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Studies on the Paua, *Haliotis iris* Martyn in the Wellington district, 1945-46

by

Mary Sinclair

Zoology Publications from Victoria
University of Wellington

No. 35

Issued June 30, 1963.

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INTRODUCTION

Haliotis has been much sought after in many countries for years on account of the food value of the muscular foot and the decorative nature of the shell. There are Haliotis fisheries in Mexico, Japan, U.S.A., South Africa, Korea, Canada, China, Channel Islands and possibly other countries. All these countries have a vernacular name to denote the genus. In Japan it is awabi, in California abalone and in the Channel Islands the ormer. These names apply to different species of large Haliotis. In New Zealand the common name of the genus is the well-known Maori name of paua, the origin of which is uncertain although three other Pacific languages, including Hawaiian, use a similar word to denote shell fish.

According to the United Nations Food and Agriculture Organisation Yearbook of Fisheries Statistics, Vol. 12, 1960 (1961), the following quantities of Haliotis

were landed in 1960:

Mexico (Abulón)		1		metric	
Japan (Awabi)			4,400	metric	tons
U.S.A. (Pacific Coast) (Abalone)			2,000	metric	tons
Union of South Africa (Klipkouse)			600	metric	tons
Korea (Chón-bok)			500	metric	tons
	less	than	50	metric	tons
China I	less	than	50	metric	tons

* 1959 figures, 1960 not available.

The paua was at one time quite a staple food of the Maori, who removed them from the rocks by means of bone implements sharpened like chisels and about 7 inches long. These implements are known as ripi and maripi (Phillipps, 1935). The Maoris relied on the paua as a staple article of diet and they were as a rule very careful of the beds of paua on which they depended. They have a saying "Remove karariwha (H. australis) from among paua and the paua will disappear". No one has so far been able to verify this. The Maori believed that once large pauas were removed from a bed it would take more than a life-time for the bed to be replenished, as they thought a specimen six inches long took from 20 to 25 years to reach that size. Little or no use was made of H. australis and H. virginea. Phillipps (1935) gives a resume of the past history of the mollusc as used by the Maori. The chief uses other than food were in inlay work of the shell either on the pa kahawai or fishing hook or in ornamentation of their carvings.

In New Zealand, since 1940, *Haliotis* has become of increased economic importance. The demand for good shell of *H. iris* for the manufacture of high-class jewellery has been fairly keen for a much greater period. Over recent years an increasing demand for the soft parts has been added to that for the shell, although collecting of animals by private persons for bait has probably always

accounted for large numbers being taken each year.

Publication of this paper has been assisted by a grant from the Publications Committee, Victoria University of Wellington.

SINCLAIR-Studies on the Paua, Haliotis iris Martyn

A count of the number of paua taken in the Cook Strait area over a period of years by one fisherman has been lodged with the Fisheries Branch of the Marine Department. This fisherman trades in both shell and soft parts. The following figures which cover the two years 1945-46 were made available to the writer:

	Oct. 1944-Sept. 1945	May 1945-March 1946
Total No. Collected	26,067	27,631
No. Sold as Food	20,904 (£194)	18,288 (£171)

These returns cover paua ranging in size from 9cm to 17cm and indicate that the income available from the sale of soft parts would not be sufficient to make a livelihood unless supplemented by sale of the shell.

The Chinese community in Wellington have occasionally sought dried soft parts for export to China, where it is used extensively in making soup. The visceral mass and mantle fringe are removed and the foot dried in the sun or in a dehydrating machine. Dried material is easily packed and light to ship A limited amount of this dried material has been exported. The paua has also found favour (sometimes under the American name of abalone) as a luncheon dish in Wellington restaurants. For this purpose the visceral mass and mantle are removed, the black pigment removed by scrubbing and the foot muscle cut into steaks. After suitable pounding they are cooked. A factory at Picton undertook to can as much paua as could be supplied for export trade and home consumption, either minced or as steaks. All this commercial work is based solely on *H. iris*. Where records have been kept, no specimen under 9cm in length has been used.

Haliotis iris Martyn was designated the type species of a subgenus of Haliotis, named Paua, established by Fleming in 1952.

No scientific work has been published on the growth and ecological habits of the paua in New Zealand and very little work has been published on this subject in other parts of the world. Stephenson (1924) published a paper on *H. tuberculata* in the Guernsey Islands in view of the serious diminution of "ormers" on the shores of that island. He concluded that overfishing and disturbance of rocks bearing seaweed food of *Haliotis* were mainly responsible for the shortage. The Guernsey States then adopted his suggestion for two years' suspension of ormering. No statistics are given in the F.A.O. *Yearbook* quoted

above, however.

In New Zealand, as elsewhere, gathering of the animal is generally carried out at low tide (more being taken during the low spring tides that at any other time). The Maori and most other collectors wade out with knives and by this means remove the paua from the rocks. It is virtually impossible to remove large paua by hand as they are strongly adhesive; but small paua can sometimes be lifted from a rock if caught in a relaxed condition. In some districts such as Taranaki the collecting of paua is a heavy task as the only habitat where they can be found is underneath large boulders which must be turned over to make the paua available and then turned back again if the bed is not to be depleted of seaweed upon which the paua feed. The Maori always make it a rule to return the stones to their former position, but Europeans are not always so careful. One commercial fisherman known to the author makes use of a gaff, a long wooden pole with a strong hook at the end, to collect paua. The hook is slipped under the lip of the shell and enters the foot of the animal so that it may be jerked off the rock and drawn up. This method enables a fisherman to collect in depths of 15 feet and fishing can be carried out quite easily at low tides other than spring tides and even at half tide.

MATERIALS AND METHODS

The present survey has been carried out principally in the Cook Strait area taking in the coast line from Karaka Bay to Karori light. Some material for the graph showing growth peaks was taken from Te Kaminaru Bay on the West Coast of the North Island (Makara). Most of the animals worked on were H. iris from the Cook Strait area, namely Chaffer's Passage, Somes Island, Island Bay, Red Rocks, The Runaround, Karori Light, Te Kaminaru Bay and Karaka Bay. A number of shells were also obtained from Turakirae Point, Eastbourne, Titahi Bay and Stewart Island. Some specimens of H. australis were collected from Island Bay and Te Kaminaru and a few H. virginea (shells only) were obtained from Stewart Island.

A number of *H. iris* were tagged and placed around the coast in the Island Bay area. Two methods of tagging were used, the first was by means of fish rings placed through the last hole in the shell and the second by means of celluloid tags attached by wire through holes punched in the posterior lip of the shell. Sixteen tagged specimens were placed in the Te Aro baths. Of all these tagged specimens none has been recovered for measuring. One tagged specimen was picked up by a fisherman near Island Bay and by mistake unfortunately thrown back into the sea. Certain pools were observed regularly and the changes in the paua population noted.

Over four hundred shells were sectioned to study the structure, particularly the number of black conchiolin layers in relation to size of the shell. The shells were cut along the longest diameter and through the nucleus by a band saw. The edges were then smoothed and polished by means of a power driven grindstone, using carborundum powder and water. The lines were counted by means of a hand lens or binocular microscope. In order to make the lines stand out more clearly the edges of the sections were polished on an oil stone or kept wet while the counting was done. The latter method was used the most, as it was much quicker. A few cut sections of shell were attached by balsam to slides and ground very thin on an emery wheel in order to study the microscopic structure of the shell. This method was at first used for counting the lines of the shell also, but was found to be unnecessary and the method described above was used as the lines could be adequately seen.

Serial sections of the mantle were cut to observe the cells which secrete the shell and the way they differ in different regions of the mantle. Also sections of mantle from pathological specimens were taken to compare with normal specimens. The method found best for killing the specimens was that used by Crofts (1929).

I am indebted to Mr Taylor of Island Bay for making available large quantities of shell from various parts of the Cook Strait area.

BIONOMICS

HABITAT AND GEOGRAPHICAL DISTRIBUTION

Haliotis occurs on exposed rocky coasts throughout New Zealand. It is common in the Wellington, Kaikoura and Stewart Island areas, where it grows to its largest size and produces the finest shell. On sheltered coasts, such as the coast around Auckland, H. iris is seldom seen (Powell, 1946), while only small shells are found in the Taranaki and Hawke's Bay districts. H. iris, however, varies to a considerable extent within small areas. This is demonstrated by specimens from the short stretch of coastline from Wellington Heads to Cape Terawhiti (see map). The shells are roughly classified into hard and soft shell. Soft shell comes from areas characterised by a sandy or muddy bottom with the seaweed often

covered with a brown slime, and holothurians, such as Stichopus, are commonly seen. This type of shell breaks in the hand and is useless commercially. "Hard shell" areas always have clean rock or shingle bottoms and although the shell may sometimes be thin it is very strong and difficult to break in the hand. From a map it can be seen that of the thirteen places from which collections were made, five gave soft shell and these are intercepted by the clear beds.

H. iris is found from just below low-tide level to a depth of approximately 30 feet. It may, however, occur at lower depths as other species of Haliotis have been found as deep as 33 fathoms, e.g. H. dalli was dredged from 33 fathoms near Charles Island, Galapagos (Bartsch, 1940). The small H. iris (1.0cm-9.0cm) are found from 1-2 feet below low-tide level and they are attached to the underside of boulders or resting on the upper surface of smaller stones beneath a boulder. The animals are never exposed to view but are always to be found out of the direct light either on the lower face of an overhanging ledge or beneath a rock. They are not attached to stones small enough to be moved by wave action unless these stones are sheltered from the direct force of the waves. The majority of small specimens occur in large shallow pools containing numerous stones and boulders and well protected from direct wave action by fringing, rocky reefs or large boulders. In some places, for example Te Kaminaru Bay, the small paua population is still extremely dense, over 300 being collected by one person in $1\frac{1}{2}$ hours from 3 pools. These pools were all less than 6 feet in longest diameter. To the west of Island Bay the writer collected approximately 60 specimens from a pool about 4 feet long and 3 feet wide containing 2 large boulders and numerous small stones (about 8 inches in largest diameter).

Medium to large specimens of H. iris (approximately 9-17cm) are found chiefly on the upper surface and sides of reefs and large boulders from 2 feet to 30 feet and possibly more below low-tide level. Sometimes, however, at a very low tide specimens have been observed out of the water. Thus they have a fairly wide range in depth and possibly the lower limit is determined by availability of food supply, mainly seaweeds. Occasional large specimens have been seen moving during daylight hours but usually they are immobile and rest, often in dense colonies not more than a few inches from one another completely covering a rock surface. H. australis is always found near H. iris although a large number of H. iris were collected without H. australis being observed. Specimens 1.2-8.4cm were found between low-tide level and approximately 3 feet below. It seems doubtful whether H. australis would occur below 4 feet under low-tide level as specimens are rarely found larger than 8.5cm and have not been recovered from deep H. iris beds. In collections made from the following areas the proportion of young H. iris to H. australis was as follows:

	Date—1946	H. iris	H. australis
Houghton Bay area	Aug. 3	169	11
	Aug. 13	139	20
	July 31	42	none
West side Island Bay	Aug. 11	23	none
	Aug. 4	99	none
Red Rocks	June 6	45	none
Te Kaminaru Bay	Aug. 11	308	seri 54 of
	wife Afrill. On stirlings on	005	Sales Con and a second
	Total:	825	35

Thus is can be seen that H. australis is in quite a small proportion to H. iris in the collections made. The habitat of H. australis appeared to be the same as that of H. iris. No living H. virginea were found although a few shells were observed on the beach at Stewart Island.

BEHAVIOUR

H. iris is a nocturnal animal. During the day it is always found away from direct light attached underneath ledges or on boulders. The small specimens are usually found on boulders or stones while the larger specimens in deeper water are generally attached to rock walls or overhanging ledges of rock. At no time during the day was a specimen seen moving unless it had been disturbed. When disturbed they cling tenaciously to the surface of the rock. Occasionally an animal would move from the exposed surface of a boulder that had been disturbed to the lower surface. This movement away from the light, however, occurred fairly frequently in the case of disturbed H. australis. Some specimens were attached to a broken piece of concrete and one had attached itself to a strip of rusty tin. This seems to point to the fact that they will attach to almost anything as long as it gives firm support and is out of direct light. It seems probable that where such a large number of specimens occurs in a small pool as described previously they must move out of such a pool during the night to feed, as often there is little or no algal growth on the rocks to which they are attached.

In one pool the writer observed a Haliotis (approximately 10cm in length) which on successive visits over a period of 3 months was still situated in the same place on the same rock. In addition, on 3 occasions on the removal of an animal from a rock there was left a definite mark on the rock where the animal had been attached. In one case a large surface of the rock was covered by small white tube worms except where a Haliotis had been removed and there remained a smooth surface of rock in the exact shape of the shell. From the above facts it is highly probable that H. iris has a homing instinct in its nocturnal movements. This view is supported by observations of the aquarium specimens. Graham (1941) expresses the opinion that Haliotis undergoes a winter migration to deeper water at Seal Point, Otago. This is a popularly held opinion. On the other hand a commercial fisherman in Island Bay, Wellington, who fishes for Haliotis throughout the year maintains that they do not migrate in the winter but can

always be obtained at the same levels.

H. australis when found in any numbers was always intermingled with H. iris and never seen in groups of more than 2 or 3 as is often the case with H. iris. It was more active than H. iris if disturbed and invariably quickly found its way back to the pool if placed out of the water on a nearby rock. On one occasion 4 small \hat{H} . iris about 2.3cm in length were placed with a H. australis of the same size in an upturned billy lid. In about half an hour the H. australis had crept over the edge of the lid at least 3 times while all the H. iris remained completely immobile. H. iris specimens show a tendency to leave a pool if disturbed. In three cases specimens were noticed in the same positions on successive visits over a varying period ranging from a few weeks to about 3 months but in every case when lifted for measuring and disturbed they disappeared very quickly from that pool. H. iris if turned on to its back will right itself in the same manner as described by Crofts (1929).

BEHAVIOUR IN AQUARIUM

A number of H. iris were kept in two small tanks for varying lengths of time. On February 21, 1946, four specimens ranging from 1.3cm-2.6cm were placed in each tank. One tank was aerated by sending a steady stream of air bubbles through the water for about 16 hours every day but the other was left undisturbed except for the removal and measurement of the specimens once a fortnight. The animals fed on algal growth present on the sides and floor of the tank. During the daytime the animals were invariably stationary, attached to the under side of a stone or the side of the tank near a corner although twice an animal

was found moving and eating in the daytime. A specimen would be in the same place during the day but would be seen moving about the tank at night. If a light were turned on immediately above them they would continue moving and

feeding for ten minutes or more.

Although *Haliotis* is said to require very high aeration (Stephenson, 1924) the specimens in the aerated tank did not live as long as those in the non-aerated tank. Foot movements appeared to be exactly the same as those described by Lissmann (1945). Specimens often moved out of the water and when put back did not live more than a day. A possible explanation of this behaviour was that there was a change in the salinity of the water.

SHELL

Structure of the Shell.

Examination of a thin longitudinal section of a shell under convergent polarised light showed a crystalline aggregate and consequently the isogyres were blurred. From the characters observed, the shell appeared to be composed of calcite intercepted with numerous conchiolin lines and an external very opaque periostracum the nature of which it was not possible to identify.

The shell of *H. iris* is unique among *Haliotis* shells by reason of the remarkable iridescence of the shell when polished. This brilliant lustre is caused in all molluscan shells by the nacreous material on the shell being laid down in very fine lamellae giving rise to blues, greens and reds through diffraction of light. All species of *Haliotis* show a certain amount of iridescence on the inner surface of the shell. *H. iris* is outstanding for the iridescence of the shell since the dark conchiolin layers alternate with nacreous material so that nowhere is there a great thickness of nacre.

Young shells of H. iris are spirally lirate like H. virginea with a few oblique rows of nodules (Suter, 1913). They remain lirate up to 2cm in length and then abruptly change the external structure of the shell to rows of low radially arranged nodules while the concentric growth lines are very distinct. Shells up to 6cm in length vary a great deal in colour from all shades of brown to dark olive-green. Sometimes a mottled effect is seen. After a length of nine centimetres has been reached the shells become covered by calcareous algae and the sculpture of the shell is no longer visible. Even before this occurs the lirate structure of the small shell has been worn away from the apical region. The small shell does not have any distinct mark on the inner surface for the muscle attachment. Not until the shell is about 7cm or more in length does the region of the muscle attachment become roughened and distinctly oval in outline. In the larger shells this roughened area is anything up to 6cm in longest diameter and is doubtless developed as a result of the need for a very firm muscle attachment. On the other hand H. australis and H. virginea lack any roughened area for the muscle attachment but have a uniform smoothness on the inner surface of the shell.

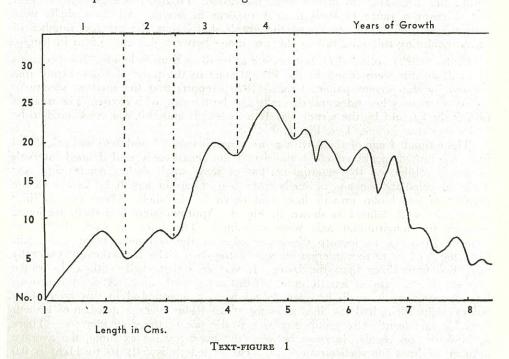
As mentioned elsewhere it is not until the shell is about 4–5cm in length that the deposition of conchiolin in definite layers begins to take place. This deposition appears to begin at the margin of the shell and spread irregularly inwards. There is a distinct demarcation line along the inner edge of the columella plate and extending down to the muscle attachment region nearest the apex so that the deposition of conchiolin on the columella plate is not continuous with that of the rest of the shell except at the margin of the plate itself. Also conchiolin is not deposited on the area of the muscle attachment after this area has become roughened. As this area of the muscle attachment increases in size the conchiolin layers terminate at regular intervals nearer the anterior lip of the shell. There is never very much conchiolin exposed on the surface at one time because by the

time the conchiolin layer is 1–2cm wide the next nacreous layer is being laid down at the margin of the shell and as the conchiolin spreads inwards so does the nacreous material. It seems, therefore, that although the growth of the shell occurs chiefly at the anterior and right margin the deposition of conchiolin and nacre can be carried out by all parts of the mantle in contact with the shell.

In a few specimens in which the shell had been broken or crushed the repair was chiefly done by deposition of conchiolin. This is also the case in the closing of the broadcast apparature.

of the branchial apertures. Growth of the Shell.

Graphs for two areas (Te Kaminaru and Island Bay) covering a total of 825 shells were made in order to find growth peaks. There was a difference of approximately one mm in shells from these two areas and this may be due to earlier settling time for larvae in one of the areas. The Te Kaminaru shells were 1mm shorter in longest diameter at each age peak, but for all practical purposes the two areas can be counted as one and when graphed in this manner produce four definite peaks as shown in text figure 1.



These four peaks came approximately 1cm apart, the first being at 1.9cm mark, the second 2.9cm, the third 3.8cm, and the fourth at 4.7cm. The peaks after the highest at the 4.7cm mark are indistinct but appear to become closer together.

Crofts (1929) considers specimens from 30 to 40mm in spring and summer are probably two years old and that growth gets progressively slower after the first few months. In this she disagrees with Stephenson (1924) who considers specimens from 20 to 40mm in summer as one year old. If the distance between troughs on the present graph is taken as indicating a year's growth, then *H. iris* agrees with *H. tuberculata* (Crofts, 1929) in being approximately 3cm in length when 2 years old. Because of this agreement in age and length of shell with the figures given by Crofts and also on account of the quite distinct peaks (approxi-

mately 1cm apart) in the present specimens, it seems reasonable to consider that the distance between one trough and another represents a year's growth. Shells that are 1.9 to 2.9cm, and 2.9 to 3.8cm in length are in their second and third years of growth respectively.

Plate 2, Fig. 3 shows an example of a small shell 4.7cm in longest diameter with well defined intervals of growth showing on the outside of the shell. These demarcations are approximately 1cm apart and would appear to lend further support to the hypothesis that 1cm growth (at least over the first three years)

represents a year's time interval.

It would appear from Text Fig. 1 that growth becomes progressively slower after the 4.7 peak. These intervals on the graph decrease from 1cm to approximately 0.5cm until the shells are 8cm in length. However, the peaks of shells greater than 4.7cm in length could not be determined accurately from this graph because as difference in growth each year becomes less, the number of shells necessary to give a definite peak is increased and sufficient quantities were not available within this size range to give a clear indication. Figures for the graph in Text Fig. 1 cover a range of shell from 1 to 8cm in length. All these shells were collected in the littoral area and the graph shows that the greatest number of shells inhabiting this area fall in the size range between 4.5 and 5.5cm in length.

Crofts (1929) collected *H. tuberculata* as small as 2mm in length. No specimens as small as this were found in the littoral zone in the parts of Cook Strait area covered by the present paper. Crofts (1929) reports that the smallest specimens are found at very low tides and this may also be the case with *H. iris*. The smallest *H. iris* shell found by the writer was 1cm in length and this was considered to be

under one year in age, Text Fig. 1.

The estimated age of shells with a size range between 1 and 5cm was calculated from the growth peaks as stated above and the occasionally well defined intervals of growth visible on the external surface of some small shells. An attempt was made to calculate the age of shells from 5 to 17cm in length by means of the number of conchiolin growth lines laid down in the shell. These growth lines are usually well defined as shown in Fig. 4. Approximately 300 shells sectioned through the longitudinal axis were examined. The lines on each shell were counted from the nucleus to the lower edge of the columella plate and again from the nucleus to the anterior margin of the shell. The former count generally gave two more lines than the latter. It was seen that shells with a size range between 4 and 5cm in length show no distinct growth lines. A definite growth line first appears in shells between 5 and 6cm in length and in this group four out of eight shells had no lines showing at all. The average number of growth lines for each centimetre group increases as the size of the shell increases. There is, however, no regular increase between the averages, for example, the average number of lines for shells from 9 to 10cm in length is 5.0; 10 to 11cm is 9.0 and 11 to 12cm is 9.9. In addition, there is a great range in the number of growth lines within any centimetre group, e.g. in the 11 to 12cm group 1 shell has only five lines while another within the same group possesses 27 lines.

It was noticed on many occasions that the growth lines were laid down in pairs. This gave rise to the idea that the growth between one line and another may represent six months' time interval. The nacreous material between the pairs is greater than between the two lines of a pair and it was thought that this greater deposition of nacre alternating with a lesser period possibly represented summer and winter seasons of growth.

The occurrence of pairs of lines is not, however, a constant feature and from examination of the data it seems unlikely that a shell 14 to 15cm in length could be 13 years old. This would be the case if half the average number of

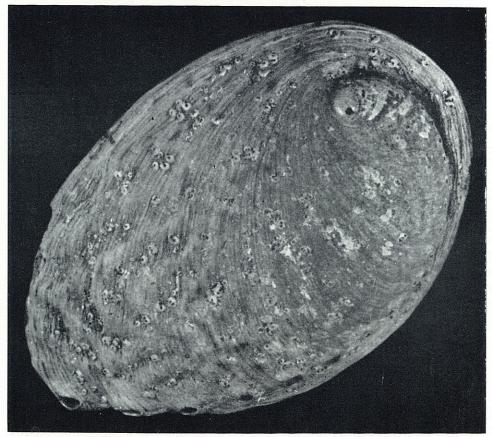


Fig. 1.—H. iris shell, photographed through the axis in order to calculate the constant angle of the shell.

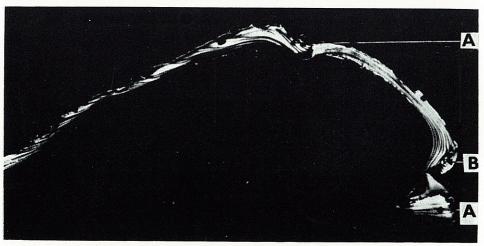


Fig. 2.—Photograph of ground section of shell through the longitudinal axis and nucleus to show the conchiolin lines. A, growth lines. B, nucleus.

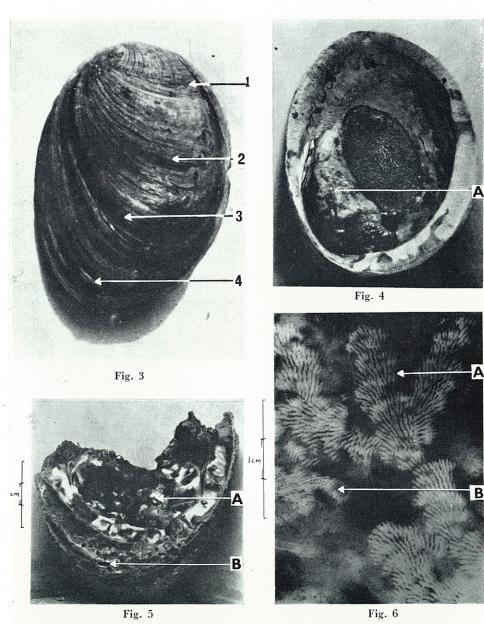


Fig. 3.—Photograph to show the well defined intervals of growth visible on the external surface of some small shells. 1, 2, 3, 4, external demarcations of growth.

Fig. 4.—Photograph to show encasement of conical caecum by the shell. A, caecum encasement.

Fig. 5.—Photograph of posterior region of a diseased shell to show the gross distortion of the shell and the numerous openings of worm tubes. A, gross distortions of the shell.

B, openings of worm tubes.

Fig. 6.—Photograph of the feeding tracks of two small Haliotis iris. A, tracks of H. iris, approximately 3cm in lengths. B, tracks of H. iris, approximately 2cm in length.

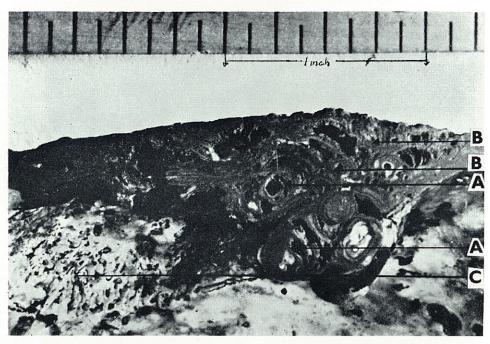


Fig. 7.—T.S. through a diseased shell to show tubercles and distortion of the conchiolin growth lines. A, tubercles. B, distortion of growth lines. C, position of insertion of shell muscle.

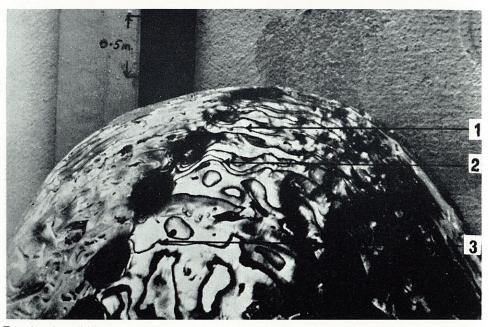
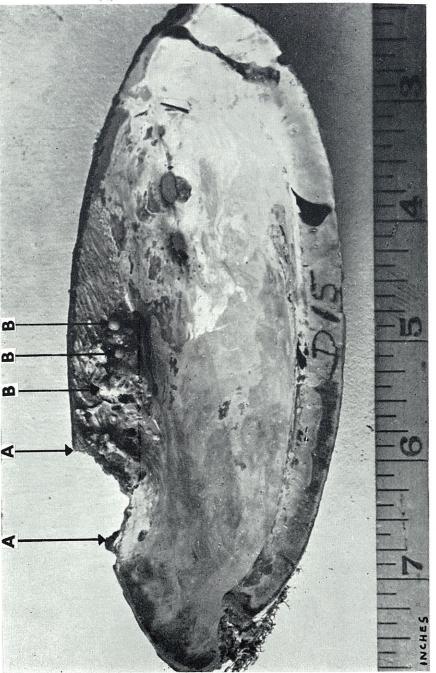


Fig. 8.—A polished specimen of *H. iris* to show the appearance of conchiolin growth lines on the outside of the shell. 1, 2, 3, growth lines.



B,

lines shown in Table I is taken, plus 4 for the four years' growth which occurs prior to the formation of conchiolin. From Text Fig. 1 it was concluded that in the first few years a shell grows approximately 1cm a year. It would be unusual if this growth rate did not decrease over a number of years. Yet a shell 14cm in length which is 13 years old would necessitate a growth of about 1cm a year for 13 years.

On the other hand the majority of the shells had the lines appearing singly and sometimes in groups of three as in Fig. 8. Therefore, it seems more probable that each growth line represents a year's growth. In this case a shell 14 to 15cm in length could be considered approximately 22 years old, i.e., the average number of growth lines plus 4. It must be remembered that the average for a group such as the 14 to 15cm group was obtained from a wide range in the number of growth lines. If a specific instance within a group is taken the age would be calculated from the number of lines actually present and not from the average for the group. For example, some old polished shells and pieces of shell have been examined with over 36 lines visible. This would mean that in some cases a shell was over forty years old. In contrast, however, some fairly large shells on the Table show very few growth lines, e.g., in the 12 to 13cm group two shells have only five lines. Therefore, their estimated age would be 9 years. This age is well below the estimated average age for the group and is open to the same objection as raised above where it was pointed out that a shell is not likely to continue growing at the same rate over a large number of years. As the rate of growth does not exceed 1cm a year the first 4 years it does not seem feasible to consider a shell 12 to 13cm in length as only 9 years old.

The only conclusion which can be drawn at present regarding the conchiolin growth lines is that these lines are put down regularly by the animal in response to some physiological need. It is not possible to state whether these lines are annual or biannual (i.e., twice yearly), or indeed give any indication of the growth-size ratio without further work being carried out.

Shell Perforations

Boutan (1886) states that the shell of *Haliotis* commences as in *Fissurella* and *Pleurotomaria* without slit or perforations and Crofts (1929) found a distinct protoconch in her smallest specimens. In the smallest specimens examined by the writer for *H. iris*, *H. virginea* and *H. australis* the protoconch was plainly visible and approximately the same size (1.5mm long) in all three species. As soon as growth begins perforations are formed and the difference in number of perforations for approximately the same length of shell is considerable in the three species.

	Number of Specimens	Long. Diam. of Shell	Total Number Perforations	Open Perforations
H. iris	1	1.10cm	15	4
H. virginea	1	.95cm	17	4
H. australis	1	1.20cm	21	5
H. iris	1	2.10cm	21	5
H. virginea	1 1	2.10cm	25	5
H. australis	1	2.20cm	32	6

Only single specimens were obtained in the size range shown above. The difference in number of perforations per unit length between the three species is due to the distinctive nature of the logarithmic spiral in each species, i.e., it follows that the constant angle of the logarithmic spiral in *H. virginea* will fall probably between that of the other two species.

There is a close correlation between the number of perforations present in the shell and the length of the shell. This can most easily be ascertained in the

smaller shells. It is very difficult to obtain an accurate count of perforations in the older shells because of the heavy encrustation of coralline algae, tube worms, etc. In a count of fifty shells taken from different areas ranging from one to seven centimetres in longest diameter the number of perforations increased regularly with the length except in one case. The average number of open perforations was five but ranged in number from 4 to 7. Suter (1913) states that open perforations in *H. iris* range from five to seven. In a count of approximately 340 shells ranging between 12 and 16cm the following estimate of shell perforations was obtained.

Number	of	Shell	Perforations

Number of Shells 2 12 50 100 140 99 34 5

It can be said that the range for open perforations for this species is from 0 to 7 while the average is from 3 to 5 rather than between 5 and 7 as stated by Suter (1913).

Crofts (1929) found in a count of 194 specimens of *H. tuberculata* of marketable size that 101 had 6 perforations and she states that the number of perforations in *H. californica* vary from 5 to 9 in young animals and from 2 to 3 in the adult. These latter figures resemble those given for *H. iris* in having fewer perforations in older shells. Crofts found only one shell imperforate and this had closed holes in the older part of the shell.

Pelseneer (1920) has described abnormalities of the shell in *Haliotis* as instances of continuous and discontinuous variation and cited the variations in the number of perforations in *H. tuberculata* and *H. californica*.

Growth Relation

Sasaki (1926) recorded the growth relation between the shorter and longer diameter in *H. gigantea* and in two varieties of *H. gigantea* from places varying in temperature in Japan. He took the ratio at Omoi as the mean (71.29) and he read his results to show that high temperature probably produced narrower shells. Crofts (1929) found the ratio for *H. tuberculata* was 68.7 in the Channel Islands.

In *H. iris* from the Runaround and Chaffer's Passage, Wellington, the ratio is 75.7 for 120 specimens varying from 9 to 17cm in longest diameter. They, therefore, are wider than *H. tuberculata* at Brecqhoua (Channel Islands) or any *H. gigantea* specimens mentioned by Sasaki. Ten specimens from Kaikoura gave a ratio of 78.1 which is wider again than any of the specimens mentioned above. In small *H. iris* varying from 5 to 50mm the shells are narrower not wider as Crofts (1929) found in *H. tuberculata* but the ratio is not constant. *H. australis* specimens give a ratio very close to that of *H. iris*, namely 70.0.

Sasaki found that the growth relation between shorter and longer diameters in H. gigantea could be expressed by the equation $S = kL^x$ where S is the shorter diameter; L the longer diameter; L the local constant and L the specific exponent. The probable specific exponent for L gigantea is 0.85 for mature specimens and for immature specimens 0.97 showing that the larger shell is the narrower. In L iris the following values for the specific exponent were obtained; 0.98 for mature specimens and 0.96 for immature specimens. These values for the specific exponent indicate that in L iris the larger shells are wider. No record of temperature range for the places in New Zealand from which the calculations on L iris and L australis were made were available to the writer. Consequently no correlation between the growth relation figures and temperature could be made as in the paper by Sasaki (1926).

Determination of Logarithmic Spiral

The large shell of H. iris has a very small apical spire and an extremely large last whorl which is very depressed with a relatively enormous aperture.

Crofts (1929) suggests that the flattened shell of *Haliotis* has been evolved from a shell with a taller spiral because of the habit of squeezing into confined spaces between rocks. The shell of *Haliotis* grows in the form of a logarithmic spiral. The form of a single curve following a logarithmic spiral is given by the expression

$$r = e^{\theta \cot \alpha}$$

where r is the radius of the shell from centre to circumference; θ is the angle of revolution which the spiral has described and α is the angle between the tangent of the curve and the radius vector of this curve, which remains constant. This is known as the constant angle of the curve and has been determined in many species of *Haliotis*. D'Arcy Thompson (1942) states that in *Haliotis* the constant angle (α) varies from about 70 degrees to 75 degrees while in the majority of gastropods it lies between 80 degrees to 85 degrees or even more.

To determine the constant angle of H. iris a photograph was taken through the axis of a shell 9.9cm in largest diameter. The curve made by the line of holes in the shell was taken as the logarithmic spiral. Plate I shows a photograph and a diagram can be drawn from it. The following expression of the formula given above was used in the actual determination of the angle.

$$\frac{\text{change of log. r}}{\text{change in } \theta \text{ deg.}} = \frac{\pi}{2.30} \cot \alpha$$

The result obtained gives $\alpha = 53$ degrees 46' which as far as the writer can ascertain is smaller than any other value of α obtained for a *Haliotis*. This means then, other things being equal, that *H. iris* has fewer whorls per unit height of shell than other species of *Haliotis*.

Moore (1936) found that the value of α in *Purpura lapillus* varied during the lifetime of the shell. The value of α calculated from a *H. iris* specimen 3.72cm in largest diameter was considerably higher in degree than in the case of the specimen 9.9cm in largest diameter. Therefore it appears probable that the value of α decreases as the shell grows.

	Longest Diameter	Constant Angle
Species	in Cms	of Spiral (α)
H. australis	7.75	72 degrees 6'
H. iris	3.72	60 degrees 53'
H. iris	9.9	53 degrees 46'

The constant angle of the spiral of H. australis in the above table shows a large increase over the values given for H. iris and is higher than some other species of Haliotis, e.g. H. tuberculata where $\alpha = 69$ degrees 48' (Moore, 1936).

Crofts (1929) states that the shell of *H. tuberculata* is so flattened that the animal is unable to retract completely into the shell. From the value of the constant angle in *H. iris* given above it follows that the shell of *H. iris* is lower in relative height; but in contrast to *H. tuberculata*, *H. iris* can retract completely within the shell when disturbed.

PATHOLOGICAL SHELLS

From over a thousand *Haliotis* examined in a period of two years no specimen was observed with macroscopic disease of the soft parts, although a number had the dorsal region in various positions affected by contact with a diseased shell. Crofts (1929) states that she found no record of parasites occurring in *Haliotis* and in her examination of approximately four hundred specimens found only

two diseased. On the other hand, in *H. iris* the crab *Elamena producta* has been found on a large number of occasions apparently living in association with the New Zealand species. On removal of the shell from *H. iris* the crab is seen to be situated between the foot and the mantle. Crofts found *H. tuberculata* shells frequently damaged by parasites, namely boring bivalves such as *Lithodomus* and various *Pholadidea*, but she does not mention tube worms. In the case of *H. iris* the shell is often heavily infested with these worms. Shells up to about 10cm in length are relatively clean on the surface and dark brown in colour. Above this size, however, out of a count of approximately 1,000 large shells all carried a heavy calcareous incrustation formed by algae covering the shell and in every case harbouring various species of annelid worm. Up to a hundred worms could be removed from one shell. These worms burrow through the periostracum of the shell and enter the nacreous portion ruining the shell for commercial use.

The most common worm found in the shell is *Polydora sp.* a member of the Spionidae. This is apparently *P. monilaris. Polydora* contains well known shell boring tube worms and has been described as causing a great destruction of oyster shells (Haswell, 1885). In some *H. iris* heavily infested with *Polydora* the calcareous crust of the shell will lift off in large pieces exposing a network of intertwining worms and their tubes. It is not known for certain how the worms burrow in the shell but it is probably by chemical means as the shell is much too hard for any mechanical means. The next most common worm found in the shell is the Terebellid *Polycirrus*. This dark brown worm has tubes very similar to those formed by *Polydora*. The tubes are not formed by many small particles adhering together but appear as thin chitin-like envelopes surrounding the worms. *Nereis* species are commonly found on *H. iris* shells although they probably do not destroy the shell as much as either *Polydora* or *Polycirrus*. The *Nereis* were identified as *Nereis kerguelensis*. Others were present. A number of

Serpulids were found and one was identified as Hydroides.

In the shell shown in Plate 4 (Figure 9) the whole posterior dorsal region was completely deformed by worms. A large specimen of Thelepus was situated in the deep indentation shown in the photograph. Although the shell in this instance may have been slightly crushed to allow entry of the worms in the first place the major destruction of the shell appeared to be due to the worms. On the ventral side of the shell the indentation was covered by nacreous material except anteriorly along the edge of the muscle attachment where a great many small round protuberances on the shell were actually embedded in the muscle itself. In addition, some of these rounded projections had become detached from the shell and were lying in the muscle. It seems that the deformation made by the worm infestation caused the shell to proliferate these small round bodies which are not nacreous but rather resemble the periostracum structure of the shell. In section they show concentric rings. Although Polydora was seen on deformed shells it could not be said to cause the deformation as many shells perfectly normal on the inner surface had numbers of Polydora living on the outer surface. Only Thelepus and Nereis were found in direct connection with malformed shells. Plate 2 (Figure 5) shows a broken shell which was picked up from the beach near Island Bay. The whole outer surface of this shell is covered with worm holes and the severe distortion of the shell is without doubt due to heavy infestation of worms.

Plate 2 (Figure 4) shows a shell with a peculiar growth almost entirely enclosing the conical caecum of the visceral hump which contains a core of liver surrounded by gonad. This portion of the shell encasing the liver caecum appears to be made of nacreous layers in a way similar to the rest of the shell although it has not the lustre of the inner surface of a normal shell. In a normal shell the nacreous layers are put down at the posterior region of the shell by the mantle

covering the visceral hump but the major part of the caecum which extends forwards passes under a sheet of mantle stretching from the edge of the muscle attachment to the edge of the mantle plate, forming as it were a pocket in which the caecum is lodged. Thus the anterior part of the caecum has no contact with the shell either dorsally or ventrally. There is a distinct line of demarcation between the portion of shell laid down by the mantle of the posterior region of the visceral hump and that laid down by the mantle covering the anterior prolongation of the liver caecum.

In Fig. 4, however, there is no marked distinction on the inner surface of the shell showing where the mantle on the visceral hump ceases deposition of nacre and deposition of nacre by the mantle of the caecum pocket begins. In this case, therefore, it appears that for some reason the conical caecum has not been enclosed in the mantle pocket but has lain in direct contact with the shell and begun to secrete shell layers. Apparently the whole surface of the lobe has taken on a secretory function as shell has been formed enclosing the whole caecum. The ventral side of this cone of shell may have been formed as protection but it is not known whether the usual ventral covering of the visceral mass was present or not. Out of many thousands of specimens, Mr Taylor of Island Bay has found not more than 12 specimens of H. iris showing this peculiar formation of the shell. In some cases the cone of shell was not as complete as that shown in Fig. 4.

In one case in which the writer was able to see the animal that had been removed from the shell the caecum was twisted dorsally and was not covered by mantle except ventrally. The whole caecum had secreted shell dorsally but not ventrally where it was covered by the ventral portion of the mantle.

The most common type of diseased shell found was that depicted in Fig. 7. This formation of protuberances or tubercles on the inner surface of the shell was found frequently in some areas. In a section of the shell as shown in Fig. 7 these tubercles can be seen to have a core surrounded by numerous layers of nacreous material alternating with the dark conchiolin lines. This abnormal growth of the shell was probably due to irritation caused by sand particles becoming lodged between the mantle and the shell or, in some cases such as in Fig. 5, to the irritation caused by worms boring in the shell. Boutan (1923) succeeded in producing pearls in Haliotis by introducing foreign bodies in a suitable manner. Pearls have been found in H. iris in close proximity with such malformations as described above. These pearls were similar in structure to those tubercles seen in section but were always very small. Small shells are not often found with any tubercle formation on the shell and it is characteristic of this abnormal formation that it always occurs near or posterior to the muscle attachment region of the shell. Perhaps this is because only in this region does the animal find it impossible to rid itself of foreign bodies which have penetrated beneath the mantle. In the few small shells that were found with the tubercles just beginning to form the shell had a rough irregular inner surface apparently due to particles of sand which had been covered over by a dark conchiolin layer.

About 200 "frosted" shells were examined. These shells completely lacked the bright lustre of the inner surface of a normal shell. All the examples seen were large shells up to 17cm in longest diameter. The frosted appearance was due to some abnormality of the nacreous material laid down. Often this nacreous layer was flecked by conchiolin unlike a normal shell where the conchiolin layers are laid down in a fairly regular pattern. In addition, the shells were thick, the "frosted" nacreous layer being much thicker than a normal nacreous layer. The shell mentioned previously with the encased caecum (Fig. 4) is an example of a "frosted" shell. These shells are of no use commercially because they will not take a polish.

FOOD AND METHOD OF FEEDING

H. iris feeds on a large variety of seaweeds. In some fifty specimens examined for gut contents the following seaweeds were identified: Xiphophora chondrophylla var. maxima, Caulerpa sedoides, Pterocladia lucida, Halopteris bordacea, Gigartina sp. and Ulva sp. Most of the animals examined were collected from Chaffer's Passage and The Runaround and they all had crop contents composed almost exclusively of brown seaweeds. Thus it can be said that in these animals which ranged from 10 to 16cm in length, brown seaweeds formed the predominating food. Crofts (1929) states for H. tuberculata that "mature animals show a preference for the delicate Algae, particularly red seaweeds such as Delesseria and Griffithsia, but will eat Chondrus as well as coarser weeds". From examination of the gut content of H. iris the reverse condition appears to be the case. In small specimens the predominant food consists of small red seaweeds. In one instance a few specimens taken from a large pool just below low water mark, i.e. where the small paua between 1-8cm are found, the green seaweed Ulva was most noticeable but all the crops examined contained principally varieties of red seaweeds. A preference for red seaweed is undoubtedly shown by the New Zealand species but not by the larger specimens, as in H. tuberculata. The areas where the best shell grows generally contain a large amount of Xiphophora chondrophylla var. maxima and sometimes a great deal of Ulva.

Specimens held in aquaria were found to eat blue-green algae and diatoms which were present on the side of the tank. The diatom was Cocconeis sp. or a species very close to it. On a number of occasions Ulva was given to the aquarium specimens when there was very little algal growth on the sides of the tanks, but on only one occasion was a specimen observed eating it. The feeding of small H. iris on the sides and floor of the tanks was observed on many occasions. Each feeding movement of the radula resulted in two minute areas on the side of the tank being cleared of Algae, as can be seen in Fig. 6. As far as could be ascertained the scraping off of the Algae was accomplished by the two lateral sets of teeth in the radula as described by Crofts (1929). Six or seven feeding movements would be taken transversely with the posterior region of the foot hardly moving at all, then the whole animal would move forward sufficiently to be in a position to clean the next area in front. This method results in the feeding tracks having a branched appearance. In Fig. 6 the feeding tracks of two small specimens are shown. The larger set of "tracks" was made by an animal approximately 3cm in length and the smaller (lower left corner) by a specimen approximately 2cm in length. The latter did not make such regular tracks.

The size of the particles of seaweed found in the gut varied with the size of the animal. The largest specimens (13–17cm in length) contained food particles averaging 5mm in length and 1.5mm in width. They may, however, reach up to 10mm in length. The shape of the particles is fairly uniform, generally pointed at both ends and slightly curved towards one side.

PROPORTION OF MALE AND FEMALE SPECIMENS

Counts of male and female specimens of *H. iris* taken from Karori Light, The Runaround and Sinclair Head were as follows:

Date	Locality	Male	Female	Ratio
2/5/46	Karori Light	251	176	1.42
3/6/46	Sinclair Head	48	38	1.26
-/6/46	The Runaround	53	32	1.62
	Total	352	246	1.43 average

Stephenson (1924) examined 127 specimens of *H. tuberculata* and found the proportion of males to females was 50 to 71. This gives a ratio of 0.7.

It is possible that the difference in relative proportions of males to females shown in the above figures was due to the different season at which they were taken. Stephenson (1924) obtained his specimens during the summer while the writer's figures are taken from specimens collected in the winter. Until a count can be taken in the summer from the Wellington areas no satisfactory comparison can be made between the two sets of figures.

SUMMARY

A brief historical survey is given of the use to which shell and soft parts of the animal were put by the Maori, and the economic importance of the shell and soft parts in New Zealand at the present time; also the figures for the number of specimens removed from Cook Strait area over a two-year period by one fisherman.

Indications of the areas from which good and bad shells can be obtained are given. *Haliotis australis* is almost without exception found in connection with *H. iris* but in very small proportions. No *H. virginea* were found in the Cook Strait area although they are known to occur further south.

H. iris is considered to have a homing instinct in its nocturnal movements but no indication was found that it undergoes winter migration to deeper water.

The shell of *H. iris* is unique in having a brilliant iridescence when polished due, probably, to dark conchiolin lines alternating regularly with nacreous material so that nowhere is there any great thickness of nacre. Conchiolin deposition commences when the shell is approximately 5cm in length and the deposition of conchiolin and nacre can be carried out by all parts of the mantle in contact with the shell.

A section of diseased mantle shows numerous dark brown granules scattered throughout the epithelial cells, connective tissue and muscle. It was not possible to determine the exact nature of these granules.

The relation of length to age for young shells was determined by graphing a number of shells from two areas and it was estimated that shells 1.9cm to 2.9cm and 2.9 to 3.8cm were in their second and third years of growth. An attempt was made to estimate the age of older shells from the number of conchiolin growth lines counted on longitudinally sectioned shells. The only conclusion able to be reached regarding these lines was that they are regularly laid down in response to some physiological need. The time interval which each line represents was not able to be determined.

A close correlation was found between the number of perforations present in small shells and the length of the shell. The number of perforations increased regularly with the length of the shell. The average number of open perforations was five in *H. iris*.

The growth relation for *H. iris* in Cook Strait area was found to be 75.7 which is wider than in *H. tuberculata* (Crofts) and *H. gigantea* (Sasaki). *H. australis* gives a ratio close to *H. iris*, namely 70.0. The constant angle of the logarithmic spiral in *H. iris* was determined as 53 degrees 46' in a specimen 9.9cm in length.

No specimens of *H. iris* or *H. australis* were observed with macroscopic disease of the soft parts, but all shells over approximately 5cm in length had some encrusting calcareous algal growth and all shells over 10cm in length had tube worms on the outer surface. Heavy infestation of tube worm sometimes led to large tubercles forming inside the shell but the most common cause of tubercle formation was considered to be irritation by sand grains. The commonest species of annelid worm present was *Polydora*. Other forms identified were *Nereis* sp., *Polycirrus* sp., *Hydroides* sp., and *Thelepus* sp.

H. iris feeds on a variety of seaweeds and diatoms. In the small specimens

the gut contents show a predominance of red seaweeds while brown seaweeds are most common in the larger specimens.

The ratio of male to female specimens in H. iris is 1.43 for a count of 352 specimens taken in the winter months.

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