THE ECOLOGY OF THE NEW ZEALAND HALIOTIS SPECIES (MOLLUSCA)

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by

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1969

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1. INTRODUCTION

1.1 A review of recent work on Haliotis and aims of this study.

Cox (1962) gave an excellent historical review of all published works on Haliotis beginning with Aristotle in the 4th century B.C. Because the genus is world-wide there is a great deal of literature including detailed anatomical studies (e.g. Crofts, 1929), studies of larval stages (e.g. Crofts, 1937; Ino, 1952) and ecological studies (e.g. Ino, 1952; Leighton & Boolootian, 1963). Many more papers have appeared since 1963.

Abalones have long been a basic food item in the Orient and are gaining appeal as a delicacy in Western countries. As the level of fishing has increased so has research, particularly in Guernsey (United Kingdom), California, Japan, South Africa and Australia. In Guernsey recent work has been done on density and on growth rate (Forster, 1962, 1967). In California, work on abalones has been associated with a five-year study of the decline of kelp beds (Leighton, 1966) and has been concentrated on their feeding habits. In Japan, research is now concentrating on ecology (Sakai, 1962 a-d) and on methods of mass culture (Oba, 1964a, b) and in South Africa and Australia on population dynamics with a view to regulating the fishery (Newman, 1966, 1967, 1968; Anon., 1967).

In New Zealand where an export fishery is just beginning, published work is limited to comments on the use of paua-shell by the Maori (Phillipps, 1935), a general ecological study (Sinclair, 1963), and papers on body proportions (Cleaver, 1966) and feeding (Tunbridge, 1967). The Marine Department has carried out other work, as yet unpublished.

This thesis is a comparable ecological study of two Haliotis species. It aims to establish basic ecological information for H. iris and H. australis at Kaikoura and to compare the species. Incidental to this are a comparison of some aspects of the ecology of H. iris at Kaikoura with that at Taylors Mistake, and some comments on H. virginea.

1.2 Taxonomy and Distribution.

The higher taxonomy of Haliotis, based on Thiele (1931) as used by Morton (1963), is as follows:

Phylum:	Mollusca
Class:	Gastropoda
Subclass:	Prosobranchia
Order:	Archaeogastropoda
Superfamily:	Zeugobranchia
Family:	Haliotidae Rafinesque, 1815
Genus:	Haliotis Linnaeus, 1758

The status of the family seems to have not been questioned since its inception but there does seem some confusion at the generic and subgeneric levels. The most recent review of the family is that of L.R. Cox (1960) in "Treatise of Invertebrate Paleontology", where "only one genus, divided into several more or less intergrading subgenera, is ... recognised, ..." He lists eleven subgenera but others have been erected in the past. In Australia, following the work of Cotton (1943), many subgenera are used as genera, e.g. Notohaliotis, Marinauris, Schismotis.

The family contains "about 130 species and subspecies" (K.W. Cox, 1962) although the exact number seems in doubt. Hybridisation of existing species in California is known (Cox, 1962) and immunochemical studies of their haemocyanins support close interrelationships (R. Meyer, pers.comm.). There is no recent overall work on the status of species within the family as a whole but some revisions of local species assemblages have appeared (Gailliard, 1958; Talmadge, 1963).

The family has an almost worldwide distribution but all individual species have limited geographical range. The greatest concentration, both in abundance and in number of species, is in the Pacific Basin: western North America, Japan, Australia, New Zealand

and the Pacific Islands. Cox (1962) discussed and figured the distribution of the family as then known. The Yucatan Peninsula, Central America can be added to this range (Harry, 1966) and Macquarie Island should be deleted (Section 1.5.1).

1.3 Common names.

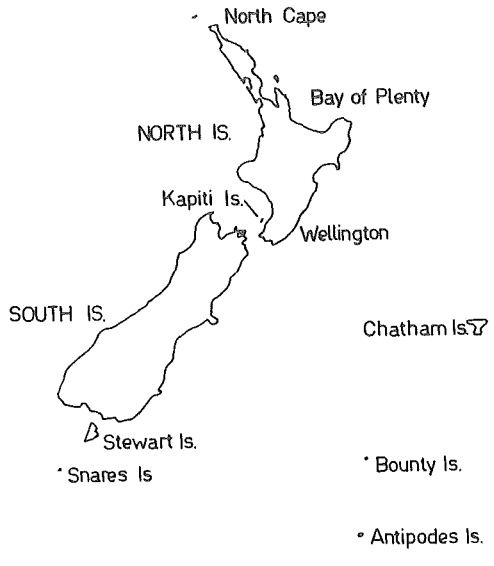
Species of Haliotis are most commonly called abalones, a North American word which has spread recently, with the commercialisation of the group, to Japan, Australia and South Africa. The origin of the word abalone can be traced to the Mexican aulone. In Guernsey, ormer is used, a contraction of the French oreille de mer (sea ear). Haliotis also means sea ear in Greek, so named because of the shape of the shell.

The Maori in New Zealand call H. iris paua and H. australis karariwha, but only the word paua has been adopted by the English language since only H. iris is utilised as meat and shell. Queen paua and virgin paua are used for H. australis and H. virginea respectively. In this work both species are referred to the more general and widely recognised name, abalone.

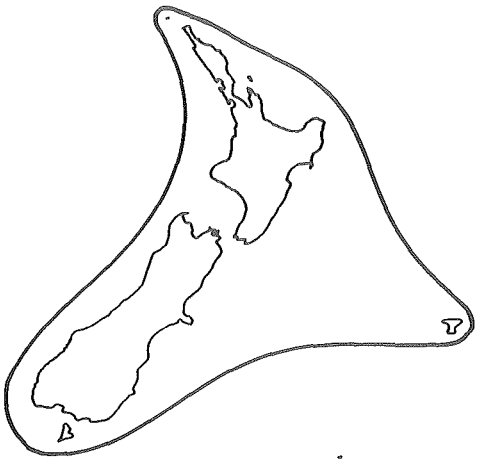
1.4 General biology of abalones.

Abalones are recognised by their loosely coiled shell with a very wide aperture and their large muscular foot with which they attach to the substrate. They range in size from a few to about 20cm in length. They are generally sedentary using the shell as protection against predators. A water current is drawn in under the shell, through the gills in the mantle cavity on the left side, and out the respiratory pores on top of the shell. Sensory organs include numerous tactile tentacles around the shell edge and a pair of eyes anteriorly. The life history involves a pelagic larval phase of 2-5 days.

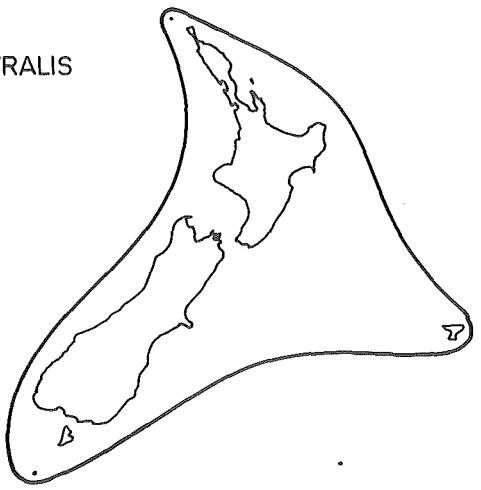
Abalones are found only on hard substrates, rock surfaces or



H. IRIS



H. AUSTRALIS



H. VIRGINEA

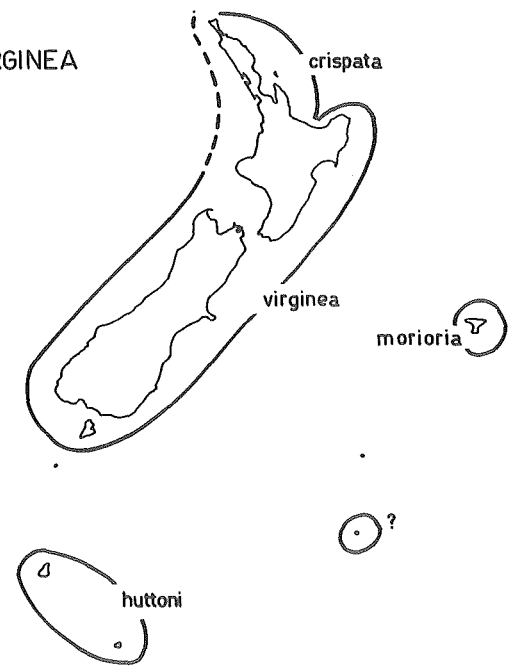


FIGURE 1.1

Distribution of three species of *Haliotis* in New Zealand and the subantarctic islands. Subspecies of *H. virginea* are marked.

boulders, often colonially in "beds". They range from the intertidal region to over 100m depth but the majority occur most abundantly in the immediate sublittoral zone. Their diet is the large seaweeds found in this region though a few may feed on diatom films.

1.5 New Zealand haliotids.

1.5.1 Extant species and their distribution.

New Zealand and its adjoining islands have three distinct species one of which has four named subspecies:

Haliotis iris Martyn, 1784.
Haliotis australis Gmelin, 1790.
Haliotis virginea Gmelin, 1790.
H. virginea virginea Gmelin, 1790.
H. virginea crispata Gould, 1847.
H. virginea huttoni Filhol, 1880.
H. virginea morioria Powell, 1938.

H. iris is placed in its own subgenus, Paua Fleming, 1952 and H. australis and H. virginea are placed in the existing subgenus Sulculus H. & A. Adams, 1854 (Fleming, 1952).

Some of the distribution records in the subantarctic islands seem a little in doubt. Specimens of H. iris in the Suter Collection of the N.Z. Geological Survey collected last century are labelled Snares Island (Dell, 1963a) but none of the several recent expeditions of the Zoology Department, University of Canterbury, to this island have collected the species (G.A. Knox, pers.comm., D.B. Cameron, pers. comm.). Dell (1963a) agrees that H. iris "would appear not to be a normal member of the fauna." Although Suter (1913) lists H. iris in the fauna of the Auckland islands, it is not contained in the Cape Expedition collections (Powell, 1955) and was not seen by a Zoology Department expedition in 1966 (P.M. Johns, pers.comm.). Thus H. iris is definitely present only on the New Zealand mainland,

Stewart Island, and the Chatham Islands (Dell, 1960).

The presence of H. australis on the Snares (Powell, 1955; Dell, 1963a) has been confirmed by a 1968-9 expedition (D.B. Cameron, pers. comm.). Its presence on Auckland Island (Suter, 1913) is in doubt (Powell, 1955) since it was not collected by a recent expedition (P.M. Johns, pers.comm.) nor by the Cape Expedition. It is definitely present also on the New Zealand mainland, Stewart Island, and on the Chathams (Dell, 1960).

H. virginea virginea occurs around the South Island, Stewart Island, Wellington and the southern coast of the North Island, H. virginea crispata occurs in the North Island between Bay of Plenty and the North Cape (Powell, 1952). The boundary between the two subspecies on the west coast is not clear but the author has collected a single specimen, probably H. virginea virginea, at Kapiti Island. H. virginea morioria is restricted to the Chatham Islands (Powell, 1938a; Dell, 1960) and H. virginea huttoni to Auckland and Campbell Islands (Powell, 1938a, 1955). A recent addition to this distribution is the discovery of several shells and one live specimen from Antipodes Island by the 1969 Zoology Department expedition (I.M. Mannering, pers.comm.). The specimens cannot be readily placed in any existing subspecies and may constitute another; work is proceeding on the subspeciation of H. virginea.

The lack of records from Bounty Island is due mainly to the fact that few expeditions have visited this island; only H. virginea would be expected. Although Macquarie Island was mentioned specifically by Cox (1962) as the southern limit of the genus, there is no reference to his source of information. No Haliotis was recorded by Dell (1963b) or by recent expeditions by members of the Mawson Institute for Antarctic Research, University of Adelaide, Australia (W.J. Merilees, pers.comm., R.D. Simpson, pers.comm.). No other antarctic or subantarctic islands have records of Haliotis (Powell, 1951). This information is summarised in Fig. 1.1.

Both H. iris and H. australis are most abundant in the immediate

sublittoral region to about 4m. At Kaikoura rare individuals are found to about 12m. While H. iris, especially juveniles, are common intertidally, H. australis are rare in this zone. H. virginea is found rarely at Kaikoura as high as the intertidal but is more common in deeper water. Dell (1960) records H. virginea in dredged samples from 15 fathoms (27m) at the Chathams, and most specimens collected in subantarctic islands are shells from the drift zone.

1.5.2 Fossil species.

The New Zealand fossil record includes a number of species of Haliotis, both extinct and extant (Table 1.1). Some of the oldest records for the genus appear in New Zealand. All records, except that of Maxwell taken from Broken River, are from the North Island. Fleming (1966) reviewed the earlier records.

1.6 Associated Species.

1.6.1 Introduction.

Cox (1962) has discussed the relationships between Californian abalones and other species, and Russell (1967) has reviewed parasites in commercially important molluscs, including Haliotis. Two commensals are reported in these and other papers, a shrimp Betaeus harfordi from the mantle cavity of all Californian species (Hart, 1964), and a polychaete, Arctonoe viltata from H. kamatschatkana (Clark, 1956). Several parasites have been recorded, Panaietis haliotis, a copepod from the mouth cavity of H. gigantea (Yamaguti, 1936), Echinocephalus pseudouncinatus, a nematode burrowing in the foot of H. corrugata and H. fulgens (Millemann, 1963), Cliona spp., sponges boring into the shell (Forster, 1967; Cox, 1962), and boring molluscs also in the shell (Cox, 1962). Predators recorded include the sea otter in California (Ebert, 1968), crabs (Olsen, 1968), and octopus (Pilson & Taylor, 1961).

TABLE 1.1. Fossil records of *Haliotis* in New Zealand.

Stage	Epoch	Species	Authors
Oturian - Recent	U. Pleistocene - Recent	*H.virginea* (1)	Fleming, 1966, pers.comm.
Nukumaruan	L. Pleistocene	*H.*sp.indet.	Fleming, pers.comm.
Opoitian - Recent	L. Pliocene - Recent	*H.iris* (2)	Laws, 1936.
Castlecliffian	Pleistocene	*H.powelli*	Fleming, 1952.
Otaian	L. Miocene	*H.flemingi*	Powell, 1938b.
Otaian	L. Miocene	*H.waitemataensis* (3)	Powell, 1938b.
Clydenian	L. Miocene	*H.* ?n.sp. (G.S.3157) (4)	Fleming, pers.comm.
Whaingaroan	L. Oligocene	*H.*sp.indet. (5)	Maxwell, pers.comm.

(1) Extant.

(2) Extant; also in U. Pleistocene (Fleming, pers.comm.).

(3) Similar to a specimen described by Powell & Bartrum (1929).

(4) A poorly preserved juvenile.

(5) Possibly in subgenus *Notohaliotis*.

1.6.2 Parasitic mites.

Both *H. iris* and, to a lesser extent, *H. australis* are host to a marine mite, *Halixodes truncipes*. Specimens were collected from abalones in subtidal and intertidal populations at Kaikoura and Taylors Mistake and are also recorded from Nelson (F.M. Climo, pers. comm.) and so seem widespread. Only large abalones were infected, with up to 50 mites per host; most were nymphs, few adults and no larvae were found. The mites, each 1-2mm long, were firmly attached to the host, especially in the groove between the most dorsal part

of the foot and the viscera surrounding it. They were also frequent around the mouth but occurred on all other surfaces. Most were hidden but a few, notably those on the edge of the epipodium, were exposed.

The diet of the mites could not be determined; it may be the tissue of the host or the mucus of the skin. The mites had no visible effect on the host.

Halixodes truncipes was originally described from "between tide marks" (Chilton, 1882) where several marine mites are known, but its occurrence below low water is unusual for mites. A second species, Halixodes chitonis, has been recorded from the chiton Cryptochonchus porosus (Brucker, 1897 cited by Stout & Viets, 1959) with a subspecies, H. chitonis stoutae from the mantle cavity of Sigapatella novae-zelandiae (Stout & Viets, 1959). Stout (pers.comm.) has identified specimens collected by the author from H. iris, H. australis, C. porosus, and Eudoxochiton nobilis as Halixodes truncipes and thinks the two species are probably synonymous.

1.6.3 Commensal crabs.

At Kaikoura large H. iris, and occasionally H. australis, are host to a commensal crab, the hymensomid, Elamena producta. The association is not obligative as the crab is often found free-living. This flat-backed crab is well fitted to its habitat in the slot between the foot and viscera, its flattened legs stretch laterally from the flat carapace and attach to the upper part of the foot muscle. Usually only one, but sometimes two or three, crabs are found per host; each may span up to 7cm.

Examination of the gut contents of several specimens of E. producta revealed crustacean fragments, most identified as large parts of amphipods. The crab has strong chelae and a pair of opposing sets of spines in the stomach and so seems predatory. The epiflora of H. iris shells supports a number of amphipods of various species and may be a ready food supply for the crab. Free-living

crabs were also found to have amphipods in their guts and one Elamena in a bowl in the laboratory ate six amphipods in two days. The abalone seems neither to benefit nor suffer from the association.

1.6.4 Predators.

Direct observations of predation of abalones in New Zealand are few but there is some indirect evidence.

Fish are definite predators on young abalones. While diving at Kaikoura the author turned a rock and exposed several H. iris, each about 30mm long. When these started to move a Banded Parrotfish (Pseudolabrus pittensis) took three and ate them whole. A small H. australis was also found in the gut of a Red Cod (Physiculus bachus) by a fisherman at Kaikoura. Predation by fish would only occur when the young abalones move out from under stones, but they rarely do this. It seems unlikely that adults are worried by fish.

Spiny lobsters (Jasus edwardsii) are probable predators on abalones. In the laboratory a small population of Jasus regularly attacked small H. iris by chipping away the anterior edges of the shell. But chipped shells on live animals have never been seen in the field and it seems unlikely that Jasus could attack a full size H. iris in this way. However, a fisherman at Kaikoura has seen spiny lobsters tip over H. iris when they are moving and feed on them. Such behaviour is more likely to occur at night when Jasus is more active. The fact that live H. iris is one of the best types of bait for lobster pots also suggests some predation.

Octopus feed on abalones in California after narcotizing them through a hole bored in the shell (Pilson & Taylor, 1962). Octopus are quite common at Kaikoura but no evidence, e.g. shells with small holes, suggests this behaviour here.

Abalones, including H. iris and H. australis, exhibit a definite escape response when they come in contact with predatory asteroids (Bennett, 1927; D.H. Montgomery, 1967) but there are few observations of actual predation in the field. The large starfish, Astrostole scabra has been observed feeding on a small H. iris, apparently

recently dead, at Kaikoura (T.G. Dix, pers.comm.) but more commonly feeds on chitons and trochid snails. Astrostole is often seen quite close to abalones but has never been seen attacking them. The rapid flight response elicited in the abalone may be a successful method to avoid capture by the asteroid. Also, experiments with H. iris suggest that the secretion of mucus from the hypobranchial gland and the shell whirling accompanying escape deter the asteroid. Only dead or dying abalones may be attacked. Asteroids respond positively to the presence of dead material in a laboratory tank for example, but no experiments have been carried out to show whether they respond positively to the presence of live abalones. All experiments have concentrated on the response of the abalone when the asteroid is purposely placed on or near it. Feder (1963) and D.H. Montgomery (1967) who worked on this problem, agree that the star Pisaster ochraceus which elicits a definite response from H. rufescens rarely preys on this species.

1.6.5 Shell-boring species.

Shells of both H. iris and H. australis are attacked by a variety of boring species. Polychaetes are the most abundant group, Polydora monilaris in particular occurs in hundreds on a single shell in chambers just under the surface. Rhamphobrachium sp., Dodecaceria sp. and Lumbrineris sphaerocephala are less common, eroding long narrow tubes through the shell. Polychaetes tend to inhabit the outer prismatic layer of the shell first and burrow into the harder nacre less readily. They are especially common in shells with a thick 'Lithothamnion' growth. The boring barnacle Cryptophialus melampygos is very abundant in both species of Haliotis as well as in other molluscs (Batham & Tomlinson, 1965). Both polychaetes and Cryptophialus occasionally break through the inside of the shell and cause the abalone to deposit a nacre blister over the hole; these are more common in H. australis. Both abalones also deposit layers of nacre internally which maintain the shell thickness as the outside

is eroded. Erosion and senility in Haliotis shells has also been noted by Talmadge (1953).

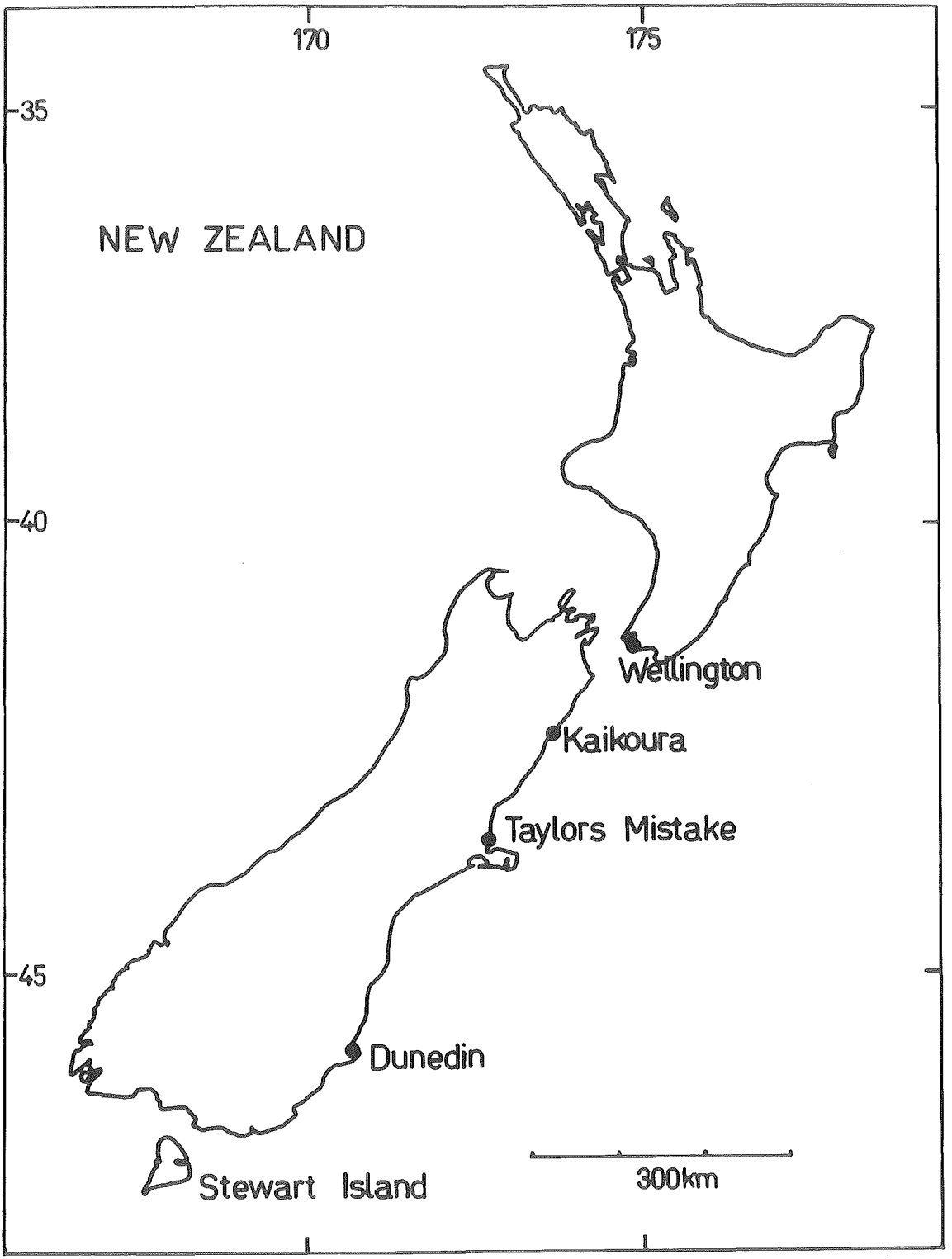

170
175
35
40
45
NEW ZEALAND
Wellington
Kaikoura
Taylors Mistake
Dunedin
Stewart Island
300km

FIGURE 1.2

New Zealand, showing place names used in text.

2. FEEDING

2.1 Introduction.

Abalones are generally herbivores browsing on the larger seaweeds of the sublittoral region and have been the subject of several recent feeding studies, especially in California and Japan (Leighton & Boolootian, 1963; Sakai, 1962a, b, c).

Apart from Sinclair's (1963) and Tunbridge's (1968) observations on Haliotis iris, little is known of the feeding habits of the New Zealand haliotids. This study attempted, firstly, to define the diets of H. iris and H. australis from two very different localities, and secondly, to establish the relative parts played by the local floral composition and by active food selection in the determination of diet. Finally, the growth rate of abalones restricted to single species diets was studied.

2.2 Methods.

2.2.1 Sampling and Gut analyses.

At two-monthly intervals between July 1967 and May 1968, six samples of about 20 each of large H. iris and H. australis were taken from Wakatu Point, Kaikoura. While each H. iris sample generally came from one or two compact colonies on the eastern side of the Point, the H. australis came from a wider area west of the Point. Both species were collected using SCUBA in 1-2m of water.

The stomach content of each individual was preserved in 10% formolsaline. The preserved gut contents consisted of small fragments of algae, a few millimetres in diameter, most of which could be specifically identified. The species were divided into six groups on taxonomy and habit (Table 2.1): I, Chlorophyta (3 spp.); II, branching Rhodophyta (9+ spp.); III, flat Rhodophyta (5+ spp.); IV, corallines (2 spp.); V, Phaeophyta (5+ spp.); VI, Angiosperma (1 sp.). Species of Group III were not easily separated as fragments

in the gut contents, so were treated together. Hymenocladia lanceolata was most often recognised though Epymenia wilsonsis, Cladhymenia oblongifolia and Hymenena semicostata were also present. Some species in Groups II and V were also lumped.

The contents of a single gut were spread in a 10cm petri dish on which were marked 50 evenly spaced points; the relative abundance of an algal species was calculated by scoring the number of points over which fragments of that species were lying. Species which did not score in this way were also noted. Only presence or absence was noted in negligible gut contents i.e. those too small to be analysed by the point system. For each monthly sample these data were converted to percentage full guts in the sample, percentage abundance and percentage occurrence of each algal species and group.

To study the effect of local flora on diet, gut samples from 20 H. iris from Taylors Mistake were examined on September 27, 1968 and compared with those from Kaikoura. The flora at Taylors Mistake is largely different from that at Kaikoura.

2.2.2 Floral analysis.

In October 1968 the composition of the flora growing in the collecting areas on each side of Wakatu Point was analysed. A metre-square quadrat was moved over the substrate in areas of concentration of Haliotis and the five most abundant algae (in terms of bulk) were listed in order; additional species were also noted. In some quadrats on the eastern side of the Point fewer than five species were present. After a few days of strong north-east seas in December 1968 the drift algae which had accumulated on the bottom were sampled with a sweep net. The drift was sorted into species, weighed and a percentage by weight for each species calculated. Very small fragments of red algal species which proved impossible to sort were omitted. These were probably too small for abalones to eat.

2.2.3 Selection experiments.

Preliminary experiments showed a difficulty in inducing Haliotis to feed in the laboratory; poor water circulation and the accumulation of silt deposits during rough weather are inhibiting factors. The experiments described were carried out in August 1968 in tanks, each 56cm by 29cm and 14cm deep, at the Edward Percival Marine Laboratory, Kaikoura. Maximum possible water circulation was maintained through them with an inlet flow of 14 litres/minute directed along the bottom of the tank.

In each experiment a diet of two species of seaweed was offered, a brown and a red. To make each species equally available the fronds were cut into discs 3cm in diameter or into squares of approximately the same area. One red species was used, Hymenocladia lanceolata, which (with other red species) makes up about 40% of the diet of both species of Haliotis. Two browns were chosen, Lessonia variegata the most abundant brown alga recognised in guts of Kaikoura abalones, and Macrocystis pyrifera, a common seaweed at Kaikoura and the dominant in the flora and in the diet at Taylors Mistake.

Three experiments were devised, differing in the species and relative amounts of food given:

Experiment No.1. Equal weights (20gm) each of Hymenocladia and Lessonia; these averaged 46 and 25 pieces of each species respectively.

Experiment No.2. Equal numbers of pieces (20) each of Hymenocladia and Lessonia; these averaged 8.5gm and 15.5gm of each respectively.

Experiment No.3. Equal numbers of pieces (20) each of Hymenocladia and Macrocystis; these were also approximately equal weights (8.5gm and 7.4gm respectively).

The amounts of algae provided were a surplus in all cases so no bias arose due to all of one species being eaten. Controls set up during the first experiment showed negligible weight changes due to water intake or loss. The laboratory water temperature was 9-10°C.

Three abalones were used for each trial and six trials per Haliotis species were run simultaneously. They spent alternately two days feeding in a separate holding tank and two days under experimental conditions. It was not found necessary to starve the animals before each experiment as Leighton (1966) did in a similar experiment. Any combination of three animals was used only once.

The procedure was as follows. The food was placed in the tank in the morning and at the same time on the next day the whole and partly-eaten fragments remaining were counted and, in Experiment No.1, also weighed. Tanks were kept in darkness during night and shaded during the day. The abalones fed only at night.

Eighteen replicates of Experiment Nos 1, 2 and 3 were carried out with both H. iris and H. australis from Kaikoura, and four replicates of Experiment No.3 were carried out using H. iris from Taylors Mistake.

2.2.4 Restricted diet experiment.

At the beginning of December 1968 a number of small H. iris were collected from the intertidal region at Kaikoura. All were about 20 months old and were selected for consistency of size. After each had been measured (shell length to nearest millimetre) and weighed (to the nearest decigram after drying on a towel) they were sorted into five groups of fourteen with similar mean lengths. The five groups were placed in separate plastic tanks (30 x 27cm) through which water flowed to a depth of 8cm. Until the experiment ended at the end of May 1969 the first group was starved, the second and third groups were fed regularly on the red alga Hymenocladia lanceolata, and the fourth and fifth groups were fed on the brown alga Lessonia variegata. The abalones were fed every four or five days on a surplus of freshly collected seaweed cut into pieces to make it more available, and at the same time the tanks were cleaned of silt and uneaten seaweed. At the beginning of every month each individual was remeasured and reweighed as before and the colours

		(a)				(b)			
		H.iris		H.australis		H.iris		H.australis	
I	Caulerpa brownii	2.86	4.08	4.91	7.13	43.9	45.6	25.2	27.8
	Ulva lactuca	1.22		2.23		4.4		3.4	
	Chaetomorpha darwini							0.8	
II	Polysiphonia sp.	22.46	36.62	8.45	39.66	83.3	97.4	21.9	71.5
	Pterocladia lucida	1.78		19.77		26.3		41.2	
	Plocamium spp.	8.76		3.02		87.7		17.7	
	Euzoniella incisa	1.57		5.58		33.3		19.3	
	Euzoniella bipartita	1.00		1.21		15.9		8.4	
	Melanthalia abscissa	0.19		1.43		7.0		22.7	
	Euptilota formosissima	0.62		0.19		17.5		6.7	
	Echinothamnion hysterix	0.24				4.4		4.2	
	Euzoniella cuneifolia					0.9			
III	Several spp.	-	44.40	-	38.08	-	78.0	-	45.4
IV	Corallina officinalis	0.14	0.14	0.45	0.64	4.4	4.4	31.1	31.1
	Jania rubens			0.19				4.2	
V	Lessonia variegata	8.27	14.76	12.30	14.49	16.7	52.6	26.1	48.8
	Marginariella boryana	4.73		1.43		28.1		5.9	
	Cystophora scalaris	1.73		0.04		18.4		8.4	
	Halopteris spicigera	0.03		0.68		1.8		10.9	
	Glossophora kunthii			0.04				2.5	
VI	Zostera nana					-	3.5		

TABLE 2.1

(a) Percentages of algal species and groups in the stomach contents of H. iris and H. australis from Wakatu Point. Each percentage is calculated from the total number of points scored throughout the year (3700 for H. iris, 2650 for H. australis).

(b) Percentages of all guts examined in which the species and groups occurred (114 for H. iris, 119 for H. australis).

of the newly deposited prismatic shell noted after cleaning with a soft brush. Mean and standard deviation of length and weight were calculated for each group each month. At the sixth and final remeasurement, May 27, all remaining animals were killed and the shells weighed.

2.3 Results.

2.3.1 Wakatu Point, Kaikoura.

Gut analysis. As there was no seasonal variation in diet all monthly samples were summed and percentage abundances and occurrence calculated for the whole year. In both H. iris and H. australis soft red algae (Groups II and III) made up about 80% of the diet and brown algae, at 15%, make up most of the remainder. Hymenocladia lanceolata was the major flat red alga recognised and within the branching reds Polysiphonia sp. made up most of the diet of H. iris and Pterocladia lucida most of that of H. australis. Lessonia was the major brown species eaten by both species. No other alga formed more than 10% of the diet of either species (Table 2.1).

Table 2.1 lists the percentage occurrence of each algal species and group summed in the same way. Although the species assume similar relative ranks, the differences between species are not as marked. (Spearman's Rank Correlation Coefficients, C = 0.896 and 0.754 for H. iris and H. australis respectively, are both highly significant at the 0.001 level.) Species are recorded that would otherwise be overlooked, e.g. Zostera nana. Species that occur often in the diet but never assume importance include Caulerpa, Pterocladia, Euzoniella incisa and Marginariella for H. iris and Caulerpa, Melanthalia and Corallina for H. australis. Closer comparison of the data of parts a and b of Table 2.1 indicates that records of presence or absence convey little information on the relative importance of components of the diet of either species.

When the frequencies of percentage abundances are tabulated it is found that only 37% of all occurrences in H. iris and 31% of all

TABLE 2.2 Frequencies of relative abundances of algae in quadrats at Wakatu Point.
(a) *H. australis* area (west side of point).
(b) *H. iris* area (east side of the point).

	(a)						(b)					
Order of relative abundance:	1	2	3	4	5	etc.	1	2	3	4	5	etc.
Ecklonia radiata	6	4	3	1		2		2				1
Carpophyllum maschalocarpum	3	6	2	1	1	3	7	1				
Pterocladia lucida	2	2	3	3	1	2		2	1	1		
Lessonia variegata	2					2						
Desmarestia firma	1	1	2			1					1	
Marginariella boryana	1		1	1		1						
Halopteris spicigera	1			3	2	3						
Glossophora kunthii		1	4		1	1						
Cystophora scalaris		1		3	4	4		1	1			1
Macrocystis pyrifera		1										
Melanthalia abscissa			1	1	2	5			1	3		
Hymenocladia lanceolata				1	4	2						
Caulerpa brownii				1	1	1			1			
Plocamium costatum				1								
Corallina officinalis						16		2	1		3	2
Asparagopsis armata						6					1	
Chaetomorpha darwini						4						
Landsburgia quercifolia						1	1		1	1		
Other flat reds						1						
Totals	16	16	16	16	16	50	8	8	5	5	5	4

TABLE 2.3 Percentages of algal species and groups in drift alga collected from Wakatu Point. A dash (-) indicates a negligible occurrence.

	Species	Percentages	
		Species	Groups
I	Caulerpa brownii	2.5	2.6
	Ulva lactuca	0.1	
	Chaetomorpha darwini	-	
II	Pterocladia lucida	3.6	25.3
	Plocamium spp.	17.7	
	Euzoniella incisa	0.9	
	Melanthalia abscissa	-	
	Euptilota formosissima	0.9	
	Gigartina sp.	2.2	
III	Miscellaneous species		36.6
V	Landsburgia quercifolia	19.8	35.5
	Lessonia variegata	5.6	
	Ecklonia radiata	-	
	Carpophyllum maschalocarpum	-	
	Cystophora scalaris	-	
	Glossophora kunthii	5.4	
	Halopteris spicigera	4.7	
VI	Zostera nana		-

occurrences in H. australis are at greater than the 10% level and that half of all species of algae never occur at levels greater than 20%. It is concluded therefore that only a few species of seaweed are important components of the diet of either species.

A marked reduction in the number of full guts of both species was apparent during the summer, i.e. during the period when the gonads are ripe (Fig. 2.1). This indicates a reduction in feeding activity during the summer. Although there were differences between the composition of diets from month to month no trends could be detected; the Kaikoura algal flora contains few seasonal species (Rasmussen, 1965).

Floral analysis. The algae from flora analysis at Wakatu Point are listed in approximate order of relative abundance (Table 2.2). On the east side only five out of the eight quadrats had more than two species of algae but in both areas brown algae dominate the flora; Ecklonia and Carpophyllum in the H. australis area and Carpophyllum alone in the H. iris area. Several species were recorded which were not recognised in gut samples: Ecklonia may at times have been confused with Lessonia but Desmarestia, growing only during the spring and summer, Carpophyllum, Asparagopsis and Landsburgia were definitely not in the guts. On the other hand, many species that were abundant in guts were not recorded or were very rare.

Drift algae. There is always some seaweed drifting on the bottom in the Wakatu Point area but the amount varies considerably. Records of sea conditions are taken daily at Kaikoura but no correlation between these and volume of gut contents was apparent.

The species composition of drift weed shown in Table 2.3 is typical of the Wakatu Point area. Soft red algae are the most abundant species but are uncommon in the area where H. iris was collected and are not dominant where H. australis is found. At Kaikoura brown seaweeds dominate the flora down to about 12m and reds are most common below this level. Drift weed then, brought

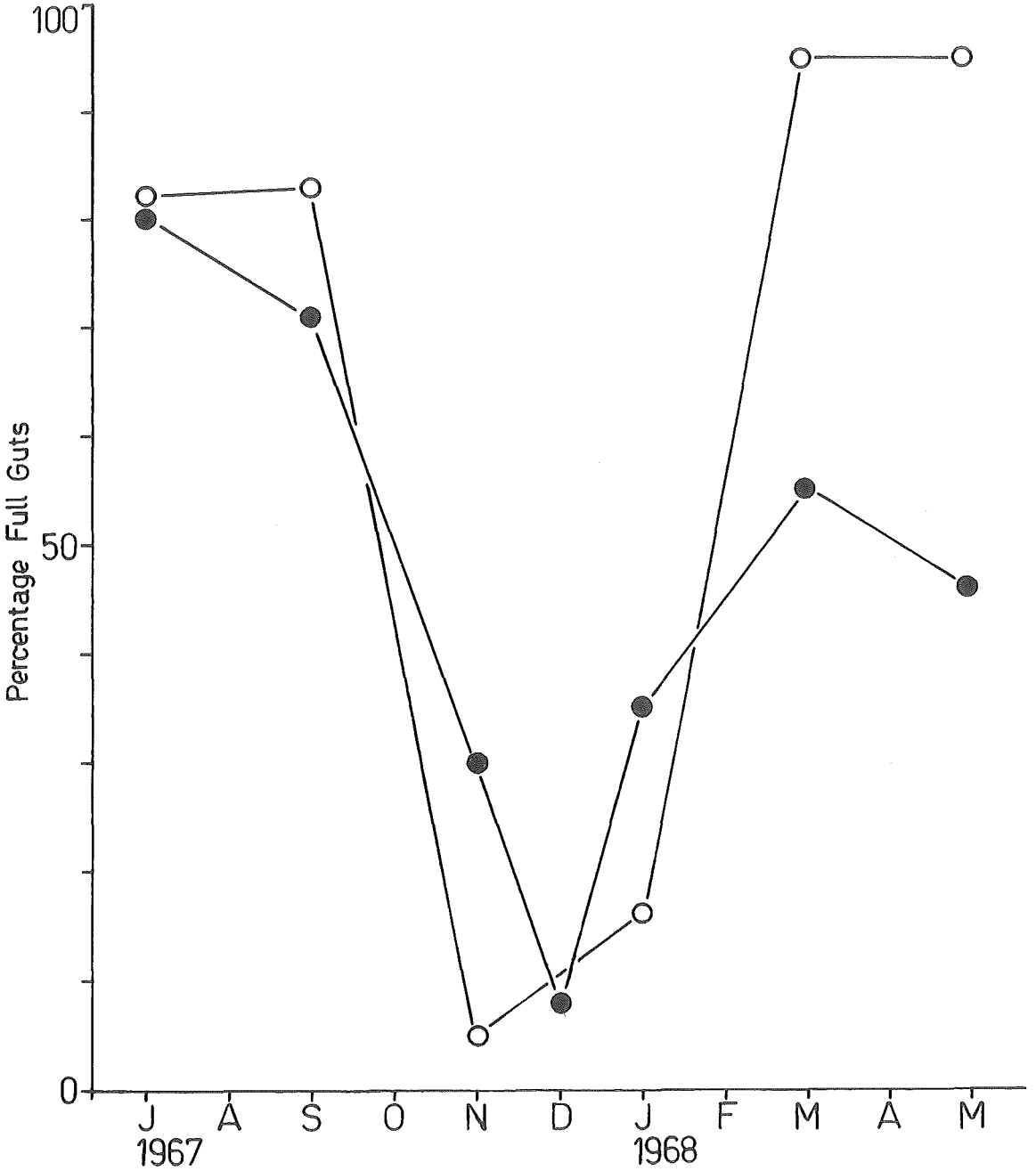

100
50
0
Percentage Full Guts
J
A
S
O
N
D
J
F
M
A
M
1967
1968

FIGURE 2.1

Seasonal trend in the percentage of full guts in samples of H. iris (open circles) and H. australis (filled circles).

TABLE 2.4 Percentage occurrences of fifteen species of algae in twenty H. iris stomachs from Taylors Mistake.

	Species	Percentage occurrences
II	Plocamium sp.	5
	Euptilota formosissima	100
III	Polysiphonia sp.	35
IV	'Lithothamnion'	50
	Corallina officinalis	45
	Jania rubens	20
V	Carpophyllum maschalocarpum	10
	Macrocystis pyrifera	100
	Ecklonia radiata	40
	Halopteris spicigera	35
	Glossophora kunthii	40
	Microzonia velutina	30
	Desmarestia firma	15
	Colpomenia sinuosa	15

in from greater depths is the main source of food of both species of Haliotis.

2.3.2 Taylors Mistake.

The percentage occurrences of algae in guts are listed in Table 2.4. Macrocystis so dominated the gut contents of all H. iris examined from Taylors Mistake that a detailed assessment of relative abundances of species was not warranted. Euptilota, which also occurred in all guts, was never abundant. The very different diet from this locality when compared with that from Kaikoura reflects the different floras of the two areas.

The flora at Taylors Mistake was restricted both in abundance and in the number of species. Macrocystis was the dominant species, its fronds floating on the water surface at low tide formed a fringe extending about 10m from the shore. All other species occupied a narrow mat just below low water level, well above the abalone colonies. Ecklonia radiata, Glossophora kunthii and Carpophyllum maschalocarpum dominated this zone but Scytosiphon lomentaria, Corallina officinalis, Jania rubens, Halopteris spicigera, Microzonia velutina, Colpomenia sinuosa and Polysiphonia sp. were also present. The only drift algae present were derived from these species.

2.3.3 Selection experiments.

The results (Fig. 2.2) illustrate several features of the feeding behaviour of the two Haliotis species. To test statistically for selection two null hypotheses are possible: (1) the weights of algae eaten are in the same ratio as the weights of algae given, and (2) the numbers of pieces of algae eaten are in the same ratio as the numbers of pieces given. Both hypotheses assume that abalones feed randomly on the seaweed fragments they encounter, but while the first is biologically more meaningful and assumes that each individual eats of constant weight of alga each night, the second may perhaps be more relevant under the limitations of the experiment.

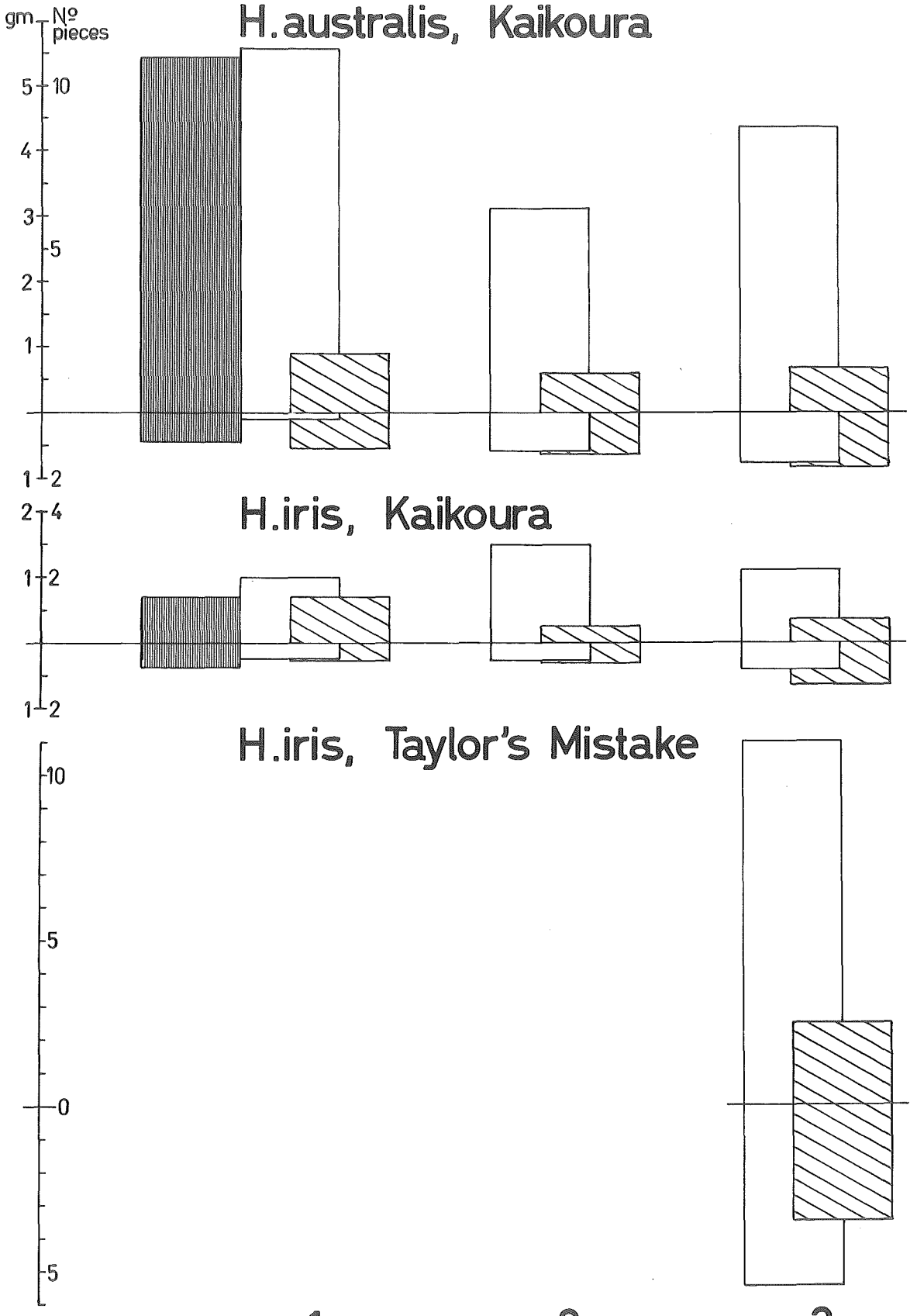

gm
№ pieces
H.australis, Kaikoura
5
10
4
3
5
2
1
1
2
H.iris, Kaikoura
2
4
1
2
1
2
H.iris, Taylor's Mistake
10
5
0
5
Experiment №:
1
2
3

FIGURE 2.2

Results of selection experiments. For each experiment the amount of red algae (Hymenocladia) eaten is shown above the axis, and the amount of brown alga (Lessonia in Nos. 1 & 2, Macrocystis in No. 3) below the axis. The weight eaten (close vertical hatching in Exp. No. 1), the number of whole pieces eaten (plain), and the number of part pieces eaten (diagonal hatching) are mean values for three individuals per trial.

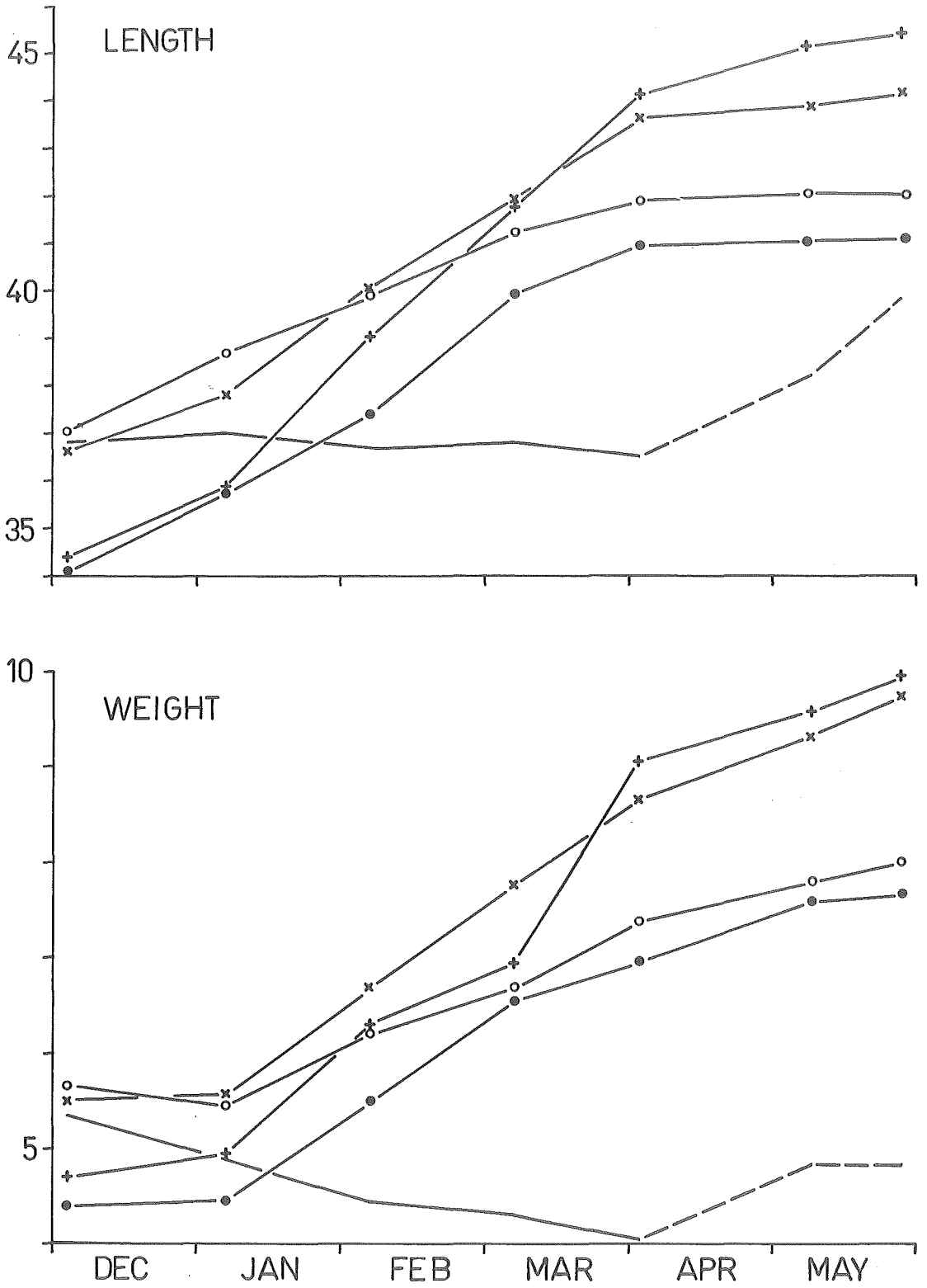

LENGTH
45
40
35
WEIGHT
10
5
DEC
JAN
FEB
MAR
APR
MAY

FIGURE 2.3

Growth rate of experimental H. iris under restricted diets. Mean lengths and weights of two groups on a diet of Hymenocladia are represented by crosses, those of two groups on a diet of Lessonia, by circles. Unmarked line represents mean size of a starved group, dashed after a number died. (Units are mm and gm).

FIGURE 2.4

The effect of starvation on *H. iris*. The one on the left was fed for 6 months on *Hymenocladia* in the laboratory and the other starved for 6 months. (Twice life size.) Photo: B. M. Dukes.

FIGURE 2.5

The influence of diet on shell colour of juvenile H. iris. (a) Bottom row, shells from abalones starved for six months. (b) Middle row, shells from abalones fed for six months on Hymenocladia, showing normal coloration of added shell. (c) Top row, shells from abalones fed for six months on Lessonia, showing the blue-green colour of added shell. (Life size.)

Photo: D. Simms.

Chi-square tests on the frequencies of pieces eaten (expected frequencies based on the weights given and the mean weights of individual pieces) gave significant differences from both null hypotheses in all experiments. There was however considerable variability between individual runs of the same experiment.

Significantly more Hymenocladia is eaten than either Lessonia or Macrocystis. Both species are therefore able to select, H. australis being the more selective. Although H. iris from Taylors Mistake had never before encountered Hymenocladia it preferred this species to its usual diet.

There is evidence suggesting that animals find brown seaweeds distasteful compared with reds. In all experiments using Kaikoura animals the number of fragments of red algae partially eaten and then discarded is small compared with the number completely eaten. The number of brown pieces discarded is always greater than the number eaten completely. Taylors Mistake H. iris, more accustomed to Macrocystis, do not reject this species as often as their Kaikoura counterparts.

H. australis is a much more active feeder in the laboratory than is H. iris, but H. iris from Taylors Mistake ate much more than the same species from Kaikoura.

2.3.4 Restricted diet experiment.

Growth rates. Abalones fed on Hymenocladia grew both in length and weight faster than those fed on Lessonia; results for two runs of the same diets are consistent (Fig. 2.3). The abalones starved showed no change in mean length but some individuals lost up to 25% of total weight before dying (Fig. 2.4).

Natural populations of H. iris grow on the average from 35mm (at age 18 months) to 50mm in six months (Chapt. 4), i.e. faster than the average recorded from either group in this experiment. The maximum growth rate of experimental H. iris feeding on Hymenocladia, between January and April, does come close to the natural rate.

The sharp increase in mean length and weight of the starved group in later months is due to the death of smaller individuals before larger ones. The numbers surviving while starved are as follows: 14 from December to February, 13 to March, 11 to April, 9 to May 8, and 5 to May 27. Six months seems to be close to the maximum survival period of H. iris of this size. Only one died in the other four tanks, one week after the start of the experiment. The mean percentage body weight of those surviving on May 27 was 58% in tank 1 and about 66% in all others - no significant difference was evident between diets. Up to 32% of body weight (excluding shell) can be lost before death occurs.

Shell colour. Fig. 2.5 illustrates the colour of new shell added by young H. iris in the experiments. Additional shell of abalones fed on Hymenocladia is indistinguishable from original shell; its colour is a dark mixture of red, orange, yellow and green, over all a dark brown. Shell added by animals feeding on Lessonia is an icy-blue to pale green colour. In the red-diet animals there is a tendency for existing shell to influence the colour of shell being laid down, i.e. longitudinal stripes persist in new shell and in very pale shells the added shell is a similar pale colour, even white in some. Some particular regions of the mantle edge lay down shell of a particular colour and there seems to be some genetic mechanism, besides the purely dietary one, determining shell colour. These influences were not obvious in the Lessonia-diet animals, probably because the particular array of pigments was inadequate.

The natural colour of the red-diet specimens suggests that red algae are the usual food of small H. iris as well as of adults.

2.4 Discussion

The data enable two comparisons to be made: (1) the diets of a single species (H. iris) may be compared from two widely differing localities, and (2) the diets of two species from a single locality may be compared. Knowing the floras of the two localities and the

preferences exhibited in experimental conditions it is possible to evaluate the influences of (a) local flora, and (b) specific preferences on diet.

H. iris has markedly different diets at the two localities, Wakatu Point and Taylors Mistake. In each case diet is limited first by the seaweed available. At Wakatu Point the abundant flora includes both growing and drift weed. In the collecting area H. iris are found on the flat boulder bottom or on low rock ridges and in such positions are almost continuously being supplied with drift weed. Consequently little movement is necessary to obtain adequate food. Both in the field (Chapt. 3) and in the laboratory movement of Kaikoura H. iris was only occasional. This means that they are poorly adapted to the relatively static conditions of the tanks and did not feed as much as the more active H. australis. At Taylors Mistake food supply is limiting and does not support such a rapid growth rate as Kaikoura. There is virtually no drift weed and the growing seaweed can be obtained only by active movement. No movement has been seen during the daytime, but at night H. iris from Taylors Mistake were more active in the laboratory than the same species from Kaikoura and were therefore able to obtain more food in the experiments (Fig. 2.3). Also, animals which were starved in the laboratory became more active at night than those which were regularly fed.

Although H. iris from both localities could select food in the laboratory when a choice was offered their ability to select in the field is limited by what is available. Kaikoura H. iris prefer red algae and get sufficient of this to make up about 80% of their diet. But at Taylors Mistake none is available and Macrocystis is eaten. At both localities the abundant Carpophyllum seems to be avoided. A few H. australis were found at Taylors Mistake and these too had mainly Macrocystis in their guts.

Examination of guts of both species from other localities around the Kaikoura Peninsula suggests that finer local differences occur.

H. iris collected from steep faces on Avoca Point contained a far greater proportion of Lessonia than those already discussed. On one occasion many individuals collected from the walls or a large cavern after a very rough sea were feeding on fragments of algae trapped under their feet. Various species were represented including Lessonia, Marginariella, Caulerpa and Desmarestia. Brown algae were growing only at some distance from the cavern so the importance of drift weed in the diet of these animals was emphasised.

A sample of twenty H. iris guts collected from sheltered Third Bay after a period of calm weather averaged 69% Lessonia and no flat red algae. Twenty H. australis collected at the same time averaged 51% Lessonia and 32% Pterocladia; there were no flat reds. Drift weed is not likely to accumulate to the same extent in this sort of habitat. Tunbridge (1967) studied the feeding habit of small H. iris in three localities at Wellington; diet varied with area, various browns and reds being eaten. Apart from avoidance of Corallina, except in one area where little else was offering, there was no evidence of selection; the relative proportions of algae in the guts and in the flora were very similar. Sinclair (1963) found mostly brown algae in large H. iris from Wellington, though reds were common in smaller specimens. In the same area R.M. Cassie (pers.comm.; Morton & Miller, 1968: 591) has observed both H. iris and H. australis moving at night, the latter up a tall Ecklonia plant which forms the major part of the diet in this particular locality. It is interesting to note the preference for Hymenocladia exhibited by H. iris collected outside the ecological range of this species. Leighton (1966) showed that Haliotis in California preferred some algal species which they did not encounter naturally.

Although H. iris and H. australis from Kaikoura have similar diets, their methods of feeding differ. Both in the laboratory and in the field H. australis is a much more active animal. Even during daylight H. australis is often seen moving about browsing on both growing and drift weed. Their usual habitat is in crevices in the rock or under large stones where they erode conspicuous shallow

depressions. Since little food finds its way into such places H. australis must be a more active feeder; it is also more active in the laboratory and consequently ate much more in the experiments than did H. iris.

Greater mobility is associated with greater selectivity both in the experiments and in the field. This is reflected in the average numbers of algal species per individual gut, 2.8 (s.d. = 2.1) for H. australis and 4.8 (s.d. = 2.2) for H. iris.

Some criticism has been levelled at gut analysis as a method of determining diet in herbivores (Leighton, 1966). The most commonly eaten foods of Californian abalones, Nereocystis and Macrocystis, are evident in their guts only as a brown algal chyme (Leighton & Boolootian, 1963). At Taylors Mistake Macrocystis is also present in gut samples as partially digested fluid but here no other alga is available in quantity. Red algal fragments are rarely unrecognisable in Kaikoura guts and partly digested brown algal chyme is infrequent.

Seasonal trends in feeding behaviour have been reported in two Japanese species of abalone, H. gigantea (Ino, 1943) and H. discus hannai (Ino, 1952). In both cases maximum feeding is associated with the winter period of gonad maturation as is the case with H. iris and H. australis. There is no reduction in feeding associated with the spring spawning of H. australis but the seasonal trends are less marked in this species (Fig. 2.1). Newman (pers.comm.) found "no apparent variation" in "settled volumes of gut contents" of H. midae in South Africa. Although no seasonal changes in the amount of algae eaten are reported for H. rufescens, Olsen (1968) has shown seasonal trends in diet associated with yearly cycles of Nereocystis and red algal epiphytes in California. A similar alternation of red and brown species occurs in the diet of H. discus hannai (Sakai, 1960).

Brown seaweeds predominate in the diets of most other abalones studied: H. cracherodii (Leighton & Boolootian, 1963), H.kamatschatkana (G.A. Robilliard, pers.comm.), H. rufescens, H. fulgens, H.

corrugata (Cox, 1962; Leighton, 1966), H. midae (Newman, 1968), H. gigantea (Ueda & Okada, 1939; Ino, 1943), and H. discus hannai (Ino, 1952; Sakai, 1962a). In most cases alternative diets are known. Although the diets of some populations of H. iris and H. australis from Kaikoura differ considerably from those of most other haliotids, those from other localities are more typical of the genus.

Several species of Haliotis have been shown experimentally to select their diet. Leighton (1966) demonstrated that, in three species of California abalone, there was a distinct preference for brown algae, in particular Macrocystis and Egraria. The only red alga tested, Gigartina armata, had a low preference value. Macrocystis is the major component of the diet of all three. A fourth species (H. cracherodii) preferred Egraria most and Gigartina next; Macrocystis rated low (Leighton & Boolootian, 1963). In Japan H. discus hannai has been shown to prefer the brown Undaria to red or green algae (Sakai, 1962a). No species documented shows the same preference for red algae demonstrated by the two New Zealand species in the experiments described.

Although food preference must play a part in determining what is eaten in the field it might not be a major one. It assumes that there is a surplus of food and that the animal actually has a choice. The more motile H. australis probably does choose but H. iris, which sits and waits for its food, may be forced to eat whatever happens to drift to it. In the case of the latter species where selection was only just significant the experimental results may indicate greater selectivity than occurs naturally. Lessonia is a much tougher species than Hymenocladia and may have been avoided for this reason; however, it does seem to be readily eaten in the field. Macrocystis, which was also avoided, was no tougher than Hymenocladia. Although brown weeds decayed much quicker in the laboratory than did Hymenocladia, this difference was minimal in the duration of the experiment. It can be concluded however, that selection is less important in determining the diet of H. iris than of H. australis.

It has been shown that in the laboratory under conditions of

equal availability H. iris grows faster when feeding on Hymenocladia than when feeding on Lessonia. While it is possible that the red alga may have a higher calorific value than the brown, further experiments will have to be carried out to estimate the weights of algae eaten and the efficiency with which they are assimilated. It is possible that more Hymenocladia was eaten than Lessonia because it is preferred and growth was faster simply for this reason. Several factors, including calorific value, palatability and availability, of the plant species influence any choice made by the herbivore, but it does seem likely that any selective behaviour on the part of the herbivore will have evolved to give the greatest energy return for the least effort, taking all these factors into account. In the laboratory at least, where the two species were equally available, Hymenocladia gave greater return, as measured by growth rate, for the same effort than Lessonia. This begins to explain why red algae (if it is possible to generalise from one species) are preferred in the field. Paine (in press) discusses calorific values of seaweeds in more detail. The two species of Haliotis have tackled this problem in different ways. While in H. iris, at Kaikoura on the one hand, selection is suppressed in favour of passive feeding on a variety of drift weeds, H. australis on the other is more selective only by being more active.

Similar experiments have been carried out with H. discus hannai where it was found that brown algae (Eisenia, Undaria) are more efficiently assimilated and promote greater growth than red algae (Pachymenia, Gelidium) (Ino, 1952; Sakai, 1962a). Although these results are the opposite to what was found with H. iris it is the preferred species that give the greatest growth in both cases. In H. cracherodii most brown algae and the red Gigartina are "effective weight producers" (Leighton & Boolootian, 1963).

The long period of starvation and high percentage weight loss of the small H. iris contrasts with some H. cracherodii starved by Leighton & Boolootian (1963) which survived only two to three months and lost between 12% and 24% weight. Thin H. iris have never been

encountered in the field at Kaikoura but MacGinitie & MacGinitie (1966) record some thin starved abalones in an area in California where freshwater had killed all the algae. The ability to withstand periods without food may be necessary if H. iris is to rely mainly on drift algae for food since this in turn relies on sea conditions.

The effect of diet on shell colour has been documented for a number of Haliotis species: H. rufescens (Leighton, 1961; Olsen, 1968); H. discus hannai (Ino, 1952; Sakai, 1962a, b); H. sieboldii and H. gigantea (Ino, 1952). In general red algae promote growth of dark-red or brown shell and brown algae, except Macrocystis, promote light blue-green shell. In the Californian species dull red-brown shell is deposited on a diet of Macrocystis; at Taylors Mistake H. iris is similar. Shells of H. australis are consistently white except for some pink tinges in small specimens; diet seems to have little effect on shell colour in this species. Comfort (1951) reviewed work done on the chemistry of pigments in Haliotis shells and concluded that shell pigments are mostly metabolic wastes.

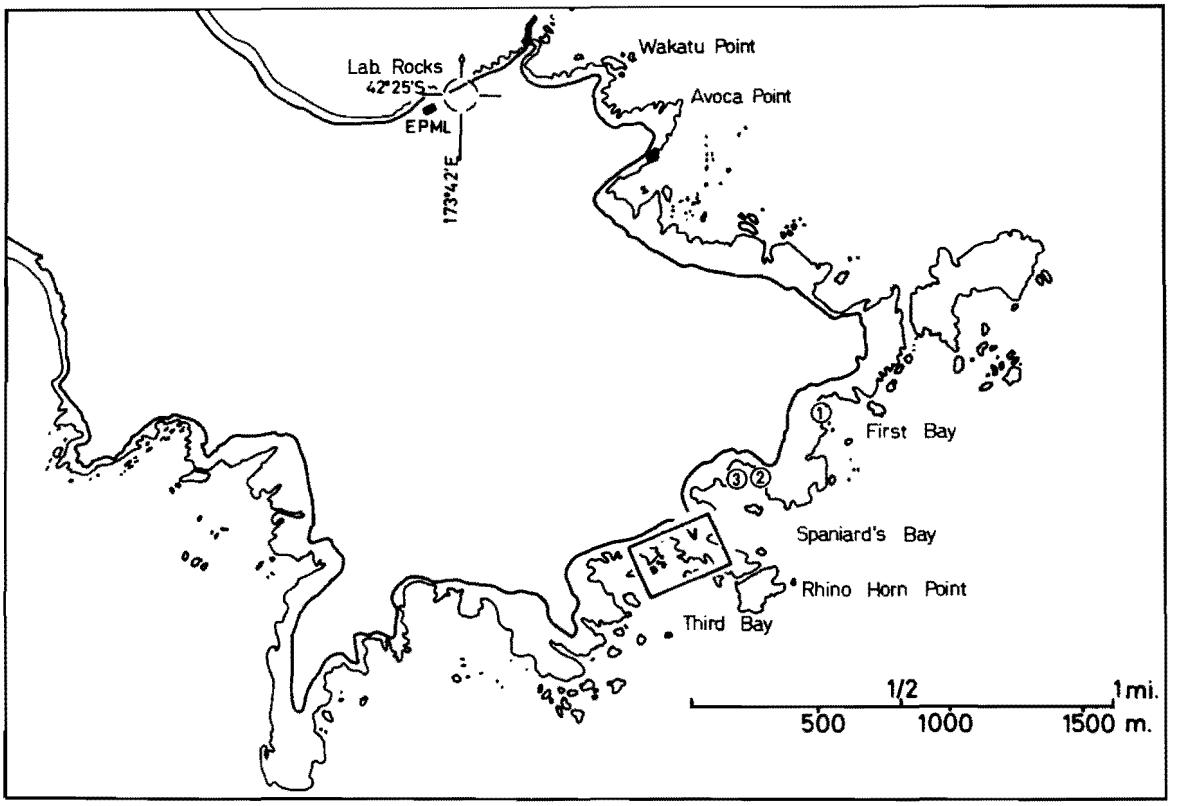

Lab. Rocks
42°25'S
EPML
173°4.2'E
Wakatu Point
Avoca Point
1
First Bay
3
2
Spaniard's Bay
Rhino Horn Point
Third Bay
1/2
1 mi.
500
1000
1500 m.

FIGURE 3.1

Kaikoura Peninsula showing the positions of the low water colonies Nos. 1-3, and the area shown in Figure 3.2.

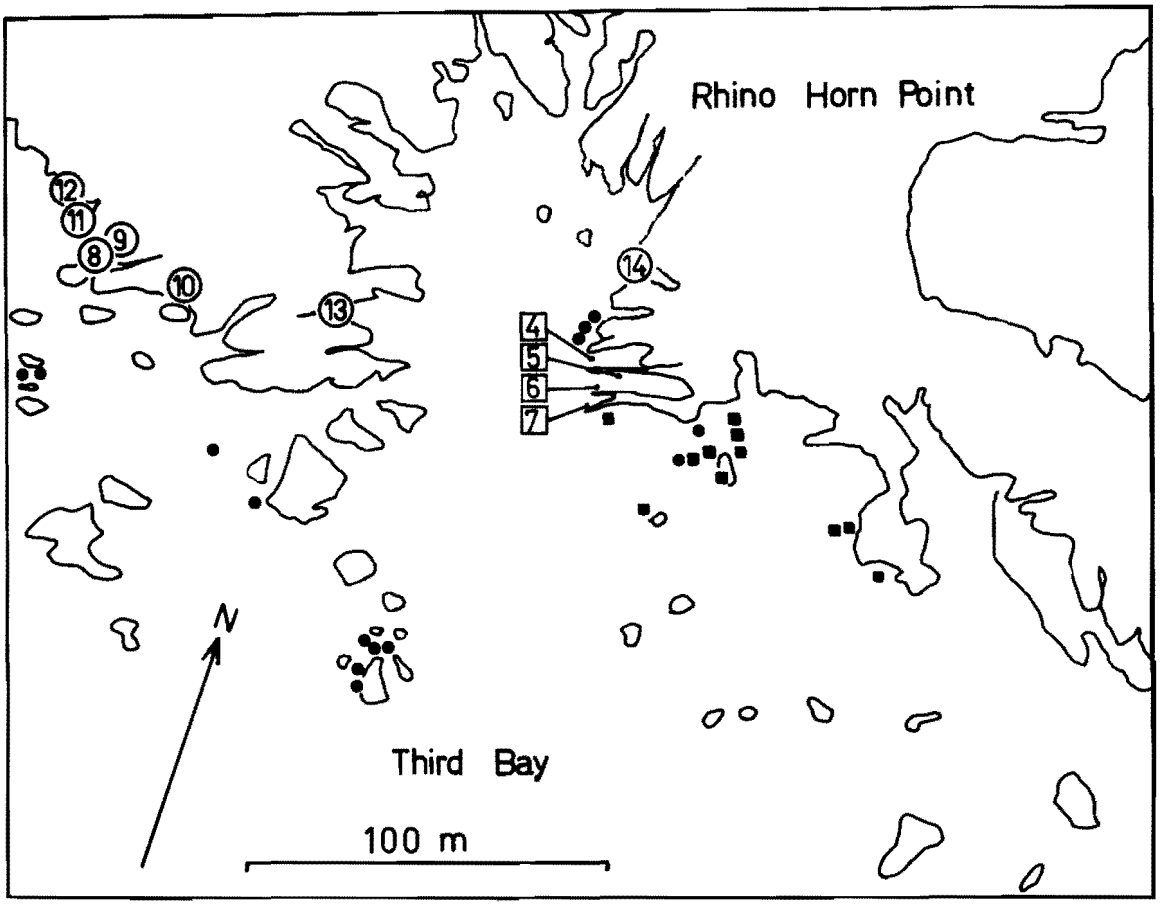

Rhino Horn Point
12
11
9
8
10
13
14
4
5
6
7
N
Third Bay
100 m

FIGURE 3.2

Map of Third Bay showing the positions of low water colonies (in circles) and subtidal colonies (in squares). Recoveries of H. iris in November 1968 beyond the tagging areas are shown by corresponding symbols (small circles and squares).

3. MOVEMENT

3.1 Long-term movement in H. iris and H. australis.

3.1.1 Introduction.

Although abalones are commercially important species very little research has been done on dispersal rates in their adult populations. Information on this subject would aid in assessing the rates of repopulation of areas following exploitation. This section, which follows a detailed study by Newman (1966) on H. midae, is concerned with two species, only one of which is of commercial interest.

The tagging program which forms the basis of the results discussed in this section was undertaken for two purposes: the first was to estimate movement in H. iris and H. australis and the second was to obtain information on growth rates of the two species. While the requirements of each study can be met by a single tagging program it does to some extent compromise both. For example, fewer adult H. iris were sampled than would have been representative because these give little information on growth rate, and the necessity for individual marking and remeasuring at frequent intervals disturbs the population more than would be required in a purely movement study. The limitations of the results arising from these points are discussed.

3.1.2 Methods.

Colonies of Haliotis were chosen in three bays on the south-eastern coast of the Kaikoura Peninsula as far away from human interference as possible (Figs. 3.1 & 3.2). Two types of colony were defined, "low water" and "subtidal", on their depth and on the way in which each was investigated. The low water colonies were recognised as the undersides of large stones or ledges just above or below extreme low water level and contained small to average sized H. iris

(Fig. 4.1). They were accessible during spring low tides though only Nos 3, 9, 11 & 12 were regularly exposed to air. SCUBA was used during collection at subtidal colonies. No. 4 was a colony of large H. iris covering the floor and sides of a small inlet with some H. australis in crevices nearby. Nos 5, 6, & 7 were systems of crevices containing mostly H. australis. The four colonies were close together in three inlets, none more than 2m deep (Fig. 3.2).

The tags used were 17 x 8mm oval, yellow plastic discs with stamped three-digit numbers, manufactured by Spinwell Products, Timaru (Size No.3). They were attached by soft 23-gauge stainless steel wire through two respiratory pores near the front of the shell so they could move freely (Fig. 3.3). A T-headed spagetti tag (Floy Tag FD-67), inserted through a single respiratory pore, was used on 27 H. iris at colony No. 8 but it was inclined to wear and be lost.

At low water colonies animals were simply removed from the rock one by one with a lever, tagged, measured, and replaced where found. But at subtidal colonies large numbers of animals were collected at once in a sack, taken to the surface, tagged, measured, and replaced as a group in the same general area. The abalones' attachment to the substrate was watched after replacement to ensure that none was washed away by waves.

Initial tagging of abalones was carried out in late October and November 1967. Successive three-month intervals from this time coincide with the generally accepted limits of the four seasons. A supplementary tagging program was carried out in May 1968 after very severe storms in April dispersed most of the low water colonies. On December 17, 1967 and January 7-9, 1968, between four and eight weeks after the initial tagging dates, the colonies were re-examined to assess the immediate effects of tagging. Tag numbers of all animals present were noted with a minimum of handling. At three-month intervals after initial tagging, i.e. in February, May, August and November 1968, all tagged animals were collected from the tagging sites and remeasured. The number of untagged animals which had

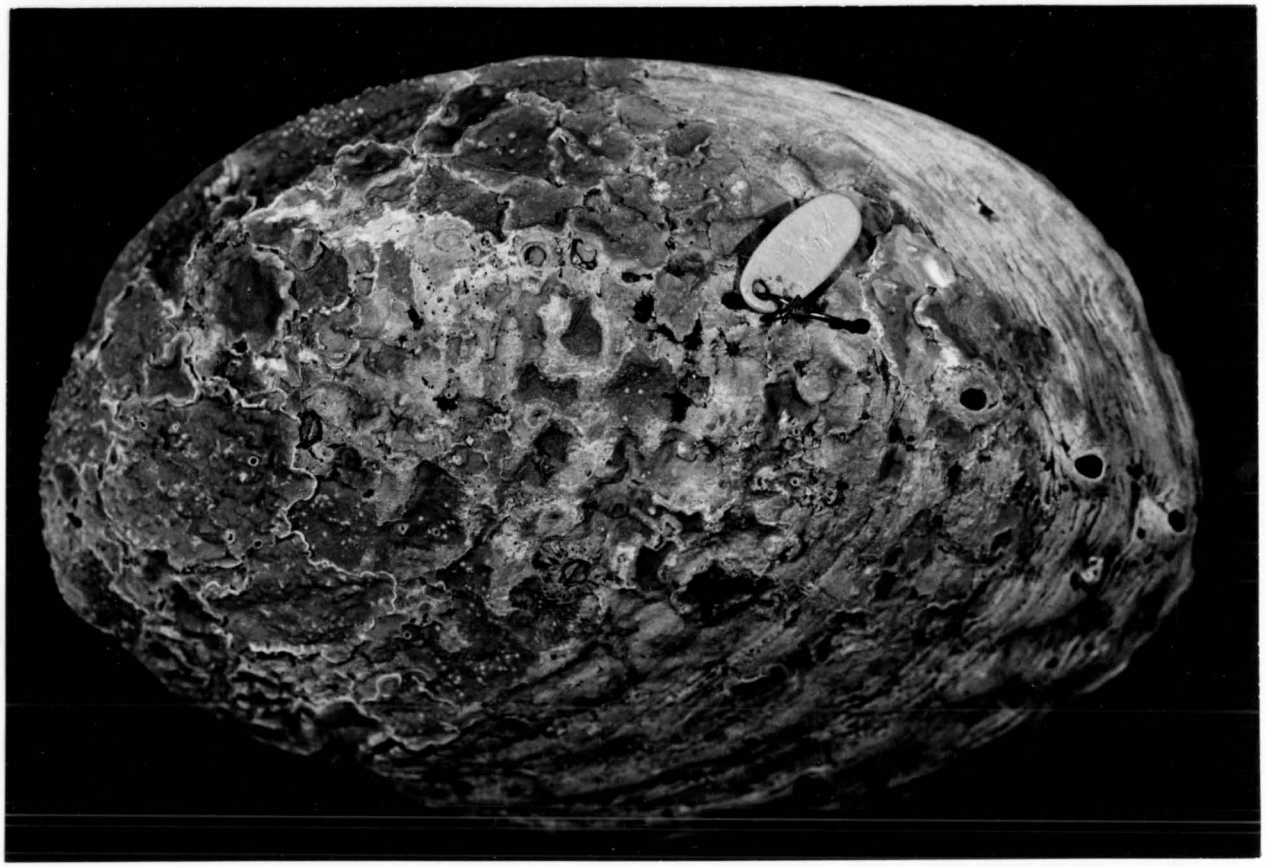


FIGURE 3.3

A tagged *H. iris*, 121 mm long. (1.3 x)

appeared was noted. Only on the last collection, one year after tagging, was an extensive search made in the areas surrounding the two major groups of colonies in Third Bay. The uneven sea bottom made systematic searching of the area with SCUBA difficult so the area was divided into several sections and each was searched by one diver. The position of abalones found was plotted on a map. The author and one other diver spent seven man hours in Third Bay in November 1968, mostly in 1-3m of water but also searching down to 10m where colonies were found at this depth.

3.1.3 Results.

The tags used were found to be suitable for abalones of a wide range of sizes; no evidence suggested interference with the animals' usual behaviour. As the shell grew the wire became smoothly covered with nacre and showed no sign of irritation. In H. australis in particular a high tag loss could be attributed to abrasion of the tag on rock in crevices or under stones. Tags attached to the shell with epoxy glues have been used by other workers (Forster, 1967; Tutschulte, 1968) on other species of Haliotis but did not prove suitable in either of the two species studied here. The high degree of infestation with boring polychaetes and barnacles and the outer coating of 'Lithothamnion' made the shell very porous and fragile, precluding a secure surface for attachment.

a. H. iris.

Tag recovery rates differ for low water and subtidal colonies (Tables 3.1 & 3.2). The final November collection includes recoveries at the tagging sites and beyond these areas. Others accounted for include animals recovered with wire only, dead tagged animals, and loose tags found.

Low water colonies. The return rate at tagging sites was high in the first examination (Table 3.1). This is especially true at

TABLE 3.1 Numbers of *H. iris* tagged and recovered at ten Low Water colonies.

Colony No.	No. tagged	No. recovered			No. tagged	No. recovered			No. others accounted for
	NOV '67	DEC-JAN	FEB	MAY	MAY '68	AUG	NOV. within area	NOV. beyond area	
1	8	6	0						1
2	28	8	0						1
3	18	16	13	0		1	0	0	1
8	43	22	6	4	22	11	5	3	5
9	40	33	26	11					2
10	49	47	40	5	8	2	1	3	1
11					16	8	9	2	0
12					5	0	0	0	0
13					22	0	0	2	0
14					13	3	0	5	0
TOTAL	186	132	85	20	86	25	15	15	11
No. recovered as percentage of recovery at previous survey		70.9	64.4	23.5	-	23.6	60.0	-	-
Percentage recovered of total tagged to date		70.9	45.7	10.8	-	9.2	5.5	5.5	4.0
							11.0		

colony Nos 3 and 10 but not so at No. 2 where there may have been interference. Lower returns at No. 8 is due at least in part to the unsuitable tags used. It seemed from this early examination that the tagging operation did not induce much movement from the colonies. A similar rate of dispersal from the colonies was recorded in February after a similar period. Only three individuals were found which had been overlooked the first time. Several untagged abalones were observed at all colonies; the greatest number was at colony No. 8 and could be explained in part by the high tag loss. Most other untagged abalones were small, their lengths not being referable to those of previously tagged abalones. Colony Nos 3 and 4 both suffered human interference.

After a series of very violent storms in April most low water colonies disappeared, i.e. the young H. iris dispersed or a few may have died. The recovery rate in May was thus drastically reduced. Stones sheltering colonies Nos 3 and 10 were overturned and the abalones had gone; they had also disappeared altogether from No. 9 though a few were found in No. 8, about 2m away. Untagged animals which had moved into the two least affected colonies, Nos 8 and 10, were tagged along with those from newly formed colonies 11, 12, 13 and 14.

Recovery rate was low in August indicating that during the winter of 1968 many abalones left the tagging sites. Three of the four new colonies disappeared during this period. More non-tagged H. iris appeared at colony Nos 8 and 11. One notable recovery was the return of a single H. iris to No. 3 after nine months absence. This suggests that movement away from the colonies is not extensive. The first half of Table 3.3 gives the frequencies of single and multiple recoveries from low water colonies, almost 80% of tagged H. iris at liberty 12 months were recaptured at least once and most of these twice.

In the final inspection a higher proportion of tagged individuals remained on the tagging sites than had done so during the two previous three-month periods. The incidence of movement seems then to vary

TABLE 3.2 Numbers of *H. iris* tagged and recovered at four Subtidal colonies.

Colony No.	No. tagged	No. recovered			No. tagged	No. recovered			No. others accounted for
	NOV '67	DEC-JAN	FEB	MAY	MAY '68	AUG	NOV within area	NOV beyond area	
4	101	58	41	19	9	4	5	9	12
5					20	7	3	2	0
6					8	4	3	1	0
7					1	0	0	0	0
TOTAL	101	58	41	19	38	15	11	12	12
No. recovered as percentage of recovery at previous survey		57.4	70.7	46.3	-	26.3	73.3	-	-
Percentage recovered of total tagged to date		57.4	40.6	18.8	-	10.8	7.9	8.6	8.6
							16.5		

seasonally at low water colonies, being greatest during autumn and winter. Rough weather may be responsible for most movement; it is known to have caused dispersal in April. During more extensive searches in Third Bay an additional 15 tagged H. iris from low water colonies were found (Fig. 3.2). Three of these were last recorded nine months previously, 10 six months, and 2 three months previously. This reflects the disturbance of colonies in April and the subsequent tag replacement. All recoveries were made in established H. iris colonies.

Subtidal colonies. The pattern of tag returns at subtidal colonies differs in several ways from that of low water colonies (Table 3.2). Poor water visibility at times, the physical difficulty of working in shallow surging water, and the dense algal cover made underwater searching for tagged animals less reliable than that in low water colonies. No extensive searches beyond the tagging sites were made except in the final survey.

No clear seasonal trend was evident in this group of colonies, although there was a marked drop in recovery rate in August after the winter. The recovery rate after 12 months was higher possibly because wave action, which upset stones sheltering some low water colonies, had less effect on colonies attached to solid substrates in deeper water.

Handling for remeasuring induced most movement at subtidal colonies since it involved longer periods out of the water and the animals could not be returned to their original positions. This was evident first in the low recovery rate during the first survey. Second, the higher recovery rate in February after the same length of time reflected the lack of interference during January when the animals were not handled. The first two recovery rates were similar at low water colonies where the effect of handling was negligible. It is probable therefore that most dispersal from subtidal colonies occurred immediately after the abalones are replaced into the water.

The disruptive effect of repeated handling of subtidal abalones

becomes clearer when colony No. 4 is compared with other untagged colonies in the same area. Several nearby colonies watched for over two years remained apparently unchanged. One in a deep crevice contained 29 large individuals every time they were counted. Its members were almost free of the coralline alga 'Lithothamnion' and clearly distinct from those of a colony of several hundred a few metres away. The larger colony was exposed to the light and all were covered with 'Lithothamnion'. Individuals in most colonies of H. iris are generally morphologically uniform, those in crevice colonies are relatively free of 'Lithothamnion' compared with those in more exposed positions. The adult size of some of these "clean" shells suggests that they never moved from the crevice, at least in daylight. Several other small groups of H. iris of between three and ten individuals were observed apparently unchanged over periods of three and six months. Little natural interchange between established colonies is suspected.

A wider search in November revealed a few of those abalones which had moved from the tagging areas (Fig. 3.2). All 12 sighted were in established colonies of untagged animals, the farthest being 150m from the tagging site. Seven of these had not been seen for 12 months. Table 3.3 shows that a high proportion of animals were recovered more than once. Only two individuals moved between the two groups of tagged H. iris colonies (Fig. 3.2), one went from No. 9 to No. 6 in nine months and the empty shell of another from No. 4 was found near No. 8 after 12 months. The two areas are separated by a broken peninsula.

b. H. australis.

No information is available on the movement of juvenile H. australis, they are rarely found intertidally as are small H. iris and the few that are seen subtidally are deep in crevices or under stones. Animals tagged ranged from 54mm to 101mm (Fig. 4.1).

TABLE 3.4 Numbers of H. australis tagged and recovered at four Subtidal colonies.

Colony No.	No. tagged	No. recovered			No. tagged	No. recovered		No. others accounted for
	NOV '67	DEC-JAN	FEB	MAY	MAY '68	AUG	NOV	
4	19	13	10	7	7	8	4	1
5	33	19	17	10	7	11	10	3
6	30	21	16	11	11	15	13	5
7	14	6	8	3	7	4	4	1
TOTAL	96	59	51	31	32	38	31	10
No. recovered as percentage of recovery at previous survey		61.5	86.5	60.8	-	60.3	81.5	-
Percentage recovered of total tagged to date		61.5	53.2	32.3	-	29.6	24.2	7.8

TABLE 3.3. H. iris. Frequencies of numbers of times recovered.

No. times recovered	LOW WATER		SUBTIDAL	
	12 months at liberty	6 months at liberty	12 months at liberty	6 months at liberty
1	46	18	27	9
2	71	10	22	7
3	13	-	18	-
4	4	-	1	-
5	3	-	0	-
TOTAL	135	28	68	16
Others accounted for	11	0	12	0
TOTAL TAGGED	186	86	101	38
Percent found at least once	72.6	32.6	67.4	42.1
Percent others accounted for	5.9	0	11.9	0

The recovery rates for each survey during the 12 month period studied were all higher than the equivalent rates for either low water or subtidal H. iris (Table 3.4). They also differed in that there was no clear seasonal trend in the pattern of recovery rates. Although there were several small H. australis colonies nearby no tagged abalones ever moved into them. Of the 209 individual recoveries made at the four colonies on five occasions, only 14 (6.7%) were not at the colony where they were liberated (Table 3.5). Most interchange was between colony Nos 5 and 6 which were in the same inlet. More than 70% of H. australis at liberty for one year were recaptured at least once and a further 10% were otherwise accounted for (Table 3.6); a high proportion were multiple recaptures.

TABLE 3.5 Frequencies of recoveries of H. australis at and beyond the colony at which they were liberated.

		Colony at which recovered three months later			
		4	5	6	7
Colony No. at which liberated	4	39		1	2
	5		58	8	
	6		1	75	
	7			2	23

TABLE 3.6 H. australis. Frequencies of numbers of times recovered.

No. times recovered	12 months at liberty	6 months at liberty
1	12	9
2	25	13
3	17	-
4	8	-
5	6	-
TOTAL	68	22
Others accounted for	10	0
TOTAL TAGGED	96	32
Percent found at least once	70.8	68.8
Percent others accounted for	10.4	0

The evidence from tag returns therefore suggests very little natural movement; that which has been observed could be induced by the handling procedures.

On all occasions several untagged animals were found in the colonies. Tag loss, discussed earlier, could partially explain this, but there was a greater likelihood of overlooking H. australis in the initial search and in later surveys because of their crevice-dwelling habits. Of a total of 209 recoveries 27 (12.9%) had been overlooked during the survey 3 months previously. Most of these were at No. 5, the most diffuse colony.

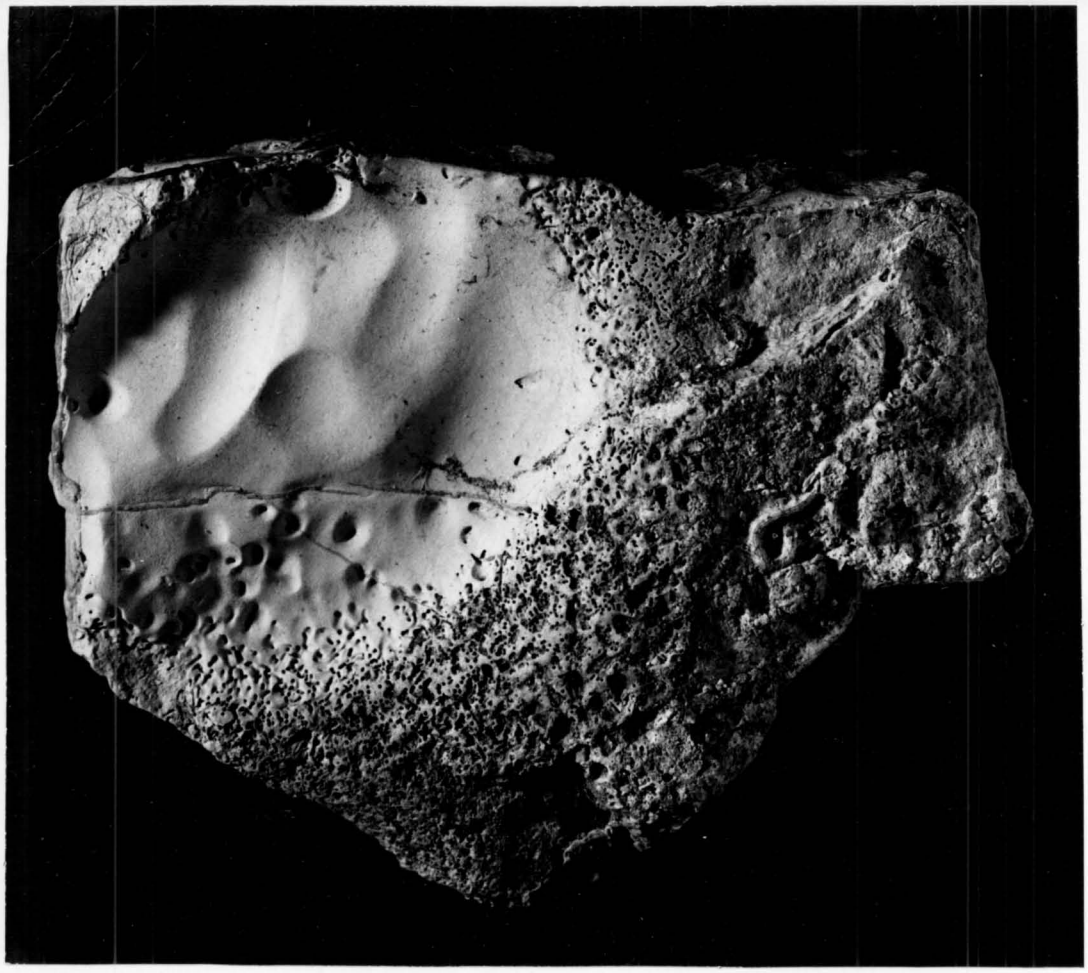
Other evidence also suggests a general lack of natural long-term movement. Older H. australis inhabit deep worn depressions in the rock surface (Fig. 3.4) and often when removed cannot clamp the shell down onto a flat surface. Some have a characteristically worn shell edge which fits the surrounding rock closely (Fig. 3.5).

3.1.4 Discussion.

All conclusions drawn from the data must be qualified to take into account any possible effects of the tagging operation and subsequent handling. Comparison of recovery rates in December - January and in February following, in the first instance, tagging and handling, and in the second, observation without handling, enables some assessment of the effect of handling to be made. As has already been pointed out, the effect of handling at low water colonies is slight while that at subtidal colonies is considerable and masks any natural movement.

Nevertheless, several conclusions can be drawn:

(1) Movement of juvenile H. iris in colonies near low water was clearly seasonal, being greatest in the autumn and winter when rough weather disturbed the habitat. This result may not be typical for the habitat in other years since rough seas may occur in all seasons at Kaikoura. The storm of April 1968 was the most severe recorded in New Zealand for a number of years and its effect on the



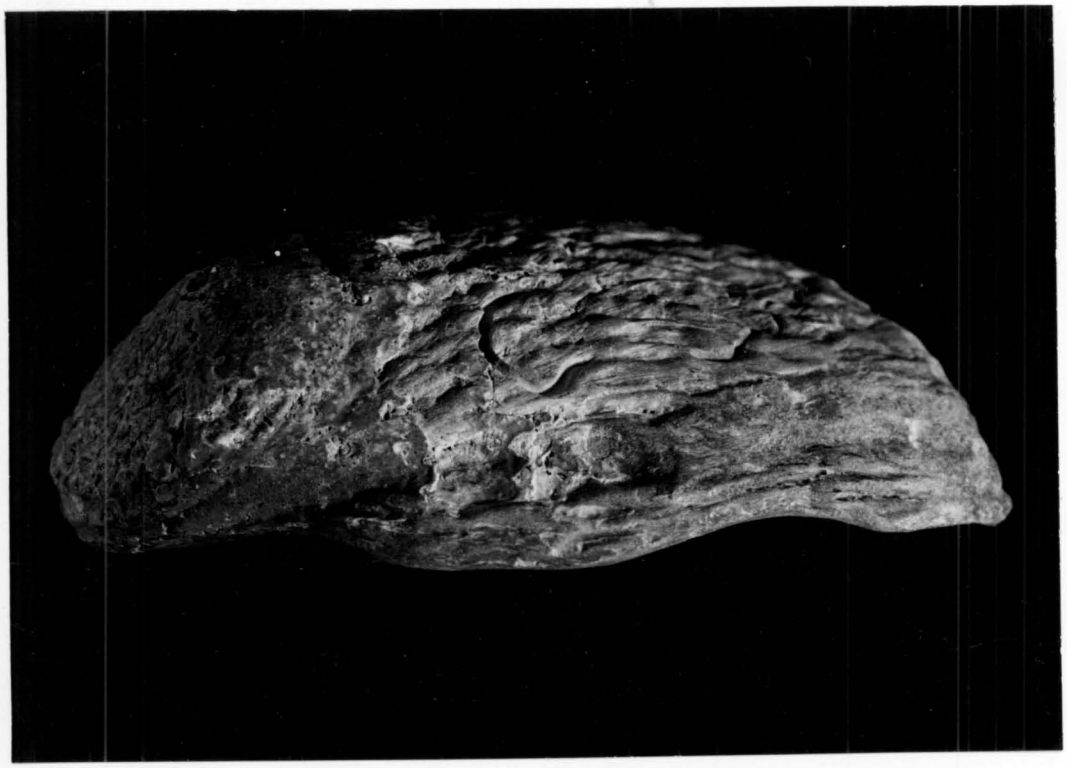


FIGURE 3.4

Area of limestone taken from a crevice at Kaikoura showing a conspicuous H. australis 'scar'. ($1\frac{1}{4}$ x)

FIGURE 3.5

H. australis shell with worn edge to fit rock surface of its home site. ($1\frac{3}{4}$ x)

intertidal habitat was devastating. Dispersal was sudden rather than gradual and may never have occurred if more usual weather had prevailed.

(2) Assessment of the importance of the tag returns for H. iris at subtidal colonies must be made in the light of other observations on non-tagged colonies. The permanence of these other colonies and individuals over periods up to two years must be weighted heavily in concluding that natural movement is negligible.

(3) Handling seems to have had less effect on H. australis than on H. iris. Over 30% of tagged animals were recovered at tagging sites or otherwise accounted for after one year. This high figure and the permanence of other colonies indicates negligible movement in this species.

Movement in H. australis has not been previously studied but two authors have mentioned movement in H. iris. Graham (1941) reported that "at Seal Point, Otago, they are abundant from October to March, but spend the winter in deeper water. That they possess a 'homing instinct' in relation to this migration, as they do in their diurnal movements, was ascertained by marking the shells". No other details were given. The present work gives no evidence of homing behaviour - the only movement recorded being out of established colonies into others. None of the colonies which broke up due to natural or observer disturbance reformed while being studied. Sinclair (1963) refuted Graham's statement but gave little evidence for either point of view.

Movement patterns have been studied in a number of other Haliotis species. A few tag returns after six months (Crofts, 1929), a four week tagging program (Brehant, 1958), and a more comprehensive tagging study (Forster, 1967) suggested that movement in H. tuberculata was slight. Cox (1962) tagged a large number of H. rufescens in California and recovered most in the tagging area one year later. Even starvation did not stimulate this species to move in search of

food (MacGinitie & MacGinitie, 1966). H. cracherodii and H. kamatschatkana also move little (Cox, 1960; D.B. Quayle, pers.comm.). Studies commencing in Australia reveal little movement in Notohaliotis ruber (Anon., 1967). H. midae differs in that dispersal over long distances was recorded in a detailed study by Newman (1966); no seasonal variation was noted. Only in H. discus hannai is a definite seasonal migration documented (Ino, 1952). Movement of adults from deeper to shallower water in summer was thought to be correlated with the requirements of spawning. In general most species of the genus are fairly sedentary, H. midae and H. discus hannai being exceptions.

In H. iris there is a clear distinction between the habitats of juveniles and adults. Young H. iris less than 100mm long show a definite photonegative response in the laboratory and occur in crevices and under stones especially on boulder bottoms, while adults are light-insensitive and inhabit more stable and exposed sites. Migration between these two habitats must occur as the animals grow, especially in the case of intertidal juveniles which must move into deeper water as adults. But no size-dependent variation in incidence of dispersal from tagging sites could be shown in H. iris at low water colonies. A χ^2 test was used to compare the length frequency distributions in 10mm size classes (refer Fig. 4.1 for initial lengths) of H. iris tagged and those recovered. Data from subtidal colonies was not included because dispersal here was not natural. Using the null hypothesis "the recovery rate on the tagging sites is the same (70.9%) for all 10mm size classes" $\chi^2 = 3.50$ with 11 d.f., $0.975 < p < 0.990$, indicating a constant recovery rate within the size range tested. No estimate of the natural rate of movement of the largest H. iris (greater than about 110mm) could be made but all available evidence suggests it is negligible. Newman (1966) who found extensive movements in H. midae, studied mainly small to average sized individuals and found a slight tendency for larger animals within this range to move faster than smaller ones. Although the test for H. iris is for incidence rather than rate of movement

a possible difference between these and Newman's results is indicated. The dispersal rate of H. australis is also size-independent (χ^2 = 1.81 with 5 d.f., p = 0.90) within the range 50-100mm but in this case it is mainly the result of unnatural disturbance. Both juveniles and adults of H. australis use the same habitats, narrow subtidal crevices or rarely under stones, so little movement of juveniles would be required.

Assuming all adult niches are full, the rate of migration of H. iris to a different habitat with increasing age will necessarily be determined by the rate at which adult habitats become available. This depends first on the mortality rate of adults and it follows that in a stable unexploited population the slow rate of dispersal of juveniles can maintain the population level. Following exploitation, the very slow growth rate (about 7 years to reach the minimum takable size, 127mm) will probably limit the rate at which an adult population is returned, even given sufficient density of juveniles and adequate dispersal rates. Repopulation by adults from other areas is unlikely on two counts: (1) adults move very little, and (2) few large deep water colonies exist beyond the reach of divers.

3.2 Diurnal movement patterns in H. iris.

3.2.1 Introduction.

Colonies of Haliotis iris and H. australis are known to persist for long periods, at least many months and probably many years and to retain the same composition of individuals (Section 3.1). It has generally been accepted, with this fact in mind, that nocturnal wandering from the colonies is necessary to feed on the surrounding algae. Sinclair (1963) for example, noted the 'scars' left on rock by adult H. iris and postulated a homing mechanism for this species as is well known for limpets and chitons. Graham (1941) also stated that homing behaviour exists in this species at Dunedin but supplied no details of experiments he may have done to demonstrate it.

Reinterpretation of this and other information suggests that, in fact, little movement may be necessary. It has been shown (Chapt. 2) that at Kaikoura both species feed mainly on drifting red algae rather than the browns which are growing nearby. Also, areas surrounding Haliotis colonies (which may contain up to several hundred individuals in a few square metres) seem never, at Kaikoura at least, any more barren of weed than equivalent areas elsewhere. The vegetation surrounding these colonies shows no signs of heavy browsing.

The observations in this study set out to determine the extent of movement of individual H. iris over a 24 hour period. Circumstances, mainly the rare occurrence of perfectly clear diving conditions, did not allow the observations to be repeated for H. australis.

3.2.2 Methods.

At 1500hrs on March 17, 1968, a colony of H. iris was selected in front of the Edward Percival Marine Laboratory at Kaikoura. The colony consisted of 19 adult animals on the tops and sides of four large boulders at a depth of about 2m at low water. The rocks were

TABLE 3.7 *H. iris* diurnal activity. Summary of observations made at eight successive three-hour periods.

	17.iii.68 0900	1200	1500	1800	2100	18.iii.68 2400	0300	0600	0900
No.not moved in period	15	14	15	11	12	17	12	15	
No.moved within colony	2	3	2	6	5	1	5	3	
No.entering					2		1		
No.lost						1	1		
Total observations	17	17	17	17	19	19	19	18	
Percentage of total moved	12	18	12	35	37	11	37	17	

TABLE 3.8 *H. iris* diurnal activity. Comparison of observations made at the end of two similar eighteen-hour periods.

	16.iii. 1500	17.iii. 0900	1500	18.iii.68 0900
No. not moved in period	13		10*	
No. moved within colony	5		6	
No. entering	0		2	
No. lost	2		1	
Total observations	19		19	
Percentage of total moved	37		47	

*includes one animal which is known to have moved and returned.

largely bare but Carpophyllum, Cystophora and corallines grew over them. Fifteen of the animals were tagged without removal from the substrate by inserting a numbered T-headed spagetti tag (Floy Tag FD-67) through one of the uppermost respiratory pores. (The next day the filament was knotted when it was found that there was a tendency for the tag to move out through the mantle cavity.) Only one abalone which moved about 30cm reacted to this treatment. The colony was mapped and the positions of all 19 individuals plotted.

Between 0900hrs March 18 and 0900hrs March 19 the colony was revisited at 3-hourly intervals and the position of all individuals marked on the map. All observations were made using SCUBA and during the night underwater lamps were used.

3.2.3 Results.

During the 42 hour period of observation none of the four untagged animals moved. In that period 10 of the 15 tagged animals moved at least once and three untagged animals entered the colony; only three tagged animals were lost, two of these before 0900hrs March 18. The two early losses may have resulted from tag loss and may account for the appearance of two untagged animals.

Table 3.7 shows the low incidence of movement during daylight and, excepting between 0000 and 0300hrs, two or three times this value during the night, 1800hrs and 0600hrs coincide closely with sunset and sunrise. Separate early and late night periods of movement are suggested. None was seen feeding at any time.

Table 3.8 compares two similar 18 hour periods; there is little difference between the patterns of behaviour during these two periods, although regular visits were made during one interval. The recorded distances moved were in general very small, i.e. within the one metre radius of the colony. However the single animal that was definitely lost moved beyond the area searched, i.e. outside a 5m radius. A single animal which moved about 2m outside the colony in one three hour period returned in the next and is the only example of homing behaviour.

3.2.4 Discussion.

The results, though limited to a single series of observations, suggest that H. iris moves very little, slightly more at night than during the day. Other observations support this. Young H. iris, which during the day are always seen intertidally under stones or ledges, are seen in the same places at low tide at night - they seem not to come out to feed. In the laboratory H. iris from Kaikoura are stationary during the day and move only slightly at night. No evidence suggests a homing behaviour.

The diurnal pattern of movement has implications in feeding behaviour. At Kaikoura H. iris feeds mainly on drift rather than attached weed (Chapt. 2) and are probably required to move very little except when this food is not available. Evidence for this point of view is found in observations on the behaviour of the species in the laboratory. H. iris from Taylors Mistake, which actively feed on growing Macrocystis in the field, are much more active in the laboratory than those from Kaikoura, and a group of small H. iris starved in the laboratory was much more active at night than a comparable group fed regularly. Both observations suggest that hunger is a stimulus for movement in search of food at night; at Kaikoura where there is a regular supply of food little movement occurs.

H. australis is a more active species, often seen moving over the substrate and plants during daylight and moving about in the laboratory at night. Since little food reaches this species in its crevices a homing behaviour seems likely. There is negligible long-term movement and there are definite home sites (Section 3.1).

R.M. Cassie (pers.comm.; Morton & Miller, 1968: 591) observed one H. iris and one H. australis moving at night in the field at Wellington; the H. australis was feeding on an Ecklonia plant. Tutschulte (1968) monitored nocturnal movements of H. corrugata in California with the aid of lights attached to their shells and a time-lapse camera. His preliminary studies "do not show any instances of foraging or homing behaviour" but the only movements

noted occurred at night (Tutschulte, pers.comm.). Ino (1943) found a diurnal pattern of feeding consumption in H. gigantea which might imply greater mobility at night. More studies must be done before any generalisations about nocturnal activity and homing behaviour in Haliotis can be made.

4. GROWTH

4.1 Introduction.

Growth rate studies are necessary for estimating desirable and sustainable yields of wild, commercially exploited species. They provide a sound basis for commercial development and conservation policy. Such studies have already been made in some areas overseas where abalones are exploited (Sakai, 1962a-d; Newman, 1968) but in New Zealand the appropriate studies have not been made despite the use of H. iris shells in jewellery for many years and increasing interest in the exploitation of its meat for overseas markets. Aside from Sinclair's (1963) data on H. iris growth rates, nothing else appears to have been published on growth of New Zealand haliotids.

The present contribution describes growth of H. iris at Kaikoura as estimated by length-frequency sampling and tagging. Comparable data for older H. australis and H. virginea, based on analysis of shell growth checks is also included.

4.2 H. iris.

4.2.1 Introduction.

All sizes of H. iris were readily accessible and analysis of time shift in length-frequencies and of growth of individually tagged animals were made. Data combined from these two techniques gave estimates of both the annual growth rate and seasonal differences in growth. Annual growth checks could not be demonstrated in this species.

4.2.2 Methods.

a. Length-frequency analysis.

Two populations of juvenile H. iris were selected at Kaikoura

in lower intertidal areas at Lab. Rocks and at Avoca Point. These areas, separated by about 1km of shore, were chosen because they supported dense populations of juveniles and were topographically isolated by rocky ridges from the surrounding areas. Being isolated in this way the populations probably mixed little with those from other areas. The young abalones were found under stones as high as about E.L.W.N. and down to below E.L.W.S.

At two-monthly intervals beginning August 1967 the areas were searched thoroughly by turning stones at low tide and the shell length of every abalone found was measured to the nearest millimetre. After measurement they were returned to the shore. The number collected varied from 67 to 307 depending firstly on mean size (larger animals being more easily found than smaller ones) and secondly on dispersal rate (largest sizes tended to move away into deeper water as their habitat requirements changes (Chapt. 3)). Human predation may also be responsible for some loss of larger animals from the intertidal region. Eleven collections were made, the last being in June 1969 (April 1969 was omitted).

The data collected each month for each area were plotted as length-frequency histograms with 2mm size classes and analysed by the probability paper method of Cassie (1950). From the change in the means of the normal curves, the growth rate of young H. iris was deduced.

b. Tagging.

The tagging and recovery program is described in detail in Chapt. 3, differing only in that an extra recovery was made in May 1969. After the initial tagging in late October and November 1967 recoveries were made at three-month intervals (to coincide with the seasons) until November 1968 and after a further six months in May 1969. The only measurement taken in the field was shell length, here defined as the greatest diameter at the base of the shell; this is not necessarily total overall length since in older shells the apex overhangs the columella by up to 10mm. The distribution

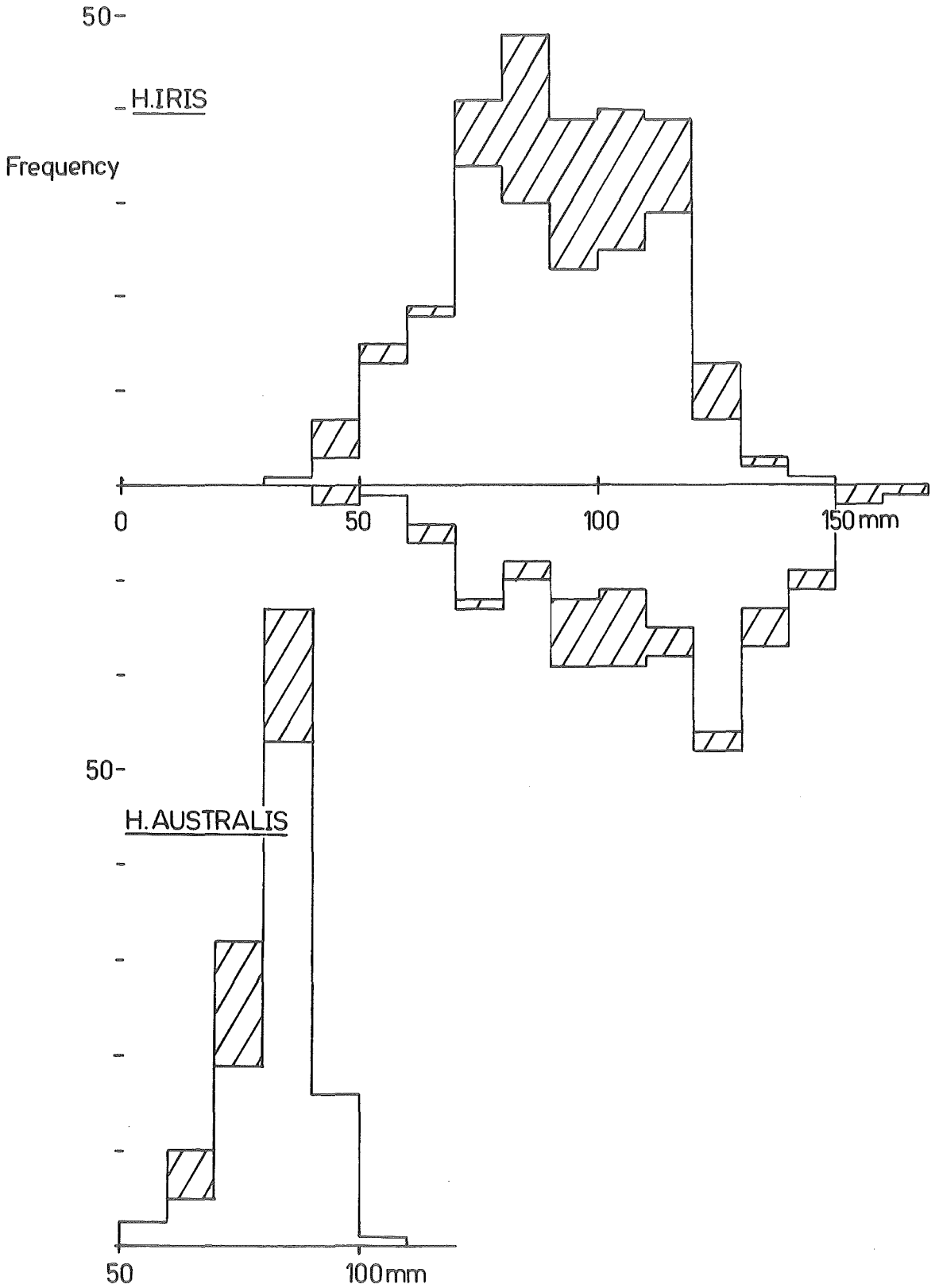

50-
H.IRIS
Frequency
0
50
100
150mm
50-
H.AUSTRALIS
50
100mm

FIGURE 4.1

Frequencies of lengths of all abalones tagged.
In H. iris, those above the axis were tagged at low water colonies, those below the axis at subtidal colonies.
Plain area represents those tagged in November 1967, hatched area, those tagged in May 1968.

of lengths of animals tagged is shown in Fig. 4.1.

Analysis of the data gave information on growth during four 3-month periods, three 6-month periods, and two overlapping 12-month periods. Recovery rates dropped in successive recaptures despite extra tagging in May. The numbers of recoveries for each period are given in Table 4.1. As sea conditions did not allow diving on predetermined dates the interval between successive recoveries of any particular individual could vary, viz. 78-115 days for 3-month period, 173-202 days for 6-month period, and 366-381 days for 12 month period. Assuming that growth rate was uniform during each recovery period each growth increment (in mm) was corrected to give the increment (to nearest 0.1mm) in 91, 182 or 365 days. For each of the nine recovery periods the corrected increment (*i*) was plotted against the initial length (*l*) for the whole sample of recovered animals and the least-square regression of *i* on *l* was calculated.

TABLE 4.1 *H. iris*. Numbers of recoveries in each recovery period used for analysis of growth rate.

Recovery Period:	3-month	6-month	12-month
Summer 1967-8	122		
		35	
Autumn 1968	27		
			19
Winter 1968	37		
		37	
Spring 1968	22		
			27
Summer 1968-9		20	
Autumn			

This technique is an alternative form of the Manzer & Taylor plot (Hancock, 1965), increment rather than final length being used. The regression equation is of the form:

$$\underline{i} = (1 - \underline{e}^{-K}) (L_{\infty} - \underline{l})$$

where K and L_{∞}, parameters of the von Bertalanffy growth equation, are the growth coefficient and the asymptotic length respectively. A statistical comparison of the regression lines for separate seasons and for separate 6-month periods enabled seasonal growth patterns to be assessed and growth rates in equivalent periods in different years to be compared.

c. Growth relationships.

In January 1969 a length-stratified sample of 152 H. iris between 10 and 170mm (not more than 10 for each cm class) was taken from Kaikoura to calculate relationships between shell length, breadth and height, total weight and body (excluding shell) weight. Shell height is the maximum height of the shell when resting on a flat surface. Measurements were to the nearest millimetre or gram. Both allometric and isometric relationships were calculated where suitable. H. iris from Taylors Mistake were similarly treated but a narrower range of sizes (80-106mm) was available.

4.2.3 Results.

a. Length-frequency analysis.

The data collected from the two areas are plotted as length-percentage frequency histograms in Fig. 4.2 and means and standard deviations for the separate size classes, calculated using Cassie's (1950) method, are plotted against time in Fig. 4.3.

When the spawning season is known it is possible to calculate the average growth rate between settling date (the larval life is only about five days) and the time when the first juveniles are

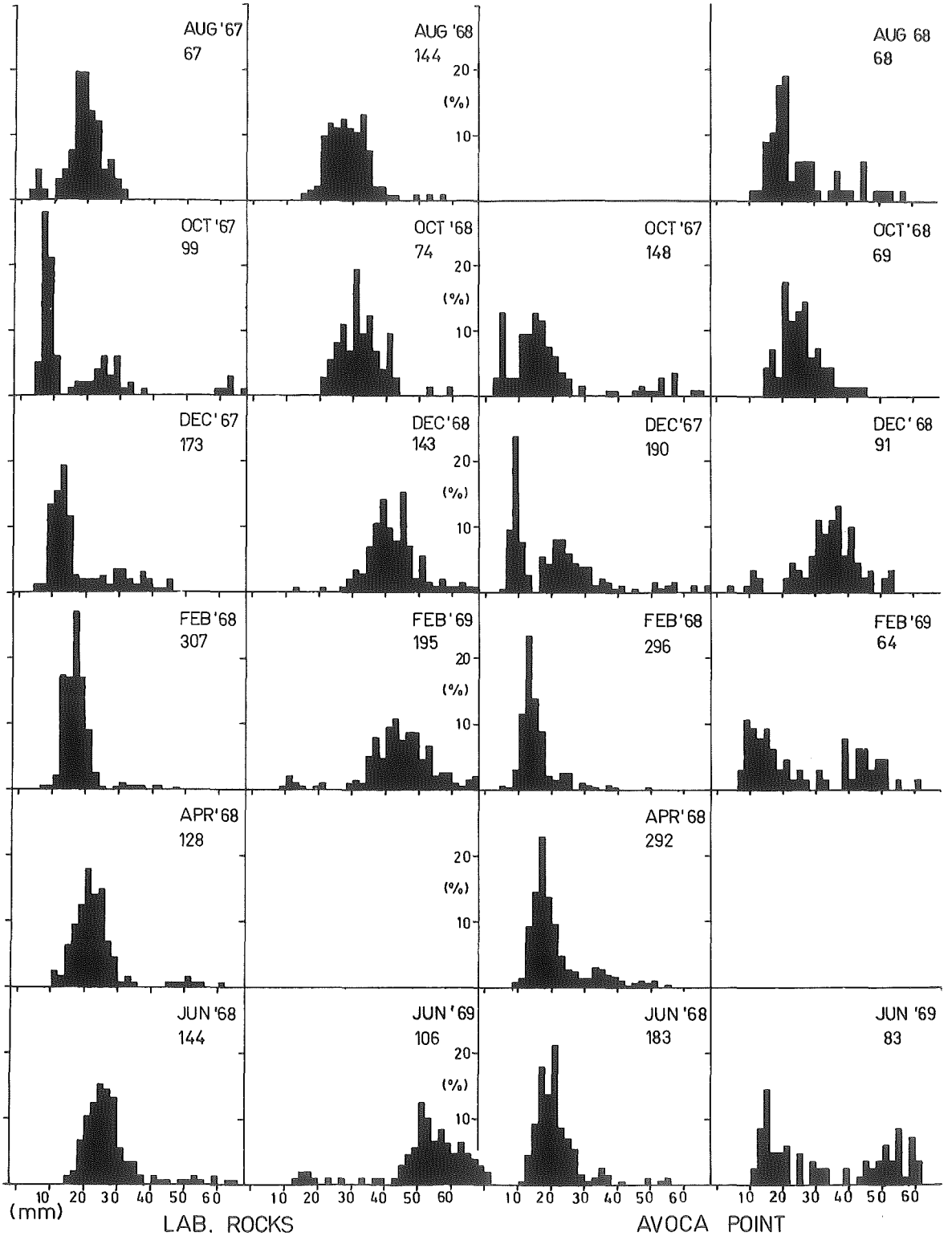
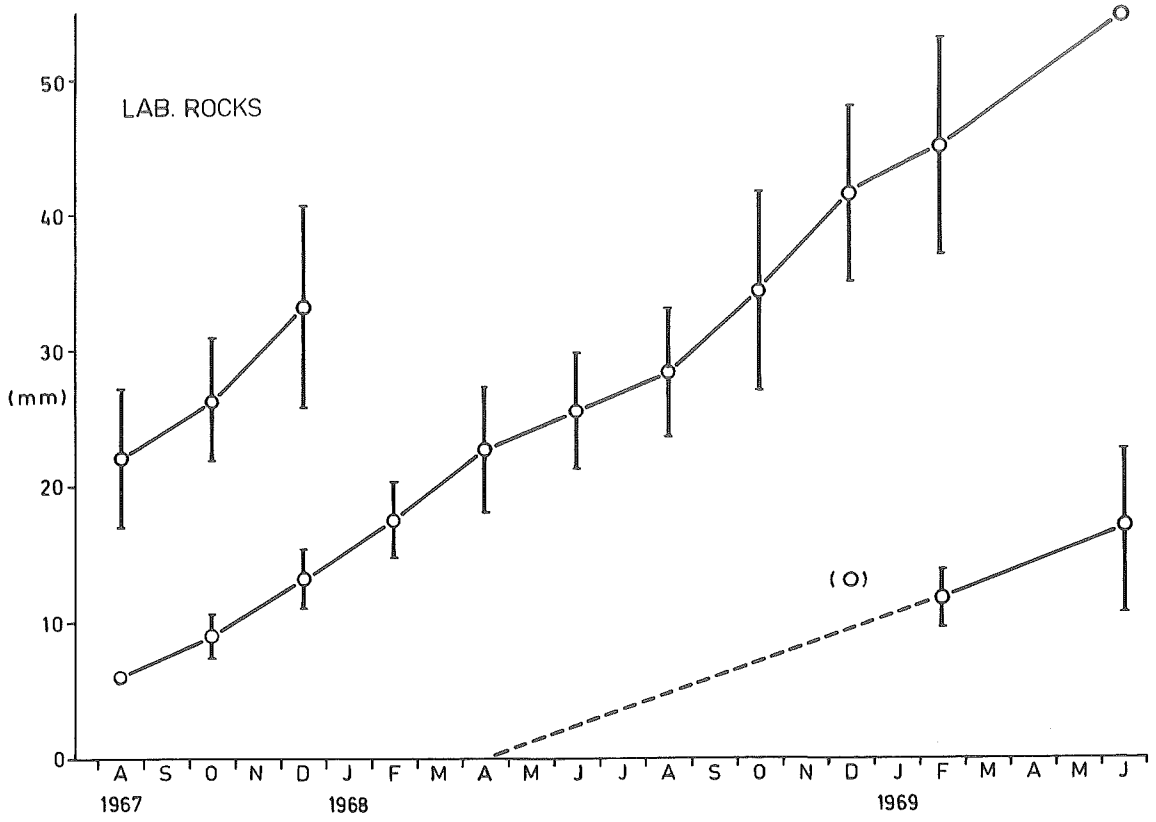

AUG '67
67
AUG '68
144
AUG 68
68
OCT '67
99
OCT '68
74
OCT '67
148
OCT '68
69
DEC '67
173
DEC '68
143
DEC '67
190
DEC '68
91
FEB '68
307
FEB '69
195
FEB '68
296
FEB '69
64
APR '68
128
APR '68
292
JUN '68
144
JUN '69
106
JUN '68
183
JUN '69
83
20
(%)
10
10 20 30 40 50 60
(mm)
LAB. ROCKS
AVOCA POINT

FIGURE 4.2

Percentage length-frequencies of juvenile H. iris measured at two-monthly intervals at two localities. Numbers under date for each histogram are totals measured.


LAB. ROCKS
50
40
30
(mm)
20
10
0
(O)
A S O N D J F M A M J J A S O N D J F M A M J
1967
1968
1969

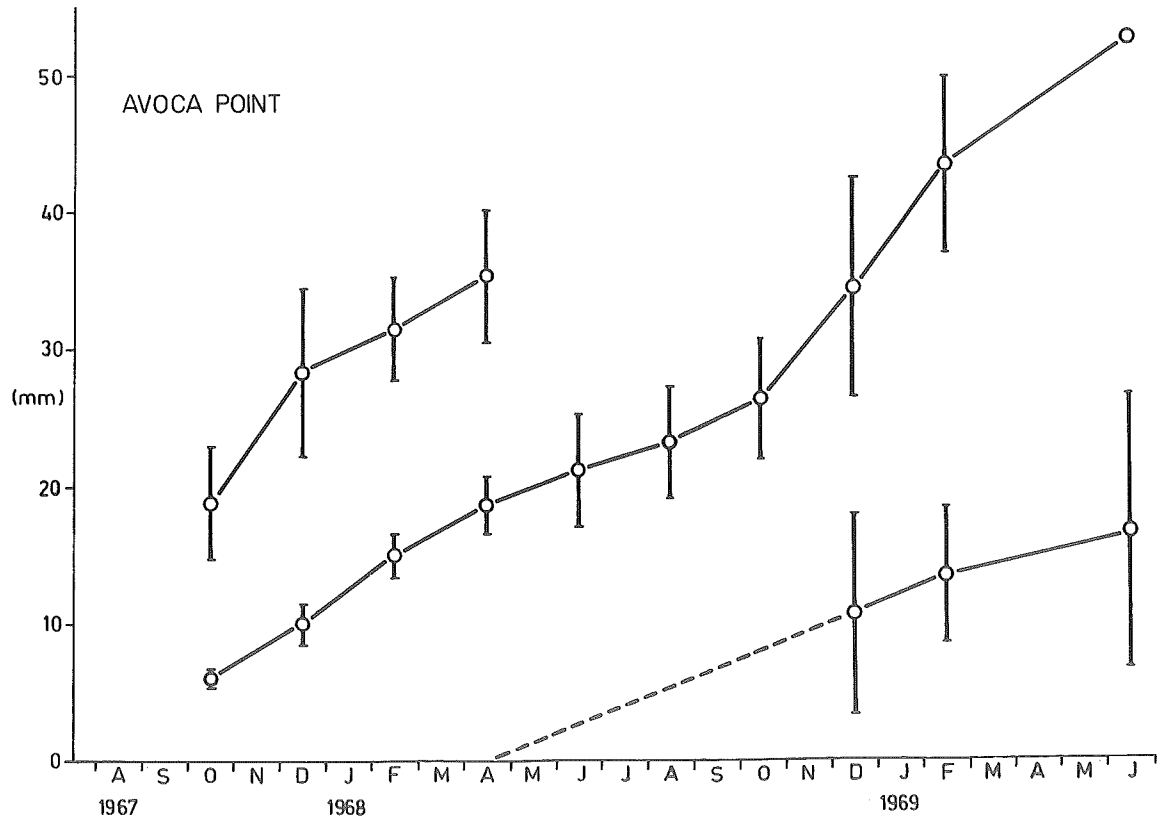

AVOCA POINT
50
40
30
(mm)
20
10
0
A S O N D J F M A M J J A S O N D J F M A M J
1967
1968
1969

FIGURE 4.3

Growth rates of year classes of juvenile H. iris derived from the means obtained by analysis of length-frequency histograms in Figure 4.2. Vertical lines indicate standard deviation. The dashed line is an extrapolation back to the probable settling date. The circle in brackets is a single specimen.

recognised. For this purpose the settling date was defined as mid-April (Chapt. 5) in 1968. Seven juveniles resulting from this spawning were first collected in December 1968 at Avoca Point with one from Lab. Rocks. The year class appeared more abundantly in February 1969. The average growth rate then in the first ten months (dashed lines in Fig. 4.3) is 1.3mm/month. While the length in February 1968 of the 0+ age class at Avoca Point is little different from that of the equivalent age class in 1969 (15.0 vs 13.7mm), it is considerably larger at Lab. Rocks (17.5 vs 11.8mm). Growth rate of the 1967 year class was greater at Lab. Rocks than that of the 1968 year class, i.e. about 1.7mm/month for the first ten months. Variability of spawning season between years cannot explain this difference since it is obvious at only one locality. The 1967 year class also grew faster than the 1966 year class as is shown when equivalent lengths of 1+ year classes in 1967 and 1968 are compared.

Variability in growth rate between localities is offset by variability within locality. Growth at Avoca Point during most of 1968 was slower than at Lab. Rocks but after October this discrepancy began to disappear.

The number of age classes at any one time never reached more than three; only two are figured since the third was always very small. Mortality, human exploitation, and a natural tendency for larger animals to move into deeper water as the habitat becomes unsuitable caused the reduction in size of larger age classes. The 1967 year class was the most abundant (286 at Lab. Rocks in February, 243 at Avoca Point in April); the equivalent age class in June 1969 totalled 9 at Lab. Rocks and 45 at Avoca Point. The degree of spawning and the success of spatfall vary remarkably from year to year; the pattern of relative abundances of year classes is repeated at the two localities and may be general for the Kaikoura area. The severe storms about settling time (April 1968) may be responsible for the scarcity of this year class.

At both localities there is a tendency for growth to accelerate

TABLE 4.2 *H. iris.* Values of K and L_∞ obtained for all tag return periods.

Recovery Period:	3-month		6-month		12-month	
	K	L_∞	K	L_∞	K	L_∞
Summer 1967-8	0.0679	156.6	0.1467	149.7		
Autumn 1968	0.0820	153.6			0.2611	148.5
Winter 1968	0.0520	143.5	0.1207	146.7		
Spring 1968	0.0781	145.3			0.3400	144.4
Summer 1968-9	-	-	0.2075	136.9		
Autumn	-	-				
Average 12-month values:					0.3104	146.2

TABLE 4.3 *H. iris.* Values of *t*, degrees of freedom and probability from *t*-tests between Manzer & Taylor regressions shown in Figs. 4.4 - 4.6.

Comparison	*t*	d.f.	*p*
Summer Autumn	0.48	145	0.6
Autumn Winter	1.48	60	0.1
Winter Spring	1.52	75	0.1
Summer-Autumn '67-8 Winter-Spring '68	0.69	68	0.5
Summer-Autumn '67-8 Summer-Autumn '68-9	0.97	51	0.3
Nov '67 - Nov '68 May '68 - May '69	1.48	42	0.2

during late spring to summer. This is evident in both 0+ and 1+ age classes (Fig. 4.3).

b. Tagging.

Figs. 4.4 to 4.6 illustrate the growth of tagged animals over 3, 6, and 12 months and the values of K and L_∞ obtained by regression are summarised in Table 4.2. The regression lines describing the Manzer & Taylor plots were compared in pairs with a t-test but although no significant difference between seasonal regressions was shown, other evidence suggests some seasonal variation in growth rate. Growth during winter is least, differing from spring and autumn at the 0.1 level of probability (Table 4.3). During tagging in October and November 1967 and in November the following year a distinct edge of new growth was obvious on many shells - spring then, probably sees the beginning of a period of rapid growth. The period of slow growth in winter is insufficient to form recognisable growth checks in the shell.

Growth during the three 6-month periods differed little and growth rates for the two overlapping year periods show no significant difference (Table 4.3).

The values of K and L_∞ over one year may be compared with those obtained for 14 tagged H. iris from Dunedin (R.J. Street, pers. comm.). Initial and final measurements were in tenths of inches and recovery periods varied from 9 to 31 months. Assuming growth to be uniform throughout the year (which it may not be) an annual increment was calculated and a Manzer & Taylor regression calculated. The values obtained, K = 0.2268 and L_∞ = 147.8mm, are little different from those for Kaikoura.

c. Absolute growth rate.

Mean lengths of year classes in the same month in two consecutive years were listed and the annual increments (the difference between the two) were calculated (Table 4.4); the annual increments are plotted against mean initial lengths in Fig. 4.7 together with the

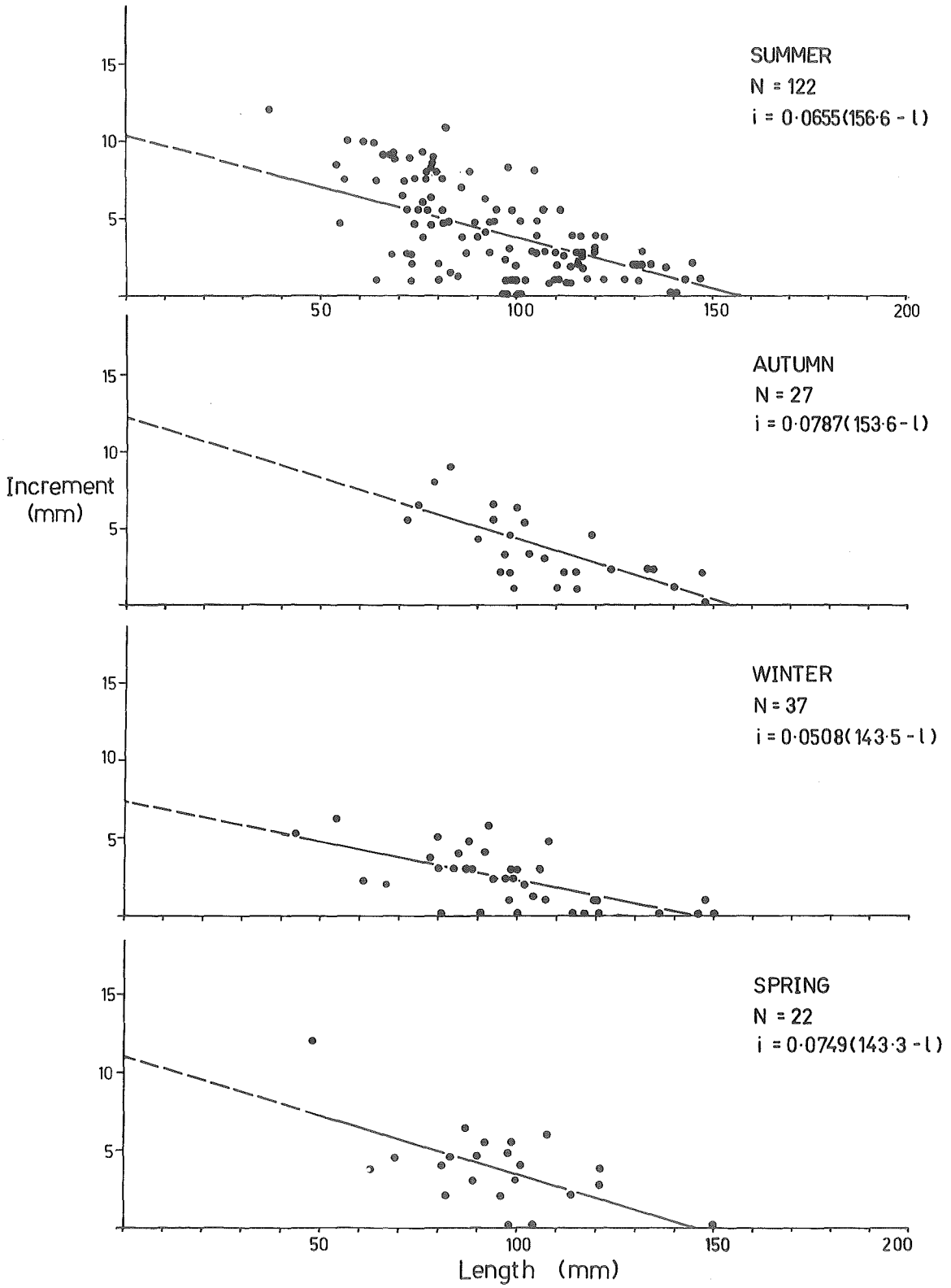

SUMMER
N = 122
i = 0·0655(156·6 - l)
AUTUMN
N = 27
i = 0·0787(153·6 - l)
WINTER
N = 37
i = 0·0508(143·5 - l)
SPRING
N = 22
i = 0·0749(143·3 - l)
Increment (mm)
Length (mm)
15
10
5
50
100
150
200

FIGURE 4.4

H. iris tag returns. Manzer & Taylor plots of increment per 3-months against initial length.

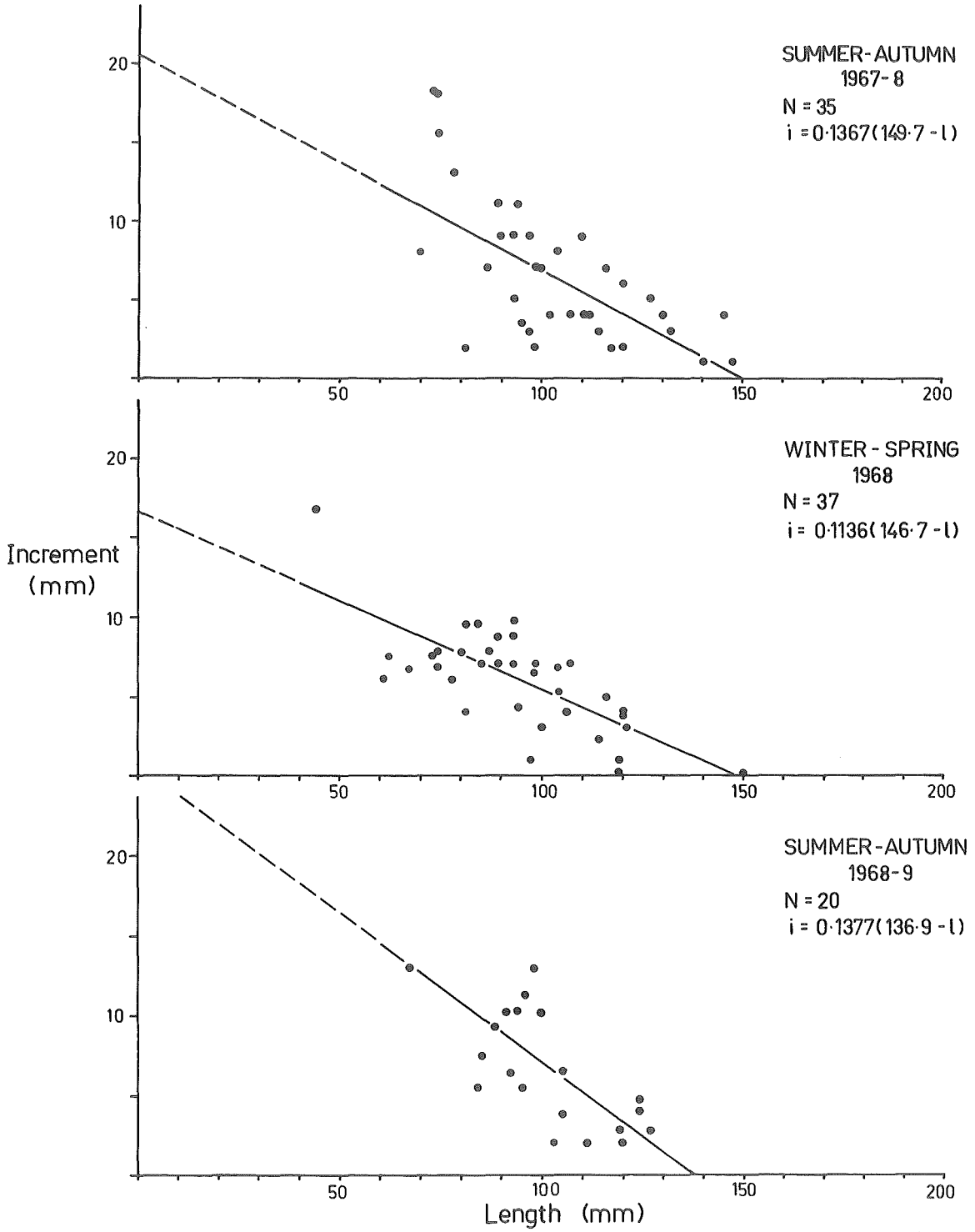

SUMMER-AUTUMN
1967-8
N = 35
i = 0·1367(149·7 - l)
WINTER - SPRING
1968
N = 37
i = 0·1136(146·7 - l)
SUMMER-AUTUMN
1968-9
N = 20
i = 0·1377(136·9 - l)
Increment
(mm)
Length (mm)
20
10
50
100
150
200

FIGURE 4.5

H. iris tag returns. Manzer & Taylor plots of increment per 6-months against initial length.

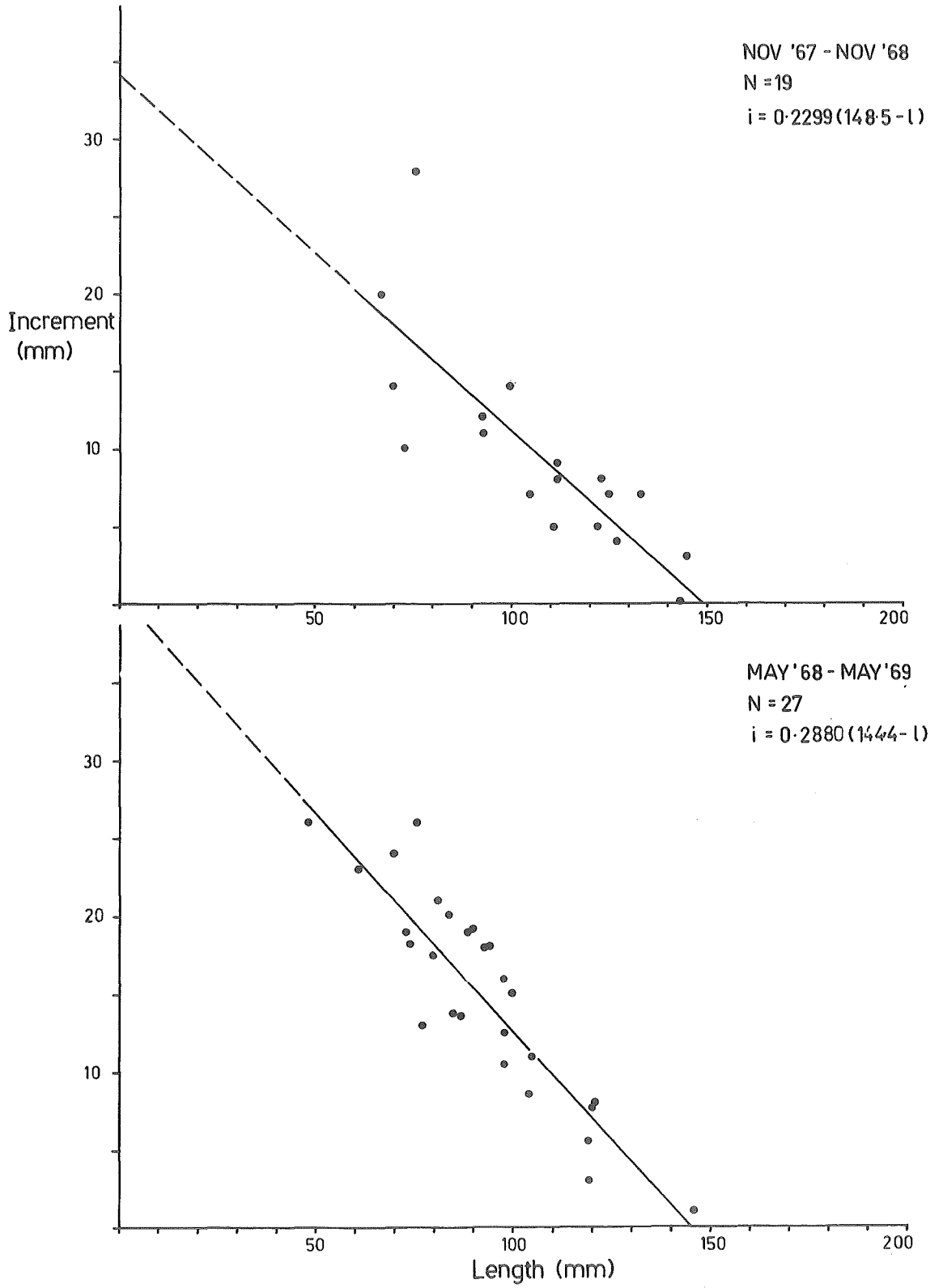

NOV '67 - NOV '68
N = 19
i = 0·2299 (148·5 - l)
MAY '68 - MAY '69
N = 27
i = 0·2880 (144·4 - l)
Increment (mm)
30
20
10
50
100
150
200
Length (mm)

FIGURE 4.6

H. iris tag returns. Manzer & Taylor plots of annual increment against initial length.

Manzer & Taylor regression obtained by averaging the two regressions from annual tag returns. A curve was fitted by eye to the points and extrapolated to intersect the regression. The following initial lengths, annual increments and final lengths can be read from the graph:

$$\underline{l}_o = 0, \quad \underline{i}_1 = 21.0, \quad \underline{l}_1 = 21.0,$$

$$\underline{i}_2 = 29.5, \quad \underline{l}_2 = 50.5.$$

$\underline{l}_2$ = 50.5mm falls within the range of the linear regression and its intercept with it lies close to the point representing growth of the smallest tag return. It is assumed then, that after the second year growth follows the von Bertalanffy equation and lengths at subsequent ages can be calculated from the regression equation. The von Bertalanffy equation is of the form

$$L_{\underline{t}} = L_\infty \left(1 - \underline{e}^{-K(\underline{t} - \underline{t}_o)} \right)$$

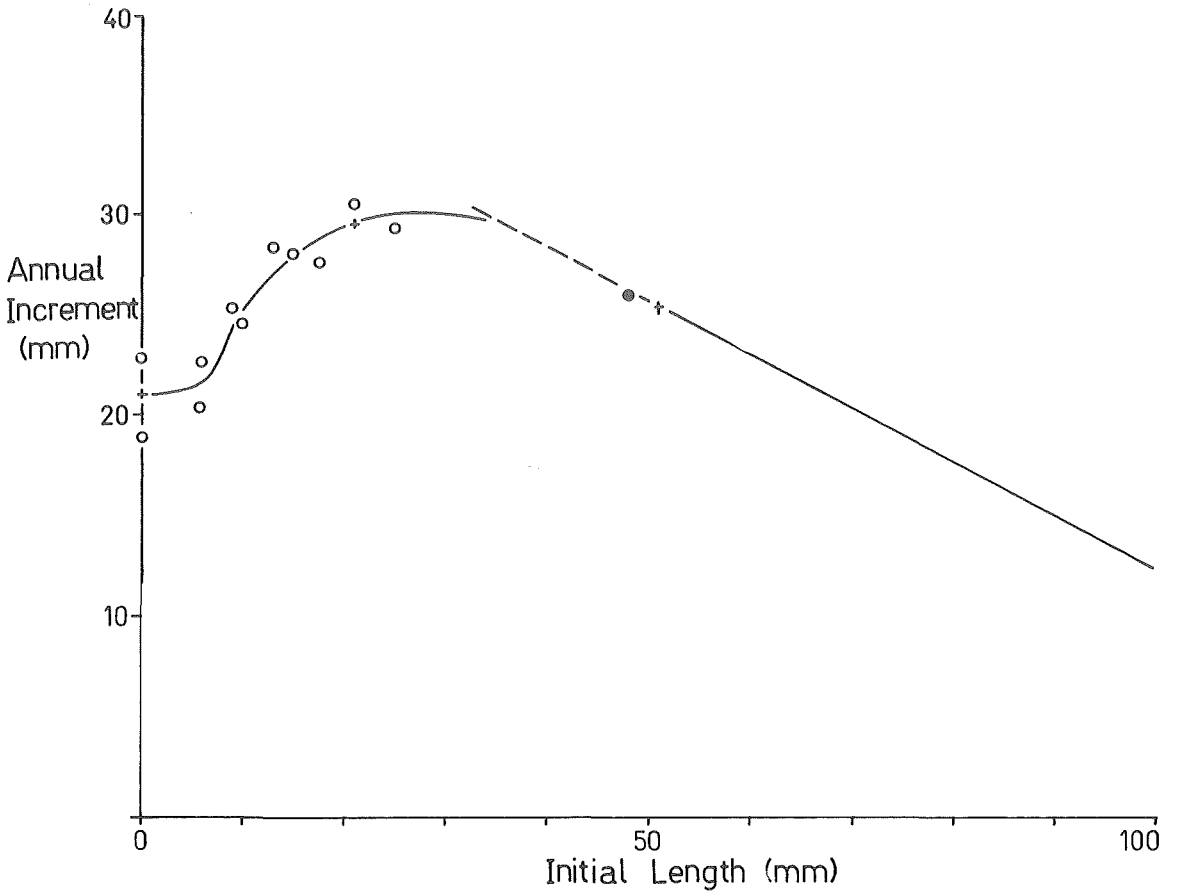
and may be transformed into the linear expression

$$\log_{\underline{e}} \left(L_\infty - \underline{l}_{\underline{t}} \right) = \log_{\underline{e}} L_\infty + K \underline{t}_o - K \underline{t}$$

(Beverton & Holt, 1957: 284). Only $\underline{t}_o$, the theoretical age at which length is zero, is unknown and may be calculated by substituting the following established values into the equation, K = 0.3104, L = 146.2mm, $\underline{t}$ = 2years, $\underline{l}_2$ = 50.5mm; this gives $\underline{t}_o$ = 0.636 years. Growth beyond the second year is described by the equation

$$L_{\underline{t}} = 146.2 \left(1 - \underline{e}^{-0.3104(\underline{t} - 0.636)} \right).$$

The growth curve for H. iris calculated in this way appears in Fig. 4.8.


40
30
20
10
Annual
Increment
(mm)
0
50
100
Initial Length (mm)

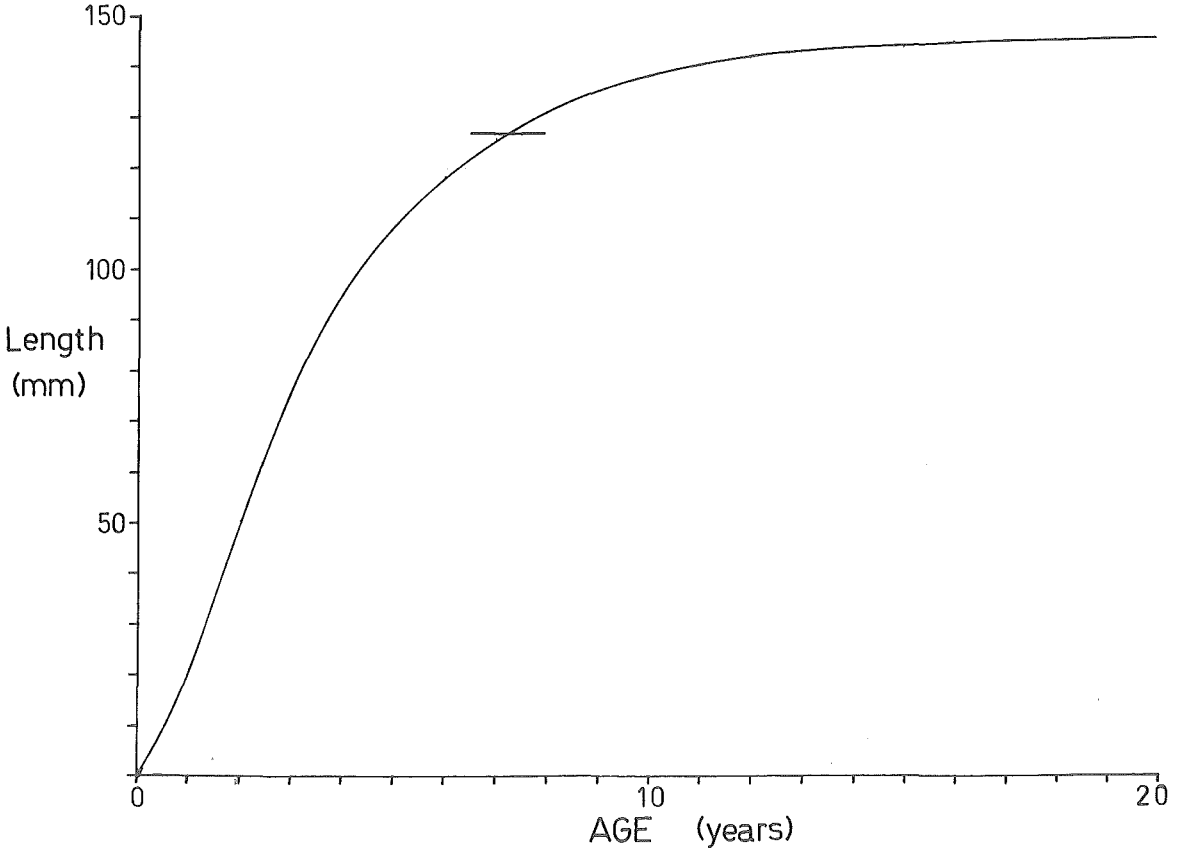

150
100
50
Length
(mm)
0
10
20
AGE (years)

FIGURE 4.7

H. iris growth. Plot of annual increment against initial length. Open circles are derived from Table 4.3, the filled circle is the annual increment of the smallest tag return, and the crosses are the initial lengths and subsequent annual increments at ages 0, 1, and 2 years. The straight line is the average Manzer & Taylor regression, the curved line is fitted by eye.

FIGURE 4.8

H. iris growth curve. The horizontal line indicates the present minimum takable size, 127mm.

TABLE 4.4. Mean annual growth increments of populations of juvenile H. iris.

Period	Locality*	Mean initial length l_t	Mean final length l_{t+1}	Annual Increment $i = l_{t+1} - l_t$
Apr '67-8	L.R.	0.0	22.7	22.7
"	A.P.	0.0	18.7	18.7
Aug '67-8	L.R.	6.0	28.4	22.4
Oct '67-8	L.R.	9.0	34.3	25.3
"	A.P.	6.0	26.2	20.2
Dec '67-8	L.R.	13.2	41.2	28.3
"	A.P.	10.0	34.5	24.5
Feb '68-9	L.R.	17.5	45.0	27.5
"	A.P.	15.0	43.2	28.2
Jun '68-9	L.R.	25.4	54.7	29.3
"	A.P.	21.2	52.6	30.4

* L.R. = Lab. Rocks; A.P. = Avoca Point.

d. Growth relationships.

The coefficients of allometry and the isometric relationships for H. iris (Table 4.9) and the total weight/length relationship (Fig. 4.15) show that the three shell parameters are related isometrically (coefficient of allometry not significantly different from one) except in the case of height and length at Kaikoura. Relative height increases with length. Taylors Mistake H. iris are relatively heavier than those from Kaikoura and have a relatively lower body weight, probably due to extra 'Lithothamnion' growth.

These relationships do not differ significantly from those given by Sinclair (1963) for smaller samples from Wellington and Kaikoura.

Cleaver (1966) related length and weights of parts of H. iris from Wellington. The proportion of shell weight is similar to that calculated here for Kaikoura. The coefficient of allometry calculated from his data relating total weight and length is higher than both those from Kaikoura and Taylors Mistake (Table 4.9).

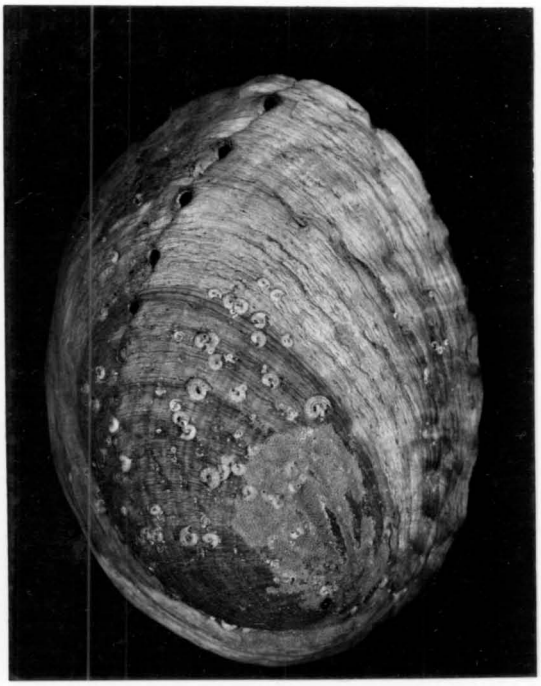
4.2.4 Discussion.

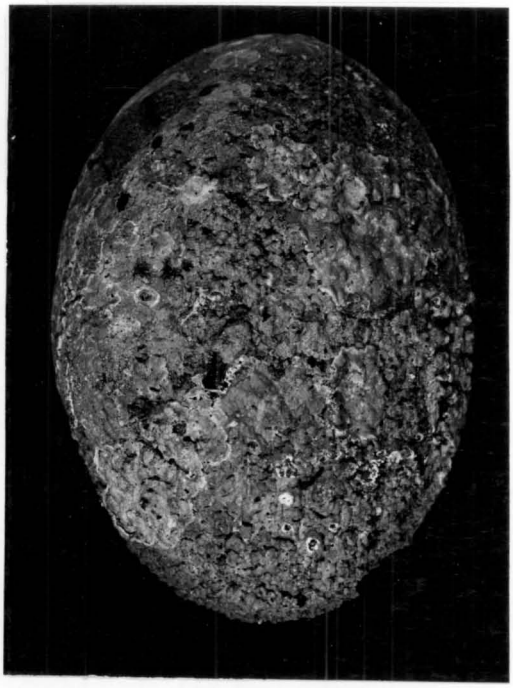
The von Bertalanffy growth equation adequately describes growth of H. iris. Had more tag returns been available, especially over a whole year, it might be shown that the equation has limitations as have been pointed out by Frank (1965) for the snail, Tegula funebralis. Frank suggested that the Walford (or Manzer & Taylor) straight line derived from the von Bertalanffy equation approximated a curve with increasing slope beyond a point of inflexion. The Walford line usually applies only above this point. To test this possibility in H. iris, the 122 tag returns from the first summer period were divided into three groups on initial length and independent regressions of increment on initial length calculated. (The rate of growth during summer is similar to the average for the whole year.) The number of points, values of K and L_∞ appear in Table 4.5 where it can be seen that the slope of the regression ($e^{-K} - 1$) increases with increasing length as Frank suggested. This also explains why the values of L_∞ obtained for the overall regressions for H. iris are lower than might be expected (Table 4.2). The largest H. iris recorded from Kaikoura was 177mm long and abalones longer than 160mm were not uncommon on other parts of the peninsula. The value of L_∞ obtained for the group of largest summer tag returns, 173.8mm, approaches the maximum. The effect of any correction to allow for this possible error will be to steepen the growth curve initially and to flatten it near the asymptote.

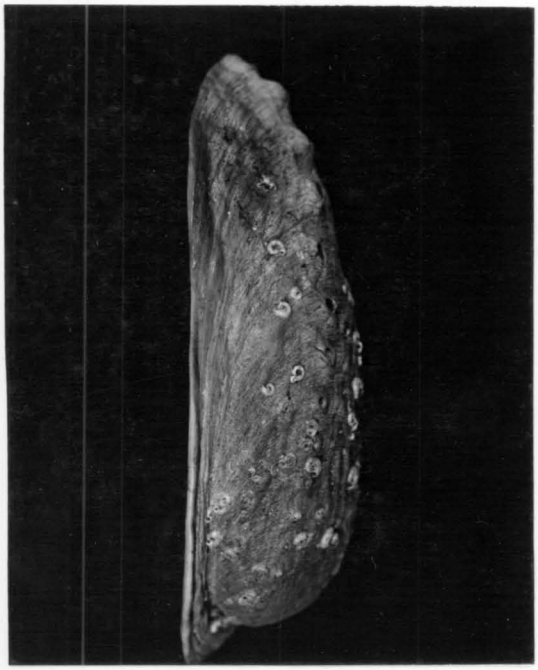
TABLE 4.5. H. iris. Values of N, K, and L_∞ for three components of the summer Manzer & Taylor plot.

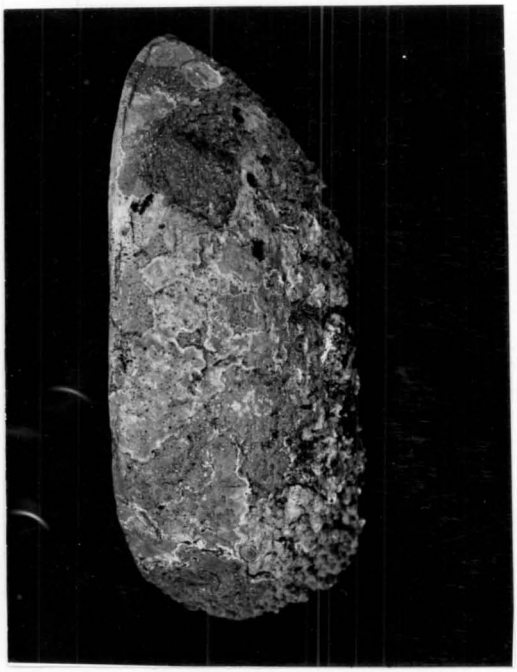
Range	N	K	L_∞
37 - 69mm	14	0.1467	-
70 - 109mm	71	0.1211	-
110 - 147mm	37	0.0394	173.8
Total	122	0.0679	156.6

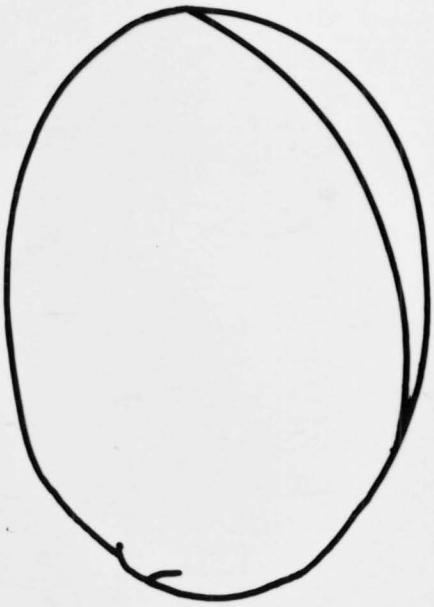
Growth has been expressed here in terms of maximum basal shell length. Growth of the spiral of the shell is only one of several factors contributing to increase of this measurement. For H. iris the angle of the logarithmic spiral (angle between radius and tangent to the spiral) decreases as the shell increases from 3.7 to 9.9cm (Sinclair, 1963). But at greater lengths the angle increases (Fig. 4.9) and growth of the shell edge becomes more lateral than anterior, so increasing the breadth/length ratio slightly. At the same time the plane of the spiral tilts downwards at the front until in older shells growth has more vertical than horizontal component (Fig. 4.9). The vertical component of growth is responsible for increasing height/length ratio. Growth of the shell length also has a negative component. Beyond about 90-100mm when the columella contributes up to 5mm of total length, the columella tilts until its edge eventually ceases to be the most posterior part of the shell (Fig. 4.9). Addition of shell material continues even in abalones which have reached their own asymptotic length; it is in the form of additional nacre alternating with layers of conchiolin laid down inside from the anterior edge of the shell backwards. The nacre strengthens the older shell as the outer prismatic layer erodes. The organic conchiolin is dark brown and is responsible for the characteristic

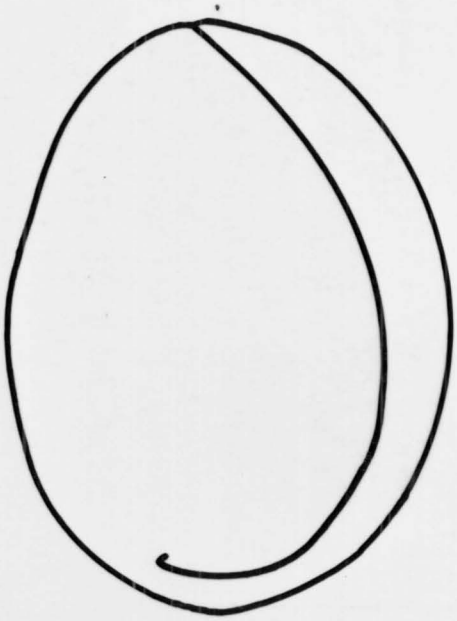












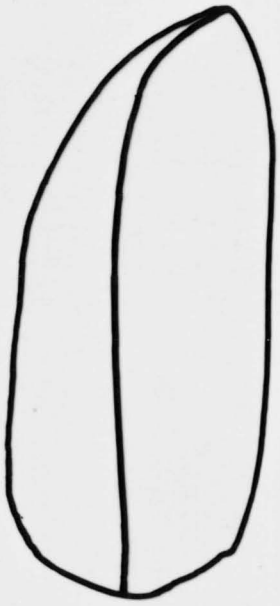


FIGURE 4.9

Growth patterns in H. iris shells. The shell on the left, shown in vertical and lateral views, 84mm long (ca natural size), shows the contribution to length made by the columella, and the flat, forward-directed angle of the spiral. The shell on the right 145mm ($\frac{1}{2}$x), shows the shell apex overhanging the base of the shell and the spiral tending to grow towards the right and downwards. The overlay diagram shows the shell spiral.

Photo: D. Simms.

patterning of the shell of this species.

This account is derived from observations on Kaikoura specimens; H. iris from Taylors Mistake differs only in that comparable changes in shape associated with growth occur at smaller sizes. Shells are proportionately taller and the columella contributes less, both due to earlier tilting of the plane of the spiral. A greater coating of 'Lithothamnion' also caused shells to be relatively higher. This and the much smaller maximum size (109mm vs 177mm) suggest a much slower growth rate at Taylors Mistake.

Sinclair (1963) used a length-frequency graph to estimate the early growth rate of H. iris. The lengths of 825 animals between 11 and 83mm plotted at 1mm intervals showed four modes below 50mm which Sinclair interpreted as four year classes 10mm apart. But if Sinclair's data are plotted at 2mm intervals only two definite modes remain, one at 19mm and the other at about 47mm. In the light of what was found at Kaikoura these modes are better interpreted as year classes.

Other workers have published data on the growth of young Haliotis species. Several have growth rates similar to H. iris. H. midae (Newman, 1968) and H. discus hannai (Sakai, 1962c, d) reach about 50mm in two years; H. diversicolor supertexta (Oba et al., 1968) reaches 28mm in one year. The smaller H. tuberculata reaches only 30mm in two years (Forster, 1967). In laboratory conditions growth can be much faster, e.g. H. discus hannai (Kan-no & Kikuchi, 1962), or in the same species, slower than in nature (Ino, 1952).

The growth rate of H. iris can be compared in more detail with that of H. midae (Newman, 1968), especially since similar techniques have been used in their estimation. The tagging analyses used differ in that remeasurement of tagged H. iris at regular intervals is substituted for a more complex statistical analysis of data from irregular recovery of H. midae. The much higher recovery rate of H. iris (Chapt. 3) enabled this to be done. Both methods enabled seasonal variations in growth to be estimated.

Growth of H. midae (Newman, 1968: Fig.12) is much more uniform throughout its life than H. iris, in 10 years it reaches only 50% of its asymptotic length while H. iris reaches 95%. This reflects the very low value of K for H. midae, 0.0593, compared with 0.3104 for H. iris and similar values for H. australis, H. virginea (Sections 4.3 and 4.4) and H. tuberculata (Forster, 1967). Few other absolute growth curves of Haliotis species have been published. H. discus hannai which is slightly smaller than H. iris, grows at a similar relative rate, reaching about 100mm in 5-6 years (Sakai, 1962c, d). Notohaliotis ruber grows even faster than H. iris (125mm in 5.5 years) (Anon., 1967).

Population sampling and analysis of length-frequency graphs was used by Oba et al. (1968) to determine the growth of young H. diversicolor supertexta. A comparison is interesting in that several features are common to both H. iris and this Japanese species. Both studies stretch over more than one year and show that equivalent age classes reach different sizes in different years and appear in the collections at different times. This can be attributed to differences in both initial settling time and in growth rate between years. The replacement of year classes by new groups of smaller animals occurs in both species; while this can be explained as mainly a natural phenomenon in H. iris, human exploitation is the cause in the Japanese species (Oba, pers.comm.).

4.3 H. australis.

4.3.1 Introduction.

The small range of sizes of H. australis readily available at Kaikoura severely limited analysis of growth rate of this species. Juvenile specimens (less than 60mm) were rarely found, probably because of their crevice-dwelling habits; this made the use of length-frequency analysis impossible and limited the usefulness of tagging. This species does, however, exhibit growth checks in the shell and tagging can be used to determine whether or not these are

annual and when they are formed.

4.3.2 Methods.

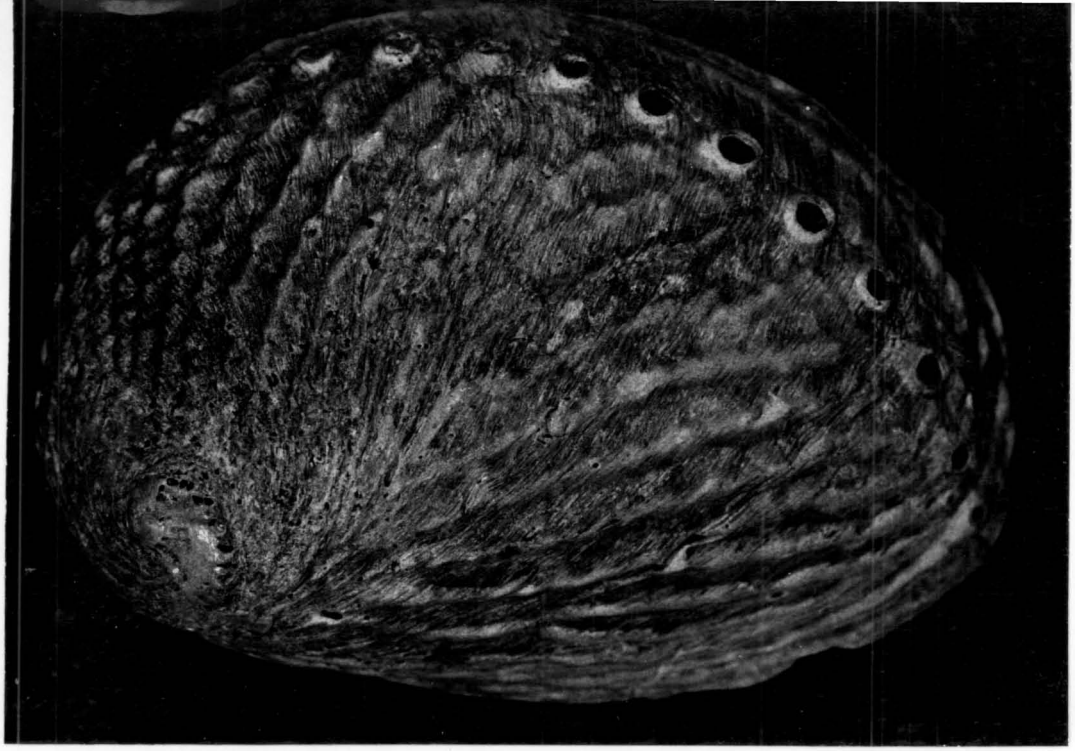
a. Tagging.

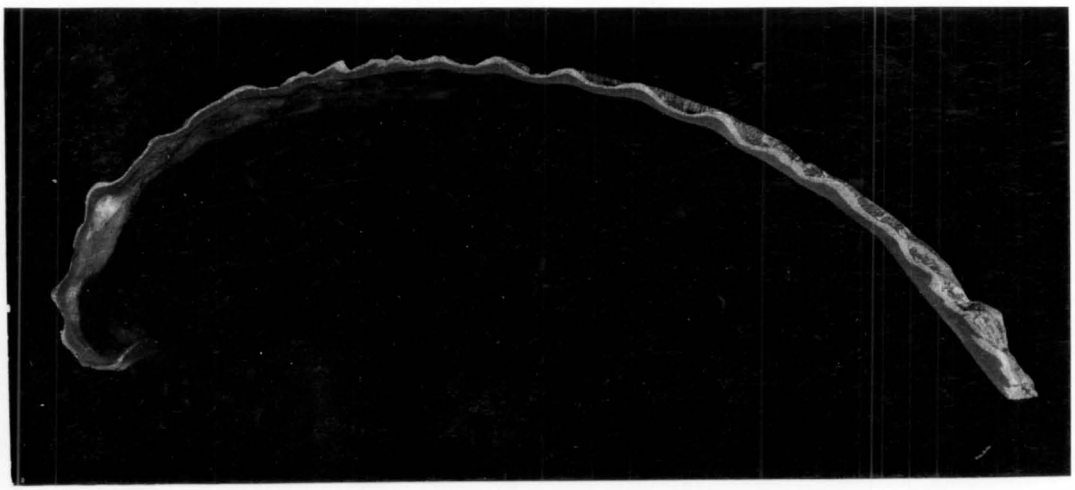
H. australis were tagged at Kaikoura in November 1967 and May 1968 and recovered at 3-monthly intervals until May 1969. Methods were the same as for H. iris (Section 4.2) and are described in more detail in Chapt. 3. Growth of those recovered was slight because only large animals could be tagged (Fig. 4.1). The formation of checks in known growth increments over a one year period was examined in the shells of those recaptured in May 1969. The final two growth lines on the shell were marked externally and the shell sectioned. The interruptions in section (see 4.3.2b) were noted and this information compared with the lengths in May 1968 and May 1969.

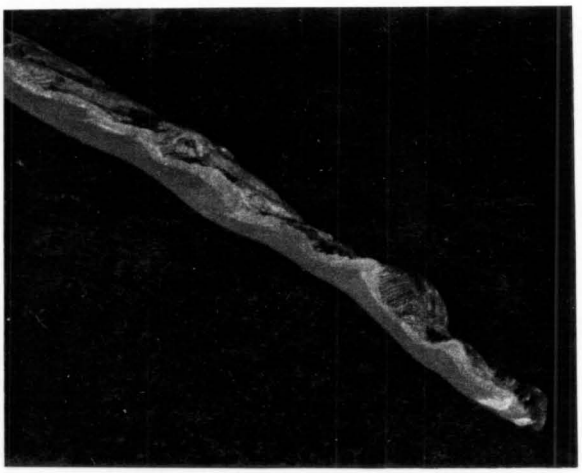
b. Growth checks.

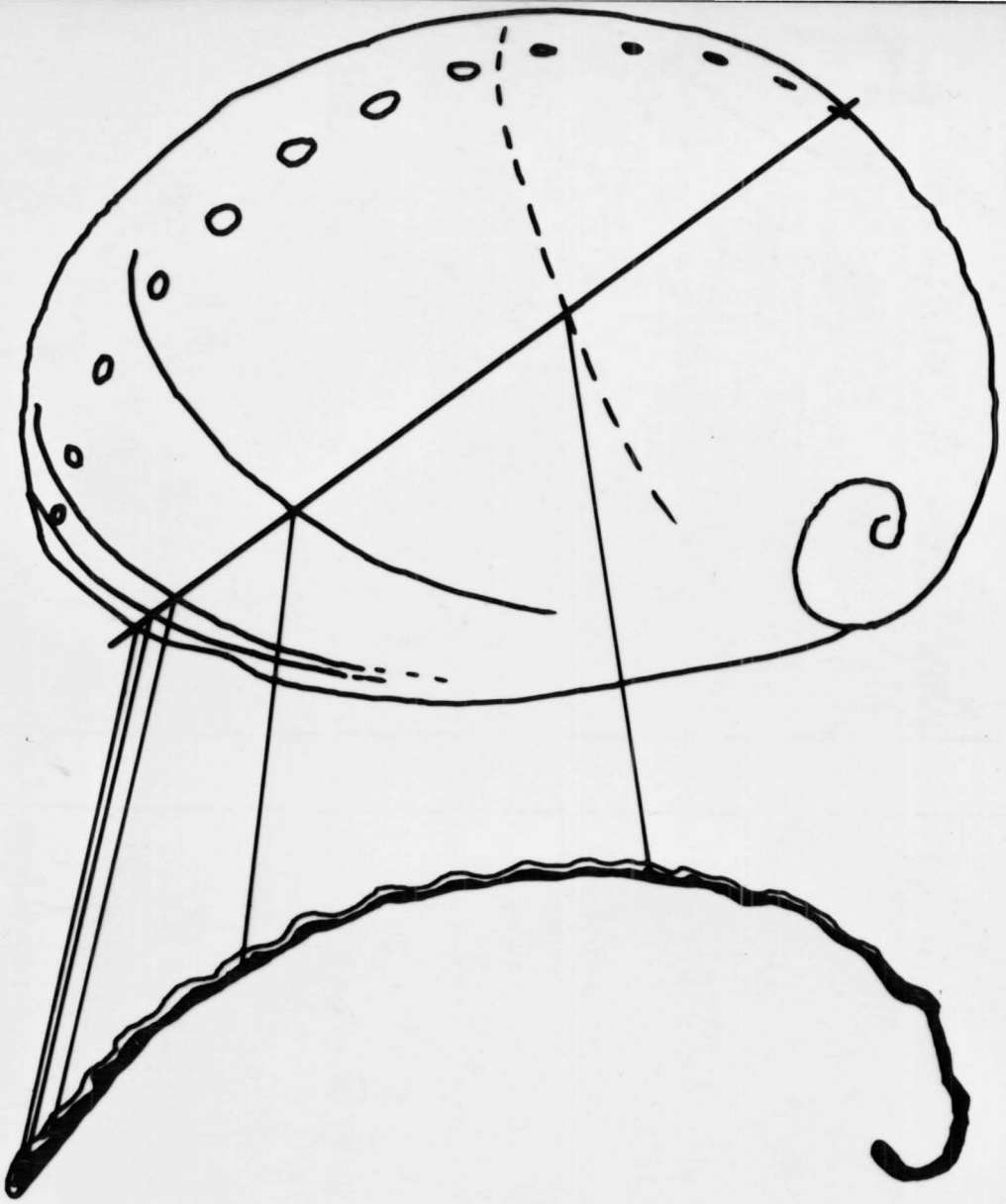
Growth checks appear externally, after any epifauna and epiflora have been cleaned off, as ridges or series of ridges which delimit a former anterior growing edge of the shell; on younger shells without secondary nacre deposition, checks are sometimes visible as lines on the nacre or as opaque areas in the partly translucent shell. On the surface of vertical longitudinal sections checks appear as interruptions in the boundary between the outer prismatic and inner nacreous layers of the shell (Fig. 4.10). Similar interruptions have been described in shells of H. discus hannai (Sakai, 1960).

Shells which had been collected monthly for estimation of gonad condition were used to establish the lengths at which growth checks were laid down; 86 from samples of 25 taken in each of five months, July, September 1967, January, February, May 1968, gave useful information. In the remainder, checks were indefinite or the shells were too eroded to be used. On the whole shell, probable growth checks were marked externally and the shell lengths at which they were formed were measured with calipers to the nearest millimetre.









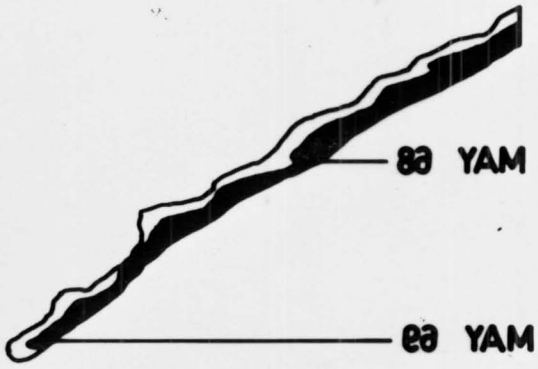

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FIGURE 4.10

External and sectional views of a shell of H. australis to show growth checks and the interruptions accompanying them in section (both $1\frac{1}{2}$ x). The nacreous layer (black on the overlay diagram) is stained with cobalt nitrate. The overlay diagram shows the line of the section and links corresponding growth checks and section interruptions between the nacreous and prismatic layers; an extra interruption on the shell edge is shown.
Photo: D. Simms.

FIGURE 4.11

Edge of typical H. australis shell sectioned in May 1969 to show growth interruptions formed on the edge and at the length in May 1968 (ca 8 x). The nacreous layer (black on overlay diagram) is stained with cobalt nitrate.
Photo: D. Simms.

TABLE 4.6 Numbers of tagged H. australis which had not grown out of total numbers of recoveries for each period. Percentages are given in brackets.

Recovery Period:	3-month	6-month	12-month
Summer '67-8	34/51 (67)		
		13/28 (46)	
Autumn '68	15/25 (60)		
			12/18 (67)
Winter '68	22/28 (79)		
		12/24 (50)	
Spring '68	14/24 (58)		
			2/14 (14)
Summer '68-9	-	4/16 (25)	
Autumn	-		

The shell was then sectioned longitudinally with a hacksaw and one of the exposed edges ground smooth on a carborundum stone. Interruptions visible on this surface were then compared with those marked externally; only checks with corresponding interruptions in section were used in the final analysis. Additional interruptions were often revealed in section close together at the edge of older shells. Although these added little to the length of the shell and were not visible externally, they were included in the subsequent analysis.

At first, shells were boiled in cobalt nitrate solution for 20 minutes staining the nacre and leaving the prismatic layer unstained. The aragonite and calcite crystal structures of these two layers allow this differential staining (Bøggild, 1930). While this made interpretation a little easier in a few cases, the treatment was abandoned. The earliest definite growth check (about 40-50mm) was not accompanied by an interruption in section and was generally much broader than later ones.

Adjacent pairs of growth checks were plotted against each other in a Manzer & Taylor plot and the least square linear regression calculated for points greater than $\underline{l}_t$ = 40 mm.

c. Growth relationships.

Allometric and isometric equations relating length, breadth and height of shell, and total weight and body weight were calculated for 93 H. australis over the size range 27-109mm. Data from not more than 10 individuals were included in any 10mm length class.

4.3.3 Results.

a. Growth of tagged animals.

The distribution of lengths of H. australis tagged is shown in Fig. 4.1. The growth of tagged animals could not be analysed in the same way as H. iris. The reason for this is evident in Table 4.6 where the numbers of animals showing no growth are listed.

The high proportion of abalones showing no growth, even over one year, suggests that H. australis may live for many years after attaining its maximum length.

b. Annual nature of the growth check.

Twenty-four tagged H. australis were recaptured in May 1969; of these three had not grown in the past year. The pattern on growth checks close to the shell edge was similar in all specimens (Table 4.7, Fig. 4.11). In all but four shells a growth check had either just formed or was forming on the shell edge in May 1969 and in all shells a growth check was present within one millimetre of its length the previous May. A growth check on a single individual between these two occurred at a length corresponding to an intermediate recovery and is therefore probably an artificially induced disturbance check. The checks observed are therefore annual and are formed in the late autumn or early winter. This period of slow growth is followed in September and October by the rapid addition of a clean band of shell anteriorly.

TABLE 4.7. Position of growth checks at the edge of shells of H. australis at liberty for one year.

A. May 1969 (edge) check:	No. shells with check forming	10	24
	No. shells with check recently formed	10	
	No. shells with no check on edge	4	
B. May 1968 check:	No. with check at length May 1968	19	24
	" " " " " " " +1mm	2	
	" " " " " " " -1mm	3	
C. Intermediate checks:	No. shells	1	

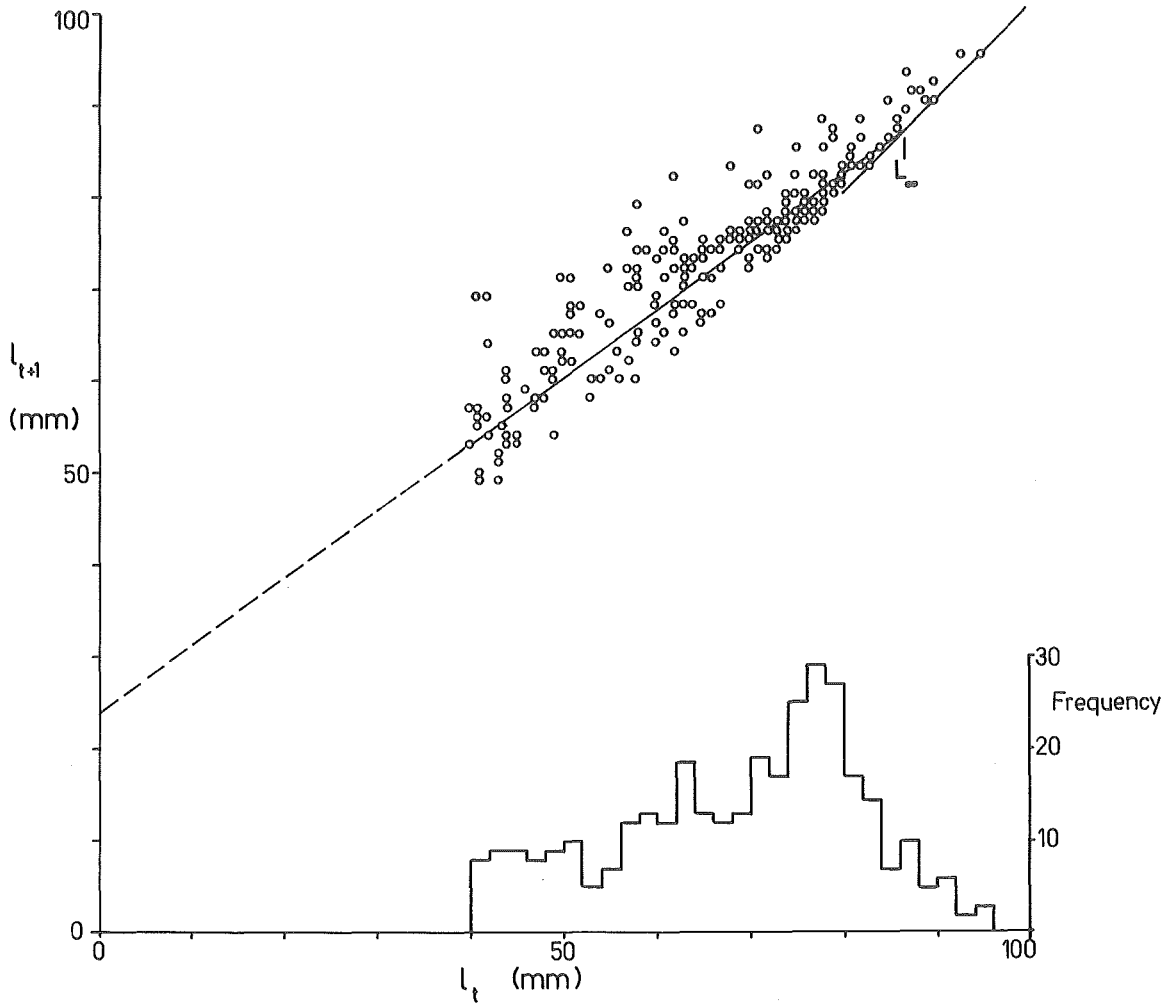

100
50
0
l_{t+1}
(mm)
L_∞
30
20
10
Frequency
0
50
100
l_t (mm)

FIGURE 4.12

H. australis growth. Manzer & Taylor plot of adjacent pairs of growth checks, and length-frequency histogram (in 2mm classes) of all growth checks.

c. Analysis of growth checks.

A total of 273 adjacent pairs of growth checks from 86 shells appear in a Manzer & Taylor plot in Fig. 4.12. The equation of its linear regression is

$$l_{t+1} = 0.7259 \left(l_t + 86.75 \right)$$

giving K = 0.3205 and L_∞ = 86.75mm.

A frequency plot of all growth checks is included in this figure but it does not aid in assessing a point of known age from which an absolute growth curve may be calculated. H. australis may have two spawning seasons a year and distinct year classes would not be expected in the size range observed.

d. Growth relationships.

Growth relationships for H. australis appear in Table 4.9 and the length/weight relationship is graphed in Fig. 4.15. As in H. iris relative shell height increases significantly with length. H. australis is relatively heavier per unit shell length than H. iris and has a lower proportion of shell weight.

4.3.4 Discussion.

An absolute growth curve cannot be calculated for H. australis since no absolute length/age relationship is known.

The factors involved in growth in length of H. australis are the same as those in H. iris excent that as there is no posteriorly directed columella, total length is always measured. The individual asymptotic length varies, i.e. the plane of the spiral slopes down anteriorly much earlier in some individuals than in others. While the maximum length recorded for this species was 109mm, most specimens reach an asymptote about 80-90mm and a few grow no further beyond 70mm. This difference between the individual and the

population growth patterns, which has been noted for fish, e.g. Tesch (1968), may also hold for H. iris, but is especially noticeable in H. australis.

4.4 H. virginea.

4.4.1 Introduction.

H. virginea is rare in the Kaikoura area but an estimate of some growth parameters was possible from examination of shells of the 19 specimens collected. A sample of 39 shells from Stewart Island was available for comparison.

4.4.2 Methods.

Larger shells of H. virginea exhibit obvious growth checks (Fig. 4.13), the positions of which can be accurately estimated externally. The lengths at which they were deposited were measured with calipers to the nearest millimetre in samples of 10 shells from Kaikoura and 38 from the drift zone at Stewart Island. No checks were evident below 20mm. A Manzer & Taylor plot of adjacent pairs of checks was drawn for each locality and regression lines calculated. In the calculation of the von Bertalanffy growth constants, K and L_∞, all checks were assumed to be annual though no direct evidence for this was obtained.

Relationships between length, breadth and height of H. virginea shells were calculated for Kaikoura specimens.

4.4.3 Results.

Manzer & Taylor plots of adjacent shell checks appear in Fig. 4.14 with the length-frequency distribution of checks. The regression equations are

Kaikoura, $\underline{l}_{t+1} = 0.6402 (\underline{l}_t + 61.51)$

Stewart Island, $\underline{l}_{t+1} = 0.7240 (\underline{l}_t + 64.35)$

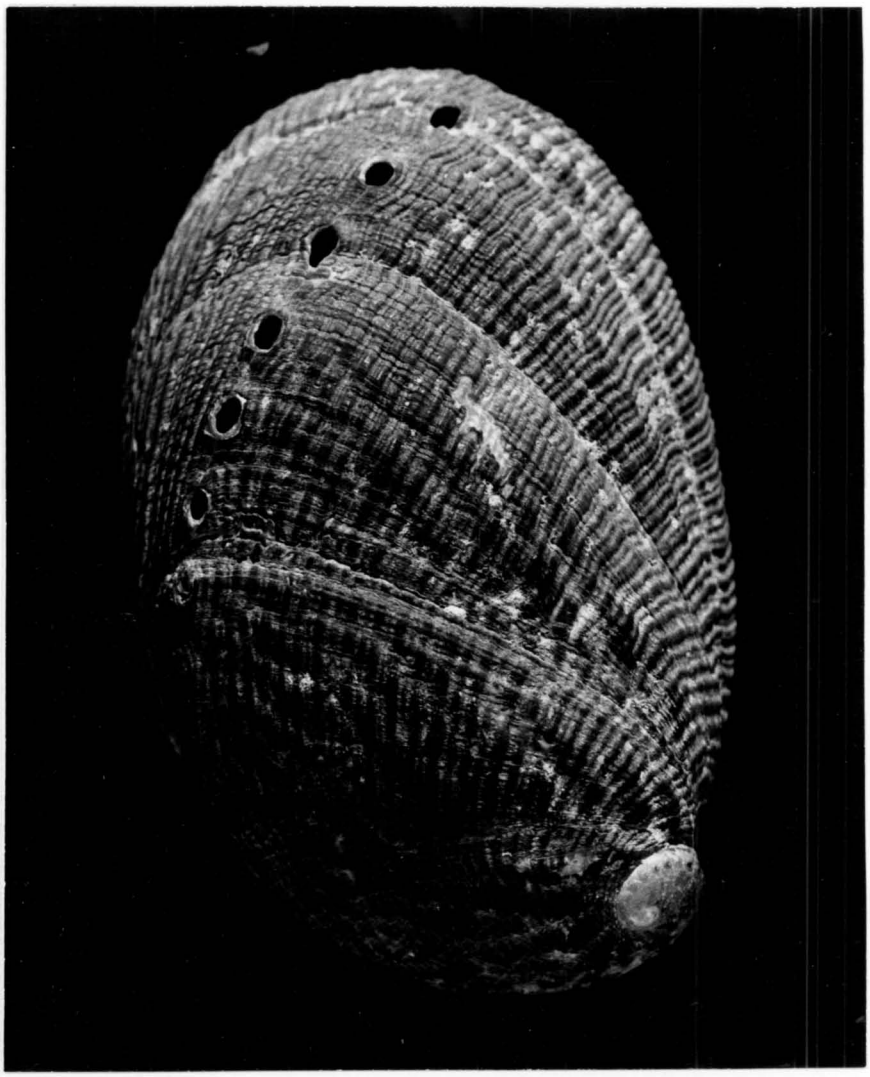


FIGURE 4.13

H. virginea shell showing three prominent growth checks. (2 x).

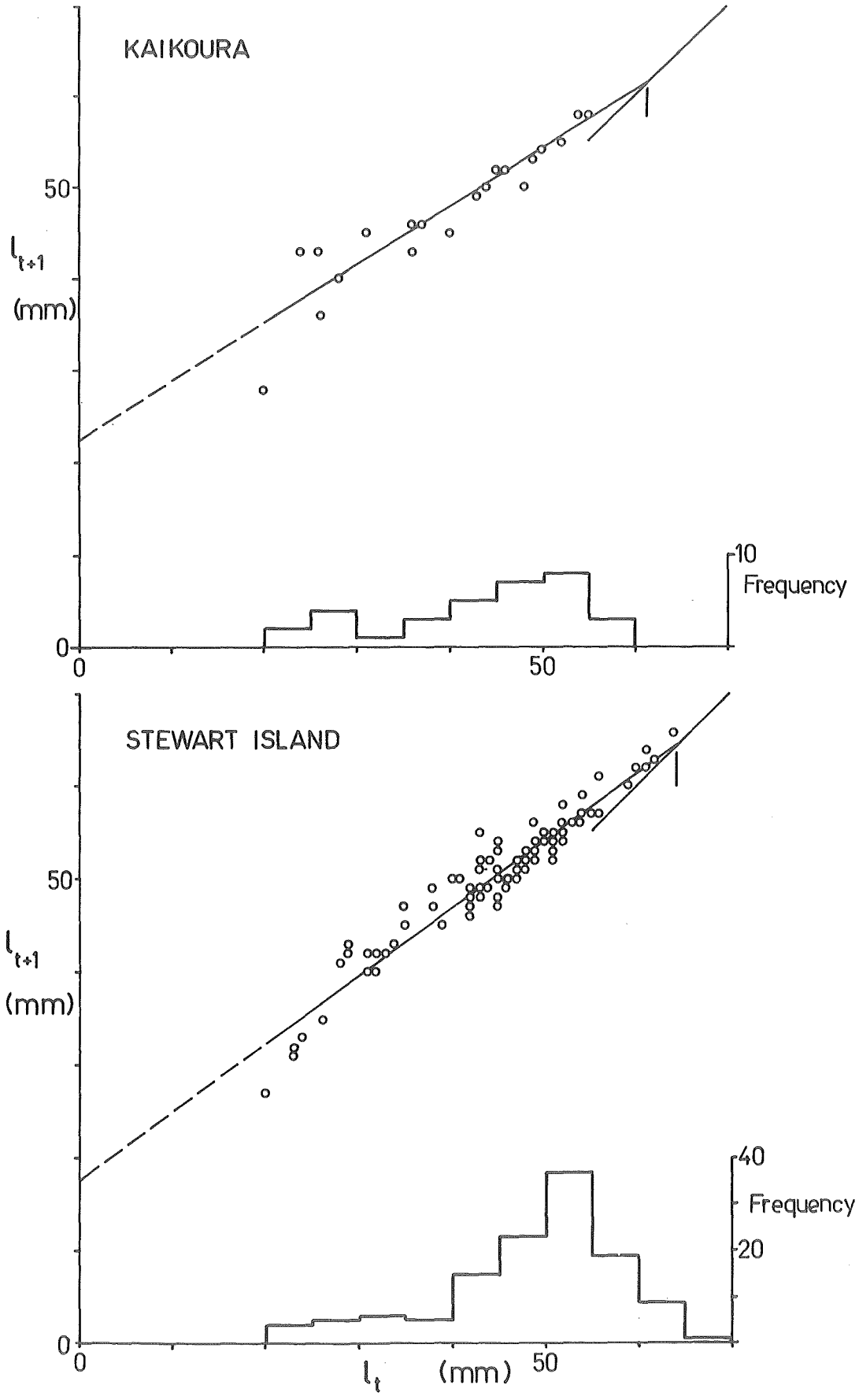

KAIKOURA
50
l_{t+1}
(mm)
0
0
50
10
Frequency
STEWART ISLAND
50
l_{t+1}
(mm)
0
0
l_t (mm) 50
40
Frequency
20

FIGURE 4.14

H. virginea growth. Manzer & Taylor plots of adjacent pairs of growth checks for Kaikoura and Stewart Island shells, and length-frequency histograms (in 5mm classes) of all growth checks.

giving the following values,

Kaikoura,	K = 0.4460	L_∞ = 61.51mm
Stewart Island,	K = 0.3231	L_∞ = 64.35mm.

The length-frequency distribution of checks of Kaikoura H. virginea shows two modes, the first of which is a possible year class with mean about 27mm. Its age is not known so it cannot validly be used as a reference point for an absolute growth curve.

Equations relating the three parameters of Kaikoura shells for the range 11-60mm (Table 4.9) show that H. virginea is proportionately narrower and higher than either H. iris or H. australis. Relative height is significantly greater in larger shells - this is not due to external encrustations in this species.

4.4.4 Discussion.

Values of K for H. virginea were similar to those for H. iris and H. australis although at Kaikoura it was a little higher. The largest specimen of the species was 64mm, 2mm shorter than the largest seen by Powell (1955). The largest collected at Kaikoura was 60mm.

The very definite growth checks in shells of H. virginea suggest considerable variation in growth rate through the year. No data were available to determine when maximum growth occurs but there is little reason to doubt that the checks were annual. Future determinations of growth rate, e.g. by tagging, must be done in populations denser than those at Kaikoura.

4.5 Conclusions.

The use of three techniques - analysis of length-frequency curves, tagging, and analysis of growth checks - has enabled estimation of absolute growth rate of H. iris and relative growth

rates of H. australis and H. virginea. The values of K, the coefficient of growth, do not differ markedly, so relative growth beyond the second or third year is similar in all three species. All available evidence, e.g. the length at which the first growth check is formed and the large proportion of H. australis which failed to grow over long periods, suggest that the shapes of the absolute growth curves of H. australis and H. virginea are little different from that of H. iris. Similar values of K (about 0.3 - 0.4) have been given for H. tuberculata (Forster, 1967) and can be deduced for H. discus hannai (Sakai, 1962c, d) and Notohaliotis ruber (Anon., 1967). This means that growth is rapid initially and slows down appreciably later. Only H. midae with K = 0.0593 has more gradual growth (Newman, 1968).

A number of species of Haliotis show some degree of seasonal growth (Table 4.8) but there seems to be no over all pattern within the genus. Nor is there any pattern in the presence or absence of growth checks which result from a period of very slow growth. While H. tuberculata, H. discus hannai, H. virginea and H. australis have them, H. rufescens, H. midae and H. iris do not; other species are not documented.

TABLE 4.8. Seasonal growth in Haliotis species.

Species	Period of most rapid growth	Author
H. tuberculata	autumn-winter	Forster, 1967
H. gigantea	winter	Ino, 1943
H. rufescens	winter	Cox, 1962
H. midae	winter-spring	Newman, 1968
H. discus hannai	winter-spring	Sakai, 1960, 1962
H. iris	spring-summer	this paper
H. australis	spring-summer	this paper
H. cracherodii	summer	Leighton & Boolootian, 1963

A correlation between the period of maximum growth and the period when the gonads are ripest and similarly, between minimum growth and maximum rate of development of gonads, has been shown in a number of species. A correlation with food availability has been demonstrated with H. discus hannai (Sakai, 1962c), and in H. iris and H. australis shell growth was inversely correlated with feeding rate (Chapt. 3). In H. iris growth rate of immature animals follows the same seasonal pattern of the adults, suggesting that the requirements of gonad production are not the sole cause of the slower growth rate; temperature is reduced during this time.

Accurate estimates of probable longevity are not possible for any species. H. australis shells, however, have a maximum of eight clear growth checks, most of them in the last few millimetres of shell. The high proportion of tagged animals which showed no growth suggests a long life at the asymptotic length. H. virginea showed a maximum of six growth checks. In neither case is the age at formation of the first check known, but in view of the fact that many older shells could not be analysed because of their erosion, longevity in both species is probably at least ten years. H. iris possibly lives much longer. Comfort (1957) cited at least 13 years as maximum age of H. rufescens.

Growth relationships have been calculated for a number of species of Haliotis: H. tuberculata (Crofts, 1929; Forster, 1967); H. gigantea (Sasaki, 1926; Nomura & Sasaki, 1928); H. discus hannai (Sakai, 1962d); H. midae (Newman, 1968); H. cracherodii (Leighton & Booloottian, 1963); H. diversicolor supertexta (Oba, 1964a). Most authors assume shell proportions to be isometrically related but some coefficients of allometry have been calculated.

There was no seasonal trend in percentage body weight in either H. iris or H. australis as has been shown in some other species (Ino & Harada, 1961; Oba, 1964a).

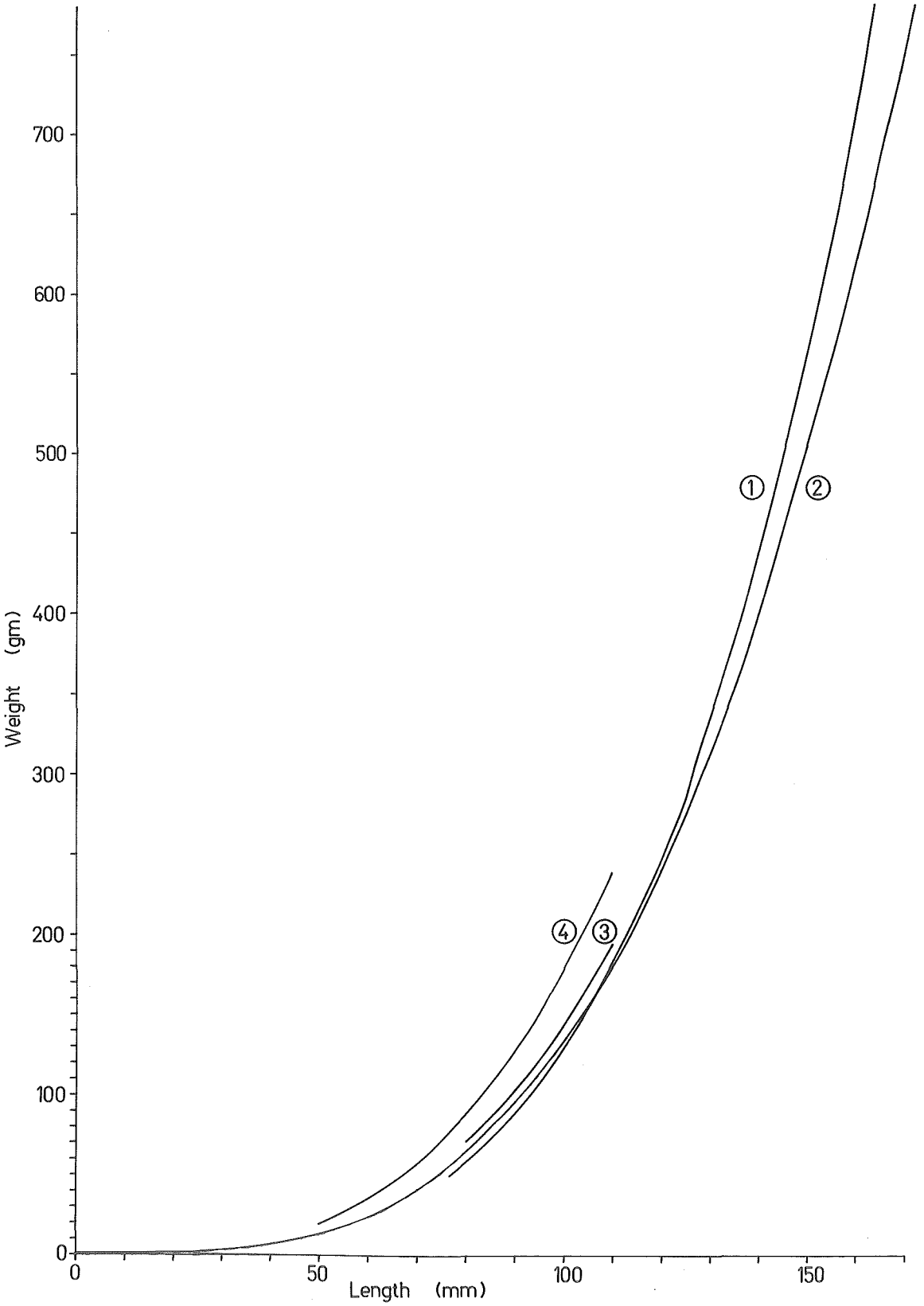

700
600
500
400
300
200
100
0
Weight (gm)
0
50
100
150
Length (mm)
①
②
③
④

FIGURE 4.15

Weight/length relationships for *Haliotis* species. 1, *H. iris*, Wellington (Cleaver, 1966); 2, *H. iris*, Kaikoura; 3, *H. iris*, Taylors Mistake; 4, *H. australis*, Kaikoura.

TABLE 4.9 Isometric and allometric coefficients for *Haliotis* species. *a* and *b* are constant and slope of isometric equation; *k* and α are constant and coefficient of allometric equation.

	ISOMETRIC		ALLOMETRIC	
	a	*b*	*k*	α
***H.iris*, Kaikoura**				
Breadth / Length	-2.6269	0.756	-0.208	1.034
Height / Length	-4.299	0.328	-0.846	1.141*
Total weight / Length	-	-	-4.331	3.228
Body weight / total weight	1.985	0.689	-	-
***H.iris*. Taylors Mistake**				
Breadth / Length	-4.631	0.755	-0.305	1.078
Height / Length	-3.093	0.333	-0.698	1.089
Total weight / Length	-	-	-4.317	3.238
Body weight / total weight	9.383	0.556	-	-
***H.iris*, Wellington (Cleaver, 1966)**				
Total weight / Length	-	-	-0.014+	3.579
Body weight / total weight	-	0.65	-	-
***H.australis*, Kaikoura**				
Breadth / Length	0.472	0.684	-0.153	0.996
Height / Length	-2.594	0.327	-0.870	1.177*
Total weight / Length	-	-	-4.041	3.144
Body weight / Total weight	1.223	0.766	-	-
***H.virginea*, Kaikoura**				
Breadth / Length	1.234	0.629	-0.146	0.979
Height / Length	-3.031	0.355	-0.931	1.229*

+ Original lengths in inches

* Coefficients of allometry marked thus are significantly different from one.

5. REPRODUCTION

5.1 Introduction.

Studies on reproduction contribute basic biological information useful in formulating regulations governing the fishery of commercial species. Knowledge of breeding seasons can be essential for the estimation of growth rates, particularly of young stages, and the relationship between age, fecundity and the minimum size at maturity must be taken into account when minimum takable size is determined.

Overseas, where Haliotis species have been fished commercially for many years, research on these aspects is extensive. Most work, however, has concentrated on the determination of spawning seasons; e.g. in Japan (Ino, 1952; Ino & Harada, 1961; Sakai, 1962d; Oba, 1964a) and in California (Boolootian et al., 1962). More comprehensive studies done in South Africa include estimations of fecundity (Newman, 1967).

No studies have been undertaken in New Zealand where H. iris is being fished on an increasing scale. In this contribution spawning seasons and fecundities of H. iris and H. australis are examined by regular sampling of populations at Kaikoura and Taylors Mistake.

5.2 Gametogenesis and Spawning seasons.

5.2.1 Methods.

Beginning July 14, 1967, monthly samples of about 25 individuals each of Haliotis iris and H. australis were taken from Wakatu Point, Kaikoura. Sampling of H. iris continued for 12 months and that of H. australis for almost two years. Samples were collected with the aid of SCUBA in 1-2m of water, all specimens were large adults (H. iris mean length = 132.1mm, H. australis mean length = 80.0mm). Shell length, total weight and shell weight were taken.

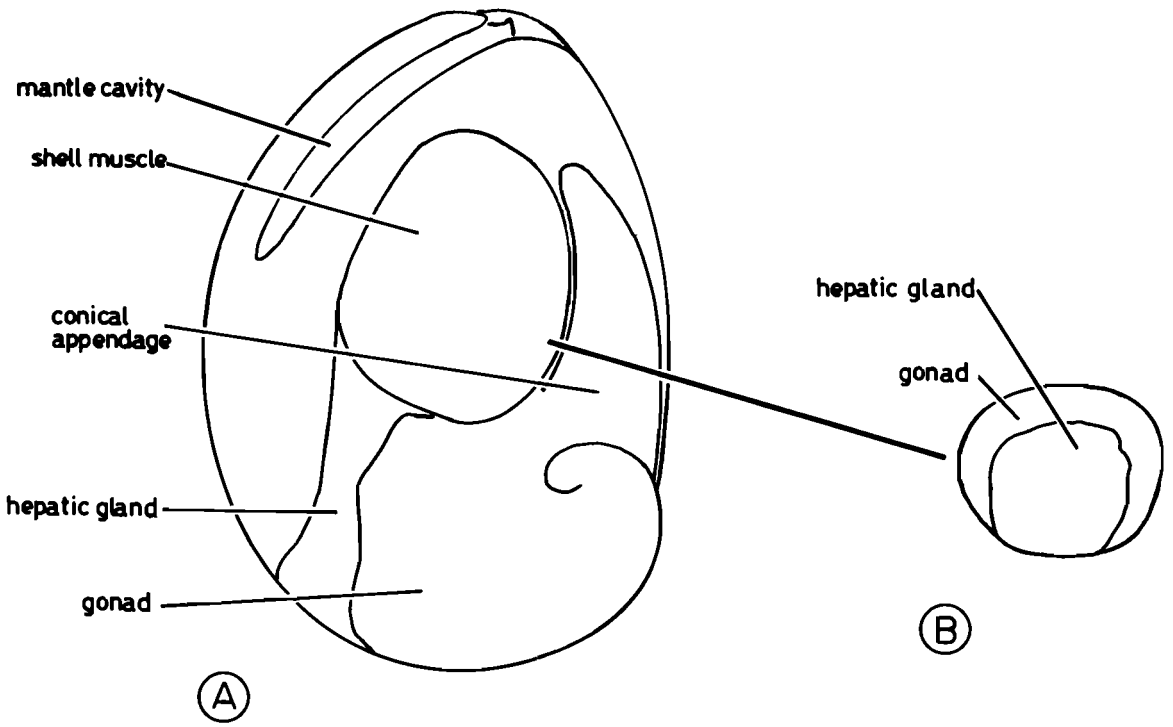

mantle cavity
shell muscle
conical appendage
hepatic gland
gonad
A
hepatic gland
gonad
B

FIGURE 5.1

Diagram of Haliotis with the shell removed to show the position of the section through the conical appendage and the shape of the exposed areas of hepatic gland and gonad used in calculation of the Gonad Index.

The conical appendage, which consists of a gonad sheath over the conical hepatic gland, was removed by cutting through the stomach region and then preserved in 10% formolsaline. When the conical appendage had hardened, it was sectioned at a point one third of the distance from the shell apex to its tip and the exposed areas of gonad and hepatic gland traced on to transparent "Permatrace" (Fig. 5.1). A planimeter was used to measure the areas either directly or after enlargement and a gonad index was determined for each individual from the formula:

$$\text{Gonad Index} = \frac{\text{gonad area}}{\text{total X-sectional area}} \times 100\%$$

This gonad index is similar to that used by Ino & Harada (1961), Boolootian et al. (1962), and Newman (1967) for Japanese, Californian and South African haliotids respectively. Because the gonad index chosen is virtually independent of length for the size range collected (Figs 5.6 & 5.8) it was not necessary to incorporate shell length as Boolootian et al. (1962) have done.

A similar series of monthly samples of H. iris was begun at Taylors Mistake near Christchurch on February 27, 1968 and continued until June 1969. Unfavourable diving conditions caused the gaps in this series. Body weight and shell weight were measured in only the first two months of the series. H. iris is smaller at this locality than at Kaikoura, mean length being 95.1mm. H. australis is not common at Taylors Mistake and was not sampled.

Although the mean gonad index showed a definite trend throughout the year microscopic examinations of ovaries were made to measure actual gametogenic activity. Small samples taken from a number of formalin hardened ovaries each month (starting September 1967) were dispersed in water with a mechanical agitator. Two reasonably distinct classes of cells were evident in all three species: (a) small cells in which the nucleus is clearly visible in the pale

cytoplasm, isodiametric when small but becoming stalked when larger, up to 130 X 50 μ ; and (b) larger yolky cells in which the nucleus is not obvious, up to 400 X 200 μ when stalked but 250 μ when rounded mature eggs. The two classes were least distinct in the post-spawning periods when the whole range of gametogenic stages was present. Bolognari (1954) gave a more complete picture of the stages of both male and female gametogenesis in H. lamellosa and Newman (1967) discussed the structure of ovaries and testes of H. midae. The percentage yolky eggs was calculated after counting the numbers of cells in each class in ten microscope fields. Because of the difficulty in removing all the smaller cells from the gonad trabeculae these were probably underestimated. Notes were made on the size and shape of the cells each month.

Searches for newly-settled individuals failed to produce results and did not help in critically delimiting the spawning season.

Temperature recordings were taken every 6 minutes by the Chart Recorder on the New Wharf at Kaikoura and the mean noon temperature for each month was calculated from these. At Taylors Mistake the temperature was taken each month with a thermometer.

To define the length of the spawning season more closely and compare spawning in two subsequent years, sampling was resumed at Wakatu Point at the beginning of February 1969 and continued into June. Samples in this series were taken weekly at first (or as sea conditions allowed) but became less frequent later. Temperature records from the Chart Recorder were retained in the hope that spawning might be correlated with some temperature change.

5.2.2 Results.

a. H. iris, Kaikoura.

One distinct short breeding season was evident in H. iris in 1968, manifesting itself as a sudden drop in Gonad Index and in percentage yolky eggs during March and April (Fig. 5.2). Notes

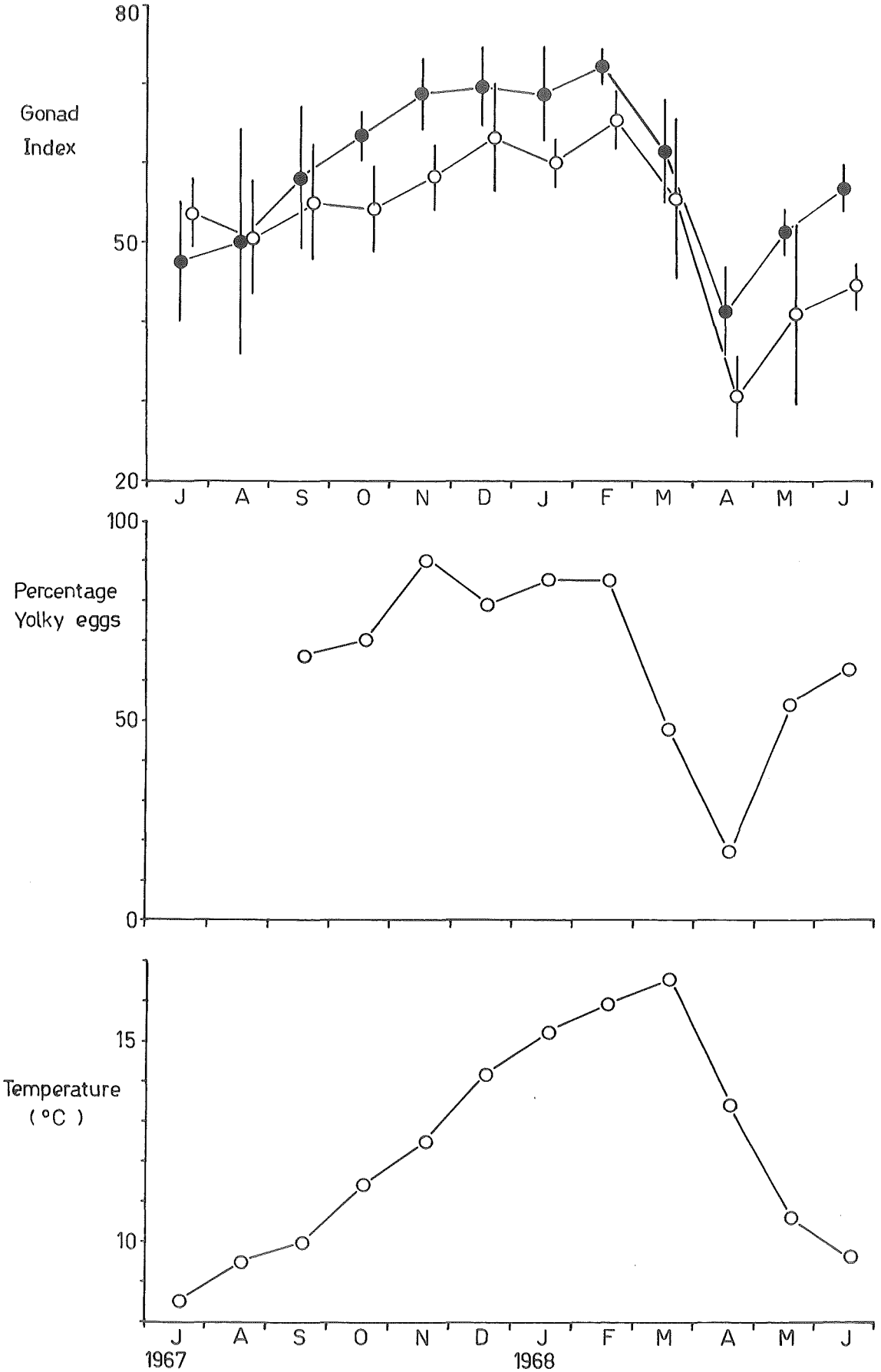

Gonad
Index
80
50
20
J
A
S
O
N
D
J
F
M
A
M
J
Percentage
Yolky eggs
100
50
0
Temperature
(°C)
15
10
J
A
S
O
N
D
J
F
M
A
M
J
1967
1968

FIGURE 5.2

H. iris, Kaikoura 1967-8. Monthly Gonad Indices (means and 95% confidence limits), percentage yolky eggs and mean monthly sea temperatures. Open circles female, filled circles male.

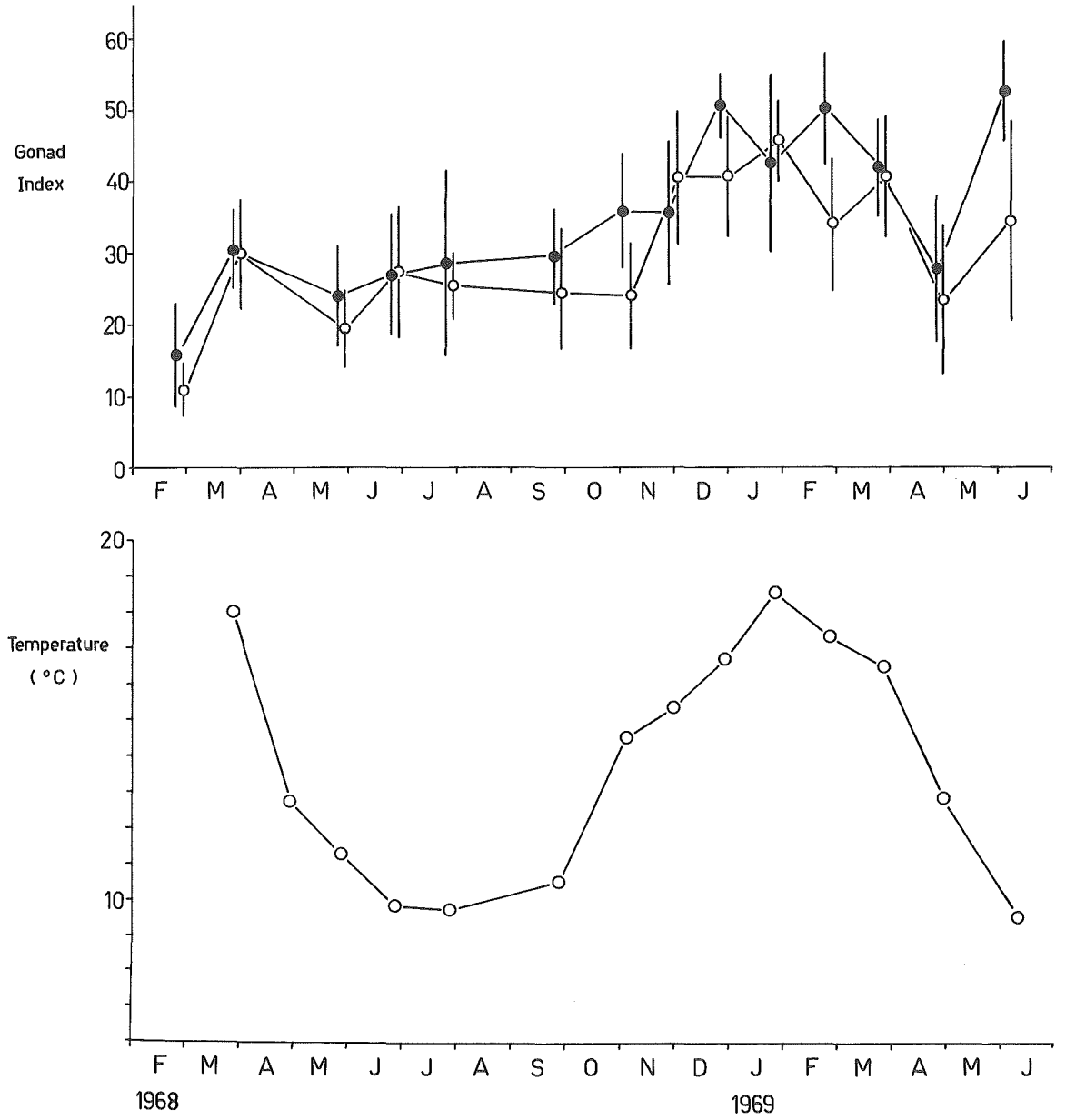

Gonad
Index
60
50
40
30
20
10
0
F M A M J J A S O N D J F M A M J
Temperature
(°C)
20
10
F M A M J J A S O N D J F M A M J
1968
1969

FIGURE 5.3

H. iris, Taylors Mistake 1968-9. Monthly Gonad Indices (means and 95% confidence limits) and monthly sea temperatures. Open circles female, filled circles male.

made on gametogenic stages present in ovaries through the year assisted in defining the season further. From September through to February the ovary consisted mainly of free rounded eggs and a few earlier stages attached to the trabeculae. In both March and April there was a marked reduction in the number of mature eggs and an increase in the number of younger stages. In mid-April a complete range of stages was present though there were few rounded eggs. In June many ripe eggs had appeared though younger stalked stages were still present; by August most stalked dense cells were replaced by rounded eggs. This suggests that spawning occurred in late February and March and may have extended into early April; rapid post-spawning recovery is suggested by the long period in which mature eggs were present. The low values of Gonad Index in June 1967 suggest that spawning occurred at a similar time in 1967.

To date (July 1969) no definite spawning has occurred at Wakatu Point or at other areas near Kaikoura (Fig. 5.5). Gonad Indices remain high and ovaries remain full of rounded eggs.

This estimation of the spawning season is supported by observations of spawning in the field and in the laboratory. Spawning at an earlier date could be induced in the laboratory and Graham (1941) recorded a female spawning in an aquarium in December at Dunedin but there is no evidence to support earlier mass spawning in the field.

b. H. iris, Taylors Mistake.

The Gonad Index graph for H. iris from Taylors Mistake follows the same general trend as that for Kaikoura (Fig. 5.3) but differs in some respects. The very low Gonad Index in February 1968 is evidence of a recent spawning, probably about a month before the equivalent autumn spawning at Kaikoura. Gonad Indices were much lower at Taylors Mistake than at Kaikoura but spawning (in 1968 at least) was virtually complete. Also, Taylors Mistake H. iris had a much slower post-spawning recovery rate than those at Kaikoura and

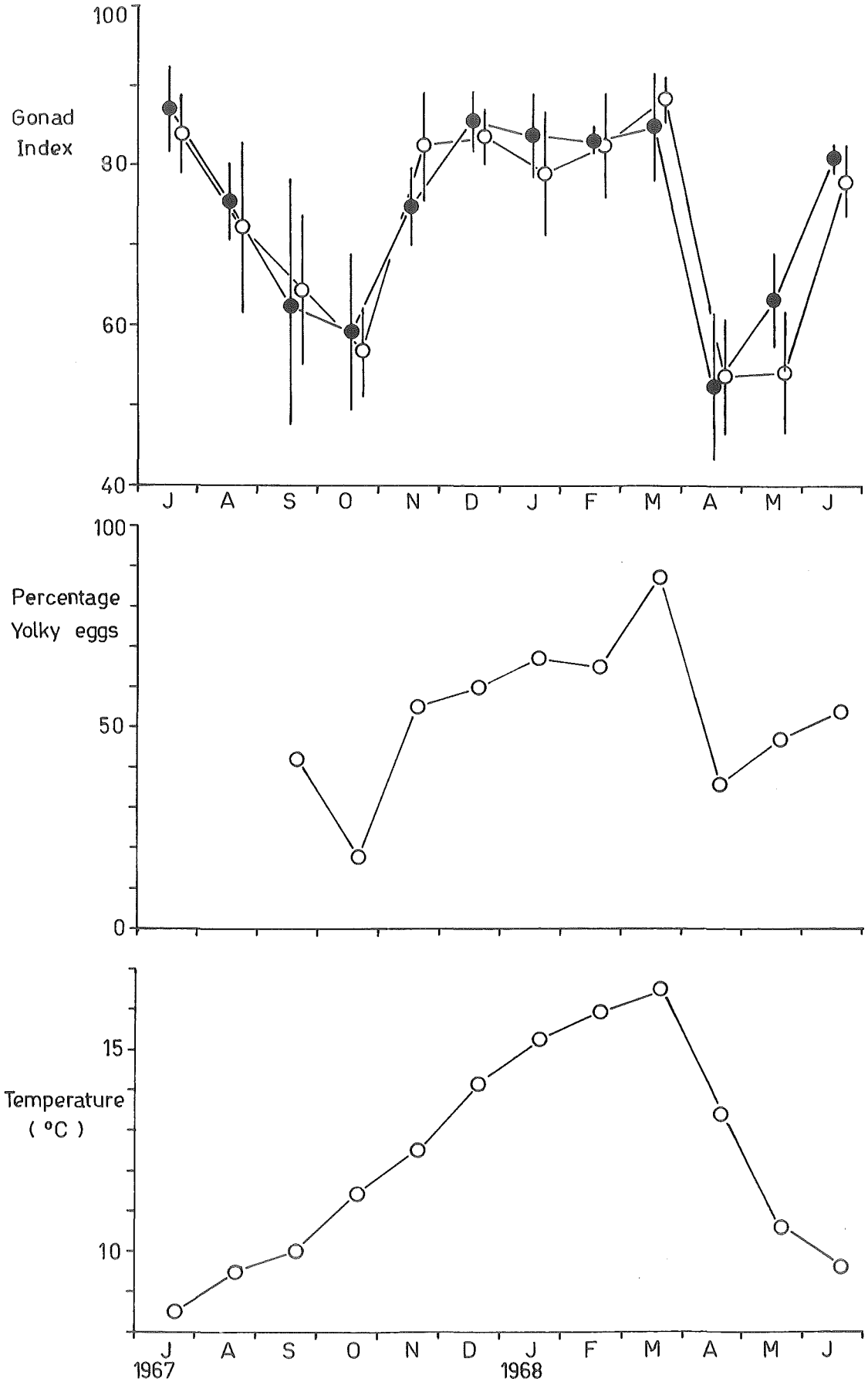

Gonad Index
100
80
60
40
J A S O N D J F M A M J
Percentage Yolky eggs
100
50
0
Temperature (°C)
15
10
J A S O N D J F M A M J
1967
1968

FIGURE 5.4

H. australis, Kaikoura 1967-8. Monthly Gonad Indices (means and 95% confidence limits), percentage yolky eggs and mean monthly sea temperatures. Open circles female, filled circles male.

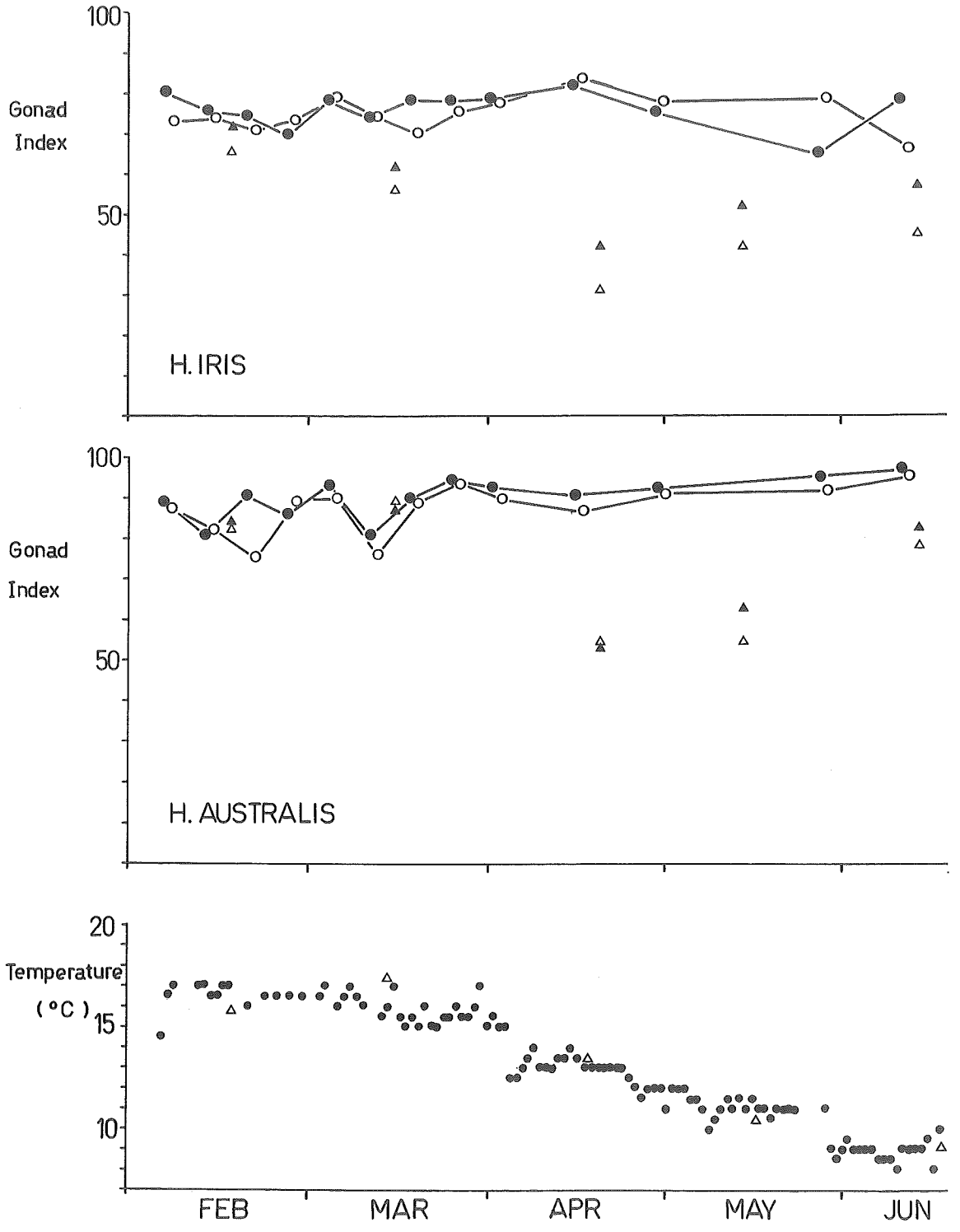

100
Gonad
Index
50
H. IRIS
100
Gonad
Index
50
H. AUSTRALIS
20
Temperature
(°C)
15
10
FEB
MAR
APR
MAY
JUN

FIGURE 5.5

H. iris and H. australis, Kaikoura 1969. Mean Gonad Indices and daily noon sea temperatures. Open circles female, filled circles male. Triangles represent monthly data from 1968 (see Figs. 5.2 and 5.4).

consequently spent a long time in a spent condition. The pattern differed in 1969 when ripe eggs were held right through the winter except for a possible partial spawning in April. This was at least two months later than in 1968 and was not as marked.

c. H. australis, Kaikoura.

The Gonad Index graph and percentage yolky eggs for 1967-8 (Fig. 5.4) indicate a more complex reproductive cycle for H.australis than H. iris. Two spawning seasons were apparent, one lasting from late winter into spring (July through to October) and another in early autumn (late March to early April). This pattern is supported by examination of gametogenesis as young stalked stages were most abundant in September and October and again in April. Rapid post-spawning recovery was indicated after both spawnings and maximum gonad size was maintained for several months before the autumn spawning. Although spawning occurred over a shorter period in autumn than in spring the relative importance of the two cannot be estimated.

All monthly samples taken from July 1968 to February 1969 had high Gonad Indices except for a slight fall of about 10% in females between August and September and a subsequent build-up. The major spring spawning of 1967 was not repeated this year. Samples from February to June 1969 showed the same failure to spawn evident in H. iris (Fig. 5.5).

H. australis was never observed to spawn in the field or in aquaria, except when artificially stimulated.

5.2.3 Discussion.

The obvious inconsistency in spawning patterns of both species between years make generalisations based on one year's observations unreliable. The delay (or failure) of spawning in 1969 occurred in both species and also at both Kaikoura and Taylors Mistake. The physical factor or factors controlling the reproductive cycle operate

on both species independently and over a wide geographical range. In contrast, the echinoid Evechinus chloroticus spawned in the early autumn in both 1968 and 1969 at Kaikoura (Dix, 1969) so either responds to different stimuli or has different thresholds of activity.

The differences could not be explained in terms of temperature cycles. Temperatures were similar in both years although the maximum in 1969 was about a month earlier than in 1968 (Fig. 5.5). Comparable monthly temperatures from Taylors Mistake are also similar (Fig. 5.3).

Spawning seasons of several species of Haliotis have been deduced by a variety of methods (Table 5.1). Of these, histological examinations and the use of gonad indices are the most reliable techniques. Few direct observations of spawning in the field have been made. Although there is a wide range of spawning seasons, most are short, two or three months. Most species spawn in the late summer or autumn, although a few have additional or alternative seasons. H. australis, H. discus hannai, and H. midae at two localities also spawn in the spring, and H. midae at a third locality spawns only in the spring. H. rufescens may spawn at all times of the year (Boolootian et al., 1962) but other authors (Carlisle, 1962; Cox, 1962) believed actual spawning occurs only over a more restricted period. Spawning seasons vary between localities for a number of species and also vary between years (Newman, 1967) though not as much as in H. iris or H. australis. These general conclusions on spawning seasons of Haliotis differ slightly from those of Boolootian et al. (1962) who also tabulated the Haliotis spawning seasons then known.

Reproductive cycles are often correlated with sea temperatures (Orton, 1920; Giese, 1959). In Haliotis the correlation is slight but autumn spawning often follows one or two months after the maximum temperature. Although temperature change has been used to stimulate spawning in the laboratory in this study and by Oba (1964b) and Ino (1952) the same phenomenon has not been demonstrated in the

Species	Author	Locality	Method	Spr			Sum			Aut			Win		
				F	M	A	M	J	J	A	S	O	N	D	J
H.discus hannai	Ino, 1952	Chiba, Japan	l							*	X	X	X		
	Ino & Harada, 1961	Ibaragi	g			X	X				X	X	X	X	
	Kan-no & Kikuchi, 1962	Matsushima Bay	-							X	X				
	Sakai, 1960, 1962d	Miyagi	-						X	X	X				
	Ono, 1932 (Ino, 1952)	Hokkaido	-							X	X	X	X		
	Tago, 1931 (Boolootian et al.)	Tokyo	-							X	X				
H.gigantea	Ino, 1943, 1952	Chiba, Japan	l							*	X	X	X		
	Kishinouye, 1894 (Ino, 1952)	warmer Japan	-										X	X	
	Tago, 1931 (Boolootian et al.)	colder Japan	-								X	X			
H.sieboldii	Ino, 1952	Chiba, Japan	l							*			X		
H.diversicolor supertexta	Oba, 1964a, pers.comm.	Chiba	g						x	x	x	X	X		
H.kamatschatkana	Quayle, pers.comm.	B.C. Canada	l					x	x	x					
	Robilliard, p.comm.	Washington	-					x	x	x					
H.cracherodii	Boolootian et al., 1962	Monterey, Calif.	g					X	X	X	X	X			
H.rufescens	Boolootian et al., 1962	Monterey, Calif.	g	X	X	X	X	X	X	X	X	X	X	X	X
	Carlisle, 1962	Monterey, Calif.	l						X	X	X				
	Cox, 1962	California	h				X	X	X	X	X				

				J	F	M	A	M	J	J	A	S	O	N	D
H. tuberculata	Crofts, 1937	Channel Is.	l						x	X	X*	X	x	x	
	Wegmann, 1884 (Boolootian *et al.*)	Roscoff, France	-							X	X*				
H. lamellosa	Bolognari, 1954	Messina, Sicily	h						x	x	X	X	x	x	
H. midae +	Newman, 1967	Stony Pt, S.A. '63-4	g,h				X	X	X			X			*
		Sea Pt, '62-3	g,h			X	X	X							
		Sea Pt, '63-4	g,h	X	X										X
		Dassen Is., '62-3	g,h			X	X				X	X	X		
		Dassen Is., '63-4	g,h	x	x						X				
H. iris +	This paper	Kaikoura, N.Z. '68	g,h								*X	X			
		Kaikoura, '69	g,h								*				
		Taylors Mistake '68	g,h							X*					
		Taylors Mistake '69	g,h							*		x			
H. australis +	This paper	Kaikoura, N.Z. '67-8	g,h			X	X				*	X			
		Kaikoura, '68-9	g,h			x					*				

TABLE 5.1 Spawning seasons of *Haliotis* species. Southern hemisphere species (+) spawning seasons have been converted to equivalent northern months. X denotes definite spawning, x probable spawning. Time of maximum water temperature is denoted thus (*) where it is known, except at Sea Pt and Dassen Is. where there is no definite maximum. The methods of estimating spawning season are as follows: g, use of a gonad index; h, examination of nature of gonads casually or by detailed histological methods; l, observations of spawning or of fertilization in the laboratory.

field. Wide and rapid temperature changes, such as are used in laboratory stimulations, are rare naturally but data from the Chart Recorder at Kaikoura show that a 2.5°C change (one quarter of the annual range) is possible in one day (Fig. 5.5). Fretter & Graham (1964) discussed the effect of environment on breeding in molluscs, noting that maturation of gametes is controlled by annual temperature fluctuations but a combination of other factors may trigger spawning. This difference between maturation and spawning stimuli was also noted by Giese (1959). Spawning stimuli may include mechanical disturbance (Medem, 1948 cited by Cox, 1962), or for females, the presence of sperm in the water (Murayama, 1935).

The demands of gonad production have repercussions in feeding behaviour and growth rate. In both H. iris and H. australis feeding was maximal in the winters of 1967 and 1968 when gonads were recovering from earlier spawnings. Growth of the shell slowed in the winter when the gonads were growing.

5.3 Minimum age of maturity and Fecundity.

5.3.1 Methods.

In January 1969 when the gonads were ripest, stratified samples of all available sizes of H. iris and H. australis were made to determine the minimum age of maturity of each species and the fecundity of females of various sizes. Ten individuals from each centimetre length class were collected from subtidal and intertidal areas around the Kaikoura Peninsula. The conical appendage of each individual was preserved in 10% formolsaline and a Gonad Index calculated for each in the manner described in Section 5.1.

Two females from each relevant centimetre size class were chosen for fecundity estimates. The ovary was carefully dissected from the hepatic gland and stomach to which it attaches, and weighed to the nearest 0.1gm. Then a fragment of about 0.1gm was weighed to the nearest 0.001gm and dispersed in water, care being taken to

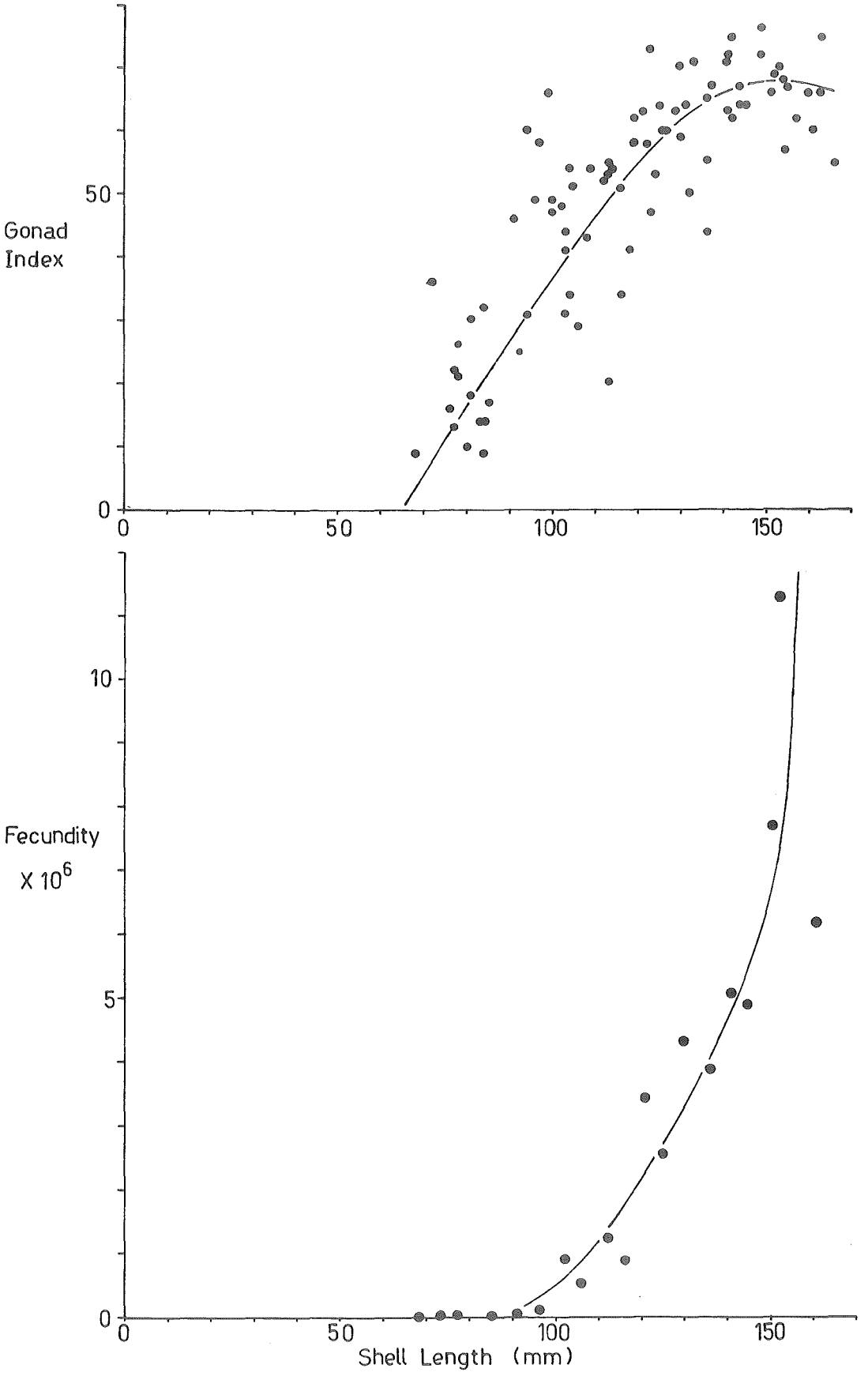

Gonad
Index
50
0
0
50
100
150
Fecundity
X 10^6
10
5
0
0
50
100
150
Shell Length (mm)

FIGURE 5.6

H. iris, Kaikoura. Gonad Index - Length relationship in January 1969; line fitted by eye.

FIGURE 5.7

H. iris, Kaikoura. Fecundities in January 1969; line fitted by eye.

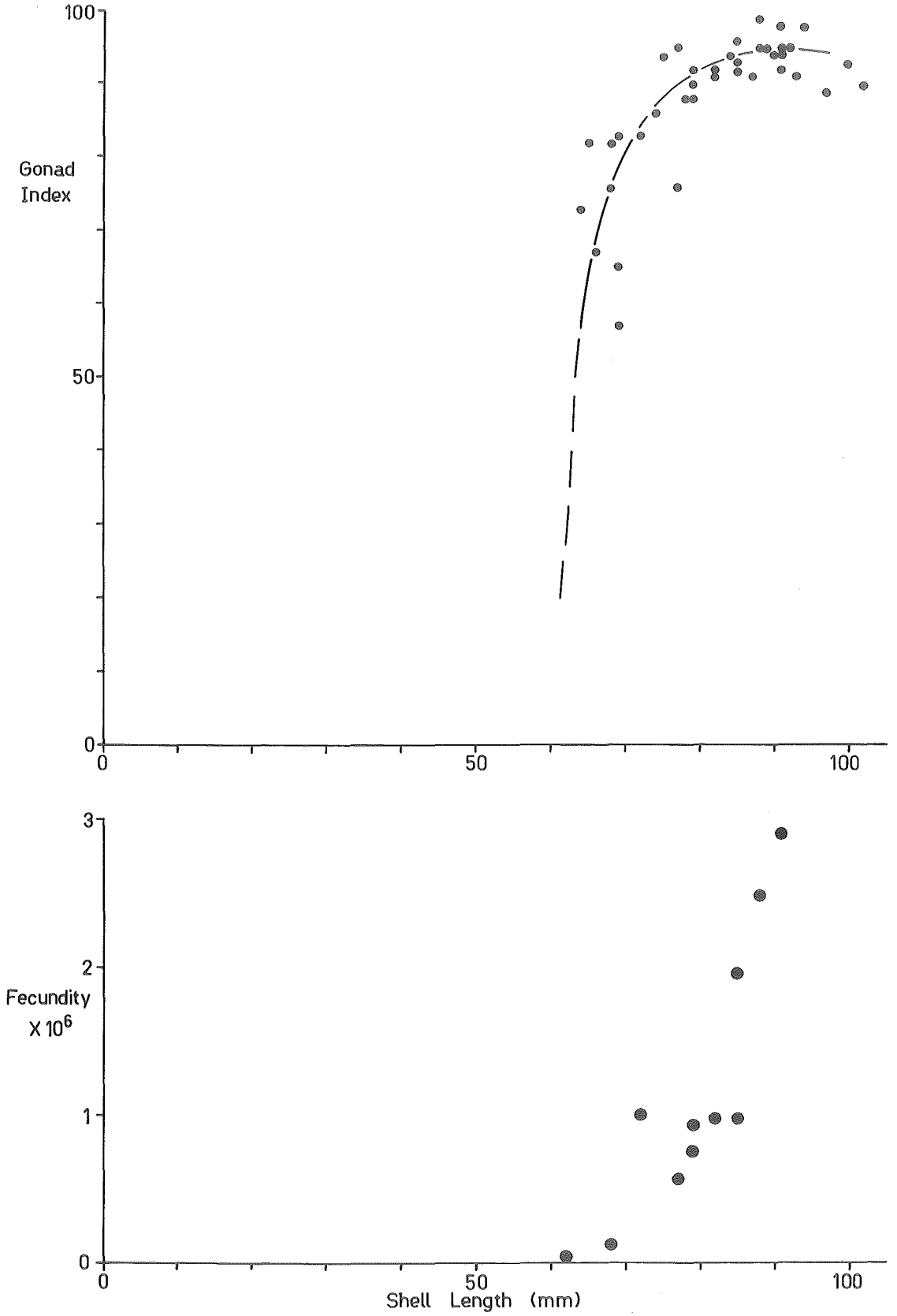

100
Gonad
Index
50
0
0
50
100
3
2
Fecundity
X 10^6
1
0
0
50
100
Shell Length (mm)

FIGURE 5.8

H. australis, Kaikoura. Gonad Index - Length relationship in January 1969; line fitted by eye.

FIGURE 5.9

H. australis, Kaikoura. Fecundities in January 1969;

remove all eggs from the trabeculae. While the eggs were spread evenly over a shallow petri dish (8.5cm diam.) those in 20 binocular microscope fields (field diam. 0.5cm) were counted. As the eggs in all individuals were roughly the same size the number counted came in the range 1150 ± 200 for both species. Fecundity, here defined as the number of ripe eggs present in the ovary prior to spawning, was calculated by multiplying by the appropriate factor. Additional fecundity estimates were made for H. australis in July 1968 prior to the spring spawning.

5.3.2 Results.

The minimum age of maturity of H. iris is indicated by the lengths of two smallest individuals containing ripe eggs, 58mm and 65mm; H. iris smaller than this do have gametogenic cells. The gonad first forms on the dorsal-inside of the conical appendage as a branching system of trabeculae. This stage which can be first recognised at 33mm corresponds to the "juvenile undifferentiated" stage of Bolognari (1954). Ripe eggs appear in number and the Gonad Index becomes measurable only above 68mm. H. iris of this length are 3 years old at this time of year.

The number of eggs counted in H. iris ranged from 1,286 at 68mm to 11,253,000 at 155mm (Fig. 5.7). The fecundity estimate for the H. iris 161mm long is disproportionately low, about 50% less than expected. A partial spawning may be indicated but there is a slight tendency for gonad indices and, from this fecundities, to be slightly lower in the largest females (Fig. 5.6).

Ripe eggs are first noted in H. australis of 55mm and the minimum age of maturity is probably 2 or 3 years in this species. The juvenile undifferentiated stage ranges from 36mm to 60mm. Recorded fecundities range from 46,000 at 62mm to 2,910,000 at 91mm (Fig. 5.9). Fecundities of H. australis in July 1968 were generally lower than those of summer. For 10 abalones between 67 and 87mm fecundity ranged from 195,000 to 1,380,000 (mean = 725,000, s.d = 368,000

The early spring spawning following this fecundity estimate was only slight (compared with a major spawning in the previous spring) so fewer eggs than this would have been released.

5.2.3 Discussion.

In its strictest sense fecundity refers to total egg production. As it is used here fecundity is the total number of eggs present in the ovary prior to spawning; very rarely are all these eggs shed in the short spawning season. Spent or empty gonads of H. iris were never found at Kaikoura, although at Taylors Mistake all gonads were spent in February 1968. Occasional spent H. australis gonads are found at Kaikoura in the autumn but generally gonads were only partially empty. Post-spawning gonads are proportionately smaller in H. australis than in H. iris (Figs 5.2 & 5.4).

The large stratified sample in January was taken about two months before the predicted spawning season. As it happened spawning was not recorded in 1969 but Gonad Indices did not increase after January (Fig. 5.5) gonads being at maximum ripeness all that time.

The minimum age of maturity, here defined as the minimum age at which ripe gonads are present, is not necessarily the minimum age at which the first substantial spawning occurs. In H. iris only 20% of the sample of 10 in the 50-59mm size class could be sexed, 30% in the 60-69mm class, 80% in the 70-79mm class and 100% of all above 80mm. But only above 100mm does the number of eggs produced reach 100,000 (Fig. 5.7). Therefore no significant contribution to the total number of eggs produced by the population in one season is made by females less than four years old. In H. australis no individuals less than 50mm could be sexed, between 50-59mm all could be sexed but few mature gametes were seen; above 60mm fecundity quickly reached a maximum (Fig. 5.9).

H. iris and H. australis differ in this respect from H. midae which was studied in detail by Newman (1967). Although the smallest individual with recognisable gonads was about 4 years old (60mm

shell breadth), at 7 years old (80mm) only 50% of the sample could be sexed and 100% only at 11 years (100mm). The relevant ages were calculated by this author from Newman (1968: Fig 12). The attainment of full maturity is therefore much slower in this species and also more variable between individuals than either New Zealand species.

Although fecundities reach higher values in H. midae (up to 25 million) they bear a similar relationship to body weight as in H. iris:

H. midae	$F = 0.0198\ W - 2.196$
H. iris	$F = 0.0170\ W - 1.528$
H. australis	$F = 0.0005\ W + 1.124$

where F is the fecundity in millions and W is the body weight in grams. H. australis differs in that fecundity and Gonad Index are little dependent on weight or length once maturity is reached (see also Figs 5.8 & 5.9). The latter species in particular supports Palmer (1907) who said "the reproductive system of Haliotis is interesting ... because of the lateness of its development and the rapidity of the same once begun."

Fecundity has been estimated in few other Haliotis species. Graham (1941) observed one female H. iris spawn "about a million eggs" on one occasion in the laboratory. Partial spawnings, such as this must have been, can be induced in laboratory conditions. One female H. sieboldii produced about 140,000 eggs in one spawning (Ino, 1952). Fretter & Graham (1964) cite 10^4 as the number of eggs produced by H. tuberculata; Crofts (1929) says the number is "extremely great". Minimum size and age at maturity have been reported in three other species of Haliotis: H. cracherodii, 8-9cm long (Palmer, 1907); H. discus hannai 8cm long (Ino & Harada, 1961), i.e. about 4 years old (Sakai, 1962d), H. tuberculata 5cm long or 3 years old (Crofts, 1927, 1937). Although Bolognari (1954) mentioned that the juvenile undifferentiated gonad first appears at

15mm in H. lamellosa he did not comment on the first appearance of ripe gametes. It is possibly similar to H. tuberculata since Gaillard (1958) considered these two morphological varieties of the same species.

5.4 Sex ratio.

The sex ratio is not significantly different from one to one in either Haliotis species (Table 5.2).

TABLE 5.2. Distribution of sexes of H. iris and H. australis.

		♂♂	♀♀	Ratio ♂♂ : ♀♀	χ^2	p
H. iris	Kaikoura	252	242	1.04 : 1	0.20	0.75 - 0.50
	Taylors Mistake	154	181	0.85 : 1	2.18	0.25 - 0.10
H. australis	Kaikoura	334	296	1.13 : 1	2.30	0.25 - 0.10

Sinclair (1963) found 352 males in a sample of 598 H. iris from Wellington, the probability of such a result under conditions of equal representation being less than 0.01. This suggests a difference in the relative numbers of each sex which is not apparent at Kaikoura or at Taylors Mistake. H. midae, H. cracherodii, H. rufescens and H. tuberculata have almost equal numbers of each sex (Newman, 1967; Boolootian et al., 1962; Crofts, 1937) though a preponderance of males has been recorded in the last species (Foster, 1962; Stephenson, 1924). However, Bolognari (1954) reported 43.10% of a sample of 2237 H. lamellosa to be female; this result was highly significantly different from equal representation of sexes. Females tend to be more numerous in populations of older

molluscs (Fretter & Graham, 1964; Comfort, 1957) but in Haliotis the trend, if any, is the other way. This is also the case for Chiton tuberculatus (Crozier, 1918).

During summer, sexes of H. iris are readily distinguished on gonad colour, males are creamy-white and females deep green. This is the case in most other species of Haliotis (Boolootian et al., 1962; Newman, 1967). In the post-spawning period, i.e. March through to May in 1968, the gonads of both sexes became pale green and could be distinguished only microscopically. The phenomenon was otherwise recorded only for H. lamellosa (Bolognari, 1954) though both Crofts (1929) and Ino (1952) noted that the colour difference is more marked in "mature" H. tuberculata and H. discus hannai. H. australis could be sexed easily on colour at all times though in this species the ovary is brown (it turns green in formalin or alcohol). H. australis can be sexed alive by pushing down the foot on the right side and noting the colour of the gonad but black pigment obscures this organ in H. iris.

No hermaphrodite specimens were seen although this condition has been recorded in H. gigantea (Murayama, 1935).

6 CULTURE OF LARVAE.

6.1 Introduction.

Culture of larvae and juveniles of Haliotis species is receiving increasing attention, especially in Japan where it is being treated as an economic feasibility to supplement harvesting of natural populations. Preliminary small scale experiments have been done and work is now being concentrated on mass culture techniques (Oba, 1964b). Detailed anatomical studies of larvae have been made for H. tuberculata (Crofts, 1937), H. discus hannai and H. sieboldii (Ino, 1952) with less detailed descriptions of other species.

No work on the culture of New Zealand species has been done; this contribution describes methods of stimulating spawning, anatomy of pelagic larval stages, and some experiments on larval behaviour.

Haliotis is dioecious and the sexes shed their gametes freely into the water through the respiratory pores. Fertilization is external and a short-lived pelagic phase is entered before settlement. H. iris and H. australis spawned in 1967 and 1968 in late summer through autumn, maintaining ripe gonads through most of the 1967-8 summer. Although gonads were ripe throughout the 1968-9 summer, natural spawning was not recorded this year. Some preliminary experiments on spawning stimulation were carried out with little success in the summer of 1967-8 but most of the work described was done between November 1968 and the end of March 1969, after the first spontaneous laboratory spawning on November 5.

6.2 Review of spawning stimulation techniques.

Natural Spawning. Gametes produced naturally by Haliotis in the laboratory have been used successfully for larval cultures (Crofts, 1937; Kan-no & Kikuchi, 1962). The appearance of gametes naturally is unpredictable and some simple methods have been used to

induce it. Simple mechanical stimuli, e.g. disturbing the water (Medem, 1948 cited by Cox, 1962) or handling (Ino, 1952), may initiate natural spawning, as may washing females with naturally produced sperm (Murayama, 1935). Both H. iris and H. australis spawned rarely in the laboratory without inducement, all those that did were males, spawning just after collection.

Electrical Stimulation. Application of electrical current to oysters or mussels (Iwata, 1950; Nagabhushanam & Sarojini, 1963) is a reliable spawning stimulus and has been used for one species of Haliotis (Kan-no & Kikushi, 1962). On several occasions a 12v current was applied across the foot of H. iris and H. australis; although the foot moved vigorously spawning was never induced.

Injection of KCl solution. Injection of isotonic (ca 0.5M) KCl solution is a reliable technique for inducing spawning in sea urchins (Tyler, 1949) but is not suitable for Haliotis. Although sperm was produced by all male H. iris injected, eggs appeared only once. H. australis never responded and both species produced copious amounts of mucus from the hypobranchial gland. Carlisle (1945) also failed to obtain a response from H. rufescens with this technique.

Exposure to Air. Carlisle (1945) found that male H. rufescens would spawn after exposure to the air for an optimum time of 75 minutes. Females, washed with sperm, spawned 6-8 hours after being replaced in water. This method gave some success with male H. iris but females did not respond.

Thermal Shock. Use of temperature change to stimulate spawning has been used in one form or another by many experimenters. A single elevation of temperature often initiates release of gametes from many molluscs (Loosanoff & Davis, 1963) but Kan-no (1962) advised repeated stimulation for clams. Thermal shock has been used for H. discus hannai, first by Ino (1952) and by Kan-no & Kikushi (1962), and is an effective part of a system devised by Oba (1964b,

pers.comm.) for H. diversicolor supertexta. Large numbers of abalones were collected and kept in tanks for 7-10 days before induction of spawning. After being exposed in air for 0.5 - 1 hour about 30 of each sex were placed in baskets in a 70 l static tank and the temperature raised from 20°C to 23-25°C in 2 - 3 hours. Males spawned first when the temperature reached its maximum and females shortly after. The eggs were fertilised immediately in the spawning tank and then washed about ten times with filtered seawater. This procedure combines Carlisle's technique, stimulation of females with sperm, and thermal shock. All successful experimental work with H. iris and H. australis was based on this system.

6.3 Thermal stimulation of spawning in H. iris and H. australis.

6.3.1 Methods.

The technique used is essentially that of Oba (1964b, pers.comm.) described above but because responses of the local species differed from those of H. diversicolor various modifications were made. A 1.5Kw immersion heater fitted with a rheostat was used in a tank of approximately 70 l of uncirculated seawater. Up to 20 abalones of each sex were placed in suspended baskets or free on the tank bottom and walls; the water was bubbled strongly to ensure even warming and adequate oxygenation. From the initial temperature (15-17°C) the water was heated about 2-4°C/hour for $1\frac{1}{2}$ - 4 hours. The temperature was brought up to a maximum of 23-30°C and then cooled suddenly by replacing with fresh seawater at the initial temperature. Some batches of animals received this treatment once a day for several days in a row, some twice a day. The treatment was applied at different times of the day and night. Before warming most animals were kept for $\frac{1}{2}$ - 2 hours in air, though some were not. A more sudden thermal shock was tried with some batches, they were removed from water at normal temperature into already warmed water.

6.3.2 Results.

Thermal shock is the only stimulus tried with H. iris and H. australis which initiated production of large amounts of eggs and sperm. Males responded more readily to this stimulus than females. But no consistent or predictable results were obtained, the same stimulus applied to the same or different groups of animals on different occasions failed to elicit the same response. Of 75 treatments applied to H. iris between mid-November and the end of March, only 8 gave good results, 7 poor results, and the remainder no response at all. Good responses were obtained on November 18, January 8, 9, 11, 16, 21, February 12, 27, that is, fairly irregularly. H. australis was treated 15 times giving good results only once (January 28) and poor results 3 times.

Good results were obtained only with elevations of between 10°C and 15°C, although adults became very weak and a few died under this treatment. Repeated high temperatures tended to produce pale, patchy eggs.

The response elicited differed from that described by Oba (1964b, pers.comm.) in that spawning never occurred while the abalones were being heated, but always in the very early morning following cooling. It sometimes continued into the mid-morning but was independent of the time the treatment was applied. In the relatively static conditions of the tanks eggs were not dispersed in the exhalent currents of the females but came to lie in thick masses on the bottom nearby. Sperm, too, often remained en masse.

6.3.3 Discussion.

Thermal shock is the only method tried which gave definite responses, but so far the response is unpredictable. The treatments which were successful were all extreme and bore no resemblance to any natural stimulus - the death of some adults under treatments supports this. The response of a population to a given stimulus may depend on some basic physiological attitude of the individuals.

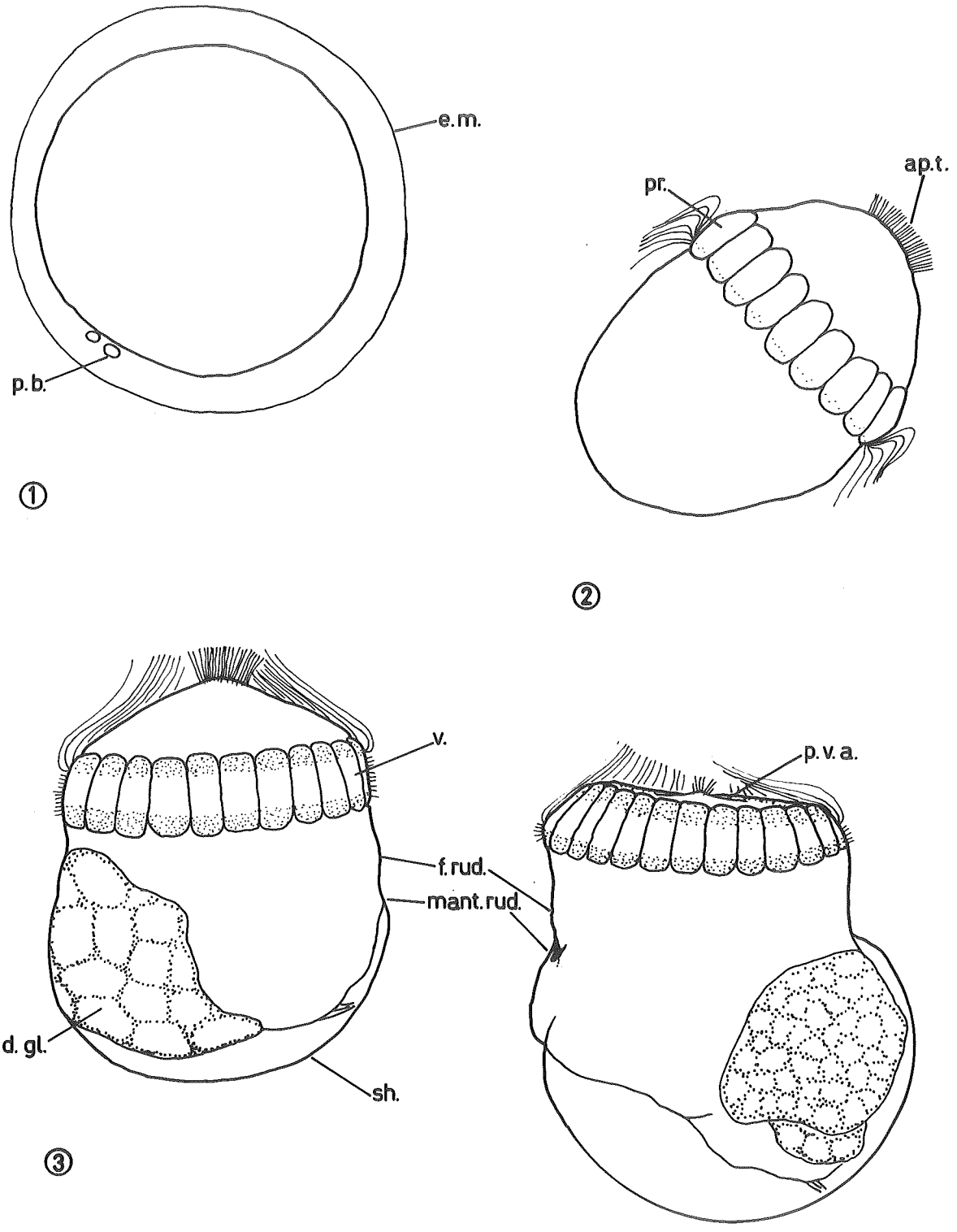
This may not always be favourable when the gonads are ripe. Such an attitude is found in some marine species where spawning is correlated with lunar cycles. The frequency of responses of H. iris through the summer of 1968-69 was very irregular and could not be correlated with such a cycle. The period when gonads were ripe through the summer of 1968-9 was unusual in that it was not followed by natural spawning in the late summer or autumn (Chapt. 5). This suggests that the susceptibility of the population to stimuli was low and a better response to the experiments may have been obtained in another year. However, successful fertilizations were made on several occasions, as early as November, so ripe gametes were present.

6.4 Larval Development.

6.4.1 Rearing methods.

In early studies where the main aim was anatomical description of larval stages (Crofts, 1937; Ino, 1952) larvae were reared in small vessels. More recently in mass culture studies larger tanks have been used (Kan-no & Kikuchi, 1962; Oba, 1964b, pers.comm.). Oba, for example, used tanks of up to 3000 l of static water.

When H. iris or H. australis eggs were obtained the technique used to prepare and rear the larvae was similar to that of Oba. Eggs lay in thick clumps on the tank bottom in the early morning together with large amounts of mucus and faeces from the adult abalones. The eggs were siphoned into a 5 l glass vessel and washed with repeated changes of filtered water. Time was allowed for fertilization to take place if it had not already occurred, but the only successful fertilizations took place before the eggs were collected. Development was completed in flat 20 l tanks, trochophores being siphoned from one to another after hatching. The water temperature remained about 17°C.



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Larval stages of *Haliotis iris*.

FIGURE 6.1

Fertilized egg with polar bodies.

FIGURE 6.2

Recently hatched trochophore, 18 hours after fertilization.

FIGURE 6.3

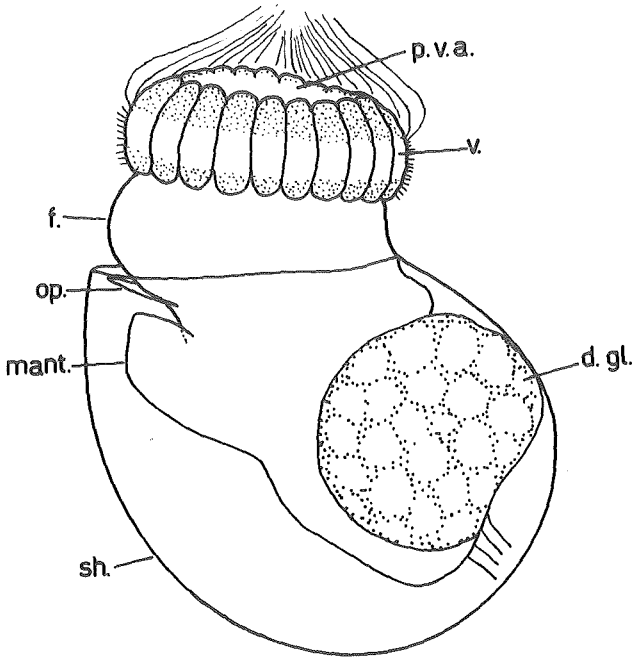
Veliger, 28 hours after fertilization.

FIGURE 6.4

Veliger, 32 hours after fertilization.

Key to lettering in Figs. 6.1 - 6.8

ap. t.	apical tuft
ceph. tent. rud.	cephalic tentacle rudiment
d. gl.	digestive gland
e. m.	egg membrane
f. (rud.)	foot (rudiment)
mant. (rud.)	mantle (rudiment)
op.	operculum
p. b.	polar body
p. v. a.	pre-velar area
pr.	prototroch
sh.	shell
v.	velum
v. r. mus.	velum retractor muscles



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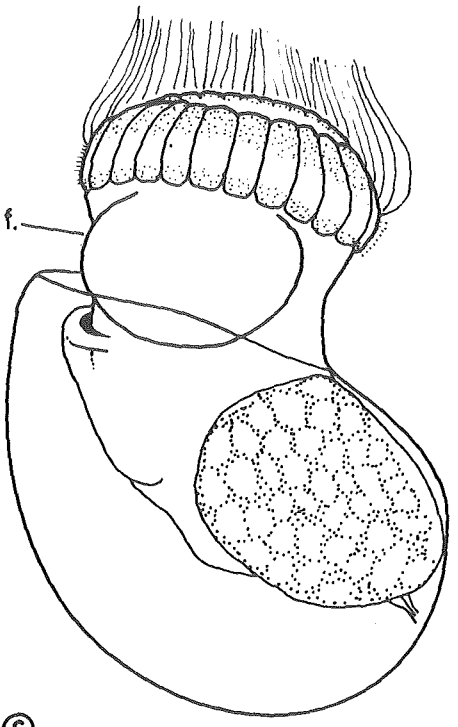

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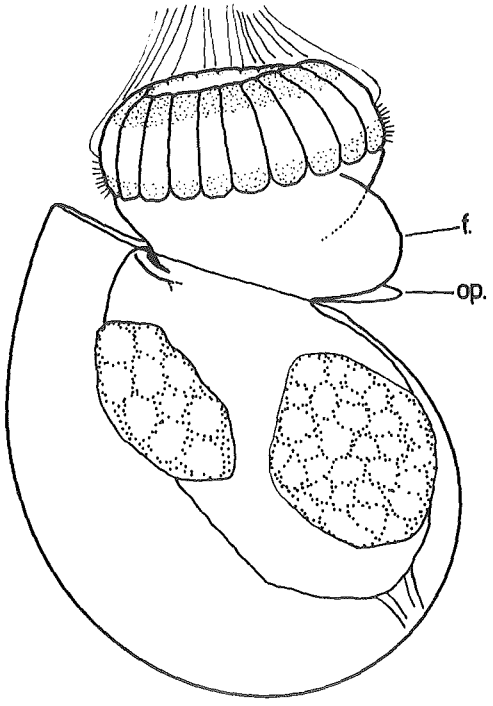

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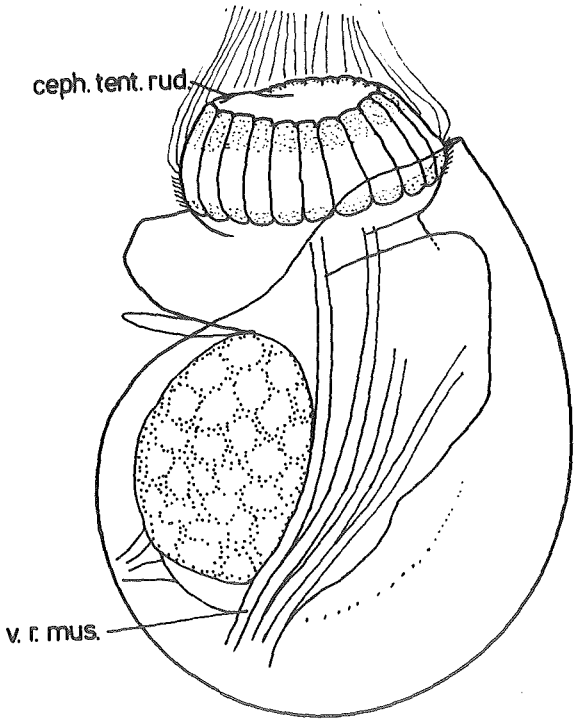


⑧

0·1mm

Larval stages of Haliotis iris (continued)

FIGURE 6.5

Veliger immediately before torsion, 39 hours after fertilization.

FIGURE 6.6

Veliger during torsion, 40 hours after fertilization.

FIGURE 6.7

Veliger, torsion completed, 41 hours after fertilization.

FIGURE 6.8

Veliger, 53 hours after fertilization.

Key to lettering on previous page.

6.4.2 Development.

Normal larval stages of H. iris were obtained three times, November 18, 1968 and January 9 & 27, 1969 and reared for $1\frac{1}{2}$ - $2\frac{1}{2}$ days. Fertilization was never observed but successful cultures were first recognized by the presence of polar bodies on fertilized eggs (Fig. 6.1) or two-cell stages. The first division occurs in most species of Haliotis within 1 - 2 hours (Ino, 1952; Murayama, 1935; Oba, 1964b) so the time of fertilization could be estimated within an hour, viz. 0600 hours on all occasions since spawning occurred only in the very early morning.

First movement of the trochophore within the egg membrane was noted 13 hours after fertilization and it hatched after 18 hours (Fig. 6.2). The trochophore was elongate with a prominent apical tuft of cilia and was slightly flattened posterior to the prototroch. It spent most of its time actively swimming near the surface of the water, stopping only momentarily. Initial deposition of larval shell was not seen but by 28 hours it had covered the posterior part of the larva, now a veliger (Fig. 6.3). The pre-velar area shortened and the foot and mantle rudiments appeared. Small secondary cilia appeared on the velum at this time below the main cilia. Up to torsion the pre-velar area continued to be flattened and the foot, mantle and shell developed (Figs. 6.4 & 6.5). The operculum formed after 33 hours. The amount of time spent actively swimming lessened, much more time being spent sinking at rest. Torsion occurred between 39 and 42 hours (Figs. 6.5, 6.6, 6.7).

By the time the larvae died after 53 hours the cephalic tentacles had begun to develop (Fig. 6.8). Larvae were not observed swimming after torsion had begun though cilia were active spasmodically. Larvae were first seen to retract into the shell in response to shock after 42 hours, although the operculum was not used to close the aperture. The larva was pale green over all but had two darker stripes on the velum.

Development of some H. australis eggs began on March 20 and one

veliger survived 40 hours, dying in the late stage of torsion. The various veliger stages could not be distinguished from the equivalent stages of H. iris except in colour. The head was pale green but the post-velar region was red-brown, similar to the red-brown colour characteristic of the ovary of adult H. australis.

Comparison of the rates of development of various Haliotis species (Table 6.1) suggests that the creeping stage of H. iris begins within 5 days and settlement is complete within 10 days. During the creeping phase the foot develops and attachment becomes more firm. The lack of swimming in cultures once torsion had begun was probably due to the inhibitory action of the particular rearing conditions; Ino (1952) noted that swimming was active after torsion in H. discus hannai. Length of pelagic life of H. australis is similar to that of H. iris, judging from observations on the single veliger reared.

TABLE 6.1. Length of larval life of Haliotis species.

Species	Author	Rearing Temp. (°C)	Time to hatch (hrs)	Veliger (hrs)	Torsion (hrs)	Creeping
H. diversicolor supertexta	Oba, 1964b	26	6	10-11	-19	43-46 hr
H. tuberculata	Crofts, 1937	-	8-13	15	29-35	2½-3 days
H. sieboldii	Ino, 1952	16-17	18	24	30-35	4-7 days
H. discus hannai	Ino, 1952	16-17	20	27-28	45-46	6-10days
" "	Kan-no & Kikuchi, 1962	25	10	14	-	-3 days
H. gigantea	Murayama, 1935	16.5-18	21-22	24	40-43	7-10days
H. iris	This paper	17	18	(20-24)	39-42	-

Larvae of various Haliotis species are similar but ciliation varies within the genus. The apical tuft is present in H. discus hannai, H. sieboldii (Ino, 1952) and H. diversicolor supertexta (Oba, 1964b) but not in H. gigantea (Murayama, 1935), H. tuberculata, except transitorily (Crofts, 1937) or H. rufescens (Carlisle, 1963). Secondary velar cilia are reported in H. tuberculata (Crofts, 1937) and are drawn in H. sieboldii (Ino, 1952) but may easily have been overlooked by other workers.

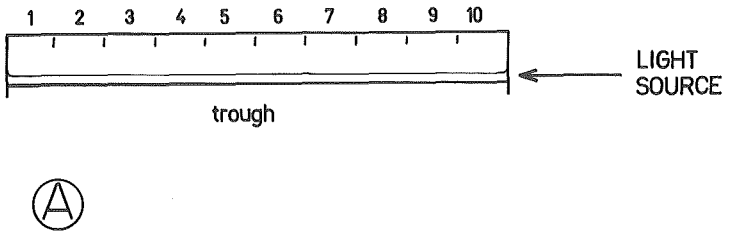
6.4.3 Abnormalities.

Frequently when gametes were shed after stimulation, fertilization occurred but only abnormal embryos developed. Cilia appeared occasionally and the motile embryos hatched and swam. The abnormalities had several consistent features though they were variable in shape. Initial cell divisions were uneven, generally one or two very large cells and many smaller cells were produced. Also the resulting cells were free and spherical rather than closely packed. Possible mechanisms interfering with development are polyspermy, non-ripe eggs and contamination. It was discovered after all experiments had been finished that the epoxy resin lining the tanks was incorrectly hardened and was leaching into the water.

6.5 Larval Behaviour.

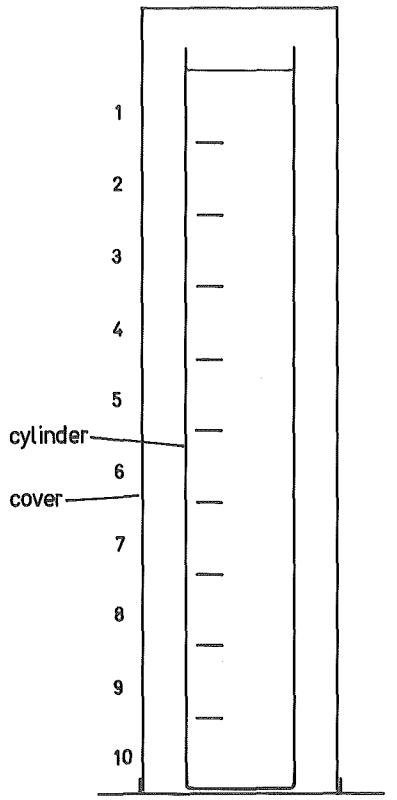
6.5.1 Introduction.

The pelagic larva of many marine benthic invertebrates is the dispersal phase in its life history. The behaviour of the larva, together with the length of pelagic life, play an important part in determining how the species is distributed. Eggs of Haliotis are dense and sink quickly after spawning so fertilization and subsequent development within the egg membrane occur on the bottom. Although it is an active swimmer, the larva, once hatched, must move into the water mass in order to be dispersed away from the adult colony.


1 2 3 4 5 6 7 8 9 10
LIGHT SOURCE
trough

Ⓐ

10 cm


1
2
3
4
5
cylinder
6
cover
7
8
9
10

Ⓑ

FIGURE 6.9

a. Apparatus used to test phototactic response of larvae.

b. Apparatus used to test geotactic response of larvae.

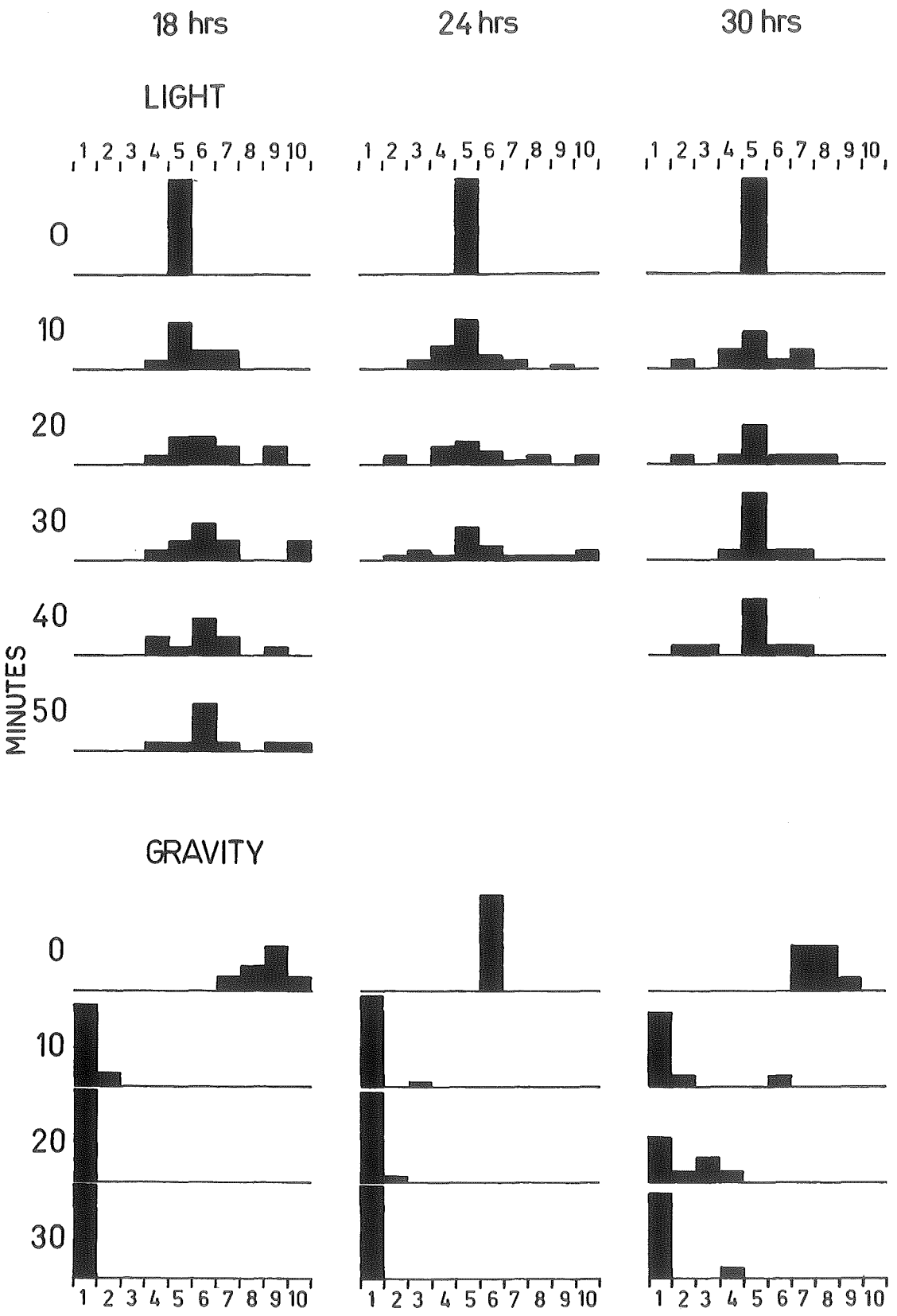

18 hrs
24 hrs
30 hrs
LIGHT
1 2 3 4 5 6 7 8 9 10
0
10
20
30
40
50
MINUTES
GRAVITY
0
10
20
30
1 2 3 4 5 6 7 8 9 10

FIGURE 6.10

Percentage frequency distributions of larvae in light and gravity experiments. Experiments were done 18, 24 and 30 hours after fertilization and the distributions measured every 10 minutes. Movement left to right (1 to 10) indicates a positive response.

Two mechanisms which may ensure this movement, phototaxis and geotaxis were investigated with larvae of H. iris. Successful experiments were carried out only for the first part of the larval life; it was not possible to test for differences at later stages. Experiments were designed to test the responses to undirectional light in the absence of gravitational effects, and to test the response to gravity in darkness.

6.5.2 Methods.

Larvae were obtained in sufficient numbers for experiments on January 7 & 28. Both times they hatched within an hour of midnight and experiments were carried out then (18 hours after fertilization) and after two subsequent 6 hour intervals. After 36 hours swimming had virtually ceased, probably due to unhealthy conditions.

Phototaxis. A plastic trough, semicircular in cross-section, with flat transparent ends was filled with about 5mm of seawater and placed in line with a variable light source in a darkened room (Fig. 6.9a). Ten larvae were pipetted gently into the middle of the trough and their positions noted every 10 mins for 30 - 50 minutes by means of the ten numbered divisions. Movement towards division 10 indicated a photopositive response. The strength of the light was varied but this did not affect the results.

Geotaxis. A tall glass cylinder filled with seawater was set up under a cover to black out all light (Fig. 6.9b). A number of larvae (7-19) were placed near the bottom of the cylinder with a long pipette and their distribution was noted in terms of the 10 vertical divisions every 10 minutes for 50 minutes. There was no change in distribution after 30 minutes.

6.5.3 Results.

The responses (Fig. 6.10) indicate a rapid negative geotaxis but no definite phototaxis. Most trochophores and veligers swam

from the bottom to the top of the 40cm cylinder in less than 10 minutes and remained on the very surface of the water until the experiment ceased. Movement in the light-response trough was a slow diffusion from the mid-point, though there was a tendency for trochophores (18 hours old) to be photopositive, but this response was negligible compared with the geotactic response. Initial observations of hatching trochophores made under a binocular microscope showed a definite photopositive response (swimming towards the microscope light) immediately on hatching but this response ceased within half an hour. The decrease in response after 30 hours (and absence of response after 36 hours) is probably due to poor health of the veligers and their decreased activity.

6.6 Discussion.

The information available obviously is limited when length of larval life and experimental responses are interpreted. Although swimming ceased prematurely in cultures and mass mortality occurred, anatomical development up to death was seemingly normal. The estimated larval life of *H. iris* is average to long for the genus but there is variability even within species. Temperature has an important effect on the rate of development, see for example *H. discus hannai* (Table 6.1) where a 8-9°C rise halves the larval life. The length of pelagic life of *H. iris* and *H. australis* will vary from the north to the south of New Zealand, and, with *H. australis* which can have two spawning seasons per year, with the time of year when spawning occurs.

Haliotis larvae are lecithopelagic in that they develop from very yolky eggs (Thorson, 1950) and do not feed in the plankton (Crofts, 1957; Oba, pers.comm.). Although they are active swimmers, they still must rely on mass water movement for dispersal. Five days in the plankton is probably ample time for a larval swarm to become well dispersed but little is known about local movement of water masses around New Zealand. Geographical isolation of

populations along the coast of New Zealand mainland is therefore unlikely and morphological variation of adult populations (Chapt. 4) is probably environmentally rather than genetically induced.

Pelagic life is sufficient to distribute all three New Zealand species of Haliotis to the Chatham Islands (600 km from the N.Z. mainland) on the West Wind drift current. Only H. virginea whose pelagic life is unknown, has a subspecies on these islands, and is distributed to the subantarctic islands (Section 1.5). Dispersal of adults, e.g. on seaweeds, seems less likely.

Fecundities of Haliotis are very high - up to 11 million per H. iris female per breeding season, for example - so a high wastage must occur. Most wastage, once failure to be fertilized and failure to develop are considered, is due to failure to find a suitable substrate or any substrate at all, and to predation in the plankton. Thorson (1950) believed predation is often underated as a source of loss. Although the larva is at the mercy of movement of water masses, its ability to swim actively combined with its tactic responses, may increase the probability of finding a substrate suitable for the adult. Both H. iris and H. australis inhabit mainly the immediate sublittoral zone close to shore though some other Haliotis species go much deeper. The strong geonegative response demonstrated in H. iris brings the larvae to the surface where, except in the breaker zone, the water mass is moving in the direction of the waves (Inman, 1963). In coastal waters wave movement is generally onshore, except perhaps at night when land breezes may set up offshore waves, so the behaviour of the larva may ensure that it remains in shallow water ready for settling. This mechanism does not preclude chance larvae getting sufficiently far offshore to be carried long distances.

Other workers with Haliotis larvae have noted the tendency to swim up but no experimentation has been done to determine the mechanisms involved. Murayama (1935) noted the phenomenon in H. gigantea trochophores and Thorson (1964) interpreted it as a photo-

positive response. Ino (1952) found both H. discus hannai and H. sieboldii larvae to be photopositive, the former more so. No previous work on geotaxis in the genus has been published.

7 CONCLUSIONS.

7.1 Summary.

The genus Haliotis consists of about 130 species and subspecies distributed around the world but concentrated mainly in the Pacific Basin. New Zealand has three species, H. iris, H. australis and H. virginea, the last with four named subspecies. The distribution of these species around New Zealand, the Chatham Islands and various subantarctic islands is described. A new geographical record for H. virginea is noted. An additional three fossil species are known from New Zealand.

Both H. iris and H. australis were found to be infested with a parasitic mite, Halixodes truncipes, and to harbour a commensal crab, Elamena producta. The predators, especially of juveniles, include parrot fish and the red cod, Physiculus bachus, probably the spiny lobster Jasus edwardsii, and possibly the asteroid Astrostole scabra. The shells of both species harbour boring organisms, including polychaetes (Polydora monilaris, Lumbrineris sphaerocephala, Rhamphobrachium sp., Dodecaceria sp.) and the boring barnacle, Cryptophialus melampygos.

At Kaikoura both H. iris and H. australis feed mainly on red algae but at Taylors Mistake H. iris, the sole species, feeds on the brown alga, Macrocystis pyrifera. The Kaikoura abalones feed mainly on drift algae, particularly reds washed in from deeper water, but H. iris at Taylors Mistake browses mainly on growing brown algae, in the virtual absence of drift algae. Selection experiments in the laboratory showed that both species preferred the red alga Hymenocladia lanceolata to either of the browns Lessonia variegata or Macrocystis pyrifera, and juvenile H. iris fed for six months on single species diets grew faster on Hymenocladia than on Lessonia. Diet is therefore determined first by availability of food species, active selection playing some part, especially in H. australis which was the more selective in the laboratory. This diet gives

the species greater growth rates. Shell laid down on a diet of red alga is a normal red-brown colour, it is blue-green on a diet of Lessonia. The amount of feeding is greatest in the winter.

Tagging of H. iris low water colonies showed that significant movement tended to occur only in autumn and winter when rough seas disturbed the habitat. These movements could vary from year to year depending on sea conditions. In contrast, subtidal colonies dispersed more gradually, seemingly induced by the tagging operation and subsequent rehandling. Other colonies which were not tagged remained apparently unchanged for up to 2 years. Subtidal H. australis colonies also did not move to any great extent; this species inhabits narrow crevices and appears to be a much more active animal than H. iris, both in the field and in the laboratory. Drift and attached algae were virtually absent from the crevices inhabited by H. australis and it seems likely that the species must forage to feed. A homing mechanism may be present because many older H. australis are found in deep scars on the rocks or have characteristically worn shell edges fitting the rock of their particular site.

A 24 hour watch on a tagged, subtidal colony of H. iris at Kaikoura showed that there was very little movement diurnally and it seems likely that feeding is passive; drift algae are available at most times. No evidence of homing behaviour was detected.

The von Bertalanffy growth equation applied to H. iris indicated that initial growth was rapid, reaching about 110mm in 5 years, 140mm in 10 years, and with an asymptote of 146mm in the populations studied. There was little seasonal variation in growth, but a slight slowing in winter. Relative growth coefficients of H.australis and H. virginea were estimated from annual growth checks in the shells but no absolute growth curve could be derived. All three species had similar relative growth coefficients, K lying between 0.3 and 0.4.

Spawning seasons, estimated from gonad indices, showed that at Kaikoura in 1967-8 H. iris spawned once in the late summer to autumn.

In contrast H. australis spawned twice, once in the spring and again in the late summer to autumn. Both patterns are typical of haliotids. But in the 1968-9 year neither species spawned; full gonads with apparently ripe eggs were maintained through the winter of 1969. No reason for this inconsistency can be offered. H. iris at Taylors Mistake followed essentially the samepattern as Kaikoura H. iris through 1968 but spawned slightly in autumn 1969.

H. iris first produces mature eggs when it is about 60mm in length and probably spawns substantially for the first time when it is four years old. Although fecundities of larger animals reached about 11 million eggs not all of these were necessarily spawned. H. australis also first produces mature eggs when it is about 60mm in length but the age at which first spawning takes place could not be determined; maximum fecundity is about 3 million eggs. The sex ratios did not differ significantly from 1 : 1 for either species.

Of the several techniques used to stimulate H. iris and H. australis to spawn in the laboratory (electrical stimulation, injection of KCl solution, exposure to air and thermal shock), only the last gave reasonable results. There was no consistent pattern in the response but spawning could be induced sporadically throughout the summer of 1968-9 by a temperature increase of 10°C. Spawning occurred only in the very early morning when thermal induction had been used on the previous day. Japanese workers have reported spawning starting during thermal induction; the time lag in the present study is unusual in comparison but the material may have been atypical as no natural spawning was detected during 1969. Larvae of both species were obtained and reared to just beyond torsion; the estimated pelagic life for both species is, at present, five days. Experiments with trochophores and veligers of H. iris demonstrated a persistent strong negative geotaxis and a negligible positive phototaxis just after hatching. This behaviour could ensure that larvae are dispersed but remain close to shore until ready for settling.

7.2 Relevance of this study to legislation of the New Zealand abalone fishery.

Although New Zealand has three species of abalone only one, H. iris, is fished at present, the others are unlikely to ever be commercial propositions. Both H. australis and H. virginea are probably too small to be processed efficiently and both are relatively inaccessible. H. australis lives mainly in crevices and is difficult to collect, H. virginea is most abundant in deeper waters in southern New Zealand.

Many points must be considered when a fishery of this sort is assessed: the biology of the species, its distribution in relation to processing facilities, the prevailing sea conditions and water visibility, the quality of the product, the availability of markets, and the effect of the commercial fishery on the sports fishery. Some of these aspects have been discussed for Californian abalones by Cox (1962).

One of the most important aspects of abalone biology relevant to the fishery, distribution and abundance, was not covered in this thesis. Lack of manpower and of finance for travelling limited any assessment of stocks. Such a project would be difficult even for a team of divers, the strip survey method used by Forster (1962) would be unsuitable because H. iris is highly colonial and occurs in beds of between a few and several hundred, scattered over wide areas. The different habitats occupied by H. iris of different sizes would also be a major problem, large abalones on rock faces would be obvious but smaller ones in crevices and under stones would require a much greater searching effort. As the species occurs only at shallow depths it is subject to heavy wave action and often high turbidity which would make surveying difficult.

Minimum age of maturity, fecundity and growth rate must be considered when legislation governing minimum takable size is imposed, the current limit is five inches (127mm). A female abalone at the

size limit produces about 3 million eggs (about 25% of those produced by a full grown specimen). Culling of animals above this limit removes those producing the largest numbers of eggs but this is compensated by the higher proportion of smaller individuals. Until mortality tables are calculated for this species it is impossible to estimate what effect exploitation will have on the fecundity of the population as a whole. The minimum takable size is about 90% of the asymptotic length calculated in this study and 72% of the maximum size recorded. Here again, the effect of this cannot be fully discussed until the size structure of the whole population is known but it is evident that only a small part of the population is being taken and that little growth occurs after the 7 - 8 years taken to reach maximum size.

Fishing methods depend on the habitat of the species. Most populations can be reached by free-diving but their generally fairly exposed habitats and often turbid water can make this difficult. (Regulations forbid the use of underwater breathing apparatus.) Weather and tides restrict diving to about one day in three and about 2 - 3 hours per day at Kaikoura. The small proportion of the population in deeper water acts as a reservoir only for spawning, movement is slight so they are unlikely to move to replace exploited populations. Areas close to shore where abalones are found are often hazardous for boats and their use may be limited. Fishing from the shore, the most commonly used technique in New Zealand, necessitates access by vehicle to carry equipment and the catch.

Fishing grounds must be accessible to either freezing or processing works. In Tasmania live holding tanks have been installed on a large mother ship to overcome this problem - it can remain at sea for several days (Anon., 1969b). (Legislation in Tasmania requires delivery of abalones live to shore installations.) The catch from the Kaikoura area at present is being frozen at the Kaikoura Fisheries and carted to Palmerston North for final processing.

Finally, the product must meet certain quality and marketability

requirements. H. iris meat is darkly coloured, there is discrimination against this in overseas markets. In California H. rufescens is favoured over the dark-fleshed H. corrugata and in Australia Schismotis laevigata is preferred to Notohaliotis ruber for the same reason. The black skin of H. iris must be removed and this reduces the final weight of the product and increases processing cost relative to other species. Nevertheless, New Zealand does have a market, especially in the United States, but it is not known how well it competes with the local or Australian product.

The paua was a traditional Maori foot item in New Zealand and there is some objection to commercialization of the species in the fear that stocks will be depleted. The size limit applies only to those taken for sale and is sufficiently large to allow reasonably sized animals to remain even after commercial fishing, so it seems unlikely that the sports fishery will be forced to cease.

The object of regulations is the attainment of the maximum sustained yield. It is difficult to say whether existing regulations (see Appendix) are adequate when stocks are just beginning to come under heavy fishing pressure, but it is felt, in the light of existing knowledge, that they probably are. Modifications that might be considered are (a) a limit on the total catch per year for a particular area, and (b) a limit to the number of fishermen and perhaps a limit to the area worked by each. The Kaikoura coast is probably saturated with divers now and catch rate will probably decline within a few years to a stable level. There is a team of about five divers on about 50 miles of suitable coastline now. Current legislation forbidding the use of underwater breathing apparatus is an effective control on the fishery, acting in the same way as a closed season by reducing the time spent diving.

More research, particularly assessment of stocks and the structure of the population, is required before additional regulations are considered. The state of Victoria in Australia collects $40,000 in licence fees from abalone fishermen and spends this money on a

current research program on the fishery. New Zealand might well follow this example.

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Appendix

THE ABALONE FISHERY

AUSTRALIA

The following account is based largely on two articles in Australian Fisheries Newsletter (Anon., 1968b, 1969a). The abalone fishery in Australia is perhaps the fastest growing in the world, now being the second largest producer after Japan. Since 1963, when the industry began to boom, the annual catch has risen to 18.7 million lb. liveweight and now has an export value of $A3.5m (Table i).

The major fishing areas are in the south-eastern states where Notohaliotis ruber and Schismotis laevigata are the main species, but there is a smaller fishery in Western Australia where Marinauris roei is the only species. In the south-east abalones are taken to a depth of 120 feet by divers using Hookah gear or less commonly, SCUBA or snorkels. Hookah gear supplies air to the divers from compressors on board boats, while baskets of abalones are brought to the surface on lines by deckhands. Generally high-speed 12 - 25 foot runabouts with outboard motors are used, but larger boats are used on more distant grounds. In Western Australia M. roei is restricted to the top 6 feet of the surf zone and the fishing methods described above are not applicable. The small size of this species, lack of suitable ports, and the greater dependence on sea conditions has restricted growth of the Western Australian abalone fishery (Anon., 1968a).

The fishery is open all year throughout Australia but regulations vary in different states. Licence limitation and size limitations are imposed in Victoria, Tasmania, South Australia and Western Australia. In Victoria for example, the number of licence holders is limited to 200, each paying a $200 fee going towards research into the abalone fishery, and the minimum size varies with

area from 4 to $4\frac{3}{4}$ inches. Research is also under way in Tasmania where Maria Island has been closed to fishermen.

Abalone is processed into frozen, canned or dried meat, or canned as soup (W.A. Montgomery, 1967). Most is exported. The main markets are Malaysia, Japan and Hong Kong but Singapore, U.S.A., Vietnam and Laos also buy from Australia. Processed, the product earns about 54 cents per lb. on the export market; the price paid to divers is 10 - 14 cents per lb. liveweight.

CALIFORNIA

Cox (1962) described and discussed the Californian abalone fishery in detail. The commercial fishery is divided into two areas: one, 35 - 40 miles of coast in the north which has only red abalone (Haliotis rufescens). It has been harvested continuously since 1929 and has yielded an average 2 million lb. per year. South of Point Conception the fishery is primarily for pink abalones (H. corrugata) which have lower quality. The fishery started in about 1945, reached peak yield in 1952 of 3.5 million lb. and has since declined to about half this level.

There is a two month closed season in the winter and size limitations are imposed. Most abalone is frozen.

OTHER AREAS

There is a traditional abalone fishery in Japan practised initially by woman divers who dive unaided. Catch (including other gastropods) has increased from 8,500 metric tons (18.7 million lb.) liveweight in 1961 to 13,000 metric tons (28.6 million lb.) liveweight in 1967 (F.A.O., 1968). There is also a fishery of long standing in Guernsey and a more recent one in South Africa.

NEW ZEALAND

The abalone (paua) fishery in New Zealand does not operate at present on the same scale as in Australia. Annual production has remained fairly static since 1964 as Table i shows, but there are signs of an increased pressure on the resource, especially on the Kaikcura coast. Exports so far have been either frozen or canned, the main market being U.S.A.

TABLE i. Liveweight and value to fishermen of abalone caught in Australia and New Zealand.

	AUSTRALIA			NEW ZEALAND	
	'000 lb.	$A'000		'000 lb.	$NZ'000
1963-4	192	20	1964	112	6.78
1964-5	996	85	1965	53	2.71
1965-6	2975	309	1966	55	3.18
1966-7	10825	1409	1967	133	9.41
1967-8	18712	-	1968	132	9.63

The New Zealand H. iris may suffer on the international market because of the dark colouration of the flesh and also because of the black pigmentation on the outside. Chemical treatments to remove the black colour are not altogether satisfactory and trimming with subsequent loss of meat is required. Removal of the black exterior is necessary only on aesthetic grounds, it does not improve the flavour.

The value to the fisherman is currently about 7 - 9 cents per lb. liveweight but this is supplemented by the value of the shell. Shells of H. iris are bright, iridescent blue internally and good

shell is used in the manufacture of jewellery and tourist souvenirs for the local and export markets. Shells fetch an average price of about 15 cents each, but range from nothing (for "dead" shell with no lustre) to over $1 (for large thick shells with good colour). Quality of shell depends on size and on locality. This means that in New Zealand fishermen can approximately double the value of the catch by selling the shells to jewellery manufacturers.

The taking of abalone in New Zealand is controlled by the Fisheries (General) Regulations 1950 (Reprint) S.R. 1966/20, regulations 103E, 103F and 106 (as amended by regulation 11 of Amendment No.10, 1968), and The Commercial Fishing Regulations 1963 (Reprint) S.R. 1968/66, regulations 15, 17 and 29.

Except in the case of holders of fishing permits, the maximum quota of abalone taken or possessed on any one day is limited to 2 gallons (measured in their shells) per person, 4 gallons for two persons, and 5 gallons for a larger party.

A fishing licence is necessary for taking shellfish for sale, fees range from $10 for a shore-fishing licence or for a boat under 40 feet, to $40 for a boat over 70 feet. Most abalone fishermen work from the shore. The minimum takable size for sale is 5 inches in greatest diameter, this refers to paua, H. iris, only. The use of underwater breathing apparatus is illegal for taking fish or shellfish for sale. Certain areas are closed, some due to the level of pollution.

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