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Novelty Interactions Between Herbivorous Fish and Sargassum: Insight into Macroalgal Phase Shifts

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**Novelty interactions between herbivorous fish and *Sargassum*:
Insight into macroalgal phase shifts**

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Abstract

Herbivores play a key role in the maintenance of algal and coral communities. A reduction in herbivory has been shown to result in a shift to a macroalgae dominated system, which can have significant effects on the biodiversity and restorative capabilities of coral reefs. Several studies have been done to better understand how herbivorous communities respond to macroalgae. These have shown that only certain herbivorous taxa are capable of removing macroalgae and there are several factors (depth, density, etc.) that affect the susceptibility of macroalgae to herbivory. However, few studies have yet to determine if the novelty of the resource will affect how herbivorous fish communities respond to a macroalgae phase shift.

This study examined the existence of a novelty response at both a community and species level at a mid-shelf reef in the Great Barrier Reef, using macroalgal arrays and aquarium. The macroalgal arrays, of *Sargassum*, did show a delayed response, however the tank experiments of a herbivorous species (*Siganus doliatus*) did not exhibit any change in preference of the familiar and novel food over time. The lack of a novelty response in the species suggests that the delayed response exhibited by the herbivorous fish community was due to the time it took the fish to find the new resource. This means that the response of herbivorous fish communities that have never experienced macroalgae should be comparable to communities with similar fish compositions that have experienced macroalgae before.

Keywords: Novelty, Phase shift, Macroalgae, *Sargassum*, *Siganus doliatus*, Herbivory
ISP Topic codes: 614, 601, 624

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1. Introduction

It is widely acknowledged that herbivores play a key role in the structure and resilience of coral reefs, specifically by managing the balance between algal and coral communities (Bellwood et al. 2004; Mumby et al. 2006; Burkepile and Hay 2008). If unmanaged, algae can have significant effects on both the recruitment of corals and the corals ability to compete for space (Lewis 1986, Tanner 1995; Kuffner et al. 2006). Overfishing and other anthropogenic factors (ie. eutrophication) have both been shown to considerably alter this balance (Littler et al. 2006). Several studies have exemplified the effects of removing herbivores from coral reefs to show the impacts of overfishing, which resulted in a shift to a macroalgae dominated system (McClanhan et al. 2001; Hughes et al. 2007). This shift in environmental composition will cause a loss in biodiversity (Jackson et al 2001; Mumby et al. 2006) and decrease the probability of restoration (Worm et al. 2006). Understanding the response of herbivores to macroalgal phase shift will be exceedingly important in the further management of these systems.

Several studies have been conducted on the response of the herbivorous fish community to the introduction of macroalgae and have shown considerable variation in feeding amongst herbivorous taxa (Steneck 1988; Bellwood et al. 2004). This has highlighted the existence of two functional groups (browsers and grazers) within the herbivorous community that occupy two very different roles in the management of algae on coral reefs (Bellwood et al. 2006). Grazers help to resist shifts to alternate states by consuming algal turfs and will typically avoid eating macroalgae strands (Bellwood et al. 2004; Nystro 2006), while browsers help to remove leathery macroalgae and possibly restore coral dominance (Hoey and Bellwood 2009; Bellwood et al. 2006). Without the presence of either group the resilience of the coral reef to macroalgae would be greatly altered (Hughes et al. 2007).

Other behavioral studies have shown that other factors exist that have a significant effect on the susceptibility of macroalgae to herbivory: density of macroalgal clumps (Lewis 1985) depth (Hoey and Bellwood 2010a) and species of macroalgae (Mantyka and Bellwood 2007a; Mantyka and Bellwood 2007b). These findings show that the ability to remove macroalgae varies significantly amongst habitats (Hoey and Bellwood 2010a), depending not only on the composition of the herbivorous fish community but also a variety of other factors. This variability in responses amongst habitats needs to be better understood in order to increase the effectiveness of further management projects of coral reefs.

While multiple studies have been done on the responses of herbivores to macroalgal phase shifts, few studies have examined if the novelty of this resource also has an effect on the responses of fish herbivores. When animals are posed with novel or unfamiliar resources they will sometimes avoid the resource (Galef 1993). This aversion will usually not last long, however the consumption of the resource may take a longer period of time to occur (Marples et al. 1998; Marples and Kelly 1999). While these studies examining novelty were conducted on birds and rats the same results should hold true for fish. Previous studies using macroalgae assays (transplanted pieces of macroalgae) have noticed a delayed response in the removal of macroalgae and have speculated that this may be attributed to a novel response (Littler and Littler 2007; Hoey and Bellwood 2010b). If fish do express this novel reaction than the way fish communities respond to macroalgae may be exceedingly different due to the differing amount of exposure each community has had to macroalgae.

Evaluations of the distribution of macroalgae within the Great Barrier Reef (GBR) have shown a decrease in the density of macroalgae from the inshore reefs to the outer shelf reefs. The inshore reefs (approximately 5-20km offshore) had 50% of Leathery macroalgal covering of

the substratum (McCook et al. 1997; Wismer et al. 2009) with less than 5% covering on the mid shelf reefs (Hoey and Bellwood 2009) and even less on the outer shelf reef (McCook et al. 2000). Based off the novelty theory the responses of herbivorous fish communities should be on average different across the three zones. The response of the herbivores in the outer-shelf and even the mid-shelf reef should be different than those fish in the inner-shelf reef that have been exposed to relatively significant amounts of macroalgae. One would expect the herbivores in the outer and mid shelf reef to have a delayed response to the introduction of macroalgae or not eat the macroalgae at all.

Hoey and Bellwood 2010b examined cross shelf variation in browsing intensity of macroalgae, specifically *Sargassum*, and noticed low removal rates in the outer shelf reef though browsers known to eat significant amounts of macroalgae (ie. *Naso unicornus*: Hoey and Bellwood 2009) were present. This result was hypothesized to be due to the lack of interactions /experience that the fish community on the outer-shelf reef would have with the macroalgae (Hoey and Bellwood 2010b). Similarly, Littler and Littler 2007 noticed a delayed response in the removal of macroalgae which they too attributed to a novelty effect. No study has yet to quantify the validity of this novelty effect in either individual species of fish or herbivorous fish communities.

1.1 Aims of Study

The aim of this study therefore is to examine the existence of a novelty effect at a community and species level through the use of macroalgal (*Sargassum*) assays and aquarium, at a mid-shelf reef in the northern GBR that has never experienced a macroalgal phase shift. Rates of removal of the assay will be used to quantify if there is a delayed response in the fish community to the addition of a novel resource. The dietary preference of an individual species,

shown to be greatly affecting the removal of the *Sargassum* through video observations, will be studied in aquarium to see if the ratio of the number of bites on *Sargassum* to turf algae increase. The results of the tank experiment will suggest whether the community delayed response, if there was one, was a result of a novelty effect or the amount of time it took the community to recognize the presence of an available resource.

2. Methods

2.1 Study Site

The study was conducted between October and November 2012 at Lizard Island (14°40'S, 145°28'E) a mid-shelf reef in the northern GBR. Two sheltered fringing reefs on the northwest side of the Island, Mermaid Cove and Turtle Bay, were selected to examine the response of the herbivorous fish community to a novel resource, macroalgae (*Sargassum* spp.). Experiments examining the response of a single species (*Siganus doliatus*) to macroalgae were also conducted using the aquarium system at the Lizard Island Research Station. Fish used in the experiments were collected from Mermaid Cove, well away from the array to ensure the individuals collected did not interact with the array.

The *Sargassum* used in both experiments was collected from the Turtle Island group (28km west of Lizard island), an inshore reef of the northern Great Barrier Reef. The Turtle group is composed of several coral keys with significant *Sargassum* spp. biomass covering the reef flat. The Turtle group is subject to terrigenous inputs into region from coastal estuaries, facilitating the growth of macroalgae.

2.2 Collection and handling of *Sargassum*

Sargassum was selected as it is one of the most common and largest forms of macroalgae found on the inner-shelf reef of the GBR (Lefevre & Bellwood 2010). Previous studies monitoring the effects of large herbivorous fish exclusion on a reef crest in the GBR showed that *Sargassum* was the main successional genus after an experimentally induced phase shift to a macroalgal dominant system (Hughes et al. 2007). *Sargassum* has also been recorded as the dominant benthic taxon following phase shifts to macroalgal dominance on east African Reefs

(Graham et al. 2006). The species of *Sargassum* collected, though difficult to distinguish (Kilar and Hanisak 1988), was most likely *S. swartzi*.

Sargassum was removed by gently pulling the algae's thallus from the benthic substrate. Care was taken to ensure the holdfast of each thallus remained intact. The *Sargassum* was then transported to Lizard Island and put into aquariums with flow through seawater within 90 mins of collection. All of the *Sargassum* were deployed onto the reefs or into experimental tanks within one week of collection. Thalli were discarded if any degradation was noted during holding.

2.3 Data Collection

2.3.1 Community Novelty in Turtle Bay and Mermaid Cove

Sargassum thalli were deployed in two plots, one in Mermaid Cove and the other off Turtle Beach, in an area measuring approximately 50m². Initially, approximately 130 thalli were deployed within each plot and algae were added every second day, resulting in an average density of 3 thalli per m². In total, the total number of thalli in each plot never fell below 100. To fix the algae to the reef, thalli were tied to six, 10 meter long, spaced approximately 60 cm apart.

An index was created in order to evaluate the overall degradation of the array (Table 1). When the index was three or below the following day *Sargassum* was added to ensure that the macroalgae in the array maintained dominance over the coral composition.

Table 2. shows the index used in the evaluation of the degradation of Mermaid Cove and Turtle bay

Index Number	Description
1	Thalli lack floats and are beginning to decompose (becoming gelatinous). Less than 10% of thalli are left.
2	Few thalli have floats or blades. 2/3 to 5/6 of the thalli have been removed.
3	Most thalli's still have floats. 1/2 to 2/3 of algae are present.
4	Majority of algae is present and show few signs of predation by herbivores.
5	No change in biomass. Macroalgae does not show any noticeable interactions with herbivores and is in a similar state to the point of collection.

The response of the herbivorous fish community to a novel resource was evaluated by measuring the change in the rate of removal of the *Sargassum*. This was done by deploying tagged thalli, to both arrays, at different time periods and measuring the height of the thalli daily until they were removed. Initially, three tagged thalli were randomly placed in both algal arrays during the initial deployment of the algae. On the fourth and sixth day of the array another seven and ten thalli (tagged) were added to each array, respectively. The average rate of removal was calculated at each site.

A macroalgal control was also used at each site to determine if the measured losses in *Sargassum* height were due to herbivory. Cages (approximately 1,000 x 500 x 500mm) made of wire mesh were used to exclude herbivorous fish. Three thalli of *Sargassum* were placed in cages at both sites in a similar location to those in the experimental algal arrays. The height of each thalli was measured daily for a total of twelve days. The rate of removal of the caged thalli was compared to the exposed, tagged thalli, from the 1st deployment, to determine the impact of herbivorous fish on degradation of the macroalgae.

2.3.2 Novelty of a model herbivore; *Siganus doliatus*

The response of individual *Siganus doliatus* to *Sargassum*, a novel resource, was assessed in a controlled aquarium study. *S. doliatus* were chosen as video monitoring showed *S. doliatus* feeding on the *Sargassum* at both arrays. *S. doliatus* has a fairly small home range approximately 180 meters (Fox and Bellwood 2012) which suggests that the fish caught in mermaid would most likely never have experienced macroalgae before this experiment.

Fourteen *S. doliatus* were collected from mermaid cove and placed in aquarium (300 L) with an excess of rubble and turf algae. Rubble was replaced every second day to ensure that turf algae did not deplete. The day after the fish were collected, thalli of *Sargassum* were placed in each tank.

Video monitoring was used to observe the number of bites taken on *Sargassum* and turf algae by *S. doliatus* over the course of six days. Videos were taken in the aquariums within one hour of mid-day and recorded for three hours. Numbers of bites of *Sargassum* and turf algae were recorded for each individual for 15 minutes at the 45 minute mark of every hour. Average bites of *Sargassum* and turf algae were calculated for each individual every day. The first 15 mins were discarded to remove observer effects of camera set up. While the videos were not recording a cylindrical cage (200mm diameter x 400mm depth), made of wire mesh, was placed around the *Sargassum* to control the specimen's access to the resource.

3. Results

3.1 Community Novelty in Turtle Bay and Mermaid Cove

Polynomial relationships were graphed for each deployment (Fig. 1-3). There was an increase in the removal rate of both arrays from the initial deployment of the *Sargassum*. While the relative shape of the polynomial curves did not differ significantly from the 2nd to the 3rd deployments for either array (Fig.2 &3), the difference between the 1st and 2nd deployments (Fig.1 & 2) were significant. The curves of the 1st deployments (Turtle $y = -0.9571x^2 + 1.3804x + 94.112$, $R^2 = 0.9595$; Mermaid $y = 0.2217x^2 - 11.775x + 103$, $R^2 = 0.917$) were flatter than the 2nd deployments (Turtle $y = 1.3733x^2 - 35.107x + 220.21$, $R^2 = 0.9965$; Mermaid $y = 4.4045x^2 - 78.953x + 343.83$, $R^2 = 0.9316$). The similarity in steepness of the curves between the 2nd deployments (Turtle $y = 1.3733x^2 - 35.107x + 220.21$, $R^2 = 0.9965$; Mermaid $y = 4.4045x^2 - 78.953x + 343.83$, $R^2 = 0.9316$) and 3rd deployments (Turtle $y = 1.3978x^2 - 45.27x + 324.8$, $R^2 = 0.9875$; Mermaid $y = 2.3119x^2 - 58.9x + 369.33$, $R^2 = 0.9982$) show that removal rates began to stabilize after about the sixth day.

The removal rates of the caged thalli at both arrays were compared to the removal rate of the arrays for each deployment (Fig. 1-3). There was very little change in height of the caged thalli at either array for each of the deployments. This showed that the removal of *Sargassum* height was almost entirely due to herbivorous interactions.

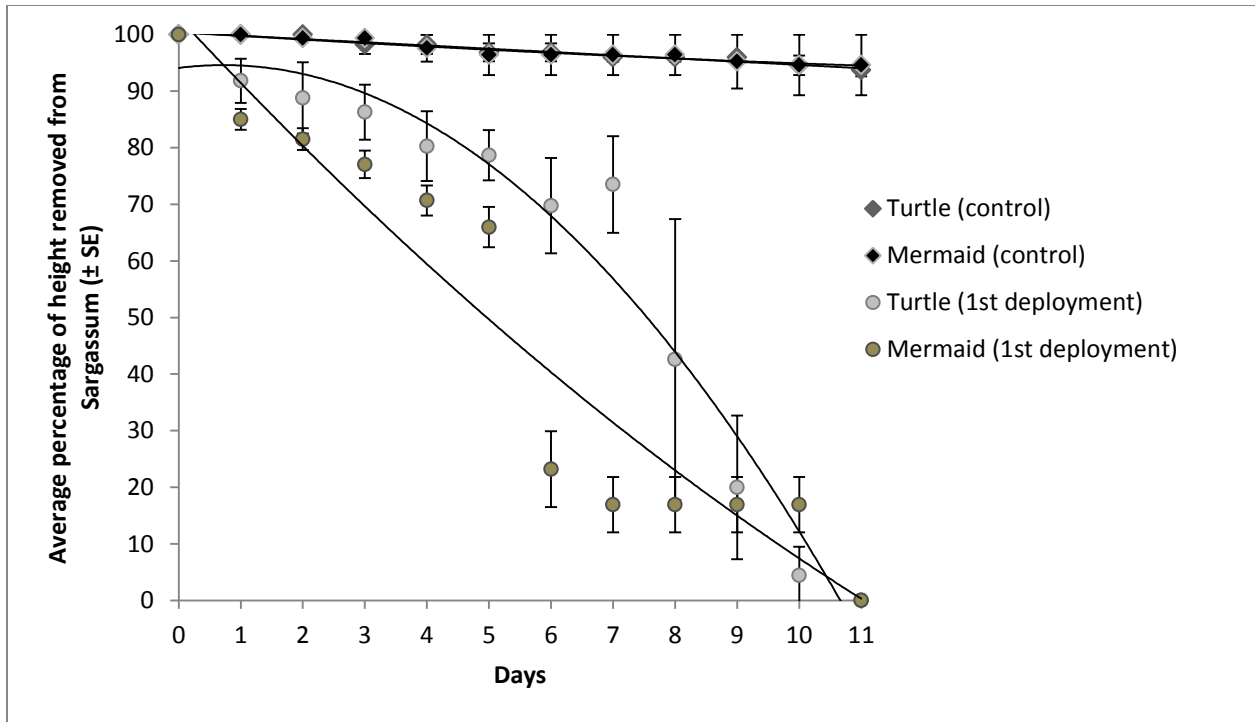


Figure 1. The average percentage of height removed for the first deployment of tagged *Sargassum* and caged *Sargassum* at both arrays over the course of eleven days. Polynomial relationships express the rate of removal over time. Turtle (control): $y = -0.0003x^2 - 0.57x + 100.36$, $R^2 = 0.9533$; Mermaid (control) $y = 0.0149x^2 - 0.7047x + 100.47$, $R^2 = 0.9396$; Turtle (1st deployment) $y = -0.9571x^2 + 1.3804x + 94.112$, $R^2 = 0.9595$; Mermaid (1st deployment) $y = 0.2217x^2 - 11.775x + 103$, $R^2 = 0.917$. Bars represent mean ± SE.

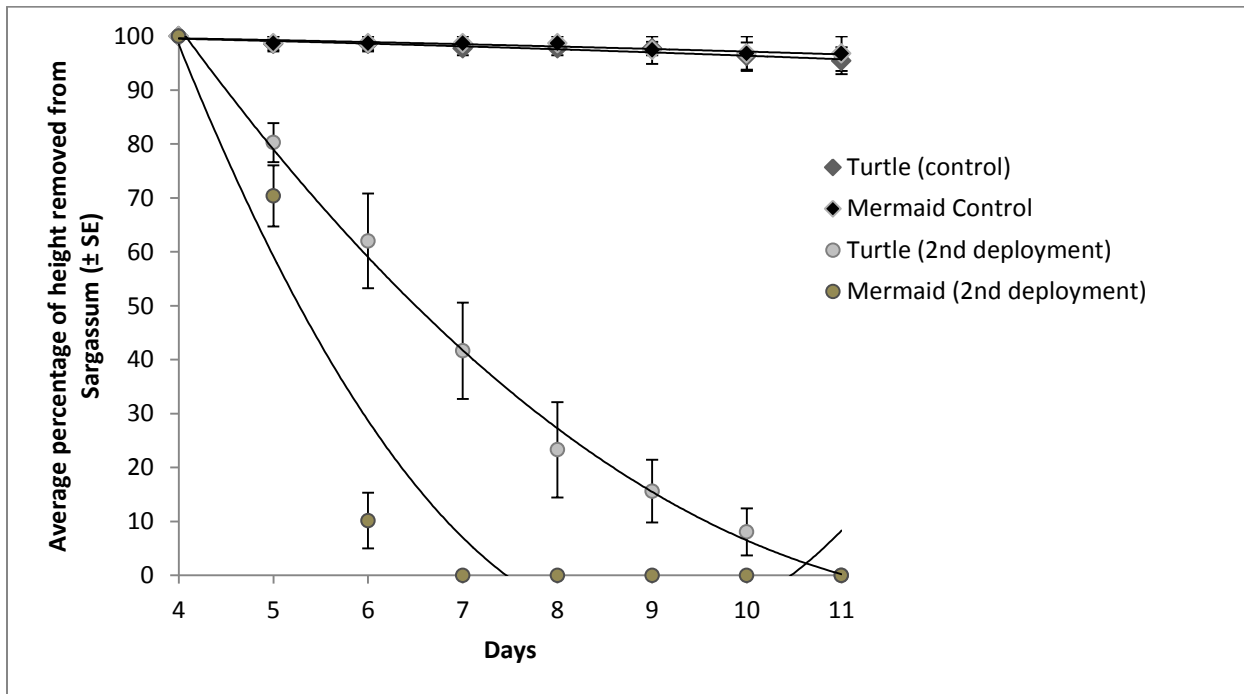


Figure 2. The average percentage of height removed for the second deployment of tagged *Sargassum* and caged *Sargassum* at both arrays for the last seven days of the array. Polynomial relationships express the rate of removal over time. Turtle (control): $y = -0.0186x^2 - 0.2654x + 100.9$, $R^2 = 0.9074$; Mermaid (control) $y = -0.0153x^2 - 0.1984x + 100.66$, $R^2 = 0.8726$; Turtle (2nd deployment) $y = 1.3733x^2 - 35.107x + 220.21$, $R^2 = 0.9965$; Mermaid (2nd deployment) $y = 4.4045x^2 - 78.953x + 343.83$, $R^2 = 0.9316$. Bars represent mean ± SE.

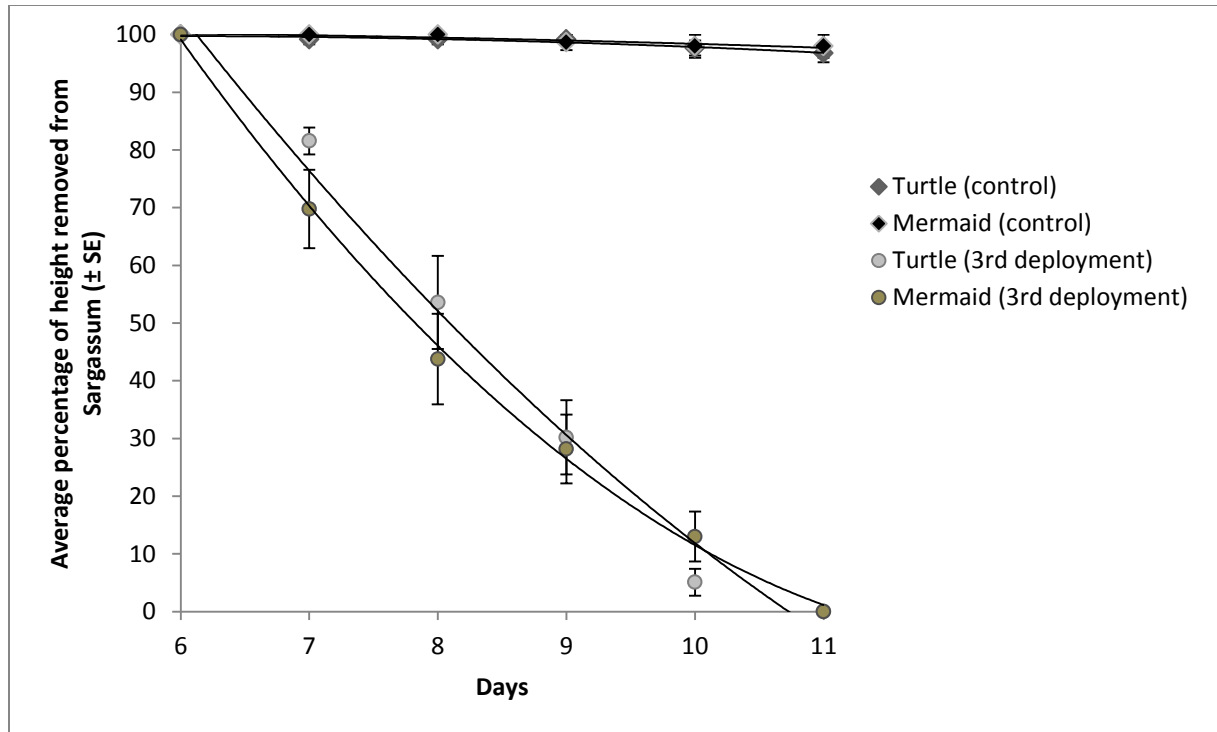


Figure 3. The average percentage of height removed for the third deployment of tagged *Sargassum* and caged *Sargassum* at both arrays for the last five days of the array. Polynomial relationships express the rate of removal over time. Turtle (control): $y = -0.1058x^2 + 1.2161x + 96.269$, $R^2 = 0.9195$; Mermaid (control) $y = -0.0476x^2 + 0.3143x + 100.02$, $R^2 = 0.8689$; Turtle (3rd deployment) $y = 1.3978x^2 - 45.27x + 324.8$, $R^2 = 0.9875$; Mermaid (3rd deployment) $y = 2.3119x^2 - 58.9x + 369.33$, $R^2 = 0.9982$. Bars represent mean \pm SE.

3.2 Novelty of a model herbivore; *Siganus doliatus*

The average percentage of bites taken on *Sargassum* was calculated for *Siganus doliatus* (n=14) over the course of five days (Fig.4). The feeding preference remained fairly consistent, showing little to no decrease or increase in *Sargassum* consumption. The initial average percentage of bites (18.2%, SE \pm 3.53) was similar to the 5th day (21.7%, SE \pm 3.7). The polynomial regression ($y = -1.6862x^2 + 10.077x + 15.696$, $R^2 = 0.6095$) shows that there were a greater number of bites on *Sargassum* on the third and fourth day. Average % of bites of the third (37.4%, SE \pm 8.35) and fourth day (30.4%, SE \pm 8.43) were slightly higher but had a much larger range of variance, relative to the other days.

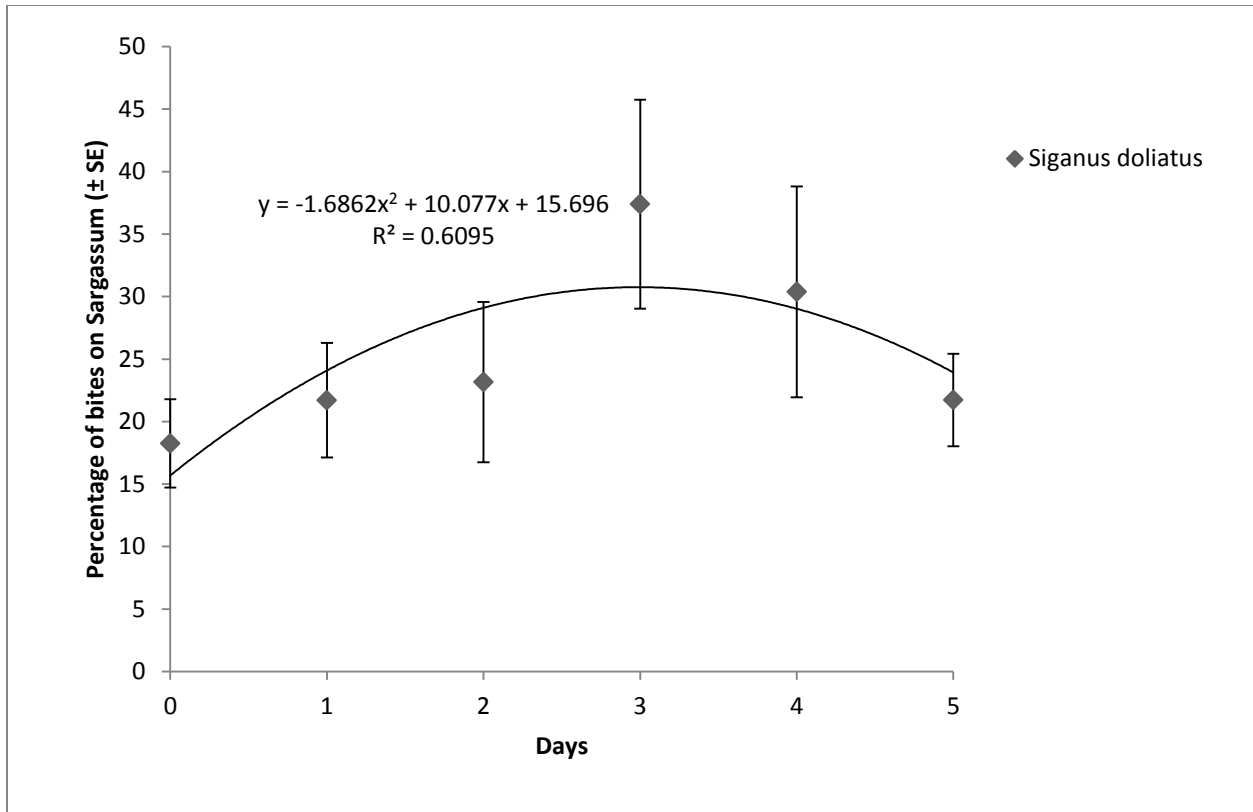


Figure 4. The average number of bites of *Sargassum*: Turf algae taken by *Siganus doliatus* over time. Polynomial relationship used to express change in dietary preference over time. Bars represent mean \pm SE.

4. Discussion

The results from this experiment represent the first time a novelty response of herbivorous fish has been quantified at both a community and species level. The novelty community experiment showed that both arrays had a delayed response in the rate of removal of *Sargassum*. This delayed response in feeding can be explained by two hypotheses: (1) as the resource was left out more herbivorous fish became aware of its presence and started to feed on the new resource over time or (2) the fish exhibited a novel response and slowly became more comfortable with the new resource, which led to an increase in removal of the resource. Both hypotheses can also explain why the removal rates in both arrays began to level out in the third deployment. If the delayed response was due to a change in the fish composition near the array eventually the influx of new fish coming to eat the *Sargassum* would decrease, resulting in removal rates to taper off; however, if the delayed response was due to a novelty response eventually more herbivorous fish would become comfortable with the resource until they all began eating the *Sargassum*, at which time removal rates would stop increasing and stay fairly consistent.

To evaluate these hypotheses a tank experiment was set up to examine the interaction of a species (*Siganus doliatus*) to the addition of a novel resource (*Sargassum*). The results of the experiment showed that the percentage of *Sargassum* to turf algae intake stayed fairly consistent over the course of five days. This result is not congruent with current expectations of novelty interactions that would suggest an increase in the consumption of a new food resource over time. While in past studies it has been suggested that this delayed response may be due to a novelty effect (Hoey and Bellwood 2b; Littler and Littler 2007) this study shows that a novelty response does not exist for *Siganus doliatus*.

These findings suggest that the delayed response experienced by the community and not the individuals (*Siganus doliatus*) is likely due to the time it takes the whole community to recognize the presence of the new available resource. An evaluation of the herbivorous fish composition in response to a macroalgal phase shift would need to be evaluated in order to more definitively state that the delayed response was in fact due to the time it takes the fish to find the macroalgae. The results from this would most likely show a noticeable increase in the density of browsers and some grazers (Bellwood et al. 2006; Mantyka and Bellwood 2007a) near the macroalgae over time.

4.1 *Ecological Implications*

The lack of a novelty effect amongst herbivorous fish provides a better understanding of how herbivorous fish will react to the introduction of macroalgae. Past studies have shown that nutrient pulses are not enough to induce a phase shift to a macroalgal system because herbivores are able to maintain the growth of the algae (McCook 1999). However, a reduction in herbivory has been shown to lead to increases in algal standing crop (McClanahan et al. 2001; Hughes et al. 2007). In areas such as the outer shelf reef of the GBR, where fish have never experienced macroalgae (Hoey and Bellwood 2010b), a novelty reaction would cause a delayed response in the consumption of the macroalgae. This could result in a reduction in herbivory that would allow macroalgae to establish. However, the present study suggests that there will be no delayed response, except the time it takes for the herbivorous fish community to recognize the presence of the algae. This is significant because it shows that habitats consisting of similar fish composition should respond similarly to macroalgal phase shifts dominated by the same species of macroalgae.

This study also highlights that if the macroalgae is not being eaten it is not because of unfamiliarity but more so because of preference. In Kaneohe Bay, Hawaii nutrient pulses (from sewage discharge) and overfishing led to a shift in the reef community composition to a macroalgae dominated system. Once the sewage discharge was diverted and fish community was established it was believed that the abundance of macroalgae (*Dictyosphaeria cavernosa*) would begin to decline; however, it remained abundant in much of the bay. This has been attributed to introduced species of algae that are preferred by the herbivores over the native algae (Stimson et al. 2001). This shows that invasive species of macroalgae that have been thought to deter fish due to their foreign nature is actually because of metabolites (Davis et al. 2005) and other properties (nutritional content, toughness, etc.) that are not preferred by fish (Mantyka and Bellwood 2007) and make the macroalgae less palpable (Littler and Littler 2007).

While *Siganus doliatus* did not exhibit a novel reaction this is not to say that another species will not. Studies done by Marples and Kelly (1999) have shown great variance in the response to a novel food source amongst species of birds. Some birds took several weeks to eat the novel food when given a choice between that and a familiar resource while other birds consumed the novel food immediately. This could have major implication on the variable response amongst habitats in the GBR and other coral reefs that have not experienced macroalgae before. If the fish composition consists of species that have a novel reaction then their ability to remove the algae before it is established may be compromised. Species that have been designated in previous studies as playing a key role in the balance between algae and coral may not be able to in areas such as the outer shelf reefs. *Naso unicornus*, recognized as an important remover of macroalgae in many habitats (Hoey and Bellwood 2009), was observed inspecting transplanted macroalgae on the outer shelf reef but not eating it (Hoey and Bellwood

2010b). If this species does in fact have a reaction to novel resources than the ability of some habitats to remove macroalgae could be severely impacted.

4.2 Additional findings

Some experiments have highlighted specific herbivores (dominant browsers) that have had a key role in the removal of macroalgae at inshore and mid-shelf reefs: *Kyphosus vaigiensis*, *Siganus canaliculatus*, *P. pinnatus*, and *Naso unicornus* (Mantyka and Bellwood 2007a; Fox and Bellwood 2008; Hoey and Bellwood 2009). A few studies have evaluated the impact of *S. doliatus* and have shown that while it does take a considerable amount of bites on many different species of macroalgae it usually does not account for the majority of the biomass removal of the macroalgae (Fox and Bellwood 2008; Cvitanovic and Bellwood 2009). In present study, video observations showed large schools of *S. doliatus* eating in the array and while no quantification was taken on the amount the school removed direct observation showed many thalli decimated after the school had left. A previous study examining schooling in an herbivorous fish has shown that the bite rates of fish traveling in the school increase by two-three fold (Welsh and Bellwood 2012). This high bite rate combined with the large number of fish within the school may have been what resulted in a significant removal of biomass from the arrays by *Siganus doliatus*. This highlights that while some fishes as individuals do not have a large impact, as a school they can be fairly effective. The potential of schooling amongst species of fish should be taken into consideration when evaluating a habitats effectiveness of macroalge removal to avoid misinterpreting the potential ability of the herbivorous fish community to reverse a macroalgal phase shift.

5. Conclusion

The aims of this paper were to “examine the existence of a novelty effect at a community and species level”. The results clearly show that *Siganus doliatus* does not exhibit any change in preference of the familiar and novel food over time. While this may not be true for all species, it does show that when given a choice between a novel and familiar food not all herbivorous fish will eat only the familiar food. This result was used to suggest that the delayed response exhibited by the community of herbivorous fish at both arrays was not a result of a novelty effect, but rather a change in the fish composition of the surrounding area.

More studies need to be done examining novelty amongst other herbivorous fish species as well as examining novelty amongst other communities, such as the outer reef of the GBR. This will help to better understand whether novelty does exist amongst herbivorous fish and if communities that have a fish composition capable of removing macroalgae will remove it even when they have never experienced it before. Future studies should also look at changes in fish composition in response to the introduction of macroalgae to determine if the delayed response is actually due to the time it takes the fish to find the array.

6. References

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