Frontispiece: A commercial fisherman's catch of eels, Waikato River.

ASPECTS OF THE BIOLOGY OF JUVENILE FRESHWATER EELS (ANGUILLIDAE) IN NEW ZEALAND

Donald John Jellyman

Submitted for the degree of Doctor of Philosophy in Zoology at the Victoria University of Wellington.

May, 1974

CONTENTS

LIST OF FIGURES

LIST OF TABLES

ABSTRACT

The early freshwater life of the two species of New Zealand freshwater eels, Anguilla australis schmidtii Phillipps and A. dieffenbachii Gray was studied involving an examination of 8131 glass-eels, 5275 migratory elvers, and 4291 resident eels of less than 26 cm. Most eels were collected from the Makara Stream, Wellington by set-net, hand-net and electric fishing.

These extensive samples together with subsidiary collections from elsewhere in New Zealand show that glass-eels of both species arrive in fresh-water from July to December. Their otoliths indicate a marine larval life of about 18 months but it is not possible as yet to locate the precise oceanic spawning areas. Migratory movements of glass-eels are in two phases: an invasion of fresh-water from the sea and an upstream migration. The former occurs only at night with a periodicity corresponding to the daily ebb-flood tidal rhythms. There is a seasonal reversal in this response which is attributable to the onset of the behavioural transition taking place prior to the second migratory phase. Increased pigmentation and changes in response to light, flowing fresh-water and schooling tendencies characterise this latter migration which occurs primarily at spring tide periods.

Such juvenile eels show specific habitat preferences and a high degree of olfactory differentiation of water types. This behaviour, together with pigment development and physical tolerances, was studied in the laboratory. Measurements of invading glass-eels show that mean length, weight and condition all decline throughout the season of arrival but mean vertebral numbers remain constant.

An upstream migration of small eels (elvers) occurs each summer and is readily observed at many hydro-electric stations. These migrations, comprising eels of mixed sizes and age groups, penetrate progressively further upstream each year.

In both species, scales begin formation at body lengths of 16.5-20 cm. All features of scale formation, including the number of scale rings, are related to length with relative differences in rate of development occurring between the species. In contrast to scale rings, otolith rings are annual in formation and become visible after grinding or burning the otolith.

Growth rates established for 273 eels to 26 cm in length from the Makara Stream, Wellington, are slow, with mean annual increments of 2.2 and 2.1 cm respectively for shortfins and longfins. In contrast, shortfins from a coastal lake near Wellington reach 26 cm in their third year of freshwater life. Length-weight relationships for small eels are given together with mean monthly condition factors.

Growth studies on elvers held in a multiple tank unit in which temperature, density, and amount and frequency of feeding could be controlled, show that young eels grow more slowly than normal under such conditions. However, growth appears optimum at 20°C with a feeding rate of 5-7% body weight per day. Feeding efficiency decreases with higher temperatures. At both glass-eel and elver stages, shortfins adapt and survive better under artificial conditions.

1 INTRODUCTION

There are two species of freshwater eel in New Zealand - a shortfinned eel growing to 90 cm in length and a longfinned eel growing to over 180 cm. The pre-anal extent of the dorsal fin is a convenient and reliable character for separating the two species and thus gives the common names shortfin and longfin.

"The fresh-water eels are probably more abundant in New Zealand than anywhere else in the southern hemisphere. For the Maori, they were of the utmost economical importance, as is evident, for instance, from the highly developed technique in methods and implements for the capture of these fish, possessed by the natives prior to the arrival of the Europeans" (Schmidt 1927: 380). The Maoris recognised by name at least a hundred varieties of eels (Hamilton 1908). These varieties were distinguished by features of size, colour, habitat, behaviour and migratory movements but are not of any systematic significance.

A comprehensive historical review of the nomenclature of both species is contained in Ege (1939). Until 1926, four species were recognised but an examination of 1500 eels from New Zealand by Schmidt (1927) convinced him that there were only two species: A. australis (shortfinned eel) and A. aucklandi (longfinned eel). The features he used for separation of the two species were the pre-anal extent of the dorsal fin and the shape of the maxillary teeth. To distinguish between Australian and New Zealand shortfinned eels which differed slightly in vertebral counts, Schmidt (1928b) proposed the two "forms" be known as A. australis Rich. forma occidentalis, the Australian shortfinned eel, and A. australis Rich. forma orientalis, the New Zealand shortfinned eel.

Subsequently, in a revision of the New Zealand marine and freshwater eels, Griffin (1936) in accordance with the rules of nomenclature, used the names A. australis schmidtii Phillipps and A. dieffenbachii Gray which are now well established.

The New Zealand freshwater fish fauna is generally sparse. About 35 species are currently recognised with half of these belonging to the family Galaxiidae. That 11% of the genera but 92% of the species are endemic to New Zealand is, according to McDowall (1964: 59) indicative of "a relatively young fauna and/or incomplete faunal isolation from other

regions". Of the two anguillids, the largest fishes in the fauna, A. dieffenbachii is endemic to New Zealand and offshore islands, whereas A. autralis schmidtii has a wider distribution. This distribution, according to Ege (1939: 218) is New Zealand, Auckland Islands, New Caledonia, Norfolk Island and perhaps Fiji and Tahiti.

Over recent years, eels have become a rapidly expanding export item. Prior to 1965 only 15-20 tonnes, worth approximately N.Z. $2,000-$2,500, were caught annually. In May 1969, the Fisheries Committee of the National Development Conference, set a target of $1m per annum for eel production by 1978. This figure was surpassed in 1971 and the export value of eels in 1972 was $1.45m. The total catch is composed of wild eels as eel farming ventures are still at the exploratory stage.

The fishery for wild eels is no longer a localised one centred on processing factories. At present, several companies operate "eel-tanker" trucks capable of transporting live eels several hundred kilometres from the area of capture to the factory. Increased fishing pressure is reflected in the number of licensed factories which process eels: in 1970 there were only nine such factories but by 1972 30 were in operation.

Relatively few areas of New Zealand are geographically inaccessible to eel fishermen. The only other areas exempt from fishing are those where physical conditions are unsuitable, or prohibited areas such as Maori reserves or National Parks. At present, the only regulations relevant to the eel fishery are those designed to protect trout and other game fish. In the past the eradication of eels for the supposed benefit of such game fish, has been actively encouraged by several Acclimatisation Societies.

The intensive fishing effort for eels has highlighted the need for further biological research to establish guidelines for the planned and rational utilisation of this resource.

Several studies have been conducted in the past on New Zealand eels, the most important being those of Cairns (1941, 1942) and Burnet (1952a and b, 1955, 1968, 1969a and b). Cairns investigated the life history of both species, including age and growth, migration, distribution, feeding relationships and sexual development. Recent research by Burnet has concerned the relationships between brown trout and eels, although he has also investigated growth rates and adult migration.

One aspect of the biology not well studied is the annual invasion of glass-eels and their freshwater migration. An understanding of these stages of the life history is vital to the eel industry as a whole, especially in view of the proposed development of commercial eel farming within New Zealand and the current international demand for glass-eels. Accordingly, this present study is primarily concerned with the movements and behaviour of glass-eels and elvers. Investigations on the age and growth of small eels together with experimental culture, have also been undertaken.

A review of the major literature on freshwater eels, reveals some confusion in terminology. Thus the "glass-eel" of New Zealand and Japan is equivalent to the "elver" of Europe and America. "Elvers" in New Zealand refers to the small adolescent eels which undergo summer migration. These are also variously referred to as "secondary migration eels" or "anguillettes".

For clarity, the term "glass-eel" has been adopted to denote the stage in the life cycle which invades fresh-water from the sea. Such eels are typically unpigmented, but after residence in fresh-water for a few weeks, become strongly pigmented (late stage glass-eels). With the attainment of the full pigmentation, stage VIB of Strubberg (1913), the juvenile eels are referred to as elvers.

Hereafter, the term "eel" refers to a freshwater eel of the genus Anguilla, unless otherwise stated. For figures and tables the name A. australis schmidtii has been shortened to A. australis, while in the text, the names "shortfin" and "longfin" are often used in place of the specific names.

The following section on "Sampling Areas and Methods", simply introduces the variety of methods used throughout this study, these methods being discussed more fully and appropriately under the relevant sections.

2 SAMPLING AREAS AND METHODS

The Makara Stream was chosen as the principal study area. This stream, which lies to the west of Wellington, is small and relatively short (see Fig. 2.1.b). However, it drains a large catchment area of 78 km^2 and so is subject to periodic rapid floods. This catchment is generally steep dissected hill country, cleared for farming. The valley and flood plain are both narrow and the outlet of the stream is restricted by a gravel bar. The extent of this bar varies according to the strength and duration of the northwest wind which causes gravel accumulation. Fig. 2.2 shows upstream and downstream views of the mouth during a period when the bar was commencing formation after being recently scoured away.

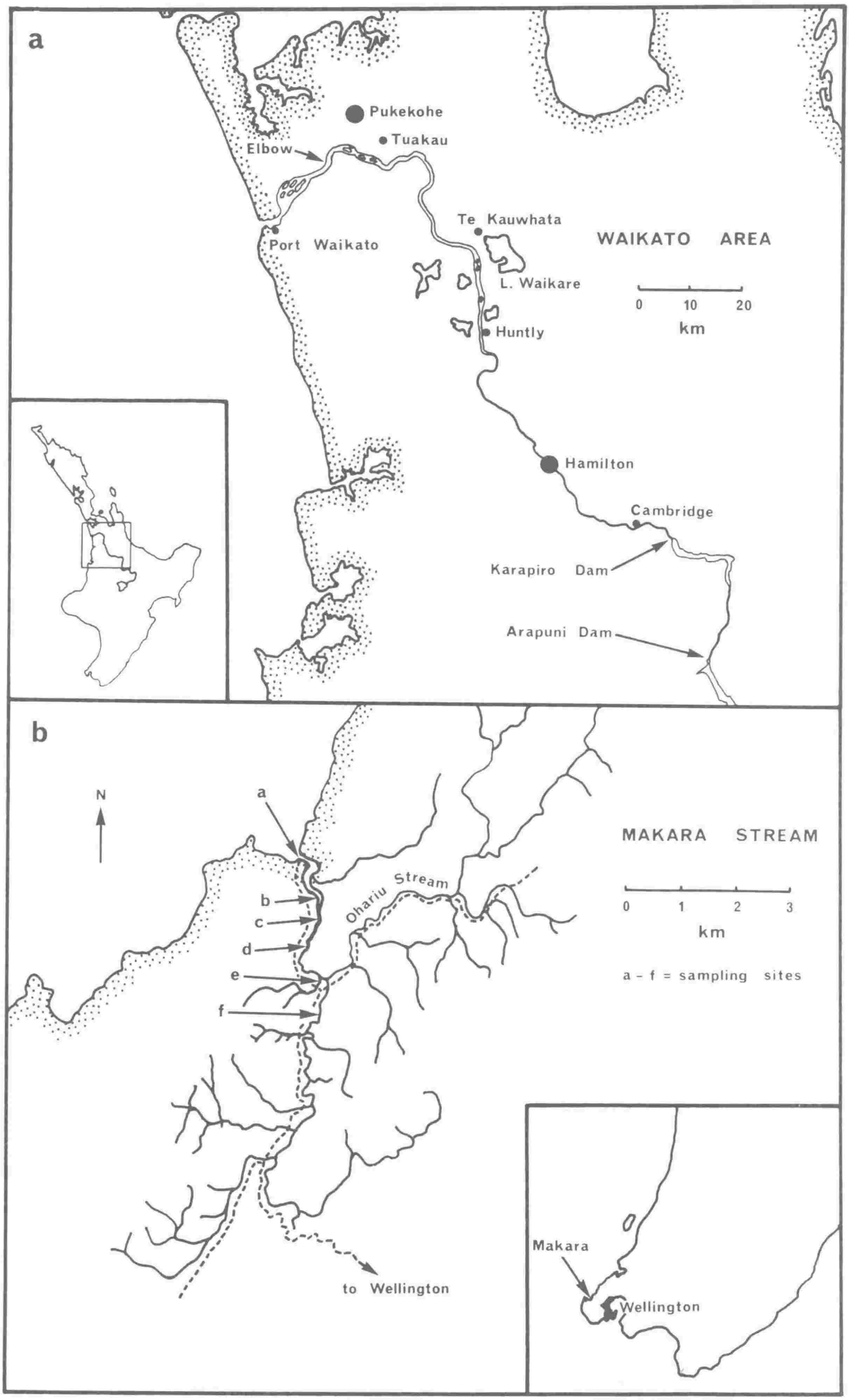
The estuary is broad and shallow, with a bottom of thick black mud. Considerable quantities of marsh gas are generated in the mud of the lower estuary. Upstream, a wide diversity of habitats occurs. In upper reaches the stream is narrow and swift with a boulder-strewn bed. In such areas there is limited cover for large fish. Downstream of this the flow is less rapid, with frequent pools and riffles. Stream margins are generally bare with some areas of secondary native bush or scrub. Finally, the lower 3 km is an area of deposition. Flow is slow with muddy undercut banks and abundant cover. Margins of the stream in this area are either bare or planted in willow.

This stream was chosen for several reasons. It is close to Wellington and accessible by road for much of its length. With the exception of the estuary and some deep holes in the lower and middle reaches, the whole stream is able to be waded and so sampled by electric fishing. Except for the discharge from two small pig farms, the stream is relatively unpolluted. Finally, the stream offers a diversity of habitats and contains populations of both species of eel.

Regular sampling sites are indicated in Fig. 2.1.b. These were concentrated along the lower 2 km, where the smallest eels were found. Monthly electric fishing samples were mainly from the vicinity of sites 'd' - 'f'. Additional eels were taken from the Ohariu tributary, and the main stream 1 km above the confluence with the Ohariu tributary. Temperatures were recorded from site 'd' over a two year period. The annual temperature regime is very similar to that given by Allen (1951: 34) for the Horokiwi Stream - a small stream 20 km northeast of Makara.

Fig. 2.1.a The Waikato district with localities mentioned in the text.

b The Makara Stream. Regular sampling sites are indicated.


a
Pukekohe
Tuakau
Elbow
Te Kauwhata
Port Waikato
WAIKATO AREA
L. Waikare
0 10 20
km
Huntly
Hamilton
Cambridge
Karapiro Dam
Arapuni Dam
b
N
a
b
c
d
e
f
Ohariu Stream
MAKARA STREAM
0 1 2 3
km
a - f = sampling sites
to Wellington
Makara
Wellington

The annual range was 4.5°-22.0°C, with a mean summer temperature (January-March) of 17.2°C and a mean winter temperature (July-September) of 9.4°C.

In addition to the Makara Stream, other important sampling areas mentioned in the text were Pukepuke Lagoon, Waimeha Stream and the Waikato River. These areas are among those shown in Fig. 3.20.

Pukepuke Lagoon is a shallow basin lake, 3.3 km inland, formed between consolidated and unconsolidated sand dunes. It has a sandy substrate overlain by a soft ooze. The lagoon has an area of 15 ha and a maximum depth of 85 cm. As it is a wildlife sanctuary, the lake has not been fished by commercial eel fishermen. The eel population is composed almost entirely of shortfins.

The Waimeha Stream is small and muddy, approximately 2.5 km long and drains an area of coastal swamp. It has an average width of 4.5 m and for the most part is 1 m deep. The bottom is fine silt-mud, while additional cover is afforded by marginal aquatic plants. The stream contains a surprisingly large variety of native fishes, including both species of eel, although shortfins predominate.

In contrast, the Waikato River is 280 km in length and drains a catchment of 14000 km^2. The average discharge recorded at Tuakau Bridge is approximately 40000 cusecs. Sampling sites mentioned in sections dealing with the migrations of glass-eels and elvers are shown in Fig. 2.1.a. In the vicinity and downstream of the "Elbow", the river edges are bordered with large plantations of willows. Those areas, together with vast banks of submerged water weed, provide excellent cover for eels, especially shortfins.

Almost all glass-eel and elver samples were obtained by net. The various glass-eel nets used in the Makara Stream are discussed later. In addition small eels were collected from beneath stones in the estuary at low tide with a small hand-net. Most elver samples were also collected with hand-nets, as the eels were found crawling over exposed obstacles - usually the lower slopes of a hydro-electric dam.

The other method of sampling used extensively, was electric fishing. Monthly samples of juvenile eels, including many late-stage glass-eels, were collected by this method. The machine used was the earth return equipment, as described by Burnet (1967). Limited use was made of a portable "pack-set" unit powered by a six volt motor-cycle battery.

Electric fishing is a convenient method of fishing in non-saline areas where the stream is able to be waded. Although sampling efficiency is

Fig. 2.2.a Mouth of the Makara Stream - view upstream.

The stick in the water near the right bank indicates the normal site of glass-eel fishing.

b Mouth of the Makara Stream - view downstream.

A gravel bar is commencing to form beyond the outlet of the stream.

greater when working downstream as paralysed eels may drift out from cover after the operator has passed, it was often found that the mud stirred up seriously reduced the visibility. As the Makara samples were not required to be quantitative, it was preferable to work upstream.

Paralysed eels were secured with a handled dip-net and placed in plastic buckets. For transport to the laboratory, the eels were placed in large plastic bins (60 x 40 x 25 cm deep). A thin film of water covered the bottom of the bin, sufficient to keep the eels moist. Watercress or other available aquatic weed was placed on top of the eels to shield them from direct sunlight. This method of transport proved most successful, and over a hundred small eels, to 26 cm, could be kept alive for several hours. If eels were completely covered with water, they soon depleted the dissolved oxygen and died from asphyxiation.

Eels of all size ranges could be collected using the electric fishing machine. Burnet (1955: 8) maintains that the method is non-selective for size, although, unless care is taken, it can easily be used selectively, especially if the stream is too large for the operator to work effectively or beyond the capabilities of the equipment. The average efficiency of fishing for a single run over one area is given by Burnet (1952b: 119) as 43%.

Of interest are the relative proportions of both species of eel recorded from the same body of water by electric fishing and netting. Thus Allen (1951: 61) recorded that less than 1% of all eels netted in the Horokiwi Stream, Wellington, were shortfins, whereas Burnet (1952b: 121) using electric fishing found 44% were shortfins. This large difference is probably attributable to the general small size of shortfins found by Burnet, where 70% were less than 30 cm. At this size, the eels are cryptozoic and this behaviour, together with size, would make them very difficult to capture by netting.

3 EARLY LIFE HISTORY

3.1 INTRODUCTION

Until early this century the life history of freshwater eels remained a mystery. The sequence of discoveries which led to the solving of this mystery is given by Bertin (1956). The first contribution of significance to the understanding of the reproductive biology was made in 1777, when Mondini recognised and described the ovaries of the female eel. The testes were identified in 1874 by Syrski.

The marine larval stage of the life history remained unknown until the end of last century. Prior to this Kaup (1856) described a small apodal fish larva as Leptocephalus brevirostris, but it was not until 1893 that Grassi and Calandruccio showed this delicate animal to be the larva of the European eel Anguilla anguilla L. The problem then remained to locate the breeding area, and this was the commission of the Danish biologist, Johannes Schmidt. During 18 years of research, Schmidt collected thousands of leptocephali from the Atlantic Ocean and adjacent seas. From these extensive collections he was able to establish the distribution of various size-classes of larvae. Consideration of the area where the smallest larvae were obtained indicated a spawning area in the western North Atlantic. The collection of larvae of less than 1.0 cm in the vicinity of the Sargasso Sea in 1920 confirmed this to be the breeding area of both the European and American eels.

The European and American eels are still the only freshwater eels for which the breeding areas are known with certainty. However, it is a reasonable assumption that all freshwater eels have a similar early life to that established by Schmidt. Matsui (1957:165) proposed that the breeding area of the Japanese eel, Anguilla japonica Temminck and Schlegel 1846, lay to the east of Taiwan. Specimens as small as 1.23 cm have recently been collected from this area but Matsui and Takai (1971:17) considered this material insufficient to confirm this proposition.

Little is known of the larval life of the New Zealand freshwater eels. Only four anguillid larvae were recorded by Jespersen (1942:13-15) from the Dana plankton collections in the South Pacific in 1928-30. Castle (1963:9) tentatively identified two leptocephali of shortfinned eels collected near New Caledonia as A. australis schmidtii. Although individual larvae of the Australian and New Zealand shortfin subspecies

cannot be separated on myomere counts, the area of collection of these specimens was within the known geographical range of the New Zealand subspecies. No larvae of A. dieffenbachii have been recorded. This lack of material precludes any delimiting of the breeding area by length-frequencies of the larvae, the method employed successfully by Schmidt. Therefore, any suggestions of possible breeding areas must come from consideration of suitable hydrological conditions together with mean sizes and arrival times of glass-eels in fresh-water.

3.2 LARVAL LIFE

With reference to Australasian shortfinned eels, Schmidt (1928:199) considered that the submarine ridge south of New Caledonia provided a physical barrier between the spawning areas of Australian and New Zealand stocks. More recently, Castle (1963:13) placed the general breeding area for southwest Pacific anguillids as "well to the east of New Caledonia - that is, between Fiji and Tahiti". The smaller of the two larvae of A. australis schmidtii recorded by Castle (1963:9) was 2.46 cm and was collected east of the New Hebrides. Based on the growth rate calculated for larvae of the European eel by Schmidt (1922:199), this larva would be approximately three months old. As considerable distance could be covered during this period, all that can be surmised from the area of collection is that a southward movement is involved during larval migration.

Indicators of Possible Breeding Areas

The above leads to a consideration of known factors which might indicate the locality of the breeding area. Distribution of both New Zealand species has already been discussed. The differences imply separate spawning areas. The validity of separation of Australian and New Zealand shortfinned eels into two subspecies based on vertebral counts, is discussed later. Further evidence for the existence of two distinct populations comes from consideration of the arrival times of glass-eels. Although the data of Schmidt (1928b:199) and Ege (1939:211) do not indicate the existence of any definite season for the invasion of A. australis australis Richardson, Buckmaster (1971:24 and pers. comm.) has found that invasion occurs from late winter to early spring. This is similar to the time for the main invasion of glass-eels into New Zealand fresh-waters.

Cairns (1941:60) and Castle (1969:2) suggested that larvae of New Zealand eels may be transported by the East Australian Current, and so arrive off the west coast of New Zealand from a southerly direction. This current is strong off the east coast of Australia and must be considered as the final agent in transportation of Australian larvae. Hamon (1965:899,921) recorded a velocity of 130 km/month for eddies of this current, and considered the volume transport of the current itself to be not more than half that of the Gulf Stream.

If there is indeed a common breeding area for both subspecies (Castle, 1972:14), the main New Zealand invasion could be expected to take place some considerable time after the Australian as both subspecies would presumably use the same current system for transport of their larvae. Few data are available for the speed of water movements across the Tasman Sea, but Fleming (1952:61) gives a known speed of "at least $4\frac{1}{2}$ miles a day, perhaps 9 miles a day". Using the 1100 miles given by Fleming for the trans-Tasman stream-line distance, the lesser speed gives a period of eight months for the crossing of the Tasman by drifting material. As previously stated no such delay occurs between glass-eel invasions in Australia and New Zealand. The alternative, that New Zealand larvae require a further year to cross the Tasman Sea is not logical, considering the relative proximity of the two landmasses.

Ege (1939:209) recorded glass-eels of A. australis from New Caledonia, at pigmentation stage VI A II of Strubberg (1913), with a mean length of 4.9 cm. This is only 0.4 cm less than the mean length for Australian specimens at the same stage also recorded by Ege, from Maroubra near Sydney, but 1.1-1.2 cm less than comparable New Zealand eels. It would be expected that growth which would take place over the distance of 1500 km separating Sydney and New Caledonia would exceed 0.4 cm. It is not surprising to find that the New Caledonian shortfin is the New Zealand subspecies. From the above, separate spawning grounds for Australian and New Zealand shortfinned eels are proposed.

The time at which maturing eels move on their catadromous migration has been recorded by a number of authors. Cairns (1941:68) states that February to April are the main months for this migration, with the shortfin run finishing by early March. Hobbs (1947:230) found migratory shortfins

at Lake Ellesmere (Canterbury) from March to April, and longfins from April to May. Dates from Burnet (1969a:237-238) for mid-Canterbury, are earlier at December to March for shortfins and October to February for longfins. Todd (pers. comm.) found the peak period in the Wellington area to be March-April, with considerable overlapping of both species, but longfin females were last to migrate. It may be concluded that the migratory season for adult New Zealand eels is late summer to early autumn, a similar season to that of the European and American eels, which are also temperate species. In contrast, it is doubtful whether the migrations of the tropical Indo-Pacific species of Anguilla are seasonal, as temperatures throughout the year are uniform (Bertin, 1956:184).

A similar seasonal correlation is found in the invasion times of glass-eels into fresh-water. European and American glass-eels arrive from late winter through spring (e.g. Schmidt 1922:203,207) with local differences according to distance from the spawning area. Similarly, New Zealand glass-eels of both species arrive from late winter through spring.

Considering these similarities in seasonal migration times of temperate eels, it would also be expected that other phases of the life cycle would be related to seasons. As A. anguilla and A. rostrata (Le Sueur) spawn in the spring and summer (Schmidt 1922:198) as does A. japonica (Matsui 1957:163), it can be predicted that New Zealand eels spawn over the equivalent period in the southern hemisphere i.e. November to February. The invasion of glass-eels commences in July, with the peak month being September. This gives a corresponding larval life of approximately six months, or a yearly increment of this. The actual length of larval life can be determined from examination of glass-eel otoliths.

Glass-Eel Otoliths

Calculation of age by examination of the otolith (sagitta) is a widely accepted technique in fisheries biology, and has been used successfully in a later section of this study to age eels. Zonation in the glass-eel otolith should reflect the length of sea-life. To determine whether the zones in the glass-eel otolith are seasonal, a comparison can be made between otoliths of American and European eels. As larvae

of the European eel spend a further year at sea than do American larvae, this should be shown as extra zones in the otolith.

It was found that otoliths from larger eels, when viewed against a black background with reflected light, show transparent zones as black areas and opaque zones as white. Glass-eel otoliths show similar zonation. Sinha and Jones (1967a:102) review knowledge of the seasonal nature of otolith zones in various fish species.

Interpretation of these zones from photographs in the relevant literature is rather unsatisfactory. Opuszynski (1965:395) records the presence of two dark rings in the glass-eel otolith of A. anguilla. This is in agreement with the description given by Sinha and Jones (1967a:103) also for the European eel. However, the latter authors mention that the outermost black ring is thin and may be incomplete or absent. In neither study do the authors attempt to relate the otolith zonation to length of sea-life. In an age and growth study of the American eel in Newfoundland, Gray and Andrews (1971) do not describe the sea-life otolith, but accompanying photographs show similar zones to those observed in New Zealand glass-eels.

To observe otoliths of American and European glass-eels directly, I tried to obtain samples of preserved eels. Unfortunately, no specimens of A. rostrata were received but a sample of 21 glass-eels of A. anguilla was kindly supplied by Dr G. R. Williamson, Inverness, Scotland. These eels, caught on 2 April 1972 in the River Severn, were in the early stages of pigmentation, indicating that they were recent arrivals in fresh-water.

The otoliths were removed and mounted on microscope slides for subsequent examination. Of the 39 otoliths examined, 17 showed a definite double white ring of sufficient clarity to be measured with a micrometer eyepiece. The division between these two rings was small and in all cases but one constituted less than 2% of the combined width of the two rings. The presence of this double ring contrasts with otoliths from glass-eels of both New Zealand species, which show a single white ring.

The known length of larval life of the European eel of two and a half years, can be correlated with the otolith zonation, as shown in Fig. 3.1.a. In the centre of the otolith, a white spot is often visible. This probably represents the growth which occurs during the first summer at sea. As hatching may extend well into summer and the otolith may not be formed until the larva is well differentiated, this spot is small or

Fig. 3.1 Photographs of glass-eel otoliths.

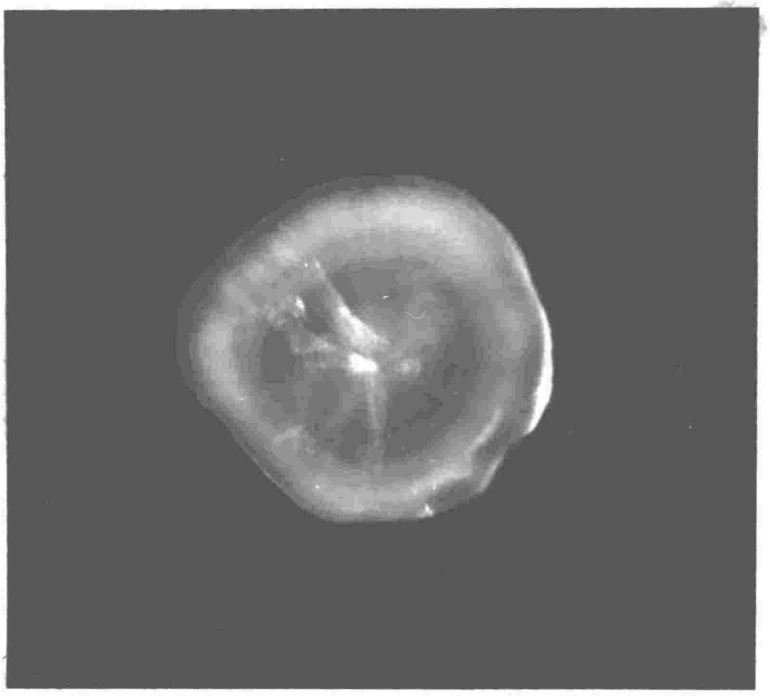
a *A. anguilla* (T.L. 6.6 cm, pigmentation stage VI A II 1)

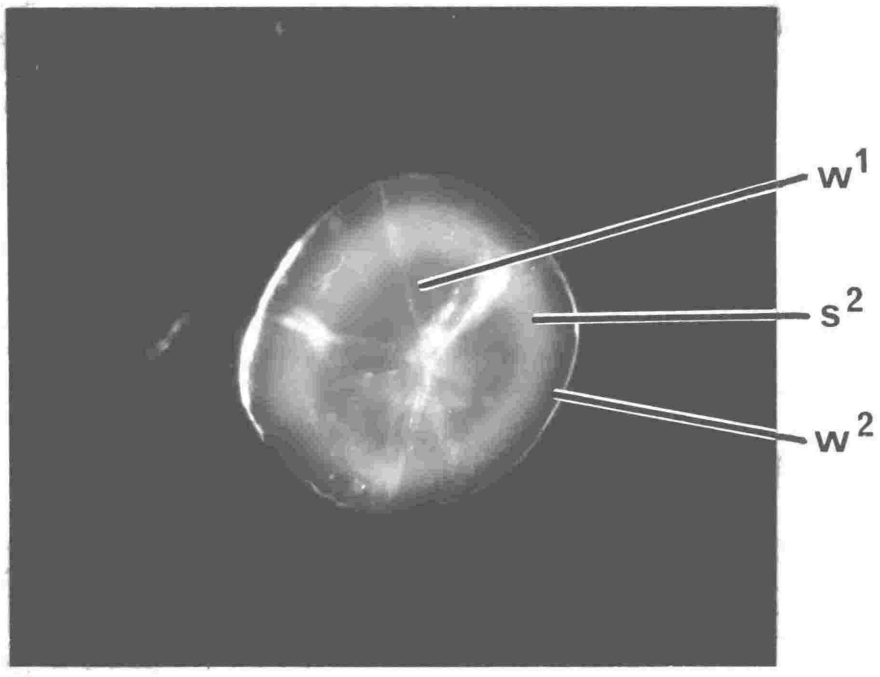
b *A. australis* (T.L. 6.0 cm, pigmentation stage V B),
showing suggested interpretation of zones:

W^1 = first winter

S^2 = second summer

W^2 = winter of arrival




w1
s2
w2

absent. Matsui (1952:234) considers that the otolith of A. japonica forms when the larva is 1.26 cm in length. Surrounding this spot is a broad black ring, formed during the first winter. Outside this is a white ring (second summer), a thin black ring (second winter), and a broader white ring representing the third summer of larval life. Between this last ring and the edge of the otolith is a black margin. At this stage the glass-eel enters fresh-water. The margin then becomes differentiated into a winter ring.

Similarly, seasons can be assigned to the otolith zonation of New Zealand glass-eels of both species. Fig. 3.1.b shows the suggested interpretation. Again a central summer spot is present, surrounded by a black ring (w^1, first winter) and a white ring (s^2, second summer). The outer black zone (w^2), represents the winter of arrival. Summation of these seasons gives a larval life of one and a half years for New Zealand glass-eels, with arrival in fresh-water during the second winter. Both MacFarlane (1936:46) and Cairns (1941:57) assume a larval life of two years.

As a further check on the validity of this interpretation, measurements were made of otoliths from invading glass-eels throughout the season of arrival. Where possible a minimum of ten eels of either species per month were examined. Mounted otoliths were measured with a micrometer eyepiece at x 100 magnification. Monthly measurements were averaged and the resulting mean zone widths expressed as a percentage of the otolith radius. Results are given in Table 3.1. The otolith radius is expressed in micrometer units, such that 40 units = 1 mm. Comparable data for A. anguilla are also given, but here the second and third summer zones are incorporated into a single measurement under s^2.

Table 3.1 shows a similar seasonal trend in both New Zealand species. A seasonal increase occurs in the width of the outer zone, the winter of arrival, with a corresponding decrease in the inner two zones. Although the actual zone measurements are not included in the table, the percentage radius occupied by zones w^1 and s^2 decreases proportionally. Also, although the mean length of the specimens decreases throughout the year, the otolith radius remains approximately the same, or in longfins increases slightly. This is due to the increasing width of the outer zone, w^2. An increasing percentage width of this zone is consistent with the seasonal interpretation of the otolith zones.

Table 3.1 Proportional zone widths of otoliths from New Zealand glass-eels per month of arrival.
Comparable measurements for a sample of A. anguilla glass-eels are also given, although the second and third summer zones have been incorporated under 'S^2'.

W^1 = 1st winter (includes the 'spot' of first summer)
S^2 = 2nd summer
W^2 = 2nd winter (winter of arrival)

A. australis				Otolith measurements		
Month	n	Mean length (cm)	Radius	w^1 (%)	s^2 (%)	w^2 (%)
July	8	6.4	6.7	65	23	12
Aug.	11	6.2	6.7	64	21	15
Sept.	18	6.2	6.8	64	22	14
Oct.	12	6.1	6.7	64	21	15
Nov.	11	5.6	6.7	63	19	18
A. dieffenbachii						
July	5	6.6	6.3	75	19	6
Aug.	11	6.7	6.6	72	21	7
Sept.	12	6.5	7.1	70	20	10
Oct.	12	6.3	6.9	70	19	11
A. anguilla						
	21	7.2	7.4	64	29	7

Thus, in early season glass-eels, this outer zone represents the second winter of larval life only, but in late arrivals it also includes a zone of summer growth as yet undifferentiated. This is verified by reference to otoliths from larger eels where the second winter zone of larval life is seen to be approximately the same width in all eels.

The difference in relative zone widths between shortfins and longfins is of interest. The high value for longfins during the first winter probably reflects a period of rapid growth during early larval life. For convenience, all zonation up to and including the second winter (w^2) is referred to as sea-life. All subsequent zonation is considered as taking place in fresh-water.

It is concluded from the above observations that zonation in glass-eel otoliths is seasonal, and is consistent with a proposed larval life of one and a half years. It remains now to delimit the spawning area.

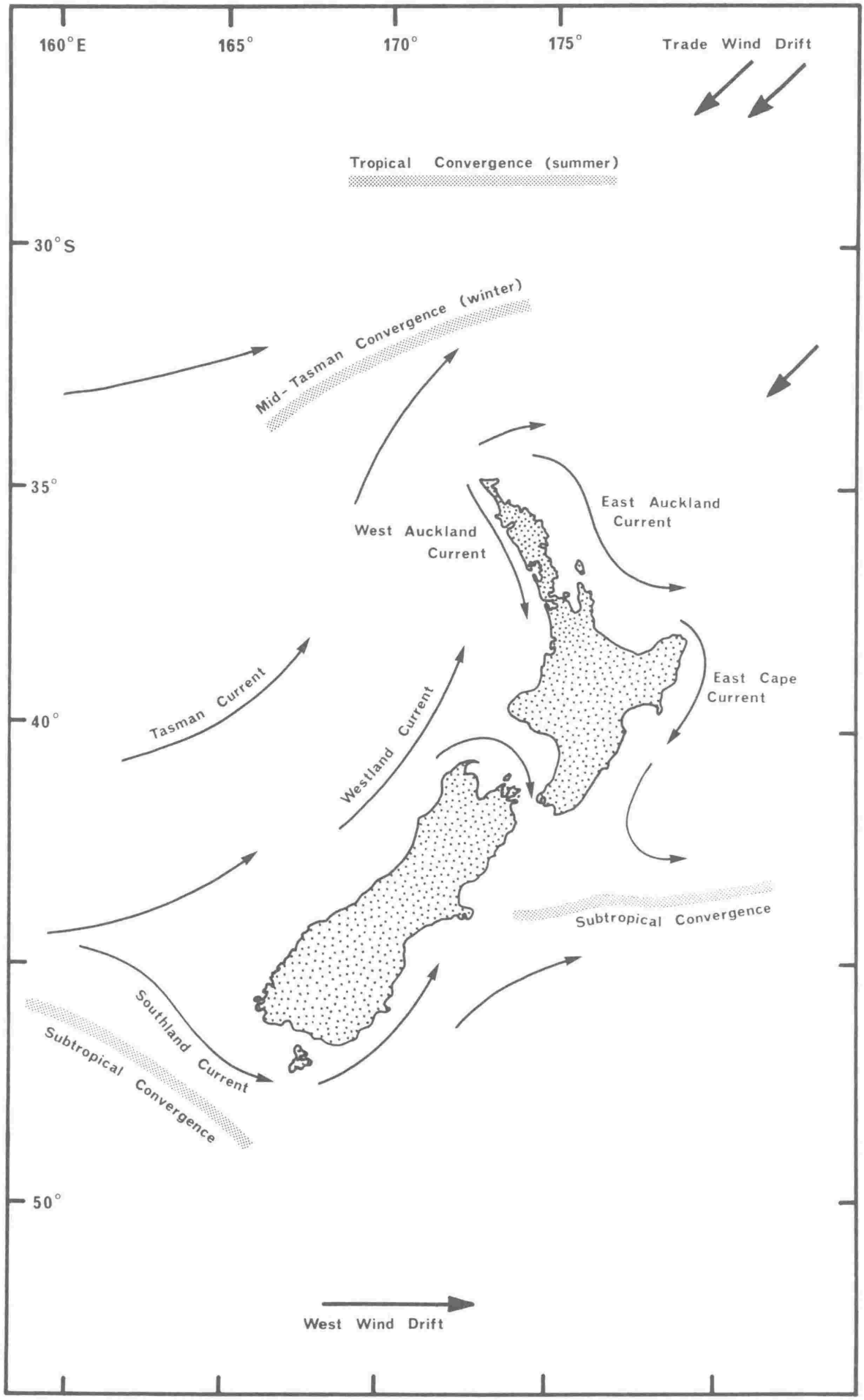
Transport of larvae of the European eel is considered to be a passive migration by water currents, although late stage and metamorphosing leptocephali can exhibit surprising activity (Schmidt 1906:178). As most are found at a depth of 25-50 m (Deelder 1970:3:11), the larvae are considered pelagic. Therefore, their direction and progress of migration are almost certainly those of surface currents. Similarly, the two larvae of the New Zealand shortfin described by Castle (1963:9), were both collected within the upper 50 m.

The following section reviews the relevant New Zealand surface hydrology.

Hydrology

Three main surface water movements give rise to the coastal circulation around New Zealand. To the south is the West Wind Drift; to the north of the North Island, the Trade Wind Drift; to the west of both islands, the Tasman Current. These water movements, together with local winds, give rise to the coastal circulation (Brodie 1960:247). These features together with others mentioned in the text are illustrated in Fig. 3.2. As the breeding areas for the three northern hemisphere temperate eels are in the vicinity of the tropics, it is assumed that both New Zealand species spawn in similar regions in the southern

Fig. 3.2 New Zealand coastal circulation showing components mentioned in the text.


160°E
165°
170°
175°
Trade Wind Drift
Tropical Convergence (summer)
30°S
Mid-Tasman Convergence (winter)
35°
West Auckland Current
East Auckland Current
East Cape Current
40°
Tasman Current
Westland Current
Subtropical Convergence
Southland Current
Subtropical Convergence
50°
West Wind Drift

hemisphere. Accordingly, the current systems of significance for larval transport are those conveying subtropical water to the coasts of New Zealand.

Subtropical water may arrive at New Zealand from two separate directions: from the west via the Tasman Current, and from the north-east via the Trade Wind Drift. As discussed below, recent research has cast some doubt on the existence of definite currents derived from the latter source.

The deflection of a branch of the east-west flowing South Pacific Equatorial Current by the landmass of Australia, gives rise to a strong southward movement of subtropical water along the east coast of Australia. This East Australian Current, during its southward passage, sheds eddies at the latitude of Sydney (Hamon 1961:10). These eddies flow eastward to the north of New Zealand in the manner given by Garner (1954:293). In discussing this west to east movement, Garner considers that floating material using this current as a vehicle, could reach the west coast of the North Island without travelling around the periphery of the Tasman Sea.

The southward flow of the East Australian Current is deflected north-eastward by the subantarctic surface water in the southern Tasman Sea. The resulting northeast drift of water, the Tasman Current, is now modified subtropical water and less well defined in its passage. It meets the east flowing water from the East Australian Current over the Norfolk Ridge, where a Mid-Tasman Convergence has been recorded in winter by Stanton (1969:141) and Stanton and Hill (1972:647). Part of the Tasman Current flows eastward through Foveaux Strait and along the Otago Coast, as the Southland Current (Brodie 1960:248, Houtman 1966:480).

In summary, the subtropical water from the East Australian Current flows towards the west coast of New Zealand, either in a direct eastward course or via the periphery of the Tasman Sea. As it approaches the New Zealand coast this current becomes markedly weaker and less well defined (Wyrtki 1962:96, Garner 1969:216).

There are varying opinions as to the origin of subtropical water flowing southward along both coasts of the northern North Island. Fleming (1950:186) proposed the existence of a warm East Cape Current to explain temperature observations. Garner (1961:62) considered that this current originated in the Trade Wind Drift. A similar origin was proposed by Brodie (1960:247) for both the East and West Auckland Currents. This "extensive flow" from the Trade Wind Drift did not show in a

circulation survey by Wyrtki (1962:97) using geopotential topographies. However, he considered that surface wind drifts would not be indicated by this survey method.

Data from the Tui cruise in 1962, analysed by Barker and Kibblewhite (1965:624), suggested that water from the Trade Wind Drift flowed southeast along the Kermadec Trench and fed the East Cape Current. These authors found that the main flow to the north of North Cape was in a northerly direction, but some water was diverted southward as the East Auckland Current. Similarly, Garner and Ridgway (1965:52) found that the Westland Current traversed the entire west coast of New Zealand and rounded North Cape to form a strong southward flow (the East Auckland Current).

Stanton (1969:136) implied that water from the Trade Wind Drift has little effect on the coastal circulation of New Zealand. He proposed a tropical convergence at the interface of water from this drift and water derived from the eastward flow of the East Australian Current. However, Garner (1970:20) found no evidence for either a tropical convergence or a southwest flowing Trade Wind Drift to the northeast of New Zealand. Contrary to Wyrtki (1962:97), Garner considered that such a surface drift should be recorded by geopotential topography. Similarly Ridgway (1970) obtained no indication of a southwest flow in the southern Kermadec Trench, as had previously been postulated by Barker and Kibblewhite (1965).

In view of these differences in interpretation, it is not possible to say definitely whether subtropical water arriving at New Zealand is completely derived from the Tasman Current or whether some originates from the Trade Wind Drift. Distribution of the two subspecies of A. australis suggests that a more direct route from the north might be taken by larvae of the New Zealand subspecies, as shortfinned eels to the west of 160° latitude are A. australis australis and to the east are A. australis schmidtii. This is not supported by known hydrological conditions, which indicate that water flowing west past New Caledonia strikes the east coast of Australia or enters the Coral Sea (Wyrtki 1962:100-102). No shorter route by-passing the eastern seaboard of Australia is known.

Thus, an analysis of the surface currents of New Zealand and adjacent waters, gives no more precise indication of a possible spawning area located in the tropics. Also, it cannot be established that glass-eels arrive at New Zealand without traversing the Tasman Sea.

Finally, a consideration of the important physical factors for spawning of the European eel may help to define possible areas in which the New Zealand eels spawn. These factors according to Bertin (1956:122) are a depth in excess of 400 m with a temperature of 16-17°C and a salinity greater than 35.5°/oo. In the southern hemisphere the warmest areas at a comparable depth occur in the vicinity of 20°S (Sverdrup et al 1942:chart V). Temperatures here are approximately 14-15°C. Depth is generally adequate over the whole southwest Pacific basin, especially east of Tonga, and salinities are relatively high. It seems logical to confine the possible spawning area to the latitude of approximately 20°S.

Estimation of possible distances travelled by larvae during the one and a half years of sea-life can also be considered. Harden-Jones (1968:77) found a good correlation between the velocity of surface currents in the North Atlantic and the proposed length of sea-life for European eel larvae. Few data are available for current velocities in the southwest Pacific. Wyrtki (1962:103) recorded an average current flow to the north of New Caledonia of 3-5 cm per second, and Hamon (1961:10) states that volume transport of the East Australian Current is approximately half that of the Gulf Stream.

Meyer-Waarden (1965) gives a migration speed for larvae of the European eel of 7 km per day, whereas the above data of Wyrtki for the western branch of the South Pacific Equatorial Current give a value of the order of 4 km per day. If this current speed is typical of that influencing New Zealand eel larvae during their 18 months larval life, a figure of 2200 km is obtained for the possible distance from New Zealand to the spawning area. In a direct northeast direction to 20°S, this estimate places the spawning area in the vicinity of the Cook Islands. However, the known distribution of A. australis schmidtii indicates a westerly component in the dispersal. The actual spawning area is probably further west of the Cook Islands, perhaps over the depths to the east of Tonga. Until more precise biological and hydrological data are available, it is not possible to be more specific.

3.3 INVASION OF FRESH-WATER. I. GENERAL

Sampling and Handling Techniques

Several set nets were constructed to sample the invasion of glass-eels from the sea and subsequent movements.

The first design was a square box net with an external collapsible frame. This net had a simple 'V' entrance and detachable 3 m wings. It was fished at sampling site 'd' in the Makara Stream (see Fig. 2.1.b) from September to November 1970. Although good catches of whitebait (Galaxias spp.) were made, only ten glass-eels were caught. Major disadvantages of this net were its large size (mouth of 75 cm x 75 cm) and lack of streamlining. It was suspected that much of the catch escaped as whitebait catches increased immediately a tapered throat was inserted. The netting itself was fibreglass insect netting with 7 meshes/cm and proved very durable.

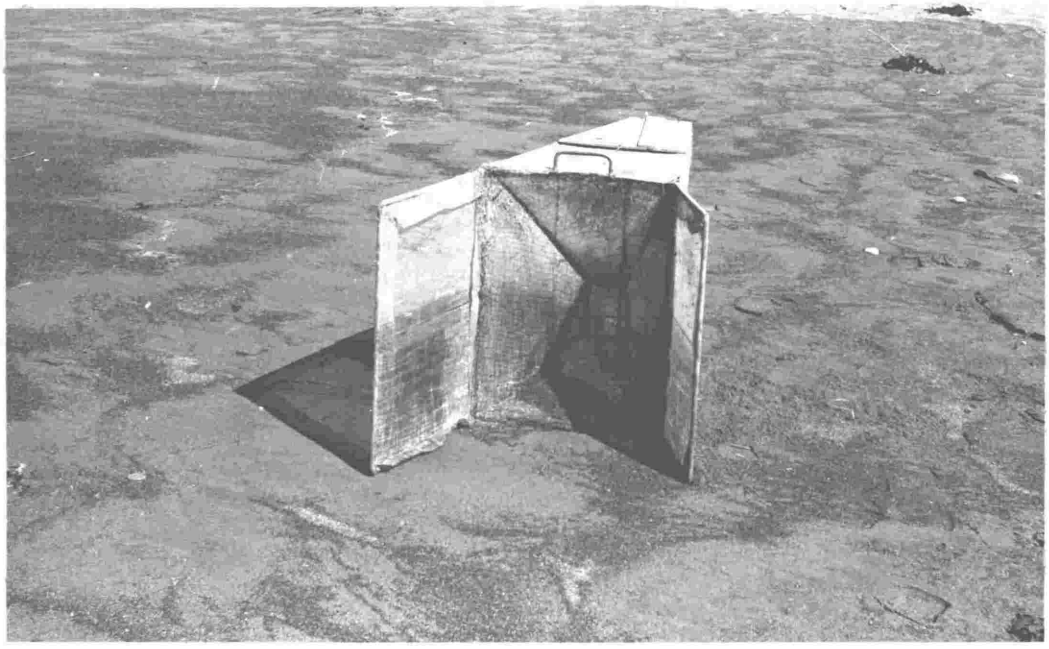
For the 1971 invasion, three further nets were constructed; one for site 'a' at the stream mouth, and two for upstream sampling at sites 'b' and 'd'. These nets had an internal frame and were covered with aluminium fly-screen netting. Seams were hand-sewn. Fig. 3.3.a shows an upstream net as used at site 'd'. These nets had permanent wings leading to a throat entrance. The upstream end was tapered to provide less resistance to the flow of water. However, upstream catches were again small. Also, site 'b' was not suited to a set-net as daily tidal fluctuations meant that the net fished effectively only half the time. One unforeseen hazard was water rats which occasionally chewed holes in these nets to get at dead whitebait.

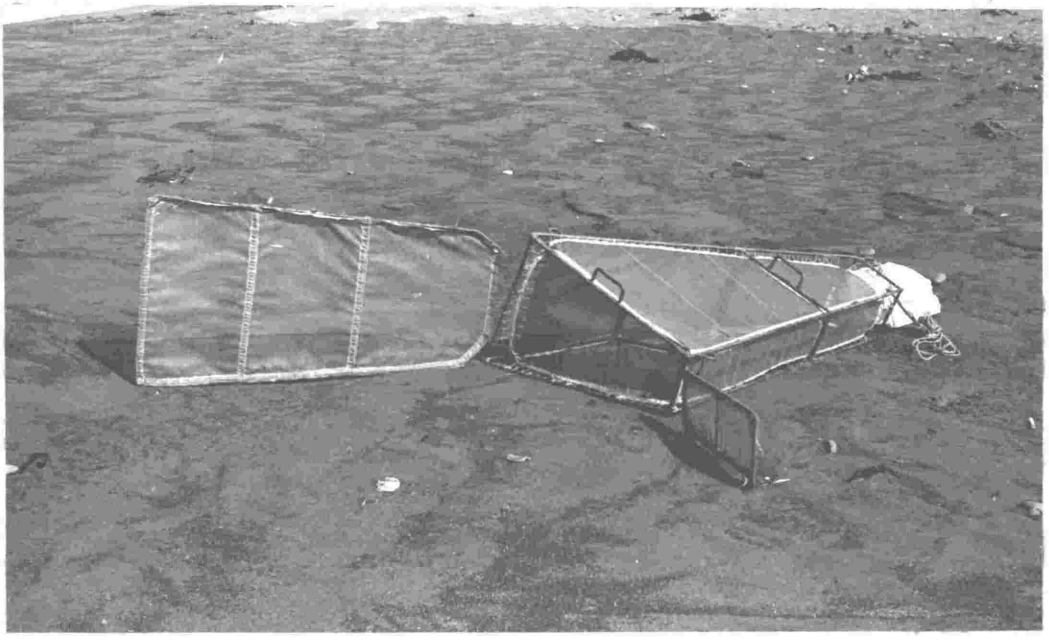
The net used for night fishing at the stream mouth proved more successful. This net had a tapered throat, detachable wings and was designed to fish the sloping stream margin. However, the internal frame meant that the leading edges were subjected to much wear and the 1972 model was designed with an external frame (Fig. 3.3.b). The latter net, again made from fibreglass insect netting, proved most efficient. A nylon skirt at the rear allowed quick emptying. It could be soundly secured with both ropes and stakes, which allowed fishing in all but the most adverse conditions. On swift flood tides a constant watch was often necessary to remove large amounts of seaweed which otherwise clogged the entrance.

Fig. 3.3 Glass-eel nets.

a Net used for upstream sampling.

b Net used to sample the 1972 invasion at the mouth of the Makara Stream.





During the 1972 glass-eel season, fishing took place on two and usually three nights each week. The net was emptied once every quarter hour, the contents tipped into a large plastic bin and the net returned immediately to the water. This operation normally took only one minute. The catch was then sorted and the glass-eels counted. Unfortunately it was not possible to differentiate between the two species in the field. Some glass-eels were caught by using a small carbide lamp as illumination and a hand net, but this method was not used extensively. The total night's catch was kept overnight in stream-water which was vigorously aerated. The eels were then measured and weighed the following morning. Some of the sequences in the fishing operation are shown in Fig. 3.4.a-d.

For measuring, eels were anaesthetised with a solution of 3% benzocaine dissolved in 95% isopropyl alcohol. This solution was used at a concentration of 2-3 ml per litre of water. As soon as the fish became immobile, they were transferred to a flat white fish, with a thin film of water covering the bottom. Using a side light and low magnification on a binocular microscope, the shadow of the dorsal fin could easily be seen. The pre-anal extent of this fin was the character used to differentiate between the two species. The stage of pigmentation, according to the scale of Strubberg (1913:4) was also recorded for each specimen.

Up to 50 eels at a time were weighed, to reduce possible percentage errors. The narcotised eels were placed on a petri-dish and weighed on a chemical balance. The weight of the glass was subtracted and the mean weight per eel calculated. Individual eels could be weighed in this way, and careful technique gave an error of less than 3% for each eel. If eels were required to be kept alive, they were removed to an aerated tank. Those for subsequent radiographic investigations were preserved by fixing in a shallow dish of 10% formalin for two days, thoroughly washed, then stored in 45% isopropyl alcohol.

When reviving narcotised glass-eels, it was noted that longfins took consistently longer to recover than did shortfins. When placed in uncirculated water, most shortfins would revive in half an hour, and all within one hour. At the end of this time, as many as 80% of the longfins would still be narcotised, while over 50% would still not have recovered after two hours. These latter fish showed opaqueness of the brain and nerve cord, characteristic signs of impending death. Further trials showed both species took the same time to become anaesthetised, but

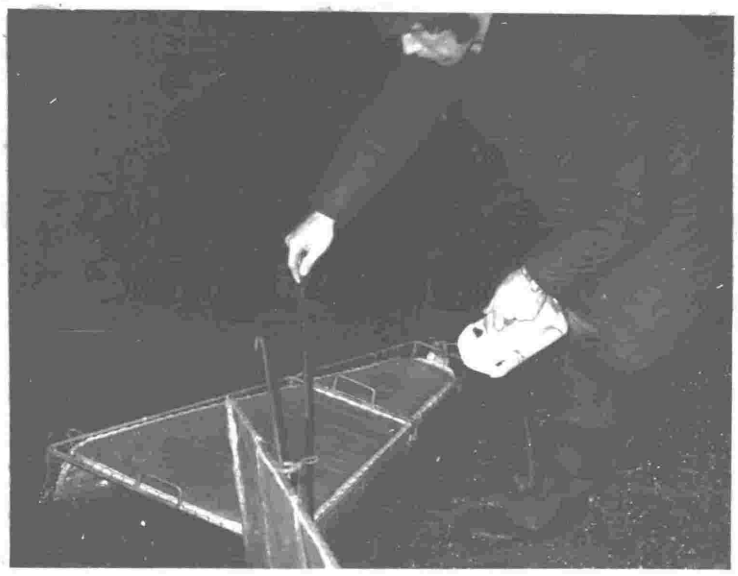
Fig. 3.4 Sequences in glass-eel fishing at night.

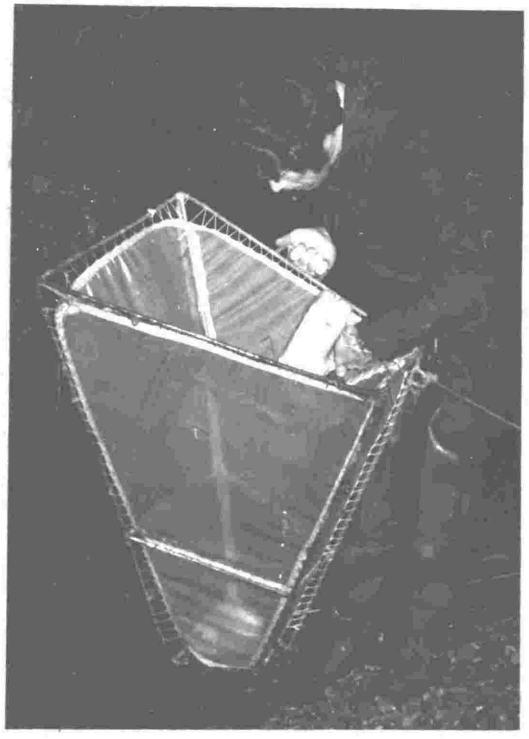
a Setting the net

b Inspecting the contents

c Re-tying the skirt after emptying the net

d Sorting the catch. In this instance the catch is completely whitebait (*Galaxias* spp.).





longfins had a slower recovery time. The recovery time in aerated water was considerably less but varied according to the strength of the anaesthetic, the time spent in this solution before removal, and the water temperature. Under normal conditions, all eels were revived within five minutes, with the shortfins again recovering more rapidly.

Other samples were obtained from various localities throughout the country. These were received either preserved in formalin or alive. Two suitable methods of transport alive were used: either the eels swam freely in a large container, aerated from an oxygen cylinder or they were packed in large plastic bags inflated with oxygen in the proportion of one part eels:one part water:20 parts oxygen. If eels were cooled prior to packing and the temperature kept between 7-10°C during transport, they could be kept this way for at least 12 hours with little or no mortality. However, during transport, if temperatures rose to 15°C and higher, the eels showed characteristic signs of distress by agitated movements and frothing of the water. Under these circumstances, considerable mortalities occurred. This method of transport, with some refinements, has been used to air-freight New Zealand glass-eels to Japan.

Whichever method was used, it was consistently found that, in proportion to the numbers present, longfins died in far greater numbers than did shortfins. For example, a large sample of several thousand glass-eels from the Waikato River, collected on 11 September 1971, was found to contain 99.8% shortfins. However, of the 72 dead eels removed from the plastic bags on arrival at the laboratory 39% were longfins. Similarly, longfins could not be kept successfully under laboratory conditions. In November 1970, a sample of 2779 glass-eels were placed in a 55 l aquarium; of these, 363 (13%) were longfins. Water was changed once weekly and the eels were fed three times weekly. Within 35 days all the longfins had died, but only 5% of the shortfins. Dead eels were not obviously in a debilitated condition, and although the cause of death was not known, it was suspected that traces of chlorine in the domestic water supply, could have been a major factor.

An analysis of living and dead glass-eels kept at a Masterton eel-processing factory showed similar results. These eels, from the Whareama River (see Fig. 3.20) were kept outside in a 300 l concrete tank, supplied with running spring-water. Although longfins comprised only 4% of a sample of 270 living eels examined, they made up 47% of a sample of 68 dead eels. As a similar water supply is used successfully to rear

brown trout fry, Salmo trutta L. (F. Salmonidae), in a nearby hatchery, it is not thought that these deaths were attributable to water quality. It would appear that longfins, at the glass-eel stage, do not adapt readily to artificial environments.

In the laboratory, the darker, more light-tolerant specimens were frequently very active, even during daylight hours and made repeated efforts to climb the aquarium sides. Their remarkable climbing ability was demonstrated when several escaped by threading their way upwards through a piece of plastic netting which had been draped over the side of the tank to hold food. Once acclimatised to an aquarium, most eels had a tendency to hang from a netting bag which was suspended in mid-water. Only a few sought cover under pieces of stone pipe provided. This behaviour greatly facilitated cleaning of the tanks by siphoning.

Little trouble was experienced in inducing the glass-eels to feed. New arrivals were left for a week to acclimatise before food was introduced. By this time, many would readily accept food and by the end of the week, almost all would be feeding. It was found that natural foods (Tubifex worms, white worms Enchytraeus albidus) were initially more acceptable than artificial foods, but once eels were feeding well, a wide variety of foods were eaten. A mixture of minced fish and liver was readily consumed but easily fragmented and clouded the water. Addition of a small amount of gelatin partially overcame this problem. Neither this food nor pelleted trout food, had the consistency of a sample of Japanese compound eel food, provided by the New Zealand Fishing Industry Board. To lessen the dispersal of food fragments in the water, floating plastic containers with perforated sides were tried. However, very few eels appeared able to locate the food and most were unwilling to enter the containers. The few that did enter the containers immediately sought a way out, and did not feed.

Some problems with disease were experienced. The most prevalent disease was Saprolegnia parasitica Coker which appeared externally as tufted growths of white fungus on any area of the body. It was normally checked by dosing tanks with a solution of malachite green and methylene blue sufficient to just colour the water. This disease, commonly encountered in eel farms, is now regarded as a secondary infection (Egusa 1965:524).

Ichthyophthirius multifiliis, "whitespot", was also encountered. Again, the above treatment proved effective and prevented reinfection

from the encysted adult form of the parasite. Tanks were dosed weekly to keep disease to a minimum. Dead fish, surplus food and faecal material were removed regularly by siphoning with a short length of plastic hose. Airlift filters removed suspended material from the water. These precautions kept the problems from disease to a tolerable level.

General Morphology and Pigmentation

As the name implies, glass-eels on arrival in fresh-water from the sea, are almost completely transparent, with the black chorioid layer of the eye being the most conspicuous feature. Fig. 3.5.a.,b shows both species at this stage. The brain and spinal cord become opaque with the onset of death. Other prominent features are the branchial area, coloured light red by the developing blood pigment; the two-chambered heart situated anterior to the liver; the large liver; the straight gut; and the kidney above and posterior to the anus. Under magnification, the circulation can be easily traced, with the dorsal aorta and the posterior cardinal veins located beneath the vertebral column.

Glass-eels invading fresh-water typically show only a few melanophores on the posterior caudal fin rays, and the commencement of pigment development around the brain and spinal cord. The chromatophores on the spinal cord form laterally one on either side of each vertebra. Development of the melanophores commences posteriorly and the spinal cord of an invading eel is generally seen as a black stripe extending two-thirds of the length of the body and formed by coalescing melanophores. At this stage, further deep-seated pigmentation develops on the membranes surrounding the brain. Again development begins posteriorly and proceeds both anteriorly and laterally, to cover the brain itself. This cerebral pigmentation or "tache cérébrale" as it is often referred to in literature of the European eel, is visible through a dorsal fontanelle in the brain-case. As the dermal bones develop to completely enclose the brain, superficial pigmentation forms on the skin above the brain and continues forward to meet the pigment now formed above the olfactory organs. Melanophore development now commences on the pericardium, peritoneum, blood vessels and branchial elements.

The external pigmentation also commences posteriorly and proceeds anteriorly along the dorsal mid-line and the lateral line. Dorso-lateral chromatophores first form at the margins of the myotomes, giving the eel

Fig. 3.5 Glass-eels at invasion (live).

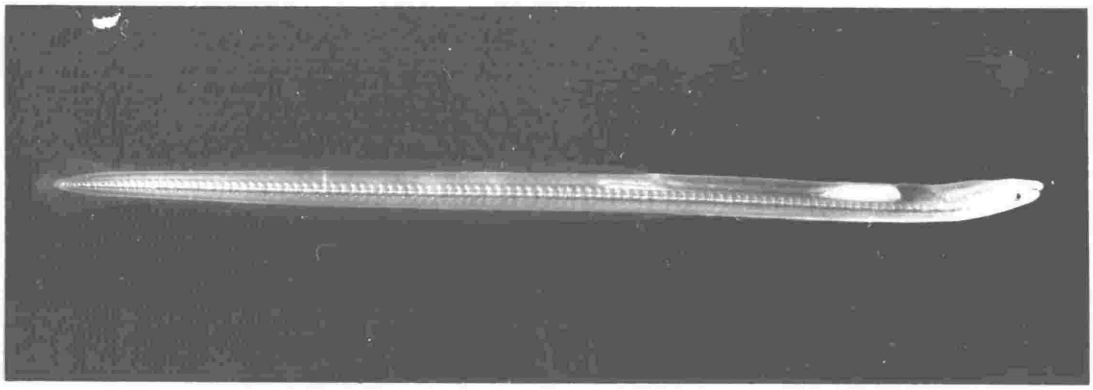
a *A. australis* 6.1 cm, stage VB.

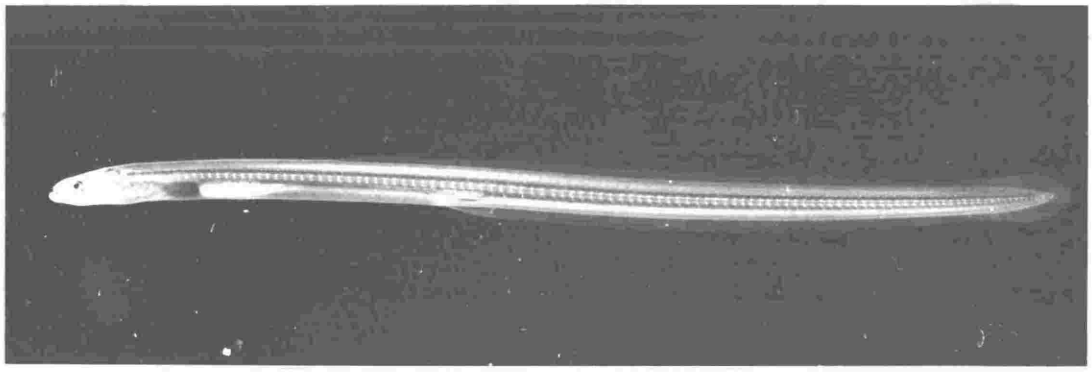
b *A. dieffenbachii* 6.5 cm, stage VB.

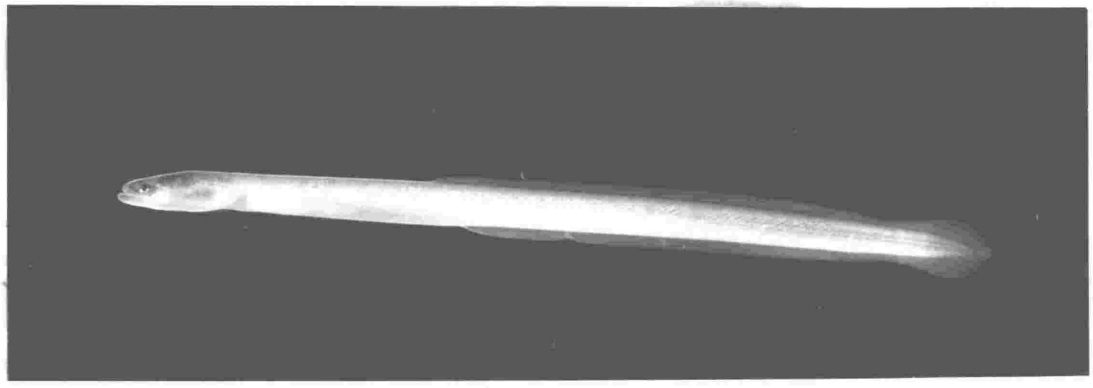
Pigmented glass-eels (preserved).

c *A. australis* 6.0 cm, stage VI A II 2

d *A. dieffenbachii* 6.3 cm, stage VI A IV 2







a characteristic chevron pattern (Fig. 3.5.d). Myotomal pigment then develops and coalesces laterally. Ventro-lateral pigmentation is somewhat slower, and by the time it appears pre-anally, the dorso-lateral pigment has reached the head. All epidermal pigment cells now coalesce to give the young eel the adult coloration.

The process of pigmentation has been divided into various stages by Strubberg (1913:4) based on the spread of superficial pigment. An abbreviated form of this scale appears in Table 3.2.

Glass-eels of both New Zealand species fit this scale well and accordingly it is adopted to characterise developmental stages.

It was found that all invading glass-eels caught at Makara, were in the earliest stages of pigmentation. Ninety percent corresponded to stage VB on the scale of Strubberg. From this it might be inferred that development of pigment is a consequence of entry into fresh-water. That this is not so for the European eel was demonstrated by Strubberg (1913:7) who found that pigmentation developed at the same rate in eels kept in salt or fresh-water. Conversely, Vilter (1944) found some evidence for the retardation of pigment development by an increase in salinity. He considered the influence of the external environment expressed itself through the endocrine system and the stage of pigmentation was not always a good index of physiological change. The comments by Bertin (1956:145) adequately summarise the above. "The two metamorphoses that the eel undergoes are dependent upon internal secretions. The external factors can only retard or accelerate the phenomenon".

To observe the sequence of pigmentation under varying conditions, three experiments were conducted on both long and shortfinned glass-eels. All trials began with fresh glass-eels at stage VB. These were caught a day prior to the experiments and either retained in salt-water or acclimatised over a day, to fresh-water.

Salinity: Ten longfins and ten shortfins were placed in a tank of salt-water. Similar numbers were placed in fresh-water. The tanks, painted black, were aerated and the eels fed three times a week with white worms. At weekly intervals, the length, mean weight and stage of pigmentation was recorded for all eels. Temperatures over the five weeks of observations ranged from 11.4°-14.2°C. The results are given in Fig. 3.6.a expressed as the percentage number of eels per pigmentation sub-stage. The histograms

Table 3.2 Abbreviated scale of Strubberg (1913) for successive stages in pigment development in glass-eels.

Stage	Pigmentation
VB	Cerebral and nerve cord pigmentation.
VIA I	Pigment developed along dorsal ridge. No mediolateral pigmentation.
VIA II	Development of mediolateral pigment post-anally. Some doubling of dorsolateral pigment on myosepta and intermyoseptal pigment developing.
VIA III	Mediolateral pigmentation extends pre-anally to the pectoral fins. Increased doubling of dorsal and mediolateral myoseptal series.
VIA IV	Development of ventrolateral pigment pre-anally with associated development of intermyoseptal pigment.
VIB	Myoseptal arrangement of pigment, both dorsally and ventrally, begins to be indistinct. Pigment developing on cheek, behind and below the eye and on pectoral fins.

show that salinity had little retarding effect on the rate of pigmentation; at the end of five weeks, both tanks were almost comparable, with eels in fresh-water showing slightly more pigment development. However, in both tanks, pigment development was more rapid in longfins than in shortfins.

Temperature: While carrying out temperature tolerance experiments, the rate of pigmentation of four eels of both species at 10° and 27°C was recorded. Unfortunately, the longfins at the higher temperature all died after one week. The results (Fig. 3.6.b) show the marked retarding effect the low temperature had on both species, while the high temperature accelerated pigment development. In this experiment, only limited cover was available for the eels, and it was thought this factor may also be important in the spread of pigment. To investigate this, a third experiment was carried out. Unfortunately only a limited number of longfins were available for this trial.

Background: Ten shortfins and three longfins were placed in a clear perspex tank with a white bottom. An equal number were placed in a black tank. Pieces of stone pipe provided cover from direct light. White worms were fed and weekly measurements of the eels taken. Temperatures recorded ranged from 12.4°-14.9°C. The results are illustrated in Fig.3.6.c and show the pronounced effect of background colouration on the development of pigmentation. The darker the background, the more rapid the rate of pigmentation to adapt to it.

The above experiments indicate that environmental factors can have a considerable effect on the rate at which pigmentation proceeds. However, as pigmentation develops almost as rapidly in salt-water as in fresh-water, the process can be considered to be initiated at larval metamorphosis. The samples of New Zealand glass-eels examined indicate stage VB to be that at which invasion into fresh-water takes place throughout the country. If post-metamorphic sea-life is extended, for whatever reason, the invading glass-eels will have commenced some superficial pigmentation. The limitations of using the scale of Strubberg as an indication of freshwater life, are discussed later.

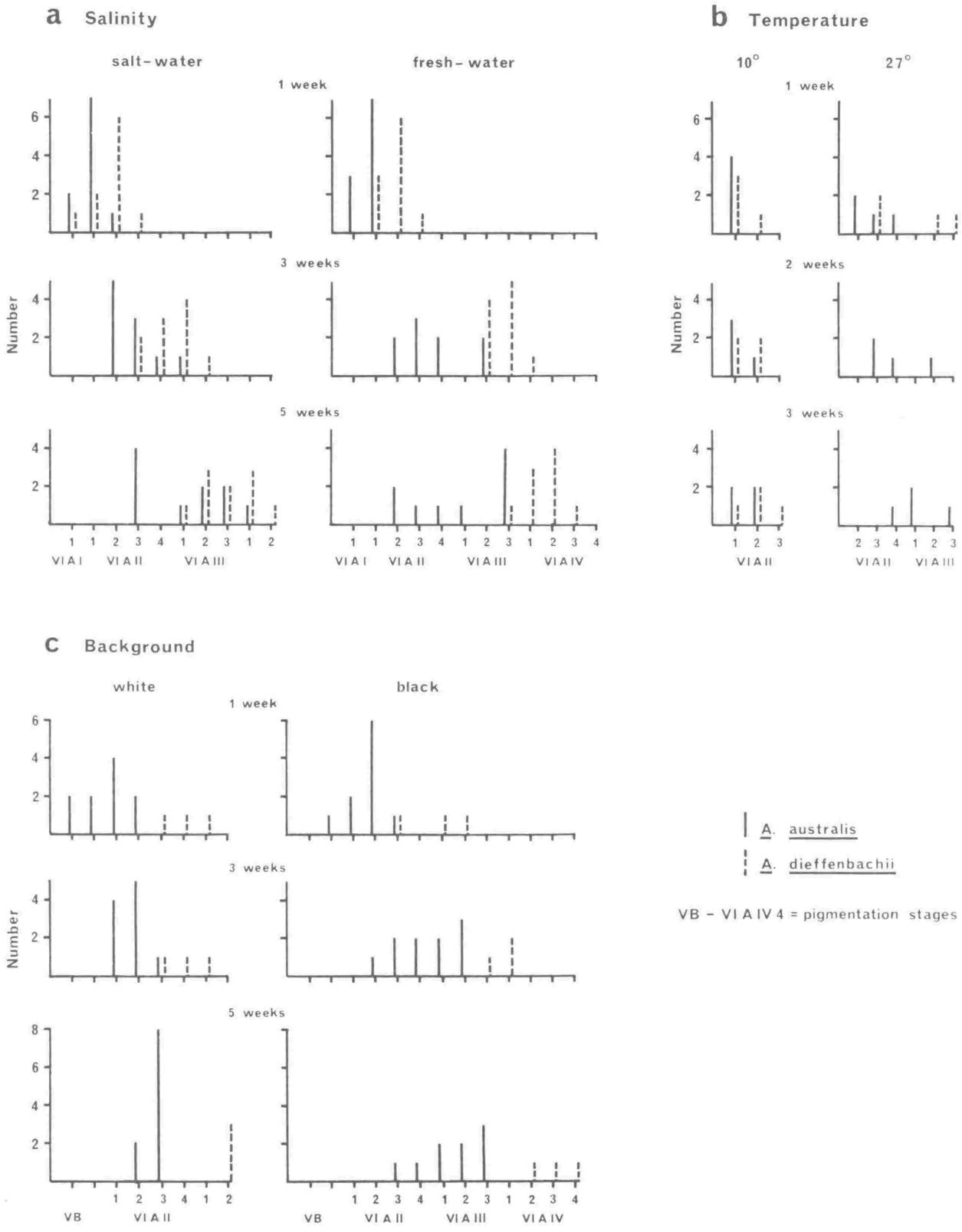
Fig. 3.6 Effects of environment on the rate of pigment development of glass-eels.

a Salinity

b Temperature

c Background colouration

All eels were at stage VB at the start of the trials.


a Salinity
salt-water
fresh-water
1 week
3 weeks
5 weeks
Number
VI A I
VI A II
VI A III
VI A IV
b Temperature
10°
27°
1 week
2 weeks
3 weeks
VI A II
VI A III
c Background
white
black
1 week
3 weeks
5 weeks
VB
VI A II
VI A III
VI A IV
A. australis
A. dieffenbachii
VB – VI A IV 4 = pigmentation stages

Shrinkage

Glass-eels invading fresh-water undergo a marked shrinkage for a period of several weeks. This decrease in both length and weight can be considered as continuous with the size reduction which takes place at metamorphosis. This reduction occurs even though the eels may be actively feeding. Thus, the eels used in the pigmentation experiments, although readily feeding, decreased in length and initially in weight also, for the five weeks of observations. This shrinkage took place in both salt and fresh-water. In fresh-water, the mean length decrease was 2.3% for shortfins and 4.4% for longfins.

Because of the variable time intervals represented by different stages of pigmentation, it is difficult to correlate the commencement of growth with any particular stage. Table 3.3.a shows the mean length per pigmentation sub-stage for a typical shortfin sample (Waikato River, 11 September 1971). No trend is obvious from the size distribution. However, if the condition factor is considered, a general trend can be seen. Table 3.3.b gives the mean condition factor per pigmentation sub-stage for shortfins collected during the month of October. The VB value is taken from Makara samples, while the other values were obtained from various live samples to give a wide coverage of stages. Condition, K, was calculated from $K = \frac{W \times 1000}{L^3}$ where W = weight in grams and L = length in cm. Insufficient data were available for longfins, and no comparable table can be given.

Table 3.3.b shows a decline in condition occurs until the onset of stage VIA III. The increase at this stage is indicative of the commencement of growth, and is attributable to increase in weight rather than a continued decrease in length, as most samples showed a slight increase in mean length during late VIA III. Similarly, Heldt and Heldt (1929:30, 36) found the reduction in length and weight of glass-eels from the Lake of Tunis to continue into stage VIA III. Hornyold (1927:108) commented that after this size reduction the pigmented eels "Qu'elles n'ont que la peau et les os" and are inedible.

To investigate the shrinkage in length further, proportional measurements were made of shortfin glass-eels and elvers. Twenty eels from each pigmentation stage were measured, using a micrometer eyepiece to calculate head length, and an accurate rule under low magnification for all

Table 3.3 a Mean length per pigmentation sub-stage of live glass-eels of A. australis collected 11 September 1971, Waikato River.

b Mean condition factor, K, per pigmentation sub-stage live glass-eels of A. australis collected during October.

a

Stage	VIA II				VIA III			VIA IV	
Sub-stage	1	2	3	4	1	2	3	1	2
Mean length (cm)	5.86	5.92	5.97	5.98	6.02	5.87	6.03	5.95	6.40
n	7	77	64	32	18	18	4	4	1

Grand mean length = 5.97 cm

N = 225

b

Stage	VB	VIA I	VIA II				VIA III			VIA IV				VIB
Sub-stage			1	2	3	4	1	2	3	1	2	3	4	
Mean condition	0.76	-	0.73	0.75	0.70	0.72	0.88	0.95	0.88	0.90	1.02	1.02	-	1.38
n	452	-	2	10	21	8	11	6	18	12	8	2	-	13

other measurements.

Measurements taken were:

Head Length (H.L.) : tip of lower jaw to branchial opening
Total Length (T.L.) : tip of lower jaw to tip of caudal fin
Pre-anal Length (PRE.A.) : branchial opening to anus
Post-anal Length (POST.A.) : anus to tip of caudal fin
Body Length (B.L.) : branchial opening to tip of caudal fin

The average measurements, expressed as percentages of the body length or total length, are given in Table 3.4.

That shrinkage is not uniform over the total length is shown by increasing proportional length of the head in pigmented eels. The actual mean head lengths for stages VB and VI A II, were 0.66 cm and 0.67 cm respectively, with body lengths of 5.40 cm and 5.19 cm. Thus, it is not a change in head length but a decrease in body length, which causes shrinkage. Similarly, measurements of A. australis schmidtii larvae given by Castle (1963:9) show that although head length increases with growth of the larvae, it does so in a decreasing proportion to growth in total length. Consequently, the major changes in body proportions which occur during larval growth are due to rapid growth in the body.

During stage VI A III, the glass-eels attain the body proportions of the elver, and from this stage on it is assumed that growth is isometric. No differences in body proportions were found in elvers examined, which covered a range in length of 5 cm.

To further localise the region of shrinkage, the body measurements excluding head length, were examined. These mean pre-anal and post-anal measurements, expressed as a percentage of body length, are also given in Table 3.4. The values show that during the stages of maximum shrinkage (VB - VI A II), the reduction in length is uniform in both pre-anal and post-anal regions. However, from stage VIA III onwards, the pre-anal region occupies a proportionally increased length.

Proportional shrinkage in both pre-anal and post-anal areas is consistent with the explanation of Ahlstrom and Counts (1958) for shrinkage observed during metamorphosis of Vinciguerria lucetia (Garman) (F. Gonostomatidae). These authors considered that shrinkage was due to compression of the unossified spaces between the centra of the vertebral column.

The change in the relative pre-anal length is considered due to onset of growth which takes place during stage VI A III. Subsequent to

Table 3.4 Proportional body measurements of glass-eels and elvers of *A. australis*

H.L. = Head Length

T.L. = Total Length

PRE.A. = Pre-anal Length

POST.A. = Post-anal Length

B.L. = Body Length

Stage	n	$\bar{l}$(cm)	H.L./T.L.	PRE.A./T.L.	POST.A./T.L.	PRE.A./B.L.	POST.A./B.L.
VB	20	6.1	10.9	27.1	62.0	30.5	69.5
VIA II	20	5.9	11.5	26.7	61.8	30.2	69.8
VIA III	20	6.6	12.3	27.3	60.4	31.1	68.9
VIA IV	20	7.3	12.7	27.5	59.8	31.5	68.5
Elvers	41	7.0-12.0	12.5	27.4	60.1	31.3	68.7

this, there has been an anterior migration of the anus during metamorphosis (Ford 1931:994) and a folding of the gut to form a looped alimentary canal. Once the eel is established in fresh-water, the role of the gut assumes more importance, as the eel enters a period of active growth, culminating in its catadromous migration.

In glass-eels at stage VB, the gut is relatively simple, being comprised of a small anterior loop, and a descending straight tube leading to the anus. During early development, the loop extends posteriorly to form the descending and ascending limbs of the stomach. The degree of stomach development in glass-eels was investigated to find whether any relationship existed between this and rate of pigment development. The extent of stomach development was determined by expressing the length of the ascending limb (A.L.) as a ratio of the length of the gut in situ (G.L.).

Measurements of early stage glass-eels (VB - VI A II 1) were made from preserved material. However, during observations on pigment development, it was possible to measure stomach development in anaesthetised eels. These eels had been fed white worms the day prior to measuring, and the full stomachs enabled the extent of development to be easily seen and measured. Although the stomach is a rather elastic organ, any distension appears to be in width and not length. As no differences were apparent in results from those eels kept in salt-water and those from fresh-water, these data were pooled, and the results plotted in Fig. 3.7.

The regression equations are:

shortfins	$Y = 4.7231(X) + 23.5029$	$r = 0.8923$	$(n = 58)$
longfins	$Y = 5.4487(X) + 17.1248$	$r = 0.9519$	$(n = 33)$

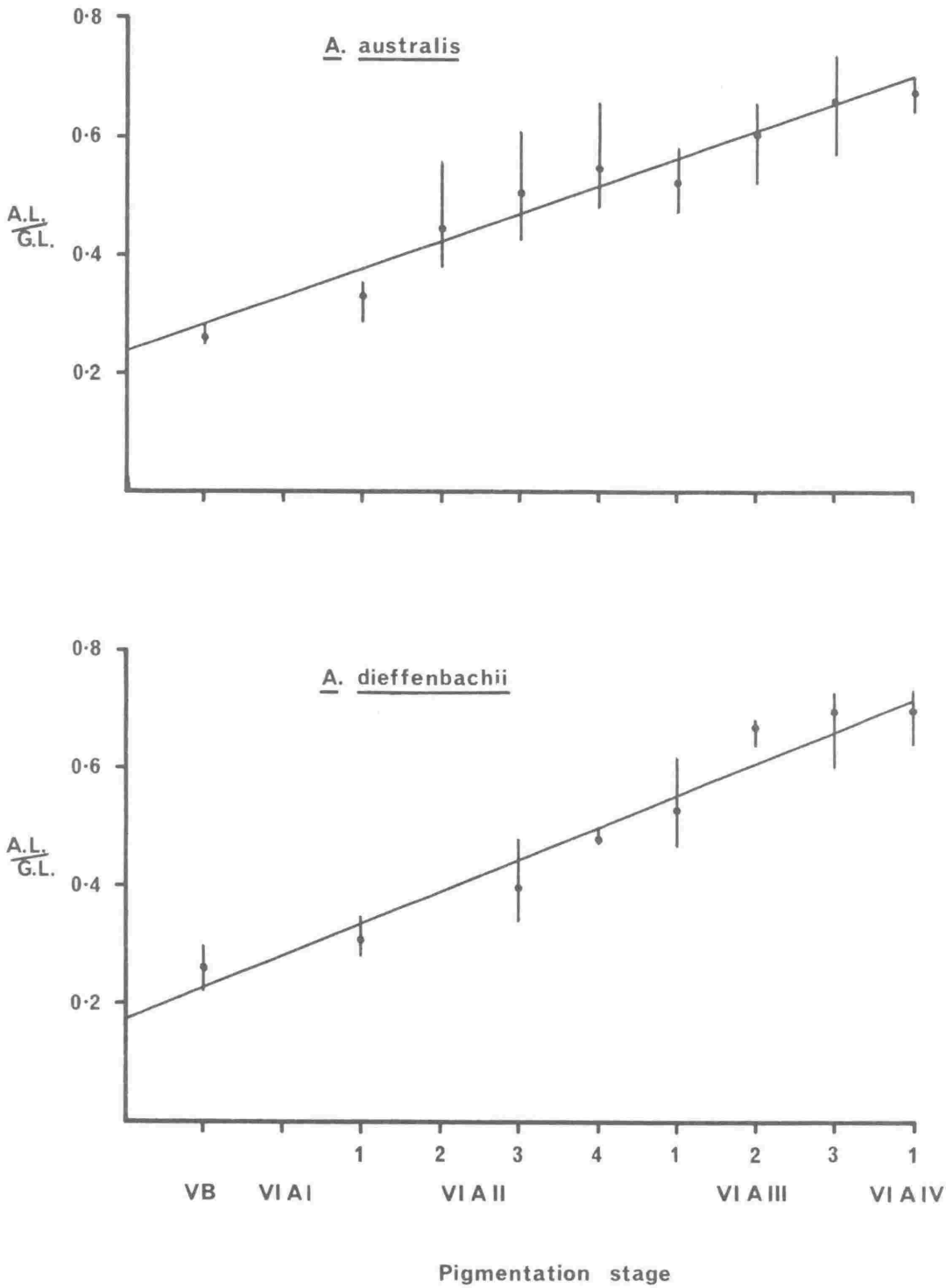
Both correlation coefficients are highly significant at the 1% level. This high degree of correlation between stomach development and stage of pigmentation also confirms the scale of Strubberg as a valid index of sequences in pigmentation development, and indicates that mean time intervals between successive stages are approximately equivalent. However, from consideration of the stage of pigmentation alone, it is not possible to make definitive statements on the length of time particular glass-eels have spent in fresh-water. As the rate of pigment development is subject to certain environmental influences and the length of post-metamorphic life, such calculations are, at best, fair estimates.

Fig. 3.7 Extent of stomach development in glass-eels at various stages of pigmentation.

A.L. = length of ascending limb of stomach

G.L. = length of gut *in situ*

Solid circles indicate the sample means and the vertical lines the ranges.


A. australis
A. dieffenbachii
A.L./G.L.
0·8
0·6
0·4
0·2
1
2
3
4
1
2
3
1
VB
VI A I
VI A II
VI A III
VI A IV
Pigmentation stage

It is suggested that the development of pigment, together with associated processes of shrinkage, stomach development and the onset of growth, take place as a result of the length of post-metamorphic life. However, as discussed in a later section, behavioural changes in response to light seem to be related directly to the development of pigmentation.

3.4 INVASION OF FRESH-WATER II. PERIODICITY AND BEHAVIOUR

Seasonal Arrival Pattern

The annual invasion of New Zealand freshwater systems by glass-eels, takes place during winter and spring. Ege (1939: 144,212) gives August to January as the months for the invasion of both species, while Cairns (1941:62) considers October to December to constitute the main invasion period. Catches during 1972 at the mouth of the Makara Stream, indicate an invasion period for this locality of July to December, but within this period different species patterns occur.

Table 3.5 gives the monthly results of glass-eel fishing at Makara for 1971 and 1972. Unfortunately it was not possible to commence fishing during 1971, until September, by which time a substantial part of the invasion had probably taken place. However, in 1972, a total of seven months was fished, with catches being recorded in six of these months. The 1972 catch is further shown in Fig. 3.8.a and b. Fig. 3.8.a shows that shortfins arrive at Makara over a period of six months, with September and October being the peak months. During 1972 these two months accounted for 72% of the total shortfin catch. The comparable value for 1971 was 69%. The longfin invasion takes place over a shorter period, from July to September, with peak months being August and September. In 1972, 79% of the total longfin catch came from these two months.

The total 1972 catch for both species combined, indicates that September is the major month of invasion, providing 37% of the seasonal total. This is followed by October (31%) then August and November with 15% and 13% respectively. Similarly the catch per fishing effort for the 1971 and 1972 seasons (Table 3.6) shows September to be the most productive month. Over the main part of the 1972 season, fishing was carried out on three nights each week to maintain a regular and constant effort. However, the effort was relaxed early and late in the season due to scarcity of glass-eels, as reflected in the low catch per effort figures.

Although the numbers of glass-eels caught at Makara were not large, they are considered to provide a good index of the relative arrival patterns of both species, for several reasons. Firstly, all sampling was carried out at the mouth of the stream and this eliminated the possibility of eels finding a suitable habitat once in fresh-water and so discontinuing

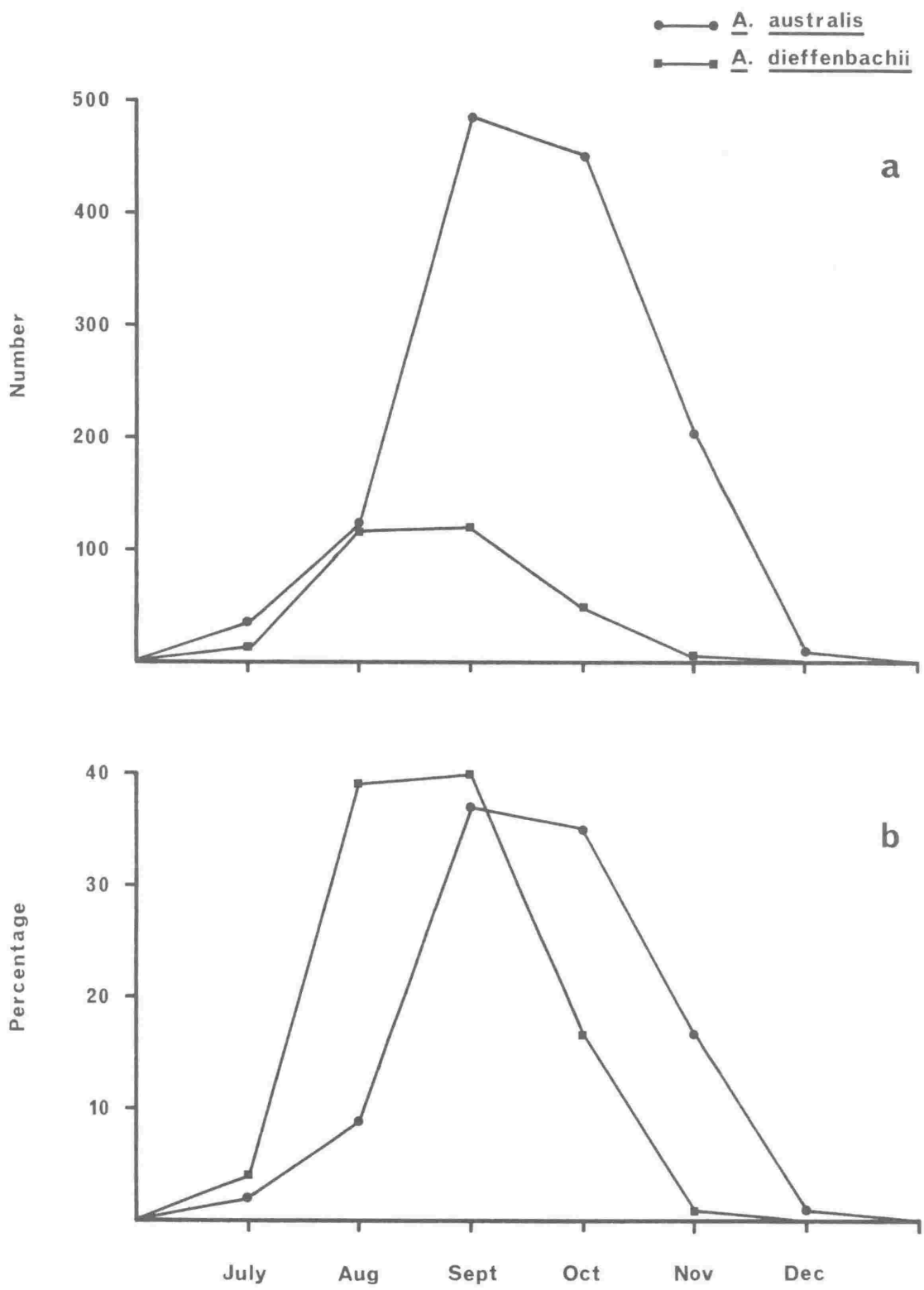
Table 3.5 Monthly glass-eel catches from Makara Stream for 1971 and 1972.

	1971				1972			
	A. australis		A. dieffenbachii		A. australis		A. dieffenbachii	
	n	%/month	n	%/month	n	%/month	n	%/month
July					31	74	11	26
Aug.					124	51	119	49
Sept.	293	94	20	6	482	80	120	20
Oct.	215	94	14	6	452	90	50	10
Nov.	225	99	1	1	205	98	4	2
Dec.	5	100	-	-	9	100	-	-
N	738		35		1303		304	
Species proportions (%)		96		4		81		19

Fig. 3.8. Makara Stream glass-eel catch, 1972.

a The number of the total catch per month for both species.

b The percentage of the total catch per month for both species.


A. australis
A. dieffenbachii
500
400
300
200
100
Number
a
40
30
20
10
Percentage
b
July
Aug
Sept
Oct
Nov
Dec

	1971			1972		
	Fishing nights	Fishing hours	Catch/ hour	Fishing nights	Fishing hours	Catch/ hour
June				2	4.00	-
July				7	20.75	2.0
Aug.				11	33.50	7.3
Sept.	7	17.50	17.9	11	35.00	17.2
Oct.	10	29.25	7.8	12	30.00	16.7
Nov.	8	24.25	9.3	8	19.25	10.9
Dec.	1	3.00	1.7	2	3.25	2.8
	26	74.00		53	145.75	
Mean catch/hour			10.4			11.0

their inland migration. Secondly, the Makara Stream supports a large population of both species. Further, the Wellington area is located "mid-way" along the north-south extent of the country; analysis of glass-eel samples from throughout the country indicates some differences in species distribution from north to south.

Provided that 1972 was a typical year, the Makara catches indicate that the majority of longfin glass-eels arrive somewhat earlier than do shortfin glass-eels.

Various glass-eel samples were obtained from the Waikato River over a period of three years. All samples came from the "Elbow" near Pukekohe (see Fig. 2.1.a) and cover a period of four months. These samples are presented chronologically in Table 3.7. Unlike the Makara data, the Waikato samples show no definite species patterns of invasion. However, the "Elbow" fishing site is located 18 km upstream from the sea, and most eels in the samples were well-pigmented, indicating a possible residency in fresh-water of approximately two weeks. As the downstream area offers varied habitats, many glass-eels may choose to remain there, rather than continue their migration. Data presented later indicate that of the two species, the shortfin glass-eel is more likely to remain in such lower reaches than the longfin. Furthermore, there is no reason to suspect that either species shows behavioural differences resulting in a bias by the sampling method of set-nets. It does not seem that the relatively small catches of longfin glass-eels are due to either the catching method or the locality of the sampling site.

From the above it is concluded that a much higher proportion of shortfin glass-eels invades the Waikato River than do longfins, but the samples do not indicate any seasonal trend in the proportions of both species.

Factors Influencing Freshwater Invasion

Glass-eels of both species caught immediately upon entering fresh-water from the sea, are typically at Stage VB of the scale of Strubberg. The stages of pigmentation for all glass-eels caught at the mouth of the Makara Stream during 1971 and 1972 are given in Table 3.8. For simplification, both species have been combined for each year. In October and November 1972, two large catches were not completely analysed, resulting in the difference shown in the total catch for 1972 between this table and Table 3.5.

Table 3.7 Glass-eel samples from the Waikato River, 1970-1972 .

	A. australis		A. dieffenbachii	
Sample date	n	%/sample	n	%/sample
13/8/72	89	100	-	-
24/8/70	300	98	7	2
11/9/71	606	99	1	1
11/9/72	501	98	8	2
21/9/72	97	91	10	9
28/9/72	503	99	2	1
9/10/71	305	95	16	5
3/11/71	320	98	5	2
6/11/70	187	90	20	10
N	2908		69	
Species proportions (%)		98		2

Table 3.8 Pigmentation stages of invading glass-eels from the Makara Stream for 1971 and 1972. Both species combined.

Figures in %/ stage/ month.

	1971					1972				
	VB	VIA I	VIA II	VIA III	n	VB	VIA I	VIA II	VIA III	n
July						100				42
Aug.						94	3	3		243
Sept.	98	1	1		313	94	3	3		602
Oct.	92	3	4	1	229	80	6	13	1	436
Nov.	77	10	13		226	87	5	6	2	215
Dec.	40	40	20		5	56	22	22		9
					773					1547
(Mean)	90	4	5	1		89	4	6	1	

Table 3.8 shows that approximately 90% of all glass-eels caught were at Stage VB. Also, the percentage of individuals at Stage VB decreases significantly throughout the season. This latter observation is discussed in a later section.

Before considering the catch data from Makara further, it is necessary to gain an understanding of the behaviour of glass-eels at sea immediately prior to their freshwater invasion. The following is a review of significant contributions in this field.

Vertical movements of migrating glass-eels have long been known. Johansen (1905: 2) discovered that newly metamorphosed glass-eels at sea exhibited a diurnal rhythm. At night they were pelagic and could be caught close to the surface, while during the day they were found on the bottom. More recently, Deelder (1952: 197-198) confirmed this and commented on the possible transport of glass-eels by tidal streams. After studying catches by tide phases, he concluded that the direction of tidal streams had no direct effect on glass-eel migration in the vicinity of fresh-water outlets.

Creutzberg (1958: 857) investigating glass-eel movements further offshore, in the Dutch Wadden Sea, found evidence for inshore movement on the flood tide and a burying or swimming close to the bottom during the ebb tide. He suggested that discrimination of the tide phases was due to salinity changes during the tidal cycle. However, after further experiments (Creutzberg 1961: 309), he concluded that this discrimination was not due to the perception of salinity changes but to olfactory stimuli. He proposed that the increased odour of inland water which occurred with the ebb tide caused the glass-eels to stay near the bottom, but with the consequent decrease in inland water odour during the flood tide, the glass-eels rose to higher water levels and were transported by the tidal stream. In a series of well-conducted laboratory experiments, he was able to confirm this.

These apparent contradictions in observations of the tidal transport of glass-eels were resolved by consideration of changes in behaviour of the eels. Deelder (1958: 136) found differences in vertical movements, schooling tendencies, and reactions to fresh-water and light between glass-eels collected well off-shore and those about to invade fresh-water. From observations at the mouth of the River Severn estuary, he assumed that newly arrived glass-eels delayed further

upstream migration until they had undergone the above behavioural changes (Deelder 1958: 145). He also postulated that a similar transitional area must exist in the Wadden Sea.

Delays between the passage of glass-eel concentrations observed in the Wadden Sea and their arrival at freshwater outlets, were recorded by Creutzberg (1961: 279). Subsequent sampling by him showed that these glass-eels had delayed their migration and had accumulated in an area of low salinity (0.5-11.0°/oo). In this transitional area they were carried to and fro by tidal streams. Although Creutzberg offered no explanation for this accumulation, it is now known that it enables the glass-eels to complete their behavioural changes before entering fresh-water.

Unfortunately neither Deelder nor Creutzberg give any indication of the stage of pigmentation of the glass-eels involved in their studies. From reference to Strubberg (1923: 17) who records the pigmentation stage of glass-eels entering Danish seas as predominantly stage VB, it is assumed Dutch glass-eels are at a similar stage. The degree of pigmentation is important, as it is suggested later in this present investigation, that certain behavioural responses are modified by increasing pigmentation.

From consideration of the above references, the glass-eel migration can now be divided into two separate stages. Firstly, the initial invasion from the sea into estuarine areas or regions of low salinity. In these transitional areas, specific behavioural changes take place. This migration is referred to in the text as the 'freshwater invasion' or 'invasion'. Secondly, a further inland penetration of freshwater systems with the assumption of the mode of life characteristic of adolescent eels. Hereafter, this movement is termed the 'freshwater migration'. Unfortunately, most authors have treated the appearance of glass-eels in fresh-water as a single phenomenon, and this leads to some confusion in discussing the migratory taxes shown by glass-eels.

The Makara glass-eel catches, typifying the phenomenon of freshwater invasion, are now examined to determine whether the periodicity of invasion is correlated with any environmental factors. Unfortunately it was not possible to distinguish between the two species in the field, and the following analyses are for both species combined.

The catches from Makara for the 1971 and 1972 seasons are shown in Figs 3.9 and 3.10 together with rainfall data and phases of the moon.

a. Water Temperature

Water temperature is a factor which could affect both the commencement of the season and the intensity of invasion. Early in the season, during winter, sea temperatures exceed freshwater temperatures, and the magnitude of this gradient could be significant to invasion. This gradient would be accentuated in swift rivers with little estuarine area, as transitional temperatures normally occur in this region.

During the 1972 season, sea temperatures at Makara were recorded adjacent to the shore, in 0.5 m of water, beyond the influence of the stream outflow. Estuarine temperatures, also taken in water 0.5 m deep, were recorded from an area 100 m upstream from the stream mouth, to ensure the readings were not influenced directly by flood tides. Temperatures in the stream itself were recorded from sampling site 'd'. Air temperatures were also taken but not used in analysis as their effect would be expressed indirectly through water temperatures. All recordings were taken at 2200 hours with the exception of the upstream temperature (site 'd') which varied according to the time spent fishing.

As anticipated, sea temperatures early in winter exceeded those of the estuary by several degrees. For example, the mean sea temperature in July 1972 was 11.1°C while the estuarine temperature was 8.3°C.

For this present analysis and subsequent ones, significant catches are considered to be those when a minimum of 20 eels per night were captured. The first such catch for 1972 was made on 31 July. Temperature recordings on this date were, sea 11.3°C, estuary 6.4°C, resulting in a gradient of almost 5°C. This was the largest gradient recorded on any 'significant' night. Prior to this date, only 18 eels had been captured.

The mean monthly sea and estuarine temperatures over the invasion season, are given in Fig. 3.11. The vertical lines show the monthly ranges. During September, both sea and estuarine temperatures became more uniform, and by October, the mean estuarine temperature exceeded that of the sea, and continued to for the remainder of the invasion season.

Fig. 3.9 Makara Stream glass-eel catch, 1971.

Nightly catches with moon phases and rainfall.

Note: all nights fished are shown on the catch analysis, including those nights when no glass-eels were caught (indicated by 'o').

Rainfall is plotted for the complete four month period.

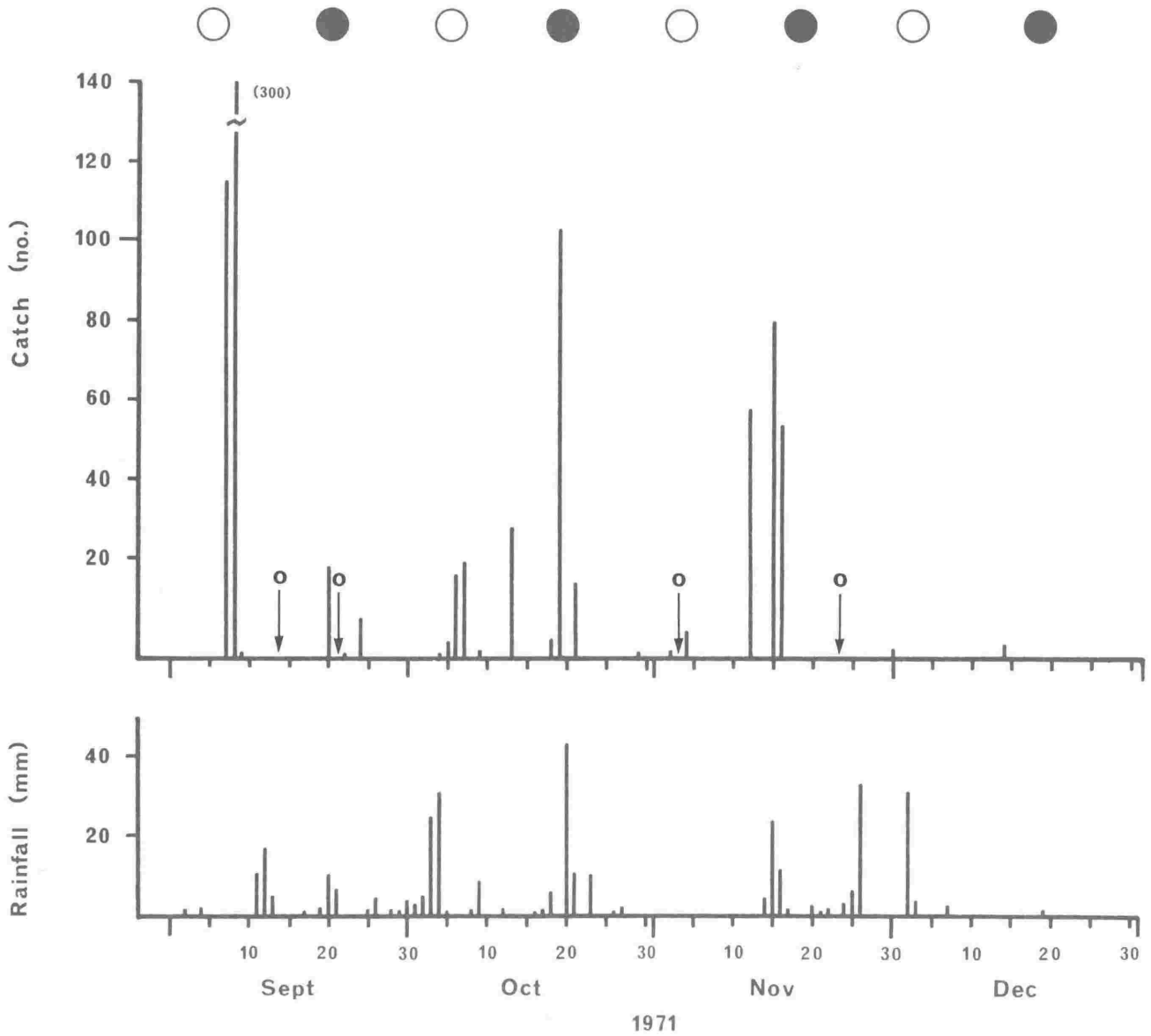

Catch (no.)
140
120
100
80
60
40
20
(300)
Rainfall (mm)
40
20
10
20
30
Sept
Oct
Nov
Dec
1971

Fig. 3.10 Makara Stream glass-eel catch, 1972.
Nightly catches with moon phases and rainfall.

Note: all nights fished are shown on the catch analysis, including those nights when no glass-eels were caught (indicated by 'o').

Rainfall is plotted for the complete six month period.

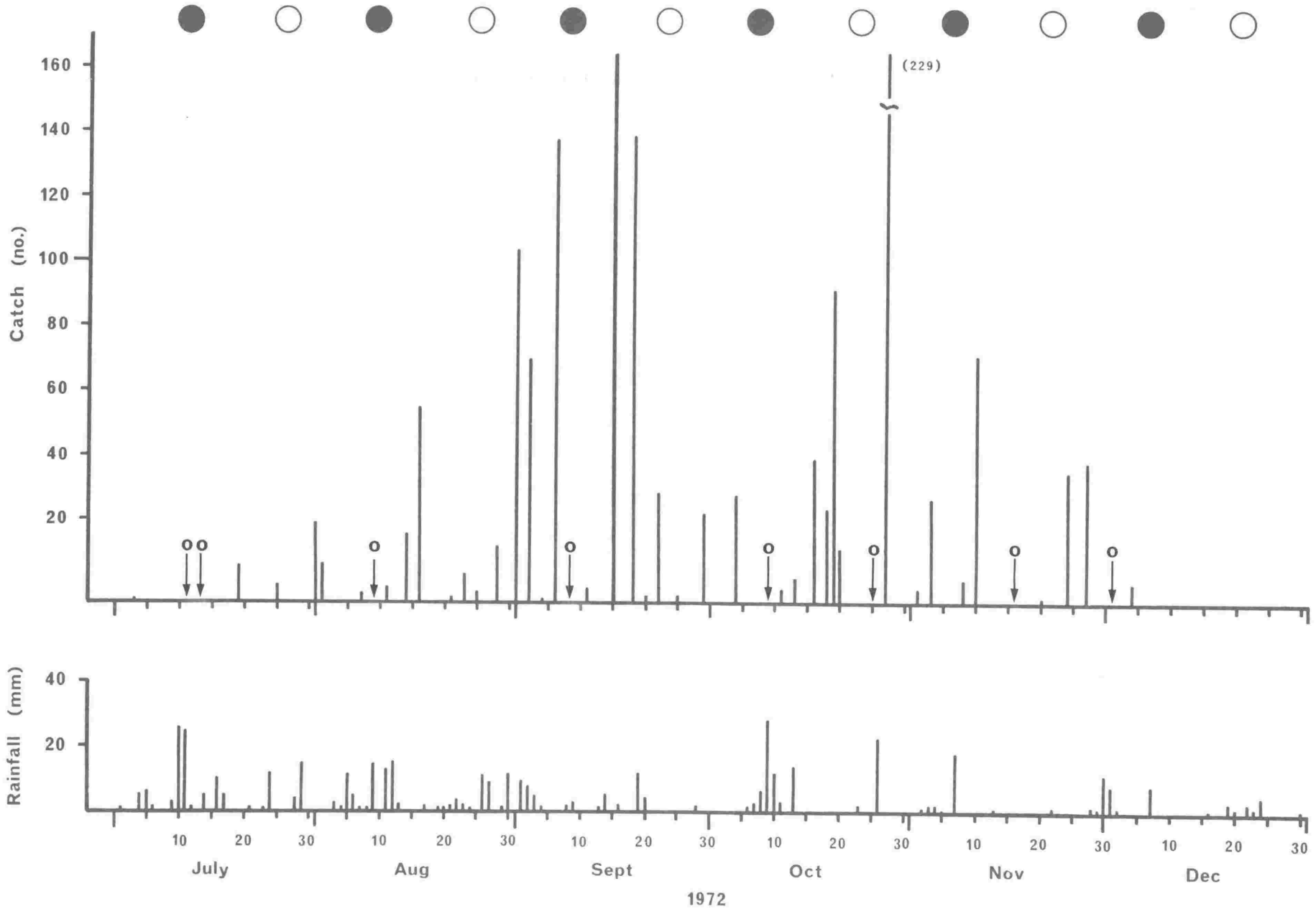
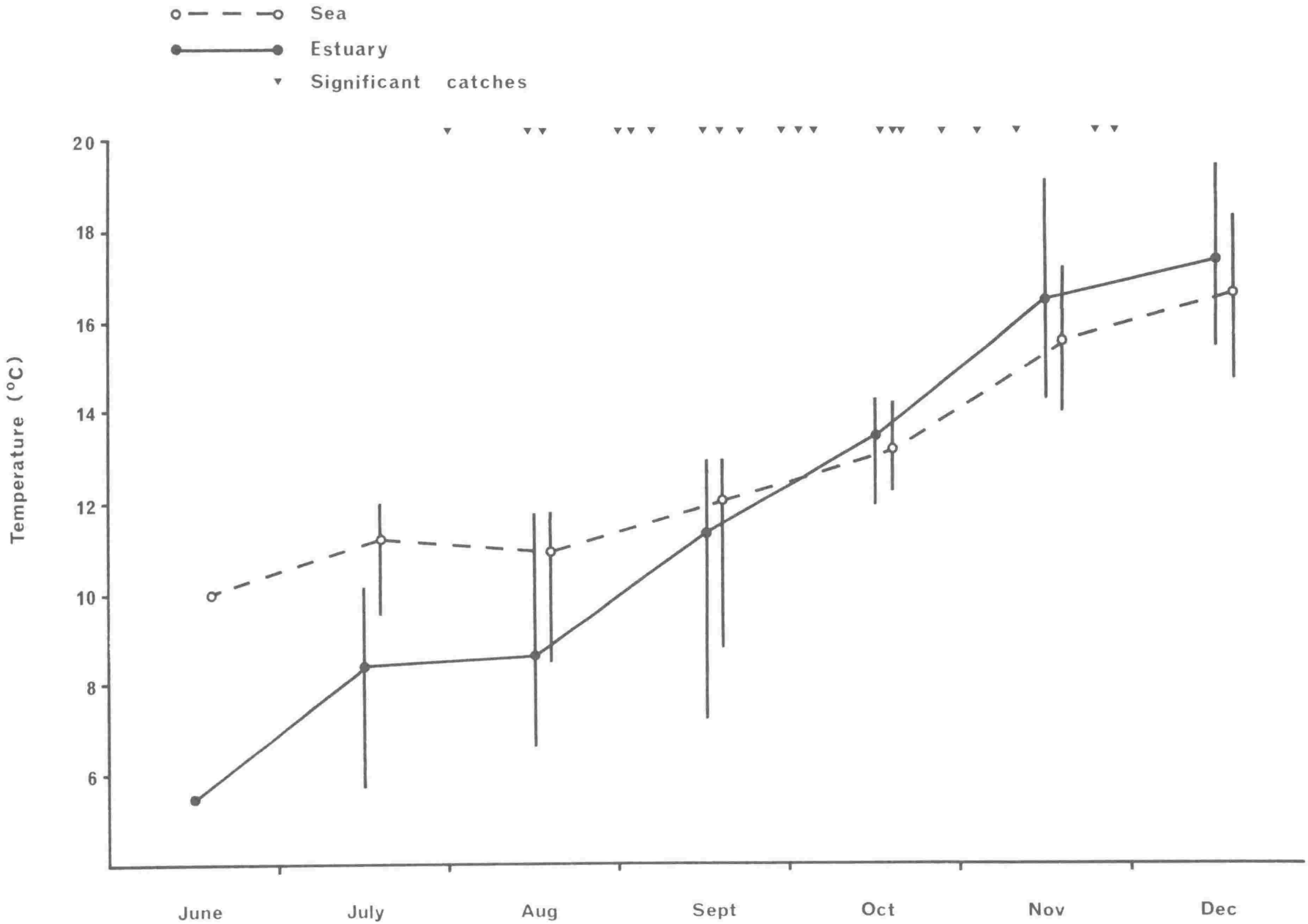

Catch (no.)
160
140
120
100
80
60
40
20
(229)
Rainfall (mm)
40
20
10
20
30
July
Aug
Sept
Oct
Nov
Dec
1972

Fig.3.11 Sea and estuarine temperatures, Makara Stream 1972.

Circles indicate the mean monthly temperatures and the vertical lines the ranges. Nights when significant catches were made are also shown.


Sea
Estuary
Significant catches
Temperature (°C)
20
18
16
14
12
10
8
6
June
July
Aug
Sept
Oct
Nov
Dec

Small numbers of glass-eels were caught on nights when low sea temperatures occurred, including 7 August when the lowest temperature for the season, 8.4°C was recorded. However, a sudden cold period in early September may have caused a temporary cessation in invasion. On 2 September (sea 12.3°C, estuary 12.2°C) 76 glass-eels were caught, but on 4 September (sea 8.8°C, estuary 7.2°C) only one was caught. By 6 September the sea temperature had risen to 12.2°C and the estuary to 11.5°C. On this date a large catch of 143 glass-eels was made. As meterological conditions were otherwise similar on these three nights, the delay in invasion seems to have been caused by the drop in temperature.

Although invading glass-eels were not deterred by an apparent temperature gradient of up to 5°C, it should be noted that such early season invasions were almost completely on flood tides. The actual temperature gradient experienced by glass-eels invading on a flood tide into the estuarine area, would be somewhat less than that encountered by invading against an ebb tide.

The highest recordings during the invasion season were from 20 November when the sea temperature was 17.2°C and the estuary 19.1°C. It is not thought that high temperature is a significant factor in ending the invasion, as temperatures in the vicinity of these increase the activity of glass-eels. Day (1941: 2) records largest movements of glass-eels of A. rostrata, take place between 20° -25°C.

The significance of water temperature as an important factor in the invasion and migration of glass-eels has been recorded by several authors. Menzies (1936: 255) found that a sudden cold period delayed the glass-eel 'run' in the River Bann, Northern Ireland. However, analyses of further large catches in this river by Lowe (1951: 311) showed no evidence of this, nor could the intensity of the migration be correlated directly with temperature. Similarly, no evidence was found for a temperature threshold for the onset of migration. Unfortunately, the only temperature records available to Lowe were air temperatures and these seldom accurately reflect water temperatures.

The existence of a threshold temperature for glass-eels below which migratory movements are inhibited, has been proposed by several workers. Sorensen (1951: 126) and Meyer and Kühl (1953: 89) give values of 15°C and 10°C respectively as the threshold for glass-eels of A. anguilla, while Matsui (1952: 232) found a value 8°C for A. japonica.

Similarly, Deelder (1952: 193, 1960a: 4) found that water temperature was a significant factor in starting or delaying migrations in European glass-eels. Once the migration had begun, temperatures above a critical value (4.5°C for glass-eels at sea) were not important. Also, the end of the invasion season was determined by the absence of glass-eels rather than by increased temperature.

Finally the results of Hiyama (1952) for thermotaxis in invading glass-eels of A. japonica can be discussed. From experimental evidence he concluded that invading glass-eels show a behavioural change during the season. Early in the season when sea temperatures are higher than river temperatures, the glass-eels move into the cooler fresh-water. When these temperatures are equal they tend to stay in sea-water, but when river temperatures exceed those of the sea the eels move into the warmer fresh-water. While the proposed seasonal change in the response of the glass-eels to temperature is of interest, it is not clear why the largest actual invasions recorded by Hiyama took place when the temperatures of the river and sea were equal.

b. Light

Despite several hours of fishing at the stream mouth during daylight hours at intervals throughout the invasion season, no early stage glass-eels (VB - VIAI) were caught. Discussions were held with local whitebait fishermen who fished the mouth of the stream regularly, using fine-meshed set nets. This non-commercial fishery is based on the freshwater migration of juveniles of Galaxias spp. but, by regulation, operates only during daylight hours from August to November inclusive. These discussions revealed that such unpigmented glass-eels were seldom captured, although it was not uncommon to find a few 'darker' stages with whitebait catches, especially later in the season.

No glass-eels were ever caught at the mouth of Makara Stream until after dark. Further evidence of the strong negative phototrophic reaction of unpigmented glass-eels could be observed by placing a few specimens in an aquarium during daylight. Such specimens immediately sought cover and remained hidden. Increased activity could be observed at night when most would be actively swimming and attempting to climb the aquarium sides. In contrast, later stage glass-eels (e.g. VIAII - VIB) showed

noticeably more activity during the day. Deelder (1952: 197) also records the avoidance of daylight by invading glass-eels.

Although such invading glass-eels avoid daylight and a strong torch beam, it was possible to catch small numbers by using a weak carbide lamp at night. In the lower estuary, with the lamp suspended on a stake 0.5 m above the surface of the water, glass-eels swam around the periphery of the beam and could be caught with a hand-net. On no occasion did the eels remain stationary in the light beam. Although this weak light had some attraction for the eels, catches were always substantially less than those made by the set-net. On nights when the lamp was used, the proportions of both species caught were similar to the larger catch made by the set-net.

Glass-eel fishermen on the River Severn, England, use a candle or faint kerosene lamp to attract newly arrived glass-eels (Deelder 1958: 136). At this stage the eels avoid a strong light beam. Deelder considers the speed of their avoidance reaction to be indicative of the behavioural change they undergo in response to light, prior to their freshwater migration.

Before continuing the discussion of the Makara glass-eel catches in relation to light and time of day, a further aspect of behaviour should be noted. This is that no schooling tendency was observed in invading glass-eels. This again contrasts with the behaviour of pigmented specimens.

Glass-eels were seen to arrive in the mouth of the stream individually, swimming at or near the surface. Any small aggregations which did occur could be explained by water flow. As the width of the stream mouth is narrow, it was not possible to tell whether the eels were endeavouring to keep close to the banks. During swift ebb tides late in season, all eels were captured very close to the bank. They were often seen slowly threading their way through the rocks and gravel of the stream margin. This behaviour was obviously enforced by the rapid outflow.

Similar observations were made by Deelder (1958: 136) who found glass-eels at this stage swam individually and were distributed throughout the water column with no obvious congregations. Creutzberg (1961: 290)

observed that glass-eel density in the open sea was relatively low in comparison to that of coastal waters.

As no schooling behaviour is shown by invading glass-eels, the time of their entry into fresh-water on any particular night can be regarded as a matter of individual 'choice'. Therefore, although the Makara catches were comparatively small they can be expected to show any preferred time of invasion per night, as the eels respond individually to migratory stimuli.

To investigate the nightly activity of the glass-eels, the significant catches for 1972 were expressed as the number of eels caught per hour. The catches per hour for each month were summed and expressed as a percentage of the monthly total. Although the intensity of invasion is known to be affected by the state of the tide and the rate of stream flow, a nocturnal pattern of invasion was established. Fig. 3.12 shows the nightly activity for August-November, and also the mean nightly activity of all significant catches. The curves were fitted by eye.

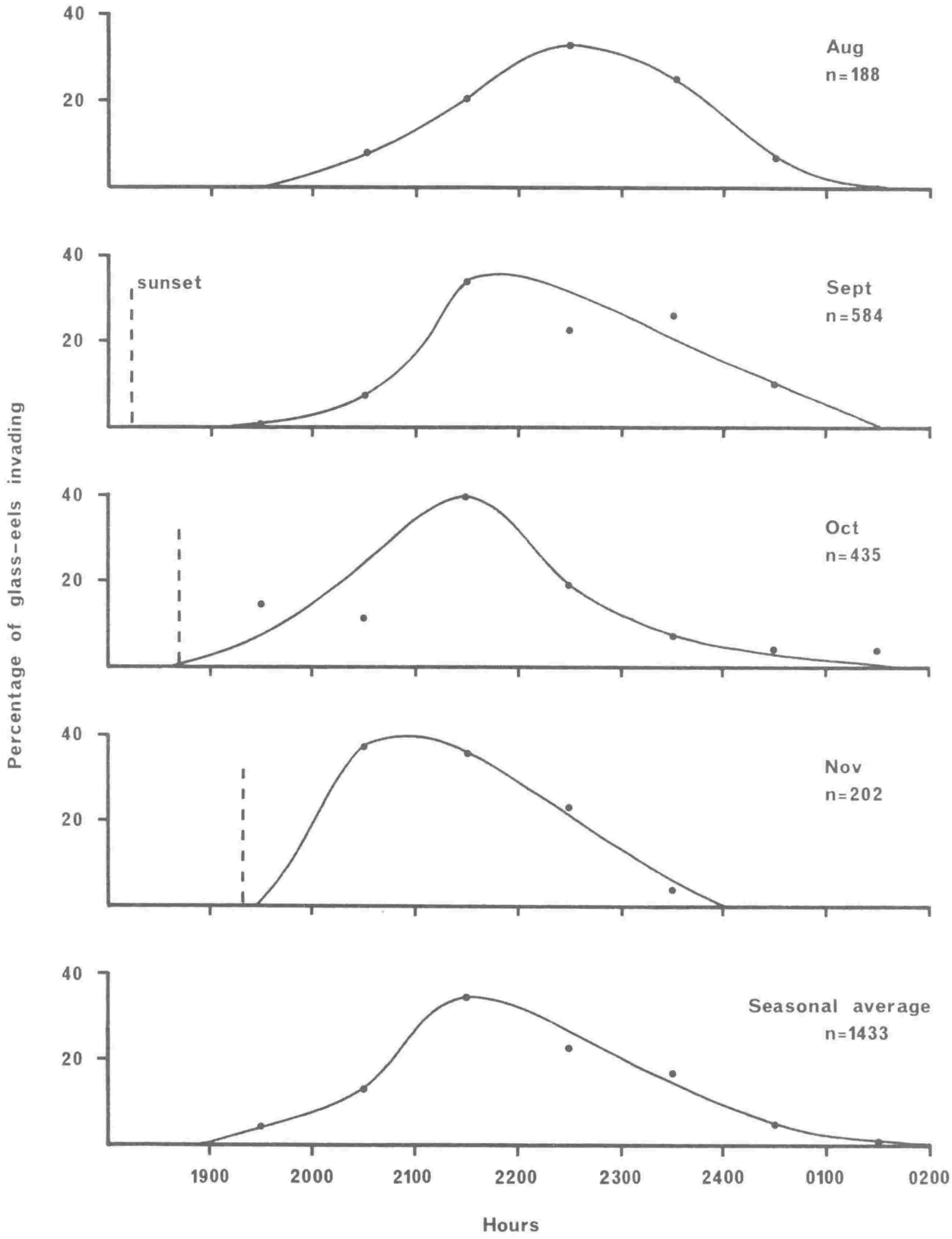
Invasion commences after sunset. No catches were made until after sunset, but during late October and in November, small numbers were taken during the twilight period. Moonlight appeared to have no inhibitory effect as several significant catches were made on nights when there was a bright moon overhead. The mean nightly activity graph shows that activity quickly builds to a peak between 2100 and 2200 hours. From this maximum, it gradually tapers off, to finish by 0200 hours, with only 7% of the invasion taking place after midnight. These latter figures do not represent a decreased fishing effort, as fishing was always continued until a 'run' had finished.

A seasonal advance in the intensity of invasion is seen by the changing skew of the monthly graphs. This advance occurs in spite of lengthening daylight. If sunset is considered as an index of darkness, it is found that this advances from 1744 hours in mid-August to 1920 hours in mid-November. However, the times of invasion commencement and peak activity do not show a corresponding staggering with decreasing darkness.

A similar advance in activity of invading glass-eels later in season was found by Deelder (1952: 198). He attributed this to increased

Fig. 3.12 Average nightly invasion periodicity of glass-eels for Makara Stream, August-November 1972.

Curves were fitted by eye.


40
20
Aug
n=188
sunset
Sept
n=584
Oct
n=435
Nov
n=202
Seasonal average
n=1433
Percentage of glass-eels invading
1900
2000
2100
2200
2300
2400
0100
0200
Hours

water temperature with consequent quicker reaction to oncoming darkness. From consideration of the Makara data it is equally possible that this advance represents an increasing tolerance to light by invading glass-eels late in the season. Although these eels still prefer to negotiate the shallow water at the stream mouth during darkness, they may commence their movement at sea towards the stream mouth before the onset of darkness. This latter explanation is in agreement with a seasonal change in response to state of the tide, as discussed in the following section.

c. Tides

The indirect effect of the moon expressed through the tides and tidal cycles, was investigated. Firstly, the daily ebb and flood tidal rhythm was examined and secondly the monthly tidal cycle.

Tidal Rhythm

To assign nightly catches to a particular state of the tide, the point at which the tide turned was taken as midway between the period when flow in one direction stopped and recommenced in the opposite direction. This was generally in good agreement with the predicted times from published tables. Table 3.9.a shows the significant catches for 1971 arranged according to the number and percentage of each nights catch caught on the flood and ebb tides. To observe any differences between the beginning and end of the season, this table has been subdivided. The 1972 catches indicated the end of September to be midway through the season, and so that date is used as a convenient division.

Although the seasonal mean values per tide phase do not indicate any obvious preference for invasion on either the flood or ebb tide, the sub-totals show marked differences for both halves of the season. During the first half of the season, represented by only three catches but comprising 51% of the total seasons catch, 77% of all eels were caught on the flood tide. During the second half of the season only 23% of glass-eels were caught on this tide.

The significant catches for 1972 are given in Table 3.9.b similarly arranged by tide phase. Both the number and mean percentage of the catches for each half-season show a similar trend to the 1971 catches. That is, for the first half of the season, most invading glass-eels were caught on

Table 3.9 Significant glass-eel catches from the Makara Stream according to tide phase

a 1971

b 1972

Results of contigency chi-square tests between both halves of the season for each year are given

c.f. $X^2_{0.01} = 6.63$

a 1971

Date	Flood tide n	%	Ebb tide n	%
7/9	109	90	12	10
8/9	225	75	75	25
20/9	10	44	14	56
	344 (77%)		101 (23%)	
6/10	17	71	7	29
7/10	19	76	6	24
13/10	10	29	24	71
19/10	45	41	64	59
21/10	8	37	12	63
12/11			64	100
15/11			87	100
16/11			60	100
	99 (23%)		324 (77%)	
N	443 (51%)		425 (49%)	

$X^2 = 252 \cdot 18$

b 1972

Date	Flood tide n	%	Ebb tide n	%
31/7	24	100		
14/8	21	100		
16/8	54	90	6	10
30/8	107	100		
1/9	72	95	4	5
6/9	34	24	106	76
15/9	162	97	4	3
18/9			140	100
22/9	2	6	32	94
29/9	25	90	3	10
	501 (63%)		295 (37%)	
2/10			39	100
4/10			34	100
16/10	34	79	9	21
19/10			95	100
27/10	44	20	180	80
3/11			39	100
10/11	10	13	66	87
24/11	15	37	26	63
27/11	13	29	33	71
	116 (18%)		521 (82%)	
N	617 (43%)		816 (57%)	

$X^2 = 288 \cdot 90$

the flood tide, but for the remaining months, the majority of eels invaded against the ebbing tide. The highly significant values obtained for the contigency chi-square tests indicate that real differences exist between half-season catches in both years.

Before considering the implications of these results, two other factors must be mentioned. Firstly, ebb tides generally afford better fishing conditions than do flood tides. The latter tides often carry large quantities of seaweed and debris which tended to clog the net. Also, the orientation of glass-eels invading on the flood tide could not be clearly established; if they were evenly distributed across the width of the stream or had a preference for mid-water, this would decrease the sampling efficiency of the net. Eels invading against the ebb tide were found swimming close to the bank. However, such a sampling bias should be consistent throughout the season and would be of lesser importance in a stream with a narrow shallow mouth, like Makara, than in a stream with a broad deep mouth.

Secondly, the physical aspects of the stream itself are variable. The locality of the stream is such that the mouth is exposed to the prevailing northwest wind. After several days of strong winds from this direction, the stream mouth may become considerably reduced to two or three metres in width, due to gravel deposited by rough seas. Such deposits require a 'fresh' in the stream to remove them. If the stream outlet is restricted in this way, the rate of tidal flow in either direction will be greatly increased. This, in turn could affect the ability of eels to invade against the ebb tide. The 1971 season was relatively free from such adverse effects and although catches were small, it is proposed that they are typical of the seasonal periodicity of invasion. Catches during the latter half of 1972 were probably affected to some extent by a gravel bar which formed offshore and restricted the outlet.

[redacted]

a tide change occurred at least one hour after the commencement of fishing. The tide cycle on these nights is divided into four periods around the change of tide. In 1971, seven of the eight nights involved showed a tidal rhythm through high-water and this was the period chosen. In contrast, the low-water period was predominant during 1972.

The tide rhythm, for 1971, is divided into the following periods:

flood tide, excluding the half hour prior to high-water (F.T.)
flood tide of the half hour prior to high-water (H.W. - $\frac{1}{2}$ hr)
ebb tide of the half hour after high-water (H.W. + $\frac{1}{2}$ hr)
ebb tide, excluding the half hour after high-water (E.T.)

The letters in brackets represent the headings given to the columns in Table 3.10.a. For the 1972 data the rhythms are based on low-water, and the headings are correspondingly reversed (Table 3.10.b). In both tables, the two middle columns cover a period of half an hour either side of slack-water respectively.

Table 3.10.a shows that most invasion for 1971 occurred during a period of directed water flow, and not over the hour 'slack-water period'. However, the number of eels caught on the flood tide decreased from 60% during the first half of the season to 43% during the second half. Unfortunately, by definition of the nights considered in this analysis, the three large catches in November cannot be included. For this reason the number of eels considered for the second half of the season is small and the percentage catch on the ebb tide (41%) is slightly less than that of the flood tide (43%).

A more definite trend in invasion by tide phase is seen from the relevant 1972 catches, as given in Table 3.10.b. During July and September, 85% of the glass-eels invaded on the definite flood tide phase. However, over the remaining months, 73% of all eels were caught on the ebb tide, but with a large proportion in the half hour prior to low-water. This increased latter movement was probably due to the physical conditions encountered by invading glass-eels. The offshore bar which formed over this period restricted the stream outlet, with the result that tide flow in either direction was swift. Only when the ebb tide was slackening prior to low-water could glass-eels negotiate the bar and make progress upstream. Accordingly, a high proportion of all movements took place over the 'slack-water period.'

Table 3.10 Significant glass-eel catches from the Makara Stream made during a tide change.

F.T. = flood tide, excluding the half hour prior to high-water

H.W.- $\frac{1}{2}$ hr = flood tide of the half hour prior to high-water

H.W.+ $\frac{1}{2}$ hr = ebb tide of the half hour after high-water

E.T. = ebb tide, excluding the half hour after high-water

L.W.- $\frac{1}{2}$ hr = ebb tide of the half hour prior to low-water

L.W.+ $\frac{1}{2}$ hr = flood tide of the half hour after low-water

a 1971

b 1972

Note: catches recorded over flood tide (F.T.) and ebb tide (E.T.) periods represent varying time intervals. Accordingly these tide periods are not directly comparable in terms of effort and catches cannot be interpreted as catches per unit time (i.e. catch rates)

a 1971

Date	State of tide: F.T. n	%	H.W. − 1/2hr n	%	H.W. + 1/2hr n	%	E.T. n	%
7/9	88	73	21	17	6	5	6	5
8/9	175	58	50	17	50	17	25	8
20/9	5	22	5	22	4	16	10	40
	268 (60%)		76 (17%)		60 (14%)		41 (9%)	
6/10	7	32	10	40	5	23	2	5
7/10	19	76			3	12	3	12
19/10	45	41					64	59
21/10	4	20	4	20	8	40	4	20
	75 (43%)		14 (7%)		16 (9%)		73 (41%)	
N	343 (55%)		90 (15%)		76 (12%)		114 (18%)	

b 1972

Date	E.T. n	%	L.W. − 1/2hr n	%	L.W. + 1/2hr n	%	F.T. n	%
31/7					1	4	23	96
14/8					5	23	16	77
16/8			6	10	14	22	40	68
30/8					3	3	104	97
1/9			4	5	3	4	69	91
15/9			4	3	20	11	142	86
29/9			3	10	8	28	17	62
			17 (4%)		54 (11%)		411 (85%)	
16/10	9	21			1	2	33	77
27/10	137	61	43	19	40	18	4	2
10/11	27	36	39	51	10	13		
24/11			26	63	10	25	5	12
27/11	8	17	25	54	12	27	1	2
	181 (42%)		133 (31%)		73 (17%)		43 (10%)	
N	181 (20%)		150 (16%)		127 (14%)		454 (50%)	

On such occasions, when the ebb tide was initially too strong to be stemmed by invading glass-eels, an interesting sequence was noted. As the tide began to slacken, whitebait (Galaxias spp. juveniles) would be caught first, followed up to half an hour later, by glass-eels. It was apparent that the whitebait were stronger swimmers than the glass-eels and able to negotiate swifter ebb tides.

In summary, the above results indicate that glass-eels invading early in the season do so on the flood tide, whereas late season eels prefer to invade against the ebb tide. As previously stated, these changes are considered indicative of different behavioural responses.

Literature on other species of Anguilla indicates that invading glass-eels are known to use flood tides for transport. Creutzberg (1958: 857) found evidence for the transport of glass-eels at sea by flood tide streams. Although Deelder (1952: 206) initially found no relationship between tidal flow and glass-eel movements at sea, he later concluded (1960a: 3) that the eels were able to discriminate between the tide phases and used the flood tide for invasion. Similar movements, also for glass-eels of A. anguilla, are recorded by Meyer and Kühl (1953: 90) and Tesch (1965: 404). Matsui (1952: 232) notes invasion by glass-eels of A. japonica on the flood tide while Day (1941: 1) gives equivalent information for A. rostrata. The data for the first half of the glass-eel season from Makara are in agreement with these observations.

In explanation of the observed seasonal change in preference by Makara glass-eels, the behavioural changes given by Deelder (1958: 136) should be recalled. He found that glass-eels which had delayed their invasion by remaining in areas of low salinity, were more tolerant of light, began to form schools and were attracted to flowing fresh-water. It is at this stage that the vast freshwater migrations commence.

Those glass-eels caught early in the season, are at the stage prior to their transition in behaviour. Thus they are carried into the stream mouth at night on the flood tide and show no schooling tendencies. It could be expected that the eels at this stage show little attraction to pure fresh-water, and so some may leave the stream on the ebb tide, but it was not possible to sample this. Those remaining in the stream would then delay further upstream migration and stay in the estuarine area until acclimatised to the new environment. As no glass-eels were found buried in the mud and small rocks of the edges of the lower

estuary, it is thought that they accumulate in the deeper areas of directed tidal streams.

Glass-eels invading late in the season show a partial change in behaviour. No schooling tendencies were observed but the eels swam against the ebb tide and seemed more tolerant of light. Although invasion still took place at night, it sometimes commenced during the twilight period.

The nocturnal invasion by glass-eels has given rise to several interesting theories among whitebait fishermen as to the spawning of eels. As whitebaiting is confined to daylight hours, very few invading glass-eels are ever caught by fishermen at river mouths. The lack of schooling behaviour in the eels at this stage also decreases the chances of catching a large quantity at any particular time. In contrast, large runs of pigmented glass-eels often occur further upstream where they may result in a temporary cessation of whitebaiting, a fact much regretted by commercial catchers. From these observations, the conclusion often reached by whitebaiters is that adult New Zealand fresh-water eels do not migrate to sea, but spawn in the river estuaries, in a similar manner to whitebait (Galaxias spp.).

As previously mentioned, invading glass-eels were occasionally caught during daylight hours at Makara, by whitebaiters, late in the season. Apparently, these showed obvious pigmentation. However, invasion is essentially a nocturnal phenomenon, even for those eels arriving late in season. These eels exhibit a positive hydrotaxis to flowing fresh-water, as shown by their invasion on the ebb tide. With the ebb tide, a substantial amount of fresh-water flows out to sea. Salinity measurements at Makara on the ebb tide have been recorded at 5°/oo, indicating a considerable content of fresh-water. Experiments by Creutzberg (1961: 309), Miles (1968: 1597) and myself all indicate that attraction to fresh-water is not due to decreased salinity but rather some organic content of the water. The amount of this substance would presumably increase with an increased volume of fresh-water.

It is suggested that adaptive changes in behaviour take place in proportion to the length of post-metamorphic sea life. The explanation for this longer post-metamorphic life of late season glass-eels is discussed later, but on this basis it can be assumed that such eels will have undergone some behavioural changes prior to their entry into fresh-water.

The corollary to the above is that the commencement of metamorphosis initiates processes resulting in specific morphological and

behavioural changes. This is important, as it might otherwise be inferred from the observations of Deelder (1952) that the behavioural changes occur in response to the proximity of fresh-water. Consideration of cerebral pigmentation illustrates the point. The precocious development of pigmentation on membranes surrounding the brain is in contrast with the typical sequence noted in other fish larvae. The appearance of this pigmentation coincides with increased tolerance towards light. Perhaps this development allows the brain protection from direct light which could otherwise penetrate through the large dorsal fontanelle. This fontanelle is readily seen in VB glass-eels stained with alizarin dye. In this way, the behaviour of the eel in response to light could be changed as a direct result of the process of pigmentation, which in turn, is initiated by metamorphosis.

Two observations by Deelder are of interest when discussing the behavioural change suggested. Firstly, Deelder (1952: 210) found different responses by invading glass-eels to tidal streams at either end of the dam enclosing the Yssel Lake. Peak invasions at the sluice at the southern end of the dam took place on the flood tide, while the most intense invasions at the northern sluice were on the ebb tide. He concluded that correlation between invasions and tide phases at the sluices was incidental. Unfortunately, no arrival dates are given but it is known that the northern sluice is some 30km from the area where the transition in behaviour occurs (Creutzberg 1961: 279), whereas the southern sluice is approximately 4 km. In view of my explanation, it seems very likely that these observations are related to the later arrival with subsequent behavioural change, of glass-eels at the northern sluice.

The second observation was made by Deelder (1958: 140) when discussing the reactions of invading glass-eels to freshwater flows. Early season glass-eels commenced their change in behaviour close to the southern sluice, but a possible explanation for a stronger positive reaction of late season glass-eels to fresh-water "could be, that of the elvers arriving in the course of the season more and more have started their change of behaviour at an earlier phase". Unfortunately, he does not discuss this possibility further.

Finally, as additional proof of the proposed change in behaviour, some results from choice experiments can be given. These experiments are fully discussed in a later section, but it was demonstrated that

glass-eels invading late in the season, showed a preference to swim into flowing fresh-water rather than sea-water. This contrasts with results obtained by both Deelder (1958: 137) and myself for early season glass-eels caught prior to commencing their transition in behaviour.

Tidal Cycle

The monthly lunar cycle is known to act as a biological clock for many of the recurring cycles found in nature. Lunar rhythms are widely distributed throughout the invertebrates and vertebrates, and are often quoted with reference to eel migrations. In the following section, the catches of invading glass-eels are investigated, to determine whether any correlation with the lunar cycle, and hence tidal cycle, is evident.

The phases of the moon in relation to the 1971 and 1972 Makara catches are shown in Figs. 3.9 and 3.10. These data are better expressed over a period of a lunar month, based on the date of the new moon as day zero (see Fig. 3.13).

Thus, Fig. 3.13 shows the 1971 catches, as numbers caught on successive days after the new moon. A large peak is seen three days after the full moon, with a further smaller peak at the new moon period. However, it should be noted that this large peak after the full moon represents only one night's catch. Also, the appearance of the full moon does not bear a constant relationship with the new moon, and the position indicated on the graph is approximate.

The 1972 figures are more reliable indicators of any lunar periodicity as they cover a period of six lunar months, and the total catch was greater than in 1971. In Fig. 3.13, the largest catches in 1972 appear to be during the neap tide periods but this relationship is not strong. For both years combined the total picture is confused, with no clear correlations.

To further examine the data for any periodicity over the actual spring and neap tide periods, Table 3.11 was compiled. In this table the position of each entry was allocated according to its relation to the date of the appropriate moon phase. This overcomes the approximation of the appearance of the full moon as made in the previous lunar month calculations.

The table assumes a period of seven days between successive moon phases. Where an eight day period occurred, the catch was divided

Fig. 3.13 Makara Stream glass-eel catches, 1971 and 1972 expressed over a period of a lunar month.

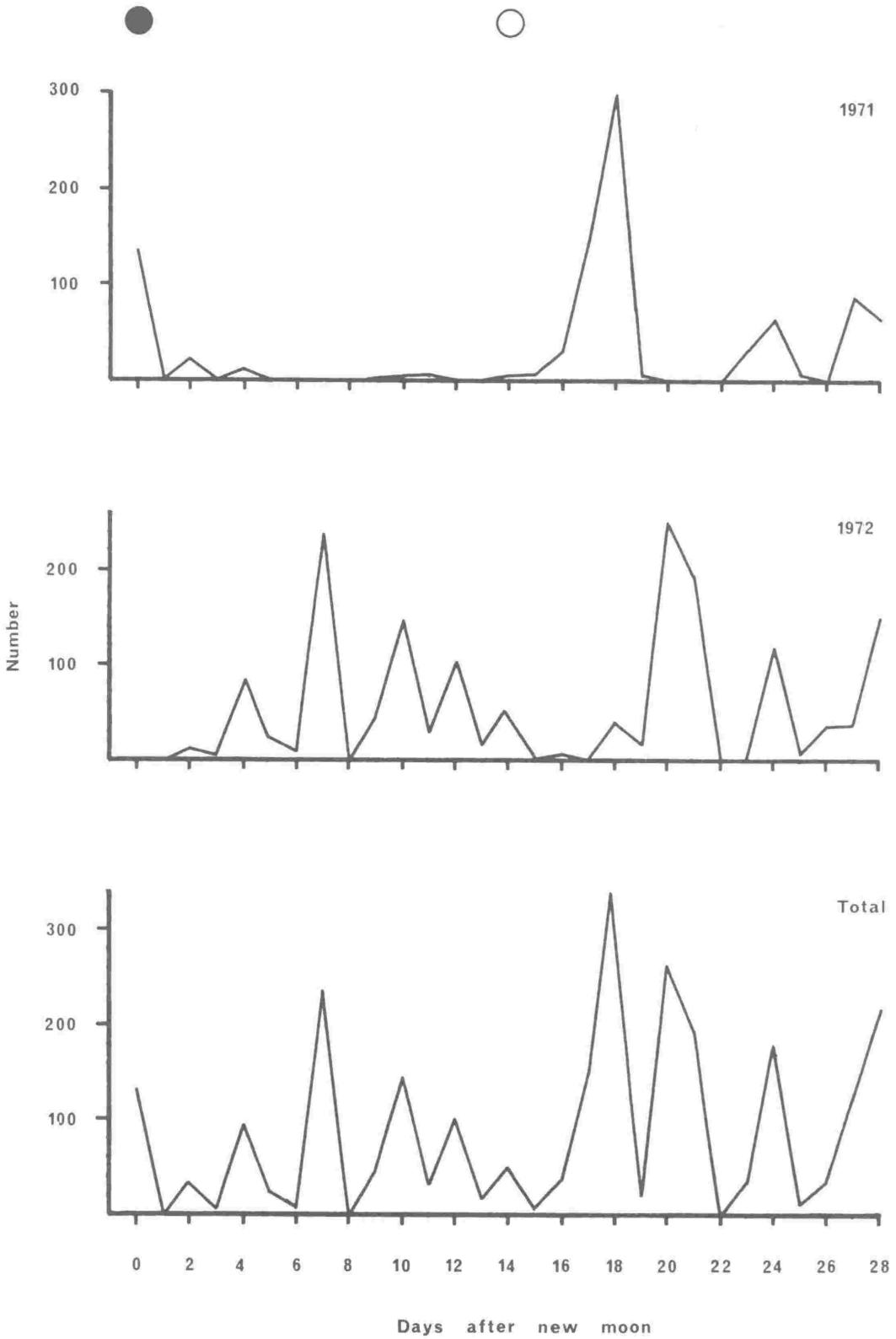

1971
1972
Total
300
200
100
Number
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
Days after new moon

Table 3.11 Makara Stream glass-eel catches during spring and neap tide periods for 1971 and 1972.

The days are given in relation to the moon phases corresponding to spring and neap tide periods.

Days		-3	-2	-1	0	+1	+2	+3	N
Spring tides	1971	5	87	74	138	32	167	305	808
	1972	87	162	41	4	1	14	105	414
	Σ	92	249	115	142	33	181	410	1222
Neap tides	1971	7	3			2	98		110
	1972	72	362	311	56	76	212	104	1193
	Σ	79	365	311	56	78	310	104	1303

equally between the days either side - days minus three and plus three. Day zero for spring tides represents full or new moon, while the same day for neap tides indicates first or last quarter. Thus, a catch made on the night prior to a full (or new) moon would be recorded in the minus one day column of spring tides. Spring tides increase to a maximum height on the day of full or new moon, or perhaps the following day. If the strength of invasion is directly related to this increased tidal amplitude, the invasion itself should closely parallel the tide cycle, building to a peak at or slightly after, the spring tide.

For 1971, the total catch over the spring tide period far exceeded that of the neap period, while the reverse was true for 1972. The totals for both years combined show that the number of eels caught through both tidal cycles was similar. From this it may be concluded that spring and neap tides exert no differential influences on glass-eel invasion.

Although the data are not presented, no differing trends could be seen when comparing early and late season catches for spring and neap tide periods. This is not unexpected as the time of high water at night for both spring and neap tides is 2100-2130 hours which allows sufficient time both before and after, for glass-eels to invade on the tide of their choice.

The lack of correlation of invasion with the lunar cycle may, in part be due to the small tidal range recorded at Makara. The mean spring tide range is only 0.3 m. However, Deelder (1952: 209) did not find any direct relationship between invasion and spring and neap tides. He considered that any monthly catch cycles were attributable to the period of flow at the flood tide. Meyer and Kühl (1953: 87), discussing glass-eel movement at Herbrum on the River Ems, found no correlation with phases of the moon, and hence tide cycles, although 'runs' did take place on flood tides at night.

d. Rainfall

Having established the different responses between early and late season glass-eels, it might be predicted that a flood or fresh in the stream late in season would provide an additional stimulus for invasion. Conversely, increased freshwater flow early in the invasion season should have little attraction.

Rainfall data for the Makara Valley were kindly supplied by the Ministry of Works Soil Conservation Station, Quartz Hill, Makara.

Distribution of rainfall throughout the 1971 and 1972 glass-eel sampling programmes is shown in Figs 3.9 and 3.10 together with the catches made. From this material the days with 10+ mm of rainfall on which fishing took place were extracted. Any significant catches on any of these nights were noted. In addition, nights when the stream was recorded as running above normal level are incorporated in the following analysis. The inclusion of these latter nights was necessary as, although no rainfall may have fallen on any one day, the stream could still have been swollen from rain on preceeding days.

The above data for both 1971 and 1972 appear in Table 3.12. A negative sign in the 'stream swollen' line indicates that stream level was normal, while a positive sign shows the stream was running high. The bottom line in these tables gives the state of the tide, or if a change occurred during the night, the phase on which the majority of the catch was made. These tide phases are approximations, as the flow of the flood tide was often greatly slowed or overcome by the increased velocity of the swollen stream.

From the table, the 1971 data show significant catches occurred on five out of the six nights when rain fell or the stream was swollen. The total number of glass-eels, 215, represents only 25% of all significant catches for the year. As anticipated, most catches during the second half of the season were made on an ebb tide.

In 1972, significant catches were recorded on eight of the twelve nights given, representing 52% of the grand total of all significant catches. In the first half of the season, four large catches were made during periods of increased flow, although predominantly on the flood tide. The two large, late season catches were made on the ebb tide. While the latter result is as expected, the former is not. As early season glass-eels appear to show no attraction towards fresh-water, a low probability of invasions during time of increased stream flow would be expected.

From reference to the fishing diary kept it was found that the increased flow noted for all five successful nights in the first half of the 1972 season, was not great, and that a definite flood tide took place close to the predicted time. This contrasts with conditions on a night when a greater 'fresh' was running, such as 27 October. The diary entry for the stream condition on this night reads: "Large fresh in stream. Swift flow holding back flood tide except for few surges."

Table 3.12 Makara Stream glass-eels. Results from fishing on nights of increased stream flow.

e = ebb tide

f = flood tide

1971

Date	20/9	4/10	6/10	21/10	15/11	16/11	N
Rain (mm)	11	32		10	23	12	
Eels (n)	24		24	20	87	60	215
Stream swollen	-	+	+	+	+	+	
State of tide	e	f	f	e	e	e	

1972

Date	11/7	11/8	14/8	16/8	30/8	1/9	6/9	9/10	13/10	16/10	27/10	10/11	N
Rain (mm)	25	13			12	10		28	14				
Eels (n)			21	60	107	76	140			43	224	76	747
Stream swollen	+	-	+	+	+	+	+	-	+	+	+	+	
State of tide	e	f	f	f	f	f	e	e	f	f	e	e	

On this night a small flood tide did take place, but 4½ hours after the predicted time.

In summary, it can be stated that if a period of increased water flow occurs late in the season, there is an increased likelihood of a significant invasion taking place. Minor floods early in the season have little inhibitory effect on invasion. It is thought that a major flood early in season would act as a deterrent to invasion. Unfortunately, the only such flood was on 11 July 1972, and although no eels were caught, this date is too early in the season to be of significance. Lowe (1951: 309) found that floods delayed 'runs' of glass-eels into fresh-water early in the season.

Summary

To determine which environmental factors are significant influences on the periodicity of glass-eel invasion, the 1971 and 1972 catches from Makara were considered.

Low water temperatures appear to have an inhibitory effect although, under normal conditions, this effect would be confined to the early part of the invasion season. Invasion takes place only after sunset and seems unaffected by moonlight. The flood and ebb tidal rhythm has a direct influence on invasion, although the monthly tidal cycle does not. Increased flow of fresh-water probably provides some additional stimulus late in the season but early season floods are liable to delay invasion.

3.5 FRESHWATER MIGRATION

After residence in the lower estuarine areas where they complete their full behavioural transition, glass-eels migrate further upstream.

The length of time spent in the estuarine area prior to upstream migration is subject to much variation, but is thought to be of the order of one to two weeks; early season glass-eels could be expected to take longer to complete their behavioural changes than late season arrivals. With the accomplishment of this change and the onset of pigmentation, the glass-eels commence their upstream migration.

Glass-eel samples, from the "Elbow" on the lower Waikato River are discussed as typifying this upstream freshwater migration. Fig. 3.14 gives the frequency of the various stages of pigmentation per month for Waikato samples received, over a period of three years. The earliest sample, from 13 August, was recorded as being taken during daylight, and so it is assumed the eels had completed their behavioural change. Surprisingly, 15% were at Stage VB as eels at this stage invariably show behaviour typical of that prior to transition. With time, glass-eels collected from the "Elbow", show increased pigmentation. The sample mode shifts from VIA II 1 for shortfins in August to VIA III 2 in November. Longfin samples were smaller and do not show trends clearly. However, the VIA II stages found in early season catches are not present by November. Finally, comparison of the histograms of both species for any month, show that longfins are further advanced in pigmentation than are shortfins. This agrees with experimental evidence of faster pigment development in longfin glass-eels.

As indicated in a previous section, the catches at the "Elbow" sampling site may not be an accurate reflection of the percentage of both species entering the river. For instance, migratory juvenile eels or elvers, caught at the "Elbow" were all shortfins, indicating many shortfin glass-eels remain in the lower parts of the river.

Typical length-frequency histograms for the Waikato material, in this instance live samples from 1971, are given in Fig. 3.15. A seasonal decline in mean length can be seen. This is due, not so much to a shift in the range of lengths as to an increase in the proportion of eels of shorter length. Not only does a decline in length occur throughout the season, but also a decline in weight, and the relationship of these two factors, expressed as condition (K). Table 3.13 gives these values for the pooled samples. Correction factors have been applied to preserved

Fig. 3.14 Waikato River glass-eels. Frequency of pigmentation stages per month.

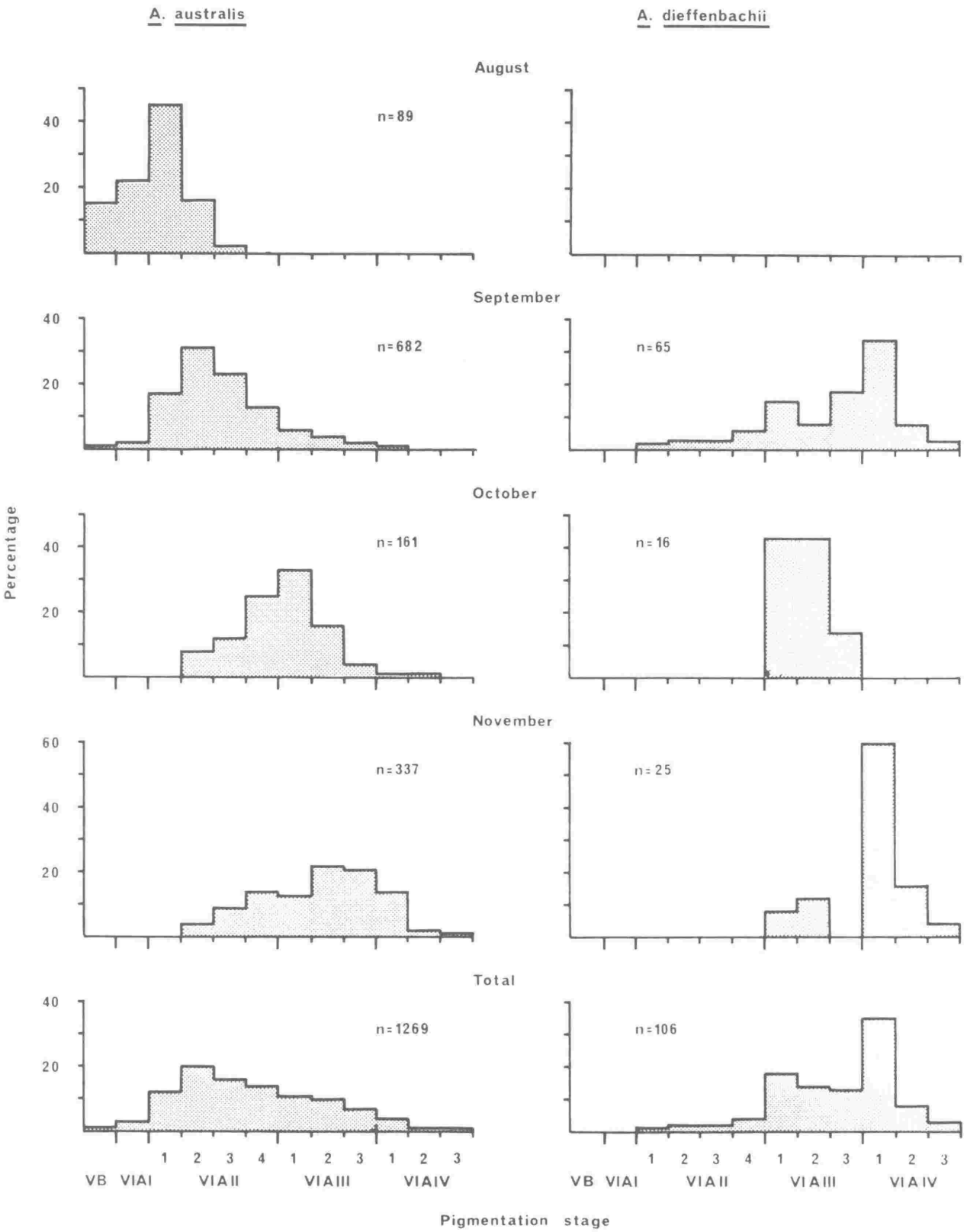

A. australis
A. dieffenbachii
August
September
October
November
Total
n=89
n=682
n=65
n=161
n=16
n=337
n=25
n=1269
n=106
Percentage
Pigmentation stage
VB VIAI VIAII VIAIII VIAIV

Fig. 3.15 Waikato River glass-eels. Length-frequencies of live eels obtained in 1971.

The number and mean length per species are indicated.

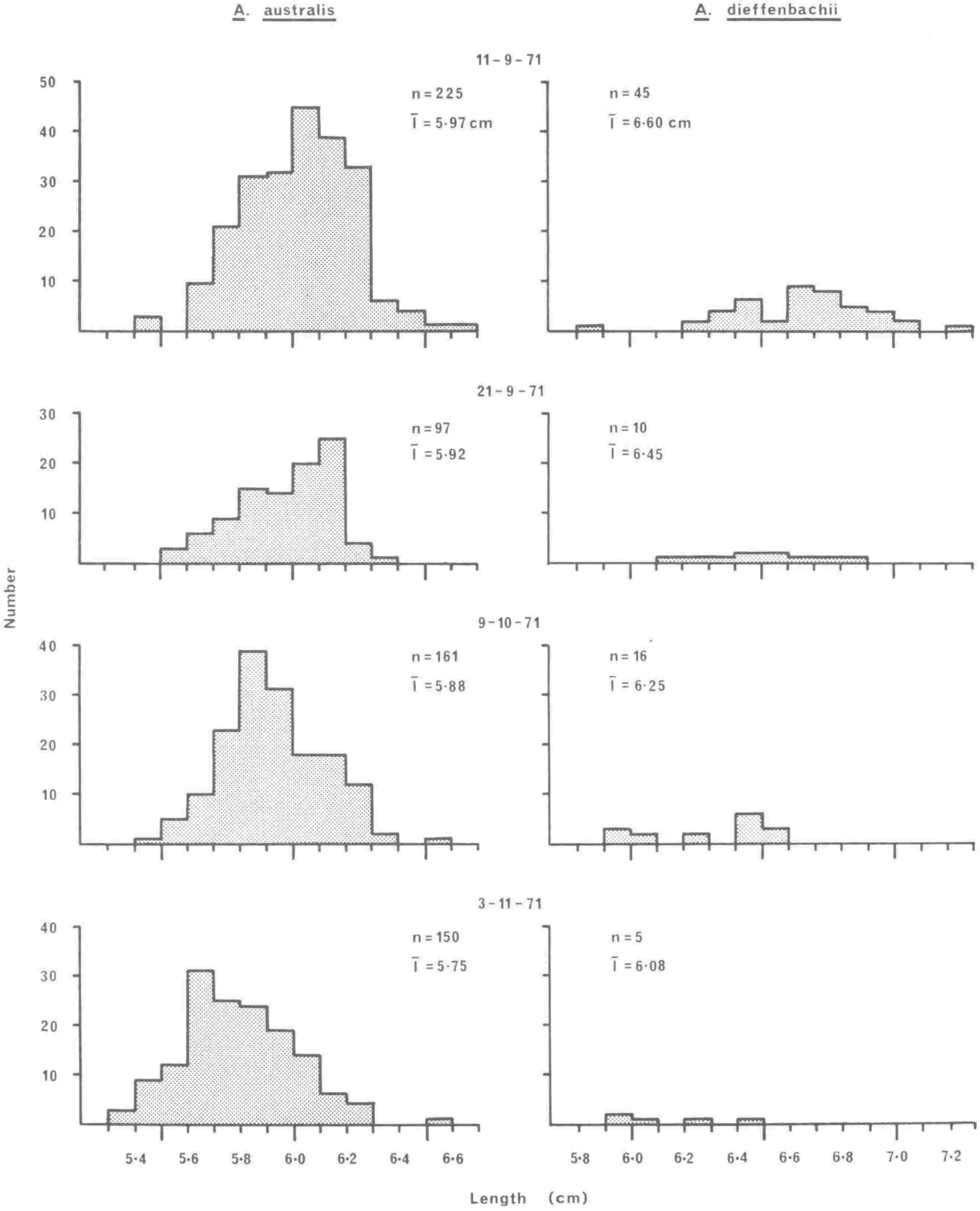

A. australis
A. dieffenbachii
11-9-71
n = 225
$\bar{l}$ = 5·97 cm
n = 45
$\bar{l}$ = 6·60 cm
21-9-71
n = 97
$\bar{l}$ = 5·92
n = 10
$\bar{l}$ = 6·45
9-10-71
n = 161
$\bar{l}$ = 5·88
n = 16
$\bar{l}$ = 6·25
3-11-71
n = 150
$\bar{l}$ = 5·75
n = 5
$\bar{l}$ = 6·08
Number
Length (cm)
5·4
5·6
5·8
6·0
6·2
6·4
6·6
7·0
7·2

Table 3.13 Waikato River glass-eels, 1970-1972.

Mean monthly length, weight and condition.

	A. australis				A. dieffenbachii			
	n	$\bar{l}$(cm)	$\bar{w}$(g)	K	n	$\bar{l}$(cm)	$\bar{w}$(g)	K
Aug.	89	6.16	0.25	1.05				
Sept.	682	6.05	0.19	0.87	65	6.58	0.27	0.94
Oct.	161	5.88	0.18	0.91	16	6.25	0.25	1.03
Nov.	337	5.81	0.16	0.82	25	6.10	0.20	0.90
N	1269				106			
Means		5.97	0.19	0.88		6.42	0.25	0.94

material. The significance of this seasonal decline in size and condition is discussed at some length in a later section.

Note: Totals in this table vary from those given in Table 3.7 because not all the eels in each sample were measured. Also, freshly dead longfins are included in Table 3.13 to give a larger number for the September sample.

Periodically throughout late winter and spring, large upstream migrations of these young eels takes place. The above samples come from such migrations. Cairns (1941: 61) records a shoal of glass-eels in the Waikato which passed a stationary point for over eight hours. This shoal was over 4.5 m wide and 2.5 m in depth. Whitebait fishermen on this river speak of vast 'runs' during the whitebait season, which move upstream apparently indifferent to light and physical obstacles. One senior citizen recalled an August migration which ran continuously for three days and four nights. The dimensions of this shoal were 0.5 - 1 m wide and 0.25 m deep, and the overall impression was of a continuous cord. However, such compacted schools are only seen in areas of steady downstream current. Similar migrations take place on a smaller scale, in other rivers throughout the country.

The opinion commonly shared amongst observers on the Waikato River, is that the shoals of glass-eels do not appear until a point at the upstream end of the estuary, approximately 8 km from the mouth. Obviously the area where the transition in behaviour occurs is downstream of this, perhaps in the areas of tidal streams in the middle or lower estuary.

The following section deals with the periodicity of these migrations. Catch statistics from three separate sources have been placed at my disposal.

In September 1970, the Fishing Industry Board commenced experimental fishing on the Waikato River, in response to requests from Japan for supplies of live glass-eels. The catch figures for the months of September and October have been made available. No private companies were permitted to catch glass-eels for export during 1970 and 1971, but in 1972 limited licences were granted. Mr T. W. Beckett, biologist to the Group Development Section of Wattie Industries Ltd, has kindly consented to the inclusion of his catch data. Similarly, Mr C. T. Scollay representing Wm. Scollay & Co. Ltd has supplied details of daily glass-eel catches, also from the Waikato River. Both the Fishing Industry

Board and Beckett fished at the "Elbow", while Scollay's site was 2 km downstream.

These daily catches, together with rainfall, river height and moon phase data, are given in Fig. 3.16. Catches are expressed as kilograms of glass-eels caught per day. The rainfall data were recorded at the Pukekohe Horticultural Research Station, while the river height came from an automatic tide recorder at Tuakau bridge (see Fig. 2.1.a) operated by the Waikato Valley Authority. The units for the river height are relative values, based on an approximate mean sea level at Port Waikato of 29.1 m.

The environmental factors investigated with reference to the glass-eel invasion, are now examined, to determine whether any influence the periodicity of upstream migration.

Water Temperature

Unfortunately, no daily water temperature readings are available for the sampling area during the season of migration. However, Beckett (pers. comm.) found that water temperature was remarkably stable throughout the season in 1972. The range from mid-August to November was 13.0°-16.5°C, and there was no apparent correlation with catches. Air temperature records from Pukekohe indicate that August is the coldest month in this area, but a water temperature of 13°C during this month is considered adequate and should not impede migration.

Light

Fig. 3.17 shows the time of day when glass-eel 'runs' were recorded by Beckett. The approximate length of daylight is indicated by the sunrise and sunset times for Auckland.

In contrast to the invading glass-eels, the movements of these pigmented glass-eels are not confined to the hours of darkness. None of the runs recorded in Fig. 3.17 were continuous from day to day, and all migrations continuing into the night showed marked declines with time; few catches were recorded after 2000 hours. In general, most 'runs' commenced about midday and continued until shortly after dark.

Daylight migrations of glass-eels have been frequently noted for the European eel, e.g. Menzies (1936: 254), Deelder (1958: 136). Similar observations for the American eel are given by Day (1941: 2). Records of migrations in the estuaries of German rivers by Tesch (1965: 404)

Fig.3.16 Daily catches of glass-eels on the Waikato River. Moon phases, rainfall and river height are indicated.

1970: data supplied by Fishing Industry Board.

1972A: data supplied by C. T. Scollay of Wm. Scollay & Co. Ltd.

1972B: data supplied by T. W. Beckett of Wattie Industries Ltd., Group Development Section.

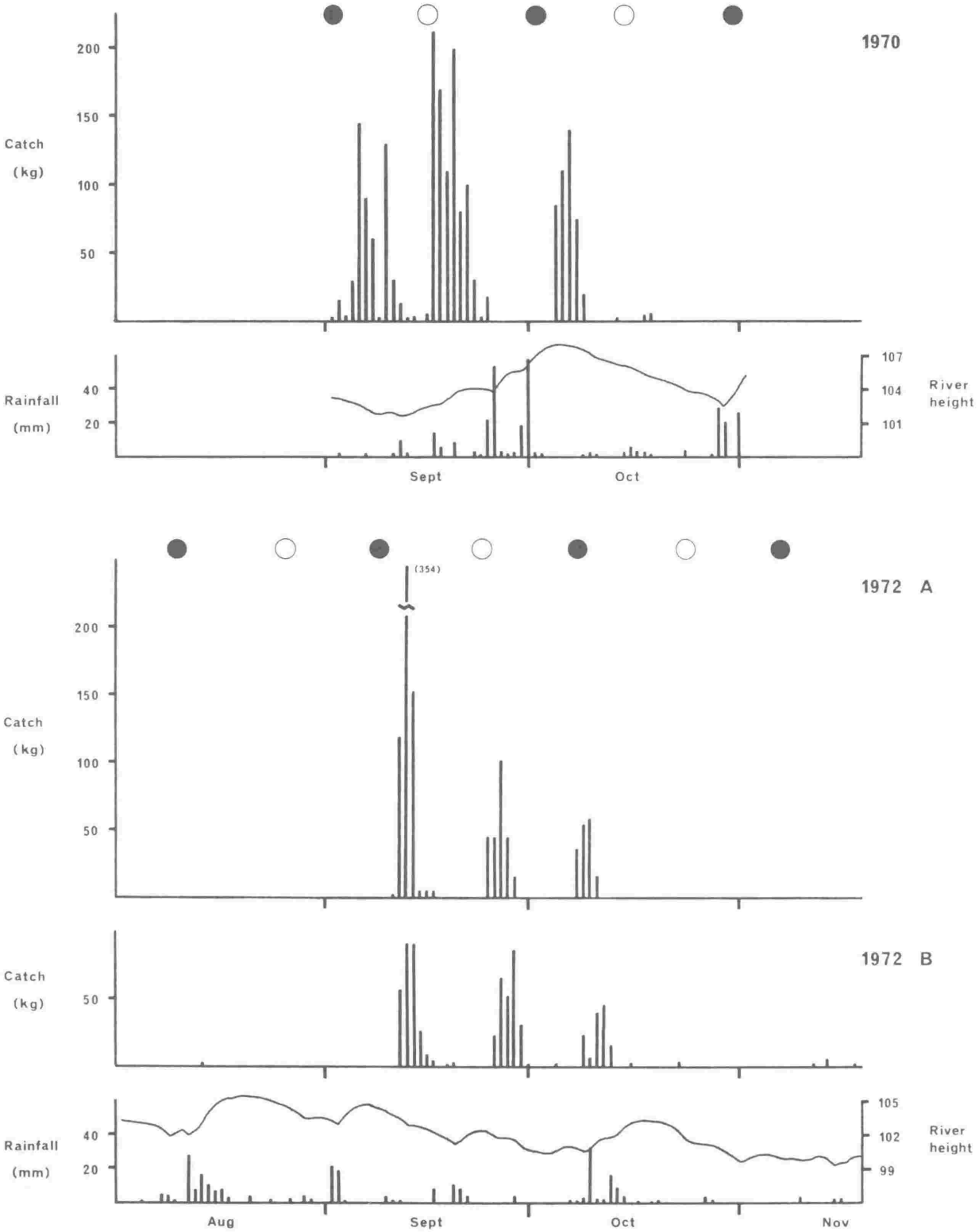
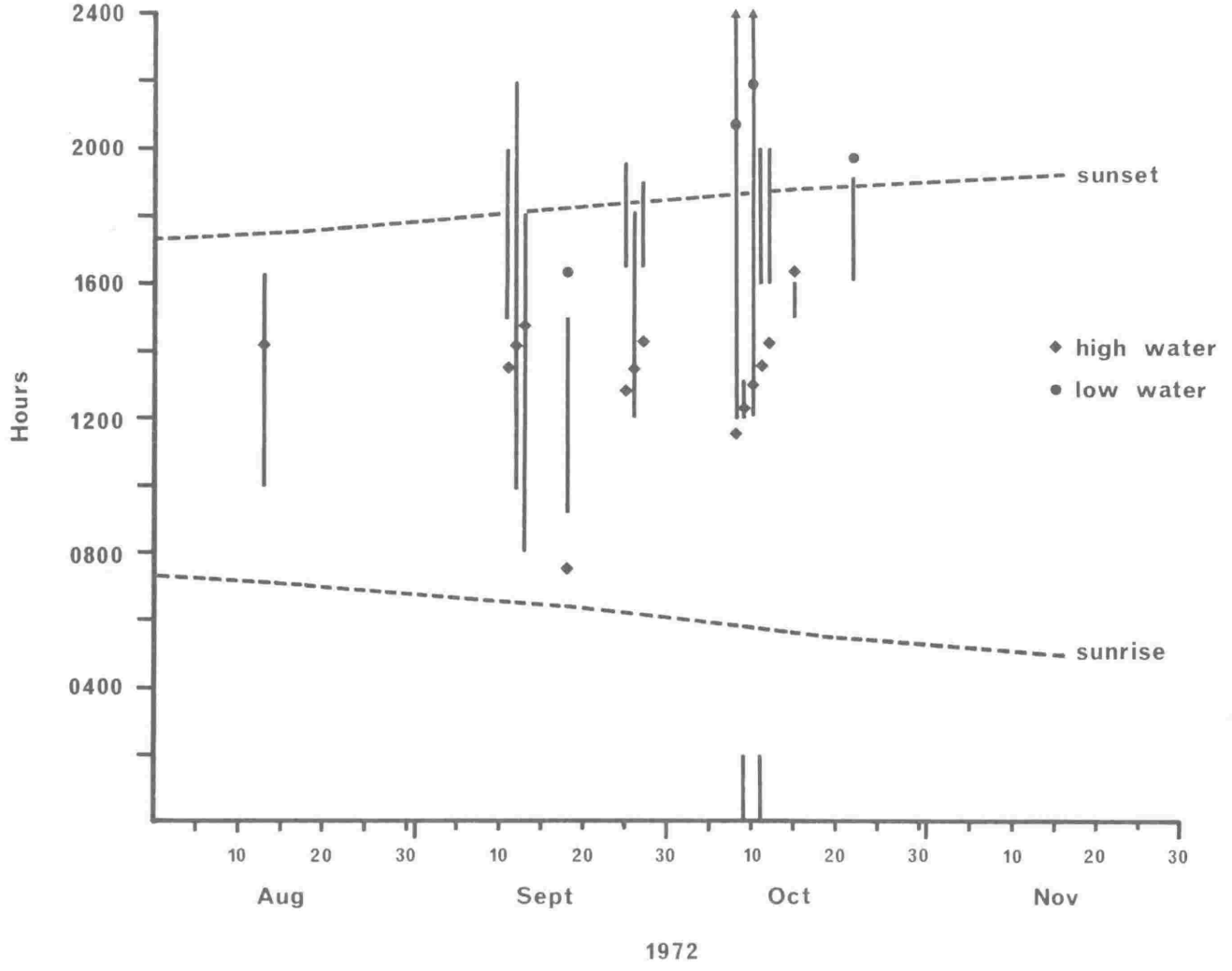

1970
Catch
(kg)
200
150
100
50
Rainfall
(mm)
40
20
107
104
101
River
height
Sept
Oct
1972 A
(354)
Catch
(kg)
200
150
100
50
1972 B
Catch
(kg)
50
Rainfall
(mm)
40
20
105
102
99
River
height
Aug
Sept
Oct
Nov

Fig. 3.17 Time of day when glass-eel "runs" were recorded at the "Elbow", Waikato River, 1972.

Data supplied by T.W. Beckett.

The approximate periods of darkness are indicated by the times of sunrise and sunset.


2400
2000
1600
1200
0800
0400
Hours
sunset
sunrise
high water
low water
10
20
30
10
20
30
10
20
30
10
20
30
Aug
Sept
Oct
Nov
1972

indicate that glass-eels move only in the early part of the morning, taking advantage of flood tides: daylight migrations may take place when the ebb tide occurs early in the morning.

Tides

a. Tidal Rhythm

The times of high and low water at the "Elbow" for days on which migrations occurred, are recorded in Fig. 3.17. These times were calculated from data on tidal delay predictions for the lower Waikato River, as supplied by the Waikato Valley Authority.

Most migrations appear to take place on the ebb tide, although the two longest 'runs' continued through a complete tidal sequence. However, at the "Elbow", the flood tide is only represented by a decreased downstream flow and a resulting increase in water level. No upstream surge occurs and the water has no measurable saline content. Furthermore, the reduced tidal amplitude combined with the lag effect of upstream tides, means that the ebb tide runs for approximately $8\frac{3}{4}$ hours, while the flood tide is only $3\frac{3}{4}$ hours in duration.

Rather than take advantage of the reduced downstream flow of the flood tide phase, the glass-eels prefer to migrate against the increased flow of the ebb tide. Perhaps the increased flow aids the eels in orienting themselves as L.P.J. Chapman (pers. comm.) observed that in areas of no current the eels were widely dispersed and appeared to swim aimlessly, whereas in an area of constant current they swam steadily upstream, only a few centimetres from the bank. The reduced catches during flood tides do not represent a more dispersed migration with subsequent less efficient fishing, as catching sites were selected as areas of steady flow.

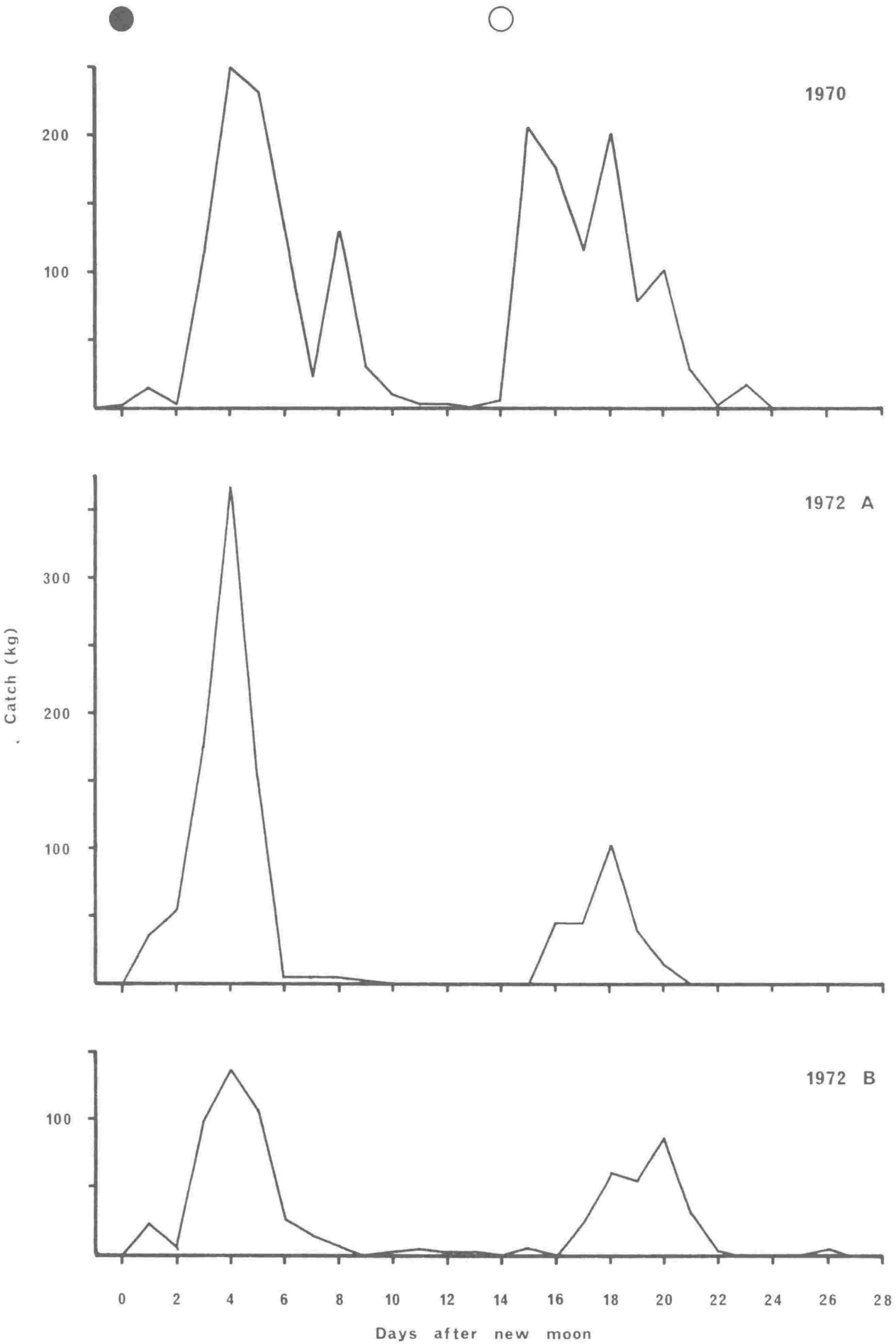
b. Tidal Cycle

The influence of the monthly lunar cycle was investigated to establish any effect it may have on the timing of migration. From Fig. 3.16 it can be seen that all large migrations took place consistently several days after a full or new moon. When these data are arranged by lunar month in Fig. 3.18, two major peaks are seen within the cycle. The larger peak occurs four days after the new moon, while the smaller peak occurs approximately the same time after the full moon.

From this it is concluded that large migrations take place on spring tides, corresponding to the new and full moon phases. It might

Fig. 3.18 Waikato River glass-eel catches expressed over a period of a lunar month.

Origin of data as for Fig. 3.17.


1970
200
100
1972 A
300
200
100
Catch (kg)
1972 B
100
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
Days after new moon

also be reasoned that the different heights of the peaks indicate that larger migrations occur on the new moon tides, which are the larger of the spring tides. Reference to the actual catches in Fig. 3.16 show that while this may be true of the 1970 catches, the differences in the 1972 catches were due to two new moon migrations but only one at full moon. The absence of a migration at full moon in October 1972 was probably due to an absence of eels, as no further migrations were recorded after this date, despite continued fishing.

The delay in time from the day of the new or full moon and the migration peak, is not unexpected. Peak catches at the downstream fishing site of Scollay's, were one or more days earlier than those made at the "Elbow" by Beckett. This indicates that large-scale migration is essentially a continuous process. As both sampling sites are some 8-10 km upstream from the area where schooling is first observed, a consequent time lag due to distance and the apparent decline in migration activity at night would be expected.

The increased tidal streams of spring tides seem to provide the stimulus to migrate upstream for those glass-eels which have completed their behavioural changes. Some initial upstream transport may take place on the flood tide but a more directed migration occurs on the ebb tide phase.

The upstream limit penetrated by the shoal of pigmented glass-eels is unknown. The inaccessibility of the river bank for several kilometres above the "Elbow" means that any movements in this area have not been recorded. A sample of small eels from Te Kauwhata collected on the night of 27 January 1971, contained some 1970 glass-eels. Whether migration was more or less continuous to this point or whether these eels were stimulated to move by the summer migration of adolescent eels, is not known. I have no records of glass-eel migrations in the Waikato River extending beyond the area of tidal influence at Tuakau.

A positive relationship between spring tides and upstream migrations of glass-eels was found by Menzies (1936: 254) for the River Bann, Northern Ireland. However, Lowe (1951: 307), in analysing further data from the same river, found that glass-eel 'runs' coincided with spring tides in years when the total number of glass-eels for the season was low. In years when the total was high, migrations took place on both spring and neap tides. From these results she concluded that the actual number of glass-eels in the estuary with the associated 'pressure' of interaction,

was a significant factor in initiating a migration. Glass-eels of A. japonica migrate upstream at night on the flood tide with definite maxima on spring tides but little movement on neaps (Matsui 1952: 232).

Rainfall

Rainfall data for the lower Waikato area were obtained from both Waiuku (16 km west of Pukekohe) and Pukekohe. A comparison of the records showed that local differences were very small and so the Pukekohe data were used as representative of the area. Rainfall recorded at Pukekohe for September-October 1970, and August-November 1972, is shown in Fig. 3.16. The periods and amount of rain are in good agreement with the river height, shown in the same figure.

Glass-eel catches show no definite correlation with rainfall and hence river height. In 1970, heavy rain on 24 and 25 September failed to stimulate any migration, as did further heavy rainfalls on 29 and 30 September. The 'run' from 4-8 October is attributable to the tidal cycle, although the river was running well above normal height over this period.

The 1972 catches are also better explained by tidal cycle rather than rainfall and river height, as the two September migrations took place while the river was dropping but the October migration commenced as the river was rising.

The increased speed of water flow during floods would stop large migrations from negotiating any open stretches of the bank with its associated lack of cover and swift flow, such as the "Elbow". Migrating glass-eels at these times would seek refuge in areas of reduced flow, where large numbers would accumulate. This would explain the observation made by several whitebait fishermen, that large 'runs' of glass-eels take place out of peripheral swamp areas during a subsiding flood.

In this instance, the effect of the flood would be a delaying one. However, if the stimulus to migrate during spring tide periods is due to the increased tidal amplitude with associated increased tidal streams, then rising flood-waters might also provide an additional stimulus. If such a stimulus does occur, it is masked by the dominance of the tidal cycle, in the catch figures presented.

A relationship between the discharge of fresh-water and the intensity of the season's migration was found by Lowe (1951: 306) such that the greater the discharge early in the season, the higher the

seasonal total of glass-eels. Also, floods tended to delay migration, especially if the seasonal total of glass-eels was low.

Summary

Although low water temperatures might have an inhibiting effect on invasion, no such temperatures were recorded over the catch periods given. It is not known whether any decrease in water temperature caused by flood-waters would be sufficient to delay migration, but it is thought that the primary effect of such a flood would be a delaying one due to increased water velocity.

Migrating glass-eels are not inhibited by light but instead show a preference for movement during daylight hours. A further preference is shown for migration during the ebb tide phase, although it should be noted that this phase occupies two-thirds of the tidal rhythm. A strong correlation exists between the tidal cycle and the periodicity of migrations; this is the dominant relationship between glass-eel migrations and environmental factors.

Unfortunately, I have never witnessed a major upstream migration of glass-eels. Reports from persons who have done so indicate an upstream movement of such determination that eels will exhaust themselves in trying to negotiate an obstacle, rather than give up. At this stage, the eels are preyed on by other freshwater fish, including longfinned eels, and also by water rats and birds.

Schooling behaviour, predictability and relative ease of capture and handling, makes glass-eels very susceptible to exploitation by man. Recent years have seen the development of a potentially large export market to Japan, where New Zealand glass-eels are used together with glass-eels imported from other countries, to supplement dwindling Japanese stocks for eel farming. Combined with this is a growing local interest in eel farming. To date, almost all glass-eels caught for either venture have come from the Waikato River. A real danger exists that if the fishing effort in this area continues at a high level or is intensified, then this recruitment will be overfished and the local river fishery will suffer accordingly.

3.6 HABITAT PREFERENCES

Investigations were made to see whether the two species of glass-eel, once established in fresh-water, occupied different habitats and hence reduced interspecific reactions.

Unfortunately it was not possible to sample the lower estuarine area by electric fishing due to the high conductivity of the water. Eels were captured from this area by using a hand-net at low tide. Results from such fishing showed that pigmented shortfins could be found intertidally in muddy backwaters. Most of these eels were at stages VI A III-IV in pigmentation, and the earliest stages collected were VI A II 4. These eels were not normally found in completely muddy areas, but were associated with small stones and rocks. Fewer eels were collected from the main stream itself, but sampling difficulties reduced the effectiveness of hand-netting in this area. The few longfin glass-eels caught came from the main stream, among larger rocks.

Electric fishing samples were obtained from sites c and d. Prior to new year, no glass-eels were found in any monthly samples taken upstream of site d, which is the upstream limit of tidal influence. To study any habitat preferences, selected areas of uniform habitat were fished, and the catches kept separate. The results of three such samples are shown in Table 3.14.a. Distinct habitat differences were shown between the species, with the shortfins preferring muddy and silty areas, while longfins were more numerous in the clear stony areas which supported large amounts of submerged water weed.

An experiment was carried out in the laboratory to see whether these preferences could be duplicated. A partition was made which could be used to separate both halves of a 15 l perspex aquarium. Various substrates were then placed in either half. Ten shortfin and ten longfin glass-eels, taken from the November and December 1971 monthly samples, were placed in the aquarium which was then left in a darkened room for two hours. When this time had elapsed the door was gradually opened to introduce light slowly and allow any eels exposed or swimming to find shelter. The partition was then placed in the centre of the tank, and the eels from both ends captured and recorded. For quick identification, the longfins were previously dyed a light pink by placing them in a weak neutral red solution. Three trials were carried out using each substrate choice. This meant it was necessary to use some of the eels twice. To reduce any bias

Table 3.14 Glass-eel habitat preferences.

a Glass-eels collected from two habitat types in the Makara Stream.

b Results of substrate choice experiments.

a

Sample date	stones and weed		mud	
	A. australis	A. dieffenbachii	A. australis	A. dieffenbachii
	n	n	n	n
Sept.1971	3	9	46	6
Nov. 1971	10	29	21	1
Dec. 1971	13	27	30	3
	26 (29%)	65 (71%)	97 (91%)	10 (9%)

b

Substrate choice	A. australis	A. dieffenbachii
	%	%
stones/gravel	100	100
sand	-	-
stones/gravel	83	100
fine mud	17	-
stones/gravel	37	70
fine mud with large stones	63	30

due to this, the twenty eels used in any trial were kept for a minimum of a week before being used again. The results of these substrate choice trials are given in Table 3.14.b.

Neither species preferred sand to loose stones and gravel. The few eels found resting along the margin of the sand and side of the aquarium immediately sought cover amongst the rocks while the partition was being introduced. In the second choice trial, only five shortfins (1%) were found in the fine mud, and these had partially squeezed down between the mud and the wall of the tank. Surprisingly, the fine mud by itself, was not attractive to shortfins, although in the wild, many shortfins are found in shallow muddy areas. However, when several large stones were placed with the mud, the resulting substrate proved more attractive to shortfins than did stones and gravel. The longfins showed a preference for the stones and gravel throughout all of the trials.

These results were similar to those from electric fishing samples and supported the observation of specific habitat preferences at the late glass-eel stage.

3.7 WATER PREFERENCE EXPERIMENTS

The specific habitat preferences exhibited by both species lead to consideration of whether invading glass-eels actively select a stream of their choice or whether the species proportions reflect random movement. To investigate this a series of preference experiments were conducted. The aims of these experiments were to observe (a) the preferences of glass-eels of both species for various water types, and (b) behaviour of early and late season invading glass-eels to fresh-water and sea-water.

A three-chambered choice apparatus was constructed, where glass-eels placed in a common chamber had the option of entering either of two upstream chambers. Water was siphoned into these two latter chambers from two 25 l containers. The rate of flow was controlled by an adjustable clamp.

Invading glass-eels from the Makara Stream were used in the experiments. For the first series of trials involving preferences of both species of eel for various types of fresh-water, glass-eels were kept in Makara Stream water for a minimum of ten days prior to use. In the second series of trials involving shortfins only, those eels for use in trials involving sea-water were acclimatised to a 50/50 mixture of sea-water/

fresh-water and kept in this water for two days before being tested. A number of invading glass-eels caught on 15 November 1971, were kept in similar water, but were tested the following day. For comparison, early season invading glass-eels captured on 27 August 1973 were treated similarly.

In those trials involving both species, the longfins were dyed light pink with neutral red solution, to enable quick recognition. They retained a distinct coloration for up to a week. Two control trials were run with dyed and undyed longfins and showed no differences in behaviour between the two states.

For each trial, ten eels were placed in the common chamber. These eels were either all of one species or five of each species. The apparatus was then left in a photographic darkroom for five minutes, after which time it was inspected and the numbers of eels which had moved into either upstream chamber recorded. All eels were then removed and new eels introduced for a repetition of the same trial. Several such trials were held for each water type tested. If it was necessary to use the same eels again, they were always left for a minimum of an hour before being tested a second time.

Water samples were taken from local streams and rivers. These were: Makara Stream, Happy Valley Stream, South Karori Stream (Wellington district); Waikanae River and Waimeha Stream (Waikanae district). Local tap-water and sea-water of various dilutions were also tested. If temperatures of the samples to be used varied by more than 1°C, the water was left to stand until temperatures had equalised. Reserve water was kept aerated, but if not used within a day of collection it was discarded.

Results are given in Table 3.15. In this table, n gives the number of trials for each choice, while the sum given is the total number of movements for the species indicated. Thus, in trial (a), 9S in column Mk indicates that from a total of four trials (n = 4), nine shortfins moved into the upstream chamber containing Makara Stream water.

In the first series of trials, involving both species, results were generally similar (e.g. Table 3.15.a-c). Thus both species preferred Makara Stream water to South Karori water, Waimeha Stream to either Waikanae River or Happy Valley. Natural waters were preferred to tap-water. However, results from Makara Stream with Happy Valley are of interest as they show that longfins seemed to have a slight preference for Happy Valley water while shortfins showed the opposite preference.

Table 3.15 Water preference experiments. Selected results.

S = shortfin (A. australis)

L = longfin (A. dieffenbachii)

note: a-f = both species

g-k = shortfins only

Mk = Makara Stream

S.K. = South Karori Stream

H.V. = Happy Valley Stream (fresh)

H.V.* = Happy Valley Stream (old)

S.W. = Sea-water

S.W. + a = 75% sea-water plus 25% Happy Valley Stream water

S.W. + b = 75% sea-water plus 25% tap/distilled-water

Wh = Waimeha Stream

Wk = Waikanae River

T.W. = Tap-water

	Mk	S.K.
a	9S	
	14L	1L
	n = 4	

	Mk	H.V.
b	14S	2S
	6L	8L
	n = 4	

	H.V.	Wh
c	8S	44S
	14L	36L
	n = 12	

	Wh	Wk
d	12S	2S
	10L	
	n = 5	

	T.W.	Mk
e	-	10S
	-	11L
	n = 4	

	T.W.	Wk
f	-	9S
	-	6L
	n = 4	

	S.W.	S.W.+a
g	-	16S
	n = 4	

	S.W.	S.W.+b
h	9S	-
	n = 4	

	H.V.	H.V.*
i	19S	8S
	n = 5	

	H.V.	S.W.
j	29S	1S
	n = 4	

	H.V.	S.W.
k	9S	31S
	n = 10	

These latter results were tested for statistical significance by means of a three-way analysis of variance after the method given by Snedecor (1956). Such a test accommodates differences between the species, successive tests, and between the two chambers. No significant differences were found at the 5% level for differences in species numbers within the chambers or between the chambers.

The second series of trials involved shortfin glass-eels only, using the same water types as above including sea-water. Again selected results are given in Table 3.15.d-h. Fresh Happy Valley Stream water was preferred to "old" water from the same stream collected five days prior to use (f). Fresh-water from any stream was preferred to tap-water, and full strength or diluted sea-water. Even the freshly invading glass-eels collected on 15 November showed no preference for sea-water (g).

However, when sea-water was tested with diluted sea-water ($27^{o}/_{oo}$ salinity), an interesting observation was made. If natural stream-water was used to dilute the sea-water (d) the glass-eels preferred the diluted water; if either tap or distilled-water was used to dilute the sea-water (e) then the glass-eels preferred the sea-water, although this preference was not strong.

The early season invading glass-eels from August 1973, showed a marked preference for sea-water which contrasts with the behaviour of late season glass-eels (g).

The results indicate that glass-eels are capable of making definite choices between water types, presumably based on an olfactory response to some factor in the water itself. The movements of the eels are not simply due to orientation and progress against a flow of water as differences in choice were consistent. Also, a trial using tap-water only which was known to be completely unattractive, produced no movements.

The acute olfactory sense of the freshwater eel is well known, although it is less pronounced in young eels (Miles 1968: 1600). Even so, Teichmann (1957) calculated that young eels could detect an odorous substance at a concentration equivalent to one or two molecules in the nasal organ. On this basis it seems well within the capabilities of a glass-eel at sea about to invade fresh-water to select which body of water it enters from those in the vicinity.

In the trials conducted to investigate this, water was taken from streams whose proportions of both species of small eels were known. In general terms, Waimeha Stream is a shortfin habitat while South Karori Stream and Waikanae River are longfin waters. Makara and Happy Valley Streams have mixed populations, although shortfins predominate. However, when Waimeha Stream water was tested with Waikanae River, both species showed a preference for Waimeha water. Makara Stream was preferred by both species to South Karori Stream, and visual differences in results from Makara and Happy Valley Streams were not statistically significant. Thus, no proof was obtained for the hypothesis that invading glass-eels of both species pre-select streams etc. according to the odour of inland water. This is in contrast to the known situation in the wild as implied above, where adjacent streams of different substrate and water type have quite different proportions of both species. Accordingly the hypothesis is not rejected but rather it is suggested that the experimental method may not have been refined enough to duplicate the natural situation. Perhaps other physical factors, oxygen content for example, are important in any selection.

An hypothesis has been proposed by Bachelier (1972: 163), that glass-eels return to the stream their parents lived in. This behaviour would require an hereditary olfactory memory. The dependence on olfactory stimuli for the homing ability of transplanted non-migrant eels has been demonstrated by Tesch (1970: 148) but inherited memory has not been demonstrated in vertebrates.

By carrying out the further tests on shortfins, it was possible to learn more about the attraction of fresh-water to glass-eels. As sea-water diluted with either tap or distilled-water proved less attractive than pure sea-water, the attraction is not merely due to a decrease in salinity. Further, the attractive substance can be detected in small amounts as 25% stream-water/75% sea-water proved more attractive than full strength sea-water. The substance gradually loses its attraction if water is left standing for any period.

These findings are similar to those of Creutzberg (1961) and Miles (1968) who investigated the attraction of freshwater types to glass-eels of A. anguilla and A. rostrata. Both authors concluded that the attractive substance was not related to salinity, could be removed by a charcoal filter and was decomposed with storage.

Finally, the difference in response of early and late season glass-eels to fresh-water, is of interest. That early season glass-eels are not actively attracted to fresh-water is in agreement with the behavioural response to tide flow previously noted - such eels invade on the flood tide. Similarly, Deelder (1958: 137) found that "Newly arrived elvers show no tendency to migrate into freshwater, they even try to escape when they get in it". Conversely, later in season, invasion takes place against the ebb tide and such eels show a preference for fresh-water.

This behaviour implies that early in the season, invasion of fresh-water is essentially a passive process as an end result of transport by the flood tide. Perhaps the directed movement <u>against</u> the current by the August glass-eels in the experiments was an avoidance reaction to escape from the freshwater influence, rather than orientation into a current. This latter behaviour is considered typical of a glass-eel which has undergone a behavioural change as outlined in a previous section. The lower percentage of total movements (40%) in trial (h) in contrast to 75% for trial (g) may be indicative of this.

The problem remains of why early season glass-eels carried into fresh-water, remain there when experimental evidence points to an avoidance reaction over-riding any active attraction. The evidence for these glass-eels remaining in estuarine areas is largely circumstantial as it was not possible to place a net facing upstream to fish water moving from the estuary into the sea. However, if these early season glass-eels did move back into the sea rather than remain in the estuary, then it would be expected that large numbers of pigmented glass-eels would be caught early in season re-entering the stream. Neither my own catches at night nor fishing during the day by myself and regular whitebaiters indicated that this was so. Rather, it is probable that such eels compromise by remaining in the more saline estuarine areas and completing their transition to fresh-water.

Unlike the experiments, movements in the wild are not from salt-water to full strength fresh-water but to brackish water. It would seem that the odorous substance peculiar to fresh-water proves more attractive to those eels which have completed their behavioural transition. Therefore, in early season glass-eels the attraction is sufficient for them to remain in estuarine areas where any freshwater odour would be correspondingly diluted, but they have no desire to enter full fresh-water where the odour would be more concentrated.

3.8 TEMPERATURE TOLERANCE EXPERIMENTS

When glass-eel fishing at Makara on nights when the air temperature was below 2-3°C, it was often difficult to remove glass-eels from the net. Upon lifting the net from the water the sudden drop in temperature caused the eels to become lethargic, and the net had to be vigorously shaken to remove them. Once placed in water from the stream these eels showed no ill effects and resumed normal activity. However, if the small volume of water containing the eels was allowed to stand, the temperature of the water rapidly dropped to that of the air, and the eels again became inactive. Addition of fresh stream-water would revive the eels, and none died as a result of such temperature fluctuations.

The ability of both species of glass-eel to survive sudden temperature changes was studied experimentally. Fresh glass-eels were acclimatised over a three day period, to pure fresh-water at 15°C. Four eels of each species were then removed and placed directly into containers at various temperatures. Temperatures were recorded graphically on a continuous recorder. By using water-bath systems of heat transfer, temperatures could be controlled to within ± 0.5°C. Hourly observations were made for the first eight hours; thereafter, daily checks were made for the 14 days the trials were run. The number of dead eels was recorded, with the point of death taken as the cessation of heartbeat.

The mean values of the temperatures used were, 2.0°, 4.2°, 7.5°, 9.9°, 20.1°, 23.4°, 26.7°, 29.4°C. Results are summarised in Table 3.16.

At 2.0°C, all eels suffered violent tremors immediately they were placed in the water. Violent shaking was accompanied by contortions of the body, with the head thrust back at a sharp angle and the gape at a maximum. After several minutes the eels relaxed and straightened a little, but were still immobile. Considerable mucus was extruded from the gills. The brain became noticeably opaque, although the heart continued to beat slowly. A few laboured swimming movements were made periodically by some eels, but these were always of short duration. On the third day, three shortfins died, followed the next day by the surviving shortfin. On the fifth day two longfins died and the further two died the following day.

The temperature shock was less severe at 4.2°C, and only one shortfin showed tremors, although the other eels were noticeably distressed. On the seventh day, two shortfins and one longfin died; on the eighth day one shortfin and three longfins died, followed by the remaining shortfin on the ninth day.

Table 3.16 Glass-eel direct temperature tolerance experiments. Deaths per day.

S = shortfin (*A. australis*)

L = longfin (*A. dieffenbachii*)

	mean °C							
Day	2.0	4.2	7.5	9.9	20.1	23.4	26.7	29.4
1								2L
2								
3	3S							1L
4	1S							1S,1L
5	2L							
6	2L						1L	
7		2S,1L						2S
8		1S,3L					1L	
9		1S						
10							1L	1S
11							1L	
12								
13								
14	no deaths recorded							

Between temperatures of 7.5°-23.4°C no deaths attributable to temperature effects occurred. However, at 26.7°, all longfins died, while at 29.4°, all eels died. At this temperature, eels were hyperactive, with the respiratory rate reaching 140 movements per minute, compared with 30 movements per minute at 15°C.

The results indicated that both species could withstand a direct temperature change of ±8°C from an ambient of 15°C, with no apparent ill effects. However, a change of ±11°C or greater was fatal for all longfins. A drop of 11°C also killed the shortfins, but they were able to tolerate the equivalent rise. Overall it appeared that shortfin glass-eels were more tolerant of the increased temperatures than were longfins, but no differences in survival rates were found at the decreased temperatures. Unfortunately lack of time and material did not allow the effect of acclimatisation to extremes of temperature, to be studied. Such a study would have given more meaningful results as temperature changes encountered by glass-eels under natural conditions, would be gradual.

3.9 ANALYSIS OF NEW ZEALAND-WIDE SAMPLES

Considerable effort was made to obtain a wide coverage of glass-eel samples from throughout New Zealand and offshore islands. In addition to letters and personal requests to interested persons, whitebait fishermen and processors, a circular was sent to all Fisheries Inspectors. Despite many promises of assistance, few samples were obtained.

Samples were preferred alive, air-freighted in the manner previously described. For frozen or preserved material, conversion factors were calculated to convert measurements to the approximate live values.

To calculate the effect of 5% formalin (formaldehyde solution) on the length and weight of glass-eels, the following trial was run. From a large sample of anaesthetised glass-eels ten were selected where possible, from each 0.1 cm length group represented. This gave a total of 99 specimens from 5.6-6.8 cm. Live lengths and weights were then recorded and the samples then preserved. They were remeasured at random intervals and the percentage changes in measurements from the original were calculated. Results are given in Table 3.17.a.

Although there was a tendency for the larger specimens to be more affected than smaller specimens, for reconverting to live values, the

Table 3.17 Percentage differences in length and weight of preserved glass-eels from live values.

a 5% formalin

b Frozen

a 5% formalin

Days after start		4	66	118	360
Length:	mean difference (%)	-0.5	-0.3	-0.5	-1.6
	range	-1.5, 0	-1.5, +1.0	-1.5, +0.2	-2.4, -0.8
Weight:	mean difference (%)	+4.4	+2.1	-4.2	-6.5
	range	-6.0,+11.2	-6.4,+10.1	-16.4,+2.8	-16.9,-0.2

b Frozen

Days after start		1	3	15	143
Length:	mean difference (%)	-4.4	-4.9	-5.6	-5.2
	range	-5.7,-3.2	-5.6,-4.2	-6.4,-4.8	-6.4,-4.2
Weight:	mean difference (%)	-23.8	-27.1	-32.6	-48.7
	range	-31.7,-20.0	-35.7,-21.7	-42.3,-25.8	-59.1,-37.8

relative differences were not significant, and so all sizes were treated uniformly. This meant that for length, preserved samples measured within four months of capture were left unaltered, but for samples left for longer than this, 0.1 cm was added to all observations. The weights showed considerably more variation according to length of preservation. However, as the ranges of differences in weights were so varied, it was not felt that live weights could be calculated with much reliability, and weight was not considered in subsequent comparisons of samples.

Woods (1964: 99) also conducted formalin preservation experiments on glass-eels, and found a decrease in mean length of 2.15% but an increase in mean weight of 13.2% after three days in 4% formalin. A series of trials conducted by Ege (1939: 81) gave a reduction in mean length in glass-eels after two weeks of 3.3% in 4% formalin, and 3.8% in a 6% solution; alcohol from 50-80% concentration, gave a reduction in length of 6.5% regardless of strength. Similar trends to my own observations were found by Parker (1963) for measurements of salmon smolts and fingerlings preserved in 3.8% formalin. After 30-40 days, length had shrunk to 96% of live length while weight increased for 1-2 days but then decreased at a decelerating rate.

As two frozen samples were also obtained, a further trial was commenced to determine length and weight changes in frozen glass-eels. The anaesthetised eels were weighed and measured, then placed in separate plastic bags. These were placed in a refrigerator and stored at -4°C. Periodically they were removed, thawed and measured. The results, Table 3.17.b show that most shrinkage in length occurred within the first day, although weight loss was progressive over the period of observation. In all specimens, the weight loss was high. This was in part due to the congealed slime which became detached from the body, but mainly to dehydration of the eels themselves. Again converted weights were liable to be too inaccurate to warrant further consideration.

Before considering the significance of the variation in mean sample lengths from throughout the country, two additional factors must be investigated. These are the seasonal and annual variations in size.

Seasonal Variation in Size

The mean size of invading and migrating glass-eels declines throughout the season of arrival. This decline occurs, not only in length and weight, but also in the relationship of these two variables, expressed as condition.

As only total sample weights and not individual weights were recorded, the condition factor, K, has been calculated from the mean sample measurement using the cube law as explained in a previous section. Assuming glass-eels correspond to this law, the condition values calculated provide a useful relative index for comparison of samples.

The mean monthly length, weight and condition of the 1971 and 1972 Makara glass-eel catches are given in Table 3.18. Similar figures for migrating Waikato glass-eels are seen in Table 3.13. The Makara data indicate that the phenomenon of the seasonal decline in size is a gradual process, with no sudden acceleration.

A similar seasonal size decline has previously been reported in the glass-eels of A. anguilla. Measurements recorded by Johansen (1905: 8) show a difference in average length about 0.5 cm between early and late arrivals. Wimpenny (1929: 390) presented length and weight data for glass-eels arriving at Tolombat in Egypt over a five month period. Mean values of both measurements decreased throughout this period. If condition is calculated from these data, a seasonal decline is also evident.

An extensive review of the size of glass-eels from northern, western and southern Europe was made by Strubberg (1923). He concluded that the seasonal decline in size was due to the ability of faster growing and hence larger larvae to show more activity during their migration and so arrive at their destination before smaller less active larvae. Also, earlier hatchers may experience better conditions for growth during their first few months of life.

Although these explanations are satisfactory for the decrease in length and weight, they do not adequately explain the decrease in condition. In the leptocephalus, it is reasonable to assume that weight is dependent on length, and small size would be represented by a proportional decrease in both, with little or no difference in condition. Any such difference would not be of the order observed over the season of invasion, where the condition of shortfins falls by 24% and longfins by 30%. The comparable decline for A. anguilla, calculated from the data of Wimpenny (1929: 390) is 26%.

The process of metamorphosis from leptocephalus to glass-eel is accompanied by drastic morphological changes, including overall shrinkage. The physical changes together with their biological significance, are discussed by Ford (1931). Menzies (1936: 258) suggested that the physical deterioration during metamorphosis is progressive until the glass-eels reach fresh-water and resume feeding. To this can be added

Table 3.18 Makara Stream glass-eels, 1971 and 1972.
Mean monthly length, weight and condition.

Results of t-tests for the same month in successive years, generated from length-frequency data
(for samples with n > 10 for both years)

A. australis

	1971				1972				
	n	$\bar{l}$ (cm)	$\bar{w}$ (g)	$\bar{K}$	n	$\bar{l}$ (cm)	$\bar{w}$ (g)	$\bar{K}$	T
July					31	6.34	0.24	0.93	
Aug.					124	6.25	0.21	0.87	
Sept.	293	6.08	0.20	0.91	482	6.26	0.20	0.82	12•40 + +
Oct.	215	6.03	0.17	0.79	452	6.07	0.17	0.76	3•21 + +
Nov.	225	5.98	0.15	0.72	205	5.90	0.15	0.73	2•40 +
Dec.	5	5.98	0.15	0.70	9	5.73	0.13	0.71	
	738				1303				

A. dieffenbachii

	1971				1972				
	n	$\bar{l}$	$\bar{w}$	$\bar{K}$	n	$\bar{l}$	$\bar{w}$	$\bar{K}$	
July					11	6.79	0.32	1.01	
Aug.					119	6.75	0.31	0.99	
Sept.	20	6.64	0.27	0.94	120	6.73	0.27	0.89	1•59
Oct.	14	6.55	0.23	0.80	50	6.69	0.27	0.89	2•34 +
Nov.	1	6.40	0.22	0.84	4	6.48	0.20	0.74	
	35				304				

+ = 5 percent significance

+ + = 1 percent significance

the observation of Strubberg (1923: 21) that the rate of metamorphosis is accelerated by high temperature. Therefore, late season glass-eels arriving in spring would metamorphose more rapidly than early season arrivals.

Arrival over the 1000 m isobath triggers metamorphosis in the European eel (Schmidt 1928a: 113), although the presence of leptocephali in the Mediterranean remains an enigma to this theory. The semi-pelagic larvae then continue their migration to the coast (Strubberg 1923: 21). As these newly metamorphosed eels do not feed (Johansen 1905: 8) it can be assumed that the longer the post-metamorphic period before invading fresh-water, the greater will be the decrease in condition.

A similar sequence can be proposed for events leading to the invasion of fresh-water by New Zealand glass-eels. Early in the season, relatively large leptocephali arrive off the coast of New Zealand. Metamorphosis commences at or about the 1000 m isobath, and continues as the eels near the mainland. Stage VB is attained just prior to invasion of fresh-water by the glass-eel. Thus there is little actual post-metamorphic life, and the eel has a high condition factor.

Later in the season, smaller larvae arrive above the 1000 m isobath and commence their metamorphosis. However, the sea surface temperatures are now markedly warmer and metamorphosis proceeds more rapidly than previously. Consequently, the young eel has a substantially longer post-metamorphic life at sea before entering fresh-water. The relative condition of the eel falls progressively, until it enters fresh-water and recommences feeding.

Associated with longer post-metamorphic sea life is progression in the sequence of pigmentation. Thus there is an increased likelihood of glass-eels invading late in season being more pigmented than early season specimens. Also, late season eels will have at least partially undergone a behavioural change prior to their entry into fresh-water. This means their subsequent upstream migration will not be delayed while this transition occurs.

Samples examined from throughout the country indicate that Stage VB is the stage of invasion, at least early in season. If metamorphosis was induced by some factor other than the proximity to land, for example contact with a specific isotherm, then metamorphosis at any one period of time would occur en masse. This in turn would mean that those invading glass-eels furthest from the area where metamorphosis took place, would be considerably more advanced in pigment development

than those glass-eels invading closer to this area. As this does not occur, it is concluded that the leptocephalus is the stage of distribution around the country, with the process of metamorphosis being initiated by proximity to land.

Two interesting observations relevant to this discussion, appear in literature on other species of Anguilla. Firstly, it has been recorded that invasion into rivers entering the Baltic Sea, is by small pigmented eels (Schmidt 1906: 213, Bertin 1956: 149). In this instance the invading eels have long since passed over the 1000 m isobath where metamorphosis commences. This observation is in agreement with the stage of pigmentation reflecting the length of post-metamorphic life.

Secondly, Jubb (1961: 26, 1964: 190) notes the migrations of 'post-elvers' of A. mossambica Peters into rivers of South Africa. No eels of less than 8.9 cm could be found in some rivers and these were only partially pigmented. From consideration of the prevailing ocean currents, Jubb postulates that many leptocephali are swept past the southwest coast into an area of colder temperature where metamorphosis is retarded. These larvae remain at sea for about a year, complete their metamorphosis, and grow to a size where they are able to stem the currents and reach the mainland.

Otoliths from these 'post-elvers' indicate a further year's sea life than do otoliths from true invading glass-eels of the same species. However, as the 'post-elvers' are only partially pigmented it would seem that their post-metamorphic life has been relatively short; probably the leptocephali swept past the coast do not metamorphose, until, as much larger larvae, they negotiate the current the following year and invade fresh-water. This is also supported by the fact that depths off the east coast of South Africa increase rapidly and larvae would have to be swept close to shore to encounter water of 1000 m depth or less.

Annual Variation in Size

In addition to seasonal variations in size, there is also an annual difference. From Table 3.18 small differences in mean sample lengths for the months of September-December 1971 and 1972, can be seen. The largest difference, of 0.25 cm occurs in shortfins for December. In September (the month with the largest samples for both species) differences of 0.18 cm for shortfins and 0.09 cm for longfins are found. Neither year is completely dominant in having all mean monthly lengths greater than

the other year. Thus, for shortfins the September and October 1972 lengths exceed the comparable 1971 lengths, while November and December 1971 means are greater than those for 1972. In longfins, the 1972 means exceed the 1971 values. T-test results are given in Table 3.18.

Waikato glass-eel measurements also show small annual size differences. For example, the mean length of 322 shortfins for September 1971 was 5.96 cm while 360 shortfins from September 1972 averaged 6.13 cm. Similarly, annual differences of up to 0.3 cm were recorded by Strubberg (1923: 9) for European glass-eels.

Considering the long larval life of the eel at sea with its dependence on water currents for transport, annual variations in size would be expected.

Mean Lengths of Samples

As the leptocephalus, an active stage of growth in the life cycle, is the stage of distribution around the country, it can be assumed that glass-eels from areas furthest from the general region of arrival of the larvae, would be of a larger size than glass-eels from areas in proximity to this arrival region. Consideration of the average sizes of glass-eels from different areas might then indicate the distribution routes followed by the leptocephali.

By this reasoning, the data of Vladykov (1966: 1009) imply a migration route northeastwards along the Atlantic coast, for larvae of A. rostrata. This is in agreement with the known current systems for this area. Comparable calculations using mean lengths of A. anguilla glass-eels are more complicated, as those eels arriving at eastern European countries have previously crossed the broad continental shelf of the East Atlantic seaboard, where metamorphosis is initiated.

For consideration of the various New Zealand glass-eel samples received, the country has been divided into seven areas (see Fig. 3.19). This separation into geographical areas is one of convenience for revealing any gross differences between samples; the boundaries are arbitrary and have no actual significance.

Ideally, comparisons of mean lengths should be made using live glass-eels of similar pigmentation stages, collected at the same time in the same year. This would eliminate both seasonal and annual size variations, and also shrinkage differences caused by both pigmentation and preservation. Unfortunately, insufficient samples are available from any one year to fulfil these requirements. Therefore, any annual

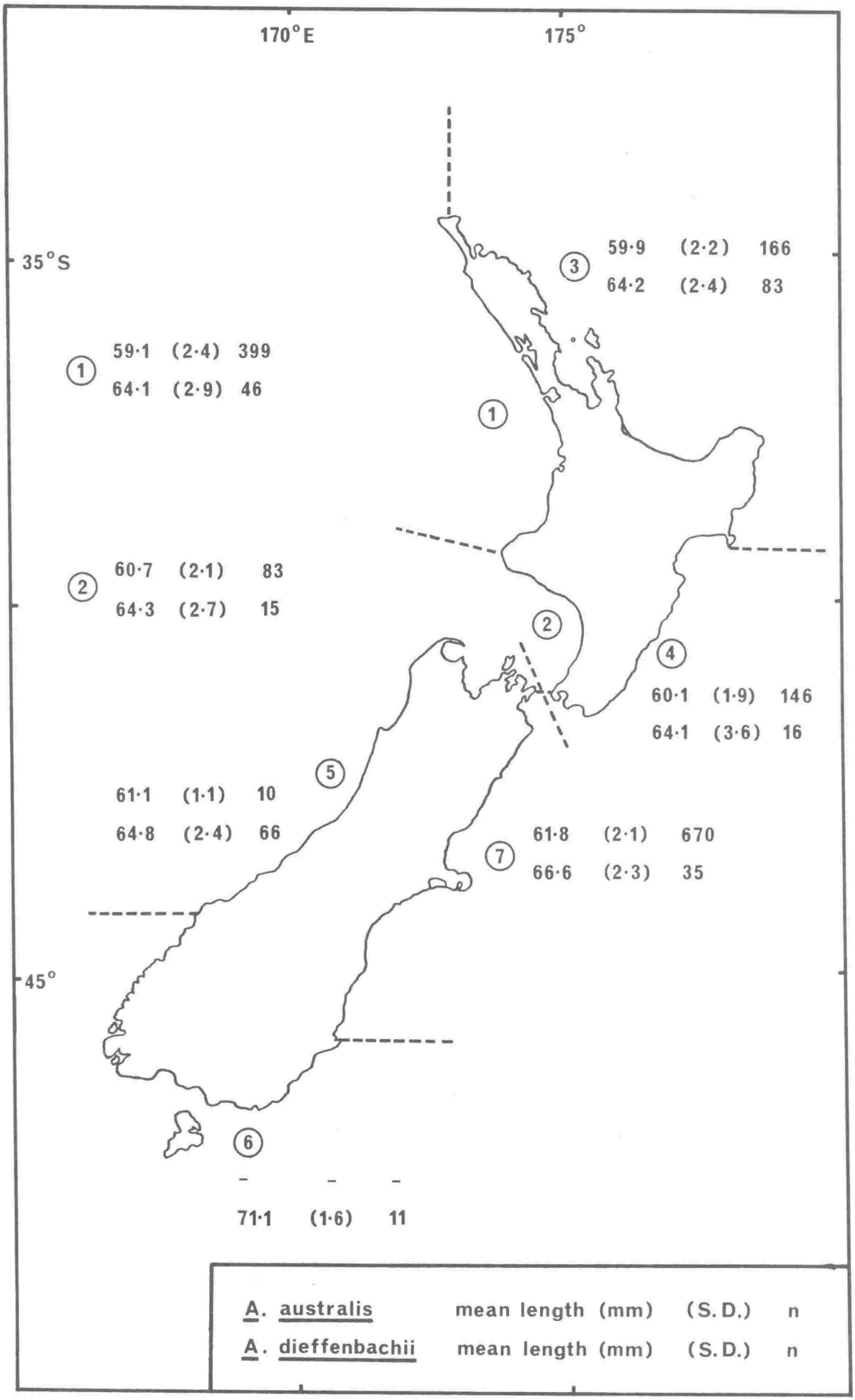
Fig. 3.19 Mean lengths of selected glass-eel samples arranged by area.

Results of one-way analysis of variance tests between areas using length-frequency distributions

Areas	d.f.	F	
A. australis			
1,2	1,481	32·0353	+ +
2,5	1,92	0·3153	
3,4	1,311	0·1554	
4,7	1,815	83·0438	+ +
3,7	1,835	96·1381	+ +
1,5	1,408	6·8547	+ +
A. dieffenbachii			
1,2,3,4,5	4,225	0·8049	
4,7	1,50	10·6143	+ +
3,7	1,117	24·9213	+ +
3,6	1,93	81·8666	+ +

\+ = 5 percent significance

\+ + = 1 percent significance


170°E
175°
35°S
45°
1
59·1 (2·4) 399
64·1 (2·9) 46
2
60·7 (2·1) 83
64·3 (2·7) 15
3
59·9 (2·2) 166
64·2 (2·4) 83
4
60·1 (1·9) 146
64·1 (3·6) 16
5
61·1 (1·1) 10
64·8 (2·4) 66
6
– – –
71·1 (1·6) 11
7
61·8 (2·1) 670
66·6 (2·3) 35
A. australis mean length (mm) (S.D.) n
A. dieffenbachii mean length (mm) (S.D.) n

variation has been ignored and no samples have been discarded because of the year of collection. To supplement my own material, measurements recorded by Ege (1939: 142, 210) have been included in the following analysis, together with unpublished data of Burnet.

As the peak of the invasion for both the Makara Stream and Waikato River was September-October, only samples from these two months were considered, with the exception of Ege's data for Hokitika and Southland. The most frequently occurring stages of pigmentation recorded in all samples were VI A II 2-4 for short-fins and VIA III 1-3 for longfins, and using these stages, the appropriate eels were assigned to one of the seven areas. After samples had been corrected for preservation shrinkage, the grand area totals were meaned. Results are shown in Fig. 3.19. For convenience in comparisons, lengths are given in mm.

The raw length-frequency data were then tested by a one-way analysis of variance to determine any north-south size differential. Results (P.65a) indicate that significant differences do occur in the length-frequency distributions for areas along a north-south axis. However, remembering that the annual difference may be of the order of 2 mm, these data must be interpreted with caution. While differences of 1 mm and more are statistically significant at the 5% level, they may not be biologically meaningful.

Despite this, it is suggested that the figures indicate a general arrival pattern of larvae from the north of New Zealand, with a subsequent southwards movement down west and east coasts. This trend is more reliably seen from the data for shortfins as the sample sizes are larger than those for longfins. Unfortunately, no shortfins were received from area six although it would be anticipated that the largest eels would occur here. All mean longfin lengths for the North Island areas are within 0.2 mm of each other and thus show no trends. However, the value from area seven is more than 2 mm greater than the North Island samples and, in conjunction with area six, indicates an arrival from the north. Although the collection date of the latter sample is not known, the eels are much larger than any others of a similar stage of pigmentation and warrant inclusion on these grounds.

Arrival from the north agrees with the pattern previously suggested from the distribution of the two subspecies of A. australis, but is contrary to the theory of transport of larvae by the East Australian Current with arrival off the southwest coast of New Zealand.

Collection Dates of Samples

To investigate any seasonal staggering of glass-eel movement in fresh-water by different areas, all known samples were arranged according to the date of collection. These included my collections, unpublished material of Burnet, and data from Ege (1939: 91, 155). These data are given in Table 3.19.

The frequencies given in this table represent variable fishing efforts. Also, the peak invasion time in a given locality may vary significantly from year to year, depending on hydrological conditions. Because of these factors, and the small sample numbers for most areas, it is not possible to make accurate predictions about the length of the glass-eel season in different areas.

However, the earliest peak in the season is found in area one, which is also the area with the smallest mean size of glass-eels. Peak periods for the South Island areas, five and seven, are later in season. The monthly totals approximate the invasion intensity calculated for the Makara data, with peak months being September, October and November.

Species Proportions

During freshwater invasion or subsequent upstream migration, both species of glass-eel are typically found together. In broad terms they have a common season of arrival and show similar behavioural responses to stimuli. However, more specific behaviour is shown in habitat preferences. The proportion of both species occurring in samples of upstream migrating glass-eels may be biased by the favourability of the downstream habitat for either species, and also vary with the time of the year.

If it is assumed that most eels remain resident in the water system they originally invade, and relative mortalities are proportional to the numbers of both species present, then the relative abundance of both species of invading glass-eel should be a reliable index of the proportion of both species present. Unfortunately, because of the nocturnal behaviour of invading glass-eels, such samples are not easily obtainable, and the majority of glass-eels in the species proportion map given, were collected during their upstream migration.

The species proportions of all data available to me are shown in Fig. 3.20. The first figure represents the percentage of shortfins and the sample number is shown in brackets. The grand species proportions from these data are, shortfins 90%, longfins 10% (n = 11557), but these cannot be considered indicative of the nation-wide pattern.

Table 3.19 Frequency of collection dates of all glass-eel samples by area.

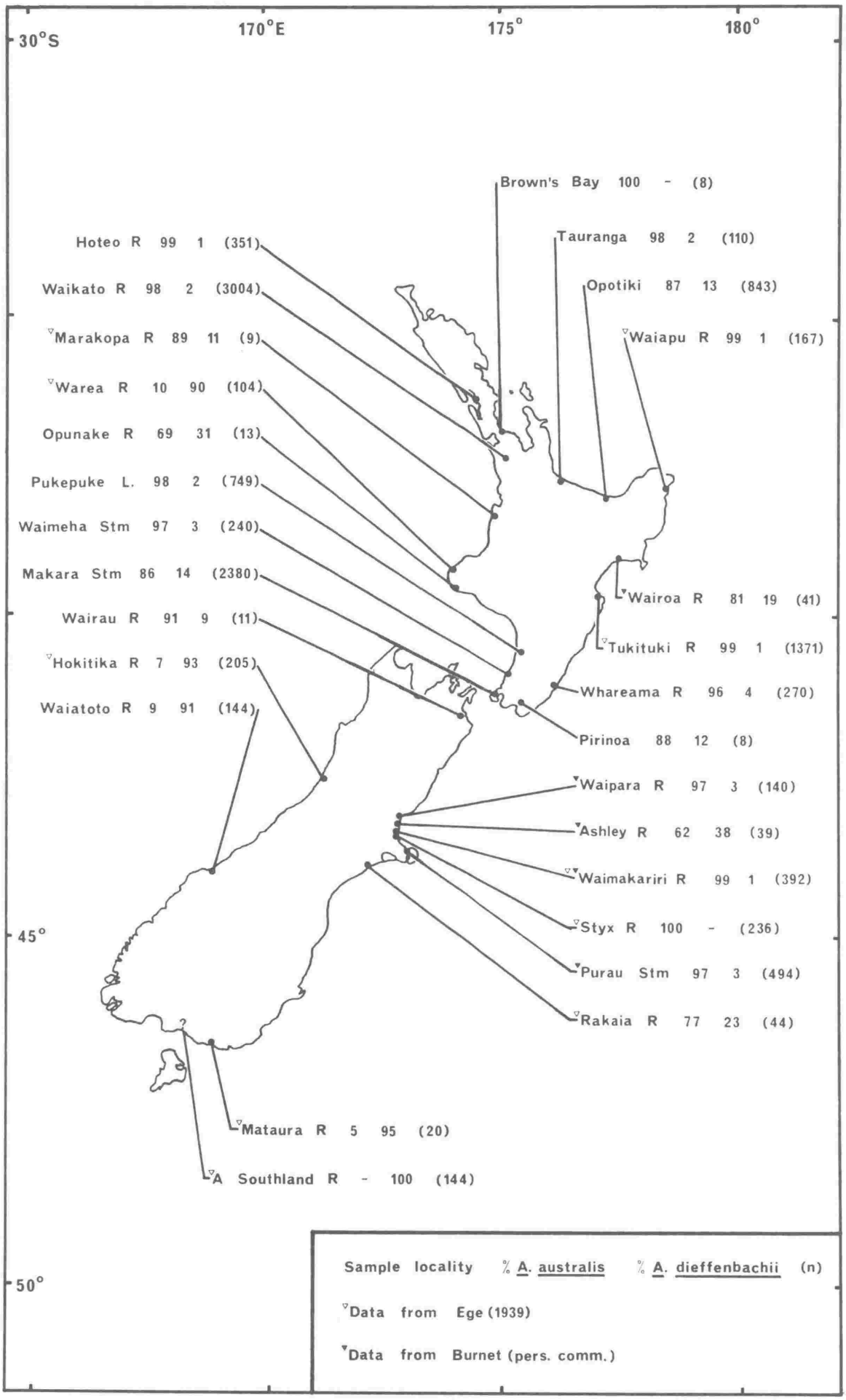
S = shortfin (*A. australis*)

L = longfin (*A. dieffenbachii*)

Areas 1-7 correspond to those given in Fig 3.19.

		Month of collection							
Area	Species	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	N
(1)	S		3	7	7	3	1		21
	L		3	7	3	3			16
(2)	S	1	1	3	3	4	1		13
	L	1	1	3	2	3	1		11
(3)	S					2	1		3
	L					1	1		2
(4)	S		1	2	1				4
	L		1		1				2
(5)	S				1	1			2
	L				1	1	2	1	5
(6)	S								-
	L								-
(7)	S			1	5	3			9
	L			1	4	1			6
	S Σ	1	5	13	17	13	3		52
	%	2	9	25	33	25	6		
	L Σ	1	5	11	11	9	4	1	42
	%	2	12	26	26	22	10	2	

Fig.3.20 Species proportions of all available glass-eel samples.


30°S
170°E
175°
180°
45°
50°
Brown's Bay 100 - (8)
Tauranga 98 2 (110)
Opotiki 87 13 (843)
▽Waiapu R 99 1 (167)
Hoteo R 99 1 (351)
Waikato R 98 2 (3004)
▽Marakopa R 89 11 (9)
▽Warea R 10 90 (104)
Opunake R 69 31 (13)
Pukepuke L. 98 2 (749)
Waimeha Stm 97 3 (240)
Makara Stm 86 14 (2380)
Wairau R 91 9 (11)
▽Hokitika R 7 93 (205)
Waiatoto R 9 91 (144)
▽Wairoa R 81 19 (41)
▽Tukituki R 99 1 (1371)
Whareama R 96 4 (270)
Pirinoa 88 12 (8)
▼Waipara R 97 3 (140)
▼Ashley R 62 38 (39)
▽▼Waimakariri R 99 1 (392)
▽Styx R 100 - (236)
▼Purau Stm 97 3 (494)
▽Rakaia R 77 23 (44)
▽Mataura R 5 95 (20)
▽A Southland R - 100 (144)
Sample locality % A. australis % A. dieffenbachii (n)
▽Data from Ege (1939)
▼Data from Burnet (pers. comm.)

The data show that shortfins were the predominant species in the North Island, especially north of Tauranga and on the east coast. In the South Island, longfins were the principal species on the west and south coasts and shortfins on the east. This distribution is of interest as it is similar to that given by Schmidt (1928: 387) who found longfins predominated in the south and west of New Zealand and shortfins in the north and east.

Assuming these agreements indicate the validity of the proposed distributions, then the differences must be attributable to one of two causes. Either the distribution is random and reflects the routes of arrival of the larvae, or both species exhibit specific habitat choices at an early stage of their arrival in coastal waters.

It has been previously stated that the leptocephalus is regarded as the stage of the life cycle at which distribution around the country takes place. However, in the vicinity of the 1000 m isobath which generally lies 50-100 km offshore, the influence of fresh-water would be barely, if at all, perceptible. For instance, Stanton (1971: 154) found a tongue of discernable "fresher water" extended for 29 km from the mouth of the Buller River on the west coast of the South Island. The average discharge from this river at the time of observation was 6000 cusecs. However, this influence extended obliquely from the shore due to the passage of the Westland Current.

The Clutha River which has the largest flow of any river in New Zealand, has a direct effect on inshore salinities recorded 100 km further along the coast (Jillet 1969: 358). However this influence is adjacent to the shore and seldom extends beyond 30 km offshore. Obviously offshore movement of fresh-water is highly variable and is largely dependent on rainfall and coastal circulation.

Thus it is extremely unlikely that the leptocephalus could show any preference for commencing metamorphosis in an area offshore to the preferred water-type of the juvenile eel. Further, the known distribution is not indicative of dispersal according to temperature preference as isotherms have a general east-west orientation. Therefore the overall distribution of both species is probably attributable to arrival routes but with local differences due to preferences shown by invading glass-eels.

However, consideration of mean lengths of glass-eels by area suggests an arrival pattern for both species from the north of New Zealand. If correct, this common route together with a similar length of larval life would in turn suggest reasonably close proximity of spawning areas

to each other. Conversely the endemism of longfins compared to the more widespread distribution of shortfins is thought to be indicative of more widely separated spawning areas.

At the present state of knowledge it is not possible to resolve these problems but it is suggested that the overall species pattern within New Zealand reflects the larval arrival routes.

The occurrence of more than one species of eel in samples of migrating glass-eels is not peculiar to New Zealand. Jubb (1964: 195) gives an instance of four anguillid species living within one river system, i.e. A. mossambica, A. marmorata Quoy and Gaimard, A. nebulosa labiata Peters and A. bicolor bicolor McClelland. The first three species are longfins while the fourth is a shortfin. Although considerable overlap in the range of these species occurs, no data are available for their relative proportions in glass-eel and 'post-elver' samples. A large sample of A. reinhardti Steindachner glass-eels examined by Ege (1939: 211) contained approximately 1% of A. australis australis. Again, the former species is a longfin and the latter a shortfin.

With the exception of inter-tropical eels which show no marked seasonal reproductive cycle (Bertin 1956: 184), catadromous and larval migrations of other freshwater eel species are seasonal phenomena. Arrival times of glass-eels of temperate species is from late winter through spring, but this may be advanced or retarded according to proximity of the spawning area. Although few data are available, it can be assumed that in areas of overlapping species, mixed species migrations are common.

3.10 VERTEBRAL COUNTS

The total number of vertebrae can be one of the most important criteria used to distinguish morphologically similar species of fish. It is the most significant character used to date to separate members of the Family Anguillidae.

Schmidt (1927: 385) investigated vertebral counts in both species of New Zealand eels, but found the differences too slight to form a distinctive distinguishing character. He considered that this fact would lead to difficulty in separating the larvae of the two species. In the course of research on Australian eels, Schmidt (1928b: 197) showed that a real difference exists between vertebral counts of Australian and

New Zealand shortfinned eels, with the former having an average of 112.68 vertebrae and the latter 111.64. Accordingly he proposed the recognition of two subspecies. Ege (1939: 205) supported this proposal and considered the meristic differences to be an expression of geographical separation. He gives mean vertebral counts for the Australian and New Zealand shortfins as 112.64 and 111.73 respectively.

Although these differences are small, Schmidt (1928b: 199) considered them indicative of geographical separation of the spawning areas of the two subspecies. He postulated that the New Caledonian submarine ridge formed a physical barrier in the breeding area, confining the Australian subspecies to the west of the ridge and the New Zealand subspecies to the east.

The question of whether phenotypic variation is environmentally or genetically determined has recently been brought to light in the controversial theory of Tucker (1959). He maintained that the American and European eels are not separate species as commonly supposed, but ecophenotypes of A. anguilla. Furthermore, the distinguishing meristic features between the two 'populations' could be attributed to temperature differences in the spawning area encountered by the developing larvae and their subsequent distribution by water currents.

This theory has been criticised by several authors including D'Ancona (1959), Jones (1959), Deelder (1960b), Bruun (1963) and Sinha and Jones (1967b). In his hypothesis, Tucker refers to experiments by Tåning (1952) who produced changes in the mean vertebral number in Salmo trutta with sudden temperature changes. Although the changes in vertebral number produced were proportionally similar to those which exist between the American and European eels, Bruun (1963: 159) concluded that the experimental conditions were in no way similar to the temperatures which affect the eel eggs during their development.

More recent evidence on the existence of two distinct species is the results of haemoglobin electrophoretic patterns of both species, investigated by Sick et al (1967). The absence of a haemoglobin allele in European eels is put forward as strong evidence against the one population concept of Tucker.

The difference between mean vertebral counts of Australian and New Zealand shortfins is one vertebra. If invading New Zealand shortfins, at some stage of the season, showed a mean vertebral count similar to that of the Australian subspecies, this would lend support to the contention of Tucker that meristic variation can be environmentally

induced. Also a common spawning area for both subspecies could be assumed, with either or both subspecies providing spawning stock. Perhaps those larvae hatching early in the season could encounter currents which would direct their migration to, for example, Australia, whereas hydrological conditions later in the hatching season might favour transport of larvae to New Zealand. Small seasonal temperature differences in the spawning area could conceivably bring about a gradual change in mean vertebral count.

Further, as any changes in temperature and current flow would be gradual, the earliest shortfin glass-eels to invade New Zealand freshwaters, could be expected to have similar vertebral counts to the Australian shortfin. As the proportion of larvae with a reduced vertebral count increases throughout the season, the mean vertebral count would become established at the value recognised for New Zealand shortfins. Such a hypothesis can be tested by examination of the mean monthly vertebral count for invading shortfin eels throughout their arrival season.

The 1972 Makara glass-eel samples, covering a six month season of arrival, provided suitable material for such an analysis. These samples had been stored in alcohol and proved satisfactory for investigation by radiography.

Where possible, a minimum of 100 eels of both species were examined each month. Longfins were included as a control, to see whether any similar vertebral count changes to those "proposed" for shortfins occur. Fifty eels were taken from the first half of the month and 50 from the second half. A fine grain radiographic film was used with a 1½ minute exposure at 25 kv giving best results. The negatives were examined with a binocular microscope, using strong reflected light.

Total vertebral counts were made. For this, the thin atlas vertebra immediately behind the cranium, was counted as the first vertebra, and the last hour-glass shaped vertebra was taken as the last but one. All structures posterior to this were counted as one vertebra. These latter centra fuse during subsequent development to become one compound vertebra. In practice it was easier to count the last neural arch as the terminal vertebra, as this consistently overlay the last two centra.

As no differences were found between half-monthly means, the data are presented as mean monthly values in Table 3.20.

Table 3.20 Vertebral counts of New Zealand glass-eels by month of arrival in fresh-water.

A. australis

No. of vertebrae	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
115		2		1	1		4
114		3	7	5	4		19
113	1	14	25	29	31	1	101
112	8	25	64	59	76	3	235
111	5	29	47	56	60	5	202
110	3	10	19	21	17		70
109		1	3	1	3		8
108		1					1
	17	85	165	172	192	9	640
Mean	111.59	111.65	111.67	111.66	111.68	111.56	111.66
S.D.	±0.84	±1.22	±1.06	±1.04	±1.00	±0.68	±1.05

A. dieffenbachii

No. of vertebrae	July	Aug.	Sept.	Oct.	Nov.	Total
115	1	1	1	1		4
114		12	11	5		28
113	2	32	19	14		67
112		36	28	18	1	83
111	1	14	7	7		29
110		1	1	3		5
	4	96	67	48	1	216
Mean	113.00	112.45	112.52	112.29	112.00	112.44
S.D.	±1.41	±0.95	±0.98	±1.10		±1.01

The seasonal range in the mean vertebral count for shortfins is small (0.12 vertebra) and does not overlap that of the Australian subspecies. Therefore, the hypothesis that early in season, New Zealand receives a proportion of shortfin glass-eels whose vertebral counts correspond with the Australian subspecies, is rejected. There is no reason to consider that Australian and New Zealand shortfins are ecophenotypes of the same species, but rather that they are separate subspecies. The seasonal mean vertebral number of 111.66 is in good agreement with the values determined by Schmidt and Ege.

The seasonal range for longfins for the months of August-October is 0.23 vertebra. Insufficient data are available for July and November. The seasonal mean of 112.44 is slightly less than the 112.66 calculated by both Schmidt and Ege, but is well within the standard deviation of $\pm$1.005 given by Ege.

4 IMMATURE EELS

4.1 INTRODUCTION

With the onset of summer each year, mass upstream migrations of juvenile eels of both species take place throughout the country.

The smallest eels commence their migration from the upper estuarine areas, where they have been resident since their arrival as glass-eels a little over a year previously. From there they make their way steadily upstream and show considerable determination in overcoming obstacles en route. The most easily observed and well known migrations are those whose progress is interrupted by hydro-electric dams.

Karapiro Dam, 130 km upstream on the Waikato River (Fig. 2.1.a), is the lowermost of several power stations on this river. The annual elver migration there is of such magnitude that it can pose considerable problems. Dam personnel reported that on one occasion, a malfunctioning turbine was stopped for inspection. During the maintenance period, elvers swam up the outlet and completely clogged the turbine chamber. They had to be manually removed before the turbine could function again.

A daytime visit to the dam during the season of elver migration typically shows the spillway festooned with the dried bodies of elvers. At night, especially during a light rain, the elvers attempt to climb the spillway or the face of the dam. The latter involves a vertical climb of 30 m. Those eels which have not negotiated the climb by daybreak and are unable to find cover in a crack or joint, are liable to become desiccated by the sun and remain adhered to the dam. That significant numbers successfully negotiate Karapiro Dam is evidenced by the later but much smaller run of elvers which occurs at Arapuni Dam, the next upstream power station.

Elvers also by-pass most waterfalls and rapids by climbing along the damp margins and so avoiding the main volume of water. However, they are unable to penetrate beyond areas where a swift current rushes over bare and smooth rock. The Huka Falls on the upper Waikato River, provide an impassable barrier to elvers, and prevent their entry into Lake Taupo. Likewise, Travers (1871) reported that a series of rapids in the Waiau River, North Canterbury, confined eels to the downstream section.

This summer migration, or secondary migration as it is commonly known, is of major importance in populating upstream areas. In large rivers, waves of small eels, grouped approximately by size, reach

progressively further upstream each year. If suitable habitat is encountered, many eels may choose to remain and establish territories, rather than progress further upstream. In this way, eels are able to disperse and occupy the available habitats along the complete river system, including territories vacated by migrant eels.

That not all eels migrate upstream from the estuarine areas is seen by the frequently large populations which estuaries contain. Such populations, especially among small eels, are largely shortfins. This is further supported by a small fishery established on the mudflats at the head of the Firth of Thames, Hauraki Gulf. Eels caught from this area seen by myself, were all shortfins and had been feeding almost exclusively on crabs.

This annual upstream migration is not confined to New Zealand eels. Skead (1959) reviewed several years observations on the migration of elvers of A. mossambica, in the Buffalo River, South Africa. Summer migrations of Australian eels are recorded by Kershaw (1911) and Whitley (1929). A similar phenomenon was witnessed in New Guinea by Herre (1930). It appears that the "dakko" stage of the Japanese eel is a migratory elver, while summer migrations of juvenile European eels have long been known.

4.2 MATERIALS

Distribution of Samples

The invasion of glass-eels into estuarine areas seems to have been regarded by Cairns (1941: 62) as a possible 'pressure' which induced the elvers to migrate in the following months. In view of the continuing summer migrations which take place throughout the first few years of life, this explanation is unsatisfactory.

However, some elvers do move upstream in the company of migrating glass-eels, over the winter and spring months. Perhaps the presence of glass-eels is sufficient to arouse a latent migratory urge in the elvers and causes them to migrate prematurely. Three small samples of such elvers were obtained from glass-eel catches from the 'Elbow' at Pukekohe, during 1970. These were transported alive to the laboratory for examination. All the 206 elvers were shortfins with a mean length of 8.6 cm (range 6.9-13.2 cm). The occasional large runs of these eels proved a nuisance to both glass-eel and whitebait fishing.

Further elvers were caught at Makara during September-December while fishing for glass-eels at the stream mouth. In 1971 a total of 86 were taken, of which 85 were shortfins. The size range was large at 8.5-30.0 cm but 85% were less than 20 cm. In 1972, although there was an increase in fishing effort, only eight elvers, all shortfins, were taken. All these elvers were in good condition and the few whose stomachs were examined indicated they had been feeding on marine organisms. It was presumed that these elvers were resident in the lower estuary or adjacent parts of the sea, and moved at will between the two.

The true elver migration over the summer months, was observed and sampled at both the Makara Stream and the Waikato River. To obtain more widespread samples, a circular was sent to all major hydro dams requesting personnel to catch samples of the migration and record any relevant information. Preserving jars and formalin were supplied to those stations which indicated they were able to help. In this way, elvers from an additional seven localities were obtained.

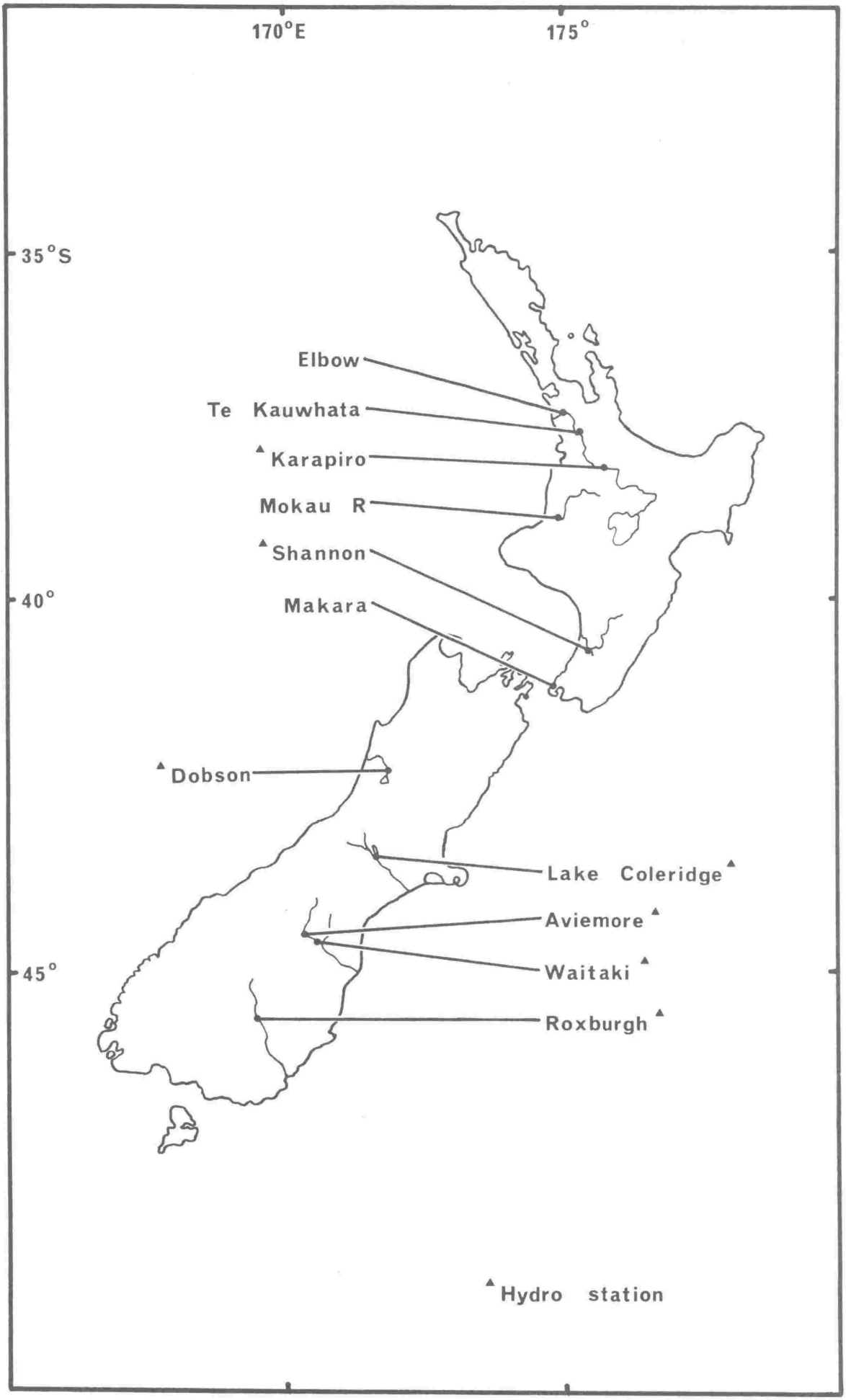
The areas from which elvers samples were received are shown in Fig. 4.1.

Period of Migration

All samples were collected from January to February. Cairns (1941: 62) noted that elvers arriving at the lowest power station on the Waikato River, then slightly above Karapiro, were very regular in their time of appearance. Dates given for four consecutive years 1936-1939, lie between January 18-22. In 1970, I visited Karapiro Dam twice in early February and saw the end of the migration. Observers stated that the run had begun in mid-January and had almost completely finished by the last week of the month. However, their criterion for defining the beginning and end of the migration was the absence of elvers during the day. It was found that although few elvers may be seen during the day, vast numbers could still be present and would swarm up the spillway at night.

During 1971, the first elvers seen at Karapiro Dam were on 18 January. Again I collected samples a week later, by which time the peak of the run was over. The run in 1972 was the smallest remembered by experienced observers. The cause for this is not known, but the commencement of large scale glass-eel fishing in 1970 may have been a contributing factor. In 1973, elvers were seen in January 17, and a substantial run occurred over the following days.

Fig. 4.1 Localities from which elver samples were received.


170°E
175°
35°S
40°
45°
Elbow
Te Kauwhata
Karapiro
Mokau R
Shannon
Makara
Dobson
Lake Coleridge
Aviemore
Waitaki
Roxburgh
Hydro station

My data are in agreement with the consistency of arrival observed by Cairns.

Nothing is known about the migration from the upper estuary to the dam itself. In this stretch, the water is often turbid and no reports of the form the migration takes have been received. It is assumed that the elvers swim close to the banks.

The Maoris were well acquainted with the annual migration of elvers. Downes (1917: 303) records the fishing season "commenced in the early summer .... and lasted for two or sometimes three months". Elvers were captured as they attempted to climb rock faces, or bundles of brush were placed in pools where the elvers had congregated. The elvers which climbed into the bundles at night would be shaken out the following morning.

4.3 ANALYSIS OF SAMPLES

Length of Elvers

The lengths of samples, as given in Table 4.1, indicate the variable size of migrating elvers from different localities. In all samples containing both species, the mean longfin length exceeds that of the shortfins. This reflects a similar trend seen in glass-eels. As expected, elvers recorded at an upstream site are larger than downstream elvers from the same river. This is seen from both Makara and Waikato, but not from the Waitaki River samples (Waitaki and Aviemore). However, these latter samples are small and cover a larger size range of 12 cm.

Typically, the length-frequencies of elvers correspond well to a normal distribution pattern. Fig. 4.2 shows four typical samples.

Within any one area, variations in mean lengths occur throughout the migratory season. This is seen in Table 4.2 where samples from Karapiro Dam are arranged chronologically. Included in this table are figures from Woods (1964: 100) for two samples taken from the same site - the base of the spillway. A range of 1.3 cm for the mean shortfin length and 1.8 cm for longfins can be seen. Of interest is the similar trend in these lengths, such that for any one sample, an increase or decrease in mean length for one species is paralleled by a similar change in the other species. The magnitude of these changes is also similar. The significance of this arrival pattern by similar "size groups" is not known.

As a check to see whether the variations in lengths recorded

Table 4.1 Migratory elvers: species proportions and mean lengths (cm).

Area	Month	n	A. australis			A. dieffenbachii		
			%	$\bar{I}$ (± 1 S.D.)	range	%	$\bar{I}$ (± 1 S.D.)	range
Te Kauwhata	Jan.	743	100	8.1 (±0.87)	5.9-11.4			
Karapiro	Jan.-Feb.	3260	62	9.0 (±0.98)	6.6-12.9	38	9.9 (±1.36)	6.8-15.1
Mokau River	Jan.	232	18	9.4 (±0.81)	7.6-11.1	82	10.2 (±0.99)	8.3-13.0
Shannon	Feb.	233	18	10.2 (±0.66)	8.3-11.6	82	11.1 (±0.80)	9.4-13.6
Makara site 'd'	Feb.	169	96	7.5 (±0.75)	6.2-11.3	4	8.1 (±0.91)	7.4-10.2
site 'e'	Jan.-Feb.	44	61	7.9 (±1.22)	6.3-11.6	39	8.4 (±0.92)	7.2-10.4
Dobson	Jan.	216	12	10.1 (±0.88)	8.1-11.8	88	11.9 (±1.30)	9.7-15.8
Lake Coleridge	Jan.	80				100	16.2 (±1.81)	12.9-21.9
Aviemore	Feb.	26				100	16.9 (±2.79)	11.6-23.7
Waitaki	Feb.	65	9	13.5 (±1.86)	10.8-16.1	91	16.7 (±2.41)	12.6-22.3
Roxburgh	Jan.-Feb.	207	1	12.0 (±0.30)	11.7-12.3	99	14.9 (±4.00)	10.8-31.5
		5275						

Fig. 4.2 Length-frequencies of four elver samples.

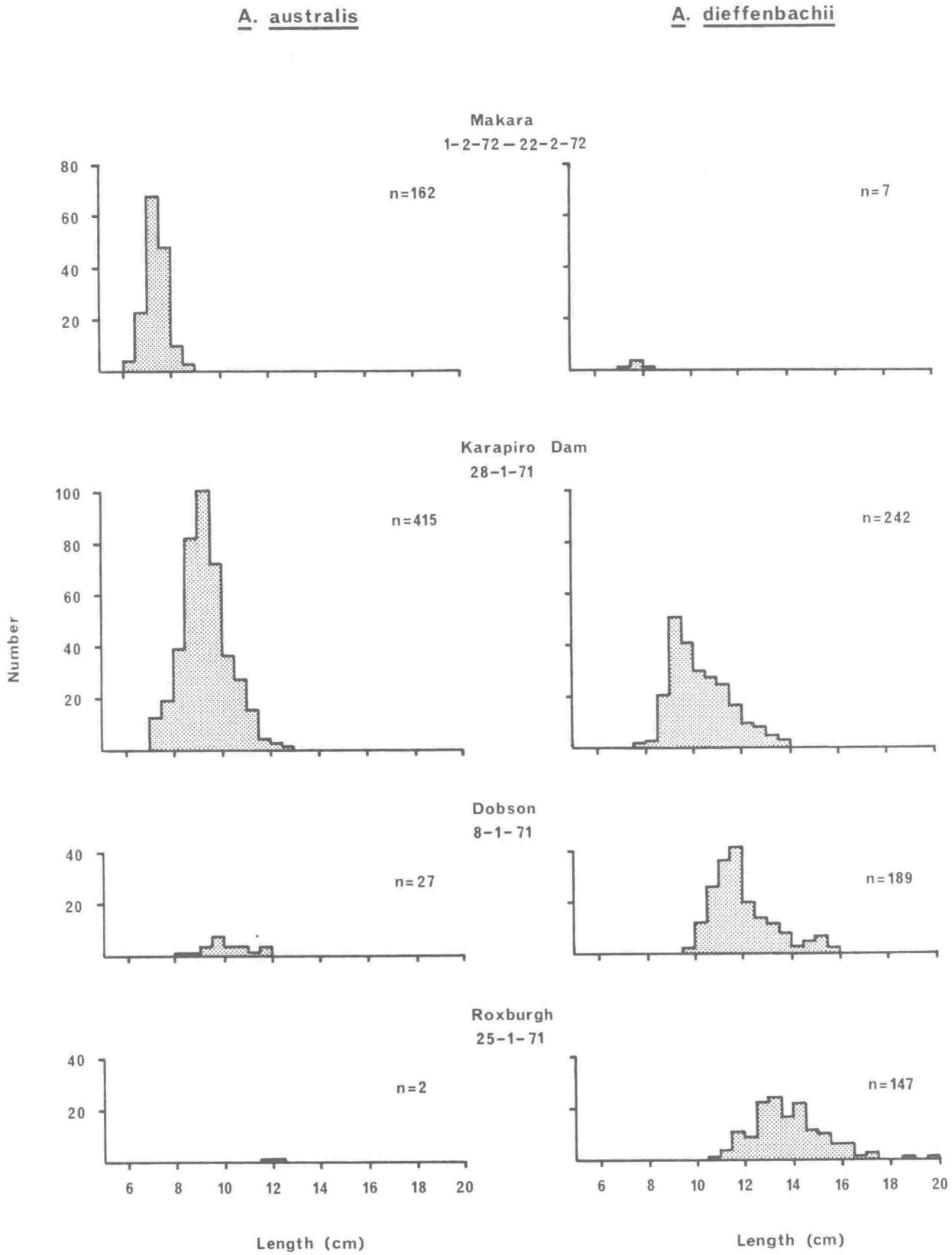

A. australis
A. dieffenbachii
Makara
1-2-72 – 22-2-72
n=162
n=7
Karapiro Dam
28-1-71
n=415
n=242
Dobson
8-1-71
n=27
n=189
Roxburgh
25-1-71
n=2
n=147
Number
Length (cm)
Length (cm)

Table 4.2 Migratory elver samples from Karapiro Dam (base of the spillway): species proportions and mean lengths (cm).

Date	n	A. australis			A. dieffenbachii		
		%	$\bar{I}$ (± 1 S.D.)	range	%	$\bar{I}$ (± 1 S.D.)	range
19/1/71	276	86	8.4 (±0.83)	6.7-10.6	14	9.0 (±0.97)	7.3-12.2
26/1/71	484	47	9.5 (±1.03)	7.4-12.9	53	10.8 (±1.29)	7.7-14.8
28/1/71	657	63	9.3 (±0.97)	7.1-12.5	37	10.3 (±1.26)	7.8-15.1
"	333	65	9.3 (±1.15)	6.9-12.4	35	10.3 (±1.13)	7.3-13.3
5/2/70	376	62	8.9 (±0.73)	7.1-11.1	38	9.3 (±1.42)	7.0-14.4
12/2/70	647	48	8.9 (±0.81)	6.6-11.6	52	9.4 (±1.14)	6.8-13.9
*27/2/62	357	74	9.3 (±2.22)		26	9.8 (±2.24)	
* 5/3/63	314	76	9.7		24	10.4	

* data from Woods (1964: 100)

were not simply due to random fluctuations within any one night, two samples were collected on 28 January 1971. Both were taken from the same place at the base of the spillway, but an hour apart. The results were identical (Table 4.2) indicating that the pattern in mean lengths was not attributable to chance but represented a real grouping.

Using this combination of samples from three separate years, it is not possible to observe any seasonal trend in the mean sizes.

Species Proportions

Table 4.1 also gives the percentages of both species for the various samples. Most specimens, 8%, came from the North Island. Here, 6% of the catch were shortfins whereas in the South Island, shortfins comprised only 6% of the species proportions. The fluctuations which occur in the proportions of both species arriving at Karapiro Dam can be seen from Table 4.2. No trend is obvious but the overall predominance of shortfins is apparent. Again, the similarity between the two samples of 28 January 1971 shows the proportions remain consistent on any night.

The Te Kauwhata sample, collected from the base of a radial flood gate at the entrance to Lake Waikare, is of interest, as it was comprised completely of shortfins. Similarly, in Makara the downstream site (d) showed a higher proportion of shortfins than did the upstream site (e). These observations are discussed in a later section.

Age Groups

Distinct age groups could not be distinguished from examination of the length-frequency data, and so some age determinations were made. The method of ageing eels from burnt otoliths is fully discussed in a following section. Samples aged were small, as it was not intended to establish growth rates but only whether several age groups were present in the samples, and the approximate proportions of each group.

From the results it was found that there was frequently an overlap in length between successive age groups. In such cases, the mid-point of the overlap was taken as the age group limit. Where successive ranges did not meet, the mid-point of the difference was defined as the group limit.

Results from Waikato and Mokau Rivers are presented in Table 4.3. Unfortunately South Island specimens were all preserved in strong formalin, and the otoliths were generally unsuitable for reading. Roxburgh and Aviemore elvers were examined, and it was found that both contained

Table 4.3 Migratory elvers: proportions of age groups in samples from Waikato and Mokau Rivers.

S = shortfin (*A. australis*)

L = longfin (*A. dieffenbachii*)

n = number aged

range = range in length of aged eels

% = percentage of total sample per age group

Area	Month	Species		Age Groups		
				0	1	2
Waikato ("Elbow")	Aug.	S	n	11	15	4
			range (cm)	6.9-8.4	8.2-10.7	11.0-12.9
			%	57	39	4
				0	1	2
Waikato (Te Kauwhata)	Jan.	S	n	7	6	2
			range (cm)	6.5-7.3	7.5-9.6	10.4-11.0
			%	21	76	3
				0	1	2
Waikato (Karapiro Dam)	Jan.	S	n	8	10	7
			range (cm)	6.6-7.7	7.9-9.8	10.2-12.3
			%	8	77	15
				0	1	2
"	"	L	n	1	15	10
			range (cm)	7.8	8.2-10.4	9.9-12.4
			%	6	63	31
				0	1	2
New Plymouth (Mokau R.)	Jan.	S	n	1	4	4
			range (cm)	7.6	8.5-9.3	9.8-11.1
			%	2	55	43
				1	2	3
"	"	L	n	5	4	3
			range (cm)	8.5-10.1	10.6-11.3	12.2-13.0
			%	57	30	13

eels from age groups three to seven, but the deterioration of otoliths prevented reliable age groups from being defined. These data are not presented.

The shortfin elvers from the "Elbow" captured during August, show high proportions of age groups 0 and 1. In the summer (January) samples from Te Kauwhata and Karapiro Dam, the age group 0 of August has been promoted to age group 1 etc. Several aspects are of interest. The high proportion of age group 1 (39%) in the August sample indicates that a considerable number of shortfins choose to spend at least the first two years of freshwater life in the upper estuarine areas. The Te Kauwhata sample is dominated by age group 1, as are the Karapiro Dam samples for both species. In these January collections, age group 0 is comprised of the previous year's glass-eels. As would be expected, this age group is more prevalent in the downstream (Te Kauwhata) sample.

Habitat preferences are discussed later, but it has already been suggested that many shortfin glass-eels and elvers remain in the upper estuary for one to two years. It might be anticipated that small longfin eels, being less suited to such areas, would migrate upstream more rapidly. Certainly the differences between the species proportions of glass-eels and Karapiro Dam elvers support this theory. However, if the upstream movement of longfins is rapid, then it would be expected that age groups 0 and 1 would predominate at Karapiro. In fact, although age group 1 is the largest of the three groups represented, age group 2 (31%) far exceeds age group 0 (6%). Therefore, it seems that large numbers of longfins elvers from age group 0 and, more surprisingly, substantial numbers from age group 1, live in the waters downstream of the dam.

New Plymouth elvers also show a predominance of age group 1. Unfortunately the exact locality on the Mokau River of this catch could not be ascertained, but the presence of age group 3 among the longfins may indicate a less rapid upstream migration than that of shortfins.

Overall, although a large percentage of shortfin glass-eels remain resident in the lower reaches of rivers, those that do migrate upstream do so more rapidly than longfins.

4.4 OBSERVATIONS

Behaviour

The behaviour of migrating elvers was observed during sampling visits to Karapiro Dam.

Both 1970 and 1971 trips took place after the peak of the migration was over. The only elvers found during daylight hours were congregated in cracks on the spillway and in a shallow pool formed on a small area of exposed ground at the base of the dam wall. Some elvers from the latter area were seen to ascend a shaded vertical wall to reach a small outlet pipe from which water trickled. Apart from these eels, no other movement was observed during daylight. This contrasts with conditions during the peak of the season as witnessed by power station operators, when elvers will actively ascend the spillway and face of the dam during daylight if rain is falling or the weather overcast.

At night, large numbers of elvers were seen. Most were congregated in shallow water at the base of the spillway. Several larger eels of both species were also present. These would immediately move out of a strong torch beam, while elvers were generally indifferent to this light.

Small streams of water flowed down sections of the spillway, and where these fanned out over the spillway base and entered the main pool,

pass over any object which caused a substantial break in contact between themselves and the substrate. Presumably the undulations of the body present a broad lateral area relative to vertical area, which prevents the eel from sliding backwards under its own weight.

A sample of elvers found ascending a vertical wall were collected for comparison with a second sample taken from the base of the spillway. The lengths of the climbing elvers were as follows with the figures in brackets being measurements from the general sample:

shortfins mean length 8.8 cm (9.5), range 7.4-11.8 (7.4-12.9)
longfins mean length 9.6 cm (10.8), range 7.9-12.0 (7.7-14.8).

Further, the percentage of eels less than 10 cm in the climbing samples was 91% and 72% for shortfins and longfins respectively. By comparison equivalent figures for the general sample were, shortfins 73% and longfins 28%. Obviously small size is an advantage in climbing as the surface area to weight ratio decreases with increasing size of the eel. Twelve centimetres which corresponds to a weight of 2.5 g, would seem to be the maximum size for vertical climbing.

Upon encountering a current, all elvers immediately orientated themselves to face into it. This positive rheotaxis could be easily induced by artificially creating a small current. Elvers also showed a distinct thigmotaxis as all crevices and pools on the spillway and elsewhere were crammed with eels. Often only a fringing circle of heads could be seen. These aggregations were partly enforced by the limited cover and resting areas available, but later laboratory observations confirmed this social behaviour.

Thigmotaxis was also demonstrated in escape reactions. If the leading members of a column of elvers crawling up a fan of water were disturbed, they immediately made vigorous attempts to escape back the way they had come. This panic reaction was rapidly transmitted through the whole column, and most elvers would re-enter the deeper water.

Mortality

Considerable mortality occurs among the elvers. In addition to the dead eels adhering to the face of the spillway, the cracks and joints in the concrete contained many dead elvers and others in a very poor condition. Continued but unsuccessful attempts to scale the dam had

exhausted such elvers, and with no food immediately available, there was little chance of their survival.

Predation is also a significant factor in mortality. In the shallow water at the base of the spillway, many large eels, up to 3 kg, were seen. Most of those were longfins. All large eels proved very wary, but 11 were gaffed and their stomach contents examined. Of these, the two shortfins contained no elvers while the nine longfins contained a total of 25 elvers. The maximum number from one stomach was seven. The cannibalistic habits of longfins are well known to eel processors but very few small eels are found in the stomachs of shortfins.

When the bodies of these large eels were thrown back into the water, they were immediately attacked by several large catfish, Ictalurus nebulosus (Le Sueur) (F. Ictaluridae). These catfish were extremely furtive and were not able to be caught, but their omnivorous feeding habit together with large numbers suggests they would eat considerable quantities of juvenile eels.

The turbulent pool below the turbine outlets also contains brown trout. These fish would also prey on elvers.

Shags, ducks and kingfishers were seen to catch elvers, especially where these had congregated in pools or were wriggling across exposed ground during daylight. Water-rats also took advantage of these concentrations, and at the outlet of Lake Waikare, Te Kauwhata, seven rats were seen in torchlight, catching elvers as they wriggled over the concrete base of the floodgate.

Finally, man now harvests varying quantities of elvers. Although no longer used directly as food, elvers have been used in recent years as "seed-eels" for stocking experimental eel ponds. If sufficient quantities of glass-eels can be obtained in the future, it is likely that this practice will discontinue.

Migratory Stimuli

The stimulus or stimuli which initiate migration are unknown. Although low temperatures (less than 10°C) could inhibit mass movements of elvers, the fact that summer migrations occur within a few weeks of each other throughout the whole country, indicates that it is not the reaching of any specific temperature which triggers migration. Temperatures recorded in the Makara Stream over the migratory period ranged from

14.2°-21.5°C, but the two 'runs' recorded at site 'd' did not correspond with any common value or fluctuation.

Similarly, the lunar cycle appears to have no direct effect, as seen by the consistency of arrival times each year at Karapiro Dam. A small migration was recorded at Makara during a 'fresh' in the stream, but the larger movement took place when the stream level was normal. Further, the water level below the Karapiro Dam is relatively constant and would provide little differential stimulus. Hardy (1950: 25) observed that increased water flow did not induce a larger number of elvers to climb the margins of a small waterfall in a North Canterbury stream.

Migration may be initiated by the summation effect of several factors. Perhaps a temperature greater than a threshold value, the increased day-length of summer, and the rapid escalation of a schooling tendency shown initially by a few elvers, all contribute to the onset of migration. Increased water flow may produce a stronger rheotaxic reaction and be a further contributing agent but is not the causative one. Any inhibitory effect of light would only be of significance where water is clear and shallow, or where elvers have to leave the water to negotiate an obstacle.

Habitat Preferences

Comparison of glass-eel and elver catches for both Waikato and Makara show gross differences in the species composition between the two stages for both areas. Thus, the grand mean of the "Elbow" glass-eel samples was 98% shortfin (n = 3004) while the grand mean for Karapiro shortfin elvers was 62% (n = 3260). The small elver catches for the Makara Stream indicated a preference by longfins for upstream areas (Table 4.1). Elvers attempting to enter Lake Waikare (Te Kauwhata) were all shortfins and local fishermen confirmed that this lake is inhabited by shortfins only.

During electric fishing operations in Wellington streams and rivers, it was frequently observed that both species of small eels showed definite habitat preferences. The Waikanae River, 50 km north-east of Wellington, was fished twice. The substrate in the areas fished was coarse gravel-rocks. The catch of eels less than 26 cm, was 94% longfin and 6% shortfin (n = 412).

In contrast, samples collected from the nearby Waimeha Stream, were predominantly shortfins. This stream was fished on four occasions and resulted in 1016 eels less than 26 cm being collected. Of these, 97% were shortfins and 3% longfins. The distance between the outlets of the Waikanae River and Waimeha Stream is 2.5 km.

To investigate any pattern in habitat selection by species, five representative areas were sampled in the Makara Stream. A portable 'pack-set' electric fishing machine was used to collect all eels below 26 cm in each area. Temperatures and flow rates were recorded, and the substrate classified according to Lagler (1952: 243). If the bottom type changed during progress upstream, fishing was discontinued until the required substrate was again encountered.

The results are summarised in Table 4.4. Flow rates in the stations paralleled the bottom types, such that the swifter the flow the coarser the substrate etc. Stations 1 and 3, although some distance apart, were similar with sluggish flow, unstable silt bottom and fringing weed. The numbers of eels from stations 1 and 5 were considerably less than the numbers from the other stations but it is assumed the species proportions recorded are valid indicators of the relative abundance of both species.

Although shortfins were predominant in all stations, Table 4.4 shows that the proportion of longfins is directly related to the bottom type, and hence water flow. Thus the percentage of small longfins in swift stony water is greater than that in slower muddy areas.

To investigate the size distribution of both species within the five stations, the percentage distribution per two cm length group was calculated. These data are given in Table 4.5 for the first five such groups; eels from 16-26 cm are given as one group.

Shortfins, more numerous in the samples, show better distribution by size than do longfins. Thus, Station 1 shows a high proportion of small shortfins (70% < 10 cm) while Station 2 does not afford a good habitat for such eels and they are noticeably absent. Station 3 would appear to be a suitable habitat for small shortfins but has only 2% < 10 cm. Although substantial numbers of small eels have penetrated these upstream waters, the predominant shortfin size group is 10-12 cm. This group also dominates Station 4 while the 12-14 cm group is the largest in Station 5.

Likewise, the small numbers of longfins show a tendency for the smaller size groups to predominate in downstream areas. Upstream, in Stations 4 and 5, the proportion of eels in the larger groups increases.

Table 4.4 Species proportions of eels less than 26 cm from selected substrates in the Makara Stream.

km = distance from stream mouth

S = shortfin (*A. australis*)

L = longfin (*A. dieffenbachii*)

Station 1 (1.4 km)	°C = 13.8 flow = 0.12 m/s catch: n = 49	bottom type = silt weed = few fringing emergents 100% S
Station 2 (2.9 km)	°C = 13.5 flow = 0.34 m/s catch: n = 108	bottom type: fine gravel weed: submerged, luxuriant 95% S 5% L
Station 3 (4.5 km)	°C = 14.8 flow = 0.18 m/s catch: n = 88	bottom type: silt weed: fringing emergents 99% S 1% L
Station 4 (5.5 km)	°C = 14.5 flow = 0.41 m/s catch: n = 140	bottom type: fine-coarse rubble weed: filamentous algae 80% S 20% L
Station 5 (6.8 km)	°C = 13.8° flow = 0.48 m/s catch: n = 38	bottom type = coarse rubble, boulders weed: few fringing emergents 63% S 37% L

Table 4.5 Percentage distribution by length groups of eels less than 26 cm from selected substrates in the Makara Stream.

A. australis

	Stations				
Length groups (x2 cm)	1	2	3	4	5
	%	%	%	%	%
6 - 8	35		3		
8 - 10	35	5	21	13	17
10 - 12	10	23	33	31	29
12 - 14	2	19	21	14	33
14 - 16	9	15	10	15	4
16+	9	38	12	27	17
(n)	(49)	(102)	(87)	(112)	(24)

A. dieffenbachii

	Stations				
Length groups (x2 cm)	1	2	3	4	5
	%	%	%	%	%
6 - 8					
8 - 10		80	100	25	14
10 - 12		20		11	50
12 - 14				11	7
14 - 16				14	7
16+				39	22
(n)	0	(5)	(1)	(28)	(14)

These results are consistent with the observation that successive summer migrations penetrate further upstream. As found with glass-eels, longfins showed a preference for swifter stony areas, whereas shortfins were less numerous in such areas but dominated muddy regions. With increase in size, the habitat requirements of eels change. Longfins up to 15 cm can find adequate cover under large stones and small rocks at the margin of a stream or river. Larger specimens are found in deep pools, weed beds or beneath undercut banks. Upstream migration would aid small eels in finding successively larger rocks and thus better cover. Although shortfins inhabit sluggish silty areas, only the small individuals, to about 20 cm, are found buried in shallow stream margins and backwaters. Larger fish prefer deeper pools and undercut banks etc.

Differences in the habitat preferences of both species of adult eel were noted by Cairns (1941: 65). He found that a change of habitat within one river produced a definite change in the species composition, with longfins inhabiting "fast-flowing boulder-strewn mountain water", while in deeper and sluggish reaches, shortfins predominated. Burnet (1952b: 119) found small shortfins, less than 30 cm, in swift-flowing and stony areas at the head-waters of river systems. The Makara samples confirm that this type of habitat is suitable for small shortfins.

Definite habitat preferences imply different feeding habits. Unfortunately few data are available to compare the feeding habits of small eels of both species. Cairns (1942: 133) combines both species for the smallest size group he examined. It would be of interest to know whether selective feeding by species occurs within an area where both species coexist.

In discussing feeding habits of longfins, Burnet (1952a: 55) concluded that selection of food organisms was not entirely due to food preference but also to the relative abundance of the organism. Also, feeding preferences were general and were readily adapted to differences in fauna. From this it would seem that differences in diet between both species merely reflect the availability of food items found within the respective habitats, and therefore it is the suitability of the habitat rather than availability of specific food types which is the primary requirement in habitat preference. Observations on relative mortalities of asphixiated glass-eels and elvers suggest that longfins have higher oxygen demands than do shortfins. This has not yet been tested experimentally. If correct, this would provide a plausible explanation for the habitat preferences shown by both species.

Such habitat preferences are ecologically important, as they allow both species of eel to inhabit the same river system, but with limited interaction and competition due to spatial separation.

Species Mortality

The elver sample from the Mokau River, New Plymouth, was sent alive, packed in an inflated plastic bag. Unfortunately, the volume of eels to oxygen was excessive and considerable mortality took place during transport. On arrival, only eight eels from a total of 232 were alive. All eight eels were shortfins, yet shortfins comprised only 18% of the total. As previously noted with glass-eels, longfins did not appear well-suited to transportation by this method which requires cutaneous respiration.

To compare survival rates of both species exposed to air, ten eels of each species were placed in plastic aquaria in a constant temperature cabinet. These ten eels comprised five less than 15 cm and five greater than this length. A thin film of water together with saturated sponge chips covered the bottom of each aquarium. This water was changed every second day to prevent the accumulation of waste products. Water of the required temperature was added as necessary to compensate for water lost by evaporation. In addition, large shallow trays of water were placed in the cabinet to maintain a moist atmosphere.

The eels were acclimatised in aerated water to the required temperature, by raising the temperature 2°C per day. After two days at this temperature they were removed and placed in the aquaria. Two eels remained in the aerated water as controls. Twice daily inspections were made and dead eels removed and recorded. The cessation of heart-beat was defined as the point of death.

The results, Table 4.6, indicate that shortfins were able to survive better under these conditions than were longfins. At 15°C, 70% of the longfins died but none of the shortfins. At 20°C, 40% of the shortfins and 90% of the longfins died while at 25°C, 100% of both species died. However, at this latter temperature, longfins died at a greater rate than did shortfins. There was no consistent difference between the survival ability of the small and larger eels.

According to Krogh (1904) eels in water receive up to 3/5 of their oxygen requirements by direct absorption through their skin. He also

Table 4.6 Survival of eels exposed to air of constant temperature. (Deaths per day).

A. australis	> 15 cm	= S
	< 15 cm	= s
A. dieffenbachii	> 15 cm	= L
	< 15 cm	= l

°C	Days 1	2	3	4	5	6	7	Total deaths
15			2L			1L	1L	4L
			1l			2l		3l
					2S			2S
			1s				1s	2s
20		1L			1L	1L	2L	5L
		1l			1l	1l	1l	4l
				1S	2S	2S		5S
			3s	2s				5s
25			3L	1L	1L			5L
		2l	3l					5l

considered that cutaneous respiration was sufficient to maintain life in the European eel, as long as the air temperature did not exceed 15°C. However, more recently, Berg and Steen (1965: 483) found that oxygen uptake from the air at this temperature was insufficient for requirements, and few eels could survive exposure of 60 hours or more.

The above data (Table 4.6) suggest that the ability of A. dieffenbachii to respire cutaneously is similar to that of the European eel, which is also a longfinned species. The shortfin appears much better suited to these conditions. As suggested in the previous section, the longfin seems to have a higher oxygen demand than the shortfin and aerial respiration at temperatures of 15°C and greater is insufficient to maintain life. In addition to differences in respiratory demand, cutaneous respiration in longfins may be less efficient than in shortfins. If so, this could be a function of skin thickness as longfins have a thicker dermal layer than shortfins. Eel processors frequently speak of the "double skin" of longfins, but this is probably a reference to the pigmented myolemma which is internal to the dermis.

The ability to tolerate prolonged periods of exposure to the air has endowed freshwater eels with additional survival capacity. Accordingly they are able to leave the water to negotiate obstacles during migrations or move from one body of water to another. Stories of eels moving across fields on damp nights are widespread. Fishermen take advantage of this respiratory ability and transport eels to processing factories in wet sacks. Air-freighting of eels in inflated plastic bags has been discussed.

4.5 SCALES AND SCALE FORMATION

During the first few years that an eel spends in fresh-water, scale development commences. The scales of freshwater eels are rudimentary and embedded in the skin. Reduction in scale size or even complete loss of scales is one of a number of morphological specialisations shown by all genera of eels which allows them to inhabit holes and crevices. All eels are adept at sudden reverse movements to withdraw back into cover - protruding and overlapping scales would hinder such movement, whereas reduced scales still afford some protection to the body surface but allow greater freedom of movement.

The following sections deal with the origin and pattern of scale development in both species of freshwater eel, while their value in age determination is discussed later.

Methods

Scale collections were made from the monthly Makara Stream eel samples. In addition, scales from a large size range of shortfins from Pukepuke Lagoon were obtained. Although this thesis is primarily concerned with eels of less than an arbitrary value of 26 cm in length, a complete size range was studied for certain aspects of scale development. This was necessary as scale development is not complete by 26 cm, and trends observable at this length could only be verified by studying larger size groups.

For easier handling, eels were first killed by prolonged immersion in benzocaine solution and were then deslimed in a strong solution of ammonia. Scales in both species were found to originate along either side of the lateral line, at a point 2/3 of the distance from the anus to the tip of the tail. Samples of scales were collected from this area by scraping a scalpel blade over the epidermis. Where available, over 100 scales were taken from each eel. These were then stored in numbered vials in a solution of 40% isopropyl alcohol to which a few drops of antiseptic had been added to prevent fungal growth.

Scales were observed using reflected light. To accentuate the zonation pattern, they were lightly stained in a 0.1% methylene blue solution. For permanent mounts, stained scales were partially dried in air to remove excess moisture. A large drop of Depex mounting medium was added and any globules of water teased away from the scale before covering with a cover slide. This procedure was necessary as scales curled immediately they became dry and were then unsuitable for further examination.

To ascertain the extent of lateral and longitudinal squamation in eels of less than 20 cm, the left side of the deslimed eel was dried and the back of a scalpel blade rubbed across the skin. The outlines of scales, visible as small pits in the skin, could then be seen. In eels with only a few scale rows, a strong methylene blue stain was found useful. A few drops of a 10% solution were painted over the surface to cover all areas known or suspected of containing scales. After half a minute the area was flooded with 100% isopropyl alcohol to destain the skin. The scales were then left stained deep blue and could be easily measured. If no scales were found on the left side of the body, the right side was also investigated as a further check.

Description and Arrangement of Scales

The scales are elongate, typically three times as long as they are wide. Mean dimensions of 20 scales from five body areas of a 67 cm shortfin are included in Table 5.1. Scales are contained in individual sacs below the epidermis, but unlike most fish they do not overlap and are able to expand in all directions. Occasionally in large eels, a small overlap of scale margins does occur and adjacent scales may even fuse to form a compound scale.

Fig. 4.3.a shows a typical scale from a small eel. The scale itself is formed by concentric rings of loculi. These loculi are of varied shape: in the centre of the scale they are square or slightly elongate but in most other areas they are quite elongate with a polygonal boundary. Waly (1940: 46) showed that contrary to general belief, these loculi were not formed of calcareous platelets, but of fibres.

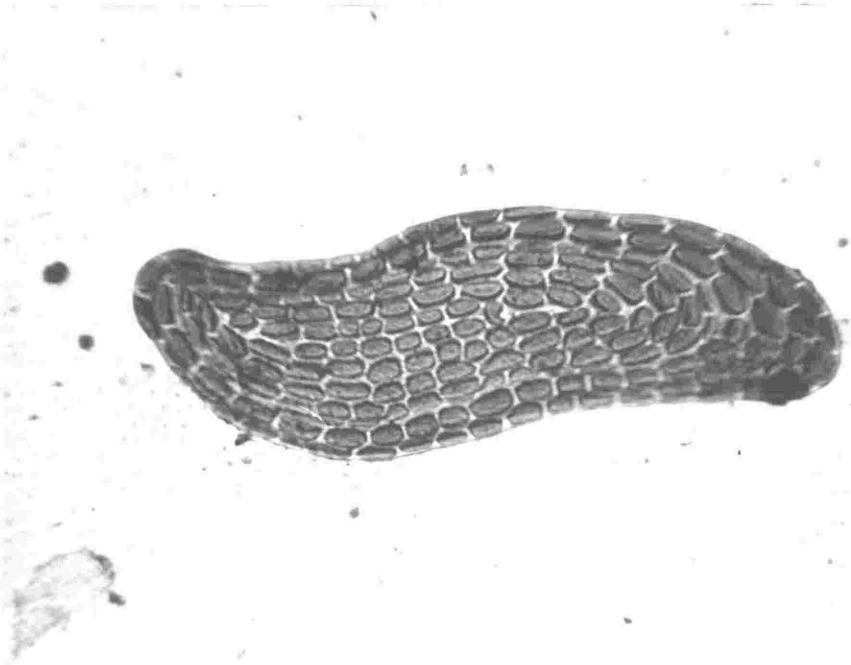
The rings of loculi are arranged parallel to the margin of the scale, but at intervals in scales of large eels, a narrow fibrous band separates the bands of loculi into zones. This distinctive zonation is seen in the figures of Hornyold (1922: 12) and Frost (1945: 32). Although such distinct zones are seen in the scales of some New Zealand eels of both species, the majority of scales examined showed less obvious zones. In most cases, a 'ring' was shown, not as a clear fibrous band but as a ring of partially formed and truncuted loculi with a flush outer margin (Fig. 4.3.b). The outer margin of these loculi was often visible as a thin line. Further, adjacent zones often took up differing amounts of stain resulting in the outermost zone being stained darker than the innermost; this aided in delimiting rings.

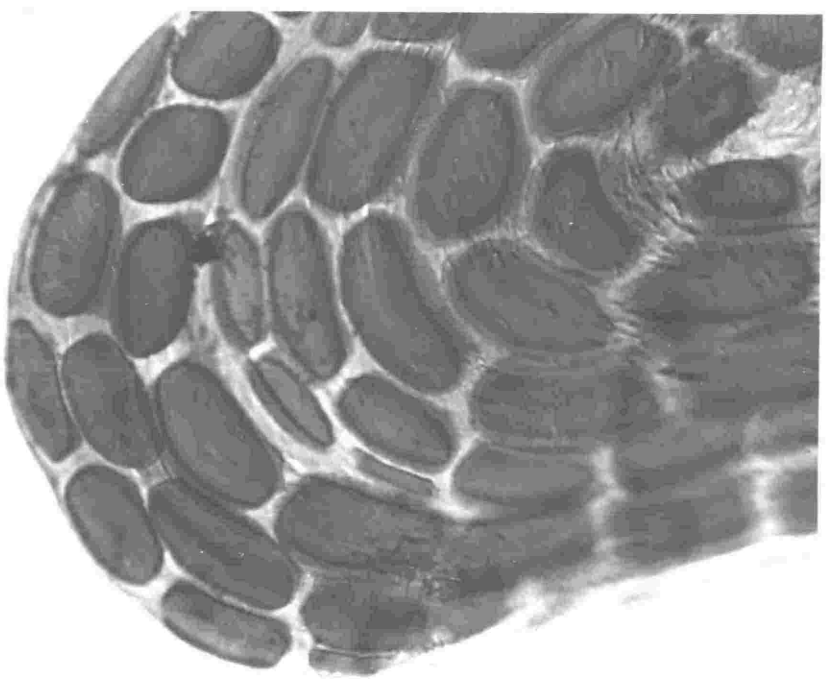
Thus, scales show definite zones which have often been interpreted as representing annual growth. These zones are most easily seen at the ends of the scale and are less distinct at the short axis where they are often crowded. Some scales, even in large eels, show no zonation at all, or perhaps a very reduced number of rings. Some of these may be replacement scales, but on occasions, half or more of the scales examined from any one eel were of these types. It is unlikely that such large numbers of scales are lost during the normal mode of life, but rather, for reasons not understood, many scales often fail to record complete zonation.

The arrangement of scales varies with different areas of the body. Over most of the trunk, scales lie in small groups, oblique to the lateral

Fig. 4.3.a Scale from a 24.4 cm *A. australis* showing one annulus. The annulus is seen as an area of truncated loculi with the loculi external to the annulus stained more heavily than those internal to it.

b Enlargement of a scale annulus showing the typical truncated loculi.





line, with the adjacent group arranged at right angles. In this way a mosaic pattern is formed, with scales lying in longitudinal rows. This is seen in Fig. 4.4.b. At the base of both dorsal and ventral fins, two to three rows form parallel to the fin. This alignment parallel to the long axis of the body, continues along most of the dorsal ridge and onto the snout.

Pattern of Squamation

a. Sequence

As previously stated, scale development in both species commences at a point approximately 2/3 the distance from the anus to the tip of the tail. From this origin, scales spread rapidly anteriorly and the greatest number of developing scale rows is found mid-way along the anal - tail tip distance. Most new scales are formed on the periphery of the area already scaled but small isolated pockets of new scales may form separately, especially along the lateral line itself.

As scales spread anteriorly, development of the rows above the lateral line proceeds more rapidly than development of rows below this line. Therefore a 'tongue' of scales spreads forward from the lateral line area immediately posterior to the pectoral fin and joins the scales which have developed on the dome of the head. Finally all ventral areas of the body become completely squamated, and scales also appear on the rays of the pectoral, dorsal and anal fins. The only areas of the body to remain free of scales are the lips and the opercular flaps, although development in the pre-orbital area and immediately posterior to the mandibular symphysis, is often incomplete.

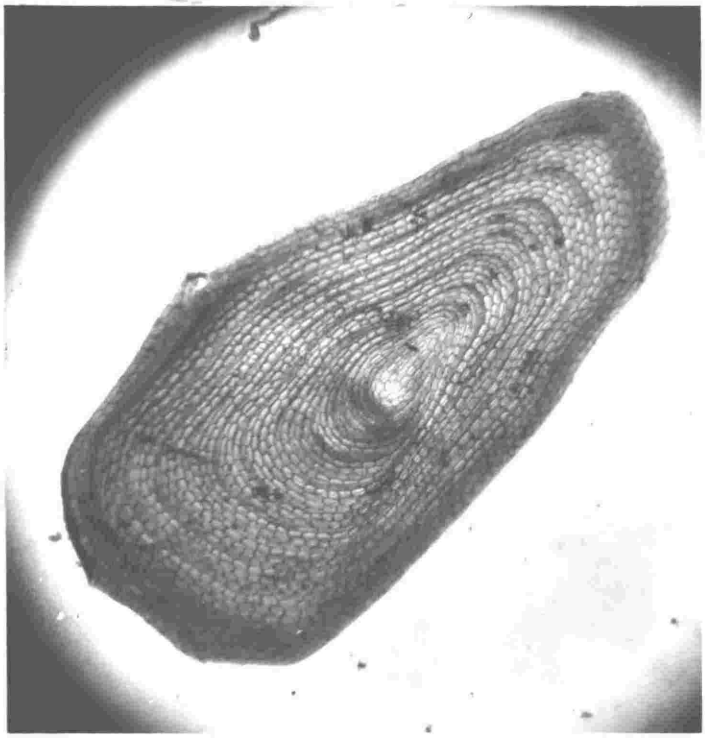
Successive stages in scale development are illustrated in Fig. 4.5.a-f.

b. Length at Appearance of Scales

From a large sample of Makara eels to 26 cm, the number in each cm group which possessed any scales were recorded. Results, Table 4.7, show that scale development takes place over a smaller size range in shortfins than in longfins and in any of the cm groups at which scales develop, the percentage of shortfins with scales present is greater than longfins. Comparative values for the Japanese eel, from Matsui (1952: 93), are also given. The minimum length at which scales were formed was 16.5 cm

Fig.4.4.a Scale from a 84.2 cm A. australis showing ten scale annuli

b Arrangement of scales on the body of a 28.7 cm A. australis. Lateral line pores are just visible in a horizontal line in the centre of the photograph.



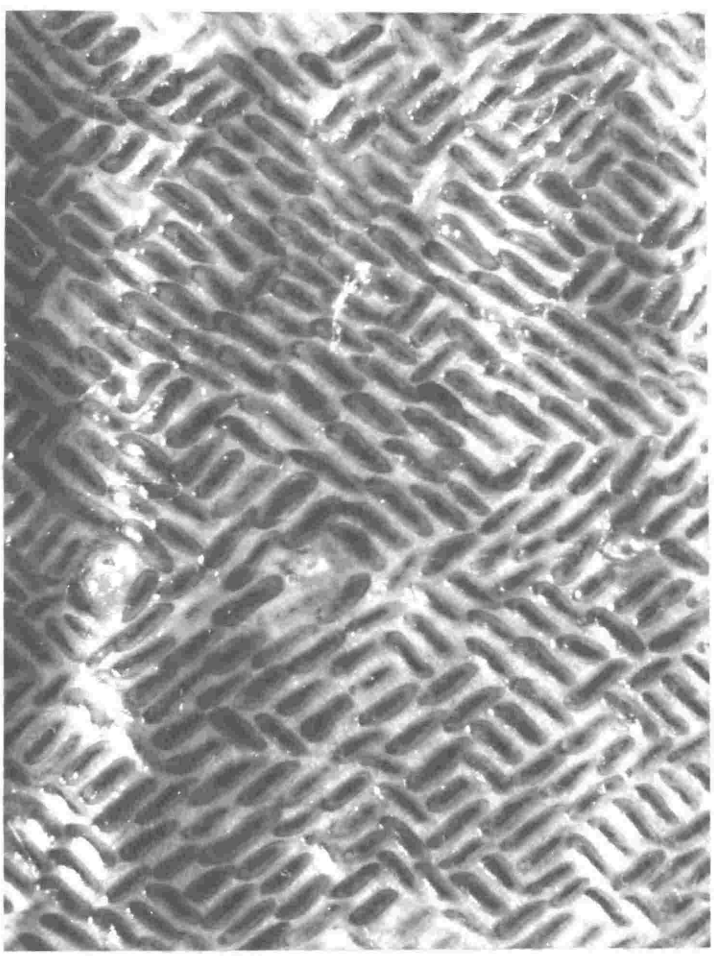


Fig. 4.5. a-f Successive stages in scale development in *A. dieffenbachii*.

g Scale sampling sites on 67.2 cm *A. australis*.

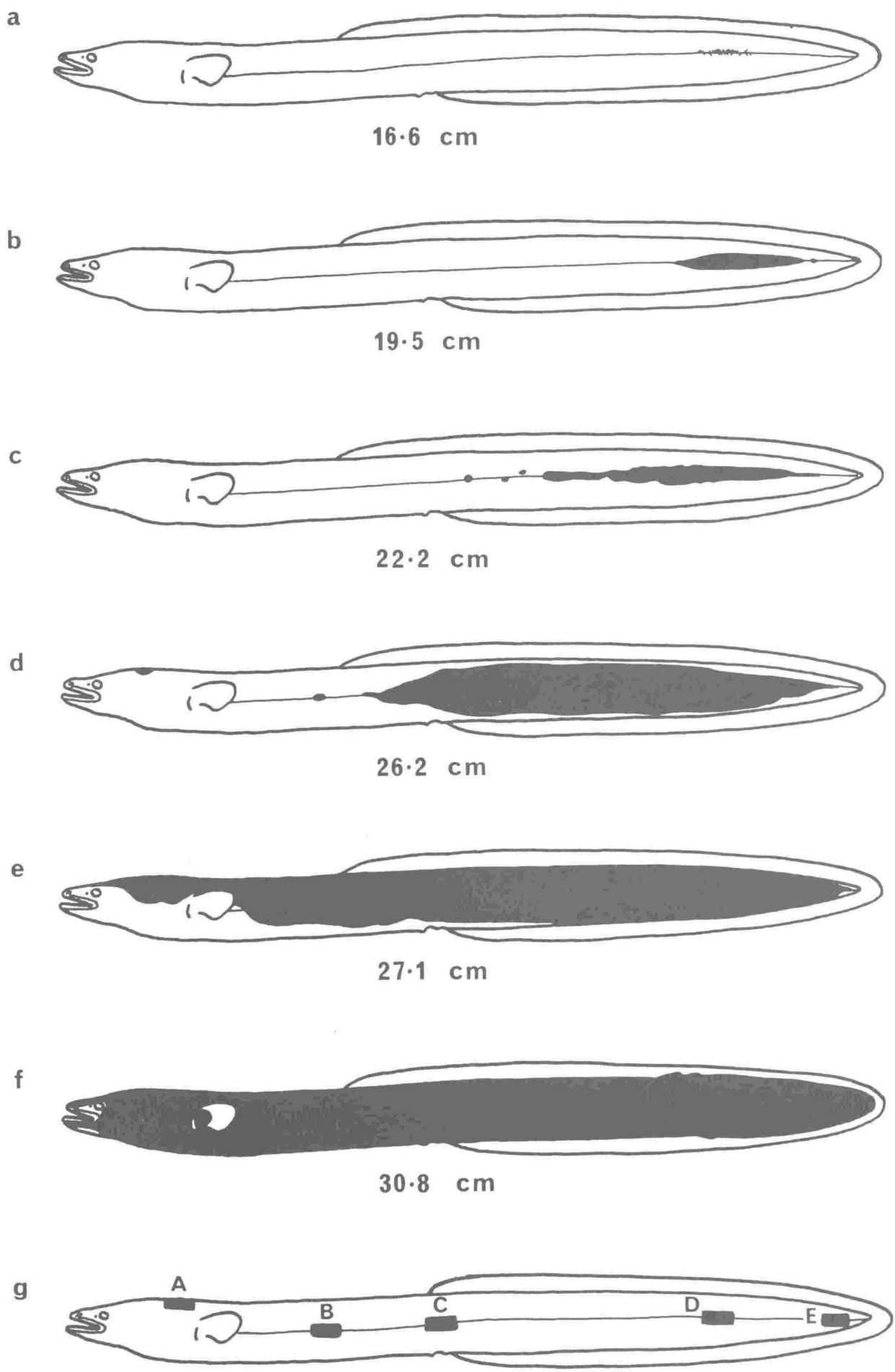

a
16·6 cm
b
19·5 cm
c
22·2 cm
d
26·2 cm
e
27·1 cm
f
30·8 cm
g
A
B
C
D
E
scale sampling sites

Table 4.7 Percentage of small eels per centimetre group with and without scales.

	A. australis			A. dieffenbachii			A. japonica*		
Cm group	Scales absent %	Scales present %	n	Scales absent %	Scales present %	n	Scales absent %	Scales present %	n
14	100	-	1	100	-	6	100	-	304
15	100	-	11	100	-	4	98	2	50
16	75	25	12	85	15	7	31	69	75
17	36	64	11	70	30	10	2	98	83
18	-	100	14	37	63	8	-	100	38
19	25	75	8	8	92	13	-	100	18
20		100	9	6	94	17		100	115
21		100	7		100	6			
22		100	4		100	7			
23		100	10		100	8			
24		100	2		100	7			
25		100	3		100	3			
			92			96			683

* data from Matsui (1952:93)

for shortfins and 16.4 cm for longfins. Conversely, the largest eels recorded which had no scales present were 19.5 cm and 20.5 cm for shortfins and longfins respectively.

These ranges in length cover two age groups for the Makara data. Additional shortfin samples from Pukepuke Lagoon gave a range of 16.3-18.0 cm for length at scale development. This latter population is faster growing than Makara shortfins, and this length range incorporates eels from age groups one and two, compared with age groups three and four for the Makara data. Together these data indicate that it is the attainment of a certain length and not age which initiates scale development.

c. Longitudinal Development

The longitudinal extent of scale development was measured, and recorded as a percentage of the total length. Only those scales which formed a continuous row were included - isolated and scattered scales some distance from a continuous row were ignored. Results for both species, expressed as the regression of percentage body length covered by scales against total length, are shown in Fig. 4.6.a.

The regressions were calculated as:

shortfins	$Y = 9.7487(X) - 150.0549$	$r = 0.8606$	$(n = 65)$
longfins	$Y = 11.1818(X) - 203.8892$	$r = 0.8708$	$(n = 66)$

Both species show a positive relationship for this aspect of scale development with correlation coefficients highly significant at the 5% level.

Longitudinal scale development commences at a shorter length in shortfins than in longfins, but in the latter species it proceeds more rapidly. Extension of Fig. 4.6.a gives maximum development in shortfins at 25.8 cm and 26.9 cm in longfins. In practice, the total length is never completely covered with scales as these do not develop on the lips and the tip of the caudal fin. These two areas comprise approximately 3% of the total body length.

d. Lateral Development

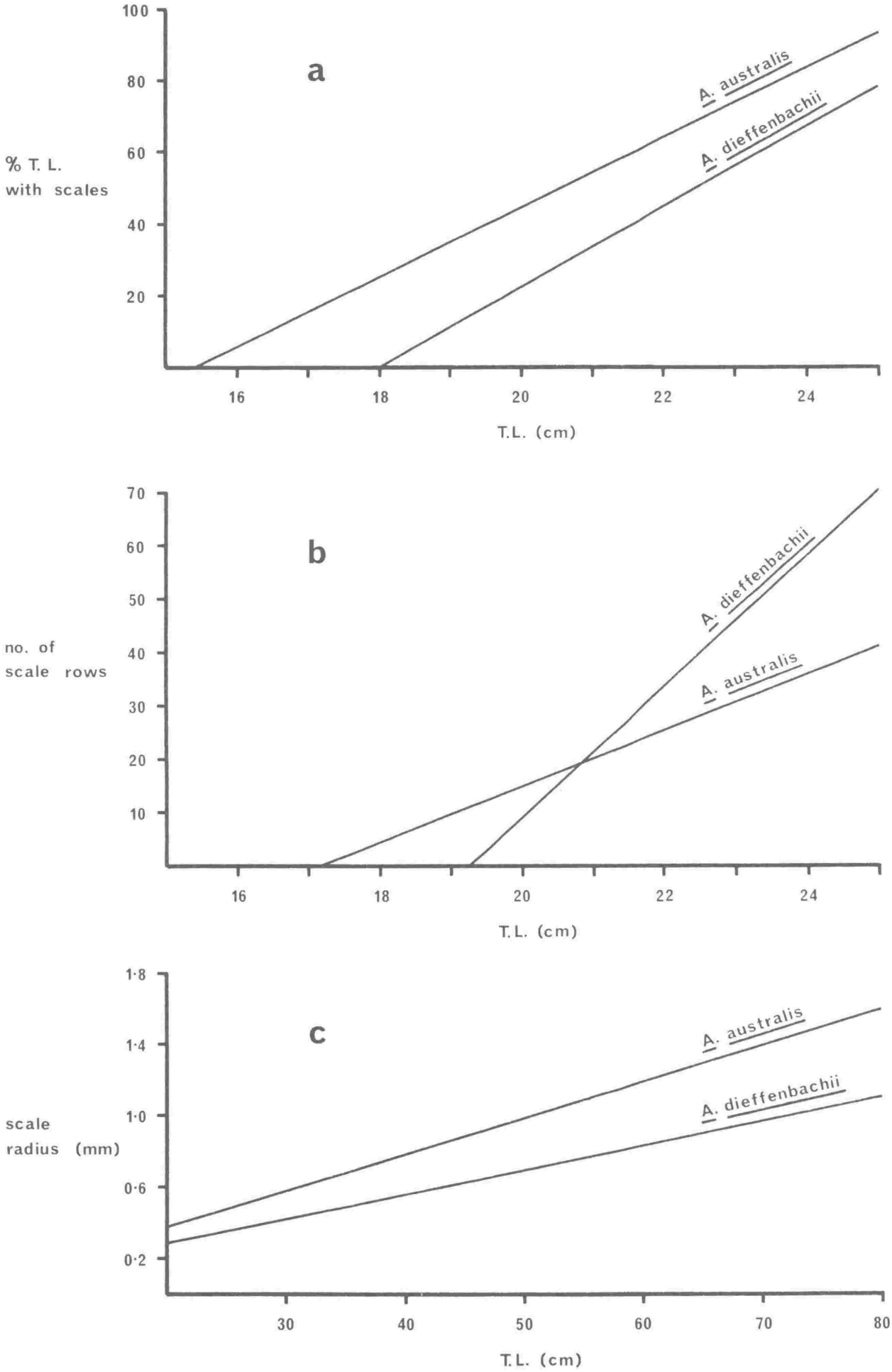
Lateral scale development was also observed in both species. For this, the sum of the number of scale rows above and below the lateral line was recorded. By definition, a row constituted a continuous line of scales

Fig.4.6 Rates of scale development for both species of eel

a Longitudinal development.

b Lateral development.

c Scale size (radius).


a
% T. L.
with scales
100
80
60
40
20
16
18
20
22
24
T.L. (cm)
A. australis
A. dieffenbachii
b
no. of
scale rows
70
60
50
40
30
20
10
16
18
20
22
24
T.L. (cm)
A. dieffenbachii
A. australis
c
scale
radius (mm)
1·8
1·4
1·0
0·6
0·2
30
40
50
60
70
80
T.L. (cm)
A. australis
A. dieffenbachii

greater than 10% of the total length of the eel. The greatest number of rows was found mid-way along the anus - tail tip distance.

The results in Fig. 4.6.b show that although such lateral scale development commences at a greater length in longfins than in shortfins, rows form more rapidly in longfins. By a length of 21 cm, both species have approximately the same number of scale rows but thereafter the number of rows in longfins exceeds that in shortfins.

The regressions for these data are:

shortfins	Y = 5.1453(X) - 87.7005	r = 0.8538	(n = 57)
longfins	Y = 12.3395(X) - 237.4486	r = 0.8494	(n = 49)

The maximum number of scale rows recorded over a large range of shortfins to 70 cm in length, was 63, with 32 above and 31 below the lateral line; the maximum for longfins was 98, with 51 above and 47 below. The mean number of rows for a sample of five eels of each species over 35 cm in length was 56 for shortfins and 90 for longfins. Extension of the regression lines in Fig. 4.6.b shows that these values are reached at lengths of 28 cm and 26.5 cm for shortfins and longfins respectively. After this, the slope of the graph could be expected to level off as few, if any, new scale rows would be added with increasing size of the eel.

In shortfins, the mean number of scale rows above the lateral line was greater than the mean number below this line. The opposite was true for longfins. However, the difference in number between the two values was small, usually one or two with a maximum of five. Because of the oblique formation of adjacent groups of scales, it was often difficult to determine the precise number of rows; accordingly it is not thought that these differences are significant.

It was also established that the number of scale rows varied according to the curved dorso-ventral distance of the body. This relationship was curvilinear. Thus, increased area is covered by an increased number of scale rows together with an increase in the size of the scales themselves.

e. Scale Size

Scale sizes were measured over a large size range, using scales taken from body area D (see Fig. 4.5.g). As a relative measure of size, the longest scale radius was used. Five regularly shaped scales from each

eel were measured using a micrometer eyepiece, and the mean radius per eel used in a regression analysis of scale radius against total length. Where available, ten eels from each ten cm length group were used, giving a total of 57 shortfins and 53 longfins. Unfortunately, few eels larger than 80 cm were obtained and analysis beyond this length was not possible.

A positive linear correlation was found for the above relationship (Fig. 4.6.c). Correlation coefficients for both species were highly significant at the 5% level, i.e.

shortfins	Y = 0.0203(X) - 0.0339	r = 0.9362	(n = 57)
longfins	Y = 0.0136(X) - 0.0125	r = 0.9199	(n = 53)

Discussion

The origin of scales in the caudal area for both New Zealand species is similar to the findings of Pantalu (1957: 270) for the Indian eel, A. bengalensis (i.e. A. nebulosa nebulosa), and Smith and Saunders (1955: 251) for A. rostrata. However, Hornyold (1922: 11), Waly (1940: 48) and Voronin and Rusetskaya (1971: 718) found scale development in A. anguilla commenced near the anus. Matsui (1952: 234) gives a similar area of origin for A. japonica. In both New Zealand species, by the time scales appear on the lateral line above the anus, the number of scale rows mid-way along the anus-tail tip distance, are at their maximum.

An investigation of scales of the European eel led Gemzöe (1908) to conclude that scale formation commenced during the third year of life in fresh-water. This was disputed by Ehrenbaum and Marukawa (1913) who found scale development to be dependent upon length rather than age. They give the 'scale size' for A. anguilla as 16-20 cm. Subsequently the consistent appearance of scales at certain lengths has been recorded by many authors.

A similar range to the above was found for A. rostrata by Smith and Saunders (1955: 251). The range for A. japonica is 15.5-17.5 cm (Matsui 1952: 92).

While the above data are in close agreement with those of the present study, Pantalu (1957: 270) records that for A. bengalensis, "all the specimens examined over 116 mm in length had well-defined scales in the caudal region". As noted by him, these results are considerably different to those known for the European eel.

Previous research on New Zealand eels by MacFarlane (1936) and Cairns (1941) indicated that scales formed regularly during the seventh year of life. Data from the present study show that all relationships of scale size and development including time of development, are directly related to length. The mean lengths given by both authors for seven year old fish are of the order of those expected for the commencement of scale growth.

MacFarlane noted that scales first appear along the lateral line in the posterior third of the body. However, Cairns (1941: 56) considered scale development to commence at the lateral line but "close to the vent". This latter statement is incorrect.

5 AGE AND GROWTH

5.1 INTRODUCTION

As is often the case with other freshwater fisheries, the wild eel fishery in New Zealand is subject to intensive and effective fishing. With the establishment of a large overseas market together with such factors as the relatively small capital outlay required for both fishing and processing, eels constitute a lucrative but nevertheless highly vulnerable resource. Their relatively long and complex life history renders them particularly liable to over-exploitation. Strict management of such a resource is essential if a long-term and stable fishery for wild eels is to be maintained.

Basic to any management practices is knowledge of the growth rate and age structure of the stock. There has been considerable research on this for the European eel in the last 60 years. A table of most of the significant contributions in this field appears in Penáz and Tesch (1970: 300-301). Previous growth studies on New Zealand eels have been conducted by Cairns (1941) and Burnet (1969b). The present study is perhaps more important from the aspect of materials and techniques rather than for the limited growth data obtained.

The ages of fish from a uniformly growing population can often be determined from the length-frequency distribution of members of the population. Individual ages are calculated from observation of the bony parts, normally scales and otoliths, but also from vertebrae, fin-rays and operculae. These structures can be variously prepared and viewed to show distinct zone patterns, which frequently correspond to annual growth. In the present study both scales and otoliths were investigated. Initially, some vertebrae were collected but this was discontinued when it was established that otoliths were suitable structures from which to determine age.

Age determination from examination of bony structures is based on the theory that fluctuations in growth rate are reflected in the optical properties and probably chemical composition of the pattern of zonation in the bony part.

With reference to interpretation of otolith zonation, much confusion has arisen as the nature of the light used has not always been defined. The terms "hyaline zones" and "opaque zones" are used to describe whether a zone

allows light to pass through it or not. When viewed under reflected light, the hyaline (transparent) zones appear black coloured while the opaque zones appear light. This is accentuated against a black background where hyaline zones appear black and opaque zones white. Conversely, under transmitted light, the hyaline zones appear light and the opaque zones dark.

Contradictory opinions exist regarding whether the opaque zones are laid down in summer or winter. Irie (1960: 220) concluded that the opaque zone was formed during winter and spring, whereas the hyaline zone formed during summer and autumn. This is contrary to the generally accepted opinion that opaque zones are formed during summer and hyaline zones in winter. Consistent with this latter opinion is the suggestion by Graham (1929) that visual changes in the otolith zones reflect metabolic changes, such that hyaline zones are formed when anabolism is low and opaque zones when it is high. Seasonal changes in temperature and availability of food would produce such metabolic changes.

In the present investigation it was established that the broad opaque zone corresponds to summer growth, while the hyaline zone is bounded by a narrow dark band formed during late winter.

The following three sections describe the preparation and interpretation of the structures investigated for possible use in age determinations. The results are those determined from otolith readings. Finally, growth as expressed by the relationship of length and weight, is discussed.

5.2 SCALES

Scales have been used in a number of investigations by various researchers as a means of determining the age of eels. In these instances, the scale annuli and zones are interpreted as representing the pattern of annual growth in the same way as narrow winter and broad summer bands appear in the otolith. From the growth rate calculated from age for length data, the time until scale formation commences can be back-calculated.

Both species of eels were examined to see whether the scale zonation reflected annual growth as calculated from otolith examination.

Sampling Site

A check was made to find which area of the body had scales with the maximum number of annuli. For this, two shortfins and two longfins greater than 50 cm in length, were examined. Results were similar and those presented are for a 67.2 cm shortfin from Pukepuke Lagoon. Scales were

collected from the five areas as indicated in Fig. 4.5.g. Ten regular scales from each area were measured to observe comparative sizes. A further ten well-formed scales were then chosen and the number of annuli for the 20 scales from each area counted. Results set out in Table 5.1 indicate that scales from area four, which have the greatest breadth for length ratio of any area, show the highest percentage of 'true' readings (60%). The largest scales came from area three but only 15% showed six scale annuli. No scales from any other area showed the maximum number of annuli.

Interpretation of Scale Annuli

From samples of Makara Stream eels of as large a size range as possible, scales from 181 shortfins and 193 longfins were examined. Ten of the largest and most regular scales were selected per eel and the maximum number of complete annuli recorded. The eels were then classified into groups according to the number of annuli recorded. Thus group 0 contained those eels whose scales had no annuli; group 1 had one annulus etc. Mean lengths of the scale groups were then calculated.

The regressions for the mean lengths per scale group are shown in Fig. 5.1.

i.e. shortfins: $Y = 6.6654(X) + 18.0250$ $r = 0.9989$

longfins: $Y = 8.0976(X) + 19.5584$ $r = 0.9963$

Shortfins show an excellent linear relationship whereas the normal type of growth curve for fish is asymptotic. Further, data from P. Todd (pers. comm.) who has aged large Makara eels, indicate that shortfins of 80 cm and larger would belong to age group 25+.

Similarly, longfins show an equally good correlation for lengths of up to 80 cm. Mean lengths per scale group for eels larger than this do not fall on a straight line and have been ignored for purposes of this correlation. Scales from such eels showed that the outer zone or zones were very wide. At approximately 80 cm and beyond, new annuli in longfin scales are laid down less frequently and the scale enlarges by addition in width of the existing outer zones rather than by laying down new zones. P. Todd (pers. comm.) found longfin eels of over 80 cm from Makara to be in age group 28+. Thus in neither species of eel do the number of scale annuli indicate the age of the eel.

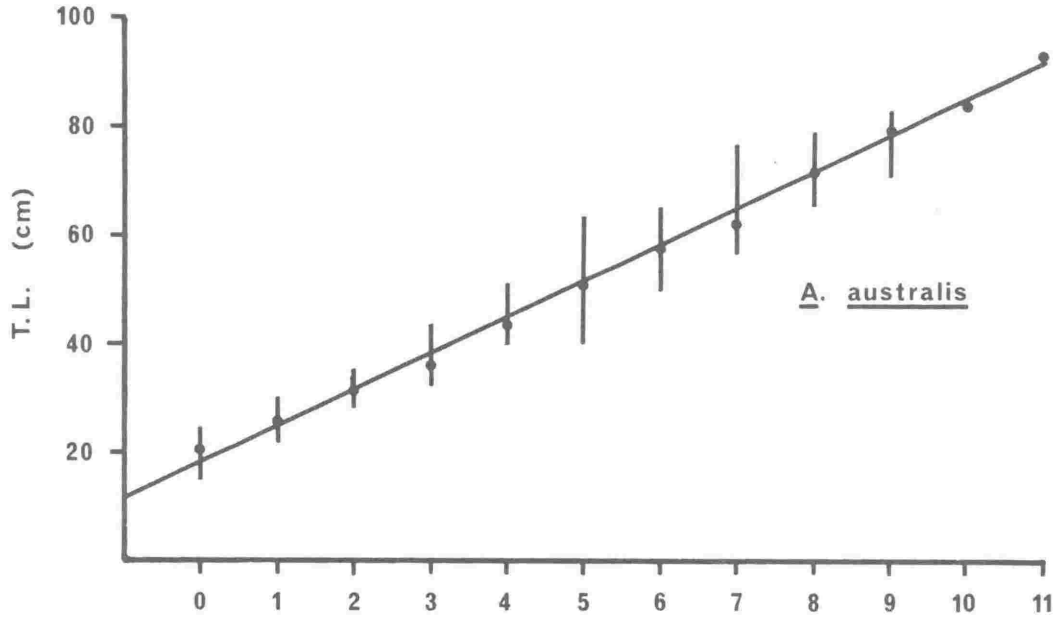
From the age groups given above for large eels of both species, it can be seen that growth rates in the Makara Stream are slow. To see whether

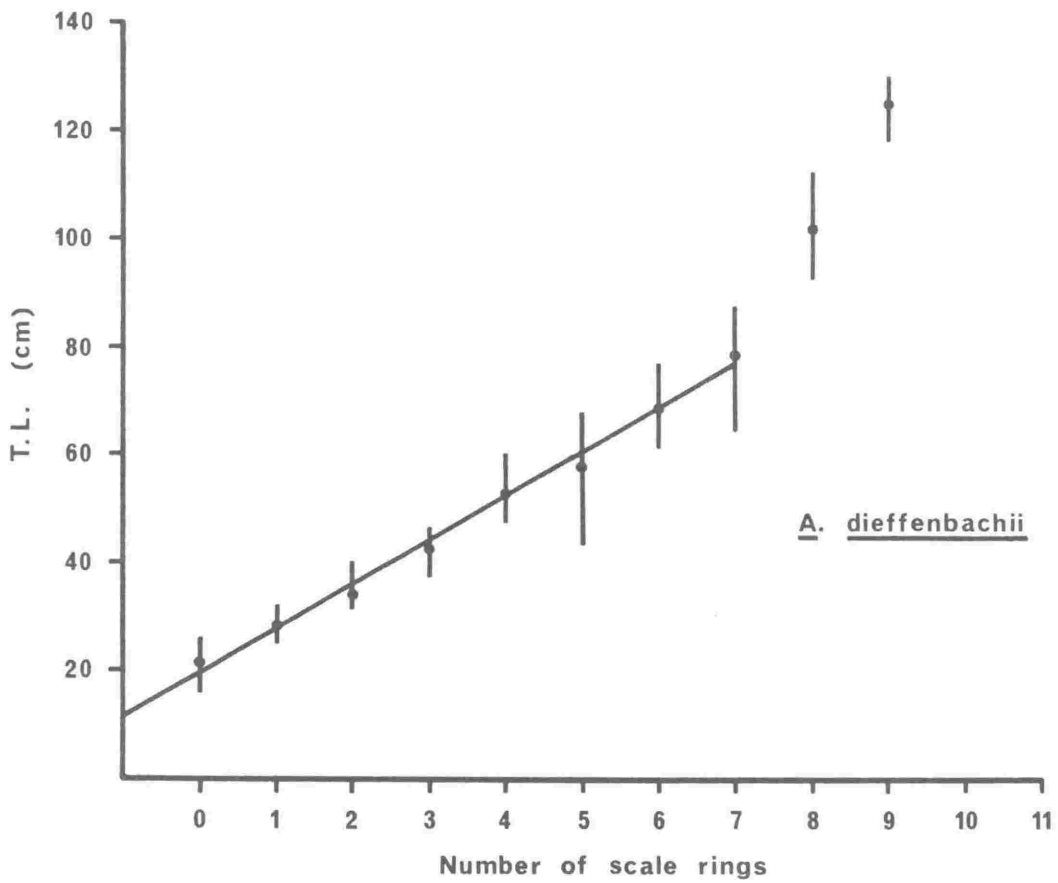
Table 5.1 Eel scales. The maximum number of annuli and mean scale size recorded at various sites along the body of a 67.2 cm *A. australis*.

The positions of these sites are indicated in Fig.4.5.g.

		Site				
		A	B	C	D	E
No. annuli	1					2
	2					1
	3	11				2
	4	9	19	3		6
	5		1	14	8	9
	6			3	12	
No. scales		20	20	20	20	20
Mean size (mm)		1.5x0.5	2.4x0.8	2.8x1.0	2.2x0.9	1.1x0.4

Fig. 5.1 Relationship of the number of scale rings to total length.


100
80
60
40
20
T. L. (cm)
A. australis
0
1
2
3
4
5
6
7
8
9
10
11


140
120
100
80
60
40
20
T. L. (cm)
A. dieffenbachii
0
1
2
3
4
5
6
7
8
9
10
11
Number of scale rings

a faster growing population showed a similar lack of correlation between known age and scale annuli, a sample of shortfins from Pukepuke Lagoon was obtained. Scales from 80 eels up to 70 cm in length were examined. Again the relationship between the number of scale annuli and mean fish length $Y = 7.2357(X) + 20.4643$ was linear ($r = 0.9943$), and differed from the mean length for age graph obtained by examination of the otoliths of these and other eels.

The slope of this regression, 7.2, is close to that obtained for Makara shortfinsi.e. 6.7. From this it is concluded that little difference exists between the mean length per scale group relationship in slow and faster growing shortfin populations and in neither instance are the number of scale annuli indicative of age.

As the annuli of scales are not annual in formation, the term "scale rings" is used hereafter with "scale zone" denoting the area between successive scale rings.

Periodicity of Scale Ring Formation

To determine whether any seasonal periodicity is involved in the formation of new scale rings, the marginal increments of monthly scale samples taken from Makara eels were calculated. For this exercise, five eels of each species per month were utilised. From each scale sample, five regular scales were selected. The marginal increment for each scale, expressed as the width of the outer zone as a reciprocal of the width of the adjacent zone, was then calculated. By this method, a newly formed ring is indicated by a low increment value.

As it was found that a new zone was laid down simultaneously in almost all the scales examined from any one eel, the five reciprocals per eel were averaged. The mean monthly values for these scale increments are shown in Table 5.2.

These data show that there is no specific period for ring formation. This is to be expected from the lack of correlation between scale rings and age. However, if the six month period from November to April inclusive is considered, mean increment values of 0.96 and 0.99 for shortfins and longfins respectively are obtained. These months include spring and summer when most growth could be expected to take place. Any check in growth, shown as a ring, should be laid down immediately prior to this period. Equivalent values for the remaining six months are 1.09 for both species.

December was chosen for further analysis as this month had the smallest increment value for both species. A further 30 eels were examined

Table 5.2 Monthly marginal increments of eel scales.

	A. australis	A. dieffenbachii
Jan.	0.94	0.88
Feb.	1.01	1.02
Mar.	0.96	0.98
April	0.93	1.15
May	0.97	1.23
June	1.27	1.08
July	1.14	0.97
Aug.	1.14	1.14
Sept.	1.00	1.19
Oct.	1.04	0.93
Nov.	1.04	1.02
Dec.	0.86	0.86
n	60	60

with five scales from each eel being measured. An increment value of 0.50 or less was considered indicative of formation of a new scale ring.

Three (17%) of the 16 shortfins examined showed new ring formation, while the equivalent longfin value was four (29%) from a total of 14. The ranges of increments were distinctive with 'new' zones being 0.21-0.47, compared with 0.89-1.40 for 'old' zones. Mean increment values were 0.99 for shortfins and 0.94 for longfins, compared with the previously calculated figure of 0.86 for both species.

Discussion

The area where scales are first formed is also the 'best' area for collecting scales for reading. Frost (1945: 34) found that scales containing the maximum number of zones in A. anguilla were formed above the anus. As previously discussed, this corresponds to the area of scale origin for this species noted by other workers.

It has been shown that the formation of rings in the scales of both species of New Zealand eels is dependent upon length. Therefore the rings are not annual in formation and are not indicative of age. However, the rings appear to be seasonal in that they are generally laid down prior to the spring-summer period. Thus the average marginal scale increment over this period is below that of the remaining months.

Therefore, at constant increments in length a new ring is laid down in the scales of an eel, with the exception of large longfins, as discussed. Such a ring is more likely to appear prior to the onset of seasonal growth. Both Frost (1945: 33) and Pantalu (1957: 272), investigating northern hemisphere eels, found scales with new marginal growth during summer and autumn, although Pantalu records that some scale growth occurs all year round.

The direct relationship between the number of scale rings and fish length is understandable, as the commencement of scale formation is similarly dependent upon length. Other phenomena in the life history of freshwater eels are also length dependent, including a change in rheotaxis for eels greater than 35 cm (Opuszynski 1965: 405), changes in feeding habits (Burnet 1952a: 54), and the onset of sexual maturity (Deelder 1970: 3: 1).

Appearance of scales on the attainment of a specific length has been shown for European, American, Japanese and Indian freshwater eels. For scales to be used in age studies, the formation of rings must be shown to be annual. In addition, the scale size and time to reach this size must be known.

Several authors have aged eels solely from scale readings, while others have used scales in combination with otoliths or length-frequencies. Recently, Voronin and Rusetskaya (1971) determined the age and growth of eels in Byelorussian lakes by scale reading. They considered that not only did scales indicate age but, by back-calculation, they could be used to study growth. Good agreement between ages determined by scale rings and length-frequencies was found by Pantalu (1957: 273) in the Indian eel, but he did not consider that scales could be used to back-calculate growth. Hornyold (1922) aged Worcester eels by otolith examination, but also compared differences in the number of zones present in otoliths and scales. He found considerable discrepancies between the two, which increased with the size of the eel.

Scales were used by MacFarlane (1936) to age A. dieffenbachii and the results correlated with otolith annuli and length-frequencies. However the data he presents are sparse and unconvincing. Both scales and otoliths were used by Cairns (1941) in age and growth studies on both New Zealand species. His contention that "the scales as well as the otoliths, are of value in determining the age of eels in New Zealand" is based on the incorrect assumption that scales form during the eels seventh year of life.

5.3 OTOLITHS

Otoliths were removed by bisecting the head sagitally. The sagitta itself could then be scraped out from the sacculus with the point of a fine scalpel, and any adhering tissue removed by rubbing between thumb and forefinger. Otoliths were then placed in numbered vials and either stored dry or in the alcohol solution used for scale storage. Both methods proved satisfactory. The otoliths from eels preserved in formalin for more than a few weeks were found to be unsatisfactory for examination. Formalin gradually decalcified and softened such otoliths.

The sagitta, the largest of the three otoliths, is oval in shape, laterally flattened with convex outer and concave inner surfaces. The sulcus is open anteriorly and extends along two-thirds of the outer surface. Cracks frequently radiate from the centre. Cairns (1941: 56) mistakenly considered these to be the result of grinding.

Otolith Diameter To investigate the relationship of otolith size and total fish length, diameters of whole otoliths from eels of up to 26 cm in length were measured. A minimum of five eels per centimetre group were used,

giving a total of 110 shortfins and 101 longfins. The regressions for these data,

shortfins: $Y = 0.0814(X) - 0.0381$ $r = 0.9747$
longfins: $Y = 0.0778(X) - 0.1042$ $r = 0.9894$

are shown in Fig. 5.2. The high correlation coefficients for both species indicate that a direct linear relationship exists between otolith diameter and fish length. This is consistent with isometric growth in eels of the above size range.

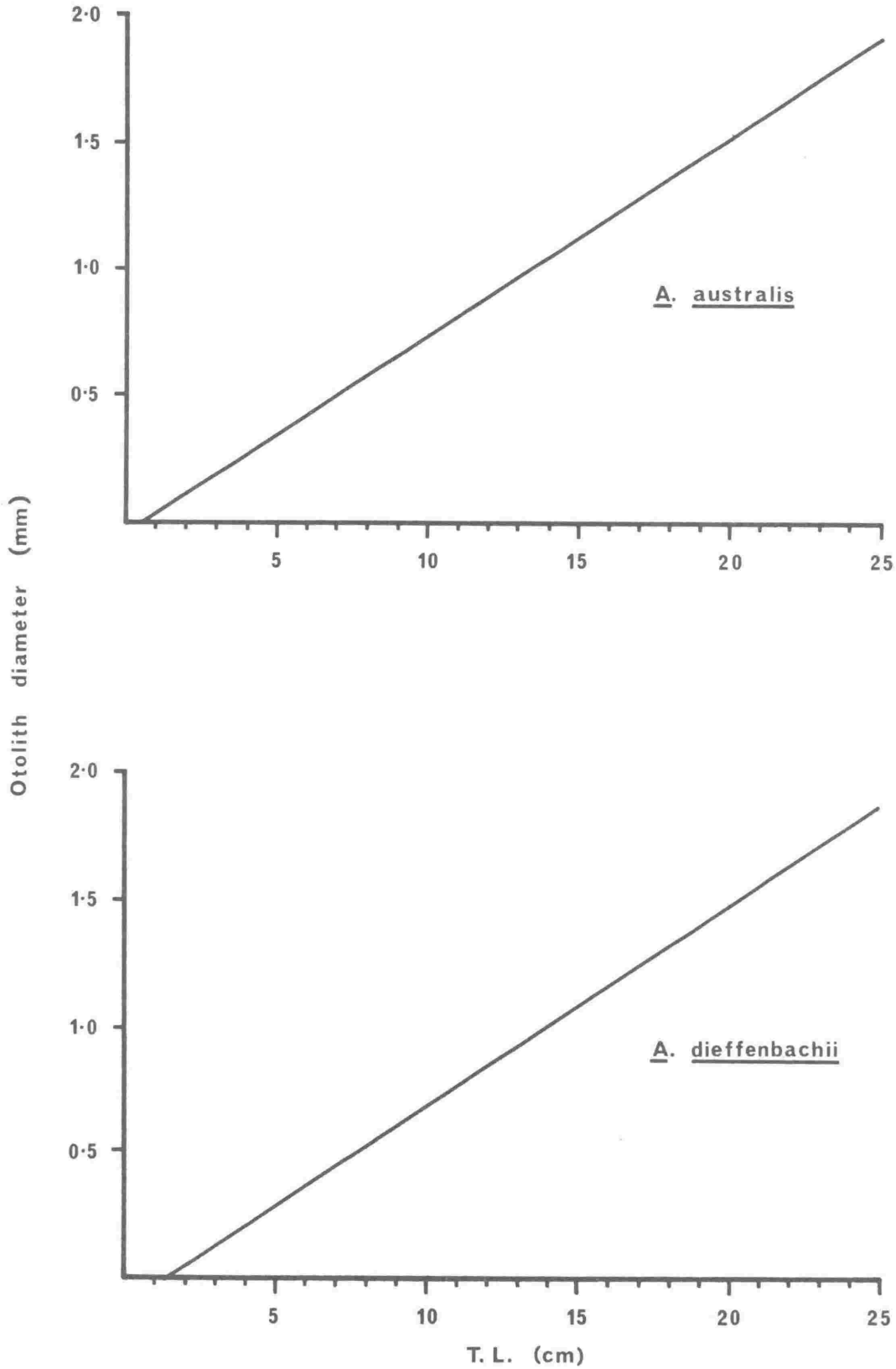
This direct relationship enables the approximate size of a small eel to be determined from measurement of the otolith. In this way the sizes of eels could be calculated from otoliths found in digested and faecal material of predatory fishes and birds. Unfortunately, it is not possible to differentiate between the otoliths of both species as they are similar in appearance. At any given body size longfin otoliths average slightly smaller than those of shortfins but considerable overlap occurs in actual measurements.

It has been assumed (Matsui 1952: 234) that the intercept of such a graph indicates the length of the larva at which the otolith commences formation. This length for longfins is thus 1.3 cm, which is a similar length to that given by Matsui for the Japanese eel. However, the equivalent value for shortfins is 0.5 cm which would seem to indicate otolith formation commences immediately upon hatching.

Diameters of otoliths from invading shortfin glass-eels do not fall on the line plotted but lie, on an average, 0.1 mm below. With the onset of growth in fresh-water, the otolith initially increases in size rapidly, especially in its greatest diameter. Otoliths from pigmented shortfin glass-eels have a diameter up to 30% greater than invading glass-eels of the same length. Differences in longfins are less marked. Due to the above, the regression for shortfins does not accurately reflect the relation of the smallest otoliths to length, and therefore the true point of intercept on the length axis is probably close to 2 cm.

Preparation of Otoliths For examination, otoliths were prepared in three ways - whole, ground or burnt. Of these methods the first was found suitable for otoliths from small eels (< 8-9 cm) only, and for eels larger than this, either of the other two methods were used.

Fig. 5.2 Relationship of otolith diameter to total length.


Otolith diameter (mm)
2·0
1·5
1·0
0·5
A. australis
5
10
15
20
25
2·0
1·5
1·0
0·5
A. dieffenbachii
5
10
15
20
25
T. L. (cm)

The clarity of otoliths to be mounted or ground was improved by placing them in beechwood creosote for 24 hours prior to usage. Various other media with high refractive indices including xylol and cedarwood oil, were investigated as possible clearing agents. However, beechwood creosote gave consistently good results and was adopted. Before mounting or grinding, the otoliths were placed on filter paper which absorbed the surface creosote.

Otoliths from glass-eels did not require clearing but were mounted on slides, using Depex as a mounting medium. Otoliths from larger eels were too dense, even after clearing, for the zones to be viewed adequately, and grinding was necessary to reduce the thickness.

Grinding of the lateral surfaces of otoliths has been widely used as a technique to prepare eel otoliths for examination. Hornyold (1922: 16) cleared otoliths in creosote prior to grinding the convex surface. A similar technique was adopted by Frost (1945: 29) and Pantalu and Singh (1962: 264). Etching of the polished surface with dilute hydrochloric acid to highlight the zonation, was used by Cairns (1941: 56) and also Sinha and Jones (1967a: 101).

In the present study several variations in grinding technique were investigated, including embedding otoliths in blocks of polyester resin for sectioning and polishing. The technique finally adopted was to place cleared otoliths on a fine carborundum stone. A short length of black plastic adhesive tape was placed on the end of the forefinger, and the otolith was ground with a circular motion with water being added as necessary. Brief final polishing was done on a rouge stone. The ground otolith was then washed in water, dried in air and mounted on a slide. These slides were dried for 24 hours in an oven at 35°C. Higher temperatures caused air bubbles to form under the coverslip. Generally, the thinner the ground otolith, the more readable it became.

Otoliths from eels less than 20 cm were approximately oval in cross-section and, with care, both surfaces could be ground without removing the outer margin. A definite concave inner surface develops in otoliths from eels larger than this and so most grinding on such otoliths was done on the convex outer surface. Excessive grinding on the inner surface soon removed the outer margin. In slow growing eels, this could mean the loss of at least one peripheral otolith zone.

To check the loss of otolith margins by grinding, the diameters of 112 otoliths from eels of 8-26 cm were measured before and after brinding. The only significant changes occurred in otoliths from eels greater than

20 cm, where 48% (22) showed a loss in diameter of less than 5%, while only one otolith recorded a decrease of greater than 5%. With care the actual amount of the margin lost remains small, and often results from chipping rather than excess grinding. However, there is an increased possibility of significant errors being introduced in large and slow growing eels where thin sections are essential to observe the full complement of rings. For this reason the technique of burning otoliths was investigated.

The burning of otoliths to determine ages of fishes including A. anguilla was described by Christensen (1964). More recently, Moriarty (1972) used burnt otoliths to age eels. His technique is described (1973) together with a useful method for making permanent mounts from the otolith fragments.

My own technique varied slightly from that of Moriarty, in that the otolith was broken prior to burning and the pieces were held directly in the flame rather than heated on a scalpel blade. The advantage in breaking the otolith first is that a good transverse fracture can be obtained which passes through the nucleus and consequently all the zones. Small otoliths when placed on a scalpel blade sometimes sprung upwards while being heated and were consequently lost.

The otoliths, stored dry, were placed between the folds of a small piece of clear plastic with the convex side uppermost. A scalpel blade was placed across the short axis. A firm press resulted in the breaking of the otolith into two approximately equal halves. The plastic covering prevented loss of these pieces.

Each piece was then firmly grasped with a pair of fine forceps and the broken margin held at the edge of an incandescent Bunsen flame until the sides of the otolith were seen to turn a deep brown colour. If the piece of otolith was heated until it turned black or grey it became very brittle and could not be handled satisfactorily.

Burnt otolith halves from the same pair of otoliths were then placed in a compartmented tray. When required they were removed from this with a fine brush. For inspection, the pieces of otolith were positioned on a piece of plasticine which was then immersed in beechwood creosote. A bright side lamp at a 45° angle was found to be the best illumination.

Using this method it was possible to burn otoliths from eels as small as 7 cm, although it was better suited to larger eels of 10 cm or more.

Appearance of Otolith Zones Ground otoliths were viewed with reflected light against a black background. The appearance of the surface of burnt otoliths proved to be similar with the opaque zones being white and the hyaline zones black. A check was made using otoliths from four adult shortfins. One otolith from each pair was ground and the other burnt. In all four instances both otoliths showed identical zonation but the burnt otoliths showed greater contrast between zones. The hyaline zones in the latter showed as a distinct heavy line whereas in ground otoliths they were broader and less definite. When read, all otoliths were awarded 'readibility' points, based on the following five point scale:

5: excellent - well defined rings of very good contrast;
4: very good - contrast good but less than 5;
3: good - readable but irregular zone widths and some multiple (secondary) zones;
2: fair - rings visible but irregular;
1: not readable.

The following description is applicable to otoliths prepared by either method.

The 'nucleus' or centre of the otolith corresponds to the sea-life of the eel and has already been described. Surrounding this glass-eel otolith is a broad opaque zone which is often divisible into two sub-zones. Bounding this zone is a hyaline ring. Depending upon the size of the eel a number of opaque and hyaline zones are seen, forming successive concentric rings. Such rings are most clearly seen along the longest axis of the otolith where they are well spaced.

Typically, the inner margin of an opaque zone shows the greatest opacity with a decline towards the outer margin until the hyaline zone is reached. This is less pronounced in burnt otoliths. Sometimes within a zone, subsidiary or secondary zones are formed. These can usually be recognised as they show various degrees of opacity and the hyaline boundary is very thin. Often such secondary zones are incomplete and do not traverse a full circle. The relative zone widths are often a useful indication of the true extent of the zone.

Interpretation of Otolith Zones To establish whether the zones in the otoliths were annual in formation, the marginal growth increments of a series of otoliths covering a year, were measured. Otoliths from ten

shortfins larger than 15 cm, per month, were examined by the burning technique. The distance from the last hyaline zone to the outer margin of the otolith was measured with a micrometer eyepiece, and expressed as a reciprocal of the width of the penultimate zone. Using this technique, the period or periods during the year when a hyaline zone is formed in the otolith can be ascertained.

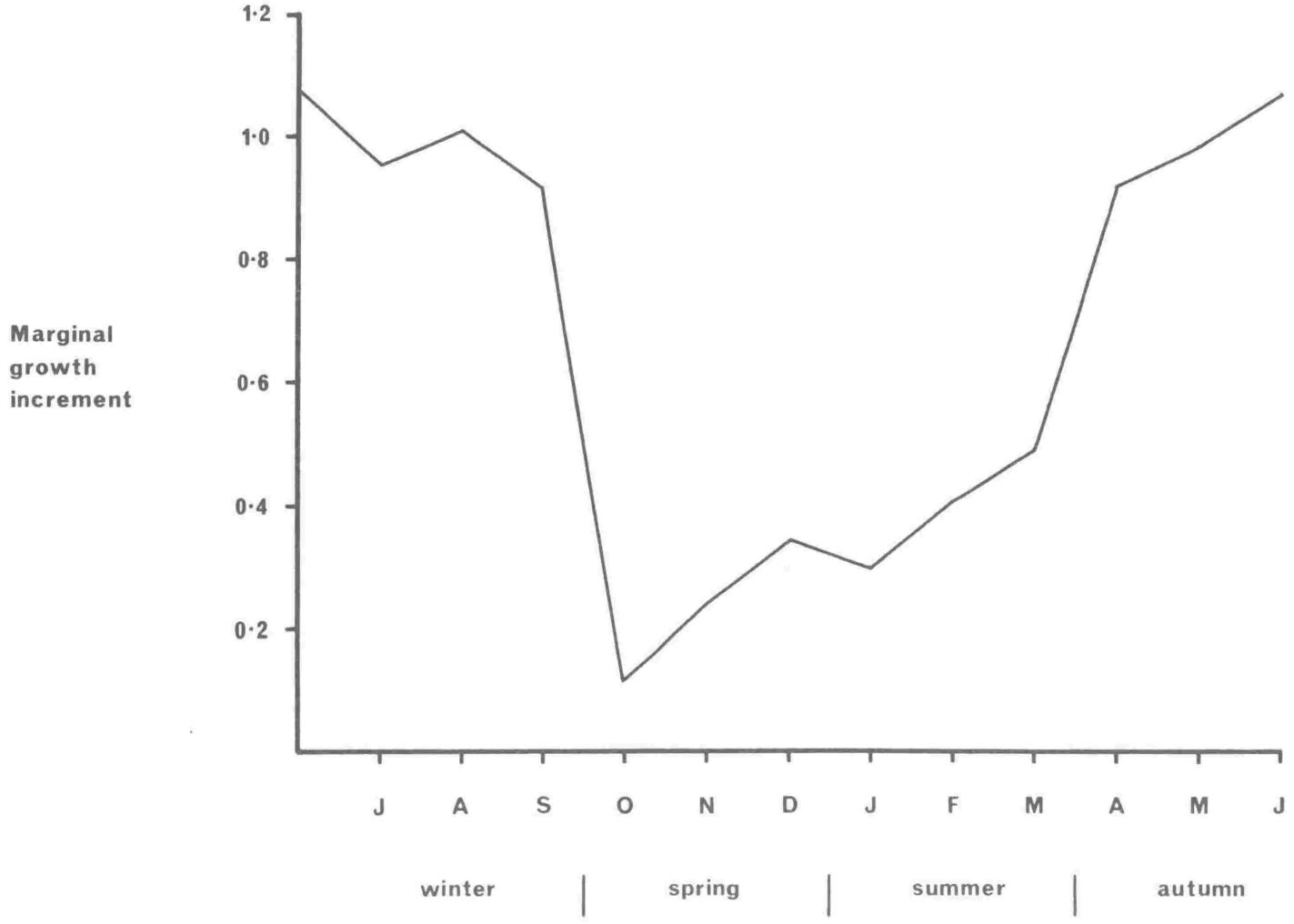
Mean monthly increment values are shown as a graph in Fig. 5.3. This graph indicates that the hyaline zone or ring as it appears in burnt otoliths, is annual in formation and is laid down between September and October. Of the ten otoliths examined from October, nine showed a discernable hyaline ring close to the outer margin. The opaque zone commences formation from October. The annual formation of these otolith zones validates the use of otoliths for determination of age in eels.

As the increasing size of the otolith is known to be directly related to growth in length of the eel, it is assumed that the marginal increment values reflect the relative rates of growth throughout the year. Surprisingly, the growth rate during summer is rather slow, with a sudden acceleration during March. The high indices from April to September indicate that little or no growth takes place over this period.

The widths of all opaque zones in otoliths from 12 of the larger Makara shortfins ($\bar{l}$ = 23.2 cm) from the months of May and June, were measured to find whether the zones corresponding to any particular year were uniformly wide. If so, this would indicate a better than average season for growth. Zone measurements for each eel were expressed as a reciprocal of the broadest zone. Results indicated that no one year was especially favourable for growth for all or most of the eels. For nine of the 12 eels, the first year in fresh-water produced the widest ring. This is in agreement with the observation that increase in the diameter of the shortfin glass-eel otolith is initially at a faster rate than that found among larger eels.

Other authors have examined the growing margin of eel otoliths to determine whether the successive zones represent annual growth. Frost (1945: 30) found the opaque zone in A. anguilla to be laid down between August and November, while Sinha and Jones (1967a: 103) recorded July-November. In both instances the authors found it difficult to determine the exact time when zones were formed as these were not well differentiated during their early formation. This is not surprising as both these studies involved ground otoliths.

Fig. 5.3 Marginal growth increment of otoliths. Mean monthly values.


Marginal growth increment
1·2
1·0
0·8
0·6
0·4
0·2
J
A
S
O
N
D
J
F
M
A
M
J
winter
spring
summer
autumn

For marginal growth to be measured, it is suggested here that the smallest otoliths that can be satisfactorily handled should be used, as growth and consequently relative zone widths should be greatest during early years. These otoliths should be burnt as this technique shows a more precise hyaline zone than does grinding.

Data from MacFarlane (1936) shows that ages calculated from otolith readings for a sample of small longfins, correlated precisely with peaks in a length-frequency distribution. The consistency of this relationship is very surprising. In his age and growth study of New Zealand eels, Cairns (1941) considers the above data of MacFarlane sufficient proof to assume that zones in the otolith are annual.

Designation of Age Groups As the winter zone in the otolith is laid down prior to October, it is appropriate to consider 1 October as the "birthday" of eels of both species. On this date all eels are promoted into the next age group. For convenience, the glass-eel otolith, which represents sea-life, is ignored. Therefore, the age group refers to those years spent in fresh-water.

Juvenile eels during their first year in fresh-water are placed in age group 0. In practice, it is possible to have eels from two different year classes in age group 0, as all glass-eels invading fresh-water prior to 1 October are "promoted" into age group 0 which already contains those eels that were glass-eels the previous year.

To calculate the age group of larger eels, the number of winter zones of freshwater life are counted and one zone is subtracted to compensate for age group 0. A series of otoliths, together with age group and size of the eel, are shown in Fig. 5.4.a-f.

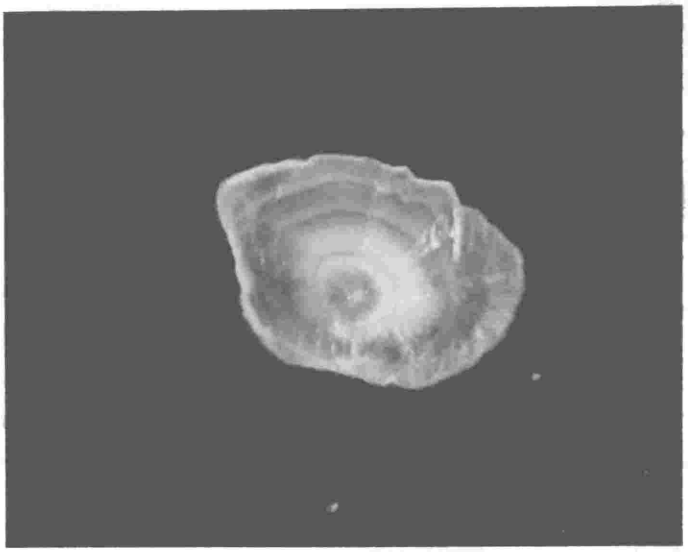
As glass-eels of A. anguilla arrive during the spring, Frost (1945: 30) proposed 1 May as their "birthday". However, as glass-eel invasion occurs at different times in various countries and, in the case of New Zealand, over a period of six months, this classification based on a mean date of invasion is not convenient for relative age comparisons. Accordingly, the above method involving the periodicity of otolith zone formation is used. A similar approach was adopted by Tesch (1928: 57) and Sinha and Jones (1967a: 104) although these authors do not propose a specific "birthday". As it is frequently difficult to distinguish when the winter zone is laid down in the otoliths of large eels, especially if growth is slow and the rings become crowded, a "birthday" provides a convenient and uniform reference date.

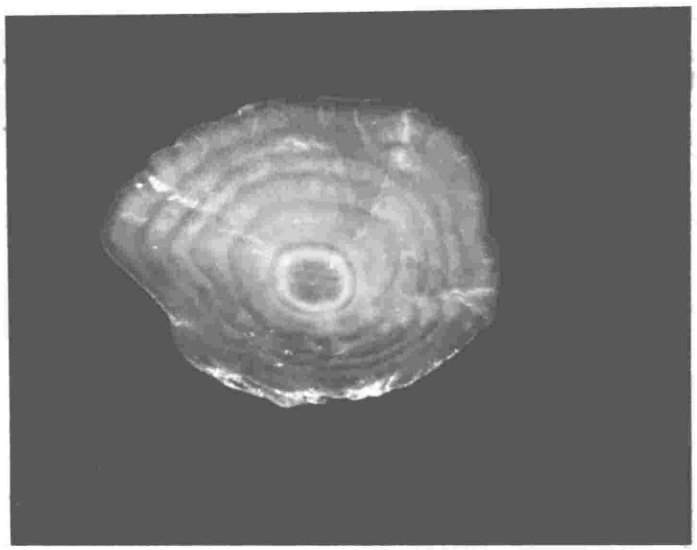
Fig.5.4 Otoliths : a-d = ground; e-f = burnt.

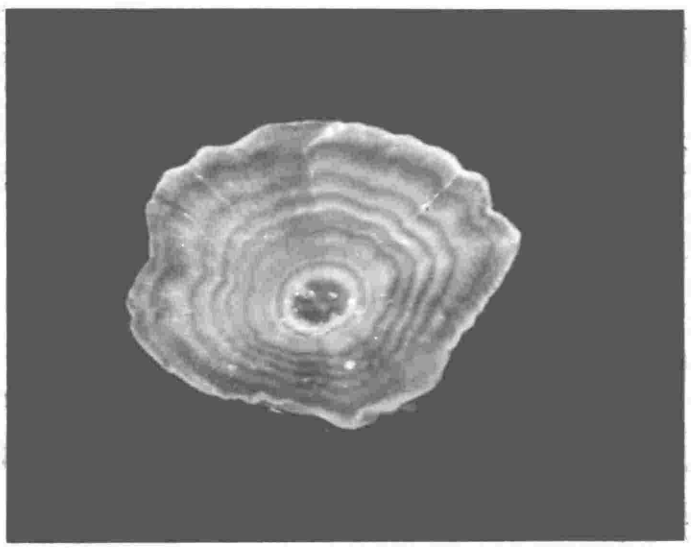
a *A. australis* 11.3 cm, age group 2 (outer ring barely visible in photograph).

b *A. australis* 16.5 cm, age group 4.

c *A. dieffenbachii* 17.9 cm, age group 4 (the apparent hyaline zone immediately adjacent to the outer margin is an effect caused by the sloping edge of the otolith and is not a new zone).



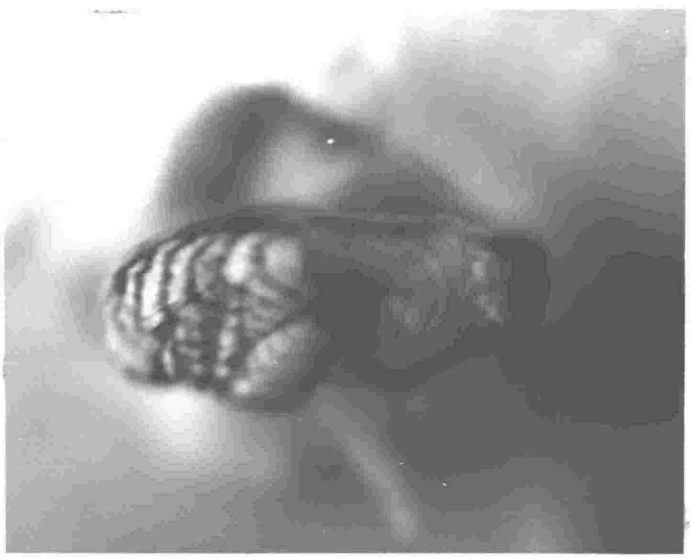


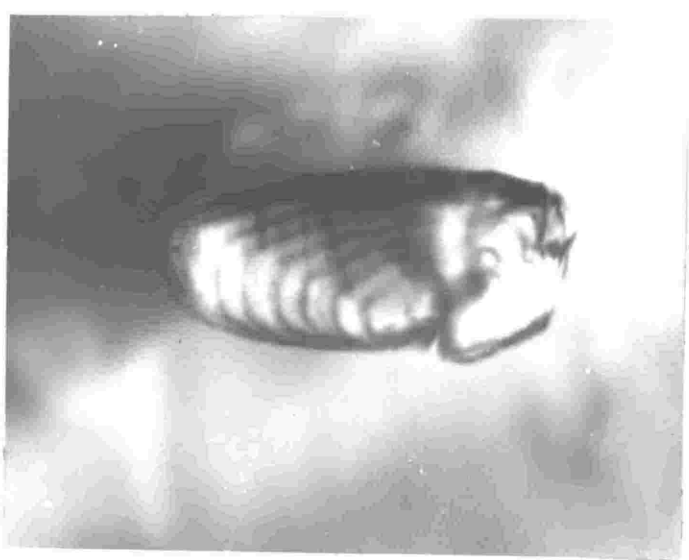


d *A. dieffenbachii* 25.2 cm, age group 8.

e *A. australis* 23.7 cm, age group 5.

f *A. australis* 24.6 cm, age group 6.





5.4 LENGTH-FREQUENCY

The lengths of all eels less than 26 cm collected during monthly sampling in the Makara Stream, were recorded and the data arranged in 0.5 cm length groups. Although the electric fishing catches were not designed to be quantitative, the samples are considered representative of small eels present in the areas fished. For later analysis, the otoliths together with length and weight data, were collected where possible from five eels per centimetre group per species.

Monthly length-frequency data are not reproduced here but they failed to show any obvious age groups with the exception of age group 0. This group could be traced through the monthly samples from their time of arrival as glass-eels until they were promoted into age group 1. From the monthly length-frequency histograms, a visual division was made between age groups 0 and 1. The mean length of the resulting members of each group was then calculated. This mean length is approximate only, as the method used does not allow for any overlap in length between successive age groups.

The mean lengths of shortfins calculated by the above method were approximately 0.5 cm less than the mean age group lengths obtained for February and August 1971 which were aged by otolith reading. This is explicable as, in the February sample aged, the known length range per age group shows that both age group 0 and 1 have a negative skew, similar to that often observed in large glass-eel samples. Such a bias is not taken into account by a stratified sampling technique as used for collecting otoliths.

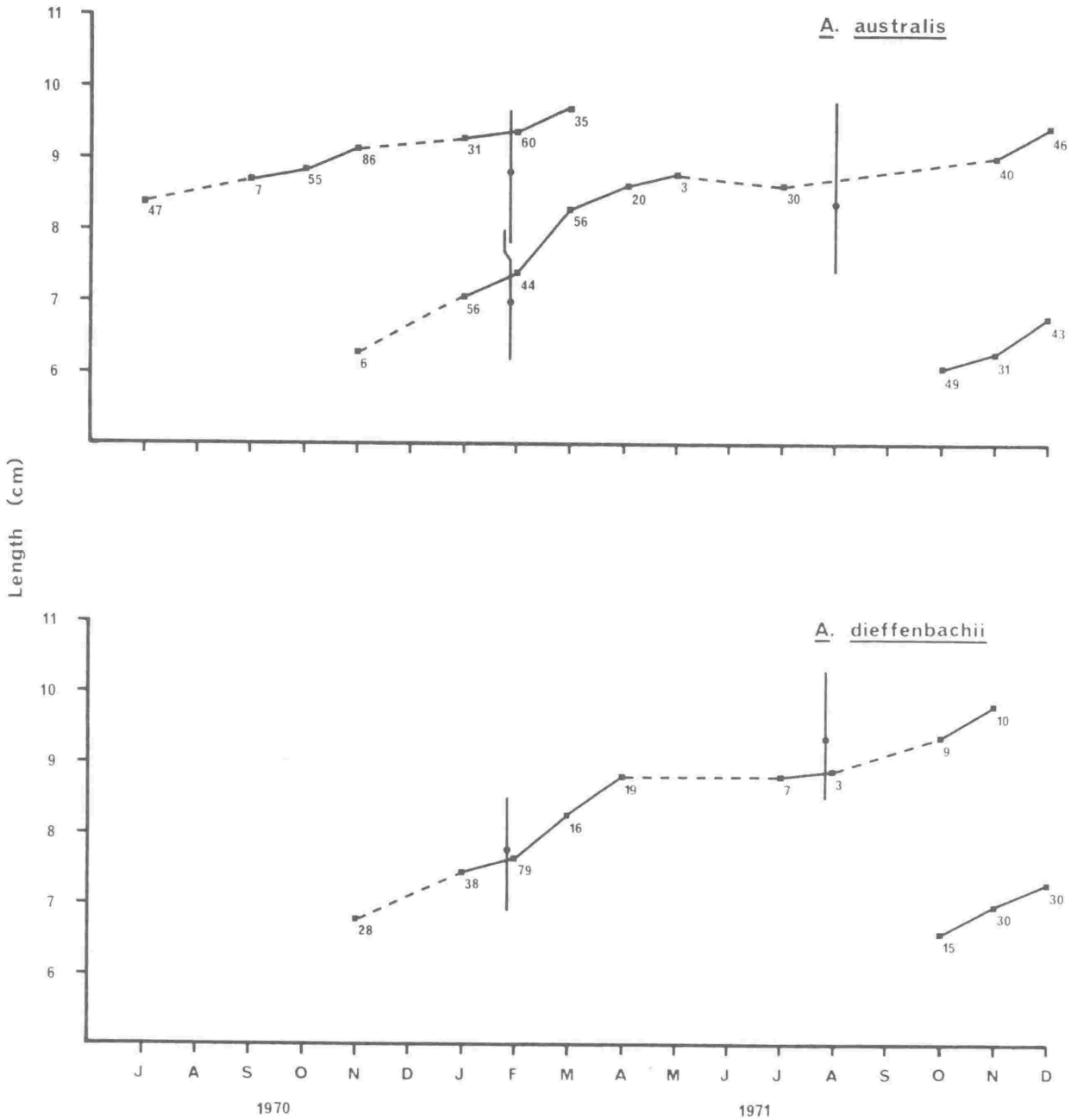
However, for both species, the mean lengths calculated by the length-frequency method are well within the ranges established for the aged samples. Also, the mean lengths of migratory elvers collected during January and February 1972 of 7.5 cm and 7.7 cm for shortfins and longfins respectively are in good agreement with the mean lengths as determined from the 1971 monthly length-frequencies.

The resulting graphs for mean monthly lengths are given in Fig. 5.5. Broken lines indicate a lack of representative samples and numbers are the number per sample. The mean lengths as calculated from the eels aged for February and August are given for comparison, with vertical lines indicating range in length. The agreement between these separate calculations is further evidence for the validity of aging by otolith reading.

Fig. 5.5 Approximate mean lengths per month of age groups 0 and 1 Makara eels, as established by visual separation of these groups from length-frequency data.

Sample numbers are shown. Dotted lines indicate no sample or the length-frequency data showed no clear separation into groups.

Solid circles and vertical lines represent the mean and range of age groups for the months of February and August 1971, as calculated from otolith readings.


A. australis
A. dieffenbachii
Length (cm)
11
10
9
8
7
6
47
7
55
86
31
60
35
6
56
44
56
20
3
30
40
46
49
31
43
28
38
79
16
19
7
3
9
10
15
30
30
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
1970
1971

These graphs show variations in the seasonal pattern of growth such that, from May to October-November, little or no growth in length occurs. From November to April, both species grow approximately 2 cm. Cessation of growth during autumn and winter is similar to the trend noted from the otolith marginal increment data.

The monthly sample of February 1971, was analysed by the probability paper method as given by Cassie (1950). This method is designed to produce a polymodal frequency distribution for size data. The February sample, which was one of those aged by otolith reading, contained 187 shortfins and 96 longfins. However, with the exception of age group 0, the data proved unsuitable, as when the graph of probabilities was constructed, an irregular series of small inflexions resulted.

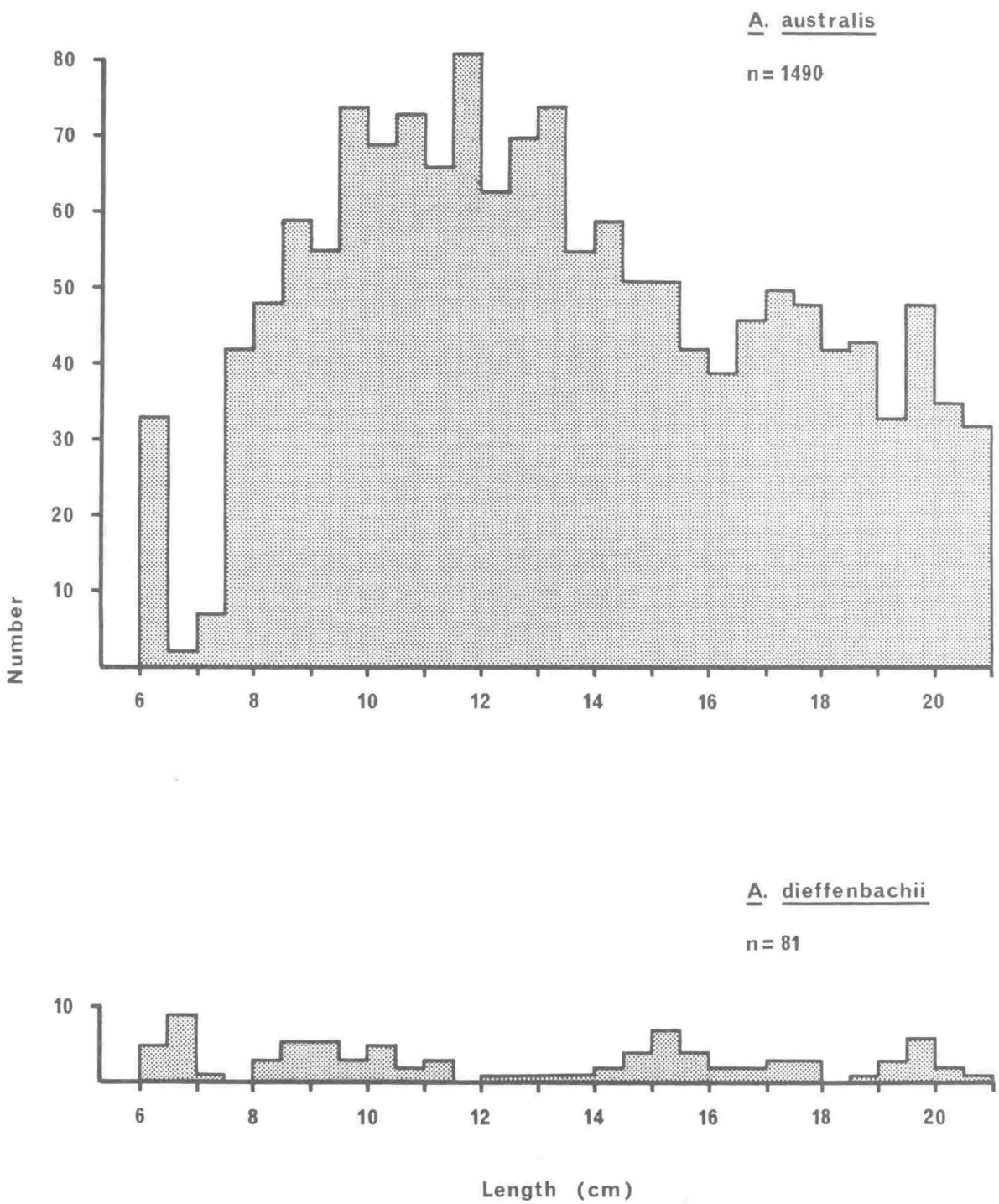
It was thought that the failure of length-frequency distributions to indicate age groups may have been partly due to small sample numbers. To increase the sample size, all Makara eels captured between the months of May to October inclusive were added together and plotted as a histogram with 0.5 cm intervals. Growth over these months has been shown to be minimal.

These months gave a total for eels of 20 cm and less of 1490 shortfins and 81 longfins. These data are shown in Fig. 5.6. Both histograms show an initial peak corresponding to glass-eels, but further age groups are obscured, presumably by overlapping ranges in length of successive groups.

The failure of length-frequency distribution to show age group patterns has been noted by several authors. Bertin (1956: 43) stated "To judge an eels age solely by its length would be to risk an error of one to five years either way." Similarly, Smith and Saunders (1955: 254), Deelder (1957: 84), Sinha and Jones (1967a: 105), Burnet (1969b: 381) and Moriarty (1972: 10), found length to be too variable to be indicative of age, especially amongst larger size groups.

Conversely, MacFarlane (1936: 46) found excellent agreement between age and length in small A. dieffenbachii. Although Cairns (1941) does not discuss the age-length relationship, the ranges in length per age group he gives for both species show only small overlaps, even in fish over 60 cm in length. Presumably, if arranged by length-frequency, these data would have shown a good age group distribution.

Fig. 5.6 Length-frequency histograms of Makara eels collected between May and October 1971.


A. australis
n = 1490
80
70
60
50
40
30
20
10
Number
6
8
10
12
14
16
18
20
A. dieffenbachii
n = 81
10
6
8
10
12
14
16
18
20
Length (cm)

Studies on A. bengalensis by Pantalu (1957: 277) and Pantalu and Singh (1962: 271) showed that the modes in length-frequency distribution were indicative of age for up to six years of freshwater life. Penáz and Tesch (1970) investigated age and growth in 8400 specimens of A. anguilla by length-frequency.

Determination of ages from the frequency of length distribution, is a convenient and quick technique for analysis of large samples. However, the use of this method should be confined to uniformly and rapidly growing species which show discernable polymodal histograms and thus little overlap between adjacent age groups. Freshwater eels would seldom fulfil these requirements.

5.5 RESULTS

From the monthly Makara samples, the months of February and August 1971 were selected for aging. These two samples were six months apart and are considered as summer and winter months respectively.

The February sample comprised 77 shortfins and 31 longfins to 21 cm in length. The August sample of 89 shortfins and 21 longfins included eels to 26 cm. To the latter sample a further 19 shortfins and 36 longfins from the following month were added to give a larger sample number.

The otoliths were ground and mounted on serially numbered slides. These slides were later viewed at a single sitting with no reference to the size of the eels. The age group was recorded, together with the readibility. From the results, mean length per age group graphs were constructed. The graphs for both species from the August sample are given in Fig. 5.7. The range in length and one standard deviation per age group are also shown.

For both species, the points plotted showed a distinct linear relationship. Regressions, fitted by the method of least squares, gave correlation coefficients of 0.9963 for shortfins and 0.9876 for longfins. The equations for these relationships were:

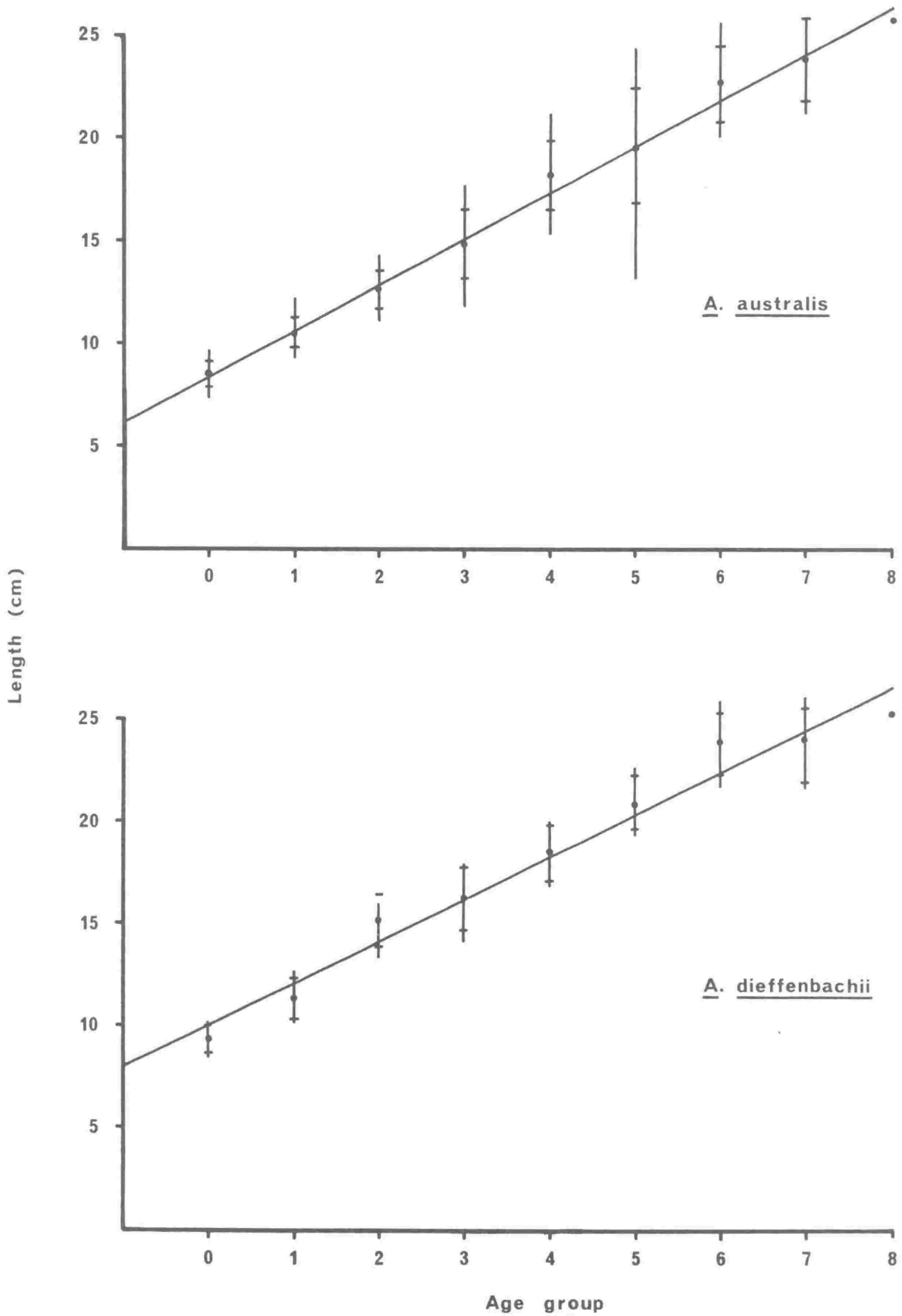
shortfins $Y = 2.2333\ (X) + 8.4911$

longfins $Y = 2.0652\ (X) + 10.0503$

Although the data are not presented, growth rates calculated from the February sample were in good agreement, and the equivalent regressions were:

Fig. 5.7 Mean length per age group for Makara eels collected in August 1971.

The solid circle indicates the mean length and the vertical line the range. The horizontal marks are one standard deviation from the mean.


25
20
15
10
5
A. australis
0
1
2
3
4
5
6
7
8
Length (cm)
25
20
15
10
5
A. dieffenbachii
0
1
2
3
4
5
6
7
8
Age group

shortfins $Y = 2.2346 (X) + 6.9162$ $(r = 0.9949)$
longfins $Y = 2.0693 (X) + 8.2393$ $(r = 0.9852)$

Because of this close agreement it was considered unnecessary to age further monthly samples.

To check the consistency in otoliths readings, the August sample was re-read, nine months after the initial reading. The results, shown in Fig. 5.8 indicate that considerable differences in interpretation occurred between the two readings. Even the classification of otoliths from the smallest eels showed differences, with four eels from age group 0 placed in age group 1 by the second reading. Overall, 63% of both readings were in agreement; 25% of the second readings were one age group less than the first reading while 9% were one greater.

However, the regressions for the mean lengths per age group from the second readings were similar to those calculated from the first readings:

shortfins $Y = 2.3607 (X) + 8.9001$ $(r = 0.9912)$
longfins $Y = 2.0500 (X) + 10.3000$ $(r = 0.9843)$

Agreement between the two sets of longfin readings was better than that for shortfins, such that the difference between mean lengths at age group seven was 0.14 cm for longfins and 1.30 cm for shortfins. These values reflect the higher mean readibility of the longfin otoliths.

The length and weight per age group data for February and August 1971 are summarised in Table 5.3.a -d. Also included are the mean weights per age group together with ranges in weight and standard deviations. The calculated weights have been obtained by substitution into the length-weight relationship (see following section).

Mean age for length graphs were constructed using the August data, and length intervals of 2 cm. Both species gave linear correlations highly significant at the 5% level. In slow growing species like eels, where large overlaps in age groups often occur for fish at a given length, such data are of limited application and so are not presented.

The graphs (Fig. 5.7) indicate that the growth rate of small eels in the Makara Stream is slow. However, the mean lengths for age groups seven and eight would, in fact, be greater than those calculated as the range in length for these age groups exceeds the 26 cm maximum of the samples.

Fig. 5.8 Comparison of repeated readings of the otoliths from Makara eels collected in August 1971.

The numbers inside the squares indicate agreements.

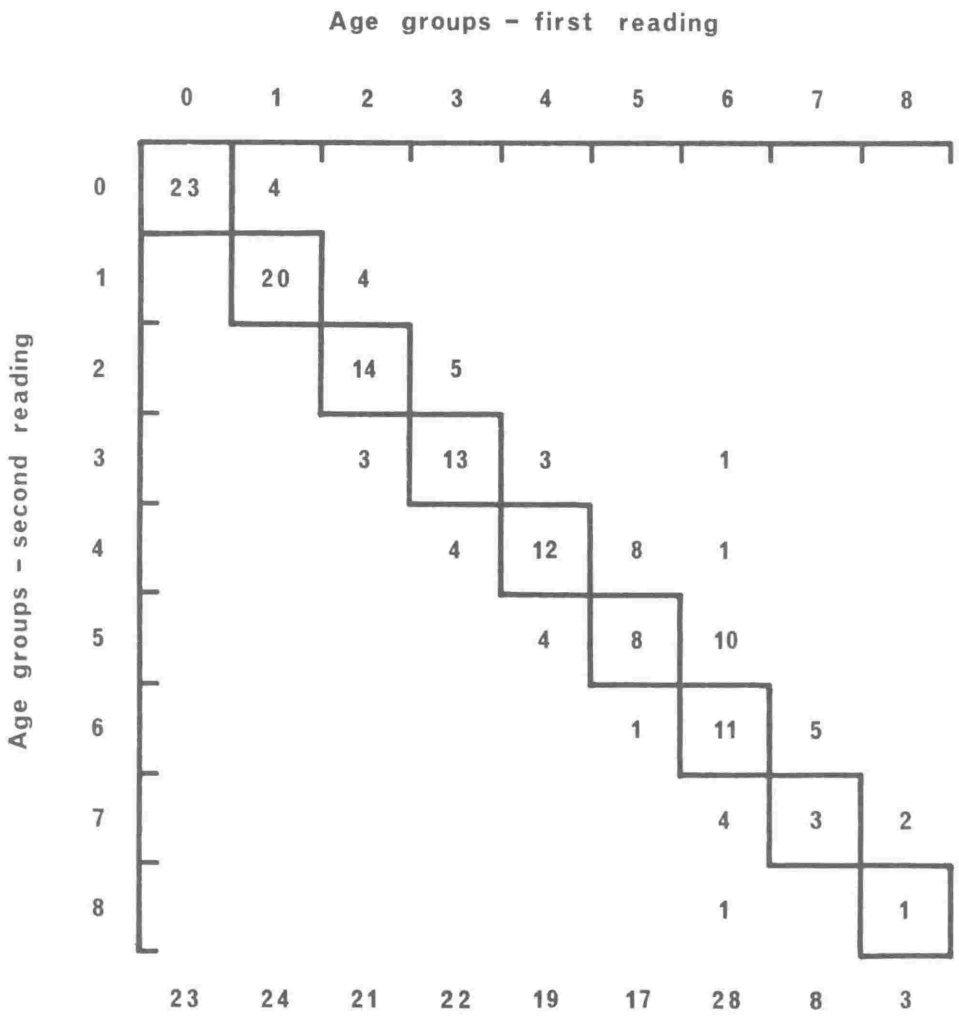

Age groups - first reading
0 1 2 3 4 5 6 7 8
Age groups - second reading
0 23 4
1 20 4
2 14 5
3 3 13 3 1
4 4 12 8 1
5 4 8 10
6 1 11 5
7 4 3 2
8 1 1
23 24 21 22 19 17 28 8 3

Table 5.3 Length and weight data per age group for eels from the Makara Stream.

a	A. australis	February 1971
b	A. dieffenbachii	February 1971
c	A. australis	August 1971
d	A. dieffenbachii	August 1971

a **A. australis**

Age groups	0	1	2	3	4	5	6	
Mean length (cm)	6.95	8.76	11.03	14.41	16.11	18.38	19.70	
Range	6.2-8.0	7.8-9.7	9.4-12.5	12.5-17.7	12.9-19.4	15.3-19.8		
S.D.	0.50	0.55	0.97	1.61	2.08	1.58		
Mean weight (g)	0.39	0.84	1.78	4.35	6.12	8.63	10.59	
Range	0.2-0.6	0.6-1.2	1.1-2.6	1.7-7.6	2.9-11.9	4.7-11.0		
S.D.	0.39	0.84	0.46	1.53	2.59	2.30		
Calculated weight	0.43	0.89	1.84	4.29	6.10	9.25	11.50	
n	15	10	14	12	19	6	1	77

b **A. dieffenbachii**

Mean length (cm)	7.71	10.13	12.60	15.00	16.80	19.60	19.30	
Range	6.9-8.5	8.7-11.1	10.8-13.9					
S.D.	0.53	0.98	1.01					
Mean weight (g)	0.61	1.41	3.05	5.50	8.50	11.70	11.29	
Range	0.4-0.9	0.9-1.9	2.0-3.8					
S.D.	0.13	0.43	0.64					
Calculated weight	0.58	1.44	2.99	5.35	7.80	13.05	12.86	
n	14	7	6	1	1	1	1	31

A. australis

Age groups	0	1	2	3	4	5	6	7	8	
Mean length (cm)	8.39	10.52	12.76	14.79	18.15	19.66	22.84	23.78	25.70	
Range	7.4-9.8	9.3-12.2	11.1-14.2	11.9-17.6	15.4-21.2	13.1-24.4	20.1-25.6	21.2-25.9		
S.D.	0.73	0.85	0.94	1.61	1.62	2.89	1.77	1.95		
Mean weight (g)	0.89	1.77	3.21	5.25	9.80	12.57	20.33	24.16	27.89	
Range	0.6-1.4	1.1-3.5	2.1-4.6	2.6-9.8	5.5-16.6	3.6-22.3	10.4-32.0	17.7-31.6		
S.D.	0.24	0.66	0.87	2.00	3.04	4.81	6.40	6.51		
Calculated weight	0.78	1.59	2.92	4.66	8.88	11.41	18.35	20.84	26.62	
n	14	20	8	14	14	14	18	5	1	108

d **A. dieffenbachii**

Mean length (cm)	9.34	11.37	15.16	16.16	18.60	20.87	23.91	24.00	25.30	
Range	8.5-10.3	10.2-12.6	13.4-15.9	14.1-17.9	16.8-19.9	19.8-22.6	21.8-25.9	21.8-25.8	25.2-25.3	
S.D.	0.63	0.98	1.27	1.49	1.33	1.51	1.48	2.03	0.07	
Mean weight (g)	1.26	2.34	6.04	7.32	10.91	17.79	25.92	27.51	30.96	
Range	0.8-1.6	1.6-3.2	3.8-11.2	5.3-9.6	8.1-13.0	14.2-24.4	17.6-35.6	18.2-36.3	26.4-35.5	
S.D.	0.28	0.65	1.93	1.98	1.83	5.75	5.66	9.02	6.41	
Calculated weight	1.10	2.12	5.54	6.85	10.95	16.10	25.32	25.64	30.66	
n	9	4	13	8	5	3	10	3	2	57

The shortfin regression has an intercept on the Y-axis at 6.26 cm, which corresponds to the length of shortfin glass-eels recorded at Makara during August 1972 ($\bar{l}$ = 6.25 cm). The equivalent intercept for the longfin regression is 7.98 cm, a significantly larger size than the mean length of 6.75 cm for August glass-eels. However, reference to the graph for longfins shows that the mean lengths for age groups seven and eight fall below the regression line for reasons given above. If the regression is re-calculated using data to age group six inclusive, the resulting line cuts the Y-axis at 7.05 cm. This is only 0.3 cm greater than the expected value.

A small sample of juvenile eels from the Waimeha Stream, Waikanae, were aged to compare growth rates with those of Makara eels. A total of 61 shortfins and five longfins from a sample taken in June 1971, were aged by burning of otoliths. The otoliths proved very readable with a mean readibility index of 4.2. Results are set out in Table 5.4.a and b.

Again the rates of growth as indicated by the mean length per age group, are slow, and the regressions are linear.

shortfins: $Y = 2.1046\ (X) + 7.6776$ $\quad r = 0.9890$
longfins: $Y = 1.7407\ (X) + 6.3825$ $\quad r = 0.9946$

The age group increments of 2.1 and 1.7 cm for shortfins and longfins respectively, are below the Makara values. It is probable that the high density of small eels in this stream is the major contributing factor to this slow rate of growth.

Finally, a sample of 127 shortfins from Pukepuke Lagoon were aged. Unlike the above eels from Makara and Waimeha Streams these eels covered the complete size range available, from 12.7-83.6 cm. During investigations on scale development it was necessary to observe scales from large eels of known age. Therefore, two samples of eels from Pukepuke Lagoon taken by fyke nets in March 1970 and 1972, were aged by the method of burnt otoliths. Negligible numbers of longfins occur in this coastal lagoon (pers. comm. P.H.J. Castle).

Unfortunately, no eels in age group 0 were available as these could not be caught by fyke nets and the conductivity of the water was generally too high for effective electric fishing.

Table 5.4 Length per age group data for eels from the Waimeha Stream, Waikanae for June 1971.

a *A. australis*

b *A. dieffenbachii*

a **A. australis**

Age groups	0	1	2	3	4	5	6	
Mean length (cm)	7.50	9.25	12.46	13.66	17.19	18.44	19.44	
Range	6.6-8.3	7.3-11.1	10.8-15.4	12.5-15.6	14.4-24.8	14.7-20.3	15.7-22.9	
S.D.	0.68	1.24	1.66	1.03	3.39	2.21	2.75	
n	5	13	13	7	8	8	7	61

b **A. dieffenbachii**

Mean length (cm)		8.9			14.85		17.75	
Range					13.7-16.0		17.1-18.4	
S.D.					1.63		0.92	
n		1			2		2	5

The results expressed as mean lengths per age group, are graphed in Fig. 5.9. Included are the range and one standard deviation. The growth rate is asymptotic with log Y = 1.2160 + 0.5237 (log X). An index of correlation, calculated according to the method given by Mills (1955) gave a coefficient of 0.87.

The growth rate for shortfins in this lagoon is therefore far more rapid than that for either Makara or Waimeha Streams.

Previous growth studies on New Zealand eels appear in Cairns (1941) and Burnet (1969b). Both authors use "age in years" rather than "freshwater life" as a measure of age, and also assume a sea-life of two years. For comparison with my data, three years must be subtracted from their figures to allow for sea-life and age group 0.

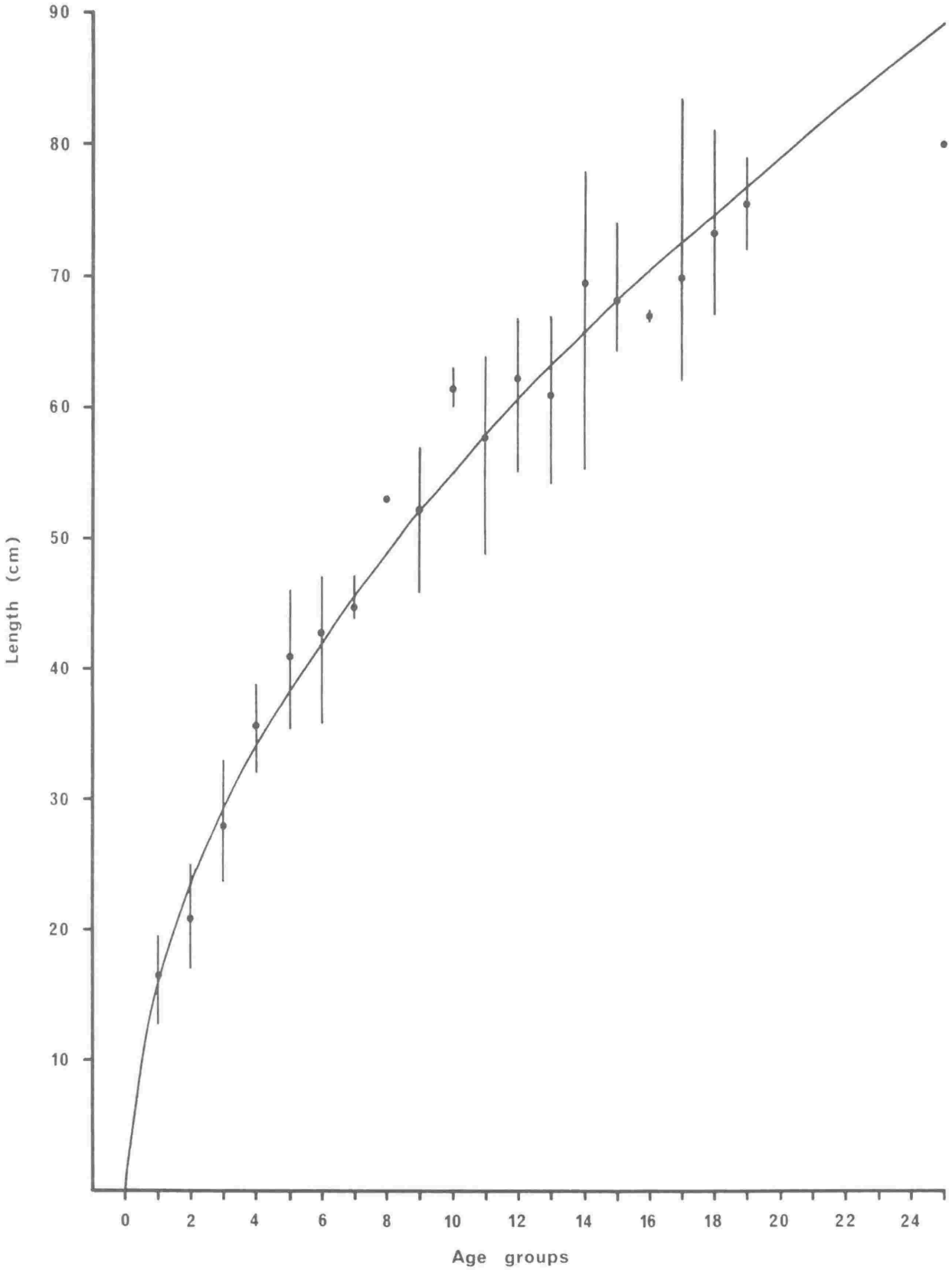
Growth rates recorded by Cairns for both species are much faster than those found by Burnet or myself. Unfortunately the rates given by Cairns appear to be based on composite samples from throughout the country. It is now well established that growth in eels shows a high degree of geographical variation and this makes the data of Cairns less meaningful.

Burnet (1969b) constructed growth curves for both species of eels in Canterbury Streams, based on tag return data from large eels and otolith readings from small eels. Although no table of lengths per age groups is given, it is possible to determine the approximate lengths from the graphs themselves (pp. 382-383).

The rate of growth of Makara Stream shortfins is intermediate between that determined by Burnet for equivalent sized shortfins in the Doyleston Drain and the South Branch. Longfins from Makara grow at a comparable rate to those in the Main Drain and more rapidly than those in the South Branch. Although no density estimates have been made for the Makara Stream, in size and temperature range the stream appears similar to both the above Canterbury streams.

The comparatively rapid rate of growth of shortfins in Pukepuke Lagoon is initially greater than that given by Cairns (1941). However, Cairns' growth rate is linear, whereas that of Pukepuke Lagoon is asymptotic and the annual increments in length decrease with age. Growth in this lagoon is very similar to that established by tag returns for shortfins in the Doyleston Drain. For this latter area Burnet (1969b: 379) found annual growth increments among small eels of up to 9 cm which are of the same order of length increases calculated for Pukepuke Lagoon. Although

Fig. 5.9 Mean length per age group of A. australis from Pukepuke Lagoon.


90
80
70
60
50
40
30
20
10
Length (cm)
0
2
4
6
8
10
12
14
16
18
20
22
24
Age groups

growth in Pukepuke Lagoon is initially more rapid than in the Doyleston Drain, from age group nine onwards, both populations show a similar rate of growth.

The variability of growth rates for small eels can be seen by comparing results for shortfins from the Makara Stream with Pukepuke Lagoon. Rates of growth in small eels may not be typical of growth in succeeding years and growth rates in small streams would not typify growth in larger bodies of water. However, such data do give grounds for caution in exploiting what is probably a relatively slow growing fish stock.

Growth rates of the European eels have been recorded by numerous authors, including Ehrenbaum and Marukawa (1913), Frost (1945), Deelder (1957), Sinha and Jones (1967a), Penáz and Tesch (1970). Both Smith and Saunders (1955) and Gray and Andrews (1971) have studied age and growth in the American eel. All these investigations gave more rapid rates of growth than those recorded for Makara although most were below those from Pukepuke Lagoon.

Slow rate of growth is frequently characterised by large overlaps in successive age groups. Such overlaps are typical of growth in eels. Nikolsky (1963: 207) considers a large growth differential to be an adaptation which enables a wider variety of food to be utilised. The linear growth curves for Makara and Waimeha eels are characteristic of dense populations with slow growth rates, whereas the asymptotic curve of the Pukepuke Lagoon shortfins is more typical of most fish populations.

The flexibility of growth in eels is well known. For instance, an eel kept in a battery jar for 57 years was only 30 cm long when it died (Harrison 1953). Conversely, Japanese eel farmers are now hopeful of growing eels to a marketable size of 150 g (approximately 40 cm) in six months, using heated water.

It is suggested that in the wild, the growth rate of eels is primarily a function of water temperature, availability of food and population density. In addition, the total volume of water available to eels is also a significant factor. Although females are known to grow more rapidly than males, it seems that the potential growth of neither sex is seldom, if ever reached in wild stocks.

5.6 LENGTH-WEIGHT RELATIONSHIP AND CONDITION

In fisheries biology, length-weight data are analysed for two reasons. Firstly, to give the mathematical length-weight relationship which enables one value to be converted into the other, and secondly, to give the condition of the fish. The term condition has been variously interpreted as indicating fatness, general "well-being" (Le Cren, 1951: 202) and the "physical capacity for survival and reproduction" (Cassie 1957: 375).

The length-weight relationship of most fish can be expressed as:

$$W = a\,L^{b}$$

where W = weight, L = length, a = a constant and b = an exponent. (n is often used in place of b, but as n is widely recognised as designating the number per sample, it is preferable to use b).

For analysis of the length-weight relationship by a straight line regression, the above formula is expressed logarithmically:

$$\log W = \log a + b \log L$$

where b gives the slope of the line and log a the elevation.

The variation observed for individual fish between the observed weight for length and the expected (theoretical) weight for the same length is an expression of the condition. Various types of condition factor, K, have been calculated, based on the "cube law" which assumes that the exponent b is equal to three as the value of b usually varies about this number.

$$\text{e.g.}\quad K = \frac{W}{cL^{3}}, \quad K = \frac{CW}{L^{3}}$$

These expressions measure the ratio between the observed and expected weights at a given length for an "ideal" fish which obeys the cube law. However, the exponent b is rarely equal to 3 and accordingly Le Cren (1951) proposed the use of a relative condition factor, Kb, such that

$$Kb = \frac{W}{aL^{b}}$$

In practice, Kb can be calculated from the ratio of the observed (W) and calculated ($\hat{W}$) weights for a fish of the same length.

$$\text{i.e.}\qquad Kb = \frac{W}{\hat{W}}$$

It is often desirable to compare the condition of various subgroups within a large group of fish. Such subgroups might represent differences in sex or reproductive state, sampling area, or time of year when caught. By using an analysis of covariance (Snedecor 1956: 394-412) the values calculated for b from the logarithmic form of the length-weight formula previously given, can be tested for homogeneity. If there is no significant difference between these values, a common regression for the pooled data can be calculated, and the values of a adjusted for this regression. Le Cren (1951: 204) states that "These adjusted values of a are accurate measures of the relative condition of the subgroups and the significance of the differences between them can be subjected to accurate statistical tests".

To analyse the monthly Makara length-weight data by the method of covariance, a computer programme was used. This programme was written and kindly made available by Dr R. D. Elder, Fisheries Research Laboratory, Wellington, and appears in Appendix 1. The programme generates values for testing residual variances, homogeneity of regression coefficients (b) and elevations (a) of the subgroup regressions. If the residual variances were found to be homogeneous, then the test for the homogeneity of the regression coefficients could be undertaken. If the differences between these coefficients were not significant then the adjusted means (elevation of the regression line) could be considered to be accurate measures of relative condition. These adjusted means, which are measures of weight relative to the calculated grand mean length, were then tested to find whether differences between them were significant.

Length-Weight Relationships The length and weight data from 1040 shortfins and 238 longfins, to 26 cm in length were analysed. These eels were from monthly Makara samples and covered a period of one year. The regression equations for these pooled data were:

shortfins: $\log W = 3.1565 \log L - 3.0251$ $(r = 0.9945)$

longfins: $\log W = 3.3355 \log L - 3.1948$ $(r = 0.9965)$

or

shortfins: $W = 0.0009443\ L^{3.1565}$

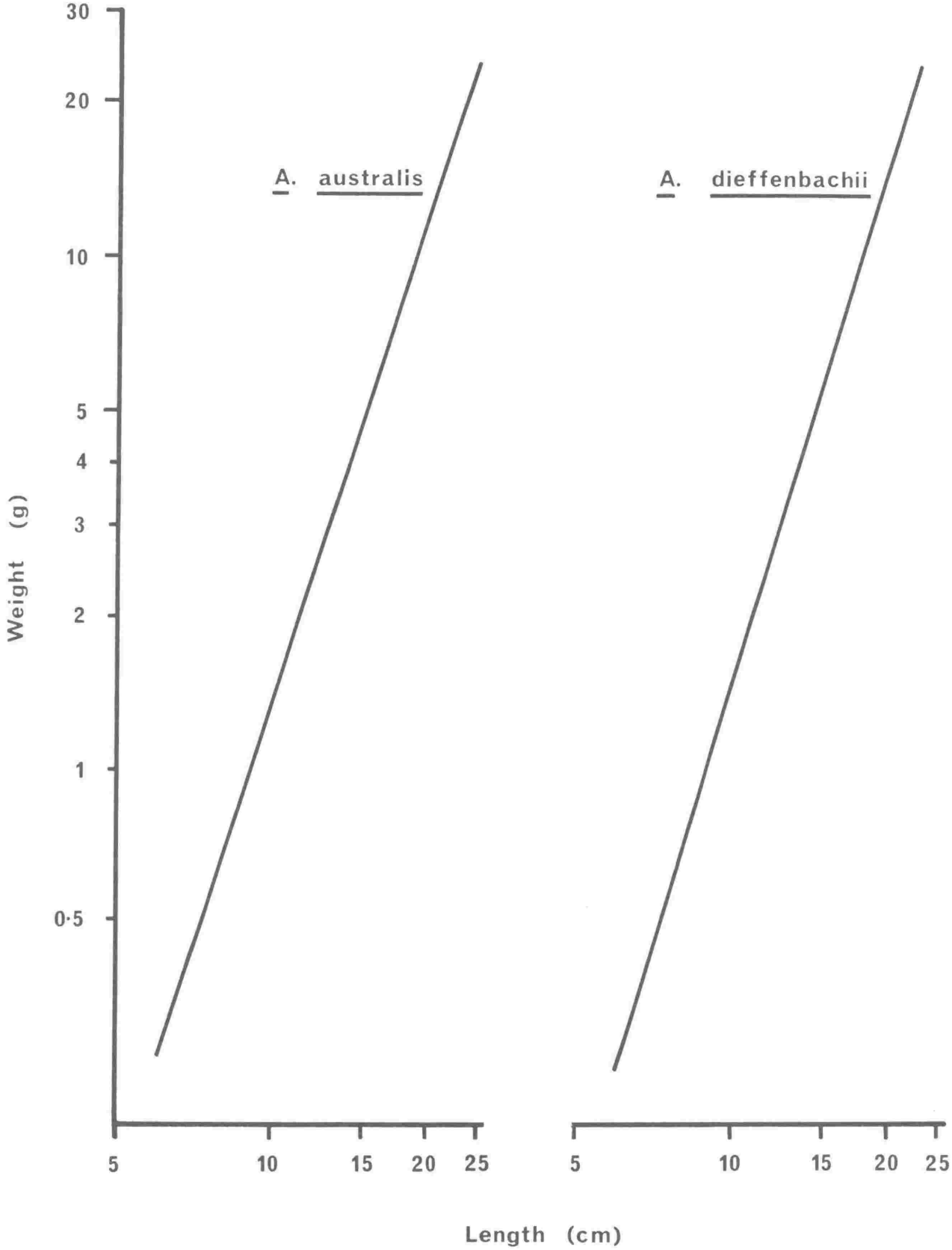
longfins: $W = 0.0006386\ L^{3.3355}$

where W = weight (g) L = length (cm)

r = correlation coefficient

These regressions are plotted in Fig. 5.10.

Fig. 5.10 Length-weight relationship for both species of eel, to a length of 26 cm.


30
20
10
5
4
3
2
1
0·5
Weight (g)
A. australis
A. dieffenbachii
5
10
15
20
25
5
10
15
20
25
Length (cm)

For given lengths less than approximately 8.5 cm, shortfins are heavier than longfins, but above this size longfins are heavier. Values for b are greater than three, indicating neither species maintains the "ideal" shape during growth. To assume the cube law would be to introduce a percentage error in weight of 32-102% for shortfins over the known length range of 6-90 cm. Equivalent errors for longfins are 23-206%.

The data were further analysed by length groups. The three length groups were 5-11 cm, 11-19 cm and 19-26 cm. Growth exponents, b were all greater than three, with the smallest size group for each species having the largest value i.e. 3.4598 for shortfins and 3.6830 for longfins. Again the regressions for these small eels showed shortfins to 8 cm were heavier than longfins to the same length. The converse was true above this length. Smallest values of b for both species were in the 11-19 cm range: shortfins = 3.0715, longfins = 3.2927.

Previous studies on New Zealand eels have included some data on length-weight relationships. Cairns (1941: 60) gives only data for eels greater than 45 cm and does not fit a regression. Similarly, Shorland and Russell (1948: 176) give length-weight data for a small range of large eels; although they do give an equation, it is not of the above type. Burnet (1952a: 49) calculated the length-weight relationship for longfins over a range of 12-50 inches as:

$$\log W = 3.305 \log L - 4.387$$

or as expressed above $W = 0.00004101\ L^{3.305}$

Unlike the above data, his measurements were recorded in inches and pounds.

Finally, regression from Woods (1964: 103) for both species over a large size range are given as:

shortfins: $W = 0.000803\ L^{3.18}$ and
longfins: $W = 0.000575\ L^{3.36}$

The exponents for these latter data are close to my own.

Values for the growth exponents of the European and American eels are also greater than three (see Frost 1945: 118, Sinha and Jones 1967a: 109, Smith and Saunders 1955: 259, Gray and Andrews 1971: 124). The two exceptions to this statement are for females of the European eel recorded by both Frost and Sinha and Jones. The greatest ranges of b as given are

2.99-3.38 for the European eel (Sinha and Jones) and 3.08-3.44 for the American eel (Gray and Andrews). These latter figures are for eels from different areas and indicate the variable effect of environment on the pattern of growth.

Analysis of Condition For analysis of condition, the adjusted mean weights obtained from the analysis of covariance were used. Although the adjusted mean weights can be substituted into the formula:

$$Kb = \frac{W}{\hat{W}}$$

to give a relative condition factor varying about one, it was felt that the actual weights gave an easily recognisable index of condition and these have been left unaltered. The monthly samples from Makara were used but only those months where more than ten eels per species were available are included in the calculations. This meant that both May and October were deleted from the longfin analysis.

Results from the analysis of covariance are given in Table 5.5. Regression coefficients for shortfins were found to be significantly different at the 5% level (although not at the 1% level), indicating that real differences exist between the monthly length-weight relationships. The adjusted mean weights for the grand mean length of 14.30 cm were also significantly different.

Conversely, neither the regression coefficients nor the adjusted mean weights for longfins were significant at either level. Thus the differences in the adjusted mean weights for longfins reflect differences within monthly subgroups rather than between subgroups. Although these adjusted mean weights, relative to a grand mean length of 12.52 cm are not significantly different they are plotted with the adjusted mean weights for shortfins for comparative purposes (see Fig. 5.11).

Le Cren (1951: 203) considered three types of variables could affect condition. These are factors related to length e.g. age, sex, maturity; sampling bias; and "long-term" features of environment, feeding, reproductive cycles etc. As the above analysis adjusts mean weights to a grand mean length per species based on the "best fit" of the regression for all data, this minimises differences related to length. Eels in the size range of those examined are in the stage of adolescence and active growth and no differences in relative condition would be attributable to maturation processes. The sampling method of electric

Table 5.5 Analysis of covariance for Makara Stream eels. Between months, by species.

	Regression coefficient			Adjusted mean weight		
	F.	d.f.	P.	F.	d.f.	P.
A. australis	2.14800	11, 1028	< .01 > .05	19.9162	11, 1039	> .05
A. dieffenbachii	1.45666	9, 229	< .05	1.03116	9, 238	< .05

fishing is not thought to be selective for "fat" or "thin" fish. Therefore, differences in relative condition should be largely related to the "longterm" features.

The hibernation of New Zealand eels during the winter is recorded by Cairns (1941: 66). Burnet (1955: 24) found feeding almost ceased below 7-8°C but had no difficulty in sampling eels throughout the winter. Similarly, Woods (1964: 104) gives 6°C as the temperature below which no feeding occurs.

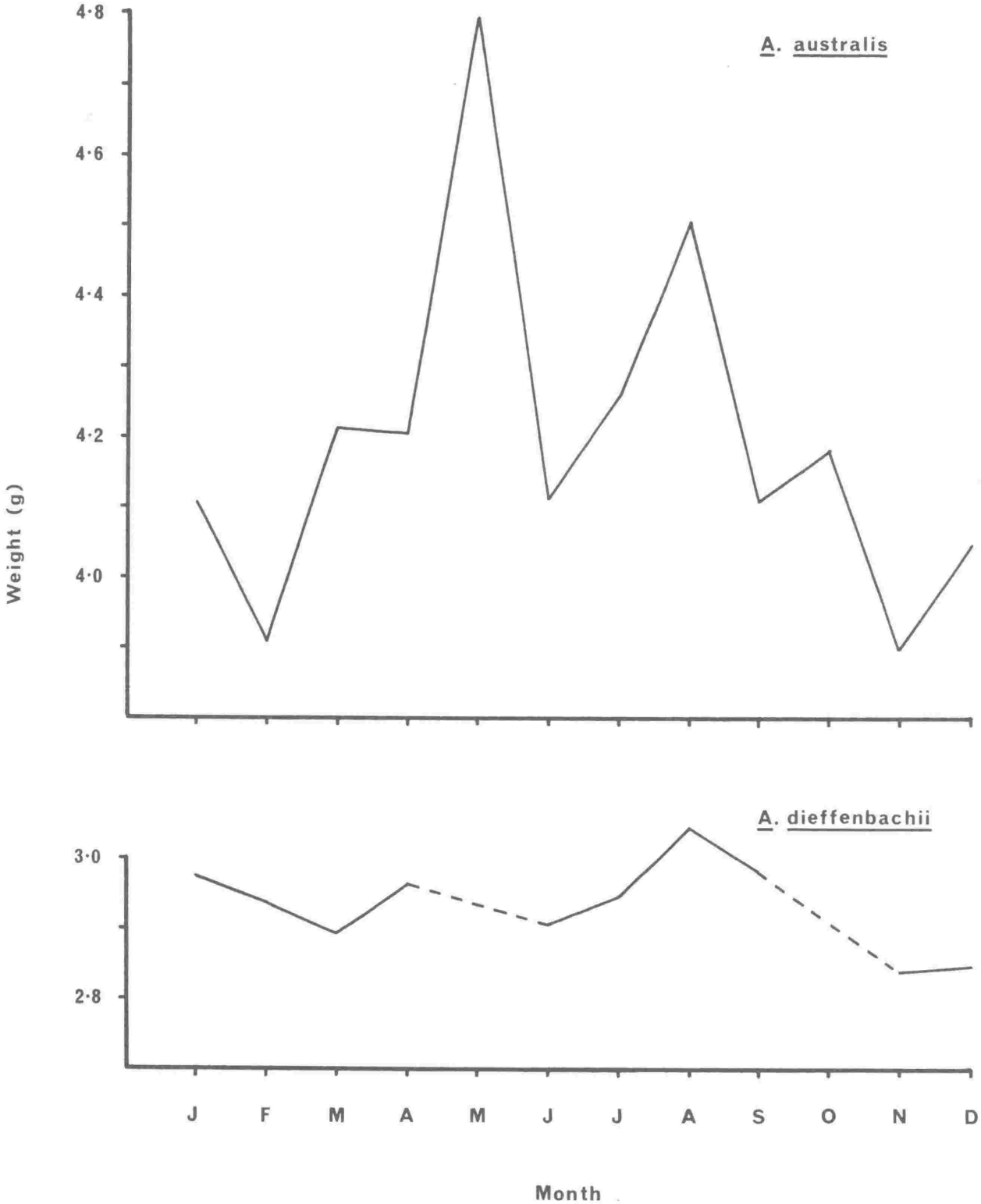
Although I have no evidence for complete hibernation in eels, they can be expected to show reduced feeding activity at low temperatures. It was thought that such overwintering, although accompanied by a decrease in metabolism, may have utilised stored body fats and so caused a gradual decline in the condition of the fish. However, reference to the graph of monthly relative condition in shortfins (Fig. 5.11) shows that this did not occur. In fact there was a tendency for condition to increase over the winter months.

The reason(s) for this trend are not clear, but the data do not support the above hypothesis of the direct relation of temperature and relative condition. Likewise, Frost (1945: 120) who calculated condition in the European eel over eight months, found a higher condition factor over the autumn-winter period than during summer. In a comparison of relative condition by month for snapper, Chrysophrys auratus Forster (F. Sparidae), Cassie (1957: 386) found a peak condition during spring which he suggested was a result of the ready availability of food. A decline in condition over the following months coincided with the onset of the spawning season, although this relationship was not supported by the state of the gonads.

Fig. 5.11 Index of relative condition throughout the year. Adjusted mean weights by month.

Weights for A. australis relative to a grand mean length of 14.30 cm.

Weights for A. dieffenbachii relative to a grand mean length of 12.52 cm.


A. australis
4·8
4·6
4·4
4·2
4·0
Weight (g)
A. dieffenbachii
3·0
2·8
J
F
M
A
M
J
J
A
S
O
N
D
Month

6 EXPERIMENTAL GROWTH

6.1 INTRODUCTION

With the rapid expansion of the wild eel fishery in New Zealand during the past few years, increasing interest has been expressed in the possible cultivation of eels to supplement the catch of wild eels. Approximately 90% of the annual Japanese eel production is of cultured eel. Matsui (1969) was optimistic about the potential of eel farming in New Zealand. However, although the principles of farming practice established in other countries can be applied to this country, the details of cultivation might best be worked out under New Zealand conditions.

The following experiments were designed to produce some guidelines in the areas of temperature range, amount of food, and species suitability for eel farming in New Zealand. Although it was recognised that results obtained under laboratory conditions may not duplicate findings from large-scale farming operations, it was considered that the trends observed would be applicable.

6.2 MATERIALS AND METHODS

To study growth in both species of eel under controlled conditions, a unit of 20 glass tanks was constructed. The tanks had a volume of 57 l each, but the overflow fitted to all tanks, reduced the actual volume to 45 l. Each tank had a supply of domestic fresh-water. This was used to replace water lost through evaporation and was also trickled into heated tanks to ensure some turn-over of water occurred in the event of air failure.

In addition, six tanks had a cold-water supply: another six had both cold-water and heaters while the remaining eight had heaters only. These appliances provided a full range of constant temperatures from 7-35°C.

Cold-water was obtained from a 500 l commercial milk chiller. As the refrigerant coils were of copper, the chiller was used as a

heat exchange system. Water from a 120 l supply tank was gravity-fed through 60 m of garden hose placed inside the chiller. By maintaining the water within the chiller itself at 2°C, an output of 5 l per minute of water at 6-7°C could be obtained. This cool water was conveyed to the tanks through a common main. Solenoid valves activated by thermostats controlled entry of cold-water into each tank.

These two-stage thermostats enabled heaters to be fitted also, giving the unit more versatility. The heaters were 150w immersion types. Fig. 6.1.a shows a tank equipped with both cold-water supply and an immersion heater, although the latter is partly obscured in the photograph. Part of the tank unit is seen in Fig. 6.1.b.

The remaining heated tanks were supplied with partially immersed bi-metallic strip thermostats, which gave a minimum differential of 1.5°C compared with 1°C for the two-stage thermostats. The power supply to each tank could be isolated by an individual switch, and the complete unit had a master switch. Additional safety was ensured by using an isolating transformer for the whole unit.

Each tank received a supply of air which both aerated and mixed the water. During experiments at temperatures of 20°C+, air-lift filters packed with nylon wool were used to remove suspended material from the water. In addition,,tanks were cleaned by siphoning twice a week.

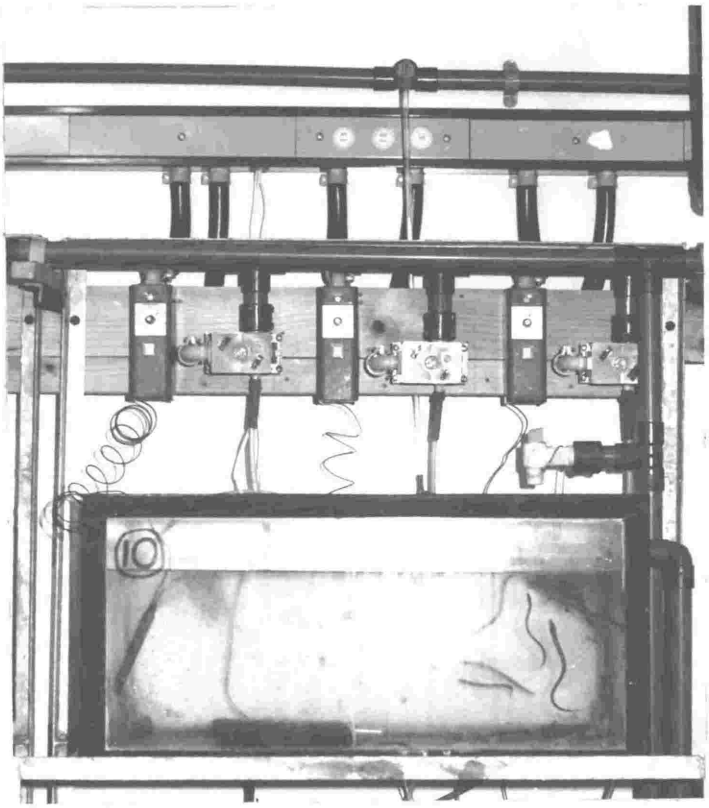
The overflow from each tank was equipped with a short outlet pipe extending 10 cm into the tank. This pipe was perforated with small holes and had sections of fine netting glued to the sides and end to increase the area available for water to escape. Because of this precaution, no tank overflows were experienced, and a 1.5 cm lip on the leading edges of the tanks ensured no eels were able to escape. The overflow water ran to waste.

The tank unit was assembled in an aquarium room where it received illumination from both fluorescent lighting and incident daylight. To provide some cover for the eels, sections of stone pipe were placed in the tanks. These were readily used by most shortfins but it was found that the longfins preferred to hang suspended from pieces of plastic netting. During the day, the majority of eels remained either

Fig.6.1.a Tank used in experimental growth trials.

The thermostat and solenoid valve on the left control the flow of cold-water into the tank. The heater is partly obscured behind the piece of stone pipe in the bottom of the tank.

b View of a section of the tank unit.


10

congregated under the pipe or in the netting, although some were always active. Activity increased at night and with increased temperature.

Originally it was intended to use both glass-eels and elvers of both species for the growth trials. However, considerable difficulty was experienced in keeping longfin glass-eels alive. Further, the much smaller size of glass-eels meant they were less readily handled than were the elvers, and so elvers only were eventually used. The opinion had been expressed (Matsui 1969: 9) that it would prove difficult to induce elvers to feed. No such difficulty was encountered. The procedure used to establish feeding patterns in elvers was similar to that already described for glass-eels. Again, natural foods of Tubifex worms, whiteworms and maggots were introduced after a week of acclimatisation.

A variety of foodstuffs were tried, to determine which proved acceptable to the eels. In addition to the above live foods, fish roe, minced liver, minced fish, assorted minced molluscs, and synthetic trout and eel preparations were all readily consumed. To provide a diet containing a variety of essential ingredients, the following was used; four parts minced fish:four parts minced liver:1 part synthetic trout food. (This trout food is a composite product with an analysis of 32% protein, 7% fat, 3% fibre - the carbohydrate content is high but unspecified). To 20 g of this mixture, 1 ml codliver oil and 1 ml gelatin solution were added. These latter ingredients helped bind the mixture and lessen fragmentation in the water.

Food was simply dropped into the centre of each tank and the eels then foraged for it on the bottom. Although this allowed all eels access to the food at the same time, it did result in problems from dispersal of food particles and made assessment of the amount of food consumed difficult. It had been hoped to train the eels to feed from floating chambers, but most seemed reluctant to enter any such apparatus, even through holes in the side.

The amount of food per tank was calculated as a percentage of the live weight of eels. Initial trials indicated a rate of 2-3% of body weight/day to be slightly above the level required for maintenance at temperatures of 15-20°C. Weekly rations were weighed out in advance and placed in cubicles in a plastic ice-block tray. These trays were then frozen until required. All food not used within a month of preparation was discarded. Most tanks were fed three times per week.

Elvers used in these experiments were obtained during January 1971, from Karapiro Dam. They were kept at the laboratory for several months until the tank unit was completed. The stocking rate was calculated on the basis of weight of eels per volume of water. The number of longfins available dictated this to be 55g/tank. This weight corresponds to a density of 1.4 kg/m^3. Matsui (1969: 11) proposed a stocking density for elvers in a large pond of 0.7 kg/m^2. Assuming such a pond to be a metre in depth (Matsui 1969: 11), this density can be considered as weight relative to volume also, and shows that my average stocking density was twice that recommended by Matsui.

The species were separated and random samples of approximately 55g wet weight were placed in numbered tanks. At the beginning and end of the trials the length and weight of each eel was recorded. It was intended to use these data in an analysis of relative condition, but the results of the trials did not warrant this.

At intervals of five weeks, the total number of survivors in each tank was counted and re-weighed en masse. This was always carried out one day after feeding. For this weighing, eels were not anaesthetised but were netted, the surplus water drained from them, and weighed in a large plastic dish. The weight of the dish together with water and mucus was then subtracted to obtain the live weight of the eels (= biomass, B). Differences in five repeated weighings to calculate the amount of error involved, varied from 1-3% with a mean value of 1.6%.

Amounts of food for the next five-week period were then calculated from this new biomass value. If a large mortality occurred between

Daily checks were made for any dead eels. These were removed, and measured and weighed before being discarded. Tanks were dosed weekly with a 2% solution of malachite green and methylene blue, to reduce the chance of fungal infection. This treatment, together with the constant slow flow of water in all tanks, prevented the outbreak of any major disease. No pathological examinations of dead eels were made.

The amount of food eaten was assessed once every two weeks. This calculation, made as follows, was both difficult and time consuming.

Firstly the tanks were carefully siphoned clean of any faecal matter and the filters turned off for the duration of the feeding time. The portion of the weekly ration was then weighed and placed in the tank. When feeding ceased completely, usually within ten minutes of introducing the food, the remaining food fragments were siphoned out. This material was strained through a fine cloth. Surplus water was then squeezed out from the residue until it had regained the consistency of the original food. This compacted residue was then weighed and subtracted from the weight of food introduced to the tank, to calculate the amount of food actually consumed.

To determine the accuracy of this method, four trials were carried out in an empty tank where a known weight of food was fragmented, left for 15 minutes before siphoning out and reweighing. In all cases there was a net decrease in the reweighed value but the mean accuracy of 93% was considered satisfactory (range: 88-96%).

The measurement of production adopted was that given by Chapman (1968: 199). i.e. the total elaboration of fish tissue during a given time interval, including that formed by individuals which die before this time expires. Wet weights were again used as results did not warrant conversion to energy equivalents.

The conversion efficiency, K, was calculated from the ratio of production to the amount of food consumed, expressed as a percentage. The usage of P (production) rather than mean weight ($\bar{w}$) or biomass (B), recognises that eels which do not survive the full period have often consumed a considerable amount of food. Conversion efficiency is also termed gross or total growth efficiency (Davis and Warren 1968: 233). An efficiency of zero usually indicates that the fish are not eating;

it may also mean that no difference in production was recorded from the previous value.

Experiments were carried out in two series. The first series ran for four five-week periods and investigated growth at varying temperatures and rates of feeding in both species. It had been planned to discard these eels after this series, but the absence of a substantial "run" of elvers at Karapiro Dam during the summer of 1972 meant that the survivors of this series had to be used again in the second series. Six weeks separated both series. Eels were acclimatised to the required temperatures over a period of ten days. For eels at 30°C this meant an increase of 1.5°C per day.

For presentation of results, the two series are treated separately as results from the second series were inconsistent and did not complement the first series.

6.3 RESULTS

Tabulations of the results for both series are given in Tables 6.1 and 6.2.

Effects of Temperature at Constant Rate of Feed (Table 6.1a-h)

Shortfins at 10°C were largely inactive and ate little. Their mean food consumption was 2% of the food given. However, because of the decreased activity, a high degree of conversion was achieved during one period. At both 15° and 20°C, eels showed a net increase in production with greater efficiency at the lower temperature. The 3% level of feeding at 25°C proved insufficient and eels lost weight.

Longfins at 10°C showed an overall loss in production but at both this temperature and 15°C, considerable mortalities occurred which probably affected results. This mortality was thought to be due to the chlorine poisoning from the domestic water supply, as both these tanks received periodic large volumes of chilled water. Ailing fish did not feed and gradually lost condition until death.

The longfins at 20°C showed a net loss in production although this took place over the last period. Prior to this an overall increase had been recorded. Unexpectedly, the eels at 25°C showed an increase in production although the efficiency was not high.

Table 6.1 Results of growth experiments at varying temperatures and rates of feeding.

Rate of feed (%) = % biomass/day

n = number of live eels

B = biomass (grams wet weight)

P = production (grams)

K = conversion efficiency

$\leq P$ = total production

$\bar{K}$ = mean conversion efficiency

		a	b	c	d
			A. australis		
	°C	10	15	20	25
	Rate of feed	3%	3%	3%	3%
	n	40	40	43	43
	B (g)	58.3	55.6	56.6	57.9
1.	n	39	39	40	43
	B (g)	51.8	56.8	52.3	53.3
	P (g)	-5.1	2.4	-2.5	-4.6
	K (%)	-29.3	5.0	-4.9	-8.2
2.	n	38	38	39	41
	B	56.5	64.1	55.6	52.0
	P	6.5	7.3	4.3	0.3
	K	32.3	15.3	9.2	0.6
3.	n	38	38	35	41
	B	51.2	71.7	52.7	51.7
	P	-5.3	7.6	1.7	-0.3
	K	-30.8	14.1	3.4	-0.6
4.	n	36	38	35	41
	B	47.6	66.7	58.5	51.6
	P	-2.5	-5.0	5.8	-0.1
	K	-15.9	-8.3	12.3	-0.2
	Σ P	-6.4	12.3	9.4	-4.7
	$\bar{K}$	-9.7	5.9	4.8	-2.2

		e	f	g	h
			A. dieffenbachii		
	°C	10	15	20	25
	Rate of feed	3%	3%	3%	3%
	n	34	33	29	34
	B (g)	54.8	57.5	44.3	49.7
1.	n	34	33	27	34
	B (g)	50.9	54.2	42.8	53.8
	P (g)	-3.9	-3.3	-0.1	4.1
	K (%)	-28.3	-8.5	-0.2	8.5
2.	n	32	32	27	34
	B	50.3	60.1	43.9	56.4
	P	1.6	7.6	1.1	2.6
	K	13.0	20.5	3.4	5.8
3.	n	21	32	26	31
	B	34.0	64.7	46.2	45.3
	P	-2.0	4.6	2.9	-8.3
	K	-16.4	11.2	8.8	-17.6
4.	n	-	1	20	20
	B	-	1.2	33.2	40.6
	P	-5.4	-13.7	-8.6	5.3
	K	100.0	-31.0	-24.6	13.9
	Σ P	-9.7	-4.8	-4.7	3.7
	$\bar{K}$	-22.2	-3.0	-3.3	2.1

		i	j	k	l
			A. australi		
	°C	20	20	20	20
	Rate of feed	1%	3%	5%	7%
	n	45	49	54	54
	B (g)	54.4	57.3	63.5	62.1
1.	n	40	49	54	53
	B (g)	45.8	55.1	59.1	62.3
	P (g)	-6.4	-2.2	-4.4	0.8
	K (%)	-32.0	-4.2	-5.5	0.8
2.	n	39	47	52	52
	B	42.5	56.3	66.0	71.7
	P	-2.8	3.2	7.5	10.7
	K	-17.5	6.3	8.6	9.1
3.	n	37	46	52	52
	B	38.7	57.6	65.3	73.8
	P	-3.4	1.7	-0.7	2.1
	K	-22.7	3.3	0	0.5
4.	n	31	44	52	50
	B	33.5	59.2	83.2	92.1
	P	-2.5	2.0	17.9	19.0
	K	-18.5	3.8	18.6	14.4
	Σ P	-15.1	4.7	20.3	32.6
	$\bar{K}$	-23.4	2.2	5.6	6.9

		m	n	o	p
			A. dieffenbachii		
	°C	20	20	20	20
	Rate of feed	1%	3%	5%	7%
	n	33	30	34	35
	B (g)	55.0	52.5	52.3	54.9
1.	n	32	30	34	34
	B (g)	49.8	48.9	51.8	46.0
	P (g)	-5.2	-3.6	-0.5	-8.9
	K (%)	-26.0	-8.6	-0.9	-12.9
2.	n	31	29	33	30
	B	51.5	47.6	50.0	44.7
	P	2.8	0.7	-0.2	1.3
	K	16.0	1.9	-0.4	2.3
3.	n	19	23	30	28
	B	29.0	40.9	50.2	44.6
	P	-13.0	-1.4	2.9	1.5
	K	-72.2	-4.0	5.4	2.7
4.	n	-	21	28	23
	B	-	30.1	48.6	39.9
	P	-1.0	-7.7	-	-1.1
	K	-13.0	-25.6	-	-2.0
	Σ P	-16.4	-12.0	2.2	-7.2
	$\tilde{K}$	-25.9	-8.4	1.0	-3.0

If the first three periods only are considered, as the fourth is less reliable due to high mortalities, the eels at 15° and 20°C show increases in production, whereas eels at 10° and 25°C show decreases. These results are similar to those observed for shortfins. However, the increase in biomass during the last period at 25°C, remains an enigma.

As explained, all tanks required some additional water from the domestic supply. Periodically this water contained sufficient chlorine to be readily detected by smell. It was thought that this chlorine content adversely affected both species of eel, especially during the last period of the first series and more generally throughout the second series. Attempted treatment of incoming water by addition of sodium thiosulphate solution did not overcome the problem and presented further practical difficulties.

Effect of Varying Rate of Feed at Constant Temperature (Table 6.1i-p).

To study the above, in the first series both shortfins and longfins were kept at 20°C and fed diets ranging from 1,3,5 and 7% of their biomass per day.

Shortfins showed reasonably consistent results. At 20°C the 1% level is below the maintenance requirement and production declined. For feeding rates of 3, 5 and 7%, both production and conversion efficiency increased, indicating that food available at these levels was in excess of that required for maintenance activities. Although the percentage of food eaten decreased with increased rations, the actual amount eaten increased. If conversion efficiencies were to be calculated on the amount of food given rather than the amount eaten, the order would be reversed.

Longfins at both 1 and 3% showed a net loss in production. Although an increase took place at 5%, a substantial decrease occurred at 7%. Comparison of the different periods shows that all tanks initially lost weight, especially the tank at 7%. Later increases in the latter tank were not sufficient to offset this first decrease in biomass. These results indicate that 3% is below the maintenance ration for longfins at 20°C, but it should be noted that at 3, 5 and 7%, longfins ate a smaller percentage of the available food than did shortfins. Thus longfins at 3% ate an amount of food which corresponded with an effective rate of 2%, while those at 5% consumed food at a rate slightly greater than 3%.

As a control, the conditions in two tanks per species were reproduced. Therefore results for eels at 20°C and a 3% rate of feeding from the trial at varying temperatures and those at varying feeding rates, should be similar. Although results for shortfins do correspond reasonably well, those for longfins do not.

For the second series of trials (Table 6.2) sufficient longfins for only two tanks were available. These were held at 25° and 30°C with feeding rates of 5 and 7% respectively (Table 6.2.a and b). The primary objective of these two trials was to observe the effect of temperature on survival. At the higher temperature all the eels died within one month of the beginning. At 25°C, all eels were dead within nine weeks. At both temperatures, eels were hyperactive, very excitable and did not feed efficiently. Death was attributed directly to the relatively high temperature.

Results for shortfins at both 25° and 30°C with feeding rates of 5, 7 and 9% were inconsistent (Table 6.2.c-h). At 25° a feeding rate of 5% was adequate - the actual amount eaten at this rate was approximately 4%. However, at the same temperature but a rate of 7%, a decrease in production took place. Unfortunately most eels at the 9% feeding rate died from accidental electrocution.

Those eels at 30°C were extremely active. A burst water hose which resulted in a rapid drop of 20.5°C killed all but one eel in the tank fed at 7%. The apparent increase in production in this tank was probably a result of endosmosis in the dead fish. Eels at the 9% rate died progressively from the sixth to the tenth week. No disease could be diagnosed and chlorine poisoning was suspected. In the remaining 30°C tank, a decrease in production occurred.

At 30°C, shortfins like longfins, became extremely excited by the introduction of food. However, they seemed unable to feed effectively and considerable wastage resulted. Although shortfins can survive prolonged periods at 30°C, even when fed excess they do not grow. At 25°C, more food, although a decreased percentage of food given, was eaten at the higher rates of feeding. The maximum amount eaten was at the 9% level and corresponded to an actual consumption of 5.5%.

Effect of Density at Constant Temperature and Rate of Feeding (Table 6.2.i-l)

During the second series of trials, four tanks were stocked with shortfins at densities of 6.1, 19.6, 56.3 and 83.0 g/tank. These densities correspond to 0.16, 0.50, 1.40 and 2.11 kg/m^3.

Table 6.2 Results of growth experiments at varying temperatures, rates and frequency of feeding, and densities.

Rate of feed (%) = % biomass/day

n = number of live eels

B = biomass (grams wet weight)

P = production (grams)

K = conversion efficiency

$\leq$ P = total production

$\bar{K}$ = mean conversion efficiency

	a	b	c	d
	A. dieffenbachii		A. australis	
°C	25	30	25	25
Rate of feed	5%	7%	5%	7%
n	30	35	32	42
B (g)	55.5	54.2	56.5	54.7
1. n	28	-	32	42
B (g)	52.0	-	58.2	60.9
P (g)	-1.3	0.9	1.7	6.2
K (%)	-2.3	11.3	2.4	5.3
2. n	-		32	36
B	-		63.8	48.6
P	-6.0		5.6	-8.5
K	-29.9		7.8	-8.7
3. n			31	33
B			60.0	43.5
P			-2.9	-2.0
K			-3.7	-2.5
4. n			29	8
B			66.7	10.4
P			6.7	-3.9
K			9.1	-19.3
Σ P	-7.3	0.9	11.1	-8.2
$\bar{K}$	-9.7	11.3	3.8	-2.6

		e	f	g	h
			A. australis		
	°C	25	30	30	30
	Rate of feed	9%	5%	7%	9%
	n	41	48	41	41
	B (g)	56.8	56.5	54.5	54.6
1.	n	40	48	40	40
	B (g)	71.5	52.4	53.9	51.2
	P (g)	15.3	-4.1	0.8	-0.5
	K (%)	11.1	-4.6	0.8	-0.5
2.	n	13	46	40	1
	B	29.3	51.1	50.4	0.7
	P	3.5	0.5	-3.5	-13.7
	K	3.8	0.6	-3.2	-85.8
3.	n	3	40	1	-
	B	9.6	39.0	1.8	-
	P	-3.8	-9.1	11.2	0
	K	-6.6	-13.5	20.0	-5.0
4.	n	-	28	1	
	B	-	24.4	1.3	
	P	-0.3	-6.0	-0.5	
	K	-1.4	-17.6	-11.8	
	Σ P	14.7	-18.7	8.0	-14.3
	Σ K	4.8	-7.0	3.0	-12.3

		i	j	k	l
			A. australis		
	°C	20	20	20	20
	Rate of feed	5%	5%	5%	5%
	n	5	14	42	59
	B (g)	6.1	19.6	56.3	83.0
1.	n	5	14	42	58
	B (g)	5.0	22.6	64.9	108.7
	P (g)	-1.1	3.0	8.6	25.7
	K (%)	0	10.5	9.6	18.2
2.	n	-	13	21	58
	B	-	21.8	28.9	105.0
	P	-0.2	0.5	-14.0	-3.7
	K	0	1.3	-33.0	-2.2
3.	n		12	4	58
	B		18.3	7.0	111.4
	P		-2.8	-5.6	6.4
	K		-7.3	-37.1	3.9
4.	n		4	-	58
	B		8.7	-	119.3
	P		-2.2	-0.4	7.9
	K		-13.7	-24.7	4.5
	Σ P	-1.1	-1.5	-11.4	36.3
	$\bar{K}$	0	-1.2	-7.7	5.6

		m	n
		A. australis	
	°C	20	20
	Rate of feed	5%	5%
	Frequency of feeding	x7/week	x 2/week
	n	42	40
	B (g)	56.8	56.2
1.	n	42	40
	B (g)	65.0	64.6
	P (g)	8.2	8.4
	K (%)	8.8	11.8
2.	n	42	30
	B	64.8	56.2
	P	-0.2	2.1
	K	-0.2	4.4
3.	n	42	1
	B	71.7	1.5
	P	6.9	-10.1
	K	6.1	-53.5
4.	n	42	
	B	76.1	
	P	4.4	
	K	3.5	
	ΣP	19.3	0.6
	$\bar{K}$	4.3	0.4

At the lowest density the five eels, although excited by the introduction of food, did not feed and died by the eighth week. Eels stocked at 19.6 and 56.3 g, after initial increases in production, appeared to lose appetite. Almost all died, probably as a result of chlorine poisoning. At the highest density, eels fed actively and consumed over 90% of all food given, resulting in a 44% increase in production. A comparable trial during the first series, of shortfins at 20°C and 5% but at a slightly lower density, produced a net increase in production of 32%.

Effect of Frequency of Feeding at Constant Temperature, Density and Rate of Feed (Table 6.2.m-n)

Two tanks were stocked with shortfins at equal densities and fed the same amount of food weekly. The first tank received rations daily while the second tank was fed only twice per week. It was hoped to relate these results to a comparable tank in the above trials which was fed at the same rate (5%) but three times per week. Unfortunately this tank was one of those affected by chlorine poisoning.

Results were inconclusive as the eels fed twice per week died prematurely. At the end of the second period this tank showed a greater increase in production than the other tank.

6.4 DISCUSSION

During the trials it became apparent that shortfins are more easily handled and adapt better to laboratory conditions than do longfins. Also, the growth trends shown by shortfins are more consistent. Behavioural differences in regard to cover have already been mentioned. In addition, longfins showed much more aggression than did shortfins. Periodically, a longfin would swim around with its mouth open and bite any other eel, regardless of size, which it came across. This behaviour did not appear to establish any "peck order" (order of dominance) or territory. No cannibalism was observed.

Generally, all eels were similar in size and so no obvious size-hierarchy developed. The exception was one shortfin, substantially larger than any other eel, which was retained in both series. In the second series this eel was placed in the 25°C and 5% feeding-rate tank. At the start of the trial it had a length of 20.7 cm, compared with the mean

tank length of 10.9 cm.

This eel clearly dominated the tank at feeding times when it fed voraciously, often intimidating smaller eels by its aggressive behaviour. If unable to find the food, as eels located food by smell and not sight, this eel would grasp another eel in its mouth and swim rapidly around the tank. The victim was never eaten but was released, apparently unharmed, as soon as the larger eel located the food. It is presumed this behaviour was a form of displacement activity. During the course of the trial, the body weight of this eel increased by 66%, whereas the mean increase for the other eels in the tank was 31%. Obviously large size conferred the eel with advantages in securing food. The importance of sorting eels to be cultivated in ponds by size, is mentioned by Matsui (1952: 242) and Koops (1967: 361).

Feeding and swimming activity were noticeably affected by temperature. At 10°C the appetite of both species became much reduced resulting in a food intake below the maintenance requirement. Matsui (1952: 243) records that the productivity of pond-cultured Japanese eels decreases below 15°C due to inactivity and loss of appetite and below 10°C, eels are not fed. He also states (1969: 7) that feeding ceases when temperatures exceed 28-30°C. Water temperature was regarded by Kubo (1936) as the major factor in determining the amount of food consumed by cultured eels.

At higher temperatures, the metabolic rate increased rapidly. In addition to increased swimming activity, the respiratory rate of eels increased. Unlike fish with large opercular apparatus, eels are not able to compensate for increased respiratory demands by an increase in amplitude of respiratory movements, but rather, must increase the rate of movements (van Dam 1938). Respiratory rate thus parallels metabolic rate.

The mean number of respiratory movements per minute for resting eels of both species was as follows (figures for longfins in brackets):

10° : 21 (19)	15° : 28 (30)	20° : 39 (40)
25° : 58 (57)	30° : 90	

To compensate for this increase in metabolic rate, the food intake must also increase. Data from shortfins indicate that above 20°C, a ration of 3% body weight/day is insufficient. Eventually a point must be reached where food intake is no longer adequate and the fish lose

condition and will eventually die. Prior to this, fish may die from thermal shock. Longfins seem unable to survive prolonged periods at 25°C and over, whereas shortfins are able to withstand temperatures of up to 30°C. Both upper and lower temperature tolerances can be increased by gradual acclimatization (Brett 1956: 76).

In the trials, shortfins at any temperature had a greater appetite than did longfins. Further, the maximum appetite of longfins was more definite and remained relatively constant at any feeding level in excess of the maintenance ration. Conversely, the appetite of shortfins was more flexible and was influenced by the amount of food available, such that the more available the greater the amount eaten. Although conversion efficiencies, calculated on the amount of food eaten, increased with increased rate of feed, so did the amount of food wasted. Ultimately the question of whether the increase in production and conversion efficiency achieved by increased feeding is warranted relative to the food wasted, is an economic one. My limited data suggest that the more rapid growth but at greater expense, would be economically feasible.

The effect of the density of fish may be considered in two ways. Firstly the volume of water available per fish and secondly, the total volume of water which contains the fish.

Shortfins at the lowest density and hence the greatest volume of water per fish, did not feed although they became excited when food was introduced. It seems that some "social stimulation" as mentioned by Brown (1957: 397) is necessary to induce effective feeding. In contrast, those eels at the highest density fed extremely well and showed a high net increase in production. The gregarious and thigmotactic behaviour of small eels probably accounts for this success.

An asymptotic relationship between stocking rates and production is given by Matsui (1952: 164) for farmed eels, with largest increases at lowest densities. However, increased density often leads to increased aggression, as found by Kinne (1960: 301) in a study of Cyprinodon macularius Baird and Girard (F. Cyprinodontidae). The same fish showed a decreased appetite when crowded.

The second aspect, of growth related to the total volume of water, is considered a major factor in the small amount of growth recorded from the overall trials. The best rate of growth recorded during the experiments was only comparable to that calculated for Makara eels - an equivalent increase in length of 2.4 cm per year for shortfins. A growth rate of

this order would be impracticably low for an economic farming venture.

However, during 1971, I was able to monitor growth in a small trial pond (20m x 10m x 0.5m deep) set up by a local eel processor. Glass-eels were introduced in October 1970 and fed a mixture of fish roe and cooked fish several times a week. Eight months after the trial commenced, I measured a random sample of 50 small eels. The size ranges were:

shortfins 7.6-11.2 cm (mean = 9.2), 0.6-2.4 g (mean = 1.2);
longfins 8.5-14.4 cm (mean = 10.3), 0.8-5.3 g (mean = 2.2)

These observations indicate the flexibility of the growth rate of New Zealand eels. Although the growth recorded in the laboratory is not directly comparable to that expected for eels cultured in large ponds, the relative differences between tanks are assumed to be valid indicators of growth trends. The restriction of growth imposed by small containers is well known amongst aquarists.

Frequency of feeding as well as the amount of food probably affects conversion efficiency, although this was not proven experimentally due to high mortalities. At higher temperatures, digestion proceeds more rapidly. Hence Burnet (unpublished data) found digestion in longfins at 20°C took from 12-18 hours while Crossland (1972: 31) recorded 18-24 hours for shortfins at 17°C. Brown (1957: 385) found that the amount of growth recorded in trout fry varied with feeding frequency. Similarly, Meske (1969) obtained slightly better growth for eels fed hourly than for those fed two-three times daily, although there were some differences in food quality between the two trials.

Few conclusions can be drawn from the limited data obtained for growth requirements in longfins. Temperatures of 25°C and greater cannot be tolerated and optimum conditions probably lie between 15°-20°C. At these temperatures a ration of 3% biomass/day is in excess of the maintenance requirements. Burnet (1952a: 59) calculated a theoretical maintenance requirement for adult longfins of 1% body weight/day.

The highest percentage increase in production (i.e. the net production expressed as a percentage of the original biomass) obtained for shortfins was at 20°C with a feeding rate of 7% when the increase was 52.5%. Increases of 43.7% and 34.0% were obtained for shortfins at 20°C and 5% but with increased density and frequency of feeding respectively. Eels at 20°C and 5% rations (normal density of 55 g) were next at 32.0%

increase, while those at 25°C and 9% recorded 25.9%. Thus, 20°C was the optimum temperature with a high feeding rate producing best results. Density and frequency of feeding were also important.

The same combination of 20°C and 7% rations produced the highest mean efficiency of 6.9%. This was followed by eels at 15°C and 3% rations, and 20°C and 5% rations. Efficiency at 25° and 30°C was generally low due to increased activity. Similarly, Kinne (1960: 307) found appetite and conversion efficiency in the desert pupfish decreased above an optimum temperature.

Recommendations by Matsui (1969) for cultivation of New Zealand eels were for temperatures of 15°C and a feeding rate of 7-10% biomass per day, depending on size of the eels and the season. Data on Japanese culture as given on Onodera (1962) indicate a feeding rate of 8% biomass/day gives a conversion efficiency of 10%. A further review of Japanese pond culture (Sanders, 1971) gives a high feeding rate for glass-eels of 30% biomass/day but reducing to 10% for eels of 20g and over. These quantities are divided into two feeds per day. Under these conditions, a marketable eel of 150g is produced in two years. It is now known that Japanese growers are hopeful of achieving this size in six months, using heated water and enclosed tanks.

Several New Zealand companies have shown interest in cultivation of eels in warm waters, and at least two pilot schemes are in operation at present. Effluent from thermal power stations offers large quantities of heated water and it is hoped full advantage will be taken of such low-cost warm water.

Either glass-eels or elvers could be used to stock culture ponds. Although elvers are larger and more easily handled, glass-eels would be preferable as, at this stage, they have not developed specific feeding habits and should prove more adaptable to an artificial environment. Their arrival during winter and spring means full advantage can be taken of the warm summer temperatures.

Further, the growth rate of elvers may in some way be governed by their residence in fresh-water prior to stocking. One company engaged in eel farming has had encouraging results in raising glass-eels but has not been able to duplicate this with elvers even though these appear to adapt satisfactorily to the culture system and feed readily. In the same way, Taiwanese eel farmers have no interest in using elvers as 'seed eels'

although large numbers are available (T. W. Beckett, pers. comm.).

At both glass-eels and elver stages, shortfins show a greater capacity for survival than longfins and also demand a higher price on overseas markets.

In addition to the identification and treatment of diseases, another major area for investigation is the availability and economics of a suitable foodstuff. Cheap fish, either reduced to fish meal and incorporated into a compound food or fed whole, forms the major food item of Japanese eel farms. At present, little low price fish is landed in New Zealand ports although the potential for large scale pelagic fishing is currently being both investigated and encouraged. This might be the only economic source of this type of food which seems most suitable for eel feed.

7 GENERAL DISCUSSION

The spawning areas of New Zealand freshwater eels are unknown. However, as the seasons of catadromous and anadromous migrations are similar to other temperate eels (which are known to spawn in the tropics), it is assumed that New Zealand eels behave similarly. The extra summer ring seen in otoliths of A. anguilla glass-eels compared with those of both New Zealand species is consistent with the known $2\frac{1}{2}$ year marine larval life for the European species and thus a $1\frac{1}{2}$ year period for New Zealand eels.

Back calculations of possible distance travelled using known current speeds and the duration of larval life, are subject to considerable error. For example, the extent to which the leptocephali actively swim as opposed to passive transportation by water movement, is unknown while current patterns and velocities are also liable to irregular fluctuations. The precise location of the spawning areas will only be found by the collection of newly hatched larvae.

Vertebral counts of New Zealand shortfins confirmed that the mean number of vertebrae differed slightly from that given for the Australian shortfins. However, as this difference was only one vertebra while the range in total vertebrae for New Zealand shortfins was eight, this character would not allow identification of individual New Zealand and Australian shortfins from a mixed sample. This small yet consistent difference together with differences in total distribution is possibly indicative of separate spawning areas for these two sub-species.

Recruitment of glass-eels consists of two phases, although this is not widely recognised. These migrations, the freshwater invasion and the upstream migration are distinguished by different responses to light and fresh-water, and also by presence or absence of schooling behaviour. The nocturnal movements of invading glass-eels means that this phase is seldom observed whereas the large upstream migrations which take place in many river systems are both well known and exploited.

The predictability of these upstream migrations means that they are susceptible to intensive fishing which may cause detrimental long-term effects to the overall fishery. Fortunately the return of larvae is not considered to be specifically to the water from which their parents originated and provided a sufficient number of migrants are available from the country as a whole, then recruitment will not decline. At

present the National Parks are the major unfished areas in the country. However, only two of the ten parks have a coastal frontage whereas waterways from the other eight pass through land accessible to fishermen. Therefore the National Parks cannot be considered as a sufficient reserve of unexploited eels to maintain the present fishery and additional protective measures are required.

An analysis of glass-eel samples obtained from throughout the country indicated that shortfins predominated in the North Island and along the east coast of the South Island while longfins were more numerous in western and southern areas of the South Island. The reasons for these differences are not understood, although it is thought that they may reflect the arrival routes of the larvae. It is known that specific habitat preferences are important factors in local distributions with longfins preferring the clear, swift and cool rivers while shortfins predominate in slower, muddy waters. Thus, even adjacent water systems of the above types will differ markedly in species composition.

Unfortunately it was not possible to demonstrate experimentally that invading glass-eels differentiate between water types such that shortfins prefer one type and longfins another. However both species did show preferences, although these were similar, and it is considered that the experimental technique may have not been refined enough to show selected species preferences. Habitat preferences are important in making more efficient use of the available cover and foodstuffs and so decreasing the amount of interspecific interaction. The physical requirements of the eels are probably more important in habitat choice than food preferences.

Mean lengths of selected glass-eel samples showed an overall increase in length from north to south. This does not agree with the situation anticipated if glass-eels arriving at New Zealand have been transported by the East Australian and Tasman Currents. In this latter instance the reverse size gradient would be expected with the larger eels occurring in the north. However the distribution of both shortfin subspecies also agrees with an arrival from the north of New Zealand. This cannot be confirmed from hydrological data.

The summer upstream migration is an important stage in repopulating upstream areas and enabling eels to find their preferred habitat types. Thus the migration is a recurring phenomenon for eels of up to 30 cm in length which have not yet become established in a suitable habitat. Th

stimulus/stimuli which initiate these movements are unknown but it is interesting to note that migrations occur throughout the country within the period of a few weeks.

It has often been assumed in freshwater eels that scale rings represent annual growth checks. However, for both New Zealand species all features of scale development including ring formation, are related to the length of the fish rather than age. This is consistent with other behavioural and morphological features of the life history which are also length dependent.

Conversely, measurements of the marginal growth increment of otoliths, and comparison of ages from the youngest year class with length-frequency distributions, showed that zonation in otoliths is annual. Again this is often assumed but the presence of subsidiary or secondary rings in many fish otoliths, including eels, is sufficient reason to warrant proof of this annual formation. Both grinding and burning techniques are suitable to show the otolith zones although the former is better suited to small otoliths which are difficult to break evenly for burning.

Results from ageing emphasised the flexibility of the growth rate in eels. Growth of eels less than 26 cm in length in two small streams, was slow - 20 cm eels were mainly in their sixth or seventh year of freshwater life. In contrast, shortfins of these ages from a coastal lake averaged 42-46 cm in length, which is a faster rate of growth than that given by most workers for the European eel. Under the more favourable feeding conditions of an eel farm it would be anticipated that a much faster rate of growth than that of wild eels could be achieved.

However, regardless of which of the above growth rates is the more typical, it is apparent that the eel fishery is based on a slow growing fish. This fact together with available markets for eels of all sizes and the development of relatively cheap and effective methods of fishing and processing, has placed substantial pressure on the fishery itself and reports of localised over-fishing are increasing.

In addition to the length-weight relationship, relative condition was calculated by an analysis of covariance. The adjusted mean weights were used for comparison of monthly condition. It had been expected that reduced activity over the winter months might be indicated by a decreas

in condition. It is known that in southern parts of the South Island, most eels hibernate over the winter months resulting in a suspension of fishing operations. Further, at temperatures below 10°C, the feeding of both species falls off markedly - the mean monthly temperature in the Makara Stream falls below 10°C from June to August. However, no annual trend in changes of relative condition was found.

Finally, laboratory growth experiments conducted on elvers of both species showed that longfins were very difficult to keep alive in the laboratory for any appreciable period - a fact that was also noted with glass-eels of this species. Shortfins were much more tolerant of the variety of conditions and survived at temperatures from 10-30°C. This is of interest as the important eels of world commerce are all longfins. In fact, of the 208 tonnes of glass-eels imported by Japan in 1972 (Folsom, 1973: 43) the New Zealand contribution of 1% probably contained the only significant number of shortfins. (Although the New Zealand eels were not sorted by species, they all came from the Waikato area and would have been 90% + shortfins).

The growth trials showed that highest rates of growth were achieved at temperatures of 20°-25°C with high rates of feeding. However, with increasing temperature, fish fed less efficiently and whether the more rapid growth is economically justified would be best determined on a larger scale pilot scheme. If the economic aspects can be satisfactorily resolved, I am confident that New Zealand eels, especially the shortfin, will prove suitable for commercial pond cultivation.

Over the last hundred years considerable research has been carried out on the European eel, resulting in an understanding of all stages of the life history. However, there is still a lack of information on population dynamics and the effects of sustained fishing. With regard to New Zealand eels, it is only in recent years that their status has risen from "nuisance value" to an important export item. Consequently the amount of research in the past has been small and discontinuous.

The work of Cairns (1941, 1942), although including all aspects of freshwater life, is frequently generalised, incorporating composite samples from unspecified localities. His figure of an annual sustainable yield of 5,000-10,000 tons (Cairns, 1945) is an intuitive estimate and not a biological deduction. However, his research remains an important contribution. Research by Burnet has been more localised but confined to large eels. Consequently there has been a gap in knowledge to date on the arrival in fresh-water and subsequent movements of glass-eels and

elvers. This present work has concentrated on these stages.

As outlined this study has been a qualitative one concerned with small eels. Large eels have been investigated for comparative aspects of scale development only. No attempt has been made to study feeding, growth by capture-recapture techniques, or detailed interspecific relationships, as these are aspects of the biology which were beyond the reach of the present investigation. However, several avenues of future research have developed.

The importance of glass-eels as an export item and for stocking of eel-farms has emphasised the need for additional research. Such research should attempt some quantitative measure of both the upstream glass-eel migration and mortality during the first year of freshwater life. The equivalent amount to this natural loss could be removed annually without endangering present stocks, although the rate of exploitation of glass-eels is ultimately a complex one as such mortality is almost certainly density dependent.

Additional and more sophisticated experiments are required to establish the precise physical criteria which both species can tolerate. For example, it seems probable that longfins have a greater oxygen demand than shortfins. Such data would prove very important as indicators for potential eel-farming areas.

Using the ageing techniques developed in this study a survey could be implemented on a closed population, to study the natural recruitment, growth, and loss by adult migration. A tagging programme would give additional data on growth, as well as movements and population numbers. Such data would provide a biological basis for regulations designed to manage existing wild stocks.

8 ACKNOWLEDGMENTS

I am grateful to the Fisheries Management Division and latterly the Fisheries Research Division of the Ministry of Agriculture and Fisheries (formerly Marine Department) for leave and financial support throughout the period of this study.

Special thanks are due to the electric fishing team of the Management Division, and to my friend and colleague Mr P. R. Todd who assisted in field-work and with whom I had many helpful discussions. The encouragement and supervision of Professor J. T. Salmon and Dr P.H.J. Castle of the Zoology Department, Victoria University of Wellington is also gratefully acknowledged.

I also wish to thank the following: Donaghy's Industries Ltd for a grant to enable construction of the experimental growth unit; the New Zealand Electricity Department, especially the staff at Karapiro Hydro Power Station, for help in collection of elver samples; the New Zealand Fishing Industry Board for provision of glass-eel samples and a grant for equipment; Mr T. W. Beckett, biologist to the Group Development Section, Wattie Industries Ltd for additional glass-eel samples and data on catches; Mr C. Scollay of Wm. Scollay & Co. Ltd for further glass-eel catch statistics; Dr R. D. Elder of the Fisheries Research Division for writing the computer programme; Mr J. H. Maindonald, biometrician to the Science Faculty, Victoria University of Wellington, for assistance with statistics; the residents of the Makara Valley especially Mr J. G. Nielsen, for allowing access to the stream; Mr G. H. Grainger of the Zoology Department Marine Laboratory for construction and maintenance of equipment; finally, to all my other friends and colleagues who assisted in a variety of ways.

9 REFERENCES

AHLSTROM, E. H., and COUNTS, R. C. 1958: Development and distribution of Vinciguerria lucetia and related species in the Eastern Pacific. Fishery Bulletin of the Fish and Wildlife Service (United States) 139: 363-416.

ALLEN, K. R. 1951: The Horokiwi Stream. A study of a trout population. Fisheries Bulletin. New Zealand Marine Department 10. 238 pp.

BACHELIER, R. 1972: Le tropisme héréditaire des jeunes d'anguilles. Bulletin Français de Pisciculture 245: 151-163.

BARKER, P. H., and KIBBLEWHITE, A. C. 1965: Physical oceanographic data from the Tui cruise, 1962. New Zealand Journal of Science 8(4): 604-634.

BERG, T., and STEEN, J. B. 1965: Physiological mechanisms for aerial respiration in the eel. Comparative Biochemistry and Physiology 15: 469-484.

BERTIN, L. 1956: "Eels, a Biological Study." Cleaver-Hume, London. 192 pp.

BRETT, J. R. 1956: Some principles in the thermal requirements of fishes. Quarterly Review of Biology 31(2): 75-87.

BRODIE, J. W. 1960: Coastal surface currents around New Zealand. New Zealand Journal of Geology and Geophysics 3(2): 235-252.

BROWN, M. E. 1957: Experimental studies on growth. In Brown, M. E. (Ed.), "The Physiology of Fishes", Volume 1, pp. 361-400. Academic, New York.

BRUUN, A. F. 1963: The breeding of the North Atlantic freshwater-eels. In Russell, F. S. (Ed.), "Advances in Marine Biology", Volume 1, pp. 137-169. Academic, New York.

BUCKMASTER, D. 1971: Eel research project at Hopkins Falls. Fur, Feathers and Fins. Fisheries and Wildlife Department, Victoria 128: 24-27.

BURNET, A.M.R. 1952a: Studies on the ecology of the New Zealand long-finned eel, Anguilla dieffenbachii Gray. Australian Journal of Marine and Freshwater Research 3(1): 32-63.

_____ 1952b: Studies on the ecology of the New Zealand freshwater eels. 1. The design and use of an electric fishing machine. Australian Journal of Marine and Freshwater Research 3(2): 111-125.

BURNET, A.M.R. 1955: "A study on the ecology of the New Zealand freshwater eels (Anguilla dieffenbachii Gray and Anguilla australis schmidtii Phillipps)." Unpublished M.Sc. thesis lodged in University of Canterbury Library. 45 pp.

_____ 1967: Electric fishing equipment design notes. Fisheries Technical Report. New Zealand Marine Department 19. 48 pp.

_____ 1968: A study of the relationships between brown trout and eels in a New Zealand stream. Fisheries Technical Report. New Zealand Marine Department 26. 49 pp.

_____ 1969a: Migrating eels in a Canterbury river (New Zealand). New Zealand Journal of Marine and Freshwater Research 3(2): 230-244.

_____ 1969b: The growth of New Zealand freshwater eels in three Canterbury streams. New Zealand Journal of Marine and Freshwater Research 3(3): 376-384.

CAIRNS, D. 1941: Life-history of the two species of New Zealand fresh-water eel. Part I.- Taxonomy, age and growth, migration, and distribution. New Zealand Journal of Science and Technology, 23(2B): 53-72.

_____ 1942: Life-history of the two species of fresh-water eel in New Zealand. II. Food, and inter-relationships with trout. New Zealand Journal of Science and Technology 23(4B): 132-148.

_____ 1945: Utilization of eels. New Zealand Science Review 3(4): 3-4.

CASSIE, R. M. 1950: The analysis of polymodal frequency distributions by the probability paper method. New Zealand Science Review 8(9-10): 89-91.

_____ 1957: Condition factor of snapper, Chrysophrys auratus Forster, in Hauraki Gulf. New Zealand Journal of Science and Technology, Section B, 38(4): 375-388.

CASTLE, P.H.J. 1963: Anguillid leptocephali in the Southwest Pacific. Zoology Publications from Victoria University of Wellington 33. 14 pp.

_____ 1969: Early life history and general distribution of eels. In Report on Eel Seminar, Fishing Industry Board (Wellington). 38 pp.

_____ 1972: Prospects for the New Zealand freshwater eel industry. New Zealand Commercial Fishing 11(10): 13-15.

CHAPMAN, D. W. 1968: Production. In Ricker, W. E. (Ed.), "Methods for Assessment of Fish Production in Fresh Waters", pp. 199-214. Blackwell, Edinburgh.

CHRISTENSEN, J. M. 1964: Burning of otoliths, a technique for age determination of soles and other fish. Journal du Conseil Permanent International pour l'Exploration de la Mer 29(1): 73-81.

CREUTZBERG, F. 1958: Use of tidal streams by migrating elvers (Anguilla vulgaris Turt.). Nature, (London) 181: 857-858.

_____ 1961: On the orientation of migrating elvers (Anguilla vulgaris Turt.) in a tidal area. Netherlands Journal of Sea Research 1(3): 257-338.

CROSSLAND, J. 1972: "Food consumption and growth of Anguilla australis schmidtii." Unpublished B.Sc. (Hons.) thesis lodged in University of Canterbury Library. 53 pp.

* DAM, L. van. 1938: "On the utilization of oxygen and regulation of breathing in some aquatic animals." Dissertation, State University of Gröningen.

D'ANCONA, U. 1959: Old and new solutions to the eel problem. Nature, (London) 183: 1405.

DAVIS, G. E., and WARREN, C. E. 1968: Estimation of food consumption rates. In Ricker, W. E. (Ed.), "Methods for Assessment of Fish Production in Fresh Waters", pp. 227-248. Blackwell, Edinburgh.

DAY, L. R. 1941: A preliminary report on elver migrations into Moser River, Nova Scotia. Fisheries Research Board of Canada, Manuscript Report of St. Andrews Biological Station 213. 3 pp.

DEELDER, C. L. 1952: On the migration of the elver (Anguilla vulgaris Turt.) at sea. Journal du Conseil Permanent International pour l'Exploration de la Mer 18(2): 187-218.

_____ 1957: On the growth of eels in the Ijsselmeer. Journal du Conseil Permanent International pour l'Exploration de la Mer 23(1): 83-88.

_____ 1958: On the behaviour of elvers (Anguilla vulgaris Turt.) migrating from the sea into fresh water. Journal du Conseil Permanent International pour l'Exploration de la Mer 24(1): 136-146.

_____ 1960a: Ergebnisse der holländischen untersuchungen über den glasaalzug. Archiv für Fischereiwissenschaft 11(1): 1-10.

DEELDER, C. L. 1960b: The Atlantic eel problem. Nature,(London) 185: 589-591.

_____ 1970: Synopsis of biological data on the eel Anguilla anguilla (Linnaeus) 1758. F.A.O. Fisheries Synopsis 80. Pages variable.

DOWNES, T. W. 1917: Notes on eels and eel weirs (Tuna and Pa-tuna). Transactions and Proceedings of the New Zealand Institute 50: 296-316.

EGE, V. 1939: A revision of the genus Anguilla Shaw, a systematic, phylogenetic and geographical study. Dana Report 16. 256 pp.

EGUSA, S. 1965: The existence of a primary infectious disease in the so-called "fungus disease" in pond-reared eels. Bulletin of the Japanese Society of Scientific Fisheries 31(7): 517-526.

EHRENBAUM, E. and MARUKAWA, H. 1913: Über altersbestimmung und wachstum beim aal. Zeitschrift für Fisherei 14: 89-127.

FLEMING, C. A. 1950: Some South Pacific sea-bird logs. The Emu 49(3): 169-188.

_____ 1952: Ecological aspects of a paleontological study. New Zealand Science Review 10(5): 60-61.

FOLSOM, W. B. 1973: Japan's eel fishery. Marine Fisheries Review 35(5-6): 41-45.

FORD, E. 1931: Changes in length during the larval life and metamorphosis of the freshwater eel (Anguilla vulgaris Turt.). Journal of the Marine Biological Association of the United Kingdom 17(3): 987-1000.

FROST, W. E. 1945: The age and growth of eels (Anguilla anguilla) from the Windermere catchment area. Parts 1 & 2. Journal of Animal Ecology 14(1 & 2): 26-36, 106-124.

GARNER, D. M. 1954: Sea surface temperature in the South-west Pacific Ocean, from 1949 to 1952. New Zealand Journal of Science and Technology, Section B, 36(3): 285-303.

_____ 1961: Hydrology of New Zealand coastal waters, 1955. New Zealand Department of Scientific and Industrial Research Bulletin 138. 85 pp.

_____ 1969: The geopotential topography of the ocean surface around New Zealand. New Zealand Journal of Marine and Freshwater Research 3(2): 209-219.

GARNER, D. M. 1970: Oceanic hydrology north-west of New Zealand. Hydrology of the North-east Tasman Sea. New Zealand Department of Scientific and Industrial Research Bulletin 202. 49 pp.

GARNER, D. M. and RIDGWAY, N. M. 1965: Hydrology of New Zealand offshore waters. New Zealand Department of Scientific and Industrial Research Bulletin 162. 62 pp.

GEMZÖE, K. J. 1908: Age and rate of growth of the eel. Report of the Danish Biological Station 14: 10-39.

GRAHAM, M. 1929: Studies of age-determination in fish. Part II. A survey of the literature. Fishery Investigations, (London) Series 2, 11(3). 50 pp.

GRAY, R. W. and ANDREWS, C. W. 1971: Age and growth of the American eel (Anguilla rostrata (LeSueur)) in Newfoundland waters. Canadian Journal of Zoology 49(1): 121-128.

GRIFFIN, L. T. 1936: Revision of the eels of New Zealand. Transactions of the Royal Society of New Zealand 66: 12-26.

HAMILTON, A. 1908: Fishing and sea-foods of the ancient Maori. Dominion Museum Bulletin, Wellington, 2. 73 pp.

HAMON, B. V. 1961: The structure of the East Australian Current. Technical Papers, Division of Fisheries and Oceanography C.S.I.R.O. Australia 11. 9 pp.

_____ 1965: The East Australian Current. 1960-1964. Deep Sea Research 12(6): 899-921.

HARDEN JONES, F. R. 1968: "Fish Migration". Edward Arnold, London. 325 pp.

HARDY, C. J. 1950: Summary of a report on eel trapping and observations at Lakes Taylor and Sheppard. North Canterbury Acclimatisation Society, Eighty-sixth Annual Report: 24-26.

HARRISON, A. C. 1953: The age and scales of freshwater eels. Piscator 7(25): 9-11.

HELDT, H. and HELDT, H. 1929: Les civelles du Lac de Tunis. Station Océanographique de Salammbô. Bulletin 14: 1-41.

HERRE, A. W. 1930: A New Guinea eel-fair. Science, (New York) 71: 16.

HIYAMA, Y. 1952: Thermotaxis of eel fry in stage of ascending river mouth. Japanese Journal of Ichthyology 2(1): 23-30.

HOBBS, D. 1947: Migrating eels in Lake Ellesmere. Transactions of the Royal Society of New Zealand 77 (5): 228-232.

HORNYOLD, A. G. 1922: The age and growth of some eels from a small Worcestershire pond. Journal of the Royal Microscopical Society 1922: 9-26.

_____ 1927: Une expérience sur la réduction de longueur et de poids chez la civelle pendant le développement du pigment. Bulletin de la Société d'Océanographie de France 38(5): 105-110.

HOUTMAN, Th. J. 1966: A note on the hydrological regime in Foveaux Strait. New Zealand Journal of Science 9(2): 472-483.

IRIE, T. 1960: The growth of the fish otolith. Journal of the Faculty of Fisheries and Animal Husbandry, Hiroshima University 3(1): 203-221.

JESPERSEN, P. 1942: Indo-Pacific leptocephalids of the genus Anguilla. Systematic and biological studies. Dana Report 22: 128 pp.

JILLETT, J. B. 1969: Seasonal hydrology of waters off the Otago Peninsula, south-eastern New Zealand. New Zealand Journal of Marine and Freshwater Research 3(3): 349-375.

JOHANSEN, A. C. 1905: Remarks on the life history of the young postlarval eel (Anguilla vulgaris Turt.). Meddelelser fra Kommissionen for Havundersøgelser. Serie Fiskeri 1(6): 1-9.

JONES, J. W. 1959: Eel migration. Nature, (London) 184: 1281.

JUBB. R. A. 1961: The freshwater eels (Anguilla spp.) of Southern Africa. An introduction to their identification and biology. Annals of the Cape Provincial Museums 1: 15-48.

_____ 1964: The eels of South African rivers and observations on their ecology. Monographiae Biologicae 14: 186-205.

KERSHAW, J. A. 1911: Migration of eels in Victoria. Victorian Naturalist 27: 196-201.

KINNE, O. 1960: Growth, food uptake, and food conversion in a euryplastic fish exposed to different temperatures and salinities. Physiological Zoology 33: 288-317.

KOOPS, H. 1967: Feeding of eels (Anguilla anguilla) in ponds. F.A.O. Fisheries Reports 44(3): 361-364.

KROGH, A. 1904: Some experiments on the cutaneous respiration of vertebrate animals. Skandinavisches Archiv für Physiologie 16: 348-357.

KUBO, I. 1936: Feeding velocity of the eel Anguilla japonica T. & S., in relation to water temperature and other environmental conditions. Bulletin of the Japanese Society of Scientific Fisheries 4(5): 335-338.

LAGLER, K. F. 1956: "Freshwater Fishery Biology." 2nd ed. Brown, Iowa. 421 pp.

LE CREN, E. D. 1951: The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (Perca fluviatilis). Journal of Animal Ecology 20(2): 201-219.

LOWE, R. H. 1951: Factors influencing the runs of elvers in the River Bann, Northern Ireland. Journal du Conseil Permanent International pour l'Exploration de la Mer 17(3): 299-315.

McDOWALL, R. M. 1964: The affinities and derivations of the New Zealand fresh-water fish fauna. Tuatara 12(2): 59-67.

MACFARLANE, W. V. 1936: "Life cycles of four New Zealand trematodes: bionomics of species of Opechona, Telogaster, Coitocaecum, and Fasciola." Unpublished M.Sc. thesis lodged in University of Canterbury Library. 71 pp.

MATSUI, I. 1952: Studies on the morphology, ecology and pond-culture of the Japanese eel (Anguilla japonica Temminck and Schlegel). Journal of the Shimonoseki College of Fisheries 2(2): 1-245.

_____ 1957: On the records of a leptocephalus and catadromous eels of Anguilla japonica in the waters around Japan with a presumption of their spawning places. Journal of the Shimonoseki College of Fisheries 7(1): 151-167.

_____ 1969: Prospects for eel cultivation in New Zealand. Report to Fishing Industry Board, (Wellington). 16 pp.

MATSUI, I. and TAKAI, T. 1971: Leptocephalae of the eel Anguilla japonica found in the waters of Ryukyu Deep. Journal of the Shimonoseki University of Fisheries 20(1): 13-18.

MENZIES, W.J.M. 1936: The run of elvers in the River Bann, Northern Ireland. Journal du Conseil Permanent International pour l'Exploration de la Mer 11(2): 249-259.

MESKE, Ch. 1969: Aufzucht von aalbrut in aquarien. Archiv für Fischereiwissenschaft 20(1): 26-32.

MEYER, P. F. and KÜHL, H. 1953: Welche milieu-faktoren spielen beim glasaalaufstieg eine rolle? Archiv für Fischereiwissenschaft 4: 87-94.

* MEYER-WAARDEN, P. F. 1965: "Der Aal. Eine kleine Monographie über einen weltberühmten Wanderfisch." Keune Verlag, Hamburg. 100 pp.

MILES, S. G. 1968: Rheotaxis of elvers of the American eel (Anguilla rostrata) in the laboratory to water from different streams in Nova Scotia. Journal of the Fisheries Research Board of Canada 25(8): 1591-1602.

MILLS, F.C. 1955: "Statistical Methods." 3rd ed. Pitman, London. 842 pp.

MORIARTY, C. 1972: Studies of the eel Anguilla anguilla in Ireland. 1. In the lakes of the Corrib System. Irish Fisheries Investigations, Series A, 10. 39 pp.

_____ 1973: A technique for examining eel otoliths. Journal of Fish Biology 5(2): 183-184.

NIKOLSKY, G. V. 1963: "The Ecology of Fishes." Academic, London. 352 pp.

ONODERA, K. 1962: Some data on eel-culture in Japan. Occasional Papers. Indo-Pacific Fisheries Council 62(6). 3 pp.

OPUSZYNSKI, K. 1965: Obserwacje nad wiekiem i biologia mlodego wegorza (Anguilla anguilla L.). Roczniki Nauk Rolniczych 86-B-2: 393-411.

PANTULU, V. R. 1957: Studies on the biology of the Indian fresh-water eel, Anguilla bengalensis Gray. Proceedings of the National Institute of Sciences of India, Series B, 22(5): 259-280.

PANTULU, V. R. and SINGH, V. D. 1962: On the use of otoliths for the determination of age and growth of Anguilla nebulosa nebulosa McClelland. Proceedings of the Indian Academy of Sciences, Section B, 55(5): 263-275.

PARKER, R. R. 1963: Effects of formalin on length and weight of fishes. Journal of the Fisheries Research Board of Canada 20(6): 1441-1455.

PENÁZ, Von M. and TESCH, F.-W. 1970: Geschlechtsverhältnis und wachstum beim aal (Anguilla anguilla) an verschiedenen lokalitäten von Nordsee und Elbe. Berichte der Deutschen wissenschaftlichen Kommission für Meeresforschung 21(1-4): 290-310.

RIDGWAY, N. M. 1970: Hydrology of the southern Kermadec Trench region. New Zealand Department of Scientific and Industrial Research Bulletin 205. 28 pp.

SANDERS, M. J. 1971: Australian studies Japanese fish culture techniques. Australian Fisheries 30(10): 3-7.

SCHMIDT, J. 1906: Contributions on the life-history of the eel (Anguilla vulgaris, Flem.). Rapports et Procès-verbaux des Réunions. Conseil Permanent International pour l'Exploration de la Mer 5: 137-274.

_____ 1922: The breeding places of the eel. Philosophical Transactions of the Royal Society, Series B, 211: 179-208.

_____ 1927: The fresh-water eels of New Zealand. Transactions and Proceedings of the New Zealand Institute 58: 379-388.

_____ 1928a: Danish fisheries investigations in the Atlantic and adjacent seas. Rapports et Procès-verbaux des Réunions. Conseil Permanent International pour l'Exploration de la Mer 47(3): 103-122.

_____ 1928b: The fresh-water eels of Australia with some remarks on the short-finned species of Anguilla. Records of the Australian Museum 16(4): 179-210.

SHORLAND, F. B. and RUSSELL, J. 1948: Observations on the oil content of New Zealand fresh water eels. New Zealand Journal of Science and Technology, Section B, 29(4): 164-200.

SICK, K., BAHN, E., FRYDENBERG, O., NIELSEN, J. T., and WETTSTEIN, D. Von. 1967: Haemoglobin polymorphism of the American fresh water eel Anguilla. Nature, (London) 214: 1141-1142.

SINHA, V.R.P. and JONES, J. W. 1967a: On the age and growth of the fresh-water eel (Anguilla anguilla). Journal of Zoology, (London) 153: 99-117.

_____ 1967b: The Atlantic eel problem. Proceedings of the Third British Coarse Fish Conference 3: 70-73.

SKEAD, C. J. 1959: The climbing of juvenile eels. Piscator 13(46): 74-86.

SMITH, M. W. and SAUNDERS, J. W. 1955: The American eel in certain fresh waters of the maritime provinces of Canada. Journal of the Fisheries Research Board of Canada 12(2): 238-269.

SNEDECOR, G. W. 1956: "Statistical Methods Applied to Experiments in Agriculture and Biology." 5th ed. Iowa State College, Iowa. 534 pp.

SÖRENSEN, I. 1951: An investigation of some factors affecting the upstream migration of the eel. Report, Institute of Freshwater Research, Drottningholm 32: 126-132.

STANTON, B. R. 1969: Hydrological observations across the tropical convergence north of New Zealand. New Zealand Journal of Marine and Freshwater Research 3(1): 124-146.

_____ 1971: Hydrology of Karamea Bight, New Zealand. New Zealand Journal of Marine and Freshwater Research 5(1): 141-163.

STANTON, B. R. and HILL, P. J. 1972: Topographic influence on the winter mid-Tasman convergence (note). New Zealand Journal of Marine and Freshwater Research 6(4): 645-648.

STRUBBERG, A. 1913: The metamorphosis of elvers as influenced by outward conditions. Meddelelser fra Kommissionen for Havundersogelser, Serie: Fiskeri, 4(3): 1-11.

_____ 1923: Elvers from north and south Europe. Report on the Danish Oceanographic Expeditions, 1908-10, to the Mediterranean and adjacent seas 3(4). 29 pp.

SVERDRUP, H. U., JOHNSON, M. W., and FLEMING, R. H. 1942: "The Oceans: their Physics, Chemistry and General Biology." Prentice-Hall, New York. 1060 pp.

TÅNING, Å. V. 1952: Experimental study of meristic characters in fishes. Biological Reviews 27(2): 169-193.

TEICHMANN, H. 1957: Das riechvermögen des aales (Anguilla anguilla L.). Naturwissenschaften 44(7): 242.

TESCH, J. J. 1928: On sex and growth investigations on the freshwater eel in Dutch waters. Journal du Conseil Permanent International pour l'Exploration de la Mer 3(1): 52-69.

TESCH, F.-W. 1965: Verhalten der glasaale (Anguilla anguilla) bei ihrer wanderung in den Ästuarien Deutscher Nordseeflüsse. Helgoländer Wissenschaftliche Meeresuntersuchungen 12(4): 404-419.

_____ 1970: Heimfindevermögen von aalen Anguilla anguilla nach beeinträchtigung des geruchssinnes, nach adaptation oder nach verpflanzung in ein nachbar-Ästuar. Marine Biology 6(2): 148-157.

TRAVERS, W.T.L. 1871: On the absence of the eel from the upper waters of the Waiau-ua and its tributaries. Transactions and Proceedings of the New Zealand Institute 3: 120-122.

TUCKER, D. W. 1959: A new solution to the Atlantic eel problem. Nature, (London) 183: 495-501.

VILTER, V. 1944: Dissociation biologique et expérimentale du complexe morphogénétique de la métamorphose chez la civelle. Compte rendu des Séances de la Société de Biologie 138(17/18): 667-668.

VLADYKOV, V. D. 1966: Remarks on the American eel (Anguilla rostrata LeSueur). Size of elvers entering streams; the relative abundance of adult males and females; the present economic importance of eels in North America. Verhandlungen der Internationalen Vereinigung für Theoretische und angewandte Limnologie 16(2): 1007-1017.

VORONIN, F. N. and RUSETSKAYA, Z. N. 1971: Determination of the age and growth of the European freshwater eel (Anguilla anguilla (L_9)) from the scales. Journal of Ichthyology 11(5): 717-724.

WALY, M. 1940: Observations on the scales of the Nile-eel. Bulletin of the Faculty of Science, Fouad I University, (Cairo) 21: 39-56.

WHITLEY, G. P. 1929: An eel-fare at Parramatta. Australian Museum Magazine 3(10): 348.

WIMPENNY, R. 1929: L'incursion des civelles Egyptiennes (1927-1928 - 1928-1929). Rapport et Procès-verbaux des Réunions, Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée, 6: 387-403.

WOODS, C. S. 1964: Fisheries aspects of the Tongariro power development project. Fisheries Technical Report, New Zealand Marine Department 10. 214 pp.

WYRTKI, K. 1962: Geopotential topographies and associated circulation in the western South Pacific Ocean. Australian Journal of Marine and Freshwater Research 13(2): 89-105.

* = not seen.

10 APPENDIX 1

Computer programme used for the analysis by covariance of length-weight data, by species by month.

```
<< JOB VIM  30,81  ALGOL LET RUNTIME 20 COMPILE 30 >>

analysis of eel data . analysis of covariance (log wt/log length)
by species, per month;

<<librar DAGYCAID ; >>

begin
      real d, x, y;
      integer mig, area, sp, i, j, mth;
      real array sx, sy, ssx, ssy, sxy, cx, cy, cxy, Sx, Sy, Sxy, r, b,
                 ss,  mms, sb, jy, my, mx, a[0:1, 1:12];
      integer array df, n[0:1, 1:12];

      real array smx, smy, smxx, smyy, smxy, crx, cry, crxy, Tx, Ty,
                 Txy, tss,  spx, spy, spxy[0:1];
      real array se1, se2, se3, se4, ms1, ms2, ms3, ms4, ms7, f1, f2,
                 dfd,  SB, B, Ybar, Xbar, A, R[0:1];
      integer array tdf, dfa, dfb, dfc, DF,  N[0:1];
      switch sw:=1 ;

     freeform (1,72) ;


      sameline;

      i:= j:= 0;
      for i:=0,1 do for j:= 1 step 1 until 12 do
            begin
                  sx[i, j]:= sy[i, j]:= ssx[i, j]:= ssy[i, j]:= sxy[i, j]:=
                   cx[i,j]:= cy[i,j]:= cxy[i,j]:= Sx[i,j]:= Sy[i,j]:=

                 Sxy[i,j]:=0;


                  r[i,j]:= b[i,j]:= ss[i,j]:= mms[i,j]:= sb[i,j]:=
                   jy[i,j]:= my[i,j]:= mx[i,j]:= a[i,j]:= 0;
                  df[i,j]:= 0;
                  n[i, j]:= 0;

                  end;

      for i:= 0,1 do
            begin

                  smx[i]:= smy[i]:= smxx[i]:= smyy[i]:= smxy[i]:=
                  crx[i]:= cry[i]:= crxy[i]:= Tx[i]:= Ty[i]:=
                  Txy[i]:= tss[i]:= 0;
                  spx[i]:= spy[i]:= spxy[i]:= 0;
                  se1[i]:= se2[i]:= se3[i]:= se4[i]:= ms1[i]:=
                   ms2[i]:= ms3[i]:= ms4[i]:= ms7[i]:= f1[i]:=
                  f2[i]:= dfd[i]:= 0;
                  SB[i]:= B[i]:= Ybar[i]:= Xbar[i]:= A[i]:= R[i]:= 0;
                  tdf[i]:= dfa[i]:= dfb[i]:= dfc[i]:= DF[i]:=  0;
                  N[i]:= 0;

            end;
```

```
11: read mig, area, d, mth, d, sp, x, y;


    if x > 0 and y > 0 then begin

    for i:= 0, 1 do begin if sp = i then
    for j:= 1 step 1 until 12 do begin if mth = j then

       begin
                x:= ln(x) * .434294481 9;
                y:= ln(y) * .434294481 9;

                 sx[i,j]:=sx[i,j]+x;
                sy[i,j]:=sy[i,j]+ y;
                ssx[i,j]:=ssx[i,j] + x*x;
                ssy[i,j]:= ssy[i,j] + y * y ;
                sxy[i,j]:= sxy[i,j] + x * y ;
                n[i,j]:= n[i,j] + 1 ;
              end;
    end;
    end;

    end;


                    if buffer + 3 then goto 11 ;

comment calculates sums, squares and products by month and species;
for i := 0,1 do for j:= 1 step 1 until 12 do if n[i,j] > 9 then

          begin
            smx[i]:= smx[i] + sx[i,j];
            smy[i]:= smy[i] + sy[i,j];
              smxx[i]:= smxx[i] + ssx[i,j];
            smyy[i]:= smyy[i] + ssy[i,j];
            smxy[i]:= smxy[i] + sxy[i,j];

            N[i]:= N[i] + n[i, j];
comment  calculates sums of sqares and products for total by month
         and species ;


             cx[i,j]:= sx[i,j] ↑ 2/n[i,j];
             cy[i,j]:= sy[i,j] ↑ 2/n[i,j];
             cxy[i,j]:= sx[i,j] * sy[i,j] / n[i,j];

comment calculates correction factors for subgroup sums of squares
        and products;

             crx[i]:= smx[i] ↑ 2/N[i];
             cry[i]:= smy[i] ↑ 2/N[i];
             crxy[i]:= smx[i] * smy[i] /N[i];
```

```
comment calculates correction factors for total sums of squares and
        productso of each subgroup;

                Sx[i,j]:= ssx[i,j] - cx[i,j];
                Sy[i,j]:= ssy[i,j] - cy[i,j];
                Sxy[i,j]:= sxy[i,j]- cxy[i,j];

comment calculates corrected sums of squares and products
        for each subgroup;

                Tx[i]:= Tx[i] + Sx[i,j];
                Ty[i]:= Ty[i] + Sy[i,j];
                Txy[i]:= Txy[i] + Sxy[i,j];


print $$L2? stage 3?;

comment adds sums of squares and products for  subgroups to give
        common sums of squares and products;

                r(i,j):= Sxy(i,j)/(sqrt(Sx(i,j)*Sy(i,j)));
                b(i,j):= Sxy(i,j)/Sx(i,j);
                ss(i,j):= Sy(i,j) - Sxy(i,j)↑2/Sx(i,j);
                df(i,j):= n(i,j)-2;
                mms(i,j):= ss(i,j)/df(i,j);

comment calulates correlation coefficient, regression coefficient,
        sums of squares of deviations from regression, d.f., and
        mean square for each subgroup;


print $$L2? stage 4?;
            tss(i):= tss(i) + ss(i,j);
            tdf(i):= tdf(i) + df(i,j);
            sb(i,j):= (sqrt(ss(i,j)/df(i,j)))/sqrt(Sx(i,j));

comment calculates within sums of squares of deviations from regression,
        d.f. and standard deviation of subgroup regression coefficients;

            spx(i):= smxx(i) - crx(i);
            spy(i):= smyy(i) - cry(i);
            spxy(i):= smxy(i) - crxy(i);

comment calculates corrected sums of squares and products for total;

            sel(i):= spy(i) - spxy(i)↑2/spx(i);
            dfa(i):= N(i) - 2;
```

```
comment  calculates total sums of squares of deviation from regression
         and d.f.;

            se2[i]:= Ty[i] - Txy[i] ↑ 2/Tx[i];
            dfb(i):= dfb(i)  + (n(i,j)-1);

end;

for i:= 0,1    do if N[i] > 9 then

      begin
                  dfb[i]:= dfb[i] - 1;

      end;

comment calculates common sum of squares of deviations from regression
        and D.F.;

for i:=0,1 do for j:= 1 step 1 until 12 do if  n[i,j] > 9 then

begin


            ms1[i]:= se2[i]/dfb[i];

comment  common mean square;

            dfc[i]:=dfa[i]-dfb[i];

comment  adj. means d.f.;


print $$L2? stage 5?;
            ms2[i]:=(se1[i]-se2[i])/dfc[i];

comment  adj means mean square;

            SB[i]:=(sqrt(ms1[i]))/(sqrt(Tx[i]));

comment  s.d. of common reg. coeff. ;

            f1[i]:= ms2[i]/ms1[i];

comment  f value for testing elevations ;


print $$L2? stage 6?;

            se3[i]:=se2[i]-tss[i];
            DF[i]:= dfb[i]-tdf[i];
            ms3[i]:=tss[i]/tdf[i];
```

```
comment  within mean square ;

print $$L2? stage 7?;

            ms4[i]:= ss3[i]/DF[i];

comment  reg. coeff. mean square ;

            f2[i]:= ms4[i]/ms3[i];

comment  f value for testing reg. coefficients ;

            my[i,j]:= sy[i,j]/n[i,j];
            mx[i,j]:= sx[i,j]/n[i,j];
            a[i,j]:= my[i,j]-b[i,j]* mx[i,j];

print $$L2? stage 8?;

comment  values for subgroup regression equations ;

                  B[i]:= Txy[i]/Tx[i];
            Ybar[i]:= sny[i]/N[i];
            Xbar[i]:= snx[i]/N[i];
            A[i]:= Ybar[i]-B[i]* Xbar[i];

comment  values for common regression equation;

            ss4[i]:= ss1[i]- ss2[i];
            R[i]:= Txy[i]/(sqrt(Tx[i]*Ty[i]));

comment  common correlation coeff.;

            ms7[i]:= ss1[i]/dfs[i];

comment  total mean square ;

            Jy[i,j]:=(sy[i,j]/n[i,j])-(((sx[i,j]/n[i,j])-Xbar[i])* B[i]);

comment  adjusted mean weight;

      end;

print  $$L3s 10? analysis of covariance table, area?, digits(3),area ;

if sp= 0 then print $$s4? short fin  ? else print $$s4? long fin?;

print $$L22$s8? month  $s9?sx2$s6? sy2$s6? sxy$s7?b$s8?df$s6?sdyx2$s6?m
      s$s8?r$s9?sb$L??;
for  i:= 0,1 do for j:= 1 step 1 until 12 do if n[i,j] >9 then

      begin
```

```
        print $$L=10??, digits(2),j,$$s??;
        print  Sx[i,j], Sy[i,j], Sxy[i,j],b[i,j],df[i,j],ss[i,j],
               mss[i,j],r[i,j],sb[i,j];
    end of print list for subgroup data, analysis of covariance table;

for  i:= 0,1 do if  N[i] > 9 then

    begin

        print  $$L2? within $s53??, tdf[i], tss[i], ms3[i],
               $$L? reg. coeff. $s48??, DF[i],so3[i],ms4[i],
               $$L? common $s12??, Tx[i],Ty[i],Txy[i],B[i],$$s??,
                    dfb[i],so2[i],ms1[i],R[i],SD[i],
               $$L? adj means $s50??,dfc[i],so4[i],ms2[i],
               $$L? total $s13??, spx[i],spy[i],spxy[i],$$s11??,
                    dfa[i],so1[i],ms7[i],
               $$L2? F reg. coeff. =?,f2[i], $$s3?d.f.?, DF[i],
                     $,?,tdf[i],$$s8? f adj. means =?,f1[i],
               $$s3?d.f.?,dfc[i],$,?,dfb[i],$$L??;
    end;
        print $$l4? the regression equations for each subgroup are
              as follows:$L??;

for  i:= 0,1 do for  j:= 1 step 1 until 12 do if n[i,j] > 9 then

    begin
        print $$L? month?, digits(2),j,$$s9??;
        print $$s6?y = ?,b[i,j],$x + ?,a[i,j];
    end;

for i:= 0,1 do if N[i] > 9 then
    begin
        print $$L4? the common regression equation is y = ?, B[i],
              $x + ?, A[i],$$L2??,
              $$L? adjusted mean weights for each subgroup with
              grand mean length = ?,
              Xbar[i],$$s? are as follows:?;

    end;

for i:= 0,1 do for  j:= 1 step 1 until 12 do  if n[i,j] > 9 then

    begin

        print $$L?month?, digits (2),j,$$s8??;
        print $$s3? adjusted mean weight = ?, jy[i,j];

end;

end;

end;
```