2006

An examination of morphological and biological traits of dominant marine plants that regulate patterns of mesograzer communities.

Yusheng M. Huang
University of Alabama at Birmingham

Recommended Citation

Huang, Yusheng M., "An examination of morphological and biological traits of dominant marine plants that regulate patterns of mesograzer communities." (2006). *All ETDs from UAB*. 5535.
https://digitalcommons.library.uab.edu/etd-collection/5535

AN EXAMINATION OF MORPHOLOGICAL AND BIOLOGICAL TRAITS OF DOMINANT MARINE PLANTS THAT REGULATE PATTERNS OF MESOGRAZER COMMUNITIES

by

YUSHENG M. HUANG

JAMES B. MCCLINTOCK, COMMITTEE CHAIR
CHARLES D. AMSLER
ROBERT W. THACKER
RICHARD B. ARONSON
JOHN F. VALENTINE

A DISSERTATION

Submitted to the graduate faculty of The University of Alabama at Birmingham,
In partial fulfillment of the requirements for the degree of
Doctor of Philosophy

BIRMINGHAM, ALABAMA

2006

ProQuest Information and Learning Company
300 North Zeeb Road
P.O. Box 1346
Ann Arbor, MI 48106-1346

AN EXAMINATION OF MORPHOLOGICAL AND BIOLOGICAL TRAITS OF DOMINANT MARINE PLANTS THAT REGULATE PATTERNS OF MESOGRAZER COMMUNITIES

YUSHENG M. HUANG

ABSTRACT

The distribution and abundance of mesograzers associated with marine plants including Antarctic macroalgae and tropical seagrasses were examined. The first chapter describes the distribution and abundance of gammarid amphipods associated with eight dominant subtidal macroalgae along the western Antarctic Peninsula. Higher abundances of amphipods occurred on the most morphologically complex macroalgae. Population densities of each amphipod species and amphipod species composition were similar within the same algal species but dissimilar on different algal species. Samples collected from different sites indicated that although the structure of species-specific macroalgal-associated amphipod communities can vary across spatial scales of 3 km, 50 % of the macroalgal species examined showed no significant inter-site differences in associated amphipod community structure.

The second chapter examines the feeding rates of three common Antarctic gammarid amphipods on ecologically important macroalgae. Feeding bioassays employing both fresh algal tissues and alginate food pellets containing homogenized algal tissues illustrated that the relative palatability of sympatric macroalgae varied in three species of common gammarid amphipods. One of the examined amphipods, *Metaleptamphopus pectinatus* failed to consume measurable quantities of fresh thalli and is likely to feed on epiphytes. Regression analysis indicated that feeding rates of the amphipods on alginate food pellets were not significantly correlated with macroalgal nutritional quality. Therefore, differences in amphipod macroalgal palatability are most likely related to other factors including physical and/or chemical deterrents.

The third chapter describes seasonal fluctuations of mesofaunal communities associated with two seagrass species and their associated epiphytes in Saint Joseph Bay, Florida. Samples collected over all 12 months revealed that *T. testudinum* seagrass blades harbored the highest levels of mesofaunal species richness and species diversity during the summer months. In contrast, aboveground blades of *Halodule wrightii* were only found in six months of the study and the highest levels of mesofaunal species richness and species diversity occurred in October. A positive correlation occurred between epiphyte biomass and abundances of blade-associated mesofauna in some of but not all months for both seagrass species. Blade-associated mesofaunal communities, (population densities and species composition) that occurred in association with blades of the two seagrasses were significantly different from one another.

ACKNOWLEDGEMENTS

I thank my mentor, Dr. James B. McClintock, and co-advisor, Dr. Charles D. Amsler, for their invaluable assistance and support during the course of my Ph.D. studies – especially for the opportunity to get involved in the Unite States Antarctic Program. I also thank Drs. Robert W. Thacker, Richard B. Aronson, and John F. Valentine for their valuable contributions and efforts as members of my dissertation committee. I would like to thank Drs. Ken Marion (Department Chairman) and Dr. Steve Watts (Program Director) for providing such a great environment for studying and training. I also want to thank Drs. Robert Angus and Kung-Ho Chen for great assistance on statistics. This research benefited greatly from field and lab assistance by Maggie Amsler, Dr. Victoria A. Fairhead, Kevin Peters, Stepheanie Weiss, and employees of Raytheon Polar Services. Special thanks to my SCUBA diving instructor, Yen Su, without him I would not have had the opportunity to explore the beauty of marine creatures. I wish to thank the numerous fellow students and lab coordinators with whom I have shared friendship. These include Patrick Erwin, Kevin Bevis, Meghana Gavand, Frank Camacho, Keela Dodd, Anne Marie LeBlanc, Philip Bucolo, Craig Aumack, Jonathan Huang, Mary Busbee, Leslie Hendon, and Raymond Odom. I thank all of my friends in Taiwan, Nick, Billy, Mike, Mark, Frank, Laura, and especially Yi-Ping, for their love and moral support.

I would not have been able to complete this work without the loving support of my families, my dad GeeKuo, my mom LiShu, and my younger sister Francine. Finally, I would like to thank my wife, HuiChien, for years of patience and sacrifice as I fulfilled a dream, and my daughter, Yun, for inspiring me to be a better scientist and human being. Funding for this research was provided by the Office of Polar Programs of the National Science Foundation to C.D.A, and J.B.M. (OPP-0125181) and B.J.B. (OPP-0125152), an Endowed University Professorship in Polar and Marine Biology to J.B.M., and the Department of Biology at the University of Alabama at Birmingham.

TABLE OF CONTENTS

Page

LIST OF TABLES

Table *Page*

PATTERNS OF GAMMARID AMPHIPOD SPECIES COMPOSITION AND ABUNDANCE ASSOCIATED WITH DOMINANT SUBTIDAL MACROALGAE ALONG THE WESTERN ANTARCTIC PENINSULA

FEEDING RATES OF COMMON ANTARCTIC GAMMARID AMPHIPODS ON ECOLOGICALLY IMPORTANT SYMPATRIC MACROALGAE

SEASONAL FLUCTUATIONS OF MESOFAUNAL COMMUNITIES ASSOCIATED WITH BLADES OF TWO COMMON SEAGRASS SPECIES AND THEIR EPIPHYTES IN THE NORTHERN GULF OF MEXICO

LIST OF FIGURES

Figure *Page*

PATTERNS OF GAMMARID AMPHIPOD SPECIES COMPOSITION AND ABUNDANCE ASSOCIATED WITH DOMINANT SUBTIDAL MACROALGAE ALONG THE WESTERN ANTARCTIC PENINSULA

LIST OF FIGURES (Continued)

Figure *Page*

FEEDING RATES OF COMMON ANTARCTIC GAMMARID AMPHIPODS ON ECOLOGICALLY IMPORTANT SYMPATRIC MACROALGAE

SEASONAL FLUCTUATIONS OF MESOFAUNAL COMMUNITIES ASSOCIATED WITH BLADES OF TWO COMMON SEAGRASS SPECIES AND THEIR EPIPHYTES IN THE NORTHERN GULF OF MEXICO

LIST OF FIGURES (Continued)

LIST OF ABBREVIATIONS

ANOSIM	analysis of similarity
ANOVA	analysis of variance
ANT	*Desmarestia antarctica*
CV	canopy volume
DAN	*Desmarestia anceps*
DME	*Desmarestia menziesii*
FL	Florida
FW	fresh weight
GIG	*Gigartina skottsbergii*
HSD	honestly significant difference
IRI	*Iridaea cordata*
IV	interstitial volume
MDS	non-metric multidimensional scaling
MYR	*Myriogramme mangini*
NB	number of branches
NC	North Carolina
PAL	*Palmaria decipiens*
PLO	*Plocamium cartilagineum*
PRIMER	Plymouth Routines In Multivariate Ecological Research

LIST OF ABBREVIATIONS (Continued)

PVC	polyvinyl chloride
SAS	statistical analysis system
SCUBA	self contained underwater breath apparatus
SD	standard deviation
SE	standard error
SPSS	statistical package for the social sciences
TV	thallus volume
USA	United States of America

INTRODUCTION

Mesograzers provide important linkages between trophic levels in terrestrial, aquatic and marine ecosystems (Schoenly et al. 1991, Brawley 1992, Crist 1998, Iken et al. 1998). In addition, mesograzers are often dominant primary consumers and key prey for a broad suite of generalist and specialist predators (Sparrevik & Leonardsson 1999). Therefore, both the distribution and the abundance of this important assemblage of grazers may be indicative of the condition and stability of ecosystems (Guerra-Garcia & Garcia-Gomez 2001). The ecology of terrestrial mesograzers, in particular the insects, has been the focus of a broad array of studies over an extensive period of years (Bernays & Woodhead 1982, Bernays 1986, 1989, Fahrig & Jonsen 1998). In contrast, studies of marine mesograzers and their relationships with their associated environments (e. g. hard and soft substrata, marine plants, etc.) has more recently attracted the attention of ecologists (Steinberg 1985, Hay et al. 1987, Hay et al. 1990, Bell 1991, Steinberg & Altena 1992, Duffy & Hay 1994, Van Alstyne et al. 1999, Cruz-Rivera & Hay 2000a, 2000b, 2001, Duffy et al. 2001, Van Alstyne et al. 2001).

Distributing across an extensive suite of marine environments, marine gastropods, amphipods, isopods, along with other smaller taxa of herbivores are commonly recognized as mesograzers. While some occur free living within the water column or are found in association with inanimate material such as rock or sand substrata, most are closely associated with living substrates including macroalgae (Hay & Fenical 1988, Hay 1997, Hay et al. 1998, Lippert et al. 2001), seagrasses and their associated epiphytes

(Nelson 1980, Nelson et al. 1982, Stoner 1983, Lewis 1984, Edgar 1992, Orth 1992, Jernakoff et al. 1996, Jernakoff & Nielsen 1997), bryozoans (Coleman 1989), and benthic macroinvertebrate sponges and ascidians (Thiel 2000). These diverse living substrates may provide mesograzers with a variety of distinctive resources including food, and refuge from predation and/or environmental stresses (Duffy & Hay 1991).

In previous studies, both biological and physical factors that regulate the distribution and abundance of mesograzers associated with marine plants, and especially seagrasses, have been broadly studied (Hay & Fenical 1988, Hughes & Gliddon 1991, John et al. 1992, Jernakoff et al. 1996). These studies have demonstrated that epiphytic structure and composition (Mukai & Iijima 1995, Pavia et al. 1999), plant chemical defenses (Stachowicz & Hay 1999), predation pressure (Wooster 1998, Sparrevik & Leonardsson 1999), complexity of the habitat (Lubchenco 1978, Parker et al. 2001), and hydrological conditions (Aikins & Kikuchi 2001, Duggins et al. 2001) can all, to varying degrees, influence aspects of patterns of distribution and abundance of mesograzers. While all of these studies have been conducted to date in temperate and tropical marine systems, it is likely that mesograzers in polar marine systems also associate with marine plants and that these interactions are important in understanding the dynamics of these communities.

Investigations of the ecology of near-shore of Antarctic benthic communities began in earnest in the 1960's and 1970's (Neushul 1965, Dayton et al. 1974, DeLaca & Lipps 1976, Moe & DeLaca 1976). Particular attention has been given to the shallow hard and soft bottom benthic invertebrate communities along the continent (Zaneveld 1966, Richardson 1977, Battershill 1990, Dayton 1990, Jażdżewski et al. 1991a, 1991b, Gambi et al. 1994, Blazewicz & Jaźdźewski 1996, Jaźdźewski & Konopacka 1999, Nonato et al. 2000, Jaźdźewski et al. 2001, Takeuchi & Watanabe 2002). Antarctic marine macrophytes, while often less abundant in continental waters, are extremely abundant along the Antarctic Peninsula and are commonly associated with a diverse assemblage of epibenthic organisms that encompass a wide range of trophic habits (Dhargalkar et al. 1988, Iken et al. 1998, Takeuchi & Watanabe 2002). For example, some epifaunal grazers may consume epiphytic colonizers in addition to host plants (Mukai & Iijima 1995, Karez et al. 2000). Both abundant in biomass (up to 1.64 – 6.34 wet kilograms per meter square (Amsler et al. 1995) and diversity (approximately 120-130 species; Wiencke & Clayton 2002), the macroalgae of the Antarctic Peninsula are known to provide a significant food resource for grazing sympatric molluscs, annelids, crustaceans, and fish (Iken et al. 1997, 1998). However, different algal species are apparently not consumed in equal frequency to their abundance as some species are frequently found in the gut contents of common herbivores whereas others are rarely ingested. Such observations have led to studies focusing on understanding whether chemical defenses mediate these patterns of grazing by sympatric Antarctic herbivores, including fish, gastropods and amphipods (Amsler et al. 1998, McClintock & Baker 1998, Amsler et al. 2001, McClintock & Baker 2001). While the role of Antarctic macroalgae in macrograzer (e. g. sea urchins, omnivorous fish) food webs has received some attention (Iken et al. 1997, Amsler et al. 1998, Iken et al. 1998), very little is known about the role of algal foods on mesograzers such as the particularly abundant amphipods. Moreover, there have been no studies of the effects of macroalgal diets on growth and survival of Antarctic mesograzers. Thus, further studies are needed to examine the role of macrophytes in providing food and structural refuge to common Antarctic mesograzers such as amphipods along with the effects of macrophytes as prey on the mesograzers themselves.

In striking contrast to our current understanding of the factors influencing the ecology of macroalgal Antarctic communities, the ecology of marine seagrass meadows and their associated fauna and epiphytes have been intensively studied (Nelson et al. 1982, Lewis & Stoner 1983, Lewis 1987, Edgar 1992, Orth 1992, Valentine & Heck 1993, Thom et al. 1995, Jernakoff et al. 1996, Bologna & Heck 1999, Boström & Mattila 1999, Leonard & McClintock 1999, Beddingfield & McClintock 2000, Duffy et al. 2001, Lee et al. 2001, Schanz et al. 2002). This is because of their ecological importance and relative accessibility (Hemminga & Duarte 2000). Seagrass meadows both directly and indirectly supply a wide range of resources for marine macro- and mesofauna including refuge for juvenile and adult life stages of invertebrates and fish (Schneider & Mann 1991a, 1991b), a rich source of prey (Buck et al. 2003), facilitation of locating mates, and abundant plant substrates for plant and animal recruitment (Kendrick & Hawkes 1988, Rooker et al. 1998, Bologna & Heck 2000). The subsequent effect of these factors is that the species diversity of epifaunal communities within seagrass is on average much higher than that in neighboring areas (Lewis 1984, Valentine & Heck 1993).

Both field manipulations (e.g. caging and tethering) and laboratory experiments (e.g. microcosm and mesocosm design) have all been used to demonstrate the mechanisms contributing to increase abundances of invertebrates and fish within seagrass beds. Although mesograzers are known to feed on diatoms and drift and coralline algae encrusting seagrass blades, seagrass can also be a direct food resource for abundant mesograzers such as isopods (Boström & Mattila 1999). Studies to date on chemically regulated seagrass-animal interactions have mainly focused on the role of seagrasses influencing the settlement of marine invertebrate larvae; however, seagrasses are also potential candidates to harbor chemical defenses against crustacean mesograzers (McMillan et al. 1980). Studies of seasonal variation of mesofaunal communities associated with seagrasses are required in order to further determine whether chemical (feeding deterrent), physical (morphology, toughness) or biological (nutrient composition, epibionts) characteristics of seagrasses are related to patterns of associated mesofauna.

In the broad picture, this dissertation investigates factors influencing the distribution and abundance of mesograzers associated with macroalgae of the polar Antarctic Peninsula and seagrasses of temperate/subtropical northern Gulf of Mexico, respectively. While all taxonomic groups of mesograzers are included in the descriptive analysis of both polar and temperate/subtropical plant communities, an emphasis is placed on gammarid amphipods in the experimental sections of the Antarctic research as they are among the most common mesograzers.

The first chapter describes the distribution and abundance of gammarid amphipods associated with eight dominant subtidal macroalgae along the western Antarctic Peninsula. The second chapter examines the feeding rates of three common Antarctic gammarid amphipods on ecologically important sympatric macroalgae. The third and final chapter describes the seasonal fluctuations of mesofaunal communities associated with two sympatric seagrass species and their associated epiphytes.

PATTERNS OF GAMMARID AMPHIPOD SPECIES COMPOSITION AND ABUNDANCE ASSOCIATED WITH DOMINANT SUBTIDAL MACROALGAE ALONG THE WESTERN ANTARCTIC PENINSULA

by

YUSHENG M. HUANG, MARGARET O. AMSLER, JAMES B. MCCLINTOCK,
CHARLES D. AMSLER, AND BILL J. BAKER

Submitted to Marine Ecology Progress Series

Format adapted for dissertation

ABSTRACT

The distribution and abundance of gammarid amphipods associated with eight ecologically dominant species of macroalgae were examined near Palmer Station, Anvers Island, on the western Antarctic Peninsula (64°46' S, 64°03' W). Divers collected ten individuals of each targeted macroalga, five each from two different subtidal sampling sites, enveloping each alga quickly in large mesh bags (mesh < 0.5 mm) to capture all associated epifauna. Samples were washed onto a sieve (0.5 mm) and all amphipods sorted to the lowest taxon possible. A suite of algal morphometrics was determined for each species including canopy, thallus, and interstitial volumes, as well as the order and number of branches. A total of 78,415 individuals belonging to 32 amphipod taxa were identified with mean abundances ranging up to 20 individuals g^{-1} algal wet wt. Regression analyses showed that higher abundances of amphipods occurred on the most structurally complex macroalgae including *Desmarestia menziesii*, *D. anceps*, and *Plocamium cartilagineum*. Non-metric multidimensional scaling (MDS) analysis demonstrated that the population densities of each amphipod species and amphipod species composition were similar on the same algal species but dissimilar on different species of algae. The most abundant amphipod taxa, *Metaleptamphopus pectinatus* and *Oradarea* spp., were found to associate predominately with the brown alga *D. menziesii*, while a third common taxon, *Jassa* spp. occurred primarily in association with the red alga *Plocamium cartilagineum*. Comparisons of amphipod communities associated with a given algal species but collected from a different sampling site indicated that although

the structure of species-specific macroalgal-associated amphipod communities can vary across spatial scales of 3 km, 50 % of the macroalgal species examined showed no significant inter-site differences in associated amphipod community structure. Compared to nearshore benthic macroalgal communities in temperate and Arctic habitats, antarctic gammarid amphipods dominate mesograzer communities. As many Antarctic amphipods are known consumers of macroalgae, their remarkable abundances are likely to play a significant role in mediating energy and nutrient transfer in nearshore Antarctic Peninsular macroalgal communities.

INTRODUCTION

Mesograzers provide key linkages within and across trophic levels in terrestrial and aquatic ecosystems (Schoenly et al. 1991, Brawley 1992, Crist 1998, Iken et al. 1998). Therefore patterns of abundance, distribution, and species composition of this functional suite of organisms may be indicative of both the condition and the stability of ecosystems (Guerra-Garcia & Garcia-Gomez 2001). Investigations of marine mesograzers and their relationships with associative habitats has increasingly attracted attention (Steinberg 1985, Hay et al. 1987, 1990, Bell 1991, Steinberg & Altena 1992, Duffy & Hay 1994, Van Alstyne et al. 1999, 2001, Cruz-Rivera & Hay 2000b, 2000a, 2001, Duffy et al. 2001).

Herbivorous representatives of the Crustacea (e.g., isopods and especially amphipods) and Mollusca (e.g., gastropods) along with a variety of additional minor taxa (referred to collectively as mesograzers) inhabit a wide suite of marine environments spanning intertidal to abyssal depths and tropical to polar latitudes (Russo 1990, Pennings et al. 1993, Iken et al. 1998, Wakefield & Murray 1998, Pavia et al. 1999, Jormalainen et al. 2001, Arroyo et al. 2004, Taylor & Steinberg 2005, Wessels et al. 2006). With diverse lifestyles, mesograzers encompass free-living planktonic and benthic organisms as well as those intimately associated with a variety of both living and inert substrates. Perhaps the largest proportion of mesograzers occur in association with other living organisms including seagrasses and their associated epiphytes (Nelson 1980a, Nelson et al. 1982, Stoner 1983, Lewis 1984, Edgar 1992, Orth 1992, Jernakoff et al. 1996, Jernakoff & Nielsen 1997, Lavery & Vanderklift 2002), macroalgae (Hay & Fenical 1988, Hay 1997, Hay et al. 1998, Lippert et al. 2001), and sessile macroinvertebrates including bryozoans (Coleman 1989), sponges (Poore et al. 2000, Thiel 2000) and ascidians (Thiel 2000). These living substrates likely provide mesograzers with a variety of prospective resources including food and/or structural or chemical refugia from predation or environmental stressors (Duffy & Hay 1991). Indicative of the extensive evolutionary history of these associative relationships, early life history stages of mesograzers are often adapted to remain in close association with their living “hosts” (Hay et al. 1990, Arrontes 1999, Sotka et al. 1999, Sotka 2005).

Both biological and physical factors are known to regulate the distribution and abundance of mesograzers associated with marine plants (Hay & Fenical 1988, Hughes & Gliddon 1991, John et al. 1992, Jernakoff et al. 1996). These factors include epiphytic architecture and community composition (Hacker & Steneck 1990, Mukai & Iijima 1995, Pavia et al. 1999), chemical defenses (Stachowicz & Hay 1999), predation (Wooster 1998, Sparrevik & Leonardsson 1999), structural complexity and toughness (Lubchenco 1978, Parker et al. 2001), nutritional factors (Cruz-Rivera & Hay 2000a), and hydrological parameters (Aikins & Kikuchi 2001, Duggins et al. 2001). While the vast majority of studies conducted to date have been in temperate and tropical marine systems, it is likely that mesograzers similarly associate with marine plants in polar marine environments and that these interactions are essential to understanding the dynamics of these communities (Richardson 1977, Iken et al. 1997, Lippert et al. 2001, Takeuchi & Watanabe 2002, Wessels et al. 2006).

Investigations of the ecology of nearshore antarctic benthic communities began in earnest in the late 1950's through the 1970's (Neushul 1965, Zaneveld 1966, Dayton et al. 1974, DeLaca & Lipps 1976, Moe & DeLaca 1976). While antarctic marine macrophytes are particularly depauperate in this region (e.g., only two species of fleshy red algae are found in McMurdo Sound), macroalgae are common along the Antarctic Peninsula where they often form dense undersea forests (Amsler et al. 1995). These macroalgal communities provide abundant food resources for a rich fauna of sympatric grazing gastropods, annelids, crustaceans, and fish (Iken et al. 1997, 1998). Such trophic relationships may be complex, and it is now evident that different antarctic macroalgal species are not necessarily consumed by grazers in proportion to their abundance (Huang et al. 2006). Such observations have facilitated recent studies examining whether chemical defenses mediate patterns of macroalgal grazing by a variety of sympatric meso- and macrograzer consumers, including amphipods, gastropods, sea urchins, sea stars, and fish (Iken et al. 1997, 1998, Amsler et al. 1998, 2005, Iken 1999, Fairhead et al. 2005).

While the role of antarctic macrograzers such as sea urchins and fish in mediating patterns of materials and energy flow in macroalgal food webs has received limited attention (Barrera-Oro & Casaux 1990, Iken et al. 1997, 1998, 1999, Amsler et al. 1998, 2005), surprisingly little is known about the prospective influence of mesograzers on the ecology of nearshore macrophytic communities in macroalgal rich regions such as the Antarctic Peninsula. To understand such relationships studies are first needed to determine the abundance and distribution patterns of the most common functional mesograzer groups such as the gammarid amphipods. If an abundant macroalgal-associated amphipod community exists, then understanding the degree to which macrophytes provide such mesograzers with structural or chemical refuge or direct or indirect sources of nutrients becomes important.

The main objectives of the present study were to determine the abundance and species composition patterns of gammarid amphipods associated with dominant species of macroalgae along the western Antarctic Peninsula. By sampling amphipods from the same macroalgal species but from two different collection sites we extended our analysis to allow for an evaluation of potential differences on a local spatial scale. In addition, for each of the algal species examined, we measured a suite of characters that define its three dimensional morphology and examined whether patterns of amphipod abundance and species composition are related to the provision of structural refuge for crustacean mesograzers. Finally, we discuss how additional characteristics not measured in the present study including macroalgal palatability (Huang et al. 2006), nutritional composition (Peters et al. 2005), and chemical defenses (Amsler et al. 2005, Fairhead et al. 2005) may play a role in mediating patterns of gammarid amphipod abundance and species composition in nearshore macroalgal communities of the Antarctic Peninsula.

MATERIALS AND METHODS

Study Site

Field collections of macroalgae and their associated epifauna were conducted in near-shore subtidal habitats near Palmer Station, Anvers Island, on the western Antarctic Peninsula (64°46'S, 64°04'W; Fig. 1). All samples were collected using SCUBA between February and April, 2003. Four different subtidal sampling sites were selected including a site on northeast Bonaparte Point (64°46.7' S, 64°04' W), a site on the northern portion of Eichorst Island (64°47.2' S, 64°03.2' W), and southern (64°48.1' S, 64°01.4' W, herein referred to as Hermit Wall) and southeastern (64°47.9' S, 64°00.4' W, herein referred to as Southeast Hermit Island) sites on Hermit Island (Fig. 1). Sea water temperatures and salinities in the vicinity of Palmer Station, Antarctica were approximately 0 ± 1°C and 28-32 ‰, respectively.

Field Survey and Sample Collection

A suite of dominant macroalgal species that occur along the western Antarctic Peninsula were targeted for this study. This suite included three common species of brown macroalgae (*Desmarestia menziesii* J Agardh, *Desmarestia anceps* Montagne, and *Desmarestia antarctica* Moe and Silva) and five common species of red macroalgae (*Gigartina skottsbergii* Setchell and Gardner, *Iridaea cordata* (Turner) Bory, *Myriogramme mangini* (Gain) Skottsberg, *Palmaria decipiens* (Reinsch) Ricker, and *Plocamium cartilagineum* (Linnaeus) P F Dixon) (DeLaca & Lipps 1976, Amsler et al. 1995). Using SCUBA, each algal sample was gently dislodged from the attached substrate and, quickly but carefully enclosed along with its associated epifauna, within a mesh collecting bag (mesh size < 0.5 mm). The collecting bags were made of fine soft fabric and the opening of each bag was framed with plastic-coated stainless wire. The mouth of the bag was supported by wire loops such that it was capable of remaining wide-open underwater for collecting purposes but could be readily twisted into a double loop for rapid closure. The overlapping wire loops were then fixed by three binder clips. Immediately following collection, algal samples were returned to the laboratory. Ten individuals of each macroalgal species were sampled to allow a quantitative analysis of all associated marine invertebrate fauna (epifaunal communities were comprised primarily of crustacean mesograzers). Individual samples of each of the macroalgal species were collected from two different locations (n = 5 samples from each location) in order to allow for a comparison of site-specific variations over a scale of 1-2 km. Collecting depths ranged 6 to 16 m.

Morphological Attributes of Macroalgae

Epifauna associated with the collected macroalgae was first removed (see the following for detail). Each macroalga was whirled by hand in a mesh bag to remove surface water and then weighed to determine fresh weight (FW). In addition, each alga was submerged in a large graduated cylinder in order to determine total thallus volume. Total abundances of epifaunal species were determined (see below) and expressed in terms of individuals per gram algal wet weight.

To facilitate measurements necessary to estimate the spatial components of algal architecture, each alga was submerged completely in a seawater tank to allow it to assume a normal vertically suspended configuration. The total spaces between fronds and branches were calculated for each of the ten individuals of each species and expressed in terms of volumetric displacement of water (ml). Measurements included: 1) canopy volume (CV), the product of the length, width and height (cm) of a plant (the holdfast is excluded), 2) thallus volume (TV), the volume occupied by an algal thallus, and 3) interstitial volume (IV), the volume of the spaces between fronds and as determined by subtracting the thallus volume from the canopy volume (Hacker & Steneck 1990).

For structural component determinations the following attributes were evaluated for ten individuals of each species: 1) degree of branching (DB), counted from the distal branch to the stem. The final branches were considered first order, and wherever two branches of the same order join, the order of the resultant branch was increased by one (Chemello & Milazzo 2002) and 2) number of branches (NB). The numbers of branches were estimated for three morphologically complex species (*Desmarestia menziesii*, *D. anceps,* and *Plocamium cartilagineum*) and for other algal species all branches were actually counted. To estimate the NB for the three largest brown algal species, each individual alga collected was cut evenly into three sections along the main axis. The branches of each section were trimmed off the main and secondary axes then counted. The total NB was the summation of the top (NB1), the middle (NB2), and the bottom (NB3) section. The shape and arrangement of interstitial spaces and branches was not measured.

The Distribution and Abundance of Gammarid Amphipods

Macroalgal-associated epifauna were separated from each alga by mixing and shaking each alga in a series of buckets (5-6) filled with seawater. Each alga was then examined further to confirm that all mobile fauna had been removed. The epifaunal invertebrates were passed through a sieve (mesh size = 0.5 mm), and fixed immediately in a solution of 5% formalin in seawater for later enumeration and identification. Gammarid amphipod samples were sorted using a dissecting microscope according to Thurston (1972, 1973). To analyze the structure of gammarid amphipod community assemblages the following variables were calculated: total abundance of individuals (N), total number of species (S), species richness (d), and Shannon-Wiener diversity (H') (Clarke & Warwick 2001).

Statistical Analyses

To investigate relationships between characteristics of algal morphology and the community composition of the associated gammarid amphipods, multivariate analyses (classification and ordination) were undertaken using PRIMER (Plymouth Marine Laboratory, Plymouth, UK; Clarke and Gorley, 2001). The descriptive algal morphometrics data matrices collected for each target macroalgal species were log (x+1) transformed to decrease the influence of outliers and then examined using Cluster Analysis (Romesburg 1984, McGarigal et al. 2000). Abundance and species composition data matrices of the amphipod species were log (x+1) transformed so that the succeeding hierarchical categorization and ordination were not determined only by the most dominant species (Clarke & Warwick 2001). The affinities among algal morphology and abundance and species composition of associated gammarid amphipods were based on the Bray–Curtis similarity index for the algal morphology data matrix and the standardized species abundance matrix. Analysis of similarity (ANOSIM) was employed to facilitate a statistical comparison of overall similarities of algal morphology and amphipod species compositions among different species of macroalgae. For further testing matched similarity matrices derived from algal morphology data and amphipod abundance and species composition data, a RELATE significance test was conducted (Clarke & Warwick 2001). In order to further demonstrate the results of the Bray-Curtis similarity, an MDS analysis (non-metric multidimensional scaling) was used based on the matrix of amphipod species composition and population densities. This technique has been found to be most robust in the analysis of community data (McCune & Grace 2002). To test the ordination, the stress coefficient of Kruskal was used (McCune & Grace 2002). Quantitative statistical comparisons of biodiversity indices and abundance of epifauna associated with all eight species of common brown and red macroalgae were conducted using a one-way ANOVA test following by Tukey's Honestly Significant Difference (HSD) tests using SAS statistical software (SAS Institute, Cary, North Carolina).

As each targeted macroalga was collected from two of the four separate field sites (five individuals from each of the two sites) we performed an analysis of similarity (ANOSIM) to evaluate whether significant differences occurred in amphipod community structure (analysis of similarity based on standardized amphipod density, species richness and species diversity) associated with each macroalga collected from different locations.

RESULTS

Morphological Traits of Macroalgae

The morphological attributes of eight ecologically important macroalgae selected for this study are presented in Table 1. According to the global test of the analysis of similarity (ANOSIM), all species are significantly ($R = 0.9$, $p < 0.05$) morphologically distinct. In terms of the morphological parameters measured, these eight macroalgal species can be categorized into two groups: branched and bladed macroalgae. The branched algal species, including *Desmarestia menziesii*, *D. anceps*, and *Plocamium cartilagineum* have higher numbers of branches per gram algal wet weight (260 ± 127.1, 191.6 ± 32.6, and 1364.6 ± 113.5 branches g^{-1} wet wt, respectively; $\bar{x} \pm 1$ SE). *D. antarctica* with ligulate branches has medium number of branches (4.5 ± 0.8 branches g^{-1} wet wt; $\bar{x} \pm 1$ SE). In addition, the high degree of branching in these four algal species contributes to an increase in complexity of alga morphology. In contrast, the bladed algal species, *Gigartina skottsbergii*, *Iridaea cordata*, *Myriogramme mangini*, and *Palmaria decipiens* have an obviously simpler morphology with both a low number of branches per gram algal wet weight and a low degree of branching. The dendrogram generated from the average values of morphological attributes demonstrated that the intraspecific morphology of each species is similar and did not vary between sampling sites (Fig 2). The morphology of *D. menziesii* and *D. anceps* were not significantly dissimilar (ANOSIM pair-wise test: $R = 0.066$, $p = 0.13$). In addition, there was a modest similarity in the morphology of *I. cordata* and *P. decipiens* (ANOSIM pair-wise test: $R = 0.233$, $p = 0.01$).

Abundance and Distribution of Amphipods

A total of 78,415 individuals representing 32 gammarid amphipod taxa were collected among the eight target macroalgal species (Table 2). The most numerically dominant amphipod species were *Metaleptamphopus pectinatus* (67%), *Oradarea* spp. (14%), *Jassa* spp. (8%), *Prostebbingia gracilis* (3%), *Gondogeneia antarctica* (2%), and *Probolisca ovata* (2%). Except for *P. gracilis* which was not found on either *Myriogramme mangini* or *Iridaea cordata*, each of remaining amphipod species were collected from at least 7 of the 8 macroalgal species. As it was not possible to identify all amphipods to the species level, four amphipod taxa were designated at either the generic or family level: *Jassa* spp., *Oradarea* spp., Lysianassidea, and Eophilantidae. These taxa were considered as independent units for ANOSIM analysis. Significant differences in amphipod abundances and species composition were determined across the algal species (ANOSIM global test: $R = 0.65$, $p < 0.01$). More than 80% of the total amphipods collected were found in association with *Desmarestia menziesii*. Additionally, more than 90 % of the total amphipods collected were associated with the brown algae in general. Thus, a relatively small percentage of the total amphipods (9.6%) were collected in association with red algal species.

To determine the similarity of the amphipod communities associated with the different macroalgae, a Bray-Curtis similarity dendrogram was employed. This test is based on amphipod species distributions and their relative population densities (number of amphipods g^{-1} wet weight algal tissue). Shown are data of amphipods associated with 10 replicates of each of the eight algal species (Fig 3). Amphipod communities collected from all *Desmarestia menziesii* replicates fell into a mono-group (similarity > 65%). In addition, amphipod communities sampled across eight of the ten *D. antarctica* replicates formed a group with similarity greater than 59%, while the other two slightly different replicates were in close proximity to the *D. antarctica* group. The distributional patterns of amphipod communities across the remaining algal species showed no clear patterns (see results of MDS analysis below). To compare the relationship of algal morphology and amphipod abundance and species composition, a RELATE significance test showed that there is no relation between the two similarity matrices derived from algal morphology data and the amphipod abundance and population density data ($\rho = 0.2$). This analysis indicated the patterns of the two dendrograms (Figs. 2, 3) were not significantly similar. Linear regression correlation analyses between parameters of algal morphology (CV, IV, TV, and NB) and total combined amphipod density yielded significant linear correlations; however, the correlation coefficients (r^2) were relatively low (Table 3).

The most abundant amphipod species, *M. pectinatus*, numerically dominated four different algal species: *Desmarestia menziesii* (81%), *D. antarctica* (74%), *Iridaea cordata* (34%), and *Plocamium cartilagineum* (27%) (Fig. 4A-H). Amphipods belonging to *Jassa* spp. were found in abundance in association with *Gigartina skottsbergii* (56%), *Myriogramme mangini* (46%), and *Desmarestia anceps* (40%). The second most abundant amphipod taxon, *Oradarea* spp., was found commonly among seven of the eight target macroalgae (range = 6 - 21%). No individuals of *Oradarea* spp. were collected from *I. cordata*. *Gondogeneia antarctica* was found most commonly associated (26%) with the red alga *Palmaria decipiens*.

The different patterns of amphipod species distributions and abundances among the eight algal species resulted in characteristic species composition patterns. Employing a non-metric multidimensional scaling (MDS) based on the species numbers and the standardized density of each amphipod species (number g^{-1} algal wet wt), we analyzed species composition patterns (Fig. 5). In most cases the differences of amphipod species composition associated with different algal species were highly significant (stress = 0.15; ANOSIM global test: $R = 0.64$, $p < 0.05$). However, amphipod species composition patterns associated with *Palmaria decipiens* and *Iridaea cordata* did not differ significantly (ANOSIM pair-wise test: $R = 0.03$, $p = 0.3$). The amphipod species compositions associated with *Desmarestia anceps* and *Gigartina skottsbergii* were slightly different (ANOSIM pair-wise test: $R = 0.12$, $p = 0.06$). When the results of the MDS analysis are analyzed in three dimensions, the amphipod species compositions (groups) associated with the algal species become more distinct (decreasing MDS stress values from 0.15 to 0.11) (Fig. 6A, B). In terms of amphipod density, *M. pectinatus* and *Oradarea* spp. were predominately found associated with the brown alga *D. menziesii* (Figure 7A,B), while *Jassa* spp. was found primarily in association with the red alga *P. cartilagineum* (Figure 7C).

Species Diversity and Total Density of Algal-associated Amphipod Communities

Both the numbers of species and diversity indices for each of the eight algal-associated amphipod communities differed significantly (ANOVA; $F_{7,72} = 15.6$ and 5.3, respectively, $p < 0.001$) from one another (Fig. 8A, B). Greatest numbers of amphipod species were detected in association with the algae *Desmarestia menziesii* (12.4 ± 3.9 species, $\bar{x} \pm 1$ SE), *D. anceps* (11.9 ± 3.4 species, $\bar{x} \pm 1$ SE), *Gigartina skottsbergii* (9.5 ± 4.2 species, $\bar{x} \pm 1$ SE), and *Plocamium cartilagineum* (7.6 ± 4.1 species, $\bar{x} \pm 1$ SE). In contrast, smaller numbers of amphipod species were found in association with *I. cordata* and *P. decipiens* (2.4 ± 1.3 species and 2.9 ± 1.8, respectively, $\bar{x} \pm 1$ SE) (Fig 8A).

Significantly higher species diversity indices were detected in association with the algae *D. anceps*, *P. cartilagineum*, and *G. skottsbergii* (ANOVA; $F_{7,72} = 5.3$, $P < 0.001$) (Fig. 8B). Although the numbers of amphipod species were highest in association with *D. menziesii*, the species diversity index was relatively low. Total amphipod densities (all amphipod species combined for each algal species) associated with each of the eight target macroalgae were significantly different from one another (ANOVA; $F_{7,72} = 48.7$, $p < 0.001$). Total amphipod density was greatest for *D. menziesii* (20.1 ± 3.8 amphipods g^{-1} g wet algal weight, $\bar{x} \pm 1$ SE) followed by *P. cartilagineum* (5.9 ± 1.1 amphipod g^{-1} algal wet wt, $\bar{x} \pm 1$ SE), and lowest for *I. cordata* (0.1 ± 0.03 amphipod g^{-1} algal wet wt, $\bar{x} \pm 1$ SE) (Fig.9).

Distributions of Amphipods among Different Sampling Sites

In order to determine whether amphipod abundance and composition patterns differ by collection site we examined algal samples from two different sites for each algal species ($n = 5$ replicates per site) (Table 4). The results of ANOSIM revealed that amphipod communities associated with *Desmarestia antarctica, Gigartina skottsbergii, Myriogramme mangini*, and *Iridaea cordata* collected from two sites that included Southeast Hermit Island, Eichorst Island, or Bonaparte Point were not significantly dissimilar ($p > 0.05$). The amphipod abundance and composition patterns associated with *D. menziesii* and *Palmaria decipiens* collected from Hermit Island and Bonaparte Point were dissimilar ($p < 0.05$). The amphipod communities associated with *D. anceps* and *Plocamium cartilagineum* collected from Hermit Wall and Bonaparte Point and Hermit Wall and Eichorst Island, respectively, were also dissimilar ($p < 0.05$).

DISCUSSION

Most studies investigating epifauna associated with antarctic hard bottom or macroalgal communities have employed either trawl or grab sampling techniques (Dhargalkar et al. 1988, Jaźdżewski et al. 1991a, 1991b, Gambi et al. 1994). As a consequence of these gross sampling techniques it is not possible to distinguish whether sampled individuals are associated with a specific living or inert substrate. Moreover, this sampling approach obscures microhabitat-specific quantitative or qualitative evaluations of the most mobile epifauna, as many likely escape such disruptive collection techniques. More recent studies in Antarctica have emphasized the analysis of algal-associated epifauna and in some cases have employed underwater sampling techniques (Iken et al. 1997, Takeuchi & Watanabe 2002). In the present study, scuba-based net collections facilitated effective capture and minimal loss of mesograzers associated with macroalgae.

Relationship between Algal Morphology and Patterns of Amphipod Abundance and Species Composition

The influence of algal morphology on the abundance of amphipod mesograzers has been investigated in two separate studies, each of which came to a different conclusion. Hacker and Steneck (1990) argue that the complexity of algal morphology (number of branches and the three dimensional space between fronds), is an important factor in determining patterns of amphipod demography on associated macroalgae. Amphipods inhabited in greater frequency highly branched algal species regardless of whether predators were present or absent. Significantly fewer numbers of amphipods were found on foliose or leathery algal species. Hacker and Steneck (1990) surmise that highly branched algal architecture provides amphipods greater interstitial space to exploit for habitat, while the smaller sizes of branches associated with highly branched forms facilitate the ability of amphipods to cling to individual branches. In contrast, Holmlund et al. (1990) found that the density of amphipods colonizing and surviving on the most structurally-complex algal species (*Hypnea musciformis* (Wulf.) Lamourous and *H. cornuta* (Lamour.) J. Agardh) were significantly lower than that found on less physically complex foliate or bladed algal species (*Padina gymnospora* and *Sargassum filipendula*) when in the presence of predatory pinfish. Holmlund et at. (1990) speculates that physically complex algal morphology (increased branching) selected against amphipods because amphipods were visually detected more often by omnivorous fish predators on branched rather than foliate or bladed algae. They offer the alternative hypothesis that lower amphipod abundances are due to pinfish visiting the structurally complex algae (*Hypnea* spp.) more frequently because it is one of their preferred algal foods.

The results of our study are similar to those of Hacker and Steneck (1990). Both amphipod abundance and total numbers of species were significantly higher on the most physically complex macroalgal species. The contrasting findings of our study and that of Holmlund et al. (1990) may be in part the result of how one defines the "morphological complexity of algae". Morphological traits of macroalgae vary from those that are relatively simple such as a single blade to those that are highly complex (e.g., highly branching kelps and rockweeds) (Bold & Wynne 1985). Measures of the complexity of algal morphology are typically linked to the numbers of branches as a function of algal tissue mass. However, this approach is not consistently applicable to different morphotypes of macroalgae. While Holmlund et al. (1990) reported that *Hypnea* spp. had greater numbers of branches, the degree of branching is low and the distance from distal branches to the main stipe is small. Consequently, the effective structural complexity that would facilitate mesograzer cover from predators is compromised. In contrast, in the present study *Desmarestia menziesii*, *D. anceps*, and *Plocamium cartilagineum* not only have higher numbers of branches per unit mass but also have branches with a higher degree of branching. This is particularly evident in both *Desmarestia* species, where the length of the secondary branches and the distance from distal branches to the main stem is great and provides significant interstitial cover from prospective fish predators. Another difference between the study of Holmlund et al. (1990) and the present work is that the morphologically more complex species in our study are highly unpalatable to omnivorous fish (Amsler et al. 2005).

Although the correlation coefficients were not high ($r^2 = 0.09 - 0.29$), linear correlation between increasing amphipod abundances (standardized by wet mass of macroalgae) and increasing numbers of branches, canopy volume, thallus volume, and interstitial volume were significant ($p < 0.01$). Amphipods collected from the target macroalgae seemed to prefer to inhabit branched algae rather than algal species characterized by blade morphology.

Patterns of Amphipod Species Composition and Abundance Associated with Macroalgae

The most abundant amphipod, *Metaleptamphopus pectinatus*, occurred on all eight macroalgal species examined but was primarily found on *Desmarestia menziesii* where it comprised 94% of total algal-mass standardized amphipod abundance.

Moreover, even when small numbers of amphipods occurred in association with a given targeted macroalga, *M. pectinatus* still comprised the greatest fraction. The tight association between *D. menziesii* and *M. pectinatus* would suggest that this alga serves loosely as a host species. Thurston (1972) similarly observed that *M. pectinatus* occurred primarily in association with *Desmarestia* spp., where it likely inhabited tufts of epiphytes on holdfasts. In laboratory feeding bioassays we found that *M. pectinatus* does not consume measurable amounts of any of the macroalgae with which they associated in the field including *D. menziesii* (Huang et al. 2006). A recent study has found that *D. menziesii* is chemically defended against grazing by the sympatric amphipod *Gondogeneia antarctica* (Amsler et al. 2005). This alga may similarly be chemically defended against *M. pectinatus,* although previous studies have shown that macroalgal chemical defenses are species-specific in terms of amphipod grazing patterns (Duffy & Hay 1994, Sotka & Hay 2002).

Microscopic examination of the guts of several *M pectinatus* revealed fragments of diatom frustules (authors' pers. obs.) suggesting that in the absence of macroalgal grazing, epiphytic diatoms may be an important component of the diet. The lack of this dominant amphipod grazing on its primary host, *D. menziesii* is paradoxical. Two factors could explain this association. First, *D. menziesii* has a comparatively complex morphology that includes a high degree of branching that may provide amphipods a physical refuge from predation. Second, Amsler et al. (2005) recently found that *D. menziesii* is chemically defended against the common sympatric omnivorous fish *Notothenia coriiceps*, a species known to include amphipods in its diet (Iken et al. 1997) and by far the most common fish in the study area (authors' pers. obs.). Thus, as has been demonstrated for amphipods associated with macroalgae in tropical and temperate latitudes (Duffy & Hay 1994, Hay 1996, 1997), *M. pectinatus* may be exploiting chemically defended macroalgae to avoid fish predation.

The second most abundant amphipod taxon, *Oradarea* spp. (likely a combination of 4-5 individual species), was collected from all the macroalgal species examined except for the red alga *Iridaea cordata*. The majority of individuals, 74 % of the total algal-mass standardized amphipod abundance, were found in association with *Desmarestia* spp. (*D. menziesii* – 60%; *D. anceps* – 14%). Gammarid amphipods of the genus *Oradarea* are characterized by having slender, elongated legs with hooked distal tips (Thurston 1972). These adaptations may facilitate clinging behaviors on the fine, highly branched, terete (cylindrical) branches that characterize *Desmarestia anceps* and *D. menziesii*, especially the latter (Wiencke & Clayton 2002). Previous gut content analyses suggest that diet may be important in this association as Graeve et al. (2001) found small pieces of *Desmarestia* spp. in gut contents of the herbivorous *Oradarea edentate*.

Smaller numbers of individuals of the gammarid *Jassa* spp. occurred on all eight species of macroalgae. Individuals were particularly abundant on *Plocamium cartilaginieum* (45% of total algal-mass standardized amphipod abundance) but were also found in equal, but lower abundances on *Gigartina skottsbergi* (19%) and *Desmarestia anceps* (20%) While *Jassa* spp. do not appear to have a primary host alga such as seen for *M. pectinatus*, its comparatively common association with *P. cartilagineum* could be related to the highly branched morphology of this alga (most highly branched on all eight algal species examined) that may provide a physical refuge from predation.

While the gammarid *Paradexamine fissicauda* occurred in very low abundance overall, more than 83 % of the total 246 individuals collected occurred exclusively on *Plocamium cartilagineum*, a clumpy red alga characterized by unilateral branches. One potential explanation for this close association is that *P. fissicauda* possesses several characteristics that may facilitate its crypticity against visual predators. These include a reddish pigmentation similar to the coloration of *P. cartilagineum*. In addition, the highly spinate pleomeres mimic the morphology of the fine, unilateral branches. This cryptic nature became evident during collections as individuals were difficult to locate amongst the branches of *P. cartilagineum* (Huang, pers.obs.). Similar to *Metaleptamphopus pectinatus* associating with its chemically defended host alga, *Desmarestia menziesii*, *P. cartilagineum* is chemically defended against a sympatric omnivorous fish (Amsler et al. 2005) and thus may provide *P. fissicauda* a chemical refuge from predation (Duffy & Hay 1994, Hay 1996, 1997). To date it is unknown whether *P. fissicauda* grazes on the tissues of its host alga, *P. cartilagineum*. We were unable to collect sufficient numbers of amphipods to provide adequate replication for feeding bioassays.

In a previous study (Huang et al. 2006) we found that the antarctic gammarid amphipods *Gondogeneia antarctica* and *Prostebbingia gracilis* generally did not consume macroalgae with which they primarily associate (present study), but did consume other species of sympatric macroalgae. This suggests that structural complexity or algal chemical defenses are more important than dietary preferences in determining patterns of amphipods associated with macroalgae. Total numbers of amphipod species associated with *Desmarestia menziesii* and *D. anceps* were the highest recorded for any of the eight macroalgal species examined (mean was approximately 12 amphipod species for each macroalga). As discussed earlier, these two macroalgal species are large, have high numbers of branches per unit wet mass as well as a high degree of branching that renders them complex in their morphology. These traits collectively contribute to a comparatively large volume of interstitial space that likely provides attractive microhabitat for a broad suite of amphipod species. This, coupled with the numerous fine, terete branches provide amphipods a suitable substrate for efficient clinging (Hacker & Steneck 1990), and the chemical feeding deterrent properties of *Desmarestia* spp. against omnivorous fish (Amsler et al. 2005) could contribute to making these macroalgae particularly attractive habitat.

Total numbers of amphipod species were moderately high in the highly branched *P. cartilagineum* and the single-bladed alga *Gigartina skottsbergii*. Although *G. skottsbergii* is not a morphologically complex branched algal species (Wiencke & Clayton 2002) and lacks chemical defenses against omnivorous fish (Amsler et al. 2005), its suitability for associated amphipods is unique when compared with other single bladed macroalgae we examined. Specifically, as a result of its multiple holdfasts, the large flattened blades rest against the benthic substrate, in contrast to remaining upright in the water column as seen in other single-bladed macroalgae, with the resultant space between the substrate and ventral blade surface forming a protective retreat for amphipods. In addition, numerous papillae on the surface of *G. skottsbergii* might provide suitable substrate for amphipod clinging. The lowest numbers of amphipod species were associated with the single-bladed macroalgae *Palmaria decipiens* and *Iridaea cordata,* each harboring only 2 species.

Patterns of species diversity indices for amphipods associated with the eight macroalgae were similar to those seen for amphipod species numbers. The one exception was the species diversity index for amphipods associated with *Desmarestia menziesii.* Here, in striking contrast to its high species number, species diversity was the lowest recorded for any of the targeted macroalgae. This discrepancy is the result of the disproportionate numerical dominance of the amphipod *Metaleptamphopus pectinatus* that comprised 81% of those amphipods found in association with this macroalga.

Site-specific Patterns of Amphipod Abundance and Species Composition

In an effort to evaluate the potential for spatial variability in community structure of macroalgal-associated amphipods, targeted macroalgae and their associated gammarid amphipods communities were collected from four different locations, each 1-2 km from one another and all within a 3 km radius of Palmer Station. While all eight species of macroalgae were not present at each of the four sampling sites, for each alga it was possible to compare its associated amphipod community with one alternate site. In general, macroalgal-associated amphipod communities were relatively similar at the Southeast Hermit Island, Eichorst Island and Bonaparte Point sites. Analysis of similarity (ANOSIM) revealed that 50% of the algae (*Desmarestia antarctica, Gigartina skottsbergii, Iridaea cordata, Myriogramme mangini*) had associated amphipod communities that were not statistically dissimilar in terms of species abundance and composition when compared with a second collecting site. The dissimilarity values for amphipod communities associated with *Palmaria decipiens* from two collecting sites are likely related to the small sample sizes of amphipods that we found in association with this alga.

Amphipod communities associated with *D. anceps* and *Plocamium cartilagineum* were dissimilar across sites (Hermit Wall and Bonaparte Point and Hermit Wall and Eichorst Island, respectively), with lower numbers of amphipods consistently found at the Hermit Wall site. It is possible that these observed dissimilarities are the result of different hydrological conditions that could be expected at Hermit Wall, a site that is exposed to high wave energy and tidal currents (Huang pers. obs.). While we have no direct evidence, it is possible that the ability of gammarid amphipods to cling to these respective macroalgae is compromised by increased water turbulence. Finally, we also found that amphipod communities associated with *D. menziesii* were dissimilar at its two collecting sites (Hermit Island and Bonaparte Point). Here it appears that there were large differences in the relative abundances of amphipods at each of these sites, with higher abundances occurring consistently at Southeast Hermit Island. Macroalgal-associated amphipod species diversity values were not dissimilar between either site.

In summary, our findings indicate that while the structure of species- specific macroalgal-associated amphipod communities can vary across spatial scales of only 3 km (seen in 4 of 8 macroalgae examined) such differences appear to be species-specific among macroalgae. Thus for select macroalgal species, extrapolating the community dynamics of their associated amphipods from one region to another, even across spatial scales as small as 3 km, is inappropriate. For those 50% of the macroalgal species that had no between-site dissimilarities in their associated amphipod communities, we would argue that macroalgal-specific factors are likely to be mediating the dynamics of their associated amphipod communities.

Comparisons to Other Regions

While patterns of amphipod communities associated with shallow-water macroalgae may vary across tropical, temperate and polar latitudes (Russo 1990, Taylor & Cole 1994, Lippert et al. 2001, present study), one must take caution in generalizing such patterns due to differences in processing methodologies (e.g., minimum mesh sizes employed) and differences in sampling and sensitivity to differences across even small spatial scales (e.g., we detected differences in macroalgal-specific amphipod communities on spatial scales of even 3 km). Nonetheless, comparisons of existing estimates of total species numbers of macroalgal-associated amphipods and their relative abundances (amphipods per unit algae) may provide useful information. While total numbers of amphipod species associated with tropical macroalgae (26 and 35 amphipod species; Lewis 1987 and Russo 1990, respectively) are similar to those determined in the present study (32 species or taxa), higher species diversity and species richness indices characterize tropical amphipod communities because of lower amphipod abundances. In temperate latitudes, total numbers of macroalgal-associated amphipod species range from 6-29 taxa (Taylor & Cole 1994, Pavia et al. 1999, Viejo 1999, Parker et al. 2001, Arroyo et al. 2004), somewhat lower than amphipod species abundances we detected in Antarctica. It is also noteworthy that in these studies total abundances of macroalgal-associated amphipods measured in temperate waters were 13-40 fold lower that those we detected in Antarctic waters.

In the present study, total abundances of amphipods are very high, particularly on finely branched species such as *Desmarestia menziesii* (20 amphipods/g algal wet wt), *D. anceps* (3 amphipods/g algal wet wt), and *Plocamium cartilagineum* (6 amphipods/g wet wt). *D. menziesii* and *D. anceps* are two of the three dominant macroalgae (the third, *Himantothallus grandifolius* was too large to be sampled quantitatively in the field), while *P. cartilagineum* is one of the more abundant red macroalgae at moderate depths (Amsler et al. 1995), and can sometimes form moderate sized patches with nearly 100% cover. For comparison with reports of total amphipod densities from other regions we have combined our mean amphipod density values with the algal biomass data collected by Amsler et al. (1995) who noted therein that their methods for algal biomass quantification favored small species and probably underestimated the biomass of larger, overstory macroalgae like *Desmarestia* spp. Although such densities should be treated only as approximations, the calculated amphipod densities are 308,000, 48,000, and 26,000 individuals m^{-2} for stands of *D. menziesii, D. anceps,* and *P. cartilagineum*, respectively. Although comparable to other reports from Antarctica (Richardson 1977, Jaźdżewski et al. 1991a, 1991b, 2001), these densities are higher, usually by 2 or 3 orders of magnitude, than most amphipod densities in temperate and tropical waters (reports from 30 locations reviewed by Nelson 1980b, Wildish 1988, Brawley 1992). Densities of amphipods associated with *D. menziesii* are above the maximum densities noted in all but one of these reports.

It is important to note that amphipod collections in the present study were completed during daylight hours. Amphipod densities on macroalgae are often observed to increase during periods of darkness (reviewed by Brawley 1992) so our total densities, although very high, may actually underestimate night time densities. It is also of note that there was a strong inverse correlation between patterns of amphipod abundance and feeding preferences, for *D. menziesii, D. anceps,* and *P. cartilagineum* were less preferred by amphipods in ground tissue feeding bioassays and also strongly deterrent as extracts (Amsler et al. 2005, Huang et al. 2006). Preferred amphipod food species including *Palmaria decipiens* and *Iridaea cordata* had very low abundances of associated amphipods (0.2 and 0.1 amphipods g^{-1} algal wet wt, respectively). *P. decipiens* and *I. cordata* are both preferred food items of the omnivorous antarctic fish, *Notothenia coriiceps* (Iken et al. 1997, 1999) so this pattern could well be the result of daylight predator avoidance behavior (cf. Brawley 1992). It seems likely that amphipod densities on palatable macroalgae like *P. decipiens* and *I. cordata* would be greater at night as has been observed for amphipods associated with the palatable alga *I. laminarioides* in Chile (Buschmann 1990).

In the Arctic, Lippert et al. (2001) found total numbers of amphipod species associated with shallow-water macroalgae to be approximately half of the numbers of species we detected in association with Antarctic macroalgae. Moreover, amphipods comprised only 4-8 % of the total epiphytic suite of Arctic fauna sampled. In another recent Arctic study conducted in shallow-water communities near Kongsfjorden, Spitsbergen, very few meso- or macro-grazers were found in association with macroalgae (Wessels et al. 2006). Moreover, levels of herbivory were very low, with only one species of amphipod found to graze on macroalgae, and the urchin *Strongylocentrotus droebachiensis* exerting only periodic and localized top-down control in this Arctic macroalgal community. Wessels et al. (2006) suggest that such low levels of herbivory lend support to latitudinal hypotheses predicting a reduction in selection for strong macroalgal defense mechanisms. In support of this hypothesis, chemical defenses appear to be rare in Arctic macroalgae examined to date (Wessels et al. 2006). This scenario contrasts markedly with the western Antarctic Peninsula where we have identified both speciose and numerically rich mesograzer crustacean communities associated with ecologically dominant macroalgae, many of which are known to possess chemical defenses (Amsler et al. 2005).

Many Antarctic mesograzer crustaceans are herbivores or omnivores that include macroalgae or their associated epiphytes in their diets (Huang et al. 2006 and refs within). While at least one omnivorous Antarctic fish (*Notothenia coriiceps*) selectively grazes on macroalgae (Iken et al. 1997), to date there appears to be little evidence that macrograzers such as urchins exert a direct impact on Antarctic Peninsular macroalgae. Although detrital food chains are important mechanisms of nutrient and energy transport within Antarctic benthic macroalgal communities (Iken et al. 1998, Dauby et al. 2001, Graeve et al. 2001), the dominance of crustacean mesograzers is likely to play a significant role in mediating energy and nutrient transfer in nearshore macroalgal communities.

ACKNOWLEDGEMENTS

We thank Anne Fairhead and Kevin Peters for assistance in the field. Assistance with amphipod taxonomy from Kathy Conlan and Ed Hendrycks is much appreciated. We thank Huichien Kuo for assistance with graphics and SAS programming. We wish to also thank those individuals employed by Raytheon Polar Services for providing valuable logistical support in Antarctica. This research was facilitated by the generous support of the Office of Polar Programs of the National Science Foundation to C. D. A. and J. B. M. (OPP-0125181) and to B. J. B. (OPP-0125152). Support from an Endowed University Professorship in Polar and Marine Biology to J. B. M. is also acknowledged.

REFERENCES

Aikins S, Kikuchi E (2001) Water current velocity as an environmental factor regulating the distribution of amphipod species in Gamo Lagoon, Japan. Limnology 2:185-191

Amsler CD, Iken K, McClintock JB, Amsler MO, Peters KJ, Hubbard JM, Furrow FB, Baker BJ (2005) Comprehensive evaluation of the palatability and chemical defenses of subtidal macroalgae from the Antarctic Peninsula. Mar Ecol Prog Ser 294:141-159

Amsler CD, McClintock JB, Baker BJ (1998) Chemical defense against herbivory in the Antarctic marine macroalgae *Iridaea cordata* and *Phyllophora antarctica* (Rhodophyceae). J Phycol 34:53-59

Amsler CD, Rowley RJ, Laur DR, Quetin LB, Ross RM (1995) Vertical distribution of Antarctic peninsular macroalgae: cover, biomass and species composition. Phycologia 34:424-430

Arrontes J (1999) On the evolution of interactions between marine mesoherbivores and algae. Bot Mar 42:137-155

Arroyo NL, Maldonado M, Perez-Portela R, Benito J (2004) Distribution patterns of meiofauna associated with a sublittoral Laminaria bed in the Cantabrian Sea (north-eastern Atlantic). Mar Biol 144:231-242

Barrera-Oro ER, Casaux RJ (1990) Feeding selectivity in *Notothenia neglecta*, Nybelin, from Potter Cove, South Shetland Islands, Antarctica. Antarctic Sci 2:207-213

Bell SD (1991) Amphipods as insect equivalents? An alternative view. Ecology 72:350-354

Bold HC, Wynne MJ (1985) Introduction to the Algae: Structure and Reproduction, Vol. Prentice-Hall, Inc., Englewood Cliffs, New Jersey

Brawley SH (1992) Mesoherbivores. In: John DM, Hawkins SJ, Price JH (eds) Plant-Animal Interactions in the Marine Benthos, Systematics Association Special Volume No 46. Clarendon Press, Oxford, p 235-263

Buschmann AH (1990) Intertidal macroalgae as refuge and food for amphipods in central Chile. Aquat Bot 36:237-245

Chemello R, Milazzo M (2002) Effect of algal architecture on associated fauna: some evidence from phytal molluscs. Mar Biol 140:981-990

Clarke KR, Warwick RM (2001) Change in marine communities: An Approach to Statistical Analysis and Interpretation, Vol. PRIMER-E, Plymouth, UK

Coleman CO (1989) *Gnathiphimedia mandibularis* K. H. Barnard 1930, an Antarctic amphipod (Acanthonotozomatidae, Crustacea) feeding on Bryozoa. Antarctic Sci 1:343-344

Crist TO (1998) The spatial distribution of termites in shortgrass steppe: a geostatistical approach. Oecologia 114:410-416

Cruz-Rivera E, Hay ME (2000a) Can quantity replace quality? Food choice, compensatory feeding, and fitness of marine mesograzers. Ecology 81:201-219

Cruz-Rivera E, Hay ME (2000b) The effects of diet mixing on consumer fitness: macroalgae, epiphytes, and animal matter as food for marine amphipods. Oecologia 123:252-264

Cruz-Rivera E, Hay ME (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

Dauby P, Scailteur Y, Chapelle G, De Broyer C (2001) Potential impact of the main benthic amphipods on the eastern Weddell Sea Shelf ecosystem (Antarctica). Polar Biol 24:657-662

Dayton PK, Robilliard GA, Paine RT, Dayton LB (1974) Biological accommodation in the benthic community at McMurdo Sound, Antarctica. Ecol Monogr 44:105-128

DeLaca TE, Lipps JH (1976) Shallow-water marine associations, Antarctic Peninsula. Antarct J US 11:12-20

Dhargalkar VK, Burton HR, Kirkwood JM (1988) Animal associations with the dominant species of shallow water macrophytes along the coastline of the Vestfold Hills, Antarctica. Hydrobiologia 165:141-150

Duffy JE, Hay ME (1991) Food and shelter as determinants of food choice by an herbivorous marine amphipod. Ecology 72:1286-1298

Duffy JE, Hay ME (1994) Herbivore resistance to seaweed chemical defense: the roles of mobility and predation risk. Ecology 75:1304-1319

Duffy JE, Macdonald KS, Rhode JM, Parker JD (2001) Grazer diversity, functional redundancy and productivity in seagrass beds: an experimental test. Ecology 82:2417-2434

Duggins D, Eckman JE, Siddon CE, Klinger T (2001) Interactive roles of mesograzers and current flow in survival of kelps. Mar Ecol Prog Ser 223:143-155

Edgar GJ (1992) Patterns of colonization of mobile epifauna in a Western Australian seagrass bed. J Exp Mar Biol Ecol 157:225-246

Fairhead VA, Amsler CD, McClintock JB, Baker BJ (2005) Within-thallus variation in chemical and physical defences in two species of ecologically dominant brown macroalgae from the Antarctic Peninsula. J Exp Mar Biol Ecol 322:1-12

Gambi MC, Lorenti M, Russo GF, Scipione MB (1994) Benthic associations of the shallow hard bottoms off Terra Nova Bay, Ross Sea: zonation, biomass and population structure. Antarctic Sci 6:449-462

Graeve M, Dauby P, Scailteur Y (2001) Combined lipid, fatty acid and digestive tract content analyses: a penetrating approach to estimate feeding modes of Antarctic amphipods. Polar Biol 24:853-862

Guerra-Garcia JM, Garcia-Gomez JC (2001) The spatial distribution of Caprellidea (Crustacea: Amphipod): A stress bioindicator in Ceuta (North Africa, Gibraltar Area). Mar Ecol 22:357-367

Hacker SD, Steneck RS (1990) Habitat architecture and the abundance and body-size-dependent habitat selection of a phytal amphipod. Ecology 71:2269-2285

Hay ME (1996) Marine chemical ecology: what's known and what's next? J Exp Mar Biol Ecol 200:103-134

Hay ME (1997) The ecology and evolution of seaweed-herbivore interactions on coral reefs. Coral Reefs 16:S67-S76

Hay ME, Duffy JE, Fenical W (1990) Host-plant specialization decreases predation on a marine amphipod: an herbivore in plant's clothing. Ecology 71:733-743

Hay ME, Duffy JE, Pfister CA (1987) Chemical defense against different marine herbivores: are amphipods insect equivalents? Ecology 68:1567-1580

Hay ME, Fenical W (1988) Marine plant-herbivore interactions: the ecology of chemical defense. Ann Rev Ecol Syst 19:111-145

Hay ME, Piel J, Boland W, Schnitzler I (1998) Seaweed sex pheromones and their degradation products frequently suppress amphipod feeding but rarely suppress sea urchin feeding. Chemoecology 8:91-98

Holmlund MB, Peterson CH, Hay ME (1990) Does algal morphology affect amphipod susceptibility to fish predation? J Exp Mar Biol Ecol 139:65-83

Huang YM, McClintock JB, Amsler CD, Peters KJ (2006) Feeding rates of common Antarctic gammarid amphipods on ecologically important sympatric macroalgae. J Exp Mar Biol Ecol 329:55-65

Hughes RN, Gliddon CJ (1991) Marine plants and their herbivores: coevolutionary myth and precarious mutualisms. Phil Trans E Soc Lond 333:231-239

Iken K (1999) Feeding ecology of the Antarctic herbivorous gastropod *Laevilacunaria antarctica* Martens. J Exp Mar Biol Ecol 236:133-148

Iken K, Barrera-Oro ER, Quartino M-L, Casaux RJ, Brey T (1997) Grazing by the Antarctic fish *Notothenia coriiceps*: evidence for selective feeding on macroalgae. Antarctic Sci 9:386-391

Iken K, Quartino M-L, Barrera-Oro E, Palermo J, Wiencke C, Brey T (1998) Trophic relations between macroalgae and herbivores. Rpt Polar Res 299:258-262

Iken K, Quartino M-L, Wiencke C (1999) Histological identification of macroalgae from stomach contents of the Antarctic fish *Notothenia coriiceps* using semi-thin sections. Mar Ecol 20:11-17

Jażdżewski K, De Broyer C, Pudlarz M, Zielinski D (2001) Seasonal fluctuations of vagile benthos in the uppermost sublittoral of a maritime Antarctic fjord. Polar Biol 24:910-917

Jażdżewski K, De Broyer C, Teodorczyk W, Konopacka A (1991a) Survey and distributional patterns of the amphipod fauna of Admiralty Bay, King George Island, South Shetland Islands. Polish Polar Res 12:461-472

Jażdżewski K, Teodorczyk W, Sicinski J, Kontek B (1991b) Amphipod crustaceans as an important component of zoobenthos of the shallow Antarctic sublittoral. Hydrobiologia 223:105-117

Jernakoff P, Brearley A, Nielsen J (1996) Factors affecting grazer-epiphyte interactions in temperate seagrass meadows. Oceanogr Mar Biol Ann Rev 34:109-162

Jernakoff P, Nielsen J (1997) The relative importance of amphipod and gastropod grazers in *Posidonia sinuosa* meadows. Aquat Bot 56:183-202

John DM, Hawkins SJ, Price JH (1992) Plant-Animal Interactions in the Marine Benthos, Vol. Oxford University Press, New York

Jormalainen V, Honkanen T, Heikkilä N (2001) Feeding preferences and performance of a marine isopod on seaweed hosts: cost of habitat specialization. Mar Ecol Prog Ser 220:219-230

Lavery PS, Vanderklift MA (2002) A comparision of spatial and temporal patterns in epiphytic macroalgal assemblages of the seagrasses *Amphibolis griffithii* and *Posidonia coriacea*. Mar Ecol Prog Ser 236:99-112

Lewis FG (1984) Distribution of macrobenthic crustaceans associated with *Thalassia*, *Halodule* and bare sand substrata. Mar Ecol Prog Ser 19:101-113

Lewis FG (1987) Crustacean epifauna of seagrass and macroalgae in Apalachee Bay, Florida, USA. Mar Biol 94:219-229

Lippert H, Iken K, Rachor E, Wiencke C (2001) Macrofauna associated with macroalgae in the Kongsfjord (Spitsbergen). Polar Biol 24:512-522

Lubchenco J (1978) Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. Am Nat 112:23-39

McCune B, Grace JB (2002) Analysis of Ecological Communities, Vol. MjM Software Design, Gleneden Beach, Oregon, USA

McGarigal K, Cushman S, Stafford S (2000) Multivariate Statistics for Wildlife and Ecology Research, Vol. Springer-Verlag New York, Inc., New York

Moe RL, DeLaca TE (1976) Occurrence of macroscopic algae along the Antarctic Peninsula. Antarct J US 11:20-24

Mukai H, Iijima A (1995) Grazing effects of a gammaridean Amphipoda, *Ampithoe sp.*, on the seagrass, *Syringodium isoetifolium*, and epiphytes in a tropical seagrass bed of Fiji. Ecol Res 10:243-257

Nelson WG (1980a) The biology of eelgrass (*Zostera marina* L.) amphipods. Crustaceana 39:59-89

Nelson WG (1980b) A comparative study of amphipods in seagrasses from Florida to Nova Scotia. Bull Mar Sci 30:80-89

Nelson WG, Cairns KD, Virnstein RW (1982) Seasonality and spatial patterns of seagrass-associated amphipods of the Indian River Lagoon, Florida. Bull Mar Sci 32:121-129

Neushul M (1965) Diving observations of sub-tidal antarctic marine vegetation. Bot Mar 8:234-243

Orth RJ (1992) A perspective on plant-animal interactions in seagrasses: physical and biological determinants influencing plant and animal abundance. In: John DM, Hawkins SJ, Price JH (eds) Plant-Animal Interactions in the Marine Benthos, Systematics Association Special Volume No 46. Clarendon Press, Oxford, p 147-164

Parker JD, Duffy JE, Orth RJ (2001) Plant species diversity and composition: experimental effects on marine epifaunal assemblages. Mar Ecol Prog Ser 224:55-67

Pavia H, Carr H, Åberg P (1999) Habitat and feeding preferences of crustacean mesoherbivores inhabiting the brown seaweed *Ascophylum nodosum* (L.) Le Jol. and its epiphytic macroalgae. J Exp Mar Biol Ecol 236:15-32

Pennings SC, Nadeau MT, Paul VJ (1993) Selectivity and growth of the generalist herbivore *Dolabella auricularia* feeding upon complementary resources. Ecology 74:879-890

Peters KJ, Amsler CD, Amsler MO, McClintock JB, Dunbar RB, Baker BJ (2005) A comparative analysis of the nutritional and elemental composition of macroalgae from the western Antarcitc Peninsula. Phycologia 44:453-463

Poore AGB, Watson MJ, Nys Rd, Lowry JK, Steinberg PD (2000) Patterns of host use among alga- and sponge- associated amphipods. Mar Ecol Prog Ser 208:183-196

Richardson MG (1977) The ecology (including physiological aspects) of selected Antarctic marine invertebrates associated with inshore macrophytes. PhD Dissertation, University of Durham

Romesburg HC (1984) Cluster Analysis for Researchers, Vol. Krieger Publishing Company, Melbourne, Florida

Russo AR (1990) The role of seaweed complexity in structuring Hawaiian epiphytal amphipod communities. Hydrobiologia 194:1-12

Schoenly K, Beaver RA, Heumier TA (1991) On the trophic relations of insects: A food-web approach. Am Nat 137:597-638

Sotka EE (2005) Local adaptation in host use among marine invertebrates. Ecology Letters 8:448-459

Sotka EE, Hay ME (2002) Geographic variation among herbivore populations in tolerance for a chemically rich seaweed. Ecology 83:2721-2735

Sotka EE, Hay ME, Thomas JD (1999) Host-plant specialization by a non-herbivorous amphipod: advantages for the amphipod and costs for the seaweed. Oecologia 118:472-482

Sparrevik E, Leonardsson K (1999) Direct and indirect effects of predation by *Saduria entomon* (Isopoda) on the size-structure of *Monoporeia affinis* (Amphipoda). Oecologia 120:77-86

Stachowicz JJ, Hay ME (1999) Reducing predation through chemically mediated camouflage: indirect effects of plant defenses on herbivores. Ecology 80:495-509

Steinberg PD (1985) Feeding preferences of *Tegula funebralis* and chemical defenses of marine brown algae. Ecol Monogr 55:333-349

Steinberg PD, Altena IV (1992) Tolerance of marine invertebrate herbivores to brown algal phlorotannins in temperate Australasia. Ecol Monogr 62:189-222

Stoner AW (1983) Distributional ecology of amphipods and tanaidaceans associated with three sea grass species. J Crus Biol 3:505-518

Takeuchi I, Watanabe K (2002) Mobile epiphytic invertebrates inhabiting the brown macroalga, *Desmarestia chordalis*, under the coastal fast ice of Lutzow-Holm Bay, East Antarctica. Polar Biol 25:624-628

Taylor RB, Cole RG (1994) Mobile epifauna on subtidal brown seaweeds in northeastern New Zealand. Mar Ecol Prog Ser 115:271-282

Taylor RB, Steinberg PD (2005) Host use by Australasian seaweed mesograzers in relation to feeding preferences of larger grazers. Ecology 86:2955-2967

Thiel M (2000) Population and reproductive biology of two sibling amphipod species from ascidians and sponges. Mar Biol 137:661-674

Thurston MH (1972) The crustacea amphipoda of Signy Island, South Orkney Islands. Br Antarctic Surv Sci Rep 71:1-133

Thurston MH (1973) Crustacea amphipoda from Graham Land and the Scotia Arc, collected by operation Tabarin and the Falkland Islands dependencies survey, 1944-59. Br Antarctic Surv Sci Rep 85

Van Alstyne KL, Ehlig HM, Whitman SL (1999) Feeding preferences for juvenile and adult algae depend on algal stage and herbivore species. Mar Ecol Prog Ser 180:179-185

Van Alstyne KL, Whitman SL, Ehlig JM (2001) Differences in herbivore preferences, phlorotannin production, and nutritional quality between juvenile and adult tissues from marine brown algae. Mar Biol 139:201-210

Viejo RM (1999) Mobile epifauna inhabiting the invasive *Sargassum muticum* and two local seaweeds in northern Spain. Aquat Bot 64:131-149

Wakefield RL, Murray SN (1998) Factors influencing food choice by the seaweed-eating marine snail *Norrisia norrisi* (Trochidae). Mar Biol 130:631-642

Wessels H, Hagen W, Molis M, Wiencke C, Karsten U (2006) Intra- and interspecific differences in palatability of Arctic macroalgae from Kongsfjorden (Spitsbergen) for two benthic sympatric invertebrates. J Exp Mar Biol Ecol 329:20-33

Wiencke C, Clayton MN (2002) Synopses of the Antarctic Benthos: Antarctic Seaweeds, Vol 9. A. R. G. Gantner Verlag KG, Rugell/Liechtenstein, FL

Wildish DJ (1988) Ecology and natural history of aquatic Talitroidea. Can J Zool 66:2340-2359

Wooster DE (1998) Amphipod (*Gammarus minus*) responses to predators and predator impact on amphipod density. Oecologia 115:253-259

Zaneveld JS (1966) The occurrence of benthic marine algae under shore fast-ice in the western Ross Sea, Antarctica. Proc Int Seaweed Symp 5:217-231

Table 1. Morphological attributes of eight dominant subtidal antarctic macroalgae ($\bar{x}$ ± 1 SE).

	Algal species							
Morphological attributes	**DME**	**DAN**	**ANT**	**PAL**	**GIG**	**MYR**	**PLO**	**IRI**
Wet Weight (g)	388 ± 91	307 ± 43	230 ± 28	40 ± 5	267 ± 47	162 ± 54	30 ± 10	83 ± 15
Width (cm)	39 ± 4	33 ± 3	39 ± 2	16 ± 1	61 ± 5	35 ± 3	19 ± 2	24 ± 1
Depth (cm)	31 ± 3	23 ± 2	26 ± 3	11 ± 1	50 ± 5	25 ± 2	15 ± 2	17 ± 2
Height (cm)	111 ± 10	136 ±11	144 ± 10	65 ± 5	10 ± 1	43 ± 3	20 ± 2	55 ± 6
Canopy volume (ml)	152299 ± 31831	113311 ± 21145	142111 ± 20750	11958 ± 1870	34395 ± 6708	43664 ± 11077	7550 ± 2713	21236 ± 2643
Thallus volume (ml)	354 ± 101	288 ± 40	202 ± 29	38 ± 5	247 ± 42	146 ± 50	27 ± 9	87 ± 15
Intestinal volume (ml)	151944 ± 31752	113023 ± 21108	141909 ± 20729	11920 ± 1866	34147 ± 6668	43519 ± 11030	7523 ± 2705	21149 ± 2634
Degree of Branch	5.2 ± 0.4	4.7 ± 0.2	3.1 ± 0.1	1.3 ± 0.2	1 ± 0	3.6 ± 0.2	7.2 ± 0.3	1.4 ± 0.2
Number of Branches 1	1738 ± 312	4291 ± 1208	82 ± 14	-	-	-	-	-
Number of Branches 2	9241 ± 1698	16561 ± 3723	403 ± 132	-	-	-	-	-
Number of Branches 3	29519 ± 4132	31188 ± 4555	546 ± 121	-	-	-	-	-
Total Number of Branches	40497 ± 4958	52040 ± 7529	1020 ± 197	1.5 ± 0.3	1 ± 0	168 ± 112	36817 ± 11612	1.4 ± 0.2
Number of Branches/g w.w.	260 ± 127	192 ± 33	4.5 ± 0.8	0.047 ± 0.013	0.006 ± 0.002	0.7 ± 0.3	1365 ± 114	0.019 ± 0.002
Sampling depth	10.6 ± 0.6	12.3 ± 0.4	10.7 ± 0.8	7.0 ± 0.1	8.1 ± 0.7	7.3 ± 0.2	13.1 ± 0.7	10.1 ± 0.7

Table 2. Species assemblages of gammarid amphipods associated with eight subtidal antarctic macroalgae. Percentage shown in parentheses.

	Algal species								
Species	**DME**	**DAN**	**ANT**	**PAL**	**GIG**	**MYR**	**PLO**	**IRI**	**Total**
Allogaussia sp.	0	0	0	0	0	0	1	0	1
Ampelisca bouvieri	0	0	0	0	2	0	0	0	2
Atyloella magellanica	1	1	0	0	0	0	5	0	7
Atylopsis sp.	1	0	0	0	0	0	0	0	1
Bovallia gigantea	76	105	0	0	8	17	24	0	230
Colomastix sp. (fissilingua)	6	2	1	0	5	1	0	0	15
Eophilantidae	253	1	1	0	19	13	3	0	290
Djerboa furcipes	7	0	0	0	18	0	0	0	25
Eurymera monticulosa	2	0	0	0	3	3	0	0	8
Gitanopsis squamosa	76	68	7	0	82	3	2	0	238
Gnathiphimedia barnardi	0	0	0	0	0	0	2	0	2
Gnathiphimedia fuchsi	4	3	0	0	0	1	0	0	8
Gondogeneia antarctica	430	477	8	20	472	442	77	16	1942
Gondogeneia redfeanri	17	509	6	4	2	6	15	0	559
Jassa spp.	189	2739	21	12	2567	590	278	22	6418
Leucothoe spinicarpa	1	0	0	0	0	0	0	0	1
Lysianassidea	37	2	0	3	0	0	0	0	42
Metaleptamphopus pectinatus	51185	500	391	19	37	10	403	24	52569
Oradarea spp.	8450	1405	38	8	539	74	154	0	10668
Paradexamine fissicauda	2	5	1	0	26	2	205	5	246
Paramoera sp.	0	0	0	0	1	0	0	0	1
Pariphimedia integricauda	6	49	0	0	15	21	5	0	96
Pontogeneia sp.	3	0	0	0	1	0	0	0	4

Table 2. (Continued)

	DME	DAN	ANT	PAL	GIG	MYR	PLO	IRI	Total
Probolisca ovata	411	515	37	7	548	90	177	3	1788
Prostebbingia brevicornis	0	3	0	0	2	0	1	0	6
Prostebbingia gracilis	2174	128	7	3	108	0	119	0	2539
Prothaumatelson nasutum	120	101	11	2	51	1	2	0	288
Schraderia dubia	8	210	2	0	82	2	24	1	329
Schraderia gracilis	2	21	0	0	34	0	1	0	58
Schraderia sp.	0	5	0	0	5	0	2	0	12
Seba sp.	0	1	0	0	0	0	0	0	1
Thaumatelson herdmani	4	16	1	0	0	0	0	0	21
Total number of individuals	63465	6866	532	78	4627	1276	1500	71	78415
	(80.9%)	(8.8%)	(0.68%)	(0.1%)	(5.9%)	(1.63%)	(1.91%)	(0.09%)	
Total number of species/taxa	12 ± 1.2	12 ± 1.1	6 ± 0.5	3 ± 0.6	10 ± 1.4	6 ± 1.0	8 ± 1.4	2 ± 0.4	
Species richness (d)	1.3 ± 0.1	1.8 ± 0.1	1.3 ± 0.1	0.9 ± 0.2	1.5 ± 0.2	1.1 ± 0.1	1.3 ± 0.2	0.7 ± 0.1	
Species diversity (H')	0.6 ± 0.1	1.5 ± 0.1	1.0 ± 0.1	0.9 ± 0.2	1.1 ± 0.2	1.0 ± 0.1	1.3 ± 0.2	0.7 ± 0.1	

Table 3. Regression analyses comparing amphipod densities to morphological parameters of algae.

Morphological parameters of algae	n	Linear Equation	r^2	P
Amphipod density vs.				
Thallus volume (ml)	80	$y = 0.04x + 137$	0.29	< 0.01
Canopy volume (L)	80	$y = 0.01x + 52$	0.24	< 0.01
Interstitial volume (L)	80	$y = 0.01x + 52$	0.24	< 0.01
Number of branches	80	$y = 19x + 153$	0.09	< 0.01

Table 4. Analysis of similarity (ANOSIM) between two different sampling sites based on the amphipod community structure associated with the alga collected. NA indicates not available. P values are shown in parentheses. Algal abbreviations are given in Fig. 1. Significance levels greater than 0.05 are shown in bold.

	Hermit Wall	**Eichorst Is.**	**Bonaparte Pt.**
Southeast Hermit Is.	NA	**ANT (0.159)**	**GIG (0.135)** DME (0.008) PAL (0.008)
Bonaparte Pt.	DAN (0.008)	**IRI (0.905) MYR (0.071)**	—
Eichorst Is.	PLO (0.016)	—	—

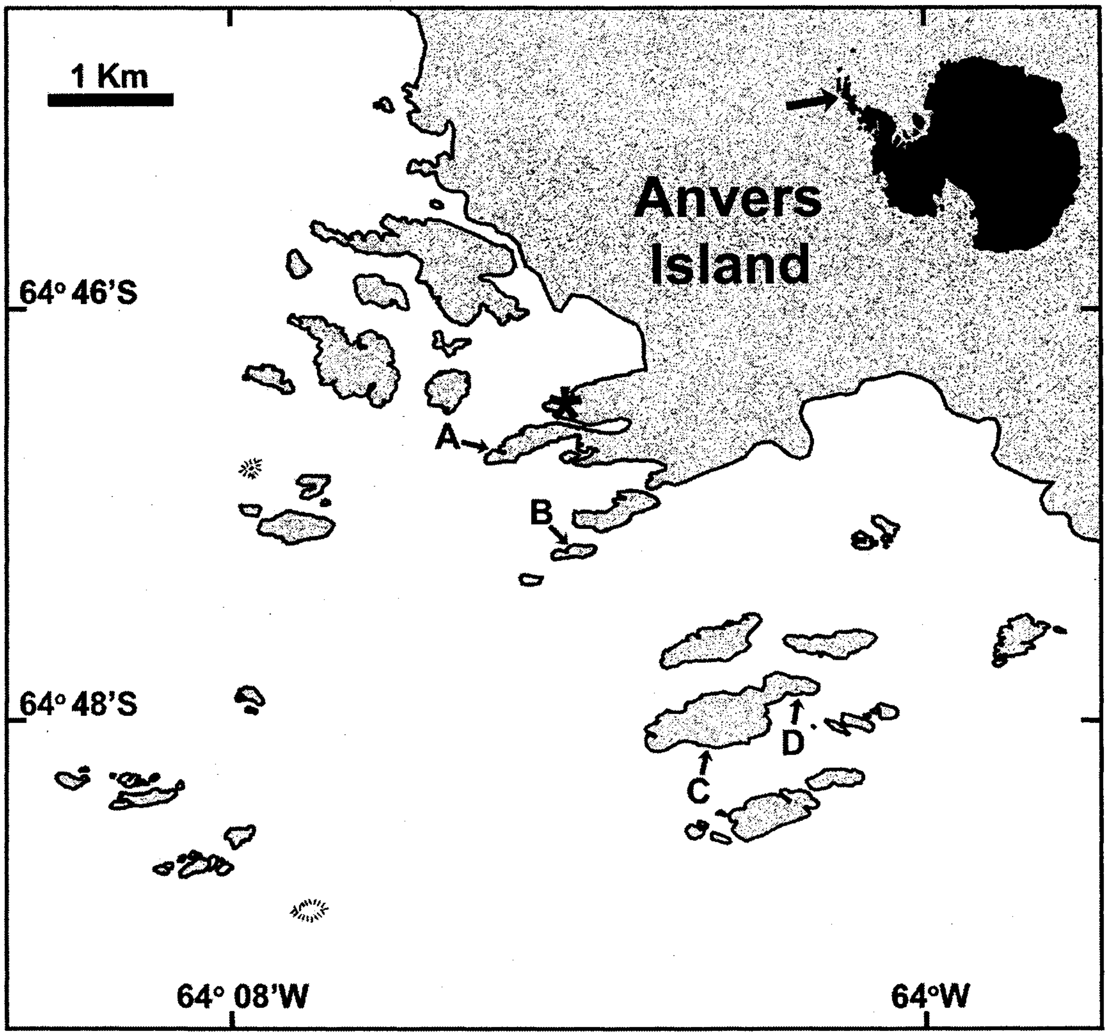

Figure 1. Sampling locations of subtidal macroalgae and associated amphipods off Anvers Island, Antarctica. Palmer Station (*), Bonaparte Point (A), Eichorst Island (B), South Hermit Island (Hermit Wall; C), and Southeast Hermit Island (D). The silhouette at the upper right corner indicates the Antarctic continent and the arrow points to the location of Anvers Island.

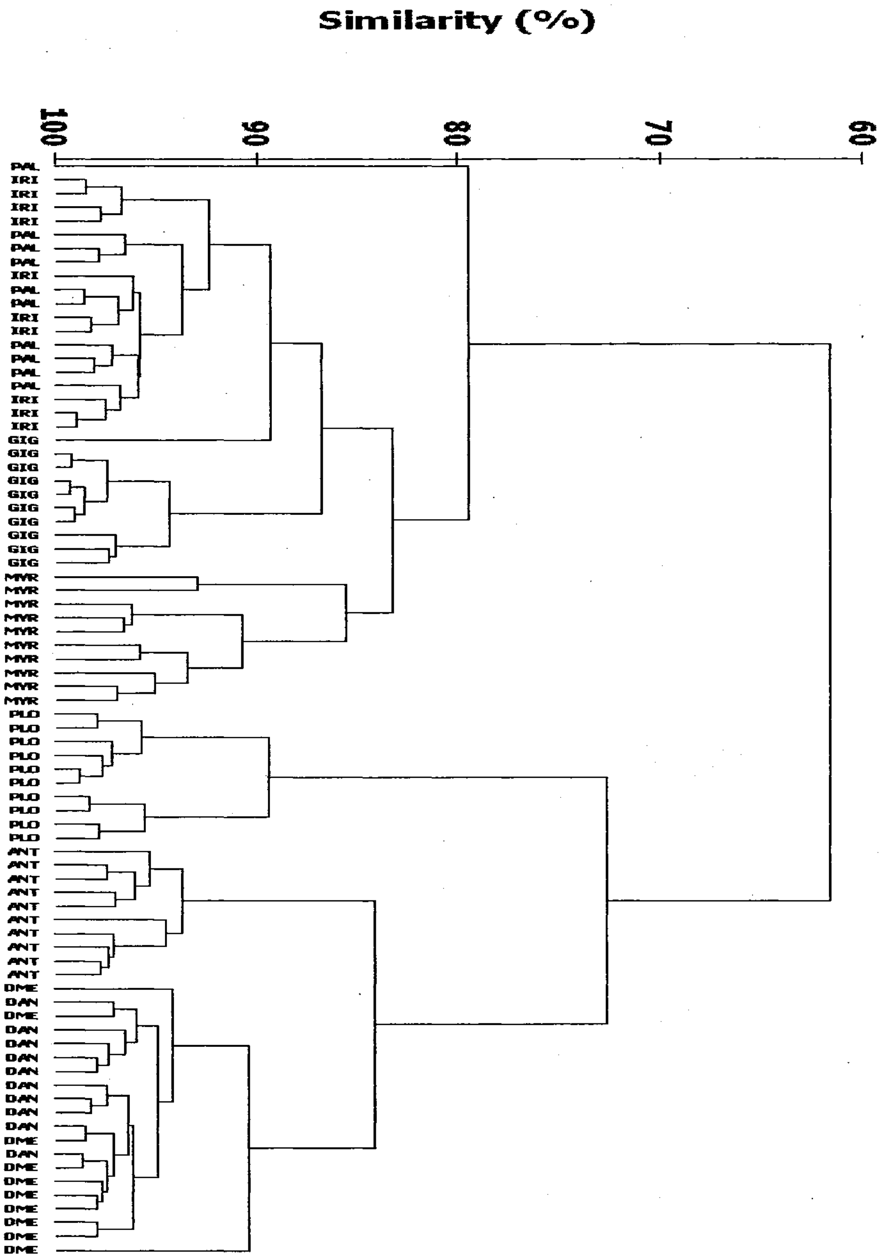

Figure 2. Bray-Curtis Cluster Analysis dendrogram generated on the basis of morphometrics of macroalgae (see Table 1). Shown is the percent similarity between 10 replicate samples of each of the eight target macroalgae. DME = *Desmarestia menziesii*; DAN = *Desmarestia anceps*; ANT = *Desmarestia antarctica*; PAL = *Palmaria decipiens*; GIG = *Gigartina skottsbergii*; MYR = *Myriogramme mangini*; PLO = *Plocamium cartilagineum*; IRI = *Iridaea cordata*.

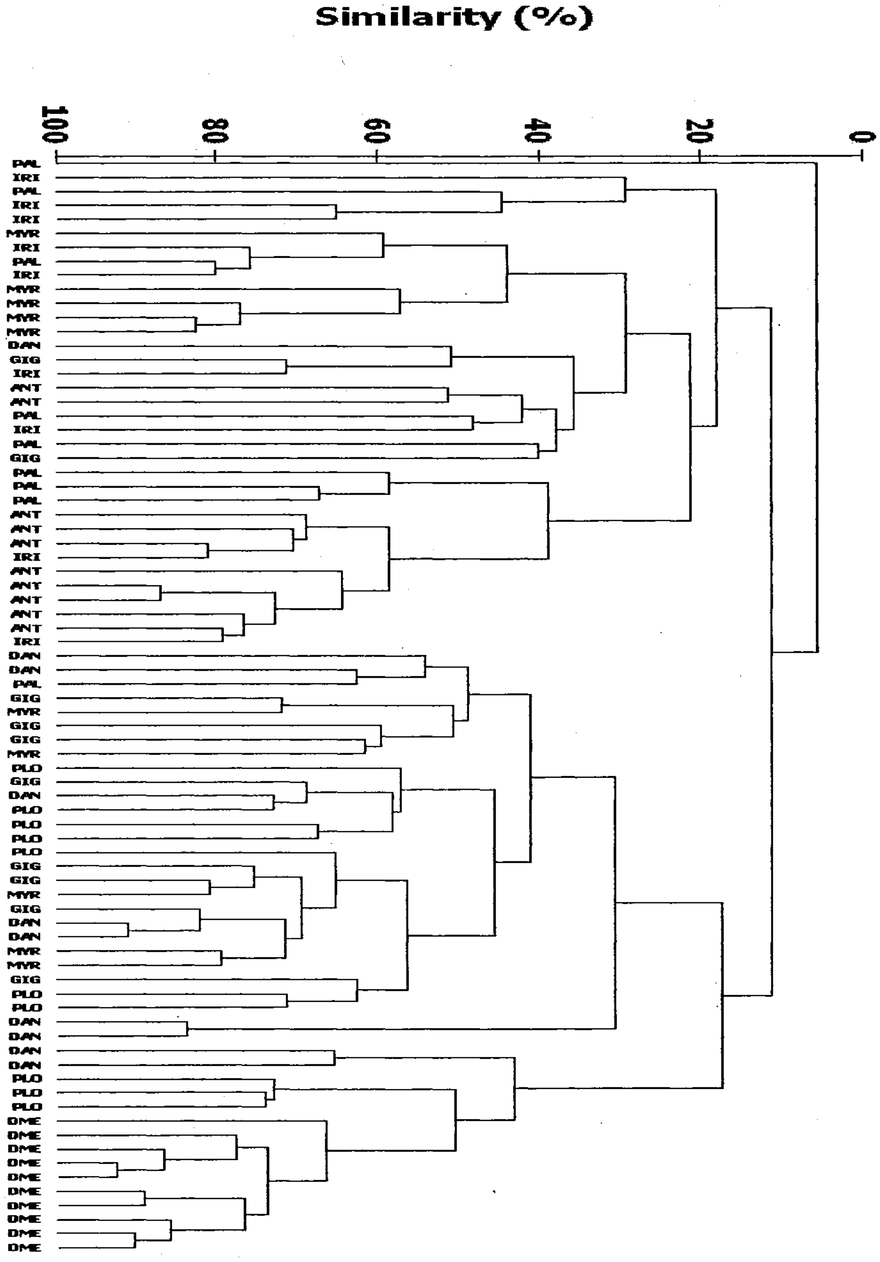

Figure 3. Bray-Curtis Cluster Analysis dendrogram generated on the basis of the standardized abundances of amphipod species distributions and their relative population densities (number of amphipods g $^{-1}$ wet weight algal tissue). Shown is the percent similarity between 10 replicate samples of each of the eight target macroalgae. (abbreviations given in Fig. 2).

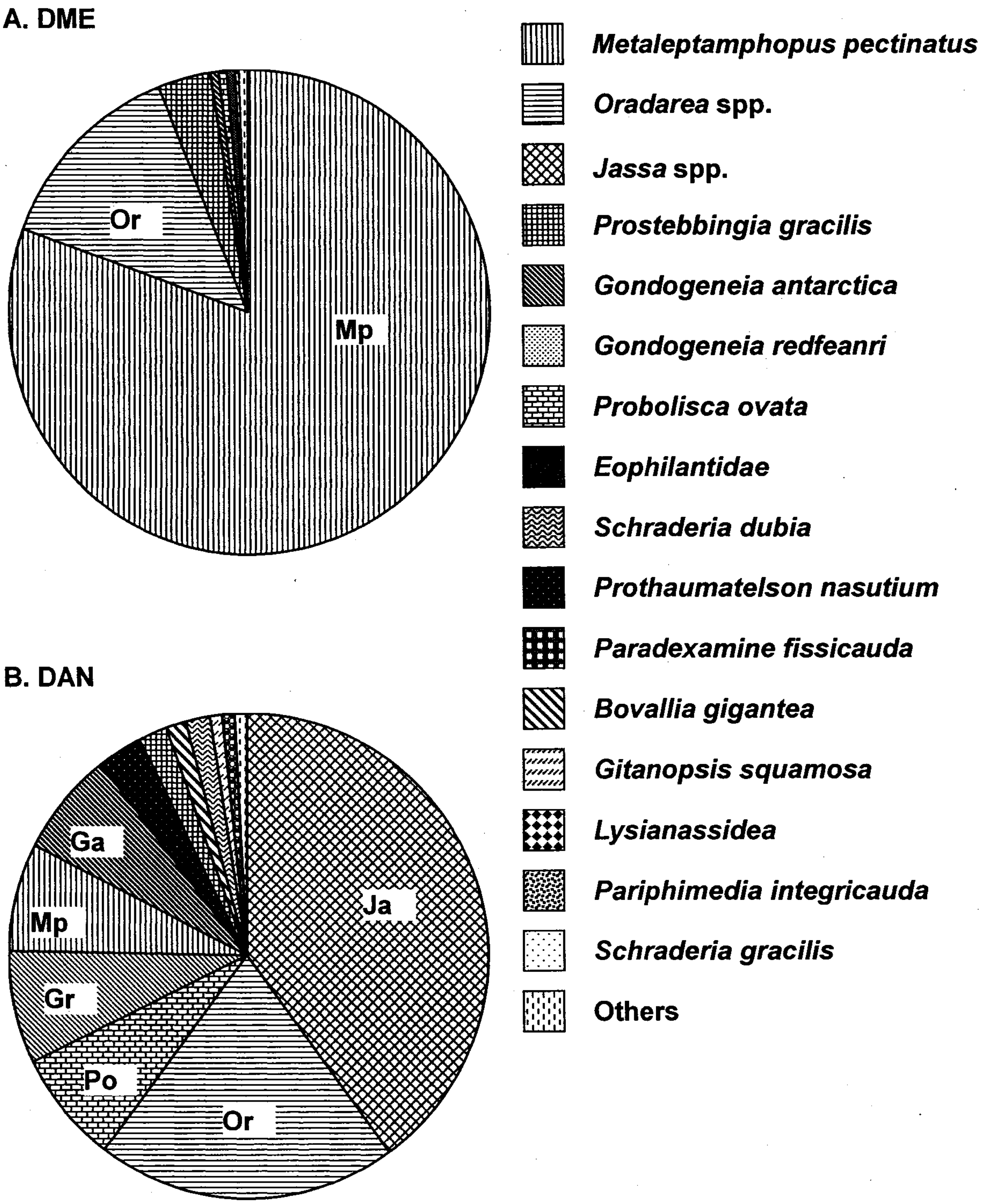

Figure 4. Species composition (%) of the 16 most common amphipod taxa associated with the eight target macroalgae. For data presented at the species level abbreviations are based on the first letter of the genus and the first letter of the species. For combined taxa the abbreviation is taken from the first two letters of the family or genus.

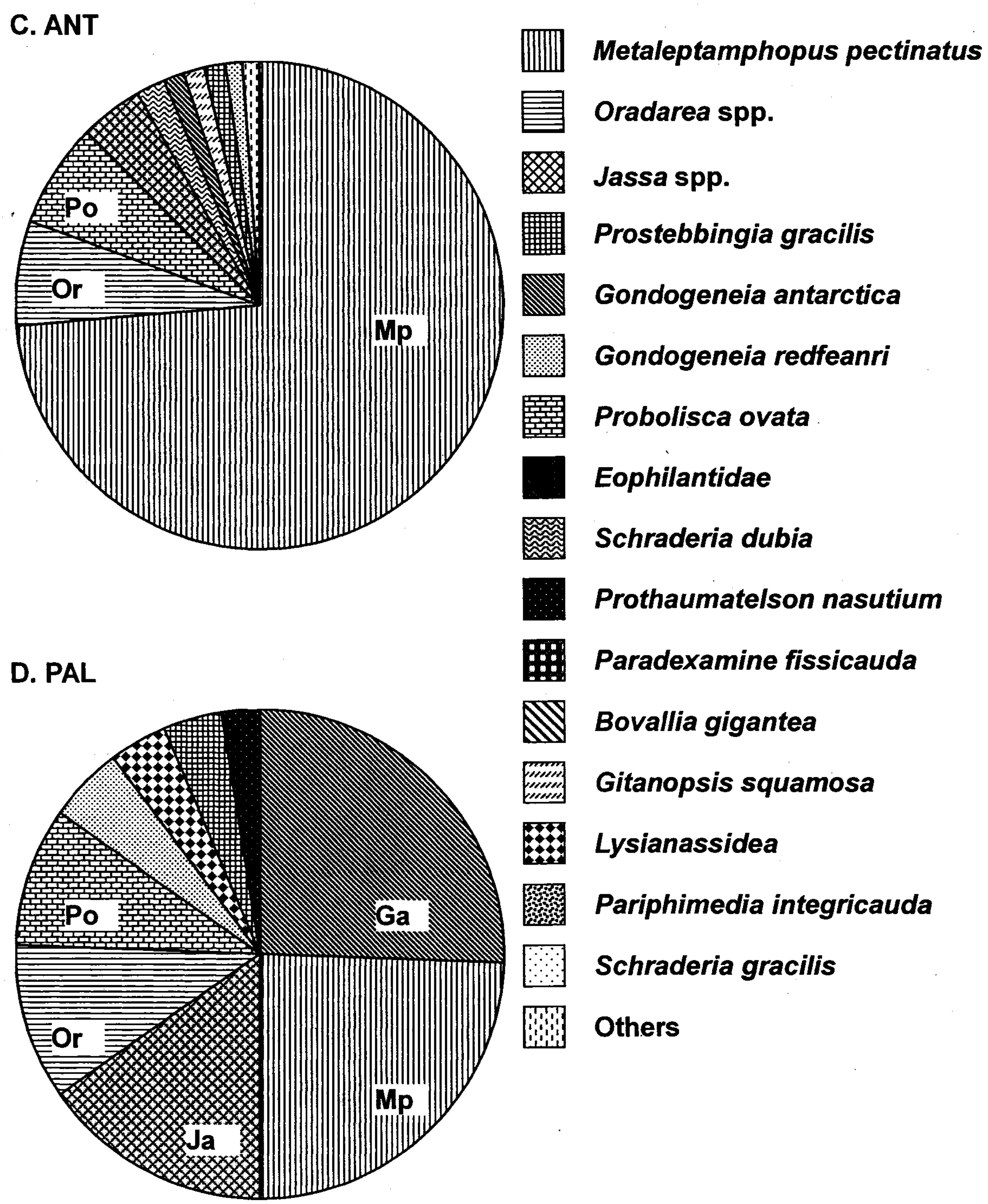

Figure 4. (Continue)

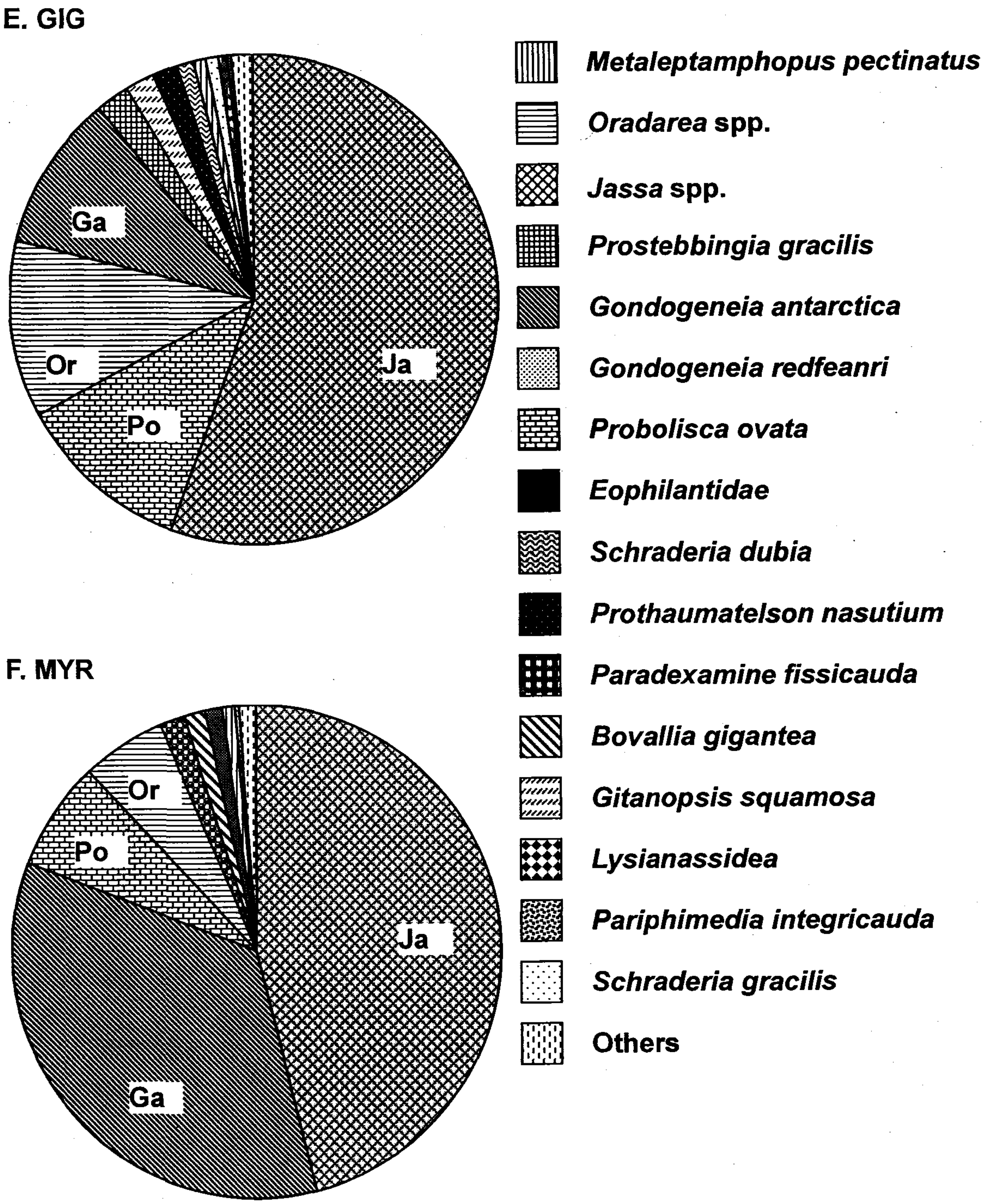

Figure 4. (Continue)

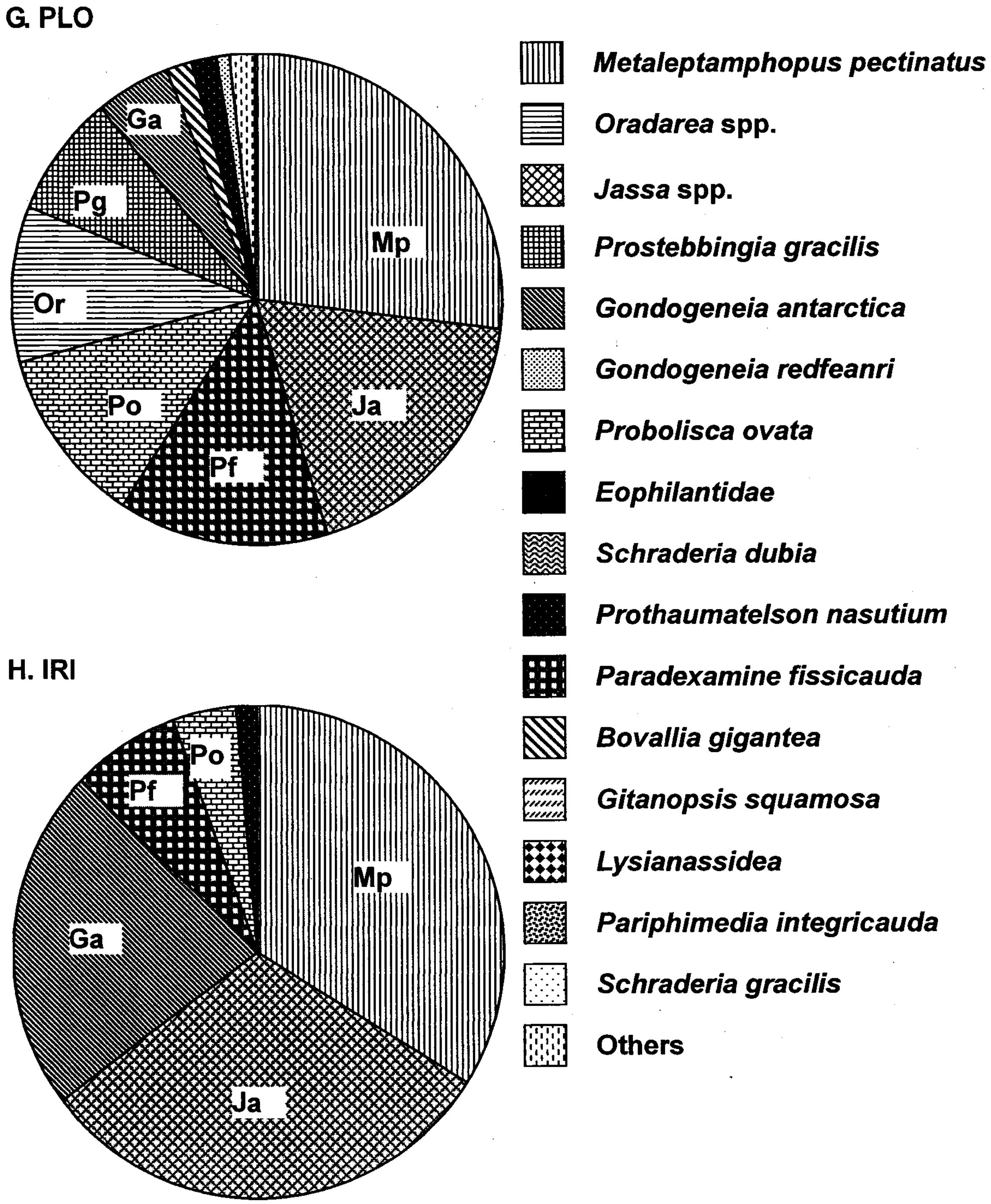

Figure 4. (Continue)

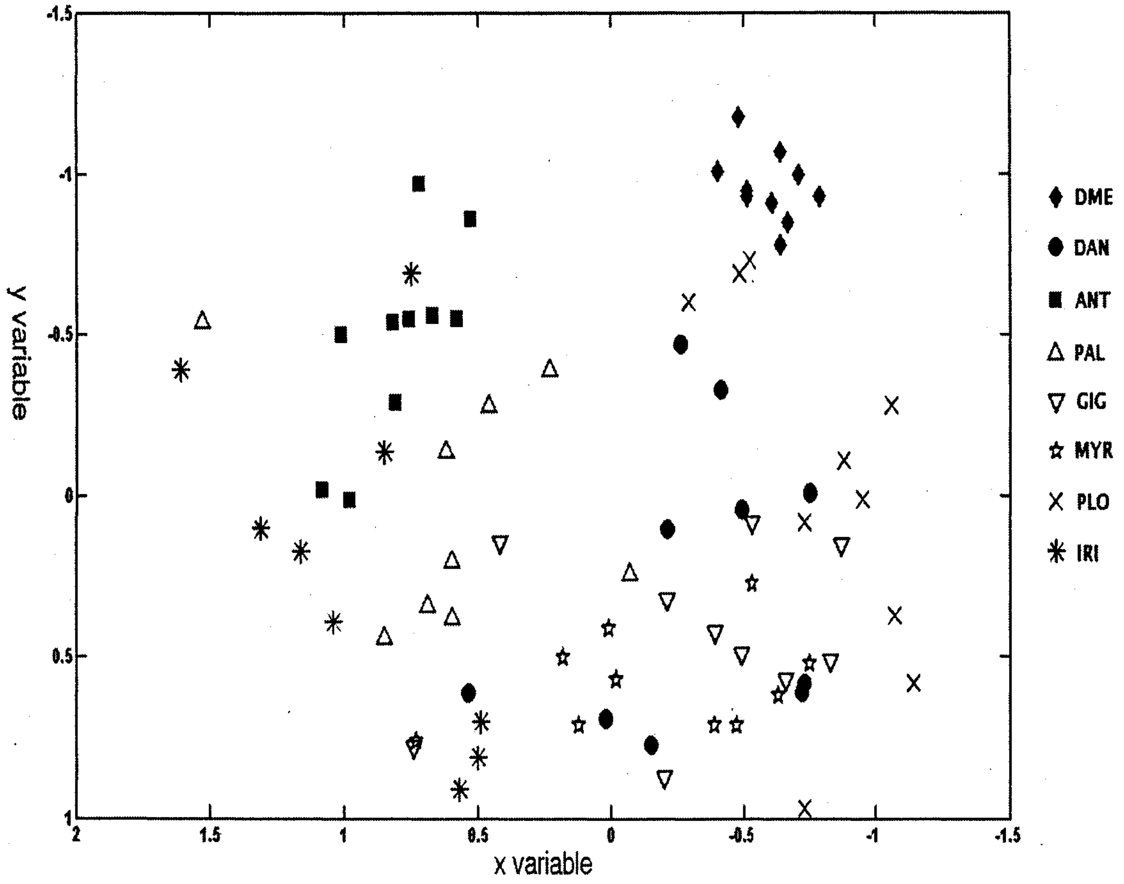

Figure 5. MDS ordination analysis of 10 replicates of each of the eight target macroalgal samples based on both the associated species abundances and compositions of 32 amphipod taxa. The MDS analysis was conducted using standardized (numbers of amphipods g $^{-1}$ algal wet wt) and log (x + 1) transformed amphipod data and presented as a 2-dimensional scatter graph using x and y variables. (stress = 0.15)

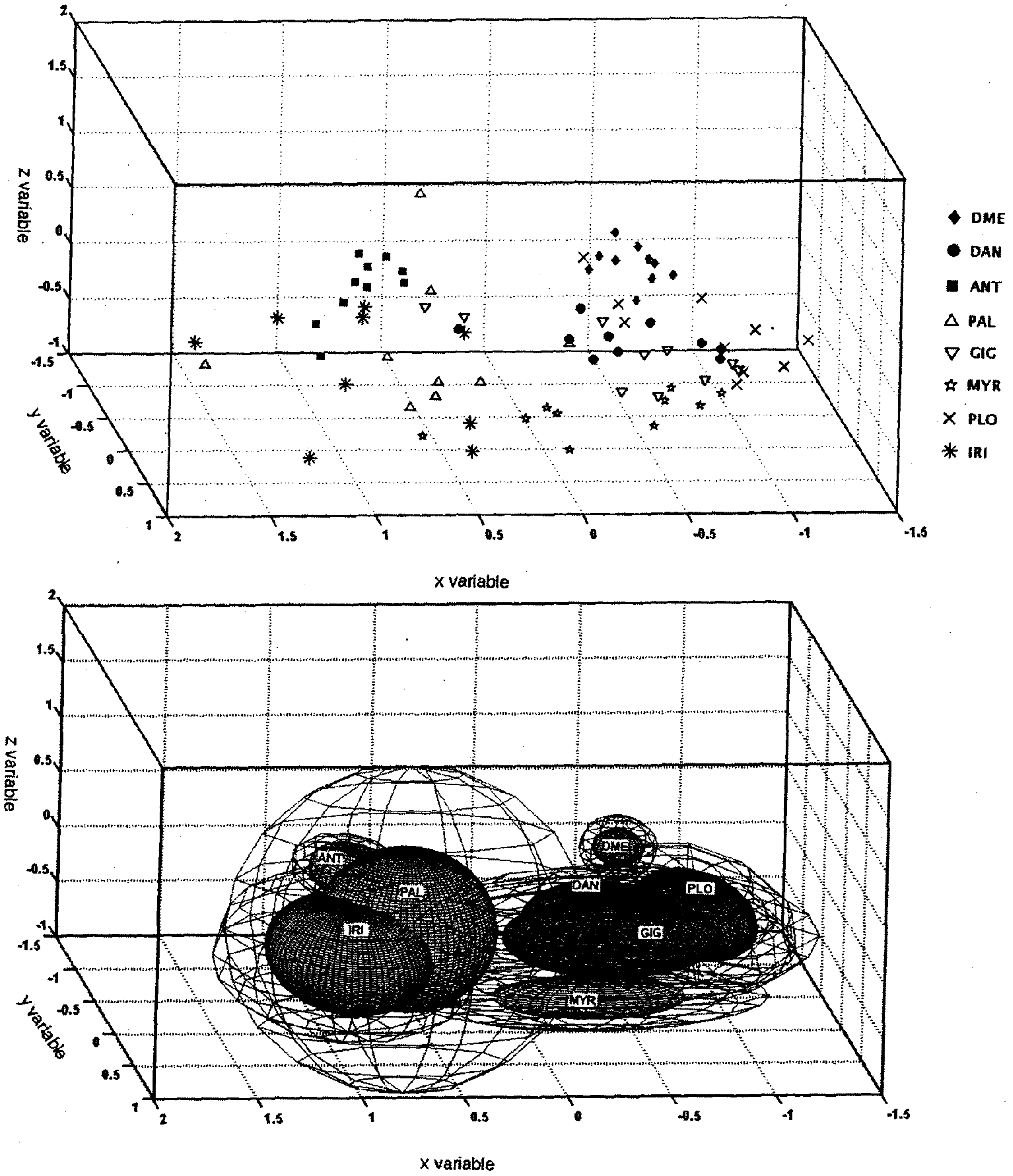

Figure 6. MDS ordination analysis of 10 replicates of each of the eight target macroalgae based on both the associated species abundance and compositions of 32 amphipod taxa. The MDS analysis was conducted using standardized (numbers of amphipods g^{-1} algal wet wt) and log (x + 1) transformed amphipod data. A. 3-dimensional scatter graph plotted using x, y, and z variable coordinates derived from MDS. B. 3-dimensional ellipsoid graph. Each solid ellipsoid represents the mean ± standard deviation of x, y, and z variables of 10 replicates of amphipod sample associated with the target macroalga. The outer mesh surface is the 95% of the maximum and minimum variables. (Stress = 0.11)

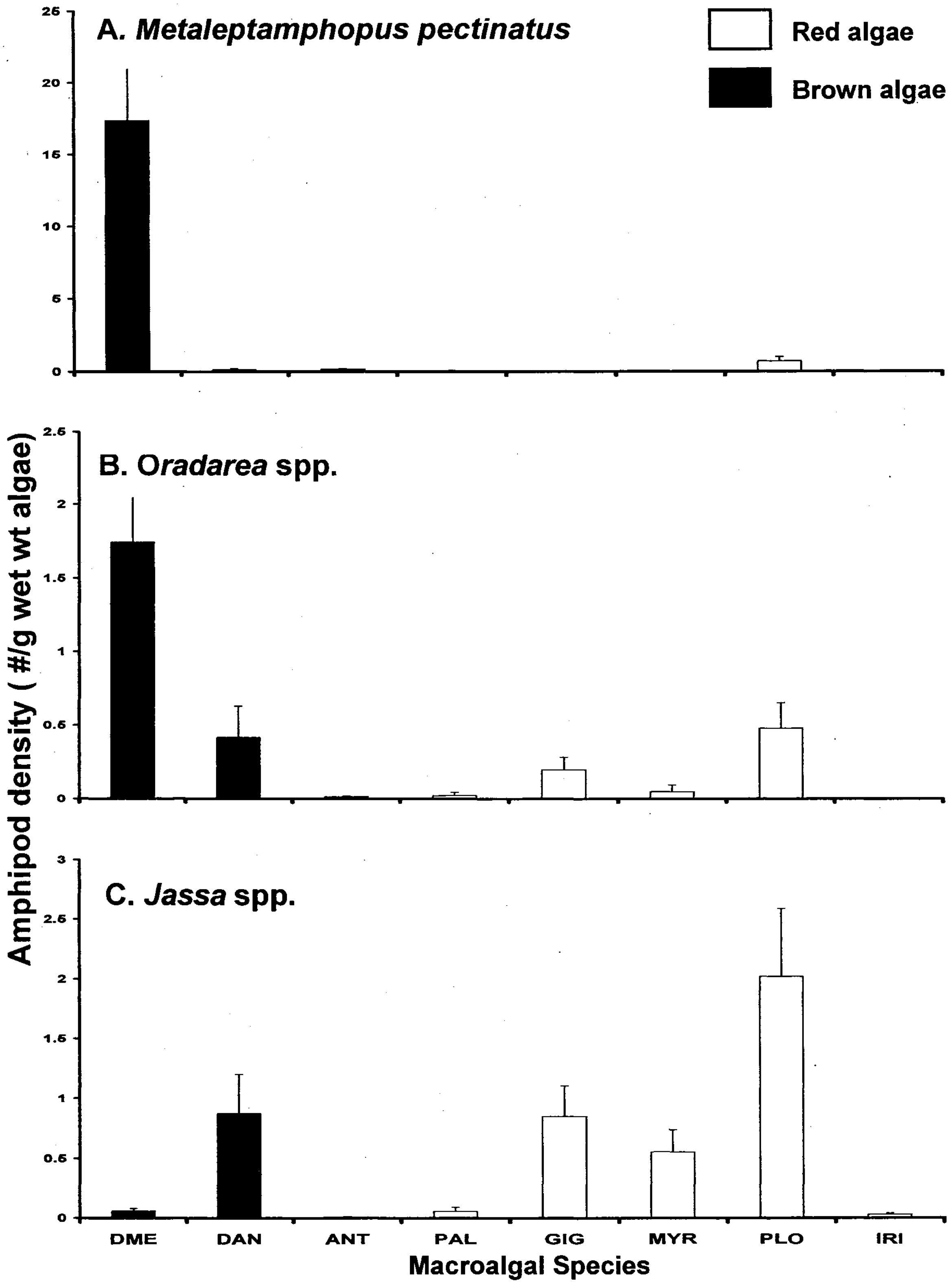

Figure 7. Densities of the three most abundant amphipod species associated with the eight target macroalgae. Data are mean ± SE; n = 10 (ANOVA; $F_{7,72}$ = 24.1, 13.3, and 8.2, respectively, $p < 0.01$). (Abbreviations given in Fig. 2).

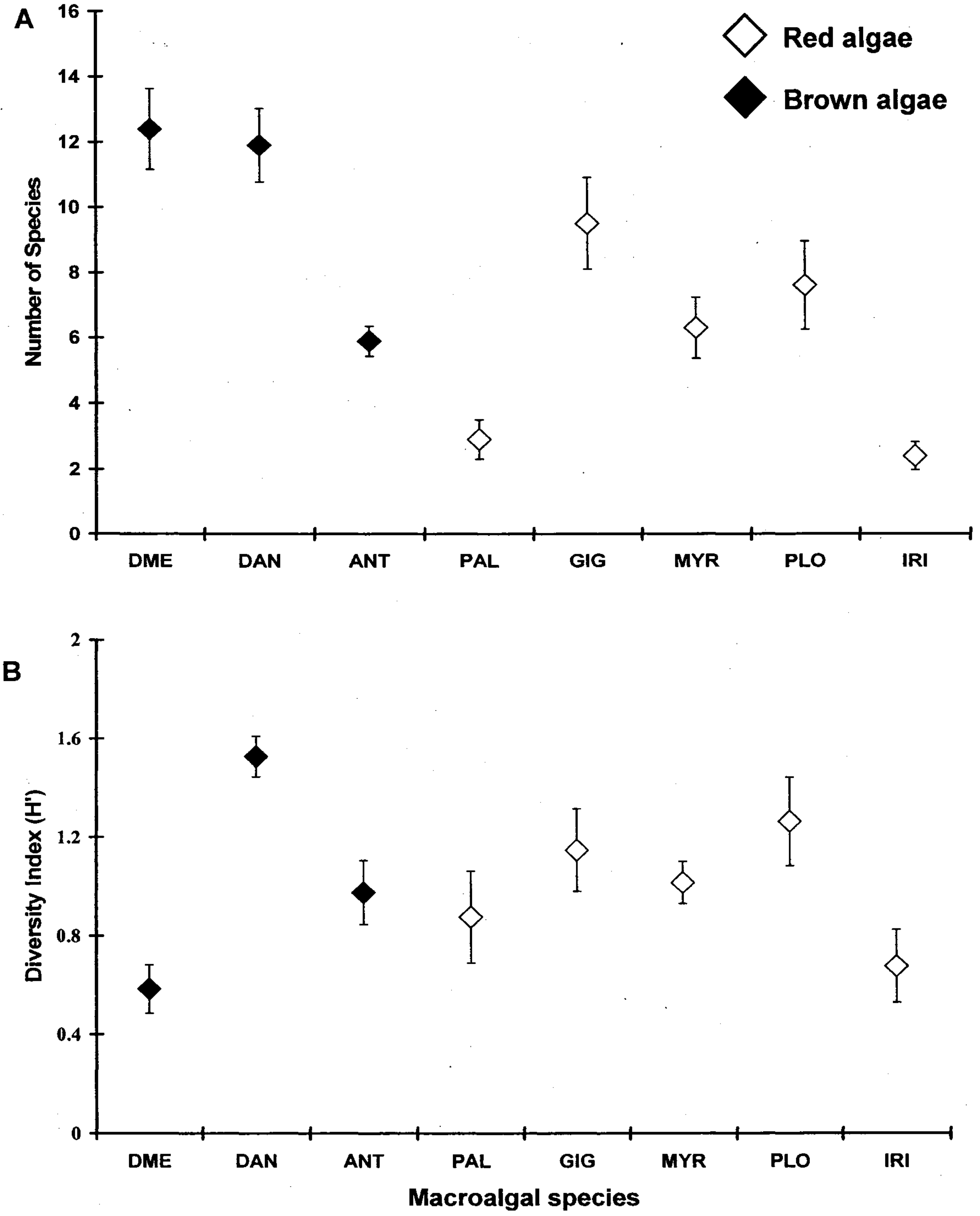

Figure 8. Numbers of species and diversity indices of amphipods associated with the eight target macroalgae. A. Number of species. B. diversity index (H') of amphipod communities associated with eight target macroalgae. Data are means ± SE; n = 10 (ANOVA; $F_{7,72} = 15.6$ and 5.3, respectively, $p < 0.01$). (Abbreviations given in Fig. 2).

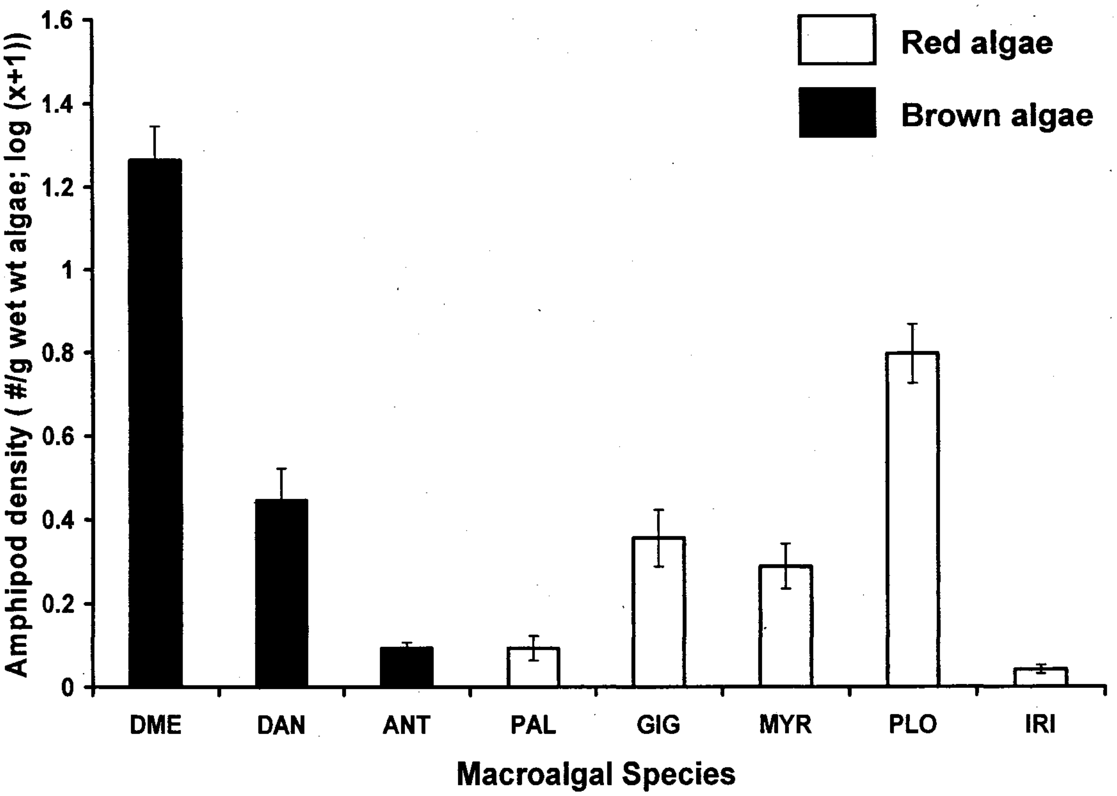

Figure 9. Total amphipod densities (number of amphipod g $^{-1}$ algal wet wt) associated with the eight target macroalgae. Data were log (x+1) transformed and presented as means ± SE; n = 10 (ANOVA; $F_{7,72} = 48.7$, $p < 0.01$). (Abbreviations given in Fig. 2)

FEEDING RATES OF COMMON ANTARCTIC GAMMARID AMPHIPODS ON ECOLOGICALLY IMPORTANT SYMPATRIC MACROALGAE

by

YUSHENG M. HUANG, JAMES B. MCCLINTOCK, CHARLES D. AMSLER, KEVIN J. PETERS, AND BILL J. BAKER

Journal of Experimental Marine Biology and Ecology
Vol. 329, pp. 55-65

Format adapted and errata corrected for dissertation

ABSTRACT

Single species feeding trials employing both fresh algal tissues and alginate food pellets containing dried finely ground algal tissues were conducted to examine the relative palatability of sympatric Antarctic macroalgae (three brown and five red macroalgal species) to three common herbivorous gammarid amphipods (*Prostebbingia gracilis* Chevreux, *Gondogeneia antarctica* (Chevreux) Thurston, and *Metaleptamphopus pectinatus* Chevreux). In fresh algal tissue bioassays, both the amphipods *P. gracilis* and *G. antarctica* consumed significantly greater amounts of the red alga *Palmaria decipiens* over all other seven species of macroalgae. The amphipod *M. pectinatus* failed to consume measurable quantities of fresh thalli of any macroalgae and therefore is likely to feed on other resources. In food pellet bioassays, the consumption rates of amphipods fed eight different species of macroalgae were compared with consumption rates on a highly palatable control green alga. Alginate pellets containing finely ground tissues of *P. decipiens* were consistently the most palatable of any of the macroalgae to *P. gracilis* and *G. antarctica*, while pellets containing the brown algae *Desmarestia menziesii*, *D. anceps* and the red alga *Plocamium cartilagineum* were not consumed by any of the three amphipod species. Regression analysis indicated that feeding rates of the amphipods *P. gracilis* and *G. antarctica* on alginate food pellets were not significantly correlated with known species-specific parameters of macroalgal nutritional quality (%N, %C, C:N ratio, soluble protein, soluble carbohydrate, and lipid). Therefore, differences in amphipod macroalgal palatability are most likely related to other factors including physical and/or chemical deterrents.

INTRODUCTION

Marine mesograzers, which include the conspicuous gastropods, amphipods, and isopods, in addition to a number of lesser taxa, are ubiquitous across a wide suite of marine environments. While some are free living within the water column or are found in association with inert materials such as rock or sand substrata (albeit coated with microbial biofilms and encrusting microorganisms), most are closely associated with living substrates such as macroalgae and seagrasses (Hay & Fenical 1988, Brearley & Walker 1995, Hay 1997, Hay et al. 1998, Duffy et al. 2001, Lippert et al. 2001). These diverse living substrates may provide mesograzers with a variety of resources including food, but also potential refuge from predation and/or environmental stress (Duffy & Hay 1991). Not surprisingly, perhaps because of these resource linkages, a variety of the life history stages of mesograzers appear to be adapted to remain in close association with their living "hosts" (Hay et al. 1990, Sotka et al. 1999).

Macroalgae, while less common around much of Antarctica, are extremely abundant in terms of biomass along the western Antarctic Peninsula (Neushul 1965, Amsler et al. 1995, Brouwer et al. 1995, Quartino et al. 2001). Commonly associated with a diverse assemblage of epibenthic organisms that encompass a wide range of trophic habits (Richardson 1977, Jażdżewski et al. 1991a, 1991b, Iken et al. 1998), peninsular macroalgae are known to provide a significant food resource for grazing sympatric gastropods, annelids, crustaceans, and fish (Iken et al. 1997, 1998, Iken 1999, 1999). However, different algal species are apparently not consumed in equal frequency to their relative abundance as some species are frequently found in the gut contents of common herbivores whereas others are rarely ingested (Iken et al. 1997, 1999). Such observations have led to studies focusing on understanding whether chemical defenses mediate these patterns of grazing by sympatric Antarctic herbivorous amphipods (Amsler et al. 1998, Ankisetty et al. 2004, Amsler et al. 2005, Fairhead et al. 2005). Despite these recent studies, much remains to be learned about the factors that mediate trophic relationships between Antarctic mesograzers and macroalgae.

Amphipods can be remarkably abundant in macrobenthic communities along the Antarctic Peninsula, in some locations constituting up to 85% of the total macrobenthos when considered in terms of their numerical abundance (Jaźdżewski et al. 1991a, Jaźdżewski et al. 1991b, Jaźdżewski et al. 2001). Three of the particularly common neritic amphipods that occur in the coastal waters along the western Antarctic Peninsula include *Prostebbingia gracilis* Chevreux, *Gondogeneia antarctica* (Chevreux) Thurston and *Metaleptamphopus pectinatus* Chevreux (Richardson 1977, Jaźdżewski et al. 1991a, 1991b, 2001). Occurring in high abundance, *Prostebbingia gracilis* is a widespread circumantarctic amphipod associated with the macroalgal habitats and mainly with *Plocamium cartilagineum* meadows (Y. Huang, pers. obs.). Its vertical distribution ranges from depths of 4 to 250 m and, in shallow marine habitats surrounding King George Island, its abundance can exceed 25% of the total amphipod community (Chevreux 1913, Jaźdżewski et al. 1991a, 1991b). *Gondogeneia antarctica* occurs not only along the western Antarctic Peninsula, but is also found on the subantarctic islands and in the Magellanic region (Richardson 1977). Its vertical distribution ranges from the shallow subtidal to depths of 40 m (Thurston 1972) and it occurs in association with a variety of benthic habitats including muds, sands, gravels, and cobbles, with many of these substrates supporting abundant macroalgae. In the benthic peninsular habitats where *G. antarctica* has been examined, this species may comprise as much as 15-20% of the total amphipod community (Richardson 1977, Jaźdźewski et al. 1991a, 1991b, 2001). *Metaleptamphopus pectinatus* has been found in shallow depths of the western antarctic sub-region as well as in sub-antarctic waters off South Georgia Island. This species primarily inhabits the mats of epiphytes which occur on the holdfasts of various genera of macroalgae including *Desmarestia* and *Himantothallus* (Thurston 1972). Richardson (1977) surveyed amphipods associated with the thalli of *Desmarestia anceps* and found that *M. pectinatus* constituted 6– 23% of total amphipod abundance over a one year period.

The objectives of this investigation were to determine whether differential palatability for sympatric macroalgae occurs in three common Antarctic amphipod mesograzers and, if so, whether these patterns are correlated with known parameters of macroalgal nutritional quality.

MATERIALS AND METHODS

All organisms were collected within 3.5 km of Palmer Station on Anvers Island, Antarctica (64°46.5'S, 64°03.3'W; see Amsler et al., 1995 for map). All collections and laboratory assays were conducted between late February and late May, 2003.

Three common Antarctic herbivorous amphipod species (see above) were selected for the feeding bioassays. *Gondogeneia antarctica* were collected using hand nets from macroalgal beds in tide pools and the shallow subtidal at Laggard Island (64°48.4'S, 64°00.5'W). These collections were supplemented with animals trapped by the Palmer Station seawater system filters (these animals were quarantined and microscopically examined before use to ensure that they were uninjured). *P. gracilis* and *M. pectinatus* were collected subtidally by divers from *Plocamium cartilagineum* (Linnaeus) P F Dixon and *Desmarestia menziesii* J Agardh, respectively, off Bonaparte Point (64°46.7'S, 64°04.0'W) at depths ranging from 5-10 m. Amphipods were maintained in 2-L plastic bottles equipped with openings covered with fine mesh screening and suspended in tanks with flowing ambient seawater (temperature ranges from -1 to 1 ^{0}C).

Fresh Thallus Bioassays

Eight species of ecologically dominant macroalgae including three representatives of the Phaeophyceae, (*Desmarestia menziesii, Desmarestia anceps* Montagne, and *Desmarestia antarctica* Moe and Silva) and five representatives of the Rhodophyceae (*Gigartina skottsbergii* Setchell and Gardner, *Iridea cordata* (Turner) Bory, *Myriogramme mangini* (Gain) Skottsberg, *Palmaria decipiens* (Reinsch) Ricker, *and Plocamium cartilagineum*), were collected by divers at depths ranging from 5-10 m off Bonaparte Point. Twelve individuals of each macroalgal species were returned to the laboratory and maintained in tanks equipped with running ambient seawater for subsequent feeding bioassays. To examine feeding preferences of herbivorous amphipods for different species of macroalgae, single species feeding trials (non-choice feeding assays) were conducted (Cruz-Rivera & Hay 2000b). For each amphipod species tested, sixteen 150-ml plastic bottles were filled to the mid- point with seawater, and then into each of eight of these bottles were haphazardly placed fifteen amphipods. Within a given amphipod species, sizes of individuals used in the experiments were similar and based on a mean adult body length (measured from the tip of the rostrum to the base of the telson) determined from a representative field sample of individuals (*P. gracilis*: 6.9±1.0 mm, n = 27; *G. antarctica*: 8.9±1.2 mm, n = 65; *M. pectinatus*: 5.0±0.8 mm, n = 38; mean ± SD). Fresh and completely un-grazed thalli (as evidenced by close visual examination) of each macroalgal species were cut into cross-sectional pieces with similar mass (mass ranged from 2 to 9 mg wet wt for *P. gracilis*; 15 to 38 mg wet wt for *G. antarctica*), blotted to remove excess seawater water, weighed and then individually placed into paired bottles, one with amphipods, and the other without amphipods (control treatment). Using this approach, we were able to calculate the precise consumption rate while negating any potential autogenic effect. Four replicate paired bottles were prepared for each experimental treatment. These were placed in a cold room at Palmer Station and room temperature maintained at 1.5 ± 0.5 ^{0}C under ambient photoperiod for a period of 33-45 hours. After this time period the pieces of fresh thallus were blotted dry and re-weighed. Amphipod algal consumption rates were calculated as the mean mg of algae consumed per day per amphipod. The thallus experiments, each consisting of four replicate paired bottles, were repeated three times to yield a total of 12 replicates (including controls) for each macroalgal species. This design in which the replicates were spread over three sets of experiments was used because it was not logistically possible to run all replicates simultaneously and unlike the pellet bioassays (see below) there was no appropriate internal control. Consequently, experimental day was included as a random factor in the statistical analyses.

Alginate Pellet Bioassays

In order to eliminate algal morphology (i.e., shape and toughness) as a potential factor influencing palatability to amphipods, alginate pellets containing algal tissues were prepared for each of the eight macroalgal species. Subtidal macroalgae were collected from Bonaparte Point, Hermit Island (64°47.9'S, 64°00.4'W), and Eichorst Island (64°47.1'S, 64°03.2'W). One individual of each macroalga was freeze-dried and then ground into a fine homogenous powder using a mortar and pestle and a commercial coffee grinder. In addition, the filamentous intertidal green macroalga *Cladophora repens* was used as a control feeding stimulant because it is a palatable alga known to be readily consumed by all three species of amphipods (Amsler et al. 2005). This alga was collected by hand from the intertidal and shallow subtidal at Laggard Island. The algal filaments were freeze dried and then ground into a fine powder using a mortar and pestle. Alginate pellets were prepared following the protocols given in Amsler et al. (2005) and Fairhead et al. (2005). Finely ground algal tissues were mixed in a 2% alginate solution to a final concentration of 5% algal tissue and then poured into a Petri dish. The mixture was then solidified by slowly pouring a cold 1 M $CaCl_2$ solution over the alginate solution. Pellets (10 mm diameter x 2 mm thickness) were punched from the hardened alginate using a cork borer. Amphipod feeding bioassays followed the same protocols as those described above for fresh thalli but with only 10 amphipods (*G. antarctica* and *P. gracilis*) per bottle and 10 sets of replicates. Twenty *M. pectinatus* were placed in to each bottle because of their relative small body size. Two of the eight different algal diet treatments and a single control treatment comprised of pellets containing *C. repens* were combined in each experimental treatment. Feeding preference of amphipods were determined by the relative consumption of an experimental algal food as a function of the consumption of the control alginate pellets containing *C. repens* (weight of the consumed treatments divided by weight of the consumed control within each experimental treatment) .

From previous feeding experiments using *Gondogeneia antarctica* (C.D. Amsler pers.obs., Amsler et al., 2005), patterns of macroalgal consumption varied across different feeding trial days. Hence, to account for such possible temporal differences in consumption rates, we presented amphipods alginate control pellets containing finely ground tissues of the intertidal green macroalga *Cladophora repens* on each day of the feeding trials. As indicated above, *C. repens* is known to be a highly palatable algal food to amphipods both in the field and laboratory (Amsler et al. 2005). By measuring the consumption of pellets containing this control alga as a function of each algal feeding treatment we controlled for both day to day variations in consumption rates and the fact that different algal species were presented to amphipods on different days.

Statistical Analyses

To compare the consumption rates of amphipods for fresh algal thalli among the different dietary treatments and different dates of trials, consumption rate data were analyzed by two-way ANOVA using SAS software (SAS Institute, Cary, North Carolina) followed by Tukey's Honestly Significant Difference (HSD) tests with experimental day as a random factor. Because the alginate pellets in all replicates came from the same preparation, a parametric ANOVA was not appropriate. Therefore, a non-parametric Friedman's test (multiple related samples ANOVA) was performed on these data using

SPSS (SPSS Inc., Chicago, Illinois) software followed by multiple t-tests using the Bonferroni adjustment for multiple comparisons (General Linear Model, SAS) to compare the percentage of algal pellet consumption among the different dietary treatments. To examine the statistical correlation between amphipod consumption rates and parameters of algal nutritional quality, linear regression analysis was perform using SAS software.

We employed regression analyses to examine whether consumption rates on macroalgal alginate food pellets by the amphipod *Prostebbingia gracilis* and *Gondogeneia antarctica* were significantly correlated with various known parameters of macroalgal nutritional quality. These parameters included percent nitrogen, percent carbon, and the ratio of carbon to nitrogen, as well as levels of soluble protein, soluble carbohydrate, and lipid, all measured in macroalgae collected during the late growing season (Peters et al. 2005). Regression analysis did not include those macroalgal species that either had negative consumption values (*Desmarestia menziesii* and *D. anceps*) or lacked complete nutritional information (*Plocamium cartilagineum*; Peters et al., 2005). Thus, for both amphipods, the macroalgae *D. menziesii* and *P. cartilagineum* were not included in the linear regression analysis. Moreover, in the case of the amphipod *Prostebbingia gracilis* the alga *D. anceps* was not included.

RESULTS

Fresh Thallus Bioassays

Single species feeding trials indicated that both amphipods, *Prostebbingia gracilis* and *Gondogeneia antarctica*, showed much higher consumption rates of fresh thalli when offered *Palmaria decipiens* over all other seven species of macroalgae (Figs. 1A,B). At the conclusion of each feeding experiment, grazing marks on the edges of the thalli of *P. decipiens* were clearly evident. The third amphipod species tested, *Metaleptamphopus pectinatus*, failed to consume measurable quantities of any of the fresh thalli. *P. gracilis* and *G. antarctica* both consumed significantly ($P < 0.0001$) more *P. decipiens* than any of the other seven species of macroalgae presented in feeding trials, respectively (Figs. 1A,B). When comparing consumption rates among different feeding trial days, both amphipod species exhibited significantly different consumption rates of algae on different days (Table 1; $p=0.01$, *P. gracilis*; $p=0.01$, *G. antarctica*). However, the interaction between algal treatments and the different days of the feeding trials had no effect on consumption rates of *G. antarctica* (Table 1; $p=0.78$). This indicates that while the consumption rates of *G. antarctica* fed the different macroalgal treatments varied from day to day, the difference in consumption rate is mainly influenced by algal palatability. In contrast, the interaction between algal treatments and the different days of the feeding trials significantly influenced consumption rates in the amphipod *P. gracilis* (Table 1; $p<0.001$). Nonetheless, the palatability of *P. decipiens* is still significantly higher than all the other algal species. For both amphipod species, two-way analysis of variance demonstrated that *P. decipiens* was consumed significantly more than all other macroalgae in each feeding trial (Table 1). Thus, we chose to present feeding rate data combined over the three consecutive days of feeding trials (see Figure 1).

Our results based on the fresh thallus consumption of macroalgae indicated that *Palmaria decipiens* is highly palatable to both the amphipods *P. gracilis and G. antarctica*. However, consumption rates of amphipods on all other algal thalli did not exhibit significant variation. In addition, the amounts of these fresh thalli consumed did not differ from zero ($p > 0.05$ for *P. gracilis*; $p = 0.05$ for *G. antarctica*). Therefore, for these reasons, we were unable to make any inferences about the relative palatability of these other seven macroalgal species.

Alginate Pellet Bioassays

The results of alginate food pellet bioassays containing ground thalli of the eight target macroalgae indicated that the amphipod *Prostebbingia gracilis* significantly ($P < 0.05$) prefers the macroalgae *Palmaria decipiens*, *Myriogramme mangini* and *Gigartina skottsbergii* over the other macroalgae (Fig. 2A, 2B). The four least preferred macroalgae were consumed at very low levels or not at all. Indeed the brown macroalgae *Desmarestia anceps* and *D. menziesii* had negative consumption values (Figure 2A). Such negative consumption values resulted when experimental pellets containing a given macroalgae were not consumed by amphipods yet absorbed greater amounts of water over the course of the feeding experiment than did autogenic control pellets (no amphipods present). In terms of net rates of consumption, *P. gracilis* consumed 2-10 fold greater amounts of the alginate pellets containing *P. decipiens* than any of the other alginate food pellets (Fig. 2B).

The general feeding patterns of *Gondogeneia antarctica* proffered alginate food pellets are similar but not identical to that of *P. gracilis* (Fig 3A, 3B). Alginate food pellets containing *P. decipiens* were significantly ($P < 0.05$) preferred over all other macroalgae, with *M. mangini* the next most significantly ($P < 0.05$) preferred species.

The remainders of the macroalgal species were consumed in very low quantities or not at all (Fig 3A). In the case of *D. menziesii*, the mean consumption value was negative.

Similar to feeding experiments employing fresh thalli, we detected no consumption of alginate food pellets by *Metaleptamphopus pectinatus*. In many cases these amphipods broke down food pellets into small pieces but this was clearly due to their locomotory activities and not from grazing.

Correlation Analyses of Macroalgal Nutritional Parameters

The results of the regression analyses indicated that for both *P. gracilis* and *G. antarctica* consumption rates were not significantly related to any of the macroalgal nutritional quality parameters (Table 2).

DISCUSSION

The results of the fresh thalli bioassays indicate that the amphipods *Prostebbingia gracilis* and *G. antarctica* exhibited their highest consumption rates when grazing on the thalli of the red alga *Palmaria decipiens*. Although the use of single species feeding trails preclude this being directly interpreted as a food preference (Peterson & Renaud 1989), *P. decipiens* is clearly the most palatable algal food among the eight macroalgal species examined. Differences in these macroalgal consumption rates may be linked to either physical and/or biological factors. In terms of physical factors, algal morphology has been shown to influence the palatability of algae to amphipod grazers feeding on macroalgae occurring on coral reefs (Hay 1997). The eight macroalgal species presented to Antarctic amphipods represent three distinct morphologies: 1) a high degree of branching and terete branches (*Desmarestia anceps, D. menzesii*, and *Plocamium cartilagineum*), 2) moderately high degree of branching and flat branches (*D. antarctica*), and 3) no or low level of branching, comprised of one to a few flattened blades (all remaining species). Moreover, some of these macroalgae possess thalli with varying degrees of toughness (Amsler et al. 2005). In the present study, each alga was cut into pieces of similar mass in order to control for interspecific differences in the morphology of thallus edges. The pieces of algae used in the experiments were necessarily of sufficient size to preclude "edge effects". Given the low rates of consumption by amphipods for all but one of the macroalgal species when presented as relatively large pieces, detection of significant differences in palatability among these species may have been obscured. This outcome precluded any meaningful evaluation of the possible statistical correlation between consumption rates of fresh algae and measures of tissue toughness conducted through penetrometry analyses by Amsler et al. (2005). Nonetheless, it is noteworthy that the most palatable alga by far, *P. decipiens*, is among the lower third of 30 species of Antarctic macroalgae in terms of toughness.

One of the three amphipod species we examined, *Metaleptamphopus pectinatus,* did not consume either fresh thalli or artificial foods of any macroalgae as evidenced by the lack of measurable changes in wet algal mass over the course of the feeding experiments. Moreover, in contrast to the other two amphipods, no discernable algal grazing scars were evident following the feeding trials. This likely indicates that *M. pectinatus* does not exploit macroalgae directly as a food source but rather may graze on epiphytic microalgae such as diatoms that colonize the surfaces of macroalgae. Our results corroborate various reports (Chevreux 1913, Schellenberg 1931, Thurston 1972) that this species inhabits epiphytic mats growing on the holdfasts of brown (*Desmarestia sp.*) and red (Gigartinacea) macroalgae at sites along the Antarctic Peninsula and at South Georgia. Other studies have noted Antarctic amphipods that feed on epiphytes including diatoms, but these studies have focused on diatoms growing on sea ice (Richardson 1977, Richardson & Whitaker 1979). Amphipods have also been observed to feed on epiphytes growing on subtropical seagrasses (Mukai & Iijima 1995, Duffy & Harvilicz 2001).

In order to control for the effects of morphological differences in the edges of fresh thalli, we also conducted amphipod feeding assays using uniformly sized artificial alginate foods impregnated with finely ground algal tissues. While there were small differences in the ranking of consumption rates of macroalgal species between the two amphipod species, similar to the fresh thalli bioassays, both *Prostebbingia gracilis* and *Gondogeneia antarctica* have the highest consumption rates when presented pellets containing the alga *Palmaria decipiens.* However, in contrast to the fresh thalli bioassays, artificial foods containing ground tissues of the macroalgae *Myriogramme mangini* and *Gigartina skottsbergii* were also consumed at relatively high rates, indeed, in the case of *P. gracilis*, consumption rates of both these algae were statistically indistinguishable from those for *P. decipiens*. The lack of consumption of *M. mangini* and *G. skottsbergii* when presented as fresh thalli suggests that toughness may play some role in its low palatability to amphipods when presented intact. Indeed, *M. mangini* is 11th in terms of toughness and *G. skottsbergii* is the toughest amongst 30 species of macroalgae examined from the Antarctic Peninsula (Amsler et al. 2005, Peters et al. 2005). It is possible that these amphipods might exploit these macroalgae as a food resource should they be dislodged from the substrate, and subsequently broken down into detritus through grazing activities of macroherbivores and through other natural degradation processes.

Information on the feeding habits of Antarctic benthic omnivores known to include macroalgae in their diets, including the common circumpolar sea star *Odontaster validus* and the Antarctic rockfish *Notothenia coriiceps,* indicates that both *Palmaria decipiens* and *G. skottsbergii* are also palatable to these sympatric macrograzers (Amsler et al. 2005). We found the amphipod *P. gracilis* also consumes food pellets containing ground tissues of the red alga *Iridea cordata*, a species palatable to the rockfish *N. coriiceps* (Amsler et al. 2005), but chemically defended against the sea star *O. validus* (Amsler et al. 2005) and the sea urchin *Sterechinus neumayeri* (Amsler et al. 1998).

Peters et al. (2005) evaluated a suite of nutritional parameters of 40 species of macroalgae from the Antarctic Peninsula including those examined in the present study. If soluble protein content is considered a proxy for nutritional value (Cruz-Rivera & Hay 2000b, 2000a), it is clear from our regression analysis that there is no significant correlation between algal nutritional value and consumption rates of amphipods presented macroalgal food pellets. Nonetheless, it should be noted that in both fresh thalli and alginate pellet assays, *P. gracilis* and *G. antarctica* preferred the macroalga *Palmaria decipiens* which had the highest soluble protein content (9.3% dry wt) among the macroalgal species (soluble protein contents of the remaining macroalgal species ranged from 2.5% - 9.2% Peters et al. 2005).

A variety of macroalgae are known to harbor defensive secondary metabolites that are deterrent to grazers (Paul et al. 2001, Van Alstyne et al. 2001, Paul & Puglisi 2004). With respect to the present study, the brown macroalgae *Desmarestia menziesii,* *D. anceps*, and *D. antarctica* and the red algae *Plocamium cartilagineum*, *Myriogramme mangini*, and *Iridea cordata* have been shown to be chemically defended against sympatric herbivores including omnivorous sea stars and fish (Amsler et al. 2005). Four of these macroalgae (*D. anceps, D. menziesii, D. antarctica, and P. cartilagineum*) have been found to be chemically defended against herbivory by the amphipod *Gondogeneia antarctica* (Amsler et al. 2005). In the present study, in both fresh thalli and alginate pellet assays, these same four species of macroalgae were either not consumed at all or consumed in very low quantities by *Prostebbingia gracilis* and *Gondogeneia antarctica,* suggesting that chemical defenses contribute to their lack of palatability.

ACKNOWLEDGEMENTS

Field and laboratory assistance from Maggie Amsler and Anne Fairhead are gratefully acknowledged. Assistance with amphipod taxonomy from Kathy Conlan, Ed Hendrycks, and Maggie Amsler is very much appreciated. We wish to also thank those individuals employed by Raytheon Polar Services Company for providing logistical support in Antarctica. This research was facilitated by the generous support of the Office of Polar Programs of the National Science Foundation to C.D.A. and J.B.M. (OPP-0125181) and to B.J.B. (OPP-0125152). Support from an Endowed University Professorship in Polar and Marine Biology to J.B.M. is also acknowledged.

REFERENCES

Amsler CD, Iken K, McClintock JB, Amsler MO, Peters KJ, Hubbard JM, Furrow FB, Baker BJ (2005) Comprehensive evaluation of the palatability and chemical defenses of subtidal macroalgae from the Antarctic Peninsula. Mar Ecol Prog Ser 294:141-159

Amsler CD, McClintock JB, Baker BJ (1998) Chemical defense against herbivory in the Antarctic marine macroalgae *Iridaea cordata* and *Phyllophora antarctica* (Rhodophyceae). J Phycol 34:53-59

Amsler CD, Rowley RJ, Laur DR, Quetin LB, Ross RM (1995) Vertical distribution of Antarctic peninsular macroalgae: cover, biomass and species composition. Phycologia 34:424-430

Ankisetty S, Nandiraju S, Win H, Park YC, Amsler CD, MCClintock JB, Baker JA, Diyabalanage TK, Pasaribu A, Singh MP, Maiese WM, Walsh RD, Zaworotko MJ, Baker BJ (2004) Chemical investigation of predator-deterred macroalgae from the Antarctic Peninsula. J Nat Prod 67:1295-1302

Brearley A, Walker DI (1995) Isopod miners in the leaves of two Western Australian *Posidonia* species. Aquat Bot 52:163-181

Brouwer PEM, Geilen EFM, Gremmen NJM, vanLent F (1995) Biomass, cover and zonation pattern of sublittoral macroalgae at Signy Island, South Orkney Islands, Antarctica. Bot Mar 38:259-270

Chevreux E (1913) Amphipoda. Crustaces II. Voyage de Ch. Alluaud et R. Jeannel en Afrique Orientale (1911-1912). In: Resultats Scientifiques, p 11-12

Cruz-Rivera E, Hay ME (2000a) Can quantity replace quality? Food choice, compensatory feeding, and fitness of marine mesograzers. Ecology 81:201-219

Cruz-Rivera E, Hay ME (2000b) The effects of diet mixing on consumer fitness: macroalgae, epiphytes, and animal matter as food for marine amphipods. Oecologia 123:252-264

Duffy JE, Harvilicz AM (2001) Species-specific impacts of grazing amphipods in an eelgrass-bed community. Mar Ecol Prog Ser 223:201-211

Duffy JE, Hay ME (1991) Food and shelter as determinants of food choice by an herbivorous marine amphipod. Ecology 72:1286-1298

Duffy JE, Macdonald KS, Rhode JM, Parker JD (2001) Grazer diversity, functional redundancy and productivity in seagrass beds: an experimental test. Ecology 82:2417-2434

Fairhead VA, Amsler CD, McClintock JB, Baker BJ (2005) Within-thallus variation in chemical and physical defences in two species of ecologically dominant brown macroalgae from the Antarctic Peninsula. J Exp Mar Biol Ecol 322:1-12

Hay ME (1997) The ecology and evolution of seaweed-herbivore interactions on coral reefs. Coral Reefs 16:S67-S76

Hay ME, Duffy JE, Fenical W (1990) Host-plant specialization decreases predation on a marine amphipod: an herbivore in plant's clothing. Ecology 71:733-743

Hay ME, Fenical W (1988) Marine plant-herbivore interactions: the ecology of chemical defense. Ann Rev Ecol Syst 19:111-145

Hay ME, Piel J, Boland W, Schnitzler I (1998) Seaweed sex pheromones and their degradation products frequently suppress amphipod feeding but rarely suppress sea urchin feeding. Chemoecology 8:91-98

Iken K (1999) Feeding ecology of the Antarctic herbivorous gastropod *Laevilacunaria antarctica* Martens. J Exp Mar Biol Ecol 236:133-148

Iken K, Barrera-Oro ER, Quartino M-L, Casaux RJ, Brey T (1997) Grazing by the Antarctic fish *Notothenia coriiceps*: evidence for selective feeding on macroalgae. Antarctic Sci 9:386-391

Iken K, Quartino M-L, Barrera-Oro E, Palermo J, Wiencke C, Brey T (1998) Trophic relations between macroalgae and herbivores. Rpt Polar Res 299:258-262

Iken K, Quartino M-L, Wiencke C (1999) Histological identification of macroalgae from stomach contents of the Antarctic fish *Notothenia coriiceps* using semi-thin sections. Mar Ecol 20:11-17

Jażdżewski K, De Broyer C, Pudlarz M, Zielinski D (2001) Seasonal fluctuations of vagile benthos in the uppermost sublittoral of a maritime Antarctic fjord. Polar Biol 24:910-917

Jażdżewski K, De Broyer C, Teodorczyk W, Konopacka A (1991a) Survey and distributional patterns of the amphipod fauna of Admiralty Bay, King George Island, South Shetland Islands. Polish Polar Res 12:461-472

Jażdżewski K, Teodorczyk W, Sicinski J, Kontek B (1991b) Amphipod crustaceans as an important component of zoobenthos of the shallow Antarctic sublittoral. Hydrobiologia 223:105-117

Lippert H, Iken K, Rachor E, Wiencke C (2001) Macrofauna associated with macroalgae in the Kongsfjord (Spitsbergen). Polar Biol 24:512-522

Mukai H, Iijima A (1995) Grazing effects of a gammaridean Amphipoda, *Ampithoe sp.*, on the seagrass, *Syringodium isoetifolium*, and epiphytes in a tropical seagrass bed of Fiji. Ecol Res 10:243-257

Neushul M (1965) Diving observations of sub-tidal antarctic marine vegetation. Bot Mar 8:234-243

Paul VJ, Cruz-Rivera E, Thacker RW (2001) Chemical mediation of macroalgal-herbivore interactions: ecological and evolutionary perspectives. In: McClintock JB, Baker BJ (eds) Marine Chemical Ecology. CRC Press, Boca Raton, Florida, p 227-265

Paul VJ, Puglisi MP (2004) Chemical mediation of interactions among marine organisms. Nat Prod Rep 21:189-209

Peters KJ, Amsler CD, Amsler MO, McClintock JB, Dunbar RB, Baker BJ (2005) A comparative analysis of the nutritional and elemental composition of macroalgae from the western Antarcitc Peninsula. Phycologia 44:453-463

Peterson CH, Renaud PE (1989) Analysis of feeding preference experiments. Oecologia 80:82-86

Quartino ML, Klöser H, Schloss IR, Wiencke C (2001) Biomass and associations of benthic marine macroalgae from the inner Potter Cove (King Geoge Island, Antarctica) related to depth and substrate. Polar Biol 24:349-355

Richardson MG (1977) The ecology (including physiological aspects) of selected Antarctic marine invertebrates associated with inshore macrophytes. PhD Dissertation, University of Durham

Richardson MG, Whitaker TM (1979) An Antarctic fast-ice food chain: observation on the interaction of the amphipod *Pontogeneia antarctica* Chevreux with ice-associated micro-algae. Br Antarctic Surv Bull 47:107-115

Schellenberg A (1931) Gammariden und caprelliden des Magellangebietes, 2(6)

Sotka EE, Hay ME, Thomas JD (1999) Host-plant specialization by a non-herbivorous amphipod: advantages for the amphipod and costs for the seaweed. Oecologia 118:472-482

Thurston MH (1972) The crustacea amphipoda of Signy Island, South Orkney Islands. Br Antarctic Surv Sci Rep 71:1-133

Van Alstyne KL, Whitman SL, Ehlig JM (2001) Differences in herbivore preferences, phlorotannin production, and nutritional quality between juvenile and adult tissues from marine brown algae. Mar Biol 139:201-210

Table 1. Two way analysis of variance comparing consumption rates of amphipods offered eight species of fresh macroalgal thalli.

Source of		***Prostebbingia gracilis***			***Gondogeneia antarctica***		
variation	***df***	**SS**	***F* ratio**	**P**	**SS**	***F* ratio**	**P**
Algal treatments	7	9.88	8.19	<.0001	75.05	48.97	<.0001
Trial days	2	1.92	5.59	0.0056	1.97	4.49	0.0145
Algal treatments x trial days	14	16.5	6.84	<.0001	2.10	0.69	0.7798

Table 2. Regression analyses comparing macroalgal nutritional parameters to amphipod consumption rates on macroalgal food pellets (nutritional parameters from Peters et al. 2005).

Nutritional Parameter	n	Linear Equation	r^2	P
Prostebbingia gracilis				
N (%)	6	y = 0.5 x + 2.3	0.33	0.23
C (%)	6	y = 0.5 x + 26.9	0.06	0.65
C:N	6	y = -1.1x +12.7	0.16	0.43
Protein	6	y = 0.1x + 5.7	0.002	0.94
Carbohydrate	6	y = 8.3 x + 11.6	0.33	0.24
Lipid	6	y = -1.2 x + 4	0.38	0.19
Gondogeneia antarctica				
N (%)	7	y = 0.02 x + 2.6	0.27	0.23
C (%)	7	y = -0.02 x + 28.9	0.05	0.62
C:N	7	y = -0.05 x + 13	0.27	0.23
Protein	6	y = 1.3 x + 30	0.02	0.80
Carbohydrate	6	y = 0.3 x + 30.2	0.04	0.69
Lipid	6	y = -6.5 x + 52	0.34	0.22

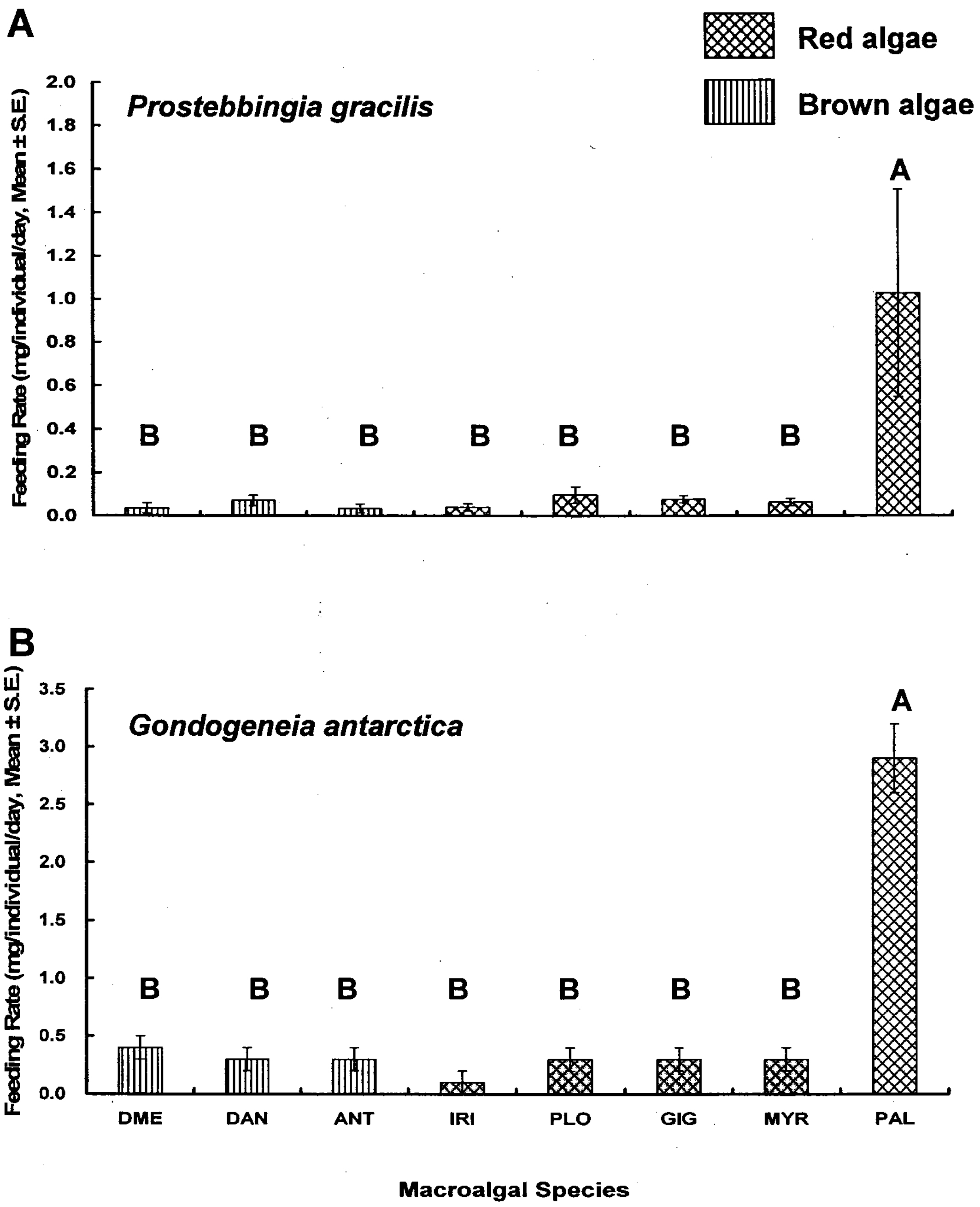

Figure 1. Results of single species feeding trials offering pieces of fresh thalli of eight Antarctic Peninsular macroalgae to the amphipods *Prostebbingia gracilis* (A) and *Gondogeneia antarctica* (B). Bars represent means ± standard error of mean (n = 12). Similar letters above bars indicate no statistical differences ($P < 0.05$) among the means (two-way ANOVA followed by Tukey's HSD). DME = *Desmarestia menziesii*; DAN = *Desmarestia anceps*; ANT = *Desmarestia antarctica*; IRI = *Iridaea cordata*; PLO = *Plocamium cartilagineum*; GIG = *Gigartina skottsbergii*; MYR = *Myriogramme mangini*; PAL = *Palmaria decipiens*. Data shown are combined across the three consecutive days of feeding trails as two-way analysis of variance indicated that statistical groupings of feeding rates did not vary between days for either amphipod species.

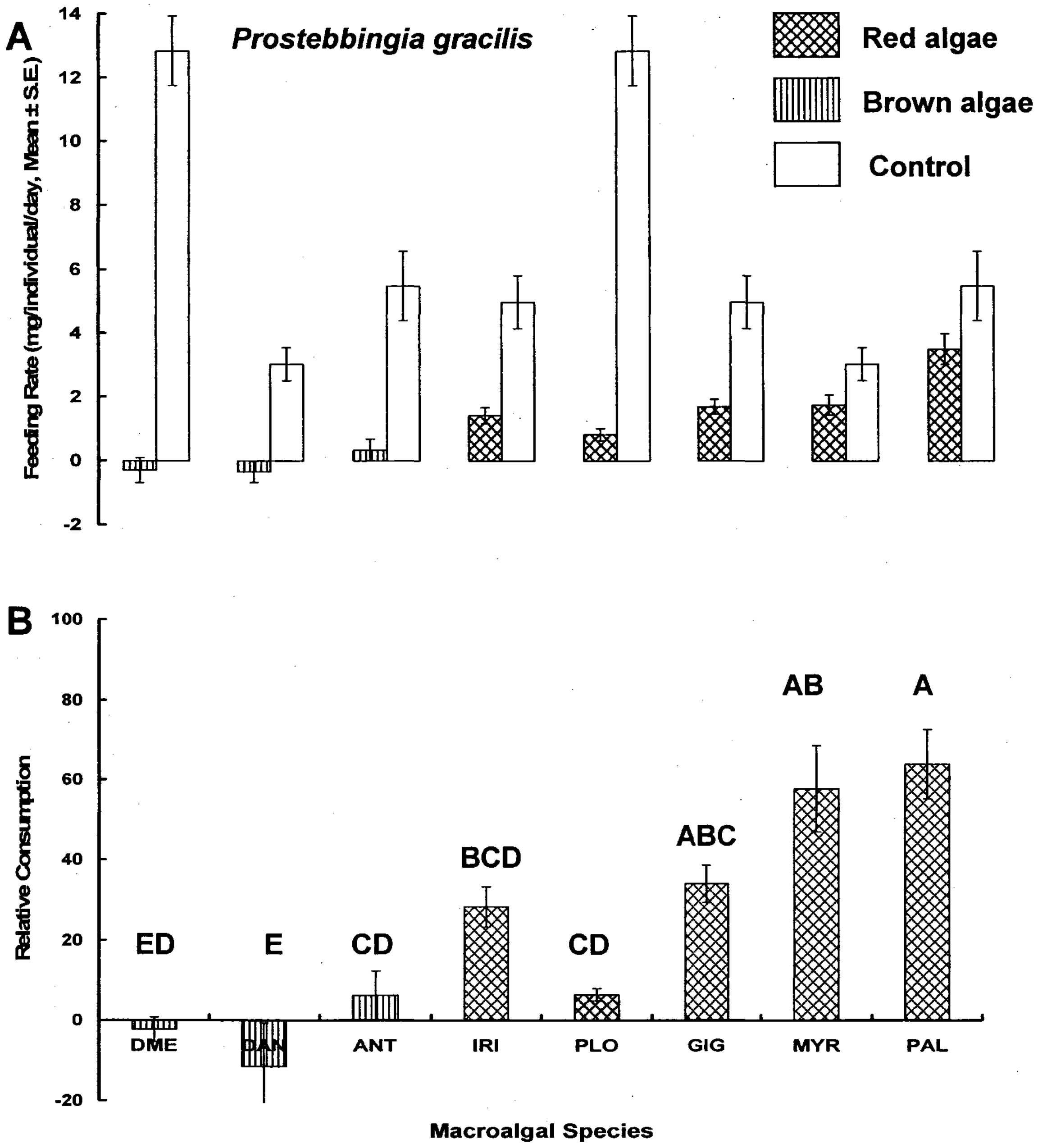

Figure 2. Results of single species feeding trials offering alginate pellets containing freeze-dried and finely ground thallus tissues of eight macroalgae to the amphipod *Prostebbingia gracilis*. (A) Net consumption rate of *P. gracilis* presented alginate food pellets containing macroalgal species. Controls consisted of alginate pellets containing the palatable green alga *Cladophora repens*. (B) Relative consumption derived from net consumption rates shown in Figure 2A. Similar letters above bars indicate no statistical difference ($P < 0.05$) among the means (Friedman's test, multiple related samples ANOVA) followed by multiple t-tests using the Bonferroni adjustment for multiple comparisons. Bars represent means ± standard error of mean ($n = 10$). See legend in Figure 1 for abbreviations of macroalgae.

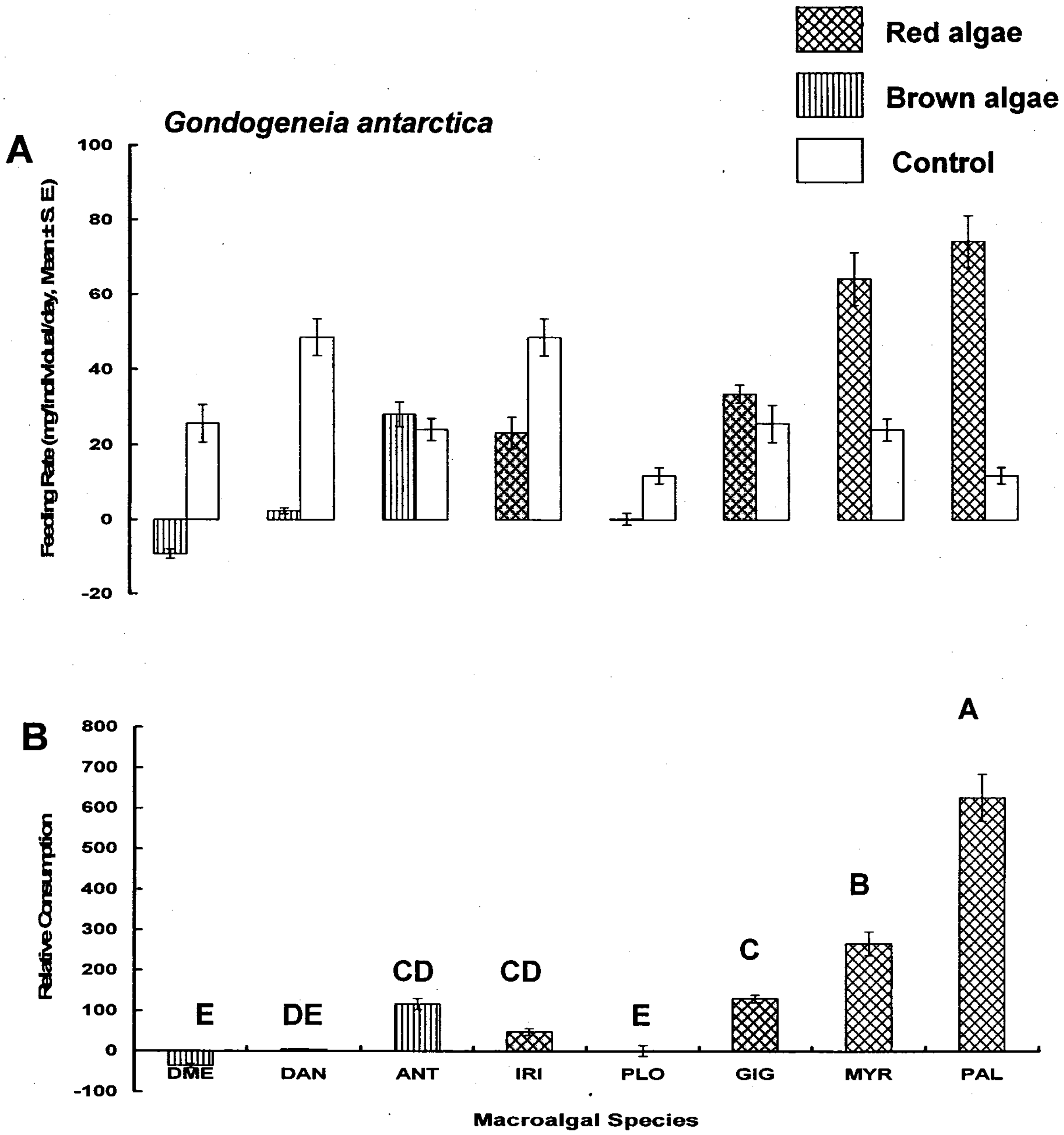

Figure 3. Results of single species feeding trials offering alginate pellets containing freeze-dried and finely ground thallus tissues of eight macroalgae to the amphipod *Gondogeneia antarctica*. (A) Net consumption rate of *G. antarctica* presented alginate food pellets containing macroalgal species. Controls consisted of alginate pellets containing the palatable green alga *Cladophora repens*. (B) Relative consumption derived from net consumption rates shown in Figure 2A. Similar letters above bars indicate no statistical difference ($P < 0.05$) among the means (Friedman's test, multiple related samples ANOVA) followed by multiple t-tests using the Bonferroni adjustment for multiple comparisons. Bars represent means ± standard error of mean ($n = 10$). See legend in Figure 1 for abbreviations of macroalgae.

SEASONAL FLUCTUATIONS OF MESOFAUNAL COMMUNITIES ASSOCIATED WITH BLADES OF TWO COMMON SEAGRASS SPECIES AND THEIR EPIPHYTES IN THE NORTHERN GULF OF MEXICO

by

YUSHENG M. HUANG, MARGARET O. AMSLER, AND JAMES B. MCCLINTOCK

In preparation for Gulf of Mexico Science

Format adapted for dissertation

ABSTRACT

Seasonal fluctuations of mesofaunal communities associated with aboveground biomass (blades) of the common seagrasses *Thalassia testudinum* and *Halodule wrightii* and their associated epiphytes were examined over a one year period in Saint Joseph Bay, Florida. Samples collected in each of 12 months revealed that *T. testudinum* seagrass blades harbored the highest levels of mesofaunal species richness and species diversity during summer. In contrast, aboveground blades of *H. wrightii* only occurred at the study sites in in six months of the study (June – Nov) with the highest levels of mesofaunal species richness and species diversity occurring in October. The most abundant groups of mesofauna to associate with the blades of *T. testudinum* were amphipods (47.9%) and gastropods (42.9%). Both groups peaked in abundance in February and April, respectively. The most abundant groups of mesofauna to associate with the blades of *H. wrightii* were gastropods (55.7%), amphipods (28%) and decapods (7.6%). These groups peaked in abundance in September, July, and October, respectively. A correlation analysis between the abundances of amphipods and gastropods and seagrass blade-associated epiphytic biomass indicated a positive correlation in some of but not all months for both seagrass species. The population densities (# per 100 g wet wt seagrass) of mesofaunal species collected from blades of both seagrasses varied significantly throughout the sampling periods. Both analyses of similarity (ANOSIM) and non-metric multidimensional scaling (MDS) demonstrated that blade-associated mesofaunal communities, (population densities and species composition) found in association with *T. testudinum* and *H. wrightii* differed significantly from one another.

INTRODUCTION

Marine mesofauna, which include the conspicuous gastropods, amphipods, isopods, and polychaetes, along with other smaller invertebrate taxa, are ubiquitous across a wide suite of marine environments. While some are free-living within the water column or occur in association with inert materials such as rock or sand substrata, most are closely associated with living substrates including macroalgae (Hay & Fenical 1988, Hay 1997, Hay et al. 1998, Lippert et al. 2001), seagrasses and their associated epiphytes (Nelson 1980, Nelson et al. 1982, Stoner 1983, Lewis 1984, Edgar 1992, Orth 1992, Jernakoff et al. 1996, Jernakoff & Nielsen 1997, Lavery & Vanderklift 2002), bryozoans (Coleman 1989), and benthic macroinvertebrates such as sponges and ascidians (Thiel 2000). These diverse living substrates may provide mesofauna with a variety of distinctive resources including food, and refuge from predation and/or environmental stresses (Duffy & Hay 1991).

Both the biological and physical factors that regulate the distribution and abundance of mesofauna associated with marine plants, and especially seagrasses, have been broadly studied (Hay & Fenical 1988, Hughes & Gliddon 1991, John et al. 1992, Jernakoff et al. 1996). These studies have demonstrated that epiphyte structure and composition (Mukai & Iijima 1995, Pavia et al. 1999), plant chemical defenses (Stachowicz & Hay 1999), predation pressure (Wooster 1998, Sparrevik & Leonardsson 1999), complexity of the habitat (Lubchenco 1978, Parker et al. 2001), and hydrological conditions (Aikins & Kikuchi 2001, Duggins et al. 2001) may all, to varying degrees, influence aspects of patterns of distribution and abundance of seagrass-associated mesofauna.

The ecology of marine seagrass meadows and their associated fauna have been intensively studied (Nelson et al. 1982, Lewis & Stoner 1983, Lewis 1987, Edgar 1992, Orth 1992, Valentine & Heck 1993, Thom et al. 1995, Jernakoff et al. 1996, Lee 1997, Bologna & Heck 1999, Boström & Mattila 1999, Leonard & McClintock 1999, Duffy et al. 2001, Schanz et al. 2002). The considerable attention given these ecological systems is related to their ecological importance and relative ease of accessibility (Hemminga & Duarte 2000). Seagrass meadows both directly and indirectly provide a wide diversity of resources for marine organisms including refugia for adult, and especially juvenile, life history stages of marine invertebrates and fish, a rich source of prey (Buck et al. 2003), facilitation in locating mates, and abundant living substrates for plant and animal recruitment (Schneider & Mann 1991b, 1991a). The collective effect of these factors is that the biomass of mesofauna within seagrass communities is on average much higher than that in neighboring unvegetated areas (Lewis 1984, Valentine & Heck 1993).

Experimental field manipulations employing techniques including caging and tethering, in addition to laboratory microcosm and mesocosm experiments, have all been employed to elucidate the mechanisms contributing to increased abundances of invertebrates and fish within seagrass beds (Nelson et al. 1982, Schneider & Mann 1991b, Boström & Mattila 1999, Zupo & Nelson 1999, Gambi et al. 2000, Hovel & Lipcius 2001, Lee et al. 2001). While many representatives of the mesofauna are known to feed on periphyton and epiphytes encrusting seagrass blades, seagrass can also be a direct food resource for mesofauna including amphipods and isopods (Boström & Mattila 1999). Studies to date on chemically mediated seagrass-animal interactions have focused primarily on the role of seagrasses in inducing the settlement of marine invertebrate larvae; however, seagrasses are also potential candidates to harbor chemical defenses against crustacean mesofauna (McMillan et al. 1980). To facilitate future studies designed to determine chemical (feeding deterrent), physical (morphology, toughness) and biological (nutrient composition, epibionts) characteristics of seagrasses as they relate to patterns of associated mesofauna, studies are first needed to compare seasonal patterns of seagrass-associated mesofaunal communities.

The main objectives of the present study were to: 1) determine and compare the seasonal patterns of abundance of seagrass biomass, associated epiphyte biomass, and a variety of parameters that characterize seagrass blade-associated mesofaunal communities (species richness and diversity, abundances of primary taxonomic groups, population density, and community composition) associated with two common species of seagrasses in a protected bay environment of the northern Gulf of Mexico, and 2) determine whether patterns of seagrass epiphytic load are correlated with the associated patterns of abundance of primary taxonomic groups of mesofauna comprising these two seagrass-associated communities.

MATERIALS AND METHODS

Study site

Saint Joseph Bay is located on the western panhandle of Florida in the northeastern Gulf of Mexico (29°N, 85.5°W) and is a semi-closed embayment well protected by an L-shaped sandy peninsula; the only connection with the Gulf of Mexico is a 3-kilometer wide opening at the northern mouth of the bay. There is little freshwater input and salinities and water temperatures range from 26 to 37 ‰ and 11 to 35 °C, respectively (Beddingfield & McClintock 2000). The mean tidal range is approximately 0.5 -1 m and wave action is minimal as the bay is well protected from the open gulf waters (Rudloe 1985). Seagrass meadows are scattered within the embayment and provide an estimated cover approximately 26 km^2 of the benthos (McNulty et al. 1972). The dominant seagrass species in the bay include the common turtle grass *Thalassia testudinum* accompanied by smaller populations of two species of eelgrasses, *Halodule wrightii* and *Syringodium filiforme* (Iverson & Bittaker 1986).

Annual fluctuation of the mesofaunal communities

Three discrete meadows of *Thalassia testudinum* and *Halodule wrightii* were identified as study sites (each meadow ranged from 10 to >100 m in diameter; *T. testudinum* – 1-2 m depth, *H. wrightii* 0 – 1 m depth). Within each of these three replicate seagrass meadows, triplicate or quadruple samples of seagrass and associated epibionts were sampled monthly over a one year period (January - December 2004). Seagrass and their associated mesofauna were collected from haphazardly selected sampling sites located approximately 3 m within the seagrass-sand border of a given seagrass bed. A PVC cylinder (103 mm radius x 600 mm height) was used to enclose above-ground blades and these were then collected by lowering the PVC sampling cylinder until it was several mm above the substratum and gently cutting the blades using scissors. Each seagrass sample and its associated mesofauna were then immediately placed in a sealed collecting bag (32.5 x 25.5 cm plastic Ziploc). Immediately following collection, seagrass samples and their associated epiphytes and mesofauna were placed in a cooler and returned to the laboratory for immediate processing. Seagrass blades were subsequently rinsed with seawater to remove all associated mesofauna, and then the collected seawater sieved through a strainer (mesh size = 1 mm) and the resultant mesofaunal organisms fixed in 5% formalin in seawater for later enumeration and identification. Epiphytes were scraped thoroughly off each seagrass blade using the edge of a glass slide and epiphytic mass determined using a microbalance (Mettler PM600). Seagrass blades from each sample were blotted to remove surface water and their fresh weight (FW) measured.

Identification of mesofauna

All collected mesofauna associated with aboveground seagrass blades were examined using a dissecting microscope (Nikon Model 77041). Taxonomic identifications of amphipods were based on keys to Florida amphipods (Thomas 1993, LeCroy 2000, 2002, 2004). Where possible molluscs were identified to genus or species (Abbott & Morris 1995). Mesofauna taxa that were not identified to genus or species levels were categorized in to broad taxonomic groupings (i.e., hermit crabs, polychaetes, nudibranchs, etc.)

Statistical analyses

The abundance of mesofauna associated with seagrasses were computed as the total number of individuals per 100g algal FW. Analysis of the structure of seagrass-associated mesofaunal assemblages included determinations of: 1) total abundance of individuals (N), 2) total number of species (S), 3) species richness (d), and 4) Shannon-Wiener diversity (H'). Quantitative statistical comparisons of monthly patterns of mesofaunal abundance and diversity associated with both species of seagrasses were conducted using a one-way ANOVA following by Tukey's Honestly Significant Difference (HSD) tests using SAS statistical software (SAS Institute Inc., Cary, NC, USA). The affinities among different seagrass species and species composition of associated mesofauna were analyzed using PRIMER (Plymouth Marine Laboratory, Plymouth, UK; Clarke and Gorley, 2001) based on the Bray-Curtis similarity index for the standardized species abundance matrix. Analysis of similarity (ANOSIM) was employed to facilitate a statistical comparison of overall similarities of mesofaunal communities associated with different seagrass species. In order to further evaluate the findings of the Bray-Curtis similarity index, a non-metric multidimensional scaling (MDS) analysis was employed that is based on a matrix of mesofaunal composition and population densities. The strength of the two-dimensional MSD display of relationships between samples is indicated by the Kruskal stress formula, with stress values < 0.1 indicative of a good outcome, and stress values > 0.2 indicative of a poor outcome. Stress values between 0.1 and 0.2 correspond to a significant depiction of relationships (McCune & Grace 2002).

RESULTS

Seagrass and epiphyte biomass

Throughout the one year study period monthly samples of aboveground blades of *Thalassia testudinum* yielded measurable quantities of blade biomass; however, aboveground blade biomass of *Halodule wrightii* was present only from June to November, 2004. Biomass (g wet wt per m^2) of aboveground blades for both seagrass species were significantly higher during the summer months (June, July, and August) and declined dramatically or disappeared in winter (ANOVA; $F_{11, 108} = 21$, $F_{5, 54} = 4.5$, respectively, $P < 0.01$; Fig 1a). Biomasses of blade-associated epiphytes also showed significant seasonal fluctuations in both seagrass species. Biomasses of blade-associated epiphytes of *T. testudinum* had significantly higher abundances in March and November when compared with other months throughout the year (ANOVA; $F_{11, 108} = 4.56$, $P < 0.01$: Fig 1b). The highest abundance of epiphytic biomass associated with the blades of *H. wrightii* occurred in July (Fig. 1b). Although not statistically significant (T-test, $P > 0.05$), the biomass of blade-associated epiphytes showed a trend of greater biomass in association with *T. testudinum* blades in March due to a temporary bloom of attached macroalgal species (e.g. *Gracilaria* sp. and *Centracerus* sp.).

Seagrass-associated mesofaunal species richness and diversity

A total of 4,174 individuals representing 53 mesofaunal taxa were found in association with blades of one or both seagrass species over the duration of the one year sampling period. Twenty of these taxa were found to occur in common, while 29 and 3 taxa, respectively, were found to be unique to *Thalassia testudinum* and *Halodule wrightii*. Monthly species richness (d) and diversity index (H') values for mesofauna associated with *T. testudinum* were lowest in January, February, March, and April and than gradually increased, reaching a peak in June (Fig. 2). Both species richness and, especially species diversity indices, for mesofauna associated with *T. testudinum* decreased in December. The species richness and diversity of mesofauna associated with *H. wrightii* over the six month period blades were present (June – Nov) were highest in

June and October and lowest in July. Except for the month of October (T-test, $P < 0.01$), species richness and diversity indices for mesofauna associated *H. wrightii* were lower that those for *T. testudinum* (Fig. 2).

Annual abundance patterns of seagrass-associated mesofaunal communities

To examine annual abundance patterns of the primary taxa comprising seagrass-associated mesofaunal communities, mesofauna were pooled into five broad categories including amphipods, isopods, decapods, gastropods, and miscellaneous taxa. Over the study period a total of 3,089 individuals were collected from the blades of *Thalassia testudinum.* These were comprised of amphipods (47.9 %), isopods (0.7 %), decapods (2.6 %), gastropods (42.9 %), and miscellaneous taxa (5.9 %) (Table 1). Total abundances of amphipods associated with *T. testudinum* were highest in February and decreased significantly in June and July (Fig 3a). Gastropods, the second most abundant taxa, were most abundant in April and then decreased throughout the winter months. With the exception of March, both isopods and decapods occurred in consistently low abundances throughout the study period (Table 1).

The annual abundance patterns of seagrass-associated mesofauna for blades of *Halodule wrightii* over the six month period (June – November) that aboveground biomass was present are illustrated in Fig. 3b. A total of 1088 individuals were collected from the blades of *H. wrightii.* These were comprised of amphipods (28 %), isopods (3 %), decapods (7.6 %), gastropod (55.7 %) and miscellaneous taxa (5.6 %). Total abundances of amphipods were highest in July, whereas other taxonomic groups occurred in significantly lower abundances during the same month (ANOVA; $F_{4,45} =$, $P < 0.05$).

A comparative analysis of mesograzer abundances between the two seagrass species indicated that the abundances of amphipods associated with *Halodule wrightii* were significantly higher than those for *T. testudinum* in June and July (T-test; $P < 0.05$). Moreover, abundances of isopods and decapods were significantly higher for blades of *H. wrightii* than for *T. testudinum* in August, September, and October and in June, September and October, respectively (Table 1). The abundances of gastropods associated with blades of *T. testudinum* were significantly higher than those for *H. wrightii* in July, Octorber, and November (T-test; $P < 0.05$).

The most numerically dominant amphipod species associated with blades of *Thalassia testudinum* were the gammarids *Cymadusa compta*, *Ampitheo longiman*, and *Erichthonius brasiliensis* (Fig. 4). *E. brasiliensis,* and the caprellid, *Paracaprella tenuis,* were collected in association with blades of *T. testudinum.* Abundances of the common isopod *Edotea montosa* were low and only occurred in association with blades of *T. testudinum* in March and June. The most numerically dominant decapod crustacean were juveniles of the shrimp *Penaeus* sp. Juvenile shrimp showed a notable increase in relative abundance in November (Fig. 4). The most abundant gastropod, *Bittium varium*, was collected from the blades of *T. testudinum* throughout the year with significant increases in abundance occurring in April. The limpet *Siphonaria* sp. was commonly found on blades of *T. testudinum* during the summer and fall (Fig. 4).

The most numerically dominant amphipod species associated with the blades of *Halodule wrightii* were the gammarids *Cymadusa compta*, *Cerapus cudjoe*, and an unidentified species (Fig. 5).. *C. compta* were collected in all sampling months except for July. Abundances of the unidentified gammarid amphipod increased significantly in the same month. The abundances of the tube-dwelling amphipod *C. cudjoe* were highest in June. Two species of isopods, *Edotea montosa* and an unidentified isopod species, occurred in relatively low abundances, with *E. montosa* detected in September and October and the unidentified species collected in every month except July. The most numerically dominant decapods were juveniles of two species of shrimp (*Penaeus* sp. and an unidentified species). Numbers of both shrimp species increased in October and November (Fig. 5). The most abundant gastropod, *Bittium varium*, was collected in June, Aug, Sept, and Nov. Hermit crabs were collected in each of the six months that *H. wrightii* blades were sampled, especially in September and October (Fig. 5).

Patterns of seagrass epiphytic biomass and mesofaunal abundances

The results of linear regression analyses between monthly epiphytic biomass and abundances of the most common mesograzers (amphipods and gastropods) are presented in Table 2. Abundances of amphipods were significantly positively correlated with *Thalassia*-associated epiphytic biomass during five of the 12 months sampled, especially during the spring and early summer (April, May, and June). Total abundances of gastropods were also significantly positively correlated with *Thalassia*-associated epiphytic biomass in May, July, and Oct. Abundances of both amphipods and gastropods were significantly positively correlated with *Halodule*-associated epiphytic biomass in two of six months that blades were sampled (July and Nov and Oct and Nov for amphipods and gastropods, respectively) (Table 2).

Mesofaunal community compositions

Mesofaunal community composition based on the population densities (# individuals per 100 g wet wt seagrass) of each species associated with blades of *T. testudinum* and *H. wrightii* were compared using analysis of similarity (ANOSIM) during the six months both seagrasses were found to simultaneously occur at the sampling sites. A Global Test for Differences between mesofaunal communities associated with blades of the two seagrass species during this six month period indicated that mesofaunal community compositions were significantly dissimilar ($R = 0.51$; $P < 0.01$). Paired tests of mesofaunal community compositions between the two seagrass species revealed these dissimilarities occurred in each month ($R = 0.50$ -0.93; $P < 0.01$) Moreover, results of a non-metric multidimensional scaling (MDS) analysis in two dimensions indicated that *T. testudinum* blade-associated mesofaunal communities were also significantly different from those associated with *H. wrightii* (Fig. 6; stress = 0.19). The stress value decreased to 0.14 when the community data were analyzed using a three dimensional approach.

DISCUSSION

Thalassia testudiun and *Halodule wrightii* are both common seagrasses in the northern Gulf of Mexico (Iverson & Bittaker 1986, Valentine & Heck 1993). Seagrasses in this subtropical region typically have their highest levels of productivity during the warmer seasons when environmental factors such as temperature, light and nutrition may be optimized for growth (Hemminga & Duarte 2000). In the present study, annual patterns of aboveground biomass of blades of both *T. testudinum* and *H. wrightii* were highest in summer months (June, July and August). This contrasts somewhat with annual patterns of aboveground biomass observed for these two seagrass species in Saint Joseph Bay, Florida by Valentine and Heck (1993). While they similarly found aboveground biomass to increase in both seagrass species from June to a peak in August, a second peak in seagrass biomasses occurred from Oct to Dec. It is possible that the much lower levels of above-ground biomass observed in the present study in the fall months are the result of lower seasonal sea water temperatures or the selection of study sites in shallower depths. Previous studies have reported that the major environmental factor influencing fluctuations of biomass of seagrasses is sea water temperature (Marbà et al. 1996, Laugier et al. 1999, Hemminga & Duarte 2000). The *T. testudnium* meadows sampled in the present study were located at the lower edge of the tidal zone with some plants experiencing aerial exposure at low tides; *H. wrightii* were located even shallower in the near-shore tidal zone at depths sufficiently shallow to routinely expose blades during diurnal low tides (Huang, pers. obs.). Although monthly sea water temperatures in Saint Joseph Bay typically range from 11 to 32.5 °C (Huang, unpublished data), winter and spring air temperatures can be as low as -4 °C (Beddingfield & McClintock 1994). Such low temperatures are likely to damage aboveground blades of seagrasses during ebb tides in Saint Joseph Bay. In the present study the potential negative effect of low temperature on the growth of *H. wrightii* meadows was particularly evident in winter and spring months (Dec – May) when aboveground biomass became undetectable. When bay sea water temperatures began to rise in the early summer (June), growth in *H. wrightii* was characterized by the rapid emergence of young blades from underground rhizomes.

The epiphytic communities associated with seagrass blades are typically comprised of a diversity of organisms including blue-green algae, diatoms, and encrusting algae, all of which are potential food recourses for grazers (reviewed by Jernakoff et al. 1996). Epiphytic assemblages associated with seagrasses in western Australia may vary significantly with seagrass species and with season (Lavery & Vanderklift 2002). Additional factors likely to influence epiphytic assemblages include seagrass morphology, age, and location (Jernakoff et al. 1996 and references inside). Although both seagrass species examined in the present study possess linear, strap-shaped aboveground blades, the width and lengths of the blades vary considerably between the species (ranges = 4-12 and 0.3 – 1 mm widths and 10-60 and 5-18 cm lengths for *T. testudinum* and *H. wrightii*, respectively). These differences may have contributed to *T. testudinum* providing a more suitable substrate for attachment of several species of drift macroalgae (*Gracilaria* sp. and *Centracerus* sp.) that were observed in the spring (March).

The higher epiphytic biomass associated with blades of *T. testudinum* occurred in summer and was attributable mainly to coralline algae that covered the majority of the surface of seagrass blades (Huang, per. obs.). Similar to *T. testudinum,* the maximum epiphytic loads (biomass) associated with the blades of *Halodule wrightii* occurred in July. This was attributable primarily to diatoms and filamentous cyanobacteria that may exploit the restricted surface areas of the blades that characterize this seagrass species. Ratios of epiphyte to seagrass biomass during the summer months were surprisingly low, a likely result of increased grazing on seagrass epiphytes by invertebrate and vertebrate macrograzers (e.g. the sea urchin *Lytechinus variegatus* and the pinfish *Lagodon rhomboides*) (Montgomery & Targett 1992, Klumpp et al. 1993, Valentine et al. 2000).

Seasonal patterns of seagrass-associated mesofaunal species richness and species diversity mirrored those of seagrass biomass. Mesofaunal species richness and species diversity was highest in the summer months, peaking in June, and generally lowest during the winter. From a macro-scale perspective, the patchy distributions of multi-species complexes of discrete seagrass meadows in Saint Joseph Bay provide a diversity of habitats for mobile mesofaunal invertebrates. During the summer months, when aboveground seagrass biomass is rapidly increasing, these increases in habitat complexity are likely to contribute to the observed increases in blade-associated mesofaunal species richness and species diversity. From a micro-scale perspective, the concomitant growth of epiphytes on the surfaces of seagrass blades during the early summer increases the heterogeneity of habitat structure, likely further contributing to higher mesofaunal species richness and species diversity (Schneider & Mann 1991b, Bologna & Heck 1999).

While few mesofauna have been observed to directly feed on seagrasses, many taxa including amphipods, isopods, and gastropods utilize seagrass-associated epiphytes directly as food resources (Mukai & Iijima 1995, Jernakoff & Nielsen 1997). In meadows of *T. testudinum,* the highest increase of blade-associated epiphytic biomass occurred in the spring (March) and was similarly reflected in an increase in both mesofaunal specie richness and species diversity. The observed decline in these variables from a peak in June to lower levels in July may be the result of top-down factors such as increased levels of pinfish predation (Nelson 1979). Both species richness and species diversity of mesofaunal communities associated with *T. testudinum* were higher than those for *H. wrightii* except for the month of October. This may be related to the larger relative surface area provided by the blades of *T. testudinum* and thus a resultant greater abundance and diversity of associated epiphytes and concomitant habitat heterogeneity that may further attract mesograzers.

Within the five primary mesofaunal groups examined in the present study (amphipods, isopods, decapods, gastropods, and miscellaneous taxa), amphipods and gastropods were the most abundant (standardized as individuals per unit seagrass mass). Both of these groups are considered to be important seagrass-associated mesograzers (Jernakoff et al. 1996). Unlike previous studies that more coarsely sampled seagrass habitats (e.g., quadrat samples, suction samples, etc), the sampling techniques employed in the present study allowed an unbiased evaluation of mesofauna that occur in unequivocal association with seagrass blades. Similar to the findings of Valentine and Heck (1993) who detected a peak abundance of amphipods associated with *T. testudinum* habitats in winter in Saint Joseph Bay, we found the abundance of *T. testudinum* blade-associated amphipods to be highest in February and gradually decrease through the spring and summer. This may be related to amphipods aggregating in higher densities upon seagrass blades during the winter months when shoot density is lower than during the summer (Huang, pers. observation). Dramatic declines in amphipod abundances associated with blades of *T. testudinum* and *H. wrightii* in July and September, respectively, may be related to increased pinfish predation as previously suggested. Mesofaunal gastropods associated with the blades of *T. testudinum* peaked in abundance in April, August, and November, generally corresponding to peaks in epiphytic biomass in March, June, and November. This suggests that mesogastropods may be exploiting epiphytes as a nutritional resource.

It is noteworthy that the July maximum in amphipod abundances found in association with blades of *Halodule wrightii* was primarily the result of the dominance of a single amphipod species (unidentified amphipod species #2). Its elongated body segments equipped with short appendages likely facilitate clinging behaviors when associating with the finer blade morphology that characterizes *H. wrightii.* During the fall (Oct, Nov), juvenile penaeid shrimp increased in abundance in association with the blades of *H. wrightii.* This contrasts with the findings of Valentine and Heck (1993) who found the highest abundances of shrimp associated with this seagrass species in the months of February and June. Previous studies of the life history of penaeid shrimp in the Gulf of Mexico have shown that the distribution and migration patterns of postlarvae are influenced by salinity (Hoese 1960, Gunter 1961). Our findings coupled with those of Valentine and Heck (1993) indicate that juvenile shrimp associate with *H. wrightii* broadly across seasons (late winter, early summer, fall) and suggest that seasonal recruitment patterns may vary interannually or within and between species (Baxter & Renfro 1966).

Epiphytized blades of the seagrass *Thalassia testudinim* have been shown to result in increased abundances and species richness of associated mesofauna (Bologna & Heck 1999). Employing artificial epiphytic structures and natural fouling epiphytes growing on artificial seagrass units, these investigators demonstrated that epiphytes function primarily as food resources rather than as shelter. Epiphytic grazing has been observed in amphipods including *Amphithoe* sp. that occurs in association with the seagrass, *Syringodium isoetifolium* (Mukai & Iijima 1995). In the present study, regression analyses indicated that abundances of amphipods were positively correlated with the biomass of epiphytes associated with the blades of *T. testudinum* and *H. wrightii* in at least some months representative of spring, summer and fall. In addition, abundances of gastropods were positively correlated with epiphytic biomass in several months of both summer and fall for both seagrass species.

A non-metric multi-dimensional scaling (MDS) analysis demonstrated that mesofaunal communities (population densities of each collected species and species composition) associated with aboveground blades of *T. testudinum* and *H. wrightii* were significantly different from one another during the entire collective six month sampling period when aboveground biomass of both seagrasses co-occurred. Moreover, an analysis of similarity (ANOSIM) revealed that the mesofaunal communities associated with blades of both seagrass species differed from one another in each of these six months. These observations are similar to previous studies that have found community level differences in blade-associated mesograzers in meadows comprised of different species of seagrasses (Lewis 1987, Schneider & Mann 1991b, 1991a, Edgar 1992, Valentine & Heck 1993). Mesofauna may actively or passively select blade-associated habitats based on a variety of factors including seagrass architecture, associated biofilms and epiphytic assemblages, hydrological conditions, and as refugia from predation (Jernakoff et al. 1996). The present study provides further evidence that studies of the dynamics of seagrass communities and their associated mesograzers and epiphytes necessitate incorporation of patterns of their temporal and spatial variation.

ACKNOWLEDGMENTS

We appreciate being provided with access to Saint Joseph Peninsula State Park, Port Saint Joe, Florida for purposes of field sampling. We also gratefully acknowledge Dr. Sara LeCroy of the Gulf Coast Research Laboratory in Ocean Springs, Mississippi who will be examining our amphipod and isopod collections to ensure that taxonomic identifications are correct prior to publication of this dissertation chapter in the peer reviewed literature. This research was facilitated by the generous support of the Department of Biology, University of Alabama at Birmingham. Support from an Endowed University Professorship in Polar and Marine Biology to J. B. M. is also acknowledged.

REFERENCES

Abbott RT, Morris PA (1995) A Field Guide to Shells - Atlantic and Gulf Coasts and the West Indies, Vol. Houghton Mifflin Company, New York, NY

Aikins S, Kikuchi E (2001) Water current velocity as an environmental factor regulating the distribution of amphipod species in Gamo Lagoon, Japan. Limnology 2:185-191

Baxter KN, Renfro WC (1966) Seasonal occurrence and size distribution of postlarval brown and white shrimp near Galveston, Texas, with notes on species identification. Fish Bull 66:149-158

Beddingfield SD, McClintock JB (1994) Environmentally-induced catastrophic mortality of the sea urchin Lytechinus variegatus in shallow seagrass habitats of Saint Joseph's Bay, Florida. Bull Mar Sci 55:235-240

Beddingfield SD, McClintock JB (2000) Demographic Characteristics of *Lytechinus variegatus* (Echinoidea: Echinodermata) from three habitats in a north Florida bay, Gulf of Mexico. Mar Biol 21:17-40

Bologna PAX, Heck KLJ (1999) Macrofaunal associations with seagrass epiphytes: Relative importance of trophic and structural characteristics. J Exp Mar Biol Ecol 242:21-39

Boström C, Mattila J (1999) The relative importance of food and shelter for seagrass-associated invertebrates: a latitudinal comparison of habitat choice by isopod grazers. Oecologia 120:162-170

Buck TL, Breed GA, Pennings SC, Chase ME, Zimmer M, Carefoot TH (2003) Diet choice in an omnivorous salt-marsh crab: different food types, body size, and habitat complexity. J Exp Mar Biol Ecol 292:103-116

Coleman CO (1989) *Gnathiphimedia mandibularis* K. H. Barnard 1930, an Antarctic amphipod (Acanthonotozomatidae, Crustacea) feeding on Bryozoa. Antarctic Sci 1:343-344

Duffy JE, Hay ME (1991) Food and shelter as determinants of food choice by an herbivorous marine amphipod. Ecology 72:1286-1298

Duffy JE, Macdonald KS, Rhode JM, Parker JD (2001) Grazer diversity, functional redundancy and productivity in seagrass beds: an experimental test. Ecology 82:2417-2434

Duggins D, Eckman JE, Siddon CE, Klinger T (2001) Interactive roles of mesograzers and current flow in survival of kelps. Mar Ecol Prog Ser 223:143-155

Edgar GJ (1992) Patterns of colonization of mobile epifauna in a Western Australian seagrass bed. J Exp Mar Biol Ecol 157:225-246

Gambi MC, Zupo V, Buia MC, Mazzella L (2000) Feeding ecology of *Platynereis dumerilii* (Audouin & Milne-Edwards) in the seagrass *Posidonia oceanica* system: the role of the epiphytic flora (Polychaeta, Nereididae). Ophelia 53:189-202

Gunter G (1961) Habitat of juvenile shrimp (Family Penaeidae). Ecology 42:5980600

Hay ME (1997) The ecology and evolution of seaweed-herbivore interactions on coral reefs. Coral Reefs 16:S67-S76

Hay ME, Fenical W (1988) Marine plant-herbivore interactions: the ecology of chemical defense. Ann Rev Ecol Syst 19:111-145

Hay ME, Piel J, Boland W, Schnitzler I (1998) Seaweed sex pheromones and their degradation products frequently suppress amphipod feeding but rarely suppress sea urchin feeding. Chemoecology 8:91-98

Hemminga MA, Duarte CM (2000) Seagrass Ecology, Vol. Cambridge University Press, Cambridge, UK; New York, NY, USA:

Hoese HD (1960) Juvenile penaeid shrimp in the shallow Gulf of Mexico. Ecology 41:592-593

Hovel KA, Lipcius RN (2001) Habitat fragmentation in a seagrass landscape: patch size and complexity control blue crab survival. Ecology 82:1814-1829

Hughes RN, Gliddon CJ (1991) Marine plants and their herbivores: coevolutionary myth and precarious mutualisms. Phil Trans E Soc Lond 333:231-239

Iverson RL, Bittaker HF (1986) Seagrass distribution and abundance in the eastern Gulf of Mexico waters. Estuar Coast Shelf Sci 22:577-602

Jernakoff P, Brearley A, Nielsen J (1996) Factors affecting grazer-epiphyte interactions in temperate seagrass meadows. Oceanogr Mar Biol Ann Rev 34:109-162

Jernakoff P, Nielsen J (1997) The relative importance of amphipod and gastropod grazers in *Posidonia sinuosa* meadows. Aquat Bot 56:183-202

John DM, Hawkins SJ, Price JH (1992) Plant-Animal Interactions in the Marine Benthos, Vol. Oxford University Press, New York

Klumpp DW, Stlita-Espinosa JT, Fortes MD (1993) Feeding ecology and trophic role of sea urchins in a tropical seagrass community. Aquat Bot 45:205-229

Laugier T, Rigollet V, De Casabiance M-L (1999) Seasonal dynamics in mixed ellgrass beds, *Zostera marina* L. and *Z. noltii* Hornem., in a Mediterranean coastal lagoon (Thau lagoon, France). Aquat Bot 63:51-69

Lavery PS, Vanderklift MA (2002) A comparision of spatial and temporal patterns in epiphytic macroalgal assemblages of the seagrasses *Amphibolis griffithii* and *Posidonia coriacea*. Mar Ecol Prog Ser 236:99-112

LeCroy SE (2000) An Illustrated Identification Guide to the Nearshore Marine and Estuarine Gammaridean Amphipoda of Florida, Vol 1, Tallahassee, Florida

LeCroy SE (2002) An Illustrated Identification Guide to the Nearshore Marine and Estuarine Gammaridean Amphipods of Florida, Vol 2, Tallahassee, Florida

LeCroy SE (2004) An Illustrated Identification Guide to the Nearshore Marine and Estuarine Gammaridean Amphipoda of Florida, Vol 3, Tallahassee, Florida

Lee SY (1997) Annual cycle of biomass of a threatened population of the intertidal seagrass *Zostera japonica* in Hong Kong. Mar Biol 129:183-193

Lee SY, Fong CW, Wu RSS (2001) The effects of seagrass (*Zostera japonica*) canopy structure on associated fauna: a study using artificial seagrass units and sampling of natural beds. J Exp Mar Biol Ecol 259:23-50

Leonard CL, McClintock JB (1999) The population dynamics of the brittlestar *Pohioderma brevispinum* in near- and farshore seagrass habitats of port Saint Joseph Bay, Florida. Gulf Mexi Sci:87-94

Lewis FG (1984) Distribution of macrobenthic crustaceans associated with *Thalassia, Halodule* and bare sand substrata. Mar Ecol Prog Ser 19:101-113

Lewis FG (1987) Crustacean epifauna of seagrass and macroalgae in Apalachee Bay, Florida, USA. Mar Biol 94:219-229

Lewis FG, Stoner AW (1983) Distribution of macrofauna within seagrass beds; an explanation for patterns of abundance. Bull Mar Sci 33:296-304

Lippert H, Iken K, Rachor E, Wiencke C (2001) Macrofauna associated with macroalgae in the Kongsfjord (Spitsbergen). Polar Biol 24:512-522

Lubchenco J (1978) Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. Am Nat 112:23-39

Marbà N, Cebrián J, Enríquez S, Duarte CM (1996) Growth patterns of Western Mediteranean seagrasses: species-specific responses to seasonal forcing. Mar Ecol Prog Ser 133:203-215

McCune B, Grace JB (2002) Analysis of Ecological Communities, Vol. MjM Software Design, Gleneden Beach, Oregon, USA

McMillan C, Zapata O, Escobar L (1980) Sulphated phenolic compounds in seagrasses. Aquat Bot 8:267-278

McNulty JK, Lindahl WC, Sykes JE (1972) Cooperative Gulf of Mexico estuarine inventory and study, Florida: phase I, area description. NOAA Technical Report NMFS 368:1-368

Montgomery JLM, Targett TE (1992) The nutritional role of seagrass in the diet of the omnivorous pinfish Lagodon rhomboides (L.). J Exp Mar Biol Ecol 158:37-57

Mukai H, Iijima A (1995) Grazing effects of a gammaridean Amphipoda, *Ampithoe sp.*, on the seagrass, *Syringodium isoetifolium*, and epiphytes in a tropical seagrass bed of Fiji. Ecol Res 10:243-257

Nelson WG (1979) Experimental studies of selective predation on amphipods: consequences for amphipod distribution and abundance. J Exp Mar Biol Ecol 38:225-245

Nelson WG (1980) The biology of eelgrass (*Zostera marina* L.) amphipods. Crustaceana 39:59-89

Nelson WG, Cairns KD, Virnstein RW (1982) Seasonality and spatial patterns of seagrass-associated amphipods of the Indian River Lagoon, Florida. Bull Mar Sci 32:121-129

Orth RJ (1992) A perspective on plant-animal interactions in seagrasses: physical and biological determinants influencing plant and animal abundance. In: John DM, Hawkins SJ, Price JH (eds) Plant-Animal Interactions in the Marine Benthos, Systematics Association Special Volume No 46. Clarendon Press, Oxford, p 147-164

Parker JD, Duffy JE, Orth RJ (2001) Plant species diversity and composition: experimental effects on marine epifaunal assemblages. Mar Ecol Prog Ser 224:55-67

Pavia H, Carr H, Åberg P (1999) Habitat and feeding preferences of crustacean mesoherbivores inhabiting the brown seaweed *Ascophylum nodosum* (L.) Le Jol. and its epiphytic macroalgae. J Exp Mar Biol Ecol 236:15-32

Rudloe A (1985) Variation in the expression of lunar and tidal rhythms in the horseshoe crab, *Limulus polyphemus*. Bull Mar Sci 36:388-395

Schanz A, Polte P, Asmus H (2002) Cascading effects of hydrodynamics on an epiphyte-grazer system in intertidal seagrass beds of the Wadden Sea. Mar Biol 141:287-297

Schneider FI, Mann KH (1991a) Species specific relationships of invertebrates to vegetation in a seagrass bed. I. Correlational studies. J Exp Mar Biol Ecol 145:101-117

Schneider FI, Mann KH (1991b) Species specific relationships of invertebrates to vegetation in a seagrass bed. II. Experiments on the importance of macrophyte shape, epiphyte cover and predation. J Exp Mar Biol Ecol 145:119-139

Sparrevik E, Leonardsson K (1999) Direct and indirect effects of predation by *Saduria entomon* (Isopoda) on the size-structure of *Monoporeia affinis* (Amphipoda). Oecologia 120:77-86

Stachowicz JJ, Hay ME (1999) Reducing predation through chemically mediated camouflage: indirect effects of plant defenses on herbivores. Ecology 80:495-509

Stoner AW (1983) Distributional ecology of amphipods and tanaidaceans associated with three sea grass species. J Crus Biol 3:505-518

Thiel M (2000) Population and reproductive biology of two sibling amphipod species from ascidians and sponges. Mar Biol 137:661-674

Thom R, Miller B, Kennedy M (1995) Temporal patterns of grazers and vegetation in a temperate seagrass system. Aquat Bot 50:201-205

Thomas JD (1993) Identification Manual for the Marine Amphipoda: (Gamaaridea) I. Common Coral Reef and Rocky Bottom Amphipods of South Florida

Valentine JF, Heck KL (1993) Mussels in seagrass meadows: their influence on macroinvertebrate abundance and secondary production in the northern Gulf of Mexico. Mar Ecol Prog Ser 96:63-74

Valentine JF, Jr KLH, Kirsch KD, webb D (2000) Role of sea urchin *Lytechinus variegatus* grazing in regulating subtropical turtlegrass *Thalassia testudinum* meadows in the Florida Keys (USA). Mar Ecol Prog Ser 200:213-228

Wooster DE (1998) Amphipod (*Gammarus minus*) responses to predators and predator impact on amphipod density. Oecologia 115:253-259

Zupo V, Nelson WG (1999) Factors influencing the association patterns of *Hippolyte zostericola* and *Palaemonetes intermedius* (Decapoda: Natantia) with seagrasses of the Indian River Lagoon, Florida. Mar Biol 134:181-190

Table 1. Mean abundance (individuals per 100 g. wet wt. seagrass) of the major taxonomic groups associated with aboveground seagrass blades in St. Joseph Bay, Florida, in 2004. T: *Thalassis testudinum*; H: *Halodule wrightii*. Bold print indicates those abundances that were statistically significantly higher than the other abundance within the same month (T-test; $P < 0.05$).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Amphipods												
T	1383	5863	1100.8	290.7	138.9	19.2	7.9	25.7	26.0	25.6	**43.4**	33.4
H						**38.3**	**311.6**	51.0	18.1	27.8	17.0	
Isopods												
T	0	42.7	88.6	0	4.6	0.6	0	0	0	0	0	2.8
H						23.4	0	**7.8**	**2.6**	**6.2**	0.8	
Decapods												
T	10	7.1	105.2	14.8	8	0.9	1.7	9.2	0.8	4.6	0.6	0
H						**28.7**	0.8	12.7	**13.8**	**65.1**	43.9	
Gastropods												
T	62	161.8	373.1	1663	156.2	101.7	**117.3**	237.4	97.2	**93.8**	**128.1**	8
H						117.8	5.5	516.8	270.1	27.8	31.2	
Miscellaneous Taxa												
T	52	72.4	27.7	67.7	48.8	28.3	12.7	19.2	15.9	2.6	13.1	1.4
H						14.1	8.2	19.6	**41.4**	**36.6**	6.3	

Table 2. Regression analyses of epiphytic biomass and abundances of two potential mesograzers (amphipods and gastropods), associated with the blades of two common seagrass species.

Thalassia testudinum associated epiphytes (biomass) versus Amphipod abundance

	N	Linear Equation	r^2	P value
JAN	10	$y = 0.007x + 0.06$	0.42	0.04
FEB	10	$y = 0.002x + 0.56$	0.02	0.68
MAR	10	$y = -0.035x + 2.48$	0.04	0.56
APR	10	$y = 0.128x + 0.10$	0.55	0.01
MAY	10	$y = 0.056x + 0.05$	0.58	0.01
JUN	10	$y = 0.339x + 0.28$	0.88	< 0.01
JUL	10	$y = 0.456x + 0.36$	0.70	0.09
AUG	10	$y = 0.018x + 0.40$	0.01	0.15
SEP	10	$y = -0.035x + 0.37$	0.04	0.58
OCT	10	$y = 0.287x + 0.47$	0.70	0.002
NOV	10	$y = -0.142x + 2.71$	0.17	0.24
DEC	10	$y = 0.001x + 0.07$	0.00	0.97

Thalassia testudinum associated epiphytes (biomass) versus gastropod abundance

	n	Linear Equation	r^2	P value
JAN	10	$y = 0.036x + 0.18$	0.10	0.38
FEB	10	$y = 0.002x + 0.56$	0.03	0.62
MAR	10	$y = -0.135x + 2.69$	0.07	0.46
APR	10	$y = 0.017x + 0.26$	0.08	0.40
MAY	10	$y = 0.059x - 0.02$	0.58	0.01
JUN	10	$y = 0.018x + 1.01$	0.02	0.67
JUL	10	$y = 0.05x + 0.15$	0.68	< 0.01
AUG	10	$y = 0.001x + 0.44$	0.01	0.82
SEP	10	$y = -0.014x + 0.36$	0.01	0.81
OCT	10	$y = 0.15x + 0.87$	0.51	0.02
NOV	10	$y = -0.065x + 2.43$	0.05	0.55
DEC	10	$y = 0x + 0.07$	0	n/a

Table 2. (Continue)

Halodule wrightii associated epiphytes (biomass) versus amphipod abundance

	n	Linear Equation	r^2	P value
JUN	10	$y = 0.164 x + 0.99$	0.03	0.65
JUL	10	$y = 0.079 x + 0.32$	0.66	<0.01
AUG	10	$y = 0.008 x + 0.28$	0.07	0.45
SEP	10	$y = 0.005 x + 0.18$	0.01	0.80
OCT	10	$y = -0.045 x + 0.38$	0.15	0.27
NOV	10	$y = 0.093 x + 0.21$	0.57	0.01

Halodule wrightii associated epiphytes (biomass) versus gastropod abundance

	N	Linear Equation	r^2	P value
JUN	10	$y = 0.057 x + 0.85$	0.15	0.27
JUL	10	$y = - 1.6 x + 2.36$	0.20	0.20
AUG	10	$y = - 0.001 x + 0.28$	0.04	0.57
SEP	10	$y = - 0.003 x + 0.20$	0.07	0.45
OCT	10	$y = - 0.076 x + 0.42$	0.55	0.01
NOV	10	$y = 0.093 x + 0.15$	0.58	0.01

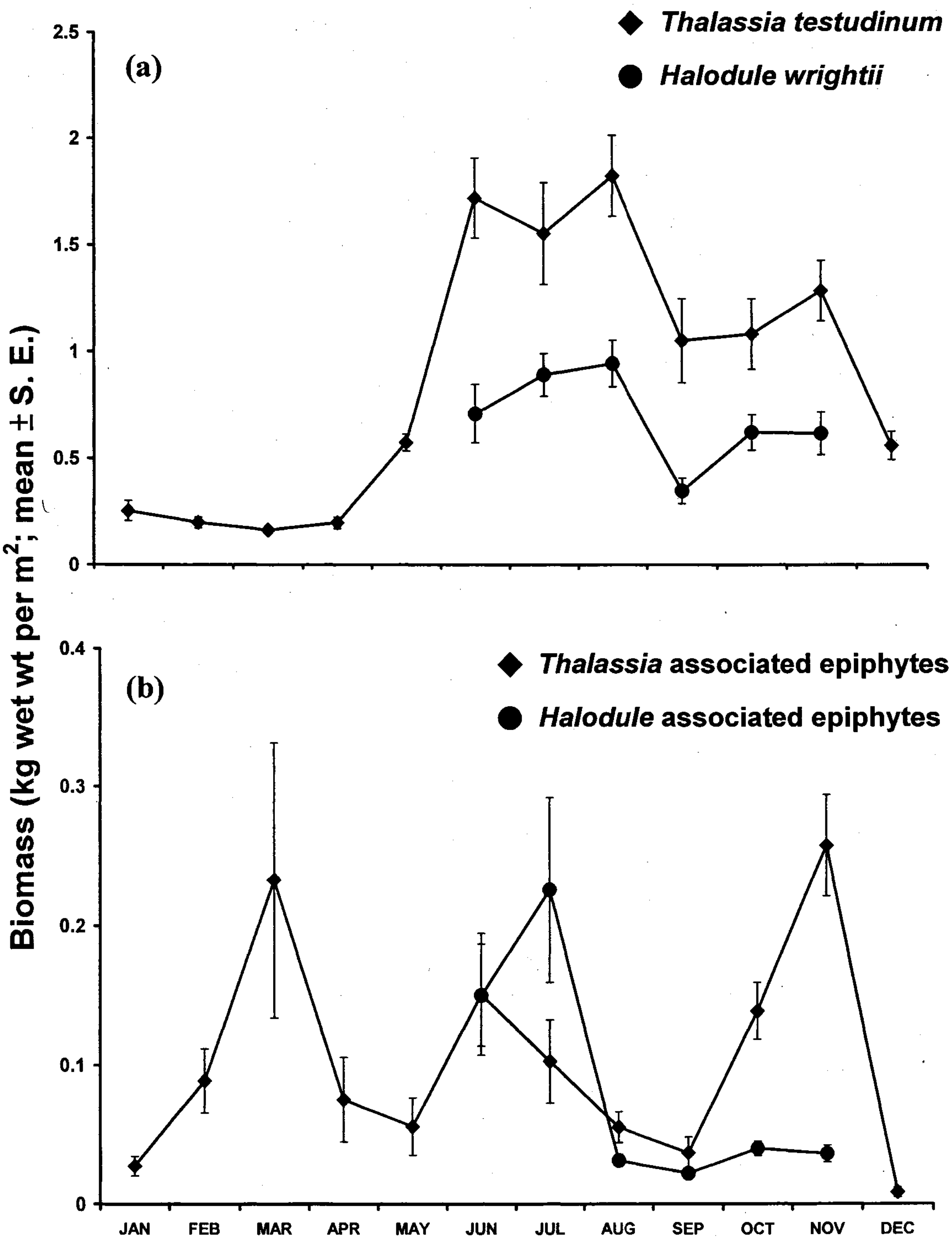

Figure 1. Mean aboveground biomass of the common seagrasses *Thalassia testudinum* and *Halodule wrightii* (Figure 1a) and their associated epiphytes (Figure 1b) in Saint Joseph Bay, Florida, from January to December, 2004. Means ± SE. One-way ANOVA; $P < 0.05$.

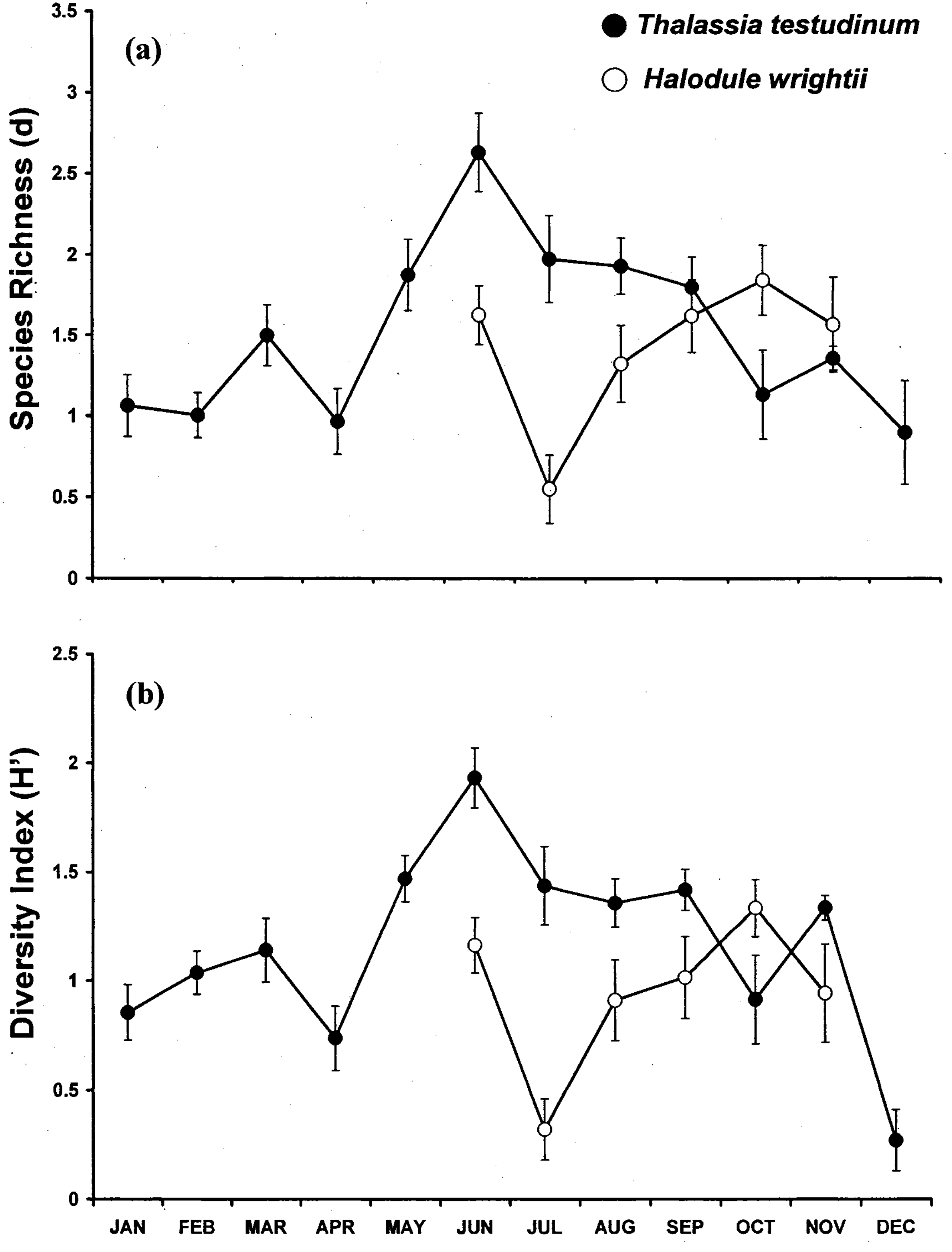

Figure 2. Mean species richness (Figure 2a) and Shannon-Wiener diversity indices (Figure 2b) of mesofaunal communities associated with blades of the common seagrasses *Thalassia testudinum* and *Halodule wrightii* in Saint Joseph Bay, Florida, from January to December, 2004. Means ± SE. One-way ANOVA; $P < 0.05$.

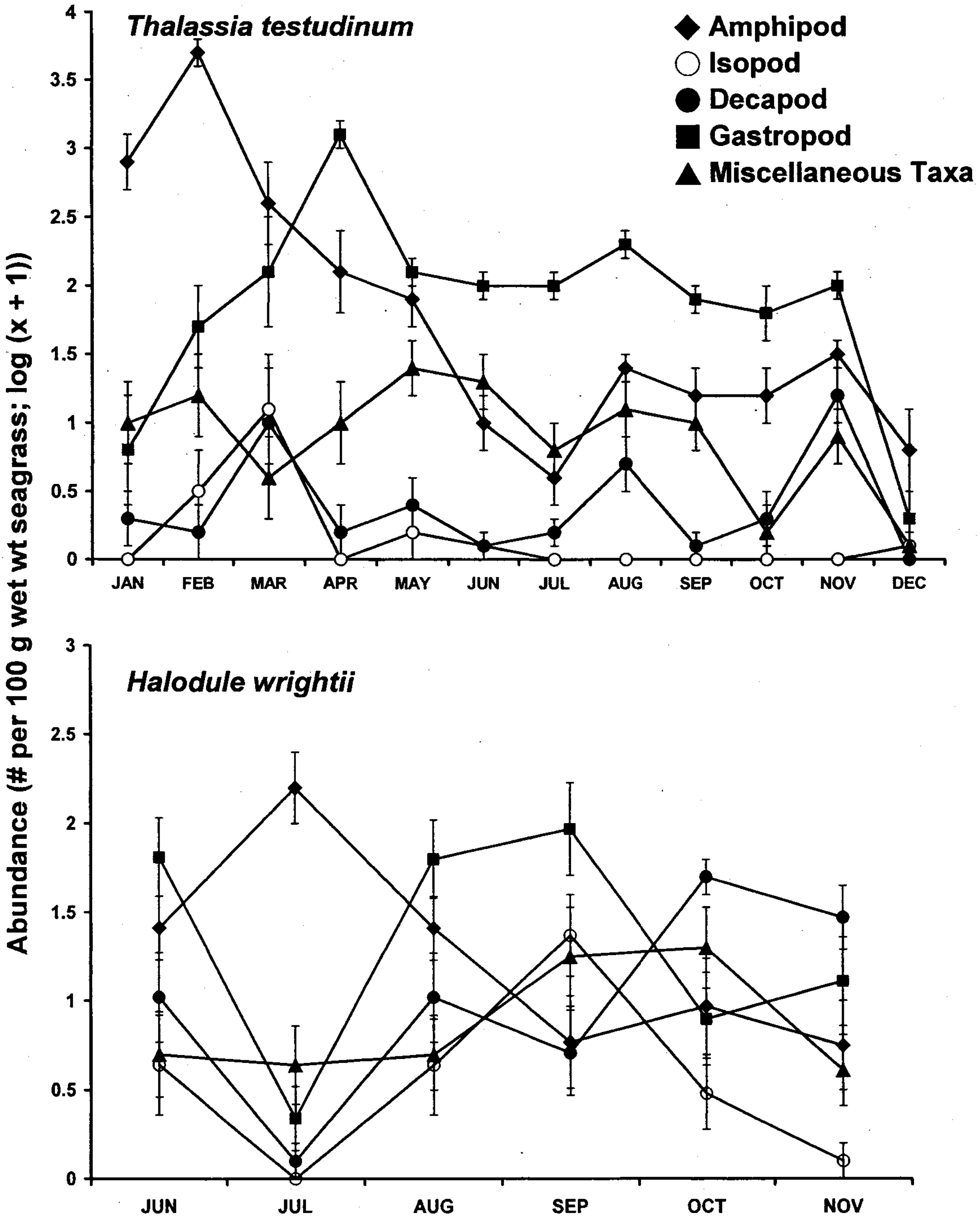

Figure 3. Abundances (# per 100 g wet wt seagrass; all data log (x + 1) transformed) of the major mesofaunal invertebrate groups associated with blades of the common seagrasses *Thalassia testudinum* and *Halodule wrightii* in Saint Joseph Bay, Florida from January to December, 2004.

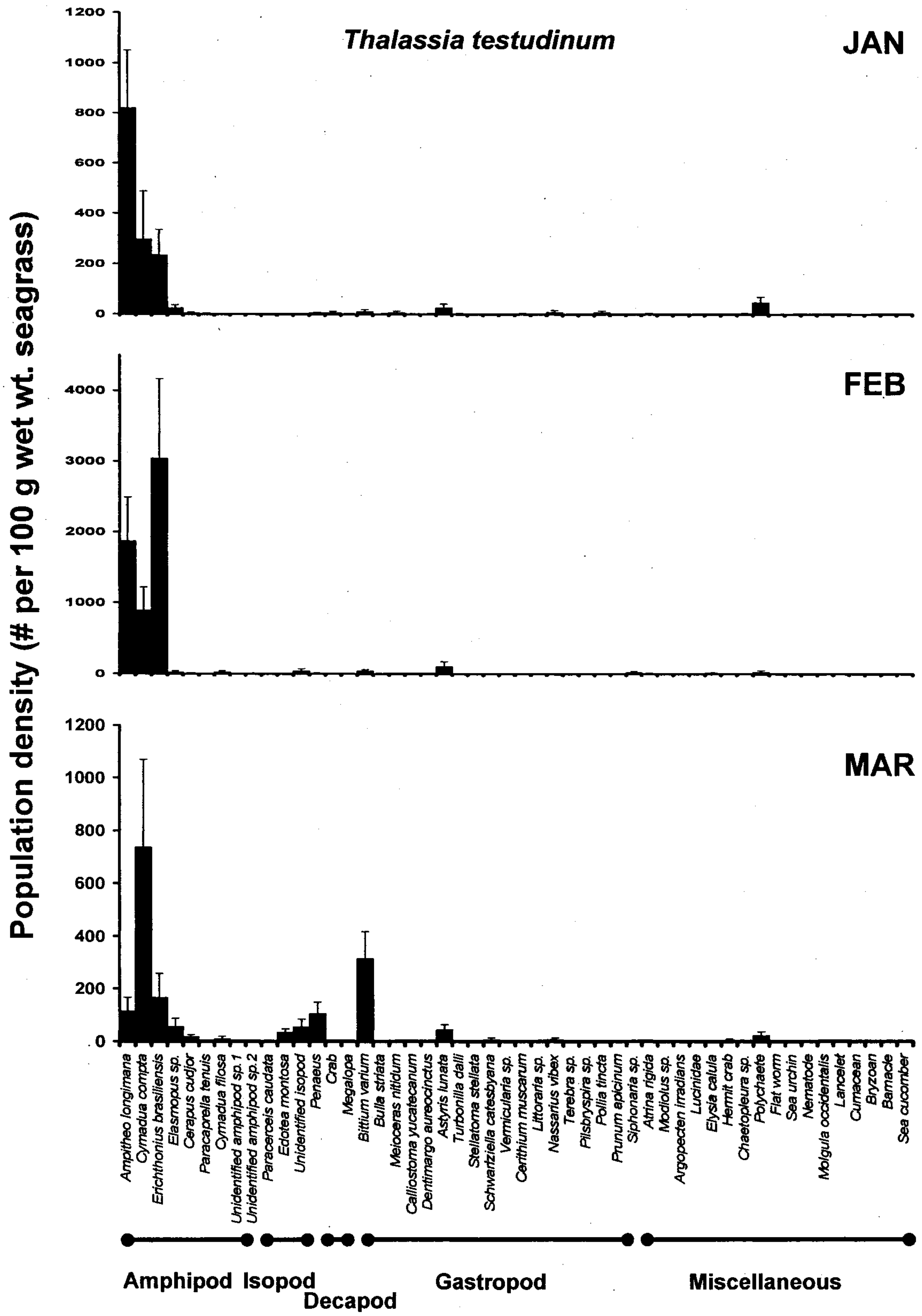

Figure 4. Population densities of mesofaunal species (# per 100 g wet wt seagrass; means ± SE) associated with the blades of *Thalassia testudinum* in Saint. Joseph Bay, Florida from Jan to Dec, 2004.

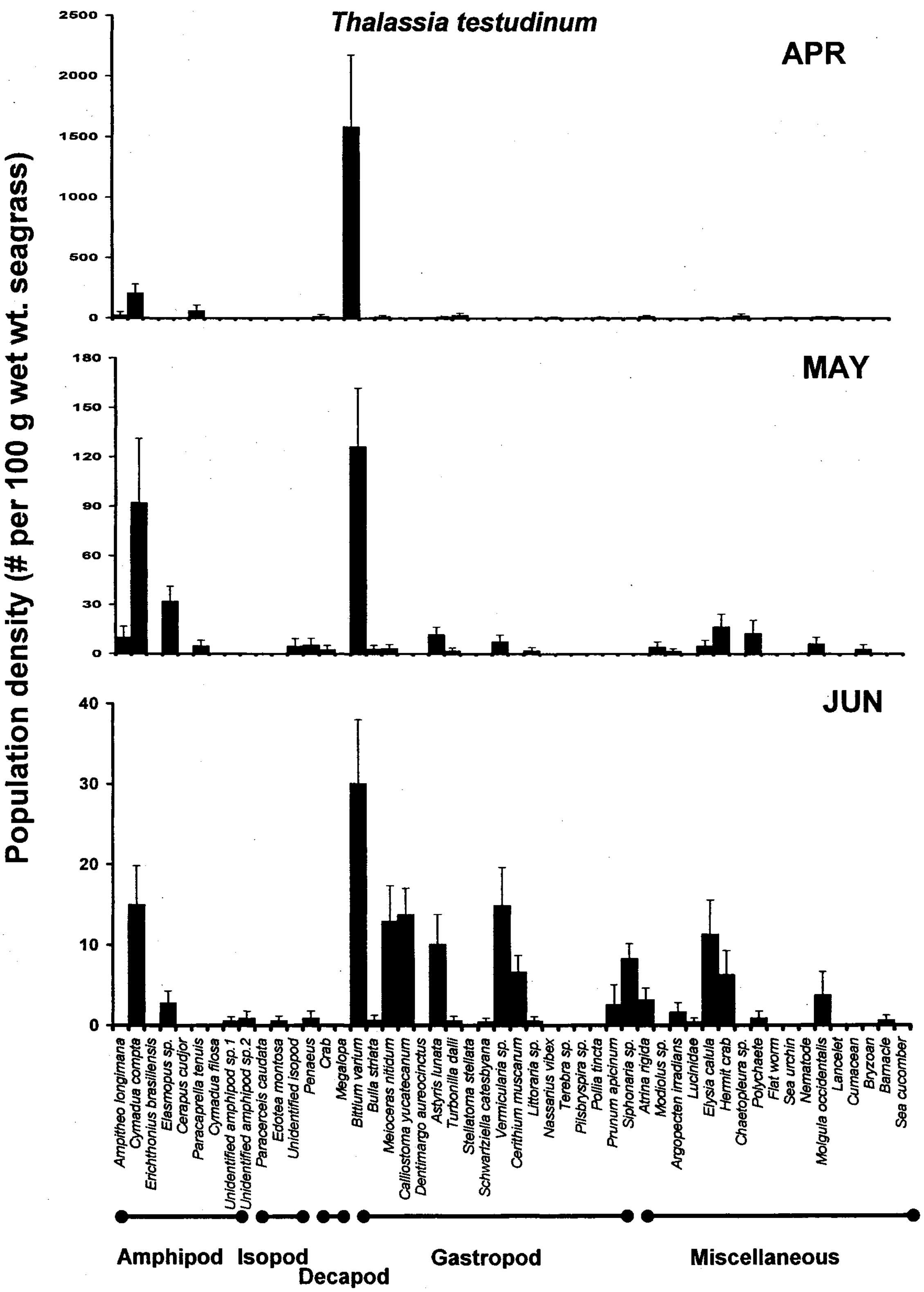

Fig. 4 (Continued)

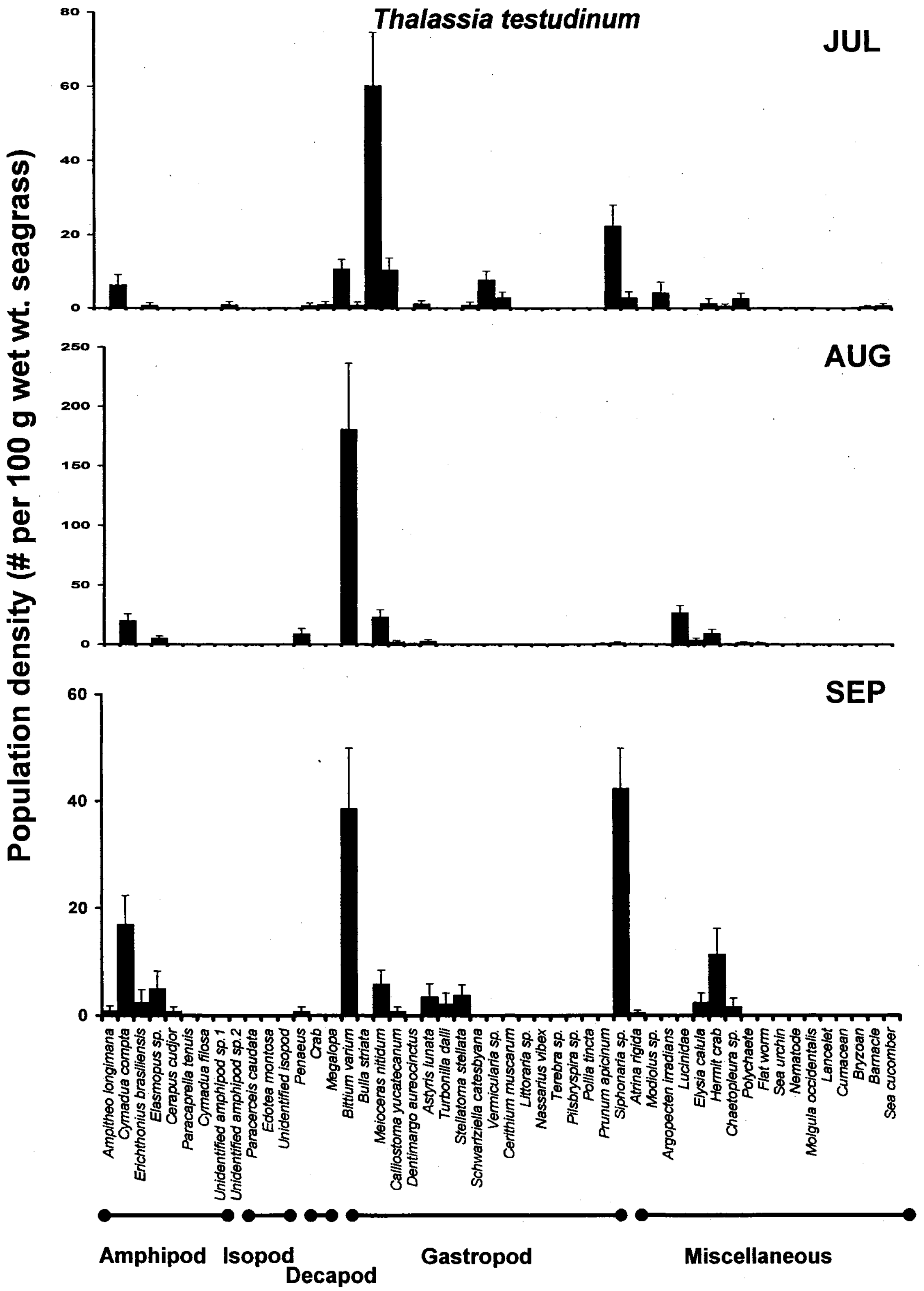

Fig. 4 (Continued)

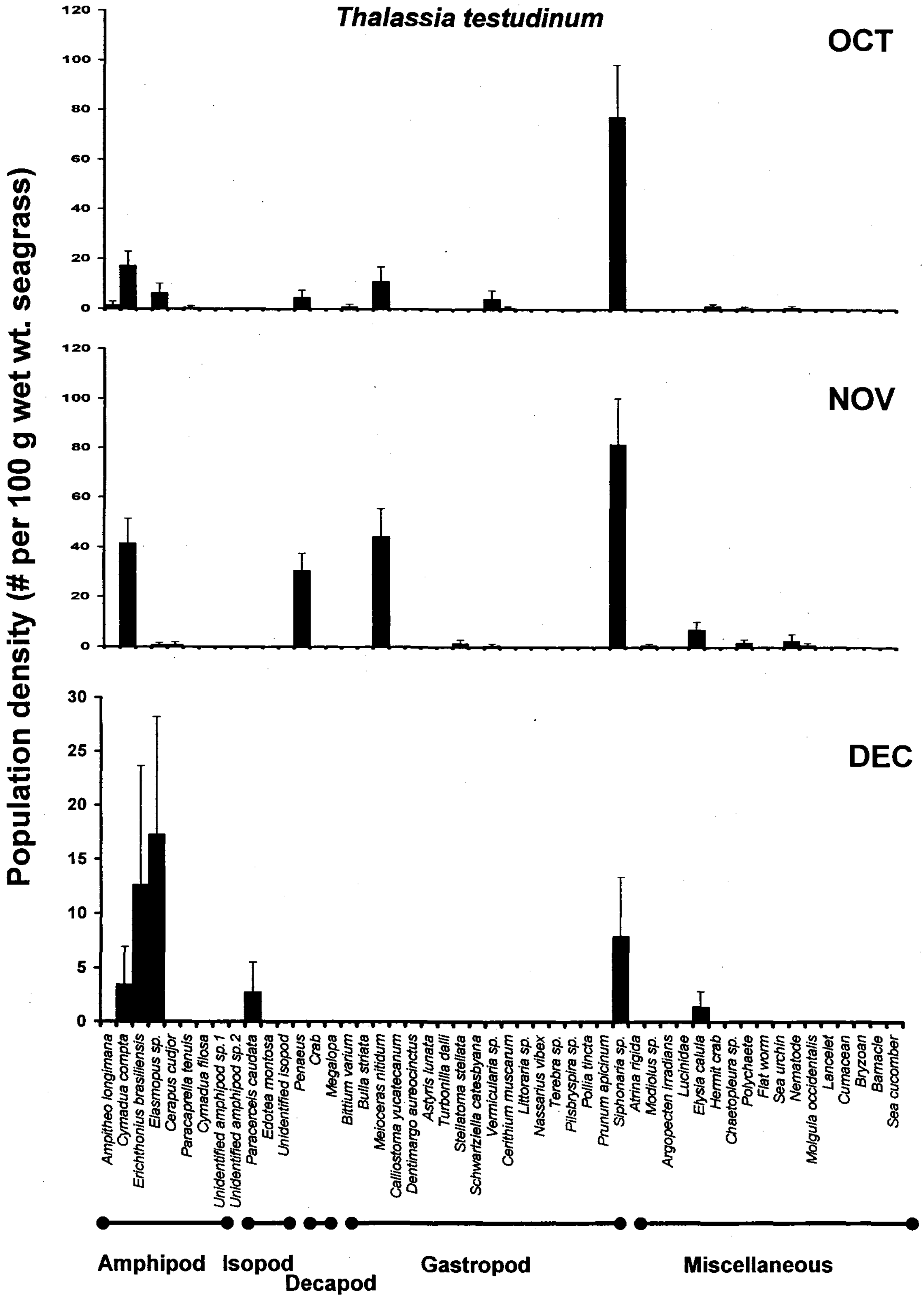

Fig. 4 (Continued)

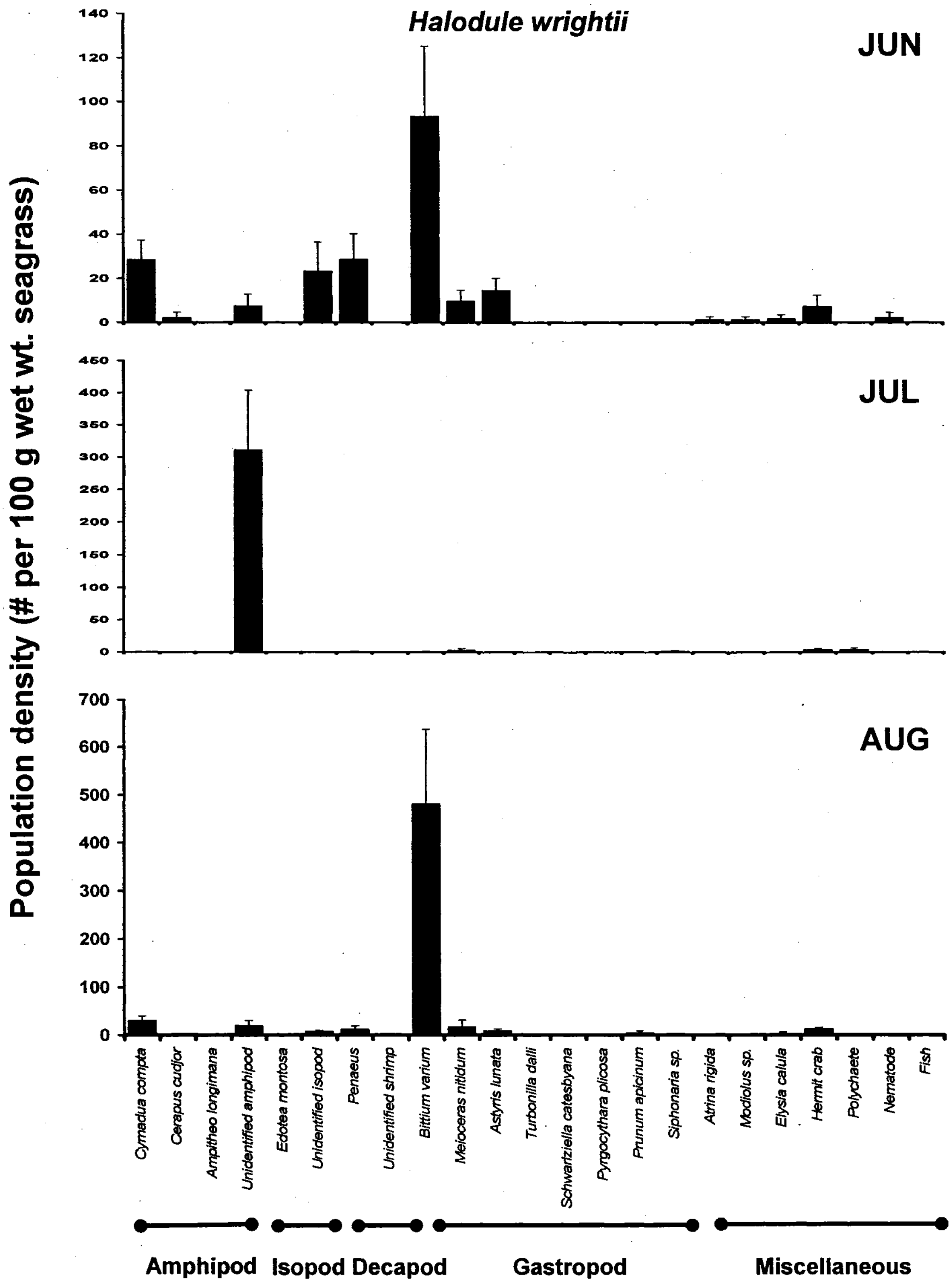

Figure 5. Population densities of mesofaunal species (# per 100 g wet wt seagrass; means ± SE) associated with blades of *Halodule wrightii* in Saint Joseph Bay, Florida from June to Nov, 2004.

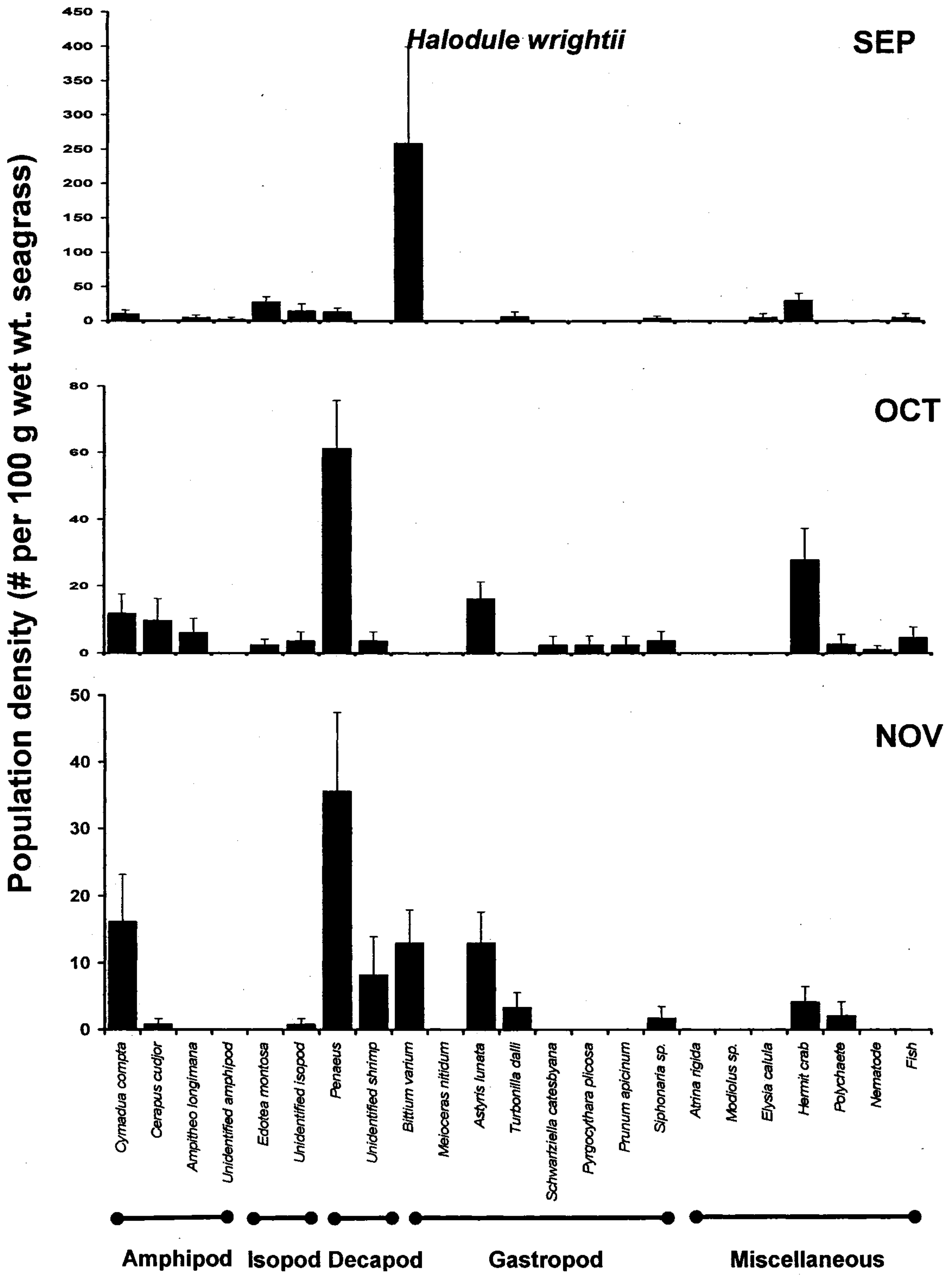

Figure 5. (Continued)

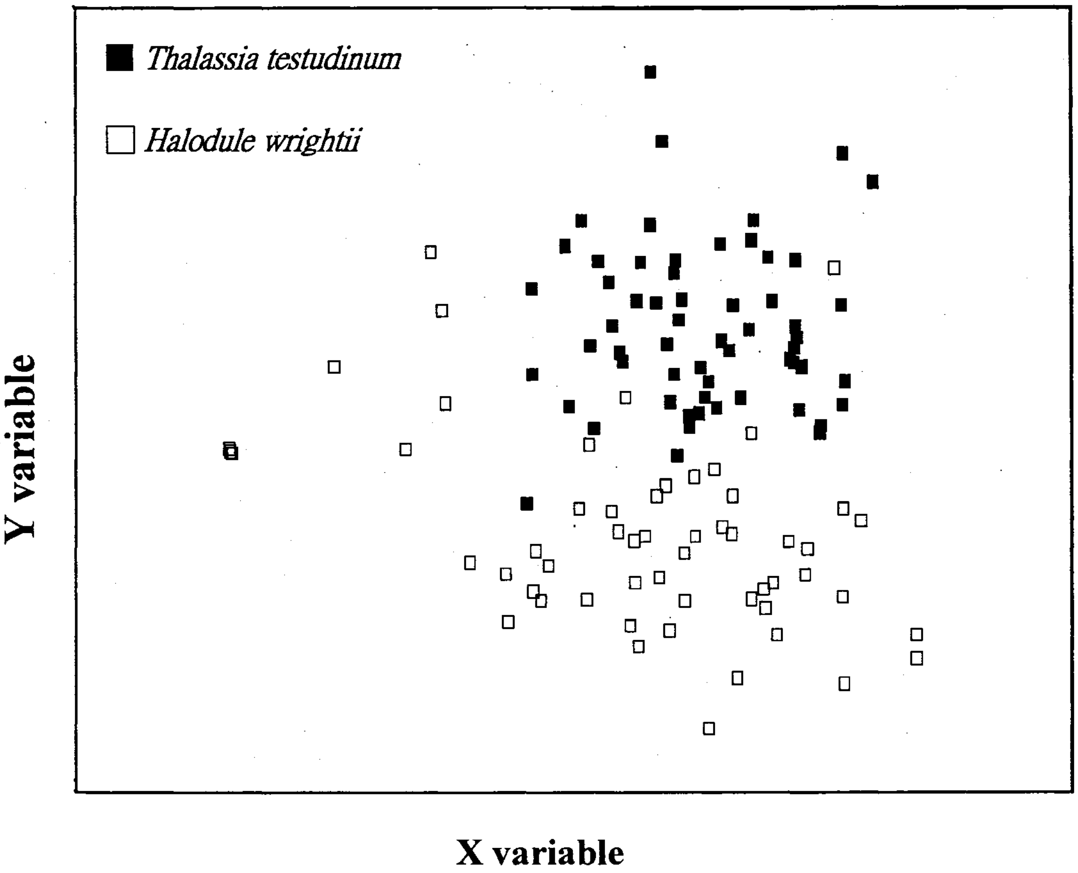

Figure 6. MDS ordination analysis of 10 replicates of mesofauna associated with blades of the common seagrasses *Thalassia testudinum* and *Halodule wrightii*. The analysis was based on the population densities and species compositions of mesofauna associated with seagrass blades collected monthly in Saint Joseph Bay, Florida from June to November, 2004. The MDS analysis was conducted using standardized (no. per 100 g wet wt. seagrass) and log (x + 1) transformed data and is presented as a two-dimensional scatter graph. (2D stress = 0.19; 3D stress = 0.14).

CONCLUSIONS

Marine herbivorous amphipods, isopods, and gastropods known as mesograzers play an important role of linking different trophic levels. Mesograzers indirectly or directly feed on marine plants (e.g. microalgae, macroalgae, and seagrasses) and their associated epiphytes. These mesograzers subsequently become prey for other nektonic invertebrate or vertebrate predators. Hence, the factors that regulate the distribution and abundance of mesograzers have been broadly examined in temperate and tropical coastal marine environments (Nelson 1979, Edgar 1983, Stoner 1983, Lewis 1984, Russo 1990, Poore & Steinberg 1999, Cruz-Rivera & Hay 2001, Duffy & Harvilicz 2001, Duggins et al. 2001, Mancinelli & Rossi 2001, Taylor & Steinberg 2005). In contrast, studies of the distribution and abundance of mesograzers in polar regions and factors regulating the patterns of distribution and abundance of these communities have received less attention (Suren 1990, Blazewicz & Jaźdźewski 1995, Brandt 1997, Brandt et al. 1997, Iken et al. 1998, Hop & Poltermann 2000, Jaźdźewski et al. 2001). This dissertation attempts to address this deficiency by comprehensively and quantitatively examining the association between mesofaunal communities and dominant macroalgae along the subtidal of the western Antarctic Peninsula. In addition, the palatability of ecologically dominant macroalgae to three model Antarctic herbivorous amphipods is examined. Finally, in a study extending plant-associated mesograzer studies to the northern Gulf of Mexico, the seasonal mesograzers communities associated with the blades of two common seagrasses in Saint Joseph Bay, Florida, are characterized.

The study laid out in the first chapter of this dissertation demonstrates that both amphipod abundance and total numbers of species are significantly greater in association with the most morphologically complex antarctic macroalgal species, *Desmarestia menziesii*, *D. anceps*, and *Plocamium cartilagineum*, with higher numbers of branches per unit mass and a higher degree of branching. This is particularly evident in both *Desmarestia* species, where the length of the secondary branches and the distance from distal branches to the main stem is great and provides significant interstitial cover from prospective fish predators. Amphipods collected from the target macroalgae seemed to prefer to inhabit branched algae rather than algal species characterized by blade morphology. A recent study has found that *D. menziesii* is also chemically defended against grazing by the sympatric amphipod *Gondogeneia antarctica* (Amsler et al. 2005). This alga may similarly be chemically defended against amphipods although previous studies have shown that macroalgal chemical defenses are species-specific in terms of amphipod grazing patterns (Duffy & Hay 1994, Sotka & Hay 2002). Two factors could explain this association. First, *D. menziesii* has a comparatively complex morphology that includes a high degree of branching that may provide amphipods a physical refuge from predation. Second, *D. menziesii* is chemically defended against the sympatric omnivorous fish, *Notothenia coriiceps*, known to prey on amphipods (Iken et al. 1997, Amsler et al. 2005). Thus, antarctic amphipods may be exploiting chemically defended macroalgae to avoid fish predation as demonstrated in studies of tropical and temperate macroalga-amphipod associated communities (Duffy & Hay 1994, Hay 1996, 1997). This, coupled with the high structural complexity (numerous fine branches) that provides amphipods a suitable substrate for efficient clinging (Hacker & Steneck 1990) may make these macroalgae particularly attractive habitat.

The different morphologies of gammarid amphipods are likely to be in part an evolutionary adaptation to the macroalgae with which they associate. For example, the antarctic genus *Oradarea* are characterized by having slender, elongated legs with hooked distal tips (Thurston 1972). These adaptations may facilitate clinging behaviors on the fine, highly branched, terete (cylindrical) branches that characterize *Desmarestia anceps* and *D. menziesii*, especially the latter (Wiencke & Clayton 2002). Although *G. skottsbergii* is not a morphologically complex branched algal species (Wiencke & Clayton 2002) and lacks chemical defenses against omnivorous fish (Amsler et al. 2005), its large flattened blades with multiple holdfasts resting against the benthic substrate provide protective space between the substrate and ventral blade surface for amphipods. In addition, numerous papillae on the surface of *G. skottsbergii* may provide suitable substrate for amphipod clinging.

Patterns of species diversity indices for amphipods associated with the eight common antarctic macroalgae examined were similar to those seen for amphipod species numbers. The one exception was the species diversity index for amphipods associated with *Desmarestia menziesii*. Here, in striking contrast to its high number of associated species diversity was the lowest recorded for any of the targeted macroalgae. This discrepancy is the result of the disproportionate numerical dominance of the amphipod *Metaleptamphopus pectinatus*. In general, the gammarid amphipod communities (population densities and species composition) associated with the macroalgal species are similar within the same macroalgal species but dissimilar across macroalgal species.

When comparing the community structure of gammrid amphipods associated with the same antarctic algal species but collected from different locations, our findings indicate that while variations do exist in species-specific macroalgal-associated amphipod communities across spatial scales of only 3 km (seen in 4 of 8 macroalgae examined), such differences seem to be species-specific among macroalgae. For those 50% of the macroalgal species that had no between-site dissimilarities in their associated amphipod communities, we would argue that the dynamics of amphipod communities are likely regulated by macroalgal-specific factors.

In the second chapter of this dissertation, fresh thalli bioassays indicate that the common antarctic amphipods *Prostebbingia gracilis* and *Gondogeniea antarctica* showed their highest consumption rates when grazing on the thalli of the red alga *Palmaria decipiens*. The eight macroalgal species offered to Antarctic amphipods represent distinct morphologies and with varying degrees of toughness (Amsler et al. 2005). It is noteworthy that the most palatable alga, *P. decipiens*, is among the lower third of 30 species of Antarctic macroalgae in terms of toughness. Results of feeding bioassays indicated that third amphipod species, *Metaleptamphopus pectinatus,* did not consume either fresh thalli or artificial foods of any macroalgae. Thus, it is likely that *M. pectinatus* does not exploit macroalgae directly as a food resource but rather may graze on epiphytic microalgae such as diatoms colonizing the surfaces of macroalgae. Our results are consistent with previous reports (Chevreux 1913, Thurston 1972) that this species inhabits, and may exploit for food, epiphytic mats growing on the holdfasts of brown (*Desmarestia* sp.) and red (*Phyllogigas* sp.) macroalgae.

In order to control the effects of morphology and toughness of fresh thalli, we also conducted amphipod feeding bioassays using uniformly sized artificial alginate foods containing finely ground algal tissues. Similar to the fresh thalli bioassays, both

Prostebbingia gracilis and *Gondogeneia antarctica* had the highest consumption rates when presented pellets containing the alga *Palmaria decipiens.* However, in contrast to the fresh thalli bioassays, artificial pellets containing ground tissues of the macroalgae *Myriogramme mangini* and *Gigartina skottsbergii* were also consumed at relatively high rates. The lack of consumption of *M. mangini* and *G. skottsbergii* when presented as fresh thalli suggests that toughness may play some role in its low palatability to amphipods. Indeed, *M. mangini* is 11th in terms of toughness and *G. skottsbergii* is the toughest amongst 30 species of macroalgae examined from the Antarctic Peninsula (Amsler et al. 2005, Peters et al. 2005). It is possible that these amphipods might exploit these macroalgae as a food resource when thalli are dislodged and subsequently decompose to become part of the detrital food web.

Peters et al. (2005) evaluated a suite of nutritional parameters of 40 species of macroalgae from the Antarctic Peninsula including those examined in this dissertation. If soluble protein content is considered a proxy for nutritional value (Cruz-Rivera & Hay 2000a, 2000b), it is clear from our regression analysis that there is no significant correlation between algal nutritional value and consumption rates of amphipods presented macroalgal food pellets. Nonetheless, it should be noted that in both fresh thalli and alginate pellet assays, *P. gracilis* and *G. antarctica* preferred the macroalga *Palmaria decipiens* which had the highest soluble protein content (9.3% dry wt) among the macroalgal species.

A variety of macroalgae are known to harbor defensive secondary metabolites that are deterrent to grazers (Paul et al. 2001, Van Alstyne et al. 2001, Paul & Puglisi 2004). With respect to the present study, these macroalgae (*Desmarestia anceps, D.*

menziesii, D. antarctica, and Plocamium cartilagineum) have been found to be chemically defended against herbivory by the amphipod *Gondogeneia antarctica* (Amsler et al. 2005). In both fresh thalli and alginate pellet assays, these same four species of macroalgae were either not consumed at all or consumed in very low quantities by *Prostebbingia gracilis* and *G. antarctica,* suggesting that chemical defenses contribute to their lack of palatability.

The study presented in the third chapter of this dissertation indicates that the subtropical seagrasses, *Thalassia testudiun* and *Halodule wrightii*, in Saint Joseph Bay, Florida, typically exhibit their highest levels of aboveground biomass during the warmer summer season (June, July and August) when environmental factors such as temperature, light and nutrition may be optimized for growth (Hemminga & Duarte 2000). Seasonal variations of epiphytic algal biomass associated with these two seagrasses occurred in both species. Epiphytic assemblages included blue-green algae, diatoms, and encrusting algae, all of which being potential food recourses for mesograzers. Factors most likely to influence these epiphytic assemblages include seagrass morphology, age, and location (Jernakoff et al. 1996 and references inside). Moreover, the much larger blades of *T. testudinum* may have provided a larger surface area for the effective attachment of several species of drift macroalgae that occurred in the spring (March). The highest epiphytic biomasses associated with blades of *T. testudinum* occurred in July and mainly resulted from an encrusting coralline algae that covered the majority of the surface of seagrass blades (Huang, pers. observation). Similar to *T. testudinum,* the maximum epiphytic loads (biomass) associated with the blades of *Halodule wrightii* occurred in the same month of July. This may have been due to a proliferation of diatoms and filamentous cyanobacteria. Throughout the entire sampling period, ratios of epiphyte to seagrass biomass during the latter summer months were surprisingly low and may have resulted from increased grazing pressure on seagrass epiphytes by macrograzers such as pinfish (Montgomery & Targett 1992, Klumpp et al. 1993, Valentine et al. 2000).

Seasonal patterns of seagrass-associated mesofaunal species richness and species diversity reflected patterns of biomass of both seagrasses. Mesofaunal species richness and species diversity were highest in the summer months, peaking in June, and generally lowest during the winter. From a large scale perspective, the patchy distributions of multi-species complexes of seagrass meadows in Saint Joseph Bay provide a diversity of habitats for mobile mesofaunal invertebrates that occur in association with seagrasses. From a micro-scale perspective, the growth of epiphytes of the surfaces of seagrass blades during the early summer similarly increases the heterogeneity of habitat structure, likely further contributing to higher mesofaunal species richness and species diversity (Schneider & Mann 1991b, Bologna & Heck 1999). In meadows of *T. testudinum,* a minor increase of blade-associated epiphytic biomass occurred in the spring (March) and was similarly reflected in an increase in both mesofaunal specie richness and species diversity. The observed decline in these variables from a peak in June to lower levels in July may be the result of top-down factors such as increased levels of pinfish predation (Nelson 1979). Both species richness and species diversity of mesofaunal communities associated with *T. testudinum* were higher than those for *H. wrightii* except for the month of October. This may be related to the larger relative surface area provided by the blades of *T. testudinum* and thus a resultant greater abundance and diversity of associated epiphytes that may further attract mesograzers.

Within the five primary mesofaunal groups examined in the present study (amphipods, isopods, decapods, gastropods, and miscellaneous taxa), amphipods and gastropods were the most abundant when standardized as individuals per unit seagrass mass. Both of these groups are considered to be important seagrass-associated mesograzers (Jernakoff et al. 1996). Similar to the findings of Valentine and Heck (1993) who detected a peak abundance of amphipods associated with *T. testudinum* habitats in winter in Saint Joseph Bay, we found the abundance of *T. testudinum* blade-associated amphipods to be highest in February and gradually decrease through the spring and summer. This may be related to amphipods aggregating in higher densities on blades during the winter months when shoot density is lower than during the summer (Huang, pers. observation). Dramatic declines in amphipod abundances associated with blades of *T. testudinum* and *H. wrightii* in July and September, respectively, may be related to increased pinfish predation. Mesofaunal gastropods associated with the blades of *T. testudinum* peaked in abundance in April, August, and November, generally corresponding to peaks in epiphytic biomass in March, June, and November. This suggests that mesogastropods may be exploiting epiphytes as a nutritional resource.

Regression analyses indicated that abundances of amphipods were positively correlated with the biomass of epiphytes associated with the blades of *T. testudinum* and *H. wrightii* in at least some months representative of spring, summer and fall. In addition, abundances of gastropods were positively correlated with epiphytic biomass in several months of both summer and fall for both seagrass species. Bologna and Heck (1999), using artificial epiphytic structures and natural fouling epiphytes growing on artificial seagrass units, demonstrated that epiphytes functioned primarily as food resources rather than as shelter. Epiphytic grazing has been observed in among amphipods including *Amphithoe* sp. that occurs in association with the epiphytized seagrass, *Syringodium isoetifolium* (Mukai & Iijima 1995).

Mesofaunal communities (population densities of each collected species and species composition) associated with aboveground blades of *T. testudinum* and *H. wrightii* were significantly different from one another during the entire six month sampling period when aboveground biomass of both seagrasses co-occurred. Moreover, an analysis of similarity (ANOSIM) revealed that the mesofaunal communities associated with blades of both seagrass species differed from one another in each of these six months. These observations are similar to previous studies that have found community level differences in blade-associated mesograzers in meadows comprised of different species of seagrasses (Lewis 1987, Schneider & Mann 1991a, 1991b, Edgar 1992).

LIST OF GENERAL REFERENCES

Aikins S, Kikuchi E (2001) Water current velocity as an environmental factor regulating the distribution of amphipod species in Gamo Lagoon, Japan. Limnology 2:185-191

Amsler CD, Iken K, McClintock JB, Amsler MO, Peters KJ, Hubbard JM, Furrow FB, Baker BJ (2005) Comprehensive evaluation of the palatability and chemical defenses of subtidal macroalgae from the Antarctic Peninsula. Mar Ecol Prog Ser 294:141-159

Amsler CD, McClintock JB, Baker BJ (1998) Chemical defense against herbivory in the Antarctic marine macroalgae *Iridaea cordata* and *Phyllophora antarctica* (Rhodophyceae). J Phycol 34:53-59

Amsler CD, McClintock JB, Baker BJ (2001) Secondary metabolites as mediators of trophic interactions among antarctic marine organisms. Am Zool 41:17-26

Amsler CD, Rowley RJ, Laur DR, Quetin LB, Ross RM (1995) Vertical distribution of Antarctic peninsular macroalgae: cover, biomass and species composition. Phycologia 34:424-430

Battershill CN (1990) Temporal changes in Antarctic marine benthic community structure. N Z Antarct Rec 10:23-27

Beddingfield SD, McClintock JB (2000) Demographic Characteristics of *Lytechinus variegatus* (Echinoidea: Echinodermata) from three habitats in a north Florida bay, Gulf of Mexico. Mar Biol 21:17-40

Bell SD (1991) Amphipods as insect equivalents? An alternative view. Ecology 72:350-354

Bernays EA (1986) Diet-induced head allometry among foliage-chewing insects and its importance for graminivores. Science 231:230-232

Bernays EA (1989) Host range in phytophagous insects: the potential role of generalist predators. Evol Ecol 3:299-311

Bernays EA, Woodhead S (1982) Plant phenols utilized as nutrients by a phytophagous insect. Science 216:201-203

Blazewicz M, Jaźdźewski K (1995) Cumacea (Crustacea, Malacostraca) of Admiralty Bay, King George Island: a preliminary note. Polish Polar Res 16:71-86

Blazewicz M, Jaźdźewski K (1996) A contribution to the knowledge of Tanaidacea (Crustacea, Malacostraca) of Admiralty Bay, King George Island, Antarctic. Polish Polar Res 17:213-220

Bologna PAX, Heck KL (2000) Impacts of seagrass habitat architecture on bivalve settlement. Estuaries 23:449-457

Bologna PAX, Heck KLJ (1999) Macrofaunal associations with seagrass epiphytes: Relative importance of trophic and structural characteristics. J Exp Mar Biol Ecol 242:21-39

Boström C, Mattila J (1999) The relative importance of food and shelter for seagrass-associated invertebrates: a latitudinal comparison of habitat choice by isopod grazers. Oecologia 120:162-170

Brandt A (1997) Abundance, diversity and community patterns of epibenthic- and benthic-boundary layer peracarid crustaceans at 75 °N off East Greenland. Polar Biol 17:159-174

Brandt A, Linse K, Weber U (1997) Abundance and diversity of peracarid taxa (Crustacea, Malacostrace) along a transect through the Beagle Channel, Patagonia. Polar Biol 18:83-90

Brawley SH (1992) Mesoherbivores. In: John DM, Hawkins SJ, Price JH (eds) Plant-Animal Interactions in the Marine Benthos, Systematics Association Special Volume No 46. Clarendon Press, Oxford, p 235-263

Buck TL, Breed GA, Pennings SC, Chase ME, Zimmer M, Carefoot TH (2003) Diet choice in an omnivorous salt-marsh crab: different food types, body size, and habitat complexity. J Exp Mar Biol Ecol 292:103-116

Chevreux E (1913) Amphipoda. Crustaces II. Voyage de Ch. Alluaud et R. Jeannel en Afrique Orientale (1911-1912). In: Resultats Scientifiques, p 11-12

Coleman CO (1989) *Gnathiphimedia mandibularis* K. H. Barnard 1930, an Antarctic amphipod (Acanthonotozomatidae, Crustacea) feeding on Bryozoa. Antarctic Sci 1:343-344

Crist TO (1998) The spatial distribution of termites in shortgrass steppe: a geostatistical approach. Oecologia 114:410-416

Cruz-Rivera E, Hay ME (2000a) Can quantity replace quality? Food choice, compensatory feeding, and fitness of marine mesograzers. Ecology 81:201-219

Cruz-Rivera E, Hay ME (2000b) The effects of diet mixing on consumer fitness: macroalgae, epiphytes, and animal matter as food for marine amphipods. Oecologia 123:252-264

Cruz-Rivera E, Hay ME (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

Dayton PK (1990) Polar Benthos. In: Polar Oceanography Part B: Chemistry, Biology, and Geology. Academic Press, p 631-685

Dayton PK, Robilliard GA, Paine RT, Dayton LB (1974) Biological accommodation in the benthic community at McMurdo Sound, Antarctica. Ecol Monogr 44:105-128

DeLaca TE, Lipps JH (1976) Shallow-water marine associations, Antarctic Peninsula. Antarct J US 11:12-20

Dhargalkar VK, Burton HR, Kirkwood JM (1988) Animal associations with the dominant species of shallow water macrophytes along the coastline of the Vestfold Hills, Antarctica. Hydrobiologia 165:141-150

Duffy JE, Harvilicz AM (2001) Species-specific impacts of grazing amphipods in an eelgrass-bed community. Mar Ecol Prog Ser 223:201-211

Duffy JE, Hay ME (1991) Food and shelter as determinants of food choice by an herbivorous marine amphipod. Ecology 72:1286-1298

Duffy JE, Hay ME (1994) Herbivore resistance to seaweed chemical defense: the roles of mobility and predation risk. Ecology 75:1304-1319

Duffy JE, Macdonald KS, Rhode JM, Parker JD (2001) Grazer diversity, functional redundancy and productivity in seagrass beds: an experimental test. Ecology 82:2417-2434

Duggins D, Eckman JE, Siddon CE, Klinger T (2001) Interactive roles of mesograzers and current flow in survival of kelps. Mar Ecol Prog Ser 223:143-155

Edgar GJ (1983) The ecology of south-east Tasmanian phytal animal communities. IV. Factors affecting the distribution of Ampithoid amphipods among algae. J Exp Mar Biol Ecol 70:205-225

Edgar GJ (1992) Patterns of colonization of mobile epifauna in a Western Australian seagrass bed. J Exp Mar Biol Ecol 157:225-246

Fahrig L, Jonsen I (1998) Effect of habitat patch characteristics on abundance and diversity of insects in an agricultural landscape. Ecosystems 1:197-205

Gambi MC, Lorenti M, Russo GF, Scipione MB (1994) Benthic associations of the shallow hard bottoms off Terra Nova Bay, Ross Sea: zonation, biomass and population structure. Antarctic Sci 6:449-462

Guerra-Garcia JM, Garcia-Gomez JC (2001) The spatial distribution of Caprellidea (Crustacea: Amphipod): A stress bioindicator in Ceuta (North Africa, Gibraltar Area). Mar Ecol 22:357-367

Hacker SD, Steneck RS (1990) Habitat architecture and the abundance and body-size-dependent habitat selection of a phytal amphipod. Ecology 71:2269-2285

Hay ME (1996) Marine chemical ecology: what's known and what's next? J Exp Mar Biol Ecol 200:103-134

Hay ME (1997) The ecology and evolution of seaweed-herbivore interactions on coral reefs. Coral Reefs 16:S67-S76

Hay ME, Duffy JE, Fenical W (1990) Host-plant specialization decreases predation on a marine amphipod: an herbivore in plant's clothing. Ecology 71:733-743

Hay ME, Duffy JE, Pfister CA (1987) Chemical defense against different marine herbivores: are amphipods insect equivalents? Ecology 68:1567-1580

Hay ME, Fenical W (1988) Marine plant-herbivore interactions: the ecology of chemical defense. Ann Rev Ecol Syst 19:111-145

Hay ME, Piel J, Boland W, Schnitzler I (1998) Seaweed sex pheromones and their degradation products frequently suppress amphipod feeding but rarely suppress sea urchin feeding. Chemoecology 8:91-98

Hemminga MA, Duarte CM (2000) Seagrass Ecology, Vol. Cambridge University Press, Cambridge, UK; New York, NY, USA:

Hop H, Poltermann M (2000) Ice amphipod distribution relative to ice density and under-ice topography in the northern Barents Sea. Polar Biol 23:357-367

Hughes RN, Gliddon CJ (1991) Marine plants and their herbivores: coevolutionary myth and precarious mutualisms. Phil Trans E Soc Lond 333:231-239

Iken K, Barrera-Oro ER, Quartino M-L, Casaux RJ, Brey T (1997) Grazing by the Antarctic fish *Notothenia coriiceps*: evidence for selective feeding on macroalgae. Antarctic Sci 9:386-391

Iken K, Quartino M-L, Barrera-Oro E, Palermo J, Wiencke C, Brey T (1998) Trophic relations between macroalgae and herbivores. Rpt Polar Res 299:258-262

Jaźdźewski K, De Broyer C, Pudlarz M, Zielinski D (2001) Seasonal fluctuations of vagile benthos in the uppermost sublittoral of a maritime Antarctic fjord. Polar Biol 24:910-917

Jaźdźewski K, De Broyer C, Teodorczyk W, Konopacka A (1991a) Survey and distributional patterns of the amphipod fauna of Admiralty Bay, King George Island, South Shetland Islands. Polish Polar Res 12:461-472

Jaźdźewski K, Konopacka A (1999) Necrophagous lysianassoid Amphipod in the diet of Antarctic tern at King George Island, Antarctica. Antarctic Sci 11:316-321

Jaźdźewski K, Teodorczyk W, Sicinski J, Kontek B (1991b) Amphipod crustaceans as an important component of zoobenthos of the shallow Antarctic sublittoral. Hydrobiologia 223:105-117

Jernakoff P, Brearley A, Nielsen J (1996) Factors affecting grazer-epiphyte interactions in temperate seagrass meadows. Oceanogr Mar Biol Ann Rev 34:109-162

Jernakoff P, Nielsen J (1997) The relative importance of amphipod and gastropod grazers in *Posidonia sinuosa* meadows. Aquat Bot 56:183-202

John DM, Hawkins SJ, Price JH (1992) Plant-Animal Interactions in the Marine Benthos, Vol. Oxford University Press, New York

Karez R, Engelbert S, Sommer U (2000) 'Co-consumption' and 'protective coating': two new proposed effects of epiphytes on their macroalgal hosts in mesograzer-epiphyte-host interactions. Mar Ecol Prog Ser 205:85-93

Kendrick GA, Hawkes MW (1988) The epiphyte Microcladia coulteri (Rhodophyta): changes in population structure with spatial and temporal variation in availability of host species. Mar Ecol Prog Ser 43:79-86

Klumpp DW, Stlita-Espinosa JT, Fortes MD (1993) Feeding ecology and trophic role of sea urchins in a tropical seagrass community. Aquat Bot 45:205-229

Lee SY, Fong CW, Wu RSS (2001) The effects of seagrass (*Zostera japonica*) canopy structure on associated fauna: a study using artificial seagrass units and sampling of natural beds. J Exp Mar Biol Ecol 259:23-50

Leonard CL, McClintock JB (1999) The population dynamics of the brittlestar Pohioderma brevispinum in near- and farshore seagrass habitats of port Saint Joseph Bay, Florida. Gulf Mexi Sci:87-94

Lewis FG (1984) Distribution of macrobenthic crustaceans associated with *Thalassia*, *Halodule* and bare sand substrata. Mar Ecol Prog Ser 19:101-113

Lewis FG (1987) Crustacean epifauna of seagrass and macroalgae in Apalachee Bay, Florida, USA. Mar Biol 94:219-229

Lewis FG, Stoner AW (1983) Distribution of macrofauna within seagrass beds; an explanation for patterns of abundance. Bull Mar Sci 33:296-304

Lippert H, Iken K, Rachor E, Wiencke C (2001) Macrofauna associated with macroalgae in the Kongsfjord (Spitsbergen). Polar Biol 24:512-522

Lubchenco J (1978) Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. Am Nat 112:23-39

Mancinelli G, Rossi L (2001) Indirect, size-dependent effects of crustacean mesograzers on the Rhodophyta *Gracilaria verrucosa* (Hudson) Papenfuss: evidence from a short-term study in the Lesina Lagoon (Italy). Mar Biol 138:1163-1173

McClintock JB, Baker BJ (1998) Chemical ecology in antarctic seas. Amer Sci 86:254-263

McClintock JB, Baker BJ (2001) Marine Chemical Ecology, Vol. CRC Press, Boca Raton, Florida

McMillan C, Zapata O, Escobar L (1980) Sulphated phenolic compounds in seagrasses. Aquat Bot 8:267-278

Moe RL, DeLaca TE (1976) Occurrence of macroscopic algae along the Antarctic Peninsula. Antarct J US 11:20-24

Montgomery JLM, Targett TE (1992) The nutritional role of seagrass in the diet of the omnivorous pinfish Lagodon rhomboides (L.). J Exp Mar Biol Ecol 158:37-57

Mukai H, Iijima A (1995) Grazing effects of a gammaridean Amphipoda, *Ampithoe sp.*, on the seagrass, *Syringodium isoetifolium*, and epiphytes in a tropical seagrass bed of Fiji. Ecol Res 10:243-257

Nelson WG (1979) Experimental studies of selective predation on amphipods: consequences for amphipod distribution and abundance. J Exp Mar Biol Ecol 38:225-245

Nelson WG (1980) The biology of eelgrass (*Zostera marina* L.) amphipods. Crustaceana 39:59-89

Nelson WG, Cairns KD, Virnstein RW (1982) Seasonality and spatial patterns of seagrass-associated amphipods of the Indian River Lagoon, Florida. Bull Mar Sci 32:121-129

Neushul M (1965) Diving observations of sub-tidal antarctic marine vegetation. Bot Mar 8:234-243

Nonato EF, Brito TAS, Paiva PCD, Petti MAV, Corbisier TN (2000) Benthic megafauna of the nearshore zone of Martel Inlet (King George Island, South Shetland Islands, Antarctica): depth zonation and underwater observations. Polar Biol 23:580-588

Orth RJ (1992) A perspective on plant-animal interactions in seagrasses: physical and biological determinants influencing plant and animal abundance. In: John DM, Hawkins SJ, Price JH (eds) Plant-Animal Interactions in the Marine Benthos, Systematics Association Special Volume No 46. Clarendon Press, Oxford, p 147-164

Parker JD, Duffy JE, Orth RJ (2001) Plant species diversity and composition: experimental effects on marine epifaunal assemblages. Mar Ecol Prog Ser 224:55-67

Paul VJ, Cruz-Rivera E, Thacker RW (2001) Chemical mediation of macroalgal-herbivore interactions: ecological and evolutionary perspectives. In: McClintock JB, Baker BJ (eds) Marine Chemical Ecology. CRC Press, Boca Raton, Florida, p 227-265

Paul VJ, Puglisi MP (2004) Chemical mediation of interactions among marine organisms. Nat Prod Rep 21:189-209

Pavia H, Carr H, Åberg P (1999) Habitat and feeding preferences of crustacean mesoherbivores inhabiting the brown seaweed *Ascophylum nodosum* (L.) Le Jol. and its epiphytic macroalgae. J Exp Mar Biol Ecol 236:15-32

Peters KJ, Amsler CD, Amsler MO, McClintock JB, Dunbar RB, Baker BJ (2005) A comparative analysis of the nutritional and elemental composition of macroalgae from the western Antarcitc Peninsula. Phycologia 44:453-463

Poore AGB, Steinberg PD (1999) Preference-performance relationships and effects of host plant choice in an herbivorous marine amphipod. Ecol Monogr 69:443-464

Richardson MG (1977) The ecology (including physiological aspects) of selected Antarctic marine invertebrates associated with inshore macrophytes. PhD Dissertation, University of Durham

Rooker JR, Holt SA, Soto MA, Holt GJ (1998) Postsettlement patterns of habitat use by Sciaenid fishes in subtropical seagrass meadows. Estuaries 21:318-327

Russo AR (1990) The role of seaweed complexity in structuring Hawaiian epiphytal amphipod communities. Hydrobiologia 194:1-12

Schanz A, Polte P, Asmus H (2002) Cascading effects of hydrodynamics on an epiphyte-grazer system in intertidal seagrass beds of the Wadden Sea. Mar Biol 141:287-297

Schneider FI, Mann KH (1991a) Species specific relationships of invertebrates to vegetation in a seagrass bed. I. Correlational studies. J Exp Mar Biol Ecol 145:101-117

Schneider FI, Mann KH (1991b) Species specific relationships of invertebrates to vegetation in a seagrass bed. II. Experiments on the importance of macrophyte shape, epiphyte cover and predation. J Exp Mar Biol Ecol 145:119-139

Schoenly K, Beaver RA, Heumier TA (1991) On the trophic relations of insects: A food-web approach. Am Nat 137:597-638

Sotka EE, Hay ME (2002) Geographic variation among herbivore populations in tolerance for a chemically rich seaweed. Ecology 83:2721-2735

Sparrevik E, Leonardsson K (1999) Direct and indirect effects of predation by *Saduria entomon* (Isopoda) on the size-structure of *Monoporeia affinis* (Amphipoda). Oecologia 120:77-86

Stachowicz JJ, Hay ME (1999) Reducing predation through chemically mediated camouflage: indirect effects of plant defenses on herbivores. Ecology 80:495-509

Steinberg PD (1985) Feeding preferences of *Tegula funebralis* and chemical defenses of marine brown algae. Ecol Monogr 55:333-349

Steinberg PD, Altena IV (1992) Tolerance of marine invertebrate herbivores to brown algal phlorotannins in temperate Australasia. Ecol Monogr 62:189-222

Stoner AW (1983) Distributional ecology of amphipods and tanaidaceans associated with three sea grass species. J Crus Biol 3:505-518

Suren A (1990) Microfauna associated with algal mats in metl ponds of the Ross Ice Shelf. Polar Biol 10:329-335

Takeuchi I, Watanabe K (2002) Mobile epiphytic invertebrates inhabiting the brown macroalga, *Desmarestia chordalis*, under the coastal fast ice of Lutzow-Holm Bay, East Antarctica. Polar Biol 25:624-628

Taylor RB, Steinberg PD (2005) Host use by Australasian seaweed mesograzers in relation to feeding preferences of larger grazers. Ecology 86:2955-2967

Thiel M (2000) Population and reproductive biology of two sibling amphipod species from ascidians and sponges. Mar Biol 137:661-674

Thom R, Miller B, Kennedy M (1995) Temporal patterns of grazers and vegetation in a temperate seagrass system. Aquat Bot 50:201-205

Thurston MH (1972) The crustacea amphipoda of Signy Island, South Orkney Islands. Br Antarctic Surv Sci Rep 71:1-133

Valentine JF, Heck KL (1993) Mussels in seagrass meadows: their influence on macroinvertebrate abundance and secondary production in the northern Gulf of Mexico. Mar Ecol Prog Ser 96:63-74

Valentine JF, Jr KLH, Kirsch KD, webb D (2000) Role of sea urchin *Lytechinus variegatus* grazing in regulating subtropical turtlegrass *Thalassia testudinum* meadows in the Florida Keys (USA). Mar Ecol Prog Ser 200:213-228

Van Alstyne KL, Ehlig HM, Whitman SL (1999) Feeding preferences for juvenile and adult algae depend on algal stage and herbivore species. Mar Ecol Prog Ser 180:179-185

Van Alstyne KL, Whitman SL, Ehlig JM (2001) Differences in herbivore preferences, phlorotannin production, and nutritional quality between juvenile and adult tissues from marine brown algae. Mar Biol 139:201-210

Wiencke C, Clayton MN (2002) Synopses of the Antarctic Benthos: Antarctic Seaweeds, Vol 9. A. R. G. Gantner Verlag KG, Rugell/Liechtenstein, FL

Wooster DE (1998) Amphipod (*Gammarus minus*) responses to predators and predator impact on amphipod density. Oecologia 115:253-259

Zaneveld JS (1966) The occurrence of benthic marine algae under shore fast-ice in the western Ross Sea, Antarctica. Proc Int Seaweed Symp 5:217-231

APPENDIX

COPYRIGHT PERMISSION FROM THE JOURNAL OF EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

ELSEVIER

7 August 2006 Our Ref: CT/jj/Aug06/J001

Yusheng Huang
Department of Biology, UAB
252 Campbell Hall
1300 University Boulevard
Birmingham, AL 35294-1170
USA

Dear Yusheng Huang

JOURNAL OF EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY, Vol 329, No 1, 2006, pp 55-65, Huang et al: "Feeding rates of common Antarctic ..."

As per your letter dated 31 July 2006, we hereby grant you permission to reprint the aforementioned material at no charge **in your thesis** subject to the following conditions:

1. If any part of the material to be used (for example, figures) has appeared in our publication with credit or acknowledgement to another source, permission must also be sought from that source. If such permission is not obtained then that material may not be included in your publication/copies.

2. Suitable acknowledgment to the source must be made, either as a footnote or in a reference list at the end of your publication, as follows:

   "Reprinted from Publication title, Vol number, Author(s), Title of article, Pages No., Copyright (Year), with permission from Elsevier".

3. Reproduction of this material is confined to the purpose for which permission is hereby given.

4. This permission is granted for non-exclusive world **English** rights only. For other languages please reapply separately for each one required. Permission excludes use in an electronic form. Should you have a specific electronic project in mind please reapply for permission.

5. This includes permission for UMI to supply single copies, on demand, of the complete thesis. Should your thesis be published commercially, please reapply for permission.

Yours sincerely

Jennifer Jones
Rights Assistant

Your future requests will be handled more quickly if you complete the online form at
www.elsevier.com/permissions

GRADUATE SCHOOL
UNIVERSITY OF ALABAMA AT BIRMINGHAM
DISSERTATION APPROVAL FORM
DOCTOR OF PHILOSOPHY

Name of Candidate Yu-Sheng M. Huang

Graduate Program Biology

Title of Dissertation An Examination of Morphological and Biological Traits of Dominant Marine Plants That Regulate Patterns of Mesograzer Communities

I certify that I have read this document and examined the student regarding its content. In my opinion, this dissertation conforms to acceptable standards of scholarly presentation and is adequate in scope and quality, and the attainments of this student are such that he may be recommended for the degree of Doctor of Philosophy.

Dissertation Committee:

Name		**Signature**
James B. McClintock	**, Chair**	
Charles D. Amsler		
Richard B. Aronson		Richard B. Aronson
Robert W. Thacker		
John F. Valentine		

Director of Graduate Program Stephen A Watts

Dean, UAB Graduate School Bryan D Noe

Date 8/25/06