

Feeding macroecology of territorial damselfishes (Perciformes: Pomacentridae)

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Received: 10 March 2008 / Accepted: 28 October 2008 / Published online: 18 November 2008
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Abstract The present study provides the first analysis of the feeding macroecology of territorial damselfishes (Perciformes: Pomacentridae), a circumtropical family whose feeding and behavioral activities are important in structuring tropical and subtropical reef benthic communities. The analyses were conducted from data collected by the authors and from the literature. A strong positive correlation was observed between bite rates and sea surface temperature (SST) for the genus *Stegastes*. A negative correlation was found between bite rates and mean body size for the genera

Stegastes and *Pomacentrus*, but this relationship was not significant when all territorial pomacentrids were analyzed together. A negative correlation between body size and SST was observed for the whole group and for the genera *Stegastes*, and *Pomacentrus*. No relationship was found between territory size and feeding rates. Principal Components Analysis showed that differences in feeding rates accounted for most of the variability in the data. It also suggested that body size may be important in characterizing the different genera. In general, tropical species are smaller and have higher bite rates than subtropical ones. This study extended the validity of Bergmann's rule, which states that larger species or larger individuals within species occur towards higher latitudes and/or lower temperatures, for an important group of reef fishes. The identification of large-scale, robust ecological patterns in the feeding ecology of pomacentrid fishes may establish a foundation for predicting large-scale changes in reef fish assemblages with expected future changes in global SST.

Communicated by S.D. Connell.

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Introduction

A major goal of macroecology is to study the general patterns of the ecological assembly and structure of biotas on a large scale (Brown 1995; Lomolino et al. 2006). Some of these patterns are surprisingly consistent; for example, there are “ecogeographic rules” (sensu Lomolino et al. 2006) in which recurring geographic gradients in the features of organisms occur across continental and/or marine realms (Gaston et al. 2008). Analyses of these gradients generally evaluate the relationships between geographical and/or environmental variables (e.g. latitude, temperature, humidity) and morphological aspects (e.g. body size, mass, color), and are the key to understanding patterns of

diversity along large-scale gradients (Lomolino et al. 2006).

Most macroecological studies have been conducted on terrestrial organisms (see Brown 1995; Eeley and Foley 1999; Kelt and Van Vuren 2001), with less focus on attempting to understand the underlying rules for aquatic organisms (Rex et al. 1997; Roy and Marteijn 2001; Alimov 2003), including fishes (Sale 1978; Macpherson and Duarte 1994; Minns 1995; Smith and Brown 2002; Floeter et al. 2005, 2007). Bergmann's rule, for example, which states that larger species or larger individuals within species (see Gaston et al. 2008) occur towards higher latitudes and/or lower temperatures, is well described for several vertebrate groups (e.g. mammals, birds, salamanders and turtles; Lomolino et al. 2006). However, there is little evidence that this pattern exists for marine fishes (see Discussions in Macpherson and Duarte 1994; Choat and Robertson 2002; Smith and Brown 2002). The present macroecological analysis is one of the first studies of its kind based on behavioral in situ observations of reef fishes (see Floeter et al. 2005, 2007).

Damselfishes as study models

In the last decades, territorial pomacentrids have been subject to a number of manipulation experiments (Robertson 1984, 1995; Ferreira et al. 1998; Ceccarelli et al. 2005), and have provided the foundation of many population and community theories. They are a widespread and abundant component of reef fish communities and are considered the numerically dominant herbivores on some reefs and in some habitats (Scott and Russ 1987; Ceccarelli 2007). They have been found to mediate algal diversity (Hixon and Brostoff 1983), affect coral zonation (Wellington 1982), and structure the benthic communities within their territories through their feeding and behavioral activities (Ferreira et al. 1998; Ceccarelli et al. 2001; Ceccarelli 2007). At Lizard Island, Great Barrier Reef, the family Pomacentridae was found to have the highest rate of body mass growth per week, showing their importance for trophic energy transmission on coral reefs (Depczynski et al. 2007).

Many studies have tried to understand the feeding and territorial activity of damselfishes in order to quantify their role in structuring reef communities (Brawley and Adey 1977; Robertson 1984, 1996; Ferreira et al. 1998; Letourneur 2000; Hata and Kato 2002; Menegatti et al. 2003; Alwany et al. 2005; Osório et al. 2006). The magnitude of their influence on coral reef communities depends on their density, size, territorial and feeding behaviors (Robertson 1984, 1996; Hixon and Webster 2002). These factors are often inter-related and influenced by environmental parameters such as water temperature (Polunin and Klumpp 1989; Ferreira et al. 1998). By addressing the nature of the

relationships between feeding behavior, size, territory size and temperature we can begin to understand how the patterns of damselfish herbivory are organized on a global scale.

Damselfish aggression may be related to their territory size, or to the amount of algae inside their territories (Jan et al. 2003). However, it is known that the algal turf the damselfish feeds on does not always encompass the entire territory area (Jan et al. 2003; Ceccarelli, 2007). Therefore, it can be said that the relationship between territorial and feeding behaviors, territory size and algal turf abundance is still poorly understood (but see Hata and Kato 2004). Given the current lack of consensus, it is possible that clearer patterns exist between damselfish feeding activity and territoriality at larger scales. One may ask the question: do individuals defending smaller territories display higher feeding rates than the ones with larger territories?

The influence of temperature on feeding activity and body size

Fishes, with few exceptions (e.g. Scombridae; Schmidt-Nielsen 2002), are thermo-dependent organisms whose metabolism is regulated according to the surrounding water temperature, which also influences their body size. It has been demonstrated that the herbivorous surgeonfish *Acanthurus bahianus* live longer and grow larger in colder waters when compared to tropical counterparts (Choat and Robertson 2002). The same pattern was observed for the Brazilian damselfish *Stegastes fuscus*: this species attains larger maximum sizes in temperate waters found along the southern Brazilian coast than in the warmer waters of northeastern Brazil (Floeter and Ferreira pers. obs.). It may be important to examine variations in body size with temperature and/or latitude in herbivorous reef fishes in general (e.g. Acanthuridae, Scarinae and some Pomacentridae), to better understand the magnitude of their roles as modifiers of the reef benthic community (Ceccarelli et al. 2005; Ceccarelli 2007) and as primary consumers in marine trophic webs (Horn 1989). We therefore ask: do damselfishes in colder waters grow larger than those in warmer waters?

The relationship between water temperature and fish metabolism tends to be one where metabolic rates increase as temperature rises (Clarke and Johnston 1999). Daily and seasonal temperature variation can therefore play an important role in the activity of reef fishes. Studies have reported that damselfishes and other herbivorous reef fishes increase their feeding activity either throughout the day or seasonally with increasing temperature (Polunin and Klumpp 1989; Ferreira et al. 1998). These relationships, however, were described for a single species at a time. In the present study, we investigated whether temperature was a relevant factor in damselfishes' feeding activity at a global scale, with the question: do damselfishes inhabiting warmer

waters display higher feeding rates compared to those inhabiting colder waters?

Fish metabolism is also related to their body mass/size, and smaller fishes generally have a higher specific metabolism (O^2 consumption/mass/time) than larger ones (Yager and Summerfelt 1993). To maintain the faster metabolism, smaller fishes must display proportionally higher feeding rates than larger ones. Menegatti et al. (2003) observed a decrease in bite rates from juveniles to adults in Brazilian damselfish *Stegastes fuscus*, which may reflect the higher metabolic rate in juveniles. Here we test whether this relationship is applicable to a broad scale analysis with several species of damselfishes, where most reach different adult sizes and assess whether larger damselfishes have lower feeding rates than smaller ones.

A global scale macroecological study of territorial damselfishes can assist with the understanding of large scale patterns for this group or fishes, and will be useful to inform future manipulation experiments trying to predict the impacts of damselfishes on reefs.

Materials and methods

Database compilation

A database was compiled using existing literature and the authors' data (Table 1) for herbivorous territorial damselfishes throughout the world (Fig. 1). It encompassed: (1) feeding rates, (2) body sizes (total length) as described in the literature or collected by the authors, (3) territory size and (4) sea surface temperature (SST). Only published data for adults collected between 11:00 h and 18:00 h were included based on herbivorous fish diurnal feeding activity (Zemke-White et al. 2002), except for Lison de Loma and Harmelin-Vivien (2002) and Lobel (1980), which contained data from earlier hours in the morning.

Authors' data

Atlantic data for *Microspathodon chrysurus*, *Stegastes adustus*, *S. planifrons* (Bocas del Toro, Panama) and *S. imbricatus* (São Tomé & Príncipe, Africa) were collected by CELF and SRF; *S. fuscus* data from the Brazilian coast were collected by DRB, SRF, CELF, DMBF and DFD using identical methods. The feeding activity and size (total length visually estimated with 1 cm precision) of individual damselfish were recorded during 5-minute observation periods; feeding rates were assessed according to the frequency of bites on the substratum during the observation periods and are expressed as bites per minute. To estimate territory size of *S. adustus* and *S. planifrons* (CELF and SRF), individual fish were observed for 15 min, and the

boundaries in which patrolling activities took place were marked with a rope divided into 10 cm intervals with lead weights. The area was calculated by measuring the circumference of each territory and using the formula for a circle of equivalent circumference.

Indo-West Pacific data for *Stegastes apicalis* (Magnetic Island, GBR, Australia), *Pomacentrus chrysurus* and *Hemiglyphidodon plagiometopon* (Orpheus Island, GBR Australia), *P. burroughi*, *P. bankanensis*, *Plectroglyphidodon lacrymatus*, *Neoglyphidodon nigroris* and *S. lividus* (Kimbe Bay, Papua New Guinea) and *P. tripunctatus*, *P. wardi* and *P. adelus* (two or more of the locations above) were collected by DMC using methods similar to those described above. Feeding observation periods were 15 min and included the assessment of territory boundaries. The boundaries were marked and measured at the end of the observation periods, and territory area estimated with the method described above. The fish were subsequently caught for gut content analysis (see Ceccarelli 2007), and total length measured in the laboratory.

Data standardization

All data were standardized to conduct the analyses. Feeding rates were transformed to bites per minute, sizes (cm) were transformed (when necessary) to total length and territory size to square meters (m^2). We transformed standard lengths (SL) into total lengths (TL) using photographs of adults (Allen 1991) from which we obtained the ratio between SL and TL.

Sea surface temperature

The high resolution sea surface temperature (SST) analysis product used in the present study was developed by Reynolds et al. (2007) using optimum interpolation (OI) version 2 (<ftp://eclipse.ncdc.noaa.gov/pub/OI-daily/daily-sst.pdf>). The analyses are global and have a spatial grid resolution of 0.25° and temporal resolution of 1 day. The analysis uses Advanced Very High Resolution Radiometer (AVHRR) infrared satellite SST data and in situ data from ships and buoys that include a large-scale adjustment of satellite biases. For this study, we used the data set between January 1985 and December 2005.

We obtained mean annual SST values over 21 years for each site from a time series of daily SST extracted from the global grids, summing 21 years of SST averages. In the same way the minimum and the maximum values of each month were extracted from the global grids to calculate the mean minimum and maximum SST for each site over 21 years. For the analyses we used the mean minimum data set as the minimum temperature may present physiological

Table 1 Feeding rates, sample sizes, mean body sizes (total length) and territory sizes of damselfishes from different localities and sources, and the minimum 21-year average sea surface temperature (SST) compiled from NOAA database for each locality

Species	Sample (n)	Bites/min	Size (cm)	Territory (m ²)	Locality	SST (°C)	Reference
<i>Hemiglyphidodon plagiometopon 1</i>	10	3.93 ± 0.70	17.78 ± 0.63	2.15 ± 0.21	Orpheus Island, GBR	22.0	This paper
<i>H. plagiometopon 2</i>	5	11.10 ± 1.60	–	–	Lizard Island, GBR	23.0	Wilson and Bellwood (1997)
<i>Microspathodon chrysurus 1</i>	11	10.71 ± 0.74	15.00 ± 0.00	–	Bocas del Toro, Panama	24.5	This paper
<i>M. chrysurus 2</i>	12	8.34 ± 0.28	16.39	–	Punta de San Blas, Panama	24.0	Robertson (1984)
<i>M. dorsalis</i>	88	2.23 ± 0.05	20.00	–	Los Frailes, Gulf of California	21.0	Montgomery (1980)
<i>Neoglyphidodon nigroris</i>	10	2.39 ± 0.66	10.00 ± 0.38	0.90 ± 0.08	Kimbe Bay, Papua New Guinea	26.0	This paper
<i>Plectroglyphidodon lacrymatus 1</i>	10	4.25 ± 0.72	7.65 ± 0.27	0.95 ± 0.03	Kimbe Bay, Papua New Guinea	26.0	This paper
<i>P. lacrymatus 2</i>	34	4.25 ± 0.72	–	–	Motupore, Papua New Guinea	23.5	Polunin and Klumpp (1989)
<i>Pomacentrus adelus 1</i>	10	3.78 ± 0.87	8.06 ± 0.15	1.06 ± 0.10	Kimbe Bay, Papua New Guinea	26.0	This paper
<i>P. adelus 2</i>	10	5.73 ± 0.93	9.37 ± 0.21	1.70 ± 0.21	Orpheus Island, GBR	22.0	This paper
<i>P. bankanensis</i>	10	5.91 ± 0.49	6.69 ± 0.15	1.19 ± 0.06	Kimbe Bay, Papua New Guinea	26.0	This paper
<i>P. burroughi</i>	10	5.87 ± 0.97	8.96 ± 0.20	1.38 ± 0.19	Kimbe Bay, Papua New Guinea	26.0	This paper
<i>P. chrysurus</i>	10	5.36 ± 0.51	7.20 ± 0.16	2.88 ± 0.40	Orpheus Island, GBR	22.0	This paper
<i>P. tripunctatus 1</i>	10	3.43 ± 0.98	8.41 ± 0.17	1.45 ± 0.08	Kimbe Bay, Papua New Guinea	26.0	This paper
<i>P. tripunctatus 2</i>	10	1.89 ± 0.25	10.84 ± 0.17	–	Orpheus Island, GBR	22.0	This paper
<i>P. tripunctatus 3</i>	10	2.96 ± 0.20	9.63 ± 0.18	0.31 ± 0.04	Magnetic Island, GBR	22.0	This paper
<i>P. wardi 1</i>	10	2.02 ± 0.26	11.35 ± 0.31	1.43 ± 0.16	Orpheus Island, GBR	22.0	This paper
<i>P. wardi 2</i>	10	4.18 ± 0.61	10.34 ± 0.21	0.85 ± 0.05	Magnetic Island, GBR	22.0	This paper
<i>Stegastes adustus 1</i>	14	13.14 ± 0.84	8.27 ± 0.28	0.89 ± 0.05	Bocas del Toro, Panama	24.5	This paper
<i>S. adustus 2</i>	12	8.07 ± 0.29	8.38	–	Punta de San Blas, Panama	24.0	Robertson (1984)
<i>S. apicalis</i>	10	4.36 ± 0.43	16.10 ± 0.54	1.57 ± 0.09	Magnetic Island, GBR	22.0	This paper
<i>S. fuscus 1</i>	22	4.08 ± 0.51	13.00	–	Florianópolis, Brazil	18.0	This paper
<i>S. fuscus 2</i>	40	4.35 ± 0.46	–	–	Guarapari, Brazil	20.5	Menegatti et al. (2003)
<i>S. fuscus 3</i>	12	2.14 ± 0.29	13.80	2.10 ± 0.08	Arraial do Cabo, Brazil	19.5	Ferreira et al. (1998)
<i>S. fuscus 4</i>	54	4.38 ± 0.22	–	–	Porto Belo, Brazil	18.0	This paper
<i>S. fuscus 5</i>	24	8.73 ± 0.50	10.00	1.99 ± 0.16	João Pessoa, Brazil	23.5	Osório et al. (2006)
<i>S. fuscus 6</i>	30	7.04 ± 0.55	9.40 ± 0.37	–	Tamandaré Reefs, Brazil	23.5	This paper
<i>S. imbricatus</i>	50	4.44 ± 0.33	10.38 ± 0.12	–	São Tomé, Africa	23.5	This paper
<i>S. lividus</i>	10	3.93 ± 0.53	9.52 ± 0.17	–	Kimbe Bay, Papua New Guinea	26.0	This paper
<i>S. nigricans 1</i>	51	10.50 ± 0.26	10.80	0.12	Réunion Island	22.0	Lison de Loma and Harmelin-Vivien (2002)
<i>S. nigricans 2</i>	51	8.17 ± 0.18	10.70	0.07	Réunion Island	22.0	Lison de Loma and Harmelin-Vivien (2002)

Table 1 continued

Species	Sample (n)	Bites/min	Size (cm)	Territory (m ²)	Locality	SST (°C)	Reference
<i>S. nigricans</i> 3	10	2.05 ± 0.16	13.62 ± 0.15	0.90 ± 0.08	Kimbe Bay, Papua New Guinea	26.0	This paper
<i>S. nigricans</i> 4	10	6.48 ± 1.00	–	–	Fanning Atoll, Line Islands	24.0	Lobel (1980)
<i>S. nigricans</i> 5	147	6.89 ± 0.23	12.10	–	Sesoko Island, Okinawa	21.0	Hata and Kato (2002)
<i>S. nigricans</i> 6	5	8.00 ± 0.40	–	–	Lizard Island, GBR	23.0	Wilson and Bellwood (1997)
<i>S. planifrons</i> 1	16	7.44 ± 0.63	8.19 ± 0.16	0.44 ± 0.05	Bocas del Toro, Panama	24.5	This paper
<i>S. planifrons</i> 2	12	7.57 ± 0.34	8.15	–	Punta de San Blas, Panama	24.0	Robertson (1984)
<i>S. rectifraenum</i>	405	8.53 ± 0.08	10.00	–	Los Frailes, Gulf of California	21.0	Montgomery (1980)
<i>S. rocasensis</i>	80	4.85 ± 0.28	11.00 ± 0.13	1.61 ± 0.23	Fernando de Noronha, Brazil	24.0	Souza (2007)

constraints to herbivorous fishes (Floeter et al. 2005). Moreover, the correlation between the minimum and the mean SST for all sites is highly significant ($r^2 = 0.99$; $p < 0.0001$).

Data analyses

Regression analyses were conducted to verify the relationship and significance between the estimated macroecological parameters (Zar 1999). The genera *Pomacentrus* and *Stegastes* were analyzed separately, as they represent the two most diverse genera of herbivorous territorial pomacentrids (Allen 1991). *Microspathodon* spp. was added to the *Stegastes* analysis of bite rates against SST due to the phylogenetic proximity of these two genera (Quenouille et al. 2004; Cooper et al. 2008). One-way analysis of variance (ANOVA) was conducted to test whether feeding rates and body size are different between *Stegastes* and *Pomacentrus*.

A Principal Components Analysis (PCA) biplot was used to summarize the overall relationship between feeding rates, body size and SST. Body size data for the species *Stegastes fuscus* 2 and 4, which were not collected, were extrapolated based on the closest species data available. All data (bites/min, body size and SST) were log₁₀ transformed to reduce the effect generated by different orders of magnitude in some of the values (i.e., bite rates ranged from approximately 6 to 13 bites/min, mean body size from 7 to 20 cm while SST ranged from 18 to 26°C). MVSP 3.1 for Windows software was used for the PCA.

Results

Feeding rates and body size versus SST

No correlation between bite rates and SST was found for the territorial Pomacentridae (Fig. 2). When the two most diverse genera of this group were analyzed separately, we observed a positive correlation for the genus *Stegastes*, but not for the genus *Pomacentrus* (Fig. 2). Data for *S. nigricans* 3 and *S. lividus* from Papua New Guinea were considered outliers and were therefore removed from these analyses (see Discussion for more details). ANOVA showed that *Stegastes* spp. have higher feeding rates than *Pomacentrus* spp. ($F_{1,30} = 7.71$; $p < 0.01$) which may explain why the mixing between different genera (Pomacentridae) was not significant.

A negative correlation between body size and SST was observed for the territorial Pomacentridae as well as the genus *Stegastes* (Fig. 3). This correlation, however, was only marginally significant for the genus *Pomacentrus* (Fig. 3).

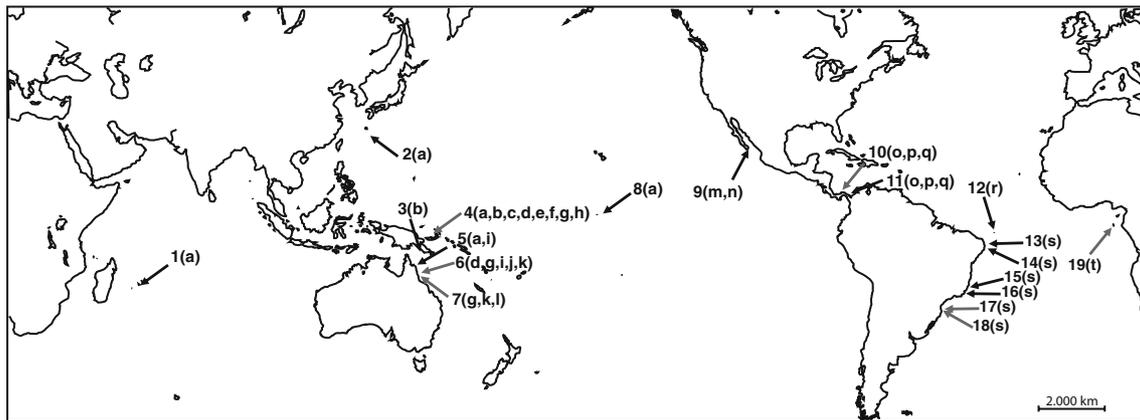


Fig. 1 World map showing the places where data were collected by the authors (gray arrows) and from the literature (black arrows). 1 Réunion Island, 2 Sesoko Island, 3 Motupore Island, 4 Kimbe Bay, 5 Lizard Island, 6 Orpheus Island, 7 Magnetic Island, 8 Fanning Atoll, 9 Los Frailes, 10 Bocas del Toro, 11 San Blas, 12 Fernando de Noronha, 13 João Pessoa, 14 Tamararé Reefs, 15 Guarapari, 16 Arraial do Cabo, 17 Porto Belo, 18 Florianópolis, 19 São Tomé.

(a) *Stegastes nigricans*, (b) *Plectroglyphidodon lacrymatus*, (c) *Neoglyphidodon nigroris*, (d) *Pomacentrus adelus*, (e) *P. bankanensis*, (f) *P. burroughi*, (g) *P. tripunctatus*, (h) *S. lividus*, (i) *Hemiglyphidodon plagiometopon*, (j) *P. chrysurus*, (k) *P. wardi*, (l) *S. apicalis*, (m) *Microspathodon dorsalis*, (n) *S. rectifraenum*, (o) *Microspathodon chrysurus*, (p) *S. adustus*, (q) *S. planifrons*, (r) *S. rocasensis*, (s) *S. fuscus*, (t) *S. imbricatus*

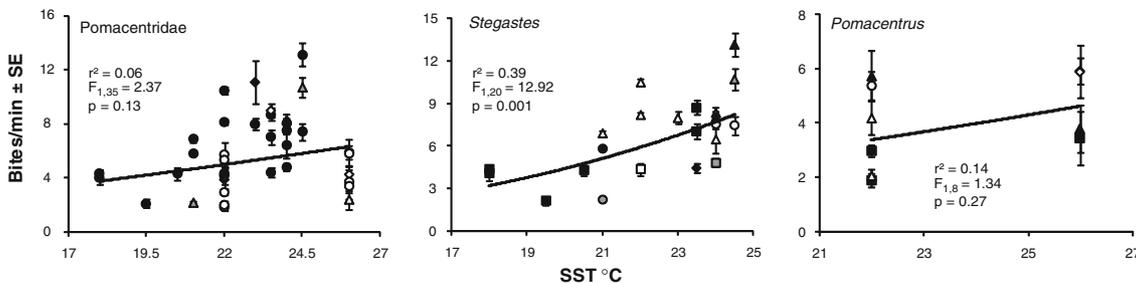


Fig. 2 Relationship between feeding rates (bites/min) and sea surface temperature (SST) in the territorial Pomacentridae and the genera *Stegastes* and *Pomacentrus*. For *Stegastes* and *Pomacentrus* graphs the black triangle represents *S. adustus* or *P. adelus*; white triangle = *S. nigricans* or *P. wardi*; black diamond = *S. imbricatus* or *P. bankanensis*; white diamond = *S. lividus* or *P. burroughi*; black circle = *S. rectifraenum*; white circle = *S. planifrons* or *P. chrysurus*; black

square = *S. fuscus* or *P. tripunctatus*; white square = *S. apicalis*; gray square = *S. rocasensis*; gray circle = *Microspathodon dorsalis*; gray triangle = *M. chrysurus*. For the Pomacentridae graph, the white triangle represents *Neoglyphidodon*; black diamond = *Hemiglyphidodon*; white diamond = *Plectroglyphidodon*; black circle = *Stegastes*; white circle = *Pomacentrus*; gray triangle = *Microspathodon*

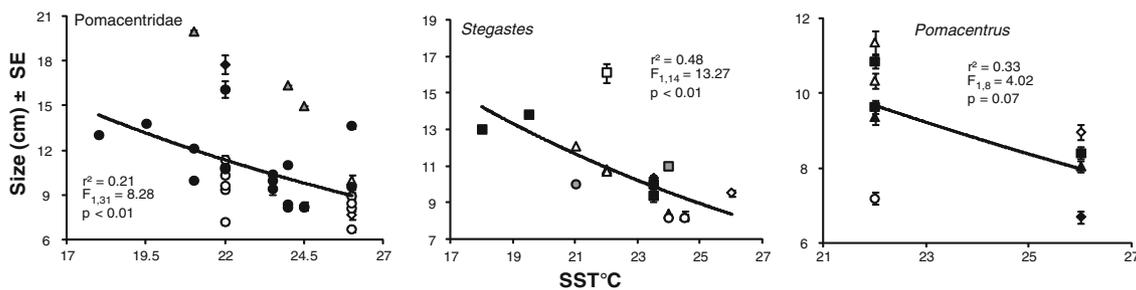


Fig. 3 Relationship between body size and sea surface temperature (SST) in the territorial Pomacentridae and the genera *Stegastes* and *Pomacentrus*. See Fig. 2 for graphic representation of species

Feeding rates versus body size and territory size

There was no significant relationship between body size and bite rates for the territorial Pomacentridae (Fig. 4). However, we found a negative correlation for both the

genera *Stegastes* and *Pomacentrus* (Fig. 4). ANOVA showed that *Stegastes* spp. are significantly larger than *Pomacentrus* spp, ($F_{1,25} = 4.40$; $p < 0.05$) which indicates that combining different genera may not be appropriate.

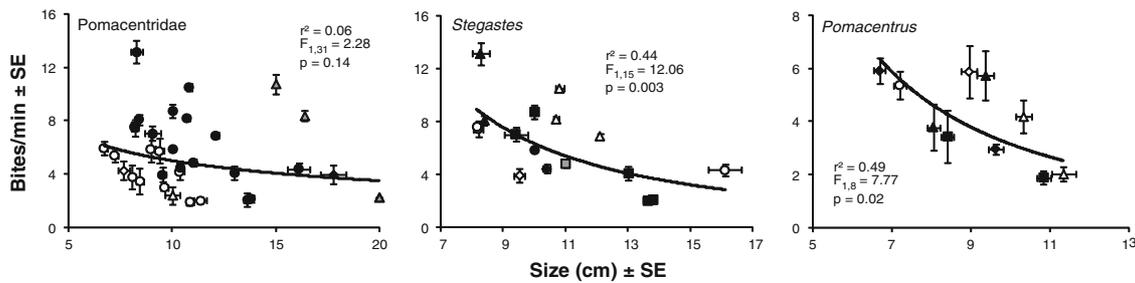


Fig. 4 Relationship between feeding rates (bites/min) and body size in the territorial Pomacentridae and the genera *Stegastes* and *Pomacentrus*. See Fig. 2 for graphic representation of species

None of the analyses showed a relationship between feeding rates and territory size: Pomacentridae ($r^2 = 0.14$; $F_{1,19} = 3.22$; $p = 0.08$); *Stegastes* ($r^2 = 0.18$; $F_{1,7} = 1.63$; $p = 0.24$); *Pomacentrus* ($r^2 = 0.18$; $F_{1,7} = 1.61$; $p = 0.24$).

Neoglyphidodon nigroris and *Plectroglyphidodon lacrymatus* are generally smaller than *Stegastes* spp.

Principal components analysis

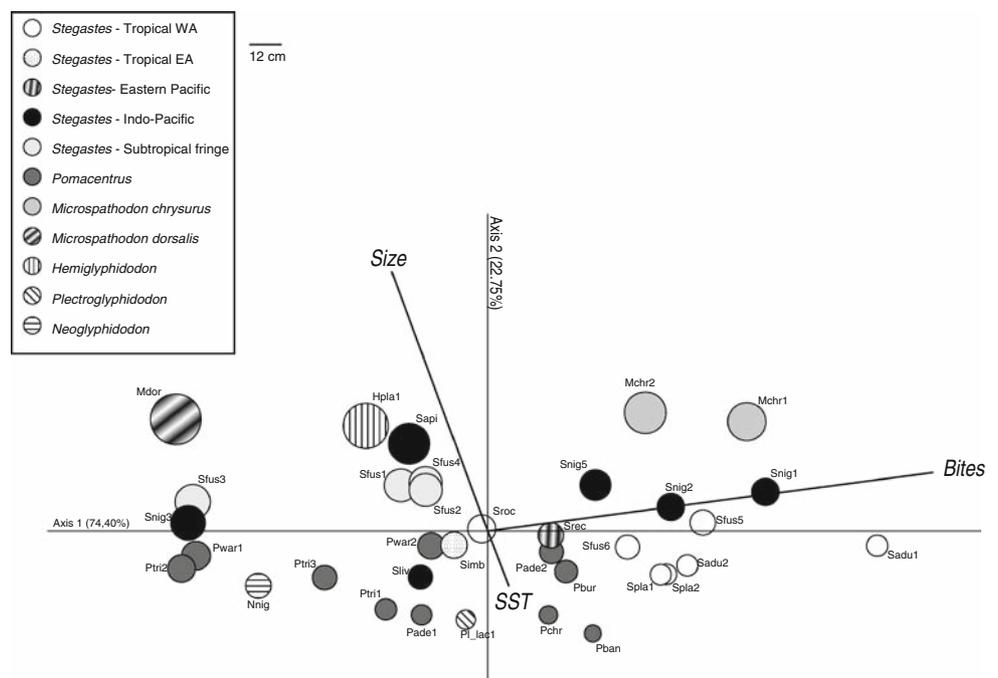
Differences in feeding rates (bites/min) explained most of the variability in the PCA (Axis 1: 74.40%; Fig. 5). Differences in body size and SST accounted for the other 22.75% (Axis 2) of the variation in the data. Larger species, such as subtropical fringe *Stegastes* spp., *Hemiglyphidodon plagiometopon* and *Microspathodon dorsalis* were characterized by having lower feeding rates than the smaller tropical Western Atlantic *Stegastes* spp. and the Indo-West Pacific *S. nigricans*. Despite the relatively large size of the tropical *M. chrysurus*, it has much higher feeding rates than its subtropical counterpart *M. dorsalis*. All species of *Pomacentrus*,

Discussion and conclusions

The influence of temperature on feeding

This study has highlighted general large-scale patterns in the relationships between temperature, body size and feeding activity in territorial pomacentrids. Temperature is a key factor in driving fish feeding activity. The higher temperatures found in the tropics are directly related to an increase in the metabolic rates of thermo-dependent organisms (Clarke and Johnston 1999; Schmidt-Nielsen 2002). Therefore, feeding activities must increase as well (Floeter et al. 2005). While there was a positive correlation between bite rates and SST in the genus *Stegastes*, this relationship

Fig. 5 Principal Components Analysis biplot of the overall relationship between sea surface temperature (SST), body size and bite rates for the territorial Pomacentridae. The length of the arrows indicates the relative importance of the three test factors. Circle sizes are proportional to body size, which is indicated by the horizontal bar. The species numbering code is based on Table 1



was not significant in the territorial Pomacentridae and the genus *Pomacentrus*. The lack of a good range of SST data for the latter – data were collected at three Indo-Pacific locations, resulting in only two different temperatures (Ceccarelli, present paper) – made the analysis of macroecological patterns with an emphasis on temperature less robust for this genus. The combining of different genera for the analysis of territorial Pomacentridae may not be appropriate, as an ANOVA showed significant differences in feeding activity of both *Stegastes* and *Pomacentrus*.

Seasonal variations in temperature account for differences in feeding activities. Previous studies have demonstrated that the bite rates of a single damselfish species (e.g. *Plectroglyphidodon lacrymatus*, *S. fuscus* and *S. rocasensis*) within the same location can vary daily and seasonally with temperature (Polunin and Klumpp 1989; Ferreira et al. 1998; Souza 2007). Our study ascertains that temperature variations have a strong influence on feeding activity in the *Stegastes* genus. However, we do not know enough about how other oceanographic (e.g. hydrodynamics) and biological conditions (e.g. density-dependent interactions) can exert some influence on macroecological fish foraging patterns (Ferreira et al. 1998).

The influence of temperature on body size

Our results show that a negative correlation between body size and SST exists for *Stegastes* spp. and the Pomacentridae family, and it is marginally significant in the genus *Pomacentrus*, confirming the applicability of Bergmann's rule to this group of fishes. Sampling *Pomacentrus* in a wider range of temperatures is likely to give a clearer view of this pattern.

Coral reefs have long been described as the richest marine ecosystem on the planet, with a complex three-dimensional structure, being compared only to tropical rain forests (Connell 1978). Being members of one of the most abundant and diverse reef fish families, territorial damselfishes display intense inter- and intraspecific competition (Robertson 1984, 1995; Ferreira et al. 1998; Ceccarelli et al. 2001; Hata and Kato 2002), may face high predation pressure (see Hixon and Webster 2002) and must deter intruding competitors (such as larger roving herbivores) from depleting the resources in their territories (Ceccarelli et al. 2005, 2006; Osório et al. 2006; Souza 2007). The cost of repelling intruders is expected to be high, and as smaller fishes allocate comparatively more energy to their metabolism than bigger fishes, the tropical environment may favor smaller and less aggressive individuals. In addition, the faster metabolism causes a larger degree of oxidative stress, which, together with possible higher predation rates, shortens their life span. This is corroborated by data showing smaller sizes and shorter life

spans for reef fish in the tropics (Choat and Robertson 2002).

This same study demonstrated that individual *Acanthurus bahianus* grow larger (and live longer) in colder waters (Choat and Robertson 2002). The authors suggested that lower temperatures reduce growth rates and/or increase life span, and that this pattern may be related to low recruitment rates in subtropical fringe areas, also leading to a longer life span. Although there are local ecological attributes to address when analyzing the body size of fishes (e.g. territorial behavior and competition; Robertson 1984, 1995, 1996; Choat and Robertson 2002; Hata and Kato 2004), we suggest that metabolic aspects were the main factor driving the observed patterns between body size and temperature in reef fishes on a macro scale analysis.

The influence of body size on feeding

There was a negative correlation between feeding rates and body size for both *Stegastes* and *Pomacentrus*, but not for the Pomacentridae combined. The difference in body size between *Stegastes* and *Pomacentrus* as showed by ANOVA indicates that combining the two genera may not be appropriate. Larger individuals tend to have lower feeding rates than smaller ones regardless temperature, as their specific metabolism (O^2 consumption/mass/time)—and therefore their feeding activity—is expected to be lower (Yager and Summerfelt 1993).

Natural variations in body size exist between and within species and genera, and this can determine the behavioral activity of individual fish. Ecological interactions between different species may play a large role in determining individual body size: the presence of larger and dominant species (Robertson 1984), intra and interspecific competition and ability (Robertson 1995, 1996), density and distribution of territories (Meadows 2001) and different feeding and 'farming' patterns (extensive vs. intensive; Hata and Kato 2004). Despite all the 'noise' that may be caused by those interactions during the life of a damselfish, we demonstrate that macroecological patterns emerge when a large enough pool of species is analyzed.

The temperature-size axis in the PCA (Axis 1) separates the genus *Pomacentrus* from the other species considered in this study. This may be due to the geographic separation of sampling sites (*Pomacentrus* spp. were only sampled in the Indo-West Pacific), but potentially indicates the importance of size, rather than feeding rates, in characterizing the different genera. Sampling *Pomacentrus* spp. more widely will offer a clearer view of this pattern.

The PCA analysis grouped *S. nigricans* 3 with subtropical fringe species due to its larger size and very low feeding rate, even though it inhabits relatively warm waters (Kimbe Bay, PNG). In terms of SST, *S. nigricans* 3 is an "outlier"

within the genus *Stegastes*, as a tropical *Stegastes* species would be expected to be smaller. A further contrast highlighted by the PCA is that *Hemiglyphidodon plagiometopon* is large, inhabits warm waters and displays a low feeding rate, while the size equivalent *Microspathodon chrysurus*, also living in warm waters, has a much higher feeding rate. Furthermore, *M. dorsalis* displays lower feeding rates than *M. chrysurus*, as would be expected for a subtropical species. Overall, it appears that within each genus there is a particular pattern for the relationship between feeding activity, body size and temperature that may or may not correspond to the pattern displayed by other genera.

Some studies show that macroecological patterns become clearer as the group analyzed becomes more restricted (Macpherson and Duarte 1994; Choat and Robertson 2002; Smith and Brown 2002). Among territorial damselfishes, territoriality may vary considerably spatially (e.g. density-dependent processes—not evaluated here; Hixon and Webster 2002), and between taxa (Ceccarelli et al. 2001). *Stegastinae* and *Pomacentrinae* are not closely related genera within Pomacentridae (Quenouille et al. 2004; Cooper et al. 2008) and have different demographic structures (Ceccarelli pers. obs.), which may be a determining factor in shaping species' body size and therefore also influence their feeding activity. *Pomacentrus* spp. are smaller (as showed by ANOVA) and less aggressive than *Stegastes* spp. (D.M.B. Frensel, D.R. Barneche, S.R. Floeter, D.M. Ceccarelli, C.E.L. Ferreira, D.F. Dinlaken, in prep.), and may be able to inhabit coral reef systems by maintaining extensive, rather than intensive, algal farming (Hata and Kato 2004). In addition, we observed that *Microspathodon* spp. data added to the *Stegastes* analysis sustained the pattern observed, and we believe that this is due to their close phylogenetic relationship (Quenouille et al. 2004; Cooper et al. 2008). When *Stegastes* and *Pomacentrus* were analyzed separately, they presented the same pattern, albeit at different scales. As a consequence, no pattern is observed when the data are pooled for the family analysis.

Feeding activity and territory area

No relationship was observed between feeding activity and territory size. We hesitate to draw conclusions from this finding due to the different approaches to territory size measurement. The overall territory area patrolled by resident fish is often not the same as the feeding area. Much of the feeding activity tends to take place on a small patch of algae within the territory (Ceccarelli et al. 2001; Jan et al. 2003; Ceccarelli 2007). Furthermore, competition with surrounding individuals and the quality of the locally available food resources can influence both territory size and feeding activity. In turn, the level of competition is likely to be

affected by the species composition of the surrounding fish community (Crossman et al. 2001; Purcell and Bellwood 2001; Russ 2003; Ceccarelli et al. 2006).

Studies have shown that larger fishes defend larger territories (Sale 1978; Letourneur 2000). The size of the 'feeding patch' may be also proportional to the feeding activity and/or the size of the occupant, but this assumption has yet to be investigated. Although our study does not analyze this aspect, we suggest that these patches may vary between taxa or even between locations for a single species.

Conclusions

On the basis of these results, we extend the validity of Bergmann's rule to territorial damselfishes, a numerically and ecologically important group of reef fishes. This ecogeographic rule applies to the territorial damselfish group in this study despite phylogenetic differences and variations in diet, aggression and sampling methods. Territorial damselfishes inhabiting warmer waters are smaller and have higher feeding rates than their subtropical counterparts. The identification of large-scale, robust ecological patterns underpins the understanding of reef fish community macroecology. Identifying these relationships for other reef fish groups may establish a foundation for predicting future large-scale changes in reef fish assemblages with expected changes in SST.

Acknowledgments We would like to thank D. Wilhelm Filho and the three reviewers for corrections and insightful comments; R.F. Yamashita for Tamadaré Reef data; H. Andrade for statistical advice. Financial support was provided by CNPq (D.R. Barneche Bolsista PIBIC do CNPq - Brazil), National Geographic Society (grant 7937-05 to S.R. Floeter), Smithsonian Tropical Research Institute (STV grants to S.R. Floeter and C.E.L. Ferreira), Universidade Federal de Santa Catarina (Funpesquisa grant 239-2006 to S.R. Floeter) and IEAPM (C.E.L. Ferreira). Data collection on Australian and PNG reefs was supported by GBRMPA and ARC grants to D.M. Ceccarelli and G.P. Jones.

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