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Ontogenetic Changes in Feeding Ecology and Habitat of the Damselfish *Neoglyphidodon melas* at Lizard Island, Great Barrier Reef

Sai-Wing Chan
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**Ontogenetic changes in feeding ecology and habitat of the Damselfish
Neoglyphidodon melas at Lizard Island, Great Barrier Reef.**



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Abstract

This study examines ontogenetic shift in habitat and feeding ecology of the black damselfish, *Neoglyphidodon melas* in three patch reef sites at Lizard Island, Great Barrier Reef. This rarely studied species is unique in its coprophagous relationship with the faeces of the giant clam *Tridacna gigas*. Distribution and habitat composition between three sites and two reef zones was estimated with 48 Visual Belt and Point Intercept Transects. 80 Focal Animal Studies revealed specific foraging strategies and aggressive behaviours. The timing of this study permitted the inclusion of juvenile recruits resulting in a more complete and comprehensive study across developmental stages. Major results showed marked ontogenetic shifts in both habitat usage and feeding strategies. Recruits fed solely on plankton and were generally found over heads of digitate *Acropora*. Older juveniles added soft coral to their diet, which was also a major benthic component in high density areas. Only adults consumed clam faeces in addition to soft coral, and larger adults consumed more faeces than smaller adults. Adult distribution was affected by soft coral and rubble, which positively affected clam occupation. Larger fish exhibited greater aggression towards conspecifics and non-conspecifics, but adult fish occupying clams had a lower rate of chasing compared with adults without clams. Protein-rich clam faeces is an important dietary component for large adult fish.

Keywords: damselfish, *Neoglyphidodon melas*, coprophagy, ontogenetic shift, feeding ecology, habitat change, *Tridacna gigas*, faeces

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1. Introduction

1.1 Study Species

Damsel fish (family Pomacentridae) are one of the coral reef's most common inhabitants, with 320 species worldwide, 120 of which are found in Australian waters (Randall et al 1997). Though the majority of pomacentrids are algal grazers, they exhibit great diversity in feeding strategies (Allen 1975). A significant proportion of *Abudefduf* and *Pomacentrus* are omnivorous, feeding on zooplankton in addition to benthic algae, while other pomacentrid species consume soft-bodied invertebrates, sponges, and fish eggs (Myers 1989). Within this generally well studied family, there is relative little literature available on the genus *Neoglyphidodon*, and even less on the black damsel, *Neoglyphidodon melas*. Much of this deficiency is due to the fish's misclassification as two separate species until the 1970's (Randall et al 1997). The juvenile phase was initially known as *Paraglyphidodon melanopus* (Bleeker), while the adult phase was identified as a separate species, *Paraglyphidodon melas*, until 1973. Such confusion was finally brought to light when colour change was observed in an aquarium setting in Kushimoto Marine Park Aquarium (Waller 2005). Generally, metamorphosis occurs when fish reach 50-65mm in length (Myers 1989).

1.2 Distribution

The majority of damsel fish are found in the Indo-West Pacific (Allen et al. 2003), with the greatest concentration of species diversity in the Indo-Malayan region (Allen 1975). *N. melas* is found in the Indo-Asian Pacific, from the Red Sea and East Africa

to Vanuatu, through South-West Japan and Northern Australia. Within these areas the black damselfish inhabits shoreline reefs, lagoons and outer slopes and areas with an abundance of soft coral (Allen et al. 2003).

1.2 Feeding ecology

Adult *N. melas* has been observed feeding on soft coral (Myers 1989, Lieske and Myers 1994, Randall et al 1997) as well as excreted pellets of clam faeces (Waller 2005, Mills unpub.). No current literature on juveniles specifically has been found. An association between the adult fish and the giant clam has been documented previously at Lizard Island as early as the 1970's (Allen 1977). Coprophagy is not uncommon in vertebrates, both in terrestrial and marine systems (Takahashi & Sakaguchi 1998, Robertson 1982, Aburto-Oropeza et al 2000, Strehan 1983) What makes this a relationship of particular interest is that clam faeces is rich in zooxanthellae (Ricard and Salvat 1977), a photosynthetic symbiotic algae found in corals.

1.3 Territoriality and Aggression

The majority of damselfish are very territorial, and will aggressively defend their plots (Randall et al. 1997, Myers 1989, Randall 2005). Among algal farming *Dischistodus* spp., the greatest amount of aggression has been exhibited towards species with the most overlap in resource use (Bay et al 2001). *N. melas* has been observed to display aggressive behaviour towards adult conspecifics of a smaller size (Waller 2005). This study attempts to carry this further and examine whether *N. melas* exhibits territoriality over particular giant clams and their faeces.

1.4 Ontogenetic shifts

Change in habitat use and behaviour between individuals of the same species of fish in different life stages has been well documented (Lecchini and Galzin 2005, Vagelli 2004). The cardinalfish *Pterapogon kauderni* exhibits a distinctive ontogenetic shift in habitat use between juvenile recruits, which are found in beds of sea grass and in association with anemones, and mature adults, which favour a coral reef habitat (Vagelli 2004). In *N. melas*, juveniles and adults exhibit a considerable difference in microhabitat use. While both are found over soft coral, giant clams (*Tridacna* spp.) are found only in adult microhabitats (Waller 2005).

1.5 Study Aim and previous study

The primary aim of this study is to determine ontogenetic differences in foraging strategies and habitat use of *N. melas*. Previous study has been conducted on this subject at Lizard Island (Mills unpub.). However, the timing of this study permits the inclusion of juvenile recruits, allowing for a more complete species study of habitats and feeding behaviour. Furthermore, this study differentiates between sizes of fish within the two developmental stages, providing insight into intraspecific interactions such as aggression. More importantly, such measures will enhance resolution in examining changes in foraging strategies and habitat use through developmental time.

2. Methods

2.1 Study Sites

Study of the damselfish *Neoglyphidodon melas* and giant clam *Tridacna gigas* were conducted during November 2007 on three patch reefs areas (in front of Casurina Beach, Corner Beach, and Loomis Beach) on the south-west side of Lizard Island on the Great Barrier Reef (14°40'S 145°28'E) (Fig.1)



Figure 1. Study sites at Lizard Island. Red = Outfront reef, Green = Corner beach reef, Yellow = Loomis beach reef. Each box equals 500 m. Photo courtesy of Dr. Andy Lewis.

These sites were selected for their ranging abundance of soft coral and *T. gigas*, as well as varying sizes of juvenile and adult *N. melas*. A previous study (Mills unpub.) was

conducted at three alternate sites (Watson's Bay, Palfrey Island, and Mermaid Cove), which are relatively sheltered fringing reef areas. The sites in this study were selected to be closer to the reef front while maintaining significant densities of study subjects. Portions of each site were designated as coral or coral-sand zones. Coral zones were characterized by a higher density and diversity of hard corals and relatively few sand patches, while coral-sand zones had a greater abundance of sand patches which interrupted patches of soft coral.

Data was collected at varying times during intermediate tides according to tide tables created for Lizard Island by Maritime Safety Queensland.

2.11 Casurina Beach reef (“Outfront”)

The reef off of Casurina Beach out front of the Lizard Island Research Station is an irregularly shaped patch reef approximately 490m in length and ranging from 53m at its narrowest point to 188m at its widest point in width. The beach side of the reef includes a coral-sand zone, which becomes a coral zone as the reef extends away from shore.

Another coral patch reef in the same vicinity was included that was 225m long and 60m wide.

2.12 Corner Beach reef

Adjacent to Corner Beach is a large patch reef approximately 300m long and 150m wide. 100m southeast of this reef is a smaller coral-sand patch approximately 113m by 75m that has been considered part of the Corner Beach reef area.

2.13 Loomis Beach reef

Loomis beach reef was composed of a well defined coral patch and a somewhat less well-defined coral-sand zone to the west. The coral reef was 225m long and 45m wide, while the coral-sand reef was approximately 340m long and 170 m wide.

All sites were dominated by soft coral, primarily *Sinularia spp.* and *Lobophytum spp.* Other major hard coral components included massive *Porites* corals and patches of branching *Acropora*. Sites contained interspersed patches of coral rubble.

2.2 Study Species

Adult *N. melas* is a jet-black fish that is distinguished from other dark damselfish by its opaque black pectoral fins (Fig. 2). Juveniles are white or grey with a yellow dorsal streak originating at the head extending caudally to the tail (Fig. 3). The pelvic and anal fins are bright blue. Mature fish may grow up to 15cm and are generally found at a depth of 1-5 m (Randall et al. 1997).



Figure 2. Adult *Neoglyphidodon melas*. Photography: Dr. Andy Lewis



Figure 3. Juvenile *Neoglyphidodon melas*. Photography: Dr. Andy Lewis

2.3 Data Collection

All data was collected on slates. Data from this study included in the results section was collected from the three aforementioned sites. Data from Mills' (unpub.) study has also been included in the results, where applicable.

2.31 Visual Belt Transects

In order to estimate abundances and densities of *N. melas* in different reefs and zones, visual belt transects were run. Each transect was 50m long and transects were conducted within habitat zones (coral or coral-sand). A transect tape was initially laid out, after which the observer swam over the tape while fish were counted in a 5m belt to either side. Each transect was conducted in about five minutes, with a swimmer speed of approximately 10m per minute. Fish were identified and categorized into six size classes. Juveniles or initial phase fishes were classified as either recruits (size class 1), which

were newly settled fish less than 20mm in length, medium-sized juveniles (size class 2, 21mm to 60mm) or large-sized juveniles (size class 3, 61mm to the maximum size observed in juvenile coloration). Adult fish with terminal phase coloration were classified as either small (size class 4, 60-80mm), medium (size class 5, 81mm-100mm), or large (size class 6, >100mm). Fish were categorized separately if they were observed hovering over a *T. gigas*. These giant clams were categorized as either juvenile clams (<500mm in shell length), adult clams with *N. melas* (>500mm) or adult clams without *N. melas*. Fish were measured visually with the aid of a sizing key during visual belt transects.

2.32 Benthic Point Intercept Transects

Benthic Surveys were conducted on the same transect tape immediately following visual belt transect fish counting. Point intercept data were collected according to the benthic constituent immediately below the tape every 0.5m, giving 100 data points per 50m tape. Life-forms were categorized according to Global Coral Reef Monitoring Network benthic code.

2.33 Focal Animal Samples

Fish were observed for ten minutes during focal animal sampling. Feeding behaviour (bites of different food sources), aggression (chasing of and chasing by conspecifics and non-conspecifics), home range size, and clam presence were noted in addition to fish size class and habitat zone. Fish were selected haphazardly on initial encounter, and a minimum observed distance was established before timing commenced. In total 54 focal studies were conducted in this study; 80 focal studies were included in the results (26 were conducted in by Mills (unpub.))

2.34 Clam microhabitat surveys

To assess differences between clams and their immediate environment, clam microhabitat surveys were conducted. If a fish was found over a clam, its presence and size were noted. In order to rate the rugosity of the microhabitat of the clam, each was given a qualitative rating of 1 to 5. A rating of 1 indicated a clam surrounded by a flat topography (for example, in the middle of a patch of sand). A rating of 5 indicated a habitat containing numerous crevices and coral cover of varying height, ideally providing ample shelter. Furthermore, the benthic components in a 5m² area around the clam were identified and assigned a percentage of the total benthic constituents.

2.35 Recruit habitat surveys

In order to estimate recruitment mortality, three sites of observed recruit habitat were selected in the Outfront reef patch. Each consisted of 1-3 heads of *Acropora* digitate coral. These sites were marked with red flagging tape, and recruits of both *N. melas* and other species were site-referenced. Individuals were identified by relative size, and each day were observed and counted during intermediate tides. Recruits remained over their head of coral throughout observation periods, thus immigration away from the area was unlikely.

3. Results

3.1 Abundance and distribution

Juveniles were significantly more abundant in the Outfront reef (mean = 4.67) and Corner beach reef (mean = 2.84) compared with Loomis beach reef (mean = 0.91), and the distribution of recruits was highest in the coral zone between all sites (total mean in coral = 5.15, total mean in coral-sand = 0.83) (Fig. 4). Of the variables in benthic composition (Fig.5), branching hard corals and encrusting coral mirrored this trend and showed significant statistical correlation with recruit abundance (ACB $p = .010$, CE $p = .030$) after running linear regression with stepwise addition of variables. Non-recruit juveniles had a greater association with foliate coral ($p = .014$) and soft coral ($p = .042$) while adults showed correlation with soft coral ($p = .002$) and rubble ($p = .025$). Soft coral represented the majority of benthic cover in both zones and in all sites. Between the two zones, the most significant difference was a greater abundance of sand and deficiency of branching hard coral and rubble in the coral-sand zone compared with the coral zone (Fig. 5).

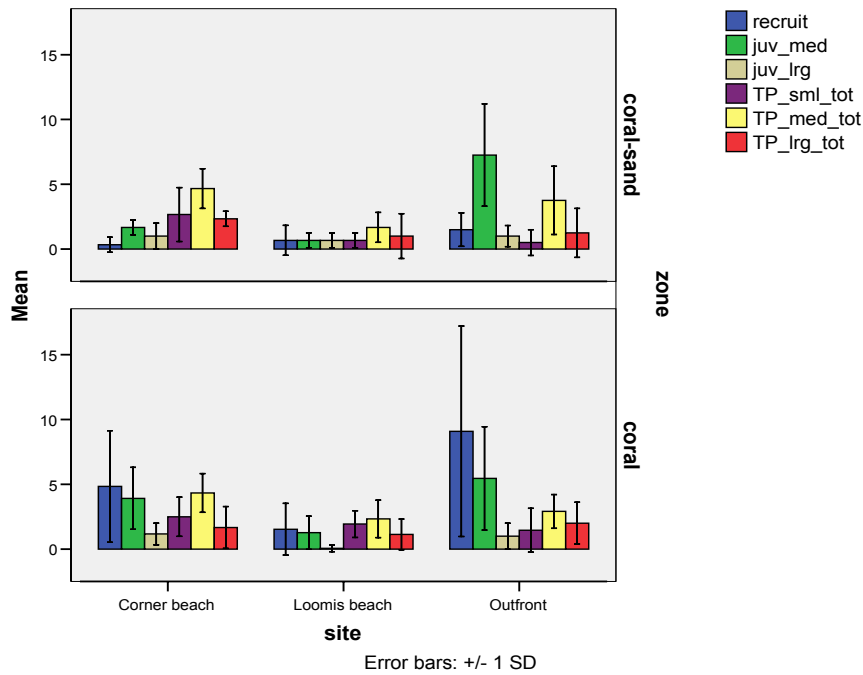


Figure 4. Average distribution of *N. melas* between sites and zones. Mean = average number of individuals found per transect. Recruit = juvenile recruit (size class 1), juv_med = medium-sized juveniles (size class 2), juv_lrg = large-sized juveniles (size class 3), TP_small_tot = total number of small adults (size class 4) including those found with and without clams. TP_med_tot = total number of medium sized adults (size class 5) and TP_lrg_tot = total number of large adults (size class 6).

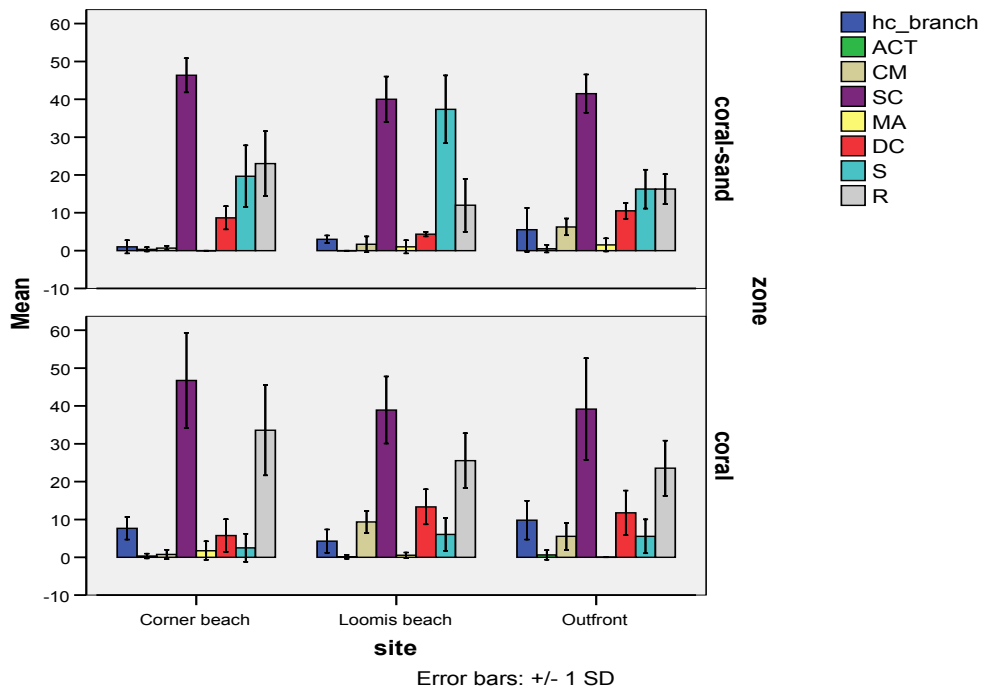


Figure 5. Benthic constituents between sites and zones. Mean = average number of individuals found per transect. hc_branch = branching hard corals, ACT = tabulate acropora coral, CM = massive coral, SC = soft coral, MA = macro algae, DC = dead coral, S = sand, R = rubble.

At all study sites, the average area used by adults far exceeded the area used by juveniles (mean area for juveniles = 2.4m², mean area for adults = 14.3m². Standard deviation = 3.2 and 19.9, respectively.) (Fig. 6)

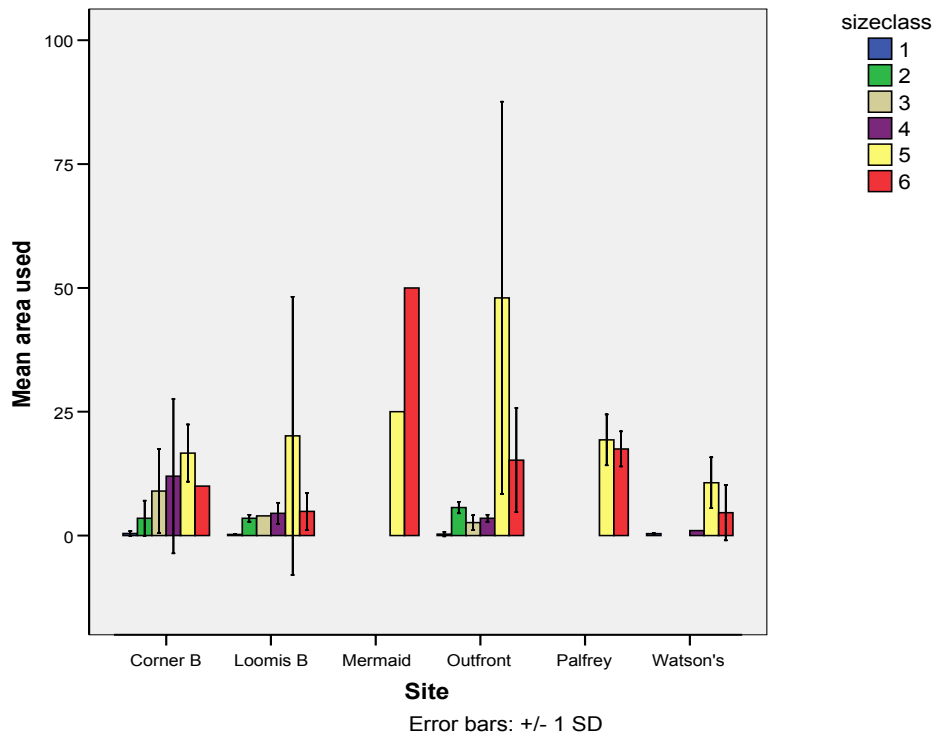


Figure 6. Average area used by fish of different size-classes, by site. 1 = juvenile recruit, 2 = medium juvenile, 3 = large juvenile, 4 = small adult, 5 = medium adult, 6 = large adult.

3.3 Feeding behaviour

Recruits consumed plankton almost exclusively (fig. 7). Soft coral was consumed by all non-recruit juvenile and adult size classes. As size class increases, average bites of plankton decreases. Bites of soft coral increase until clam faeces consumption begins. Only adults consumed faecal pellets, and consumption of this food source increased with size as consumption of other food sources decreased.

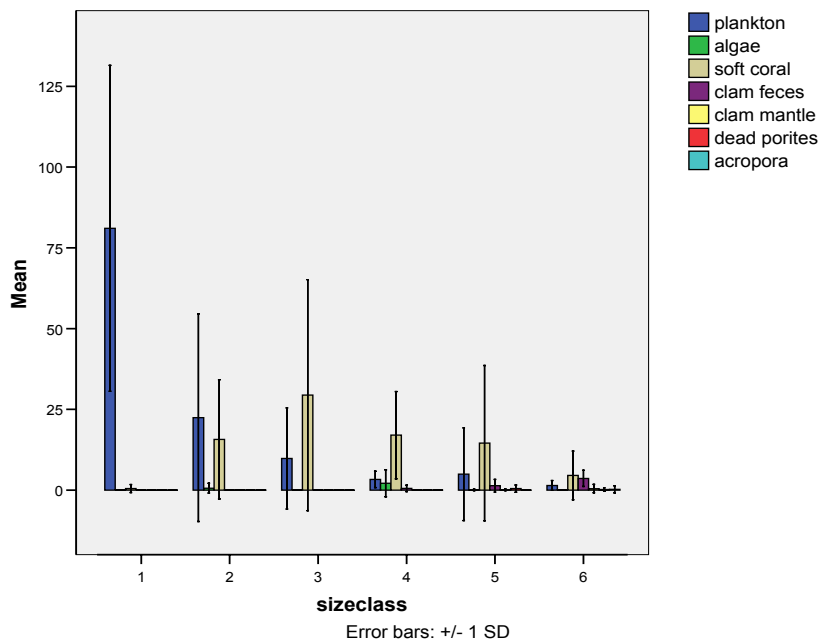


Figure 7. Average bites of food source by size-class. 1 = juvenile recruit, 2 = medium juvenile, 3 = large juvenile, 4 = small adult, 5 = medium adult, 6 = large adult.

Averaged among all size classes, more bites of soft coral were taken than any other food source (mean # bites = 9.76). Adult fish in particular took more bites of soft coral than any other food source (fig 8 & 9.)

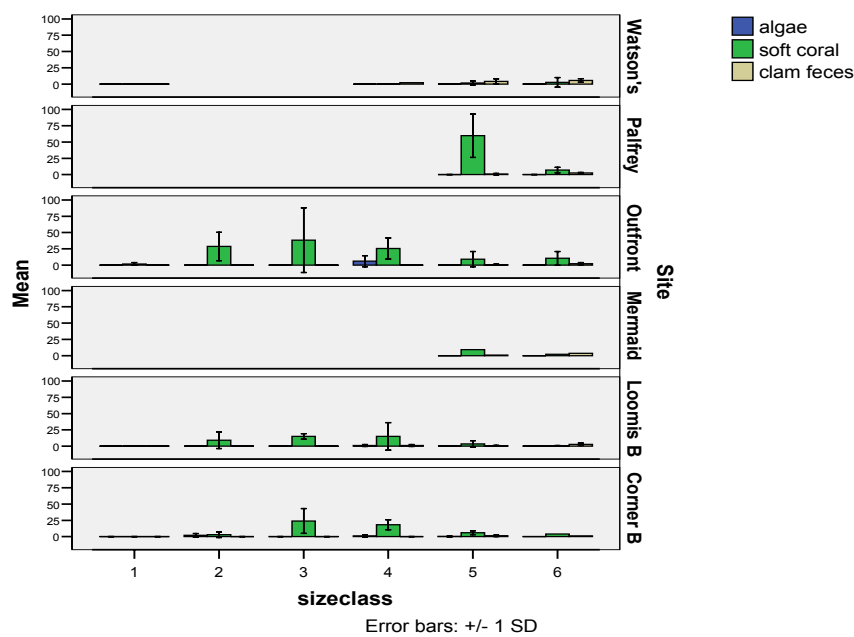


Figure 8. Average bites specific food sources by site and size-class. 1 = juvenile recruit, 2 = medium juvenile, 3 = large juvenile, 4 = small adult, 5 = medium adult, 6 = large adult.

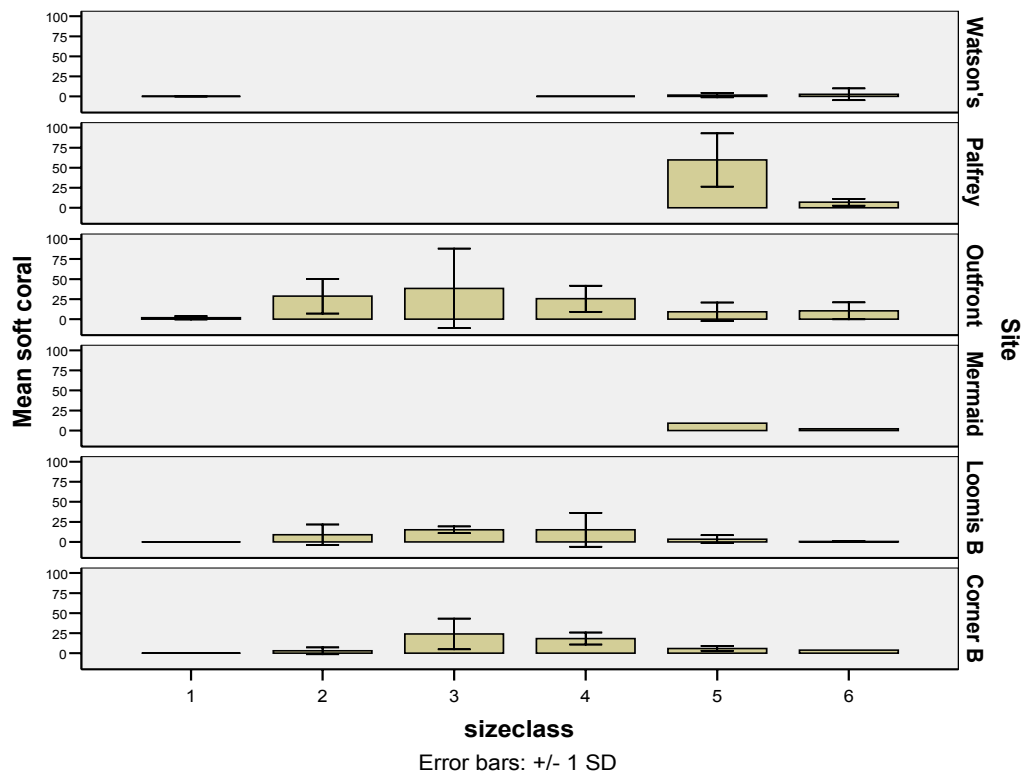


Figure 9. Average bites of soft coral by size-class and site. 1 = juvenile recruit, 2 = medium juvenile, 3 = large juvenile, 4 = small adult, 5 = medium adult, 6 = large adult.

Only adult fish consumed clam faeces (Fig. 10). Among fish that were “successful” at consuming at least one faecal pellet per observation period (10 min), larger adult fish consume a greater number of pellets than smaller adult fish (Fig. 11). Within this group, the number of adults eating any pellets at all increased with size. Only two size-class 4 individuals were able to consume pellets, while size-class 5 fish had twelve and size-class 6 fish had nineteen individuals consuming pellets.

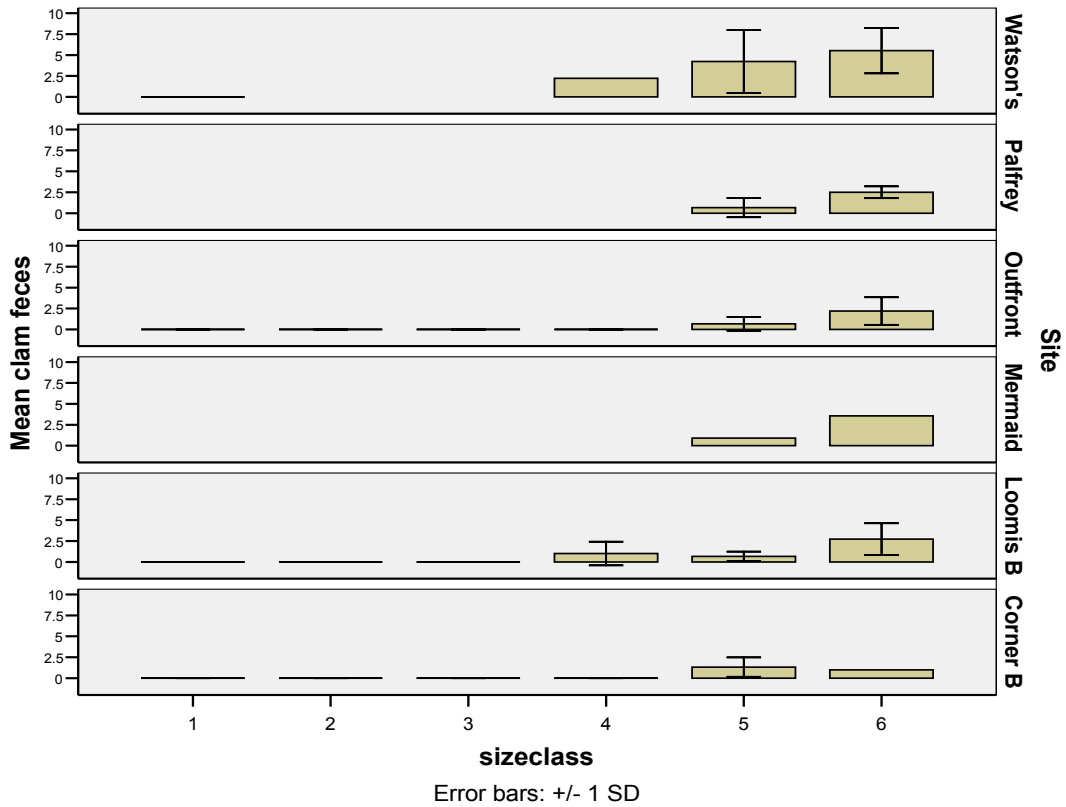


Figure 10. Average faecal pellets eaten (= bites of faeces), by size-class and site. 1 = juvenile recruit, 2 = medium juvenile, 3 = large juvenile, 4 = small adult, 5 = medium adult, 6 = large adult.

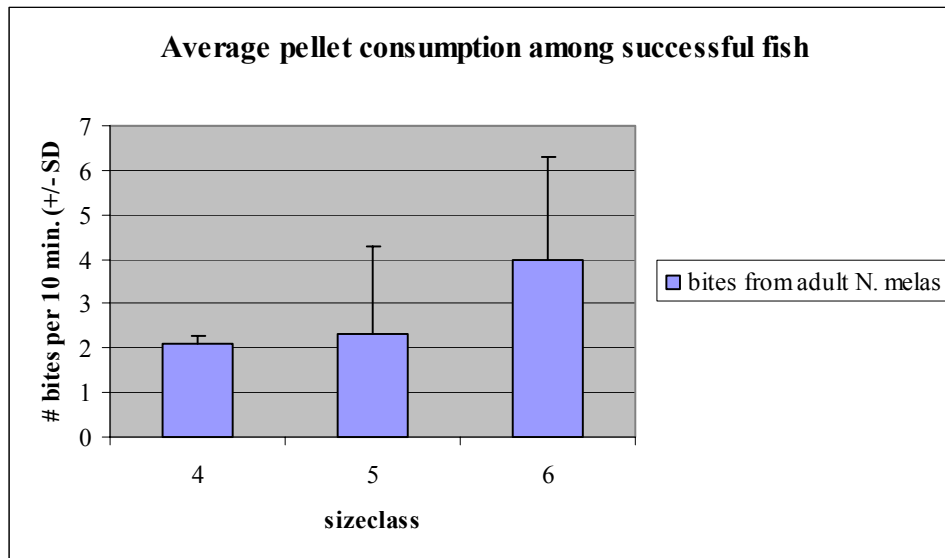


Figure 11. Average faecal pellet consumption among successful adult fish. 4 = small adult, 5 = medium adult, 6 = large adult.

3.4 Clam occupation and aggression

The majority of *T. gigas* were associated with at least one adult *N. melas* (Fig. 12). Furthermore, giant clams with fish were found in much greater abundance in the coral zone than in the coral-sand zone. Both zones contained similar numbers of adult *T. gigas* without *N. melas*. However, on average more adult fish were found without a clam than with a clam (Fig 13). Between the two zones, the coral zone had higher rates of clam occupation, with approximately one third of the total adults associated with a clam.

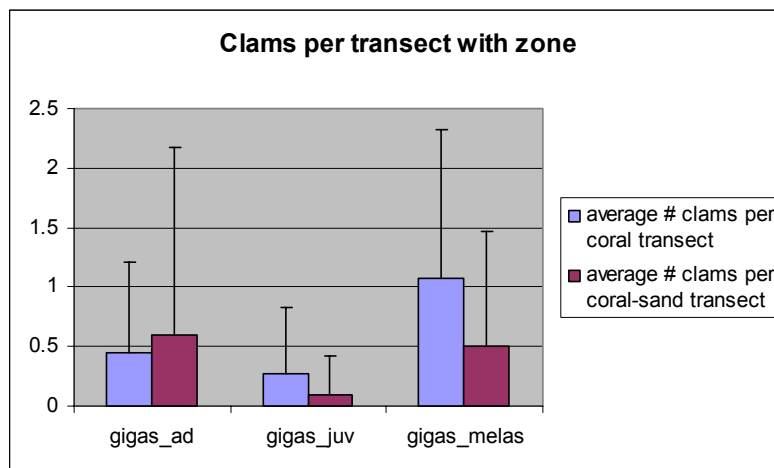


Figure 12. Average number of clams per transect with respect to zone. gigas_ad = adult *T. gigas*, gigas_juv = juvenile *T. gigas*, gigas_melas = *T. gigas* found with *N. melas*.

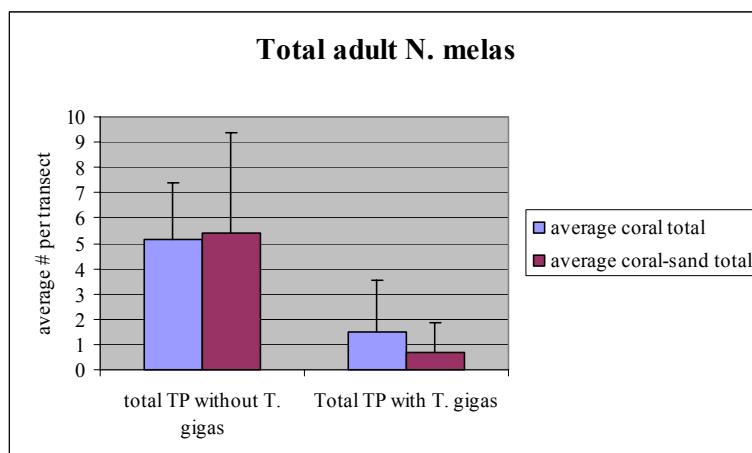


Figure 13. Adult *N. melas* distribution of clam users and non-users, by zone. TP = terminal phase (adult) *N. melas*.

When differentiating between sites, coral-sand zones of Corner beach reef and Loomis beach reef were very low in overall clam density (Fig. 14). These areas also had the highest abundances of sand and showed high levels of variability in benthic cover between the two zones (Fig. 5). In contrast, the Outfront reef showed similarity in clam distribution between the two zones; it also showed the least amount of variation in benthic cover between zones (Fig. 5).

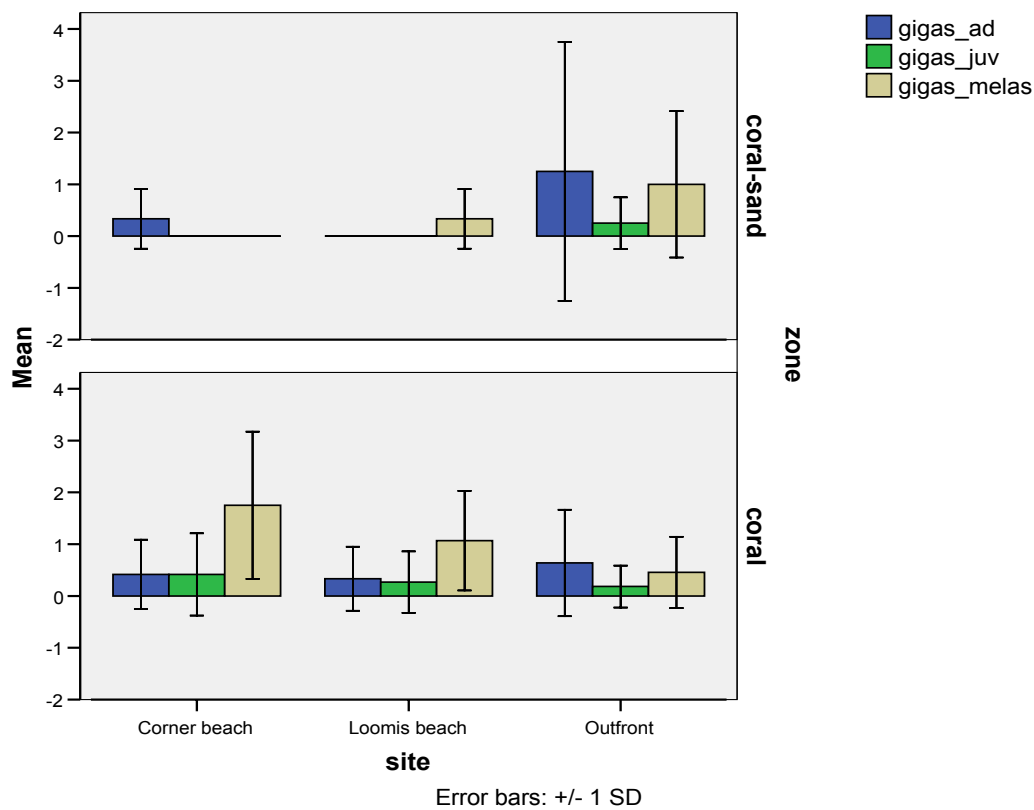


Figure 14. Clam density by site and zone. Mean = average number found per transect. gigas_ad = adult *T. gigas*, gigas_juv = juvenile *T. gigas*, gigas_melas = *T. gigas* found with *N. melas*

When examining clam occupation status among adults, larger adults exhibited higher proportions of clam occupation relative to total abundance within their size-class (Fig 15). Among small adults (class 4), medium adults (class 5) and large adults (class 6),

11.49%, 21.57% and 28.38% of fish occupied clams, respectively.

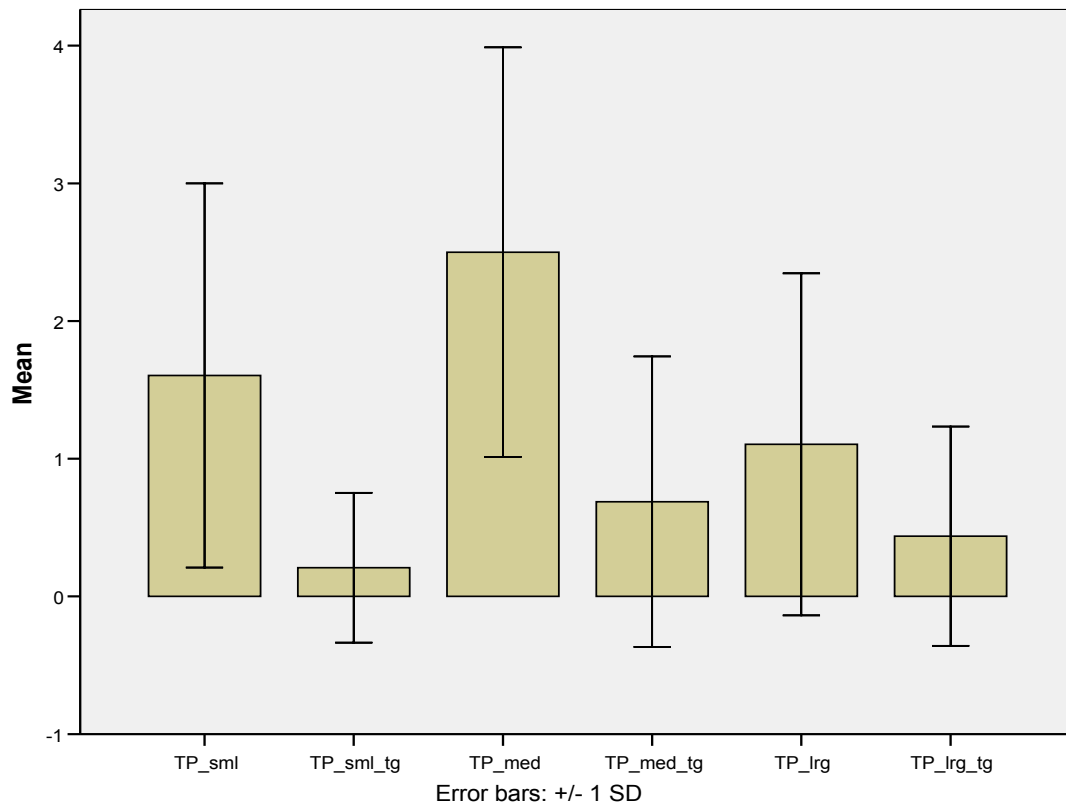


Figure 15. Average number of adult *N. melas* per transect by size class. Mean = average number of individuals found per transect. TP = terminal phase (adult) *N. melas*, _tg = *N. melas* found with *T. gigas*.

Smaller adults chased conspecifics less than medium and large sized ones.

Conversely, smaller adults were chased by conspecifics more frequently than medium adults. Large adults experienced the least amount of chasing by conspecifics (Fig 16).

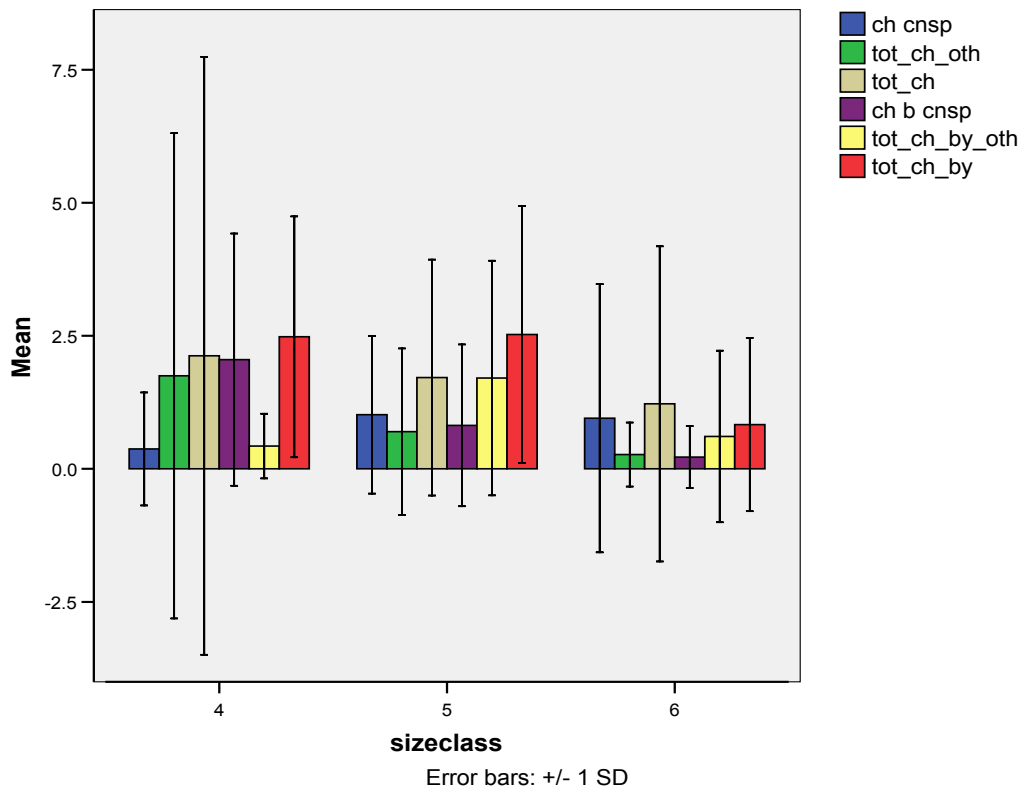


Figure 16. Average number of chasing/chased events by size class. Ch cnsp = chased conspecifics, tot_ch_oth = chased other non-conspecifics, tot_ch = chased all species. Ch b cnsp = chased by conspecifics, tot_ch_by_oth = chased by other non-conspecifics, tot_ch_by = chased by all species.

Significantly more chasing activity was exhibited by fish not occupying a clam, especially among large adults. These fish were much more aggressive than those of smaller size, and were not chased by any other fish at all. In general fish occupying clams were chased by other fish marginally more than they themselves chased fish.

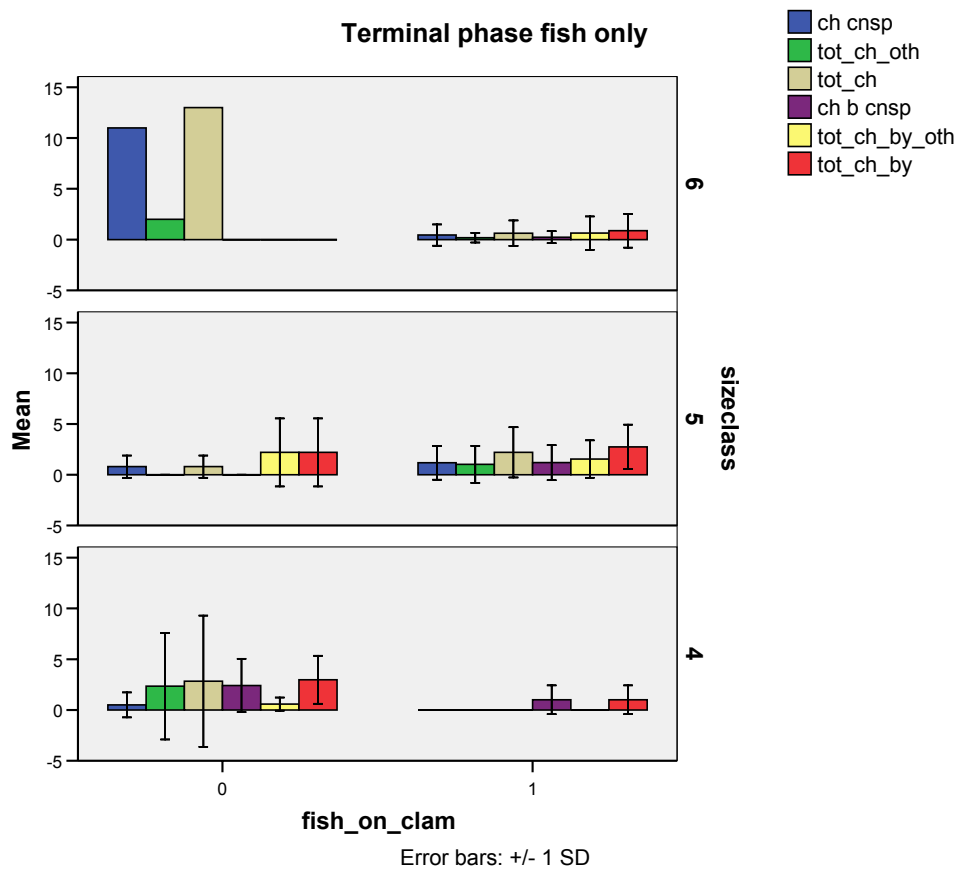


Figure 17. Mean chasing/chased events by adult size class and clam occupation. 0 = fish without a clam, 1 = fish with a clam. . Ch cnsp = chased conspecifics, tot_ch_oth = chased other non-conspecifics, tot_ch = chased all species. Ch b cnsp = chased by conspecifics, tot_ch_by_oth = chased by other non-conspecifics, tot_ch_by = chased by all species.

Clam occupation was correlated with rugosity of the microhabitat in which fish/clams were found. Adults fish occupying a clam were found in microhabitats with higher values of rugosity, while adults without a clam had microhabitats with lower values. Clams that were found without any fish were in lowest rugosity microhabitats.

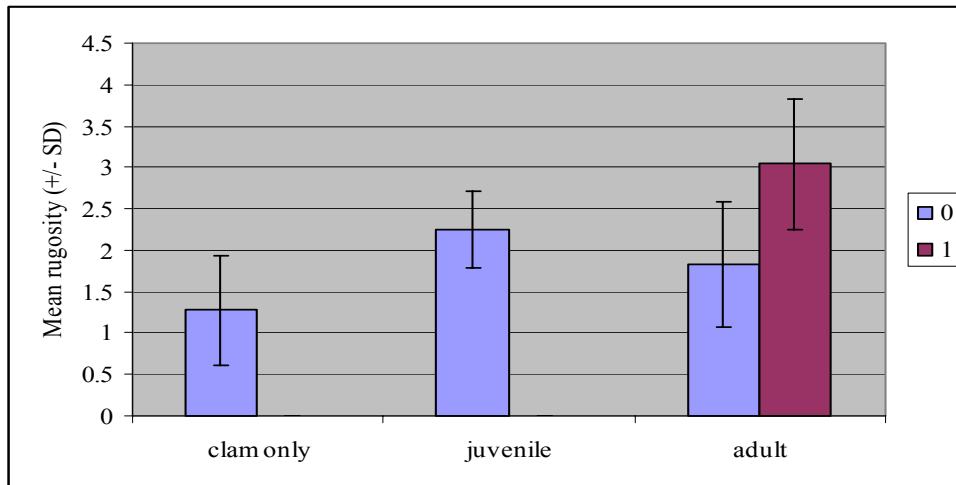


Figure 18. Mean rugosity of clam and fish microhabitats. 0 indicates that clam and fish were not found together, 1 indicates that fish were found with a clam. Higher values indicate higher rugosity.

3.5 Recruit mortality

N. melas recruits did not experience severe rates of mortality over five days (Fig. 16). Of all four species observed in the study sites, *P. moluccensis* experience the highest mortality. In all species, a reduction in number of recruits occurred only during one interval; mortality does not appear to be gradual.

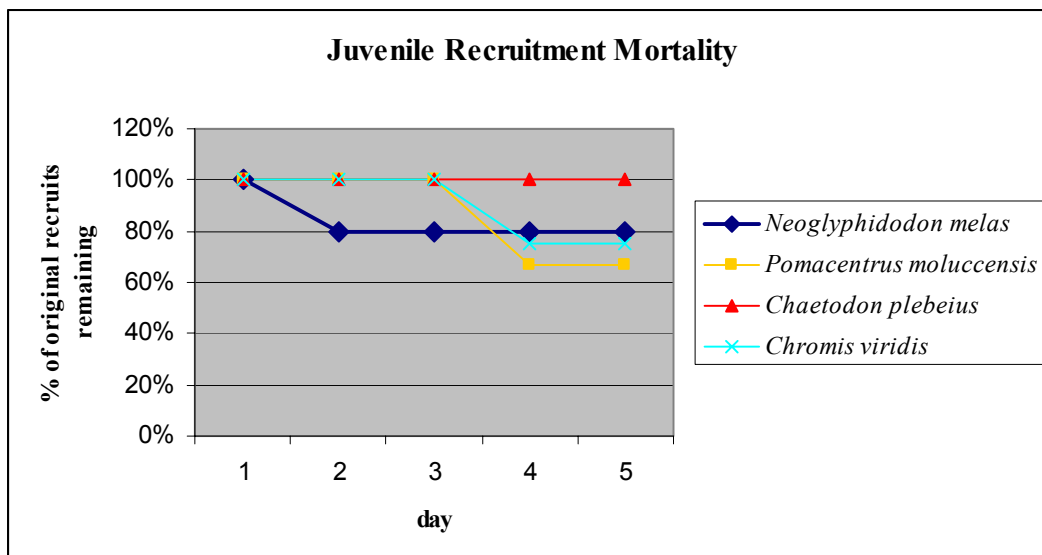


Figure 19. Juvenile recruitment mortality over five days.

4. Discussion

4.1 Ontogenetic Shift

N. melas showed significant change in habitat and feeding ecology through developmental time. Mills (unpub.) found niche separation between juvenile and adult phases, and this study supports that conclusion while showing the gradual shift from juvenile recruit to large adult. Juvenile recruits were found to have statistically significant correlation with branching hard coral. Furthermore, the majority of recruits were found over heads of digitate *Acropora*, supporting this association (pers. obs.) Recruits fed exclusively on plankton, which also gives insight into the minimal area used. They need not actively forage for soft coral; plankton is found readily within the water column. Thus the risk of predation resulting from foraging extensively for a ubiquitous food source outweighs the benefits. This is particularly true for a small individual whose resource consumption is unlikely to be limited by feeding area. In addition, small recruits are often at greater risk for predation compared with large adults (Sogard 1997). It has been experimentally shown that individuals are able to more effectively evade pursuit when using more familiar terrain (Clarke et al. 1993), therefore minimizing one's home range (resulting in greater familiarity of that range) reduces the risk of predation. As recruits mature into larger juveniles, their habitat shifts and soft coral become an important component. This shift occurs simultaneously with a change in foraging strategies. Soft coral becomes a secondary dietary component in medium-sized juveniles, and becomes a primary food source as fish size increases. With the transition from large juveniles to small adults, clam faeces become a new food source. Waller (2005) found that the largest difference in microhabitat between juveniles and adults was the presence of giant clams found only in the habitats of the latter. This study establishes that, in

addition to soft coral, adult fish densities showed significant correlation with rubble, which was more abundant in the coral zone. Concurrently, clams occupied by adult fish were also more abundant in the coral zone.

Ontogenetic shift in both habitat and feeding ecology is not uncommon in coral reef systems. In a study conducted by Lecchini and Galzin (2005), 12 out of the 20 most abundant species in the study area underwent some ontogenetic habitat shifts, including the four Pomacentridae species *Abudefduf sexfasciatus*, *Chrysiptera leucopoma*, *Stegastes albifasciatus* and *S. nigricans*. Of these, *A. sexfasciatus* utilized different habitats between juvenile and adult phases, while *C. leucopoma* experienced a reduction the number of occupied habitats. Lecchini and Galzin explain that in some species this is due to changes in morphology and behaviours, which necessitate relocation in order to maintain survive. Changes in nutritional requirements may also play a part in these shifts.

4.2 Consumption of Clam Faeces

There was a clear positive relationship between fish size and numbers of individuals consuming pellets, as well as pellets consumed per individual. This may have been due to intraspecific competition in which larger adults were able to out-compete smaller adults for a limited resource. Fish were extremely aggressive when pellets were ejected, thus it comes as little surprise that larger fish ate more pellets. As clam faeces consumption increased, bites of soft coral decreased. Although the number of bites of soft coral outnumbered bites of faeces, the amount of biomass within each bite of faeces (in most cases this was an entire pellet) was probably significantly greater than any single bite of soft coral (pers. obs.) In order to determine the relative amounts of soft

coral and clam faeces actually consumed, future studies should examine the gut contents of adult *N. melas*.

Coprophagy in nature occurs for a variety of reasons nutritional and digestive reasons. In the rodent nutria (*Myocastor coypus*), coprophagy is an important method of ingesting extra protein, in particular the amino acids Met and Lys (Takahashi and Sakagushi 1998). Infant koalas (*Phascolarctos cinereus*) are known to feed on soft faeces from its mother. This is believed to inoculate the infant's caecum with micro-organisms necessary for the fermentation and eventual detoxification of phenolic compounds and cyanide precursors present in eucalyptus leaves, their predominant food source (Strahan 1983).

In a study by Ricard and Salvat (1977) it was found that faeces of the giant clam (*Tridacna maxima*) was composed of 80% undigested zooxanthellae, which was similar to those found in the mantle of the clam. This symbiotic algae, present in all members of the genus *Tridacna*, provides nutrition for the clam via photosynthesis. Other components of faeces included plankton which was filtered and passed out. Chemical analysis revealed that these pellets consisted of 29% to 35% protein and 0.32% to .042% chlorophyll. Where these clams are abundant, faeces and the undigested zooxanthellae therein provide substantial protein supplement for marine organisms. With this understanding, it is not surprising that *N. melas* has adapted to make use of this untapped resource in order increase protein intake. From personal observation, the adult black damselfish are the only species at Lizard Island to habitually take advantage of this food source.

The rugosity of clams seems to have an affect on its utilization by adult *N. melas*. Fish were found with clams where micro topography was diverse and rugosity was high,

while clams with less rugosity were unoccupied. A more rugose environment would ideally provide greater protection from predators, and thus clams in such an environment would have a higher probability of being occupied.

In this study, fish were found to have more chasing behaviour when not associated with a clam. This may be due to utilization of a larger home range necessary for foraging for other food sources such as soft coral. When a larger area is used, interaction and thus chasing with other fish is more likely to occur. These large fish also chased other fish the most but were not chased themselves, indicating a possible dominance hierarchy based on size, which is well documented in reef systems (Coates 1980, Booth 1995, Schwarz 1995). However, the data indicates that occupying clams did not have distinctly elevated levels of chasing behaviour. Nevertheless, focal observation showed consistent competition over pellets once they were ejected. This suggests that fish exert greater competition over pellet that is already present, compared with one that may be imminent.

5. Conclusion

N. melas exhibits a distinct ontogenetic shift in both feeding ecology and habitat, not only between juvenile and adult phases, but continuously throughout its life history. Foraging strategies change from exclusively plankton in recruits to a combination of plankton and soft coral in older juveniles. This is followed by a shift to include clam faeces in the diet, which is accompanied by colour change that distinguishes juveniles from adults. As adults grow larger, they consume proportionally more clam faeces and less soft coral.

Shifts in habitat occur concurrently. Recruits are found near heads of digitate *Acropora* and branching coral, while older juveniles and adults are associated with soft corals.

Adults were associated with rubble, which was found in greatest abundance in the coral zone where there was the greatest density of occupied clams.

The consumption of giant clam faeces by adult *N. melas* is unique in that other fish do not regularly make use of this feeding strategy. The high protein content in these faeces makes them an ideal food source, despite the apparent indigestibility of the live zooxanthellae (Maruyama and Heslinga 1997) within may be a deterrent to other fishes. Further study should be conducted to analyse gut contents of adult *N. melas*. Such a study would reveal how much of the fish's diet is actually composed of faeces, and whether these zooxanthellae are digestible by the fish.

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