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Diatom diet selectivity by early post-larval abalone *Haliotis diversicolor supertexta* under hatchery conditions*

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Abstract Benthic diatoms constitute the primary diet of abalone during their early stages of development. To evaluate the dietary preferences of early post-larval abalone, *Haliotis diversicolor supertexta*, we analyzed the gut contents of post-larvae that settled on diatom films. We compared the abundance and species diversity of diatom assemblages in the gut to those of the epiphytic diatom assemblages on the attachment films, and identified 40 benthic diatom species in the gut contents of post-larvae 12 to 24 d after settlement. The most abundant taxa in the gut contents were *Navicula* spp., *Amphora copulate*, and *Amphora coffeaeformis*. *Navicula* spp. accounted for 64.0% of the cell density. In the attachment films, we identified 110 diatom species belonging to 38 genera. Pennate diatoms were the dominant members including the species *Amphiprora alata*, *Cocconeis placentula* var. *euglypta*, *Cylindrotheca closterium*, *Navicula* sp. 2, and *A. coffeaeformis*. Nano-diatoms (<20 μm in length) accounted for a considerable proportion of the total species number and cell density of the diatom assemblages in the gut contents and on the films. This suggests that nano-diatoms are important to the efficient production of abalone seed. The difference of the composition and abundance of diatoms between in the guts and on the biofilms suggests that early post-larval grazing was selective. An early post-larval abalone preferred nano-diatoms and the genera *Navicula* and *Amphora* during the month after settlement.

Keyword: benthic diatoms; feeding; *Haliotis diversicolor supertexta*; post-larval abalone

1 INTRODUCTION

Abalones are commercially important in many countries. Mass culture of abalone began in the mid 1980s in China and developed rapidly in the 1990s. *Haliotis diversicolor supertexta* is the species most commonly cultured in south China, constituting around 65% of the total yield of abalone in 2000 (Nie et al., 2004). In recent years, nursery rearing has become more difficult because mortality occurs frequently during the first month after settlement. Maintaining viable juveniles past settlement is the biggest challenge for abalone seed production. It is generally believed that an inappropriate diet is the major cause of high mortality in this (Nie et al., 2004; Zhang et al., 2004) and other species of abalone (Gordon et al., 2006).

Benthic diatoms are the primary food choice for early post-larval abalone. In abalone seed production hatcheries, diatom films on plastic plates have been used as a settlement substrate and an initial food source for post-larvae (Ebert et al., 1984; Kawamura, 1996; Nie et al., 2004). Successful seeding is closely related to the quantity and quality of benthic diatoms.

At present, the dietary value of the different diatom species is still not well understood. A number of studies have examined the relationship between post-larvae growth and feeding behavior using a range of diatom species. The dietary value of benthic diatoms is influenced by their morphology, attachment strength, frustule strength (Kawamura et al., 1995a, 1998a; Kawamura et al., 1995b; Roberts et al., 1999), the biochemical composition of

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the diatom cell contents (Dunstan et al., 1994; Gordon et al., 2006), and digestibility. In addition, post-larval size has a significant effect on their ability to consume different sized diatoms (Xing et al., 2008). However, research into juvenile abalone diets has focused on the use of monocultured species of benthic diatoms. Little is known about the use of hatchery diets or feeding behavior in newly settled larvae. Most hatcheries rely on a benthic diatom community that forms on plastic plates placed in the tanks. Thus, the post-larvae ingest a variety of diatoms, rather than a single species. Given this, knowledge of post-larval feeding preferences in the natural environment is likely to be invaluable for producing diets that allow successful culture of post-larval abalone.

The dietary preferences of post-larval abalone can be determined by identifying the algal species that are present in the gut. If certain species are preferred, they are likely to be over-represented in the gut contents. Spawning and larval rearing of *H. diversicolor supertexta* occurs between May and June in hatcheries in Dongshan, Fujian Province on the southern coast of China. We analyzed the composition and structure of the diatom community in the gut of post-larvae during this rearing period in 2003. We also documented the species composition and abundance on the surrounding diatom films. We then compared the composition and abundance of diatoms in the gut and on the diatom films.

2 MATERIAL AND METHOD

2.1 Sampling

We obtained *H. diversicolor supertexta* post-larvae in-situ from an abalone farm in Dongshan between May and June, 2003. The larvae were reared at the hatchery in flow-through tanks (30 m^3) filled with plastic plates at a temperature of 24.7±0.5°C. Approximately 6 d after spawning, the larvae had settled on the plastic plates that had been coated with a thin film of naturally occurring diatoms. Seawater (salinity 29.6) was pumped from Dongshan beach and filtered before it entered the tanks.

We randomly sampled 10 post-larvae from the diatom films 12, 16, 20, and 24 d after settlement. The larvae were dislodged with a fine needle, washed with filtered sea water to remove external diatoms, then placed into a bottle and preserved in 4% formalin. We measured the shell length (SL) of each individual under a microscope with an ocular graticule. The mean SLs were 654±111 μm, 832±84 μm, 1 285±192 μm, and 1 570±290 μm on days 12, 16, 20, and 24, respectively.

We used a sterilized blade to collect a sample of diatoms from a 10×10 cm^2 area surrounding the post-larvae. Each blade was rinsed with 10 mL filtered sea water to flush the diatoms into a 10-mL sample bottle, to which a few drops of formalin were added.

2.2 Treatment

The analysis of gut contents was conducted in accordance with the method of Norman-Boudreau et al. (1986). The post-larval abalones were treated with EDTA and sodium hypochlorite to decalcify the shell and dissolve the tissue, leaving only the siliceous frustules of the diatoms for counting and identification. Frustules were preserved in distilled water.

2.3 Relative abundance

To determine the cell density of diatoms in the gut contents and on the films, we placed 1 mL of the preserved sample into a chamber slide. The number of cells was enumerated under a phase contrast microscope. In addition, we calculated the size of each cell. We calculated relative abundance using the following formula:

$$\text{Relative abundance (\%)} = (N/N_0) \times 100$$

where N is the number of cells of one species per mL, and N_0 is the total number of cells per mL.

We ignored cell frustules that were too damaged to be identified.

We tentatively identified the diatoms during the counting procedure. Identifications were made in more detail by scanning electron microscopy (Philips XL30) and transmission electron microscopy (JEM2100). Diatom taxonomic determination was based on Jin et al. (1965, 1982, 1992).

3 RESULT

3.1 Diatom assemblages in the gut contents of post-larval abalone

We identified 40 diatom species belonging to 13 genera in the gut contents of the post-larvae (Table 1). Among these, pennate diatom species (38 species, representing 11 genera) accounted for 95.0% of the total number. The most common genera were: *Navicula*, *Nitzschia*, and *Amphora*.

The diatom taxa shown in Fig.1 were representative of the most common diatoms in the

Table 1 List of diatom species identified from settlement films and also (†) from post-larval abalone guts

Achnanthes amoena Hustedt * †	*Gyrosigma* sp. †
A. bremeyeri Lange-Bertalot *	*Hantzschia amphioxys* (Ehr.) Grunow *
A. brevipes Agardh †	*Haslea* sp. †
A. brevipes var. *angustata* (Grev.) Cleve †	*Licmophora californica* Grunow
A. brevipes var. *parvula* (Kuetz.) Cleve * †	*L. flabellata* (Carm.) Agardh
A. campechiana Hustedt	*Melosira moniliformis* (O. F. Muller) Agardh
A. citronella (Mann) Hustedt	*M. juergensi* Agardh *
A. delicatula (Kuetz.) Grunow *	*Navicula britannica* Hustedt et Aleem
A. javanica var. *subcontricta* Meister	*N. complanata* Grunow
A. punctifera Hustedt	*N. duerrenbergiana* Hustedt
Achnanthes sp. 1 * †	*N. cryptocephala* var. *veneta* (Kuetz.) Rabenhorst* †
Achnanthes sp. 2 *	*N. gregaria* Donkin *
Achnanthes sp. 3 *	*N. johanrossii* Giffen
Actinocyclus ehrenbergi Ralfs	*N. mollis* (W. Sm.) Cleve *
Actinoptychus undulates (Bail.) Ralfs	*N. perminuta* Grunow * †
Amphipleura rutilans (Trent.) Cleve	*N. ramosissima* (Ag.) Cleve †
Amphiprora alata (Ehr.) Kuetzing *	*N. orthoneoides* Hustedt *
Amphora angusta Gregory †	*N. retrocurvata* J. R. Carter *
A. coffeaeformis (Ag.) Kuetzing * †	*N. subminuscula* Manguin * †
A. coffeaeformis var. *borealis* (Kuetz.) Cleve †	*N. voigtii* Meister *
A. copulata (Kuetz.) Schoeman & Archibald * †	*Navicula* sp. 1 * †
A. cymbelloides Grunow *	*Navicula* sp. 2 * †
A. graeffii (Grun.) Cleve * †	*Navicula* sp.3 †
A. incrassata Giffen *	*Nitzschia alexandrina* (Chol.) Lange-Bertalot et Simonsen* †
A. laevis Gregory *	*N. constricta* (Kuetz.) Ralfs * †
A. laevis var. *laevissima* Gregory *	*N. dissipata* (Kuetz.) Grunow * †
A. micrometra Giffen * †	*N. dubiiformis* Hustedt
A. ostrearia Brebisson	*N. constricta* (Kuetz.) Ralfs*
A. proteus var. *oculata* Peragallo H. et M.	*N. frustulum* (Kuetz.) Grunow * †
Amphora sp. * †	*N. frustulum* var. *indica* Skvortzow * †
Arcocellulus mammifer Hasle, Von Stosch & Syvertsen *	*N. frustulum* var. *symbiotiea* Lee et Reimer * †
Asterionella notata Grunow	*N. laevis* Hustedt * †
Bacillaria paradoxa Gmelin	*N. longissima* (Breb.) Ralfs
Biddulphia aurita (Lyngbye) Brebisson et Godey	*N. obrusa* var. *scalpelliformis* Grunow
Chaetoceros sp. *	*N. ovalis* Arnott *
Cocconeis diruptoides Hustedt *	*N. paleacea* Grunow * †
C. disculus (Schumann) Cleve * †	*N. panduriformis* Gregory
C. placentula var. *euglypta* (Ehr.) Cleve * †	*N. panduriformis* var. *minor* Grunow *
C. pseudomarginata Gregory	*N.* af. *pusilla* (Kuetz.) Grunow emend. Lange-Bertalot *
C. scutellum var. *parva* Grunow *	*N. sigma* (Kuetz.) W. Smith
C. sublittoralis Hendey †	*Nitzschia* sp. * †
Coscinodiscus sp.	*Pleurosigma aestuarii* (Breb.) W. Smith
Cyclotella atomus Hustedt *	*P. intermedium* var. *dongshanense* Chin et Liu
C. striata var. *baltica* Grunow	*Rhizosolenia setigera* Brightwell
Cylindrotheca closterium (Ehr.) Reimann et Lewin †	*Skeletonema costatum* (Grev.) Cleve * †
Cymbella pusilla Grunow *	*S. potamos* (Weber) Hasle *
Denticula sp. *	*Stauroneis* sp.
Diploneis bombus Ehrenberg †	*Striatella unipunctata* (Lyngbye) Agardh
D. incurvata (Greg.) Cleve	*Synedra laevigata* Grunow
D. smithii (Breb.) Cleve * †	*S. investiens* W. Smith
Extubocellulus cribriger Hasle, von Stosch & Syvertsen *	*S.* af. *tabulata* var. *parva* (Kuetz.) Hustedt
E. spinifer (Hargr. & Guill.) Hasle, von Stosch & Syvertsen *	*S. ulna* var. danica (Kuetz.) Grunow
Gomphonema pseudexiguum Simonsen * †	*Synedra* sp. †
Grammatophora marina (Lyngbye) Kuetzing	*Thalassiosira minima* Gaarder * †
G. oceanica var. *macilenta* (W. Sm.) Grunow	*Tropidoneis* sp.

* nano-diatoms

diet of the abalone we examined. The most abundant taxa in the gut contents were *Navicula* spp., *Amphora copulate* and *A*. *coffeaeformis*.

Navicula was always the most common genus (Fig.2), and accounted for 64.0% of the average total cell density (range: 43.2%–91.5%). The relative abundance of *A*. *copulate* was 15.5% on day 12, 2.0% on day 16, and 38.2% on day 24. The relative abundance of *A*. *coffeaeformis* varied between 2.3% and 8.5% during the experiment.

We often observed aggregations of diatom cells in the gut contents (Fig.3a). Many diatom frustules were broken in the position of girdle bands (Fig.3a, b, c). Among these, some diatom valves were also broken (Fig.3c, d).

3.2 Diatom assemblages in the settlement films available for post-larval abalone

We identified 110 diatom species (including varieties) belonging to 38 genera from the diatom films (Table 1). The diversity of diatom species taken from the settlement plates was 2.5 times greater than that in the abalone gut contents (Table 1). The diatoms were primarily pennate diatoms (85.5 % of the total number of species) from six genera: *Nitzschia*, *Navicula*, *Achnanthes*, *Amphora*, *Cocconeis*, and *Synedra*.

The dominant diatom species were *Amphiprora alata*, *Navicula* spp., *Cylindrotheca closterium*, *Cocconeis placentula* var. *euglypta*, and *A*. *coffeaeform*.

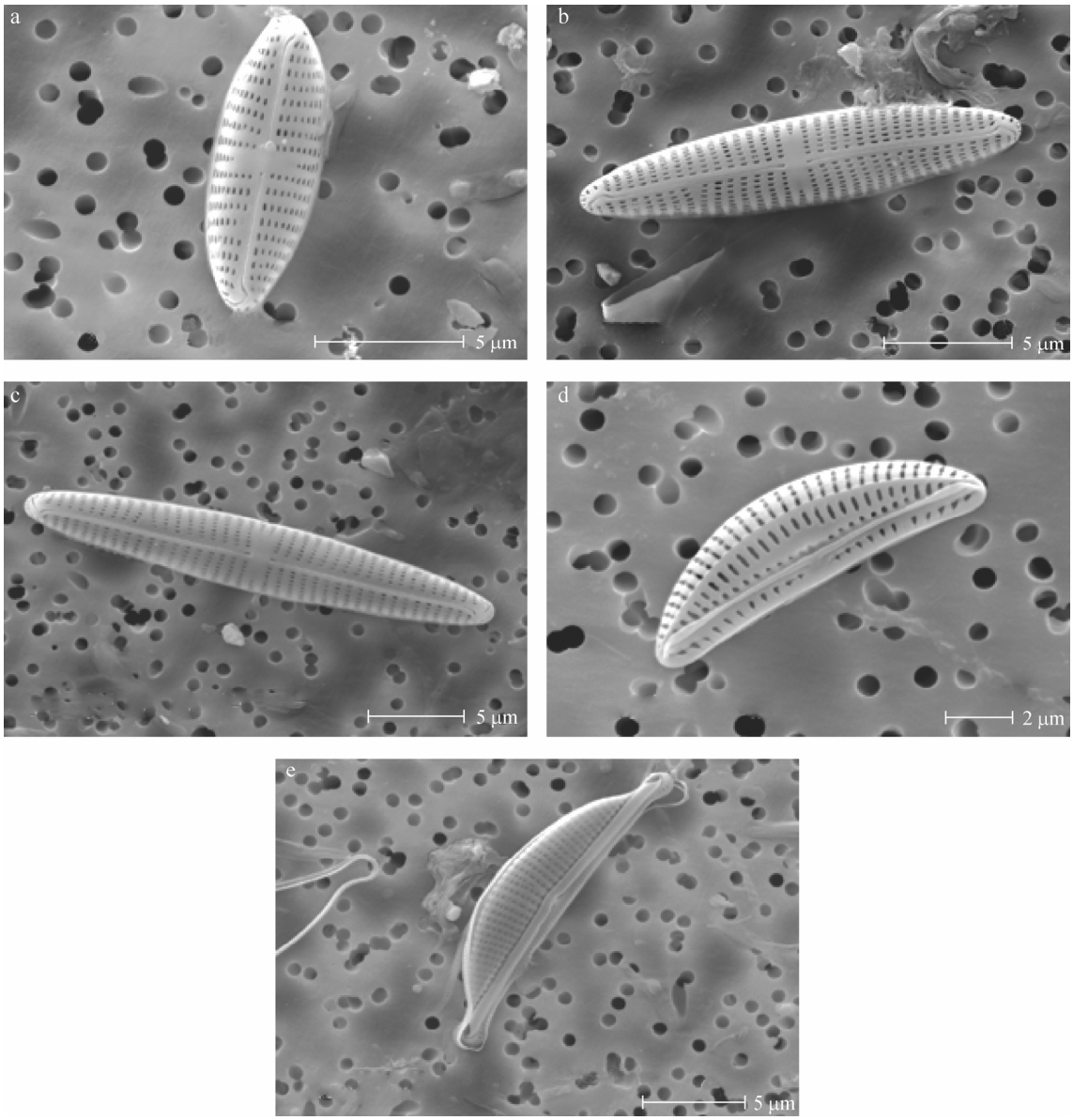

Fig.1 Predominant species from *H*. *diversicolor supertexta* post-larval guts

a. *Navicula* sp. 1; b. *Navicula* sp. 2; c. *Navicula* sp. 3; d. *Amphora copulate* (Kuetz.) Schoeman & Archibald; e. *Amphora coffeaeformis* (Ag.) Kuetzing

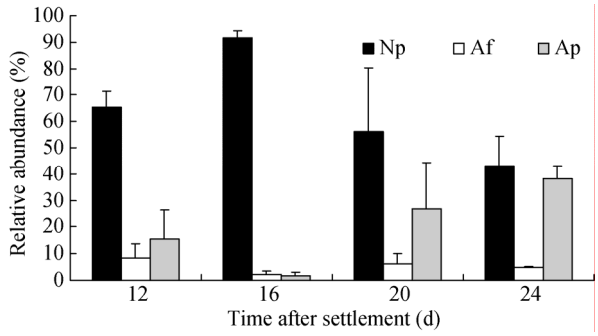

Fig.2 Relative abundance of the principal groups of diatoms in early post-larval abalone guts

Np: *Navicula* spp.; Af: *Amphora coffeaeformis*; Ap: *A. copulate*. *N*=10 for each sampling time point

A. alata was the most dominant species and accounted for 31.6% of the total cell density on average. *Navicula* spp. and *C. closterium* accounted for 30.2% and 14.0%, respectively.

Navicula spp. and *A. coffeaeformis* were abundant both in the guts and on the films, while *A. copulate* was abundant only in the guts (Fig.4). The other dominant species found in the diatom films were seldom observed in the guts.

3.3 Nano-diatoms found in the guts and diatom films

Nano-diatoms (<20 μm in length) were dominant

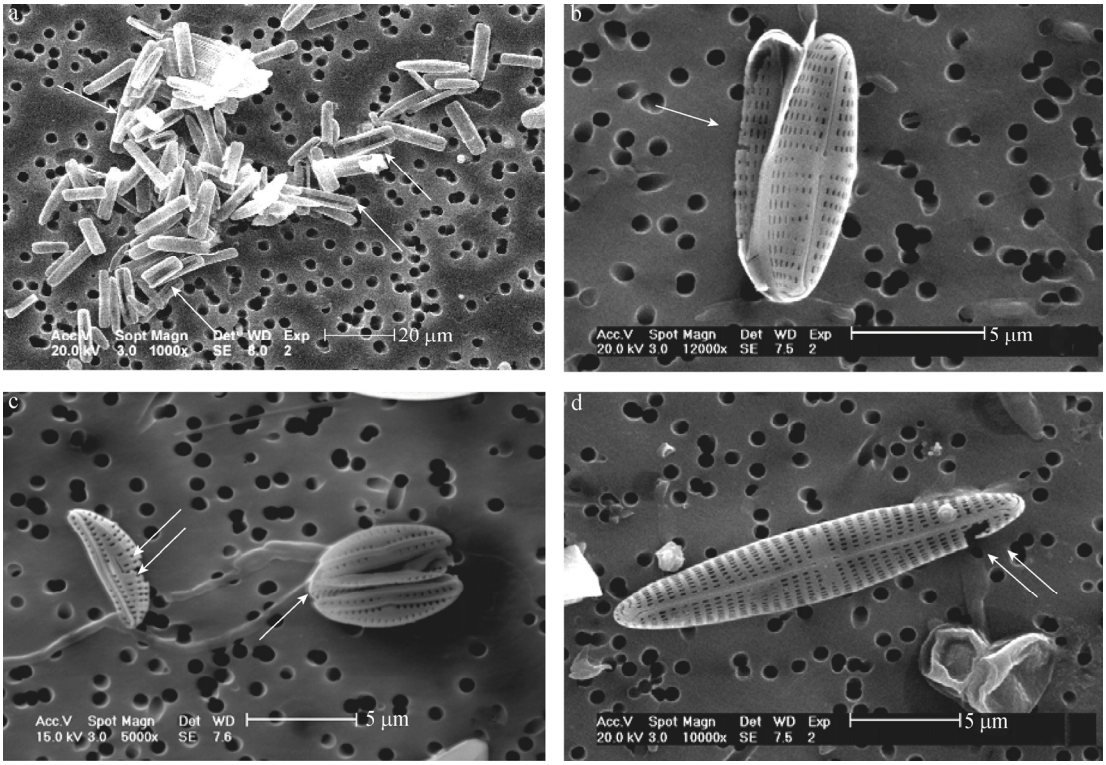

Fig.3 Broken diatom frustules in the gut contents of *H. diversicolor supertexta*

↑ girdle band broken; ↑↑ valve broken

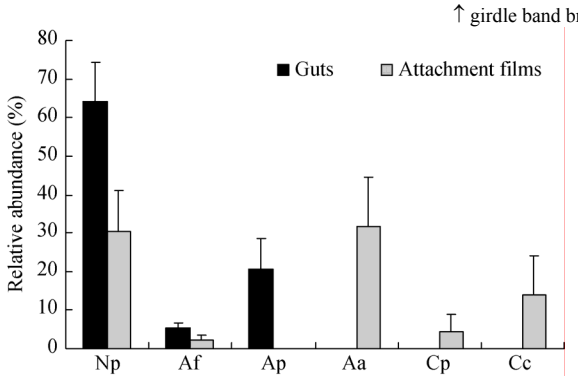

Fig.4 The mean relative abundance of dominant species from post-larval guts and attachment films during the investigation

Np: *Navicula* spp.; Af: *Amphora coffeaeformis*; Ap: *A. copulate*; Aa: *Amphiprora alata*; Cp: *Cocconeis placentula* var. *euglypta*; Cc: *Cylindrotheca closterium*. *N*=10 for each sampling time point.

both in the gut contents and on the diatom films, accounting for 70.0% and 52.7%, respectively, of the total number of species (Table 1). The average relative abundance was >90% in the gut contents and >60% on the biofilms (Fig.5). Nano-diatom species consisted primarily of *Navicula* and *Amphora* in the gut contents and *Amphiprora* and *Navicula* on the biofilms.

4 DISCUSSION

Our results represent a significant advance in our understanding of the diatom preferences of post-larval abalone. The abalones were sampled in-situ from an abalone farm which has successfully reared seed abalone, not from an array of cultured microalgae.

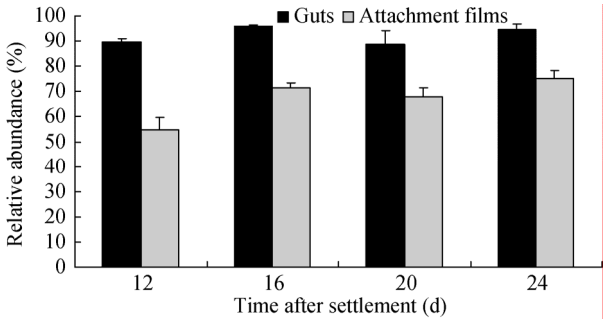

Fig.5 Relative abundance of nano-diatoms in the guts and the films during the investigation

Therefore, our findings are more representative of dietary preferences in the hatchery environment.

Kawamura et al. (1998b) suggested that post-larval abalone that are less than 600–800 μm SL gain adequate nutrition from yolk reserves, dissolved organic matter, or the components of biofilms. Post-larvae that are larger than 600–800 μm SL are able to digest diatoms, and therefore grow more rapidly. Martinez-Ponce et al. (1998) noted that the grazing rates of post-larval abalone feeding on *Navicula incerta* increased abruptly above a SL of 470 μm. The post-larvae in our study were all larger than 600 μm SL so were large enough to digest diatoms. The presence of large amounts of diatoms in the post-larval guts suggested that the yolk reserves and biofilm components no longer provided adequate nutrition for *H. diversicolor supertexta* post-larvae, and that diatoms had become an important food source.

The post-larval abalones are unable to digest the siliceous frustules of diatoms. By analyzing the composition of diatoms in the gut contents, we can estimate the composition of the diatom diet of post-larvae and determine their dietary preferences. During the fixation process, all organic materials in the post-larvae, except the siliceous diatom frustules, were oxidized by sodium hypochlorite.

Many of the diatom frustules in the gut contents were damaged, particularly at the position of the girdle bands (Fig.3). Girdle band silica is one of most delicate parts of the valve silica (Dusan et al., 2007). Thus, girdle bands can be easily broken by the post-larval radula when post-larvae ingest diatoms. Post-larvae are often able to extract the cell contents without totally crushing the frustules.

The composition and abundance of diatom species differed between the gut contents and the settlement films. The species diversity of diatoms taken from diatom films was 2.5 times greater than that in the abalone guts. The dominant species from the diatom films and the abalone guts were not the same. *A. copulate* was common in the gut contents but was uncommon in the diatom films. Likewise, most of the major species in the biofilms were seldom observed in the guts (Fig.4). This suggests that the diatoms were grazed selectively by *H. diversicolor supertexta* post-larvae.

There were no significant changes in the composition of diatom species in the gut contents during the investigation period. *Navicula* and *Amphora* were the dominant genera at all sampling times. Their average relative abundance was 64.0% and 26.0%, respectively, which was higher than their abundance on the biofilms (30.2% and 2.2%) (Fig.4). Thus, we hypothesize that *H. diversicolor supertexta* early post-larvae prefer these two species. Moreover, the success of larval rearing at the abalone farm suggests that *Navicula* and *Amphora* are beneficial to early post-larval growth. There is evidence that *Navicula* and *Amphora* support high post-larval growth and survival rate when supplied in combination (Gordon et al., 2004, 2006; Daume, 2000). The biochemical composition of diatom cell contents can affect post-larval abalone growth. Gordon et al. (2006) conclude that the suitability of *Amphora luciae* and *Navicula* cf. *lenzii* for enhancing growth and survival of post-larvae can be attributed to their complementary and balanced nutritional properties.

Navicula spp. occurred frequently in the gut contents as clumps containing numerous individuals, similar to those seen in Fig.3a. The ingestion of large numbers of *Navicula* spp. cells may be explained by the low adhesive strength of this species and their ability to form clumps, thus facilitating their ingestion by the abalone. Siqueiros-Beltrones et al. (2000) noted that *H. rufescens* post-larvae exhibited grazing selectivity. The guts of this species contained a high proportion of *Navidula incerta*, which are rare or absent from samples of the surrounding flora. Laboratory experiments suggest that *Navicula* is both a good food source for early post-larval abalone and a suitable substratum for settlement and metamorphosis of larval abalone (Martínez-ponce et al., 1998; Daume et al., 1999, 2000; Gallardo et al., 2003; Gordon et al., 2004; Xing et al., 2008). Besides the contents of *Navicula* cells, their extracellular mucus is also beneficial to the growth and survival of early abalone post-larvae (Daume et al., 2000).

Amphiprora alata, which accounted for a high percentage of the biomass in the diatom films, was seldom found in the guts. This may be due to their

morphology whereby solitary cells are twisted about the apical axis and the raphe is raised in a keel. Thus, they cannot be easily ingested by the post-larvae. *C. placentula* var. *euglypta* was also commonly observed in the diatom films but is seldom seen in the guts. Kawamura et al. (1995b) report that *Cocconeis* spp., although a suitable substratum for settlement and metamorphosis of larval abalone, is not a good food source for early post-larval abalone. This species exudes relatively small quantities of extracellular substances that serve as a food source for the post-larvae. In addition, early post-larvae do not ingest any *Cocconeis* spp. cells due to the high adhesive strength of these diatom species (Kawamura et al., 1995a; 1998a). However, *Cocconeis* species support good growth once post-larvae reach a size where they can efficiently ingest the diatom (Kawamura et al., 1998b).

In this study, *C. closterium* was also common in the diatom films. However, cell fragments were observed only occasionally in the guts. We suspect that this is because *C. closterium* cells are too large to be entirely ingested by post-larvae. In addition, *C. closterium* cell walls are weakly silicified, and their cells are relatively easily broken by the abalone radula, which may contribute to their rare occurrence in the gut.

Nano-diatoms accounted for a considerable portion of the total species number and the cell density of diatoms in the gut contents of post-larval abalone. Our observations suggested that early post-larvae abalone exhibit size selectivity for diatoms. Thus, the size of diatom cells is a critical factor determining their dietary value, especially for small post-larvae. Given this, the value of nano-diatoms in abalone seed production cannot be ignored. Diatom cell size affects how efficiently the radula passes food into the mouth (Kawamura et al., 1998b). Early post-larvae are not able to ingest the larger celled/longer stalked diatoms. Nano-diatoms were generally handled more efficiently, so their cell contents and extracellular secretions may be an important source of food for *H. diversicolor supertexta* early post-larvae. Seki et al. (1981) report that early post-larval *H. discus hannai* only ingest diatoms that are <10 μm in length. Likewise, Norman-Boudreau et al. (1986) noted that diatoms ingested by 6 d-old *H. rufescens* post-larvae were 30 μm in length and 10 μm in width.

Understanding abalone feeding ecology in early life stages is important for the improvement of rearing techniques in abalone hatcheries. In this study, we examined the diatom species composition in the guts of early post-larval *H. diversicolor supertexta* during the month after settlement. The post-larvae exhibited a preference for nano-diatoms and the genera *Navicula* and *Amphora*. The dietary value of different species of benthic diatoms is likely to change with the growth of the abalone. Therefore, further experiments are required to gain a better understanding of the dietary preferences for each developmental stage of the abalone.

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