ECOLOGICAL STUDIES OF *GRACILARIA ASIATICA* AND *GRACILARIA LEMANEIFORMIS* IN ZHANSHAN BAY, QINGDAO

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Abstract

Natural populations of *G. asiatica* Zhang & Xia and *G. lemaneiformis* (Bory) Weber van Bosse were studied during 1984 and 1986 in Zhanshan Bay, Qingdao (36°4'N, 120°21'E). Rapid growth (length, weight) of these plants occurred between mid-May and late June (water temperatures, 15–20°C). The major epiphyte of *G. asiatica* was *Enteromorpha linza*, while *Punctaria latifolia* was the major epiphyte of *G. lemaneiformis*. Epiphytism declined throughout early summer, and epiphytes were rare after mid-July (1984); they did not reappear in late summer, although macrophyte growth declined abruptly after early July. Populations of *G. asiatica* varied during late spring-early summer between adjacent sandy and rocky portions of the intertidal zone; plants at the sandy site were larger and epiphyte-free. Amphipod densities were low on both species of *Gracilaria*, but the most abundant species were *Ampithoe lacertosa*, *Caprella equilibra*, *C. krøyeri*, *C. scaura* and *Pontogeneia rostrata*. Additional information on general community structure is provided for the *G. asiatica* zone.

INTRODUCTION

We have studied intertidal and subtidal communities in Zhanshan Bay, Qingdao (People's Republic of China) in order to obtain information on the ecology of two of the dominant macrophytes, *Gracilaria asiatica* Zhang & Xia and *G. lemaneiformis* (Bory) Weber van Bosse. *Gracilaria* spp. are of international interest as mariculture crops (Chapman and Chapman, 1980; Tseng, 1981; Waaland, 1981), and are potentially important to Chinese mariculture. Seasonal studies of these plants in their natural habitats should provide information helpful in artificial cultivation.

MATERIALS AND METHODS

These studies were done during 1984 and 1986 in Zhanshan Bay slightly east of Qingdao City, Shandong Province at 36°4'N, 120°21'E (Fig. 1). Underwater visibility was usually 0.5–2 m, occasionally 3 m, during this study. After mid-May the lowest low-tide occurred at night, resulting in little or no daytime exposure and desiccation of *G. asiatica* during the summer. Changes in water temperature during the study are given in figure 2.

G. asiatica and *G. lemaneiformis* were collected from Zhanshan Bay in 1984 (every 3–4 weeks,

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dependent upon weather, Table 1, Fig. 3) using a 0.25 m^2 PVC-frame to obtain information on macrophyte length, wet weight, density, habit, composition and biomass of associated epiphytes, and composition and density of associated mesoherbivores (e.g., amphipods). Collections were made underwater (with snorkel and SCUBA) beginning 1. 5 h before

Table 1 Number of 0.25 m^2 quadrats / sampling date (1984)

G. asiatica			*G. lemaneiformis*		
4/27	5	(93 plants)	5/13	5	(44 plants)
5/18	5	(40 plants)	5/18	4	(32 plants)
6/20	6	(73 plants)	5/31	6	(75 plants)
7/18	6	(84 plants)	6/28	6	(52 plants)
8/13	6	(101 plants)	7/28	2	(50 plants)
			8/15	6	(74 plants)

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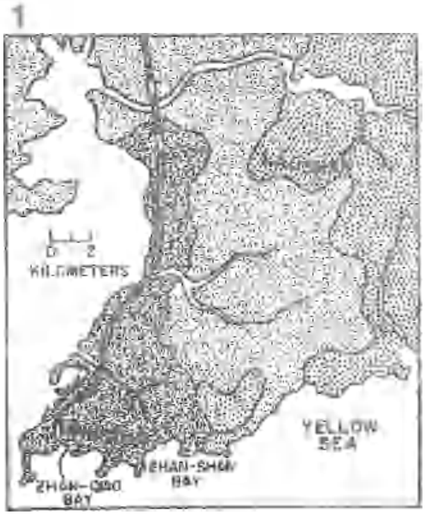

Fig. 1 Field work in Zhanshan Bay, Qingdao

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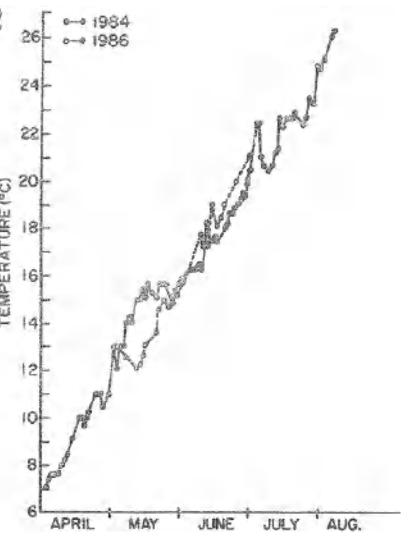

Fig. 2 Sea temperatures near the entrance to Zhanqiao Bay at a depth of 2 m

low tide; sampling was completed within a 2 h period. Following April 27, sampling of *G. asiatica* was made with random tosses of the quadrat throughout the mid-intertidal zone where this species was a dominant space holder. For the April 27 quadrats and all *G. lemaneiformis* sampling, a populated area was located and then random throws were made. To eliminate sampling bias, quadrat tosses were made above water. Plant wet weight was determined by separating epiphytes from *Gracilaria* plants, rinsing material briefly with fresh water and then patting the plants dry with cheesecloth. Some diatoms remained attached to plants, but at times when a substantial portion of the epiphytic biomass consisted of diatoms, most could be rubbed off the plants.

It was impossible to collect all the amphipods associated with plants in quadrat samples, because, unless plants are bagged underwater quickly, some of the more mobile species (e.g., *Pontogeneia rostrata*) escape. However, it was desirable to have data on amphipod association that

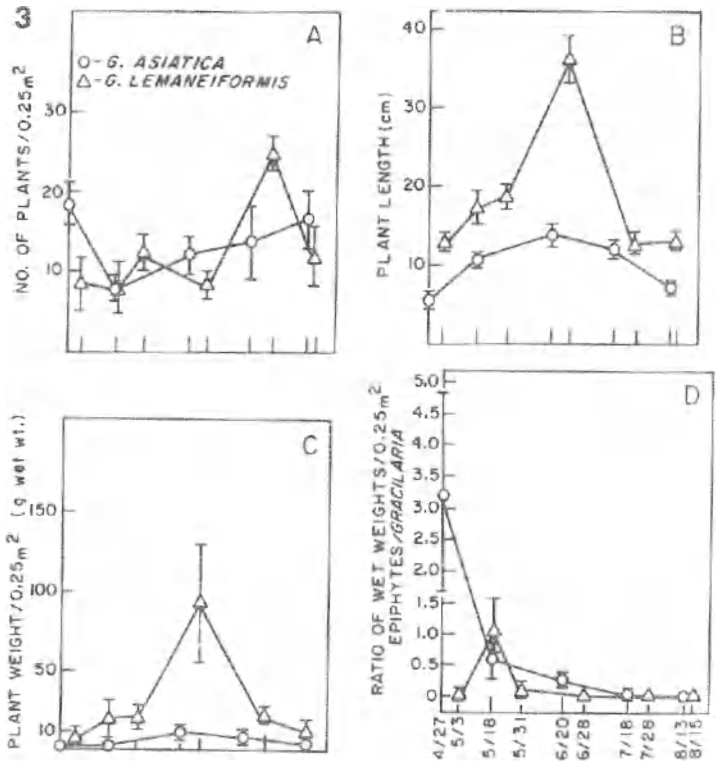

Fig. 3 Seasonal changes in density. A: length B: biomass C: and epiphytism D: of *G. asiatica* and *G. lemaneiformis* at Zhanshan Bay (mean ± standard error, see Table 1 for sample sizes)

would relate temporally and spatially to other data. With this objective in mind, we collected the two plants closest to a diagonal across the quadrat before disturbing the area during collection of plants within the quadrat. Bagged plants were analyzed in the same way as quadrat plants to determine features such as *Gracilaria* wet weight and epiphyte wet weight. However, they were first shaken in 50% ethanol in seawater to kill the amphipods, most of which fell off plants immediately (plants were inspected to make sure all amphipods had been removed). Amphipods retained by a 0.25 mm (pore diameter) sieve were sorted by size (plus sex for *A. lacertosa* and *C. acherusicum*) using a dissecting scope.

In 1986, we marked a transect parallel to the shore (at 0.87 m above LLW) through the *G. asiatica* zone sampled in 1984. A 0.25 m^2 quadrat having 100 evenly-spaced intersections (formed by rows of strings glued to the frame and intersecting each other at 90°) was constructed. This quadrat was placed along every 5 m of the linear transect, and the percentage composition of different species was noted by identifying components below each of the point-intersections. Ten quadrats were counted. A line placed parallel to the permanent transect, but 2–3 m seaward, was used to collect *G. asiatica* for determination of length, wet weight and epiphyte coverage. This line was placed along the easternmost 13 m of the transect. It was also placed (at the same tidal height) on the sand beach just east of the rocky intertidal zone in which our main collecting took place. At both sites, plants were collected within a 6 cm strip along each side of the rope.

RESULTS

The objective of studies of natural populations of *G. asiatica* and *G. lemaneiformis* was to provide seasonal data on epiphytism of these macrophytes and to assess the density and species composition of resident mesoherbivores. *G. asiatica* was abundant in rocky (granitic) areas of the mid to low intertidal zone at Zhanshan Bay. *G. lemaneiformis* was abundant in patches throughout the sandy, shallow subtidal zone (to about 3 m); plants "growing on sand" were often found to be attached to buried hard substratum, and most patches were on the landward side of large (submerged), boulders.

We observed substantial changes in the length, wet weight, and amount of epiphytes of both *G. asiatica* and *G. lemaneiformis* during our studies in 1984 (Fig. 3). *G. asiatica* plants were short and sparsely branched from a single main axis in April. By mid-May, plant length had increased substantially, peaking in late June and decreasing after mid-July (Fig. 3B). A similar pattern was observed for seasonal changes in wet weight (Fig. 3C). Changes in length and wet weight of *G. lemaneiformis* were similar seasonally to those observed for *G. asiatica*; however, *G. lemaneiformis* plants were longer and very bushy, even in late April (see data for May 3 in Fig. 3). The presence of multiple axes indicated regrowth of plants following physical and/or biological damage, and observation of such plants in spring showed that the *G. lemaneiformis* population might be perennial. There were significant increases in plant length for both *G. asiatica* ($P < 0.001$, Mann-Whitney U test) and *G. lemaneiformis* ($P < 0.05$, Mann-Whitney U test) between the earliest pair of sampling dates (Fig. 3); this was not true of plant weight. Thus, for both *G. asiatica* and *G. lemaneiformis*, growth (increased wet weight and length) was observed in the field between mid-

Table 2 Length, biomass and epiphytism of *G. asiatica* in 1986 along adjacent rocky and sandy portions of Zhanshan Bay. Data are presented as means (± S.D.).

	5-28-86 Rocky	5-28-86 Sandy	6-27-86 Rocky
A. Plant length (cm)	5.8 (2.3)^{d,e}	17.7 (7.9)^{c,d}	13.9 (7.2)^{c,e}
B. Plant fresh weight (g)	0.13(0.13)^{e,f}	0.78(1.09)^{f}	0.63(1.06)^{e}
C. Ratio of epiphyte to *G. asiatica* wet weights (E/*G*)	0.36(0.65)^{d}	0.23(1.42)^{b,d,e}	0.34(0.40)^{e}
D. Number of plants (*G. asiatica*)	19	37	46
E. Percentage of plants with epiphytes	47%	5%	48%

a A transect in the sandy area was not repeated 6-27-86 because of extensive collecting in this area: however, large plants were still observed there.

b only 2 plants had epiphytes, the epiphytes weighed 8.64 g and 0.01 g.

c $P < 0.05$. between pair of dates so marked, Kruskal-Wallis test. followed by Dunn's nonparametric multiple comparison test (Zar, 1984. p. 198).

d $P < 0.01$

e $P < 0.001$

May and late June, corresponding to water temperatures between 15–20°C.

Data (Table 2) on length and weight of *G. asiatica* in 1986, from an overlapping region of the rocky intertidal zone sampled in 1984, fit the trends found in 1984 (Fig. 3). Water temperature was cooler during May 1986 compared to 1984 (Fig. 2), and this may explain, in part, the shorter plants in late May 1986 compared to 1984. However, as shown in Table 2, long *G. asiatica* plants were found in Zhanshan Bay in late May; they were present in the adjacent, sandy intertidal zone. *G. asiatica* were larger and more numerous in the portion of the rocky transect closest to the sandy beach (data not shown).

Table 3 Percentage composition (mean ± S.D.) of components within the *G. asiatica*, lower intertidal zone community in Zhanshan Bay. Based upon counts (see methods) within a 0.25m² quadrat ($n = 10$) along a permanent transect.

	5–23–86	6–26–86
Anemone	0.1(0.3)	1.7(3.1)
Bryopsis corticulans Setch.	—	2.0(3.1)
Cladophora fascicularis (Mert.) Kuetz.	—	0.7(1.1)
Corallina pilulifera Post. & Rupr.	0.9(1.9)	3.9(4.4)
Enteromorpha linza (L.) J. Ag. + *Ulva pertusa* Kjellm.	87.6(13.) **	63.4(18.1)
Gracilaria asiatica Zhang & Xia	—	2.8(4.4)
Punctaria latifolia Grev.	2.0(5.3)	—
Rock (bare)	2.8(7.2) *	12.6(13.7)
Sand	4.7(6.8)	11.9(16.3)
Sargassum thunbergii (Mert.) O'Kuntze	0.3(0.9)	0.4(0.8)
Scytosiphon lomentaria (Lyngbe) C. Ag.	1.6(3.7)	—
Symphyocladia latiuscula (Mert.) Yamada	—	0.6(0.7)

** $P < 0.01$, Mann–Whitney U test.

* $P < 0.05$

Both in 1984 and 1986, a June storm of about 3 d duration removed much of the benthic (and epiphytic) *E. linza* and *Ulva pertusa*, reflected in data on community composition (Talbe 3). The decrease in cover from May to June of these ephemeral, green algae may have permitted or facilitated recruitment of *G. asiatica*.

Epiphytism is difficult to quantify at a species level because many of the epiphytes are unicellular algae or immature macrophytes. We used several methods to characterize seasonal changes in epiphytism of *G. asiatica* and *G. lemaneiformis* at Zhanshan Bay. Changes in epiphyte to *Gracilaria* wet weight per quadrat are given in figure 3D and, per plant, in Table 2; Table 4 contains a list of most of the epiphytic species (an exhaustive species list was not prepared) with relative abundance indicated at each timepoint. These relative abundances of multicellular epiphytes are based upon quantitative data such as those given in Table 5 for *Enteromorpha linza*, the most common multi-cellular epiphyte of *G. asiatica*, and for *Punctaria latifolia*, the most common multi-cellular epiphyte of *G. lemaneiformis* (Fig. 4). We tried a number of semi-quantitative schemes (e.g., thickness of layer from plant surface at predetermined intervals along the axis) for evaluating the diatomaceous component of the epiphytic biomass, but none were satisfactory. Thus, the diatom component is described qualitatively below.

Table 4 Multicellular epiphytes of *G. asiatica* and *G. lemaneiformis. See Tseng (1983) for additional information on these species in China.**

G. asiatica:			1984			
Chlorophyta:	4/27	5/18	6/20	7/18	8/13	
Enteromorpha linza (L.) J. Ag.	+ +	+ +	+	—	—	
Ulva pertusa Kjellm.	+	+	+	—	—	
Rhodophyta:						
Polysiphonia japonica Harv.	+	+	—	—	—	
Polysiphonia spp.	+	+	—	—	—	
Porphyra tenera Kjellm.	+ +	+	—			
Phaeophyta:						
Ectocarpus confervoides (Roth) Le Jolis	+	+				
Leathesia difformis (L.) Aresh.	+	+				
Punctaria latifolia Grev.			—			
Sphacelaria subfusca S. et G.	+	+				
G. lemanaeformis Chlorophyta:	5/3	5/18	5/31	6/28	7/28	8/15
Enteromorpha linza (L.) J. Ag.	+	—	—	—		
Ulva pertusa Kjellm.	—	—	—	—		
Rhodophyta:						
Plocamium telfairiae Harv.			—	—		
Polysiphonia japonica Harv.	—	—				
Polysiphonia spp.	—	—				
Porphyra tenera Kjellm.	—					
Phaeophyta:						
Ectocarpus confervoides (Roth) Le Jolis	+	—	—			
Leathesia difformis (L.) Aresh		—				
Punctaria latifolia Grev.	+ +	+ +	+ +	—		
Sphacelaria subfusca S. et G.		—				

* + + = abundant
+ = common
— = rare
Based upon quantitative data for epiphytic species such as that in Table 5.

The ratio of epiphyte to *Gracilaria* wet weights decreased steadily during our 1984 study, except for a transient increase on *G. lemaneiformis* during May (Fig. 3D). As noted above, epiphytic wet weight includes most of the diatomaceous component of epiphytic biomass because, at times when substantial diatom fouling occurred, the diatoms could be rubbed off plants with other epiphytes and blotted dry. The transient increase in epiphytic biomass on *G. lemaneiformis* during May was due to growth of *P. latifolia* (Table 5). Between late June and mid-July, macroscopic

Table 5 Seasonal decline of *Enteromorpha linza* as an epiphyte of *G. asiatica* and of *Punctaria latifolia* as an epiphyte of *G. lemaneiformis*. (X ± S.D.)

	Apr. 27 (n=5)	May 18 (n=5)	June 20 (n=6)	July 18 (n=6)	August 13 (n=6)	
Mean length of epiphytic *E. linza* (>1 cm only)/0.25 m²	5.0(3.7)	3.8(2.1)	6.0(1.6)	3.2(4.9)*	0	
Mean number of epiphytic *E. linza* (>1 cm)/plant/0.25 m²	1.1(0.8)	0.9(1.5)	0.5(0.4)*	0	0	
Mean number of epiphytic *E. linza* (≤1 cm)/plant/0.25 m²	0.5(0.1)*	0.1(0.3)	0.1(0.1)	0	0	
	May 3 (n=5)	May 18 (n=4)	May 31 (n=6)	June 28 (n=6)	July 28 (n=2)	August 15 (n=6)
Mean length of epiphytic *P. latifolia* (>1 cm only)/0.25 m²	1.2(0.6)	3.2(2.0)	2.8(1.4)*	0	0	0
Mean number of epiphytic *P. latifolia* (>1 cm)/plant/0.25 m²	6.8(12.6)	3.1(3.2)	4.2(4.4)**	0	0	0
Mean number of epiphytic *P. latifolia* (<1 cm)/plant/0.25 m²	3.0(3.1)	7.3(9.4)	1.8(1.6)**	0	0	0

* = $p \leq 0.05$, Mann-Whitney U test

** = $p \leq 0.01$

epiphytes disappeared from *G. lemaneiformis*. Multicellular epiphytes on *G. asiatica* had decreased substantially by late June; however, *E. linza* was still common. By mid-July, *E. linza* was uncommon and other epiphytes, rare; *G. asiatica* remained free of multicellular epiphytes through mid-August. Thus, the decline of epiphytism (by multicellular species) on *G. asiatica* and *G. lemaneiformis* occurs, generally, with the onset of *Gracilaria* growth (Fig. 3); however, these epiphytes do not reappear as *Gracilaria* growth declines in July and August.

G. asiatica in the rocky intertidal zone in 1986 had an epiphytic load very similar to that observed in 1984 (compare Table 2 and Fig. 3D); however, plants growing in the sandy intertidal zone were very clean, and only 5% of the plants had any (measurable) epiphytes, compared to half of the plants along the rocky transect.

The major diatomaceous epiphyte of both *G. asiatica* and *G. lemaneiformis* was *Licmophora* sp. These diatoms formed a macroscopic layer on surfaces of *G. asiatica* and *G. lemaneiformis* throughout May in 1984. *G. asiatica* plants were free of diatoms when first sampled in late April and both *G. asiatica* and *G. lemaneiformis* were diatom-free from mid-June through late August with the exception of a short period in mid-July (absent June 20, present July 18, absent July 28) when a macroscopic coating of diatoms was observed again. This period co-occurred with some of the calmest weather of the summer. Diatomaceous cover on *G. asiatica* was sparse or absent in 1986.

Weather may have influenced epiphytism in a number of ways (e.g., nutrient enrichment and/or osmotic stress during heavy rains, sand scour and whiplash during storms). Storms of about

4 days duration occurred on June 3 and 21 (1984) and the bottom appeared scoured when the June 28 collections were made. In particular, the larger epiphytic and benthic *E. linza* had disappeared, as noted above; similar events occurred in 1986. From late July through mid-August, typhoon-related storms passed Qingdao, resulting in high waves and poor visibility underwater; it was still rough in mid-August (8/13–15) when the last quadrat collections were made. Fine silt covered the bottom. Both *G. asiatica* and *G. lemaneiformis* were obviously shorter. The change in the habitat of *G. lemaneiformis* was especially striking. Most of the plant's branches were frayed and short, but a few long axes, sometimes close to 0.5 m, remained (Fig. 5). Polychaetes (*Platynereis bicanaliculata* Baird) were common in the *G. lemaneiformis* at this time and may have contributed to decreased plant length.

We determined the amphipod species present on *G. lemaneiformis* and *G. asiatica* in order to set up meaningful experiments to assess what effects such small herbivores might have on algal community structure. Tables 6 and 7 present, respectively, a list of all species found and quantitative data on associations of amphipods with *G. asiatica* and *G. lemaneiformis*. The most abundant species were *Ampithoe lacertosa*, several species of *Caprella* (especially *C. equilibra, C. krφyeri*, and *C. scaura*) and *Pontogeneia rostrata*. Some features of our *P. rostrata* are different from Gurjanova's type description, including orange eyes and the even length of rami on the third uropod of our specimens. *Jassa falcata* was the next most abundant species but was only common in late June on *G. lemaneiformis* plants (23% of all amphipods collected on June 28 belonged to *J. falcata*). *Paradexamine* sp. were collected on plants only in late summer; our animals are identical to those figured by Nagata as *P. barnardi* but this appears to be a new species (J.L. Barnard, pers. comm.).

Fig. 4 A common epiphyte *Punctaria latifolia* on *G. lemaneiformis* in Zhanshan Bay. Background scale in cm.

Fig. 5 Common habitat of *G. lemaneiformis* in Zhanshan Bay in late summer

Information on amphipod density is presented in two ways in Table 7, as animals/plant and animals/g *Gracilaria* (wet wt.). Some amphipod species (e.g., *Pontogeneia rostrata*, *Caprella* spp.) are potentially very mobile, while other species (e.g., *A. lacertosa, J. falcata*) build tubes on plants

Table 6 Amphipods present on *G. asiatica* and *G. lemaneiformis* in 1984 at Zhanshan Bay. Representative specimens are in collections of the U.S. National Museum (#362479)

Allorchestes angustus Dana (Hyalidae)
Ampithoe lacertosa Bate (Ampithoidae)
Caprella equilibra Say (Caprellidae)
Caprella kröyeri De Haan
Caprella scaura Templeton
Caprella septentrionalis Kroyer
Cheiriphotis sp. (Isaeidae)
Corophium acherusicum Costa (Corophiidae)
Jassa falcata (Montagu) (Ischyroceridae)
Paradexamine sp. (Dexaminidae)
Pontogeneia rostrata Gurjanova (Eusiridae)

and are less mobile. Hence, calculation of animal density per plant is important in evaluating herbivore effects, even though this does not take into account seasonal variation in plant length or wet weight.

Amphipod densities were low on both species (Table 7) except on *G. lemaneiformis* in late May. Epiphytes were still common on *G. lemaneiformis* in late May but the ratio of epiphytic to *Gracilaria* wet weight had just decreased at that time. Most of the amphipods present on *G. lemaneiformis* in late May were *A. lacertosa* (55%) and *P. rostrata* (12%). Amphipods were uncommon on plants after June when epiphytes disappeared. Amphipods / plant and epiphytic biomass / plant correlated positively ($r^2 = 0.560$, $n = 43$, $p < 0.01$) from May 31–August 15 (see Edgar, 1983 and Gunnill, 1982 a, b, 1983, 1984 for similar correlations on other macrophytes). No correlation existed between *Gracilaria* biomass and amphipod density. In contrast, there was a positive correlation ($r^2 = 0.752$, $n = 34$, $p < 0.01$) between amphipods / plant (June 20—August 13) and wet weight of the *G. asiatica* plants. Amphipods / plant and epiphytic biomass / plant were not correlated ($r^2 = 0.020$, $n = 34$) for *G. asiatica*; however, biomass data were not collected for the May 4 and 18 samples, so these important times could not be included in this analysis. Amphipod density / plant and amphipod density / g (wet wt.) *G. asiatica* were highest in mid-July when diatom cover had reappeared on plants.

In the course of the studies reported above, we observed (1984, 1986) the yellowfish *Hexagrammos otakii* Jordan et Starks (Hexagrammidae) throughout the lower intertidal-subtidal zones of Zhanshan Bay at a density of about 1 fish / m^2. This fish feeds on a wide variety of small invertebrates (Brawley & Fei, submitted). At night (1986), numerous small (carapace diameter < 3 cm) crabs fed upon the algae within the lower intertidal zone where the *G. asiatica* studies took place. They were found in rock crevices by day. The role of these organisms in regulating the cycles described above deserves additional study.

DISCUSSION

Detailed, baseline data on the rocky intertidal, *G. asiatica* community and the rock / sand subtidal, *G. lemaneiformis* community presented above present a complex picture of the natural cycle of epiphytism. Epiphytism is an important subject for ecological investigation because

Table 7 Selected mesoherbivores associated with *G. asiatica* and *G. lemaneiformis* at Zhanshan Bay (X ± S.D.) in 1984.

A. *Gracilaria asiatica*	5/4	5/18	6/20	7/18	8/13
n (plants)	12	6	12	12	10
Number of n plants with amphipods	6	3	6	9	4
Gracilaria wet weight (g)	—	—	1.61(1.14)	3.78(3.42)	1.13(0.60)
Gracilaria length (cm)	—	—	25.6(9.2)	22.1(9.1)	12.2(3.6)
Epiphyte/*Gracilaria* wet weight [quadrat]	3.24(3.10) (Apr. 27)	0.55(0.61)	0.24(0.14)	0.01(0.03)	0
Epiphyte/*Gracilaria* wet weight [plant]	—	—	0.16(0.18)	0.07(0.17)	0
Amphipods/g (wet wt.) of *Gracilaria*	—	—	0.7(0.9)	2.3(3.6)	1.0(1.5)
Amphipods/plant	1.3(1.9)	0.8(1.2)	1.3(2.8)	5.1(5.2)	1.3(1.8)
(total number of amphipods from all plants)	(16)	(5)	(16)	(61)	(13)
Caprellids/plant	0.2(0.4)	0	0.2(0.4)	1.1(1.8)	0
(% represented in total sample)	(13%)	(0%)	(13%)	(21%)	(0%)
A. lacertosa/plant	0.2(0.6)	0.2(0.4)	1.0(2.6)	0.2(0.4)	0.3(0.7)
	(19%)	(20%)	(75%)	(3%)	23%)
P. rostrata/plant	0.9(1.8)	0.7(1.2)	0	2.0(2.4)	0
	(69%)	(20%)	(0%)	(39%)	(0%)
Isopods (*Synidotea* sp.)/plant	0	0	0	0.1(0.3)	0
B. *Gracilaria lemaneiformis*	5/18	5/31	6/28	7/30	8/15
n (plants)	8	12	12	7	12
Number of n plants with amphipods	6	11	10	4	3
Gracilaria wet weight (g)	—	4.41(4.16)	9.36(7.87)	8.84(13.44)	2.78(2.68)
Gracilaria length (cm)	—	—	30.2(19.9)	46.2(38.1)	22.5(8.5)
Epiphyte/Gracilaria wet weight [quadrat]	1.05(1.19)	0.12(0.10)	0	0	0
Epiphyte/*Gracilaria* wet weight [plant]	—	0.20(0.24)	0	0	0
Amphipods/g (wet wt.) of *Gracilaria*	—	7.3(8.1)	1.7(2.4)	0.2(0.3)	0.4(1.1)
Amphipods/plant	11.6(15.7)	31.0(37.7)	12.7(15.5)	0.9(0.9)	0.7(1.3)
(total amphipods from all plants)	(93)	(372)	(152)	(6)	(8)
Caprellids/plant	3.8(10.6)	0.7(1.2)	1.6(4.0)	0	0
(% represented in total sample)	(32%)	(2%)	(13%)	(0%)	(0%)
A. lacertosa/plant	4.9(9.3)	17.1(24.1)	2.7(6.2)	0.3(0.5)	0.2(0.6)
	(42%)	(55%)	(22%)	(33%)	(25%)
P. rostrata/plant	0.9(1.4)	3.8(6.7)	1.5(2.4)	0.4(0.5)	0.1(0.3)
	(8%)	(12%)	(12%)	(33%)	(13%)
Isopods/plants	0.1(0.4)	0.2(0.6)	6.4(15.3)	5.7(11.2)	0.3(0.6)
Gastropods (juveniles, 1–2 mm)/plant	0.2(0.7)	0	37.0(41.8)	9.4(17.2)	19.3(36.0)

epiphytes can affect community succession in several different ways. Sousa (1979) observed that some species were more subject to epiphytes than others, and that this led to removal of these plants by storms, to the advantage of later successional species. Similar results were reported by D'Antonio (1985) working with *Rhodomela larix* on the Oregon (U.S.A.) coast. Epiphytes inhibit macrophyte growth by shading the plant and creating a diffusion barrier (e.g., Brawley & Adey, 1981; D'Antonio, 1985; Sand-Jensen et al., 1985). Further, when epiphytic algae are common, many of these species also exist freely attached to the substratum where they can inhibit attachment of macrophytic spores and zygotes (Hruby & Norton, 1979).

Present hypotheses concerning epiphytes suggest that they may be reduced by: 1) rapid growth, accompanied by sloughing of outer cell wall layers with adherent epiphytes (Filion-Myklebust & Norton, 1981; Moss, 1982) and chemical defenses (Sieburth & Conover, 1966; Sieburth & Tootle, 1981; Harrison & Durance, 1985) 2) mesoherbivores (Brawley & Adey, 1981; Robles & Cubit, 1981; Shacklock & Croft, 1981; Kangas et al., 1982; Warwick et al., 1982; Cattaneo, 1983; Lubchenco, 1983; Shacklock & Doyle, 1983; D'Antonio, 1985) 3) and / or physical effects such as sand scour or whiplash in heavy waves (D'Antonio, 1985, and references therein). This baseline work supports each of these as a factor potentially responsible for the disappearance of epiphytes from *G. asiatica* and *G. lemaneiformis* in Zhanshan Bay in early summer.

One of the most interesting findings of this study is that epiphytes do not reappear on plants after they stop growing (see Results, especially Fig. 3). Epiphytism of plants at Zhanshan Bay remained very low during July and August (1984) when water temperatures were high, but diatoms briefly reappeared on *G. asiatica* in July during a short period of calm weather. Heavy storm waves were present throughout most of the summer (June–August), and plants were continually abraded against rock / sand surfaces by wave action. In addition to direct effects of sand scour upon epiphyte removal, reduced light penetration accompanying suspended sediment also may have contributed to decreased epiphytism. Ephemeral species do not recruit well in some kelp forests because of severe light reduction under stable canopies (Reed & Foster, 1984).

Our 1986 data demonstrate that some aspect of the sandy environment is beneficial to *G. asiatica*, permitting rapid growth and reducing epiphytes. However, there is also a seasonal decline in epiphytes on *G. lemaneiformis* (subtidal plants on sand), which makes the interpretation of these results complex. Future studies of this community should address these questions:

1) Does a spring bloom of ephemeral, green algae inhibit establishment of *G. asiatica* in the rocky intertidal zone compared to adjacent sandy areas?

2) How do normal and storm-generated levels of sand scour influence *Gracilaria* growth and general community structure? The seasonality and intensity of storms should be studied in connection with changing community structure, and

3) Does "amphipods / plant" or "amphipods / g *Gracilaria*" reflect the majority of grazing by amphipods to which *Gracilaria* and its epiphytes are exposed? Most amphipods collected from plants at Zhanshan Bay were 2–6 mm in length, but larger (> 1 cm) *A. lacertosa* were collected in patches of nearby *Corallina* turf.

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