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ニュージーランドの開放海岸に生息する大型深潜没二枚貝トヘロア（チドリマスオガイ科）の底質にもぐる速さと位置・方位

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Burrowing Ability and Life Position of Toheroa (*Paphies ventricosa*: Mesodesmatidae), an Unusually Large, Deep-Burrowing Ocean Beach Bivalve Endemic to New Zealand

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Abstract: *Paphies ventricosa*, commonly known as "toheroa", is an unusually large, ocean beach bivalve endemic to New Zealand. The burrowing rate, depth of burial and azimuthal shell orientation of toheroa were observed on Muriwai beach, northwest of Auckland, North Island. Many individuals were found with their commissure planes parallel to the shoreline, or aligned with their dorsal side seaward. This attitude is similar to that resulting from the shell orientation during movement by receding waves, after being washed out on the beach. Toheroa displayed almost the maximum rate of burrowing performance amongst the bivalves reported to date, being similar to members of the Donacidae. The depth of shell burial is about 10 cm for individuals of 10 cm shell length. This is unusually deep for ocean beach bivalves. The adaptation shown by toheroa is interpreted as a forced compromise in a very harsh environment between shallow and rapid burrowing, and permanent or almost immobile and deep burrowing.

Introduction

Paphies ventricosa is an unusually large (up to 14 cm shell length) mesodesmatid bivalve endemic to New Zealand. Aside from the size, its adaptation to ocean beaches appears unusual, with its deep-burrowing habit, while still retaining a very active burrowing ability. This animal is well-known as toheroa in New Zealand due to its exploitation in commercial and recreational fisheries earlier this century. Its population has been so unstable that sudden disappearance and quick recovery were common. However, there has been no major recovery after the 1970's on the west coast of the North Island (Stace, 1989), and the beds were closed. Much attention has accordingly been paid to the population dynamics (Rapson, 1954; Cassie, 1955; Greenway, 1969), predation (Rapson, 1954; Haddon, et al., 1987), distribution (Waugh, 1967; Redfearn, 1982), growth (Rapson, 1952), larval ecology (Redfearn, 1982), along with some taxonomic studies (Dawson, 1959; Beu, 1971, Beu and De Rooij-Schuiling, 1982). Redfearn (1974) summarized all aspects of biology of this animal.

However, studies of the functional shell morphology and other ecological attributes, such as burrowing ability and life orientation were quite limited. Adaptation of this somewhat unusual bivalve has remained unappreciated to date. The ecological and adaptive-morphological studies of the mesodesmatid bivalves are also limited (Allen, 1975; Narchi, 1981). Besides the general ecological account by Morton and Miller (1973), only Hoby (1933) provided pertinent information, but part of the study needs revaluation from the standpoint of subsequent progress in bivalve shell morphology and ecology, (e.g., Stanley, 1970), and has remained an unpublished thesis. In addition, owing to a strict conservation policy, even the digging of this animal is prohibited and opportunity for observtion is limited today. We thought, therefore, that our brief ecological observation may deserve publication.

This note describes the mode and rate of burrowing, and life orientation of toheroa, and discusses the adaptation of this bivalve, compared with other mesodesmatid bivalves, and with better-known ocean beach bivalves belonging to Donacidae.

Field Observation

Observations were made near a dense bed of toheroa, the middle intertidal zone of a highly exposed sandy beach north of Muriwai, northwest of Auckland at low tide on the afternoon of 8 April, 1994. Azimuthal shell orientation was measured against the shoreline. Life position, including long axis inclination and depth of shell burial, were measured directly by digging. Mode and rate of burrowing were observed and measured by video recording. Seven individuals were chosen to cover as wide a range of size classes as possible. They were allowed to burrow three times successively in nearby sandy substrate slightly covered with water. Each time the individuals burrowed, time and number of burrowing sequences from the erection of the shell, to complete burial when the shell became invisible, were measured to be within about five minutes. The water temperature was 19°C.

The burrowing performance was compared with those for other species, based on the Burrowing Rate Index (B. R. I.)(Stanley, 1970),

$$\text{B.R.I.} = \frac{\sqrt[3]{\text{shell mass (g)}}}{\text{burrowing time (sec.)}} \times 100$$

Burrowing Sequence, Orientation and Performance

As in other bivalves, the burrowing sequence of toheroa consists of a series of steps; (1) initiation of a wavy motion of the foot, (2) penetration of the foot into the substrate, (3) initiation of the burrowing, (4) erection of the shell, (5) complete burial of the shell, (6) attaining the final position within the substrate.

The erect probing orientation of toheroa, that is the orientation when the shell is erected in the initial stage of burrowing (Stanley, 1970), is significantly inclined (Fig. 1, right),

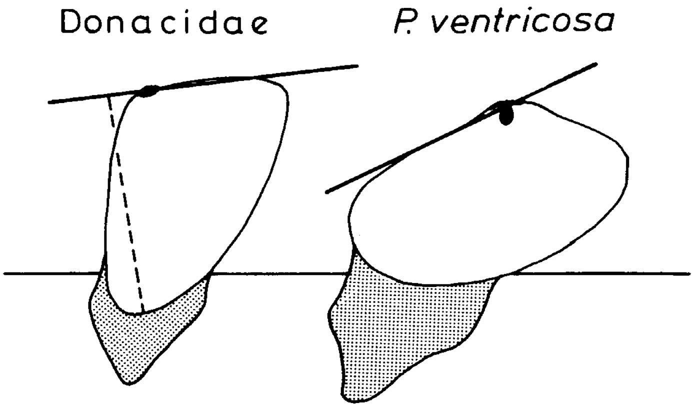


Fig. 1. The erect probing orientation of toheroa (right), as compared with that in Donacidae (left) shown by Stanley (1970). トヘロア（右図）とナミノコガイ科（左図）の直立潜入姿勢の比較. ナミノコガイの姿勢はStanley (1970)による.

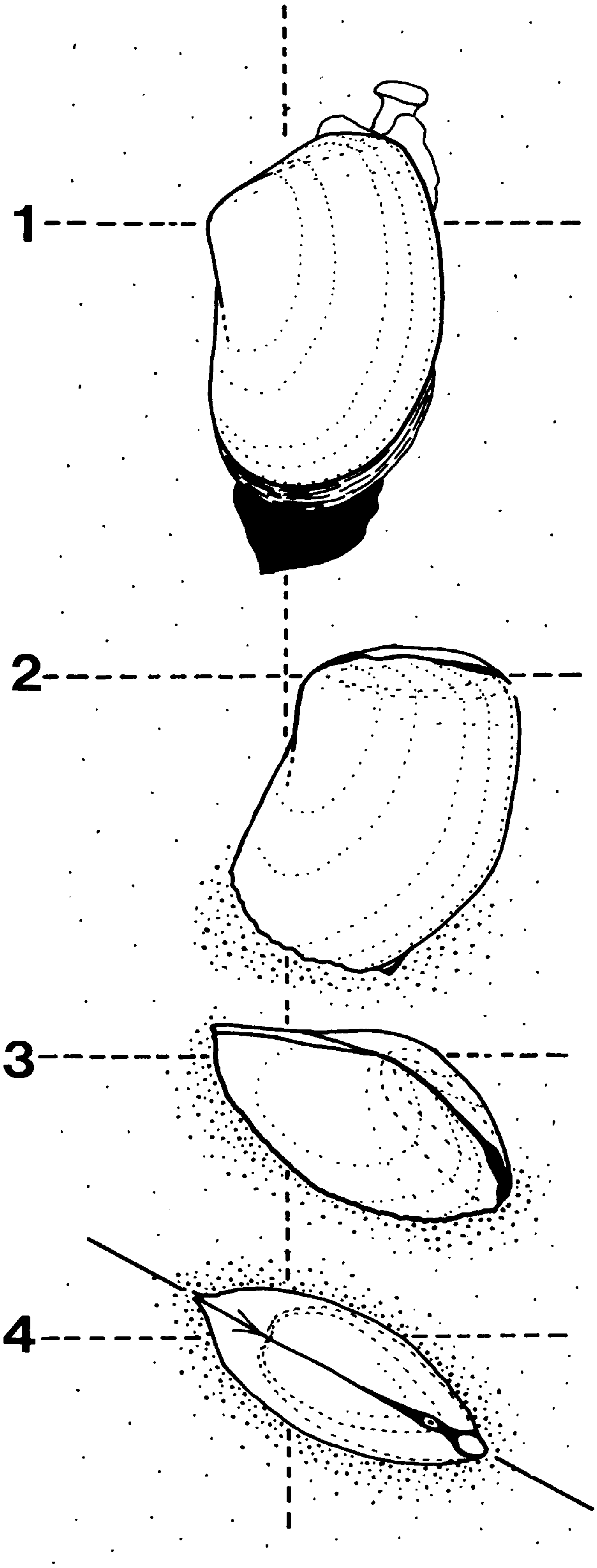
in contrast to the almost vertical orientation of the long axis shown by Donacidae (Fig. 1, left; Stanley, 1970). This appears to be the result of the heavy weight of the shellfish, but even the smallest individual of 27 mm shell length, was also slightly inclined. After the erection of the shell, they showed very little rocking motion, but buried themselves straightforwardly in an anterior-downward direction, similar to the burrowing of Donacidae. This indicates that they are efficient burrowers. The orientation during burrowing is with the long axis about 40-50° inclined from the vertical. They must rotate their shell postero-ventrally to attain the final feeding orientation after burial. The normal feeding orientation was observed with the long axis almost vertical or only slightly inclined.

The azimuthal orientation of the dorso-ventral axis became somewhat rotated during the stages from (1) to (3) of Fig. 2. This happens because an anchorage is gained by inflating the dosal part of the foot and contracting it ventrally.

In our observation, the burrowing time was measured from (4) to (5), as in Stanley

Table 1. Burrowing rate index (B.R.I.). The weight was estimated from the data by Rapson (1952), using the established relation between the shell length and animal weight. 潜入速度指標. 貝の重量は, Rapson (1952) の殻長と重量の関係から算出した.

Shell length (mm)	Weight (g)	Burrowing time (second)	B. R. I.
27	2.2	12	11
77	60	41	10
79	65	72	6
86	85	166	3
97	118	154	3
98	120	not completed	
100	126	245	2


1
2
3
4

(1970), to compare with other burrowing bivalves of the western Atlantic. As a result, toheroa was shown to be a moderate to very rapid burrower, with the B. R. I. ranging from 2 to 11 (Table 1). There is a notable difference in the B. R. I. between juvenile and adults; the smallest individual showed the greatest value, 11, and the largest one the smallest, 2. For comparison, B. R. I. of *Donax denticulatus* is 17, and *Donax variabilis*, 7.

This ontogenetic change in the B. R. I. is exceptional, compared with the roughly constant value for most of the burrowing bivalves described by Stanley (1970). It might then be claimed that the juvenile and adult toheroa differ in their adaptation, and that the juvenile has a more donacid like mode of life. Redfearn (1974) described the supporting observation on the partly voluntary emergence and movements by wave of the juveniles, which is similar to the habit of Donacidae.

Toheroa requires a high rate of burrowing for survival in its habitat, that is, the middle intertidal zone of highly exposed ocean beaches. Also, rapid burrowing is essential for toheroa who are constantly confronted with predators including birds, snapper and paddle crabs (Haddon et al., 1987).

Azimuthal Orientation

Azimuthal orientation was measured for twenty four specimens. It was variable (Fig. 3), but not random ($\chi^2 < 0.05$). Many individuals were found roughly parallel to the NW-SE trending shoreline. Individuals with the dorsal portion directed upshore, were rare. This observation is very similar to that described by Hoby (1933). Figure 4 summarizes Hoby's interpretation; it was found that the heaviest portion of the animal, that is the posterior end and less commonly the dorsal edge, pointed towards the sea in the receding

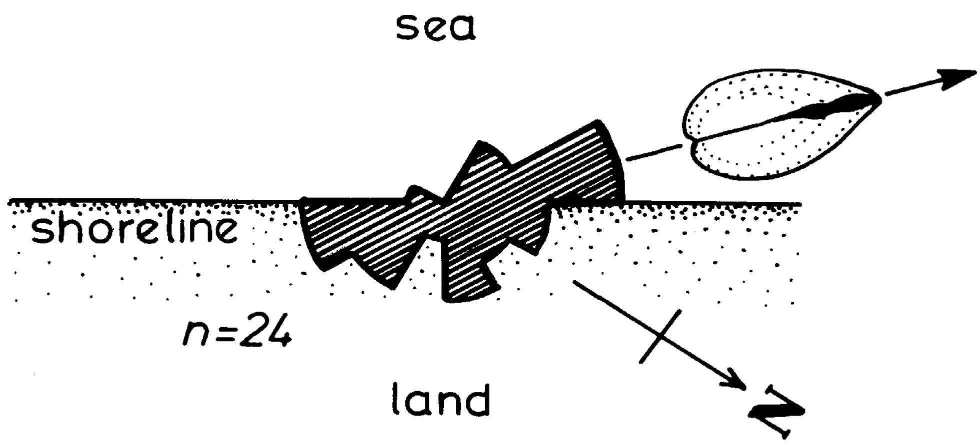


Fig. 3. The azimuthal life orientation of toheroa at Muriwai beach. ムリワイ海岸におけるトヘロアの方位.

Fig. 2. Plan view of toheroa showing the shell orientation during burrowing. Note the slight dorsally rotation during erection of the shell. トヘロアが底質にもぐる時の貝殻の向きを示す上面図. 貝殻を立てる段階で，殻が腹側に少し回転することに注意.

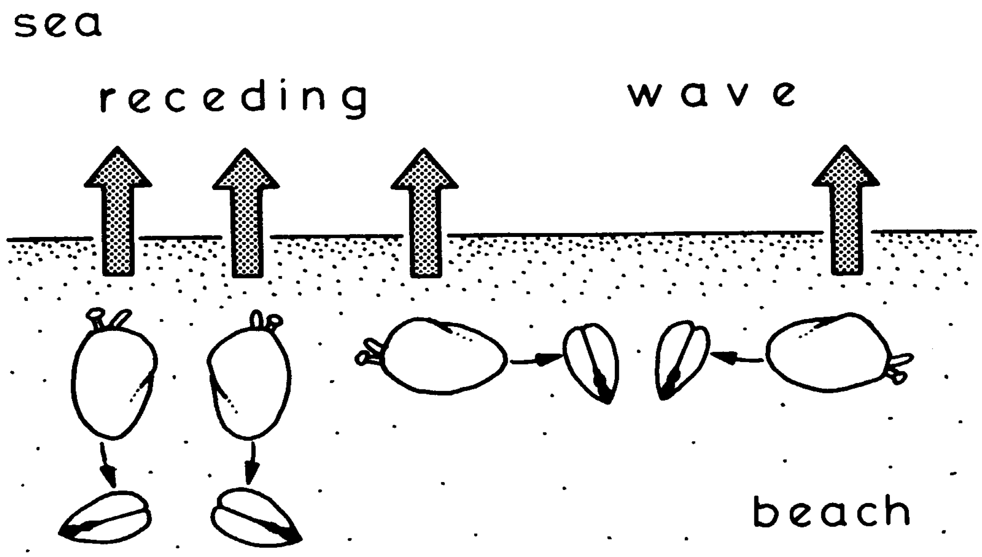


Fig. 4. Schematic diagram explaining the azimuthal orientation of toheroa. トヘロアの海浜での方位を説明する模式図.

wave, and the former resulted in the shore-parallel orientation and the latter the orientation with the dorsal edge towards the sea. Also Hoby (1933) noted that the shore-parallel orientation became more common on those days which follow a storm or when there is a strong surf. The azimuthal shell orientation of toheroa has been thus interpreted as mechanically determined. Considering that toheroa are often washed out on beaches, resulting in large mortalities (Eggleston and Hickman, 1972), this explanation appears plausible. The mechanically determined azimuthal orientation is in contrast to the more constant orientation with the dorsal edge towards the sea shown by the two Japanese beach clams *Chion semigranosus* and *Donax (Latona) cuneatus* (Unpublished data). We suggest that this type of preferred orientation common in Donacidae is an adaptation for effective suspension-feeding in the receding waves.

Interpretation of a slightly asymmetrical orientation to the normal axis to the shoreline (Fig. 3) is unclear. This may have resulted from an asymmetric wave on this beach.

Depth of Burial

From the observed depth of burial (Fig. 5), there appears a reverse relation between depth of burial in the substrate and the shell length of the animal, although the variation is quite large in moderately large specimens and the size range of the available specimens was quite limited. As few very small specimens were found, and they were only a few centimeters below the surface (not shown in the diagram), there should be a general tendency that small individuals are shallowly buried and larger specimens burrow more deeply.

A similar pattern regarding depth of burial and shell length was reported for *Dosinorbis japonicus* from the sandy intertidal zone of Japan (Kondo, 1987). *Dosinorbis japonicus* is a moderately deep burrower in absolute depth down to 15 cm from the surface. In a relative sense, it is a very deep burrower, with the maximum burrowing depth attaining

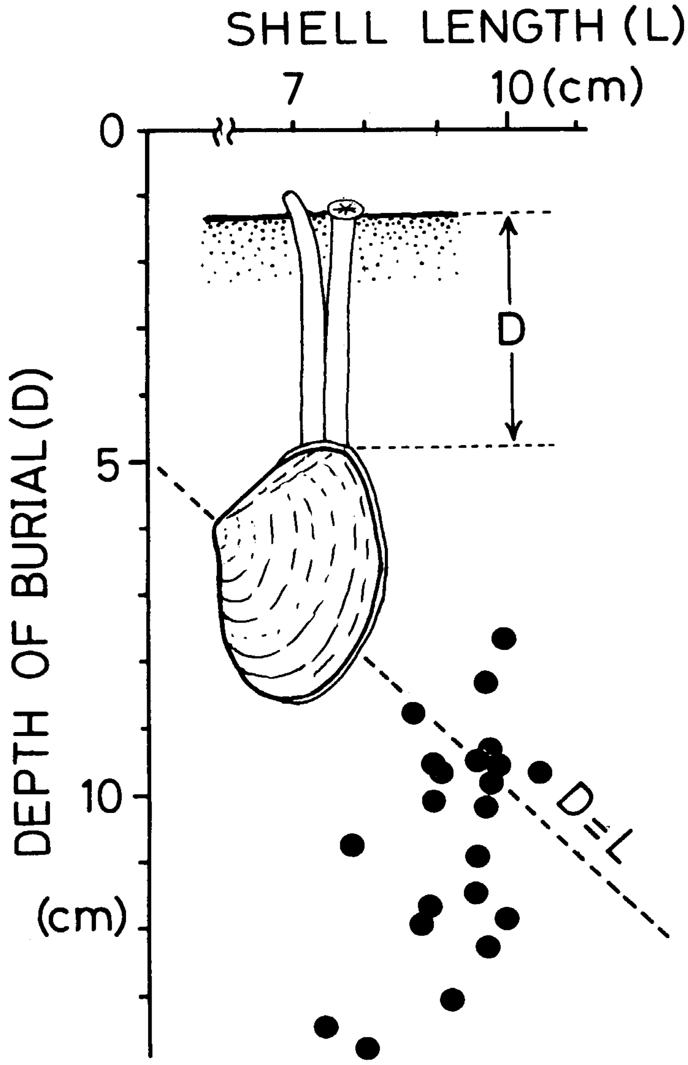


Fig. 5. The depth of burial by toheroa on Muriwai beach.
ムリワイ海岸におけるトヘロアの潜入深度.

five times the shell length for juvenile. Juvenile specimens are found invariably in a deeper zone near the maximum depth of their ability. Adult specimens, however, burrow much less deeply in a relative sense, about twice the shell length, and the individual variation is larger. This pattern may indicate a relatively secure situation for adult individuals having thicker shells and hence physical stability, while juveniles having thinner shells need to burrow as deeply as they can, to avoid disinterment and predation. The observed depth distribution pattern for toheroa may be interpreted similarly.

Haddon et al. (1987) experimentally verified the general idea that deep burial within the substrate provides significatnly more secure protection for toheroa from predation by the paddle crab *Ovalipes catharus*. They also demonstrated that the high population density produced a significantly lower predation rate. Their experiments thus answered the question why toheroa burrowed deeply and occur in dense beds.

Discussion

Shallow sea soft-bottom infaunal bivalves have two different adaptive strategies for coping with physical and biological disturbances; shallow burrowing with active burrowing ability and deep burrowing abandoning reburrowing ability (Stanley, 1972; Kondo, 1987). Here, the former is tentatively called "exposed strategy" and the latter "sheltered strategy". A distinct exception to this general rule is burrow-dwelling bivalves, such as Solemyacea and Solenacea, which can burrow very deep in their maintained burrows, but still retain active burrowing ability.

Toheroa may be another exception to this rule. The maximum burrowing depth of toheroa is about 1.7 times the shell length and is not very deep compared with common bivalves in Japan (cf. *Ruditapes philippinarum*, 2.6; *Dosinorbis japonicus*, 5.0; Kondo, 1987), for example. Nevertheless it is still much deeper than the other two species of the same genus living in exposed ocean beaches in New Zealand, *Paphies subtriangulata* and *P. donacina*. Also owing to its large shell size, absolute depth is moderately deep, down to about 18 cm (Hoby, 1933). However, toheroa is, as shown in this paper, a rapid burrower. The adaptive strategy of toheroa appears to lie somewhere between the exposed and sheltered strategies.

One of the most successful bivalves on ocean beaches is Donacidae which adopt an extremely exposed strategy. Some of them even make use of the extremely unstable wave-swept environment, using the uprush and backwash to be transported and maintain their position at the water edge (Mori, 1938, 1950; Wade, 1967; Ansell and Trevallion, 1969). Their distribution is limited to tropical and subtropical waters. Ansell and Trevallion (1969) stated that the burrowing of Donacidae is very rapid in tropical waters *(Donax incarnatus)*, and much less rapid on the colder British coasts (*Donax vittatus*). To burrow rapidly and repeatedly in the harsh environments, which is essential to survive the life on ocean beaches, appears to require high temperature to maintain activity. The generally small size of the Donacidae indicate that rapid burrowing is more important than physical stability, in contrast to the large size of toheroa.

Closely related species of the same genus *Paphies* in New Zealand, *P. subtriangulata* and *P. donacina* show similar adaptation to that shown by Donacidae with rapid burrowing habit and wedge-shaped shell morphology, except that they are larger than Donacidae. North-western Atlantic species of the same family, *Mesodesma arctatum* distributed north to Greenland (Stanley, 1970; Allen, 1975) also shows similar shell shape and environmental preference to Donacidae. Some of the members of the Mesodesmatidae are thus temperate and cold water ecological equivalent to the Donacidae. Distribution of such Mesodesmatidae and Donacidae do not overlap in most areas.

In the intertidal zones of highly exposed ocean beaches, even deep burrowing may not assure as secure a life, as most of the more sheltered soft bottom locations, because substrate disturbances, particularly reworking, are so great and easily exceed the usual limit of burrowing ability, that is, 50–70 cm of extremely deep bivalves, such as *Panopea japonica* (Kondo, 1987). From the senior author's observation of the fossils of the living species *Panopea japonica* in the Pleistocene Shimosa Group exposed in Chiba Prefecture, Japan, the species is found in a variety of sedimentary facies from sheltered muddy sediments to shelly substrate inferred to have been deposited off moderately exposed beaches. This indicates that an extremely deep burrowing mode of life can successfully colonize a wide variety of substrates. However, even *Panopea japonica* cannot colonize the intertidal zone of ocean beaches. Seasonal beach cycles of a constructional and destructional phase is probably the major cause of the large-scale fluctuation of substrate level, in addition to more rapid scouring and burial by constant strong wave action. The sheltered strategy, abandoning mobility, cannot thus be effective on ocean beaches. A burrow-dwelling mode of life also appears difficult to adopt; maintenance of a burrow appears difficult in the well-sorted clean sand of such beaches.

The adaptive theme shown by toheroa, therefore, appears to be a forced compromise between the exposed and sheltered strategies. Also the large size of the adult shell apparently increases their physical stability in keeping their position on the beaches.

Judging from the published information, the most similar adaptation is found in *Mesodesma mactroides* living in the ocean beaches of South America (Narchi, 1981). This species is a thin-shelled bivalve, living in the lower intertidal zone of the exposed ocean beaches of eastern South America, and it burrows deeply, down to 20 cm. Considering that the average shell size is only 5 cm, the depth of burial is very deep in a relative sense. Moreover it burrows rapidly. There is, however, no information on the B. R. I. measurement. According to information available, the mode of life of this bivalve is generally similar to that of the toheroa, but it appears to prefer a slightly more sheltered mode of life.

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要　　約

トヘロアはニュージーランドの開放海岸潮間帯に密集層を形成して生息するチドリマスオガイ科の大型二枚貝である。オークランド北西のムリワイ海岸でその生息位置，方位，運動能力を観察した。多くの個体は，殻を海岸線と平行，または背縁を海側に向けている。これらの殻の向きは，波に洗い出された貝が引き波に流されながら再びもぐる向きと一致しており，最も開放的な海岸の潮間帯に適応したトヘロアが，頻繁に洗い出されているという事実とよく合う。トヘロアは，Stanley (1970) の潜入速度の指標値で，2-11を示し，急速潜没二枚貝であることが確かめられた。幼貝の指標値は特に大きく，二枚貝の中で最もすばやくもぐるナミノコガイ科の値と同程度に達する。一方，底質にもぐる深さは，平均的な殻サイズ10cmの個体で約10cmであり，開放海岸潮間帯の二枚貝としては例外的と言えるほど深い。物理的に不安的な生息場所である浅海砂泥底の内生二枚貝に普通に認められる適応型は，底質に浅くもぐりながら洗い出されてもすばやくもぐる能力を発達させるものと，洗い出される危険をほとんど回避できるほど深くもぐるかわりに再潜入能力を放棄するものの二つであるが，トヘロアは両者の折衷した特異な適応を示している。

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