Prey selectivity of planktivorous fish:
Analysis of stomach contents in four Pomacentrids at Lizard Island, Great Barrier Reef

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May 2008

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Submitted in partial fulfilment of requirements for *Australia: Natural and Cultural Ecology*

Abstract:

Coral reef planktivores are important to coral reefs by concentrating and delivering nutrients and allochthonous carbon from the plankton to reef building corals. In an otherwise very oligotrophic system this function may be of major importance. Planktivorous Damselfish (Pomicentridae) were analysed for prey selectivity through enumeration of stomach contents. Simultaneous plankton tows were conducted to establish the plankton community composition of the waters they were taken from. There was a statistically significant variation between the stomach composition and that of the water column. While there was not a significant difference among Simpson's diversity indices of the stomach contents, there was a significant difference between the mean diversity indices for the reef zones. The diversity index of the fish stomachs (.13 of back flat fishes and .15 of front flat fishes) was found to be significantly different from diversity index of the water column (.37 of the back flat and .36 of the front flat)

Chesson's index of selectivity was calculated from the average number of individuals per plankton category within each species and the difference between these calculated values were found to be statistically significant. Amphipods were heavily selected for, while Chaetognaths, Pteropods, and gelatinous organisms were completely avoided, possibly due to chemical defenses. The combined average selectivity of back flat fishes was compared to that of front flat fishes and no statistically significant difference was found. The combined averages were not significant, but the difference between the means of individual fish was found to be significant. This supports the idea that the selectivity of each species is independent of reef zone and possibly confounded by another variable, perhaps individual size (total length in mm). This led to an acceptance of the second null hypothesis (H_{0b}) which states that there is no statistically significant difference in the selectivity between front flat fishes and back flat fishes. Future study should be conducted to asses the size preference of planktivores as well as the changes in selectivity along the reef flat within one species.

Acknowledgments

This investigation would not have been possible without the knowledge and assistance of Jacob Johansen (James Cook University) in the collection, analysis, and interpretation of the data. The facilities of the Lizard Island Research Station (Australian Museum) far exceeded my expectation, and the privilege to live there for 5 weeks I spent there were unforgettable. The staff of LIRS including Anne Hoggett, who assisted with laboratory supplies, Lyle Vail who assisted with nautical manoeuvres during data collection, Bob Lamb who transformed my unreliable boat motor into a precise machine and helped keep my leaky boat afloat, and Tania Lamb who took extremely good care of me. Their constant support and hospitality was beyond anything I could have expected.

Thanks to Tony Cummings for the brainstorming sessions, editorial advice, and flexibility that allowed me to stay on the island continuously. Thanks to Reef Teach for their hospitality in allowing us to use their business as our work station. Thanks to Sea Education Association for bringing in world class lecturers (Scott Doney and Deborah Steinberg) and teaching me to identify plankton (Jan Witting, Kara Lavender, Skye Moret, Caroline Lipke, and Patrick Erbland).

Finally, thank you to my family. Without their constant love and support I would not be where I am today.

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0 Introduction

0.1 Plankton

Plankton comes from the Greek word ‘planktos’ which means wanderer. This is a general term for organisms in the ocean that have no significant control over their locomotion. The plankton vary greatly in size, ranging from viruses 20 nanometers across to gelatinous organisms up to 30 meters long (*Physalia physalis*). Planktivorous damselfish consume plankton 0.2 to 5 mm in size called mesoplankton (Lecture: Steinberg 2007).

Plankton play an important role in allochthonous carbon deposition on coral reef systems. Through photosynthesis, phytoplankton transform CO_2 and water into glucose using a complex pathway powered by sunlight. Zooplankton concentrate the energy created by consuming these producers. The zooplankton then serve to transport the concentrated energy to higher trophic levels, such as opisthobranch filter-feeders, baleen whales, and in the context of coral reef systems, planktivorous fish like the Pomicentridae.

0.2 Damselfish

The family Pomacentridae is made up of 321 species in 28 genera (Allen, 1991). They are an important family of reef fish composing 15% of the standing biomass by weight, consuming 36% of the total dissolved oxygen consumed, and accounting for 24% of the abundance observed (Depczynski et al., 2007). Four species that are abundant and easily captured in the Lizard Island group are *Pomacentrus moluccensis* (Bleeker), *Dascyllus aruanus* (Linnaeus), *Neopomacentrus azysron* (Bleeker), and *Pomacentrus coelestis* (Jordan and Starks).

0.3 Nutrient transport

Coral reef ecosystems have very high average vertebrate densities (Sale, 1978) and are often closed systems where nutrients and energy flow is tightly recycled among residents with limited inputs of energy or nutrients into the system (Arias-Gonzalez et al., 1997). Water flowing around and over coral reefs are typically low in nutrients (oligotrophic), and one pathway for import of nutrients to reefs is through zooplanktivores. Carbon produced by phytoplankton is moved up trophic levels by zooplankton and zooplanktivores at which point it is excreted as feces (Peduzzi, 1992). Robertson (1982) found zooplanktivores actively produce feces while feeding in the water column and defecated at much lower rates when they were traveling or resting close to the substrate. Feces produced by zooplanktivores are of low density and sink very slowly, sometimes spending up to 5 minutes in the water column and moving more than 50 meters laterally before being eaten or sinking to the substrate (Robertson 1982). Only 6-19% of the feces produced by Pomacentrids that feed within 2 meters of the reef substrate is ingested by coprophagous fish (Robertson, 1982). This low ingestion rate increases the rate of carbon removal from the water column. Increased rates of removal transport carbon into the reef system from the water column as the coral sequesters it for the formation of its $CaCO_3$ skeletal structure. As a result, coral reefs are globally significant reservoirs of carbon, with relevance for global climate change (Kinsey & Hopley, 1991).

0.4 Prey Selectivity

Variation in plankton consumption by Damselfish is dependent upon many variables including location on the reef, plankton composition of the water column, social rank of the individual, and time of day. Species of Damselfish have been observed to prefer different microhabitats within the reef. *D. aruanus* tend to prefer shallow and quieter locations with either branched Acropora or Pocilloporan corals (Coates, 1977). *P. moluccensis* prefer to live on live coral near other conspecifics while *P. coelestis* prefer to aggregate over coral rubble (Ohman et al. 1998).

It has been said that the abundance of zooplankton affects the distribution of planktivorous reef fishes (Hobson & Chess, 1978; Bray, 1981; Kingsford & MacDiarmid, 1988; Shapiro & Genin, 1993). This could give support to the idea that planktivores reduce much of the zooplankton entering a reef area on a flooding tide because of predation (Anderson and Sabado, 1995). Position on the reef can be related to the quality of plankton that passes over a given area and allows fish on the front flat and crest to be less selective. This also could result in an increase in selectivity in back flat planktivores in order to ingest the same quality food with limited availability, but has not been previously investigated.

0.5 Aims:

The aim of this study was to determine the prey selectivity of four planktivorous damselfish by comparing the plankton collected in the water column to the plankton in their stomachs. The carbon content of the plankton in the water column was measured to determine the quality of food and possibly the amount of carbon transported from the plankton to the reef substrate through the feces of planktivorous fish. Ultimately, the study may help to gain a better understanding of allochthonous carbon from the plankton.

0.6 Hypotheses

The first null hypothesis (H_{0a}) is that there is no statistical significance between the stomach contents and the water column. The first alternative hypothesis (H_1) is that there is a significant difference between the stomach contents and the water column. The second null hypothesis (H_{0b}) is that there is no significant difference in selectivity between front flat and back flat fish. The second alternative hypothesis (H_2) is that the two species on the front flat are more selective than the two species on the back flat. The third alternative hypothesis (H_3) is that the two species on the back flat are more selective than the two species on the front flat.

1 Methods:

1.1 Study Site:

Study organisms and plankton tows were conducted during two days in April of 2008 at Lizard Island (14°40'S, 145°28'E). Lizard Island is situated in the northern portion of Australia's Great Barrier Reef, 270 km north of Cairns, Queensland. It is a high granite island about 7 square kilometres in size, with three smaller islands nearby (Palfrey, South and Bird). Samples were gathered on the reef between Bird and South Island (figure 1.1).

Figure 1.1: an Aerial photo of the Lizard Island group. In red is the study reef. **b** Enlarged aerial photo with different zones of the reef marked in red.

The reef studied consisted of a long reef flat made up of soft coral and coral rubble that sloped steeply down at the crest on the oceanic side. At the lagoonal side of the flat, the coral rubble began to be punctuated by patches of sand, and eventually transitioned to complete sand and a gently downward slope towards the deep water of the lagoon.

1.2 Study Species:

1.2.1 Pomacentridae:

Four species of Damselfish (Actinopterygii: Perciformes: Pomacentridae) were selected based on abundance at different parts of the reef and ease of capture. They were: the Lemon Damsel (*Pomacentrus moluccensis*), The Humbug Damsel (*Dascyllus aruanus*), the

Yellowtail Demoiselle (*Neopomacentrus azysron*), and the Neon Damsel (*Pomacentrus coelestis*) (figure 1.2). These small fish are planktivorous and are abundantly found in the waters surrounding the Lizard Island group. *P. moluccensis* and *D. aruanus* are found in abundance on the back flat of the reef (called back flat fishes) and *N. azysron* and *P. coelestis* are found on the along the length of the reef, but have been observed to prefer the front of the flat or the reef crest (called front flat fishes) (Ohman et al., 1998). Ethics permits were obtained that allowed for the killing of 8 fish from each species.

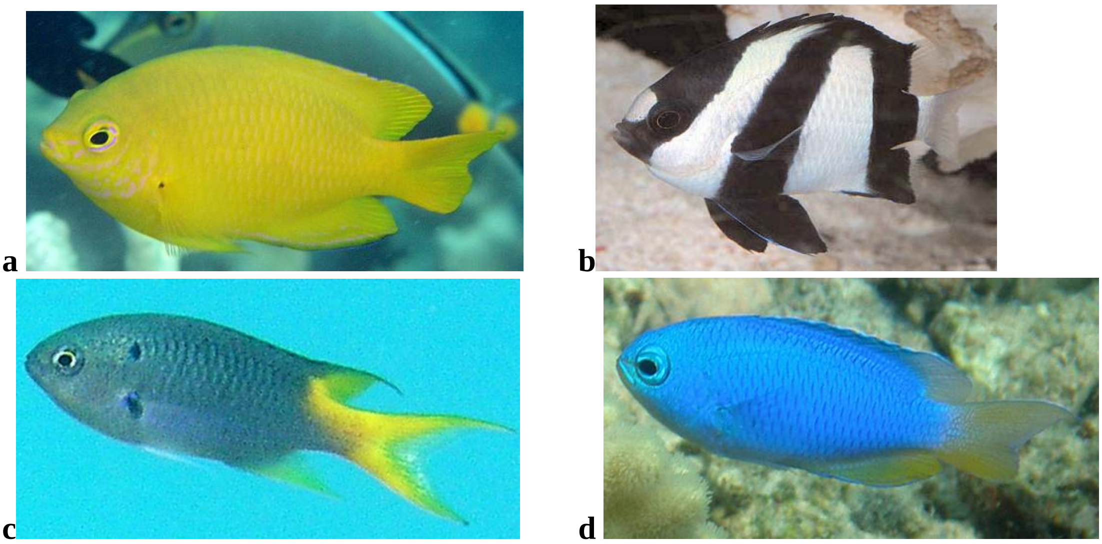


Figure 1.2: Study species. **a** *P. moluccensis* **b** *D. aruanus* **c** *N. azysron* **d** *P. coelestis.*

1.2.2 Planktonic Species

The mesoplankton (0.2 – 5mm) analysed in this investigation were divided into 11 categories: Copepods, Amphipods, Decapods, Isopods, Chaetognaths, Zoea larvae, Larvaceans, Ostracods, other Crustaceans, and Gelatinous organisms. Copepoda (Dahl, 1956) is a subclass of Maxillopoda in the subphylum Crustacea in the phylum Arthropoda and contains over 14,000 species. Decapoda is an order within the class Malacostraca in the subphylum Crustacea. Isopoda (Latreille, 1817) is in the same class as the decapods. Chaetognatha (Leukart, 1854) is a phylum with 120 species in 20 genera. Zoea larvae are larval Crustacea within the order Decopoda. Larvacea is a class in the subphylum Urochordata in the phylum Chordata. Ostracoda is a class within the subphylum Crustacea.

Other Crustaceans were all in the subphylum Crustacea. The category of gelatinous organisms was broadly defined as containing organisms with no exoskeleton including the phyla Cnidaria, Ctenophora and individuals from Chordata (Thaliacea: Urochordata: Chordata).

1.3 Data Collection:

Table 1.1: Astronomical and Tidal data at times of data collection.

Date	Time	Height	Difference	Movement	Moon Phase
10 Apr 2008	10:15	1.8	0.6	Slack	23%
20 Apr 2008	08:30	0.9	2.1	Ebb	99%

1.3.1 Stomach Contents

Fish were collected by the project supervisor Jacob Johansen under his permits (Ethics: A 1267). Clove oil and barrier nets were used to anesthetize and capture them, and also to kill them upon return to the dive boat. As soon as they were aboard, they were placed on ice for transport back to the research station.

Back in the laboratory their viscera were removed through decapitation and a rostral-caudal incision from the operculum to the anus. The gonads, liver, and heart were discarded and the stomach was preserved in 4% formalin. The stomach contents were enumerated through a dissecting microscope to determine type of plankton consumed.

1.3.2 Plankton Tows:

Samples were gathered in triplicate from five different places in the study area: one from the lagoon, one from the back flat, one from the mid flat, one from the front flat, and one from the ocean (figure 1). A conical net 38.1 cm in diameter with a pore size of 153 microns was used to collect plankton. A flowmeter (General Oceanics) was used to determine the distance towed. Distance towed multiplied by area of the net opening was equal to the volume of water filtered. When a flowmeter was unavailable, a measuring tape was used to measure a distance of 40 meters. The tows were conducted by swimming out and back from the boat, a total distance of 80 meters. Any currents encountered on the outbound leg were cancelled out by the inbound leg of the tow.

Tows were conducted starting one hour before slack high water and finished no later than one hour after. This was done to allow sufficient stratification of oceanic plankton as it flowed across different zones by predation by planktivores. High tide was chosen because of the opportunity to collect still unpredated upon plankton from the oceanic site. Sampling at low tide would have increased the proportion of lagoonal plankton collected across reef zones.

After the net was brought back aboard it was briefly rinsed, and the cod-end jar was removed. The sample was filtered by pouring the contents of the cod-end jar back through a small area of the net. That part of the net was rinsed with pre-filtered sea water until the entire sample was suspended in 200 ml. The sample was then preserved with 100 ml of 95% ethanol to produce a solution of approximately 30% ethanol. The net was rinsed through immersion and agitation in ocean water three times before a new cod-end jar was attached and the tow procedure repeated.

In the lab, the contents of the jar were filtered through 200-micron mesh, and approximately .05 grams (3mm x 3mm x 3mm) was taken from the solid biomass for enumeration under a dissecting microscope. The remaining biomass was transferred to labelled, pre-weighed aluminium foil, and masses recorded. They were place in a drying oven at 60°C for 48 hours until a constant weight was achieved and dry weights were recorded. They were baked at 500°C for 6 hours to burn off organic content. The difference between this ash free dry weight (AFDW) and the dry weight is due to the combustion of carbon in the sample (Nagao et al., 2001). Carbon content can be expressed as a percent of the total dry mass of the sample by dividing the AFDW by the dry weight and subtracting this fraction from 1.

1.4 Data Analysis

Simpson's Index of diversity was calculated for each sample of plankton from the water column and stomachs.

$$S = \sum (n_i (n_i-1) / N (N-1))$$

Where n is the number of species in group *i* and N is the total number of individuals in all groups. This equation yields values between 0 and 1, indicating high diversity and low diversity, respectively. Since this is counter intuitive, S is commonly subtracted from 1 to get D (1-S=D). D can range from 0 to 1, indicating low diversity and high diversity, respectively and intuitively.

A chi-square one sample test for goodness of fit was performed on the plankton in the water column and fish stomachs for each species. This is a test for the difference between distributions and variation from theoretical expected values (no variation across zones or taxa). The test specifies that no expected value can be less than 1, and not more than 20% of the expected values can be less than 5. However, Roscoe and Byars (1971) suggest that these criteria are conservative, and serve only to ensure a sufficiently large sample. If the average number of expected values across all categories is at least 6, the test is still reliable (Roscoe and Byars 1971).

$$\chi^2 = \sum (o - e)^2 / e$$

Where o is the observed value and e is the theoretical expected value. If the chi-square value is less than the critical value, the null hypothesis is accepted; else, the alternative hypothesis is accepted.

The Kruskal-Wallis test was performed to determine if there was a statistically significant difference between mean of more than two. This test is used when analyzing non-parametric independent samples of equal or unequal size (Ambrose et al., 2002). This test does not indicate what the difference between the means is, only if the difference is statistically significant.

$$H = 12/N\,(N+1) + \sum R i^2/n_i - 3(N+1)$$

Where N is the number of observations, n_i is the number of items in group *i* and R_i is the sum of the ranks assigned to values in sample *i*. If H is less than the critical value, the null hypothesis is accepted; else, the alternative hypothesis is accepted.

Spearman's Rank Correlation was used to determine the existence of a correlation between fish size and stomach content diversity and also the correlation between plankton density and distance from the ocean.

$$r_s = 1 - (6\sum d^2) / (n^3 - n)$$

Where d is the difference between the rank values assigned to x and to y and n is the number of observations. If r_s is less than the critical value, the correlation is not statistically significant, else, it is.

Chesson (1983) improved Manly's (1979) selectivity index which was used to determine the difference between the proportion of a category *i* in the stomach compared to the proportion of that category in the environment.

$$E = (am)-1)) / ((m-2)\,a + 1)$$

$$a_i = (r_i/n_i) / \sum (r_j/n_j)$$

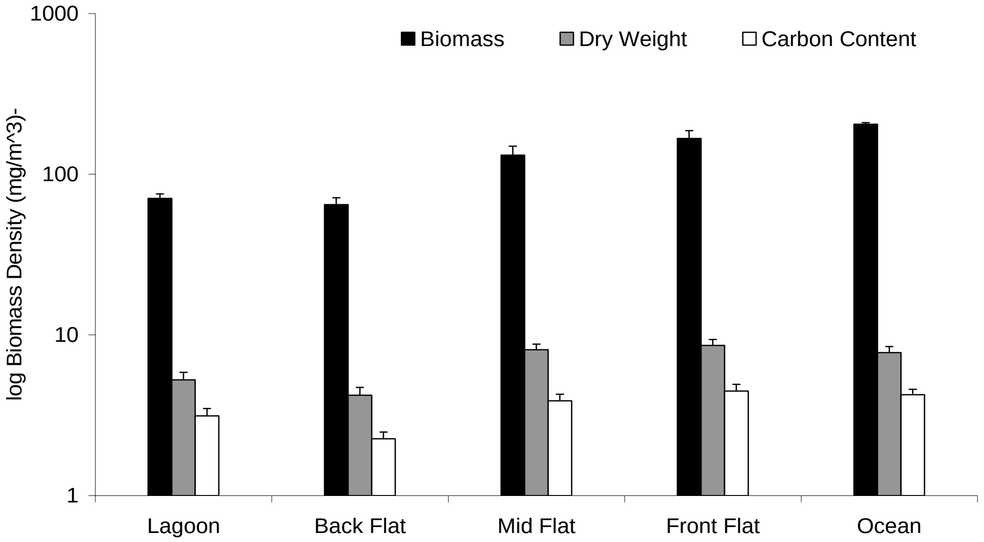
Where m is the number of categories, r_i is the number (or proportion) of category *i* in the stomach, r_i is the number (or proportion) of category *i* in the environment. r_j is the number (or proportion) of category *j* in the stomach and r_j is the number (or proportion) of category *j* in the environment. *j* represents each category from 1 to m. Foraging ratio (a_i) is the probability that the next individual picked from the entire sample will be of type *i*. Neutral selection is indicated by a value of 1/m. Values larger than this indicate selection and those smaller than this indicate avoidance. E is the index of selectivity that scales a_i to values from -1 to 1. An E value of 1 indicated positive selection and a value of -1 indicates avoidance (Chesson, 1983).

2 Results

2.1 Plankton Tows

2.1.1 Density

Analysis of plankton tows yielded information about the density and carbon content as well as the community composition of the zones sampled. Figure 2.1 shows biomass density (mg/m^3), dry weight (mg/m^3), and the carbon content (mg/m^3). Oceanic tows collected the densest biomass and tows from the front flat collected the densest plankton once dried out as well as the most carbon. The back flat of the reef consistently had the least dense biomass, dry weight, and carbon content. A Kruskal-Wallis test revealed that the difference in the means is statistically significant ($p<0.05$) for the biomass density, dry weight, and the carbon content.



H=16.28 Biomass, H=14.15 Dry Weight, H= 9.51 Carbon Content, critical value = 9.49

Figure 2.1: The biomass density (black), dry weight density (grey) and carbon content (white) across the reef zones sampled. A logarithmic y-axis was used in order make visual comparison across the zones easier. Standard error bars are included.

2.1.2 Carbon Content

Percent of the plankton samples (by weight) that were carbon also varied across reef zones (figure 2.2). The lagoon had the highest percent carbon, and the mid flat had the lowest percent carbon. A Kruskal-Wallis test was performed and the difference between the means was found to be significant ($p<0.05$).

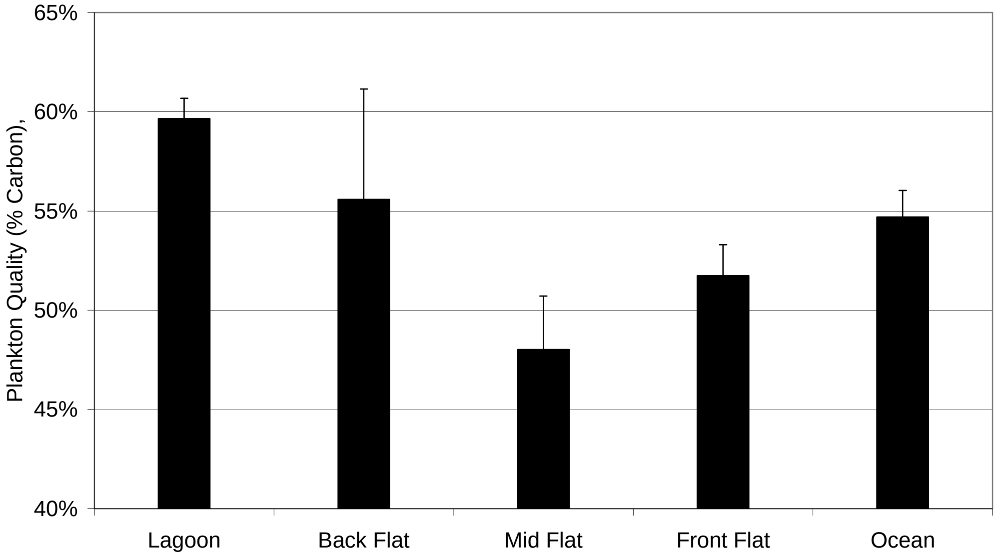
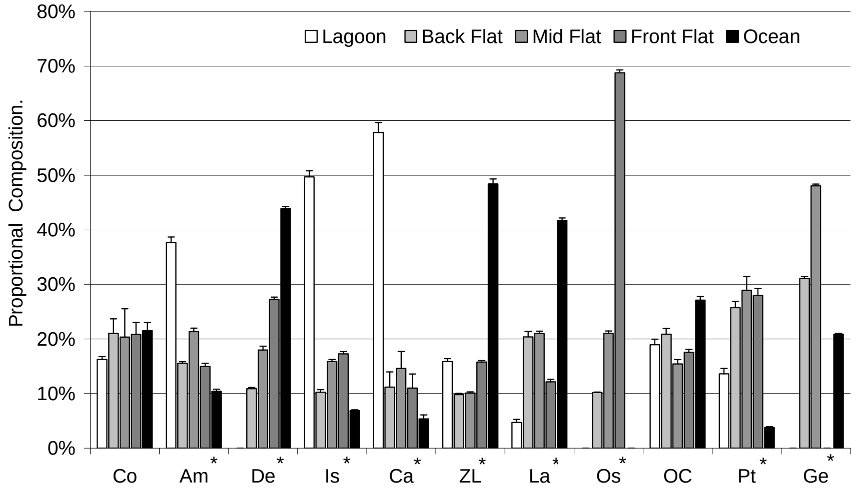


Figure 2.2: Average percent of carbon (by weight) in each of the reef zones. Standard error bars included.

H=13.20, d.f.= 4, critical value = 9.49

2.1.3 Plankton Tows by Category

The plankton community composition based on the proportional contribution of each reef zone varied by category. Copepods and other Crustaceans had a fairly even distribution across the different reef zones, and did not differ significantly ($\chi^2 = 0.90$ and 3.96, respectively) from the expected value of 20% (equal distribution between five zones). All of the other nine categories of plankton analysed differed significantly ($p<0.001$) from the expected values (figure 2.3)



Chi-Square critical value = 18.46, d.f.= 4

Figure 2.3: Proportion within each category collected at different reef zones. All the percent values within one category add up to 100%. Note the relative evenness of the Copepods and other Crustaceans. Standard error bars are shown. * Indicates statistical significance (P<0.001). Co: Copepods, Am: Amphipods, De: Decapods, Is: Isopods, Ca: Chaetognaths, ZL: Zoea larvae, La: Larvaceans, Os: Ostracods, Pt: Pteropods, Ge: Gelatinous organisms.

2.1.4 Plankton Tows by Reef Zone

The plankton community composition was dominated in every case by Copepods. In the lagoonal zone, Chaetognaths composed approximately one quarter of the individuals counted, however, in other zones, they accounted for less than 10% (figure 2.4). All of these values differ significantly ($p<0.001$) from the expected values of 9.09% assuming an equal distribution between 11 categories.

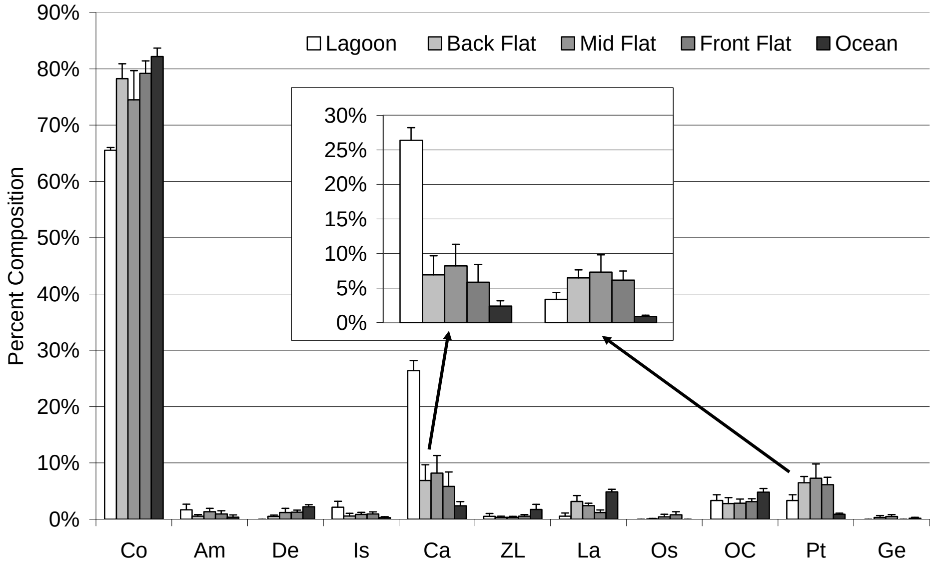


Figure 2.4: Percent composition within each reef zone by category. All of the values for each reef zone add up to 100%. Note that the lagoonal tow collected a lower abundance of Copepods than tows in the other zones did. Also note the relative abundance of Chaetognaths in lagoonal tows and that of Pteropods in tows from the reef flat. Standard error bars are shown. Co: Copepods, Am: Amphipods, De: Decapods, Is: Isopods, Ca: Chaetognaths, ZL: Zoea larvae, La: Larvaceans, Os: Ostracods, Pt: Pteropods, Ge: Gelatinous organisms.

Diversity at each reef zone was calculated using Simpson's index of diversity (figure 2.5). A significant difference between mean diversity indices at each zone was calculated using the Kruskal-Wallis test ($p<0.05$)

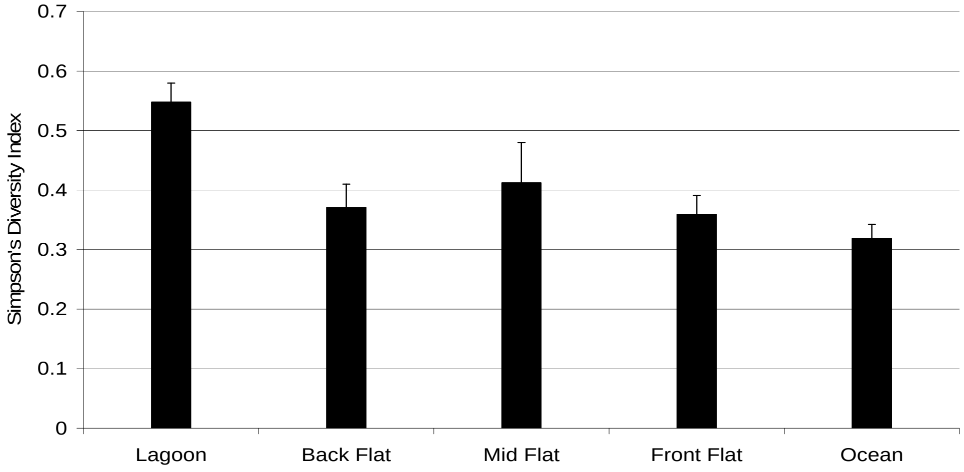


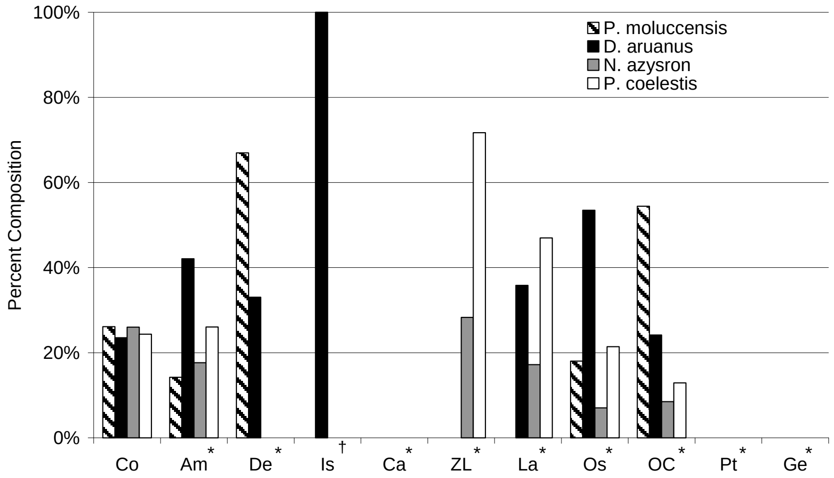
Figure 2.5: Average values of Simpson's diversity index at each reef zone. The lagoonal site had the highest diversity index value, and the oceanic site has the lowest. Standard error bars are shown.

H=6.76, Critical value = 5.99, n=24

2.2 Stomach Contents

2.2.1 Contents by Category

The percent contribution of each species varied based on category of plankton. Copepods had a fairly even distribution across all species, and did not differ significantly ($\chi^2 = 0.909$) from the expected value of 25% (equal distribution between 4 species). All of the other categories of plankton analysed differed significantly ($p<0.001$) from the expected values (figure 2.6).



Chi-square critical value = 16.27, d.f.= 3, n=29

Figure 2.6: Proportion within each category collected from different species' stomachs. This does not infer anything about abundance, only the percentage of the total number in the category consumed by each species. Also notice the skewness of Zoea larvae consumption. Also note the relative evenness of Copepod consumption across all species. Variations in consumption from the expected value of 25% of each category were calculated. * Indicates statistical significance ($p<0.001$). † One *D. aruanus* individual had one Isopod in its stomach, accounting for this extreme skewness. Co: Copepods, Am: Amphipods, De: Decapods, Is: Isopods, Ca: Chaetognaths, ZL: Zoea larvae, La: Larvaceans, Os: Ostracods, Pt: Pteropods, Ge: Gelatinous organisms.

2.2.2 Contents by Species

The percent composition of the stomachs of each species contained an abundance of Copepods (figure 2.7). Chaetognaths, Pteropods, and gelatinous organisms were not found at all. The proportion of other categories varied from zero to 12%.

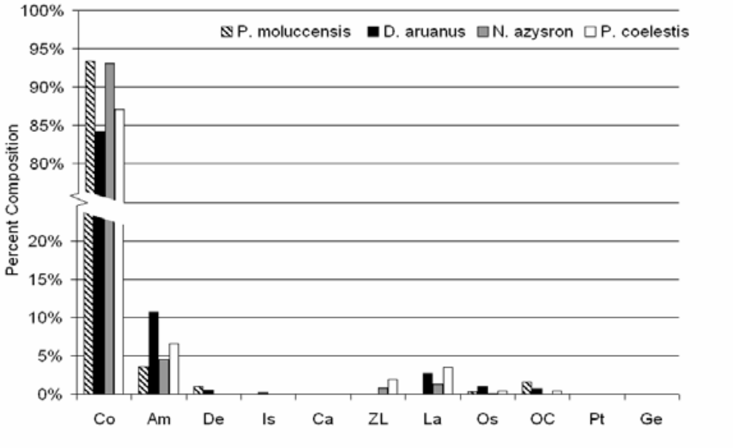


Figure 2.7: Contents of stomachs by percent composition of the study species. Note the extremely high abundance of Copepods consumed by all four species. Also note the complete absence of Chaetognaths, Pteropods and gelatinous organisms across the four species. Co: Copepods, Am: Amphipods, De: Decapods, Is: Isopods, Ca: Chaetognaths, ZL: Zoea larvae, La: Larvaceans, Os: Ostracods, Pt: Pteropods, Ge: Gelatinous organisms.

Average diversity values were calculated for each species and analyzed for significance through the Kruskal-Wallis test. No species of fish was found to consume significantly more diverse prey than the others.

2.3 Difference between Water Column and Stomach Contents

Percent composition of each reef zone was compared to the percent composition of the stomach contents of the fish caught in that zone. Figure 2.9 shows the difference between the contents of the stomachs, and the contents of the waters they were caught in. This acts as a rough indication of selectivity. Copepods and Amphipods were proportionally consumed more often while Chaetognaths, Pteropods, and other Crustaceans were consumed proportionally less often.

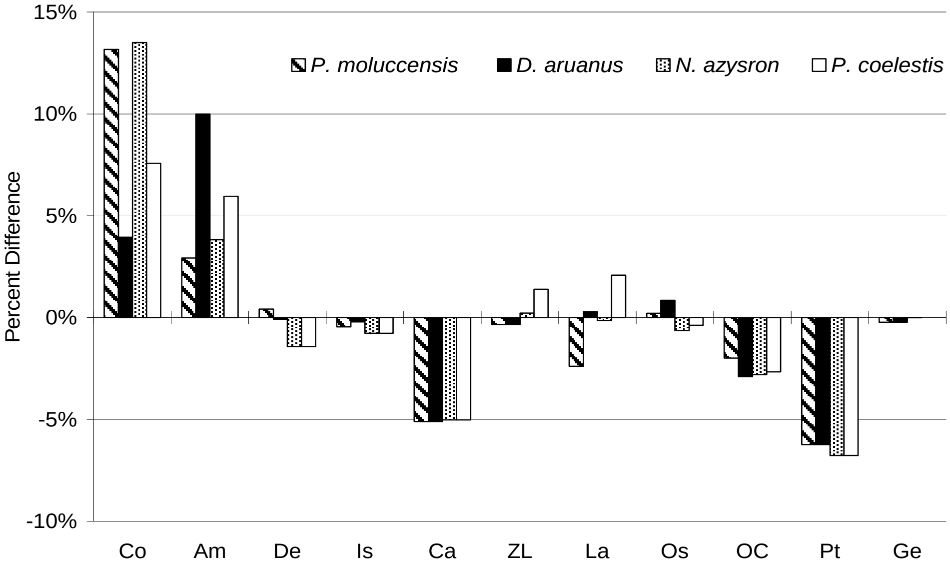
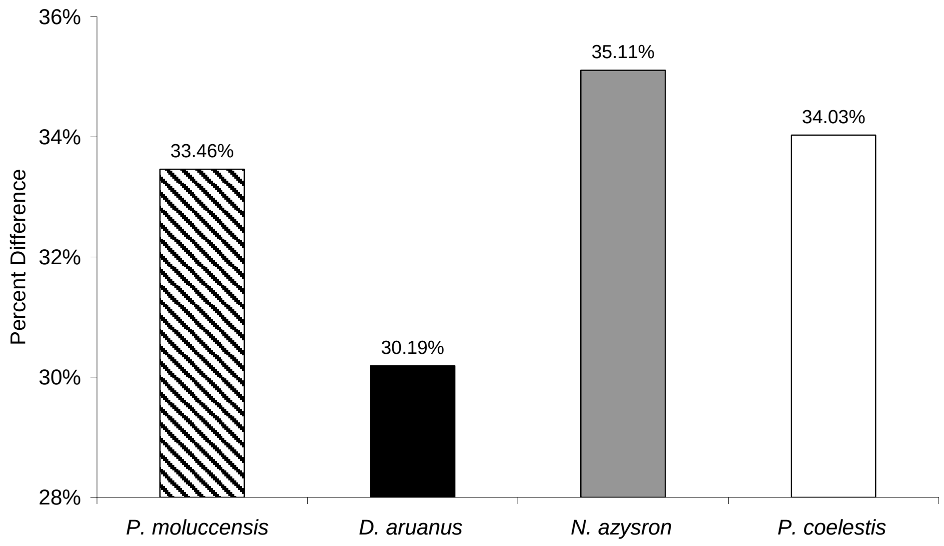


Figure 2.8: Difference in percentage composition of the study species and the water they were taken from. P. moluccensis and *D. aruanus* were taken from the back flat and *N. azysron* and *P. coelestis* were taken from the front flat. Positive values indicate groups that were present in a higher proportion in the stomach than in the environment. Note that Copepods and Amphipods composed a larger part of the stomach contents than they did the water column. Also, that Pteropods, Chaetognaths, and other Crustaceans composed a smaller percentage of the stomach contents of all four species than they did in the water column. Co: Copepods, Am: Amphipods, De: Decapods, Is: Isopods, Ca: Chaetognaths, ZL: Zoea larvae, La: Larvaceans, Os: Ostracods, Pt: Pteropods, Ge: Gelatinous organisms.

The sum of the absolute values of the percent differences (figure 2.9) were calculated and a Kruskal-Wallis test was performed. It was found that the means of the total percent differences were significantly different from one another ($p<0.01$).



H=12.82, critical value =7.81, n= 44

Figure 2.9: Total percent difference calculated by taking the sum of the absolute values of the percent differences shown in figure 2.9. Note the generally higher percent difference among front flat species and the lower percent difference among back flat fishes.

The results of a χ^2 analysis (table 2.1) show significant variations between all species and the water column. These data support the alternative hypothesis (H_1) that there is a significant difference between the observed plankton in the stomachs and the expected plankton in the water column.

Table 2.1: χ^2 values for the variation between the expected valued from the plankton tows and the observed values from the stomach analysis.

Species	χ^2	Critical Value	Degrees of Freedom	α
P. moluccensis	29.1	23.21	10	$p<0.01$
D. aruanus	118.0	29.59	10	$p<0.001$
N. azysron	32.2	29.59	10	$p<0.001$
P. coelestis	57.0	29.59	10	$p<0.001$

2.4 Selectivity

Foraging ratios (figure 2.10) indicate the probability that an individual selected at random is of a given category. A probability of 1/k (in this case 1/11 = 9.09%) indicates neutral selection of a given category. Values below this neutral selection threshold indicate avoidance and values above this threshold indicate selection.

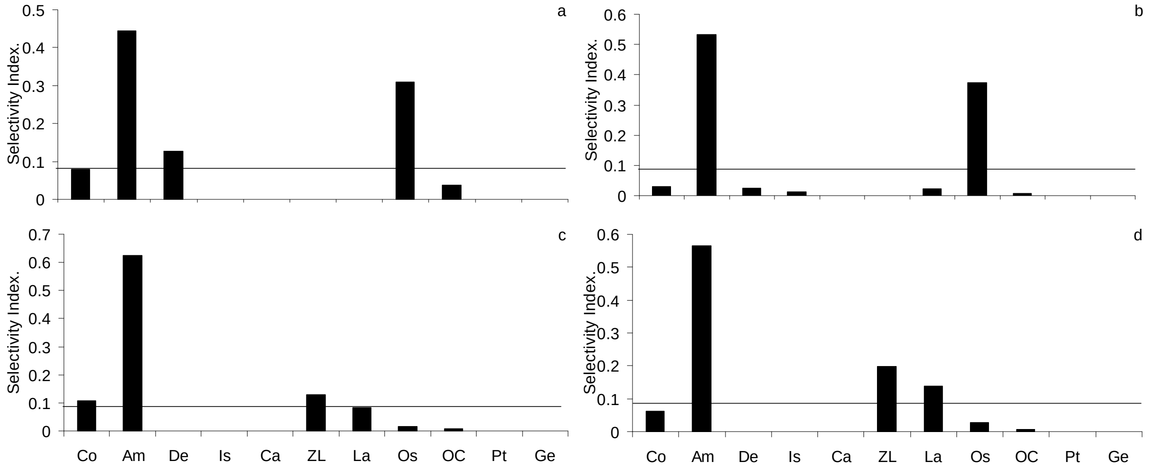


Figure 2.10: Foraging ratios among the four species. The horizontal line (at 1/k) indicates neutral selection. A: *P. moluccensis*, B: *D. aruanus*, C: *N. azysron*, D: *P. coelestis*.

Foraging ratios scaled to Chesson's selectivity index (from -1 to 1) are shown in figure 2.11. Note the variation in selection for Copepods, Decapods, Zoea larvae, Larvaceans, and Ostracods and the positive selection for Amphipods across all species. Among mixed values of selection, Zoea larvae are selected for by front flat fish and avoided by back flat fish. Conversely, Ostracods are selected by back flat fish and avoided by front flat fish.

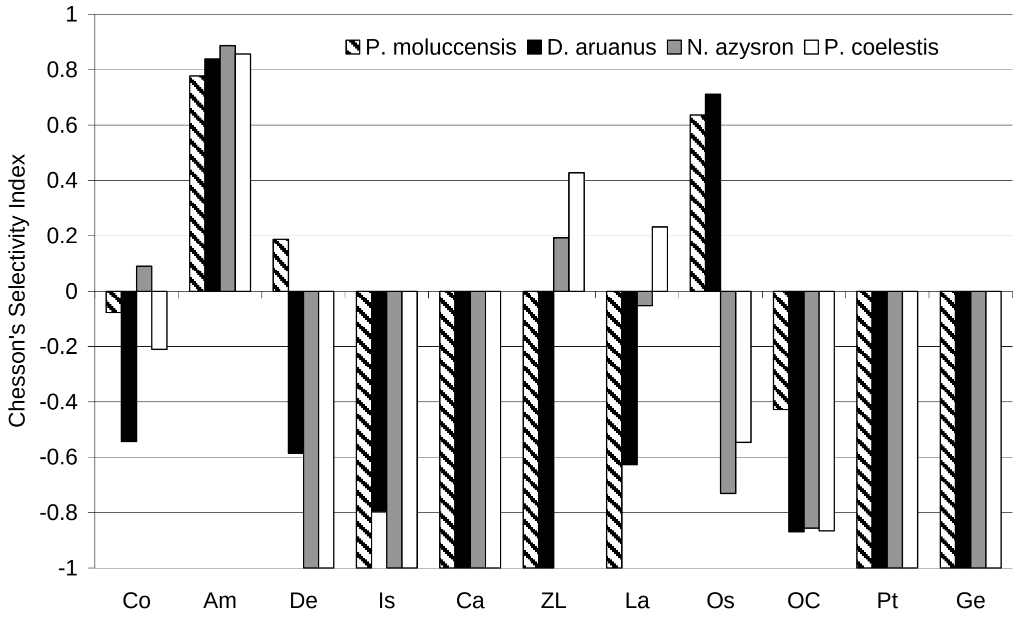


Figure 2.11: Chesson's selectivity index for the four species. Positive values indicate selection of the given category and negative values indicate avoidance. A value of zero indicates neutral selection. Note the high selection of Amphipods and low selection of Isopods, Chaetognaths, Pteropods and gelatinous organisms. There is a variation in selection for Copepods, Decapods, Zoea larvae, Larvaceans, and Ostracods between the fish species.

Shown in figure 2.12 are the data displayed in figure 2.11 grouped by fish species instead of category. This allows for a visual interpretation of selectivity by fish species.

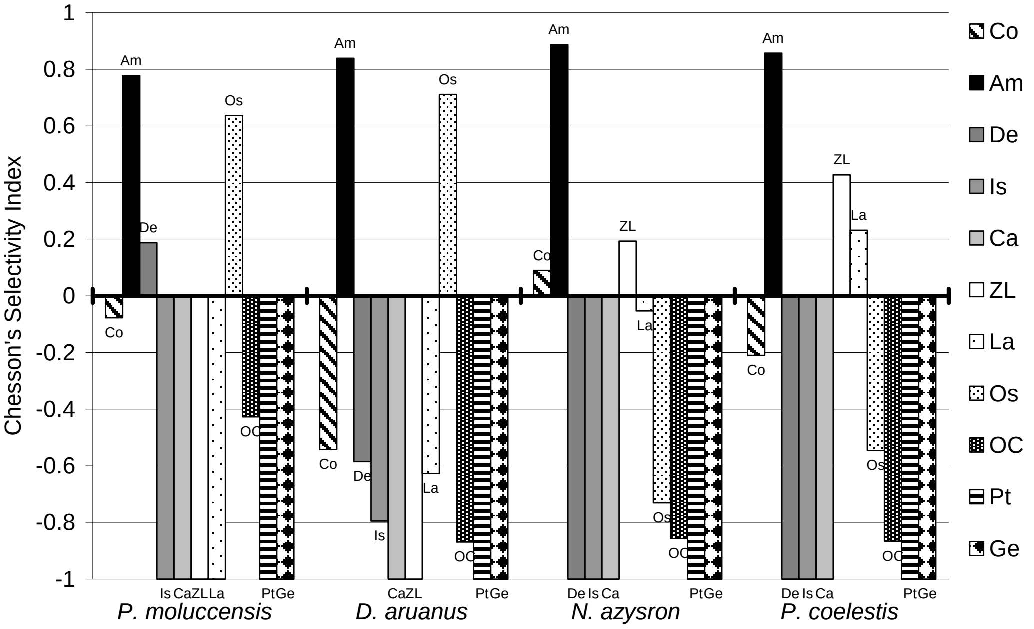
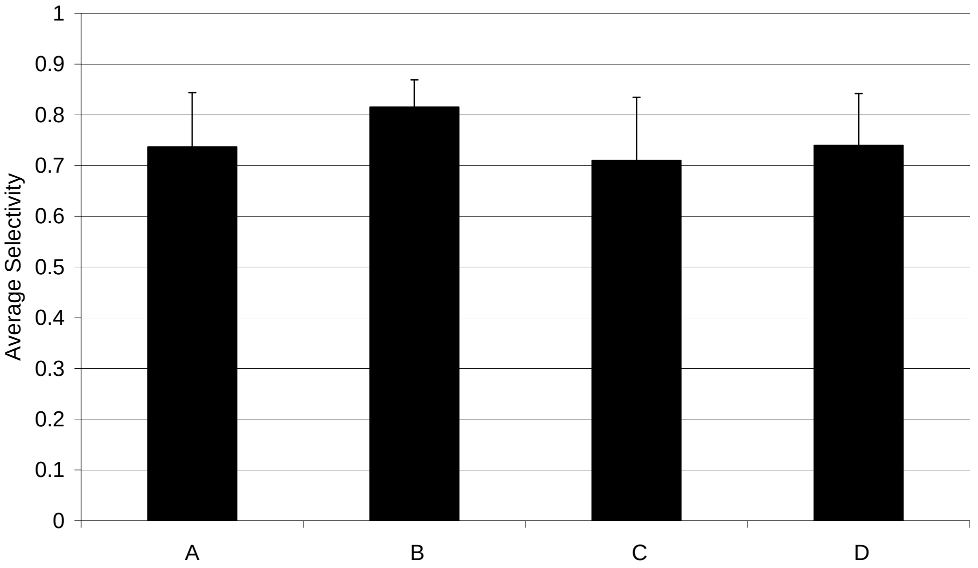


Figure 2.12: Chesson's index of selectivity grouped by fish species. Note the selection for Amphipods in all species, Ostracods in back flat species, and Zoea larvae in front flat species.

The average selectivity each fish species is shown in figure 2.13. This value was calculated by taking the mean of the absolute value of Chesson's selectivity index. A Kruskal-Wallis test was performed, and the difference between the means was found to be statistically significant (P<0.05). The combined mean for back flat fishes was .776 and .725 for front flat fishes and was not shown to be statistically significant.

Figure 2.13: Total selectivity as calculated from the sum of the absolute values of Chesson's selectivity index. A: *P. moluccensis*, B: *D. aruanus*, C: *N. azysron*, D: *P. coelestis.*



H= 12.29, d.f.= 3, critical value = 7.81

A Rank Sum test was performed on the combined means of species back flat fishes and front flat fishes. No significant difference between the means was found, which led to the acceptance of the second null hypothesis (H_{0b}). There was no difference in mean selectivity of front flat fishes and back flat fishes.

2.5 Size

It was found that the longer (and therefore larger) a fish is, the more diverse the contents of its stomach (figure 2.14). The correlation coefficient of 0.53 was found to be statistically significant at the alpha level of $p<0.05$.

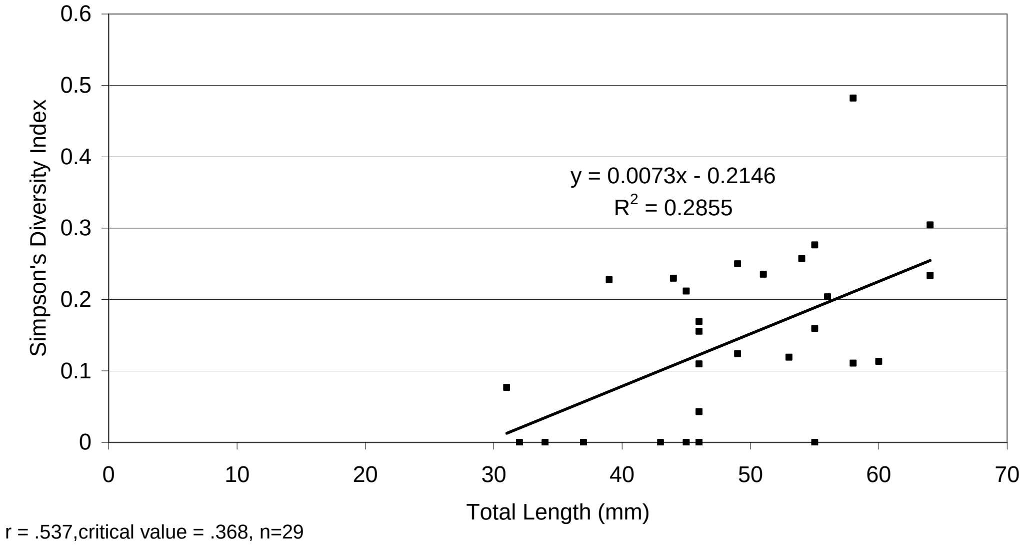


Figure 2.14: Scatter plot of fish size (total length in mm) against Simpson's diversity index for each individual fish. A trendline is shown and the correlation is significant ($p<0.05$).

Results for average fish size (total length in mm) are shown in table 2.2. A Kruskal-Wallis test was performed on the lengths and a significant ($p<0.05$) difference was found between the means.

Table 2.2: Average fish size and standard error.

Species	Size (total length in mm)	Standard error
P. moluccensis	42.71	3.11
D. aruanus	48.71	2.85
N. azysron	47.25	3.14
P. coelestis	55.57	2.47

3 Discussion:

3.1 Plankton Tows

The results of the plankton tows indicate that there was a higher biomass density in the oceanic tows than in the lagoonal tows, and exhibit a gradient between those two zones. This finding, combined with that of Shapiro and Genin (1993) that zooplankton density affects planktivore distribution results in the possibility that planktivores also affect the biomass density of zooplankton in the water column.

This would explain the difference observed because as a parcel of water from the ocean flows over the reef flat with the flooding tide, the plankton in it are predated upon by planktivores along the distance of the reef flat. The data support this because the lowest values of biomass, dry weight, and carbon content are seen from the back flat. Once the parcel of water reaches the lagoon, levels remain relatively constant due to the lack of planktivores that would further decrease the biomass.

This has implications for the selectivity of fish at different reef zones based on quality and quantity of food available during flooding tides. Back flat fishes have to be more selective in their feeding patterns in order to maintain a certain quality of food. The data support this (based on the difference in the means of front flat (.725) and back flat (.776) fishes). This theory was the basis of the development of the third alternative hypothesis (H_3) that back flat fishes are more selective than front flat fishes.

3.2 Carbon content

The results for carbon content were largely unexpected. The highest value was at the lagoonal site, and the lowest was at the mid flat. When considering this is a measure of carbon percent by density, an explanation can be offered. Consider a sample with a large biomass density and small dry weight (e.g. gelatinous organisms) will have a larger carbon content [(1-(AFDW/dry weight))/m^3] than would a sample of similar biomass density and larger dry weight (e.g. copepods). This example explains the difference between mean percent carbon content by density at the lagoonal site and at the oceanic site.

3.3 Percent Difference

The difference between the stomach contents and the water column illustrate the discrepancy between what is available and what is eaten. The variation between the plankton in the stomachs and the plankton in the water was found to be statistically significant through χ^2 analysis. This supports the first alternative hypothesis (H_1) which states that a difference exists.

3.4 Selectivity

By contrasting selectivity (figure 2.12) with proportional composition of plankton in the water column (figure 2.4) and plankton in the stomachs (figure 2.7), an accurate picture of plankton selectivity can be drawn. Copepods were found most abundantly in all zones (figure 2.4) but were found to have a selectivity index between -.53 and .15 indicating a range between avoidance and slightly positive selection. This is not what would be expected, but they still composed a large proportion of the diet of each species because they were so overwhelmingly abundant in the water column. Foraging ratios of Copepods were low (figure 2.10) because they were more common in the water column than other organisms in addition to the fact that they were more common in the stomach contents.

Both Decapods and other Crustaceans, are found in higher proportions in stomachs of back flat fishes than in stomachs of front flat fishes (figure 2.6) despite the fact that the are found in higher proportions on the front flat (figure 2.4). As a result, back flat fishes need to have higher selectivity values for Decapods (.19 and -.59) and other Crustaceans (-.43 and -.87) to consume a higher proportion than front flat fishes (-1 and -1 for Decapods and -.86 and -.87 for other Crustaceans).

Zoea larvae were found most abundantly in the oceanic tows and synchronously were selected for and consumed only by *N. azysron* (E= .19) and *P. coelestis* (E= .43). Back flat fishes did not consume Zoea larvae at all although they were present, albeit in lower but still significant proportions. Zoea Larvae have large spikes which can deter predation. Front flat fishes, which encounter a higher proportion of Zoea larvae, may be more accustomed to predating upon these spiky morsels than the back flat fishes which would encountered less frequently, and therefore, avoided.

An opposite pattern was found with Ostracods. They were selected for by the back flat fishes and avoided by the front flat fishes. Ostracods spend the daylight hours at depth in the ocean and come up at night to feed during their deil vertical migration. The depth at oceanic and lagoonal sites allowed deil vertical migration below the habitat of planktivores, but in the shallow reef flat, migrating downwards during the day only brought them closer to the planktivores. This could explain the higher proportional abundance of Ostracods found on the reef flat during the day. This increased proportional abundance is a factor in the increased selectivity towards Ostracods by back flat fishes.

Chaetognaths, Pteropods and gelatinous organisms were all avoided by all species. Some Chaetognaths are known to have a highly toxic tetrodotoxin on the hooks surrounding their mouths. This may have acted as a successful defense against predation.

Pteropods have shells made of $CaCO_3$ that when digested with stomach acid produces gaseous CO_2 (Lecture: Lewis, 2008). This addition of positively buoyant gas could be a major problem for a fish trying to maintain neutral buoyancy. If a fish is unable to stay near the reef substrate, its lifespan could be drastically shortened when it is unable to take refuge in rocks or coral. Also, McClintock and Janssen (1990) found an Antarctic pelagic species that had a chemical in their shell that was a predator deterrent. Either of these reasons could explain why they were avoided by all species.

There was a complete avoidance of gelatinous organisms across all species. Gelatinous organisms typically have high water content and offer poor nutrition. However, Shenker (1985) pointed out that the non-gelatinous parts such as the gonads, feeding structures, and stomach can be rich in nutrients. Additionally, the gonads of a jellyfish can weigh eight grams and contain the same amount of carbon as a larval fish (Shenker, 1985). Considering their complete avoidance by the planktivores studied, there must be some kind of defense. Since these organisms are typically sluggish and lack structural defenses, McClintock et al. (1985) thought the deterrence must be chemical. Such is the case with the class *scyphomedusa* (Shanks and Graham, 1988). The presence of a chemical deterrent would explain the complete avoidance of this concentrated food source.

While there was no statistical difference between combined mean selectivity indices for front flat fishes and back flat fishes, there was a significant difference in the means of each of the species. This suggests that one zone does not encourage the planktivores inhabiting it to be more or less selective as the planktivores are selective independent of reef zone.

3.5 Fish Size and stomach diversity

Total length was weakly positively correlated (r=.53) with the diversity of stomach contents. This could indicate that bigger fish, which are more dominant in the group, experience a wider range of prey to choose from. This was also found by Coates (1980) in a study of prey-size intake in *D. aruanus*. This also could indicate that smaller fish are less selective because they can't ingest some of the larger plankton that larger fish would be able to, so they have to take any that they can. Fish size could have acted as a confounding variable in the relationship between selectivity and reef zone.

Looking at Copepod consumption in back flat fishes, fish size seemed to be a determining factor in selectivity. Based on the theory that plankton is actively picked off by planktivores as oceanic water floods the reef on a rising tide, the size of the Copepods could be smaller at the back flat than at the front flat due to the selection of larger prey. Frost (1954) demonstrated that the size of prey in the stomachs of fish correlates well with the total length of the fish. *D. aruanus* was an average of 6 mm longer than *P. moluccensis* (table 2.15) and also was more avoidant of Copepods than *P. moluccensis*. This is an instance of average prey size being decreased as the prey traverse the reef flat and this size difference affecting selection. This avoidance of possibly smaller prey could also be the case in Decapod and other crustacean selectivity, which are both avoided more by *D. aruanus* than by *P. moluccensis*.

3.6 Sources of Error

3.6.1 Difference between Percent Difference and Selectivity Index

The difference between percent composition of the stomach and the water can act as a crude predictor of selectivity, but is prone to error. Looking at percent difference of Copepods compared to the percent difference of Amphipods, one of the possible errors is made clear. There is a larger mean percent difference in Copepods (9.55%) than there is in the mean percent difference in Amphipods (5.67%) (figure 2.8). When the mean foraging ratios (proportional differences) are calculated, it is obvious that the Amphipods (.542) are selected for much more readily than the Copepods (.068) (figure 2.12).

3.6.2 Selection with replacement

All the analysis of selectivity assumes that there is such a high abundance of plankton in the water, that predation by planktivores does not affect their relative proportions over time within that reef zone. Effectively, every time an individual plankter is consumed, it is immediately replaced because of the vast abundance of the plankton. However, this assumption is not valid over all reef zones due to the time elapsed and longer distance travelled from the ocean to the lagoon. Over this distance, the static population is degraded by predation (figure 2.1).

3.6.3 Stomach Contents

Stomach contents were the only indication of selective feeding in the fishes studied. It was impossible to observe and record their feeding habits *in situ* because plankton are simply too small to be identified without using microscopy.

Several factors affected the enumeration of the stomach contents. Stomach fullness had an effect on the accuracy of enumeration because if the stomach was mostly empty, it was difficult to separate the individual organisms from the stomach lining. Full stomachs produced the most accurate enumeration. Type of organism counted also had an effect on accuracy. The absence of an exoskeleton in some of the organisms counted was thought to affect the time it took to digest them. Organisms with an exoskeleton were less digested and positively identified more often than the partially digested, unidentifiable gelatinous organisms without an exoskeleton.

3.6.4 Sample Size

The ethics permits obtained for this investigation were limited in the number of individuals per species (eight) we were able to kill. An ethics permit that provided for a larger sample size than 8 could have reduced variation within species.

The number of replications of the plankton tows was too few as well. Each zone should have been sampled in triplicate at three or more different times. Three or more replications of the sampling method allow for the exclusion of an outlier. One of the two replicates that were conducted in this investigation could have been an outlier and would not be evident due to the lack of repetition.

3.7 Future Study

This study provides a baseline level of data to determine selectivity among planktivorous damselfish at Lizard Island. In the future, affects upon reef zone on selectivity should be investigated. This could be studied in a similar method as this one in a follow-up study or it could be studied by isolating one species abundant at all reef zones (such as *D. aruanus* or *N. azysron*). Another topic of future study is the size of prey consumed in relation to size and weight of the individual. This could also be studied across several species, or within one species.

4 Conclusion

In this investigation of prey selectivity of planktivorous damselfish and carbon content of plankton entering a reef system, it was found that there was a significant difference between the plankton in the water column and plankton in the fish's stomach. Copepods, Decapods, Zoea larvae, Larvaceans, and Ostracods had mixed selectivity among the fish species studied. Chaetognaths, Pteropods, and gelatinous organisms were always selected against, possibly because of chemical defenses. Amphipods were highly selected for in all species. There was no significant difference in the mean selectivity index values of front flat fishes (.725) and back flat fishes (.776); however, there was a significant difference between the mean index values of the different species. This indicates that there was no difference in selection based on reef zone, and that selectivity amongst species is independent, although possibly confounded by predator size. Future studies of the relationship between selectivity and reef zone within one species as well as the relationship between predator size and selectivity would be important in the broader context of prey selectivity in planktivorous fish.

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6 Appendix:

6.1 Density Biomass, Dry Weight, and AFDW Raw Data

Table 6.1: Raw data from plankton tows: biomass, density, and AFDW.

Site	Water Volume	Tare	Biomass (mg)	Dry Weight (mg)	AFDW (mg)
Back Flat	8.5387	-0.3218	346.5	20.7	7.10
Back Flat	7.9535	-0.1889	634.6	32.6	10.50
Back Flat	9.4058	-0.1780	673.4	35.5	10.80
Back Flat	9.1207	-0.1528	760.8	57.3	31.40
Back Flat	9.1207	-0.1535	510.4	39.1	20.80
Back Flat	9.1207	-0.1306	514.4	40.3	24.80
Mid Flat	7.9658	-0.1284	1044.2	52.5	25.10
Mid Flat	6.8230	-0.1221	838.4	46.8	24.30
Mid Flat	7.0038	-0.1102	1275.6	64.8	27.40
Mid Flat	9.1207	-0.1239	1669.6	99	55.50
Mid Flat	9.1207	-0.1210	801.6	68.7	37.80
Mid Flat	9.1207	-0.1386	746.4	68.2	40.10
Front Flat	8.5357	-0.1142	1388.5	63.1	28.70
Front Flat	8.3794	-0.1400	1896.7	91.9	39.40
Front Flat	7.2090	-0.1440	1047.3	56.5	30.50
Front Flat	9.1207	-0.1403	1508.4	70.5	34.50
Front Flat	9.1207	-0.1317	1909	100.1	50.10
Front Flat	9.1207	-0.1408	834.5	61.2	29.50
Lagoon	4.1851	-0.1350	328.5	26.2	10.80
Lagoon	4.7059	-0.1310	334.7	24.8	9.50
Lagoon	6.5779	-0.1662	412.1	27.7	11.50
Ocean	9.1207	-0.1370	1817.7	58.6	26.30
Ocean	9.1207	-0.1402	1835	79.5	38.00
Ocean	9.1207	-0.1322	1950.5	74.5	32.20

6.2 Plankton Tow Raw Data

Table 6.2: Enumeration of Plankton Tows.

Zone	Co	Am	De	Is	Ca	ZL	La	Os	OC	Pt	Ge
Back Flat	62	0	1	0	4	1	6	0	0	8	0
Back Flat	68	0	0	0	15	0	4	0	0	5	0
Back Flat	72	0	0	3	15	0	4	0	2	4	2
Back Flat	212	1	2	0	3	1	2	1	10	7	0
Back Flat	156	2	2	1	5	1	3	0	13	17	0
Back Flat	138	3	0	0	3	0	2	0	7	14	0
Mid Flat	58	2	0	0	19	1	1	0	0	19	0
Mid Flat	53	2	2	2	6	0	3	2	4	1	1
Mid Flat	75	4	5	1	19	0	2	0	4	7	2
Mid Flat	213	0	1	1	7	1	7	0	4	13	0
Mid Flat	142	0	0	1	5	0	4	0	7	14	0
Mid Flat	124	0	0	1	1	1	4	0	4	6	0
Front Flat	131	0	2	2	12	0	0	3	6	10	0
Front Flat	93	2	0	2	22	0	1	4	3	5	0
Front Flat	64	3	1	2	7	1	0	0	4	1	0
Front Flat	167	0	6	1	2	1	6	0	9	20	0
Front Flat	162	1	3	0	2	3	4	0	3	14	0
Front Flat	112	0	1	0	1	0	2	0	3	12	0

Lagoon	43	1	0	2	16	1	0	0	1	1	0
Lagoon	37	2	0	0	14	0	0	0	2	2	0
Lagoon	33	0	0	2	18	0	1	0	3	3	0
Ocean	215	3	7	1	7	3	13	0	10	3	0
Ocean	168	0	3	1	2	1	8	0	12	2	1
Ocean	157	0	5	0	7	7	11	0	9	1	0

6.3 Stomach Content Raw Data

Table 6.3: Enumeration of Stomach Content.

Species	Fish	Fish length(mm)	Co	Am	De	Is	ZL	La	Ca	OC
Pomacentrus moluccensis	1	44	71	3	2	0	0	0	1	4
Pomacentrus moluccensis	2	55	22	2	0	0	0	0	0	0
Pomacentrus moluccensis	3	34	12	0	0	0	0	0	0	0
Pomacentrus moluccensis	4	49	58	3	0	0	0	0	0	1
Pomacentrus moluccensis	5	32	17	0	0	0	0	0	0	0
Pomacentrus moluccensis	6	46	90	2	0	0	0	0	0	0
Pomacentrus moluccensis	7	39	15	1	1	0	0	0	0	0
Dascyllus aruanus	8	37	13	0	0	0	0	0	0	0
Dascyllus aruanus	9	53	61	2	0	0	0	0	0	2
Dascyllus aruanus	10	45	2	0	0	0	0	0	0	0
Dascyllus aruanus	11	49	94	9	0	0	0	1	4	1
Dascyllus aruanus	12	56	101	13	0	0	0	0	0	0
Dascyllus aruanus	13	58	74	20	2	1	0	10	0	0
Dascyllus aruanus	14	43	2	0	0	0	0	0	0	0
Neopomacentrus azysron	15	46	71	5	0	0	1	0	1	0
Neopomacentrus azysron	16	45	78	5	0	0	3	2	0	0
Neopomacentrus azysron	17	46	115	6	0	0	1	0	0	0
Neopomacentrus azysron	18	46	37	0	0	0	0	0	0	0
Neopomacentrus azysron	19	60	96	4	0	0	0	0	0	2
Neopomacentrus azysron	20	58	115	2	0	0	1	4	0	0
Neopomacentrus azysron	21	46	166	11	0	0	0	4	0	0
Neopomacentrus azysron	22	31	49	2	0	0	0	0	0	0
Pomacentrus coelestis	23	64	64	6	0	0	2	3	1	1
Pomacentrus coelestis	24	64	28	2	0	0	0	2	0	0
Pomacentrus coelestis	25	55	28	3	0	0	0	2	0	0
Pomacentrus coelestis	26	55	31	0	0	0	0	0	0	0
Pomacentrus coelestis	27	54	49	4	0	0	3	1	0	0
Pomacentrus coelestis	28	51	21	2	0	0	0	1	0	0
Pomacentrus coelestis	29	46	3	0	0	0	0	0	0	0