

Feeding plasticity of reef fish

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Abstract. Understanding conditions where feeding plasticity can occur is particularly important as the assessment of reef health and resilience is currently partially achieved by examining the abundance and biomass of key fish feeding guilds. The classification of fish species into a guild is based on their niche, however there has been little consideration of the effect of habitat quality on niche breadth. The study examines whether or not plasticity in guild membership is driven by environmental conditions including habitat quality and competitive interactions. The species studied belong to different feeding guilds although both are in the family Pomacentridae and abundant throughout the Indo Pacific. *Plectroglyphidodon lacrymatus* is conventionally classed as a territorial herbivore and *Amblyglyphidodon curacao* as predominately a planktivore. The research was conducted on three reef sites of varying quality within the Wakatobi Marine Park, South East Sulawesi, Indonesia. This study identified that *P. lacrymatus* is capable of switching to plankton feeding under different conditions; however *A. curacao* showed no variation in feeding across all the sites but did graze on benthic macroalgae as well as feeding on plankton. The results suggest that competition was the driver for niche expansion for *P. lacrymatus* as the expansion occurred on the same two reefs where: higher frequencies and durations of inter/intraspecific aggressive behaviors were recorded; territory volume was significantly smaller; the abundance of competitors/fish was higher; and the overall reef quality was higher.

Key words: Niche expansion, Feeding plasticity, Competition, Herbivore, Planktivore.

Introduction

Reef fish play important functional roles within coral reef systems and the importance of one such role, herbivory, is well documented as essential in maintaining a healthy ecosystem through the removal of algae to allow coral to recruit and grow (Hay, 1981; Lewis, 1986; Hoey and Bellwood, 2009). The assessment of reef health, vulnerability and resilience is partially achieved by estimates of the total biomass of specific functional guilds and the number of species that contribute to this biomass (Bellwood et al, 2004; Hughes et al, 2010; Nyström et al, 2008). It is particularly important to understand how degrading habitats influence levels of redundancy and reef resilience. Accurately assessing and predicting functional biomass depends on our knowledge of niche characteristics of a species, be it fundamental or realized, and how this may vary across environmental gradients.

The intention of this study was to increase our understanding of the flexibility of trophic guild membership and thereby increase our ability to build environmentally driven plasticity into behavioral models and concepts of reef functionality. The two study species were *Plectroglyphidodon lacrymatus* and *Amblyglyphidodon curacao*. Both belong to the Pomacentridae, which is one of the most abundant

and diverse fish families on coral reefs and the dominant visually conspicuous fish family on the study sites. *P. lacrymatus* is a territorial herbivore (Jones et al, 2006; Frédérick et al, 2009) and *A. curacao* is a facultative planktivore (Hobson and Chess, 1978).

There have been some reports of feeding plasticity for the *P. lacrymatus*. During a coral spawning event, the species was observed feeding in the water column, suggesting that the species' behavior is able to rapidly adapt to changing environmental conditions and thus questions their designation as herbivores. *Amblyglyphidodon curacao*, although classed as a planktivore, has been reported to graze benthic macroalgae (Hobson and Chess, 1978). Trophic switching has been reported by Bellwood et al (2006) although the prevalence, drivers and the consequences of such activity for our understanding of reef functionality remains to be seen. The question then arises whether or not the ability to switch guilds is rare, common, driven by prevailing environmental conditions, opportunistic food availability or inter-specific interactions? Is this guild plasticity predictable? Identifying how these factors influence niche breadth of reef fish is essential if we wish to understand the effects of declining reef quality on ecosystem function. It is particularly important to

focus on those species that represent a significant proportion of the functional biomass. If flexible behavior is prevalent amongst functionally important species then our understanding of trophic interactions, trophic modeling, and functional redundancy need to be reassessed. Within this study we tested the hypothesis that environmental conditions, including habitat quality and competition would significantly influence the relative feeding contribution of *P. lacrymatus* and *A. curacao* to herbivory and planktivory, respectively.

Material and Methods

The study took place in the Wakatobi Marine Park, South East Sulawesi, Indonesia in 2008 and 2009.

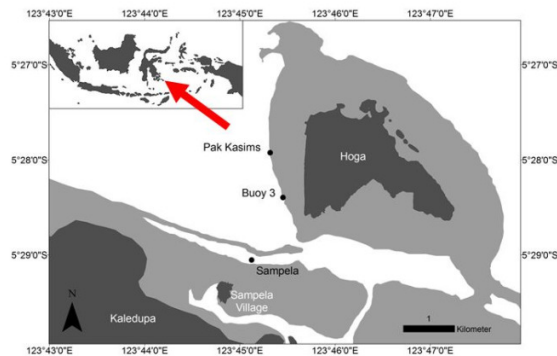


Figure 1: The location of the Wakatobi Marine Park, in South East Sulawesi, Indonesia and the three study sites.

The reef habitat data was collected using the continual intercept method and fish data was collected using time (25 minutes) and distance restricted belt transects; both methods used 50 meter transects. In the case of the fish surveys a 5m wide 50m belt transect was used. Surveys were replicated (n=3) at reef flat, crest, and slope at each site.

Ethological Observations

Key behavioural traits were identified through 15 hours of initial observation and continuous time budget analysis used to characterize behaviours. The optimum time for an observation period for both species was assessed through these preliminary observations of up to an hour. A period of ten minutes was determined to be optimum for observations of *P. lacrymatus* and *A. curacao*. Observations were conducted of adult individuals, where fish had full adult markings and were of an adult size (larger than 5cm standard length). Observations were replicated in the morning and afternoon at various states of tide (ebb and flood) and lunar states (spring, neap, and

waxing/waning) and equally across reef zones. A total of 263 individual fish equating to 43.83 hours of observations were conducted across the three sites. Observations were conducted only once per individual and a note of territory positions of *P. lacrymatus* was made to ensure no repeat observations were conducted. *A. curacao* observations were performed on one individual per shoal and from different locations along the reef sites to reduce the possibility of repeated observations to ensure data independency.

Competitive Pressure

A measure of competitive pressure for the sites was determined by assessing: the frequency and durations of aggressive inter and intraspecific events; the abundance and structure of fish assemblages; and the assessment of territory size of *P. lacrymatus* across sites. The mapping of territory size was conducted by observing an individual fish for a 10 minute period and dropping markers at 30 second intervals. The mapped boundary was recorded with a digital photograph and territory size was calculated using image analysis software (Coral Point Count 4.0). As territories are not planar and surface area for algal growth would be important, the surface complexity through territories were additionally determined through mean height measurements taken from within the territories to calculate the volume.

Isotope Analysis

The analysis of stable carbon and nitrogen isotope signatures from fish tissues can provide information both on food sources and trophic position (Peterson and Fry, 1987; Arrington and Winemiller, 2002). Stable isotope analysis of carbon and nitrogen was carried out on muscle tissue of the species *P. lacrymatus* at a dedicated stable isotope analysis laboratory. This analysis was replicated for five individuals from each of the reef sites but only at the reef flats. The muscle tissue sample was taken from the caudle peduncle and preserved in salt for trophic analysis (Arrington and Winemiller, 2002). Mass spectrophotometry was used to determine the isotopic ratio of carbon and nitrogen. The isotopic ratios were compared to a standard and reported as a delta value. The delta value is determined by the following equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

Where X = ¹³C or ¹⁵N and R is the corresponding ratio of ¹³C/¹²C, ¹⁵N/¹⁴N respectively. An increase in the stable isotope value indicates an increase in the amount of a heavier isotope relative to the standard.

The $\delta^{13}\text{C}$ is predicted to increase 0-1‰ per trophic level and indicates the source of energy. The ratio of nitrogen isotopes will be compared to atmospheric nitrogen to determine the $\delta^{15}\text{N}$ isotopic signature where $\delta^{15}\text{N}$ is predicted to increase by 3‰ per trophic level and indicates trophic level.

Statistical Analysis

Homogeneity of variance in the data was assessed by Levene's test and transformations for normality applied where necessary (arcsine for behavior percentage data). Where heteroscedasticity was still apparent a non-parametric Kruskal-Wallis test was performed. Permutational multivariate analyses of variance (PERMANOVA) with a nested design were performed to further assess the significance of factors within the behavioral data relative to each site (Anderson, 2001). Site was treated as a random factor with 3 levels and the time of day was treated as a fixed factor (2 levels), tidal state as fixed (2 levels), and the lunar state as fixed (3 levels). Pair-wise post-hoc comparisons were conducted to identify between which factors, years or sites, the differences occurred. Where sample sizes were small, PERMANOVA P-values were obtained through the Monte Carlo test. Non-metric multi-dimensional scaling (nMDS) based on 9999 permutations and the Bray-Curtis similarity matrix were used to visualize patterns in the data. The fish abundance data was examined in terms of the number of individuals and diversity assessed with Hill's N1 index (Hill, 1973).

Results

The three reef sites varied in habitat quality as indicated by percentage coral cover (see Table 1). Buoy 3 had the highest coral cover whereas Sampela had the lowest quality reef with significantly low coral cover and higher coverage of algae in comparison to the other sites. Additionally the abundance of fish was significantly lower at Sampela to that of the other sites; diversity did not vary spatially (see Table 1).

	Pak Kasims		Buoy 3		Sampela	
Hard coral % cover	25.9	±4.7*	49.30	±1.9*	13.53	±3.5*
Algae % cover	7.65	±1.4	5.90	±1.9	60.50	±4.8*
Abundance /250m ²	437.5	±29.1	509.2	±82.9	268.7	±41*
Fish diversity /250m ²	25.2	±1.5	21.3	±3.8	21.9	±1.8

Table 1: Reef site quality summary (±SE). The data shows the mean percentage cover of hard coral and algae cover; with the mean fish abundance and diversity. The asterisk's denote significant differences across sites.

There were site differences in the behavior of *P. lacrymatus* (see Fig. 2) but not for *A. curacao*. The spatial differences in behavioral data were mainly due to plankton feeding (see Fig. 2). Plankton feeding was observed at Buoy 3 and Pak Kasims but not at Sampela, the most degraded site (see Fig. 2 and 3). Algae grazing did not differ across sites (see Fig. 3).

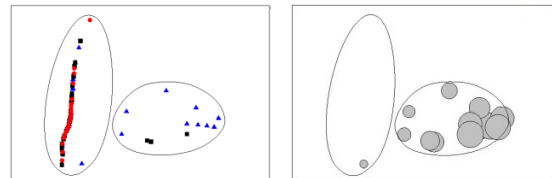


Figure 2: MDS ordination of *P. lacrymatus* feeding behavior data with bubble overlay of percentage time planktonic feeding. Plots have a cluster similarity level grouping of 60%. Stress level 0.03. The symbols represent site; red dots represent individuals from Sampela, black squares represent Buoy 3 and blue triangles represent Pak Kasims.

Planktivorous activity was highest at Buoy 3, which was the site with the highest abundance of coral and fish. The tidal state the only factor to significantly influence this behavior, with feeding only occurring on flood tides; lunar state and time of day had no effect. No significant interactions between factors were identified for either feeding mode. However, the isotopic analysis did not support the ethological findings as the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ratios demonstrated no differences between sites (see Fig. 4).

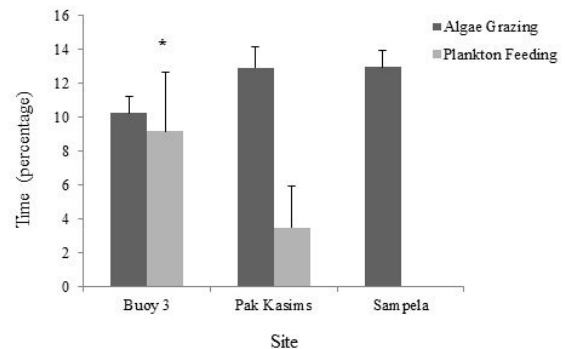


Figure 3: The percentage of total observation time of herbivory and planktivory for *P. lacrymatus* at the three sites (±SE).

The abundance of the species *A. curacao* and the proportion of time spent plankton feeding did not vary spatially. The species was observed spending the same amount time grazing on macroalgae across all of the sites. The algal feeding only contributed to a relatively small percentage of time (15.3±3.0%) in comparison to plankton feeding (76±3.6%).

The abundance of the study species *P. lacrymatus* and *A. curacao* showed no variation between sites. The abundance of the total fish assemblage, however,

was lowest at Sampela and of the fish assemblage the abundance of herbivores, planktivores, and fish belonging to the Pomacentridae family was again lowest at Sampela.

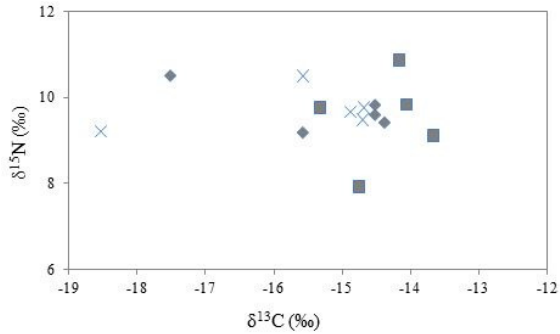


Figure 4: Plot of $\delta^{15}\text{N} \text{ ‰}$ versus $\delta^{13}\text{C} \text{ ‰}$ isotope ratios from individuals of *P. lacrymatus* muscle tissue from the site Buoy 3, Pak Kasims, and Sampela taken in 2008. Diamonds represent Buoy 3, squares represent Pak Kasims, and crosses represent Sampela.

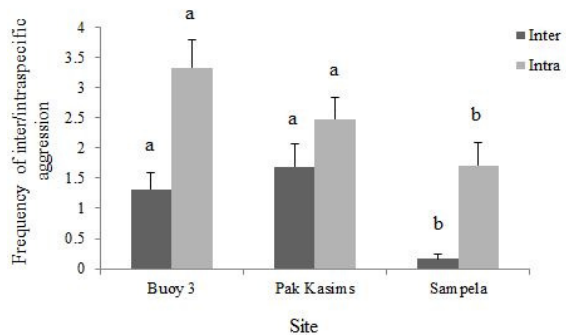


Figure 5: The frequency of inter/intraspecific events per *P. lacrymatus* observation at each site (\pm SE). The alphabetical letters denote significant differences across sites.

Time investment in to aggressive behaviors was significantly reduced at the low quality Sampela site. The frequency of aggressive events also was lowest at Sampela in comparison to the other sites (see Fig. 5). The species most frequently engaged with *P. lacrymatus* during interspecific events was *Pomacentrus moluccensis* at Buoy 3 and Pak Kasims, but this species was not recorded in aggressive interactions at Sampela. The species at Sampela with the highest frequency of interactions with *P. lacrymatus* was *A. curacao*.

Territory area was the same across sites although volume was highest at Sampela ($H=13.55_{(2)}$, $P<0.001$) (see Fig. 6).

Discussion

The study species both showed a degree of flexibility in trophic guild membership. The herbivore *P. lacrymatus*, was found to be capable of planktonic feeding. This planktivorous behavior occurred at two

higher quality reefs of the three study sites and only on flood tides (lunar cycles and time of day had no effect on their feeding behavior). The lack of plankton feeding at the degraded site could have been a result of lesser abundance of the resource or the turbidity of the water. Furthermore, the highly abundant benthic algae at the site could make planktivorous feeding unbeneficial or unnecessary.

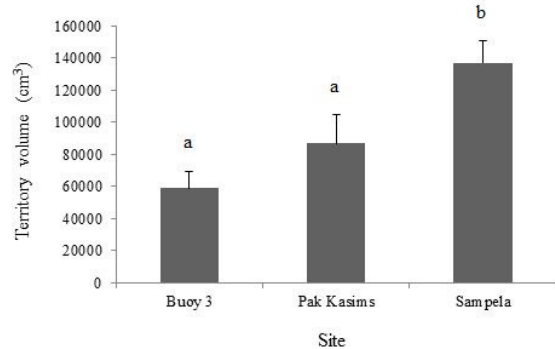


Figure 6: The mean volume of territory size for *P. lacrymatus* at the three sites (\pm SE). The alphabetical letters denote significant differences across sites.

However, the ethological results obtained for the planktivorous species *A. curacao* suggest that resource limitation was not the key factor, as the species plankton feed equally across the sites. It has been found that fish learn to eat new food types by social observation of other conspecifics and these individuals are termed as ‘demonstrators’ (Magnhagen and Staffan, 2003). The absence of *P. lacrymatus* demonstrators at Sampela may be an explanation for the lack of plankton feeding recorded at the site. Perhaps a future transplant experiment of *P. lacrymatus* individuals between the sites would be able to test this hypothesis. The species *A. curacao* also exhibited feeding plasticity as the species supplemented plankton feeding with algal grazing. This plasticity occurred at all the sites studied and is seemingly unaffected by environmental conditions.

Niche theory predicts that niche size will expand in the absence of competition (competitive release) and contract under competition (Werner, 1976). However, the data from this research found the opposite – competition resulted in niche expansion of *P. lacrymatus* with spatial behavioral plasticity coinciding with an increase of competitive pressure. The measure and difference in competition across sites was supported by three sets of data: fish abundance, behavioral aggression, and territory size. Firstly, the total fish abundance data showed higher numbers of fish at Buoy 3 and Pak Kasims than at Sampela. Secondly, the percentage of time spent in and the frequencies of inter and intraspecific

aggressive behaviors were higher at Buoy 3 and Pak Kasims than at Sampela. Thirdly, the territory data, the area data showed no differences between the reef sites. However area of territory is only comparable where territory habitat utilization and vertical profile are the same across sites. The problem arises when comparing territories with different vertical profiles. When the complexity of the territories was also considered the volume of the territories was found to be largest at Sampela. Interestingly Sampela is the reef which had the least complex substratum; this indicates the fish at Sampela are selecting a highly complex area for territories. Perhaps the lack of competitive pressure allows *P. lacrymatus* to select and maintain territories which are highly complex, these areas would be beneficial as the surface area is greater for algal growth. Thus the territory data supports the spatial pattern of the lower fish abundance and lower durations and frequencies of aggressive interactions as larger territories were found at Sampela. In conclusion, the data indicates a higher competitive pressure at Buoy 3 and Pak Kasims is linked to opportunistic feeding behavior of *P. lacrymatus* at these sites.

This study has identified an opportunistic feeding behavior and additionally determined the factors that are possibly driving this expansion in niche. The switch in feeding guild at two of the sites was not supported by a significant difference of the isotope ratios. However, the planktonic behavior was sporadic and the isotope sample small and thus individuals which exhibited this behavior may have been missed by the sampling. This together with the complication of multi-source diets and the variation in the benthic sources may have resulted in a lack of difference between sites. Replication of this study across a larger spatial scale and across regions would determine if this behavior is localized or a common trait of this species. Published research has shown variation in reef fish diet across a large scale (Sano, 1987). Understanding whether this diet variation is a result of resource availability, competition or learnt behavior is vital to an understanding of the structuring and functioning of reef systems and how they will respond to disturbance.

In summary guild membership for both species was not exclusive, with both species being capable of algal grazing and plankton feeding. The spatial variation in *P. lacrymatus* feeding was correlated with higher site quality and the increase of competition within the environment and not as previously recorded an opportunistic response to food availability (Pratchett et al, 2001). It is concluded that behavioral adaptability and expansion of the recognized niche at a species level needs to be taken

into account for reef fish trophic modeling and the predictions of reef fish functionality through the identification of total guild biomass to ensure more effective conservation management can take place.

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