

# Feeding Ecology of an Abalone, *Haliotis discus hannai*, in Their Early Life Stages

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**Key Word:** abalone, feeding, growth, *Haliotis discus hannai* nutrition, survival

## Abstract

Recent studies on the feeding ecology of abalone, *Haliotis discus hannai*, during the early life stages were reviewed in this article. The feeding habits of *H. discus hannai* changed with growth, and three major changes in the feeding were identified. The first change occurred at the time of the metamorphosis of 0.28 mm in shell length (SL), namely a shift from lecithotrophy (yolk absorption) to exogenous feeding. The energy source of abalone is gradually transferred from yolk to particulate food after metamorphosis by the size of 0.3-0.4 mm SL. Several days of food limitation after metamorphosis leads to a failure to shift to exogenous feeding. In the second change, when the SL reached values of about 0.6-0.8 mm, post-larvae were able to digest diatom diet. They grew more rapidly, feeding on efficiently digested diatoms, whereas those fed poor diatom diet will generally grow slowly. The differences in the dietary value of diatoms for abalone were controlled mainly by the digestibility of diatoms. The final change consisted of a shift from a biofilm-dominated diet to a macroalgal dominated diet. Abalone (>1.8 mm SL) were able to utilize juvenile macro algae efficiently. Juvenile macroalgae provide a much higher biomass per unit area than small-volume, two dimensional diatom films. The energetics of diatom ingestion became insufficient to support rapid growth. These changes in feeding habits were closely related to ontogenetic changes in the digestive enzyme activities and the development of the radula morphology. The activity of macroalgal polysaccharide-degrading enzymes showed marked increase at 2 mm SL. The morphological development in the radula occurred mostly in abalone less than 4 mm SL, to complete adult radula which is suitable to graze macroalgae.

## Introduction

The food deprivation tolerance of newly metamorphosed *H. discus hannai* is extremely low, and limiting food over several days has a harmful effect on the survival of post-larvae (Takami *et al.*, 2000). Growth rates in the early life stages of *H. discus hannai* are considerably affected by the diet and the ability of the individuals to utilize available food (Kawamura and Takami, 1995; Kawamura *et al.*, 1995; Seki, 1997; Takami *et al.*, 1997a, b). In many abalone hatcheries, low survival and growth rates are often observed in the first few months, and these are probably caused by inadequate or inappropriate diets. Thus, understanding of the abalone feeding ecology in the early life stages is considered important for the improvement of rearing techniques in abalone hatcheries.

This article will review studies on the feeding ecology in the early life stages of *H. discus hannai* with a focus on the feeding transitions associated with the development of the digestive ability.

## Feeding Transitions in Abalone *Haliotis discus hannai*

### Shift from Lecithotrophy to Particulate Matter Feeding

Abalone species have planktonic larval stages before metamorphosing to benthic stages. Larval abalone are lecithotrophic (non-feeding) and carry a yolk derived from the egg that fuels larval life and metamorphosis. However, this diet could be supplemented by dissolved organic matters (Manahan and Jaeckle, 1992; Shilling *et al.*, 1996). Larval *H. discus hannai* require about 3-4 days at 20°C before becoming able to metamorphose (Seki and Kan-no, 1977). When settlement cues are provided, able larvae attach to a substratum and subsequently metamorphose into benthic post-larvae.

Larval abalone delay metamorphosis if they fail to detect an appropriate environmental stimulus (Roberrts and Lapworth, 2001; Takami *et al.*, 2002). Delayed metamorphosis of lecithotrophic larvae causes a depletion of yolk reserves, which has a negative effect on metamorphosis success, post-metamorphic survival, and growth. Larval *H. discus hannai* remained competent to metamorphose in extended larval period and can metamorphose successfully after 19 days from fertilization at 20°C. Survival and growth of the post-larvae are influenced by an extended larval swimming period. Post-larval survival and growth rates do not differ significantly between larval swimming periods  $\leq 15$  days, but become significantly lower for post-larvae with a 19-day swimming period, compared with post-larvae with a 15-day swimming period. These results suggest that the amount of residual yolk reserves available for post-larvae declines as the duration of their larval period become longer and has a significant effect on the survival and growth of newly metamorphosed individuals as an initial energy source (Takami *et al.*, 2002).

During the metamorphosis, larval abalone shed the velum, develop enlarged gills and a foot, and start peristomal shell formation. Post-larval abalone commence particle feeding using the radula immediately after completion of the metamorphosis. Newly metamorphosed post-larvae still have a visible yolk and initial survival and growth can still be supported by the yolk supply in addition to particle feeding when the shell length (SL) increases from 0.28 mm at the time of metamorphosis to 0.5 mm. The primary nutrition source for post-larval *H. discus hannai* is gradually transferred from yolk to particulate food after the metamorphosis (Takami *et al.*, 2000).

Under hatchery conditions, *H. discus discus* show massive mortality when the SL is 0.5 mm if there is a lack of food (Ohashi, 1993). Under experimental conditions, *H. discus hannai* with a SL below 0.5 mm die when they are fed unsuitable food sources (Takami *et al.*, 1997a, b, 2000). In the natural habitat, a number of dead or dying *H. discus hannai* with a SL of 0.4-0.5 mm were often observed, presumably due to starvation (Sasaki and Shepherd 2001). It was suggested that food limitation for several days after metamorphosis led to a failure to shift to exogenous feeding (Takami *et al.*, 2000). Thus the initial habitat should provide enough food for the post-larval abalone.

In natural habitats, larval *H. discus hannai* preferentially settle on crustose coralline algae (CCA) and grow on CCA for at least several months (Saito, 1981; Sasaki and Shepherd, 1995, 2001; Takami, 2002). Grazing gastropods are usually found at high densities on CCA (Ayling, 1981; Choat, 1982; Kawamura *et al.* 1992; Takami, 2002), and CCA rely on their grazing to prevent surfaces from being covered with competitively superior algae (Paine, 1992; Steneck, 1983). Grazing-resistant algae with strongly adhesive prostrate forms such as benthic

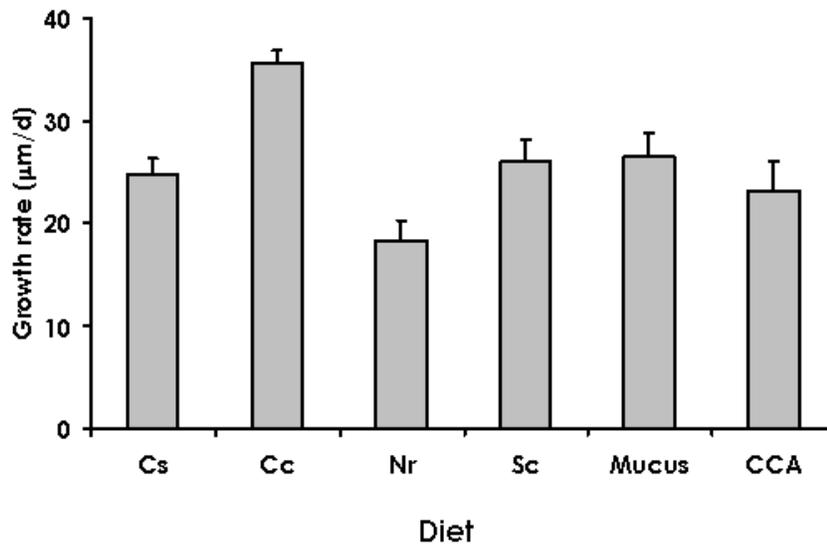
diatoms *Cocconeis* spp. tend to dominate on the CCA surface, and dense patches of *Cocconeis* spp. were often observed on CCA where post-larval and juvenile abalone were present (Kawamura *et al.* 1992; Takami, 2002).

In many Japanese abalone hatcheries, pre-grazed plates are used as substrata for the settlement of larvae and as rearing plates for post-larvae. The pre-grazed plates are first covered with a film of naturally occurring microalgae, and then the plates are grazed by juvenile or adult abalone (> 10 mm SL). Grazing-resistant algae such as *Cocconeis* spp. also dominate on the plates (Ioriya and Suzuki, 1987; Suzuki *et al.*, 1987). Both CCA and pre-grazed plates strongly induce larval settlement and are considered to supply adequate food sources for post-larval abalone.

In post-larval habitats in the natural environment and hatcheries, (1) CCA themselves, (2) benthic diatoms which dominate on CCA and on pre-grazed plates such as *Cocconeis* spp., and (3) the trail mucus left by herbivorous gastropods, including juvenile or adult abalone creeping on the substrata, appear to be food sources for the newly metamorphosed abalone. The growth rates of the newly metamorphosed *H. discus hannai* (< 0.6-0.8 mm SL) were compared among mono-cultured diatom diets including *Cocconeis* spp., CCA *Lithophyllum yessoense* which was not attached to any diatoms, and the trail mucus of juvenile *H. discus hannai* (30 mm SL) to determine the possible food sources for post-larvae on CCA and pre-grazed plates (Kawamura and Takami, 1995; Takami *et al.* 1997a, b).

Differences in the diatom species feed did not alter appreciably the growth rates of the post-larvae (**Fig. 1**). Diatom species *Navicula ramosissima* and *Stauroneis constricta* passed through the post-larval abalone gut alive, whereas *Cylindrotheca closterium* were ruptured and lost their cell contents. Post-larvae fed *Cocconeis scutellum* did not ingest any diatom cell material, probably due to the high adhesive strength of this species. These results and observations suggest that smaller post-larvae (< 0.6-0.8 mm SL) can grow well without high levels of absorption of the diatom cell contents. It appears that the extracellular substances of diatoms are an important source of food for smaller post-larvae (Kawamura and Takami, 1995).

The newly metamorphosed individuals (< 0.5 mm) fed CCA showed comparable growth rates to those of individuals fed on benthic diatoms (**Fig. 1**). Since post-larvae do not ingest CCA fragments, individuals utilize biofilm components such as extracellular products plus bacteria (Takami *et al.*, 1997a). The trail mucus of conspecific juveniles also supports adequate growth of post-larvae smaller than 0.7 mm (**Fig. 1**). On the pre-grazed plates, the extracellular materials of *Cocconeis* spp. and conspecific trail mucus were possibly the main food sources for smaller post-larvae (Takami *et al.*, 1997b).



TAKAMI FIG. 1

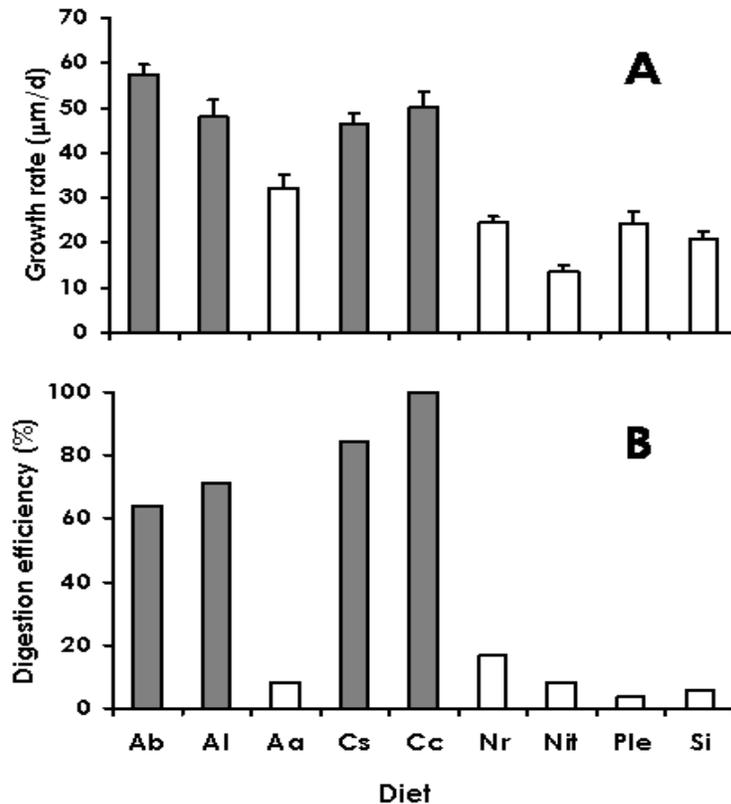
**Figure 1:** Growth of newly metamorphosed *Haliotis discus hannai* ( $\mu\text{m}$  per day) fed 4 benthic diatom species, mucus trail of juvenile *H. discus hannai* (30 mm in shell length) and crustose coralline alga *Lithophyllum yessoense*. Cs: *Cocconeis scutellum*, Cc: *Cylindrotheca closterium*, Nr: *Navicula ramosissima*, Sc: *Stauroneis constricta*, Mucus: mucus trail of juvenile *H. discus hannai*, CCA: crustose coralline alga. Each bar represents mean + SE. Data from Kawamura and Takami (1995) and Takami *et al.* (1997a, b).

Food sources from the CCA themselves enabled post-larvae with a SL above 0.5 mm to remain alive but were not adequate to support rapid growth (Takami *et al.*, 1997a). Post-larvae larger than 0.7 mm were not able to grow and survived by feeding on conspecific trail mucus only or extracellular substances of *Cocconeis scutellum* (Kawamura and Takami, 1995; Takami *et al.*, 1997b). Larger post-larvae need to utilize diatom cell contents for adequate growth.

#### Changes in Digestibility of Diatoms

Post-larval abalone with a SL above 0.8 mm became able to digest diatom diets and grew more rapidly on efficiently digested diatom species. The term “digestibility” refers to the proportion of diatom cells that lost cell contents when ingested and passed through the abalone gut (Kawamura *et al.*, 1995). **Figure 2A** shows the growth rates of larger post-larvae (1-2 mm) fed 9 diatom species. All the post-larvae fed these algae displayed an active feeding behavior but significant differences were observed between the growth rates of abalone fed different diatom species. The mean growth rates of the post-larvae fed the diatom species, *Achnanthes brevipes*, *A. longipes*, *Cocconeis scutellum*, and *Cylindrotheca closterium*, were significantly higher than those of the post-larvae fed the species, *Amphora angusta*, *Navicula ramosissima*, *Nitzschia* sp., *Pleurosigma* sp., and *Synedra investiens*. The differences in the

dietary value of diatoms for larger post-larvae were controlled mainly by the digestibility of diatoms. The digestion efficiency (Kawamura *et al.*, 1995) of each diatom species, which was calculated as the percentages of diatom cells that lost their contents by abalone grazing as a proportion of the total number of cells in the feces, is presented in **Figure 2B**. The 4 diatom species with a higher dietary value for post-larvae showed a higher digestion efficiency. In contrast, the digestion efficiency of the other species of diatoms was lower, and many live diatom cells were observed in the fecal material of the post-larvae.



TAKAMI FIG. 2

**Figure 2.** The mean (+SE) growth rates of post-larval *Haliotis discus hannai* with a shell length of 1-2 mm ( $\mu\text{m}$  per day) fed 9 benthic diatom species (A) and the mean digestion efficiency of diatoms grazed by post-larval *H. discus hannai* (B). Ab: *Achnanthes brevipes*, Al: *Achnanthes longipes*, Aa: *Amphora angusta*, Cs: *Cocconeis scutellum*, Cc: *Cylindrotheca closterium*, Nr: *Navicula ramosissima*, Nit: *Nitzschia* sp., Ple: *Pleurosigma* sp., Si: *Synedra investiens*. Data from Kawamura *et al.* (1995).

A limited number of diatoms showed high digestion efficiencies and induced rapid growth in larger post-larvae (Kawamura *et al.*, 1995, 1998; Roberts *et al.*, 1999a). Diatom attachment strength was one of the factors that affected the diatom digestibility for post-larval abalone. Strongly attached diatoms such as *Cocconeis* spp. and *Achnanthes* spp. required a

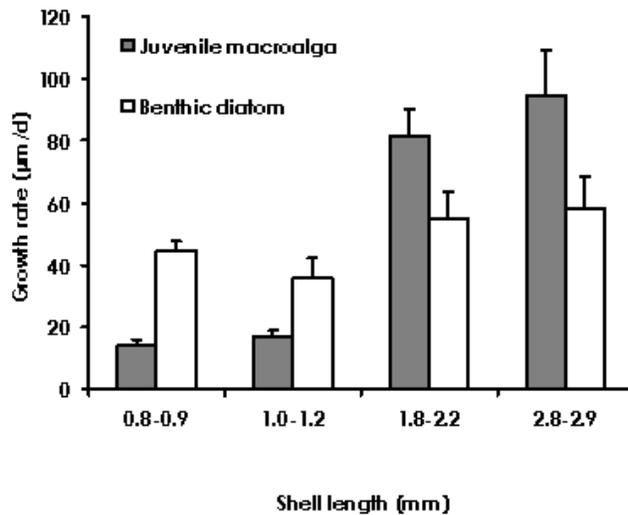
considerable strength to be detached from the substrata and were usually ruptured if dislodged. In contrast, many diatoms with a low adhesive strength were ingested without cell rupture, and the majority of the ingested cells passed through the gut alive and unbroken. There were some exceptions such as *Cylindrotheca closterium*, which had a low attachment strength, but showed a high digestion efficiency and induced rapid growth for post-larvae probably due to its structurally weak silica frustule.

Post-larvae may require diatom cell contents for rapid growth and abalone larger than 0.6-0.8 mm to begin to ingest *Cocconeis* spp. efficiently. These diatom species often dominate in the habitats of post-larval abalone both in the natural environment and on the pre-grazed plates used in abalone hatcheries. Benthic diatoms *Cocconeis* spp. are probably the main diet for larger post-larvae. In contrast, it has been suggested that juvenile abalone with a SL above 10 mm do not graze on *Cocconeis* species if more suitable foods are available (Ioriya and Suzuki, 1987; Suzuki *et al.*, 1987), because *Cocconeis* spp. are not efficient food sources for these large juveniles due to their small-volume cells and prostrate growth form (Takami *et al.*, 1996).

#### Changes from Diatom Feeding to Macroalgal Feeding

Large juveniles and adults of *H. discus hannai* prefer to feed on brown macroalgae of Laminariales (Kikuchi *et al.*, 1967; Sakai, 1962; Uki, 1981) and show rapid growth rates when fed these algal species (Kikuchi *et al.*, 1967; Uki, 1981; Uki *et al.*, 1986). Evidence from natural habitats suggests that the diet of the abalone is dominated by macroalgae as the juveniles grow (Shepherd and Cannon, 1988; Tomita and Tazawa, 1971). The dietary value of microscopic algal stages (juvenile sporophytes) of *Laminaria japonica* and the benthic diatom *Cylindrotheca closterium* for different developmental stages of *H. discus hannai* were compared to determine the size at which the abalone began to utilize macroalgae efficiently (Takami *et al.*, 2003).

Considerable variations were observed in the growth rates of the abalone between both algal types and the developmental stages of the abalone (**Fig. 3**), although most individuals were feeding actively. The post-larvae growth rates with a SL below 1.2 mm that were fed juvenile macroalgae of *L. japonica* were significantly lower than those of the post-larvae fed the benthic diatom *C. closterium*. In contrast, for post-larvae with a SL above 1.8 mm, feeding on juvenile macroalgae led to a significantly faster growth than those fed benthic diatom. Smaller post-larvae (< 1.2 mm SL) repeatedly grazed the surface of juvenile sporophytes without detaching these algae. Larger post-larvae (> 1.8 mm) could ingest large amounts of juvenile macroalgae. The dietary value of juvenile macroalgae for post-larval abalone depended on whether individuals could efficiently ingest algal fronds or not. The ingestion efficiency of post-larvae on algal diets was largely influenced by the radula morphology (see next section).



TAKAMI FIG. 3

**Figure 3.** Growth of post-larval *Haliotis discus hannai* ( $\mu\text{m}$  per day) fed juvenile sporophyte of *L. japonica* and benthic diatom *Cylindrotheca closterium* at four developmental stages. Each bar represents mean + SE. Data from Takami *et al.* (2003).

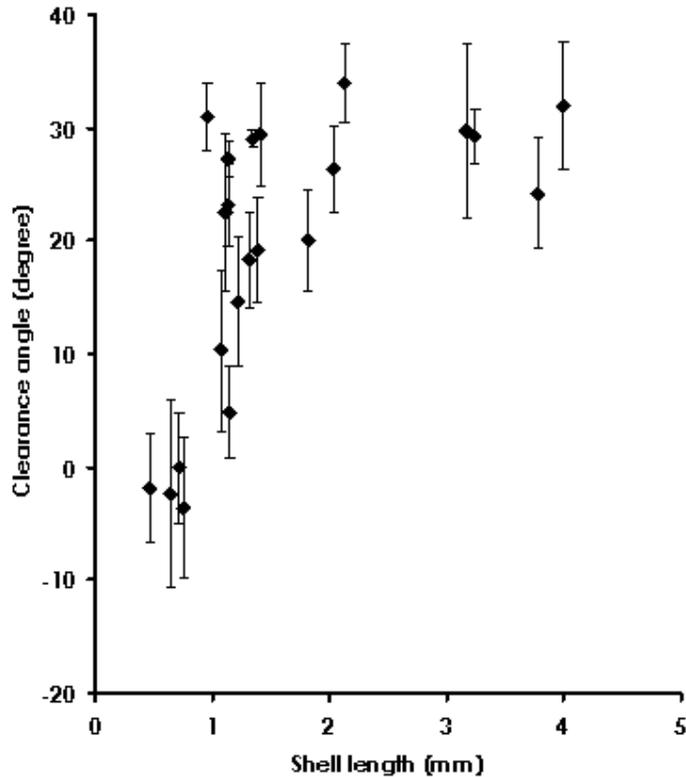
Although post-larvae fed the benthic diatom *Cylindrotheca. closterium* actively grazed and efficiently ingested diatom cells at all the post-larval stages, the relative dietary value of *C. closterium* decreased as post-larvae grew, compared with that of juvenile sporophytes of *L. japonica*. This implies that juvenile sporophytes provide a much higher biomass per unit area than small-volume, two-dimensional *C. closterium* films, if post-larvae are able to detach and ingest the juvenile sporophytes. *Cocconeis* films, which are suitable food sources for post-larvae > 0.8 mm in SL, also become energetically inadequate as abalone grow (Takami *et al.* 1996). The size at which the abalone begin to feed on macroalgae could be highly variable and probably depends on the macroalgal species, but it is apparent that *H. discus hannai* with a SL above 1.8 mm can utilize juvenile macroalgae *L. japonica* efficiently. Therefore the main food source may shift from a biofilm-dominated diet to a macroalgal-dominated diet from this size.

### **Possible Mechanisms Underlying the Feeding Changes**

#### Ontogenetic Changes in Digestive Enzyme Activities

Brown macroalgae contain a significant amount of polysaccharides such as cellulose, alginate and laminarin. These polysaccharides are an important energy source for adult abalone which have high enzyme activities against these polysaccharides (Anzai *et al.*, 1991; Onishi *et al.*, 1985). Changes in the activity of the digestive enzymes for brown algal polysaccharides

(carboxymethylcellulose, alginate, and laminarin) were measured in post-larval *H. discus hannai* at 7-46 days after the metamorphosis (Takami *et al.*, 1998). Enzyme activities were not detected in post-larvae about 0.5-0.6 mm SL, but by 1 mm SL, there was a detectable activity for all the enzymes (Fig. 4). In individuals > 1.5 mmSL, the total activities of the enzymes increased rapidly as they grew.



TAKAMI FIG. 6

**Figure 4.** Relationship between total activities of digestive enzymes ( $\mu\text{g RS/individual/h}$ ) and shell length (mm) in post-larval *Haliotis discus hannai*. Data from Takami *et al.* (1998).

*H. discus hannai* with a SL above 1.8 mm began to utilize juvenile brown macroalgae as described above. The developmental process for the digestive enzyme activities shows that a series of enzymes useful for digesting brown algal polysaccharides is produced by post-larvae with a SL about 1 mm. This suggests that post-larvae with a SL about 1 mm may use brown algal polysaccharides if they can ingest either the algal cells or their surface biofilm.

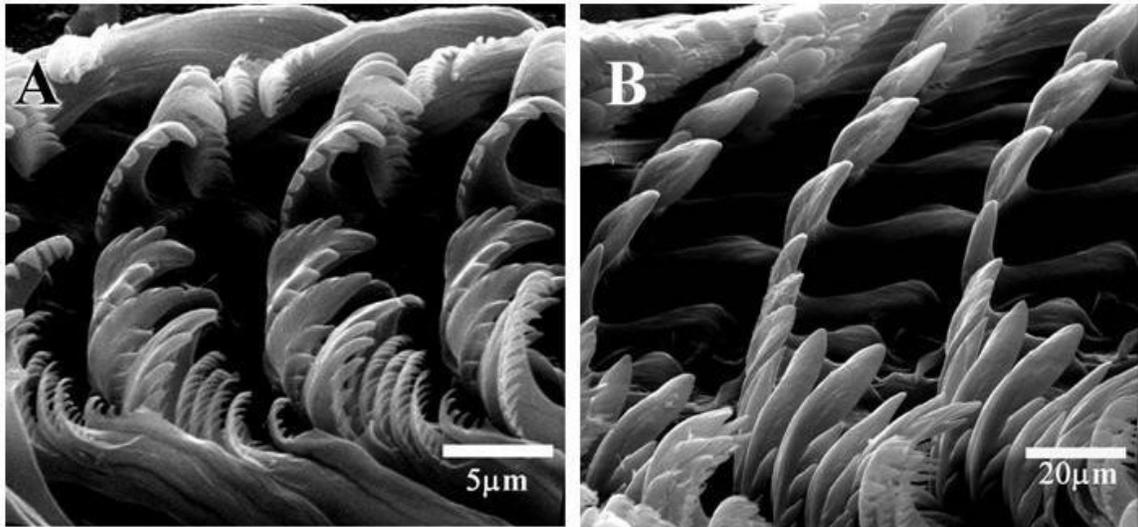
#### Development of Radula Morphology

The post-larva's ability to ingest and digest the algae appears to be affected by the radula, as the abalone gut lacks any grinding mechanisms (Crofts, 1929). The developmental sequence of the radula morphology could be closely related to the changes in feeding (Roberts

*et al.*, 1999b). Changes in the radula morphology were examined for *H. discus hannai* from larval to adult stages using a scanning electron microscope (Kawamura *et al.*, 2001).

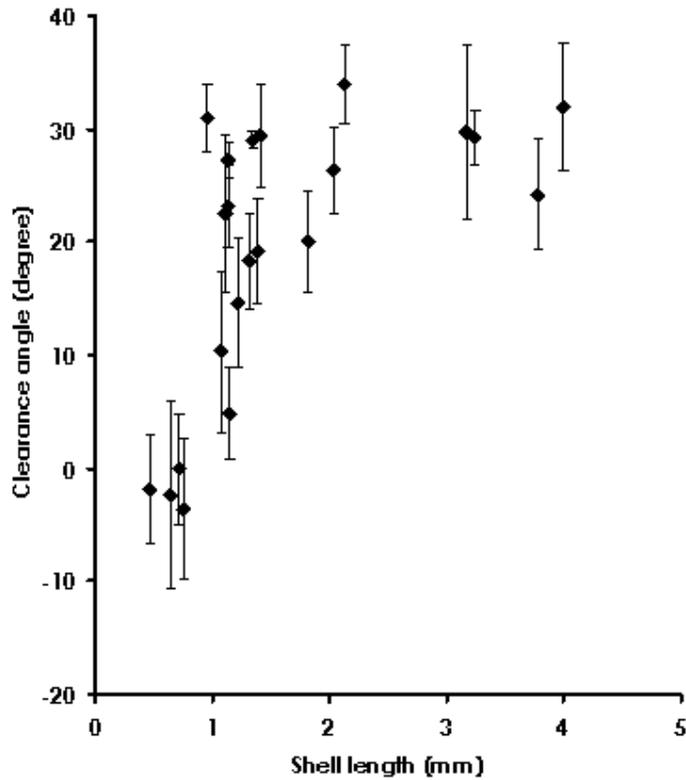
Most of the structural changes in the radula occurred at the post-larval stage (< 4 mm SL). The number of transverse rows of teeth in the radula increased from 10-11 to 25-30 during the days following the metamorphosis, but then remained constant throughout the post-larval period. The initial increase in the number of rows of teeth seems to be related to the first change in feeding from lecithotrophy to particle feeding.

Post-larvae < 1 mm in SL had highly curved teeth (**Fig. 5A**) with values of the clearance angles being approximately or less than zero (**Fig. 6**), whereas larger abalone had straight teeth (**Fig. 5B**) with values of the clearance angles above 0 (**Fig. 6**). The clearance angle of the teeth was adopted by Padilla, who suggested that it provided information about the function of radula teeth (Padilla, 1985). Clearance angles with a zero value may result in a tooth sliding across the surface rather than cutting it (Padilla, 1985). The curved radula teeth of the post-larvae < 1 mm in SL probably function as scoops, which are suitable for collecting biofilm components such as extracellular secretions of diatoms and CCA. The clearance angles with values above 0 of the larger post-larvae (> 1 mm SL) may allow them to 'cut' rather than just slide across the substratum. The increase in the value of the clearance angle in the abalone with a SL of approximately 1 mm could contribute to the post-larva's ability to detach strongly attached diatoms such as *Cocconeis* spp.



TAKAMI FIG. 5

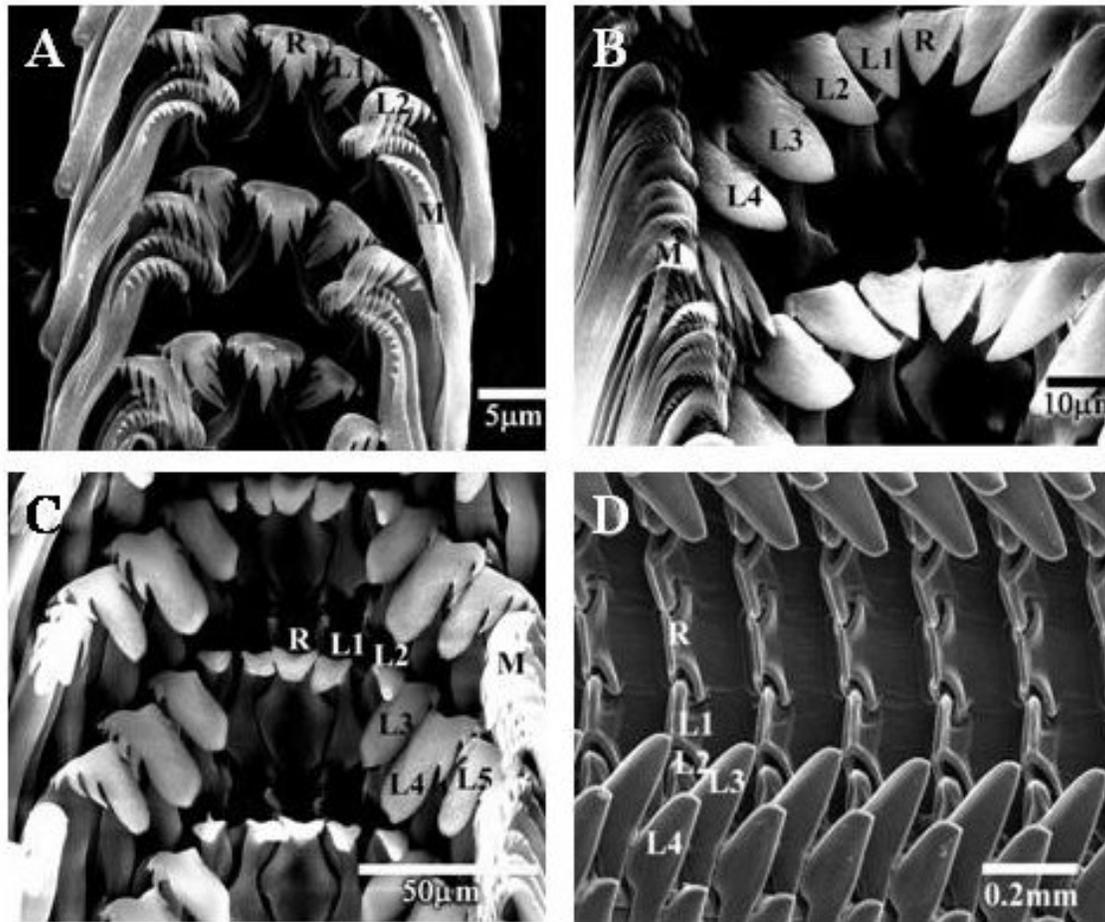
**Figure 5.** SEM photographs showing lateral views of the post-larval radula. A: Strongly curved rachidian and lateral teeth of post-larvae with a shell length of 0.72 mm on Day 11 post-settlement, with values of clearance angles near or less than zero. B: Radula teeth with clearance angles with values above 0 in a 3.24 mm post-larva on Day 63. Data from Kawamura *et al.* (2000).



TAKAMI FIG. 6

**Figure 6.** Relationship between value of clearance angle of teeth and post-larval shell length. Each data point shows the mean  $\pm$  SE of 9-12 teeth on one radula. Data from Kawamura *et al.* (2000)

In post-larvae < 1 mm in SL, only 2 pairs of lateral teeth (L1, L2) were present in the radula (**Fig. 7A**). Three pairs of lateral teeth (L3-L5) were added gradually as the SL of the post-larvae increased from 0.9 mm to 1.9 mm (**Fig. 7B**). The serrations on the working edges of the rachidian (R) and lateral teeth became less pronounced as the abalone grew. Nearly all the serrations disappeared from the rachidian (R) and inner lateral teeth (L1, L2) when the SL was 2 mm, and the outer lateral teeth (L3-L5) became longer and more pointed (**Fig. 7C, D**). The reduction in tooth serrations suggests that the radula is less able to handle very small food particles such as bacteria and small diatoms, while the well developed L3-L5 teeth are more able to cut the macroalgae. These radula changes appear to be related to the changes in feeding habits from microbial to macroalgal diets.



**Figure 7.** SEM photographs of the radula showing developmental stages. Radula formulae represent the numbers of teeth in a transverse row as follows: M+L+R+L+M (Voltzow 1994). R, Rachidian tooth; L1-L5, lateral teeth 1-5, M, marginal teeth. A: Post-larva 0.47 mm in shell length on Day 6 post-settlement, 3+2+R+2+3. B: Post-larva 1.9 mm in shell length on Day 49. Differentiation of the lateral teeth has started,  $\sim 15+(2+2)+R+(2+2)+\sim 15$ . C: Post-larva 3.2 mm in shell length on Day 63. L3-L5 teeth are larger and longer than R, L1 and L2.  $?+(3+2)+R+(2+3)+?$ . D: Juvenile 29.9 mm in shell length. L3-L5 teeth are much longer and more pointed than the central teeth (R, L1, L2).  $?+(3+2)+R+(2+3)+?$ . Data from Kawamura *et al.* (2000).

### Summary

Three major changes in the diet that were closely related to the developmental changes in the digestive enzyme activities, and radula morphology were identified as the abalone grew. The first change consisted of a shift from lecithotrophy (yolk absorption) to particle feeding. This change occurred around the time of metamorphosis with an overlap in nutrition sources. During this period, the abalone immediately developed the radula to acquire an effective feeding organ.

Post-larvae with a SL of 0.6-0.8 mm were able to digest diatom diets and grew more rapidly on efficiently digested strains. The factors that control the digestibility of a diatom strain were complex, but diatoms with a high attachment strength such as *Cocconeis* spp., which often dominated on both CCA in the natural habitat and the pre-grazed plates used in the hatcheries, generally showed high digestion efficiencies. Post-larvae < 0.8 mm in SL were not able to efficiently detach *Cocconeis* cells from substrata. The morphological changes in the radula of the abalone appeared to contribute to the post-larva's ability to detach *Cocconeis* cells.

Post-larval abalone > 1.8 mm in SL became able to utilize juvenile macroalgae *L. japonica* efficiently and the main food sources gradually shifted from a biofilm-dominated diet to a macroalgal-dominated diet from this size. The activity of the macroalgal polysaccharide-degrading enzymes was detected in post-larvae with a SL of about 1 mm and showed a marked increase at 2 mm SL. The morphological development of the radula of *H. discus hannai* occurred mostly in post-larvae with a SL below 4 mm up to the level of the adult radula which was suitable for the grazing of macroalgae.

Food availability exerts a considerable impact on the survival and growth of post-larval *H. discus hannai*. It is important to prepare a suitable diet for each developmental stage of the abalone for constant and efficient production of hatchery seeds.

#### Literature Cited

- Anzai, H., Y. Enami, T. Chida, A. Okoshi, T. Omuro, N. Uchida and E. Nishiide.** 1991. Polysaccharide digestive enzymes from midgut gland of abalone. *Bull. Coll. Agric. Vet. Med. Nihon Univ.* 48: 119-127.
- Ayling, A. M.** 1981. The role of biological disturbance in temperate subtidal encrusting communities. *Ecology* 63: 830-847.
- Choat, J. H. and D. R. Schiel.** 1982. Patterns of distribution and abundance of large brown algae and invertebrate herbivores in subtidal regions of northern New Zealand. *J. Exp. Mar. Biol. Ecol.* 60: 129-162.
- Crofts, D. R.** 1929. *Haliotis*, in "L.M.B.C. Memoirs on Typical British Marine Plants & Animals XXIX" (ed. by Johnstone J. and Daniel R. J.), The University Press of Liverpool, Liverpool. pp. 1-174.
- Ioriya, T. and H. Suzuki.** 1987. Changes of diatom community on plastic plates used for rearing of abalone *Nordotis discus*. *Suisanzoshoku* 35: 91-98.
- Kawamura, T., H. Yamada, M. Asano and K. Taniguchi.** 1992. Benthic diatom colonizations on plastic plates in the sublittoral zone off Oshika Peninsula, Japan. *Bull. Tohoku Natl. Fish. Res. Inst.* 54: 97-102.
- Kawamura, T. and H. Takami.** 1995. Analysis of feeding and growth rate of newly metamorphosed abalone *Haliotis discus hannai* fed on four species of benthic diatom. *Fisheries Sci.*, 61: 357-358.

- Kawamura, T., T. Saïdo, H. Takami and Y. Yamashita.** 1995. Dietary value of benthic diatoms for the growth of post-larval abalone *Haliotis discus hannai*. *J. Exp. Mar. Biol. Ecol.*, 194: 189-199.
- Kawamura, T., R. D. Roberts and C. M. Nicholson.** 1998. Factors affecting the food value of diatom strains for post-larval abalone *Haliotis iris*. *Aquaculture*, 160: 81-88.
- Kawamura, T., H. Takami, R. D. Roberts and Y. Yamashita.** 2001. Radula development in abalone, *Haliotis discus hannai*, from larva to adult in relation to feeding transitions. *Fisheries Sci.*, 67: 596-605.
- Kikuchi, S., Y. Sakurai, M. Sasaki and T. Ito.** 1967. Food values of certain marine algae for the growth of the young abalone *Haliotis discus hannai*. *Bull. Tohoku Reg. Fish. Res. Lab.*, 27: 93-100.
- Manahan, D. T. and W. B. Jaecle.** 1992. Implications of dissolved organic matter in seawater for the energetics of abalone larvae *Haliotis rufescens*: a review, in "Abalone of the World: Biology, Fisheries and Culture" (ed by. Shepherd S. A. Tegner M. J. and Guzman del Proo, S. A.), Fishing News Books, Oxford, pp. 95-106.
- Ohashi, S.** 1993. Yolk absorption of plantigrade juvenile abalone *Nordotis discus discus*. *Bull. Nagasaki Pref. Inst. Fish.*, 19: 23-25.
- Onishi, T., M. Suzuki and R. Kikuchi.** 1985. The distribution of polysaccharide hydrolase activity in gastropods and bivalves. *Bull. Jpn. Soc. Sci. Fish.*, 51: 301-308.
- Padilla, D. K.** 1985. The structural resistance of algae to herbivores. A biomechanical approach. *Mar. Biol.*, 90: 103-109.
- Paine, R. T.** 1980. Food webs: linkage, interaction strength and community infrastructure. *J. Anim. Ecol.*, 49: 667-685.
- Roberts, R. D., T. Kawamura and C. M. Nicholson.** 1999a. Growth and survival of post-larval abalone (*Haliotis iris*) in relation to their development and diatom diet. *J. Shellfish Res.*, 18: 243-250.
- Roberts, R. D., T. Kawamura and H. Takami.** 1999b. Morphological changes in the radula of abalone (*Haliotis iris*) during post-larval development. *J. Shellfish Res.*, 18: 637-644.
- Roberts, R. D. and C. Lapworth.** 2001. Effect of delayed metamorphosis on larval competence, and post-larval growth and survival, in the abalone *Haliotis iris*. *J. Exp. Mar. Biol. Ecol.* 258: 1-13.
- Saito, K.** 1981. The appearance and growth of 0-year-old Ezo abalone. *Bull. Jpn. Soc. Sci. Fish.* 47: 1393-1400.
- Sakai, S.** 1962. Ecological studies on the abalone *Haliotis discus hannai* Ino-I. Experimental

- studies on the food habit. *Bull. Jpn. Soc. Sci. Fish.*, 28: 766-779.
- Sasaki, R. and S. A. Shepherd.** 1995. Larval dispersal and recruitment of *Haliotis discus hannai* and *Tegula* spp. on Miyagi coasts, Japan. *Mar. Freshwater Res.*, 46: 519-529.
- Sasaki, R. and S. A. Shepherd.** 2001. Ecology and post-settlement survival of the ezo abalone *Haliotis discus hannai*, on Miyagi coasts, Japan. *J. Shellfish Res.*, 20: 619-626.
- Seki, T. and H. Kan-no.** 1977. Synchronized control of early life in the abalone, *Haliotis discus hannai* Ino, Haliotidae, Gastropoda. *Bull. Tohoku Reg. Fish. Res. Lab.*, 38: 143-153.
- Seki, T.** 1997. Biological studies on the seed production of the northern Japanese abalone, *Haliotis discus hannai* Ino. *Bull. Tohoku Natl. Fish. Res. Inst.*, 59: 1-71.
- Shepherd, S. A. and J. Cannon.** 1988. Studies on southern Australian abalone (genus *Haliotis*) X. Food and feeding of juveniles. *J. Malacol. Soc. Aust.* 9: 21-26.
- Shilling, F. M., O. Hoegh-Guldberg and D. T. Manahan.** 1996. Sources of energy for increased metabolic demand during metamorphosis of the abalone *Haliotis rufescens* (Mollusca). *Biol. Bull.*, 191: 402-412.
- Steneck, R. S.** 1983. Escalating herbivory and resulting adaptive trends in calcareous algal crusts. *Paleobiology*, 9: 44-61.
- Suzuki, H., T. Ioriya, T. Seki and Y. Aruga.** 1987. Changes of algal community on the plastic plates used for rearing the abalone *Haliotis discus hannai*. *Nippon Suisan Gakkaishi*, 53: 2163-2167.
- Takami, H., T. Kawamura and Y. Yamashita.** 1996. Dietary value of benthic diatoms for the growth of juvenile abalone *Haliotis discus hannai*. *Suisanzoshoku*, 44: 211-216.
- Takami, H., T. Kawamura and Y. Yamashita.** 1997a. Contribution of diatoms as food sources for post-larval abalone *Haliotis discus hannai* on a crustose coralline alga. *Moll. Res.*, 18: 143-151.
- Takami, H., T. Kawamura and Y. Yamashita.** 1997b. Survival and growth rates of post-larval abalone *Haliotis discus hannai* fed conspecific trail mucus and/or benthic diatom *Cocconeis scutellum* var. *parva*. *Aquaculture*, 152: 129-138.
- Takami, H., T. Kawamura and Y. Yamashita.** 1998. Development of polysaccharide degradation activity in postlarval abalone *Haliotis discus hannai*. *J. Shellfish Res.*, 17: 723-727.
- Takami, H., T. Kawamura and Y. Yamashita.** 2000. Starvation tolerance of newly metamorphosed abalone *Haliotis discus hannai*. *Fisheries Sci.*, 66: 1180-1182.

- Takami, H.** 2002. Studies on the feeding, growth, and survival in early life stages of an abalone *Haliotis discus hannai*. PhD thesis, The Univ. Tokyo, pp.220.
- Takami, H., T. Kawamura and Y. Yamashita.** 2002. Effects of delayed metamorphosis on larval competence, and postlarval survival and growth of abalone *Haliotis discus hannai*. *Aquaculture*, 213: 311-322.
- Takami, H., D. Muraoka, T. Kawamura and Y. Yamashita.** 2003. When is the abalone *Haliotis discus hannai* first able to utilize brown macro-larvae? *J. Shellfish Res.*, 22: 795-800.
- Tomita, K. and N. Tazawa.** 1971. On the stomach contents of young abalone *Haliotis discus hannai* Ino, in Rebun Island, Hokkaido. *Sci. Rep. Hokkaido Fish. Exp. Stn.*, 13: 31-38.
- Uki, N.** 1981. Food value of marine algae of order Laminariales for growth of the abalone *Haliotis discus hannai*. *Bull. Tohoku Reg. Fish. Res. Lab.*, 42: 19-29.
- Uki, N., M. Sugiura and T. Watanabe.** 1986. Dietary value of seaweeds occurring on the Pacific coast of Tohoku for growth of the abalone *Haliotis discus hannai*. *Bull. Jpn. Soc. Sci. Fish.*, 52: 257-266.
- Voltzow, J.** 1994. Gastropoda: Prosobranchia, in "Microscopic Anatomy of Invertebrates, Vol. 5, Mollusca I" (ed. by Harrison F. W. and Kohn A. J.) Wiley-Liss, Inc., New York, pp. 111-1152.