AMPHIPODS ASSOCIATED WITH *CODIUM* SPECIES IN KOREA

BY

SUCHANA CHAVANICH[1,3]), VORANOP VIYAKARN[1]) and HEUNG-SIK PARK[2])

[1]) Department of Marine Science, Faculty of Science, Chulalongkorn University, Bangkok 10330, Thailand

[2]) Marine Living Resources Research Department, Korea Ocean Research and Development Institute, Ansan, Korea

ABSTRACT

A comparison was made of amphipod assemblages on different species of the green alga, *Codium* both from a protected marine area and from a disturbed area. In addition, a laboratory experiment was conducted to determine habitat selection by amphipods. A total of five species of amphipods was found on *Codium* species. Amphipods were more abundant in the protected marine area; however, high numbers of amphipod species occurred on *Codium fragile* where that was a fouling organism in the disturbed area. The results from the experiment showed that amphipods preferred *C. fragile* as their habitat over any of the other species of *Codium*. The formation of canopies, the morphology of the plant species, and amphipod morphology, are all likely to influence the distribution and habitat selection by amphipods.

RESUMEN

Se compararon los ensambles de anfípodos en diferentes especies de *Codium*, en un área marina protegida y en otra alterada. Adicionalmente, se llevó a cabo un experimento de laboratorio para determinar la selección del hábitat efectuada por los anfípodos. Un total de cinco especies de anfípodos se encontraron en las especie *Codium*. Los anfípodos fueron más abundantes en el área protegida; sin embargo, un número alto de especies de anfípodos ocurrieron en un *Codium fragil*e contaminado en el área alterada. Los resultados del experimento mostraron que los anfípodos prefirieron el *C. fragile* como su hábitat más que cualquier otra especie de *Codium*. La formación de colonias de especies, la morfología de la planta y la morfología de los anfípodos son, probablemente, los factores que influyen en los anfípodos para la selección de su hábitat.

INTRODUCTION

Amphipods are considered one of the most dominant groups associated with a variety of macroalgae on rocky shores. They use these algae both as their habitat

[3]) Corresponding author; Fax: +66.22550780; e-mail: suchana.c@chula.ac.th

Also available online: www.brill.nl/cr

Crustaceana 83 (7): 795-807
DOI:10.1163/001121610X504306

and their food (Buschmann, 1990; Hacker & Steneck, 1990; Duffy & Hay, 1991; Chavanich & Wilson, 2000; Chavanich, 2006). The selection of macroalgae by amphipods can be influenced by both biological and physical factors (McBane & Croker, 1983; Buschmann, 1990; Hacker & Steneck, 1990; Duffy & Hay, 1991; Viejo & Arrontes, 1992). Some studies have shown that amphipods tend to choose algae that have a more complex structure as their habitats, while they prefer soft algae, like green algae and ephemeral red algae, as their source of food (Hacker & Steneck, 1990; Duffy & Hay, 1991).

Codium is a green macroalga that is found at both temperate and tropical latitudes. *Codium fragile* (Suringar) Hariot has evoked particular interest for many years because its subspecies, *tomentosoides* (Van Goor) P. C. Silva invaded many habitats in many countries (Silva, 1957; Fralick & Mathieson, 1972; Carlton & Scanlon, 1985; Trowbridge, 1995). The form *tomentosoides* has now been redescribed and is accepted as a subspecies of *fragile* (cf. Provan et al., 2007). *Codium fragile* is native to Korea and Japan, where a centre of distribution of *C. fragile* is assumed (Silva, 1955; Goff et al., 1992; Provan et al., 2005; Chavanich et al., 2006). Organisms associated with *C. fragile* can be both sessile and mobile (Harris & Mathieson, 2000; Harris & Jones, 2005; Chavanich et al., 2006), and amphipods contribute one of the epifaunal groups associated with *C. fragile* both in native and non-native habitats (Cruz-Rivera & Hay, 2001; Chavanich et al., 2006; Schmidt & Scheibling, 2006). Those amphipods use *C. fragile* as their habitat and as their food (Cruz-Rivera & Hay, 2001; Chavanich et al., 2006; Schmidt & Scheibling, 2006). There are studies on the distribution and feeding of amphipods on *C. fragile* in non-native habitats (Cruz-Rivera & Hay, 2001; Schmidt & Scheibling, 2006), but little is known on the distribution patterns of amphipods associated with *C. fragile* in native habitats (Chavanich et al., 2006).

The purpose of this study was to examine the species composition and distribution of amphipods on *C. fragile* in comparison to other species of *Codium* in a native habitat, Korea. In addition, the distribution patterns of amphipods associated with *Codium* spp. at different depths were investigated. A comparison was also made of amphipod assemblages both from a protected marine area and from a disturbed area.

MATERIAL AND METHODS

Sampling was conducted at three locations in the southern part of Korea: (1) Munseom Islet (previous name: Munsom), (2) Seopseom Islet (previous name: Supsom), and (3) Tongyeong (previous name: Tongyong) (fig. 1). The islets Museom and Seopseom are located closed to Jejudo (previous name: Cheju

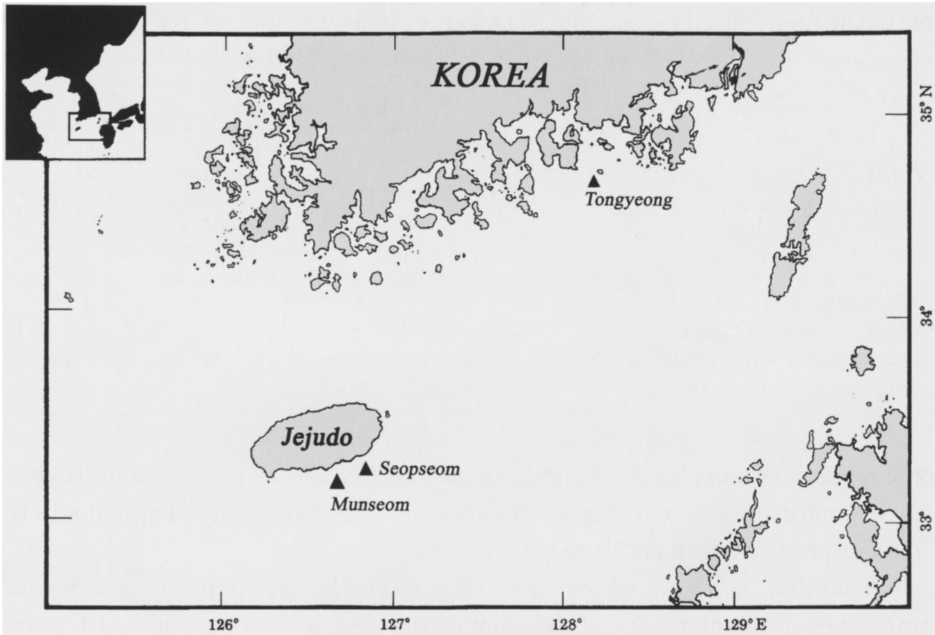

Fig. 1. Map of southern Korea showing the three study sites.

Island). The difference between these three locations is, that Tongyeong is a disturbed area where many species of kelp and invertebrates have been harvested as human food, while Museom and Seopseom are in an environmentally protected marine area.

At each site, surveys were conducted at three different depths: at 4, 9, and 18 m below mean seawater level, except at Tongyeong where the bottom becomes silty and muddy below 9 m depth, and there is no *Codium*. Therefore, at Tongyeong, samples were collected at 3, 6, and 9 m depth, and also *Codium fragile* samples from the floating docks and piles at the surface. Chavanich et al. (2006) reported 4 species of *Codium* to occur at these sites: *Codium adhaerens* C. Agardh, *Codium cylindricum* Holmes, *Codium fragile* (Suringar) Hariot, and *Codium minus* (Schmidt) Silva. *Codium fragile* can be found at all depths and all sites. The species of *Codium* and the depths that were sampled are shown in table I. Five samples of each species were collected at different depths at each location. All samples were collected from June to August 2000, when water temperatures averaged 20-25°C. To collect amphipods associated with *Codium*, a whole plant plus the attached amphipods were covered with a plastic bag and removed from the substratum. All samples were brought back to the laboratory in the Korean Ocean Research and Development Institute for later analysis. In the laboratory, the amphipods were removed from the *Codium* samples, fixed in 75% ethanol, and identified to species level. Algae were then blotted, dried, and weighed for calculating densities of

TABLE I
Samples of *Codium* spp. (X) that were collected at different depths and sites

Sampled species of algae	Localities/Depths									
	Munseom			Seopseom			Tongyeong			
	4 m	9 m	18 m	4 m	9 m	18 m	Floating docks (Surface)	3 m	6 m	9 m
Codium adhaerens C. Agardh		X			X	X				
Codium cylindricum Holmes					X			X	X	X
Codium fragile (Suringar) Hariot	X	X	X	X	X	X	X	X	X	X
Codium minus (Schmidt) Silva	X				X					

amphipods per gram alga dry weight. A one-way ANOVA test followed by Tukey's pairwise mean comparison was used to test differences in density of amphipods on *Codium* species at different depths.

In addition, a laboratory experiment was conducted to investigate habitat preferences of the amphipods. The amphipod, *Ampithoe valida* Smith, 1873 was chosen for the experimental trial because it occurred on most *Codium* spp. In each aquarium (500 ml), ten amphipods were offered an approximately equal wet weight (0.2 g) of four species of *Codium*. Then, the experiment was run for 12 hours. After 12 hours, the amphipods were removed from each alga and counted. A total of 10 replicates was conducted. A one-way ANOVA test followed by Tukey's pairwise mean comparison was used to test differences in the numbers of amphipods in the different habitats.

RESULTS

A total of five species of amphipods was identified from the various species of *Codium*. These included *Ampithoe valida* Smith, 1873, *Caprella penantis* Leach, 1814, *Eusiroides monoculoides japonicus* Hirayama, 1985, *Gammaropsis japonica* Nagata, 1961, and *Jassa falcata* (Montagu, 1808). Amphipods were found on almost all *Codium* species, with the exception of *C. cylindricum* in Seopseom and Tongyeong, and *C. minus* in Munseom (table II, fig. 2). The highest number of amphipods (3 species) was found on fouling *C. fragile* at Tongyeong (fig. 2). *A. valida* was the dominant species (table II).

In this study, *C. fragile* was found at every sampling depth, and as deep as 18 m. In Tongyeong, it also occurred as a fouling organism growing on floating docks. The results from the sampling surveys showed that at 18 m depth, the only amphipod found associated with *C. fragile* was *E. monoculoides japonicus*

TABLE II

Average density of amphipods per gram alga dry weight found on *Codium* spp. at three sites: 1, Munseom; 2, Seopseom; and 3, Tongyeong. N/A (not applicable) if no algal sample could be collected in the area due to the absences of algae

Amphipod species	*Codium adhaerens* C. Agardh			*Codium cylindricum* Holmes			*Codium fragile* (Suringar) Hariot			*Codium minus* (Schmidt) Silva		
	1	2	3	1	2	3	1	2	3	1	2	3
Ampithoe valida Smith, 1873	4.37	0.61	N/A	N/A	0	0	0	2.27	1.96	0	0.23	N/A
Caprella penantis Leach, 1814	0	0	N/A	N/A	0	0	0	0	3.20	0	0	N/A
Eusiroides monoculoides japonicus Hirayama, 1985	0	0	N/A	N/A	0	0	1.82	0.85	0	0	0	N/A
Gammaropsis japonica Nagata, 1961	0	0	N/A	N/A	0	0	1.82	0	0	0	0	N/A
Jassa falcate (Montagu, 1808)	0	0	N/A	N/A	0	0	0	0	0.6	0	0	N/A

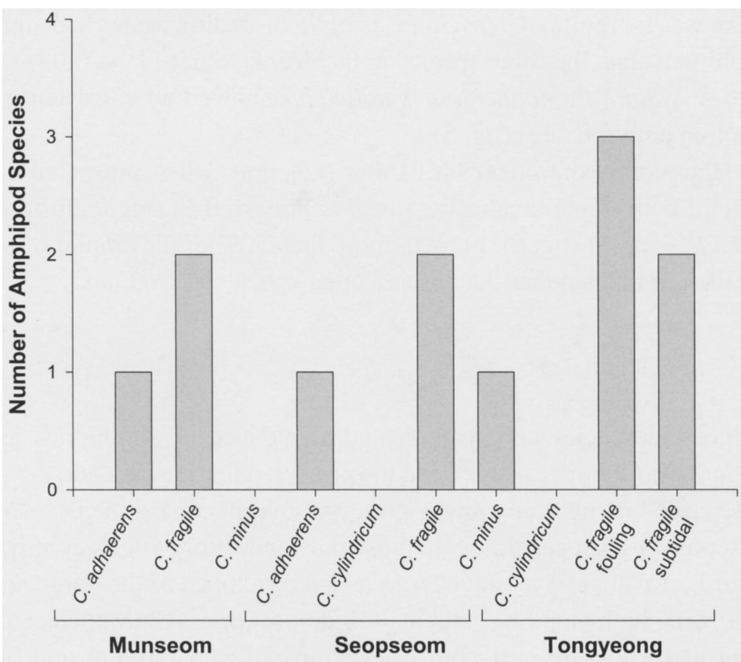

Fig. 2. Number of amphipod species associated with *Codium* species at three locations.

TABLE III

Amphipod species found on *Codium fragile* (Suringar) Hariot at three sites and at different depths. Presence (+) or absence (−) are shown for each depth at each study site

Amphipod species	Localities/Depths									
	Munseom			Seopseom			Tongyeong			
	4 m	9 m	18 m	4 m	9 m	18 m	Fouling on floating docks (Surface)	3 m	6 m	9 m
Ampithoe valida Smith, 1873	−	−	−	+	+	−	+	+	+	+
Caprella penantis Leach, 1814	−	−	−	−	−	−	+	−	+	−
Eusiroides monoculoides japonicus Hirayama, 1985	−	+	+	+	+	−	−	−	−	−
Gammaropsis japonica Nagata, 1961	+	+	−	−	−	−	−	−	−	−
Jassa falcate (Montagu, 1808)	−	−	−	−	−	−	+	−	−	−

(table III). The distribution of associated amphipods on *C. fragile* at different depths is shown in figs. 3-5. At Tongyeong, both *A. valida* and *C. penantis* were more abundant on fouling *C. fragile* ($P < 0.05$) (figs. 3-4). However, in Seopseom where there was no fouling *C. fragile*. *C. fragile* in shallow water had significantly more amphipods than the same species in the deeper water ($P < 0.05$) (fig. 3). In contrast to *A. valida*, *E. monoculoides japonicus* showed no consistent pattern in its distribution between sites (fig. 5).

In the laboratory experiment on habitat selection, when presented 4 *Codium* species for 12 hours simultaneously, *A. valida* preferred *C. fragile*, followed by *C. adhaerens* ($P < 0.05$) (fig. 6). In total, more than 50% of the amphipods chose *C. fragile* as their habitats rather than of any other species of *Codium*.

DISCUSSION

Differences in species composition and abundance of amphipods associated with different *Codium* species between the protected marine area and the disturbed area are described in this study. In the protected marine area at the islets Munseom and Seopseom, *Codium* species were present as understory vegetation, whereas in the disturbed area, at Tongyeong, *C. fragile* had developed as the dominant canopy species, growing both on pilings and in the subtidal zones (Chavanich et al., 2006). Tongyeong had a low diversity of algae compared to Munseom and Seopseom (Chavanich et al., 2006), and this can affect the choice of the associated fauna. When comparing between different *Codium* species, the highest species richness

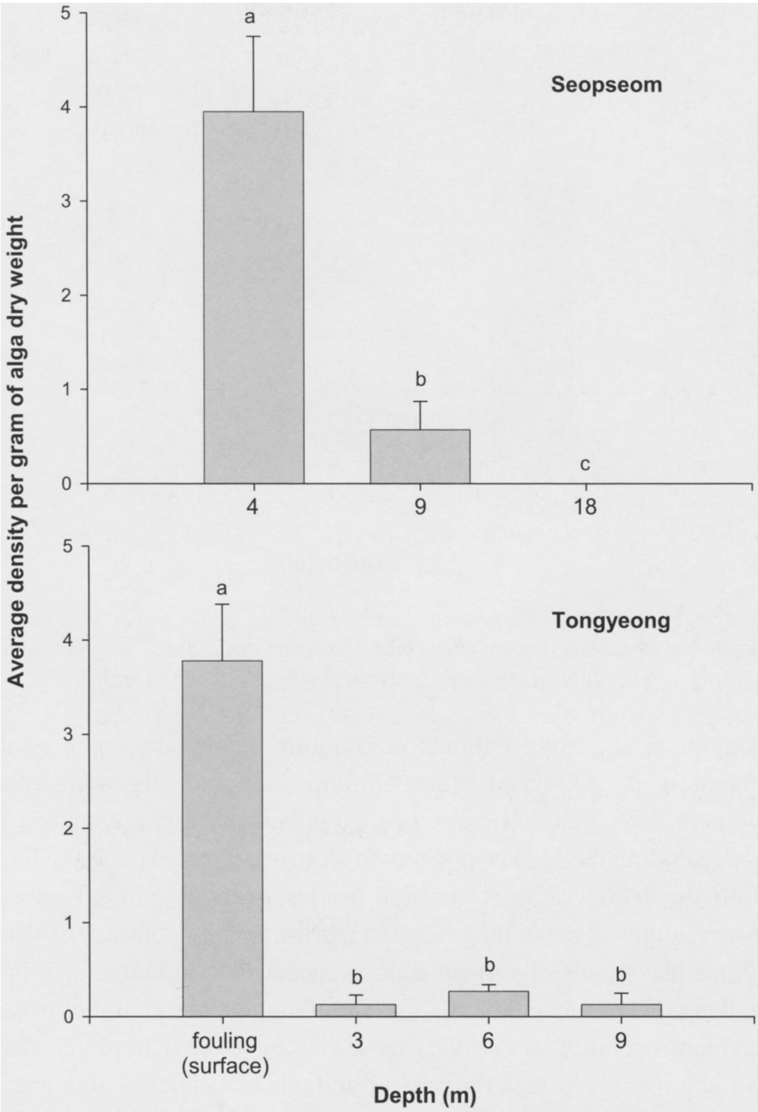

Fig. 3. Average density of *Ampithoe valida* Smith, 1873 on *Codium fragile* (Suringar) Hariot at different depths at Seopseom and Tongyeong. Letters above each histogram designate density of amphipods that differ significantly between depths ($P < 0.05$).

of associated fauna occurred on *C. fragile* at Tongyeong in the disturbed area (Chavanich et al., 2006; this study). However, the overall density of amphipods associated with *Codium* species was highest in the marine reserve area (table II).

The formation of canopy species has an effect on the composition of understory species and fauna. The formation can alter both physical and biological factors such as light, water flow, sedimentation, recruitment, and predator-prey relation-

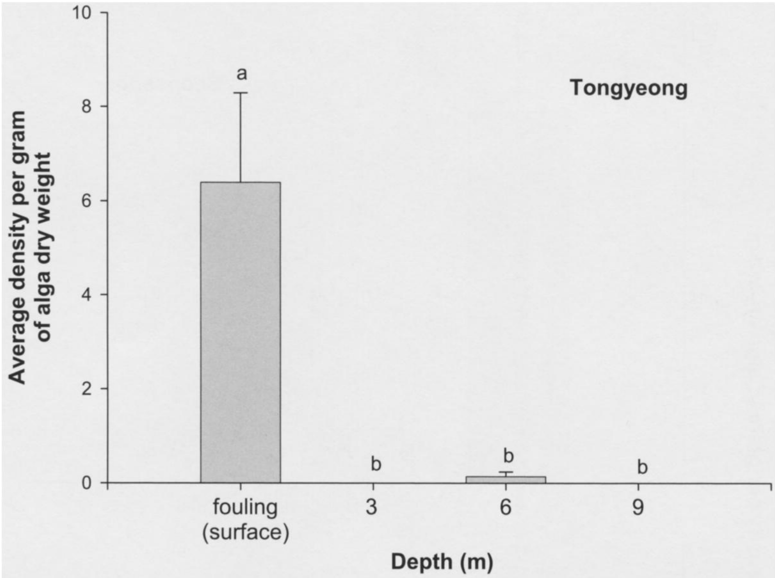

Fig. 4. Average density of *Caprella penantis* Leach, 1814 on *Codium fragile* (Suringar) Hariot at different depths at Tongyeong. Letters above each histogram designate density of amphipods that differ significantly between depths ($P < 0.05$).

ships (Duggins et al., 1990; Echman & Duggins, 1991; Chavanich et al., 2002, 2004; Edgard et al., 2004). At Munseom and Seopseom, the dominant canopy species were brown algae, *Ecklonia cava* Kjellman and *Sargassum* spp., while all other algae including the species of *Codium* were understory species (Chavanich et al., 2006). In the field, we observed a high species diversity of mobile invertebrates on the brown canopy algae in the protected marine area. In contrast, at Tongyeong, *C. fragile* had become the dominant canopy species due to human overharvesting of brown algae (Chavanich et al., 2006). Even though a high number of species of associated fauna occurred on *Codium fragile* at Tongyeong (Chavanich et al., 2006; this study), the overall species richness of animals associated with algae was low compared to the protected marine area, where the algal community was not altered through human activities (S. Chavanich, unpubl. data). The effective removal of the kelp canopy at Tongyeong appeared to also have an effect on the amphipod assemblage. A higher total number of amphipod species was found on fouling *C. fragile* than on that species in the subtidal zone. In contrast, in the protected marine area, the densities of amphipods were high in the shallow subtidal zone (fig. 3). When there were limitations of choice or environmental constraints, animals may show a different behaviour in habitat selection. For example, grazers may utilize algae that are more abundant, as their habitat and food source (Cronin & Hay, 1996). Interestingly, the density of amphipods on fouling *C. fragile* in the disturbed area

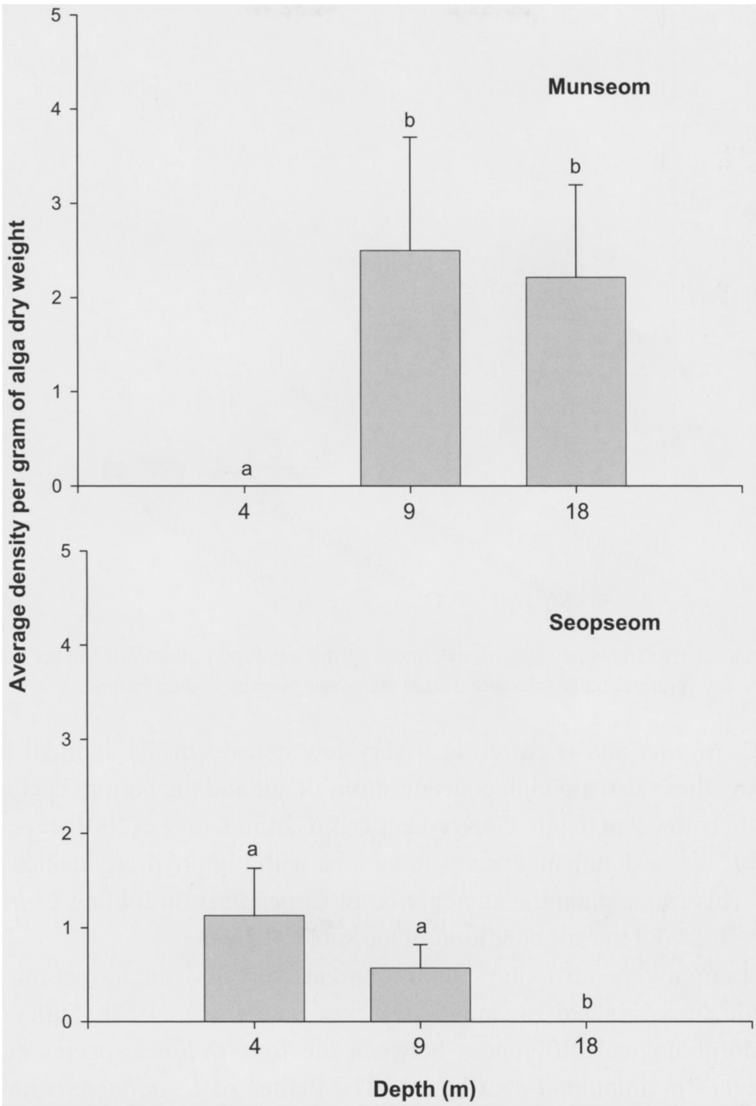

Fig. 5. Average density of *Eusiroides monoculoides japonicus* Hirayama, 1985 on *Codium fragile* (Suringar) Hariot at different depths at Munseom and Seopseom. Letters above each histogram designate density of amphipods that differ significantly between depths ($P < 0.05$).

was as high as on *C. fragile* in the shallow subtidal zone in the protected marine area (fig. 3).

Behaviour and morphology can be factors affecting the distribution of amphipods inhabiting algae. *Caprella penantis* has a parallel posture that allows to attach to the substratum in exposed habitats (Guerra-García & Garcia-Gómez, 2001; Guerra-García et al., 2002). In this study, *C. penantis* was found abundantly on

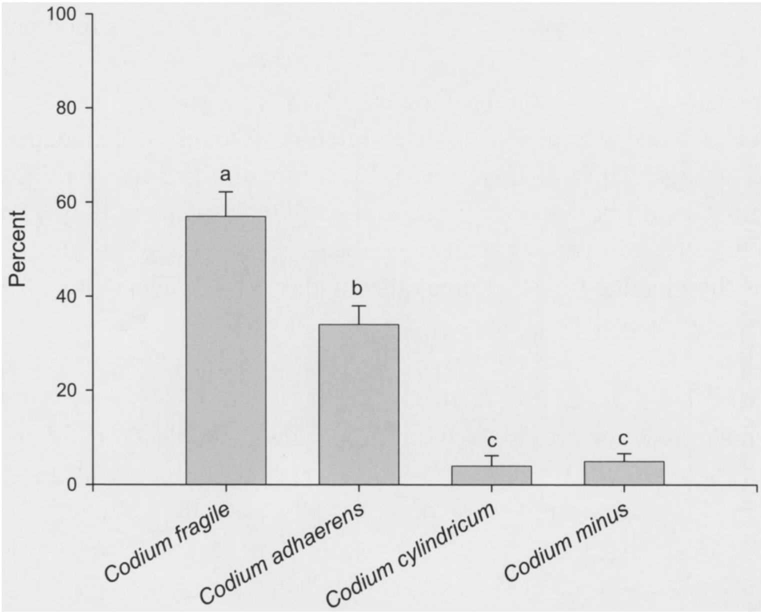

Fig. 6. Mean relative frequency (%) of specimens of the amphipod, *Ampithoe valida* Smith, 1873 preferentially selecting different *Codium* species as their habitat.

fouling *C. fragile*, and occurred at a very low density in the subtidal zone. At Tongyeong, there also are high concentrations of silt and the bottom becomes silty and muddy below 9 m depth. Guerra-García & Garcia-Gómez (2001) reported that *C. penantis* was a dominant species in an area with high hydrodynamics and low siltation. This can explain the aggregation of *C. penantis* on fouling *C. fragile*, as a response to avoid the silt condition in the subtidal zone.

Plant morphology also plays an important role in habitat section and the distribution of associated organisms (Hacker & Steneck, 1990; Duffy & Hay, 1991). Morphological differences between the four *Codium* species can result in differences in amphipod distribution. The thallus of *C. adhaerens* has a mat-forming morphology, while *C. cylindricum* has a branched and erect morphology in which the branches are broader than thick below each node (Verbruggen et al., 2007). On the other hand, the thallus of *C. fragile* has a cylindrical branched morphology, while *C. minus* has a spherical morphology (Verbruggen et al., 2007). It has been shown that fronds of *Codium fragile* ssp. *tomentosoides* support a higher density of amphipods than those of a blade-like structure such as in kelp, *Laminaria* (cf. Schmidt & Scheibling, 2006). Since amphipods need to cling on to the algae (Hacker & Steneck, 1990), *Codium* species that have a branched structure such as *Codium fragile*, can be preferred as a habitat, as shown by the experiment reported in this study (fig. 6).

The distribution of amphipods can also be influenced by their food preferences and by chemical defenses of the algae (Duffy & Hay, 1991; Viejo & Aarrontes, 1992). Habitat selection is also influenced by the various feeding strategies of amphipods and the ability to use different feeding modes depending on food availability (Duffy & Hay, 1991). Even though there was no difference in thallus morphology between *C. fragile* and *C. cylindricum*, except that the branch broadening differed (Verbruggen et al., 2007), the amphipods still preferred *C. fragile* as their habitat (fig. 6). Some other studies have shown that *C. fragile* was not a preferred food for amphipods and other mobile invertebrates (Cruz-Rivera & Hay, 2001; Chavanich & Harris, 2002, 2004). *Codium fragile* also has a low nutritional value (Cruz-Rivera & Hay, 2001). In addition, chemicals produced by algae can attract herbivores and have influence on their selection of food (Hay & Fenical, 1988; Prince & LeBlanc, 1992). *C. fragile* lacks a chemical attractant, and is known to be an unpalatable alga for herbivores (Prince & LeBlanc, 1992; Cruz-Rivera & Hay, 2001). Thus, choosing *C. fragile* over other *Codium* species by the amphipods in this study may not be related to their food preference.

In conclusion, a combination between the formation of canopies, the morphology of the plant species, and amphipod morphology are all likely to influence the distribution and habitat selection by amphipods at both the protected marine area and the disturbed area. Future studies of amphipod-*Codium* relationship may provide an insight into their interaction.

ACKNOWLEDGEMENTS

We would like to thank Jong-Geel Je, Rae-Seon Kang, Larry G. Harris, and Jose Cruz Escamilla Casas for comments and suggestions on the initial projects. We also thank J. C. von Vaupel Klein and an anonymous reviewer who provided constructive comments to improve the manuscript. This work was supported by grants from a Korea Summer Fellowship, the National Science Foundation (NSF, U.S.A.), the Korea Foundation for Advanced Studies' International Scholar Exchange Fellowship for the academic year of 2008-2009, and the Asia Research Center at Chulalongkorn University to S.C.

REFERENCES

BUSCHMANN, A. H., 1990. Intertidal macroalgae as refuge and food for Amphipoda in central Chile. Aquat. Bot., **36**: 237-245.

CARLTON, J. T. & J. A. SCANLON, 1985. Progression and dispersal of an introduced alga: *Codium fragile* ssp. *tomentosoides* (Chlorophyta) on the Atlantic coast of North America. Bot. mar., **28**: 155-165.

CHAVANICH, S., 2006. The occurrence of *Hyale nilssonii* in the rocky intertidal zone in New Hampshire, U.S.A. Crustaceana, **79**: 1005-1010.

CHAVANICH, S. & L. G. HARRIS, 2002. The influence of macroalgae on seasonal abundance and feeding preference of a subtidal snail, *Lacuna vincta* (Montagu) (Littorinidae) in the Gulf of Maine. Journ. Moll. Stud., **68**: 73-78.

— — & — —, 2004. Impact of the non-native macroalgae, *Codium fragile* (Sur.) Hariot ssp. *tomentosoides* (Van Goor) Silva, on the native snail, *Lacuna vincta* (Montagu), in the Gulf of Maine. Veliger, **47**: 85-90.

CHAVANICH, S., L. G. HARRIS, J. JE & R. KANG, 2006. Distribution pattern of the green alga *Codium fragile* (Suringar) Hariot, 1889 in its native range, Korea. Aquat. Invasions, **1**: 99-108.

CHAVANICH, S. & K. A. WILSON, 2000. Rocky intertidal zonation of gammaridean amphipods in Long Island Sound, Connecticut. Crustaceana, **73**: 835-846.

CRONIN, G. & M. E. HAY, 1996. Susceptibility to herbivores depends on recent history of both the plant and animal. Ecology, **77**: 1531-1543.

CRUZ-RIVERA, E. & M. E. HAY, 2001. Macroalgal traits and the feeding and fitness of an herbivorous amphipod: the roles of selectivity, mixing, and compensation. Mar. Ecol. Prog. Ser., **218**: 249-266.

DUFFY, J. E. & M. E. HAY, 1991. Food and shelter as determinants of food choice by a herbivorous marine amphipod. Ecology, **72**: 1286-1298.

DUGGINS, D. O., J. E. ECKMAN & A. T. SEWELL, 1990. Ecology of understory kelp environments II. Effects of kelp on recruitment of benthic invertebrates. Journ. exp. mar. Biol. Ecol., **143**: 27-45.

ECKMAN, J. E. & D. O. DUGGINS, 1991. Life and death beneath macrophyte canopies: effects of understory kelps on growth rates and survival of marine benthic suspension feeders. Oecologia, **87**: 473-487.

EDGAR, G. J., N. S. BARRETT, A. J. MORTON & C. R. SAMSON, 2004. Effects of algal canopy clearance on plant, fish and macroinvertebrate communities on eastern Tasmanian reefs. Journ. exp. mar. Biol. Ecol., **12**: 67-87.

FRALICK, R. A. & A. C. MATHIESON, 1972. Winter fragmentation of *Codium fragile* (Suringar) Hariot ssp. *tomentosoides* (Van Goor) Silva (Chlorophyceae, Siphonales) in New England. Phycologia, **11**: 67-70.

GOFF, L. J., L. LIDDLE, P. C. SILVA, M. VOYTEK & A. W. COLEMAN, 1992. Tracing species invasion in *Codium*, a siphonous green alga, using molecular tools. American Journ. Bot., **79**: 1279-1285.

GUERRA-GARCÍA, J. M., J. CORZO & J. C. GARCIA-GÓMEZ, 2002. Clinging behaviour of the Caprellidea (Amphipoda) from the Strait of Gibraltar. Crustaceana, **75**: 41-50.

GUERRA-GARCÍA, J. M. & J. C. GARCIA-GÓMEZ, 2001. The spatial distribution of Caprellidea (Crustacea: Amphipoda): a stress bioindicator in Ceuta (North Africa, Gibraltar area). Mar. Ecol., **22**: 357-367.

HACKER, S. D. & R. S. STENECK, 1990. Habitat architecture and the abundance and body-size-dependent habitat selection of a phytal amphipod. Ecology, **71**: 2269-2285.

HARRIS, L. G. & A. C. JONES, 2005. Temperature, herbivory and epibiont acquisition as factors controlling the distribution and ecological role of an invasive seaweed. Biol. Invasions, **7**: 913-924.

HARRIS, L. G. & A. C. MATHIESON, 2000. Patterns of range expansion, niche, shift, and predator acquisition in *Codium fragile* ssp. *tomentosoides* and *Membranipora menbranacea* in the Gulf of Maine. In: J. PEDERSON (ed.), Marine Bioinvasions: Proceeding of the First National Conference, Massachusetts Institute of Technology, Massachusetts: 46-56.

HAY, M. E. & W. FENICAL, 1988. Marine plant-herbivore interactions: the ecology of chemical defense. Annu. Rev. Ecol. Syst., **19**: 111-145.

McBane, C. D. & R. A. Croker, 1983. Animal-algal relationships of the amphipod *Hyale nilssoni* (Rathke) in the rocky intertidal. Journ. Crust. Biol., **3**: 592-601.

Prince, J. S. & W. G. LeBlanc, 1992. Comparative feeding preference of *Strongylocentrotus droebachiensis* (Echinoidea) for the invasive seaweed *Codium fragile* ssp. *tomentosoides* (Chlorophyceae) and four other seaweeds. Mar. Biol., Berlin, **113**: 159-163.

Provan, J., D. Booth, N. P. Todd, G. E. Beatty & C. A. Maggs, 2007. Tracking biological invasions in space and time: elucidating the invasive history of the green alga *Codium fragile* using old DNA. Diversity Distrib., **14**: 343-354.

Provan, J., S. Murphy & C. A. Maggs, 2005. Tracking the invasive history of the green alga *Codium fragile* ssp. *tomentosoides*. Mol. Ecol., **14**: 189-194.

Schmidt, A. L. & R. E. Scheibling, 2006. A comparison of epifauna and epiphytes on native kelps (*Laminaria* spp.) and the invasive green alga (*Codium fragile* ssp. *tomentosoides*) in Nova Scotia, Canada. Bot. mar., **49**: 315-330.

Silva, P. C., 1955. The dichotomous species of *Codium* in Britain. Journ. mar. biol. Ass. U.K., **34**: 565-577.

— —, 1957. *Codium* in Scandinavian waters. Svenska Bot. Tidskr., **51**: 117-134.

Trowbridge, C. D., 1995. Establishment of the green alga *Codium fragile* ssp. *tomentosoides* on New Zealand rocky shores: current distribution and invertebrate grazers. Journ. Ecol., **83**: 949-965.

Verbruggen, H., F. Leliaert, C. A. Maggs, S. Shimada, T. Schils, J. Provan, D. Booth, S. Murphy, O. De Clerck, D. S. Littler, M. M. Littler & E. Coppejans, 2007. Species boundaries and phylogenetic relationships within the green algal genus *Codium* (Bryopsidales) based on plastid DNA sequences. Mol. Phylogenet. Evol., **44**: 240-254.

Viejo, R. M. & J. Arrontes, 1992. Interactions between mesograzers inhabiting *Fucus vesiculosus* in northern Spain. Journ. exp. mar. Biol. Ecol., **162**: 97-111.

First received 21 February 2009.
Final version accepted 14 January 2010.