

UNIVERSIDAD SAN FRANCISCO DE QUITO USFQ

Colegio de Posgrados

**Impacto de peces herbívoros en macroalgas y el crecimiento de
Posillopora damicornis y *Posillopora capitata* en la Isla de la Plata, Ecuador**

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Trabajo de titulación de posgrado presentado como requisito
para la obtención del título de Magíster en Ecología

Quito, marzo de 2016

UNIVERSIDAD SAN FRANCISCO DE QUITO USFQ

COLEGIO DE POSGRADOS

HOJA DE APROBACIÓN DE TRABAJO DE TITULACIÓN

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RESÚMEN

Los arrecifes de coral son altamente diversos y productivos, pero se ven amenazados debido a una serie de factores antropogénicos y variaciones climáticas. Un tema de preocupación para la supervivencia de los corales es la proliferación de algas, debido a la eliminación de los herbívoros y al escurrimiento de nutrientes. La herbivoría es un proceso ecológico clave en los sistemas marinos ya que, mantienen a las algas bajo control. El propósito de mi estudio fue estudiar experimentalmente los efectos de la herbivoría en dos especies de corales *Posillopora capitata* y *Posillopora damicornis* y sus comunidades asociadas. El experimento se llevó a cabo en La Isla de la Plata, Ecuador. Para estimar los impactos de los peces de algas marinas coloqué placas dentro de cuatro tratamientos que consistían en vallas cubiertas totalmente, vallas cubiertas parcialmente y una parcela de control abierto que limita selectivamente el acceso a los diferentes tipos de peces en su interior, con fragmentos de coral en cada uno y grabé las vallas para cuantificar la diversidad de peces y caracterizar su comportamiento alrededor de las unidades experimentales. Se encontró que los herbívoros no tuvieron ningún impacto sobre la abundancia de los grupos funcionales de las algas, a través del tiempo y el espacio o ningún impacto sobre las especies, la riqueza, la diversidad y la uniformidad de los grupos funcionales de algas, pero después de un año de estudio, todos los corales trasplantados crecieron en promedio un 40% en todos los tratamientos. Mi hipótesis es que meso-consumo de menos de 2.5 cm podrían desempeñar un papel clave en la regulación de las algas.

PALABRAS CLAVE: Herbivoría . Algas . Peces herbívoros . Corales . *Posillopora* . Meso consumidores . Micro herbívoros . Organismos sésiles.

**Impact of herbivorous fish on macro algae and the growth of
Posillopora damicornis and *Posillopora capitata* in La Plata Island, Ecuador**

ABSTRACT

Coral reefs are highly diverse and productive but threatened due to a myriad of anthropogenic factors and due to climatic variations. One issue of concern for coral survival is the proliferation of algae due to the elimination of grazers and nutrient runoff. Herbivory is a key ecological process in marine systems that keep algae under control. The purpose of my study was to study experimentally the impacts of herbivory on two species of corals *Posillopora capitata* and *Posillopora damicornis* and its associated communities. The experiment was conducted in La Plata Island, Ecuador. To estimate the impacts of fish on marine algae I placed settlement plates inside four treatments that consisted of total fences, partial fences and an open control plot that selectively restricted the access to different types of fish inside them with coral fragments each one and recorded the fences to quantify the diversity of fish and characterize their behavior around the experimental units. We found that grazers did not have any impact on the abundance of any functional groups of algae through time and space or any impact on species, richness, diversity and evenness of functional groups of algae but after a year, all the transplanted corals grow on average 40% in all treatments. I hypothesize that meso-consumer smaller than 2.5 cm could play a key role regulating algae.

KEY WORDS: Herbivory . Algae . Herbivory fishes . Corals . *Posillopora* . Meso consumers . Micro herbivores. Sessile organism.

Introduction

Coral reefs are highly diverse, comparable only to tropical forests due to the structural complexity they provide to many other species. Corals are highly productive (Hay & Rasher 2010) and provide a range of key provisioning, cultural and regulatory services for humans such as biodiversity conservation, formation of beaches, erosion control, food, research and tourism (Moberg & Folke 1999). For example, nearly a third of the world's species of marine fish are found in coral reefs (McAllister 1991) and 10% of the fish consumed by humans (Smith 1978).

However, corals and coral reefs worldwide are threatened due to a myriad of anthropogenic factors and due to climatic variations (Bruno *et al.* 2009, Rasher & Hay 2010, Kaneryd *et al.* 2012). The main threats are pollution, over-fishing, trawling, by catch, destructive fishing, diseases, climatic factors and tsunamis (Bruno & Selig 2007, Glynn & Ault 2000, Glynn 2003, Glynn *et al.* 2009, Cortés 2003, Wellington 1997, Bryant *et al.* 1998). It is anticipated that many of these natural phenomena will intensify in the future due to human induced climate change (Hughes *et al.* 2007, Kaneryd *et al.* 2012, Mumby & Harborne 2010, Rasher & Hay 2010).

Environmental and biological factors may interact with each other, with impacts that may be antagonistic. For example, overfishing, pollution and eutrophication might lead to a reduction in coral cover, increased proliferation of microalgae, reduced local biodiversity (Hay & Rasher 2010) and a reduction and degradation in quality and quantity of

environmental goods and services provided by corals (Bellwood *et al.* 2006, Kaneryd *et al.* 2012).

One issue of concern for coral survival is the proliferation of algae due to the elimination of grazers and nutrient runoff. Algae can compete with corals through different mechanisms such as allelopathy, overgrowing, abrasion, shading, recruitment barrier, and epithelial sloughing (McCook *et al.* 2001, Rasher & Hay 2010). In the Caribbean and Pacific microalgae caused coral bleaching and sometimes death through the transfer of toxic compounds from the surfaces of microalgae (Rasher & Hay 2010). Macro algae can also transmit diseases to corals by exuding metabolites that stimulate coral damaging microbes and sometimes death (Hay & Rasher 2010, Nugues *et al.* 2004, Smith *et al.* 2006).

Herbivory is a key ecological process in marine systems, herbivores can keep algae under control (Burkepile & Hay 2008, 2009, 2010). Herbivores remove three to four times more biomass than terrestrial herbivores and this impact is more important in tropical systems. It is estimated that on average they can remove 68% of the biomass of the algae (Poore *et al.* 2012), thus significantly influencing the structure and dynamics of corals (Hughes *et al.* 2007).

However, the impact of grazers depends on a number of factors, such as the morphology, abundance and, diversity of herbivores (Gaines & Lubchenco 1982). At the same time, the impact of herbivores can be modulated by environmental factors such as temperature, the nutritional quality of primary producers, and primary productivity of the

system under study and wave action (Poore *et al.* 2012, Burkepile & Hay 2008, 2009, 2010, Lewis 1985, Glynn & Ault 2000, Hay & Rasher 2010, Vinueza *et al.* 2014).

Among the diverse array of grazers from tropical latitudes, fish from the families Scaridae, Acanthuridae and Pomacentridae are key to the functioning of coral communities and may affect the wealth, abundance, distribution and productivity of communities of microalgae and corals (Burkepile & Hay 2010). They can influence recovery and maintenance of coral communities and alter the competition for space between microalgae and corals (Glynn *et al.* 1979, McClanahan *et al.* 2011, Carpenter 1986, Hughes *et al.* 2007). Similarly, the corallivorous organisms (that feed on corals) can influence growth rates of corals.

The impact of consumer often causes changes in the diversity of their prey (Burkepile & Hay 2010). For example an increase in the number and diversity herbivores resulted in a reduction of algae that facilitates the survival and growth of corals (Burkepile & Hay 2008, 2010, Lewis 1985, Glynn 2000, Hay & Rasher 2010). Complementarity between feeding herbivorous fish can suppress coverage and biomass of microalgae upright, leading to an increase to a 22% increase in surface area and prevents coral mortality (Burkepile & Hay 2008, Hay & Rasher 2010). Therefore, herbivores on coral communities control the growth of seaweeds and facilitate the establishment, growth, survival and resilience of corals (Burkepile & Hay 2008, 2009, 2010, Hay & Rasher 2010).

However, overfishing has affected the functioning of many marine ecosystems through removal of disproportionately important species and reduction of functional

diversity at all trophic levels (Burkepile & Hay 2008). This has contributed, along with other factors to a transformation of coral dominated ecosystems to completely alternative stable states that are characterized by the dominance of algae, whose ecological and economic value to humans is lower than the healthy coral communities. (Graham *et al.* 2006)

The purpose of my study was to study experimentally the impacts of herbivory on two species of corals *Posillopora capitata* and *Posillopora damicornis* and its associated communities. I conducted these studies on La Plata Island, inside Machalilla National Park. I hypothesized that:

H1. Herbivorous fish affect the richness and abundance of algae

H2. This pattern is consistent through time and space

H3. Herbivorous fish alter the competitive interactions between algae and corals by consuming algae, indirectly speeding the growth of corals.

I predicted that algal diversity will increase in treatments that exclude fish, reducing coral growth. I expect this pattern will be consistent across time and space for the duration of the experiment (Burkepile & Hay 2008, 2010, Glynn *et al.* 1979, McClanahan *et al.* 2011, Hughes *et al.* 2007, Vinuela *et al.* 2014).

Study area

The study was conducted in La Plata Island, an island located on the Central Coast of Ecuador, to the south west of the province of Manabí, inside the Machalilla National Park, which includes about 56,184 of land area and 14,430 ha of marine area (Martinez *et al.* 2011) (Fig. 1).

The experiment was conducted at two sites: Bahia Drake and Palo Santo, in March 2013, both sites are in close proximity (500 meters Source: Dustin, Raymond). Bahia Drake presents *Posillopora damicornis* patches and *Posillopora capitata* interspersed with *Pavona spp.* patches and register with the formation of two species. Palo Santo registers the presence of coral communities interspersed with sand and pebble space.

Experimental design

Physical parameters

Temperature Sea surface was extracted from satellite data provided by INOCAR. Basically, I used the daily average to calculate the monthly mean and standard error.

Water flow is an important parameter that can affect the growth rates of coral (Palardy & Witman 2014). In order to monitor the flow of water in the two study sites, gypsum blocks three centimeters in diameter and three centimeters high were prepared

with PVC pipes. Plaster Stone Type III (100 g), was mixed with 32 ml of water. Each month six gypsum blocks were placed in each of the sites randomly an interval of two hours, a total of twelve gypsum blocks were placed every month.

Impacts of grazers on functional groups of algae

To estimate the impacts of fish on marine algae I placed settlement plates inside four treatments that consisted of total fences, partial fences and an open control plot that selectively restricted the access to different types of fish inside them.

The fences were assembled with a plastic mesh that was 25 cm wide and 25 cm high. The mesh size was 2.5 cm. The first treatment, an open control (Fig. 2A) consisted of a ring 15 cm wide that was fixed to the substratum. This treatment allowed access to all herbivores. The second treatment, a fence open at the top (25 x 25 cm) excluded sea urchins and allowed the entry of all consumers smaller than 25 cm from the top (Fig 2B); The third treatment excluded all consumers that were greater than 2.5 cm (Fig 2C). The fourth treatment was a procedural control (Fig 2D). This treatment consisted of a semi open fence and closed top.

Inside these fences settlement plates for algae made of polypropylene (1/2' 5 x 5 cm) were attached to the base of each replicate with cable ties. One set was changed every three months, while the other set was left for the entire experiment (1 year). I estimated the percent cover of the entire sessile organism that attached to the plates in the lab. The

organisms were classified to the highest taxonomic level possible and later a grouped into functional groups (Steneck & Dethier 1994).

The role of fishes

To quantify the diversity of fish and characterize their behavior around the experimental units' four underwater cameras (GoPro Hero 3 Silver), two on each site were randomly placed for around two-hours (depending on battery life). Videos were observed to characterize the diversity, abundance and behavior around the cages. The cameras were tied with cable ties to cement blocks to keep them fixed on the substrate and placed in front of randomly chosen treatments, the videos were made once a day for each site between 11:00 am and 3:00 pm, every month for a year. To quantify the number of pecking each video is reviewed and counted the number of times that each species of fish pecked treatments, the species were identified and grouped by families.

Impact of fish on growth rates of *Posillopora damicornis* and *Posillopora capitata*

I experimentally manipulated the access of herbivores to branches of *Posillopora* that were placed inside the experimental unites described above. For this purpose, I collected fragments of *P. damicornis* and *P. capitata* around Bahia Drake and Palo Santo. These fragments were on average 8 cm. The weight of each branch was estimated at the onset of the experiment in March 2013. Afterwards, these coral fragments were assigned randomly to each one of the treatments and their respective replicates. These fragments

were left for a year at the study site and were collected at the end of the experiment to estimate the change in growth that occurred after a year.

Statistical analysis

Percent cover of functional groups was transformed using the arcsine of the square root of the proportion. Differences among treatments were analyzed using ANOVA with site and treatment level as fixed factors and percent cover, diversity indexes or growth rates of coral as dependent variables. Diversity indexes were calculated using PRIMER 6.2. Similarities among experimental units and sites were established using Bray Curtis Similarity Matrixes and non-metrical multidimensional scaling (nMDS). The routine ANOSIM was used to detect significant differences among treatments and sites.

Results

Physical parameters

Sea surface temperature ranged from $26 \pm 0.4^{\circ}\text{C}$ during the warm phase (Dec to April) and $24 \pm 0.3^{\circ}\text{C}$ during the cool season from May to November (Fig 3A).

Water flow measured as the rate of dissolution of plaster blocks was similar at both sites. BD 3.2 ± 0.4 g/h and PS 3.1 ± 0.5 g/h. December the highest rates of dissolution (4.8

g/h) followed by February (4 g/h) for both BD and PS. January and August had the lowest rates of solution (1.5 g/h) (Fig. 3B).

Impact of grazers on functional groups of algae

Grazers did not have any impact on the abundance of any functional groups of algae at any site (Table 1 for ANOVA of plates collected every three months). Marginal but non-significant interactions between site and treatment were observed for articulated coralline ($p = 0.0048$) and crustous algae ($p = 0.013$) (Fig. 4B and 4C). Filamentous algae was more abundant at BS ($p = 0.015$), while empty substrate was more abundant at PS ($p = 0.002$). Crustous algae abundance peak in September and December for both sites ($p = 0.007$) with a coverage of $33.8 \pm 4.7\%$. Bare Rock was more abundant on PS during March reaching $29 \pm 14.5\%$ cover. In June bare rock was more abundant in BD ($p = 0.001$).

Herbivores did not have any impact on species, richness, diversity and evenness of functional groups of algae (Fig. 5). Both species richness and diversity were generally higher for all treatments in June 2013 with few exceptions, control plots for BD and procedural controls and total exclusions for PS. For most treatments richness and diversity fluctuated with no pattern related to treatment and generally declined at the end of the experiment in March 2014 (Fig. 5A and 5B).

Multivariate Analysis of Community Structure

Spatial ordination of communities did not show any consistent pattern related to time or treatment (Appendix A1 and A2). For BD, only in June all treatments formed a separated cluster with 75% of similarity (Appendix A1). For PS no temporal pattern emerged, control plots formed another group, sharing 50% of similarity (Appendix A2).

The role of fishes

In total 767 fishes were observed. In BD, herbivorous fish was the most abundant group reaching 52.2%. *Stegastes flavious* (88 individuals observed) was the most abundant in this group. Predatory fish accounted for 46% of the abundance with *Thalassoma lucasanum* (81 individuals observed) as the most abundant group. Omnivorous fish represented 1.8% of the total individuals observed. For PS, predatory fish were the most abundant with 59% of 767 observed group. The most representative species of this site was *Thalassoma lucasanum* (112 individuals observed). Herbivorous fish accounted for 24% with *Prionorus laticlavus* and *Stegastes acapulcoensis* as the most abundant (24 individuals observed each). Omnivores was less representative with 16.9% of observed group (See Table 3A and 3B).

The differences in the intensity of foraging for fish between the two study sites was not significant $p > 0.05$, but we find a significant differences between site and month $p=0.009$. From August to December we observed an increase in foraging rates for both sites

(Fig 6A and 6B). More grazing fish in BD (4.7 ± 1.3 forag /s) and PS (3.2 ± 1.2 forag/s). The fish species most frequently observed foraging in PS were *Prionurus laticlavus* (7.1 forag/s), followed by *Holacanthus passer* (2 forag/s). In BD they highlighted *Chromis atrilobata* (1 forag/s) and *Prionurus laticlavus* (1 forag/s).

Impact of fish on growth rates of *Pocillopora damicornis* and *Pocillopora capitata*

Growth rates (percent) were transformed using Arcsin (Warton & Hui 2011) logarithmic function. The distribution was normal (Anderson-Darling Test). No significant differences between treatments and site existed $p > 0.05$ were observed (Table 2).

After a year, the transplanted corals grow on average $49 \pm 8.2\%$ at PS and $43 \pm 9\%$ at BD (Fig 7). No consistent pattern among treatments and site was observed. On PS, coral grew only $30 \pm 7.4\%$ in total exclusions, compared to other treatments that grew between $45 \pm 7.4\%$ and $60 \pm 9.7\%$ (Fig 7), however, differences were not significant ($p > 0,453$ Table 2). For BD both total exclusion and procedural controls had the highest growth rate with $50 \pm 12\%$ and $52 \pm 13.4\%$ respectively, while walls and open control plots had the lowest growth rates with $35 \pm 5.5\%$ and $36 \pm 5.2\%$ respectively.

Discussion

Contrary to my hypothesis and predictions, macro herbivores did not have a significant impact in the control of functional groups of algae or the species, richness, diversity and evenness of functional groups of algae. Furthermore, at the community level samples did not group by treatment, site, season or month (Appendix A). Based on other studies (Burkepile & Hay 2008, 2010; Vinueza *et al.* 2006, 2014; Hay & Rasher 2010), I expected upright forms of macro algae (i.e. filamentous algae, articulated coralline algae), these patterns were consistent in time and space with few exceptions.

Impact of grazers on functional groups of algae

I expected upright forms of macro algae (i.e. filamentous algae, articulate coralline algae) to flourish inside treatments that excluded fish (i.e. total exclusion and procedural control) (Hixon & Brostoff 1996, Steneck 1983).

I also expected a higher abundance of crustous algae and empty substrate on plates that were placed inside open control plots where all fish had access as they usually dominate landscapes with high grazing intensity and that this pattern was maintained over time but we didn't find similitudes (Fig 2, 4) (Hixon & Brostoff 1996, Burkepile & Hay 2010). While crustous algae occupied $32 \pm 4\%$ and $36 \pm 5\%$ of primary space on BD and PS respectively and Filamentous algae $30 \pm 3\%$ and $16 \pm 2\%$ at BD and PS respectively, their abundance were

not related to grazing. These results are different from other studies that found a significant impact of fish on the type and abundance of algae (Bruno & Selig 2007, Ceccarelli *et al.* 2001, Burkepile & Hay 2010, 2011, Aburto *et al.* 2007).

Alternatively, algal growth might have been inhibited by shading; an unintended artifact due to the mesh. However, fenced treatments with open roofs (W) and control plots (C) did not have a higher abundance of upright algae as opposed to the total exclusion and procedural control treatment that had mesh on top and could have inhibited algal growth (Fig 4). It is also possible that plates I used inhibited algal growth; however these same settlement plates have been widely used in Galapagos and Oregon with successful results (L. Vinueza personal communication). For example, in Galápagos, Vinueza *et al.* (2014) found that inside total exclusion treatments *Ulva sp* was present and dominated the landscape at sites of low productivity, such as Genovesa but was nearly absent in open control plots.

Another possibility is that nutrient levels were particularly low around La Isla de la Plata. According with the INOCAR between 2013 and 2014, the nutrients for wet season was 6.5 ± 3.5 ug/L and for dry season were 2 ± 1.2 ug/ L. Vinueza *et al.* (2014) said that high nutrients favor growth of all algae, in special in the absence of macro herbivores. In comparison with Galapagos (Vinueza *et al.* 2006, 2014), this can be another explication why the algae growth in Isla de la Plata is very slow.

An alternative scenario is that small meso-consumers (< 2.5 cm) such as juvenile fishes, blennies, crabs and sea stars observed inside my cages could play an important

ecological role and might be able to control the abundance of algae. I realize this issue while I was conducting my experiment and placed additional plates inside cages that have a smaller mesh, 1 x 1 cm, rather than the mesh of 2.5 cm that I used to manipulate the presence of fish (Fig 2). Several studies (Silliman & Bertness 2002, Whitlach & Osman 2009, Palmer 1979, Nydam & Stachowicz 2007) indicate that the exclusion of large predators may lead to changes in the communities of prey through trophic cascades where predators become small meso-predators. Sams & Keough (2007) worked with two types of mesh size to manipulate consumers one of 1x1 cm and the other 2x2 mm. While the smaller mesh was effective at excluding all types of predators, a smaller mesh size can block light intensity, water flow and harm the coral.

Sessile organism such as ascidians, barnacles and tube worms could be better colonizers and repel algae. For example *Didemnum sp.* is an invasive species that can grow on top of any substrate, including macro algae (Daniel & Therriault 2007). This ascidian was first observed in my experiments in June 2013. While they were observed inside all the experimental units they did not settle any coral fragment inside the experimental units.

It is likely that meso-predators and micro herbivores that live associated with the corals prevented the spread of this ascidian (Fig 8D). According Lavender *et al.* (2014) numerous studies examining the interaction prey-consumer failed because they do not take into account the effects of meso consumers that might use the cages as refuge against predation. Based on the evidence presented above, I presume that the meso predators and micro herbivores had some impact on the study, I discuss this hypothesis below.

The role of fishes

The impacts of fishes greater than 2.5 cm on algae were not apparent in our experiment. I presume that meso-predators, including small fish could have an important role in controlling algae. For example, blennies were always present inside treatments (Fig 8C). This family appears to be important in controlling algal growth according to other studies (Allen 1991; Burkepile & Hay 2008; Hixon & Brostoff 1996).

Prionurus Laticlavus (8 forag/s) spends more time foraging in BD and PS than any other species of fish. Based on this evidence I hypothesize that this species could have a greater role at controlling algae. This species, forms large aggregations of hundreds of individuals that graze on marine algae in shallow reefs and affect the abundance of reef macro algae (Miller 1998; Hixon 1997). Burkepile & Hay (2010) concluded that fish of this family improved the growth of corals and kept algae under control.

Chormis atrilobata, a member of the Pomacentridae family, was the second species foraging around the cages in BD (1 forag/s). Burkepile & Hay (2011) and Ceccarelli *et al.* (2001) concluded that damselfish have important impacts on benthic communities. This family in general can increase diversity and are considered “Keystone” species (Hixon & Brostoff 1996; Allen 1991; Gochfeld 2010). I recorded some *Chromis atrilobata* inside most treatments that had mesh. I observed some attacks by individuals of this species when I was cleaning the fences. This evidence supports my view that smaller meso - consumers might

play a key ecological role in the regulation of coral communities around La Plata Island and attract other species of fish.

Holacanthus passer was abundant as well and spends more time foraging in PS (2forag/s). I recorded this specie foraging actively around my experimental units. Aburto *et al.* (2000) observed that the presence of *H. passer* was associated with the presence of the damselfish *C. atrilobata*; they found a clearly trophic association between *C. atrilobata* schools and *H. passer* the later species fed on damselfish feces in the water column.

However, my observations on feeding behavior should be taken with caution. Burkepile & Hay (2011) suggested that it is better to standardized all bite rates by the length of each tape because feeding behavior is difficult to quantify rigorously on videotapes and many fishes had access to the treatments all the time and could pass through the mesh making their responses to cage removal less informative.

Impact of fish on growth rates of *Posillopora damicornis* and *Posillopora capitata*

Contrary to my predictions, coral growth was similar across all treatments. In all cases coral grew $40 \pm 8.6\%$ after a year. I never observed any diseases, bleaching or competitive displacement by algae on any single treatment. In fact, no algae were observed on top of all the transplanted coral fragments. However, algal growth was evident on top of the mesh that I use to build the fences (Fig 8A and 8B). Similarly algal growth around my

experimental units was evident, particularly around entangled fishing lines and on top of dead branches of coral around my experiment.

According Wellington (1982) and Gochfeld (2010), *Posillopora* species are protected from predation by their highly branched morphology, the rapid regeneration of their polyps and because they provide shelter to corallivorous and herbivores. In my experiment, corals did not show any signs of stress or predation irrespective of the treatment to which they were assigned. Contrary to my expectations, exclusion treatments had higher growth rates than the same control (C) plots (Fig. 7). We believed that corals remained healthy inside exclusion plots because meso predators took advantage of the protection offered by the mesh. Vinueza *et al.* (2006, 2014) used a mesh size of 2.5 cm to exclude grazers on the intertidal zone in the Galapagos Islands. They found smaller organisms (< 2.5 cm) such as isopods, copepods, limpets, newly recruited sea urchins, fish, and crabs inside their cages. However, in this particular case, meso consumers did not have an apparent effect on the abundance of algae.

This is one of the first studies carried out in mainland Ecuador to experimentally evaluate the role of fish on algae and the growth rates of coral reefs. While fish did not have an important role in the regulation of coral communities, further studies should be focused on measuring other important parameters such as nutrient levels, light intensity that can affect algal growth and consider the presence of meso predators. Also it is important to know the abundance of large predators in La Plata Island because it could be that their population can be affected for overfishing and that could be one of the reasons why the

meso predators had a real impact in this study because their population is growing without large predators in common.

References

- Aburto, O., E. Sala., G. Paredes., A. Mendoza., and E. Ballesteros. 2007. Predictability of reef fish recruitment in a highly variable nursery hábitat. *Ecology* 88: 2220-2228.
- Adam, T., D. Burkepile., B. Ruttenberg., and M. Paddack. 2015. Herbivory and the resilience of Caribbean coral reefs: knowledge gaps and implications for management. *Mar. Ecol. Prog. Ser.* 520: 1-20.
- Allen, G. 1991. *Damselfis of the World*. Mergus Press, Germany: 271pp.
- Ateweberhan. M., D. Feary., Sh. Keshavmurthy., A. Chen., M. Schleyer., and Ch. Sheppard. 2013. Climate change impacts on coral reefs: Synergies with local effects, possibilities for acclimation, and management implications. *Mar. Pollut. Bull.*
- Baums. I., J. Boulay., and M. Hellberg. 2012. No gene flow across the Eastern Pacific Barrier in the reef-building coral *Porites lobata*. *Molecular Ecology*. Uncorrected Proof.
- Bellwood. D., A. Hoey., J. Ackerman., and M. Depczynski. 2006. Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. *Global Change Biology* 12: 1587-1594.
- Bryant, D., L. Burke, J. McManus and M. Spalding. 1998. *Reefs at risk, a map-based indicator of threats to the world's coral reefs*. World Resources Institute, Washington, D.C. 56 p.
- Bruno, J., and E. Selig. 2007. Regional Decline of Coral Cover in the Indo-Pacific: Timing, Extent, and Subregional Comparisons. *PLoS ONE* 2(8): e711.
- Bruno, J., H. Sweatman., W. Precht., E. Selig., and V. Schutte. 2009. Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. *Ecology* 90: 1478-1484.
- Burkepile, D. and M. Hay. 2008. Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *PNAS* 105: 16201-16206.
- Burkepile, D and M. Hay. 2009. Nutrient versus herbivore control of macroalgal community development and coral growth on a Caribbean reef. *Mar Ecol Prog Ser* 389: 71–84.
- Burkepile, D and M. Hay. 2010. Impact of Herbivore Identity on Algal Succession and Coral Growth on a Caribbean Reef. *PLoS ONE* 5(1): e8963.

- Burkepile, D and M. Hay. 2011. Feeding complementary versus redundancy among herbivorous fishes on a Caribbean reef. *Coral Reefs*.
- Carpenter, R. 1986. Partitioning Herbivory and Its Effects on Coral Reef Algal Communities. *Ecological Monographs* 56: 345-364.
- Ceccarelli, D., G. Jones., and L. McCook. 2011. Interactions between herbivorous fish guilds and their influence on algal succession on a coastal coral reef. *Experimental Marine Biology and Ecology* 399: 60-67.
- Cortés, J. 2003. Latin American Coral Reefs. *Coral Communities and Coral Reefs of Ecuador*. Elsevier Science B. V. 449-468.
- Daniel, K and T. Therriault. 2007. Biological synopsis of the invasive tunicate *Didemnum* sp. Canadian Manuscript Report of Fisheries and Aquatic Sciences :1-53.
- Glynn, P., G. Wellington., and Ch. Birkeland. 1979. Coral Reef Growth in the Galapagos: Limitation by Sea Urchins. *Science, New Series* 203: 47-49.
- Glynn, P and J. S. Ault. 2000. A biogeographic analysis and review of the far eastern Pacific coral reef region. *Coral Reefs* 19: 1-23.
- Glynn, P. 2003. Coral communities and coral reefs of Ecuador. *Latin American coral reefs*. Elsevier science B. V. 449-472.
- Glynn, P., B. Riegl., A. Correa., and I. Baums. 2009. Rapid recovery of a coral reef at Darwin Island, Galapagos Islands. *Galapagos Research* 66: 6-13.
- Gochfeld, D. 2010. Territorial damselfishes facilitate survival of corals by providing an associational defense against predators. *Mar Ecol Prog Ser* 398: 137-148.
- Graham, N., Sh. Wilson., S. Jennigs., N. Polunin, J. Bijoux., and J. Robinson. 2006. Dynamic fragility of oceanic coral reef ecosystems. *PNAS* 103 (22): 8425-8429.
- Hay, M and D. Rasher. 2010. Coral reefs in crisis: reversing the biotic death spiral. *F1000 Biology Reports* 2: 71.
- Hixon, M., and W. Brostoff. 1996. Succession and herbivory: effects of differential fish grazing on Hawaiian coral-reef algae. *Ecological Monographs* 66 (1): 67-90.
- Hixon, M. 1997. Effects on reef fishes on corals and algae. *NSF* 10: 230-248.

- Hughes, T., M. Rodrigues., D. Bellwood., D. Ceccarelli., O. Guldberg., L. McCook., N. Moltschaniwskyj., M. S. Pratchett., R. S. Steneck., and B. Willis. 2007. Phase Shifts, Herbivory, and the Resilience of Coral Reefs to Climate Change. *Current Biology* 17: 360–365.
- Kaneryd. L., Ch. Borrvall., S. Berg., A. Curtsdotter., A. Eklo., C. Hauzy., T. Jonsson., P. Munger., M. Setzer., T. Saterberg., and B. Ebenman. 2012. Species-rich ecosystems are vulnerable to cascading extinctions in an increasingly variable world. *Ecology and Evolution* 2(4): 858–874.
- Lavender, J., K. Dafforn., and E. Johnson. 2014. Meso-Predators: a confounding variable in consumer exclusion studies. *Experimental Marine Biology and Ecology* 456: 26-33.
- Lewis. S. 1985. Herbivory on Coral Reefs: Algal Susceptibility to Herbivorous Fishes. *Oecologia* 65: 370-375.
- Lubchenco, J., and S. Gaines. 1981. A unified approach to marine plant- herbivore interactions. I. Populations and communities. *Ecol Syst* 12: 405-37.
- Martínez. P., F. Rivera., and F. Proaño. 2011. Ambientes coralinos del Parque Nacional Machalilla y Reserva de Producción Faunística Marino Costera Puntilla de Santa Elena. Un caso de estudio para el manejo y conservación de los corales en Ecuador. Instituto NAZCA de investigaciones marinas: 1-49.
- McAllister, D.E. 1991. What is the status of the world's coral reef fishes? *Sea Wind* 5: 14–18.
- McClanahan. T., B. E. Huntington., and B. Cokos. 2011. Coral responses to macroalgal reduction and fisheries closure on Caribbean patch reefs. *Mar Ecol Prog Ser* 437: 89–102.
- McCook. L., J. Jompa., and G. Díaz-Pulido. 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* 19: 400-417.
- Miller, M and M. Hay. 1998. Effects of fish predation and seaweed competition on the survival and growth of corals. *Oecologia* 113: 231-238.
- Moberg, F and C. Folke. 1999. Ecological goods and services of coral reef ecosystems. *Ecological Economics* 29: 215–233.
- Mumby, P., and A. Harborne. 2010. Marine Reserves Enhance the Recovery of Corals on Caribbean Reefs. *PLoS ONE* 5(1): e8657.
- Nugues, M., G. Smith., R. Hoodonk., M. Seabra., and R. Bak. 2004. Algal contact as a trigger for coral disease. *Ecology Letters* 7: 919-23.

- Nydam, M and J. Stachowicz. 2007. Predator effects on fouling community development. *Mar Ecol Prog Ser* 337: 93-101
- Palardy, J., and J. Witman. 2014. Flow, recruitment limitation, and the maintenance of diversity in marine benthic communities. *Ecology* 95(2): 286-297.
- Palmer, A. 1979. Fish predation and the evolution of gastropod shell sculpture: experimental and geographic evidence. *Evolution* 33: 697-713.
- Poore, A., A. Campbell., R. Coleman., E. Graham., J. Veijo., P. Reynolds., E. Sotka., J. Stachowicz., R. Taylor., M. Vanderklift., and J. Duffy. 2012. Global patterns in the impact of marine herbivores on benthic primary producers. *Ecology Letters* 15: 912-922.
- Rasher, D and M. Hay. 2010. Chemically rich seaweeds poison corals when not controlled by herbivores. *Proc Natl Acad Sci USA* 107: 9683-8.
- Salvat. B. 1992. Coral reefs a challenging ecosystem for human societies. *Global Environ. Change* 2: 12–18.
- Sams, M and M. Keough. 2007. Predation during early post-settlement varies in importance for shaping marine sessile communities. *Mar Ecol Prog Ser* 348: 85-101.
- Silliman, B., and M. Bertness. 2002. A trophic cascade regulates salt marsh primary production. *Proc Natl. Acad. Sci.* 99: 10500-10505.
- Smith. S.V. 1978. Coral-reef area and the contribution of reefs to processes and resources of the world's oceans. *Nature* 273: 225–226.
- Smith JE., M. Shaw., R. Edwards., D. Obura., O. Pantos., E. Sala., S. Sandin., S. Smriga., M. Hatay., and F. Rohwer. 2006. Indirect effects of algae on coral: algae-mediated, microbe-induced coral mortality. *Ecology Letters* 9: 835-45.
- Steneck. R. 1983. Escalating herbivory and resulting adaptive trends in calcareous algal crusts. *Paleobiology* 9: 44-61
- Steneck, R., and M. Dethier. 1994. A functional group approach to the structure of algal-dominated communities. *Oikos* 69: 476-498.
- Vinueza. L., G. Branch., M. Branch., and R. Bustamante. 2006. Top-Down herbivory and bottom-up El Niño effects on Galápagos Rocky-shore communities. *Ecological Monographs* 76(1): 111-131.

- Vinueza, L., B. Menge., D. Ruíz., and D. Palacios. 2014. Oceanographic and climatic variation drive top-down/ bottom-up coupling in the Galápagos intertidal meta-ecosystem. *Ecological Monographs* 84 (3): 411-434.
- Warton, D and F. Hui. 2011. The arcsine is asinine: the analysis of proportions in ecology. *Ecology* 92: 3-10.
- Wellington, G. 1982. Depth zonation of corals in the Gulf of Panama: control and facilitation by resident reef fishes. *Ecological Monographs* 52: 223-241.
- Wellington GM. 1997. Field guide to the corals and coral reefs of the Galápagos Islands, Ecuador. *Proc. 8th Int. Coral Reef Symp., Panamá* 1: 185-202.
- Whitlatch, R and R. Osman. 2009. Post-settlement predation on ascidian recruits: predator responses to changing prey density. *Aquatic Invasions* 4: 121-131.

Legend Figures

Figure1. Map of La Plata Island, Ecuador, showing the sites of study Bahia Drake (BD) and Palo Santo (PS).

Figure2. Experimental design: Open control 2A (C), fence open at the top 2B (W), total exclusion 2C (TE), procedural control (PC). Plates design: every three months (3M), annual plates (AP) and plates small cages (PSC).

Figure3. Time series charts of Temperature per month (3A) and dissolution rate per month for Bahia Drake (BD) and Palo Santo (PS) (3B).

Figure4. Percentage of algae coverage ($X \pm SE$) by functional groups per month in Bahia Drake and Palo Santo. Treatment types: open control (C), fence open at the top (W), total exclusion (TE) and procedural control (PC).

Figure5. Index diversities: species richness (S), diversity (H) and evenness (J) for percentages of algae coverage of plates collected every 3 months. By treatments: open control (C), fence open at the top (W), total exclusion (TE) and procedural control (PC).

Figure6. Foraging Intensity ($X \pm SE$) for herbivores, predators and omnivores per month in Bahia Drake (6A) and Palo Santo (6B).

Figure7. Coral growth rate ($X \pm SE$) of *Pocillopora* spp. by open control (C), fence open at the top (W), total exclusion (TE) and procedural control (PCI) in Bahia Drake (BD) and Palo Santo (PS).

Figure8. Figure 8A and 8B shows how algae cover the Total Exclusion treatment (TE), inside the same treatment it is possible to see *Didemnum* and other algae but the coral is healthy and alive. Figure 8C shows how *Didemnum* invasive all the treatment but the coral not, also it is possible to see a fish from bleniidae family inside de cage too. Figure 8D During the project we commonly saw crabs into the branches of my corals.

Legend Tables

Table1. Two-way Analysis of Variance (ANOVA) to determine the effect of treatment (T) and Site (S) on the different Algae functional groups (1A) and two-way ANOVA of index diversities to determine the effect of month (M) and treatment (T) in the algae percentage coverage (1B).

Table2. Two-way Analysis of Variance (ANOVA) to determine the effect of treatment (T) and Site (S) on the growth of corals in the genus *Pocillopora*, Isla de la Plata, Manabí.

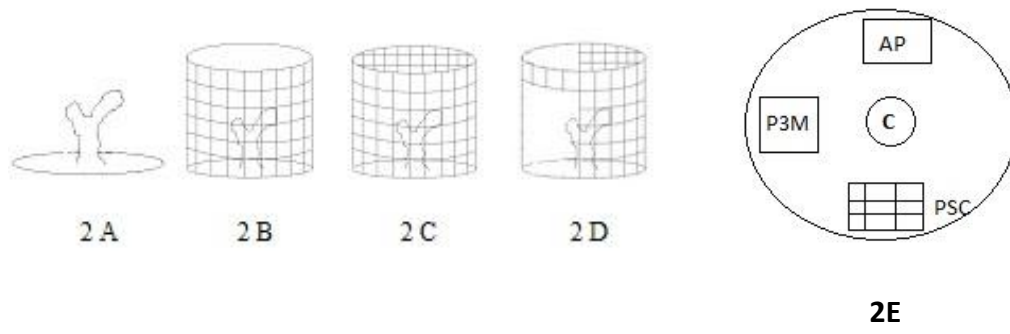
Table3. Specie, family and number of fishes found in Bahia Drake (3A) and Palo Santo (3B).

Figures

Figure 1



Figure 2



2 F

Figure 3A

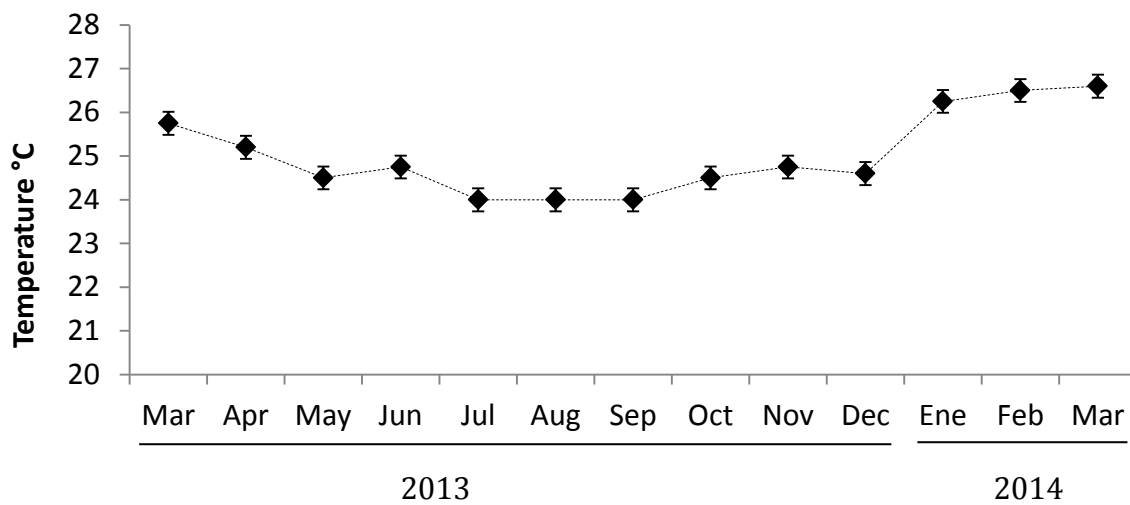


Figure 3B

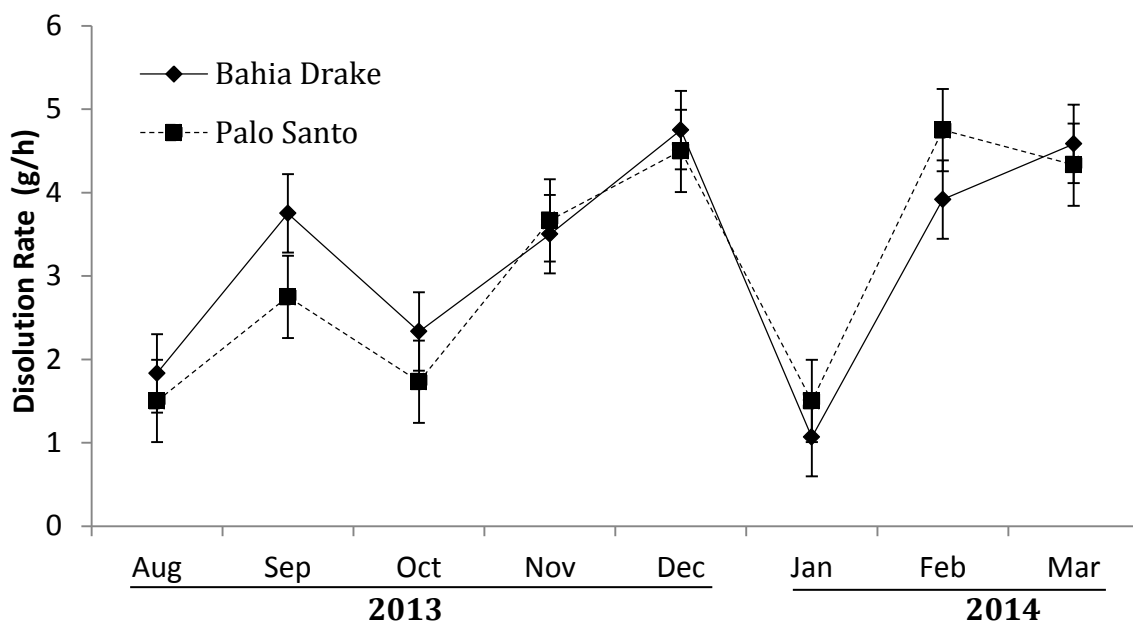
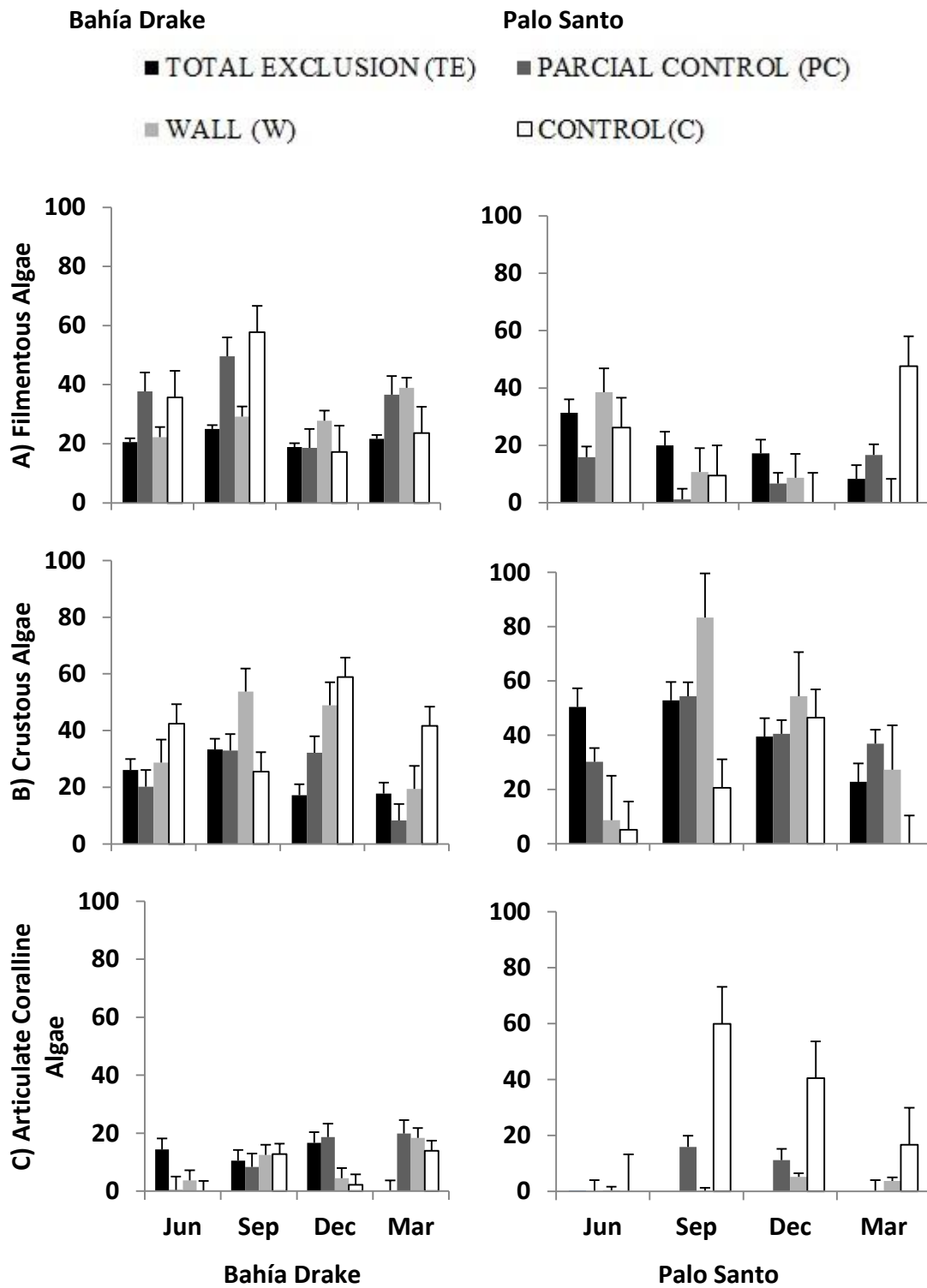


Figure 4



TOTAL EXCLUSION (TE)
 PARCIAL CONTROL (PC)

WALL (W)
 CONTROL (C)

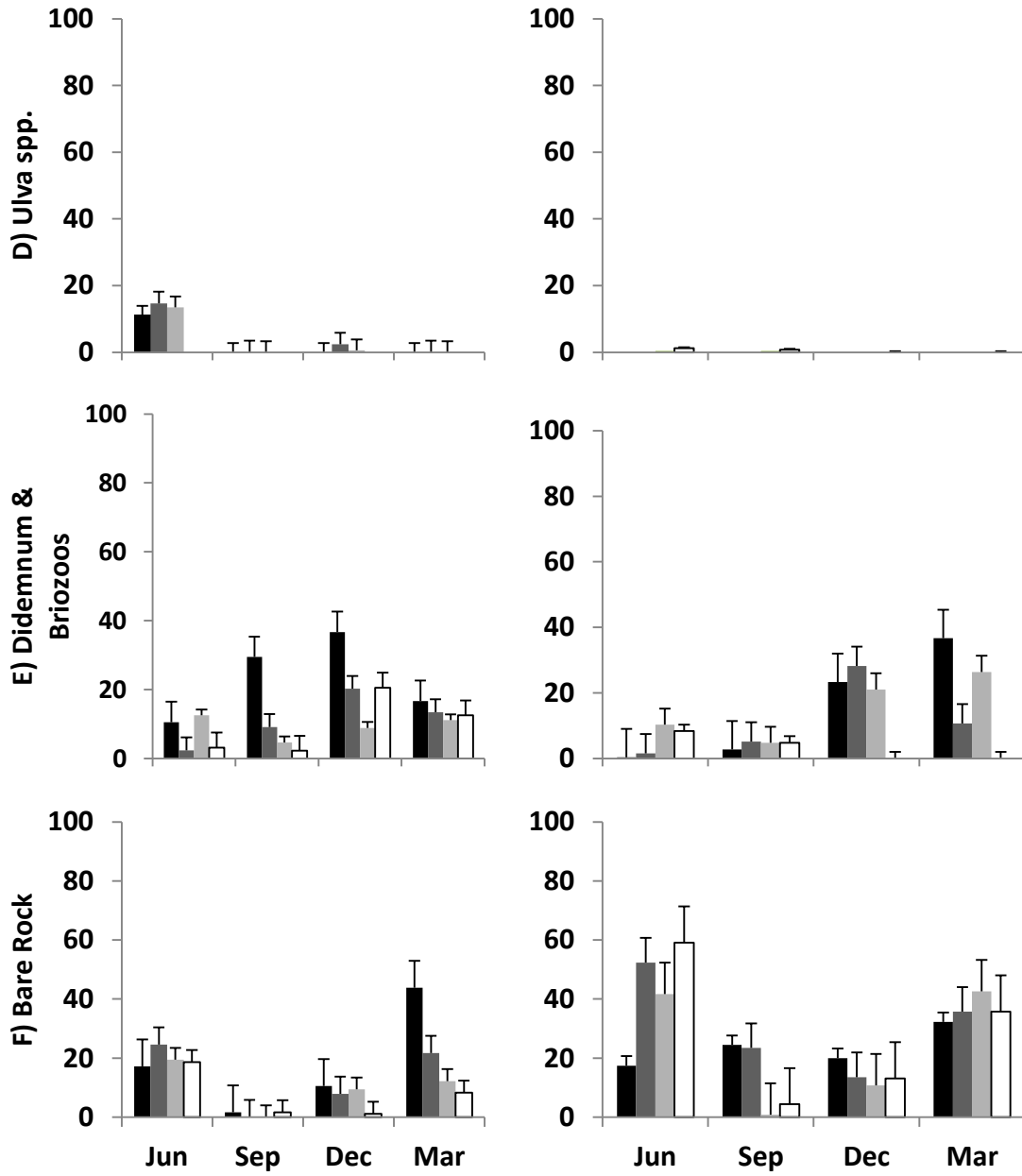


Figura 5

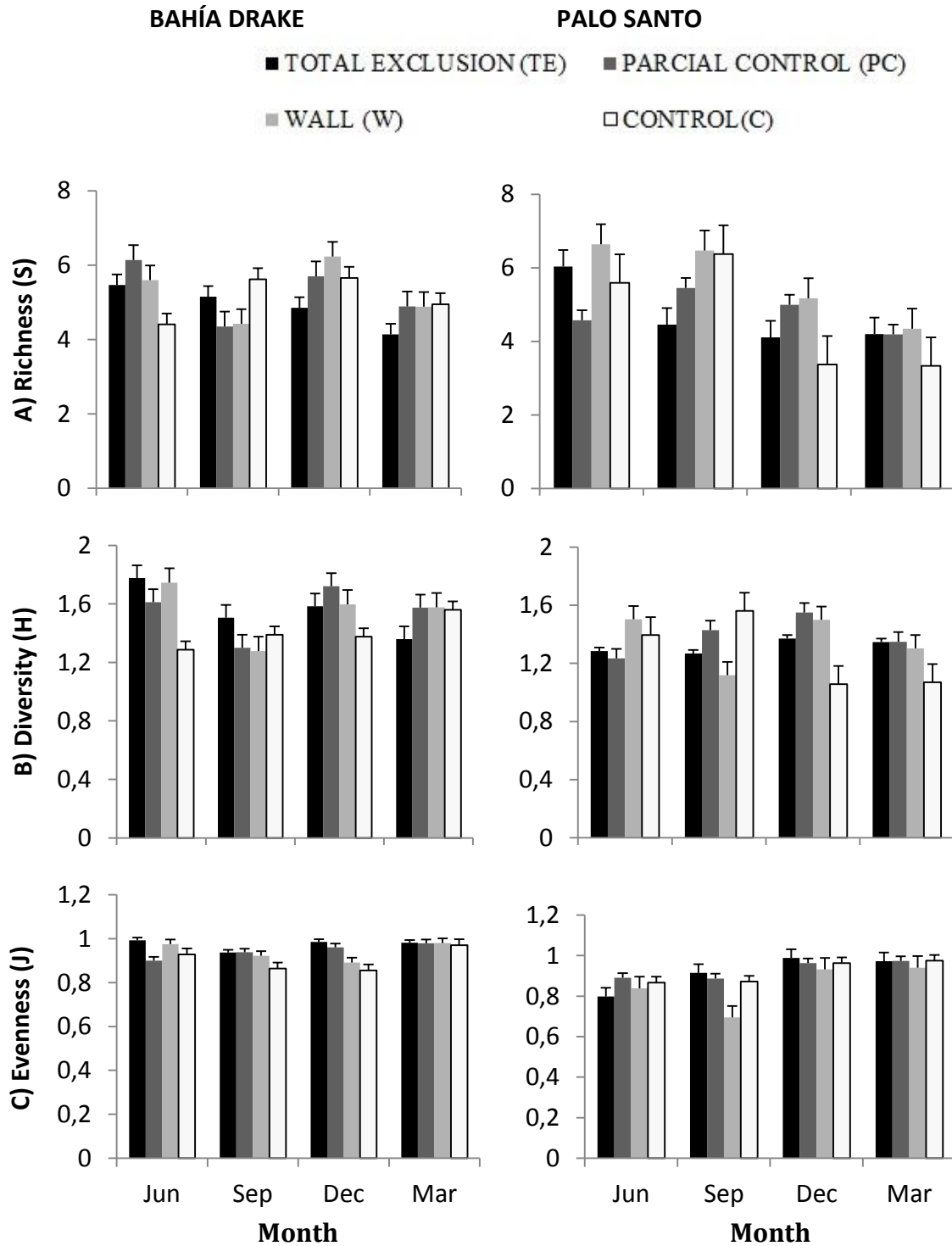


Figure 6A

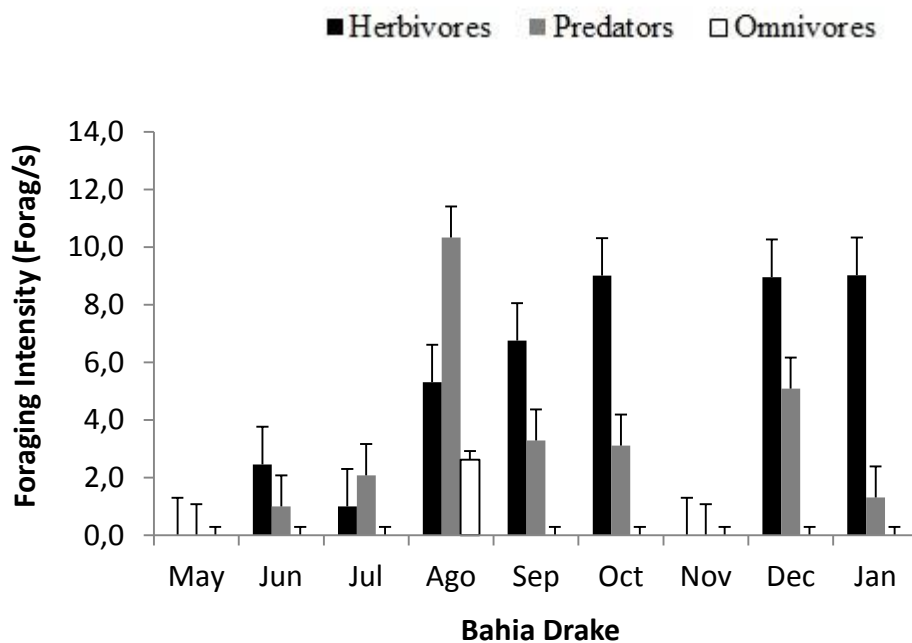


Figure 6B

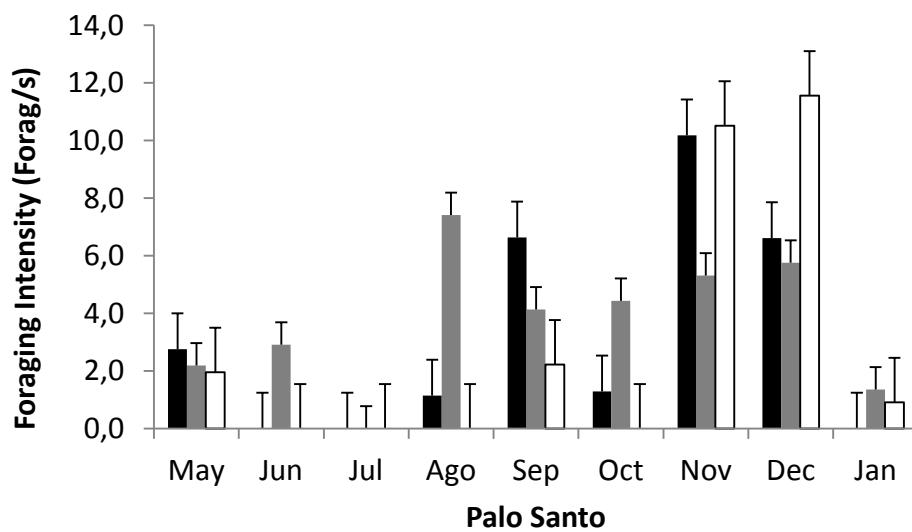


Figure 7

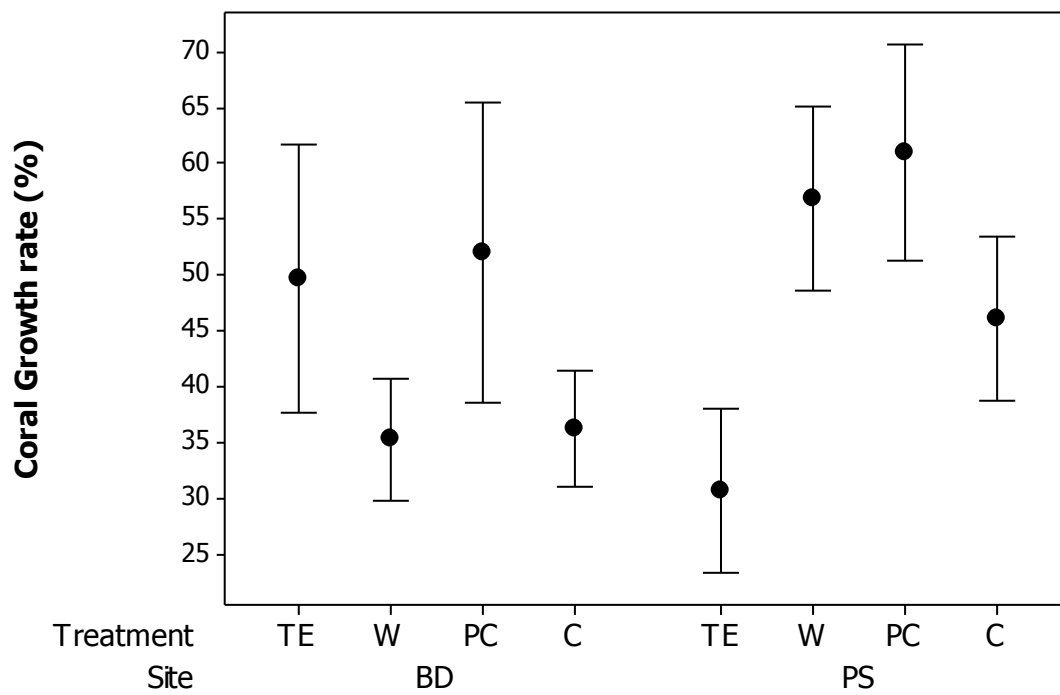


Figure 8

8A



8B



8C



8D



Table 1A**A) Filamentous Algae**

Source	DF	Adj SS	Adj MS	F-Value	P-Value
Site (S)	1	0,34019	0,34359	8,91	0,015
Month (M)	3	0,16769	0,05590	1,46	0,288
Treatment (T)	3	0,01447	0,00482	0,13	0,942
Site*Month	3	0,13531	0,04510	1,18	0,370
Site*Treatments	3	0,09303	0,03101	0,81	0,519
Month*Treatments	9	0,19240	0,02138	0,56	0,800
Error	9	0,34359	0,03818		
Total	31				

B) Crustous Alga

Source	DF	Adj SS	Adj MS	F-Value	P-Value
Site (S)	1	0,00471	0,00471	0,24	0,637
Month (M)	3	0,45390	0,15130	7,69	0,007
Treatment (T)	3	0,08873	0,02958	1,50	0,279
Site*Month	3	0,08509	0,02836	1,44	0,294
Site*Treatments	3	0,38294	0,12765	6,48	0,013
Month*Treatments	9	0,33108	0,03679	1,87	0,183
Error	9	0,17719	0,01969		
Total	31				

C) Articulate Coralline Algae

Source	DF	Adj SS	Adj MS	F-Value	P-Value
Site (S)	1	0,04646	0,04646	1,58	0,241
Month (M)	3	0,27021	0,09007	3,06	0,084
Treatment (T)	3	0,18913	0,06304	2,14	0,165
Site*Month	3	0,04445	0,01482	0,50	0,690
Site*Treatments	3	0,34838	0,11613	3,94	0,048
Month*Treatments	9	0,40108	0,04456	1,51	0,274
Error	9	0,26524	0,02947		
Total	31				

D) Ulva spp

Source	DF	Adj SS	Adj MS	F-Value	P-Value
Site (S)	1	0,032077	0,032077	5,39	0,045
Month (M)	3	0,128113	0,042704	7,17	0,009
Treatment (T)	3	0,012013	0,004004	0,67	0,590
Site*Month	3	0,086885	0,028962	4,86	0,028
Site*Treatments	3	0,037942	0,012647	2,12	0,167
Month*Treatments	9	0,031308	0,003479	0,58	0,782
Error	9	0,053591	0,005955		
Total	31				

E) Didemnum & Briozoos

Source	DF	Adj SS	Adj MS	F-Value	P-Value
Site (S)	1	0,02828	0,02828	0,98	0,348
Month (M)	3	0,21465	0,07155	2,48	0,127
Treatment (T)	3	0,18406	0,06135	2,13	0,167
Site*Month	3	0,01409	0,00470	0,16	0,919
Site*Treatments	3	0,08276	0,02759	0,96	0,454
Month*Treatments	9	0,17203	0,01911	0,66	0,725
Error	9	0,25951	0,02883		
Total	31				

F) Bare Rock

Source	DF	Adj SS	Adj MS	F-Value	P-Value
Site (S)	1	0,33566	0,33566	18,24	0,002
Month (M)	3	0,83557	0,27852	15,13	0,001
Treatment (T)	3	0,04685	0,01562	0,85	0,501
Site*Month	3	0,02312	0,00771	0,42	0,744
Site*Treatments	3	0,04092	0,01364	0,74	0,554
Month*Treatments	9	0,17778	0,01975	0,74	0,459
Error	9	0,16565	0,01841		
Total	31				

Table 1B**A) Richness (S)**

Source	DF	Adj SS	Adj MS	F-Value	P-Value
Month (M)	3	6,2603	2,08675	2,97	0,063
Treatment (T)	3	2,0521	0,68402	0,97	0,430
M*T	9	3,7730	0,41922	0,60	0,782
Error	16	11,2538	0,70336		
Total	31	23,3390			

B) Diversity (H)

Source	DF	Adj SS	Adj MS	F-Value	P-Value
Month (M)	3	0,08601	1,05130	0,81	0,508
Treatment (T)	3	0,08599	0,0286649	0,81	0,508
M*T	9	0,31104	0,0345599	0,97	0,496
Error	16	0,56825	0,0355159		
Total	31	1,05130			

C) Evenness (J)

Source	DF	Adj SS	Adj MS	F-Value	P-Value
Month (M)	3	0,042172	0,0140572	3,49	0,040
Treatment (T)	3	0,012121	0,0040405	1,00	0,417
M*T	9	0,013901	0,0015445	0,38	0,926
Error	16	0,064468	0,0040292		
Total	31	0,132662			

Table 2

Posillopora Coral Growth

Source	DF	Adj SS	Adj MS	F-Value	P-Value
Site (S)	1	0,01929666	0,019296662	0,37	0,5441
Treatment (T)	3	0,13810229	0,046034096	0,89	0,4531
S*T	3	0,25573766	0,085245886	1,66	0,1931
Error	37	1,90424817	0,051466167		
Total	44	2,33355436			

Table 3A

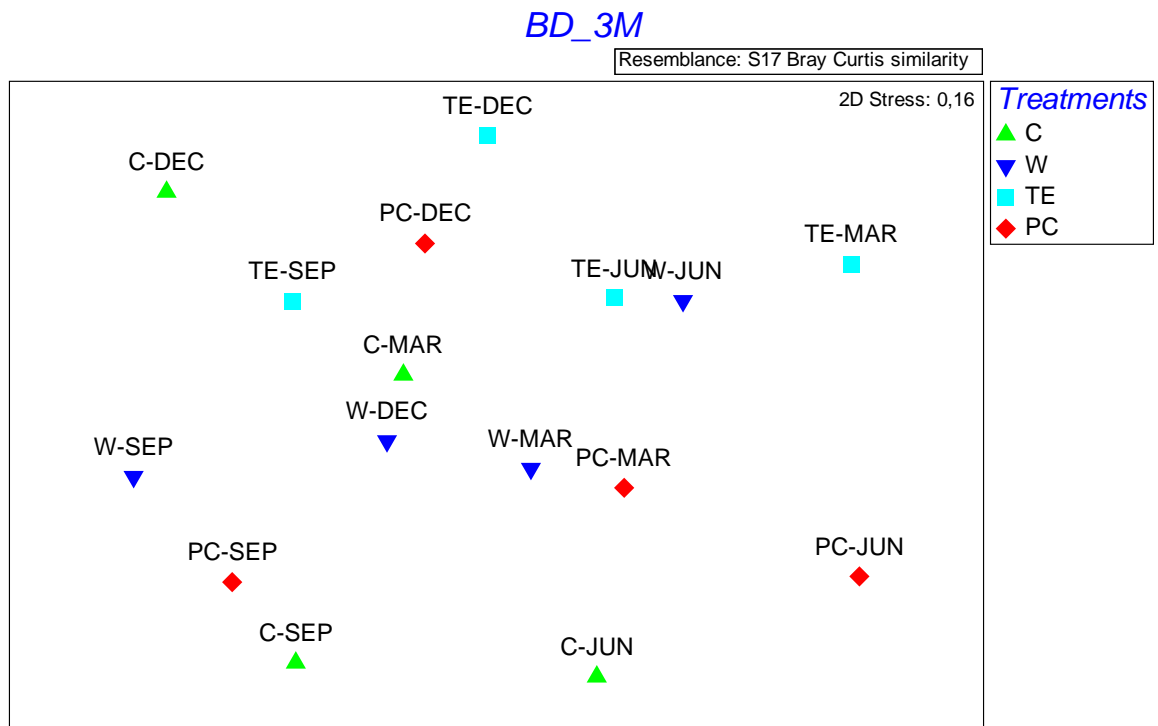
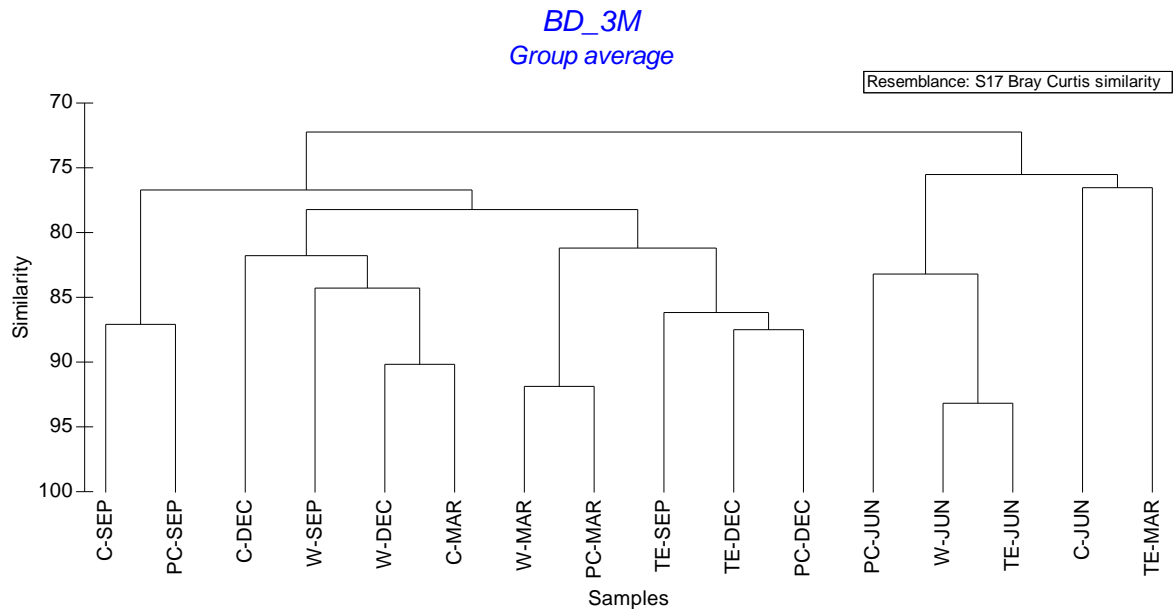
Type	Specie	Family	# Individuals
HERBÍVORES	<i>Prionurus laticlavus</i>	Acanthuridae	25
	<i>Scarus perrico</i>	Scaridae	3
	<i>Abudefduf troschelii</i>	Pomacentridae	16
	<i>Chromis atrilobata</i>	Pomacentridae	1
	<i>Stegastes acapulcoensis</i>	Pomacentridae	59
	<i>Stegastes flavilatus</i>	Pomacentridae	88
	<i>Ophioblennius steinchechneri</i>	Blenniidae	35
PREDATORS			0
	<i>Chaetodon falcifer</i>	Chaetodontidae	
	<i>Chaetodon humeralis</i>	Chaetodontidae	11
	<i>Heniochus nigrirostris</i>	Chaetodontidae	0
	<i>Johnrandallia nigrirostris</i>	Chaetodontidae	3
	<i>Halichoeres notopilus</i>	Labridae	43
	<i>Halichoeres chierchiae</i>	Labridae	11
	<i>Halichoeres dispilus</i>	Labridae	36
	<i>Halichoeres nicholsi</i>	Labridae	3
	<i>Paranthias colonus</i>	Serranidae	3
	<i>Bodianus diplotaenia</i>	Labridae	9
	<i>Thalassoma lucasanum</i>	Labridae	81
	<i>Canthigaster punctatissima</i>	Tetraodontidae	0
OMNIVORES	<i>Holacanthus passer</i>	Pomacanthidae	7
	<i>Zanclus cornutus</i>	Zanclidae	0
	<i>Pseudobalistes naufragium</i>	Balistidae	1
	<i>Diodon holocanthus</i>	Diodontidae	0
Total			435

Table 3B

Type	Specie	Family	# Individuals
HERBÍVORES	<i>Prionurus laticlavus</i>	Acanthuridae	24
	<i>Scarus perrico</i>	Scaridae	6
	<i>Abudefduf troschelii</i>	Pomacentridae	0
	<i>Chromis atrilobata</i>	Pomacentridae	0
	<i>Stegastes acapulcoensis</i>	Pomacentridae	24
	<i>Stegastes flavilatus</i>	Pomacentridae	8
	<i>Ophioblennius steinchechnei</i>	Blenniidae	18
PREDATORS	<i>Chaetodon falcifer</i>	Chaetodontidae	1
	<i>Chaetodon humeralis</i>	Chaetodontidae	39
	<i>Heniochus nigrirostris</i>	Chaetodontidae	5
	<i>Johnrandallia nigrirostris</i>	Chaetodontidae	10
	<i>Halichoeres notopilus</i>	Labridae	0
	<i>Halichoeres chierchiaie</i>	Labridae	0
	<i>Halichoeres dispilus</i>	Labridae	12
	<i>Halichoeres nicholsi</i>	Labridae	1
	<i>Paranthias colonus</i>	Serranidae	0
	<i>Bodianus diplotaenia</i>	Labridae	15
	<i>Thalassoma lucasanum</i>	Labridae	112
	<i>Canthigaster punctatissima</i>	Tetraodontidae	1
	OMNIVORES	<i>Holacanthus passer</i>	Pomacanthidae
<i>Zanclus cornutus</i>		Zanclidae	2
<i>Pseudobalistes naufragium</i>		Balistidae	0
<i>Diodon holocanthus</i>		Diodontidae	1
Total			332

Appendixes

Appendix A1



Appendix A2

