AN ABSTRACT OF THE THESIS OF Allison Elaine Palmer for the Master of Science in Biology presented November 5, 2003.

Title: Seasonality of Macroalgae and Benthic Cyanobacteria on Reef Flats of Guam.

Approved: Valerie J Paul
Dr. Valerie J. Paul, Chairperson, Thesis Committee

Macroalgal and cyanobacterial abundance data were collected on the reef flats at five sites around Guam over four and a half consecutive years (Apr. 1998-Oct. 2002) to discern if patterns of seasonality occur. Abundance data of the seven most common species at each site were compared with wave height data to determine whether wave action was a controlling factor in the formation or the demise of blooms of macroalgae and cyanobacteria.

Results showed no association of abundance of macroalgae with abundance of cyanobacteria at the five study sites. Maximum wave heights prior to algal data collection dates had no significant effect on abundance of macroalgae or cyanobacteria at all sites. This suggests that normal wave activity is not a controlling factor of algal community dynamics on the reef flats of Guam. There was one major occurrence of extreme wave action during Typhoon Chata'an on July 5, 2001, which devastated algal communities. Distinct peaks and dips in the algal communities from year to year mostly coincide with juvenile rabbitfish (Siganidae) runs.

TO THE OFFICE OF GRADUATE SCHOOL AND RESEARCH

The members of the Committee approve the thesis of Allison Elaine Palmer presented November 5, 2003.

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SEASONALITY OF MACROALGAE AND BENTHIC CYANOBACTERIA ON REEF FLATS OF GUAM

BY

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I dedicate this thesis to my mother, Sandra Palmer, who supported me endlessly through my endeavors with this project and who was a good role model to follow. Without her, I would not have succeeded.

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INTRODUCTION

As coastal areas are becoming more populated, shifts in coral reef communities due to anthropogenic factors are increasingly apparent. Communities that were once dominated by a diversity of corals are now filled with coral skeletons covered in turf and fleshy algae as well as cyanobacteria (blue-green algae).

Algal blooms, sudden increases in algal abundance, can have negative impacts on tropical coral reef communities and on recreational activities in Guam waters. Macroalgae and cyanobacteria compete with corals for space and inhibit coral recruitment and growth (Miller and Hay 1996, McClanahan et al. 2000, and Jompa and McCook 2002). Some marine algae are toxic to humans and to other marine life. On Guam, there have been cases of illness and three deaths associated with the ingestion of the red alga *Gracilaria tsudae* (Yasumoto 1993). Some seaweeds may be associated with toxic, epiphytic cyanobacteria.

An algal bloom can be a nuisance to beach-goers. On Guam, tourism forms the basis of the local economy, particularly marine-based tourism, which relies on healthy beaches and coral reefs (Amesbury et al. 1993). Algae can be visually unpleasant and, as they decompose in the sun, emit a noxious odor. Occasionally, beaches on Guam are closed due to toxic cyanobacteria in the water. One such occurrence of these toxic blooms happened at one of the present study sites, Ypao Beach Park. The outbreak occurred simultaneously with the massive fish kill of juvenile *Siganus argenteus* and *Siganus spinus* in May 1994 (Nagle and Paul 1998).

Seasonality has not been shown previously for all species of macroalgae and benthic cyanobacteria at the present study sites. Tsuda and Kami (1973) found little algal seasonality in a slightly deeper lagoon environment, i.e., Cocos Lagoon in southern Guam. Instead, they found that succession to an algal climax community could be reached in less than a year. These authors determined that selective feeding by herbivores and reduced light conditions were controlling factors leading to a cyanobacteria-dominated community structure.

Tsuda (1974), however, reported obvious algal seasonality, specifically for Phaeophyta, at other locations in Guam. For example, *Sargassum cristaefolium* (referred to as *S. duplicatum*) is present in Pago Bay between January and August, while *Jania capillacea* and *Amphiroa fragilissima* (Rhodophyta, calcareous red algae) are present from October to December (Tsuda 1971). Tsuda (1971, 1974) concluded that algal seasonality on shallow reef flats was caused by desiccation during low tides when the reefs are exposed during the noon hours and by annual precipitation, which alters salinity. Nagarkar and Williams (1999) found clear vertical zonation of cyanobacteria throughout the year on a tropical shore in Hong Kong, and marked temporal variation in species distribution, abundance and biomass. They suggested that the variation might have been due to fluctuating environmental factors, mainly temperature and precipitation.

Macroalgae incorporate a wide range of morphologies from fleshy, frondose plants to smaller turf-forming species. Benthic cyanobacteria are photosynthetic organisms that form macroscopic filamentous mats or clumps. Many factors play roles in determining which species bloom, where they occur and how large the blooms become.

Wave Action

Wave action can have damaging effects on attached marine algae and has been previously mentioned as an important ecological parameter worthy of investigation

(Kingsbury 1962, Jones and Demetropoulos 1968, Bustemante and Branch 1996). Mechanically, waves may break and tear seaweeds, although stipes of some macroalgae have excellent flexibility (DeWreede et al. 1992). Prior to breaking, wave height is directly proportional to flow speed; high waves have a faster flow (Denny and Gaylord 2002). The force exerted on the reef as waves break can vary due to tide changes. During high tides, waves break closer to shore, whereas lower tides break closer to the reef crest. Production of foam can inhibit algal growth by hindering light penetration. Conversely, waves can bring in nutrient-rich water and remove waste, allowing for enhancement of algal growth (Kingsbury 1962). Wave velocities can reach 10-20 $m \cdot s^{-1}$ (Dudgeon and Johnson 1992) and those close to shore may exceed 20 $m \cdot s^{-1}$ (Denny 1999).

Wave action can also be damaging to the substratum on which algae attach. FitzGerald (1978) reported a direct relationship between water movement and minimum size of substratum required to provide anchorage for thalli of *Enteromorpha clathrata* greater than 5 cm in length inhabiting the intertidal shore in Tumon Bay, Guam. Findings from the same study found seasonal variations of *E. clathrata* were correlated with wave height (FitzGerald 1978).

There is an abundance of information on wave-swept attached algae for temperate rocky shores (John et al. 1992, DeWreede et al. 1992, and Dudgeon and Johnson 1992), but little is known about wave-swept tropical benthic marine macroalgae and cyanobacteria. Tropical benthic macroalgae can commonly be observed, during or following high wave action, unattached and floating in the water column. Some macroalgae have evolved structural or morphological differences to withstand wave action. Turf-forming algae tend to survive better than large, frondose individuals and mat-forming species on the reef flat (Hay 1981). Macroalgal species found on the reef flat are usually much shorter and spread over more of the substratum than the same species found at depth. Some species will grow intertwining together to form tough mats.

Thacker and Paul (2001) used preliminary data from the present study to compare algal growth with several environmental factors such as nutrient enrichment, wave action, temperature, salinity, rainfall and wind. They wanted to determine what environmental factors, if any, were limiting or enhancing growth and distribution, and whether cyanobacteria were competing with macroalgae. Nutrient availability and competition with macroalgae showed no significant effects on the growth and distribution of cyanobacteria. They saw a negative correlation between macroalgal abundance and cyanobacterial abundance. One of their sites showed differences in abundance due to wave height (Thacker and Paul 2001).

Other than the above-mentioned wave height and macroalgal correlations, no real trends were observed by Thacker and Paul (2001), when cyanobacterial abundance was compared to environmental factors. Nevertheless, large changes in percent cover can be seen in the macroalgal and cyanobacterial abundance data from year to year.

I hypothesize that macroalgal abundance is positively associated with cyanobacterial abundance and that wave height is negatively correlated with macroalgal and cyanobacterial abundance at the present study sites. As wave action, herbivory and competition increase, abundance of some species may decline and abundance of other species may increase as space becomes available.

Other Factors Controlling Algal Dynamics: Herbivory and Nutrients

Annual runs of juvenile rabbitfishes *Siganus spinus* and *S. argenteus* (Siganidae) occur on the reef flats of Guam. The juveniles of these fish are herbivorous and are of some importance to the local economy of Guam. Juvenile siganids usually appear at the third quarter moon in April and feed until May, during which time they are caught by fishers (Kami and Ikehara 1976). Occasionally, there is a second, smaller run from June to October. Depending on the size of the schools, they can alter the algal community around Guam.

Gut contents were examined and it was determined that they fed mostly on filamentous algae and non-calcareous fleshy algae, i.e. *Caulerpa racemosa* and *Hypnea pannosa* (Tsuda and Bryan 1973). Feeding assays with *Siganus* spp. have shown an order of algae preference: 1) *Enteromorpha,* 2) *Hincksia* and *Derbesia*, and 3) *Cladophoropsis*. Juvenile *Siganus* spp. usually avoided the following genera, although some were observed eating the younger stages of the algae, i.e., *Avrainvillea, Codium, Dictyota, Gelidium, Gracilaria, Padina and Jania* (Tsuda and Bryan 1973, Paul et al. 1990). In a study by Paul et al. (1990), it was determined that juvenile *S. argenteus* preferred algal genera that were not calcified or tough, and they did not always select against defensive chemistry that was unpalatable to adults.

Although this study will not cover nutrient limitation as a factor that controls algal blooms, I acknowledge that it may be important. Previous studies showed nutrient enrichment from eutrophication and herbivory as major factors in fleshy algal abundance (Belliveau and Paul 2002, Hixon and Brostoff 1996, Miller et al.1999, Lapointe 1997 and Raffaelli et al.1998). In one such experiment, cages were used to exclude herbivorous fishes, and slow release fertilizers were placed inside the cages for nutrient influx. Cages that excluded herbivores showed increases in fleshy algae abundance and decreases in abundance of crustose coralline algae, which are important for coral settlement (Belliveau and Paul 2002).

METHODS

Site Selection and Sampling

Cyanobacterial and macroalgal abundance were monitored on the reef flats in Tanguisson Beach Park, Tumon Bay and Pago Bay, Guam (Table 1, Figures 1-4). Shallow water depth at all sites allowed for good light availability. Transects were positioned to ensure best coverage of the survey area. Transects were surveyed approximately every four to six weeks for four and a half consecutive years (April 1998-October 2002). A 0.5-m x 0.5-m quadrat was placed every 6 m on each transect. The quadrat was sectioned into one hundred 5-cm x 5-cm cells. All macroalgal and cyanobacterial species were counted as present or absent in each cell and were combined to give total percent cover. There was overlap of some species but usually they could all still be identified and were counted. Mean percent cover was determined for each site. Total percent cover of cyanobacteria and macroalgae was estimated at each site using these data (Sutherland 1996).

Tumon Bay had two transects that were 60 m long and positioned perpendicular to shore for each of the three sites. The Pago Bay site and the Tanguisson Beach Park site had three transects each, 30 m and 60 m long, respectively. Transects were positioned parallel to shore— along or near the reef crest, central and shoreward. The shore runoff and freshwater seeps at Tumon and Tanguisson may cause spikes of nutrients or salinity changes that may not have been measured in previous studies (Thacker and Paul 2001), but may have a noticeable influence on algal abundance. At all sites, juvenile and adult fish were diverse and moderately abundant (pers. obs.). Observers collecting algal abundance data took note of juvenile siganids during their

Table 1. Description of algal transect sites.

Site	Depth (MLLW)	Location	Figure
Tanguisson Beach Park	43 to 109 cm	north on the west side of Guam	2
Tumon Bay:	2.5 to 81 cm	south of Tanguisson site	3
Sails		north side of bay adjacent to the beach bar formerly called Sails Beach Bar	
Pia Marine		west of the Pia Marine Hotel and south of Sails site	
Ypao Beach Park		southernmost part of Tumon Bay, adjacent to the Hilton Hotel	
Pago Bay	-10 to 20 cm	east side of Guam, south of the University of Guam Marine Laboratory	4

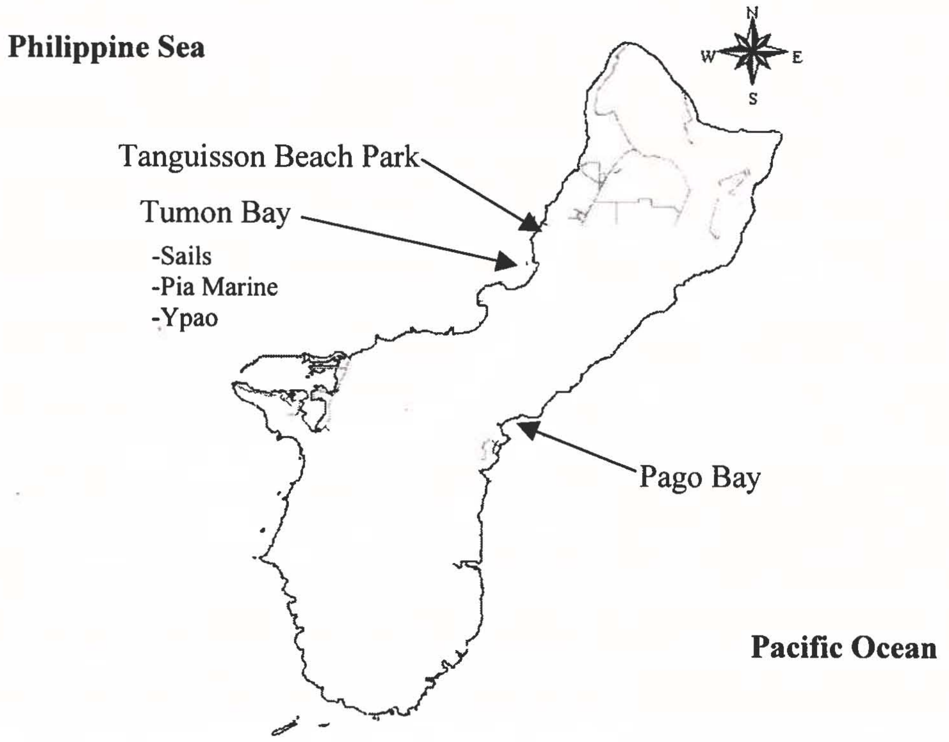


Figure 1. Algal transect site locations on Guam.

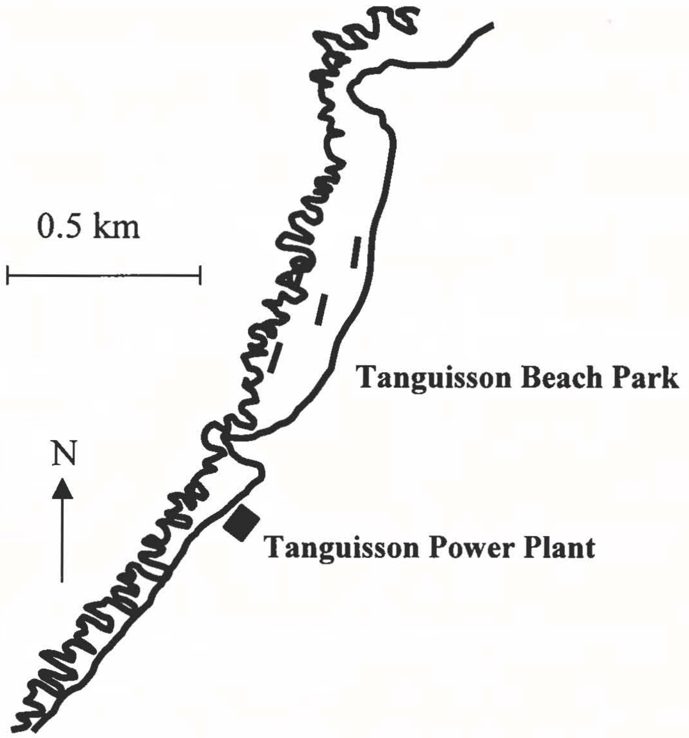


Figure 2. Tanguisson Beach Park transect locations at 13° 33′ N, 144° 48′ E. (Taken from 1978 USGS Topographical Map of Guam).

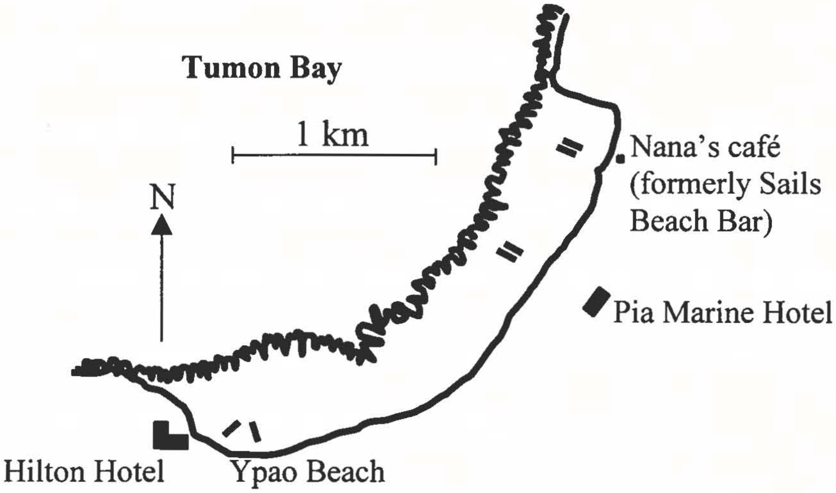


Figure 3. Sails, Pia Marine and Ypao transect locations at 13° 32′ N, 144° 48′ E. (Taken from 1978 USGS Topographical Map of Guam)

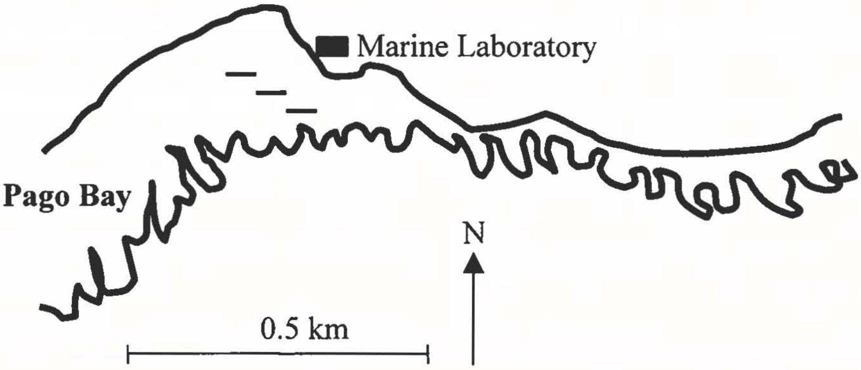


Figure 4. Pago Bay transect locations at 13° 25′ N, 144° 48′ E. (Taken from 1978 USGS Topographical Map of Guam)

annual runs, henceforth, referred to as “siganid events”, and took note of bite marks on algal species.

Collection of Wave Height Data and Data Analysis

Wave height data were obtained from the NOAA National Weather Service office at Tiyan, Guam. Their data are based on visual observations of wave height recorded twice daily from the University of Guam Marine Laboratory (near the Pago site on the east side of Guam) and from Agana Boat Basin (south of the Tumon and Tanguisson sites on the west side of Guam) and are shown in Figure 5.

The seven most frequently occurring algal species were chosen at each site for correlation analysis with the maximum wave height that occurred since the previous data collection. Macroalgal and cyanobacterial abundance data did not meet the assumptions of normality. Spearman’s rank correlations were performed to test associations among wave height and algal seasonality and to test associations between overall abundance of macroalgae and cyanobacteria at all of the five sites. Spearman’s rank analyses were corrected according to Holm’s procedure and, as they are non-parametric analyses, no transformations were applied to the data.

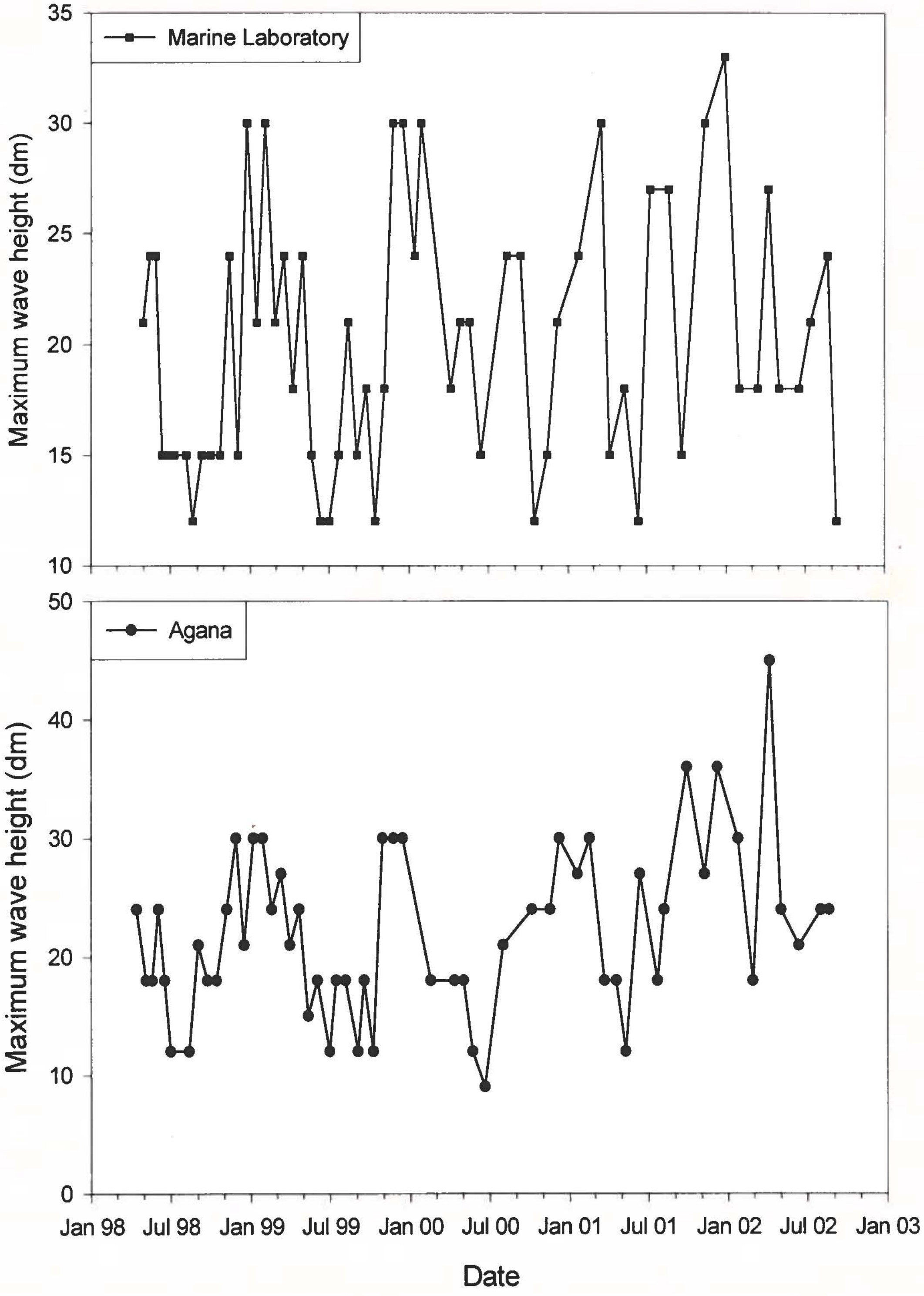


Figure 5. Maximum wave height data obtained from National Weather Service.

RESULTS

Thirty-seven macroalgae and fifteen cyanobacteria species were counted and are listed in Tables 2 and 3, respectively. Some algal species were not identified with certainty, i.e., no vouchers collected, and some only to genus level. Therefore, some species, mostly cyanobacteria, were not identified to species level in the data set. Species that were more common, i.e., most frequently occurring, were chosen for analysis.

Ypao had a significant negative rank correlation (r_s= -0.34976, $p \leq 0.01$) between total cover of macroalgae and total cover of cyanobacteria (Figure 6). At the other sites, there was no significant correlation between macroalgae and cyanobacteria.

Macroalgae

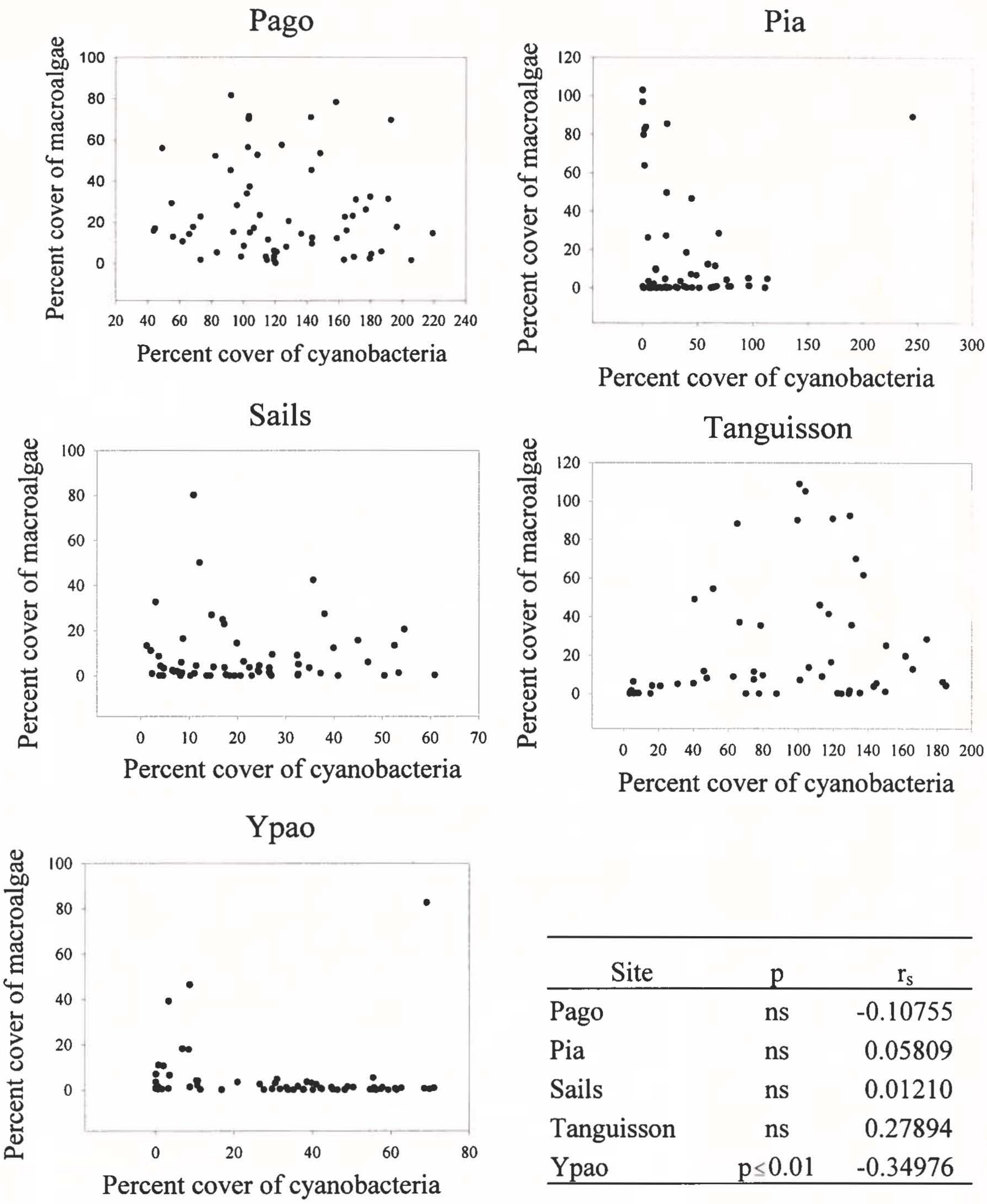
Most species of macroalgae were removed from the reef by typhoon Chata'an on July 5, 2002. The few left were mostly found as mere holdfasts on the reef. *Acanthophora spicifera* (Figure 7) had blooms once a year, but the timing was not the same every year for the red alga. *Boodlea composita*, (Figure 8) a crunchy green turf alga, at Pago, Pia and Sails showed distinct blooms occurring around May to July and November to December. *Caulerpa racemosa* is a fleshy green alga thought to be a preferred species for juvenile siganids (Tsuda and Bryan 1973). *C. racemosa* showed declines at Pago and Tanguisson shortly after siganid events (Figure 9). *Dictyota bartayresiana,* a frondose brown alga, at Pago (Figure 10) had small blooms during the siganid events or shortly thereafter. Figure 11 shows early spring and late summer blooms for the red alga, *Gracilaria salicornia*. *Padina boryana*, a calcified brown alga, at Pia and Ypao (Figure 12) had a steep drop-off in September 1999 at Ypao. Blooms were apparent but not temporally uniform. *Dictyota* and *Padina* are two of the less

Table 2. List of species of macroalgae found at five sites on Guam.

Macroalgae species	Author
Acanthophora spicifera	(Vahl) Børgesen
Actinotrichia fragilis	(Forsskål) Børgesen
Amphiroa fragillisima	(Linnaeus) Lamouroux
Asparagopsis taxiformis	(Delile) Trevisan
Avrainvillea sp.	Probably *A. obscura* (C. Agardh) J. Agardh
Boergesenia forbesii	(Harvey) Feldmann
Boodlea composita	(Harvey) Brand
Bryopsis pennata	Lamouroux
Caulerpa cupressoides	(Vahl) C. Agardh
C. racemosa	(Forsskål) J. Agardh
C. serrulata	(Forsskål) J. Agardh
C. sertularioides	(Gmelin) Howe
C. taxifolia	(Vahl) C. Agardh
C. urvilleana	Montagne
Chlorodesmis fastigiata	(C. Agardh) Ducker
Chondrophyllum papillosa	(C. Agardh) Garbary & Harper
Chrysophaeum taylori	Lewis & Bryan
Codium arabicum	Kützing
Dictyosphaeria cavernosa	(Forsskål) Børgesen
Dictyota bartayresiana	Lamouroux
Enteromorpha clathrata	(Roth) Greville
Galaxaura marginata	(Ellis & Solander) Lamouroux
Gelidiella acerosa	(Forsskål) Feldmann & Hamel
Gracilaria salicornia	(C. Agardh) Dawson
Halimeda macroloba	Decaisne
Halimeda opuntia	(Linnaeus) Lamouroux
Hydroclathrus clathratus	(C. Agardh) Howe
Hypnea pannosa	J. Agardh
Jania capillacea	Harvey
Lobophora variegata	(Lamouroux) Womersley ex Oliveira
Mastophora rosea	(C. Agardh) Setchell
Neomeris annulata	Dickie
Padina boryana	Thivy in Taylor [=*P. tenuis* (C. Agardh) Bory]
Rhodymenia divaricata	Dawson
Sargassum cristaefolium	C. Agardh
Sargassum polycystum	C. Agardh
Turbinaria ornata	(Turner) J. Agardh

Table 3. List of species of cyanobacteria found at five sites on Guam.

Cyanobacteria species	Author or description for unknowns
Hormothamnium enteromorphoides	Grunow
Lyngbya majuscula	(Dillwyn) Harvey
L. semiplena	(C. Agardh) J. Agardh
Lyngbya sp. 1	dark, cotton-like balls
Lyngbya sp. 2	green iridescent (cf. *L. semiplena*)
Oscillatoria margaritifera	(Kützing) Falkenberg
Oscillatoria sp. 1	light mat
Oscillatoria sp. 2	brown film
Oscillatoria sp. 3	unknown
Schizothrix mexicana	Gomont
Schizothrix sp. 1	dark pink balls
Schizothrix sp. 2	hard golden buttons
Schizothrix sp. 3	dark mat
Symploca hydnoides	(Harvey) Kützing
Tolypothrix byssoidea	(Berkeley) Kirchner



Site	p	r_s
Pago	ns	-0.10755
Pia	ns	0.05809
Sails	ns	0.01210
Tanguisson	ns	0.27894
Ypao	$p \leq 0.01$	-0.34976

Figure 6. Correlation between percent cover of macroalgae and cyanobacteria. The data are presented by site. Each point represents total percent cover for a collection date. Percent cover exceeds 100% due to overlapping algae. Table on bottom right shows Spearman's rank correlation coefficients for each site.

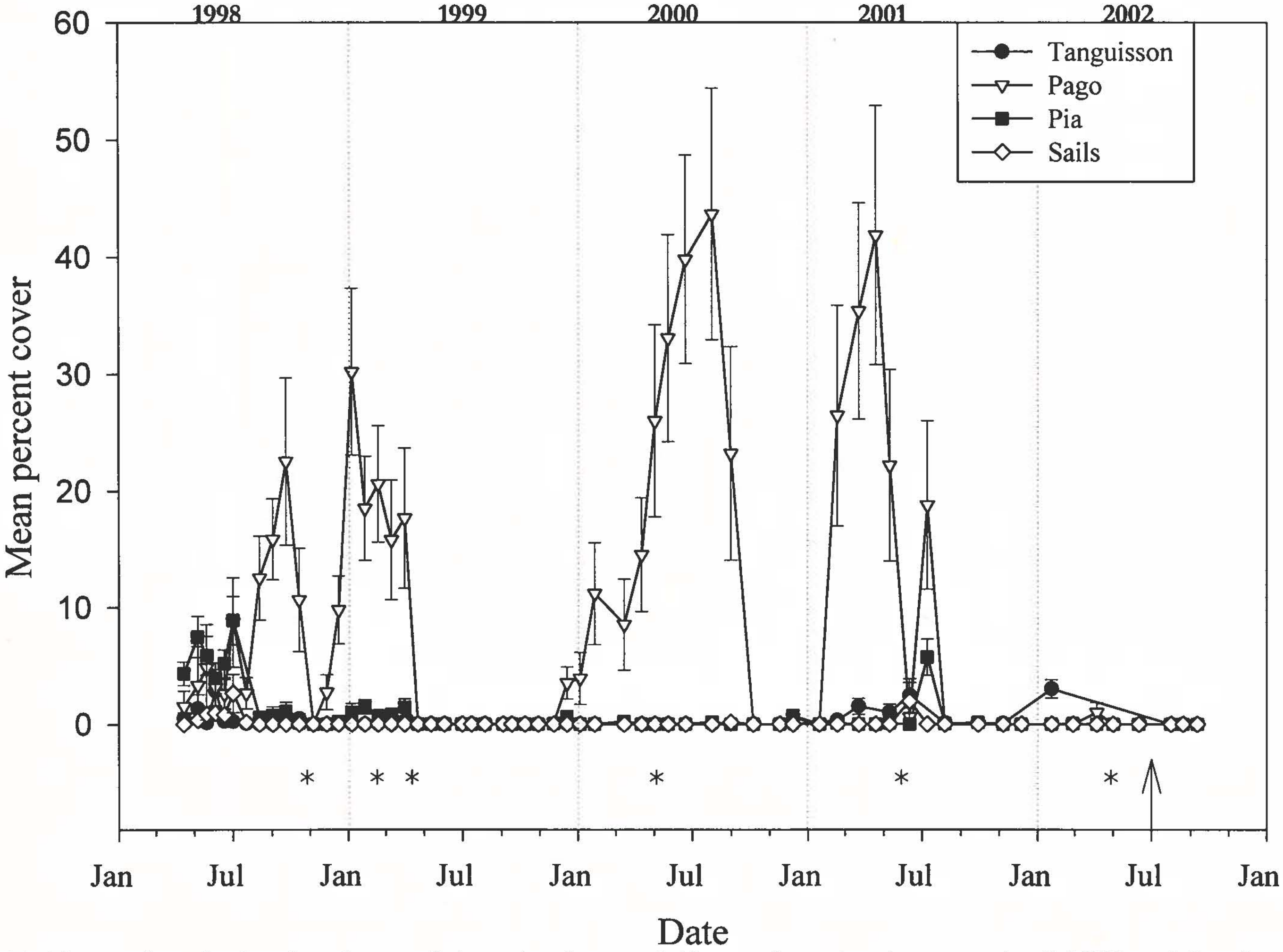


Figure 7. Fluctuations in the abundance of *Acanthophora spicifera* at four sites between April 1998 and October 2002. Asterisks represent visual observations of juvenile siganid groups. The arrow represents Typhoon Chata'an.

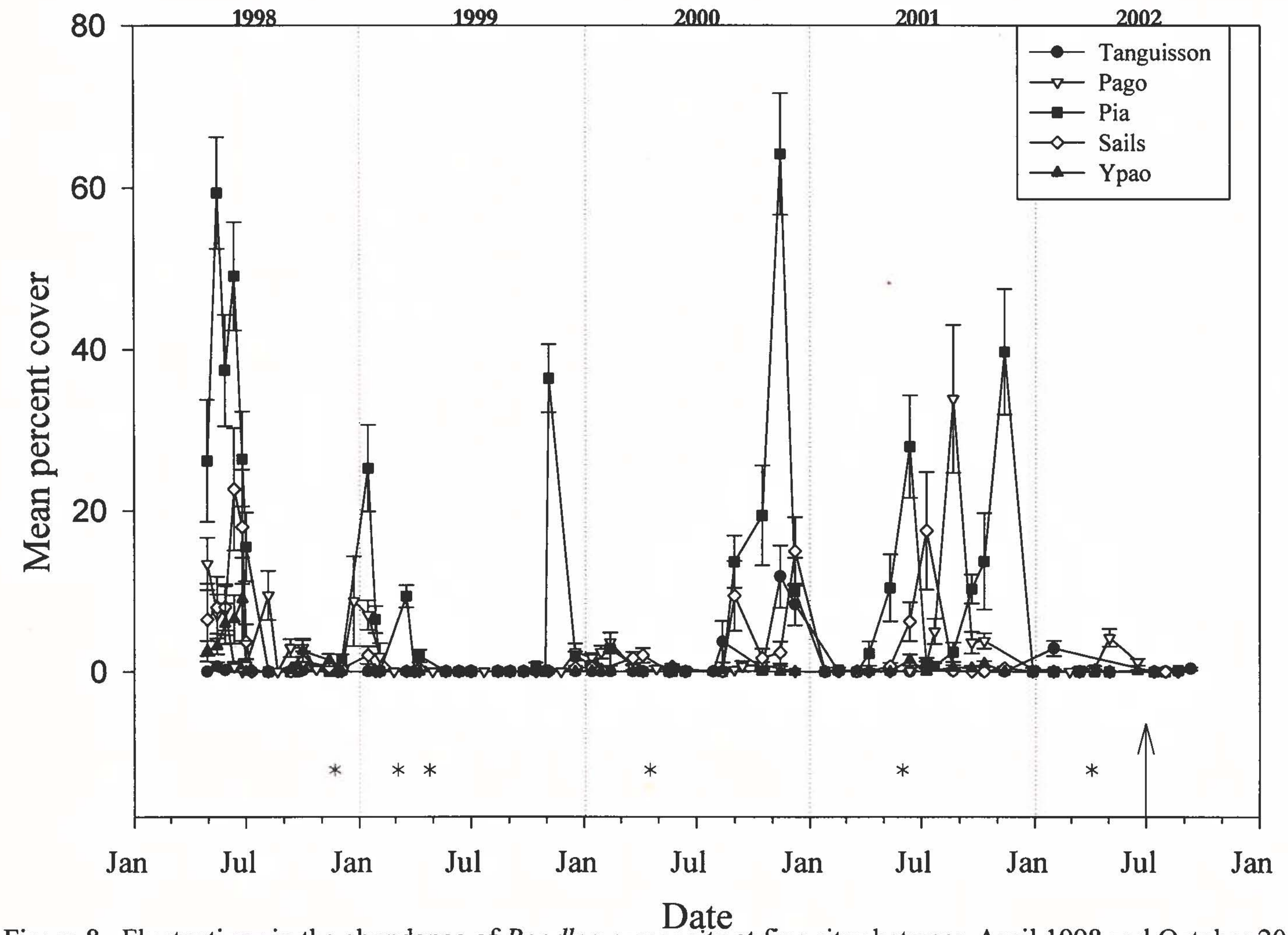


Figure 8. Fluctuations in the abundance of *Boodlea composita* at five sites between April 1998 and October 2002. Asterisks represent visual observations of juvenile siganid groups. The arrow represents Typhoon Chata'an.

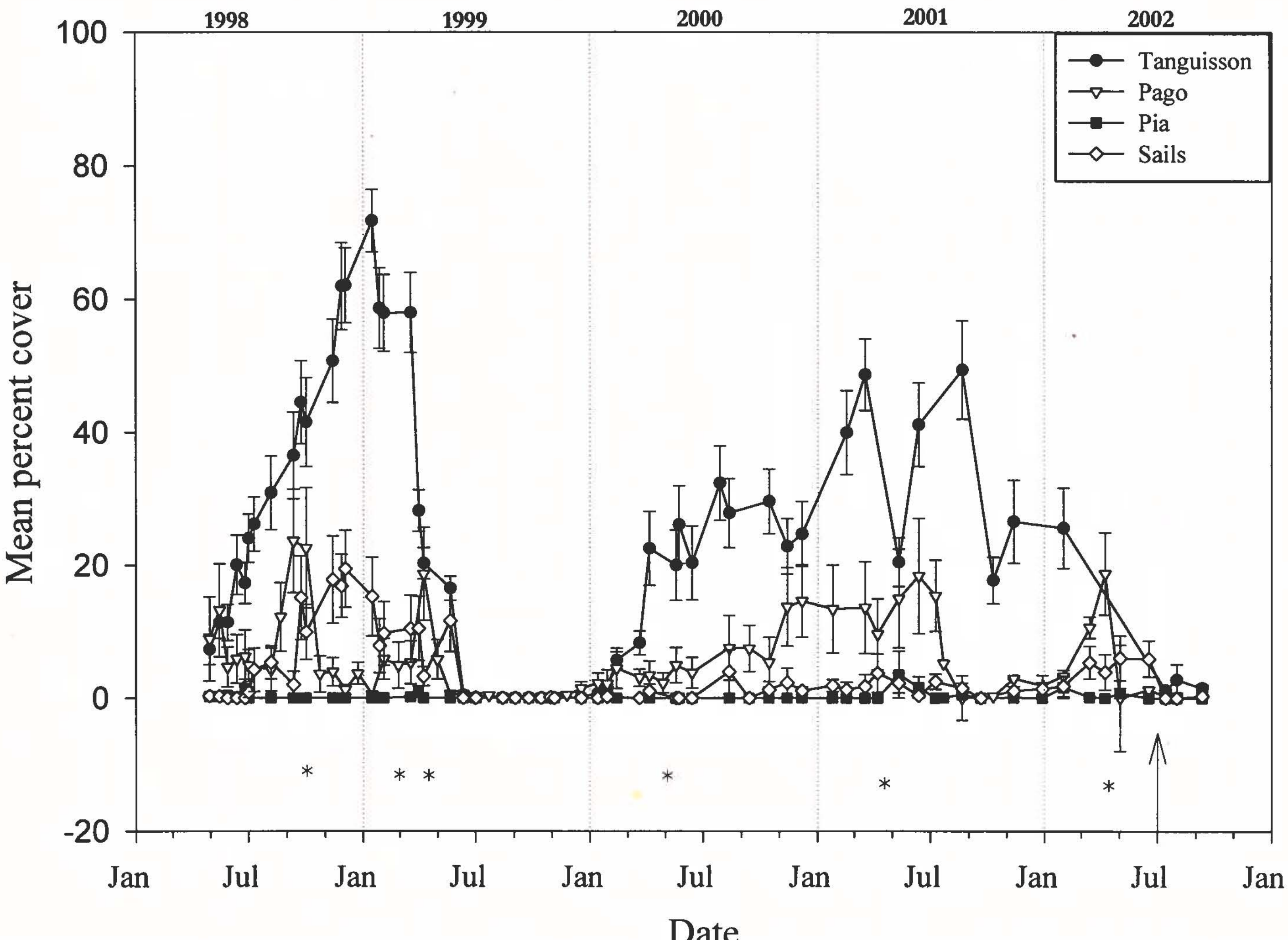


Figure 9. Fluctuations in the abundance of *Caulerpa racemosa* at four sites between April 1998 and October 2002. Asterisks represent visual observations of juvenile siganid groups. The arrow represents Typhoon Chata'an.

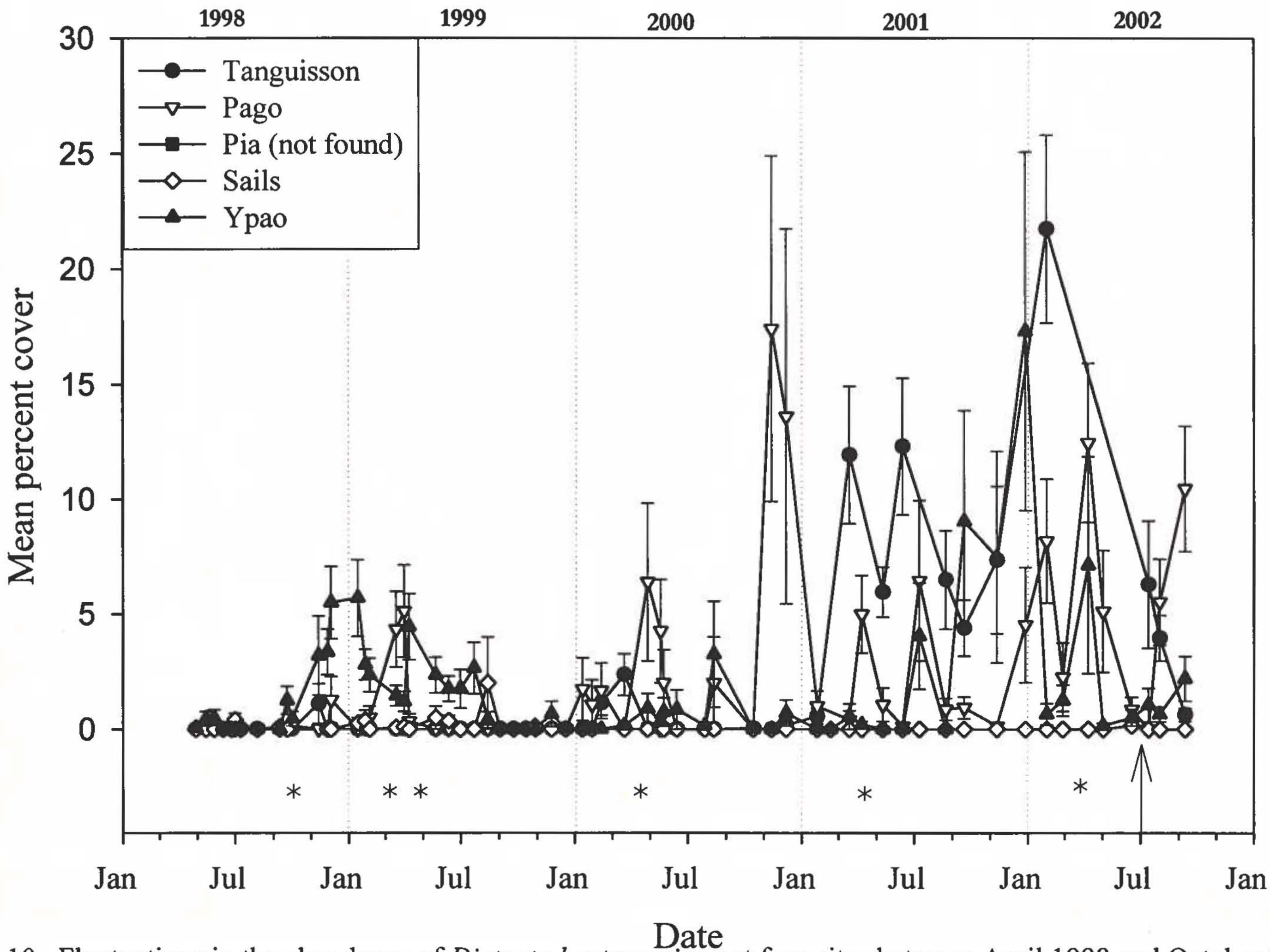


Figure 10. Fluctuations in the abundance of *Dictyota bartayresiana* at four sites between April 1998 and October 2002. Asterisks represent visual observations of juvenile siganid groups. The arrow represents Typhoon Chata'an.

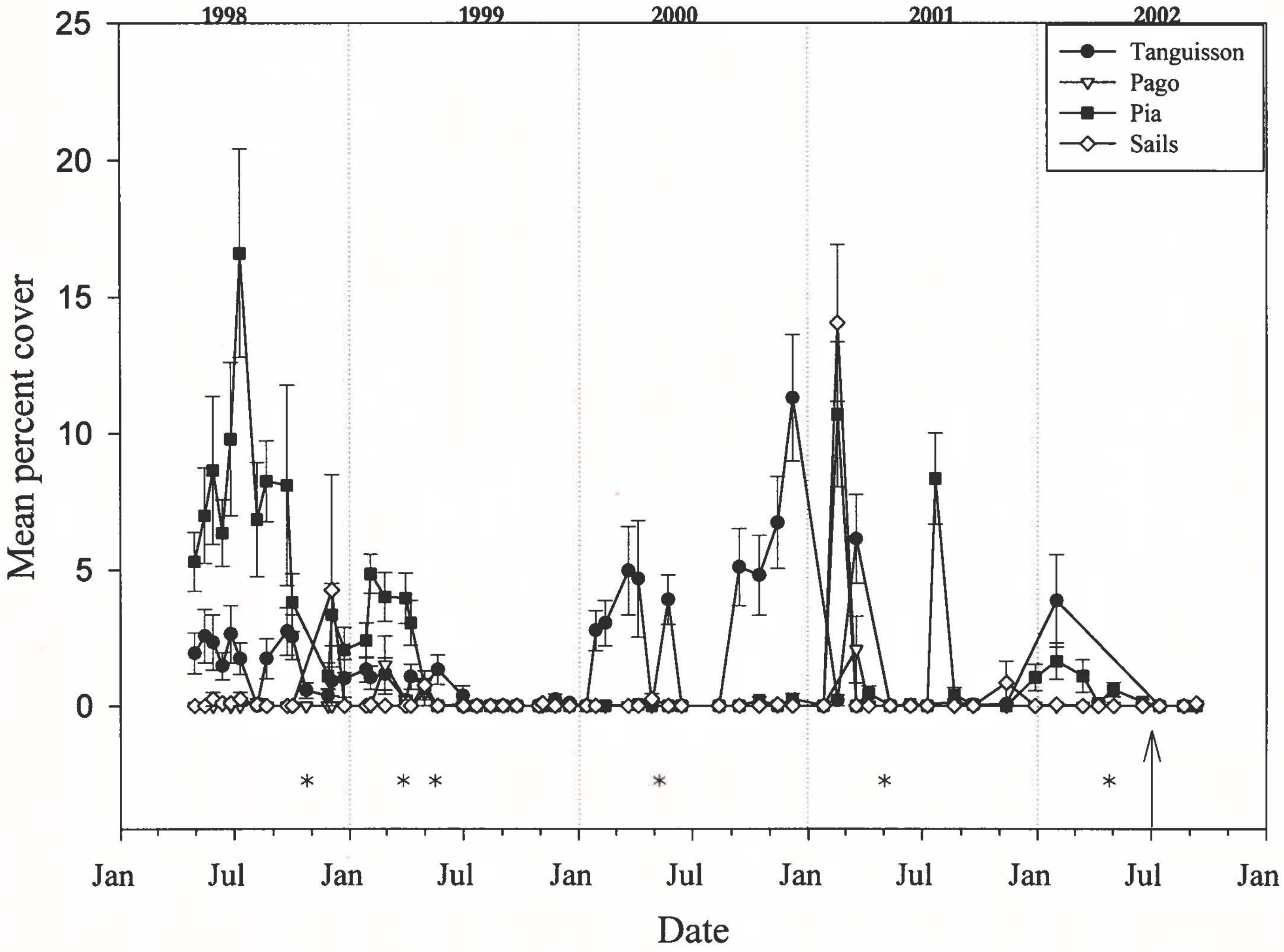


Figure 11. Fluctuations in the abundance of *Gracilaria salicornia* at four sites between April 1998 and October 2002. Asterisks represent visual observations of juvenile siganid groups. The arrow represents Typhoon Chata'an.

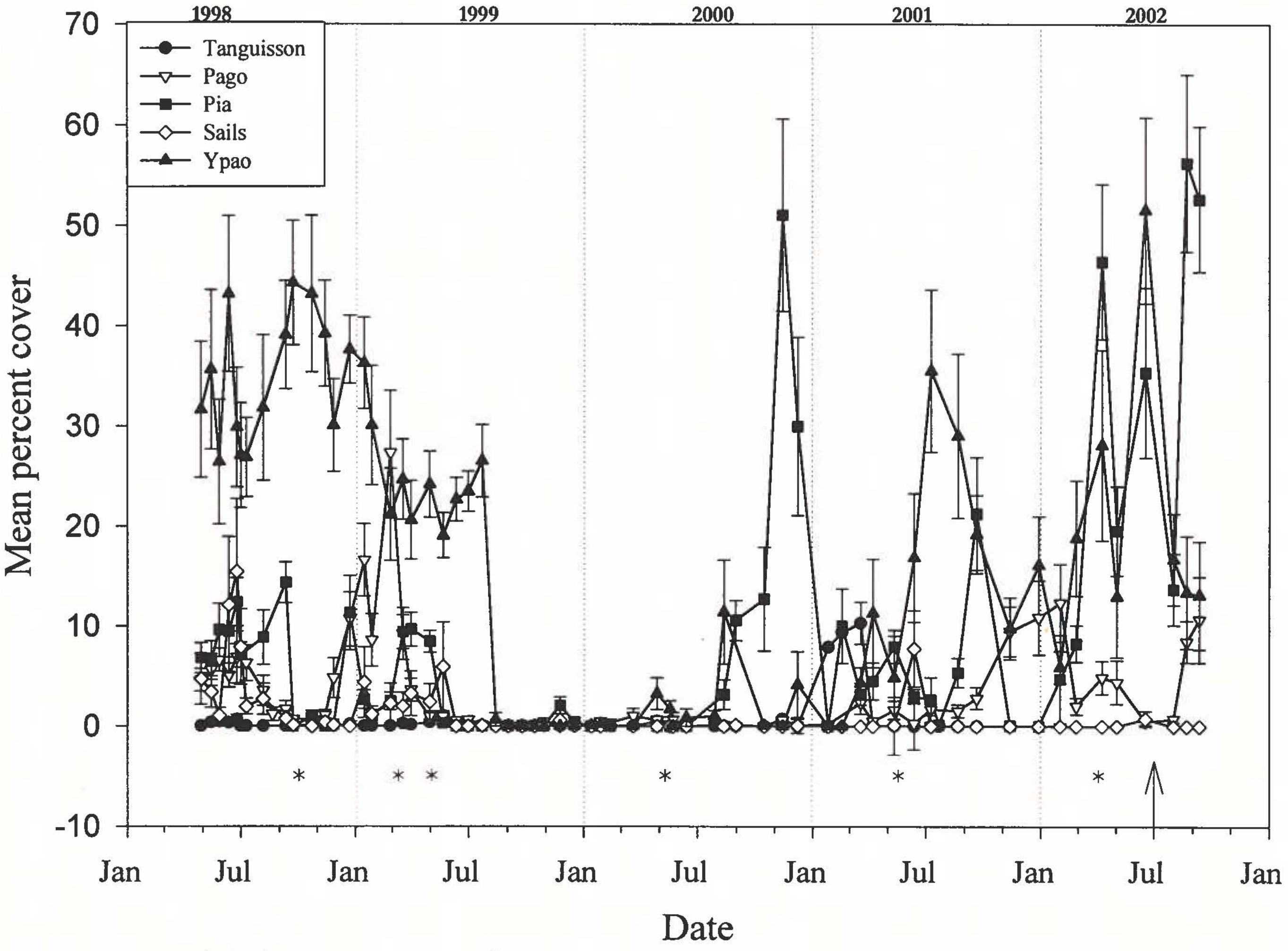


Figure 12. Fluctuations in the abundance of *Padina boryana* at four sites between April 1998 and October 2002. Asterisks represent visual observations of juvenile siganid groups. The arrow represents Typhoon Chata'an.

preferred genera by juvenile siganids (Tsuda and Bryan 1973). Some macroalgae may have been exposed during extreme low tides at Pago possibly causing substantial desiccation. Some species of macroalgae, such as *Acanthophora spicifera* at Pago, bloomed but did not fall in the transect area and, therefore, did not show up in the data set (pers. obs.).

Cyanobacteria

Most species of cyanobacteria were no longer apparent after Typhoon Chata'an. *Lyngbya* spp. form delicate filaments, which usually appear hair-like and sway with movements in the water column. *Lyngbya semiplena* (Figure 13) has blooms at Pia every year around April. There was a *L. semiplena* bloom at Pia in April 2002 outside of the transects (pers. obs.). *Lyngbya* sp. 1 (dark cotton-like, Figure 14) had multiple blooms and declines of blooms after August 1999. *Lyngbya* sp. 2 (green iridescent small clumps, Figure 15) only had one big bloom, which occurred simultaneously with the juvenile siganid run of 2000. *Oscillatoria* spp. are usually mat-forming, encrust any part of the substratum and may have small filaments that grow up into the water column. *Oscillatoria* sp. 2 (Figure 16), which we called brown film, has very distinct October blooms every year at Pia. Similar blooms around September or October can be seen for the same species at Sails and Tanguisson. Two closely related species, *Oscillatoria* sp. 1 (light mat, Figure 17) at Pago and *Oscillatoria* sp. 3 (mat, Figure 18) at Ypao occurred less repeatedly, but were still apparent, usually blooming early spring to summer. *Schizothrix* spp., have microfilaments, i.e., much smaller than the other two genera examined, that are very morphologically diverse. Some form dense clumps that

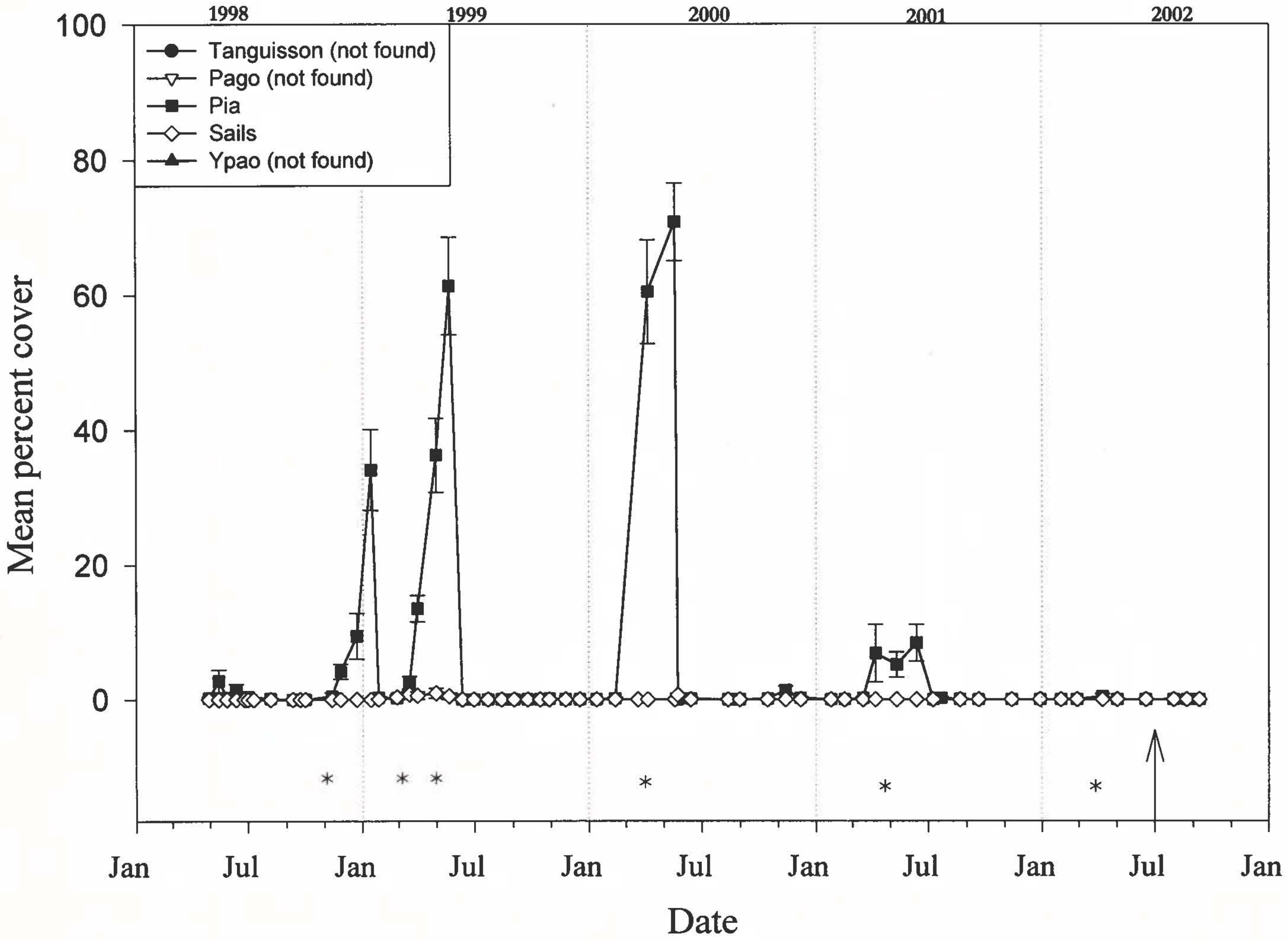


Figure 13. Fluctuations in the abundance of *Lyngbya semiplena* at two sites between April 1998 and October 2002. Asterisks represent visual observations of juvenile siganid groups. The arrow represents Typhoon Chata'an.

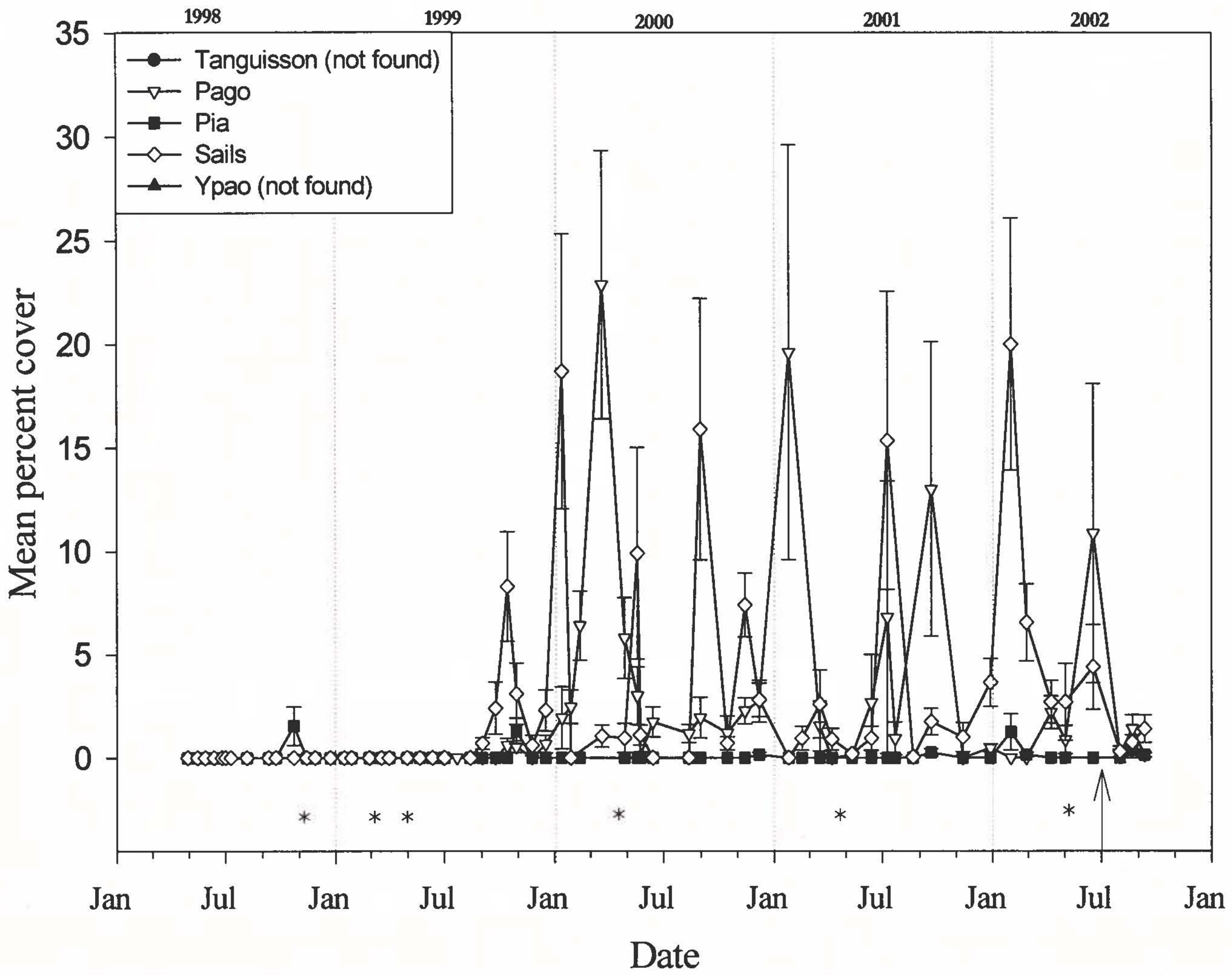


Figure 14. Fluctuations in the abundance of *Lyngbya* sp. 1 at three sites between April 1998 and October 2002. Asterisks represent visual observations of juvenile siganid groups. The arrow represents Typhoon Chata'an.

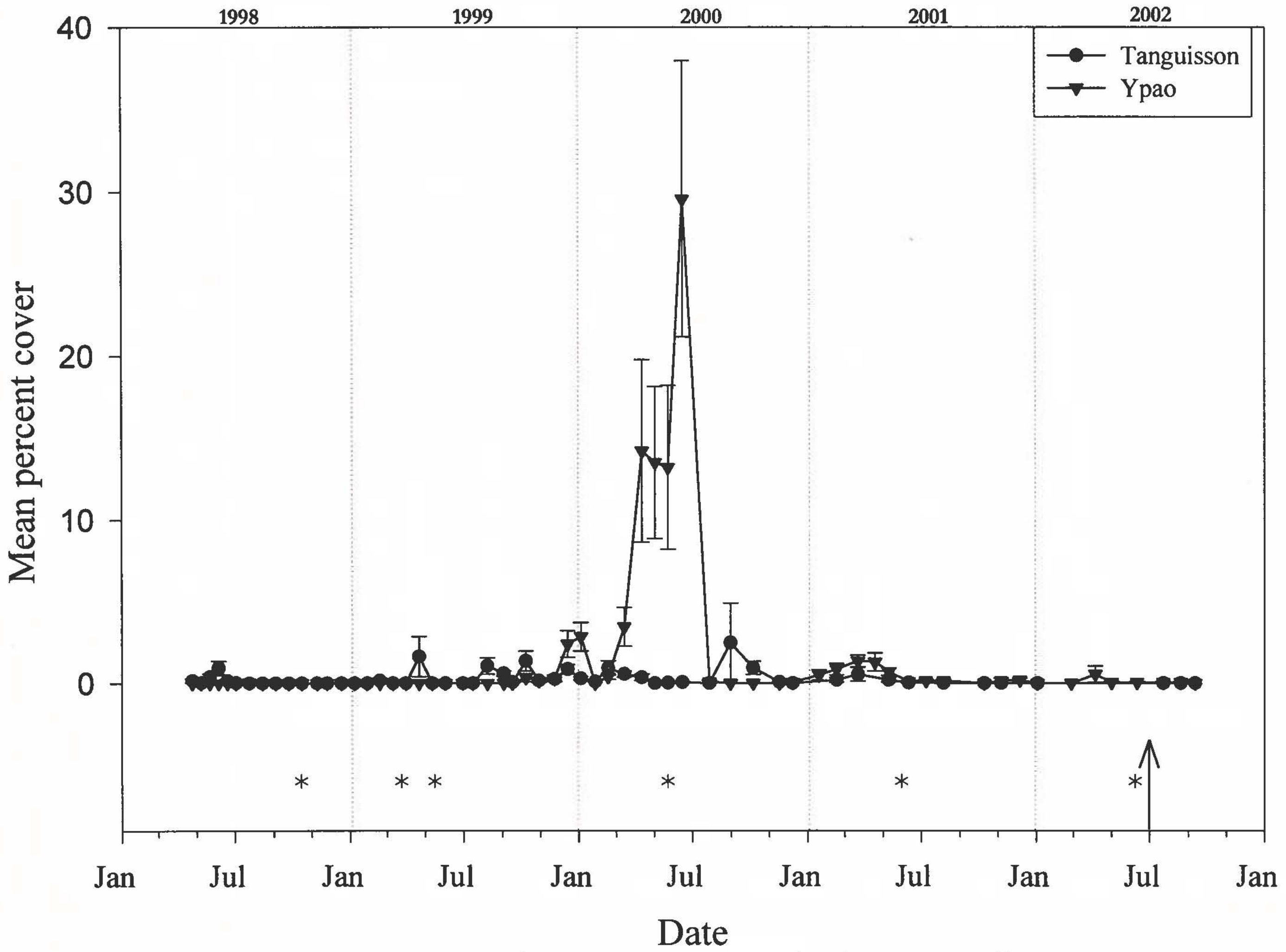


Figure 15. Fluctuations in the abundance of *Lyngbya* sp. 2 at two sites between April 1998 and October 2002. Asterisks represent visual observations of juvenile siganid groups. The arrow represents Typhoon Chata'an.

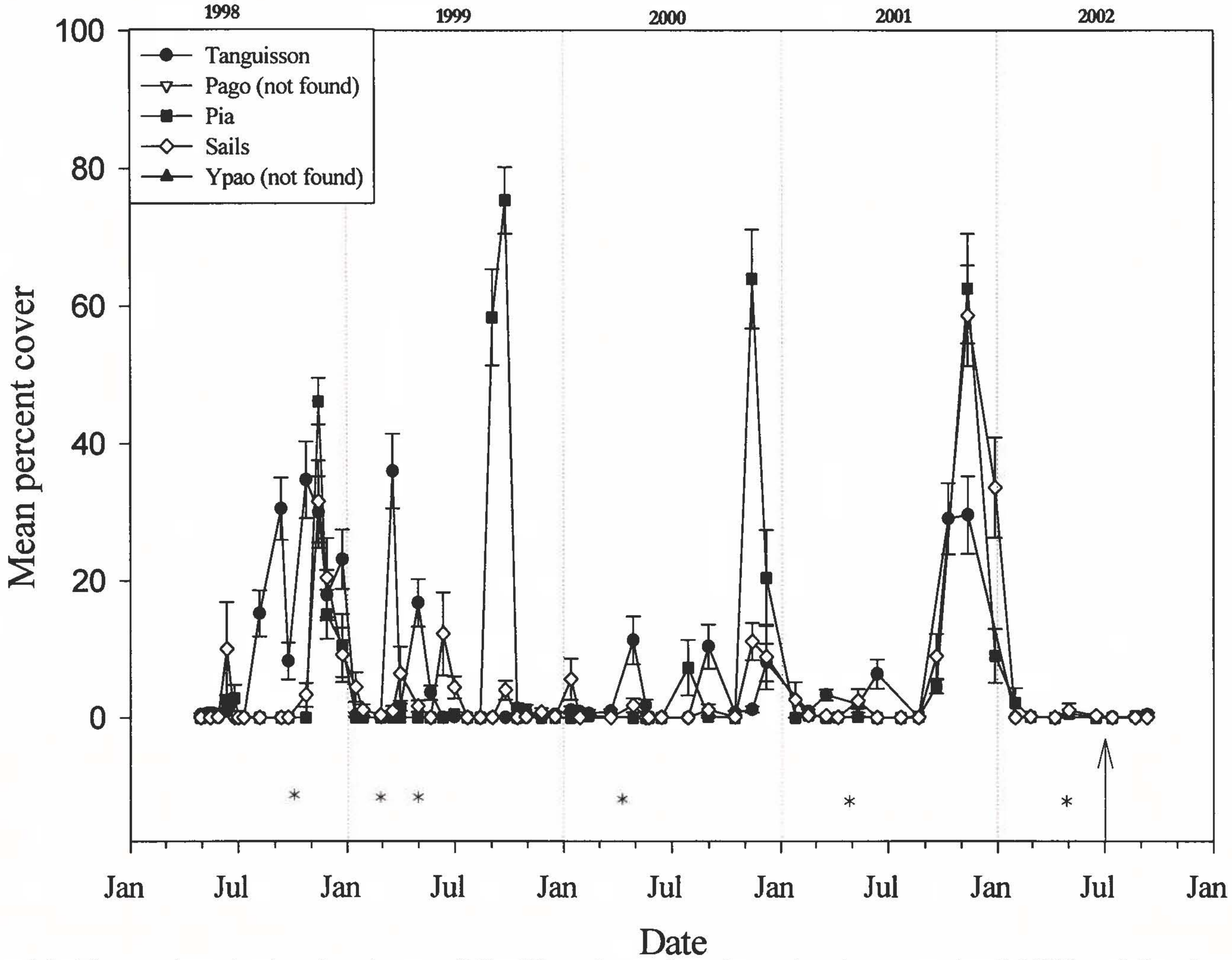


Figure 16. Fluctuations in the abundance of *Oscillatoria* sp. 2 at three sites between April 1998 and October 2002. Asterisks represent visual observations of juvenile siganid groups. The arrow represents Typhoon Chata'an.

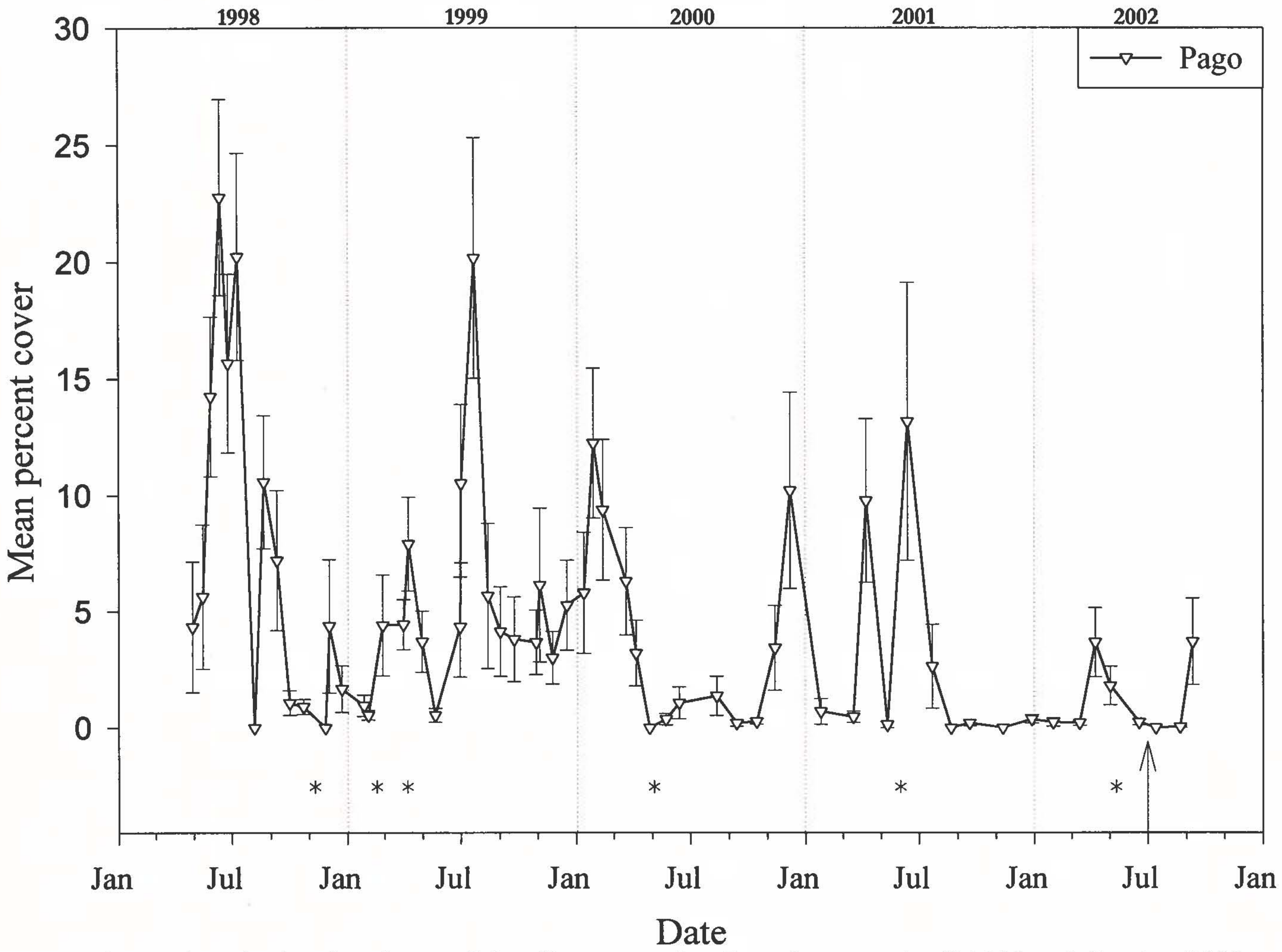


Figure 17. Fluctuations in the abundance of *Oscillatoria* sp. 1 at Pago between April 1998 and October 2002. Asterisks represent visual observations of juvenile siganid groups. The arrow represents Typhoon Chata'an.

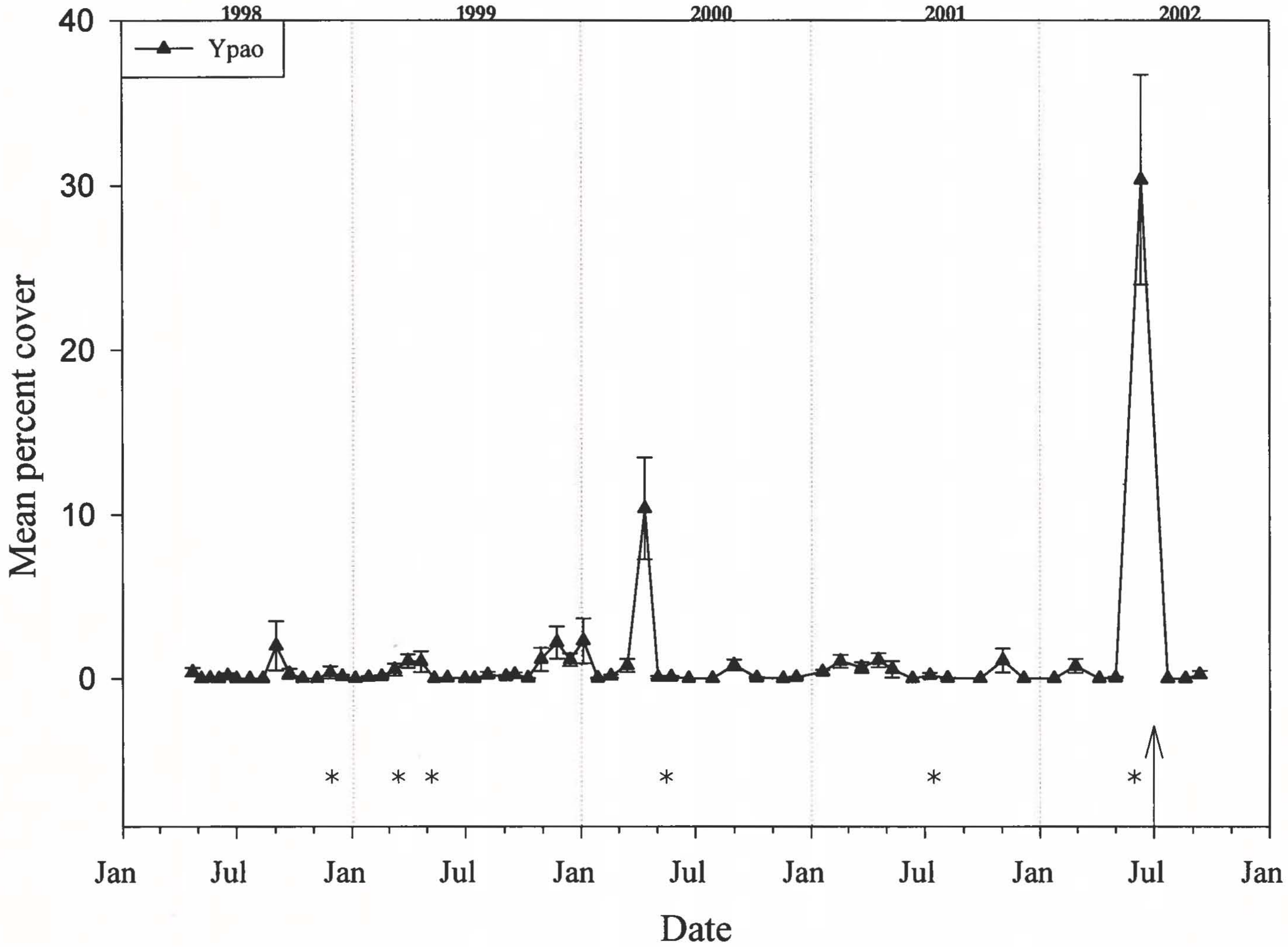


Figure 18. Fluctuations in the abundance of *Oscillatoria* sp. 3 at Ypao between April 1998 and October 2002. Asterisks represent visual observations of juvenile siganid groups. The arrow represents Typhoon Chata'an.

grow on hard substrata and others form encrusting mats. *Schizothrix* sp. 3 (Figure 19), a dark encrusting mat form, had blooms that began in July 1998 and May 2001 at Pago. Each bloom only lasted a few months.

Wave Action

No significant correlations were apparent between maximum wave height and abundance of any species of macroalgae or cyanobacteria (Table 4). The passing of Typhoon Chata'an was the only storm in four and a half years that produced "extreme" wave action, i.e., wave heights exceeded 5 m in the study areas.

Herbivory

Fish bite marks were observed on *Acanthophora spicifera, Schizothrix* spp., and *Caulerpa* spp. at the study sites, especially during the annual siganid runs. Estimates of numbers of juvenile siganids during their annual run were recorded inconsistently; hence, these data could not be used for analysis. The demise of certain algal species could be seen following the annual runs, as well as blooms preceding them. Some macroalgae grew rapidly during the juvenile siganid runs. *Acanthophora spicifera* at Pago, *Dictyota bartayresiana* at Ypao and Pago and *Padina boryana* at all sites but Tanguisson all bloom about the time these fish are apparent.

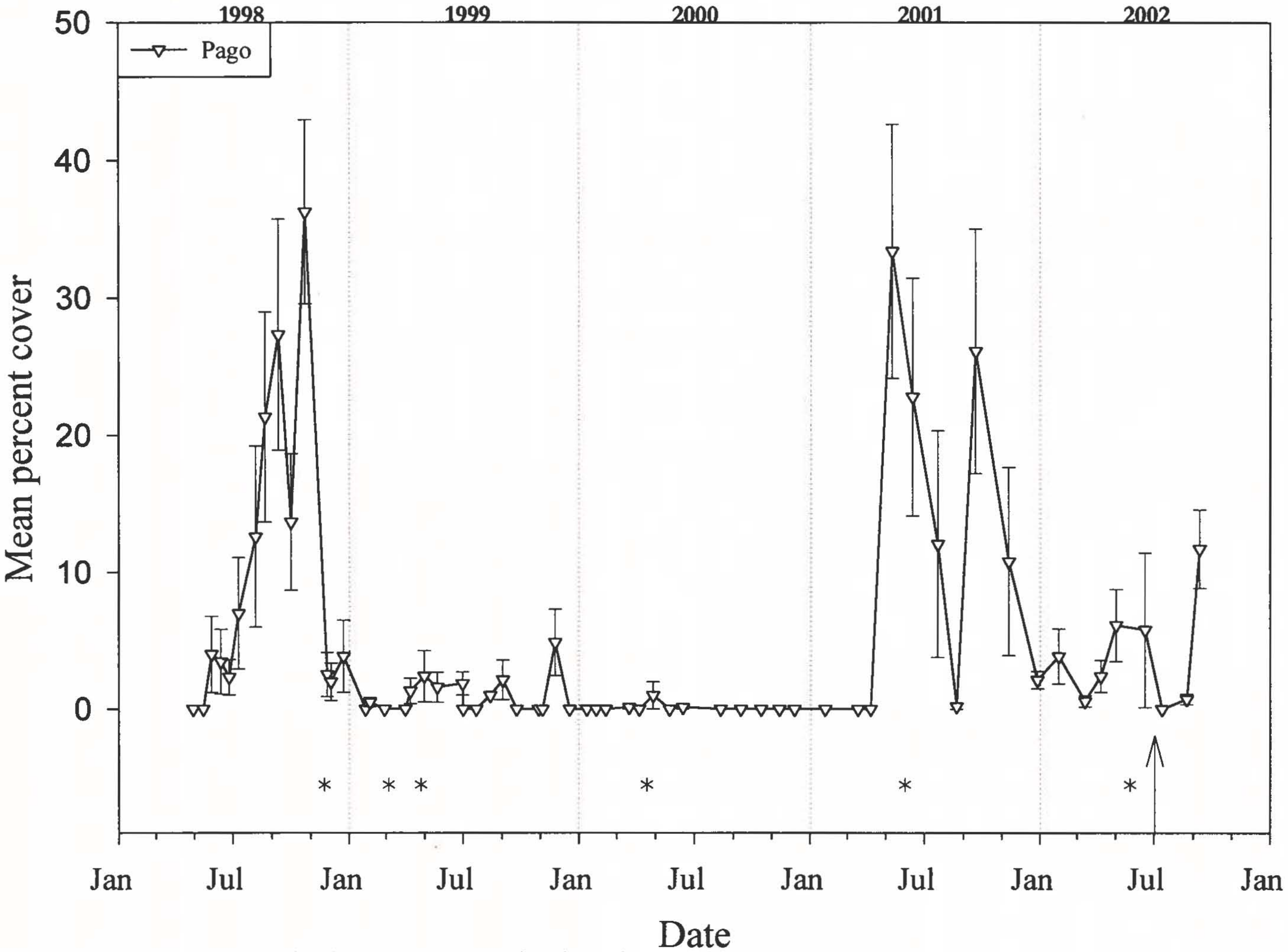


Figure 19. Fluctuations in the abundance of *Schizothrix* sp. 3 at Pago between April 1998 and October 2002. Asterisks represent visual observations of juvenile siganid groups. The arrow represents Typhoon Chata'an.

Table 4. Spearman's rank correlations (Holm's procedure corrected) of abundance of macroalgae or cyanobacteria to wave height. (ns=not significant)

Site/Species	n	p	r_s	Site/Species	n	p	r_s
Pago				Ypao			
Acanthophora spicifera	60	ns	0.14500	*Boodlea composita*	61	ns	-0.12629
Caulerpa racemosa	60	ns	0.06934	*Dictyota bartayresiana*	61	ns	0.23905
Gelidiella acerosa	60	ns	0.04512	Farmerfish turf	61	ns	0.09164
Jania capillacea	60	ns	0.20462	*Halimeda opuntia*	61	ns	0.08102
Mastophora rosea	60	ns	0.25290	*Lyngbya* sp. 2	61	ns	-0.02792
Oscillatoria sp. 1	60	ns	-0.27067	*Oscillatoria* sp. 3	61	ns	0.27783
Sargassum spp.	60	ns	0.02839	*Padina boryana*	61	ns	-0.10548
Pia				Tanguisson			
Boodlea composita	58	ns	0.20331	*Caulerpa racemosa*	53	ns	0.21971
Gelidiella acerosa	58	ns	0.29916	*Caulerpa urvilleana*	53	ns	-0.00231
Gracilaria salicornia	58	ns	0.08627	*Dictyota bartayresiana*	53	ns	0.20722
Halimeda opuntia	58	ns	0.12542	*Gelidiella acerosa*	53	ns	0.09465
Lyngbya semiplena	58	ns	-0.08063	*Jania capillacea*	53	ns	0.01326
Oscillatoria sp. 2	58	ns	0.06189	*Oscillatoria* sp. 2	53	ns	0.16186
Padina boryana	58	ns	0.23161	*Rhodymenia divaricata*	53	ns	0.15527
Sails							
Boodlea composita	59	ns	-0.02568				
Caulerpa racemosa	59	ns	0.24415				
Gelidiella acerosa	59	ns	0.28742				
Halimeda opuntia	59	ns	0.17396				
Lyngbya sp. 1	59	ns	0.22398				
Oscillatoria sp. 2	59	ns	0.26258				
Padina boryana	59	ns	-0.10290				

DISCUSSION

General Algal Community Structure

Ecologists have tried to determine what processes cause algal blooms (Done 1992, Hughes 1994, Lapointe 1997, Thacker and Paul 2001). There are both top-down and bottom-up factors that control fluctuations in algal populations, such as herbivory and disturbance or nutrient fluctuations, respectively. Macroalgae and cyanobacteria compete for space and nutrients not only with each other but also with all other biota on the reefs. Competition between macroalgae and cyanobacteria may not be important in structuring the community; rather, environmental factors may favor growth of both macroalgae and cyanobacteria (Thacker and Paul 2001).

Data for the first year at the present study sites in addition to four other sites were used in a preliminary study that found a negative association between abundance of macroalgae and abundance of cyanobacteria at Togcha River reef flat (Thacker and Paul 2001). One of the present study sites, Ypao Beach Park, also displayed a significant negative rank correlation (see Figure 6) between abundance of macroalgae and cyanobacteria. Communities of macroalgae and cyanobacteria at the present study sites are considerably different. Tanguisson and Pago have more diverse algal assemblages than any of the three sites located in Tumon Bay. The Ypao site had the lowest species abundance and diversity, which may give reason, at least in part, for the significant negative rank correlation. Results from the present study, showing significant association only in one out of five sites, and from Thacker and Paul (2001), showing significant association in one out of nine sites suggests that there may be no significant association between macroalgae and cyanobacteria. Hence, it is not clear (1) whether macroalgae and cyanobacteria compete with each other, (2) whether the factors influencing the growth of one enhance growth in the other, (3) whether site differences have some bearing on growth of algae and cyanobacteria or (4) whether any assumptions can be made about the results.

Some species that were expected to bloom occurred outside of the transects (i.e., *Lyngbya semiplena* and *Acanthophora spicifera*). This suggests that macroalgae and cyanobacteria are spatio-temporally heterogeneous and may be why these blooms do not show up in data figures when expected. Moreover, seasonal blooms of the species in this study do not occur synchronously. It seems that all algal and cyanobacterial species have independent roles.

Effects of Wave Action on Algal Communities

Contrary to previous findings (Kingsbury 1962, and Thacker and Paul 2001), there is no evidence to show wave action as a controlling factor of algal blooms for any species at any sites. Typhoon Chata'an was the only major storm over a four and a half year period. This suggests that wave heights over a long temporal scale, with few to no extreme events, i.e., typhoons, show little significance affecting algal community dynamics. Correlative evidence for wave height affecting algal cover of some species may not have been seen because these sites are so regularly swept with waves that certain wave-resistant genera remain dominant. These genera include, but are not exclusive to, *Dictyosphaeria, Gelidiella, Halimeda, Jania* and *Mastophora*, which are not usually preferred by juvenile siganids. However, "extreme" wave action or major disturbances (typhoons) may still scour the wave-resistant algae.

On July 5, 2002, Typhoon Chata'an removed the majority of the biomass in the algal communities (see Figures 7-19). Most species of macroalgae and cyanobacteria were diminished, save the few calcified turf forming species, leaving space for new algal colonization and succession to start over. Data were inconclusive for much of the wave sizes because agencies taking data were closed during and after the storm. The data may have been incomplete, i.e., missing the most extreme wave heights, such as those during the landfall of Typhoon Chata'an, which may have produced unreliable or inaccurate results. Those data immediately following typhoon Chata'an were either missing or recorded after the wave heights had already receded.

Algae that grow on reef flats are usually able to recover from disturbance faster than fleshy, frondose uprights because of vegetative reproduction (Hay 1981 and Airoldi 1998). There were between-site differences in algal composition seen due to differing wave exposures. Overall species diversity was higher at Pago and Tanguisson possibly due to waves having more direct contact with the reef flat at those two sites. The other three sites in Tumon Bay are on the inner reef flat and are not regularly scoured by direct wave contact.

Most studies done on algal communities and wave exposure cover only temperate intertidal macroalgae. This study incorporates wave action effects on benthic macroalgae and cyanobacteria on tropical reefs in Guam. Wave height may have a threshold that it must reach before noticeable scouring takes place. Up to that threshold, herbivory or other environmental factors may have a greater control on macroalgal and cyanobacterial communities. When wave heights reduce in size there may be a shift of control of algal fluctuations to herbivory, as fish are able to readily feed on the reef flats during these periods. The lack of wave action, however, may allow algal succession to move forward and cyanobacterial or algal blooms may occur. These calm periods may be when extreme increases (peaks) in certain algal abundance are happening. Algae will grow until they reach a size that is unable to withstand wave pressures and they will break away. Plants in intertidal zones are relatively smaller than plants in more protected areas (Denny 1999).

Extreme wave exposure affects algal communities. It can be seen anytime after high waves move across the reef flat. Benthic algae break into pieces or become unattached by waves and float into the water column only to be tumbled into smaller pieces, to succumb to herbivory, or to terminate as beach drift at the high water line. Strong currents and waves can bring in nutrients, keep temperature, pH and salinity more constant and sweep away waste (Kingsbury 1962). It has been shown that waves affect temperate intertidal macroalgae such as red algae, *Chondrus crispus* and *Mastocarpus stellatus* (Dudgeon and Johnson 1992), and *Mastocarpus papillatus* (Carrington 1990). Gaylord et al. (1994) discuss size restrictions of wave-swept algae. One brown and two red macroalgae were studied to analyze constraints that hydrodynamic forces have on size of the plants in the intertidal zone. Drag coefficients of flexible plants decreased with an increase in velocity, but they admitted that drag alone is not the primary factor limiting the sizes of algae. In addition to this conclusion, they also mention that characteristics of the substratum may determine strength of the holdfast to remain or become dislodged.

In the present study, I stated that algal abundance should be significantly affected by wave action. This hypothesis was rejected because there is no evidence showing waves affect abundance of any species of macroalgae and cyanobacteria at the present study sites over four and a half consecutive years.

Effects of Herbivory or Nutrients on Algal Communities

Herbivory is an important controlling factor in algal populations (Duffy and Hay 1990). Herbivorous fishes can have noticeable effects on reef macroalgal communities because the dynamics of competition among algal species may change due to intense grazing (Hay 1991, Glynn 1997). Turf algae are predominantly the preferred food by herbivorous fish (Choat 1991), although they will graze on whatever is available when turf algae are not available.

Algae are commonly defended either structurally, chemically, or both to deter herbivory (Hay 1991, Paul 1997). Different algae are selected by herbivores according to their palatability. Low preference algae are often those with both chemical and structural defenses (Paul and Hay 1986). Genera, such as *Halimeda*, which are chemically and structurally defended, can only be eaten by specialized herbivores, i.e., parrotfishes with fused teeth and pharyngeal mills (Paul and Hay 1996, Paul 1997). Chemical defenses have been recognized as key factors influencing the bloom and resolution of *Lyngbya majuscula* and *Hormothamnium enteromorphoides.* Pennings et al. (1997) conducted bioassays using several generalist fish and determined that most, but not all, were deterred by these cyanobacteria. Although secondary metabolites of algae and cyanobacteria are usually considered unpalatable, studies have shown that deterrence may decrease if digestion is not seriously affected by the chemistry. Hunger stress may make herbivores more susceptible to toxins. Fish can learn to avoid defensive chemistry, but this learning does not occur when access to food is limited (Thacker et al. 1997). Hence, as more palatable algae become less abundant, fish will eat from a broader range of algal species. Thacker et al. (2001) demonstrated in caging experiments that removing herbivorous fish could shift macroalgal communities from relatively less palatable to relatively palatable species. Herbivorous fish in Guam have been observed grazing on cyanobacteria, which are usually considered less palatable (V.J. Paul, pers. comm.).

Apart from chemical and structural defenses, algae and cyanobacteria have other methods for deterring predators. Seaweeds avoid predation by inhabiting cracks. The present study sites have numerous fissures and boulders for algae to escape predation. Some seaweeds are indirectly protected spatially by damselfish "gardens", which have relatively low herbivore pressure (Duffy and Hay 1990). Lassuy (1980) found that two common damselfish in Guam, *Eupomacentrus lividus* and *Hemiglyphidodon plagiometopon*, weed out less preferred algae in their defended territory. Damselfish are commonly found in the present study sites protecting their home ranges, within which they usually keep algal gardens with multiple species. It has been suggested that consumers may be able to prevent a macroalgal bloom, reduce its intensity or accelerate its decline (Raffaelli et al. 1998). Algae that grow intertwining to form tough "turfs" have been deemed less appealing to herbivores because 1) there are fewer refuge holes in areas where these algae occur (Hay 1981), 2) fish are unable to bite at tightly packed uprights (Hay 1981) and 3) the protein content is higher in species forming these bundles (John et al. 1992).

Juvenile siganids have been observed lying on their sides on the reef flats in Tumon Bay and Pago Bay. They are cryptically colored among the background of adult and juvenile *Padina,* which were commonly found in abundance during the seasonal runs of at least one of the present study years. In this study, certain years underwent blooms or demises of blooms of certain species of macroalgae and cyanobacteria following siganid events.

Herbivorous fish, when grazing, cause small nicks on algae, thereby causing weakness. A previous study (DeWreede et al. 1992) showed that the structural integrity of kelp can be damaged by herbivores and should the damage be sufficient, the stipe would break entirely. In the present study sites, abrasions to algae by certain factors, including herbivory or human contact, can cause deterioration of the algal strands. This can lead to weakening of the algae to other factors, such as wave action.

Nutrient enrichment has shown inconclusive results towards the growth or abundance of macroalgae and cyanobacteria. Laboratory experiments by Kuffner and Paul (2001) showed that phosphorus enrichment might enhance cyanobacterial growth. A similar nutrient study showed nutrient enrichment to be insignificant in the growth of cyanobacteria (Pangilinan 2000). Thacker and Paul (2001), from field observations, concluded that there was no significant effect of nitrogen and phosphorous availability on the abundance of cyanobacteria. Other research has tested nutrient limitation in the laboratory, but few have monitored long-term, i.e., more than one year, algal growth and surrounding conditions on tropical reefs (Lapointe 1997, Larned 1998). One field study showed that phosphorus was a limiting factor for growth of *Gracilaria tikvahiae* over one year in Florida (Lapointe 1987). Miller and Hay (1996) conducted field studies in temperate waters that showed herbivory and nutrient availability act synergistically on seaweeds. Nutrient addition to caged (herbivore-exclusion cages) corals in the field tended to suppress coral growth, whereas seaweeds were stimulated. Overall seaweed abundance was not affected by herbivores; rather, species composition was altered (Miller and Hay 1996). Hixon and Brostoff (1996) concluded that herbivory of fishes can affect the succession of Hawaiian benthic algae over small spatial scales.

CONCLUSIONS

Macroalgae and cyanobacteria are two common components of the reef flat communities on Guam. Many species show distinct patterns of seasonality. For years, herbivory and wave action have been seen as factors that control algal community dynamics. This study supports the idea that wave action has no significant control over abundance of macroalgae and cyanobacteria on the reef flats of Guam. There are other factors that contribute to algal community dynamics. Major herbivory events, such as the annual juvenile siganid runs in Guam, may be one of the controlling factors of blooms or demises of blooms in macroalgae and cyanobacteria on Guam's reef flats.

Future studies should incorporate other methods for more unambiguous results. For instance, the use of a maximum wave velocity recorder such as that used by Bell and Denny (1994) or a maximum drag recorder used by Jones and Demetropoulos (1968) would allow direct measurement of wave speed and drag. Although wave height is directly proportional to velocity across the substratum (Denny and Gaylord 2002), there may have been some observer bias in the data collected from outside sources. Other studies should also use a spring scale to measure algal attachment to the substratum, although most cyanobacterial species are unable to be measured because they tend to disintegrate upon contact. For spring scale tensile strength experiments, researchers may want to follow similar methods to those used by Jones and Demetropoulos (1968), Dudgeon and Johnson (1992) or Gaylord et al. (1994). Obtaining all ecological parameters including environmental data, i.e., temperature, salinity, nutrients, may aid in the comprehension of the factors controlling algal communities.

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