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Prorocentrum (Prorocentrales: Dinophyceae) populations on seagrass-blade surface in Taklong Island, Guimaras Province, Philippines

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Abstract: The cell densities of *Prorocentrum* on the upper tip, middle and base areas of seagrass blades, *Enhalus acoroides*, were investigated during the southwest monsoon, July–September 1999. The seagrass blade samples were taken from two adjacent coves in Taklong Island one cove of which has seagrass exposed during low tide while in the other cove it is submerged. The benthic dinoflagellates were invariably composed of *Prorocentrum*, which constituted 5.3 to 22.8% of the microbenthic algal classes found on seagrass blades. There were six *Prorocentrum* species observed and *Prorocentrum lima* was the dominant species during the study. The *Prorocentrum* mean cell densities per month on the blades ranged from nil to 606 cells cm^{-2}. There were significant differences ($p<0.01$) in the *Prorocentrum* cell densities on the three blade sections. Exposure during low tide had no significant effects on the *Prorocentrum* populations. It is likely that a combination of physical factors particularly strong water movement and the separation of withering or decaying upper tips of seagrass bring about the entry of *Prorocentrum* into the coastal food web.

Key words: *Prorocentrum* population, seagrass, microbenthic algae

Introduction

Several studies have focused on the presence and distribution of toxic benthic dinoflagellates particularly *Gambierdiscus toxicus* Adachi et Fukuyo on algae in tropical reefs and coastal areas (Fukuyo 1981; Bomber et al. 1989; Heil et al. 1998; Holmes et al. 1998; Turquet et al. 1998). However, there are indications that other toxic dinoflagellate species aside from *G. toxicus* inhabit seagrass substrates in ciguatera endemic areas (Bomber et al. 1985). In an earlier study on the occurrence of benthic dinoflagellates in Guimaras Province, we observed that seaweeds were distributed in patches in some reefs and coves (Marasigan et al. 1999). These patches tend to be interspersed together with seagrasses. For example in Taklong Island Guimaras, there were coves where seagrasses were more abundant than seaweeds. Consequently, it would be difficult to decide whether to take algal samples in order to assess benthic dinoflagellate distribution or simply just move on to other site where seaweeds are most abundant. However, it can also be presumed that benthic dinoflagellate species that are adapted to seagrass blade habitats occur. Knowledge of benthic dinoflagellate ecology in tropical reef areas can be broadened through investigations on their occurrence in sites where seagrasses are the dominant intertidal flora.

From our initial samples taken from Taklong Island, *Prorocentrum* were the most common and dominant benthic dinoflagellates on blades of the seagrass *Enhalus acoroides* (L.) Rayle. Members of the genus *Prorocentrum* are either planktonic or benthic. The benthic *Prorocentrum* species are usually epiphytes but can also be found attached to coral rubble, floating detritus or even living interstitially between sand grains (Faust 1995; Morton & Faust 1997; Lebour 1925). Earlier studies indicated that benthic microalgae washed out by waves and tidal currents were important components of coral reef plankton (Glynn 1973; Sorokin 1993). Faust (1995) reported that interstitial *Prorocentrum lima* (Ehr.) Dodge and *Prorocentrum mexicanum*

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Tafall and other toxic benthic dinoflagellates as tychoplankton modified the phytoplankton assemblage and comprised the major species in algal blooms in warm shallow lagoons. *Prorocentrum* species such as *P. concavum* Fukuyo and *P. mexicanum* have been reported elsewhere to produce potent ciguatera-like toxins (Anderson & Lobel 1987). Furthermore, *Prorocentrum lima* produces diarrhetic shellfish toxins such as okadaic acid and methyl okadaic acid (Yasumoto et al. 1987; Morton & Tindall 1995).

The objectives of our study were to evaluate the *Prorocentrum* populations associated with seagrass in two types of coves and relate the growth of three species of *Prorocentrum* under laboratory conditions to their distribution on seagrass blades. We also elucidated the significance of the entry of benthic *Prorocentrum* into the coastal detrital and plankton based food web systems.

Materials and Methods

Study site

The study was conducted on Taklong Island, Guimaras Province, Philippines (10°24.679′N, 122°30.191′E) from July to September 1999. The University of the Philippines in the Visayas operates a marine biological field station on the island that was declared a Marine Reserve Area by the Department of Environment and Natural Resources in 1991. Two coves with extensive seagrass communities, mostly *Enhalus acoroides*, were selected for their unique characteristics. One cove faces the open sea and drains completely during low tide. The other cove faces an islet which forms a channel and the seagrass community remains submerged during low tide.

Measurements of environmental parameters

Duplicate samples of bottom sediments (approximately 2–3 cm deep) were collected randomly once a month from the study site from July–September with a simple plastic corer to determine organic matter content. Likewise, duplicate water samples for temperature and salinity profiles were taken during high tide in 10 cm depth using polythene 500-ml bottles.

Biological sampling

Three clumps of seagrasses were randomly collected at each site. Samples were taken by placing self-sealing plastic bags over the seagrass clumps to reduce the loss of epipythic microbenthic algae to the water column. The samples in plastic bags were kept in a styrofoam box and transported to the laboratory in Miag-ao, Iloilo Province, about 70 km away.

Sample preparation and cell counts

Upon arrival at the laboratory, the seagrass contents were taken out and discrete 5-cm sections were cut from the tip, middle and base areas of the blades. Two healthy blades per clump were cut to take discrete sections for microscopic analysis. The seagrass blade sections were placed into labeled 150-ml polythene screw capped bottles. The bottles were sonicated for 3 min; after which they were vigorously shaken and the suspensions filtered over four sets of stainless steel screen sieves: 250, 125, 38 and 20 μm. Cells from the 38- and 20-μm size fractions were placed into 30-ml capacity polythene vials. A final volume of 20 ml was made for each sample and they were preserved with 10% neutralized formalin-seawater solution.

Microsocopic analysis

Identification of the *Prorocentrum* was based on morphological characteristics described by Fukuyo (1981) and Faust (1990). Thecal plates were dissociated using 5% sodium hypochlorite solution and stained with chloral hydrate, potassium iodine and iodine solution under a light microscope Nikon Optiphot 2 with differential interference optics. Two subsamples were taken for each sample and cells were counted with a Sedgwick Rafter counting chamber under a Reichert Jung inverted microscope. Cell densities were estimated as number of cells per unit surface area of the seagrass blade (Lobel et al. 1988).

Culture conditions and test species

Single cells of *Prorocentrum lima*, *P. concavum* and *P. hoffmannianum* Faust were isolated from the 38- and 20-μm filtered sample suspensions collected from Taklong Island on 21 July 1999 using sterilized capillary pipettes. About 50 cells of each species were inoculated into 5 ml of sterile culture medium in capped polypropylene test tubes. The resulting uni-algal and non-clonal cultures were maintained for a month to acclimate the test species to laboratory culture conditions. The growth study was conducted by inoculating single cells from the maintenance culture into each well of a Corning sterile polystyrene plate with 24 wells. The well plates were sealed with parafilm wax. Prior to inoculation, each *Prorocentrum* cell was washed at least 3 times in sterile culture medium. Direct counts were made using an inverted microscope at 0900 h every day during the culture period and the count data were used to determine growth rates as divisions d^{-1} (Guillard 1973). The maintenance and growth experiments were conducted under the following culture conditions: aged seawater filtered with 0.45-μm filter and sterilized in autoclave, 24°C, 12 : 12 L/D cycle with fluorescent tube and Keller and Guillard's (1985) K media added to enrich the aseptic seawater.

Ecological data analysis

The tabulated cell count values were transformed to $\ln(n+1)$. The cell densities for each species were subjected to two-way analysis of variance (Zar 1984). Statistical analysis was carried out using SYSTAT Version 4 for microcomputers (Wilkinson 1986).

Results

Environmental parameters

The tabulated environmental parameter values such as salinity, temperature and organic matter content of the sediments were similar at both sampling sites (Table 1).

Prorocentrum distribution on seagrass blade

The genus *Prorocentrum* is the largest genus, containing 6 member species. It was the most abundant genus attached to the seagrass blade surface. The relative numerical contribution of *Prorocentrum* to the seagrass microbenthic algal population ranged from 5.3 to 22.8% (Fig. 1). The *Prorocentrum* cell densities at the 2 sampling sites were tabulated (Tables 2, 3). The tabulated cell count values are means for the 2 sampling periods per month, although the cell count per sampling period, i.e. twice a month, was used in the statistical analysis. Among the *Prorocentrum* species, *Prorocentrum lima* was the most dominant species over the entire blade area, i.e. tip, middle and base. The tip area of the seagrass invariably hosted the highest number of *Prorocentrum* cells compared to the middle and base areas. Analysis of variance (Table 4) conducted on the *Prorocentrum* cell counts showed no significant differences between trial factors: site, site by species ($p<0.01$). Thus, exposure of seagrasses during low tide had no significant effects on the *Prorocentrum* population. However, significant differences were obtained for the following factors : species, blade area, site by blade area, species by blade area, site by species by blade area.

Table 1. Environmental parameters (mean±SD) measured for the two sampling sites during low tide in Taklong Island, Guimaras Province with seagrass exposed and submerged, July–September 1999.

Sampling Site	Temperature (°C)	Salinity (‰)	Organic Matter (%)
Exposed Cove	27.4±0.5	32.8±0.8	0.35±0.07
Submerged Cove	27.2±0.2	32.5±0.5	0.41±0.07

Prorocentrum growth rate

The highest growth rate was obtained for *Prorocentrum lima* culture (Fig. 2). The failure of most *P. concavum* and *P. hoffmannianum* isolates to reproduce after the first cell division resulted in low growth rates during the culture period. We observed that *P. lima* vegetative cells were mostly motile and settled to the well plate bottom only during active cell division. After cell division, the *P. lima* daughter cells became motile. On the other hand, *P. concavum* and *P. hoffmannianum* daughter cells settled at the bottom of the culture well plates after the first cell division and enveloped themselves with a mucus secretion. Apparently, most of the *P. concavum* and *P. hoffmanianum* cells discontinued reproduction once the cells had been enveloped in mucus.

Discussion

Seagrass blade as habitat for benthic *Prorocentrum*

The results of the present study suggest that seagrass blades can be as important as seaweed as habitat space for microbenthic algae particularly dinoflagellates. The results

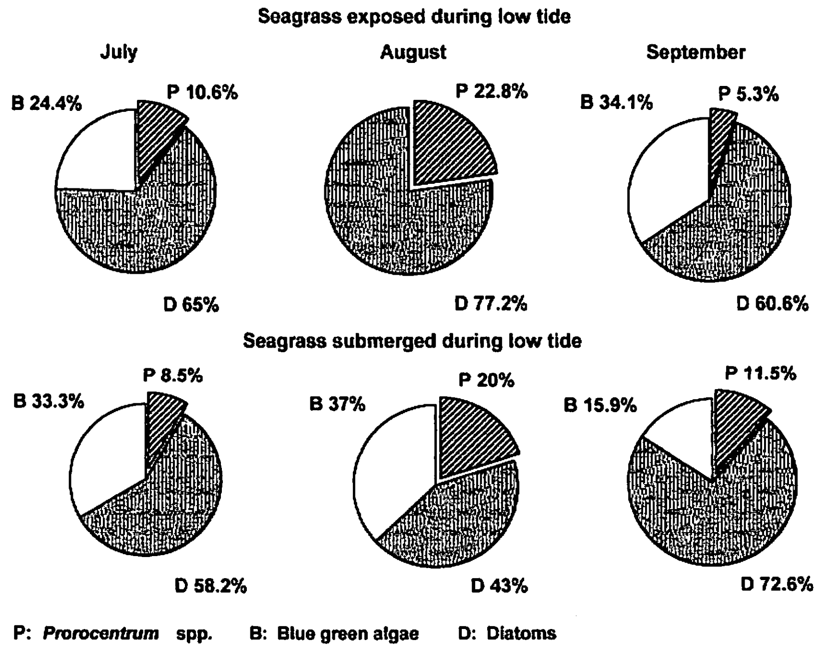

Fig. 1. Microbenthic algal populations (cell counts) on seagrass blades. Lawi Cove, Taklong Island, Guimaras, Philippines.

Table 2. *Prorocentrum* distribution (cell cm^{-2}, mean±SD) on seagrass, *Enhalus acoroides*, exposed at low tide in Taklong Island, Guimaras, Philippines from July to September 1999.

Species	Tip Area			Middle Area			Base Area		
	July	Aug.	Sept.	July	Aug.	Sept.	July	Aug.	Sept.
P. lima	606±578	140±120	458±277	51±27	133±53	295±276	13±18	117±51	170±253
P. emarginatum	27± 28	68± 58	125± 82	9±11	29±31	117±128	0	36±21	61± 78
P. concavum	27± 33	68± 58	121± 42	0	34±12	80± 95	0	42±35	53± 25
P. mexicanum	34± 42	68± 58	45± 79	4± 9	38± 9	38± 40	0	2± 5	23± 20
P. hoffmannianum	15± 20	40± 43	72± 29	6± 5	15±22	61± 12	0	51±24	11± 19
P. ruetzlerianum	0	4± 9	0	0	2± 5	0	0	4± 9	0

Table 3. *Prorocentrum* distribution (cell cm^{-2}, mean±SD) on seagrass, *Enhalus acoroides*, submerged at low tide in Taklong Island, Guimaras, Philippines from July to September 1999.

Species	Tip Area			Middle Area			Base Area		
	July	Aug.	Sept.	July	Aug.	Sept.	July	Aug.	Sept.
P. lima	330±54	261±118	193±132	210±471	206±63	170±110	21±46	134±53	121±113
P. emarginatum	6±10	49± 50	57± 49	6± 10	85±95	72± 56	0	15±21	45±20
P. concavum	13±15	38± 33	80± 55	13± 32	38±38	45± 35	0	36±37	27±33
P. mexicanum	6±10	21± 15	19± 17	2± 5	34±31	15± 19	2± 5	42±33	11±12
P. hoffmannianum	15±22	36± 40	18± 13	15± 22	25±40	6± 13	0	3±5	19±30
P. ruetzlerianum	0	0	0	0	8±19	3± 8	0	0	0

Table 4. ANOVA of the two sampling sites, *Prorocentrum* species and discrete seagrass blade areas. The effects of sampling period was excluded.

Source	DF	SS	MS	F-value	p-value
Site	1	7.644	7.644	1.534	0.226^{ns}
Species	5	975.722	195.144	39.095	0.000*
Blade area	2	94.305	47.152	46.091	0.000*
Site/species	5	16.080	3.216	0.084	0.994^{ns}
Site/blade area	2	18.291	9.146	8.940	0.000*
Species/blade area	10	49.952	4.995	4.883	0.000*
Site/species/blade area	10	57.585	5.759	5.314	0.000*

^{ns} no significant difference
* significant difference ($p<0.01$)

of our study corroborate earlier findings that seagrasses support larval and juvenile epibenthic animal grazers (Fortes 1993). In a related study, for example, salt marsh cord grass provided shelter and grazing areas for the larvae of blue crab, *Callinectes sapidus* Rathbun, and grass shrimps *Callinectes sapidus* Holthius during their premolt and molt stages (Welch et al. 1997).

The tip area of the seagrass blade with its high densities of *Prorocentrum* can be considered to be a habitat with a mature or climactic epifloral community. It is likely that nutrient exchange is greater at the seagrass blade tip as the blades undulate with water movement, most vigorously at the tip. *Enhalus acoroides* at the two sampling sites formed canopies with its relatively long blades of about 18–25 cm in length and presumably reduced light exposure at lower levels. The tip areas would likely have experienced greater light exposure while the middle and base areas would be shaded by the canopies. Vergara et al. (1997) reported that light was attenuated and suboptimum under canopies of the green seaweed, *Ulva lactuca* Linneaus, in a shallow estuary.

Factors influencing *Prorocentrum* distribution

The consistent high cell densities obtained for *Prorocentrum* suggest that the benthic members of this genus are well adapted to seagrass blade habitats although there are

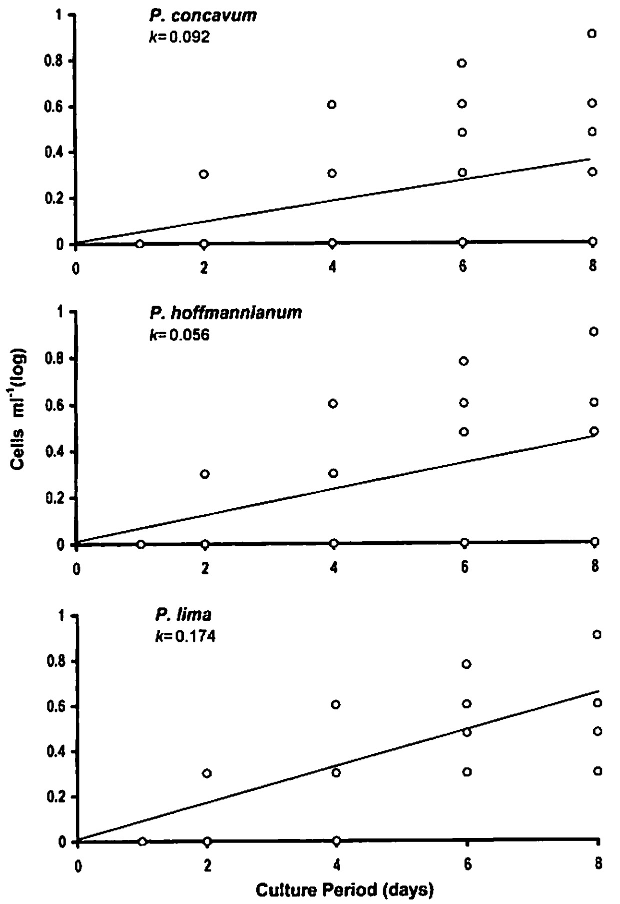

Fig. 2. Growth rates of *Prorocentrum* spp. isolates from Taklong Island under laboratory conditions.

no previous records of this observation. The values we obtained for percentage numerical contribution of *Prorocentrum* to the total microbenthic dinoflagellate population on seagrass blades were comparable to the proportion of *Prorocentrum* to dinoflagellates attached to macroalgal habitats in the Southeastern Barrier Reef, Australia (Heil et al. 1998). Apparently, *Prorocentrum* is widely distributed in the Pacific and can adapt to various types of habitats (Fukuyo 1981).

Prorocentrum has the attributes of an *r*-strategy organism. *Prorocentrum* cells, particularly those of *P. lima*, were obtained from the base of seagrass blades even if other benthic microalgae had failed to colonize this section. Among the *Prorocentrum* species attached to seagrass blades, the morphologically small *P. lima* was ubiquitous and successful in reproduction, as suggested by its high cell densities. The competitive advantage of *P. lima* may either be due to its wide temperature tolerance range or high growth rate or to a combination of these that favored higher populations on seagrass blade surfaces than for other *Prorocentrum* species. *P. lima* is found in both cold temperate seas as far as Nova Scotia, Canada, in the Northern Hemisphere down to Northland, New Zealand, in the Southern Hemisphere and warm tropical coastal waters of the Pacific and Atlantic (Faust 1995; Rhodes & Syhre 1995; Morton & Tindall 1995; Lawrence et al. 1998). Earlier studies showed that tropical isolates of *P. lima* have a wider temperature tolerance range than *P. mexicanum*, and *P. concavum* (Morton et al. 1992). This suggests that *P. lima* would be able to resist the adverse effects of temperature fluctuations in the shallow coastal waters where seagrass beds usually abound. Moreover, the occurrence of large populations of *P. lima* in several types of habitats may also be attributable to its highly reproductive characteristic when compared to other *Prorocentrum* species. In our growth experiments on *P. lima*, *P. concavum*, and *P. hoffmannianum*, we observed the highest doubling rates for *P. lima*. Our growth rate values for the *P. lima* culture experiment were lower than the doubling rate values, 0.20–0.35 doublings d^{-1} recorded by Morton & Tindall (1995) for *P. lima* clones isolated from Heron Island, Australia, under culture conditions using 2500-ml aliquots of modified K media at 28°C and a 16:8 photoperiod. These differences in growth values are likely the result of the lower incubation temperature used in our culture experiment. However, the growth rates we obtained were still within the range, 0.12–0.4 doublings d^{-1}, for *P. lima* clones from Heron Island (Morton & Tindall 1995). The poor growth of *P. concavum* and *P. hoffmannianum* cultured in our experiment may be due to technical limitations imposed by the smaller culture volume in the well plates, the general lack of turbulence in the culture media, or even the comparatively shorter photoperiod length.

Although the present study suggests that *Prorocentrum* spp. compose a high proportion of the microbenthic algal populations in seagrass communities, it is not yet clear as to the position that *Prorocentrum* spp. from seagrass blades take in the reef food web system. Faust (1990, 1993) noted the presence of various *Prorocentrum* species on floating mangrove detritus. Wave action due to wind stress would likely favor sloughing off and breakage of seagrass tips that may allow the entry of *Prorocentrum* into the food web via detritus feeders or possibly as tychoplankton in the water column. Although Lawrence et al. (1998) implicated that the occurrence of *Prorocentrum lima* on the brown filamentous algae *Pilayella littoralis* (L.) Kjellman found on mussel culture rafts was linked to an outbreak of DSP in Nova Scotia, there was no detailed evidence on the route of *P. lima*'s entry into the food web. Morton et al. (1999) showed that DSP levels in mussel digestive glands collected from the coast of Maine were related to the populations of *P. lima* attached to the thalli of the brown alga, *Ectocarpus*. The presence of DSP toxins in blue mussels and *P. lima* cells isolated from *Ectocarpus* and the general absence of DSP toxins in the phytoplanktonic populations of known DSP toxic species of *Dinophysis* in water samples from Maine present evidence that benthic *P. lima* can enter the food web in shallow coastal environments either through the detrital or tychoplankton pathway. These mechanisms may also be at work for the entry of *Prorocentrum* attached to seagrass blades in areas with large seagrass communities.

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