates their feeding on small molluscs and polychaete worms. Two rivers enter Pittwater which exert a seasonal influence on the salinity. Chlorinity varies from 14.68‰ in winter to 20.00 ‰ in summer (oceanic values for this part of Tasmania: 19.29 ‰ - 19.50 ‰); the slightly higher value of 20.00 ‰ being due to evaporation in mid-summer. Temperatures range from 8° - 20° C, the minimum reading occurring in July and the maximum in January. Thus it is apparent that R. tapirina can tolerate a substantial range of salinity and temperature, as it is present in the locality in numbers at all times of the year. Port Welshpool, in south-eastern Victoria, possesses a similar type of habitat but on a larger scale. It has the same topography of channels and mud or sand flats covering an area of about 140 square miles. The inlet has a tide range of six to eight feet and the depth of water varies from five to sixty feet. The Port Welshpool and adjoining Corner Inlet areas provide more flounders than any other in Australia and supply fifty-one per cent. of the total Victorian catch of this species.

Port Arthur, in southern Tasmania, is a good example of a non-estuarine habitat, being in direct contact with the open sea. The port itself is about five miles long and varies in width from one to two miles. Water of depth from twenty to thirty fathoms occupies most of the area and shallow flats are confined to the environs of the mouths of a few small creeks. The waters of Port Arthur can be described as oceanic and support large beds of *Macrocystis pyrifera* (L) Ag. The range in temperature is from 12.1 - 17.8° C. Flounders are not found there in the quantity they are in the estuaries but are nevertheless numerous enough to be fished for commercially.

Two further localities in Tasmania which are topographically similar and which provide suitable conditions for flounders are George's Bay (St. Helens) and Port Sorell. The tidal flow in George's Bay, however, is smaller than in Port Sorell and in this regard it is comparable with Corner Inlet.

Whilst flounders can be regarded as an estuarine fish and all sizes of the adult form are found in shallow waters throughout the year, the location of spawning grounds remains doubtful. It will be shown later in the section on spawning, that the number of running ripe fish in samples was extremely small as was the percentage of male fish. The largest proportion of males in any one sample was 12.7 per cent. and the lowest nil.

IV. FISHING METHODS

(a) Amateur fishing

A considerable quantity of flounders are taken by amateur or sport fishermen largely by the light and spear method.

Although it is impossible to gauge the extent of this type of fishing in Tasmania it is known that it accounts for a large proportion of flounders taken and gives rise to many a grievance on the part of the professional fishermen. This is so because amateurs generally are not much concerned with the observance of the minimum length laws, usually taking every fish they see and often spear undersize fish for sport. The author has seen instances of amateur spearers filling an apple case with young fish in the course of a night's fishing, and then emptying them on the shore before leaving. Many areas are worked by both professional and amateur fishermen and it is fairly common for the former to cover the same ground closely following the latter taking any small fish which may have been discarded. There is a five months closed season for flounders in Tasmania extending from June to October which applies to amateur and professional fishing alike so that the main fishing period occurs during the warmer months. This gives every encouragement to flounder spearers who usually wade to waist depth while fishing. The winter temperatures of Tasmanian estuaries which fall to from 8 - 12° C would greatly reduce the number of spearers, were fishing allowed at that time of the year.

In Victoria where there is no closed season certain areas are marked off for either amateur or professional fishing. This gives the professional grounds some local protection from amateurs during the summer but does not lessen the effect of extensive spearing on the population generally.

The beach seine is not much used by amateurs due to the more expensive gear and accurate local knowledge essential for this type of fishing.

As there are no present means of assessing the quantity of fish taken by amateur spearers their effect on the fishery cannot be gauged. But it is considerable, and is added to by the depredation of juvenile fish that accompanies their activities.

(b) Commercial fishing

Due to its availability and eating qualities the greenback flounder was amongst the first fishes to be exploited in the early years of the settlement of Tasmania. Although there are no official records of quantities taken, evidence given before the Royal Commission on Tasmanian Fisheries, 1882, suggests that they were at times much more abundant during the last century than in the present one. Passages quoted from this

Commission are given below:-

"Between thirty and forty years ago flounders were very scarce indeed, then they appeared in great numbers and were sold as low as ninepence per dozen. I have known 50 dozen to be taken in a haul at Brown's River Beach......" "I have heard of 150 dozen large fish being taken in two consecutive shots of the net thirty years ago in the Tamar. For some years past the fish have been scarce, in fact it had almost disappeared out of the Tamar and the fishermen had to go to Port Sorell for them. Latterly, however, the fish have reappeared and fishermen report that they are nearly as numerous as formerly."

The gear used at that time was mostly the seine net with the dimensions as follows. Length 40-60 fathoms, depth 9-13 feet and with mesh varying from 1-1.5 inches. Mesh nets were also employed using 3-4 inch mesh with the length varying from 300-500 fathoms. The efficiency of the mesh nets was improved by catching up the leadline to form pockets. As early as 1882 a minimum legal length of 9 inches had been assigned to the flounder although fishing was permitted throughout the year. However, during the Royal Commission of 1882 it was stated "flounder are at a certain season unfit for food - November to February. Their sale should be prohibited during these months". Another witness proposed a close season of two months "with heavy penalties" as the answer to depleted grounds.

Nowadays the bulk of the commercial flounder catch is taken by seine nets although in some places due to rough and unsuitable bottom spearing is employed. The nets vary from 30-60 fathoms in length, 9-12 feet in depth with mesh 3-4 inches, knot to knot. As the technique of beach seine netting is well known further description is unnecessary except that flounder nets are often worked parallel to the shore-line in shallow water instead of at right angles to it. A catch of five dozen marketable flounders in the one haul would be considered good fishing by present-day standards. According to fishermen flounders are very susceptible to weather conditions and the state of the tide. The moon also is said to play an important role in the movements of the fish shorewards. Conditions for fishing are considered ideal when the tide has just commenced to flood, the wind is very light, and there is no moon. Under these conditions flounders leave the deep water they prefer during the daylight hours and move across the flats to feed. Under favourable conditions of moon and tide but with rough weather, it has been found that fishing is very poor. The author has also noticed whilst fishing in Tasmania that scarcity of flounders appeared to be associated with low barometric pressures, other conditions being considered satisfactory.

Professional spearing, unlike the amateur method, is usually done from a dinghy in depths of up to eight feet. Tasmanian regulations do not allow more than three prongs to each spear and most fishermen prefer to use three barbless prongs fashioned from motorcycle wheel spokes or wire of the same gauge. The light used to illuminate the fish on the bottom consists of a small six volt battery-operated lamp with reflector suitably mounted on a handle about four feet long. This method of fishing can only be used when the surface is unruffled by wind. Under such conditions it is possible for an expert fisherman to take as many fish in this way as would be caught by netting over a similar period of time.

Mesh nets are very rarely used at present due, no doubt, to the relative scarcity of flounders compared with the early days.

V. THE COMMERCIAL CATCH

It is not proposed to deal with the study of flounder catches over the years in detail for the following reasons.

The fisheries statistics compiled by the State Departments are inaccurate and do not truly represent the amount of fish taken. Two factors contribute to this. A considerable quantity of fish is caught by amateur fishermen who are not required by law to furnish returns and professional fishermen who are required to submit returns either do not or fail to disclose their catches accurately.

To establish the state of a fishery it is necessary to determine the effort in terms of the number of men engaged in it, the time spent actually fishing, and the effect of market prices on supply. In Tasmania where the present investigation was made, records are scanty prior to 1944 when an attempt was made to implement a system whereby fishermen were issued with a book containing forms to be filled in to give relevant details of their fishing operations month by month. These records were not available to the writer but yearly totals of flounder catches from these returns compiled by the Fisheries Division of the Department of Agriculture were supplied. All figures quoted before 1944 are taken from the records of fish buyers and wholesalers.

(a) The Tasmanian Flounder Catch - Economic Importance

The total fish catch of Tasmania fluctuates from year to year, often greatly, due to the varying abundance of the barracouta. For example, for the years 1945 and 1955 the catches of all fish, not including crustacea and molluscs, were 8.77 million lb and 3.33 million lb respectively. However, the barracouta catch for those years was 6.11 million lb and 1.22 million lb. Thus if the barracouta catch is neglected the totals of all other species amounted to 2.65 million lb in 1945 and 2.11 million lb in 1955. In the comparison of the flounder catch with the total catch of the State the barracouta will therefore not be taken into account.

The percentage by weight of flounder of the total fish production varies from approximately one to two per cent. Table 1 shows the Tasmanian fish catch by species for the two years 1945 and 1955. (These data are also shown in Figure 2 (barracouta and shark omitted for convenience) where the relative sizes of the catches can be more easily compared.)

The Tasmanian flounder catch from available records of the period 1931-1956 is shown graphically in Figure 3. The fluctuating nature of the histogram from 1931 to 1939 is no doubt due to a certain extent to the inadequacies of the statistical records. But as it seems likely from evidence given at the Royal Commission referred to earlier allowance must be made here for natural changes in abundance. The war years contribute to the lack of information between 1939 and 1945 and in this regard it is noteworthy that from 1941 to 1945 (when lack of manpower manifested itself in most other fisheries) the flounder catch is maintained around 40,000 lb. It should be pointed out that during the war, blackout restrictions prohibited the use of underwater lights which gave the fish protection from amateurs and no doubt enabled the population to build itself up; so that in 1945-47 with the release of fishermen from the services and in Fig. 3 the catch rises to circa 60,000 lb.

By 1946 returns from fishermen had improved to the extent where they gave a fairly reliable indication of the catch

TABLE 1

THE TASMANIAN SCALE FISH CATCH BY SPECIES FOR THE YEARS 1945 AND 1955 SHOWING THE RELATIVE IMPORTANCE OF GREENBACK FLOUNDER

1945		1955	
SPECIES	WEIGHT LB	SPECIES	WEIGHT LB
Barracouta	6,116,652	Shark	1,265,644
Shark	877,767	Barracouta	1,219,193
Salmon	335,514	Salmon	337,431
Whitebait	332,500	Flathead	103,422
Rock Cod	312,623	Trumpeter	67,559
Flathead	304,214	Garfish	66,944
Trumpeter	109,391	Rock Cod	65,135
FLOUNDER	59,938	Trevally	35,835
Mullet	30,994	Whitebait	33,167
Perch	18,011	Mullet	24,363
Mackerel	16,938	FLOUNDER	19,321
Garfish	15,048	Trout	10,092
Trevally	14,956	Perch	9,493
Parrot fish	8,587	Tuna	7,632
Bream	7,735	Parrot fish	3,291
Other species	205,855	Other species	62,653
Total catch	8,766,723	Total catch	3,331,175

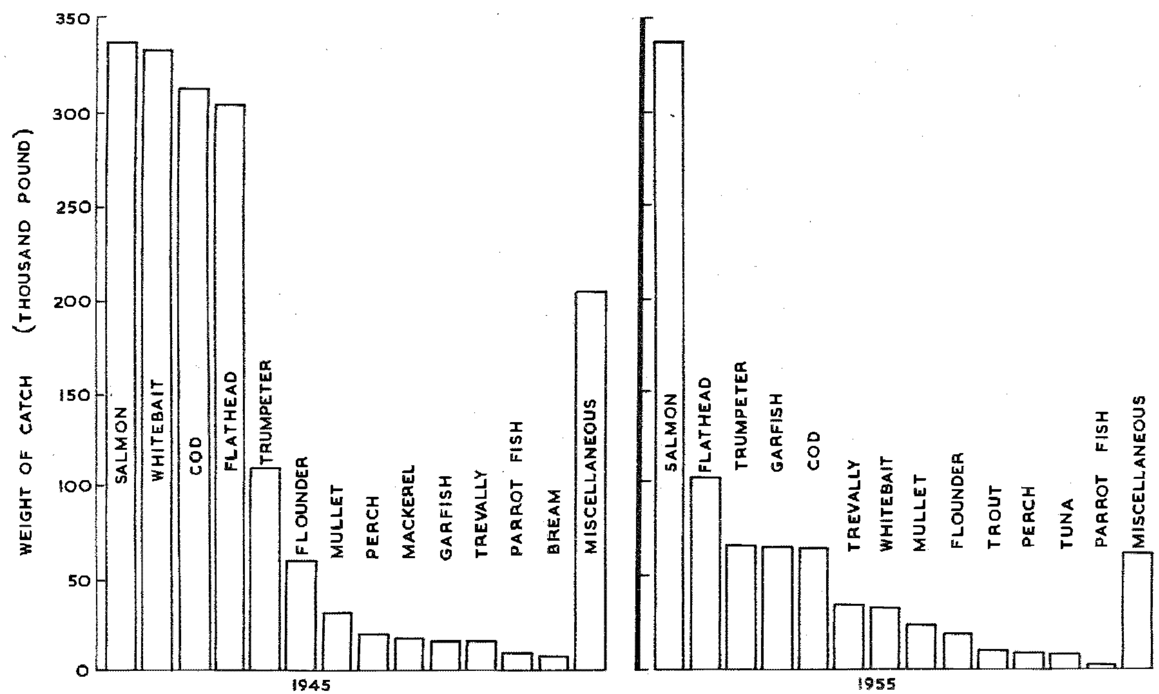

Fig. 2 A comparison of the Tasmanian fish catch for two selected years showing the quantitative importance of the various species. The greatly fluctuating barracouta (_Thyrsites atun_) and school shark (_Galeorhinus australis_) catches are omitted.

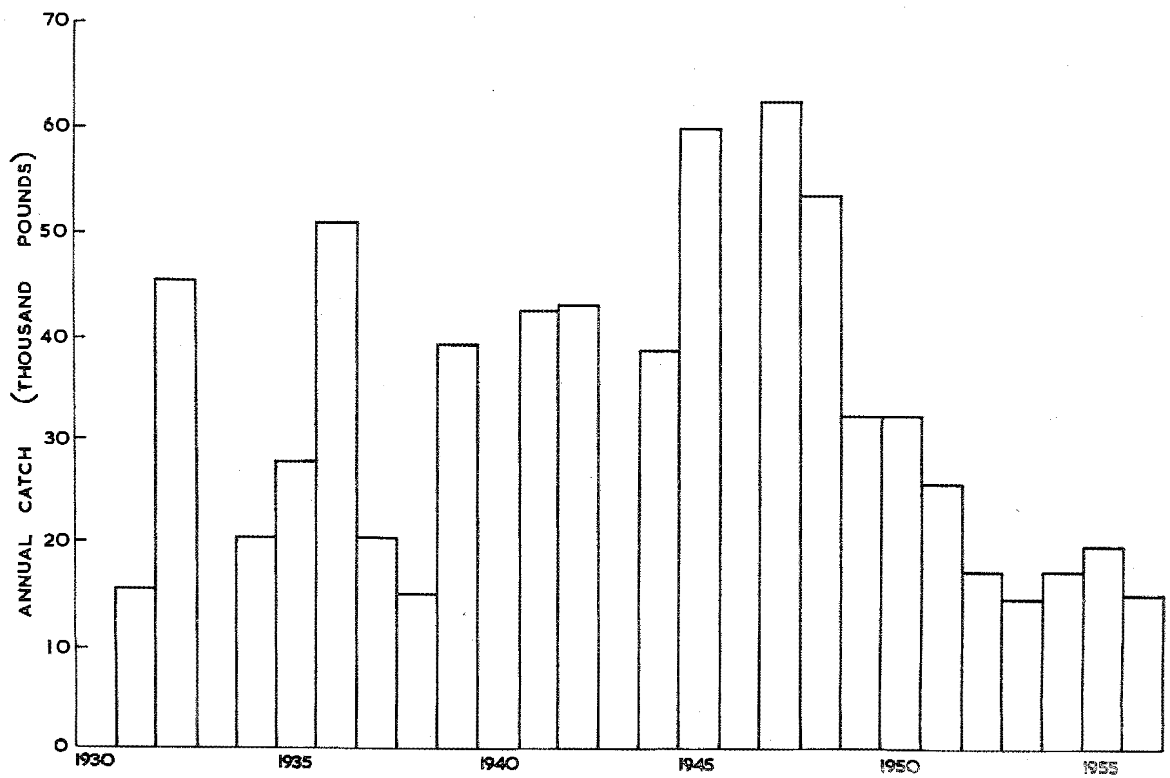

Fig. 3 Some Tasmanian greenback flounder catches 1931-56.

(Smith 1946). The decline from 62,000 lb in 1947 to 14,000 lb in 1953 is sharp but steady and it would appear that this represents a fall in abundance. It may be argued that there is insufficient evidence to make such an assumption without assessing the fishing effort. However, it is the author's opinion that in the case of the greenback flounder the fishing effort is largely regulated by the abundance of fish for the following reasons:-

(1) The flounder is amongst the highest priced fish and subject to an unsaturated demand. If they are there the fishermen will fish for them.

(2) Men engaged in the fishery usually are equipped to catch other estuarine fish such as salmon and mullet and are unlikely to be forced out of the industry by a dearth of flounder alone.

(3) The effect of a sudden increase in the number of men in the fishery can be disregarded because of the local knowledge required for seine netting which cannot be gained in a short period. In other words the potential number of flounder fishermen is fairly constant and their active participation in this fishery would be largely determined by availability of fish.

From 1952-1956 inclusive the catch fluctuates between 14,000 lb and 19,000 lb which is approximately equivalent to the catch for 1938 and 1939 although as stated the records from those years are merely an indication of the true weight of fish taken.

In view of possible natural changes in population density due to environmental and other causes, the rapid downward trend from 1947 cannot be definitely ascribed to over-exploitation of the stocks. However, this trend is significant in that the period follows one during which the fish had some respite from spearing and the returns for the years 1947-1956 are a more accurate assessment of the catch than those of previous years.

As individual fisherman's returns were not accessible the monthly variation in the catch cannot be given. Half-yearly figures, however, have been prepared since 1951 and these are of interest. The half-yearly catches for four years are given in Table 2.

The closed season for the years quoted operated only during the second half-yearly period, namely from July 1 to September 14 inclusive. Latterly it has been extended a month to October 14 in some parts of the Island. From the table it is evident that fishing is about 300 lb a month better during spring and early summer than it is during late summer and autumn. It would be expected that following the rest from fishing during the winter more fish would be on the fishing grounds but against this must be weighed the fact that unsuitable fishing weather is more prevalent in spring than late summer and autumn when long periods of light winds and generally calm conditions occur.

Professional fishermen generally claim that the increase

TABLE 2

THE TASMANIAN FLOUNDER CATCH FROM 1951 - 1955

FOR THE FIRST AND SECOND HALF OF EACH YEAR

FLOUNDER CATCH IN LB

YEAR	JAN. 1 - JUNE 30	JULY 1 - DEC. 31
1951	16,369	8,956
1952	no record	no record
1953	7,928	6,204
1954	10,146	6,703
1955	11,143	8,178

Average catch per month		Average catch per month	
for 6 months =	1,899 lb	for $3\frac{1}{2}$ months =	2,145 lb

in amateur spearing has adversely affected the fishery. In order to compare the size composition of flounders from an area relatively inaccessible to spearers with that of fish from readily accessible Pittwater some experimental hauls were made in Lime Bay. This Bay, although only twelve miles by water from Pittwater, being situated at the northernmost tip of the hook-shaped Tasman Peninsula, is isolated by virtue of its distance from well populated areas and lack of roads. The length distribution of flounders from three hauls from this area together with that of fish from a similar number of shots of the same net made in Pittwater is shown in Figure 4. The samples were collected in March 1954 on successive days and the same netting technique was employed in both cases. The histograms show a distinct difference in the proportion of fish 20 cm and greater available in the two localities. In the Pittwater sample only 28 per cent. of the total number taken fall into the 20 cm or greater group but in Lime Bay this group forms 57 per cent. of the total number taken. As both places are fished commercially but only Pittwater is visited extensively by amateurs the apparent correlation between their activities and the scarcity of larger fish is worthy of consideration. Significant also is the fact that juvenile fish are abundant in Pittwater and the sharp downward trend in the histogram of that sample commences at 19 cm at which length the flounder is large enough to be edible, although still 4 cm below the minimum

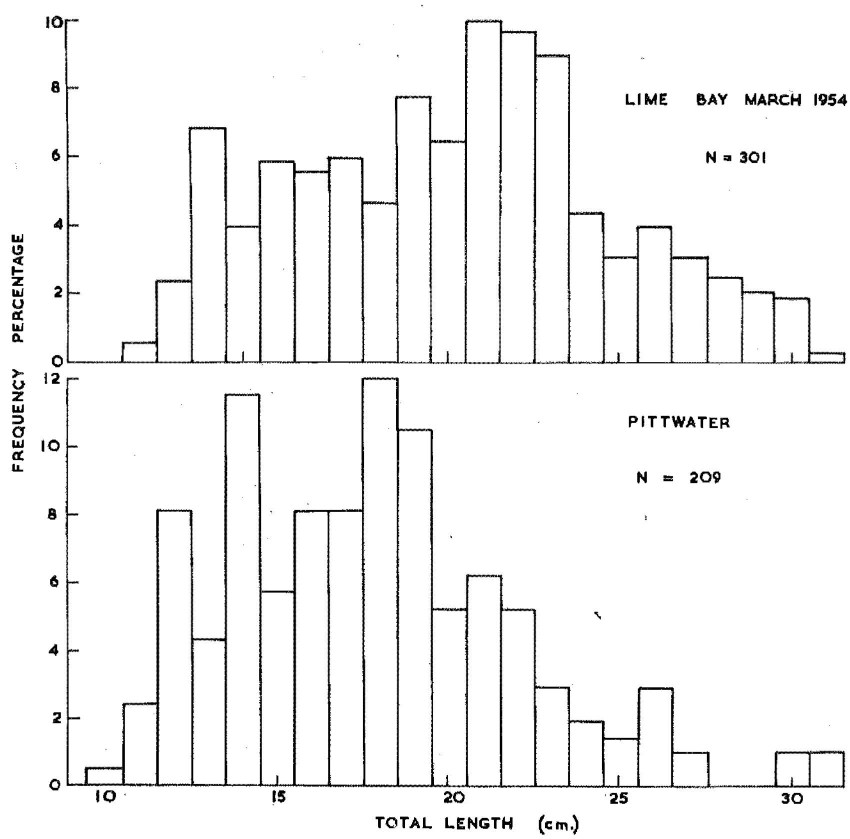

Fig. 4 The length distribution of experimentally netted flounders from Lime Bay compared with a similar sample from Pittwater.

legal length. In advancing the above contention it is assumed that professional fishermen do not take any quantity of fish below the legal length (230 mm) and considering the difficulty of disposal for profit the author feels that this is a safe assumption.

It is realized, however, that the samples represented by the two histograms are insufficient either in size or duration to be anything more than a basis on which to advance a hypothesis regarding the effect of amateur spearers on the flounder population. However, it appears that if spearing has been detrimental to the professional fishery it has operated through limiting the number of flounders attaining legal size rather than reducing the fecundity of the population.

(b) The Victorian Catch - Economic Importance

Of the forty-three main species of edible teleostean fish taken in Victorian waters the flounder lies tenth in order of catch weight and commands the highest price. The South Australian spotted whiting Sillago punctata, Cuvier, is the most expensive fish on the market in Victoria varying from six to nine shillings per pound as against from five to six shillings per pound for flounder. From 1946 to 1955 inclusive the annual fish catch of Victoria ranged from 10.7 - 12.8 million lb and during that period the percentage of flounder in the catch varied between 1.3 - 1.7 per cent. Figure 5 shows the 1956 teleostean catch by species in order of weights.

In Victoria, unlike Tasmania, there is a well organized central fish market situated in Melbourne through which the bulk of the fish sold in the State passes. There is a tendency for flounders to be bought direct from the fishermen, to a limited extent, by guest-houses, hotels, and the like but it is safe to assume that this amount is small enough to be disregarded for the purposes of general observations on the flounder catch. Data shown in Figure 5 and Table 3 are taken from market records and have been checked with figures from fishermen's returns. Fish sold privately are not usually included in their returns.

Figure 6 shows the magnitude of the flounder catch from 1931-1936 in histogram form with a superimposed trend curve obtained by smoothing the data with a moving average of three. The drop in the mid thirties shows the effect of the economic depression during that time and the even lower catches in the early forties result from lack of manpower due to the war. But it is significant that even after enjoying a respite during the latter period the postwar fishery does not attain its prewar level as in Tasmania, and after 1947 a slight downward trend is evident. The same conditions as regards numbers of fishermen and the market demand for flounder apply to Victoria, as has been outlined for Tasmania.

(c) Conclusions

Tasmania.-

(i) The lack of reliable catch data prior to 1945, limit

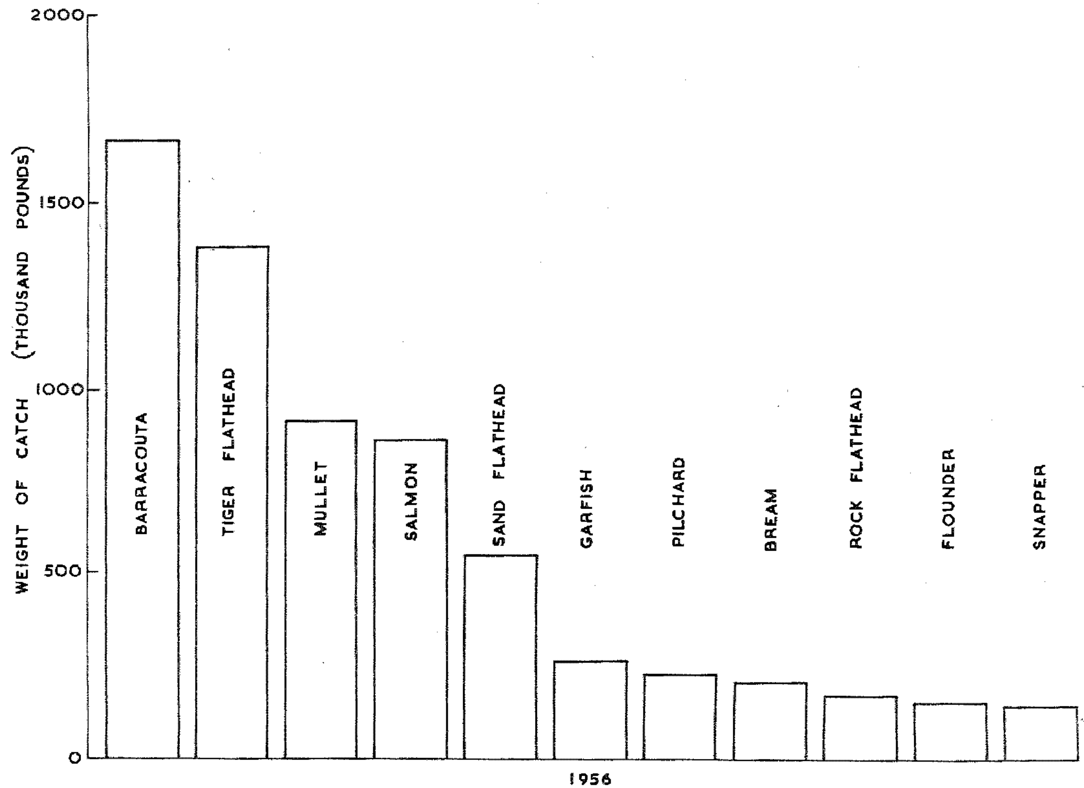

Fig. 5 The Victorian scale fish catch by species for 1956 in order of landed weight.

TABLE 3

VICTORIAN ANNUAL FLOUNDER CATCH 1931 - 1956

The Tasmanian catch for the same period
is also given for comparison.

YEAR	VICTORIA LB	TASMANIA LB
1931	330,254	15,360
1932	251,759	45,382
1933	216,728	
1934	212,384	20,224
1935	180,849	27,625
1936	192,577	50,835
1937	239,653	20,166
1938	196,221	16,685
1939	189,208	39,104
1940	271,163	
1941	165,788	42,390
1942	105,709	42,976
1943	84,388	
1944	107,568	38,760
1945	165,933	59,938
1946	134,861	
1947	199,359	62,303
1948	182,761	53,283
1949	186,540	32,112
1950	180,606	30,638
1951	162,905	25,235
1952	185,155	16,394
1953	187,012	14,132
1954	150,916	16,849
1955	164,482	19,321
1956	147,977	14,698

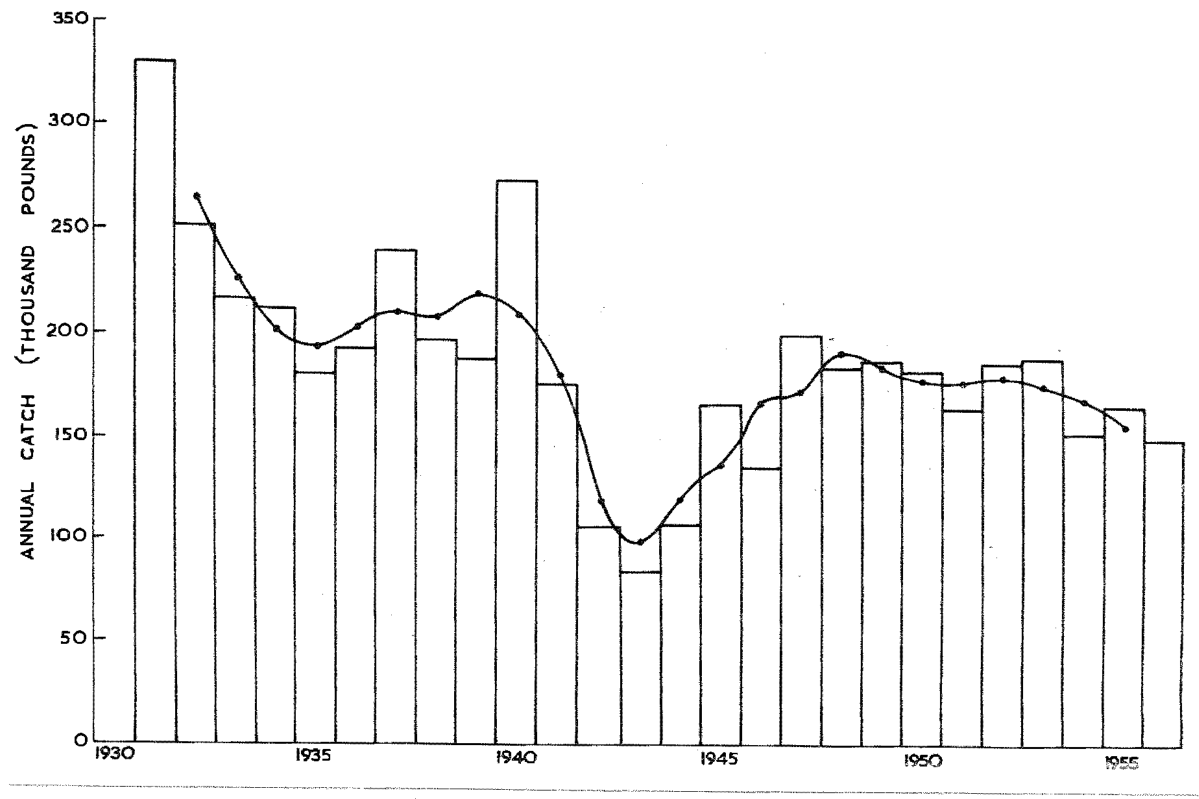

Fig. 6 The Victorian greenback flounder catch 1931-56. The trend is indicated by the curve obtained by smoothing the data with a moving average of three.

to the ensuing ten years the period from which any conclusion can be drawn as to the state of the flounder fishery in Tasmania.

(ii) Although it cannot be established that the decline in total catch since 1945 has in part been due to a decrease in abundance there is some evidence that the activity of spearers may have limited the numbers of legal fish available.

(iii) The present minimum legal length of nine inches does not give the maturing fish adequate protection. (This question will be covered in a later section of this paper.)

(iv) The decline is a phase of a natural fluctuation due to environmental factors which are unrelated to (a), (b), or (c).

(d) Conclusions

Victoria.-

(i) The statistics available are a reasonable indication of the catches for this State but until more detailed information such as the number of shots of the net made throughout the year, the quantity of gear used, and the selectivity of the mesh it will be impossible to assess accurately the fishing effort.

(ii) The Victorian fishery is more stable than that of Tasmania, showing smaller fluctuations in the catch from year to year. However, the period from 1946-1956 can be regarded as a more accurate indication of the state of the fishery because during these recent years prices have been high and the demand for flounders unsatisfied. Prior to 1946 demand was affected by the economic depression of the 1930-1938 period and production declined with manpower shortage during the war years.

During the war years the population had an opportunity to increase its strength and any subsequent steep decline could be explained as a depletion of the accumulated stock.

After the war handling facilities such as transport, quality, and supply of ice improved which encouraged maximum production.

Thus the slight downward trend since 1946 cannot in the light of available statistics be attributed to a decline in the population due to over-exploitation.

VI. SAMPLING

(a) Sampling Methods

It was not possible to adopt the accustomed procedure of large-scale observations on fish market material in this investigation as a central market ceased to exist in Tasmania soon after the first world war. All fish is sent direct to several buyers some of whom have their own retail shops and the demand for flounders is such that they are sold to consumers almost immediately. In addition it is the custom to cook and serve the flounder complete save for the viscera which are removed by the fishermen as soon as possible after catching. It is also impossible to remove the ovaries without affecting either the appearance or the weight of the fish. Hence these considerations made it necessary for all fish used in the investigation to be either fished for or purchased from commercial fishermen. The last-mentioned avenue of supply had understandable financial limitations.

Samples collected by the author were obtained by netting which provided the majority of immature fish used. These were supplemented by regular monthly samples of about a hundred fish taken by an experienced fisherman over a period of nineteen months.

(i) Netting.- What is commonly called a "garfish net" was used as a seine to fish estuarine beaches. Dimensions of the net were: length, 30 fathoms; depth, 4 feet; and 3 inch mesh throughout. The net was weighted with moulded leads and four foot six inch lead tipped spreader-poles were used at each wing to keep the leadline at the extremities of the net on the bottom when nearing the end of each haul. The net was worked from an eleven foot dinghy using ten fathoms of coir hauling line on each wing to enable the working of the net in the deep channels bordering the flats. The net was bunted up on the flats. A three inch mesh was found to be suitable for the regular capture of flounders as small as 10 cm and from time to time smaller sizes were found entangled in seaweed in the bunt meshes.

(ii) Spearing.- For the most part the monthly samples were speared. The fish were collected in the following manner. Using the equipment described in an earlier section of the paper and fishing from a dinghy every fish sighted was speared or at least an attempt was made. The number of fish escaping through not being securely speared or missed altogether was generally less than 10 per cent. It was always possible to obtain the sample of one hundred in the one night and the size composition of a night's speared catch when compared with that of a netted catch showed no more variation than that between two successive catches of one or the other method of fishing. The samples can therefore be regarded as random.

Other methods of specimen and data collection will be discussed in the sections of the paper dealing with specific aspects of the investigation.

(b) Measuring Methods

All fish were measured to the nearest millimetre by placing them blind side down on a standard fish measuring-board. The total length was read to the extremity of the caudal rays. In order to obtain the standard length the distance from the caudal peduncle to the end of the caudal rays was measured with dividers and subtracted from the total length. All other measurements were taken with dividers. Weighing was done on a "Mormal" pan balance while the fish were wet although all excess water was first shaken off. All weights were recorded to the nearest gram. The majority of the weighing was done either in the laboratory or in the cabin of the launch used in the investigation where sheltered conditions made accurate weighing possible.

VII. TOTAL LENGTH - STANDARD LENGTH RELATIONSHIP

It is more convenient for practical purposes to express lengths of fish in terms of total length but to ascertain whether the standard length is a truer value for the purposes of growth study in the case of the flounder, its relationship with total length was investigated.

The total length measurements of a sample of 1723 specimens ranging from 110 mm to 370 mm were grouped to the nearest centimetre and the mean standard length was calculated for each centimetre group. The resulting graph is shown in Figure 7. Apart from the extreme values derived from relatively few specimens all the points lie about a straight line passing through the origin. Thus the standard length was found to be 81.20 per cent. of the total length which relationship is constant throughout the life of the fish. This proportion approximates that found in two other species of flatfish namely, the California sand dab *Citharichthys sordidus* (Girard), Arora (1951), and the starry flounder *Platichthys stellatus* (Pallas), Orcutt (1950). The standard lengths of these fish are 84.00 per cent. and 81.95 per cent. of their total lengths respectively.

For the greenback flounder, if Y = total length and X = standard length conversion from one to the other can be made by using the equations:

$$X = 0.812\,Y$$

or

$$Y = 1.231\,X$$

VIII. WEIGHT/LENGTH RELATIONSHIP

The weight/length relationship was investigated for the following reasons:

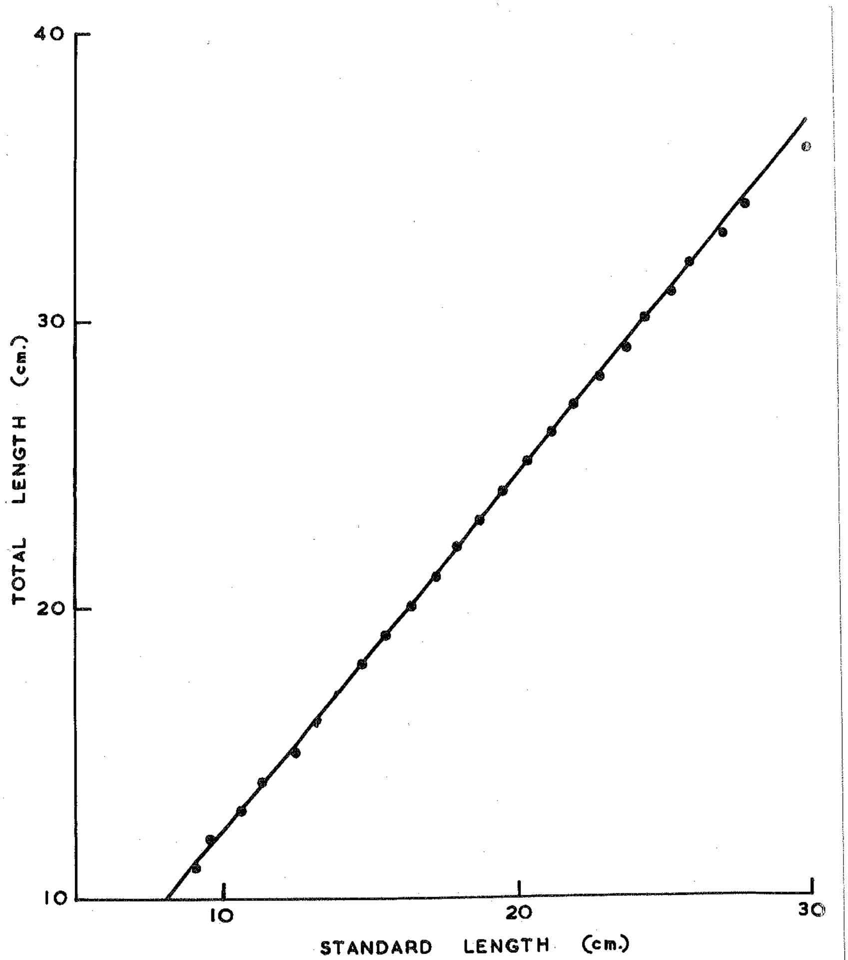

Fig. 7 The total length/standard length relationship in the greenback flounder. Measurements are taken from representatives of both sexes.

Firstly to measure the seasonal change in the relationship and to correlate it with increased weight due to gonad development.

Secondly to determine the length at which the weight increase is suitable to define an optimum size for fishing.

Thirdly to compare the weight/length relation of two representative samples of flounders from two populations possessing significantly different meristic characteristics.

That the weight/length index of a species varies considerably with the time of year, state of gonads, and feeding conditions has been shown by Clark (1928) and Ancona (1937). Thus to arrive at a mean value it was thought necessary to treat data from a series of samples extending over a period of twelve months. Although the most obvious cause of changing weight/length value is the increase and decrease in gonad weight, the changes occurring throughout the year are not due to this alone. It appears that linked with the development of the gonad to maturity is the building up of body fats and tissue. This will be evident when the seasonal variation of the condition factor C for males and females over a period of eighteen months is considered where the variation in C for males shows comparable fluctuations with the female values although the relative weight of gonad per weight of fish is very different for the sexes. A ripe ovary usually forms about 17.5 per cent. of the total weight of the fish and when spent about 1.1 per cent. In the male however the testis when ripe rarely exceeds 1.3 per cent. and when spent 0.4 per cent. of the total weight.

(a) Methods

Two samples of fish were used for weight/length determinations. The first consisting of 286 females and 129 males was collected during the month of March 1954. The range in total lengths of fish in this sample was from 110-240 mm and was therefore largely composed of immature fish. The second, comprised of 1172 females and 58 males within the range 180-340 mm total length, was collected over the period of twelve months from June 1954 to May 1955, there being approximately one hundred fish in each monthly sample.

In both samples the mean weight of each ten millimetre group was calculated and log length plotted against log weight. This relationship was found to be linear as is shown in Figures 8 and 9. Data from which the calculations were made are shown in Table 4.

The raw data of Table 4 are plotted in Figures 10 and 11 and the points are seen to lie about the curves drawn using the mean calculated weights for each class. Calculated weights were derived from the expression: $\log W_c = \log C + n \log L$. Where C is the condition factor from the expression $C = \frac{W_a}{L^b}$. W_c = calculated mean weight; W_a = actual mean weight and n = the regression coefficient. The total length of the fish is represented by L. The choice of the above expression as

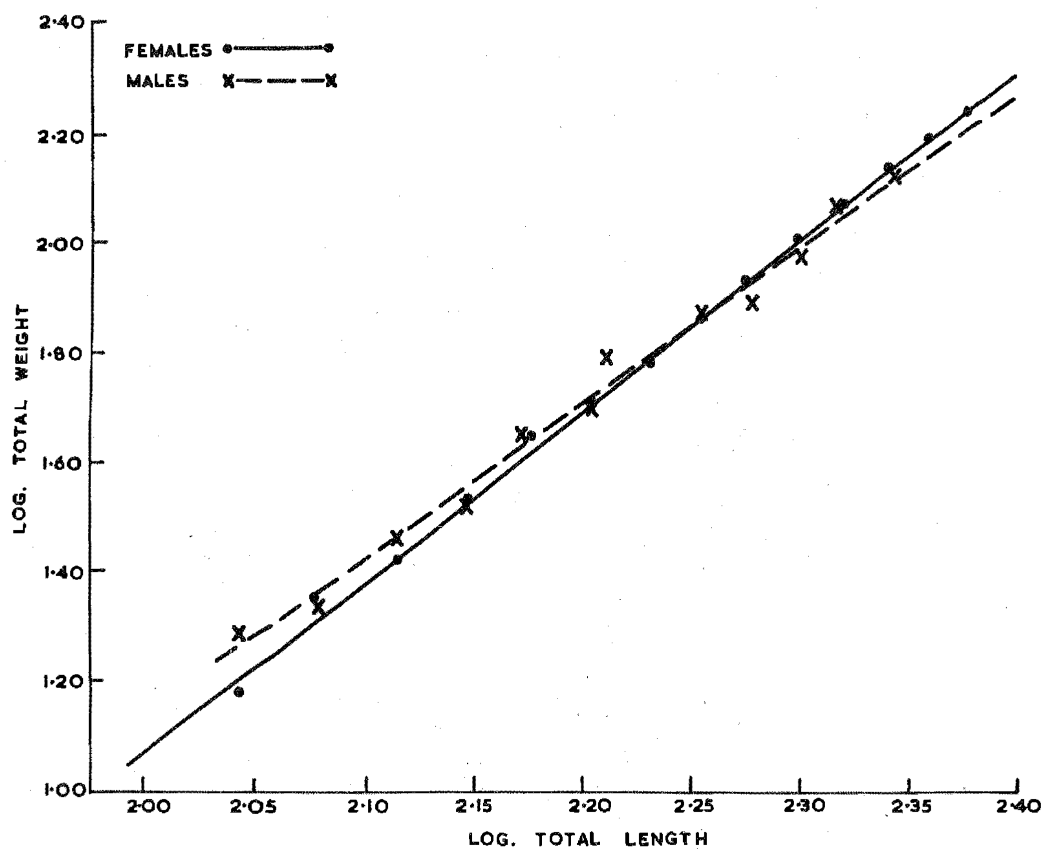

Fig. 8 The regression of log weight on log length for juvenile male and female flounders from Pittwater, March 1954.

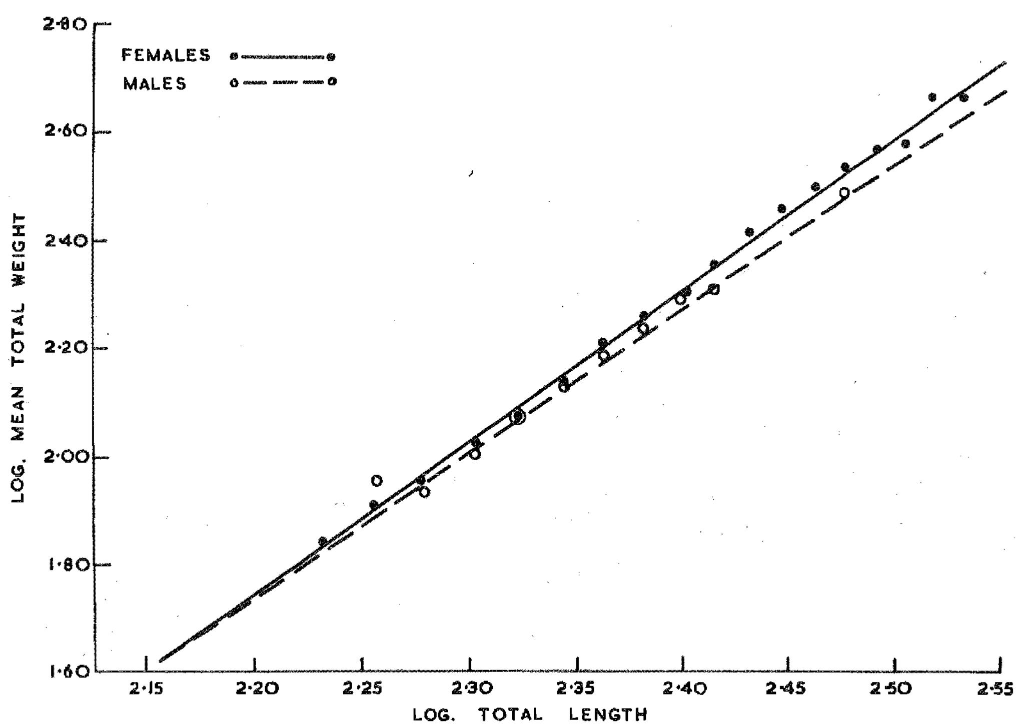

Fig. 9 The regression of log weight on log length for adult male and female flounders from Pittwater, for the twelve months June 1954 to May 1955.

TABLE 4

THE MEAN WEIGHT OF JUVENILE AND ADULT PITTWATER FLOUNDERS FOR EACH CENTIMETRE OF TOTAL LENGTH

INTERVALS OF TOTAL LENGTH mm	MEAN WT. GM.		MEAN WT. GM.	
	Males (110-230 mm)	Females (110-240 mm)	Males (180-300 mm)	Females (170-340 mm)
105-114	19.5	15.3		
115-124	22.0	22.5		
125-134	30.0	26.5		
135-144	33.8	34.5		
145-154	45.3	45.1		
155-164	51.1	51.4		
165-174	61.6	60.7		69.5
175-184	73.8	73.5	90.0	83.0
185-194	78.7	85.1	86.0	89.3
195-204	95.3	101.1	100.3	105.3
205-214	120.0	117.0	118.0	119.7
215-224	133.7	137.4	134.6	137.9
225-234		157.8	154.3	158.8
235-244		176.2	173.5	178.8
245-254			195.0	199.1
255-264			201.0	228.1
265-274				252.2
275-284				287.6
285-294				313.5
295-304			313.0	339.1
305-314				370.9
315-324				379.4
325-334				466.6
335-344				466.1

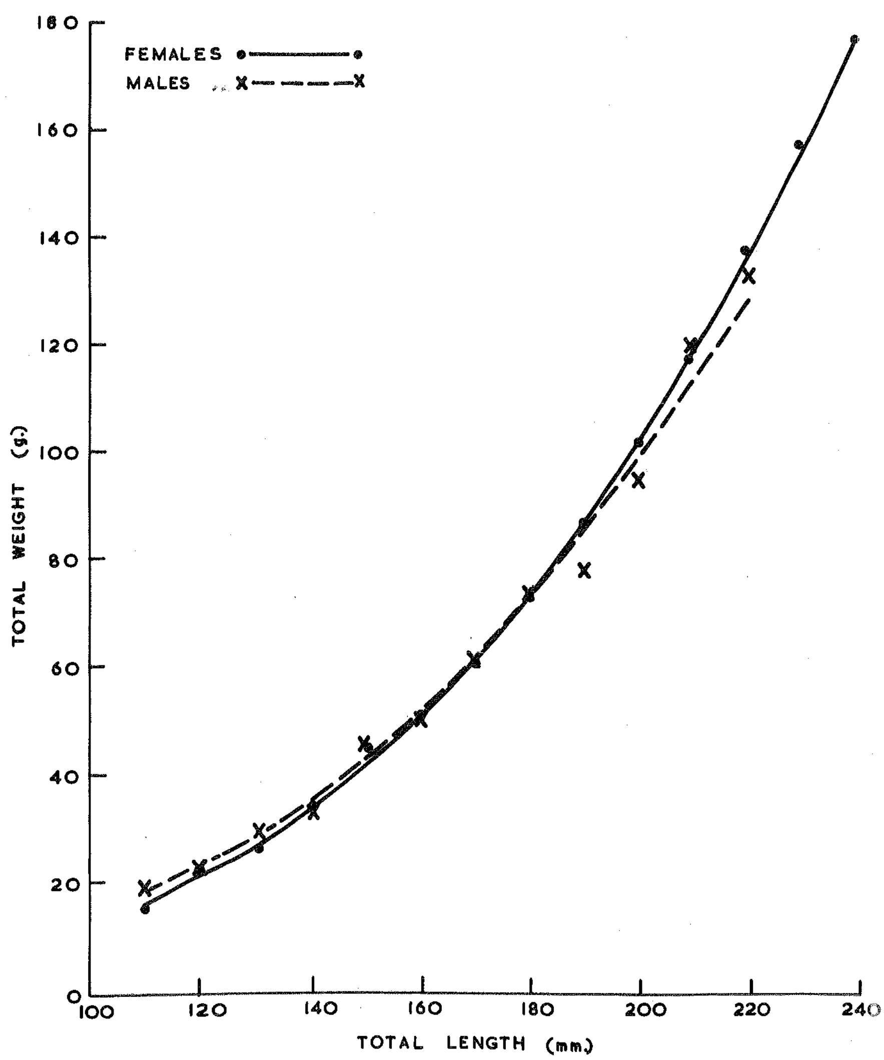

Fig. 10 The weight/length relationship in juvenile male and female flounders from Pittwater, March 1954.

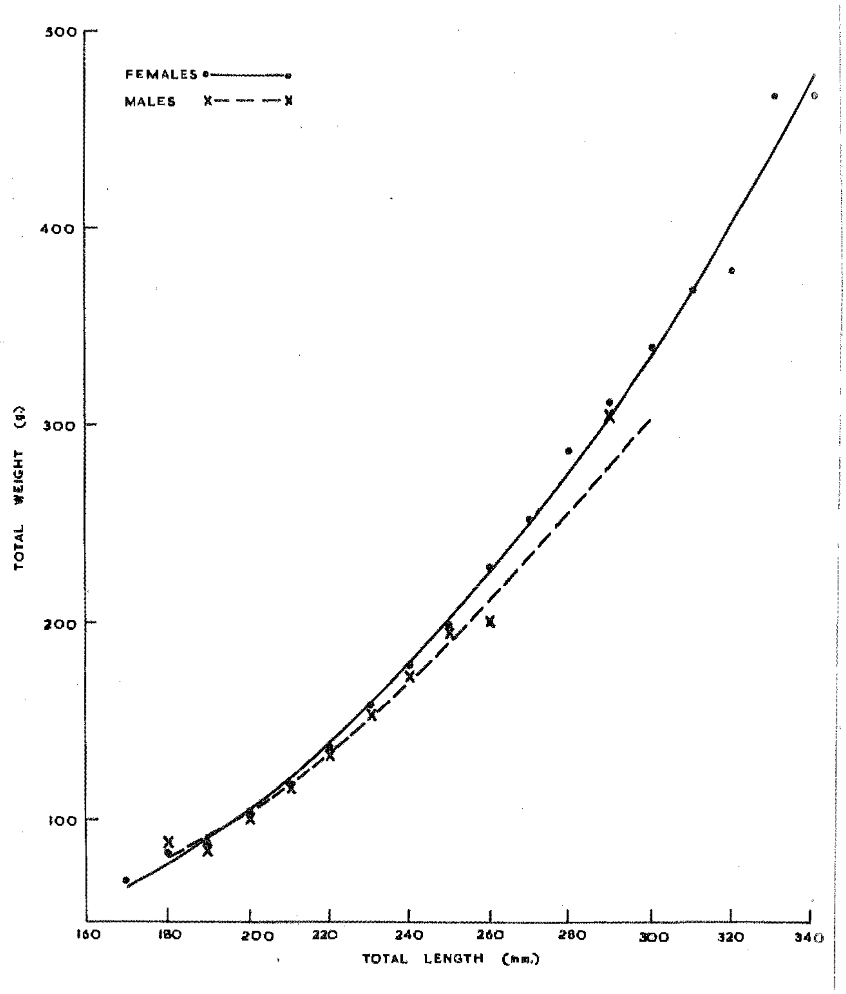

Fig. 11 The weight/length relationship in adult male and female flounders from data collected over the period of twelve months, June 1954 - May 1955.

against another well-known variation, $K = W/L^3$ will be discussed later in this section.

If Y is the weight expressed in gm and X the total length in mm equations for the curves are:

March 1954 sample (Fig. 10)

Males $\quad \text{Log } Y = \bar{5}.5427 + 2.802 (\text{Log } X)$ or $Y = .00003489\ X^{2.802}$

Females $\text{Log } Y = \bar{5}.0108 + 3.040 (\text{Log } X)$ or $Y = .00001025\ X^{3.040}$

June 1954 - May 1955 sample (Fig. 11)

Males $\quad \text{Log } Y = \bar{4}.0165 + 2.611 (\text{Log } X)$ or $Y = .0001039\ X^{2.611}$

Females $\text{Log } Y = \bar{5}.5347 + 2.823 (\text{Log } X)$ or $Y = .00003426\ X^{2.823}$

(b) Discussion

The values of "n" for females were found to be 3.040 for the 110-240 mm fish and 2,823 for the larger 170-340 mm fish. For males the corresponding figures were 2.802 and 2.611. The difference in values of "n" between the samples (0.138 for females and 0.212 for males) was due to the larger fish being collected throughout twelve months whilst the smaller fish constituted a single month's sample.

It is evident that as they get older the female fish increase in weight for length at a slightly greater rate than the males although this relationship does not hold for young fish. The curves of the 110-240 mm fish show that up to 170 mm male fish have a greater weight/length factor than females. This is also evident in the intersection of the regression lines for log weight/log length plots of the same sample. That this is not just an abnormality due to sampling is borne out by the curves for the 170-340 mm fish which also intersect at approximately 190 mm. The regression lines for this sample also show a tendency to meet.

Hagerman (1952) and Orcutt (1950) show log weight/log length regressions for both sexes of Dover sole and starry flounder respectively in which the male and female regression lines are parallel to each other. The weight/length curves for Dover sole are also parallel but as the data are largely from mature fish they are not strictly comparable with those for greenback flounder. However, Orcutt measured starry flounders down to 100 mm standard length at which all were certainly immature. The curves for the two sexes of starry flounder appear to meet at about 180 mm although the regression lines do not show it. Thus a different condition has been met with the greenback flounder than apparently occurs in two other species of flatfish.

It will be shown in a later section that the ovaries of immature flounders begin to mature when the fish is about 160 mm in length and at 200 mm may contain ova that will be spawned during the coming season. It is significant therefore that it is while the length is between these limits that the female fish becomes proportionately heavier than the male.

Unlike a large number of other teleosts the ovaries of flatfishes do not lie wholly in the visceral cavity but are placed posteriorly between the haemal spines and the body wall.

In the ripe female the posterior extremity of the ovary closely approaches the caudal peduncle. However, the testis is considerably smaller than the ovary (not more than 0.06 the weight of an ovary from a similar sized fish) and therefore does not penetrate the posterior tissue to the same extent. In the immature female fish it is possible to pass a probe backwards between the haemal spines and the body wall through the post visceral cavity of the coelom that will ultimately be taken up by the ovary. In the male fish such a space does not exist and the muscular tissue is closely applied to the spines. Thus the low relative density of the immature female due to the allowance for gonad development seems a possible explanation of observed unusual weight/length differences in young fish. As development of the ovaries takes place the female weight/length factor becomes greater than that of the male and the curves assume the form generally found with most fishes.

(c) Weight/Length Relationship of Fish from Two Areas

In order to ascertain any differences in this relationship between two distinct areas 265 fish were collected from Port Sorell and 285 from Pittwater. Only females were used and flounders less than 185 mm or greater than 304 mm in total length were discarded.

All fish were collected over a period of three months, namely from July-September 1955.

The data are shown in Table 5 and the regression of log weight on log length for these two samples is presented in Figure 12. The two coefficients differ by 0.085, Pittwater fish being 3.052 and Port Sorell having a value of 2.967. The equations for the curves are:

Pittwater $\quad \text{Log } Y = \bar{6}.9675 + 3.052 (\text{Log } X)$

or $\quad \underline{Y = .000009279\ X^{3.052}}$

Port Sorell $\quad \text{Log } Y = \bar{5}.1481 + 2.967 (\text{Log } X)$

or $\quad \underline{Y = .00001406\ X^{2.967}}$

Bearing in mind that both samples contain fish of the same size composition and were collected simultaneously the variation in the weight/length ratio must be due to one or more of the following causes.

(i) Intrinsic population characteristics.

(ii) Difference in mean gonad condition and spawning period.

(iii) Environmental factors influencing food supply.

It will be shown in a later section of the paper that there are significant differences in certain meristic characters in flounders from the two areas but it is thought that the cause of weight/length variation more justifiably lies with (ii) than (i). Insufficient information is available to consider the implications of (iii).

As the curves and the regression lines converge towards their lower limits it seems highly probable that the weight/length ratio of immature fish would be closely comparable for both areas. The mean weights of the 190 mm group differ by

TABLE 5

THE WEIGHT/LENGTH RELATIONSHIP OF ADULT FEMALE FLOUNDERS FROM TWO LOCALITIES

INTERVALS OF TOTAL LENGTH mm	MEAN WEIGHT GM	
	Port Sorell	Pittwater
185-194	83.1	82.8
195-204	96.4	96.9
205-214	106.8	115.8
215-224	124.7	131.1
225-234	139.2	149.4
235-244	165.7	170.6
245-254	177.5	201.1
255-264	204.6	210.3
265-274	236.0	244.2
275-284	249.5	261.9
285-294	279.2	299.8
295-304	330.1	354.3

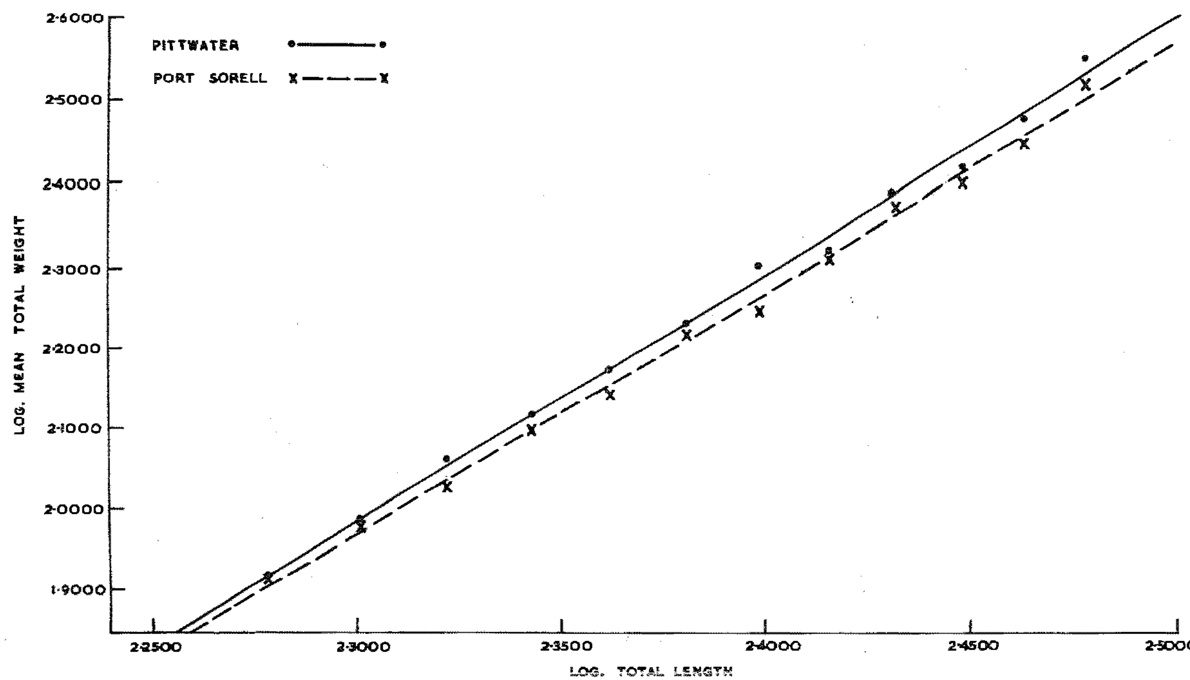

Fig. 12 Log. Weight - log. length relationship of female adult flounders from Pittwater and Port Sorell compared. Both samples were collected during July, August, and September, 1955.

only 0.3 gm whilst the 280 mm group which would consist of mature fish have a difference of 12.4 gm. Furthermore, the sharp decline in mean ova diameter at the end of the spawning season in 1955 (Figure 24) commenced three months earlier at Port Sorell. Although it was not feasible to collect enough material to determine the limits of the spawning period of flounders from this area it seems certain that it is more protracted in Pittwater where as can be seen in Figure 24 the temperature of the water remains cooler for at least two months longer in the spring than at Port Sorell. From this evidence the weight/length differences between the two samples could be attributed at least in part to differing relative weights of gonads in mature fish.

In the treatment of the seasonal fluctuation of the weight and length of male and female flounders the "condition factor" C was used as the index. Hart *et al.* (1940) have stated that the alternative relationship $K = W/L^3$ gives an index of weight relative to that which would be expected under conditions of isogonous growth in all body dimensions. However, the procedure of using the relationship $C = W/L^n$ gives an index of the weight relative to the mean weight at any length which Hart *et al.* regarded as more applicable to the determination of the seasonal trend in relative heaviness. It was thought therefore that C was preferable to K for the present purpose as the comparison of the relationship of the seasonal variation of condition factor with the spawning period is shown more by the trend in relative heaviness than "form". Also as is the case with many other species the cube law does not strictly hold for R. tapirina; that is it will be shown that "n" is not exactly equal to three and in fact is considerably less.

Some further workers who have made use of and modified both C and K as indices of "condition" are Clark (1925), Keys (1928), Hile (1936), Kesteven (1942), Le Cren (1951), and Cassie (1956).

In the present analysis "n" was determined by linear regression as outlined previously in which case it becomes the coefficient of regression of weight on length. C was then calculated from the expression $C = W/L^n$ or $\text{Log } C = \text{Log } W - n(\text{Log } L)$ where W and L are the mean weights and mean lengths of each monthly sample.

Attention is drawn to the small number of male fish in all samples (Table 6). Whereas the proportion of males to females was approximately 1 : 2 in the March 1954 collection of largely immature flounders the ratio in the adult samples is 1 : 23. It is difficult to accept this latter figure as representing the normal balance of the sexes and it is concluded that as they mature male fish do not generally inhabit the shallow water to the same extent as the females. This will be referred to in the section on spawning. It is possible that the fishing methods were selective to some degree as there

TABLE 6

MALE TO FEMALE RATIO IN SAMPLES OF GREENBACK FLOUNDERS USED IN WEIGHT/LENGTH CALCULATIONS

MONTH	RATIO OF MALES TO FEMALES	NUMBER EXAMINED
Jun.	1 : 16.0	96
Jul.	1 : 50.0	100
Aug.	1 : 50.5	101
Sept.	1 : 59.2	105
Oct.	1 : 50.0	100
Nov	1 : 59.2	105
Dec	0 :103.0	103
Jan.	0 : 98.0	98
Feb.	1 : 7.8	92
Mar.	1 : 16.8	96
Apr.	1 : 8.4	92
May	1 : 6.8	89
Jun.	1 : 14.1	99
Jul.	1 : 19.6	98
Aug.	1 : 28.6	86
Sept.	1 : 37.8	113
Oct.	1 : 54.5	109
Nov.	1 : 21.0	105
Dec.	1 : 35.6	107

is a higher proportion of male flounders in the three monthly Port Sorell samples than in corresponding Pittwater samples. The former were all taken by beach seine and the latter by spear.

Monthly values of C are listed below and presented graphically in Figure 13. For convenience both male and female values have been multiplied by 10^3.

Whilst the condition factor of greenback flounders does not vary greatly during the year, what fluctuations do exist can be broadly correlated with the spawning cycle. The species has a winter spawning season that extends over a period of up to eight months depending on suitable temperature conditions, and for the remaining four months from November to February, although occasionally fish may be found in roe the majority of them are in the spent condition. In 1954 the condition factor begins to fall in August, the male value more sharply than the female, until it reaches its minimum in October. However, in November it commences to rise again until January of the following year when it reaches a point not much short of the maximum for that year. The sudden drop in February is surprising but coincides with the month at which the mean ova diameter is at its lowest (see Figure 23). During the remainder of 1955 "C" at no time reaches the equivalent of its maximum value of 1954 which leads to the assumption that environmental conditions were not suitable for as long a period in the latter year. This effect also shows up to the same degree in the male graph.

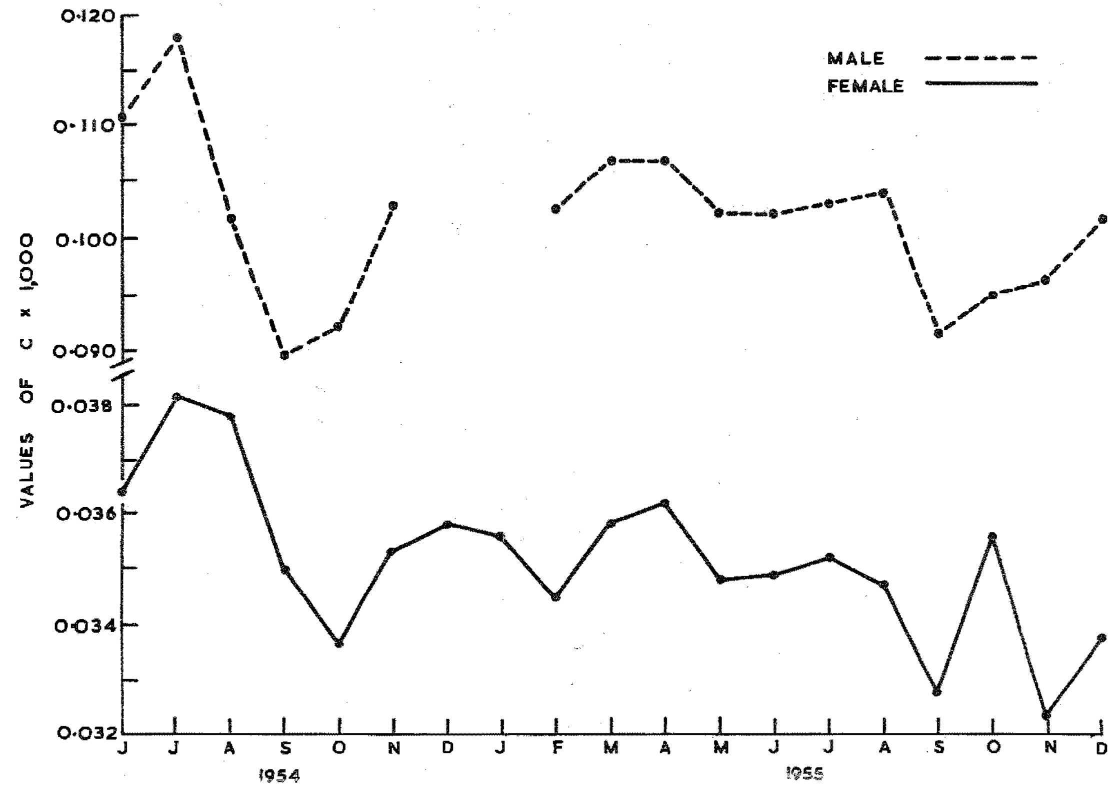

Fig. 13 The seasonal variation of the "condition factor" C for male and female flounders from Pittwater 1954-55. Values of C have been multiplied by 1000 for simplicity in plotting.

The sudden rise in "C" in October is obviously due to a late spawning run as a similar peak occurs for that month in Figure 23.

It has been pointed out that there is a great difference in weight between the gonads of the two sexes. Notwithstanding the two curves are of similar form and trend which indicates the possibility that other factors such as the formation and absorption of fat tissue and availability of adequate seasonal food contribute to the degree of variation of "C" throughout the year.

IX. GROWTH RATE AND AGE DETERMINATION

Four well-known methods of approach to the problem of age and growth determination were considered in the present study.

(a) Scales

Unlike some northern hemisphere flatfish the scales of the greenback flounder are useless for age determination. Scales from different parts of the body were examined without finding any indication that they might be of use.

(b) Otoliths

When otoliths were first studied the writer was under the impression that these also were unsatisfactory for growth investigation and collection of them was not as extensive as it might have been. However, in the absence of other criteria they were reverted to and by exercising care in the selection of readable material it became possible to follow the growth for the first three years of life. As the fish length approached 300 mm a high proportion of otoliths became unreadable due to their increased opaqueness and no fish longer than 320 mm possessed otoliths that could be read with certainty.

In order to ascertain whether grinding the older otoliths facilitated reading, several specimens were thus treated to no advantage. The obscurity of the annuli was found to lie not in the actual thickness of the otolith but in the tendency of the annuli to become opaque as the age of the fish increased.

It was found that the otoliths could be most satisfactorily removed from the flounder by severing the head with a sharp knife midway between the eyes and the insertion of the right pectoral fin. The otoliths can then be lifted out of their sacculi which remain in the portion of the head which has been severed. They were not immediately visible and had to be felt for with forceps. After the otoliths had been cleaned by rubbing between the fingers they were stored in small envelopes upon which was written the length of the fish together with the place and date of collection. Where possible both otoliths were collected as nearly 10 per cent. exhibited varying degrees of crystallization of one or the other. In some cases both otoliths were affected by this condition.

For reading purposes the otoliths were placed under water in a Petri dish, the bottom of which was covered by a coating of black wax, and viewed by means of a low power dissecting microscope. Illumination was provided by a microscope lamp placed about nine inches from the stage in such a manner that the otolith could be read by reflected light. One side of the flounder otolith is almost flat whilst the other is slightly convex and it was found that reading was facilitated by placing it with the latter side uppermost.

About half-an-hour after being placed in water a degree of clearing was noticed which sharpened the distinction between zones but clearing with clove oil and xylol did not render the otoliths more readable. The alternating rings of white opaque and translucent material could be distinguished in the otolith without magnification although the detail could only be seen under a lens.

Molander (1947) working on plaice and flounder has shown that the opaque zone is associated with the fast growth during spring and summer whilst the hyaline or translucent zone is formed during the slow growing winter period. The greenback flounder's otolith conformed to Molander's exposition of seasonal zone formation with the first appearance of the opaque ring occurring in November and its almost certain presence in fish taken in December. The hyaline zone made its first appearance during the month of April. A large variation in the structural composition of the zones and their relative width is presumably due to the extended spawning season of the species. A small proportion of otoliths possessed translucent nuclei. It is thought that fish possessing such were spawned in late summer and their early development took place during what is a normally slow growing period. On the whole the otoliths were not easy to read owing to the frequency of supernumery or false annuli.

Before employing the use of otolith measurements for calculating intermediate lengths the proportional growth of fish and otolith must be established. Although Jensen (1938) discovered that for the plaice and dab growth was disproportionate quite satisfactory agreement was found between the two for the greenback flounder. Both length and width of the otolith as well as the distance from the nucleus to the ventral and posterior margins were compared with the fish length and it was found that of these measurements the best correlation with the fish length was found using the distance from the centre of the nucleus to the ventral margin. This measurement will be referred to as the otolith width.

The regression line of otolith width on fish length in Figure 14 indicates that the growth of fish and otolith is proportionate in flounders between 13 - 32 cm total length. As the regression line intercepts the Y (otolith width) axis at 1 scale division and does not pass through the origin this was subtracted from both the otolith width measurements and the distance from the nucleus to each annulus in the determination of intermediate lengths. This adjusts the proportionality and so permits the use of the formula $L_i = (L_f/W)l_a$ to calculate the

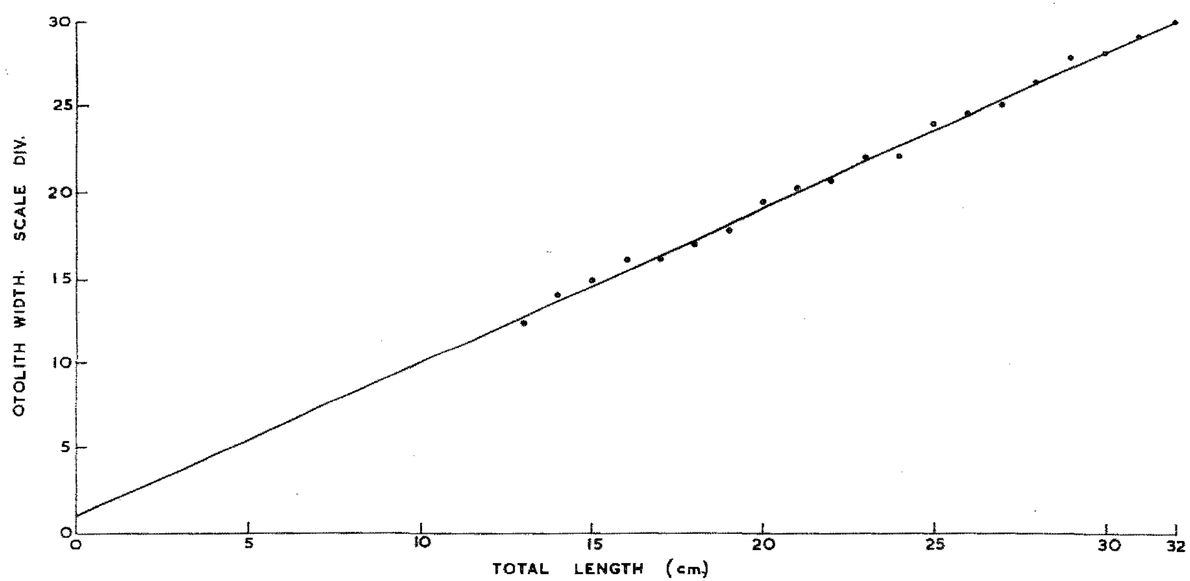

Fig. 14 The regression of otolith width on fish length.

intermediate lengths. The following notation is used in the above expression.-

L_i	=	intermediate length
L_f	=	total fish length
W	=	width of otolith measured from centre of nucleus to ventral or more curved margin.
l_a	=	distance from centre of nucleus to outside edge of annulus

Successive annuli are designated l_{a1}, l_{a2}, and l_{a3}, and likewise intermediate lengths L_{i1}, L_{i2}, and L_{i3}.

It was necessary to use the outside edge of the annulus as a reference point for measurements because it was often difficult to judge the position of the centre.

For purposes of relating the otolith measurements to age it is necessary to select a birthday month. This month represents the period during which the fish pass from one age group to the next and it is usually convenient to choose the month during which spawning is most concentrated. The long spawning season of R. tapirina makes the choice of such a birthday month difficult. As the month of July lies approximately in the middle of the spawning season it was chosen as the birthday month and the 31st day as the birthday. The formation of the mid point of the annulus may also be taken to occur in July, the whole period of the laying down of the annulus lasting from May to September.

Thus if the intermediate lengths of the age groups are calculated using the distance from the nucleus to the outside edge of the annulus formed in September, each length will be greater than the birthday length by approximately three months' growth. To account for this period the age groups have been designated 0+, I+, II+, and so on.

The minimum water temperature of all the Tasmanian localities from which samples were drawn occurs in either July or August, concurrently with the peak of the spawning season. As has been pointed out the annulus is also laid down during this period so that in the greenback flounder its formation is contemporaneous with the spawning season and the months of lower temperatures.

The mean otolith size and corresponding values of l_a and L_i for fish between 130 and 320 mm are given in Table 7. The figures have been corrected according to the Y intercept of the regression line as previously mentioned.

The number of flounders in each age group from which otoliths were read in conjunction with the intermediate length calculations is shown in Table 8. It will be noticed that the overlap of age groups is not great which is due to the shortness of the period over which the sample of fish was collected.

The growth curve in Figure 15 has been drawn using the means of the intermediate lengths.

(c) Marking Experiments

(i) Methods.- All flounders used in the tagging programme

TABLE 7

THE MEAN OTOLITH WIDTH AND CALCULATED INTERMEDIATE LENGTHS FOR EACH CENTIMETRE GROUP OF FISH LENGTH. (l_a = DISTANCE OF ANNULUS FROM NUCLEUS. l_i = INTERMEDIATE LENGTH)

Fish Length (cm groups)	Mean Otolith Width (scale divs.)	l_{a1} (scale divs.)	l_{a2} (scale divs.)	l_{a3} (scale divs.)	l_{i1} (scale divs.)	l_{i2} (scale divs.)	l_{i3} (scale divs.)
13	11.4	9.0			10.3		
14	13.0	9.5			10.2		
15	13.9	10.0			10.7		
16	15.1	10.5			11.1		
17	15.1	9.6			10.8		
18	16.0	9.9			11.1		
19	16.8	9.4			10.6		
20	18.4	9.6			10.4		
21	19.2	9.4			10.3		
22	19.6	9.6	16.2		10.7	18.2	
23	21.0	9.6	16.3		10.5	17.9	
24	21.0	8.4	17.0		9.6	19.4	
25	23.0	9.1	17.0		9.9	18.5	
26	23.5	11.0	18.3		12.1	20.2	
27	24.0	8.5	17.5		9.6	18.7	
28	25.3	9.7	17.9		10.7	19.8	
29	26.7	10.0	19.0		10.9	20.6	
30	27.0	8.3	16.7	23.0	9.2	18.6	25.6
31	28.0	9.5	19.0	25.0	10.5	21.0	27.7
32	29.0	9.0	18.0	24.0	9.9	19.9	26.5
Mean Intermediate Lengths (cm)					10.5	19.4	26.6

TABLE 8

THE NUMBER OF FLOUNDERS CONTAINED IN EACH AGE GROUP FOR EACH CENTIMETRE OF TOTAL LENGTH

Total Length (cm groups)	Number in Age Group 0+	I+	II+	III+
13	1	2		
14	3	1		
15	1	7		
16		11		
17		24		
18		20		
19		9		
20		10		
21		8		
22		2	1	
23		1	3	
24		2	7	
25		1	2	
26			4	
27			2	
28			7	
29			4	
30			1	2
31			1	1
32				1

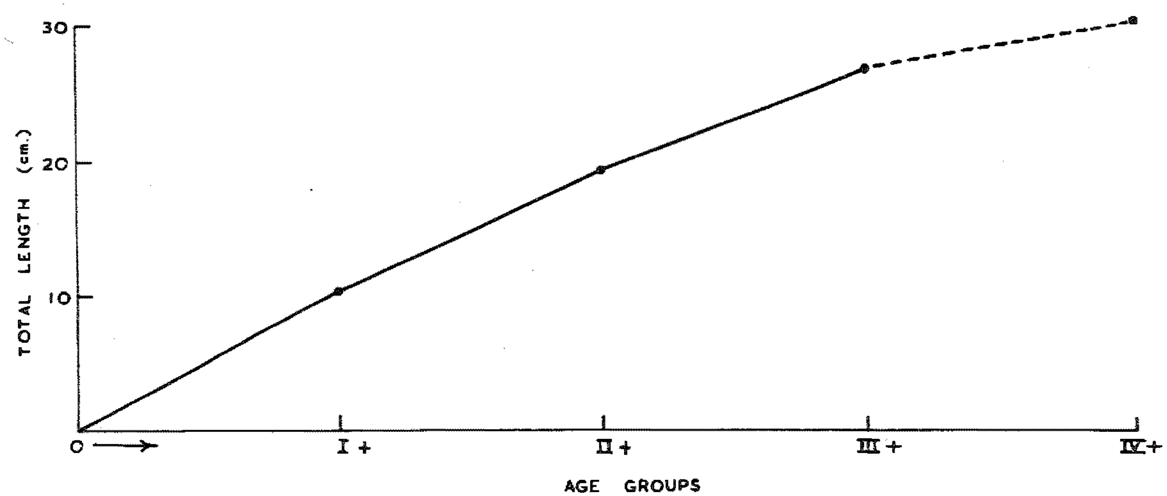

Fig. 15 The growth curve of the greenback flounder for the first four years of life as derived from otolith measurements. The dotted line indicates fourth year growth of a single tagged fish.

were caught by beach seine and transferred as soon as possible to the well of the netting dinghy. Experimental fishing was usually done between 9 p.m. and 3 a.m. and all fish reserved for tagging were kept in the well until about 9 a.m. so that any fish suffering damage from handling could be rejected. In this way only the most active fish were used for tagging.

Petersen disc tags were used exclusively and were affixed in the following manner with silver wire. The flounder was held in the left hand in such a way that the snout lay in the palm with the blind or left side uppermost. The body-wall was punctured with a long slender awl at the midpoint of the line from the centre of the lateral line to the dorsal fin, and the prepared wire loaded with the blank backing-disc passed through the fish. The tag was then slipped onto the emergent wire which was given two turns with pliers and the turns then bent down close against the outside surface of the tag. The tags were rather loosely affixed to allow for growth. At the outset of the programme white celluloid tags were placed on the blind side of the fish but abrasion by sand particles when it was in close contact with the bottom tended to wear away the numbers on the tag as evidenced by the return of worn tags that had been out for only a month. Grey tags were then used and placed on the uppermost side. It was considered that white tags placed on this side, whilst desirable for their conspicuousness to fishermen, would render the fish more evident to natural predators.

To observe the effect of the tags on the fish several small flounders 13 - 15 cm long were tagged and placed in a small aquarium tank in the laboratory. They commenced feeding on nereid worms a week later and although they did not grow appreciably were all alive and healthy for twelve weeks when they died due to an overnight breakdown of the aerator.

(ii) Discussion.- In all, 474 southern flounders were tagged in two localities, Pittwater and St. Helens. Total lengths of the fish ranged from 10 - 30 cm and the number of tags recovered was 28 or 5.91 per cent. of the total released. Of this number 22 (4.64%) were returned with full information regarding length, place, and date of capture. The number of fish that were available for accurate measurement amounted to 8 or 1.69 per cent. of the total returns and this figure included flounders recaptured by the author during the experimental fishing operations. It was found that where fish had been measured by fishermen and then returned to the laboratory for checking differences of up to 1 cm between the two lengths occurred. Fishermen tended to measure to the nearest half inch by placing a rule along the side of the fish often after keeping them alive in caufs or wells for a week or so as curios.

The periods of freedom varied from nine to nine hundred and seventy-eight days, with a mean of one hundred and sixty-six days. With the exception of one fish, all were retaken within the tagging area. The fish referred to travelled from Pittwater to the Carlton River, a distance of nine miles in one hundred and eight days. From this it appears that generally the southern flounder does not travel extensively but rather tends to spend its life within a restricted area. It might be expected that the percentage return of tags should have been higher than it actually was, taking into account their limited movements and the intensity of fishing. It may well be that the mortality of tagged flounders was abnormally high, as was found in the case of the lemon sole (*Parophrys vetulus*) by Manzer (1952). This author estimated by extrapolation that over a period of a year the rate of tagging mortality without competition from other types of mortality was from 41 - 49 per cent.

In the present investigation no indication of high mortality was noticed other than the relative small percentage of returns.

Table 9 shows the number of fish tagged from each centimetre group of total length together with the number and percentage of tags returned. The contents of this table are arranged graphically in Figure 16 for easier comparison. It is noticeable that none of the 10 - 15 cm fish were returned and that the highest proportion lay in the larger size groups. A possible explanation of the absence of the small sizes is that professional fishermen would rarely catch them and amateur spearers, if they did take them, would be loth to disclose the

TABLE 9

THE FREQUENCY DISTRIBUTION OF TAGGED AND RECAPTURED FLOUNDERS

TOTAL LENGTH (cm groups)	NUMBER TAGGED	NUMBER RECAPTURED	% RECAPTURED
10	1	0	0
11	14	0	0
12	20	0	0
13	24	0	0
14	14	0	0
15	23	0	0
16	24	1	4.17
17	24	0	0
18	20	2	10.00
19	28	2	7.14
20	40	2	5.00
21	51	1	1.96
22	68	4	5.88
23	51	6	11.76
24	23	4	17.39
25	20	2	10.00
26	14	4	28.57
27	9	0	0
28	3	0	0
29	1	0	0
30	2	0	0

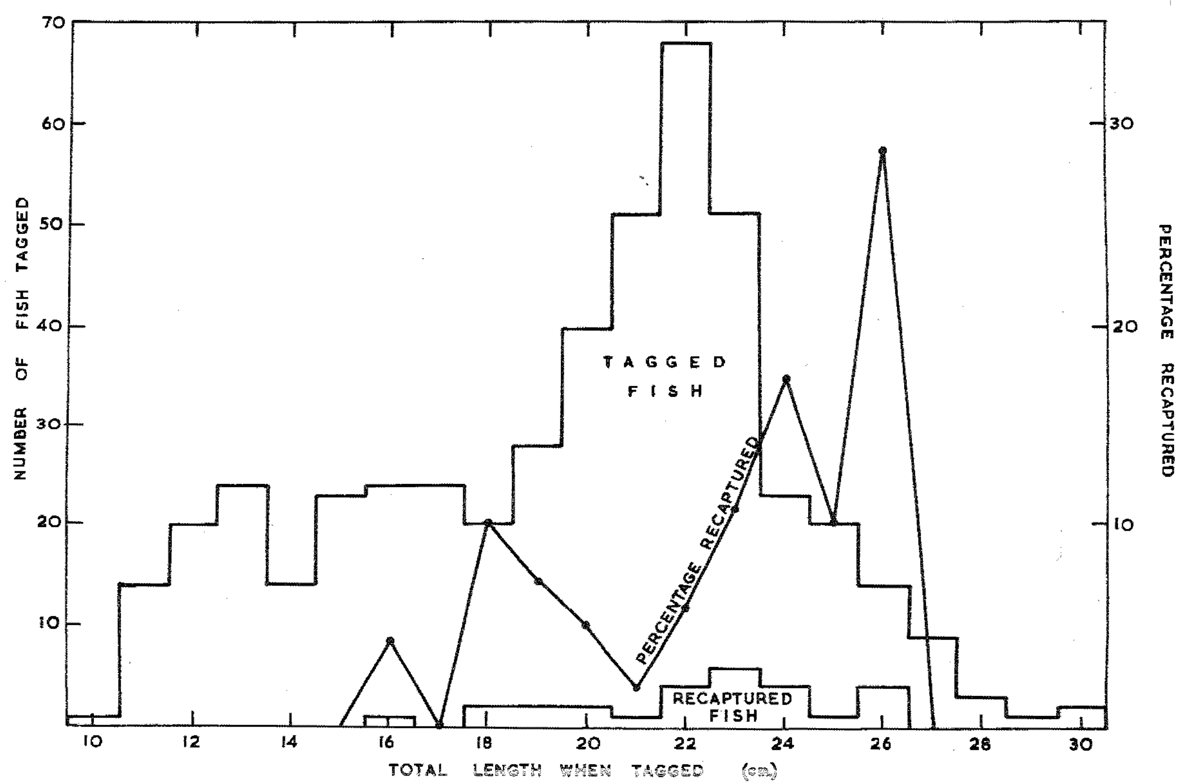

Fig. 16 The length distribution of tagged and recaptured flounders and the percentage of recaptures for each centimetre of total length.

information, for obvious reasons. On the other hand the mortality in the small fish could have been high due to both natural causes and the effect of the tags. Manzer (1952) found that the size of the fish could not be related with either the number of deaths or the rate at which they took place but the smallest fish tagged during his investigation were in the 25 - 27 cm group. When the two histograms in Figure 16 (data Table 10) are compared not only do the means differ (19.65 cm and 22.93) but the principal mode of the returned fish is one centimetre greater than that of the tagged sample. This may indicate that mortality decreases with age although one would expect that any differing physical effects of tagging on 20 and 26 cm fish would be negligible.

The period between July and October when the flounder fishery is closed accounts for the lack of returns during these months. Only one tagged fish was caught in the experimental hauls made during the closed season.

The increase in length of individual fish during their release is presented in Figure 17. The time axis covers four years and the points at the extremities of the lines represent the lengths and dates at tagging and recapture. The lines are numbered to correspond with the figures in the last column of Table 11 where other details of each particular fish may be consulted. The lines marked with an asterisk indicate the specimens which were accurately measured both times by the author.

TABLE 10

STATISTICS OF TAGGED AND RECAPTURED FLOUNDERS TREATED AS TWO SEPARATE SAMPLES

	TAGGED FISH	RECAPTURED FISH
Mean Length	19.65 cm	22.93 cm
Number	474	28
S.D.	± 4.231	± 2.596
S.E.	± 0.1943	± 0.4905

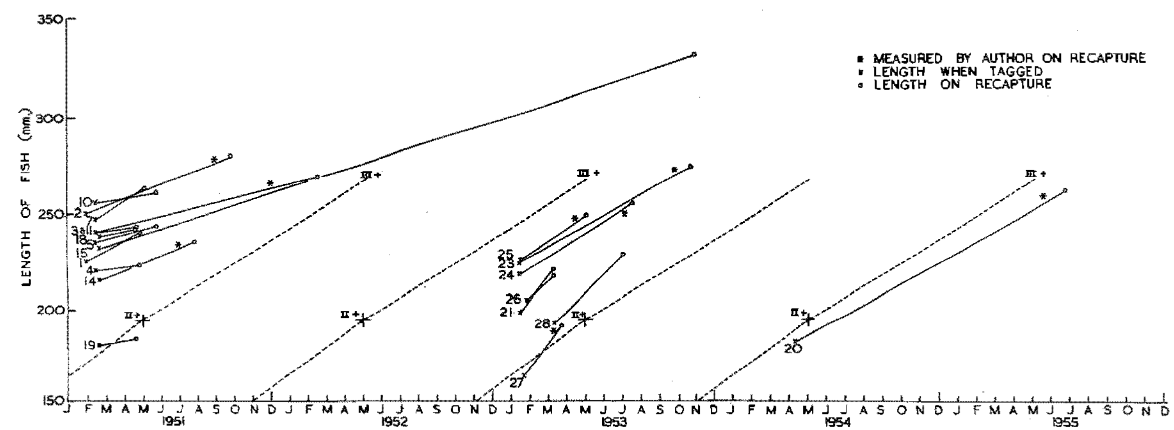

Fig. 17 The growth of tagged flounder during varying periods of freedom. The dotted lines represent the calculated growth and the figures adjacent to each tag return refer to the serial numbers in the extreme right-hand column of Table 11 where more detailed data are shown.

TABLE 11

RESULTS OF TAGGING EXPERIMENTS AT PITTWATER (PW) AND ST. HELENS (SH)

TAG NO.	RELEASES			RECAPTURES			DAYS FREE	INCRE-MENT	GRAPH NO.
	Date	Locality	Length	Date	Locality	Length			
A2329	31. i.51	S.H.	225 mm	28. iv. 51	S.H.	240 mm	88	15 mm	1
A2384	31. i.51	S.H.	250	27. x. 51	S.H.	279	270	29	2
A7522	16.ii.51	P.W.	240	20. iv. 51	P.W.	243	63	3	3
A7530	16.ii.51	P.W.	220	27. iv. 51	P.W.	223	70	3	4
A7533	16.ii.51	P.W.	235	25. v. 51	P.W.	243	99	8	5
A7539	16.ii.51	P.W.	225	?	P.W.	235	?	10	6
A7544	16.ii.51	P.W.	247	5. v. 51	P.W.	262	79	15	7
A2266	16.ii.51	P.W.	232	?	P.W.	235	?	3	8
A2267	16.ii.51	P.W.	260	?	P.W.	260	?	0	9
A2280	16.ii.51	P.W.	255	25. v. 51	P.W.	260	99	5	10
A2283	16.ii.51	P.W.	240	19. ii. 52	P.W.	268	368	28	11
A7551	22.ii.51	S.H.	260	3.iii. 51	S.H.	260	9	0	12
A7565	22.ii.51	S.H.	210	?	S.H.	214	?	4	13
A7571	22.ii.51	S.H.	225	27.vii. 51	S.H.	235	155	10	14
A7581	22.ii.51	S.H.	232	27. x. 53	S.H.	330	978	98	15
A7582	22.ii.51	S.H.	220	?	S.H.	220	?	0	16
A7587	22.ii.51	S.H.	185	?	S.H.	186	?	1	17
A7589	22.ii.51	S.H.	238	20. iv. 51	S.H.	242	57	4	18
A7594	22.ii.51	S.H.	180	20. iv. 51	S.H.	184	57	4	19
C3554	9.iv.54	P.W.	182	20. vi. 55	P.W.	260	376	78	20
C3214	14. i.53	P.W.	198	10.iii. 53	P.W.	220	55	22	21
C3216	14. i.53	P.W.	255	24. i. 53	P.W.	255	9	0	22
C3201	14. i.53	P.W.	224	23. x. 53	P.W.	273	282	51	23
C3221	14. i.53	P.W.	218	17.viii.53	P.W.	254	215	36	24
C3234	16. i.53	P.W.	225	4. v. 53	Carlton R.	248	108	23	25
C3293	20. i.53	P.W.	204	9.iii. 53	P.W.	216	47	12	26
C3312	21. i.53	P.W.	162	20.iii. 53	P.W.	190	57	28	27
C3338	10.iii.53	P.W.	192	2.vii. 53	P.W.	228	114	36	28

The broken lines drawn at yearly intervals are corresponding parts of the growth curve determined by otolith reading.

It is apparent from the agreement between the calculated growth lines and the growth of the tagged fish that the otolith interpretation is essentially correct. Good agreement occurs in the case of the asterisk-marked lines, but it is only fair in the remainder where the accuracy of measurement cannot be vouched for. The accelerated growth taking place in the summer months shows up in lines 21, 26, and 27, but due to the absence of any reliable short-term returns over the winter the extent to which it falls off during this period cannot be determined. Lines 2 and 11 indicate the slowing down of growth in the third and fourth year. Had it been possible to obtain more reliable returns from the 20 - 25 cm group over a longer period the calculated growth curve could be extended beyond the stage when otoliths become unreadable. However, it has not been attempted with the figures available as the only return that might have been of use, line 15, is not strictly accurate. This fish which remained free for over two and a half years was reported by the finder to have the "tail almost eaten away" and its length was estimated at 330 mm on having a standard length of 295 mm. However, interpolating the growth arrived at by this approximation it seems that a flounder at the end of its fourth year would have a total length in the vicinity of 300 mm.

(d) Length Frequency Observations

The successful use of the Peterson method for estimating growth in fishes depends primarily on the species under consideration having a relatively short breeding season, and also upon fish at the same size having approximately the same growth rate. The greater range in lengths of each year brood resulting from an extended spawning tends to obscure yearly modes in the frequency distributions, although this may be overcome to some extent by large sampling techniques.

In the present investigation the interpretation of length frequency modes was severely limited as the sampling was not great enough to overcome the irregularities caused by the extended spawning season of the species.

There being no fish market in Tasmania it was not possible to measure large numbers of flounders and the collections made by the author were rarely greater than 100 fish for any one month. In addition the fishing methods were probably selective as regards the limited areas fished and the gear used. Practical considerations prevented making large experimental collections of juvenile fish at regular intervals and usable data on I+ fish were therefore lacking. There were also insufficient numbers of IV+ and V+ fish to provide any clue to growth in these two groups.

However there is some indication of the presence of genuine age groups over a short period in some samples whilst others display a modal shift commensurate with growth.

The length frequencies of female fish from nineteen monthly collections in Pittwater are presented graphically in Figure 18. All length measurements were grouped to the nearest centimetre. Only female fish were used as the number of males taken was too small to be of consequence in monthly plots.

In the curves for the months June to October 1954 it is seen that there is a modal shift of 2 cm over the four months period. From the calculated curve the annual growth rate of II+ (19-26cm) flounders was established to be 0.6 cm per month or 2.4 cm for four months. As growth is presumably slower in winter there is reasonable agreement between these two figures. The growth cannot be followed directly in November where two modes occur at 21 and 23 cm. In this sample the 21 cm mode probably represents the I+ fish as they become II+, and the 23 cm mode is possibly due either to sampling error or the existence of two main spawning periods in the protracted breeding season. That growth is greatly retarded in winter is evidenced by the primary modes of the May - August 1955 samples remaining static at 22 cm and then showing an increase of 1 cm in September. The growth of II+ and III+ fish from August 1954 to April 1955 indicated by modal shift in Figure 19 is comparable with the calculated growth for the period shown by the broken lines drawn through the curves. The III+ group can be followed more easily than the II+ but in both it is

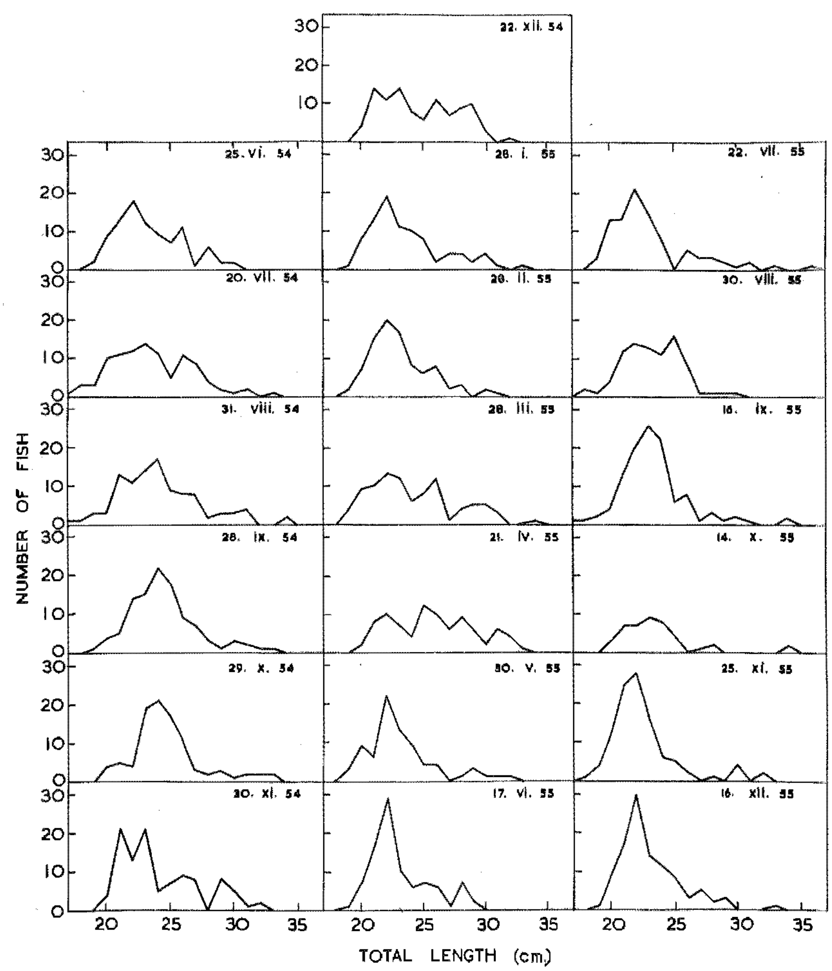

Fig. 18 Length composition of female greenback flounders from Pittwater as shown by measurements of nineteen consecutive monthly collections, June 1954–December 1955. Statistical data shown in Table 12.

TABLE 12

STATISTICS OF FEMALE FLOUNDERS FROM WHICH THE DATA PLOTTED IN FIGURE 18 WERE TAKEN (MEASUREMENTS IN MM)

n = NUMBER EXAMINED
A.M. = ARITHMETIC MEAN
S.D. = STANDARD DEVIATION
S.E. = STANDARD ERROR OF THE MEAN

MONTH	RANGE (T.L.)	n	MODE	A.M.	S.D.	S.E.
1954						
June	19-30	92	22	23.4	± 2.64	± 0.28
July	17-33	96	23	23.6	± 3.21	± 0.33
August	17-34	102	24	24.1	± 3.21	± 0.32
September	19-33	105	24	24.5	± 2.68	± 0.26
October	20-33	96	24	24.6	± 2.82	± 0.29
November	20-32	104	21 & 23	24.2	± 3.09	± 0.30
December	20-32	98	21 & 23	24.6	± 2.91	± 0.29
1955						
January	19-33	88	22	23.6	± 2.74	± 0.29
February	19-31	100	22	23.1	± 2.15	± 0.21
March	19-34	93	22	24.1	± 3.40	± 0.35
April	20-33	87	22	25.7	± 3.38	± 0.37
May	19-33	86	22	23.2	± 2.92	± 0.31
June	19-29	93	22	23.0	± 2.38	± 0.25
July	19-36	91	22	23.1	± 3.20	± 0.34
August	18-30	85	22	23.3	± 2.25	± 0.24
September	17-34	113	23	23.4	± 2.74	± 0.26
October	20-34	43	23	23.5	± 2.98	± 0.45
November	18-32	102	22	22.3	± 2.63	± 0.26
December	19-33	104	22	23.0	± 2.41	± 0.24

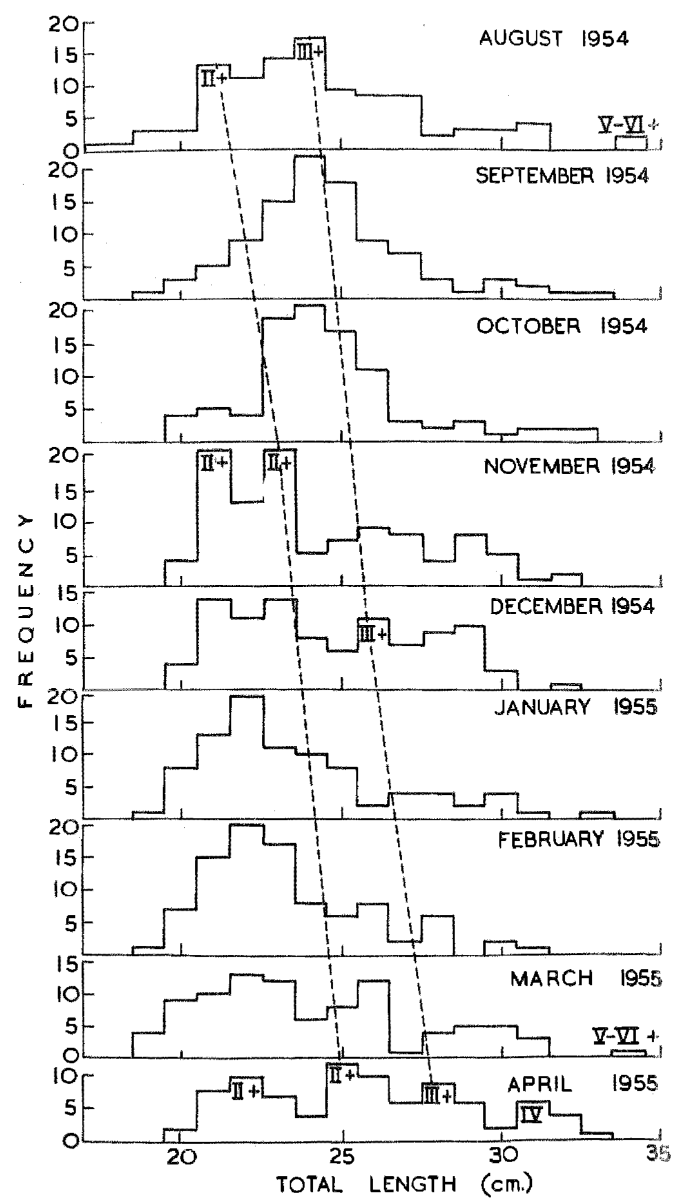

Fig. 19 Length frequencies of nine consecutive monthly flounder samples from Pittwater covering the fast growing period during spring and early summer. The dotted lines indicate the suggested modal progression for II+ and III+ year groups.

apparent that the fastest growth is during the period November to February.

The summed frequencies of all male and female flounders examined together with those of a twelve months sample of females appear in Figure 20. The arithmetic means of the two female samples differ by less than 0.5 cm and the mean length of males is 1.92 cm less than the value for the corresponding female sample. The statistics of the curves are in Table 13.

(e) General Conclusions on Growth Rate

From the study of otoliths it appears that in its first year of life the greenback flounder could be expected to attain a length of approximately 10.5 cm at a mean rate of 8.75 mm a month. During its second year the growth rate decreases to 7.35 mm a month and reaches a length of 19.4 cm. The mean monthly growth rate during the third year is 6.0 mm and approximate length at the end of the year 26.6 cm.

The second and third year calculated growth rates are corroborated by tag returns and modal progression of length frequency curves, which also demonstrate a retardation from May to August and an acceleration from November to February.

Although it was not possible to calculate fourth year growth it is estimated to be of the order of 2.8 mm per month and the length attained approximately 30.0 cm.

X. SPAWNING AND GONAD MATURITY

The documentation of maturity spawning and progressional

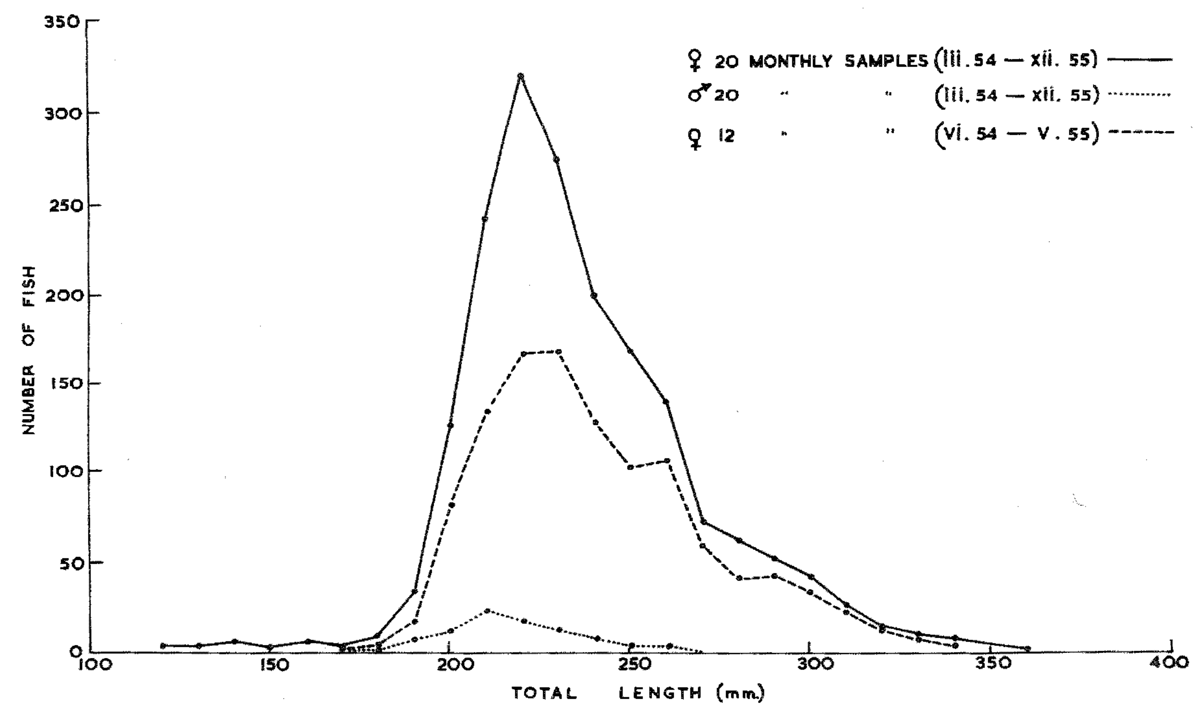

Fig. 20 The length frequency curves of all flounders examined during the investigation. The statistics of the curves are presented in Table 13.

TABLE 13

STATISTICS OF LENGTH FREQUENCY CURVES SHOWN IN FIG. 20

n = NUMBER EXAMINED
A.M. = ARITHMETIC MEAN
S.D. = STANDARD DEVIATION
S.E. = STANDARD ERROR OF THE MEAN

SAMPLE	RANGE IN TOTAL LENGTH (mm)	n	MODE	A.M.	S.D.	S.E.
March 1954-Dec. 1955 (Females)	12-36	1,818	22	23.6	± 3.01	± 0.07
June 1954-May 1955 (Females)	17-34	1,123	23	24.1	± 3.07	± 0.19
June 1954-May 1955 (Males)	17-27	89	21	21.7	± 1.76	± 0.09

development of ova in R. tapirina was made somewhat difficult by four factors.

Firstly, the spawning season was found to be greatly prolonged; secondly, the proportion of male fish in the samples was low; thirdly, running ripe females were rare; and finally, the external appearance of the ovary varied only slightly during the various stages of maturity.

As the length of the spawning season will be dealt with later in this section it will be sufficient to state briefly that spawning takes place over a period of eight months, although some fish with maturing or ripe ova may be encountered in any month of the year. The manner in which a prolonged spawning affects growth determination has been mentioned in the previous section and the study of adolescence and age at maturity is similarly rendered difficult by this condition. The more prolonged the spawning season the greater will be the range in size of developing ova at any chosen time of observation. This gives rise to complications when following the growth of ova in frequency distributions from month to month.

Secondly, because of the difficulty of capturing mature and ripe males during the investigation, and the absence of adequate observational staging criterion, it was necessary to confine the study of maturity and spawning to female fish. Although in the 10 - 17 cm flounders the percentage of males varied between 25.0 and 56.7 per cent., as maturity was reached the proportion quickly fell away to 17 per cent. and this downward trend continued among the larger fish. The smallest fish taken from which "milt" flowed freely was 18 cm long so that the bulk of fish represented by the part of the curve lying between 18 and 27 cm in Figure 21 would be mature. Reference to the percentage curve in the same figure shows the steady decline in the proportion of males from 17.0 - 0.6 per cent. over the length limits of mature fish. Considering the almost equal proportion of the sexes amongst immature fish the question of what factor or factors determine the change in sex ratio presents itself. Although Kawasaki and Hatanaka (1951) found that for two groups of Limanda angustirostris Kitahara the sex ratio remained constant at 1:0.999, in other species the proportion of females may either increase or decrease with age. Hile (1935) showed that the number of female ciscos per one hundred males increased from one hundred in the first year of life to 1100 in the sixth year. He was of the opinion that the differential mortality of the two sexes was probably the result of their innate physiological mechanism the manifestation of which could vary from one population to another. Previous work on the Lake Huron herring by Van Oosten (1929) demonstrated the reverse condition in which the males, although not abundant in age groups I+ and II+, predominate in older age groups. Van Oosten attributed the shifting sex ratio to the earlier attainment of sexual maturity in females and a resulting

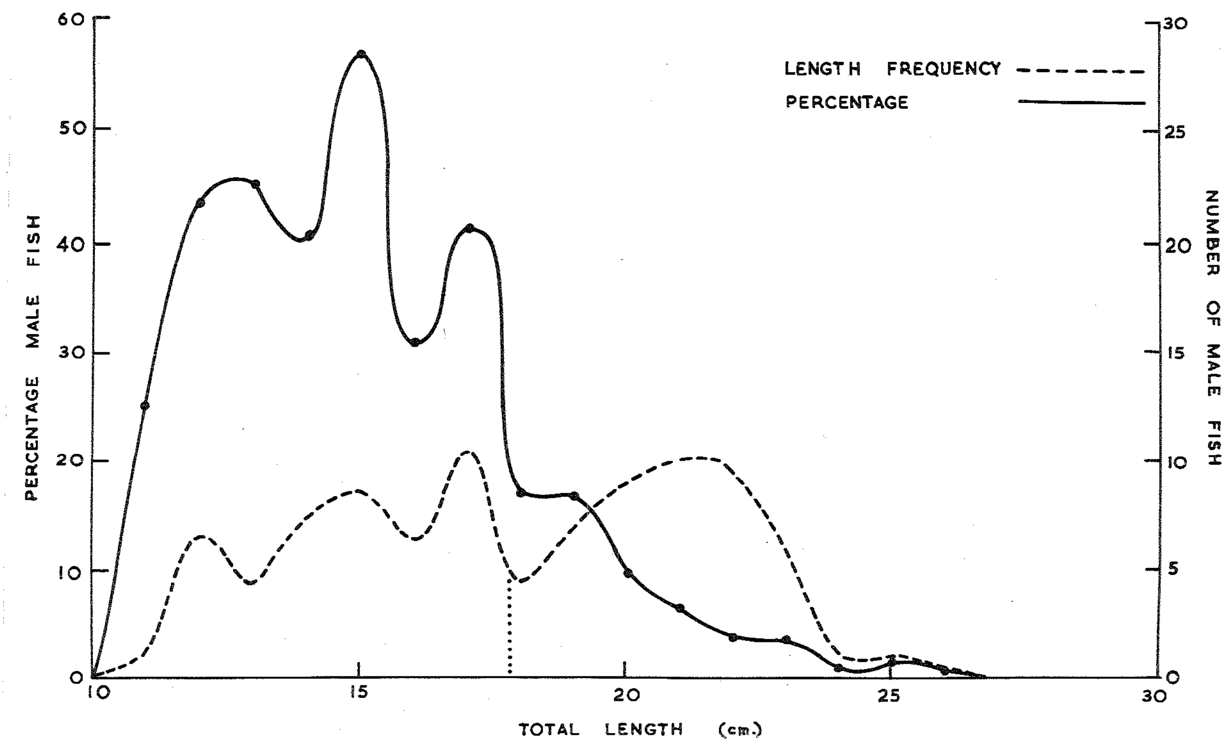

Fig. 21 The numbers of male flounders in each cm. of total length expressed as a percentage of total number examined. The broken line indicates the length composition of male fish.

tendency for them to appear in the commercial catch at an earlier age.

The reason for the change in sex ratio in the greenback flounder is not clear from the data available. Possibly, as Geiser (1923, 1924) concluded, the differential mortality of the sexes is due to the greater inherent ability of the females to survive adverse environmental conditions. A further possibility is that males, as they mature, tend to move to sea and remain there. That there is a higher mortality amongst older male fish seems apparent from a study of the length composition of the two sexes in the collections from June 1954 to May 1955. In Figure 20 the mean length of males is only 2.31 cm less than the female mean length although there is a difference of 8 cm between the largest male and female fish measured. At no time during the investigation was a male taken longer than 26 cm while the largest female flounder measured 36 cm.

(a) Methods

Because the changes in appearance of the developing ovary were few the author decided to pursue the study of the growth and development of the ovarian ova and use it for the determination of the age at maturity and the spawning season. Ova diameter measurements as maturity criteria have been used by several workers and sytematized by Clark (1934). The measuring technique used in the present study was similar but in view of several minor changes it will be as well to outline the procedure.

Ovaries were taken from about 1800 flounders over a period of a year and a half. The flounders were collected at regular monthly intervals from Pittwater, each sample being randomly speared and consisting of approximately one hundred fish.

Additional collections of small, immature fish were netted by the author from time to time for the investigation of age at maturity. Where possible the whole of the ovary was preserved by placing it in a 4" x 1" tube containing a ten per cent. solution of formaldehyde. Where the size of the ovary precluded its entire preservation a large transverse section of the anterior portion was used. Examination established that the size classes of ova were homogeneously distributed throughout the ovary. Any shrinkage or distension caused by preservation was not detectable even in mature eggs although a certain amount of distortion due to pressure exerted by the walls of the tube was evident. Hardening of the ova was completed within a week after which they could be handled without causing any alteration in diameter.

For measuring purposes a small piece of ovary was teased out with needles, placed on a slide, and covered by a suitable amount of water so that the largest eggs were completely submerged. This enabled the material to be viewed without the use of a coverslip which simplified and speeded up the operation. A movable stage microscope was used to make the actual measurements in conjunction with an eyepiece micrometer in which one scale division equalled 0.015 mm.

Twenty to thirty of the largest ova were measured from each ovary and the mean diameter noted. Generally the majority of eggs were symmetrical but to obviate errors caused by any that may have been distorted the micrometer was always kept in a vertical position and the diameter measured parallel to the graduations. When it was required to make measurements of groups of eggs of varied sizes within the one ovary a fraction of the gonad was teased out, and all ova in the field measured. The field was then changed and measuring continued until from 200 to 300 eggs had been accounted for.

(b) Terminology

The maturity of fish can be expressed either in terms of the maturity of its ova, or by the state of development of its ovary. Whilst the changes in appearance of the ovary itself are usually adequate to define the state of maturity of the fish the use of ova diameter measurements is subject to certain qualification. Because it is possible for an adolescent and an adult fish to contain maturing ova it is necessary to draw up a series of terms that will avoid confusion when referring to the maturity of ova as distinct from the maturity of ovaries. Furthermore, as it is necessary to apply the terminology of eggs and gonads to the state of the fish itself the different stages of maturity are listed under three headings, as follows.

(c) Description of Ovarian Ova

(i) Ovarian Ova.- It became evident at the outset of the gonad study that the ovarian eggs could be separated into one or more of three size groups depending on state of maturity.

GroupI: this group comprised the immature egg stock from which eggs destined to mature would be drawn. The range in ova diameter was found to be from 0.015-0.135 mm and the ova were largely transparent with a granular translucent nucleus approximately half the total ova diameter in size. The smaller eggs tended to remain in clusters after the tissue had been teased out on a slide whilst the larger ones were often separated by this operation. Group I ova were visible in all ovaries in all stages of maturity.

Group II: eggs in this group measured 0.150-0.525 mm and had begun to form yolk which gave them a granulated appearance. The granulation gradually became general throughout the egg, rendering it more opaque as the size increased although the nucleus could be distinguished in eggs up to 0.250 mm in diameter. From 0.350-0.525 mm the eggs were darkly opaque, except for a thin transparent periphery.

Group III: all ova ranged from 0.630-0.800 mm in diameter and were closely approaching or had undergone maturation in preparation for spawning. They were translucent with a very thin semi-transparent peripheral layer and therefore markedly different from Group II eggs. The nucleus was visible if maturation had not taken place and from one to three dark brown oil globules were present which varied in size from $\frac{1}{8}$ to $\frac{1}{4}$ the egg diameter. The largest eggs in the group were found to be identical with those of the species found in the plankton.

(ii) The Ovary.- (1) Immature. An ovary which contained Group I eggs only. The immature ovary could be infallibly distinguished from one that had spawned and was recovering as in the spent ovary the largest ova fell into Group II. (2) Maturing. There were two types of maturing ovaries. Adolescent: those which had never reached full maturity but would produce ripe eggs in the approaching spawning season. Recovering: ovaries which had previously spawned and had begun to mature the next season's ova.

Both adolescent and recovering ovaries contained Group II and Group III eggs, but were readily distinguished by differences in shape and appearance. As in the plaice (Cole and Johnston 1901) the spent ovary of the greenback flounder does not revert to its adolescent form. The recovering ovary is elongated and shrunken with well developed blood vessels whereas that of the adolescent is of a lighter appearance, more rounded and lacks prominent blood vessels. (3) Mature: ovaries which contained Group III ova which were usually in process of being spawned.

(iii) The Fish.- To overcome ambiguity in the application of ova diameter and gonad stage criteria to the maturity of the fish three further terms were introduced. Young: the ovary contained Group I ova only. Adolescent: had never spawned but possessed Group II ova. Adult: had spawned previously and contained Group II or III ova or may not have spawned but contained Group III ova.

These terms will be adhered to throughout the present paper.

(iv) Discussion.- The size limits of the ova in each group together with their relationship with the maturity of the fish were determined from the measurements of from two hundred to three hundred ova chosen at random from each of four adult flounders with different stages of mature and maturing gonads. The resulting ova frequency distribution from (A) maturing, (B) mature, (C) partly spent, and (D) fully spent ovaries are shown in Figure 22. In all four distributions the immature stock of Group I ova is clearly seen with a mode at 0.075 mm. In (A) secondary modes at 0.105 and 0.135 mm indicate that portion of the stock has commenced to increase in size as the first step in the maturing process has been taken. Two important features of the behaviour of the developing ovary shown by the distributions are:

Firstly, the spawning act is completed in two stages with an unknown interval between each stage. In the mature ovary (B), two distinct size groups are present, those about to be spawned and a secondary group ranging in size from 0.360 to 0.495 mm. The question arises whether this group of ova mature and are spawned in the current season, whether they constitute the stock from which the following season's eggs will be drawn,

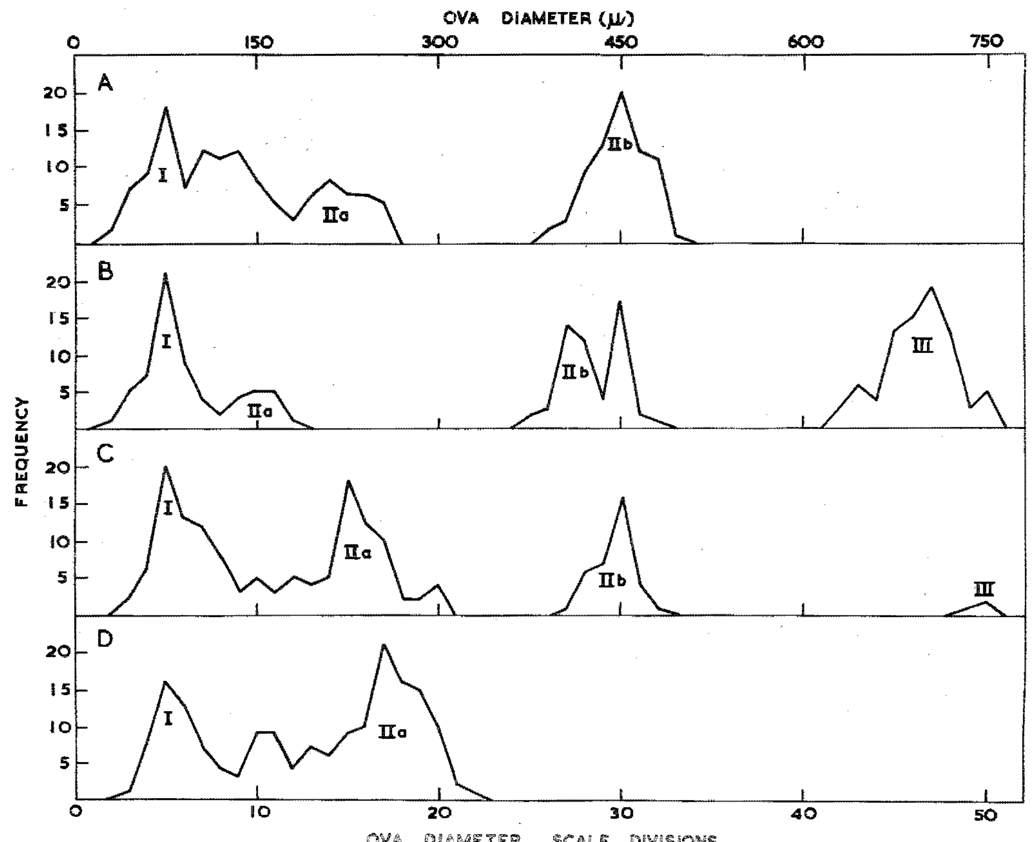

Fig. 22 The size distribution of randomly selected ova from four ovaries in different stages of maturity.

"A" represents the condition in an ovary that has begun to mature, "B" an almost ripe ovary, "C" a running ripe and partly spent ovary, and "D" a fully spent ovary.

The small letters merely distinguish the two size groups of Stage II ova mentioned in the text.

or whether they degenerate and are resorbed. It is common in some species of flatfishes for all mature eggs to be discharged at spawning, only the immature stock remaining in the ovary. This condition is met with in the dab (Wheeler 1924), the starry flounder (Orcutt 1950), and the Dover sole (Hagerman 1952) all of which, during the spawning season, contain no intermediate groups of ova between ripe and immature stages. Conversely in the California sand dab (Arora 1951) and plaice (Franz 1910) a stock of unripe maturing eggs remains after spawning which are ultimately reabsorbed. Such is the case with the greenback flounder.

Observation of running ripe ovaries showed that a large number of ova were released during the spawning act which left the ovary quite flaccid. This indicates that the ova which undergo maturation in preparation for spawning do so in a body and not in small batches over a considerable interval of time. The ultimate fate of the secondary group of ova must now be considered. Two types of readily recognizable ovaries were found to be consistently present in spent fish, one containing the group of maturing eggs in question and the other in which it was lacking. (See graphs (C) and (D). Fig. 22). The study of ovaries of type (B) showed that at the time when the mature ova were lying freely in the lumen the secondary group of ova were firmly attached to the walls and in such quantity that they were estimated to be potentially as numerous as those already mature. No instance of the breaking down and resorption of this group was noticed throughout the study. Once it has been established that these eggs do become mature the question of the interval between spawning of the two groups presents itself. That the secondary group are the stock from which the ova destined for the following year are drawn is discounted by curve (D) in which the largest ova are seen to be in the 0.180 - 0.315 mm class. While no accurate assessment of the time lapse between maturing batches of ova could be made it is likely, considering the length of the spawning season, that it may be a period of weeks or even months.

The second noticeable characteristic is that not all ova that begin to mature are destined to achieve final maturity. Examination of fully spent and maturing adolescent ovaries showed the presence of two ova groups measuring 0.045 - 0.135 mm and 0.135 - 0.180 mm respectively. The smaller group represents the immature stock whilst the larger comprises the succeeding season's crop which has already entered the maturing stage. In some cases there occurred a further class ranging from 0.180 - 0.330 mm which, if in spent adults showed signs of degeneration. It appears that these were ova in which, for some reason, development did not continue and it may well be that they formed a "reservoir" from which any losses due to mortality in later stages were replenished. That they did ultimately degenerate was borne out by microscopical observation and confirmed by their general absence in ovaries from November to February when the modal ova diameter was 0.150 mm.

The monthly ova frequency data in Figure 23 show that the growth of eggs from 0.150 to 0.450 mm in the adult and adolescent flounder is accomplished in four to five months. During this period growth is regular as is demonstrated by the occurrence of all intermediate size groups in the month to month samples. However, once the ova reach a size ranging from 0.330 - 0.450 mm, development appears to be halted and a stock of ova awaiting maturation is formed. The existence of this prematuration group is clearly seen in the frequency histograms for the spawning period. From June to October 1954 (Fig. 23), with the exception of two fish in August and one each in September and October, the largest group of eggs have their mode at 0.450 mm. During the same period mature ova measure 0.675 - 0.825 mm which draws attention to the noticeable absence of 0.450 - 0.675 mm eggs.

Light has been thrown on the absence of eggs in the intermediate stages of the final maturation process by Fulton (1897) working on haddock. He concluded that the relative scarcity of such ova was due to sudden change from the densely opaque condition to the distended transparent form and added that the actual extrusion of eggs took place as quickly. Hickling (1930) also attributed the low percentage of "running ripe" female hake on the spawning grounds at the height of the spawning

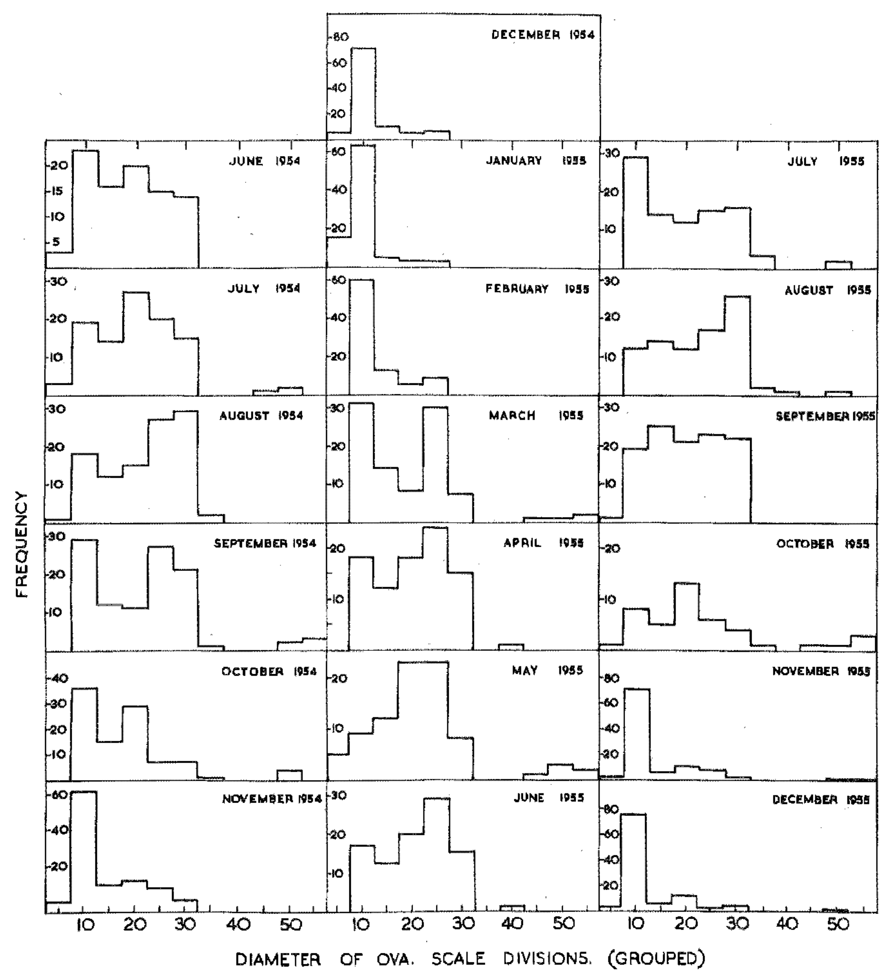

Fig. 23 Diameter frequency histograms of ova from Pittwater flounders sampled monthly from June 1954 to December 1955. The raw data have been grouped about intervals of 5 scale divisions (1 scale div. = 15 micra). Relevant statistical data are given in Table 14.

TABLE 14

MONTHLY VARIATION IN MEAN OVA DIAMETER (RIPE OVA EXCLUDED) OF PITTWATER FLOUNDER FROM JUNE 1954 TO DECEMBER 1955. CLASS INTERVAL FIVE SCALE DIVISIONS WHERE 1 SCALE DIVISION = 15 MICRA

MONTH	MEAN DIAM. (Sc. Div.)	S.D.	S.E.	n	MEAN DIAM. (Micra)
1954					
June	18.46	± 7.365	± 0.772	91	277
July	19.44	± 7.066	± 0.714	98	292
August	21.92	± 7.572	± 0.742	104	329
September	20.01	± 7.772	± 0.773	101	301
October	16.68	± 6.514	± 0.668	95	250
November	13.99	± 6.179	± 0.606	104	210
December	11.82	± 4.628	± 0.465	99	177
1955					
January	10.28	± 4.039	± 0.426	90	154
February	12.88	± 4.951	± 0.531	87	193
March	18.22	± 7.161	± 0.755	90	273
April	20.35	± 6.939	± 0.744	87	305
May	19.63	± 6.998	± 0.782	80	294
June	20.70	± 6.705	± 0.695	93	310
July	19.10	± 8.092	± 0.858	89	287
August	22.44	± 7.657	± 0.835	84	337
September	20.00	± 7.054	± 0.670	111	300
October	19.21	± 7.211	± 1.170	38	288
November	13.00	± 5.477	± 0.548	100	195
December	12.40	± 5.320	± 0.527	102	186

season to the ova ripening in batches and being shed at once. The final maturation process in the greenback flounder appeared to follow this pattern for not only were no eggs between 0.525 mm and 0.630 mm encountered throughout the study but the number of running ripe females was extremely small.

(d) The Place of Spawning

It is generally accepted by fishermen that the greenback flounder seeks the shallow waters of estuaries and tidal rivers in which to spawn and the author's observations supported this belief. Female flounders about to spawn, or actually in the running ripe condition together with males from which it was possible to express milt, were found in this type of locality often in extremely shallow water. Confirmatory evidence was provided by the similar occurrence of planktonic ova and juvenile fish. However, it is suspected that spawning is not confined to the estuarine environment as running ripe males and females have been taken offshore in depths down to fifteen fathoms from time to time by Danish seiners. (Fairbridge, unpublished data 1947.) As there are but scanty details recorded from flounder caught in deep water no certain opinion can be given regarding the relative proportion of fish spawning in the two habitats. There is also no apparent seasonal variation in abundance in mature estuarine fish that might suggest the occurrence of a spawning migration and consequently the inshore habitat is regarded as normal for all months of the year including those in which spawning takes place.

(e) Spawning Times

The length of the spawning season for flounder in Tasmania has been a subject for argument and speculation ever since the first fishing regulations were drawn up during the middle of last century. Opinions given before royal commissions and enquiries into fisheries regulations varied between a short spawning season of two months in the middle of winter to continuously throughout the year. The results of the present investigation show that the spawning period, although prolonged, can be defined and that a marked cycle exists. It must be emphasized, however, that it was not possible to investigate the effect of environmental factors on spawning from one locality to another and the results presented are indicative of the condition found in one estuary only, namely Pittwater.

The monthly frequency distributions of ova diameters (Table 14, Fig. 23) show a decided seasonal periodicity over nineteen successive months. The histograms were constructed by grouping the raw data in class intervals of five scale divisions with values of 5, 10, and 15 scale divisions as mid points. It was thought that as there was often a degree of distortion in preserved ova which exceeded two scale divisions nothing was lost by grouping and the much tidier distribution shown subsequent to grouping justified this treatment of the raw data.

In considering the curves it should be borne in mind that ova in the class measuring 30 scale divisions (0.450 mm) are those awaiting maturation. Because of the suspected rapid development from this stage to full maturity and also considering the few fish obtained containing fully ripe or spawning ova the presence of those 0.450 mm in diameter were taken to be as indicative of incipient spawning as was the presence of ova measuring 0.600 - 0.800 mm.

The ovaries contain a large proportion of well developed eggs from March to September but during the remaining months (October to February) the number of large ova is considerably diminished and their place taken by small ones which form a distinct mode at 0.150 mm. This rather short period when the great majority of ova are not much larger than the immature stock is brought to an abrupt end with their growth during March and April. As growth proceeds the proportion of 0.150 mm eggs naturally decreases and this condition holds, apart from the suggestion of a recession in July, until September when a sharp decline in frequency of large ova commences. The seasonal fluctuation in egg maturity is more apparent in Figure 24 where the mean ova diameter of each monthly sample is plotted. Because ripe ova are almost twice the size of those awaiting maturation and also the number of running ripe fish in a sample is not truly indicative of the maturity of the sample, Stage III eggs are excluded in the calculation of the means.

The curve shows that a definite spawning peak occurs in August of both years but in 1955 the ova achieve a comparable size as early as May. In both 1954 and 1955 the decline in mean diameter takes place in September although at a more rapid rate in the former year. As it can be assumed that samples of flounders whose eggs have a mean diameter of .300 - .345 mm are in a position to spawn the season may be said to last from March to September, although as the value for October 1955 indicates, a fair proportion of fish may spawn during this month.

It is unfortunate from the standpoint of checking the length of one spawning season against another that it was not possible to commence the investigation before June 1954. As only half the season of that year was covered it cannot be proved that the tendency of the 1955 curve to be bimodal is characteristic of each year. The bimodality of the 1955 curve raises the strong possibility that two spawning concentrations exist and which account for the two classes of ova found in the mature ovary. It has been shown that following the extrusion of ripe eggs numerous ova .390 - .495 mm remain which show no sign of breaking down and which are destined to be released ripe at a later stage. The theory that the first stage of spawning takes place about March followed by a second and final stage in the extrusion of eggs in September as suggested by the curve must be considered in the light of the probable relationship of spawning and temperature.

In fishes the stimulus to spawn may be provided by a number of factors other than temperature. For a number of freshwater species the importance of such agents as the presence of certain types of vegetation, the nature of the bottom and changing levels of water has been shown by Fabricius (1950). However, as these conditions in the habitat of the present species are relatively stable compared with lakes and rivers subjected to a continental climate and the eggs of flounders are pelagic, it is assumed such influence would be extremely small. The importance of temperature and length of day as controlling spawning of the minnow (Phoxinus laevis) has been outlined by Bullough (1939), who found that whilst variations in light influenced gonad development temperature was the more critical to the extent that spawning could not take place until the temperature of the water had risen above 17°C. Furthermore, the change from potential maturity to functional maturity was induced by the rise in temperature and it was the rise itself and not the height of temperature reached that was considered the important factor.

Now the greenback flounder in common with most other Heterosomata spawns during the winter months and consequently the development of ovarian ova can be correlated with falling temperature. During the months of 1954-1955 in which spawning took place in Pittwater the temperature was less than 13°C, and a general rise in temperature above this reading was concomitant with a decrease in mean ova diameter, resulting from the cessation of ova development. In fact, as Figure 24 shows, the close inverse correlation between temperature and ova diameter during the whole period of the investigation is worthy of attention.

Whether any significance can be attached to the close agreement of the points at which the two curves intersect between October and November in both years is problematical but it is clear that the relatively rapid rise in temperature in 1954 and the somewhat slower rise in 1955 is reflected in the egg diameter curve.

If indeed egg development is induced by a fall in temperature an earlier or sharper decline at the end of summer would bring about a more rapid maturing of ova than would a slow or late fall which would have a direct influence on the length of the spawning season. That the rate of fall in autumn temperature is subject to variation in successive seasons is indicated by a temperature curve of Pittwater for 1950 and 1951. (See Fig. 25) In 1950 the April temperature of 14.6°C was 3.9° higher than in the same month of 1951, and did not fall to below 11° until a month later. In 1955 an even sharper fall occurred and the temperature was such that it permitted spawning to commence in April. Thus the 1955 spawning season may have been abnormally long and the occurrence of large ova from April to June simply the direct result of

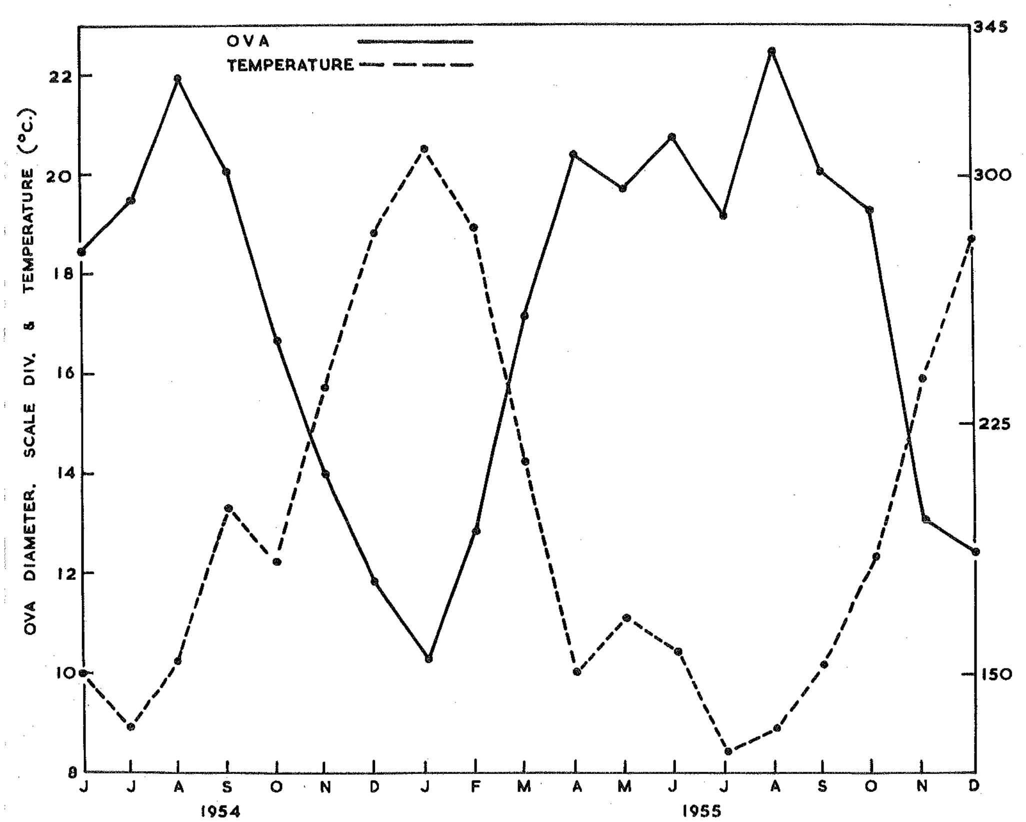

Fig. 24 Monthly variation in mean diameter of eggs from Pittwater flounders during 1954-55, with the corresponding mean water-temperature curve.

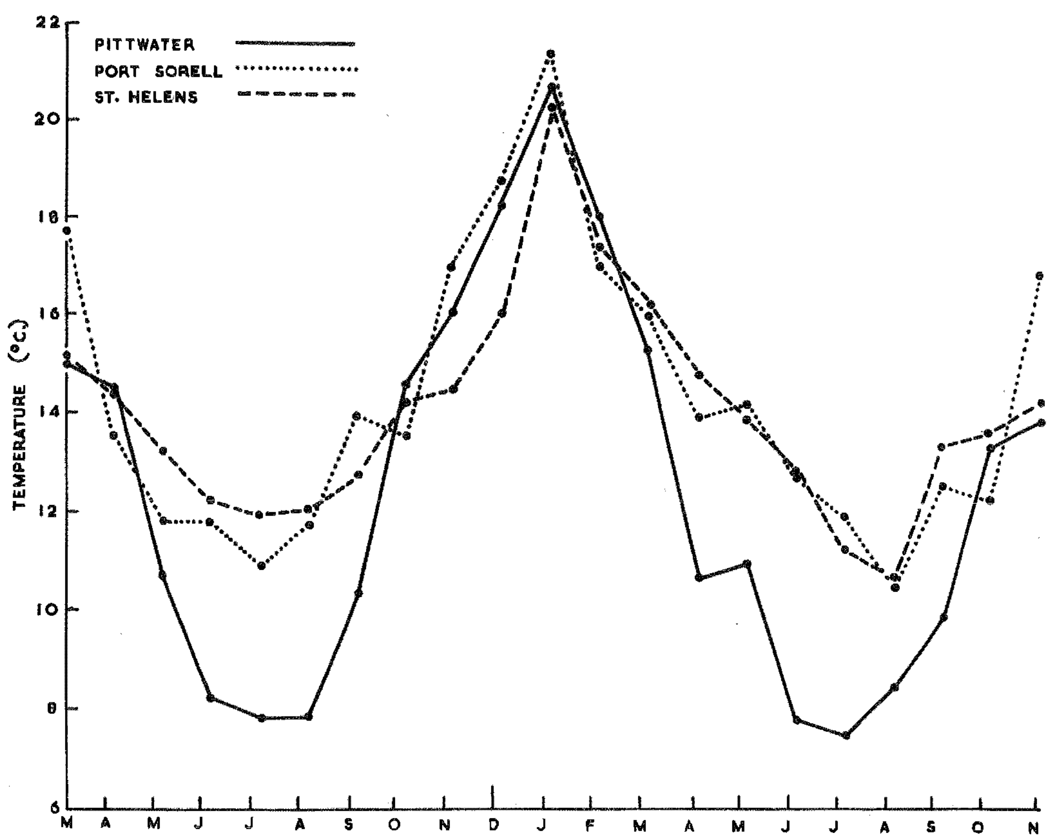

Fig. 25 The comparison of seasonal water temperature variation at Pittwater, Port Sorell, and St. Helens.

sudden temperature drop and consequent early maturation of ova. The drop in mean value for July 1955 may be due to a small rise of one degree in May which had the effect of halting or slowing down maturing process and for this reason a shadow of doubt is thrown on the interpretation of the two modes representing two spawning concentrations. Whether or not there is a critical temperature that must be reached before the maturing process commences, or that this is induced by a fall in temperature could be made conclusive by laboratory experiment only. But there is a strong suggestion from the appearance of the curves that temperature is an important factor in the development and spawning of eggs in the species.

The implications of temperature effects open up the question of the possibility of varying lengths of each year's spawning season. For instance the mean temperature of Pittwater over twelve months in 1954-1955 was 13.5°C and the months during which the water remained below this temperature extended from April to October, a period of seven months. For a corresponding period during 1950-1951 the water was colder than the mean of 13.2°C for only six months, and during the winter of 1950 for only five months. Thus from these records alone the possibility of a variation of two months in the limits of any two spawning seasons must be allowed if gonad development is induced primarily by falling temperature as seems highly probable.

The present regulation which prohibits the taking of flounders from July 1 to October 14, was designed to give protection to the fish during the spawning season. This aim has been achieved as far as the spawning peak in September is concerned but in 1955, for instance, would have covered only half the period in which the ovaries were in a high state of maturity and during which running ripe fish were encountered. The position holding in 1954 is of course not clear as sampling did not begin until June but the similarity between the temperature curve for that year and that for 1951 suggests that a seven months' period of water temperature below 13°C with a correspondingly lengthened spawning is fairly common in Pittwater. Thus if it were deemed necessary to protect the flounder for the whole of the spawning season every year this could only be ensured by a closure from April to October inclusive. However, recommendations of this nature can only be made after a thorough understanding of the composition and condition of the stocks has been reached. This involves intensive investigation of catch and fishing effort based on reliable records over a large number of years and was therefore quite beyond the scope of this investigation.

XI. LENGTH AND AGE AT FIRST MATURITY

The number of mature or nearly mature male fish taken in the collections during the spawning season was small enough to be considered inadequate for purposes of determining age at maturity and the study was therefore confined to females. However, it was observed that males 17 cm in length frequently displayed signs of maturity and during the spawning season fish of 19 cm and greater, possessed testes in a ripe or approaching ripe condition.

The length and age of female fish at maturity was obtained from the study of the diameters of ova present in each centimetre group of fish length from a sample of 862 flounders taken during the spawning season of 1955. The lengths of the flounders used for this purpose varied from 12 to 36 cm.

The presence of ova falling in the 0.350 - 0.800 mm diameter range was used as the criterion of maturity as it was assumed that fish with eggs developed to this extent would spawn in the current season. The consideration of ova greater than 0.350 mm was prompted by the doubt that eggs smaller than this would reach full maturity by the end of the season as evidenced by the breakdown and resorption of the 0.180 - 0.330 mm class mentioned earlier in the paper. This group of eggs remaining in adult fish following spawning is certainly resorbed as the histograms of Figure 23 show. It is also evident that the eggs of adolescent flounders may develop to the 0.330 mm stage a year before spawning takes place but are resorbed without further development. This condition was illustrated by the increasing percentage of this group of eggs found in fish from 17 to 20 cm without the single occurrence of larger ova. In addition frequent breakdown of these eggs was noticed in fish of this size range.

The number of fish of each length class examined together with the percentage which had become mature is presented in Table 15. These data are plotted in Figure 26, where the trend is indicated by an eye-drawn curve. The curve shows that the greenback flounder begins to mature at 20 cm with 60 per cent. maturity reached at a length of 24 cm. That the percentage mature values for lengths at which all fish are obviously fully mature does not reach the 100 per cent. level is due to the spread of the spawning season over a considerable period. Theoretically if maturity were gauged on the possession of fully ripe eggs the curve could be expected to reach 100 per cent. only if all fish spawned simultaneously. Arora (1951) in using the diameters of largest ova present in the ovary to establish the maturity of the sand dab confined his observations to one month during the height of the spawning season and attributed 100 per cent. maturity to all fish greater than 250 mm. In view of the proportion of spent fish containing only small ova that must have surely been present in the sample at that time of the spawning period one can only conclude that a further criterion of maturity was applied although this is not staged. Spent flounders were readily recognizable from the appearance of the ovary and on this basis it was found that all fish greater than 29 cm were invariably adult either in a spawning or spent condition.

However, using ova diameter alone it can be stated that

TABLE 15

THE LENGTH FREQUENCY DISTRIBUTION OF MATURE FEMALE FLOUNDERS. THE FIGURES IN THE RIGHT-HAND COLUMN REPRESENT THE PERCENTAGE MATURE IN EACH CENTIMETRE GROUP

FISH LENGTH (cm. groups)	NO. EXAMINED	PER CENT MATURE
16	6	-
17	3	-
18	9	-
19	17	-
20	62	7
21	121	12
22	154	21
23	107	41
24	95	55
25	78	73
26	62	64
27	37	67
28	30	80
29	26	61
30	20	72
31	13	76
32	9	71
33	9	100
34	3	60
35	-	-
36	1	100

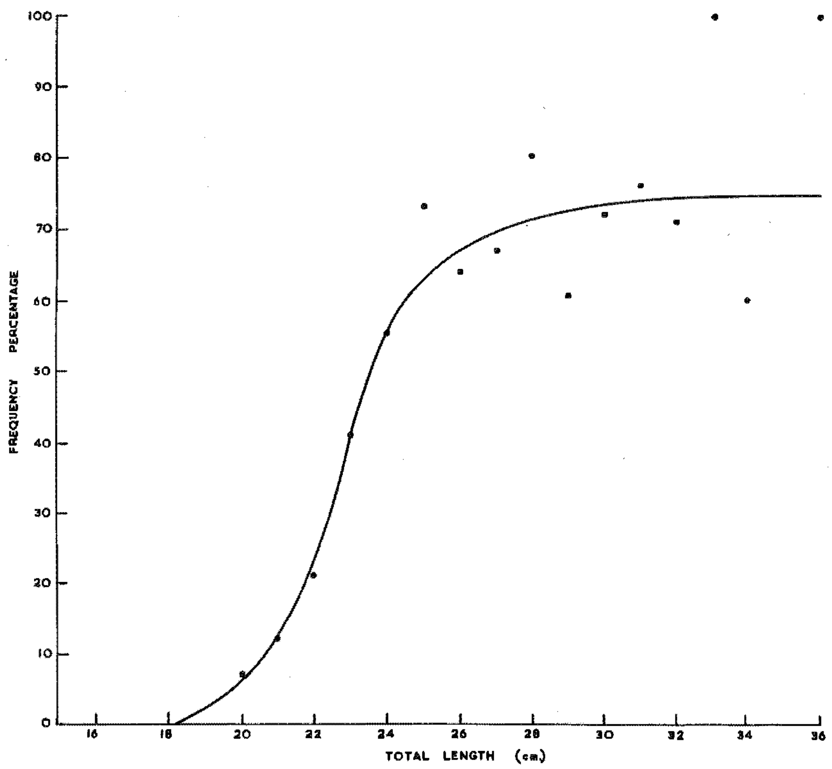

Fig. 26 The maturity of the female greenback flounder. The eye drawn curve indicates the percentage of fish in each centimetre group possessing ova within the 0.390-0.800 mm size range. Ova in this group are either ripe or will become so during the current spawning season.

a mean value of approximately 75 per cent. of total mature fish observed at any one time possessing 0.350 - 0.800 mm eggs indicates 100 per cent. maturity. This is to say at any one time during the spawning season about one quarter of the mature female population are spent fish.

Length at maturity may be converted to age by reference to the growth curve in Figure 15. The range in total lengths of fish arriving at maturity is seen to be from 20 - 27 cm with the majority becoming mature at approximately 24 cm. This falls largely in the third year of life although as Table 8 indicates maturity may be achieved by larger second year fish whilst a small percentage probably do not become mature before entering their fourth year. However, it may be safely said that 70 per cent. of flounders reach adulthood and have spawned at the completion of the third year of life.

The present legal length of the greenback flounder is 23 cm (9 ins.) which from Figure 26 protects approximately 40 per cent. of the spawning population. Should additional conservational measures be deemed necessary further protection of immature fish could be brought about by raising the minimum length to 255 mm (10 ins.). An increase of one inch would result in the reduction in the percentage of immature fish likely to be taken by more than 10 per cent.

XII. HANDEDNESS REVERSAL AND AMBICOLOURATION

It is well known that during the metamorphosis of flatfishes one of the eyes migrates to the side of the head upon which the other eye is situated. Whether it is the right or left eye that takes part in this transformation is thought to be determined genetically and usually within a species it is the eye of the same side that makes the migration. Hence some species normally have their eyes on the right side and are said to be dextral whilst others have them on the left side and designated sinistral. The word normally is used as in certain cases some members of the same species may be either dextral or sinistral in varying proportion according to geographical location or other causes although one condition generally predominates. Thus species are regarded as being either normally sinistral or normally dextral and any right handed fish belonging to what is predominately a left handed species and vice versa is said to be reversed and such are termed reversals.

Some idea of the number of sinistral and dextral species has been given by Gudger (1935) who estimated that of the approximate 289 known species of Heterosomata 87 were normally dextral and 202 normally sinistral. In Arctic and cold water species dextrality tends to predominate in the ratio of 60 to 47 whereas in tropical and warm temperate species the ratio is 155 sinistral to 27 dextral.

The problems associated with handedness have been considered by many authors and have been conveniently summarized by Hubbs and Hubbs (1945). These authors conclude that all Pleuronectidae with the exception of two species of the genus Platichthys and possibly Rhombosolea were normally dextral and any occurrence of sinistrality is so rare as to appear teratological. They qualified this statement by remarking that adequate data on the number of rights and lefts in the genus Rhombosolea were not available.

Little more than casual observations have been made on instances of reversal in this genus but it appears from Hutton (1876) that in R. plebeia such forms are not uncommon and indeed gave rise to the description of Apsetta thomsoni by Kyle (1900) which was subsequently regarded as merely a sinistral form of R. plebeia itself.

According to Norman (1926) there has been but a single recorded instance of reversal in R. tapirina although Gudger (1935) drew attention to two reversals of the species reported by Hutton (1874 and 1876) who in the latter paper reported finding in a collection from Dunedin, New Zealand, as many lefts as rights but did not give the size of his collection.

The rarity of reversal in R. tapirina was also confirmed by the author in the present investigation to the extent that only one reversed greenback flounder was encountered throughout the study in which over three thousand specimens were observed. Furthermore, no fishermen questioned, remembered having seen such a fish.

A further abnormality common to flatfishes is the condition known as ambicolouration. This phenomenon, characterized by the fish possessing varying degrees of pigmentation on the normally unpigmented blind side, is well known in the turbot and European dab and is often associated with the failure of the appropriate eye to complete its migration. Usually correlated with the arrested migration of the eye is the failure of the dorsal fin to complete its development with the result that the structure terminates in a fleshy hook-like process and is not carried forward to the snout as in the normal fish. The incidence of ambicolouration in Rhombosolea is thought to be rare although Haast in 1873, discussing R. plebeia and leporina quoted fishermen as saying that such examples were far from uncommon. The author was able to find but a single record of an ambicolourate greenback flounder. This fish was taken at Coorong, South Australia, and forwarded to the British Museum where it was described by Norman (1926). In consideration of the apparent rarity of ambicolourate greenback flounders the description of a specimen 221 mm long taken by the author in 1953 is given.

This specimen differs from the normal R. tapirina in the formation of the head, the position of the left eye, the possession of a left pelvic fin, and the extensive pigmentation of the blind side. Certain peculiarities of the lateral line in the region of the head are also evident.

The fleshy hook formed by the incomplete development of the dorsal surface is more pronounced than that of the ambi-colourate halibut described by Gudger and Firth (1935) and the similar four spotted flounder (Paralichthys oblongatus) by the same authors in 1936. In both of these cases, however, the eyes are almost normal in position which may explain the relative smallness of the hook. As can be seen in Figure 27 the extremits of the process in R. tapirina is level with the anterior margin of the left eye which is situated almost on top of the head being slightly towards the right side. The prominent snout, typical of the species, is lacking which gives a pig-like expression to the mouth region. Two equal pelvic fins lie side by side and are joined posteriorly by a common membrane but are unconnected with the anal.

Pigmentation and scale formation on the blind side is similar in intensity to that of the right side, except for a small part of the head which retains the normal whiteness of the blind side. The extent of the unpigmented portion of the head is shown by the unstippled area in Figure 28.

The arrangement of the anterior portion of the lateral line differs markedly from the normal fish. Instead of the line branching slightly forward of the operculum with one fork continuing on between the eyes and the other bearing away towards the dorsal it bends almost at right angles towards the dorsal before branching, after which both forks diverge in that

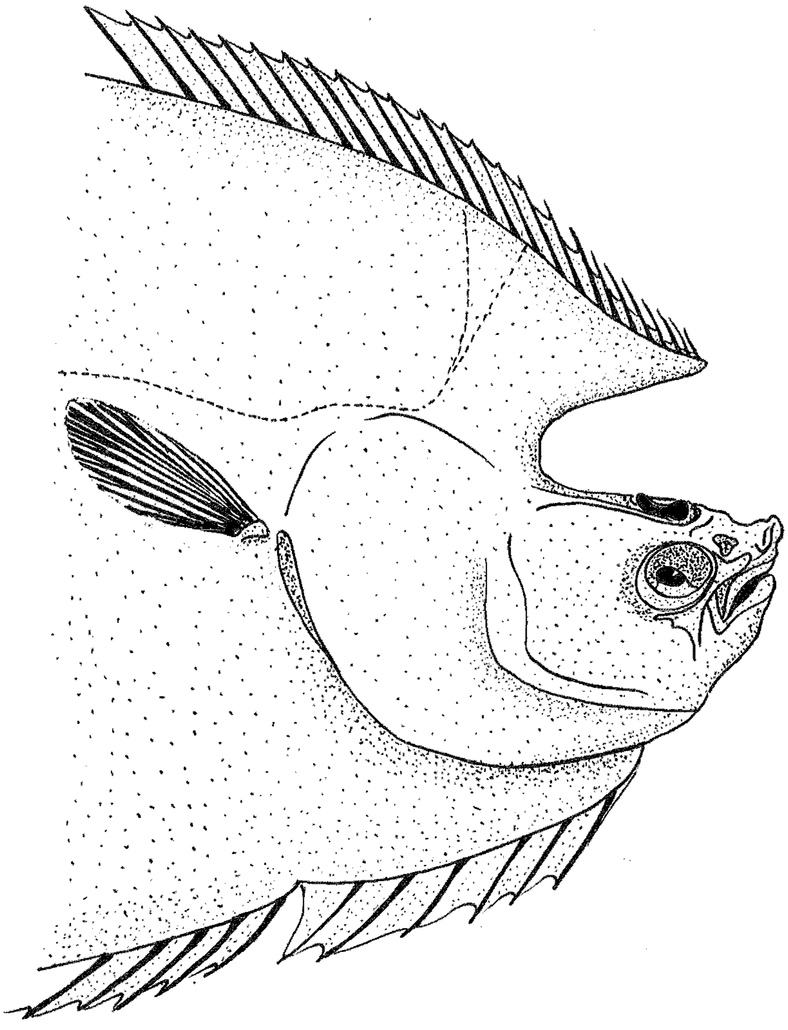

Fig. 27 Dextral view of the ambicolourate specimen of
<u>Rhombosolea tapirina</u>.

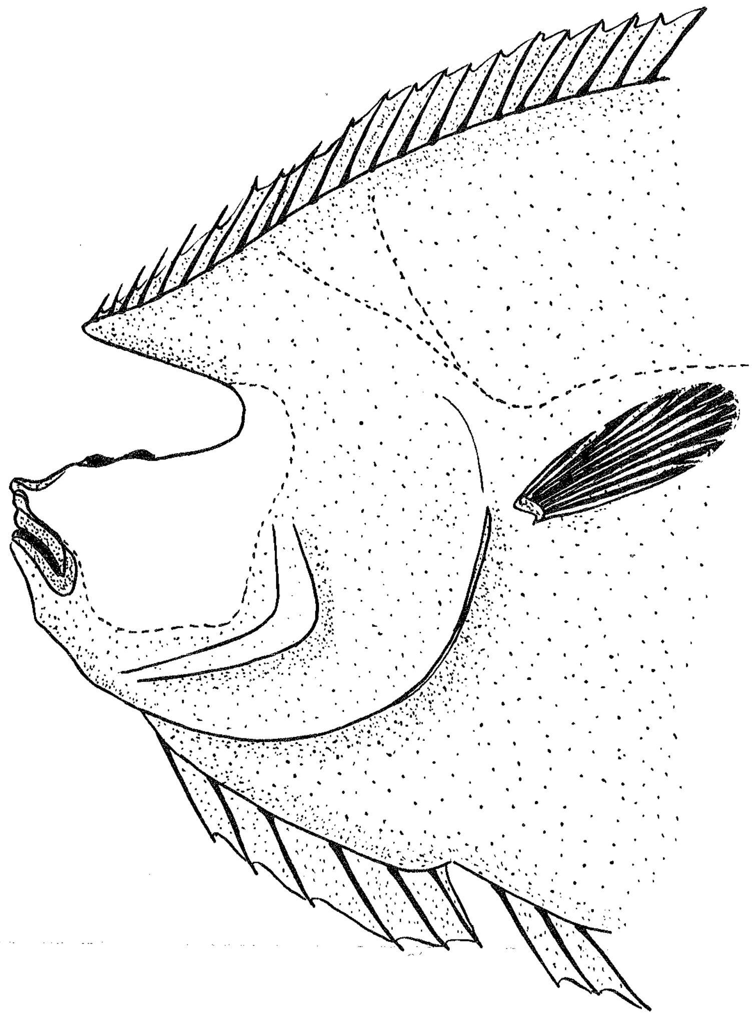

Fig. 28 Sinistral view of the ambicolourate specimen of *Rhombosolea tapirina*.

direction at an angle of about 30° to each other.

Meristic and morphometric characteristics of the ambicolourate specimen are compared with those for the species in Table 16.

All characters of the ambicolourate specimen are seen to be commensurate with the normal flounder with the exception of those pertaining to the head and eyes. The head length of the former is proportionately shorter than is usual and although the loss of the snout would be contributory to this it does not entirely account for the difference. This appears to be due to a general compression of the anterior part of the head and all relationships incorporating the head length are consequently affected.

The relatively wide interorbital space is of course due to the arrested migration of the eye.

The hindered development of the dorsal fin apparently does not invariably lead to a reduction in the number of fin rays. The specimen in question possesses 59 rays which comes well within the range for the species. Although the specific range for the species is given as 56-69 the mean number of dorsal rays for the population to which the ambicolourate example belongs is 61 so that it is highly probable if reduction in fin rays is associated with the condition it is only slight.

From time to time speculation has arisen regarding the swimming and feeding habits of ambicolourate flatfish. It

TABLE 16

MORPHOMETRICS OF THE AMBICOLOURATE SPECIMEN OF R. TAPIRINA COMPARED WITH THE RANGE IN CHARACTERS OF NORMAL SPECIMENS. (s = sinistral; d = dextral)

CHARACTER	AMBICOLOURATE SPECIMEN	RANGE IN SPECIES
Body depth in length	2.0	1.7 - 2.1
Head length in total length	3.9	3.1 - 3.7
Lower jaw in head	2.9	3.0 - 3.7
Eye diam. in head	4.4	4.8 - 6.0
Orbital width in eye diam.	2.4	4.0 - 5.0
Number of dorsal fin-rays	59	56 - 69
" " anal "	42	40 - 50
" " caudal "	18	16 - 21
" " pelvic (s)"	6	absent
" " " (d)"	6	6
" " pect. (s)"	11	10 - 13
" " " (d)"	11	10 - 13
Total length	221 mm	
Standard length	181 mm	
Depth of body	110 mm	
Sex	Female	

has been suggested that markedly ambicolourate forms with a high placed eye may swim in the vertical plane as is normal with other fish and in Heterosomata prior to metamorphosis. In view of this it may be well to record that the specimen described above was taken by spear whilst swimming in the horizontal position normally assumed by flatfishes.

XIII. PARASITES

The greenback flounder was found to be fairly free of both endo- and ecto- parasites. A small percentage of livers were infested by encysted nematodes and larval acanthocephalids occasionally occurred in the gut wall.

The only ectoparasite encountered was a previously undescribed piscicolid leech belonging to the genus *Austrobdella* which has been named *Austrobdella bilobata* by Ingram (1957).

Approximately 12 per cent. of the flounder population was found to carry at least one leech although as many as seven were found on the one fish. Leeches were found throughout the year, there being no indication of seasonal fluctuation in infestation.

From a collection of 296 greenback flounders from Pittwater 51 leeches were counted and the number of specimens per fish is given in Table 17.

With one exception all leeches were found attached to the right side of the body in the region of the mouth and gills where they produced ulcerated patches and extensive scars. The

TABLE 17

THE INFESTATION OF GREENBACK FLOUNDERS BY
AUSTROBDELLA BILOBATA

Number of Fish Examined	Number of Leeches Present
261	0
25	1
8	2
1	3
1	7

single individual observed on the left side was thought to be a recent infection which was probably making its way to the normal position on the right or uppermost side. In no instances were leeches found on the fins.

XIV. RACIATION

Attention has already been drawn to differences in weight/length ratio and termination of spawning season found to occur in the samples of greenback flounders from Pittwater and Port Sorell. Now it is proposed to consider further variations found in certain meristic characters and use them to prove the existence of two distinct populations with a limited east-west geographical distribution. It will also be submitted that there is justifiable evidence that the two populations constitute sub-species on the grounds of significant meristic and geographical distinctiveness.

Differences apparent in the mean number and range of dorsal and anal finrays of Pittwater and Port Sorell flounders first aroused the suspicion that some significant degree of variation might occur within the species. Accordingly efforts were made to collect samples from as many places as possible with a view to applying statistical tests to any variations in meristic or morphometrical characters so found. However, it proved very difficult to make large collections in many places due both to the expense and time involved in fishing for a species characterized by great fluctuations in availability. Furthermore, the localities in which they are taken commercially are relatively few. Thus the data were limited to collections of about a hundred fish from Pittwater, Port Arthur, St. Helens and Port Sorell with smaller samples from Stanley, Port Welshpool and Macquarie Harbour. The location of these points of collection are shown in the chart in Figure 1. A considerable number of morphometric measurements was made which gave random results only and the study of variation was therefore limited to dorsal and anal finrays, gillrakers and vertebrae all of which showed comparable agreement in the separation of the two populations.

The data are summarized in Figure 29 after the manner of Hubbs and Perlmutter (1942) in which the significance of the differences between the means may be visually estimated.

In the figure the means are represented by the vertical lines, the horizontal lines indicate the range, the heavy portion of the horizontal one standard deviation on each side of the mean and the hollow rectangle twice the standard error of the mean on each side of the mean.

It is readily seen that the samples from Pittwater, Port Arthur and St. Helens fall into a group whilst the remaining ones, Port Sorell, Stanley, Port Welshpool and Macquarie Harbour constitute another with a marked uniformity of samples within the groups.

Reference to Figure 30 will show that these two groups lie in two geographically distinct areas east and west of the 147th meridian. Later the separation of these two populations will be discussed in some detail but it is necessary to give

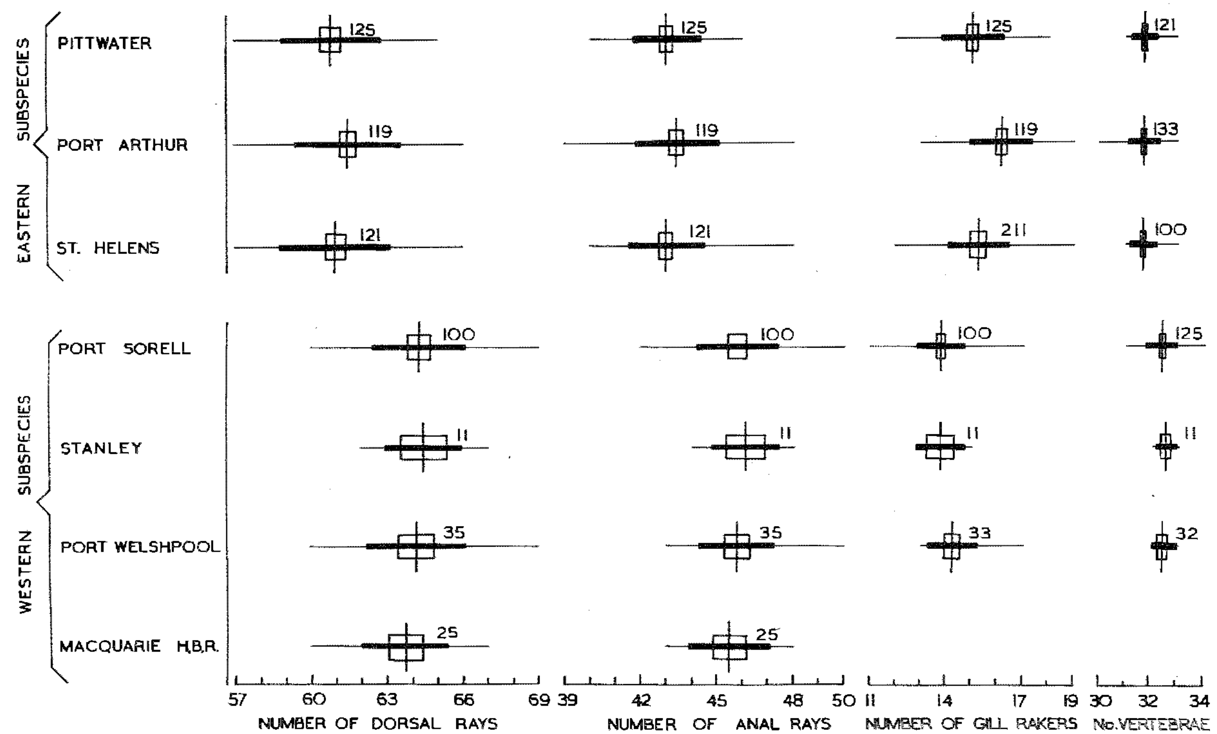

Fig. 29 Summary of dorsal ray, anal ray, gill raker, and vertebral counts from seven sampling localities. The range is indicated by the fine horizontal line, the mean by the vertical line, one standard deviation on each side of the mean by the heavy horizontal line, and twice the standard error of the mean by the hollow rectangle. The figures to the right of each diagram indicate the number of specimens examined.

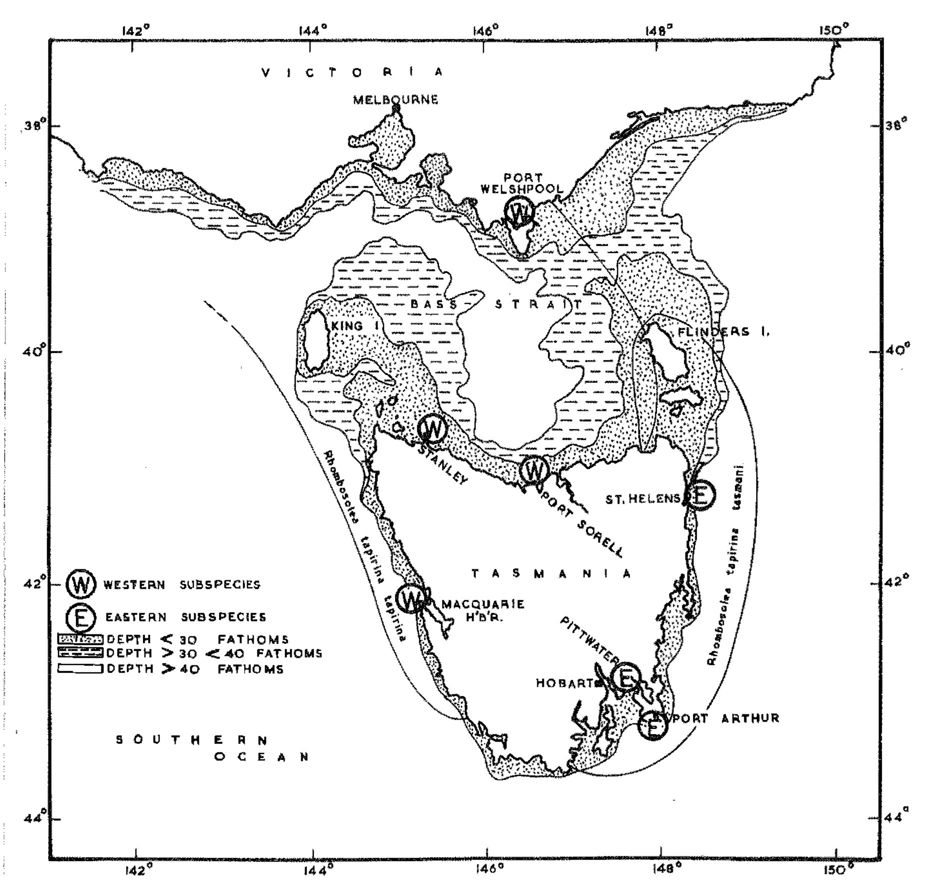

Fig. 30 Sketch chart of Bass Strait showing the position of the Pleistocene Bass Land Bridge as indicated by the 30 and 40 fathom contours taken from the current Admiralty chart. Sampling localities and the geographical range of the two subspecies of Rhombosolea tapirina are also shown.

them descriptive names at this stage to facilitate reference to tables. Thus the terms Eastern population (E) and Western population (W) will be used in the following sections to distinguish the two groups.

(a) Test of Significance

The degree of apparent uniformity of characters within each population indicated in Figure 29 along with the relationship of samples with all others was tested statistically by the use of a variation of the well known "t" test. The process propounded by Simpson and Roe (1939) tests the significance of the difference between two samples in terms of the standard error of difference between their means. The standard error of difference between the means of the two samples is expressed by $d/\ sigma_d$ where d equals the difference between the two means and $sigma_d$ is the estimate of the standard error of difference between them. The last mentioned value may be calculated from several expressions the most commonly used being

$$sigma_d = sigma_{M1}^2 + sigma_{M2}^2$$

where $sigma_{M1}$ and $sigma_{M2}$ are the standard errors of the means of the two populations being considered. However, the authors claim that the above formula is correctly used only when it is required to see whether two separate species differ significantly in the mean for some variate. In order to adequately test whether two samples could be drawn from the one population the formula

$$\text{sigma}_d = \frac{N1}{N2}\,\text{sigma}^2_{M1} + \frac{N2}{N1}\,\text{sigma}^2_{M2}$$

should be used. N1 and N2 are the number of specimens in the two samples. As a large number of calculations in the comparison of the different samples had been made using the first formula before the author was aware of the existence of the second both were applied to several selected pairs of samples and in no case did the difference in the final values of d/sigma$_d$ warrant the application of the more lengthy expression. This was the case even when N1 was up to six times as great as N2.

The criteria of significance using the d/sigma$_d$ test is as follows:

d/sigma$_d$	3.0	almost always significant
"	2.5	usually significant
"	2.0	sometimes significant
"	2.0	not significant

These criteria are obtained from the transference of criteria of significance of P (probability) into corresponding values of d/sigma$_d$.

All samples in the comparison calculations were regarded as statistically "large". Although the specimens collected from Stanley numbered only 11 it was found that this sample could be safely tested using the same formula as for the other samples.

Values of d/sigma$_d$ obtained in the comparison of each of the six samples with the remaining five are listed in Table 18.

TABLE 18

THE COMPARISON OF SAMPLES FROM EACH LOCALITY WITH THOSE FROM ALL OTHER AREAS AS EXPRESSED BY THE $d/\sigma d$ TEST OF SIGNIFICANCE. (S.= significant, N.S. = not significant)

E = eastern subspecies
W = western subspecies
D. = dorsal rays
A. = anal rays
G.R. = gill rakers
V. = vertebrae

	CHARACTER	PORT ARTHUR (E)	PITTWATER (E)	PORT WELSHPOOL (W)	ST. HELENS (E)	STANLEY (W)
Pt. Sorell (W)	D.	10.920	13.580	0.401	12.640	0.306
	A.	10.950 (S)	14.180 (S)	0.609 (N.S.)	13.480 (S)	0.651 (N.S.)
	G.R.	25.800	8.630	2.160	10.110	0.000
	V.	9.361	9.365	0.272	8.360	0.630
Stanley (W)	D.	6.081	7.386	0.536	4.645	
	A.	6.422 (S)	7.598 (S)	0.649 (N.S.)	7.478 (S)	
	G.R.	8.407	4.230	1.291	5.060	
	V.	5.845	5.793	0.329	6.250	
St. Helens (E)	D.	1.858	0.387	8.510		
	A.	1.980 (N.S.)	0.056 (N.S.)	5.890 (S)		
	G.R.	6.144	1.650	5.357		
	V.	0.832	0.994	6.738		
Pt. Welshpool (W)	D.	7.278	8.750			
	A.	8.330 (S)	10.360 (S)			
	G.R.	10.250	4.160			
	V.	8.340	6.290			
Pittwater (E)	D.	2.300				
	A.	2.630 (N.S.)				
	G.R.	7.940				
	V.	0.199				

Where samples from within one population have been compared with those from the other it will be noticed that for all characters examined the d/sigma$_d$ relationship is strongly significant with values lying between 4.160 and 25.800. On the other hand where samples have been compared with others belonging to the same population, not significant values result for all characters with the exception that comparisons involving Port Arthur approach the level of significance with regard to finrays. For gill-rakers the results are strongly significant. However, this does not justify the suspicion that a third population may be present because the difference in the means of the finrays approach significance with respect to Port Arthur and Pittwater only and in any case it is slight compared with the differences between the means of the two populations. Some factors contributing to quantitative differences in meristic characters of fishes and the possibility of their operative effect on greenback flounders will be discussed later when the subject of population boundaries and the east-west separation of the two groups will be considered.

It is therefore clear that flounders from the six localities may be divided into two well defined groups and in order to calculate the parameters of each group the data from Pittwater, Port Arthur, and St. Helens were combined and likewise those for Port Sorell, Stanely, and Port Welshpool. The resulting frequency distributions are shown in Figure 31 and relevant statistics in Table 19. The separation is most marked in the case of the finrays

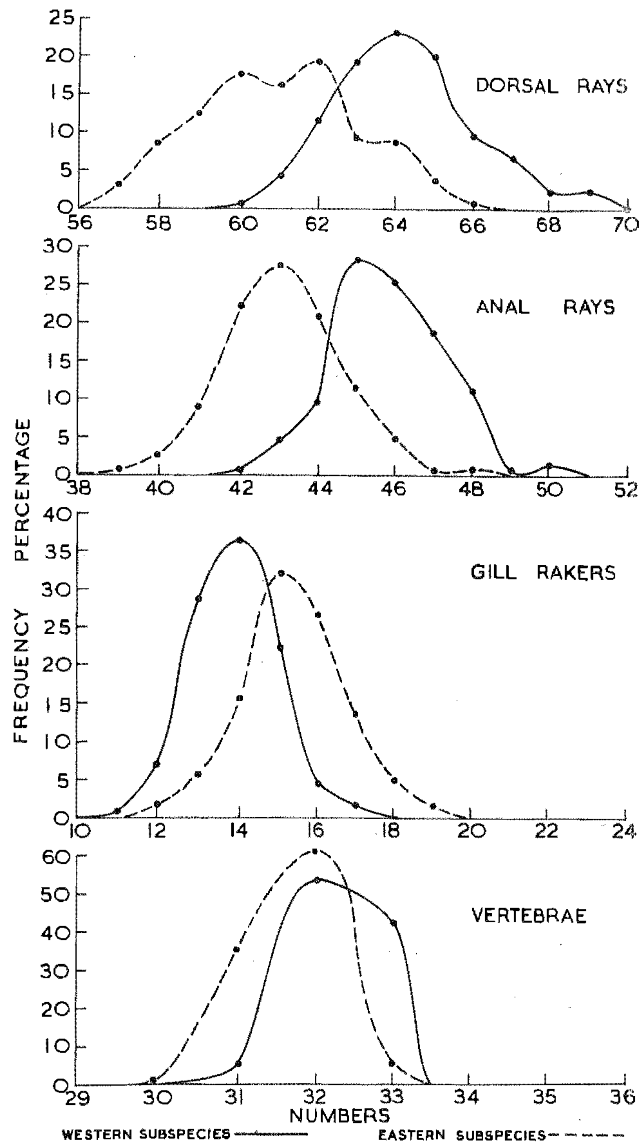

Fig. 31 Frequency distribution curves of four meristic characters of flounders from the eastern and western subspecies. The data from Port Arthur, Pittwater, and St. Helens, is summed in the eastern curve and that from Port Welshpool, Port Sorell, and Stanley, similarly treated in the western curve. Statistics are given in Table 19, and the results of the tests of significance in Table 20.

TABLE 19

STATISTICS OF THE SUMMED MERISTIC DATA FROM SAMPLES
WITHIN EACH SUBSPECIFIC AREA

	CHARACTER	RANGE	A.M.	S.D.	S.E.	n
Western sub-species Population	Dorsal Rays	60-69	64.207	± 1.775	± 0.1474	145
	Anal Rays	42-50	45.836	± 1.441	± 0.1193	146
	Gill Rakers	11-17	13.903	± 1.063	± 0.0886	144
	Vertebrae	31-33	32.379	± 0.563	± 0.0433	169
Eastern sub-species Population	Dorsal Rays	57-66	61.033	± 2.017	± 0.1055	365
	Anal Rays	39-48	43.126	± 1.426	± 0.0746	365
	Gill Rakers	12-19	15.425	± 1.222	± 0.0640	365
	Vertebrae	30-33	31.691	± 0.556	± 0.0295	356

and to a lesser degree for gill-rakers and vertebrae, but as Table 20 indicates the differences are all highly significant with d/sigma_d varying from approximately 13 to 17.

In addition to the six samples mentioned dorsal and anal ray counts were available from a sample of 25 specimens from Macquarie Harbour on the west coast of Tasmania. As data on gill-rakers and vertebrae were not taken from these specimens the results were not incorporated in the calculations in which each sample was compared with all others in turn but was simply tested against the parameters for the two populations. There is no doubt that Macquarie Harbour flounders belong to the Western population as is clear from Table 21. The d/sigma_d values 1.176 and 1.007 for dorsal and anal rays respectively when compared with the Western population indicate that the sample could have been drawn from any of the other samples in this population. On the other hand when compared with the means of the Eastern population d/sigma_d values of 5.961 and 6.082 for the same characters are significant and the chances that the samples could have been drawn from a homogeneous population are extremely small.

(b) Status of the Populations

Once it has been established that a species has within it two or more distinctly recognizable populations their rank should be decided and if necessary subspecific names allotted. The question of the constitution of suitable subspecific, racial and

TABLE 20

RESULTS OF TESTING THE SIGNIFICANT DIFFERENCE OF MERISTIC CHARACTERS BETWEEN THE TWO SUBSPECIES. (S. = significant)

CHARACTER	d/sigma$_d$
Dorsals	17.510 S
Anals	19.265 S
Gill Rakers	13.920 S
Vertebrae	13.132 S

TABLE 21

THE COMPARISON OF THE MEAN DORSAL AND ANAL FIN-RAY COUNTS OF THE MACQUARIE HARBOUR SAMPLE WITH THE MEANS OF THE EASTERN AND WESTERN SUBSPECIES.
(S. = significant; N.S. = not significant)

	EASTERN SUB-SPECIES	WESTERN SUB-SPECIES
	$d/\sigma d$	$d/\sigma d$
Macquarie Harbour:		
Dorsals	5.961 (S)	1.176 (N.S.)
Anals	6.082 (S)	1.007 (N.S.)

varietal criteria is controversial and is the subject of an extensive literature. However, a practical definition was advanced by Ginsburg in 1938 which has much to commend it and seems particularly applicable to the fishes where speciation is based on quantitative characters such as finrays, vertebrae, etc.

Briefly Ginsburg's method involves the measure of the degree of intergradation of the degree of divergence of one or more specific characters between two related populations and using these measures in an arithmetical definition of the relationship of the populations. Other things being equal a given population is considered a race with respect to another closely related population when the average intergradation of the character showing the greatest divergence is between 30 per cent. and 40 per cent; a subspecies constitutes a population intergrading between 15 per cent. and 25 per cent; it is considered to be a full species when the degree of intergradation is not more than 10 per cent. The measure of divergence is arrived at by subtracting the measure of intergradation from 100 per cent. hence the divergence between races is 75 per cent. to 85 per cent. between subspecies 60 per cent. to 70 per cent. and full species diverge to extent of 90 per cent. or more.

The measure of intergradation is equal to the area enclosed by the two overlapping histograms representing the two populations constructed on a percentage basis expressed as a percentage of the sum of their total areas. The dividing line that forms the basis of the determination of the measure of intergradation is taken as the position of intersection of the two polygons. In Figure 31, for instance, the intersection of the dorsal-ray polygons lies between 62 and 63 rays and by arranging the frequencies as percentages (Table 22) the percentage intergradation of one population with the other can be calculated. The mean of these two percentages is the measure of intergradation.

The percentage measure of intergradation for all characters investigated for Rhombosolea tapirina is given with the percentage divergence in Table 23.

The application of Ginsburg's criteria to this species shows that the percentage divergence for both dorsal and anal rays are well within subspecific limits and for gill rakers and vertebrae it closely approaches the lower limit. Whilst a definition of the rank of two populations within a species based on quantitative characters is perhaps the most desirable it cannot be regarded as comprehensive as the observed differences may be due to inadequate sampling. It is well known that the environmental factors of temperature and salinity play an important role in the numerical determination of meristic characters and the examination of small samples from habitats within the population area with a great variation in these factors may result in the accumulation of spurious data. Furthermore, gradual changes in environment produce character-

TABLE 22

THE PERCENTAGE FREQUENCY DISTRIBUTION OF DORSAL AND ANAL RAYS GILL RAKERS AND VERTEBRAE IN FLOUNDERS BELONGING TO THE EASTERN AND WESTERN SUBSPECIES

	NUMBER OF DORSAL RAYS													
SUBSPECIES	57	58	59	60	61	62	63	64	65	66	67	68	69	
Eastern	3.0	8.5	12.3	17.8	16.4	19.2	9.3	9.0	3.6	0.8				% No. of fish
Western (b)				0.7	4.1	11.7	19.3	23.4	20.0	9.7	6.8	2.1	2.1	% No. of fish
	NUMBER OF ANAL RAYS													
	39	40	41	42	43	44	45	46	47	48	49	50		
Eastern	0.5	2.7	9.0	22.2	27.4	20.8	11.2	4.9	0.3	0.8				% No. of fish
Western				0.7	4.8	9.6	28.1	25.3	18.5	11.0	0.7	1.4		% No. of fish
	NUMBER OF GILL RAKERS													
	11	12	13	14	15	16	17	18	19					
Eastern		1.4	5.5	15.3	32.1	26.3	13.2	4.9	1.4					% No. of fish
Western (b)	0.7	6.9	28.5	36.1	22.2	4.7	1.4							% No. of fish
	NUMBER OF VERTEBRAE													
	30	31	32	33										
Eastern	0.2	34.8	60.4	4.5										% No. of fish
Western		5.1	53.8	42.0										% No. of fish

TABLE 23

INTERGRADATION OF THE EASTERN AND WESTERN SUB-SPECIES
WITH RESPECT TO FOUR MERISTIC CHARACTERS

CHARACTER	% INTERGRADATION OF EASTERN WITH WESTERN	% INTERGRADATION OF WESTERN WITH EASTERN	% AVERAGE INTERGRADATION	% DIVERGENCE
Dorsal Rays	22.7	16.5	19.6	80.4
Anal Rays	17.2	15.1	16.2	83.8
Gill Rakers	22.2	28.3	25.3	74.7
Vertebrae	4.5	58.9	31.7	68.3

gradients or clines which, as Huxley (1939) points out, when extending through the area of one or more populations or subspecies may be marked by a very gradual slope within the subspecies area but steep across the interbreeding zones. The demarcation of interbreeding zones or population boundaries and the understanding of conditions contributing to their formation and maintenance must be ascertained before the true relationship between the populations can be fully understood. The importance of geographical distribution in the problem of speciation was also emphasized by Huxley (1939) in his statement " .... a subspecies is a natural or real taxonomic unit in the sense that it is a self-reproducing group with a characteristic geographical distribution distinguished from other similar groups by measurable character differences which can be determined on any reasonably sized series".

However, the number of specimens examined and the uniformity of samples within the two populations of R. tapirina removes without reasonable doubt the question of sampling error and therefore the subspecific separation of the two populations is justified in so much as it fulfils the requirements of Huxley's (1939) statement with regard to meristic characters. The ensuing section will show that the geographical distribution of the two populations is also in agreement with his concept of subspeciation.

(c) Intra-specific Variation

Intra-specific variation of meristic characters in fishes was first recorded by Gill (1863) who found, amongst certain labroid fishes of the western coast of North America, the tendency of a cold water environment to bring about the laying down of more vertebrae than occurred in fishes inhabiting warmer waters. However, Cox (1903) discovered that three species of flatfishes (Pleuronectes americanus Walbaum, Limanda ferruginea Storer and Pleuronectes glauber Gill) from northern New Brunswick on the Atlantic seaboard had reduced finray counts compared with specimens from more southern habitats. In his paper Cox did not assume this to be normal for the species he dealt with but drew attention to the greater range in temperature occurring in New Brunswick waters than much farther south as a probable explanation of anomalous variation. Confirmation of this effect was provided by Tåning (1951) who subjected developing eggs of Salmo trutta to various temperatures and was able to demonstrate that the highest number of rays were laid down at intermediate temperatures whilst at extremely high or low temperatures a fewer number of segments resulted. Cox had put forward the idea that the very young larval fish is plastic enough to be modified by changes of the environment and Tåning found that although this is true the number of segments were actually determined shortly before the "eyed egg" stage is reached.

A study of the variation in finrays and vertebrae of the starry flounder (Platichthys stellatus) from three points on the western North American coast from Alaska to Puget Sound was undertaken by Townsend in 1937 who recorded differences in the means of these characters between the three places. A further study of the same species carried out by Orcutt (1950) was extended to Monterey Bay, California, where fish showed no significant difference from Puget Sound specimens. However, when Californian fish were compared with those from Alaska a value approaching significance was noted. The starry flounder belongs to the family Pleuronectidae and possesses approximately the same number of finrays and vertebrae as the greenback flounder. It is interesting therefore to compare the meristic counts of the two species with respect to their latitudinal range and the corresponding sea temperature differences during the winter months when development takes place. This is presented in Table 24.

Although any two samples within each sub-species could have been used in the comparison in the table, St. Helens and Port Sorell have been selected as records of seasonal variation of temperature was available for them and in this aspect the environments may be regarded as similar.

In the absence of experimental evidence on the behaviour of the developing embryo of R. tapirina under extremes of temperature and salinity the suggestion that observed differences in meristic characters are not the result of phenotypical influences cannot be fully substantiated. But assuming the variation found in P. stellatus is fairly representative of

TABLE 24

THE DIFFERENCE IN MEAN NUMBER OF DORSAL RAYS, ANAL RAYS, AND VERTEBRAE OF STARRY AND GREENBACK FLOUNDERS SHOWING GEOGRAPHICAL SEPARATION INVOLVED

SPECIES	LOCALITIES COMPARED	LATITUDINAL SEPARATION	DIFFERENCE IN WINTER TEMP.	DIFFERENCE IN MEAN NO. OF			NO. EXAMINED
				DORSALS	ANALS	VERT.	
Starry Flounder	Puget Sound - Alaska	1,000 miles	4° C	2.05	0.34	0.05	313
Greenback Flounder	St. Helens - Port Sorell	30 "	1° C	3.38	2.69	0.72	221
Greenback Flounder	St. Helens - Pittwater	104 "	3° C	0.07	0.13	0.07	246

the extent which the formation of the number of segments is controlled by temperature it appears very doubtful whether the differences between the eastern and western sub-species of R. tapirina could be attributed to it alone. The disparity in mean temperature between the most northerly and southerly area samples is not greater than 3°C and the actual monthly fluctuation over a period of 21 months for three representative sampling localities is revealed by Figure 25. Port Sorell and St. Helens closely agreed in both the extreme range and seasonal change of water temperature during at least two winters and presuming that the normal spawning seasons of both populations are comparable all developing embryos would be subjected to somewhat similar conditions irrespective of their location.

The inverse correlation between temperature and spawning has been mentioned previously and in the section on weight/length attention has been drawn to the more abrupt termination of the spawning season at Port Sorell in August 1955 which was two months earlier than in Pittwater. It should be remembered that a three months' observation of gonads in a single year does not justify the conclusion that the Port Sorell spawning season differs from Pittwater as in the particular period when the data were collected (July to September) the possibility of abnormal conditions of flooding from an early thaw and its effect on spawning flounders cannot be overlooked. However, if the spawning season in Port Sorell is normally concurrent with that in Pittwater the case for sub-specific separation is strengthened and the consideration of differences in finray counts etc. being a result of unequal temperature during development becomes secondary.

Further evidence contrary to the possibility of temperature-induced meristic variations is provided by the absence of a definite gradient from south to north and the unusual fact that the fish from habitats bordering Bass Strait which have a warmer environment possess more segments than those from the southern portion of Tasmania for instance, where the winters are considerably colder. If the effect of great temperature range noted by Cox (1903) in Miramichi Bay and Bay des Chaleurs were to be involved amongst any of the areas under consideration Pittwater should show it because of its somewhat greater range of temperature. But as Table 23 indicates although there is a greater difference between St. Helens and Pittwater in distance and temperature than there is between St. Helens and Port Sorell the meristic divergence is much greater between the two latter localities. The difference between these two places which is greater than the divergence of the most widely geographically separated samples from Port Arthur and Port Welshpool draws attention to the longitudinal nature of the division between the two populations. This in turn leads to the consideration of possible genotypical factors which may be responsible for the existing variation.

(d) Geographical Isolation of the two Sub-species

It is now generally accepted by competent evolutionists (Carter 1951, Huxley 1940 and Mayr 1942) that infra-specific variation is the product of the isolation of two or more parts of a monotypic species. Although four types of isolation are recognized, namely geographical, ecological, biological and genetic, the first of these almost always occurs in association with the remaining three. Huxley (1942) points out that it is impossible for this reason to separate them into mutually exclusive categories so that when any one of these four terms are employed to describe an isolation the one used must be the primary isolating mechanism.

Thus in the case of the greenback flounder for which it was not possible to undertake a study of the ecological and genetic factors affecting the two populations it is proposed to consider geographical isolation as the primary isolating principle and regard the remaining factors as consequent to it.

Reference to the chart in Figure 30 shows the distribution of the two sub-species to lie on either side of a line approximately 147°E. At present no apparent geographical barrier exists between the two areas separated by this line which would prevent the free interchange of flounders except on the most southern portion of the Tasmanian coast. There it could be expected that the replacement of shallow sandy beaches by a somewhat rugged coastline with fairly deep water close inshore would discourage any tendency of the species to venture into these waters. This was borne out by the observed dearth of the species in Port Davey in the southwest corner of the island.

Attention should then be turned to the northern boundary of each sub-species which must lie somewhere between St. Helens and Port Sorell. Notwithstanding the absence of a present-day physical barrier between these two places today there is abundant evidence that such did exist until fairly recently in geologic time. To understand the implications of such a statement it is necessary to consider the geological evidence available on the history of Bass Strait and its application to the fish population during the latter part of the Cenozoic era. The most comprehensive account of the geological evolution of the Australian continent available appears to be that of David (1932) and this work will be used in the application of geological aspects to the following discussion.

During the Oligocene period the greater part of the southern portion of southern Australia was submerged and remained so until the late Pliocene. As comparatively modern forms of heterosomata are known to have existed in the Middle Eocene of Egypt (Woodward 1910) and the Miocene of California (Jordan and Gilbert 1919) it is reasonable to suppose that an ancestral form of the genus Rhombosolea was present in southern Australian seas during that period. In the paper referred to Jordan and Gilbert draw attention to the similarity of the characteristic fish fauna of Miocene California and the present-day forms found there. With the commencement of the Pleistocene Period and its accompanying ice ages the sea level of most parts of the world including the Australian region was lowered considerably and from one half to one-third of Tasmania became covered by a thick mantle of ice. If, as David (1932) has suggested, the sea level during the Pleistocene was no less than 200 feet lower than it is at present the approximate area enclosed by the 40 fathom contour line in Figure 30 would have been above sea level, thus effectively separating the waters of western Bass Strait from the Tasman Sea. The 30 and 40 fathom contour lines in the figure which show well the pattern of the connexion of the two land masses were obtained from depths given on the current Admiralty chart of the area.

Thus the flatfish population could have become divided by the formation of the so-called Bass Land Bridge and the differentiation of the characters of each population initiated. It is conceivable that during the period of isolation, which later will be shown to have persisted until the Late Pleistocene, the environments of the eastern and western sides of the Bass Bridge differed considerably for the following reasons. Firstly geological evidence shows that the Pleistocene ice capping and subsequent glaciation of Tasmania was confined to from one-third to one-half the total area of the island, mainly on the north-western and western portion.

It has been estimated that ice from 1,000 to 1,500 feet in thickness covered the Macquarie Harbour region which descended almost if not actually to sea level. With the sea level lowered as shown in the chart Bass Strait would have taken the shape of a large bay or gulf into which poured the cold glacier-fed rivers of the north coast with the result that both the temperature and salinity of the sea would have been lowered. The western population would therefore be subjected to an environment greatly changed from that which existed prior to isolation.

Secondly, the eastern seaboard with the land relatively free of ice and glaciation was probably under the influence of a warm northern current from the tropical regions. During this period the southern part of the Australian continent itself was ice-free apart from a culotte on the Kosciusko Plateau which did not come down below 5,000 feet above sea level, so that its influence on the sea of the eastern continental coast would have been small. It is thought that the greater part of the run-off from the Kosciusko Plateau flowed west into the Murray basin to be discharged into the eastern end of the Great Australian Bight. If the warm current flowed south along the east coast as it does at the present time, and the lack of ice on the east Tasmanian coast appears to suggest this, the environment of the eastern population of fishes could be expected to be markedly different in both temperature and salinity from that of the western population. Today the southerly limit of the Coral Sea current from October to April is thought to be affected by the flow through Bass Strait of the South-West Tasman water mass (Rochford 1957) but with the Strait closed this warm current could be expected to extend much further south along the east coast of Tasmania. Rochford (personal communication) considers that a lowering of sea level to the extent described would still have permitted uninterrupted flow of tropical water from the Coral Sea.

It would be expected that the two isolated populations of the species living in these hypothetically different environments would undergo differentiation. Carter (1951) is of the opinion that differentiation of this type is slow, even to the sub-specific stage taking many thousands of years, and it will now be shown that in this case an interval of not less than about 800,000 years elapsed between the time of isolation and the removal of the barrier separating the populations.

The final drowning of the Bass Bridge is thought to have been concurrent with the end of the Pleistocene Period and the rise in sea level following the melting of the great ice caps. It was certainly after the arrival of the Tasmanian aborigines who possessed no sea-going craft but before the coming of the Australians and the dingo judging by the complete absence of fossil evidence of the latter in Tasmania. As the antiquity of the aboriginal in Tasmania indicated by the presence of bones and artefacts in glacial deposits is set between 20,000 and 100,000 years ago it may be taken that Bass Strait assumed its present form about this time.

The majority of workers in the evolutionary field agree that differentiation will always occur between populations that are sufficiently isolated and much of it will be adaptive to conditions of the habitat. This is followed by the formation of a polytypic species through a process of microevolution the greater part of which is caused by micromutation. With regard to the significance of microevolution in problems characteristic of the present one in *R. tapirina*, Dobzhansky (1937) points out that quantitative infraspecific differences are characteristics of micro-mutation. The supposed differing environment of the two populations referred to earlier in which the western group would have been subjected to colder temperatures and lower salinity than the eastern group may have caused meristic character differentiation to follow the pattern observed in natural populations of flatfish whereby colder waters of low salinity favour increased segmentation than do warmer waters of higher salinity. If this was so and through a process of micro-mutation the number of segments in the populations became genetically controlled the higher mean meristic counts of flounders which at present live in the warmer environment may be accounted for. That is that genetic differences evolved during the period of isolation persist even although the barrier no longer exists.

Mayr (1942) suggested that once a species has become polytypic due to the action of geographical barriers two alternate processes may follow. (i) Greater differentiation follows and isolating mechanisms bring about a new species that does not interbreed with the parent species.

(ii) The removal of the barrier permits interbreeding and the formation of hybrids between the two populations. It is thought that (ii) possibly describes the present condition of the two flounder populations because the differences found between them are not of a specific degree and nothing is known of the extent to which hybridization occurs. Of course, the view that the sub-species are still in process of differentiation and will eventually become full species might be supported by the absence of clines and the strongly significant difference between the means of Port Sorell and St. Helens. During the investigation the author was aware of the importance of examining specimens from the boundary area around Flinders I. to find evidence of population interchange but was unable to make any collections. This was due primarily to unsuccessful fishing which may indicate that the species, with its natural tendency towards remaining in the estuary of birth as demonstrated by tagging returns, has not yet become fully established in the regions where the barrier once existed.

The hypothesis thus far advanced may be briefly summarized as follows.

Due to the lowering of the sea level during early Pleistocene a single species of Rhombosolea became isolated into two parts by the Bass Land Bridge. The two populations thus formed remained isolated for about 800,000 years during which time there took place a differentiation of meristic characters selected by differences in environment with regard to temperature and salinity. The isolating barrier was removed by a rise in sea level about 20,000 to 100,000 years ago but due to the differentiation becoming genotypic through a process of micro-evolution quantitative differences in meristic counts persist to the present day.

The subspecific name tasmani is proposed for the Eastern subspecies and for the Western subspecies R. tapirina tapirina.

The writer presents the hypothesis aware that much more light could be thrown on the problem by more extensive sampling particularly in the boundary areas as well as in the South Island of New Zealand where the species also occurs but where it has not been possible to make collections.

XV. SUMMARY

The distribution and habits of the greenback flounder (*Rhombosolea tapirina* Gunther) are recorded with reference to the commercial fishery in Victoria and Tasmania.

Some of the more fundamental aspects of the biology of the species are presented with particular reference to growth, maturity and speciation. The assessment of growth and age by otolith interpretation is compared with relevant data from length measurements and marking experiments. Age at maturity and seasonal spawning cycle is related to measurement of ovarian ova.

The variation in the number of finrays, gill-rakers, and vertebrae is used to separate the greenback flounder stocks of southern Australia into two populations for which subspecific rank is proposed.

Possible factors contributing to the existence of the two subspecies are examined and a theory contingent on past geological history of the Bass Strait area is presented.

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XVII. REFERENCES

Ancona, M.U. (1937).- La Croissance chez les Animaux Mediterranees. Rapp. Comm. Int. Mer M'edit. 10: 163-224.

Arora, H.L. (1951).- An investigation of the California sand dab. Citharichthys sordidus (Girard). Calif. Fish Game. 37 (1): 1-42.

Blackburn, M., and Fairbridge, W.S. (1946).- Report on the Danish-Seining trials by the M.V. "Liawenee" in southern Tasmanian waters. J. Coun. Sci. Industr. Res. Aust. 19 (4): 404-413.

Boulenger, G.A. (1902).- Ichthyology in Rep. Coll. Nat. Hist. "Southern Cross" 5: 158.

Bullough, W.S. (1939).- A study of the reproductive cycle in the minnow in relation to the environment. Proc. Zool. Soc. Lond. 109: 79-102.

Carter, G.S. (1951).- Animal Evolution, a study of recent views of its causes. Sidgwick and Jackson (Lond.)

Cassie, R.M. (1956).- Condition factor of snapper, Chrysophrys auratus Forster, in Hauraki Gulf. N.Z. J. Sci. Tech. B 38 (4): 375-388.

Castelnau, F. de (1872).- Contributions to the ichthyology of Australia. Proc. Zool. Soc. Vic. 1: 168.

Clark, F.N. (1925).- The life history of Leuresthes tenuis an atherine fish with tide controlled spawning habits. Calif. Fish and Game Comm., Fish Bull. 10: 51p.

Clark, F.N. (1928).- The weight/length relationship of the California sardine (Sardina caerulea) Calif. Fish and Game Comm., Fish Bull. 26: 20p.

Clark, F.N. (1934).- Maturity of the California sardine (Sardina caerulea) determined by ova diameter measurements. Calif. Fish and Game Comm., Fish Bull. 42: 49p.

Cole, F.J., and Johnstone, J. (1901).- Pleuronectes. L.M.B.C. Mem. 8: 252p.

Cox, P. (1903).- Reduction in the number of fin-rays of certain flatfishes. Proc. Miramichi Nat. Hist. Ass. 3: 42-47.

David, T.W.E. (1932).- Explanatory notes to accompany a new geological map of the Commonwealth of Australia. C.S.I.R. Aust. 177p.

Dobzhansky, T. (1937).- Genetics and the origin of species. Columbia Univ. Press (New York).

Fabricius, E. (1950).- Heterogeneous stimulus summation in the release of spawning activities in fish. Rep. Inst. Freshw. Res. Drottning. 31: 57-99.

Franz, V. (1910).- "Die Eiproduktion der Scholla" and Zur Eiproduktion der Scholle Nachtrage Wiss. Meeres. Untersuch. N.S. 9: 217-224.

Fulton, T.W. (1897).- On the growth and maturation of the ovarian eggs of teleostean fishes. Fish. Bd. Scot., Ann. Rep. 1897.

Geiser, S.W. (1923).- Evidences of a differential death rate of the sexes among animals. Amer. Midl. Nat. 8 (7): 153-163.

Geiser, S.W. (1924).- The differential death rate of the sexes among animals with a suggested explanation. Wash. Univ. Stud. Sci. Ser. 12 (1): 73-96.

Gill, T.N. (1863).- On the labroids of the western coast of North America. Proc. Acad. Nat. Sci. Philad. (1863): 22.

Ginsburg, I. (1938).- Arithmetical definition of the species, sub-species, and race concept with a proposal for a modified nomenclature. Zoologica. N.Y. 23 (3): 253-286.

Graham, D.H. (1953).- "Treasury of New Zealand Fishes." (Reed: Wellington).

Gudger, E.W. (1935).- Abnormalities in flatfishes (Heterosomata). I. Reversal of sides. A comparative study of the known data. J. Morph. 58: 1-39.

Gudger, E.W., and Firth, F.E. (1935).- An almost totally ambicolourate halibut Hippoglossus hippoglossus with partially rotated eye and hooked dorsal fin - the only recorded specimen. Amer. Mus. Novit. 811: 7p.

Gunther, A.C.L.G. (1862).- Cat. Fish. Brit. Mus. (Lond.) 4 (3): 458-460.

Gunther, A.C.L.G. (1863).- Bibliographical notices. Ann. Mag. Nat. Hist. 11 (3): 117.

Hagerman, F.B. (1952).- The biology of the Dover sole, Microstomus pacificus (Lockington). Calif. Fish and Game Comm., Fish Bull. 85: 48p.

Haast, J. (1872).- Some undescribed fishes of New Zealand. Trans. Proc. N.Z. Inst. 5: 277.

Hart, J.L., *et al.* (1940).- Proximate analysis of British Columbia herring in relation to season and condition factor. *J. Fish. Res. Bd. Canada.* 4: 478-490.

Hickling, C.F. (1930).- The natural history of the Lake. *Fish. Invest. Lond. Ser 2.* 12 (1): 3-78.

Hile, R. (1936).- Age and growth of the cisco, *Leucichthys artedi* (Le Seur) in the lakes of the north-eastern highlands, Wisconsin. *Bull. U.S. Bur. Fish.* 48: 211-317.

Hubbs, C.L., and Hubbs, L.C. (1945).- Bilateral asymmetry and bilateral variation in fishes. *Pap. Mich. Acad. Sci.* 30: 229-310.

Hubbs, C.L., and Perlmutter, A. (1942).- Biometric comparison of several samples with particular reference to racial investigations. *Amer. Nat.* 76: 582-92.

Hutton, F.W. (1873).- Notes on some New Zealand fishes. Ann. Mag. Nat. Hist. 4 (12): 401.

Hutton, F.W. (1874).- Contributions to the ichthyology of New Zealand. *Trans. Proc. N.Z. Inst.* 6: 106.

Hutton, F.W. (1876).- Contributions to the ichthyology of New Zealand. *Trans. Proc. N.Z. Inst.* 8: 215.

Huxley, J.S. (1939).- In a "discussion on sub-species and varieties." *Proc. Linn. Soc. Lond.* 151 (2): 105-114.

Huxley, J.S. (1940).- The new systematics. Oxford Univ. Press.

Huxley, J.S. (1942).- Evolution, the modern synthesis. (Harper and Brothers, published N.Y.). 298.

Jensen, A.J.C. (1938).- Factors determining the apparent and the real growth. Rapp. Cons. Explor. Mer. 108 (1): 109-114.

Jordan, D.S., and Gilbert, J.Z. (1919).- Fossil fishes of southern California. II. Fossil fishes of the (Miocene) Monterey formations of southern California. Leland Stanf. Univ. Publ. Univ. Ser. (1919).

Kawasaki, T., and Hatanaka, M. (1951).- Studies on the populations of the flatfishes in Sendai Bay. I. Limanda angustirostris Kitahara. Tohoku J. Agric. Res. 2 (1): 83-106.

Kesteven, G.L. (1942).- Studies in the biology of the Australian mullet. I. Account of the fishery and preliminary statements of the biology of Mugil dobula Gunther.

Keys, A.B. (1928).- The weight/length relation in fishes. Proc. Nat. Acad. Sci. Washington. 14: 922-925.

Kyle, H.M. (1900).- Contributions towards the natural history of the plaice (P. platessa L.) Rep. Fish. Bd. Scot. 18: 189-241.

Macleay, W. (1882).- Descriptive catalogue of Australian fishes. Proc. Linn. Soc. N.S.W. 6: 130-132.

Manzer, J.I. (1952).- The effects of tagging on a Pacific coast flounder Paraphrys vetulus. J. Fish. Res. Bd. Canada 8 (7): 479-485.

Marr, J.C. (1943).- Age length and weight studies of three species of Columbia River salmon (Onchorhynchus keta, O. gorbuscha, and O. kisutch). Stanf. ichthyol. Bull. 2 (6): 157-197.

Mayr, E. (1942).- Systematics and the origin of species. (Columbia Univ. Press, New York).

McCulloch, A.R. (1921).- Notes on fishes of N.S.W. Aust. Zool. 2: 36.

McCulloch, A.R. (1929).- A check list of the fishes recorded from N.S.W. Mem. Aust. Mus. 3: 282.

Molander, A.R. (1947).- Observations on the growth of the plaice and on the formation of annual rings in its otoliths. Svenska hydrogr. - biol. Komm. Skr. N.S. 2 (8): 11p.

New Zealand Marine Department (1928).- Report of fisheries for year ended 31st March (Govt. Printer: Wellington).

Norman, J.R. (1926).- A report on the flatfishes (Heterosomata) collected by the F.I.S. "Endeavour". Biol. Results "Endeavour" 5: 219-308.

Orcutt, H.G. (1950).- The life history of the starry flounder. Platichthys stellatus (Pallas). Calif. Fish and Game Comm. Fish. Bull. 78: 64p.

Phillips, W.J. (1921).- Notes on the edible fishes of New Zealand. N.Z. J. Sci. Tech. 4: 122.

Phillips, W.J. (1927).- Bibliography of New Zealand fishes. N.Z. Mar. Dept. Fish. Bull. 1: 29.

Rapson, A.M. (1940).- The reproduction, growth, and distribution of the lemon soles (Pelotretis flavilatus Waite) of Tasman Bay and Marlborough Sounds. N.Z. Mar. Dept. Fish. Bull. 7: 56p.

Rochford, D.J. (1957).- The identification and nomenclature of the surface water masses in the Tasman Sea (Data to the end of 1954). Aust. J. Mar. Freshw. Res. 8 (4): 369-413.

Simpson, G.G., and Roe, A. (1939).- Quantitative Zoology. (McGraw Hill, New York).

Tåning, A.V. (1952).- Experimental study of meristic characters in fishes. Biol. Rev. 27: 169-193.

Tasmania (1882).- Royal Commission on Tasmanian fisheries. (Govt. Printer: Hobart).

Thomson, J.R., and Anderton, T. (1921).- Notes on Rhombosolea. Bull. N.Z. Bd. Sci. Art. 2: 84.

Townsend, L.D. (1937).- Geographical variation and correlation in Pacific flounders. Copeia 1937. 2: 92-103.

Van Oosten, J. (1929).- Some fisheries problems on the Great Lakes. Trans. Amer. Fish. Soc. 59: 63-95.

Waite, E.R. (1906).- Notes on Australian and Tasmanian fishes. Rec. Aust. Mus. 4 (3): 197.

Waite, E.R. (1909).- New Zealand fishes. Subantarctica Isle N.Z. Vertebrata. 25: 590.

Waite, E.R. (1911).- Scientific results of the New Zealand Government trawling expedition, 1907. Pisces part 2. Rec. Canterbury (N.Z.) Mus. 1 (3): 202-209.

Waite, E.R. (1921).- Illustrated catalogue of the fishes of South Australia. Rec. S. Aust. Mus. 2: 158.

Waite, E.R. (1923).- Fishes of South Australia. (Govt. Printer: Adelaide).

Wheeler, J.F.G. (1924).- The growth of the egg in the dab. Quart. J. Micr. Sci. 68: 641-660.

Whitley, G.P. (1929).- R.M. Johnstone's memoranda re fishes of Tasmania. Pap. Proc. Roy. Soc. Tas. 1929: 44-68.

Woodward, A.S. (1910).- On a fossil sole and fossil eel from the Eocene of Egypt. Biol. Mag. N.S. 5 (7): 402-405.

Woodward, B.H. (1902).- West Australian fishes. W.A. Yearbook. 1900-1: 272.