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REVIEW

Dietary Changes in the Abalone, *Haliotis discus hannai*, and Relationship with the Development of the Digestive Organ

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Abstract

The feeding habits of the Ezo abalone, *Haliotis discus hannai*, changed with growth. Three major changes in the feeding of *H. discus hannai* were identified by reviewing recent studies on the feeding habits of this species. The first change occurred at the time of the metamorphosis, namely a shift from lecithotrophy to particle feeding. In the second change, when the shell length (SL) reached values of about 0.6–0.8 mm, post-larvae were able to digest diatom diets and they grew more rapidly on efficiently digested strains. The final change consisted of a shift from a biofilm-dominated diet to a macroalgal-dominated diet. Post-larval abalone (> 1.8 mm SL) were able to utilize juvenile macroalgae efficiently. These changes in the feeding habits were closely related to ontogenetic changes in the digestive enzyme activities and the development of the radula morphology.

Discipline: Aquaculture

Additional key words: feeding, growth, nutrition, post-larval abalone, survival

Introduction

The Ezo abalone, *Haliotis discus hannai*, is the most abundantly harvested abalone species in Japan, and the total catch rapidly decreased from 3,000 t in 1969 to the current level of < 1,000 t. The culture of *H. discus hannai* was promoted due to the decline in catch. At present, this abalone is being successfully reared from egg to adult under artificial conditions and is becoming a very important aquaculture species in Japan, China and Chile.

The tolerance of newly metamorphosed post-larval *H. discus hannai* to starvation is extremely low and limitation of food over several days exerts a harmful effect on the survival of post-larvae[46]. Growth rates at the early life stages of *H. discus hannai* are considerably affected by the diet and the ability of the individuals to utilize available food[13,14,37,43,44]. In many abalone hatcheries, low rates of survival and growth are often observed in the first few months, presumably due to inadequate or inappropriate diets. Initial food availability could be one of the main factors controlling abalone recruitment in the natural environment. Analysis of feeding habits at the early life stages of the abalone is important for the improvement of rearing techniques in abalone hatcheries and for a better understanding of the mechanisms of natural recruitment.

In this article, we will review studies on the feeding habits at the early life stages of *H. discus hannai*, with emphasis placed on the feeding changes associated with the development of the digestive ability.

Major feeding changes in abalone *Haliotis discus hannai*

1. Shift from lecithotrophy to feeding on particulate matter

Abalone species display planktonic larval stages before undergoing metamorphosis to benthic stages. Larval abalone are lecithotrophic (non-feeding) and carry a yolk supply derived from the egg that fuels larval life and metamorphosis. However, this diet could be supple-

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mented by dissolved organic materials[20,39]. Larval *H. discus hannai* require about 3–4 days at 20°C before being able to undergo metamorphosis[36]. When settlement cues are provided, larvae become attached to a substratum and subsequently undergo metamorphosis to benthic post-larvae.

Larval abalone delay metamorphosis if they fail to detect an appropriate environmental stimulus[30,49]. Delayed metamorphosis of lecithotrophic larvae leads to a depletion of yolk reserves, which exerts an adverse effect on metamorphosis success, post-metamorphic survival, and growth. Larval *H. discus hannai* remain able to undergo metamorphosis over the extended larval period, and metamorphosis can be successfully achieved after 19 days 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 ≤ 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 decreases as the duration of their larval period increases and exerts a significant effect on the survival and growth of newly metamorphosed individuals as an initial energy source[49].

During the metamorphosis, larval abalone shed the velum, develop enlarged gills and a foot, and peristomal shell formation is initiated. Post-larval abalone start feeding on particles using the radula immediately after completion of the metamorphosis. Newly metamorphosed post-larvae 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 supply to particulate food after the metamorphosis[46].

Under hatchery conditions, *H. discus discus* show massive mortality when the shell length is 0.5 mm if there is a lack of food[24]. Under experimental conditions, *H. discus hannai* with a SL below 0.5 mm die when they are fed unsuitable food sources[43,44,46]. 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[35]. It was suggested that food limitation for several days after metamorphosis led to a failure to shift to exogenous feeding[46]. 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[32,34,35,48]. Grazing gastropods are usually found at high densities on CCA[3,4,11,48], and CCA rely on their grazing to prevent surfaces from being covered with competitively superior algae[27,40]. 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 observed on CCA where post-larval and juvenile abalone were present[11,48].

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. dominate on the plates[8,41]. 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[13, 43,44].

Differences in the diatom species fed 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 on *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[13].

The newly metamorphosed individuals (< 0.5 mm) fed on 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[43]. The trail mucus of conspecific juveniles also supports adequate growth of post-larvae smaller than 0.7

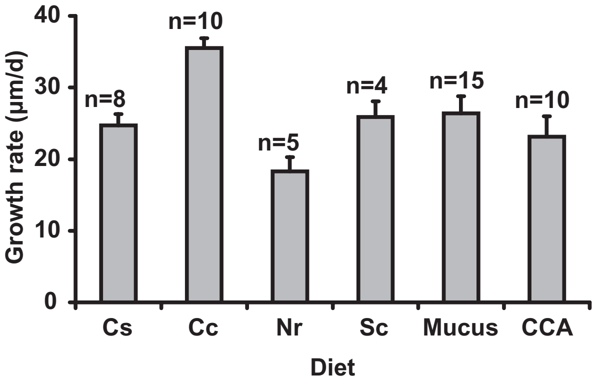

Fig. 1. Growth of newly metamorphosed *Haliotis discus hannai* (µm per day) fed 4 benthic diatom species, mucus trail of juvenile *H. discus hannai* (30 mm in shell length) and crustose coralline alga *Lithophyllum yessoense*

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.

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[44].

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[43]. 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*[13,44]. Larger post-larvae need to utilize diatom cell contents for adequate growth.

2. 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[14]. Fig. 2A shows the growth rates of larger post-larvae (1–2 mm) fed on 9 diatom species. All the post-larvae fed on these algae displayed an active feeding behavior but significant differences were observed between the growth rates of abalone fed on different diatom species. The mean growth rates of the post-larvae fed on the diatom species, *Achnanthes brevipes*, *A. longipes*, *Cocconeis scutellum*, and *Cylindrotheca closterium*, were significantly higher than those of the post-larvae fed on 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[14] 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 Fig. 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.

A limited number of diatoms showed high digestion efficiencies and induced rapid growth in larger post-larvae[14,15,28]. Attachment strength of diatoms 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

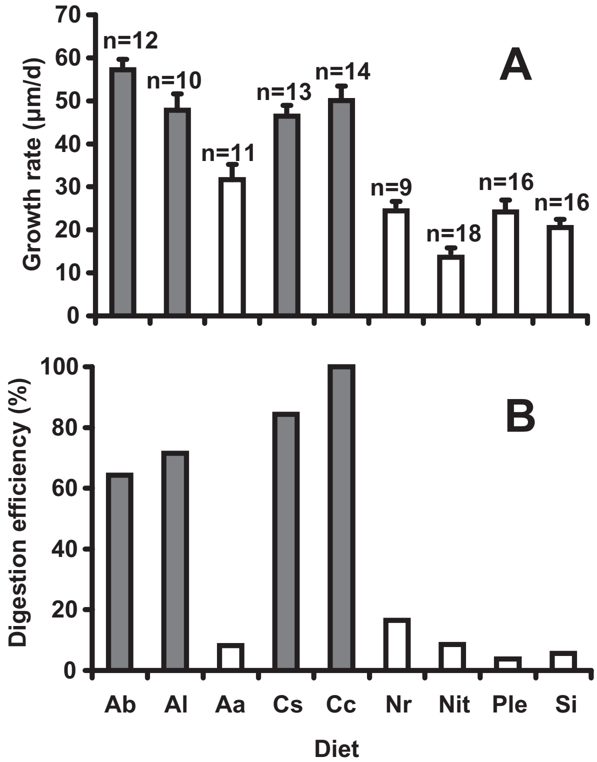

Fig. 2. Growth of post-larval *Haliotis discus hannai* with a shell length of 1–2 mm (µm per day) fed 9 benthic diatom species (A) and digestion efficiency[14] of diatoms grazed by post-larval *H. discus hannai* (B)

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*.
Each bar represents mean + SE.

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 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 *Cocconeis* species if more suitable foods are available[8,41], because *Cocconeis* spp. are not efficient food sources for these large juveniles due to their small-volume cells and prostrate growth form[42].

3. Changes from diatom feeding to macroalgal feeding

Large juveniles and adults of *H. discus hannai* prefer to feed on brown macroalgae of Laminariales[17,33,51] and show rapid growth rates when fed these algal species[17,51,52]. Evidence from natural habitats suggests that the diet of the abalone is dominated by macroalgae as the juveniles grow[38,50]. 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* was compared to determine the size at which the abalone began to utilize macroalgae efficiently[48].

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 growth rates of the post-larvae with a SL below 1.2 mm 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 that on the 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[16,29] (see next section).

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[42]. 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.

Generally the germlings or juvenile stages of macroalgae are susceptible to grazing by herbivores[2,6,7,18,19,21,27,31,53,54]. Also, the sloughing of epithallial cells from the surface crust of CCA prevents other macroalgae from becoming established[9,22,23]. Therefore, it may be difficult for juvenile algae to settle and grow on CCA surfaces. However, since northern Laminarian species show a remarkable reproductive output, they have a considerable potential for dense recruitment if the grazing pressure is low[10]. The sexual reproductive season of *L. japonica* along the Iwate and Miyagi coast extends from late autumn to midwinter when grazers' activities are reduced due to the low

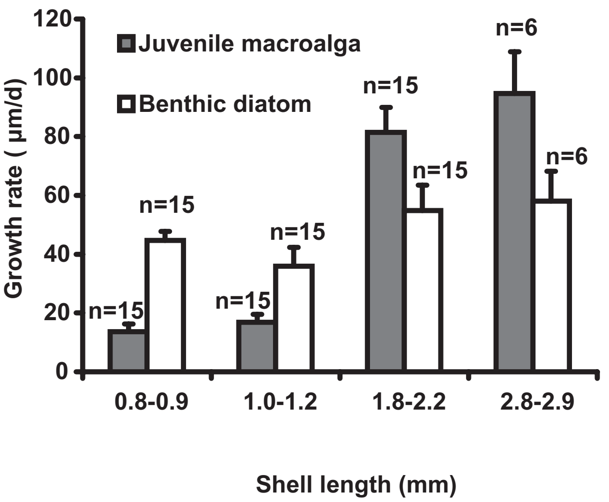

Fig. 3. Growth of post-larval *Haliotis discus hannai* (µm per day) fed juvenile sporophyte of *L. japonica* and benthic diatom *Cylindrotheca closterium* at 4 developmental stages

Each bar represents mean + SE.

water temperature. By this time, most of the *H. discus hannai* less than one year old reach a SL above 2 mm[34,35,48], at which they can efficiently ingest juvenile sporophytes of *L. japonica*. Therefore juvenile *L. japonica* could be an important food source for the abalone in their early life.

Possible mechanisms underlying the feeding changes

1. 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[1,25]. 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[45]. Enzyme activities were not detected on Day 7 (0.52 mm mean SL), but by Day 17 (0.97 mm SL), there was a detectable activity for all the enzymes. Changes in the total activities of the enzymes showed a similar pattern to that of the growth rate, which increased rapidly after Day 37 (1.59 mm SL) (Fig. 4). However, specific activities did not show appreciable changes in the total activities (Fig. 5). These results suggest that the rapid increase of total activities observed after Day 37 was mainly due to the increase in the production of digestive enzymes.

H. discus hannai with a SL above 1.8 mm began to utilize juvenile brown macroalgae[48]. The developmental process for the digestive enzyme activities shows that a series of enzymes useful for digesting brown algal polysaccharides is produced even by post-larvae with a SL below 1 mm. This suggests that post-larvae may use brown algal polysaccharides if they can ingest either the algal cells or their surface biofilm.

2. 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

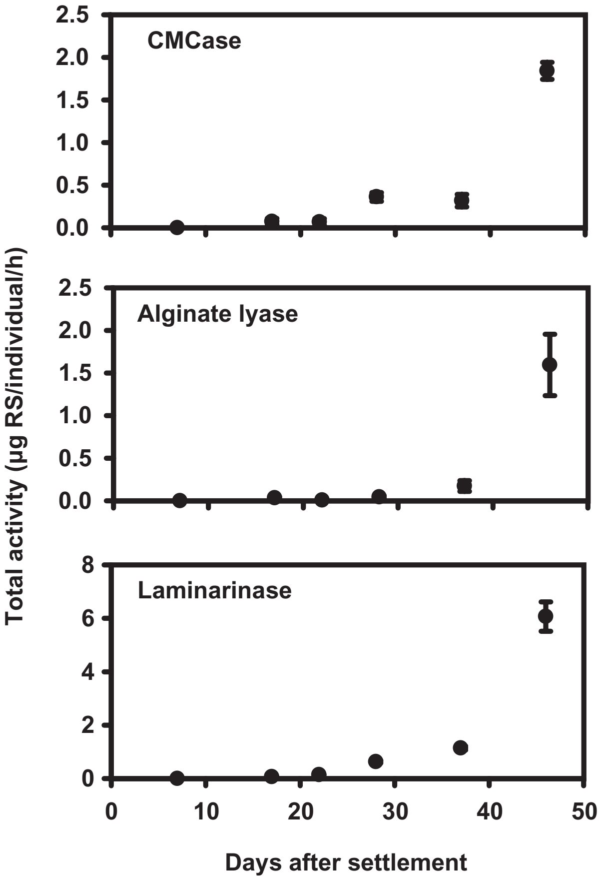

Fig. 4. Relationship between total activities of digestive enzymes (µg RS/individual/h) and age (in d) in post-larval *Haliotis discus hannai*
Data indicate the mean ± SE (n = 6).

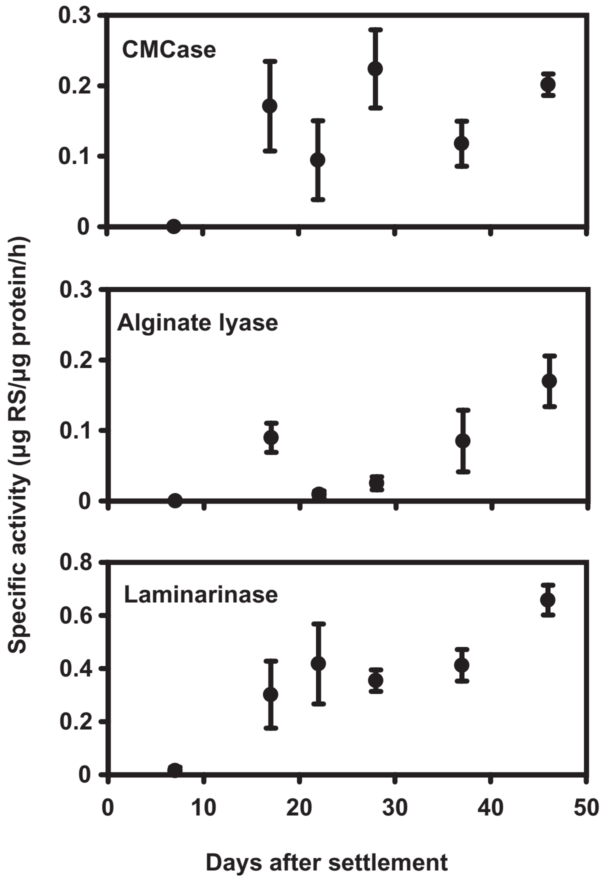

Fig. 5. Relationship between specific activities of digestive enzymes (µg RS/µg protein/h) and age (in d) in post-larval *Haliotis discus hannai*
Data indicate the mean ± SE (n = 6).

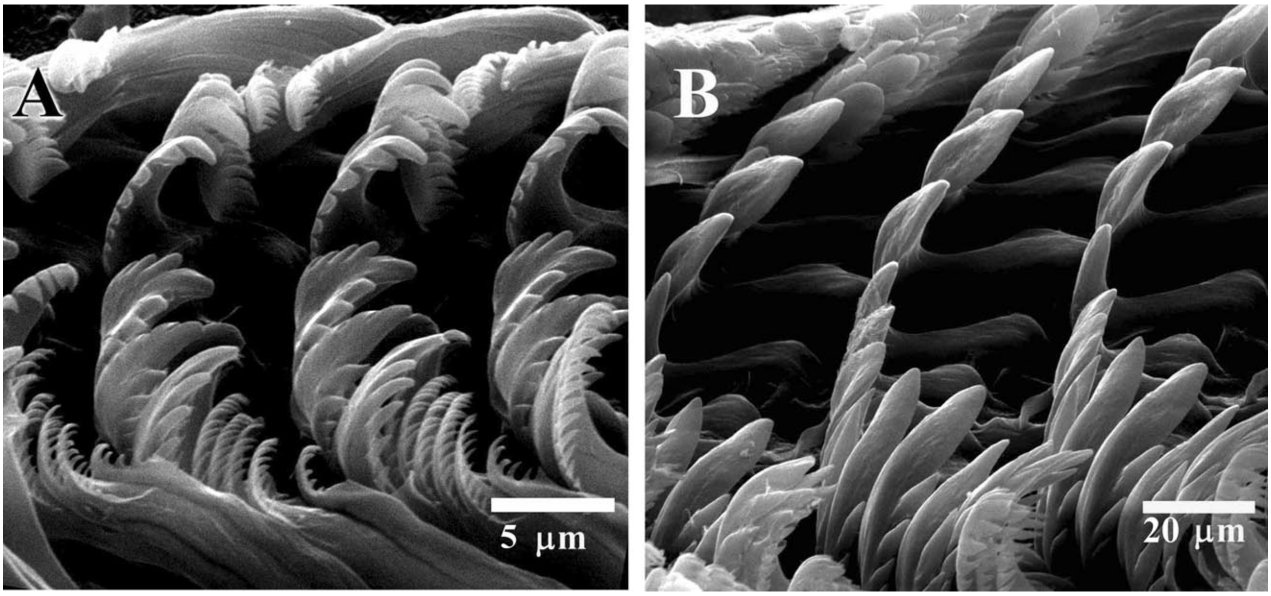

Fig. 6. SEM photographs showing lateral views of the post-larval radula
A: Strongly curved rachidian and lateral teeth of post-larvae with a shell length of 0.72 mm on Day 11 post-settlement, with values of clearance angles near or less than zero. B: Radula teeth with clearance angles with values above 0 in a 3.24 mm post-larva on Day 63.

lacks any grinding mechanisms[5]. The developmental sequence of the radula morphology could be closely related to the changes in feeding. Changes in the radula morphology were examined for *H. discus hannai* from larval to adult stages using a scanning electron microscope[16].

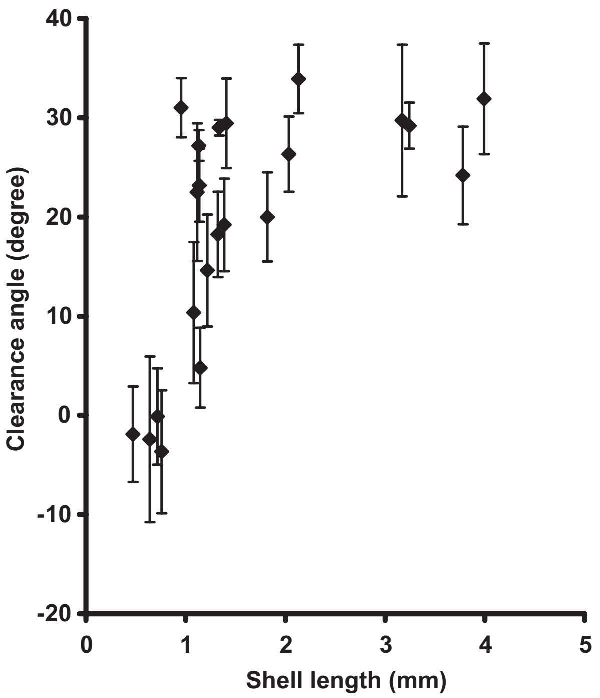

Fig. 7. Relationship between value of clearance angle of teeth and post-larval shell length
Each data point shows the mean ± SE of 9–12 teeth on one radula.

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. 6A) with values of the clearance angles being approximately or less than zero (Fig. 7), whereas larger abalone had straight teeth (Fig. 6B) with values of the clearance angles above 0 (Fig. 7). The clearance angle of the teeth was adopted by Padilla, who suggested that it provided information about the function of radula teeth[26]. Clearance angles with a zero value may result in a tooth sliding across the surface rather than cutting it[26]. 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

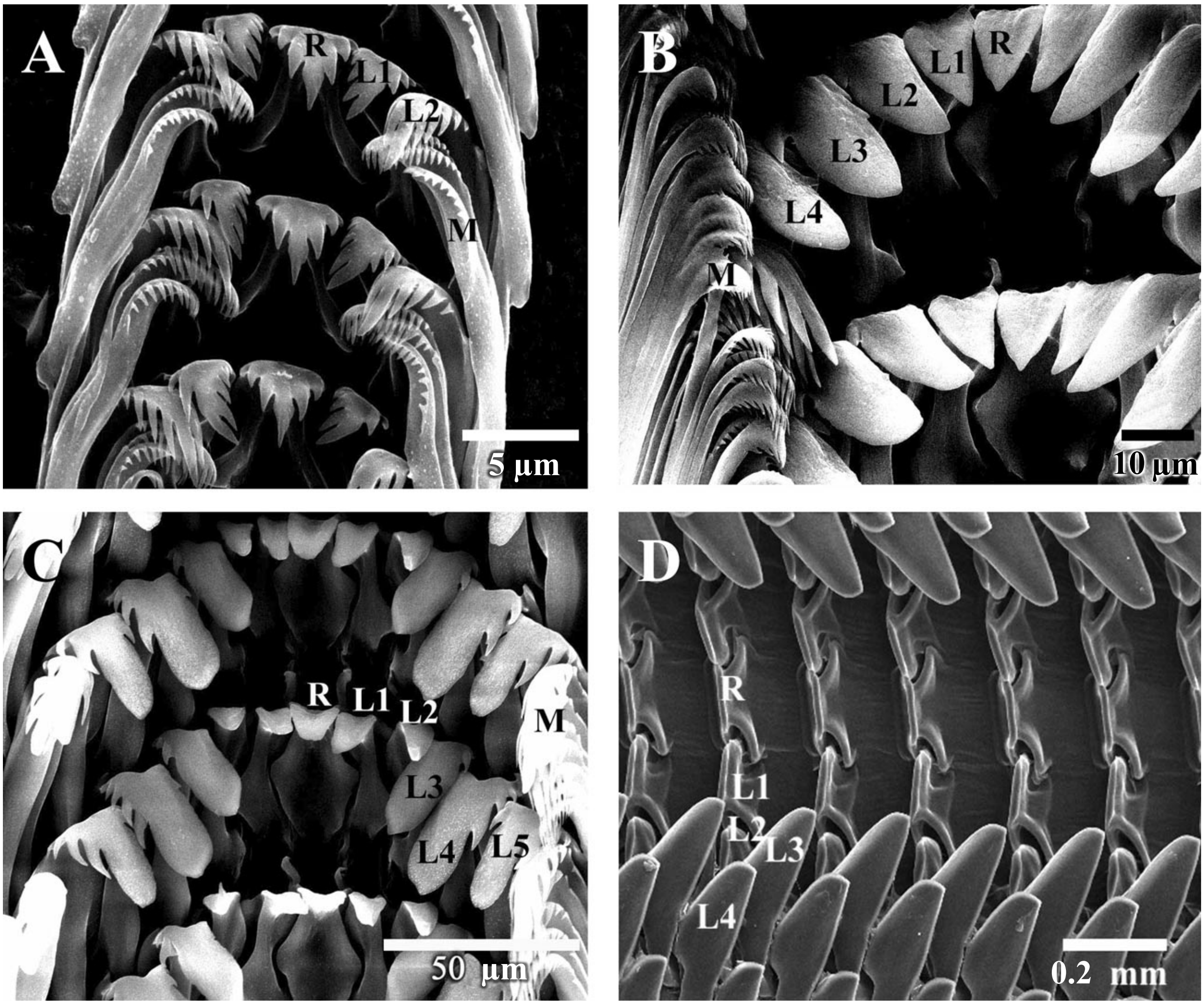

Fig. 8. SEM photographs of the radula showing developmental stages

Radula formulae represent the numbers of teeth in a transverse row as follows: M+L+R+L+M[55]; 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, ~15+(2+2)+R+(2+2)+ ~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. ?+(2+2)+R+(2+2)+?.

D: Juvenile 29.9 mm in shell length. L3-L5 teeth are much longer and more pointed than the central teeth (R, L1, L2). ?+(2+2)+R+(2+2)+?.

diatoms such as *Cocconeis* spp.

In post-larvae < 1 mm in SL, only 2 pairs of lateral teeth (L1, L2) were present in the radula (Fig. 8A). Three pairs of lateral teeth (L3-L5) were added gradually as the SL of the post-larvae increased from 0.9 to 1.9 mm (Fig. 8B). 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. 8C, 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.

Summary and conclusions

Three major changes in the diet that were closely related to the developmental changes in the digestive

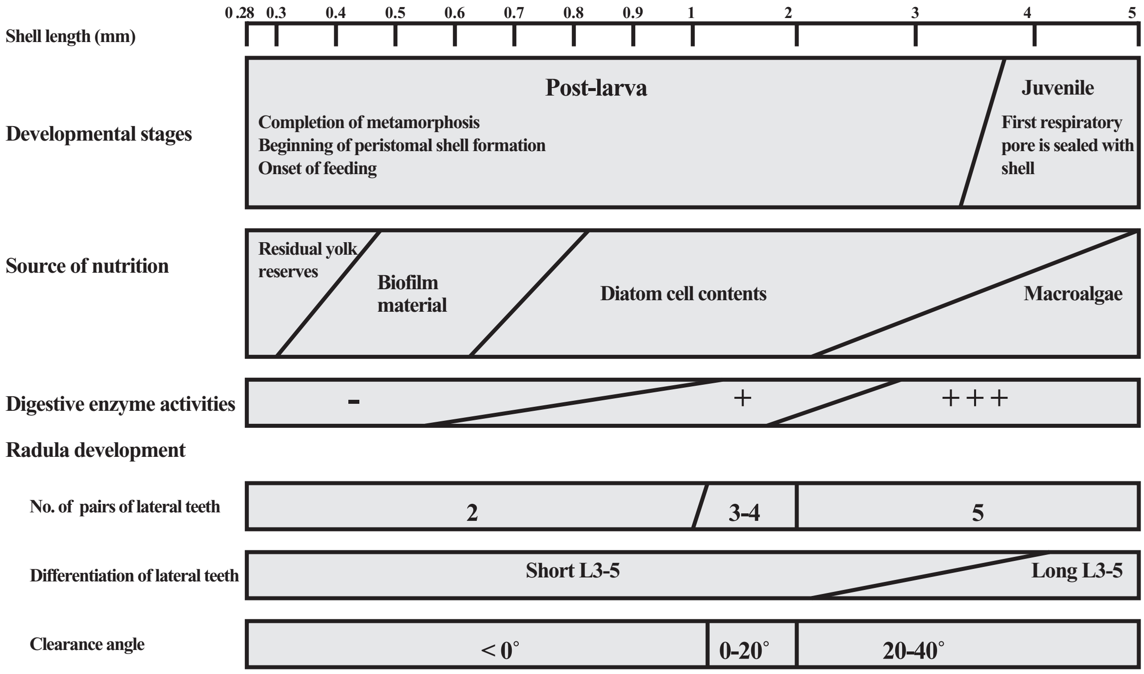

Fig. 9. Feeding changes, development of digestive enzyme activities and radula morphology in post-larval and juvenile *Haliotis discus hannai*

enzyme activities and radula morphology were identified as the abalone grew (Fig. 9). 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. In the natural fishery grounds of abalone, the presence of juvenile and adult abalone at relatively high densities is probably associated with a sufficient amount of food for post-larvae. This is because juveniles and adults do not compete for food with post-larvae and may even exclude small herbivorous gastropods, which were found to be strong competitors for suitable diatoms with post-larval abalone[12,47]. The grazing of adult and juvenile abalone provides a trail mucus and promotes the presence of *Cocconeis* spp. Research on the feeding ecology of post-larval *H. discus hannai* in the natural environment is limited. It is important to carry out further field experiments to link laboratory work to field studies.

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