A Review of the Structural and Digestive Capability of Juvenile Abalone Species in Relation to Diet and Growth Rate

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Abstract: Within the aquaculture industry, growth rates of juvenile abalone can be accelerated by identifying the optimum type of feed. Both natural and artificial feed were reviewed in relation to the structural and digestive capabilities of abalone. The consumption of diatoms was largely dependent on their morphology, specifically their attachment strength to the substrate. *H. discus* hannai less than ~500 μm Shell Length (SL) initially consumed diatomic secretions and thereafter the diatoms themselves. The diatoms consumed at ~500 μm SL were easily consumed as they were loosely attached to the substrate, for example *Navicula ramosissima*. However, *N. ramosissima* was not digested efficiently and was passed out of the digestive system whole. The radula of *H. discus* hannai between 500-1000 μm SL had undergone various morphological changes. The clearance angle of the radula increased so that the abalone could efficiently excavate strongly attached diatoms from the substrate. For *H. discus* hannai and *H. rubra* >1000 μm SL, larger highly adhesive diatoms, for example *Achnanthes longipes* were more suitable because during grazing the frustule was ruptured allowing the abalone to consume the cell contents. The contents of artificial feeds can be manipulated to induce accelerated growth rates in abalone, therefore making them a suitable substitute for natural feeds. The optimum level of proteins, lipids and carbohydrates was found to be 27-35, <5.58 and 30-60%, respectively. High levels of proteins and carbohydrates in the feed were tolerated as abalone produced sufficient proteases and carbohydrases to digest the feed efficiently. However, the low levels of lipids in the feed could be attributed to the low lipase activity in the digestive system. Fishmeal was identified as being the optimum source of protein for accelerated growth rates in *H. midae*. However, there was insufficient data to determine the optimum sources of lipids and carbohydrates. The metabolism of many gastropods including abalone, is based on the utilization of carbohydrates, therefore future research should be focused on carbohydrates when developing nutritionally balanced feeds.

Key words: Abalone, aquaculture, feed development, gastropods, growth rate, nutrition, mollusks

INTRODUCTION

Abalone aquaculture and fisheries are primarily driven by their economic importance. The growth of the abalone industry can be attributed to two main contributing factors:

- The increased global demand for abalone meat
- The high economic value of abalone meat (Lee-Anne, 2006)

To satisfy global demands, abalone stocks in the wild are being put under great pressure from overexploitation (Steinberg, 2005). Aquaculture has been the main alternative to provide the deficit of abalone for global markets, as abalone stocks are declining in the wild. The growth of juvenile abalone to marketable size is dependent upon three main contributing factors:

- The types of feed that are suitable for consumption
- The capability of the abalone to consume the feed
- The capability of the abalone to convert the feed to biomass (Onitsuka *et al.*, 2007)

Understanding of the digestive system in juvenile abalone is imperative to accelerate growth rates on different abalone feeds.

The radula and digestive enzymes (protease, carbohydrase and lipase) are the two main components that facilitate feeding in the digestive system of abalone species (Fleming *et al.*, 1996). For *Haliotis rubra* the mechanical breakdown of the feed was facilitated by the radula whereas digestive enzymes facilitated the chemical break down of the feed (Johnston *et al.*, 2005). It was essential that the morphology of the radula through the juvenile stages be reviewed as it determined the ability of the abalone to consume the feed. Commercially, there is

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much debate over the growth performance of abalone consuming natural and artificial feeds. The growth rate of abalone fed a diatom diet depends upon the physical characteristics of the diatom and the ability of the abalone to rupture the cell wall of the diatom in order to consume its contents (Kawamura *et al.*, 1998a). Artificial feeds consist mainly of proteins, lipids and carbohydrates that accelerate the growth rate of abalone (Fleming *et al.*, 1996). Different ratios of proteins, lipids and carbohydrates in artificial feeds can induce different levels of enzymatic responses in abalone (Garcia-Esquivel and Felbeck, 2006). The type of feed that is utilized in culture system needs to complement the digestive system of the abalone so that maximum growth rates can be achieved.

The motivation for this review was to provide information to the abalone industry on the best diet that would achieve accelerated growth rates in juvenile abalone. Juveniles were selected over adult individuals because the feeding structures and digestive ability changed in relation to the types of feed that were consumed. The last known review which covered the feeding of juvenile abalone was in 1998 (Kawamura *et al.*, 1998b). Since 1998, there have been great advances in research on the feeding of juvenile abalone. Through compiling this review, aspects of feeding that are not adequately covered in existing literature can be identified and focused on in future studies. This review examines the types of feed that are best suited for juvenile abalone species to achieve accelerated growth rates in relation to their structural and digestive capabilities.

FEEDING TRANSITIONS, MORPHOLOGY OF THE RADULA AND DIGESTIVE SYSTEM IN JUVENILE ABALONE

The type of feed that is best suited for abalone growth is dependent on an understanding of the feeding transitions, as well as the morphology of the radula and digestive system. Abalone undergoes three feeding transitions throughout their lifetime (Onitsuka *et al.*, 2007).

Figure 1 shows that the first feeding transition takes place when abalone changes from lecithotrophy (yolk absorption) to particle feeding (Onitsuka *et al.*, 2007). This transition takes place between 280-500 μm Shell Length (SL). The second transition occurs when abalone are capable of feeding on diatom cell contents which is at about 10 days old (Fig. 1) (Onitsuka *et al.*, 2007). The final transition is from a predominantly diatom diet to a macroalgal diet at around 102 days old (Fig. 1) (Onitsuka *et al.*, 2007). These transitions are
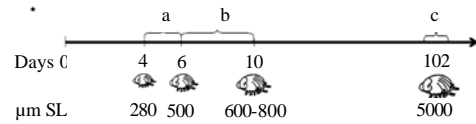

Fig. 1: General schematic timeline illustrating the feeding transitions of abalone throughout their lifetime: a) Feeding transition from lecithotrophy to particle feeding; b) Feeding transition from particle feeding to diatom cells; c) Feeding transition from diatom cells; *Not drawn to scale; SL = Shell Length
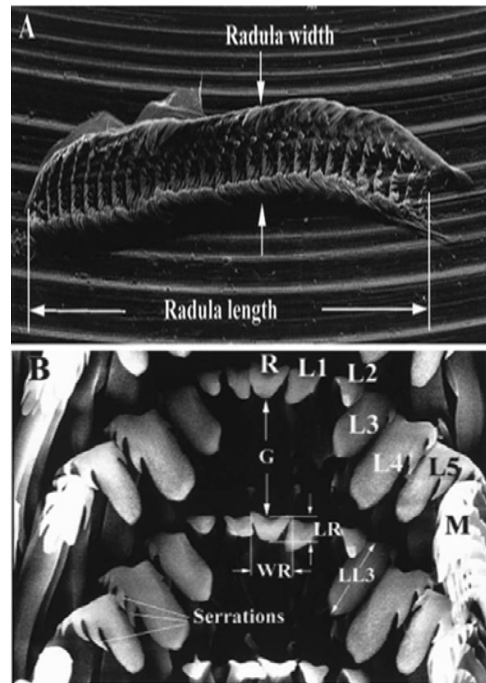

Fig. 2: Scanning electron microscope photographs: A) A complete radula illustrating length and width; B) Transverse rows of radula teeth; R = Rachidian tooth; L1-L5 = Lateral teeth 1-5; M) Marginal teeth; G = Gap between rachidian teeth of adjacent transverse rows; WR = Width of Rachidian tooth; LR = Length of Rachidian tooth; LL3 = Length of L3 tooth (Kawamura *et al.*, 2001)

largely affected by the morphological changes of radula and the digestive system which facilitate feeding in abalone.

The radula consists of many rows of teeth (Fig. 2) (Kawamura *et al.*, 2001). The arrangement of teeth on each row consists of a central rachidian tooth, lateral teeth on either side of a central rachidian tooth and marginals on the outer edge (Fig. 2) (Kawamura *et al.*, 2001). The digestive system of *H. rubra*, as described by

Johnston *et al.* (2005) consists of a mouth followed by a buccal region and an oesophagus that extends posteriorly at the end of which is a crop. The stomach extends from the crop, then loops 180° at posterior end of the abalone and extends anteriorly to the style sac. The intestine consists of five regions which extends from the style sac anteriorly and concludes with the anus. The digestive gland which covers the crop and the stomach is connected through tubules to other digestive organs.

This review determines the type of feed that is best suited for juvenile abalone through the feeding transitions. This will be accomplished by examining the morphological changes of the radula and the biochemical changes of the digestive system (Onitsuka *et al.*, 2007; Johnston *et al.*, 2005).

DIATOMS

Factors affecting diatom consumption: Growth forms of benthic diatoms are classified into seven types based on their form of attachment, motility, adhesive strength and whether solitary or colonial (Kawamura *et al.*, 1995; Onitsuka *et al.*, 2007). Diatom attachment strength was one of the main characteristics that determined if the frustule of the diatom was ruptured during grazing and cell contents consumed by juvenile abalone (Onitsuka *et al.*, 2007).

Kawamura *et al.* (1995) reported that diatom species, *Navicula ramosissima* was characterised by low attachment strength to the substrate and was easily ingested by *Haliotis discus* hannai without cell rupture. *N. ramosissima* passed through the digestive system alive as the digestive system could not digest the frustule efficiently (Kawamura *et al.*, 1995). Therefore, the abalone could not access the contents of the cell, resulting in slower growth rates (Kawamura *et al.*, 1995). Onitsuka *et al.* (2007) reported that diatom species, *Cocconeis sublittoralis* was highly attached to the substrate, therefore require a great deal of force to dislodge them. The frustule of the diatom was ruptured by the force used during detachment and the cell contents consumed by *Haliotis diversicolor* resulting in accelerated growth rates (Onitsuka *et al.*, 2007). Therefore, although easily consumed, diatom species with low attachment strength are not necessarily more beneficial than diatoms with high attachment strength. There were some exceptions, for example *Cylindrotheca closterium* which had low attachment strength but owing to its' weak silicate frustules the diatom could be digested efficiently by *H. diversicolor* resulting in accelerated growth rates (Onitsuka *et al.*, 2007).

The size of the diatom cell plays a significant role on its ability to be consumed. Two strains of *Achnanthes longipes* with different cell sizes and stalk length were fed to *Haliotis iris* (<1300 μm SL) (Kawamura *et al.*, 1998a). Kawamura *et al.* (1998a) reported that the strain that had larger cells and longer stalks had not been consumed. This suggests that the morphology of the diatom cell influences its dietary value (Kawamura *et al.*, 1998a).

In light of the mention earlier, small, highly adhesive diatom species such as *Co. sublittoralis* and *Cy. closterium* are best suited for abalone consumption in intensive abalone culture. However, this is largely dependent on the feeding ability (radula development and biochemical digestion) of the abalone.

Diatoms best suited for post-larval abalone less than ~500-800 μm SL: In culture systems, plastic plates with diatom films that have been previously grazed upon by adult abalone are used as a substrate for the settlement of early veliger larvae (Kawamura *et al.*, 1995). The first feeding transition of abalone from lecithotrophy to particle feeding takes place after settlement and once metamorphosis has been completed (Kawamura *et al.*, 2001). Post settlement juveniles feed on the mucus trail left behind by adult abalone and/or extracellular diatomic secretions (Kawamura *et al.*, 1995). Both mucus from juvenile abalone and extracellular diatomic secretions appear to be a good source of food for *H. discus* hannai up to the ~600 μm SL (Kawamura *et al.*, 1995). During the first transition there were slight variations in the morphology of the radula suggesting that abalone were making preparations for particle feeding (Onitsuka *et al.*, 2007).

The radula of abalone <800 μm SL was adapted to be used as scoops rather than a means of cutting diatom cells (Kawamura *et al.*, 2001). Onitsuka *et al.* (2007) reported that *H. diversicolor* could consume *N. ramosissima* owing to their low attachment strength to the substrate. However, *H. diversicolor* could not detach *C. sublittoralis* because of its high attachment strength to the substrate and *A. longipes* because of its mucus stalk (Onitsuka *et al.*, 2007). This could be owing to the radula of *H. diversicolor* not being developed enough to dislodge the diatom. For *H. discus* hannai <800 μm SL clearance angles of the rachidian and lateral teeth were zero, making them more suitable for sliding across the substrate acting as scoops rather than a means of cutting the surface (Kawamura *et al.*, 2001). The scoops suggested by Kawamura *et al.* (2001) were used for scooping extracellular diatomic secretions and/or mucus trails secreted by juvenile abalone. The use of the radula as a scoop and not a means of cutting concur

with the findings by Onitsuka *et al.* (2007) that the radula is not structurally adapted to dislodge the diatom (*C. sublittoralis*) from the substrate at this stage (Kawamura *et al.*, 2001).

Using diatom cells as the primary feed for abalone ~<500 µm SL may not be suitable. However, utilizing mucus trails of juvenile abalone first and subsequently diatoms may be more appropriate. Kawamura *et al.* (2001) suggested that the rachidian and lateral teeth of *H. discus* hannai form scoops which were used for scooping extracellular diatomic secretions. One would assume that mucus trails would be a more appropriate feed. However Takami *et al.* (1997), compared the growth rates of post-larval *H. discus* hannai fed conspecific mucus trails and/or benthic diatoms. It was found that the growth rates of abalone that settled on mucus and diatom substrate were significantly higher than abalone that settled on the mucus substrate (Takami *et al.*, 1997). This suggested that abalone initially fed on trail mucus left by adult abalone then consumed diatoms as they grew older (Takami *et al.*, 1997). Therefore, a mucus and diatom substrate would be more appropriate after settlement of the veliger larvae. Inspite of the mention earlier, little is known about the digestive capabilities (enzyme activity and morphological changes to the digestive tract) of abalone to efficiently digest mucus as well the shell length at which abalone make the switch from consuming mucus to consuming diatoms.

Diatoms best suited for post-larval abalone more than ~1000 µm SL: The second feeding transition occurs when abalone become capable of consuming diatom cell contents owing to morphological changes of the radula (Kawamura *et al.*, 2001; Onitsuka *et al.*, 2007). For *H. rubra* at ~1000 µm SL, the serrations on lateral teeth pair 1 (L1) and lateral teeth pair 2 (L2) was reduced and the gaps between rows of teeth on the radula increased (Johnston *et al.*, 2005). These changes resulted in the radula being more suited for consuming larger food sources (Johnston *et al.*, 2005). For *H. discus* hannai between ~500 and 1000 µm SL, the clearance angle of the rachidian increased from 0° to ~5-35° (Kawamura *et al.*, 2001). An increase in the clearance angle of the rachidian allowed, the abalone to dislodge diatom cells from the substrate and in the process, rupturing the frustule (Kawamura *et al.*, 2001). In rupturing the frustule of the diatom cell, the cell contents of the diatom became available to the abalone for consumption resulting in accelerated growth rates (Kawamura *et al.*, 2001). The reduction of serrations on L1-L2 and an increase in the clearance angle of the rachidian facilitates the second feeding transition.

Abalone between ~900 and ~1900 µm SL grow 3 more pairs of lateral teeth on each row of teeth on the radula (Kawamura *et al.*, 2001). Owing to lateral teeth 3 (L3) lateral teeth 5 (L5) being slightly cusped, abalone are able to excavate tightly attached diatoms rather than just scraping of the surface (Kawamura *et al.*, 2001). Through the formation of L3-L5 on the radula, *H. discus* hannai was able to detach *A. longipes* from the substrate rupturing the frustule in the process, thereafter consuming its cell contents (Kawamura *et al.*, 2001; Onitsuka *et al.*, 2007). Hence, for accelerated growth rates at ~1000 µm SL diatom species with high attachment strength to the substrate, for example *A. longipes* are appropriate as the radula can efficiently consume the diatom and its cell contents. The full set of teeth for *H. rubra* was completed at around ~1500 µm SL, thereafter the length and width of the radula increased with increasing shell length (Johnston *et al.*, 2005). From 2000-4000 µm SL there were no major morphological changes to the rows of teeth on the radula. Rather, the number of rows of teeth on the radula increases with increasing shell length (Johnston *et al.*, 2005). This suggested that *H. rubra* at 5000 µm SL were now equipped to consume a macroalgal diet which they continue throughout their adult life.

Between 900 and 1900 µm SL the digestive tract undergoes various morphological changes to increase the digestive capacity of the abalone with feeding transitions (Johnston *et al.*, 2005). The crop expands and becomes increasingly folded which allows digesting food to come into greater contact with microvilli to absorb nutrients (Johnston *et al.*, 2005). Enzymes that are secreted by the digestive gland are capable of digesting proteins, lipids and carbohydrates; increase over time, increasing the digestive capacity of the abalone (Johnston *et al.*, 2005). High activity of the carbohydrate digestive enzyme laminirase was detected in *H. rubra* which was owing to the high concentration of carbohydrates in the ingested diatom. High activities of laminarinase correspond with morphological changes of the radula reiterating that the abalone have adapted to eating larger food sources (Johnston *et al.*, 2005).

ARTIFICIAL FEEDS

Natural versus artificial feeds: There is much debate over whether a natural feed or an artificial feed would induce accelerated growth rates in abalone. Over the past 15 years, research has been primarily focused on developing artificial feeds that would substitute the use of natural feeds in intensive abalone culture (Fleming *et al.*, 1996). The main obstacles during the weaning phase were maintaining the supply, the quality (nutritional value) and the quantity of diatoms (Knauer *et al.*, 1996). The rationale for this research was

to investigate the ability to manipulate the contents of artificial feeds inducing accelerated growth rates (Bautista-Teruel and Millamena, 1999). The use of artificial feeds provides a controlled alternative to natural feeds as the nutritive value of the artificial feed is maintained (Bautista-Teruel and Millamena, 1999).

Knauer *et al.* (1996) conducted a comparative study on the growth performance and digestive enzyme activity of juvenile *Haliotis midae* fed on diatoms and an artificial feed. There was no significant difference in the growth rates between abalone on the diatoms and the artificial feed. This suggested that there was a high possibility of replacing natural feeds with artificial feeds during the weaning phase (Knauer *et al.*, 1996). Owing to the artificial feed having high protein content, an elevated level of protease was detected in the digestive system of *H. midae*, illustrating the capability to deal with high levels of protein (Knauer *et al.*, 1996). It further showed a degree of flexibility in their digestive system that can be altered by their diet (Knauer *et al.*, 1996). Abalone are capable of dealing with varying levels of components (proteins, lipids and carbohydrates) in their feed within the boundaries of their physiology (Fleming *et al.*, 1996). However, determining the optimum levels and best source of the components is vital to determining abalone growth rates.

There was no difference in the morphology of the radula and digestive system when fed natural and artificial feeds (Johnston *et al.*, 2005). However, the final feeding transition took place when abalone changed from a predominantly diatom diet to a macroalgal diet. Artificial feeds are substitutes for macroalgae therefore future studies should focus on the structure (shape, size) of the artificial feed that would be best suited for the morphology of the radula to ensure efficient consumption.

PROTEIN

Protein sources: Most research has been primarily focused on protein as it is the most expensive component of artificial feeds (Mai *et al.*, 1995b; Bautista-Teruel and Millamena, 1999). In the context of aquaculture where abalone is cultured intensively using artificial feeds, this will result in higher production costs. Therefore, there is a need to develop cost effective feeds that will allow optimum utilization of protein to achieve accelerated growth rates (Bautista-Teruel and Millamena, 1999). Identifying a cheap source and optimum level of protein that would induce accelerated growth rates is the key to developing any cost effective feed.

Britz (1996b) reported a study in which casein was regarded as the best protein source for inclusion into artificial feeds (Uki *et al.*, 1985). However because of the

high cost of casein, it cannot be used in intensive abalone culture (Uki *et al.*, 1985). Therefore, an alternative source of protein is required that would provide the same type of growth rate as would casein but still be readily available and cost effective. Britz (1996b) evaluated the suitability of various protein sources (fishmeal, casein, soya oil cake and torula yeast) for inclusion into artificial feeds for *H. midae*. The results from this study suggested that *H. midae* fed fishmeal produced accelerated growth rates and higher shell length increments than other protein sources (Britz, 1996b).

Surprisingly, *H. midae* that were fed fishmeal had a higher growth rate than *H. midae* fed casein. The differences between the growth rates could be attributed to the source and processing of the fishmeal (Britz, 1996b). Although, abalone fed fishmeal had a Feed Conversion Ratio (FCR) of 0.8, it was marginally close to 0.7 for the casein, suggesting a relatively high efficiency of conversion to body weight (Britz, 1996b). The high FCR and growth rates obtained with the fishmeal are encouraging with respect to artificial feed development as it is readily available and relatively cheap (Britz, 1996b).

Optimum level of protein to include into artificial feeds: A linear trend has been identified for *Haliotis fulgens* that as protein levels in artificial feeds increase growth rates increase (Gomez-Montes *et al.*, 2003). A study conducted by Britz (1996a) confirmed this statement as there was an increase of 18% in the weight gained by *H. midae* fed between 27 and 47% protein in their feed. However, the optimum level of protein for *H. midae* was not identified as there was no control on the amount of energy in the diet (Bautista-Teruel and Millamena, 1999). The optimum level of protein for *Haliotis asinina* has been identified as being 27% of the feed (Bautista-Teruel and Millamena, 1999). Similar results were obtained by Mai *et al.* (1995b) which identified the optimum levels of protein for *Haliotis tuberculata* to be between 22.3-32.3% and between 23.3-35.6% for *H. discus* hannai. The variation among the species could be attributed to their energy requirement, as well as the initial size of the animal (Mai *et al.*, 1995b). Should the diet contain sub-optimal levels of energy, such energy would be obtained from the protein sources therefore, growth rate would be reduced (Bautista-Teruel and Millamena, 1999). To achieve maximum growth rates, an effective protein energy ratio must be maintained (Gomez-Montes *et al.*, 2003). The optimal energy level for *H. asinina* was identified as being 3150 kcal kg^{-1} metabolizable energy with a dietary protein level of 27% (Bautista-Teruel and Millamena, 1999). However, the optimum energy level for *H. fulgens* was found to be 4060 kcal kg^{-1} metabolizable energy with a

dietary protein level of 40.45%. Therefore, further studies would have to be conducted on other abalone species as the protein energy ratio could be species and diet specific.

Proteases: The highest concentration of proteases was detected in the digestive gland as it synthesizes proteases. However, protease activity was uniform throughout the gut (Johnston *et al.*, 2005). Artificial feeds contain between 30-40% proteins whereas natural feeds only contain protein within the region of 10-20% (Johnston *et al.*, 2005). Johnston *et al.* (2005) reported that trypsin activity increased as the levels of protein in the artificial feed increased for *H. rubra*. Similarly, Britz (1996a) reported increased levels of proteases with increased levels of protein in the artificial feed for *H. midae*. From the studies of both Johnston *et al.* (2005) and Britz (1996a), it is clear that abalone can efficiently digest high levels of protein. In contrast, Edwards and Condon (2001) reported that trypsin activity was not influenced by the level of protein in the feed of adult *H. rubra* suggesting that adult abalone lack digestive flexibility. A Protein Efficiency Ratio (PER) of 6.6 was reported by Knauer *et al.* (1996) for large juvenile *H. midae*. However, Britz (1996a) reported a PER of 2.4 for small juvenile *H. midae*, therefore suggesting that smaller *H. midae* are more efficient users of protein.

LIPIDS

Lipids are important dietary components as they provide concentrated energy and essential fatty acids (Mai *et al.*, 1995a). There are various sources of lipids such as corn oil, vegetable oil and menhaden fish oil (Mai *et al.*, 1995a). There are no known studies that primarily focus on the optimum sources of lipids that will provide accelerated growth rates in abalone (Mai *et al.*, 1995a). However, there are a few studies that focus on the optimum dietary level of lipids to include in artificial feeds.

Thongrod *et al.* (2003) reported accelerated growth rates for *H. asinina* when fed artificial feeds containing lipid concentrations between 1.3-5.58%. However, growth rates decreased when lipid concentrations exceeded 5.58% (Thongrod *et al.*, 2003). As lipid levels in natural feeds are low, abalone are inefficient in digesting high concentrations of dietary lipids in artificial feeds, thus retarding their growth (Knauer *et al.*, 1996). Similar results were obtained by Mai *et al.* (1995a) who illustrated the optimum lipid level for *H. discus* hannai to be between 3.11-7.09% whereas the optimum lipid level for *H. tuberculata* to be 3.11%. The lipid requirements of abalone are very low, however they are very efficient

users of the low concentrations that are in their diet (Mai *et al.*, 1995a). Lipase activity in *H. rubra* that were fed artificial feeds was low as the feeds contain low levels of lipids (Johnston *et al.*, 2005). The digestive gland consists of various interconnecting tubules that are made up of both epithelial duct cells and epithelial crypt cells (Johnston *et al.*, 2005). The crypt cells have no secretory function (Johnston *et al.*, 2005). However, the duct cells synthesis enzymes that are capable of digesting lipids, carbohydrates and proteins (Johnston *et al.*, 2005). Therefore, for the abalone to efficiently digest high levels of lipids in the artificial feed the ducts cells will have to be stimulated in order to produce sufficient lipase. Further studies will have to be conducted to determine the catalyst that will stimulate the duct cells in the digestive gland.

CARBOHYDRATES

Energy is primarily supplied as a carbohydrate in artificial feeds, contributing 30-60% of the feed (Fleming *et al.*, 1996). Sources of carbohydrate include wheat, soybean meal, maize, rice and starch (Fleming *et al.*, 1996). However, little is known about their nutritional value and which sources will provide accelerated growth rates in abalone. A study conducted by Bautista-Teruel and Millamena (1999) primarily focused on the optimal protein levels and secondarily discovered optimal carbohydrate levels in *H. asinina*. The optimum carbohydrate level was identified as 40% for *H. asinina*. Future studies, should primarily focus on carbohydrates as the metabolism of many gastropods is based on the utilization of carbohydrates (Emerson, 1967). Abalone appears to be efficient users of carbohydrates. Garcia-Esquivel and Felbeck (2006) compared enzyme activity in *Haliotis rufescens* fed both natural and artificial feeds. Garcia-Esquivel and Felbeck (2006) reported high activity of carbohydrases throughout the entire gut when fed artificial feeds. Higher levels of cellulase and lysozyme were also detected when fed artificial feeds suggesting that abalone were efficient users of carbohydrates (Garcia-Esquivel and Felbeck, 2006).

CONCLUSION

Abalone initially feed on trail mucus of adult abalone and extracellular diatomic secretions (Takami *et al.*, 1997), thereafter highly adhesive diatoms would be more appropriate as the radula would have developed enough to rupture the frustule of the diatom cell, allowing the abalone to consume its contents (Onitsuka *et al.*, 2007). The appropriate feed should be fed at the appropriate

shell length in order to gain accelerated growth rates in abalone throughout its life time. Although, the diatom species can induce accelerated growth rates, their nutritional value is highly variable producing heterogeneous abalone sizes (Bautista-Teruel and Millamena, 1999). Artificial feeds provide a constant nutritional value, resulting in a constant growth rate of abalone producing homogenous shell length. The growth rate of abalone fed artificial feeds can be accelerated by manipulating the levels of proteins, lipids and carbohydrates in the feed (Fleming *et al.*, 1996). This is highly beneficial to abalone farmers as abalone take prolonged periods of time to grow to marketable sizes, therefore farmers would be able to grow more abalone in short space of time. The optimum levels of proteins, lipids and carbohydrates are 27-35, <5.58 and 30-60%, respectively. Further research would have to be conducted on stimulating the duct cells in the digestive gland to produce digestive enzymes (lipase, protease and carbohydrase) that would allow for optimum use of the artificial feed. The metabolism of gastropods is based on the utilization of carbohydrates (Emerson, 1967). Therefore, future studies should focus on the use of carbohydrates and the optimum source of carbohydrates that would induce accelerated growth rates in abalone.

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