THERMAL TOLERANCE AND METABOLIC RESPONSES OF
BRUSHTAIL TANG, ZEBRASOMA SCOPAS

A thesis submitted in partial fulfillment of the requirements for the degree of
Master of Science in Biology
by
Lorna J. McFarlane

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Thesis of Lorna J. McFarlane is approved:

__________________________________________
Dr. Robert E. Espinoza                          Date

__________________________________________
Dr. Wayne A. Bennett                            Date

__________________________________________
Dr. Larry G. Allen, Chair                       Date

California State University, Northridge
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ABSTRACT

THERMAL TOLERANCE AND METABOLIC RESPONSES OF BRUSH TAIL,  

Zebrasoma scopas

By:  

Lorna J. McFarlane  

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The brushtail tang (Zebrasoma scopas) is an important herbivorous fish species that plays a vital role in the maintenance of coral reef health though algal grazing. Algal grazing prevents algal overgrowth and thus a shift in reef ecology from dominant coral to pervasive algae. My project aimed to quantify the effects of rising ocean temperatures on the survivorship and metabolic rates of brushtail tang on the reefs surrounding Hoga Island, Indonesia. Fish were housed at 26 and 30°C for the duration of the experiment, consistent with current and predicted sea-surface temperatures over the next century. Stop-flow respirometry was used to determine the resting metabolic rate of Brushtail tang at both temperatures, and total oxygen consumption was used to estimate resting metabolic rates. Metabolic compensation ability was assessed using individually derived Q_{10} values for fish acutely exposed to warmer waters, and measurements were taken over
a time series of 1, 3, 7, and 10 days to test the effect of acclimation to warmer water. The temperature tolerance of brushtail tang was also determined as the critical thermal maximum (\(\text{CT}_{\text{max}}\)) with inversion as the endpoint. The ability of brushtail tang to metabolically compensate when acutely exposed to warming waters was found to be greater than that of other tropical reef fishes. However, acclimation was not found to further increase the compensatory metabolic ability of this species. Acute exposure to elevated temperatures increased \(\text{CT}_{\text{max}}\), however acclimation did not to further increase \(\text{CT}_{\text{max}}\). My data may be useful for predicting how this species responds to rising sea temperatures, which are likely to be encountered over the next century.
Introduction

By the end of the century, global warming is anticipated to cause up to a 3°C rise in mean sea-surface temperature (Meehl et al., 2007; Munday et al., 2008; Pandolfi et al., 2011) while the Indo-Pacific regions are projected to experience an increase of up to 4°C (IPPC, 2014). Coral reefs are especially vulnerable to the threat of warming waters (Paladino et al., 1980; Poloczanska et al., 2007), and serve a variety of economic and ecological functions including: supporting fisheries, promoting tourism, protecting coastlines, and increasing coastal biodiversity (Dikou, 2010). While many studies have examined coral responses to high water temperature, far fewer focus on the effects of rising ocean temperatures on reef-associated fish species. Herbivorous fishes exert system-wide influences on reefs by limiting algal overgrowth, which can negatively impact or even kill corals (Dikou, 2010). In addition to acting as integral species, herbivorous reef fishes are also an important income source for local fishermen. Unfortunately, reductions in herbivorous fish populations from overfishing, habitat degradation, and changing sea temperatures could shift reefs from coral-dominated to algae-dominated systems (Hughes, 1994; McClanahan et al., 2007). An ecological shift of this type would diminish the ability of coral to recover from natural disturbances like hurricanes, leaving them even more susceptible to anthropogenic disturbances. Therefore, it is important to begin addressing questions of how climate change may impact herbivorous reef fishes (Hughes et al., 2003).

I quantified the effects of increasing water temperature on the thermal tolerance and metabolic responses of the brushtail tang (*Zebrasoma scopas*), a herbivorous reef fish common to Pacific coral reefs (Figure 1). Hoga Island, Indonesia represents an ideal
study location, as the Indo-Pacific is the most diverse marine region in the world with an estimated 4000 fish species (Springer, 1982; Myers, 1999). Indonesia lies at the center of this biologically rich region with nearly 2500 fish species (Val & Randall, 2005), and also marks the center of the Indo-Pacific Warm Pool. The Indo-Pacific Warm Pool is the warmest region of any ocean, and recent findings suggest it may have also been as warm as temperatures predicted for 2100 during the Medieval Warm Period (950–1300 BP). Such historical fluctuations suggest that persisting species may exhibit greater thermal plasticity than originally predicted (Oppo et al., 2006).

![Brushtail tang, Zebrasoma scopas.](https://commons.wikimedia.org/wiki/File:Zebrasoma_scopas.jpg)

*Figure 1. Brushtail tang, Zebrasoma scopas. An acanthurid perciform common along the coast of East Africa, the Indo-Pacific, and well into the South Pacific. (https://commons.wikimedia.org/wiki/File:Zebrasoma_scopas.jpg)*

Brushtail tang are of particular interest given their ecological importance and their known preference for slightly deeper, potentially cooler tropical waters (Robertson et al., 1979). The species is widely distributed on reefs from East Africa, across the Indo-Pacific, and well into the South Pacific (Randall, 2001). Strictly herbivorous marine fish
are uncommon (Choat et al., 2002). Brushtail tang are explicitly herbivorous, grazing primarily on red turfing, fleshy or filamentous, and smaller thallate algae (Bailey & Robertson 1982, Choat et al., 2002). Although data are limited, some red algae exhibit increased or stable growth rates with increasing temperature (Gerung and Ohno, 1997). *Eucheuma denticulatum*, the species fed to fish in my study and prevalent around Hoga Island, grows optimally at water temperature ranging 22–32°C (Nishihara et al., 2013).

The morphological characteristics of brushtail tang, including a rounded, laterally compressed body with large sail like fins, a small truncate tail, and a small semicircular mouth at the end of a long rostrum, have also been shown to aid the fish in the exploitation of resources and habitats many others species cannot utilize (Robertson et al., 1979). It is apparent that brushtail tang fill an ecological niche that may be vital to ecosystem stability. Furthermore brushtail tang are fairly common in the aquarium trade industry and as these individuals are wild caught, the species provides both commercial and job market economic value.

Relatively little data exist on the predicted response of brushtail tang to changing thermal conditions, although the capacity for adaptation is key to determining an organism’s resilience to climate change (Seebacher and Franklin, 2012; Stillman, 2003; Somero, 2010). It is not known whether brushtail tang will be able to metabolically compensate to temperatures 3–4°C higher than current conditions (measured as resting metabolic rate). Likewise, the upper thermal limit of this species is also unknown (measured as $CT_{\text{max}}$). Significant uncompensated increases in metabolic rate would have a number of detrimental energetic consequences for recruitment, growth, and reproduction of brushtail tang populations; potentially leading to both negative
population-level effects, as well as negative effects the on coral reefs stemming from algal overgrowth (Randall, 1961; Vine, 1974).

To assess the thermal response of brushtail tang I first quantified metabolic response to an acute temperature increase. Second, I measured the upper thermal tolerance at both current and predicted reef temperatures. And third, I determined metabolic and thermal tolerance changes over time at both current and predicted reef temperatures. This allowed for the assessment of metabolic responses to warming waters, along with the effect of thermal acclimation by testing the following null hypotheses:

**H01:** Brushtail tang acclimated to laboratory housing at 26°C for 14 days and acutely exposed to 30°C will exhibit no significant change in routine metabolic rate.

**H02:** Brushtail tang acclimated to laboratory conditions at 26°C for 14 days, then acclimated at 30°C will exhibit no significant differences in metabolic rates as measured on days 1, 3, 7, and 10.

**H03:** Brushtial tang acclimated to laboratory conditions at 26°C for 14 days, then acclimated at 30°C will exhibit no significant differences in heat tolerance as measured on days 1, 3, 7, and 10.

**Methods**
Study Location

My study was conducted on Hoga Island, southeast Sulawesi, Indonesia (05° 27.53’ S, 123° 46.33’ E; Figure 2) in collaboration with Dr. Wayne Bennett from the University of West Florida and Operation Wallacea. Hoga Island is a small island within the Wakatobi National Park, the second largest national park in Indonesia, and is a “no take area” for fishermen. The quality of the reef habitat surrounding Hoga is considered among the highest in the Wakatobi with good water quality (Bell and Smith, 2004).

Figure 2. Location of Operation Wallacea Hoga Island Research Center, Southeast, Sulawesi Indonesia.

Fish Husbandry and Initial Acclimation

Seventy-two adult brushtail tang were collected via hand nets in the surrounding reef by local fishermen and transported to the Hoga Island Research Center. Fish were held in a 409-L tank filled with seawater at 26 ± 1°C, the approximate reef temperature in
Wakatobi National Park (Eme & Bennett, 2009) and maintained via routine water changes and occasional ice bottles to reduce the tank temperature as needed. Fish were visually assessed for physical appearance, absence of infections or parasites, consistent feeding, and normal swimming for 24 h. Animals that displayed signs of distress were released. Remaining fish were acclimated to laboratory tanks for 2 wk at 26 ± 0.05°C, and then placed into randomly assigned groups in 100-L treatment tanks for the remainder of the study. While in captivity, fish were fed twice daily for 1 h or to satiation with a diet of freshly collected and rinsed Eucheuma denticulatum mixed with sinking Spirulina pellets. Eucheuma is the overwhelmingly prevalent red alga found where the fish were collected, and was the only algal species they ate in the laboratory when offered six species to choose from. A 20% water exchange was performed after each feeding to insure water quality. Water temperature was recorded every 4 h. Fluctuations in water chemistry were negligible as water exchanges were both frequent and substantial. Fish were released back onto the reefs following experimental trials, as permitted on Hoga Island.

Resting-Routine Metabolic Rate (RMR)

Following the 2-wk acclimation period at 26°C, fish were randomly separated into two groups. One control group of 30 fish remained at the initial acclimation temperature of 26°C, and a second experimental group of 30 fish were moved to 30°C and subject to an acute temperature increase of ~0.2°C min⁻¹. Time-series measurements of resting metabolic rate (RMR) were determined for subsets of five fish from both treatment groups on days 1, 3, 7, and 10. Prior to the RMR trials, fish were fasted for 12 h
to ensure a post-absorptive state, thus avoiding specific dynamic action effects on oxygen consumption (Hopkins & Cech, 1994; Di Santo & Bennett, 2011). On the appropriate day stop-flow respirometry, was used to determine the RMR of each fish (see Steffensen, 1989; Cech, 1990). Briefly, fish were individually transferred into a respirometer (1535 ml) and held at a constant temperature (± 1°C) via a recirculating water bath and a Techne XX-W heater (TE-10A, Staffordshire, U.K.). To reduce stress, fish were habituated to the respirometry chamber for 40 min prior to measurements. This interval also allowed them achieve the temperature of the chamber (Brett 1971). During this period I observed the fish for normal swimming behavior. The respirometry chamber was surrounded by a water bath, which was connected to incoming and outgoing ports that continuously flushed the jacket with filtered sea water (63 μm plankton net). The respirometer was then sealed and water recirculated through the chamber. An oxygen meter (Yellow Springs Instrument 550A, Yellow Springs, Ohio) continuously monitored oxygen levels (mg min^-1) from the sealed respirometry chamber. Oxygen concentration and trial time was recorded once O₂ levels inside the chamber were reduced by approximately 20% because a greater reduction could result in hypoxia-induced metabolic adjustments (Hughes, 1973; Clark et al., 2013). The RMR of each fish was measured at least five times. Between trials, the respirometry chamber was flushed with fresh seawater until the oxygen concentration returned to pre-trial levels. Trials were not included in analyses if I experienced technical problems or if fish became agitated or excessively active. The oxygen consumed during the trial (mg O₂ g^-1 h^-1) was derived from the equation:

\[ ((O_2(i) - O_2(f))(V_{respirometer} - (M_{fish}*C))/T) - O_2(blank), \]
where \( O_{2(i)} \) and \( O_{2(f)} \) were initial and final oxygen concentrations in the respirometer (mg/L). \( V_{\text{respirometer}} \) was the volume (L) of the respirometer, \( M_{\text{fish}} \) was the wet mass (g) of the fish multiplied by the constant \( C \) (1.05), which uses specific gravity to correct for the displacement of water caused by the mass of the fish’s swim bladder. \( T \) was the time of the trial (min) and \( O_{2(\text{blank})} \) was the volume of non-fish respiration, if any, which was determined by running a trial with an empty respirometer (blank). Blank trials were run with each group of fish to determine whether there was any \( O_2 \) uptake not attributable to the fish (e.g., bacterial or planktonic respiration).

Comparisons between the 26°C (control) and 30°C (high temperature) groups at each acclimation interval (days 1, 3, 7, and 10) were made to assess changes in RMR. The mean total oxygen consumption for individual fish at both temperatures was used to calculate temperature-specific grand means. Differences in grand means were tested using a two-way analysis of covariance (ANCOVA) with acclimation time and temperature as factors, and mass a covariate. ANCOVA was preformed in preference to a two-way ANOVA with mass corrections, as oxygen consumption did not exhibit allometric scaling, or vary as a fixed proportion of body mass (Packard and Boardman, 1999).

**Acute Resting Metabolic Rate Trials**

An additional subset of five fish were subject to RMR trials before and after an acute temperature increase, also at a rate of \( \sim 0.2^\circ C \text{ min}^{-1} \); however these fish were not acclimated as described above. Total oxygen consumption from fish before and after acute exposure to the temperature increase was used to determine the temperature
quotient, or $Q_{10}$ values. The temperature quotient represents the increase in metabolic rate observed following a $10^\circ C$ temperature rise following the equation:

$$Q_{10} = \left(\frac{K_2}{K_1}\right)^{(10/(T_2 - T_1))},$$

where $Q_{10}$ is the temperature quotient, and $K_1$ and $K_2$ are grand means of metabolic rates of each temperature group at temperatures $T_1$ and $T_2$ (Schmidt-Nielsen, 1997; Dabruzzi et al., 2012). The resulting $Q_{10}$ value is used as an index for thermal sensitivity.

**Temperature Tolerance Trials ($CT_{\text{max}}$)**

The upper thermal tolerance of individual fish was measured following the RMR trials. Individual measurements were grouped by acclimation interval (1, 3, 7, or 10 d) and averaged to calculate the critical thermal maximum ($CT_{\text{max}}$) for each acclimation interval. $CT_{\text{max}}$ is a standard procedure for estimating thermal tolerance (Cox, 1974; Becker & Genoway, 1979; Paladino et al., 1980; Beiting et al., 2000; Eme et al., 2011) where fish experienced a temperature increase of $\sim 0.2^\circ C$ min$^{-1}$ until loss of equilibrium is observed. A shift from a normal upright swimming position to a horizontal orientation lying on the bottom on the tank was used as the endpoint for $CT_{\text{max}}$ (Cox, 1974; Lutterschmidt & Hutchison, 1997; Beiting et al., 2000). As for RMR, comparisons between the 26$^\circ C$ (control) and 30$^\circ C$ (high temperature) groups at each acclimation interval, and after acute exposure were made to assess changes in $CT_{\text{max}}$. A two-way ANCOVA was used to test for differences in $CT_{\text{max}}$ attributable to acclimation with acclimation time and temperature as main factors and individual mass was as a covariate.
Results

An increase in temperature was found to increase to the resting-metabolic rates of brushtail tang, as expected. The resting-routine metabolic rates of brushtail tang at 26°C and acutely exposed to 30°C were found to be significantly different (one-tailed t-test; \( t = 6.168, \text{df} = 4, p = 0.002 \)) when comparing raw VO\(_2\) consumption. This trend was further supported by the Q\(_{10}\) value. The Q\(_{10}\) for brushtail tang acutely exposed to warmer waters was found to range from 1.29–7.63, with a mean Q\(_{10}\) of 1.86 for raw VO\(_2\) consumption, and 1.92 for mass adjusted (adjusted with a 0.79 scaling exponent) VO\(_2\) consumption.

Acclimation to warmer water had no effect on RMR across acclimation days (ANCOVA: \( F_{3,31} = 2.40, p = 0.087 \); Figure 3). Only temperature and mass had a significant effect on RMR (ANCOVA: \( F_{3,31} = 8.67, p = 0.006; F_{1,31} = 2.50, p = 0.001 \), respectively). Finally, there was no significant effect of acclimation to warmer water on CT\(_{\text{max}}\) across acclimation days (ANCOVA: \( F_{3,31} = 2.72, p = 0.061 \); Figure 4); however temperature, was found to have a significant effect on CT\(_{\text{max}}\) (ANCOVA: \( F_{1,31} = 29.67, p < 0.001 \)).
Figure 3. No effect of acclimation on RMR was found (n = 5 fish temperature\(^{-1}\) day\(^{-1}\)) for brushtail tang when ANCOVA analysis was run on log VO\(_2\) consumed, with no mass adjustment. Data are reported in mg O\(_2\) min\(^{-1}\). The RMR of fish maintained at 26°C rose over time, however all treatment groups were housed in the same conditions negating a treatment effect. Fish in the lab were fed to satiation and did not experience predation pressure or costs of foraging, so it is reasonable to conclude that such an increase in consumption may lead to an increase in metabolic rate.
Figure 4. No significant effect of acclimation was found for the $CT_{\text{max}}$ ($n = 5$ fish temperature$^{-1}$ day$^{-1}$) of brushtail tang, however there is a clear effect of initial exposure to warmer waters.
Discussion

My study quantifies the temperature dependence of the metabolic rates of brushtail tang by first determining the species Q\textsubscript{10}, the factor by which metabolic rate increases over a 10°C interval. The estimated Q\textsubscript{10} of 1.92, means this species has a temperature-dependent metabolic rate that places the species within the range reported for other Indo-Pacific Perciformes (Table 1). Interestingly, previous studies have demonstrated such temperature increases to yield a 2–3-fold rise in metabolic rate in large coral trout (*Plectropomus leopardus*) (Johansen et al., 2015). For brushtail tang, a Q\textsubscript{10} of 1.92 equates to a 26–35% increase in metabolic demand for a 4°C temperature increase, as projected for the next decade. To avoid compromising overall health, growth, and recruitment, such an increase in metabolic demand would need to be met by food intake. While the ability of brushtail tang to adequately increase their energy intake for periods of time greater than 10 d remains unknown, their behavior and current energetic expenditure is encouraging. Brushtail tang exhibit only mildly territorial behavior in comparison to other reef fishes (Robertson et al., 1979) so it is reasonable to postulate that only a small proportion of their total energy budget is dedicated to aggressive territorial defense. This may be a favorable trait in light of increasing water temperature projections, as the increase in metabolic demand is more likely to be met if the increase in food intake is allocated to vital physiologic functions and not territorial behavior.

Although the Q\textsubscript{10} value of 1.92 was recorded for fish acutely exposed a temperature increase, short-term acclimation time was also found to have no significant effect on metabolism throughout my study. Though the acclimation time was limited to 10 d, other tropical fish species acclimate to temperature increases in a week or less,
suggesting longer acclimation would not have affected the final outcome (Barrionuevo & Fernandez, 1998; Nilsson et al., 2009). This finding is consistent with other short-term acclimation studies of tropical coral reef fishes, highlighting the fact that metabolic response to increased temperatures varies among species (Tullis and Baillie, 2005; Nilsson et al., 2009, 2010). Although a 1.5-year acclimation study of Acanthochromis polyacanthus found evidence of partial acclimation, this study noted reduced growth and overall condition, suggesting acclimation was costly (Donelson et al., 2011). Resting metabolic rate for brushtail tang at 26°C was also similar to other Indo-pacific Perciformes (Table 2), however no data exist for other species at 30°C.
Table 1. Comparison of $Q_{10}$ values for adult brushtail tang and juveniles of five Indo-pacific reef fishes from $^1$Eme and Bennett (2009) and $^2$Dabruzzi et al. (2013). All species are Perciformes and common in the Wakatobi National Park.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean wet mass (g)</th>
<th>Mean standard length (cm)</th>
<th>Mean Q10</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sandflat goby$^1$ Bathygobius sp.</td>
<td>0.34</td>
<td>2.71</td>
<td>1.06</td>
</tr>
<tr>
<td>Common goby$^1$ Bathygobius fuscus</td>
<td>0.91</td>
<td>3.12</td>
<td>1.12</td>
</tr>
<tr>
<td>Blackspot sergeant$^1$ Abedudefduf sordidus</td>
<td>0.19</td>
<td>6.06</td>
<td>1.26</td>
</tr>
<tr>
<td><strong>Brushtail tang Zebrasoma scopas</strong></td>
<td><strong>34.06</strong></td>
<td><strong>8.63</strong></td>
<td><strong>1.92</strong></td>
</tr>
<tr>
<td>Nine-banded cardinalfish$^1$ Apogonidae novemfasciatus</td>
<td>1.11</td>
<td>3.30</td>
<td>2.29</td>
</tr>
<tr>
<td>Sergeant major$^2$ Abudefduf saxitilis</td>
<td>0.21</td>
<td>16.0</td>
<td>2.40</td>
</tr>
<tr>
<td>White-tail humbug$^1$ Dascyllus aruanus</td>
<td>0.39</td>
<td>1.81</td>
<td>2.65</td>
</tr>
</tbody>
</table>
Table 2. Comparison of resting metabolic rates, given no acclimation time, of brushtail tang with five other Indo-Pacific reef Perciforms from ¹Eme and Bennett, 2009. Note that numbers here are not raw values as used in ANCOVA analysis of the effect of acclimation, but rather the values are mass adjusted using 0.79 as a scaling exponent for comparison purpose. Smaller fishes have a much higher mass adjusted metabolic rate due to allometric scaling.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean wet mass (g)</th>
<th>Mean standard length (cm)</th>
<th>Mean mg O₂ g⁻¹ h⁻¹ at 26 °C</th>
</tr>
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<tbody>
<tr>
<td>Brushtail Tang Zebrasoma scopas</td>
<td>34.06</td>
<td>8.63</td>
<td>0.31</td>
</tr>
<tr>
<td>Nine-banded cardinalfish¹ Apogon novemfasciatus</td>
<td>1.11</td>
<td>3.30</td>
<td>0.36</td>
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<tr>
<td>Common goby¹ Bathygobius fuscus</td>
<td>0.91</td>
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<td>0.34</td>
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<tr>
<td>White-tailed humbug¹ Dascyllus aruanus</td>
<td>0.39</td>
<td>1.81</td>
<td>0.71</td>
</tr>
<tr>
<td>Blackspot sergeant¹ Abeduufduf sordidus</td>
<td>0.19</td>
<td>6.06</td>
<td>1.41</td>
</tr>
</tbody>
</table>

My study demonstrates that the upper thermal limit for brushtail tang is well above the predicted sea surface temperature increase for the next century; however, simple exposure without extended acclimation does significantly increase the CTmax. Assuming brushtail tang can meet and sustain the increased energetic demand, we can anticipate the continued survival of brushtail tang based solely on the projected rise in global sea surface temperatures.

It is reasonable to predict a shift in some populations, which could result in reorganization of the food web. While my study examined the plasticity of metabolic responses of adult brushtail tang to acute warming and to short-term acclimation, it did not account for the effects of developmental plasticity. The potential for genotypic
temperature adaption, along with the influence if a myriad of other changing oceanic conditions and their interactions, remain to be determined. A large proportion of coral reef fishes experience broad temperature ranges because of their large latitudinal ranges (Nilsson et al., 2009), which are also genetically connected among populations (Planes, 2002). For example, yellow tang (*Zebrasoma flavescens*) migrate over large distances and multilocus genetic surveys suggest population connectivity across their distribution range, with no population subdivision noted within the Hawaiian Archipelago or across the tropical and subtropical Pacific (Eble et al., 2009, 2011, respectively). Although the larval connectivity of brushtail tang is not known, should the pattern even remotely resemble that of the yellow tang, there is reason to anticipate at least some degree of genotypic temperature adaptation.

The potential for such adaptation, combined with other life-history traits, such as lack of aggressive behavior and a herbivorous diet, bode well for the persistence of brushtail tang and their positive effects on coral reefs. In addition to being one of a few tropical marine herbivorous fish species, brushtail tang also exhibit comparatively high feeding rates (Robertson et al., 1979). The large consumption of algae is already a known contributor to the maintenance of coral reefs, through the prevention of a macroalgal phase shifts. As algal growth increases with warming sea-surface temperatures, an increase in algal consumption by brushtail tang, and other herbivorous fishes, may be exactly what coral reefs need.
Literature Cited


