BURROWING SHRIMPS AND SEAGRASS DYNAMICS IN SHALLOW-WATER MEADOWS OFF BOLINAO (NW PHILIPPINES)
BURROWING SHRIMPS AND SEAGRASS DYNAMICS IN SHALLOW-WATER MEADOWS OFF BOLINAO (NW PHILIPPINES)
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BURROWING SHRIMPS AND SEAGRASS DYNAMICS IN SHALLOW-WATER MEADOWS OFF BOLINAO (NW PHILIPPINES)

DISSERTATION
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by

Hildie Maria Nacorda
born in Lucena City, Philippines
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Preface

This research project was carried out following the PhD sandwich scheme of the UNESCO-IHE Institute for Water Education in Delft with the Marine Science Institute (MSI) of the University of the Philippines in Diliman. The detailed proposal had been prepared and some laboratory analyses were carried out at IHE, the actual research has been implemented in the Philippines, mostly in Bolinao, Pangasinan, and all the chapters were completed and finalized at MSI in Diliman. A WOTRO fellowship through IHE (WB84-413) afforded me the opportunity to undertake this research project, which was supplemented later on by a scholarship contract from MERF-MSI, through the SARCS/WOTRO/LOICZ project “Economic evaluation and biophysical modeling of the marine environment in Bolinao in support of management for sustainable use”.

My sincere thanks to Dr. ir. Jan Vermaat, his extraordinary commitment, academic recommendations, constant guidance and motivation, and unfaltering support as adviser and co-promotor, and to Prof. Miguel Fortes, who, as co-adviser, gave big brother counsel and encouragement during various turning points. Jan and Sir Mike had endorsed my participation in the EU Project CERDS (Responses of Coastal Ecosystems to Deforestation-derived Siltation in Southeast Asia, TS3*-C-T92–0301) and in various scientific meetings, all of which proved beneficial to the research project – the 5th International Crustacean Congress, the Seagrass Biology Workshops, the 4th Symposium of the Marine Biology of the South China Sea, and several symposia of the Philippine Association of Marine Science (PAMS).

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Last but not least, a big hug to my family for the unreserved support (Raul and his family deserve special mention for the hospitality in Sydney), the incredible amount of patience (I apologize for having missed birthdays/ holidays), and inspiration through the years. I will always be grateful for my mother’s advice and unceasing prayers; I was drawn to complete this work so that we can have stories to tell the children.

Hildie Maria E. Nacorda
January 2008
Summary

Natural disturbances contribute to the dynamics of seagrass meadows. This thesis intended to assess the importance of small-scale disturbance (bioturbation) by burrowing shrimps as a determinant of sediment mobility and as a factor limiting the establishment, expansion, and species composition of mixed-species beds in the Philippines. The specific aims of the studies were to describe the spatial distribution of burrowing shrimp disturbance in seagrass beds along a siltation gradient and its consequences to the vertical properties of bed sediments, to quantify the behavior of burrowing alpheid shrimps, and to determine the effects of short-term burial and leaf harvesting on the growth patterns of the dominant seagrass *Thalassia hemprichii* (Ehrenberg) Ascherson.

Burrow openings and sediment gaps were common in the meadows and were associated with either the caridean shrimp *Alpheus macellarius* Chace, 1988 or the larger, deeper burrowing species of Thalassinidea. Wave-sheltered beds harbored more frequent and larger sediment gaps than the exposed beds; shrimp burrows and mounds were also more prevalent in clear-water than in turbid seagrass areas. The disturbance by *A. macellarius* was found greater than that due to thalassinidean shrimps, overall, and alpheid distribution was found to be largely limited to vegetated fine-sand substrates. Areas of *A. macellarius*-reworked sand patches represented 15 ± 2% of the meadows (at scaled-up densities of 102 ± 5 per 100 m²; cf. cover photograph) while sand mounds of thalassinidean shrimps covered 5 ± 1% (at densities of 52 ± 7 per 100 m²). Burrowing shrimps altered the vertical profiles of sediment properties differently – *A. macellarius* relocated a significant proportion of coarse grains in the top 10 cm while thalassinidean shrimps consolidated finer fractions from 10 down to 20 cm of the sediments and concentrated organic matter. Both shrimps decreased sediment nitrogen by 20-73% in the top layer and by 4-46% at deeper than 10 cm. No significant changes in the sediments’ phosphorus profiles were observed due to the shrimps.

*In situ* observations of the aboveground behavior of *A. macellarius* revealed its active sediment reworking and occasional harvesting of seagrass leaves during the dry months in a clear-water meadow. The shrimps allocated only 12% of its daily active period for these activities and were in their respective burrows during the remainder of daytime. In wet months, the rates of aboveground activities became reduced by at least 34% and within-burrow periods increased by 5% as a consequence. On average, *A. macellarius* remobilized ~300 g DW of sediment d⁻¹ (or 112 kg y⁻¹), and harvested 0.8 g DW of leaves d⁻¹ (or 291.3 g y⁻¹). The estimated sediment reworking rate is considerable (0.8 to 1.4 kg m⁻² d⁻¹) for an average shrimp density of 2 individuals m⁻², and the leaf harvesting rate represents moderate herbivory (0.4 to 2.3 g m⁻² d⁻¹), equivalent to 12 to 42% of leaf production.

Subsequent laboratory observations that examined the role of bed sediment type – sand, muddy sand, and sandy mud – on the behavior of *A. macellarius* showed that the shrimps immediately commenced with burrowing upon contact with the substrates. In the sand substrate, early success in concealment was achieved (first burrows within 2 hours) despite considerable burrowing effort and extensive tunnel lengths were also attained. Burrowing activities became reduced and wandering evident in all the substrates after the fifth week of observation. Feeding became conspicuous – mainly as particle ingestion, occasional suspension-feeding bouts,
and direct grazing on seagrass leaves. Burrowing, grooming, and surveying behavior were predominant during the day while wandering and feeding were extended at night. Burrowing, however, remained significantly higher in sand than in the other two substrates. Overall, soft carbonate sand sediments together with reinforcement from dense seagrasses presented greater support for the burrowing behavior of *A. macellarius* and this is in line with the observed higher densities in these habitats in the field. In contrast, shrimp burrowing appeared limited and was substituted by concealment strategies in the terrigenous substrates, and, with less support from the sparse vegetation, burrow numbers were significantly lower in these habitats in the field.

The series of manipulative experiments mainly on the seagrass *T. hemprichii* provided evidence of the tolerance of vegetative shoots to the small-scale disturbance imposed by burrowing shrimps. In apical shoots, single burial events lasting at least 14 days induced accelerated leaf growth, while leaf clipping and combined treatments had minimal effects on either leaf or rhizome growth. Seedlings also survived defoliation but were sensitive to burial events – clipping alone did not cause changes in seedling growth but this significantly and continuously decreased with burial, applied alone and combined with clipping disturbance. Exclusion from shrimp activity did not influence leaf growth rates of mature shoots. Only *Halophila* densities were enhanced, particularly after 21 weeks of the 13-month lasting experiment, and both *T. hemprichii* growth and shoot densities of other coexisting seagrass species exhibited strong temporal variation as expected.

In short, this thesis established that the two types of burrowing shrimps – the alpheids and thalassinideans – that are common in the seagrass beds redistribute considerable quantities of sediment with significant substrate effects on depth gradients of organic matter, grain size, and nitrogen. Only the alpheids have a tight connection to the seagrass, i.e., they feed on it and remove a moderate component from primary production, but these do not affect the established clonal seagrass stands markedly. Probably they affect seed and seedling recruitment negatively, but this may not necessarily have a severe impact on the established stands these shrimps inhabit.
Chapter 1

General introduction

The ecosystem services provided by seagrass meadows, and valued at about a tenth of the total global flow value (Constanza et al. 1997), are central to current advocacies for resource restoration and conservation (Duarte 2002, Orth et al. 2006). Seagrass meadows are coastal ecosystems that often exhibit high primary production (Duarte and Chiscano 1999), which supports diverse floral and faunal assemblages and large marine animals (McConnaughey and McRoy 1979, Lewis and Stoner 1983, Howard et al. 1989, Hily and Bouteille 1999). Bed sediments and the leaf canopies serve as habitat and refugia to benthos and resident and transient fish (Bell and Westoby 1986, Bell and Pollard 1989, Connolly 1994, Loneragan et al. 1997, Sheridan 1997, Heck et al. 2003). Seagrass canopies modify currents and attenuate wave energy, a case of autogenic ecosystem engineering (sensu Jones et al. 1994), thus, trap sediment, seston, and larvae (Grizzle et al. 1996, Duarte et al. 1999, Koch 1999, Terrados and Duarte 2000, Vermaat et al. 2000, Gacia and Duarte 2001, Evrard et al. 2006), affect the storage of primary production within the system (Duarte and Cebrián 1996) or its export (Slim et al. 2006), and contribute to buffering adjacent sensitive habitats against the direct effects of water turbulence (Koch et al. 2006) and riverine siltation (Kenworthy et al. 1982, Cebrián et al. 2000). Belowground, the production of roots and rhizomes is substantial (45% of the meadow’s total biomass; Vermaat et al. 1995), hence, probably fundamental to substrate stability (Duarte et al. 1998).

The persistence of seagrass meadows depends on vegetation processes and the plants’ continuous response to various natural and anthropogenic disturbances. Seagrass meadows are dynamic systems composed of vegetative shoots in clonal networks that undergo demographic increases through branching, and decreases following senescence and mortality (Duarte et al. 2006). The recruitment of seeds and seedlings occurs periodically and may account for patch initiation (Duarte and Sand-Jensen 1990, Olesen et al. 2004). The rates of module production, ramet integration, colonization, and mortality vary with the size of the species (Marbá et al. 1996), habitat conditions, and season (Lee and Dunton 1996, Ramage and Schiel 1999). Disturbances may cause discontinuities in the landscape and affect these vegetation processes. These discontinuities are caused by medium- to large-scale natural events – dune migrations (Marbá et al. 1994a), waves and storms (Patriquin 1975, Fonseca and Bell 1988, Preen et al. 1995), and grazing (Ogden et al. 1973, Thayer et al. 1984, Valentine and Heck 1999, Sheppard et al. 2007) – that result in the dislodgment of the plants or their negative response to redistributions of sediments, eutrophication, and light reduction (Duarte et al. 1997, Terrados et al. 1998, Guidetti and Fabiano 2000).

Small-scale biological disturbance in seagrass meadows, prominent in benign environments, is caused by seagrass-associated animals (Jacobs et al. 1981, Hall et
Burrowing shrimps are a specific group of benthic invertebrates that may occur in association with seagrass environments, often conspicuous because of sediment gaps produced by their bioturbation (Fig. 1). In particular, the bioturbation by thalassinidean shrimps is well-studied and known to affect plant dynamics (Suchanek 1983, Valentine et al. 1994, Duarte et al. 1997, Dumbauld and Willey-Echeverria 2006), patch expansion (Townsend and Fonseca 1998), the benthos (Branch and Pringle 1987, Berkenbusch et al. 2000, Pillay et al. 2007), and processes at the sediment-water interface (Koike and Mukai 1983, Murphy and Kremer 1992, Forster and Graf 1992, Forster 1996, Gilbert et al. 1998). Another group of burrowing shrimps, the alpheids (Caridea), could also dominate the range of biological interactions in seagrass ecosystems, e.g., *Alpheus edamensis* De Man in Barang Lompo (Indonesia), the activities of which were shown to prevent the export of organic matter, hence, contributed to the conservation of nutrients (Stapel 1997). These interactions are probably altered in mixed-species beds of tropical regions such as SE Asia, where human pressure on the coastal zone has increased due to development initiatives (Fortes 1988, Milliman and Syvitski 1992, Duarte 2002, Orth et al. 2006). The degree of sediment mobility determines the life span, extension, and horizontal mobility of seagrass patches (Marbá et al. 1994a, Vermaat et al. 1997), and the species that compose the beds differentiate along a size and age range that may be used to distinguish their response to siltation by clonal leaf and rhizome growth (Duarte et al. 1994, Vermaat et al. 1995). Sediment mobility is primarily driven by river inputs but at the lower end of the siltation gradient, biological modifications may become important, along with physical reworking caused by tidal currents, wind- and wave-induced resuspension, and bed load movement, all likely to be severe during monsoonal rains and storms.

The present thesis intends to examine the role of small-scale disturbance by burrowing shrimps and its interaction with seagrass performance against a changing background of anthropogenically altered sediment dynamics. It describes the results of fieldwork within the 27 km² seagrass beds off Santiago Island in Bolinao.
GENERAL INTRODUCTION

(northwestern Philippines) (McManus et al. 1995) and of outdoor experiments carried out in the hatchery facility of the Bolinao Marine Laboratory (BML) of the University of the Philippines-Marine Science Institute (UPMSI). These results of work conducted between June 1997 and April 2001 are reported in the succeeding four chapters. In Chapter 2, the distribution of burrowing shrimp disturbance (as apparent marks on the beds – burrows openings, pits, sand patches/mounds – Fig. 1) in various seagrass and adjacent sediment environments is described. Apart from the beds on reef flats off the Bolinao-Anda region, the beds on selected islands of North Palawan, the Tubbataha Reef Atolls, and the reef flats off Naawan and Sulawan in northern Mindanao were visited to provide a comparative contrast to exposure conditions of the Bolinao-Anda region. The sediments disturbed by the shrimps are also characterized based on profiles of grain sizes, organic matter contents, and nutrients (nitrogen and phosphorus).

Chapter 3 quantifies the aboveground behavior of the snapping shrimp *Alpheus macellarius*, Chace, 1988 from its early morning emergence to prolonged retreat to the burrow by late afternoon to early evening. Observations were made *in situ* during three periods in a clear-water meadow off Silaki Island (Bolinao). The chapter also provides estimates of the significance of the shrimps’ sediment reworking and seagrass harvesting. Because *A. macellarius* spent a considerable amount of time in its burrow based on field observations, an outdoor experiment was setup to determine the shrimp’s behaviour within the burrow and to test the effect of sediment type on its activities. This study is organized as Chapter 4, which presents aspects of shrimp behaviour – burrow construction, feeding, and other within-burrow activities, activity pattern – as observed in glass cuvettes.

Chapter 5 contains results from a series of manipulative experiments that show the effects of short-term burial and leaf clipping on the growth patterns of the dominant seagrass *Thalassia hemprichii* (Ehrenberg) Ascherson. The manipulations involved monitoring leaf growth and rhizome elongation of apical shoots on clonal rhizome runners (Expt. 1, in situ) and leaf and root growth in seedlings (Expt. 2, outdoor). Experiment 3, also in situ, used exclosures to block all shrimp activity and tested the effect of the exclusion of shrimp disturbance on leaf growth and densities at the meter-scale. The thesis concludes with a synthesis (Chapter 6) that ties up results and conclusions in thematic sections, i.e., the role of bioturbation by burrowing shrimps in seagrass meadows, foraging strategies of *A. macellarius* and its mutualistic symbiosis with *Cryptocentrus* spp., shrimp disturbance and *T. hemprichii*, and, finally, small-scale disturbance and large-scale dynamics.

**References**


Chapter 2

The distribution of burrowing shrimp disturbance in Philippine seagrass meadows

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Abstract

Small-scale disturbance of seagrass meadows by burrowing shrimps was assessed by mapping and quantifying apparent disturbance marks (burrow openings, sand patches, sand mounds, shafts) and obtaining vertical profiles of sediment properties (grain size composition, organic matter and nutrient contents). The densities and sizes of sediment gaps and burrow openings were determined within sampling quadrats in various meadows and were correlated with ambient bed and site characteristics. Effects on sediment properties were determined in a comparison of disturbed and undisturbed areas in two beds with contrasting organic matter sources. Burrow openings and sediment gaps were common in all the meadows and were associated with either the snapping shrimp \textit{Alpheus macellarius} Chace, 1988 (Alpheidae, Caridea), or species of Thalassinidea. Alpheid shrimp disturbance was more frequent than that of thalassinidean shrimps. The distribution of sand mounds and associated shafts of thalassinidean shrimps were random, whereas the distribution of sand patches and burrow openings of alpheid shrimps on the beds appeared regular and clumped, respectively. The densities and sizes of sediment gaps and openings were higher and larger in wave-protected than in exposed beds ($p < 0.05$). Shrimp disturbance was more prevalent in clear-water than in turbid seagrass areas of the Bolinao-Anda region. The distribution of thalassinidean shrimps, however, was wider than that of \textit{A. macellarius}, which was observed to be
limited to vegetated fine-sand substrates. Overall, alpheid shrimps reworked sand patch areas of 14 ± 2% of the meadows while thalassinidean shrimps produced sand mounds that covered 4 ± 1%.

Burrowing shrimps altered the vertical profiles of sediment properties – *A. macellarius* relocated a significant proportion of coarse grains in the upper 10 cm while the thalassinidean shrimps consolidated finer fractions from 10 to 20 cm down the core, and consequently concentrated organic matter. Both shrimps reduced nitrogen by 20-73% in the top 10 cm sediment layer, by 4-36% in sediment deeper than 10 cm, but did not affect profiles of phosphorus.

**Keywords**: sediment gaps, *Alpheus macellarius*, Thalassinidea, burrows, seagrass canopies, sediment characteristics, Philippines

**Introduction**

Discontinuities in seagrass landscapes can result from disturbances that can have natural causes, such as rapid currents and exposure to waves (Patriquin 1975, Fonseca et al. 1983, Fonseca and Bell 1988, Hemminga and Duarte 2000), cyclones (Preen et al. 1995), as well as grazing by large mammals (De Jong et al. 1995, Preen 1995, Sheppard et al. 2007), rays (Valentine et al. 1994, Townsend and Fonseca 1998), and urchins (Ogden et al. 1973, Heck and Valentine 1995, Rose et al. 1999). Man-made causes of discontinuities include blast fishing (Jennings and Kaiser 1998), boat moorings (Walker et al. 1989, Hastings et al. 1995, Francour et al. 1999), and propeller scars (Dawes et al. 1997, Kenworthy et al. 2000). Small discontinuities in the meadows are due to disturbance by lugworms (Philippart 1994), crabs (Woods and Schiel 1997, Townsend and Fonseca 1998), and herbivorous birds (Jacobs et al. 1981, Nacken and Reise 2000), but sediment gaps – sand patches and mounds – result primarily from bioturbation by burrowing shrimps (Suchanek 1983, Stapel et al. 1997, Dumby and Wyllie-Echeverria 2003). The mechanisms by which small-scale shrimp disturbance contributed to the maintenance of one tropical clear-water seagrass meadow were determined by Duarte et al. (1997) in their assessment of each species’ response – shoot density, vertical growth, branching – to sediment burial. However, the more general extent of such disturbance has remained unclear in coastal systems such as in the Southeast Asian region, where siltation events often threaten coastal habitats (Milliman and Meade 1983, van Katwijk et al. 1993, McClanahan and Obura 1997, Terrados et al. 1998, Barnes and Lough 1999, Wesseling et al. 2001).

Burrowing shrimps generate small- to intermediate-scale disturbance (Hall et al. 1992). They modify the sediment environment primarily through their foraging and turbative behavior. Most deposit-feeding thalassinidean shrimps (Thalassinidea, Decapoda) produce conspicuous mounds and construct shallow cylindrical shafts and funnels around the mounds (Nickell and Atkinson 1995). The mounds arise from the shrimps’ ejections of fine sediments from belowground (Waslenchuk et al. 1983, Stamhuis et al. 1996), a behavior that has been associated with food sorting (De Vaugelas and Buscail 1990, Nickell and Atkinson 1995) and burrow ventilation (Stamhuis et al. 1996). The shafts are sites where the shrimps obtain food from surface sands while simultaneously maneuvering freely (De Vaugelas and Buscail 1990). Some species of alpheid shrimps (Alpheidae, Caridea, Decapoda) dump
tunnel sediments on the bed surface through the burrow openings and stack rubble and shell fragments opposite to the dumping site (Karplus 1987). The dumping of sediments is a typical penultimate behavioral state during tunnel extension and appears as a means by which alpheid shrimps access the sediment surface. The stack of rubble and shells, which resembles a roof and which may continue down as the burrow wall, provides structural support to the burrow opening (Karplus 1987, Dworschak and Ott 1993).

We hypothesized that where high densities of burrowing shrimps occur, sediment properties and processes may be affected at the larger meadow scale (e.g., Chapin et al. 1997). As an initial approach to address this issue, therefore, we implemented a survey programme that assessed the presence of apparent disturbance marks in various seagrass environments. We related the distributions to bed characteristics to serve as a qualitative basis for the estimation of the significance of these animals for sediment disturbance and seagrass herbivory in our subsequent work (Nacorda et al., Chapter 3, this Thesis). We also looked at profiles of sediment attributes to describe the shrimps’ disturbance region and the extent by which the animals particularly altered distributions of grain sizes and organic matter as well as concentrations of nitrogen and phosphorus in the sediments.

Materials and Methods

Study sites
We surveyed selected shallow seagrass areas in three locations – north-western, western, and southern Philippines (Fig. 1, a-c). These beds were on wave-protected reef flats (i.e., Bolinao-Anda and northern Mindanao), leeward zones of islands (Nangalao) or open to wind and waves (Pangaldaan, northern Palawan and in the Tubbataha Reef atolls) (Table 1). Within the Bolinao-Anda region (I), we also examined unvegetated substrates of lagoons in the reef flat (Sites 3 and 5), which were adjacent to the seagrass sites, and of sandy areas that followed reef slopes (Sites 1, 6, and 14) (Table 1).

Mapping of apparent shrimp disturbance and calculations
Rope quadrats (n = 3, size 9 to 25 m², laid 5 m apart and perpendicular to the shore) were set and corners were pegged into the substrate, then 1-m² grids were made within each quadrant to facilitate mapping. On rapid surveys in the Tubbataha Reefs and in Lopez Jaena (Misamis Occidental), short transects of 50-m and 20-m lengths, respectively, were installed instead, and mapping involved a 1-m² steel quadrat laid at 5-m intervals on both sides of the transect.

Systematic mapping proceeded by plotting the positions of thalassinidean shrimp sand mounds, funnels and shafts, alpheid shrimp burrows, and surrounding sand patches in all the 1-m² squares within the sampling quadrant. Measures of the following were determined: base diameter for sand mounds, longest length (L), and widest width (W) for sand patches, and diameters for burrows and shafts. Based on these measurements, the area was calculated, which was used to indicate the potential effects to the meadows in question. The base area of sand mounds covered a circle, hence:

\[ A = \pi r^2, \]
Figure 1. The locations of the three regions surveyed in the Philippines – (a), Bolinao-Anda reef system (Sites 1, 3-17); (b), North Palawan islands (Sites 18-19) and the Tubbataha Reef atolls (Sites 20-21); and (c), Iligan Bay in northern Mindanao (Sites 22-25). The specific seagrass habitats surveyed are indicated by (●) and the unvegetated habitats by (♦). Boxed areas in map (a) have turbid water; sediment core samples for detailed characterization were collected from two seagrass sites marked (®, 5 and 12). (Base maps courtesy of R. Abesamis and P. van der Wateren)
### Table 1. **Broad site characteristics of areas examined for the distribution of burrowing shrimp disturbance.**

<table>
<thead>
<tr>
<th>Region/ Sites</th>
<th>Site description</th>
</tr>
</thead>
<tbody>
<tr>
<td>I. Bolinao-Anda seagrass (● in Fig. 1, a)</td>
<td>Waters from the South China Sea and the Lingayen Gulf overlying the seagrass-dominated reef flat that is protected from outside waves by an intertidal reef crest (McManus et al. 1992); siltation gradient apparent from clear-water Site 5 (Silaki Is.; 16.4435 N, 119.9214 E) to turbid Site 17 (Batiarao; 16.2282 N, 120.0042 E) (McManus and Chua 1990); turbid conditions in Sites 9 (Pislatan; 16.3781 N, 119.9626 E) to 13 (Carot; 16.3496 N, 119.9650 E) also due to the organically loaded water mass of the Caquiputan Channel (Rivera 1997) and to discharges from fishponds and from the Sta. Rita River in Cabarruyan Island (Anda); bed substrate 90% coarse and fine sand with at least 8% silt and 4% organic matter (Kamp-Nielsen et al. 2002); mixed seagrass community dominated by <em>Thalassia hemprichii</em> (Ehrenberg) Ascherson (Vermaat et al. 1995) and declined in species richness above a 15% silt threshold (Terrados et al. 1998); sites intertidal to 5 m deep</td>
</tr>
<tr>
<td>I. Bolinao-Anda unvegetated substrata (● in Fig. 1, a)</td>
<td>Site 1 (Guiguiwanen; 16.3823 N, 119.9112 E) within an embayment, clear-water to turbid, with freshwater input from groundwater; Site 3 (Lucero; 16.4235 N, 119.9044 E) on western reef flat of Santiago Island, clear-water; both Sites 1 and 3 with muddy-sandy substrates and depths of 3 to 5 m; Site 6 (Malilnep; 16.4430 N, 119.9439 E) within a channel and Site 14 (Cangaluyan; 16.3678 N, 120.0059 E) after the reef slope</td>
</tr>
<tr>
<td>II. North Palawan Islands seagrass (● in Fig. 1, b)</td>
<td>Overlying water from the Sulu Sea, clear; Site 18 (Pangaldaan; 11.4931 N, 120.1426 E) exposed to waves, and with short <em>T. hemprichii</em> and <em>Cymodocea rotundata</em> Ehrenberg et Hempich ex Ascherson on coarse coralline substrata; Site 19 (Nangaloa; 11.3478 N, 120.1633 E) at the leeward side of the island with stands of mostly <em>Enhalus acoroides</em> (L.f.) Royle and <em>T. hemprichii</em> on white sandy substrate mixed with coral rubble</td>
</tr>
<tr>
<td>II. Tubbataha Reef Atolls seagrass (● in Fig. 1, b)</td>
<td>Sulu Sea clear water also overlying the seagrass-dominated reef flats; both Sites 20 (South Islet; 8.8756 N, 119.8730 E) and 21 (North Islet; 8.9616 N, 119.9767 E) with white sandy substrates mixed with coral rubble; short shoots of <em>T. hemprichii</em> and <em>C. rotundata</em> found</td>
</tr>
<tr>
<td>III. Northern Mindanao seagrass (● in Fig. 1, c)</td>
<td>Bohol Sea water overlying the seagrass-dominated reef flats; Sites 22 (Kapayas Island) and 23 (Danlugan) in Lopez Jaena (8.6206 N, 123.7527 E) both on the west coast of Iligan Bay; Site 22 more seaward, exposed, and with clearer water than Site 23; <em>T. hemprichii</em> dominant in Site 22, <em>E. acoroides</em> in Site 23; Sites 24 (Naawan; 8.4601 N, 124.2620 E) and 25 (Sulawan; 8.6244 N, 124.3999 E) flanked the outer east coast of Iligan Bay (Misamis Oriental); Site 24 nearshore and on a narrow reef flat, with water turning turbid due to river discharge; dense population of <em>Halodule uninervis</em> (Forsskal) Ascherson found, occasionally with <em>C. rotundata</em> and <em>Syringodium isoetifolium</em> (Ascherson) Dandy (Uy et al. 2001); Site 25 in a remote cove of Tabajon (Lagundingin), a clear-water area with ~110 ha of mixed seagrasses dominated by <em>T. hemprichii</em> (Arriesgado 1999)</td>
</tr>
</tbody>
</table>
while the area of irregularly shaped sand patches was estimated from

\[ A = L \times W, \]

an approach applied to similarly shaped corals (English et al. 1994).

Seagrass species richness and densities for each site were determined from either samples collected using a Rambo corer (diameter = 20 cm, area = 0.03 m²; \( n = 10 \)), \textit{in situ} counts within 50 x 50 cm quadrats (\( n = 3 \); haphazardly thrown outside the mapped rope quadrat), or obtained from literature, in the case of sites in northern Mindanao, i.e., Arriesgado (1999) and Uy et al. (2001). Sediment samples were also collected for the determination of grain size structure (corer diameter 4 cm, length = 10 cm; \( n = 3 \)); water depths at sampling time were recorded in all sites.

**Core sampling, sediment characterization, and laboratory analyses**

A separate set of sediment samples were obtained from Sites 5 (Silaki; clear-water; \( K_d \) from 0.1 to 0.7 m⁻¹, Rollon 1998) and 12 (Rufina; turbid; \( K_d \) from 0.1 to 2.0 m⁻¹, Rollon 1998) (Fig. 1, a) using PVC corers (10 cm diameter x 35 cm length). The samples were collected near sand patches with burrow openings (core type #1, \( n = 3 \)), sand mounds with shafts (core type #2, \( n = 3 \)), and on the homogeneously vegetated section of the meadow (core type #3, \( n = 3 \)). All the core samples were kept upright and soaked in ambient water during transport to the laboratory.

Each core sample was sliced into sediment sections at depths 3, 6, 9, 12, 15, 20, 25, 30, and 35 cm from the surface. Each section was rid off of plant matter, subsampled for total organic matter (TOM) and nutrient analyses, then oven-dried altogether at 105°C for 24 h, cooled, and weighed. TOM was determined as material lost from the dried sample after ignition for 6 h at 550°C (Buchanan 1984). The rest of the each slice was analyzed for grain size distribution, i.e., characterized by wet sieving after soaking up to 100 g of dried samples in Calgon (sodium hexametaphosphate; Buchanan 1984). Fractions retained on each sieve were similarly oven-dried and weighed as described above. The grain size profile for each site was summarised as mean (\( \mu, \phi \)), standard deviation or sorting (\( \sigma, \phi \)), and skewness (Leeder 1982).

Nitrogen (N) and phosphorus (P) of sediments were analyzed at the Environmental Engineering Laboratory of UNESCO-IHE. Known weights of oven-dried sediment samples (grain size <1 mm) were first digested with a mixture of sulphuric acid, selenium, and salicylic acid (Kruis 2000) prior to the analyses. Total N (as \( \text{NH}_4\text{-N} \)) was determined from the resulting digests following straightforward procedures and utilized a Perkin-Elmer Lambda 20/2.0 nm UV/VIS spectrometer. The standard addition technique was utilized for the analyses of total P (as \( \text{PO}_4\text{-P} \)) in a Tecator-Aquatec autoanalyser (APHO 1992 in Kruis 2000).

**Data analyses**

Each apparent disturbance point (burrow openings, sand patches, sand mounds, shafts) on seagrass areas of Region I was scored and analyzed for pattern using quadrat analysis, where variance-mean ratios (VMR) are calculated then interpreted, i.e., VMR approximates 1 for random distributions, <1 for uniform, and >1 for clustered distributions (Rogerson 2001). Mixed analyses of variance in SPSS were used to test the quadrat dataset of all sites. Densities of the disturbance marks were compared among regions (I-III), among habitat types (seagrass, reef flat lagoon, reef...
lagoon), and among sites for the Bolinao-Anda region (I). Sampling depth, sediment descriptors, mud content, seagrass parameters, and sediment gap densities and sizes were entered as covariates during the analyses and their sums of squares remained additive. *Post-hoc* comparisons were carried out where regional or habitat differences emerged, maintaining an experimentwise error rate of 0.017 (Sokal and Rohlf 1995). Appropriate transformations were carried out on heteroscedastic data. Attributes in the sediment dataset were compared across core types and sections for each site using two-way ANOVAs. *Post-hoc* comparisons were similarly carried out as described.

### Results

#### Mapping survey – comparisons of regions

The shallow meadows surveyed had sandy substratum, were poorly sorted, and were fine-skewed except for Region II which was coarse-skewed (Table 2). Substrate type was finer in the deeper and unvegetated lagoons of the Bolinao-Anda region (I), indicating low energy environments comparable to the meadows surveyed. The mixed meadows visited were dominated by *Thalassia hemprichii*, and those composed of as much as 7 species occurred in the relatively protected meadows (Table 2).

The marks of shrimp disturbance were evident in all the sites surveyed (Table 3). Some sand mounds occurred within huge sand patches and some alpheid shrimp burrows opened from mound margins as well. The burrows within the sand patches were inhabited by *Alpheus macellarius*, Chace, 1988, which live in symbiosis with species of *Cryptocentrus*. We noted the presence of craters of fish (e.g., *Amblygobius phalaena*) and crabs (e.g., *Callinectes* sp.) in silty environments, and of pits occupied by *Corallianassa* sp. in the intertidal zone of Site 3 (Lucero) (Fig. 1, a) and in wave-exposed Site 18 (Pangaldaan) (Fig. 1, b).

The exposed sites of Region II had reduced densities and sizes of sand patches, burrow openings, and mound-associated shafts (Table 3). Sand mounds were low and appeared as ‘moon-scapes’ that covered 9 ± 4% of the bed. In the protected beds of Regions I and III, we observed our sampling quadrant of 9 m² to include 9 ± 1 sand patches of alpheid shrimps (maximum = 2 m²) with altogether 20 ± 5 burrow openings (maximum = 10 m²), 3 ± 1 sand mounds of thalassinidean shrimps (maximum = 3 m²), and 3 ± 1 mound-associated shafts (maximum = 3 m²) within funnel-shaped surface openings. The sand patches bared 13 ± 2% of the bed (maximum = 52%) and its burrows opened ~ 0.1 ± 0.02% of the patch surface (maximum = 1%). Mean sand mound height was 9 ± 0.3 cm from the bed (maximum = 48 cm). Sand mound cover was significantly lower at 4 ± 0.7% of the meadows (maximum = 32%) compared with mound cover in Region II. Mound-associated shafts opened 0.05 ± 0.01% of the bed surface (maximum = 0.5%).

Sand patch numbers and sizes positively correlated with the number of burrow openings (Fig. 2, a and b). Mound sizes covaried positively with corresponding densities and with water depth (Table 4). There were also significant among-site variations in seagrass species richness and shoot densities of *T. hemprichii*, *H. uninervis*, and *E. acoroides* ($p < 0.05$, Table 4). Sediment skewness emerged as a positive correlate of seagrass species richness and the presence of sand mounds seemed to indicate a negative effect on shoot densities of *T. hemprichii* but
Table 2. Mean values of (± SEM) depth, sediment characteristics, species richness and shoot densities of seagrasses on the 3 regions (25 sites) surveyed in the Philippines. Legend: (a), the species was found in the meadow but was missed in the quadrats or cores; –, the species was not found in the quadrats or cores; superscripts denote similar or significant differences among means after post-hoc comparisons at $\alpha = 0.017$)

<table>
<thead>
<tr>
<th>REGION</th>
<th>Bolinao-Anda reef system (NW Phils)</th>
<th>N Palawan &amp; Tubbataha Reefs</th>
<th>N Mindanao (S Phils)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parameters</td>
<td>After reef slope</td>
<td>Reef flat lagoon</td>
<td>Seagrass</td>
</tr>
<tr>
<td>Sampling depth, m</td>
<td>4.65 (0.26)</td>
<td>4.12 (0.17)</td>
<td>0.89 (0.06)</td>
</tr>
<tr>
<td>Sediment parameters:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean grain size, $\mu$, in $\phi$</td>
<td>+ 2.39b (0.32)</td>
<td>+ 1.48b (0.02)</td>
<td>+ 1.17a (0.06)</td>
</tr>
<tr>
<td>Sorting, $\sigma$, in $\phi$</td>
<td>+ 1.81a (0.22)</td>
<td>+ 2.35b (0.36)</td>
<td>+ 1.92a (0.06)</td>
</tr>
<tr>
<td>Skewness</td>
<td>+ 0.21 (0.06)</td>
<td>+ 0.72 (0.01)</td>
<td>+ 0.06 (0.02)</td>
</tr>
<tr>
<td>Mud content, %</td>
<td>10.4 (2.4)</td>
<td>9.9 (2.2)</td>
<td>5.2 (0.4)</td>
</tr>
<tr>
<td>Seagrass parameters:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of species</td>
<td>no seagrass</td>
<td>no seagrass</td>
<td>4 (0.01)</td>
</tr>
<tr>
<td>Shoot densities, per sq. m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cymodocea rotundata</td>
<td>36 (6)</td>
<td>88 (13)</td>
<td>33 (19)</td>
</tr>
<tr>
<td>Cymodocea serrulata</td>
<td>27 (4)</td>
<td>-</td>
<td>32 (22)</td>
</tr>
<tr>
<td>Enhalus acoroides</td>
<td>22 (2)</td>
<td>(a)</td>
<td>57 (19)</td>
</tr>
<tr>
<td>Halophila ovalis</td>
<td>15 (4)</td>
<td>19 (17)</td>
<td>20 (8)</td>
</tr>
<tr>
<td>Halodule uninervis</td>
<td>32 (6)</td>
<td>-</td>
<td>466 (287)</td>
</tr>
<tr>
<td>Syringodium isoetifolium</td>
<td>27 (6)</td>
<td>-</td>
<td>210 (133)</td>
</tr>
<tr>
<td>Thalassia hemprichii</td>
<td>180a (18)</td>
<td>622b (123)</td>
<td>516c (138)</td>
</tr>
</tbody>
</table>
Table 3. Mean density and space occupied (± SEM) by sediment gaps of burrowing shrimps in the three regions (25 sites) surveyed and in 3 habitats of the Bolinao-Anda region. Differences among regions were detected by ANOVA for alpheid shrimp sand patch densities and subsequent sizes, as well as sizes of thalassinidean shrimp sand mounds. Sand mound densities and sizes of alpheid shrimp burrow openings, sand mounds, and shaft opening sizes also differed across substrata in Region 1. Results of subsequent post hoc comparisons of regions are indicated by the lowercase superscripts, and of substrate comparisons by uppercase superscripts ($\alpha = 0.017$).

<table>
<thead>
<tr>
<th>REGION</th>
<th>VARIABLES</th>
<th>Bolinao-Anda reef system (NW Phils)</th>
<th>N Palawan Islands &amp; Tubbataha Reefs</th>
<th>N Mindanao (S Phils)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>After reef slope</td>
<td>Reef flat lagoon</td>
<td>Seagrass</td>
</tr>
<tr>
<td></td>
<td>Number of quadrats sampled</td>
<td>16</td>
<td>8</td>
<td>71</td>
</tr>
<tr>
<td></td>
<td>Densities (numbers/ 9 m$^2$)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Alpheid shrimp sand patches</td>
<td>-</td>
<td>-</td>
<td>$9^b$ (0.5)</td>
</tr>
<tr>
<td></td>
<td>VMR (range)</td>
<td></td>
<td></td>
<td>0.1 – 0.7</td>
</tr>
<tr>
<td></td>
<td>Alpheid shrimp burrow openings*</td>
<td>31 (9)</td>
<td>33 (21)</td>
<td>$2^b$ (2)</td>
</tr>
<tr>
<td></td>
<td>VMR</td>
<td></td>
<td></td>
<td>1.3 – 4.8</td>
</tr>
<tr>
<td></td>
<td>Thalassinidean shrimp sand mounds</td>
<td>29$^b$ (8)</td>
<td>19$^b$ (3)</td>
<td>$4^a$ (0.5)</td>
</tr>
<tr>
<td></td>
<td>VMR (range+)</td>
<td></td>
<td></td>
<td>0.8 – 1.2</td>
</tr>
<tr>
<td></td>
<td>Mound-associated shafts/ pits</td>
<td>6 (1)</td>
<td>5 (2)</td>
<td>$3^b$ (0.6)</td>
</tr>
<tr>
<td></td>
<td>VMR</td>
<td></td>
<td></td>
<td>0.8 – 1.2</td>
</tr>
</tbody>
</table>

Sizes (% of space occupied/ 9 m$^2$)

<table>
<thead>
<tr>
<th>VARIABLES</th>
<th>Bolinao-Anda reef system (NW Phils)</th>
<th>N Palawan Islands &amp; Tubbataha Reefs</th>
<th>N Mindanao (S Phils)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>After reef slope</td>
<td>Reef flat lagoon</td>
<td>Seagrass</td>
</tr>
<tr>
<td>Alpheid shrimp sand patches</td>
<td>-</td>
<td>-</td>
<td>15.8$^b$ (1.8)</td>
</tr>
<tr>
<td>Alpheid shrimp burrow openings</td>
<td>0.7$^b$ (0.4)</td>
<td>1.0$^b$ (0.9)</td>
<td>0.1$^a$ (0.03)</td>
</tr>
<tr>
<td>Thalassinidean shrimp sand mounds</td>
<td>10.6$^b$ (2.9)</td>
<td>16.6$^b$ (5.1)</td>
<td>3.3$^a$ (0.6)</td>
</tr>
<tr>
<td>Mound-associated shafts/ pits</td>
<td>0.1$^b$ (0.1)</td>
<td>0.2$^b$ (0.00)</td>
<td>0.03$^a$ (0.01)</td>
</tr>
</tbody>
</table>

Legend: *VMR – variance to mean ratio, here given as the range of the most frequent pattern; *Alpheus macellarius – Cryptocentrus sp. burrows were observed to be restricted to seagrass beds; those found on unvegetated substrata were occupied by different alpheid shrimp – goby associations.
explained only little of the total variance. Densities of sand patches were negatively correlated with shoot densities of *H. uninervis*; depth emerged as a negative correlate of shoot densities of *E. acoroides*.

**Bolinao-Anda region (I): comparisons within seagrass sites and across habitats**

Within the 20-km latitude covered by the survey, shrimp disturbance appeared to be more frequent in the northern beds of Santiago Island (Bolinao) than either midway, where turbid conditions existed, or in the beds of the reef flat of Cabarruyan Island (Anda) in the south (Fig. 1, a). When sites were regrouped *a posteriori* based on water clarity, the disturbance by alpheid shrimps became more pronounced in clear-water than in turbid seagrass areas (Fig. 3, top graphs). Sand mounds were similar in both environments, on average, but mound maxima, shaft densities, and shaft maxima were reduced in turbid areas (Fig. 3, bottom graphs). The distribution patterns of shrimp disturbance were not similar, with sand patches occurring more regularly in the quadrats than the sand mounds and shafts, which occurred at random (Table 3). The distribution of burrow openings, on the other hand, appeared clumped (Table 3).

There was a clear overlap in the densities and sizes of sand patches and burrow openings of alpheid shrimps with those of sand mounds and of associated shafts of thalassinidean shrimps, especially on the shallow seagrass areas (~1 m depth) (Fig. 4, a). More sand mounds were also recorded on the bare substrates than in seagrass areas (*p* < 0.05; Fig. 4, b; Table 3), the latter having projected areas of 12 and 14% of our grid (1 m²) (maximum = 40 and 45%; maximum heights = 31 and 57 cm). The sizes of alpheid shrimp burrow openings were also significantly higher in the bare sediments than on seagrass beds (*p* < 0.05, Table 3; Fig. 4, b). We noted, however, that the unvegetated substrates had other shrimp-goby associations that accounted for the observed increase and not by the *A. macellarius–Cryptocentrus* sp. symbiosis that occurred in the seagrass beds. In Site 6 (Malilnep), for instance, we found occurrences of two banded *Alpheus* sp. individuals that alternated in expelling chela-loads of burrow sediment, and recognized the prawn goby *C. polyophthalmus* guarding several burrows.
Table 4. Variables that showed significant variation among regions (n=3) based on mixed analyses of variance versus in-situ bed characteristics (as covariates). All covariates were entered in each analysis but only the significant ones* are presented below (error term in this case is 'within sites'; \( \alpha \approx 0.05 \)). The association of the covariables with the dependent variable is given as + or –.

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Region</th>
<th>% variance explained by Region</th>
<th>% variance explained by Covariables in model</th>
<th>Covariables in model</th>
<th>% variance explained by Covariables in model</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sand patch density (1)</td>
<td>0.043</td>
<td>1 91 9</td>
<td>+ Burrow opening density 3 &lt;0.001</td>
<td>- Sand mound density 1 0.003</td>
<td>+ Shaf/ pit density 1 0.048</td>
<td>- H. uninervis shoot density 1 0.042</td>
</tr>
<tr>
<td>Sand mound size (2)</td>
<td>&lt;0.001</td>
<td>9 87 13</td>
<td>+ Depth 2 0.003</td>
<td>- Sand patch size 1 0.019</td>
<td>+ Shaf/ pit opening size 2 0.002</td>
<td>- Sand mound density 4 &lt;0.001</td>
</tr>
<tr>
<td>n seagrass species (3)</td>
<td>&lt;0.001</td>
<td>2 96 96</td>
<td>+ Skewness 1 0.018</td>
<td>- Sand patch density 1 0.020</td>
<td>- Sand patch size 1 0.026</td>
<td>+ Sand mound density 2 0.016</td>
</tr>
<tr>
<td>Thalassia hemprichii shoot density (4)</td>
<td>&lt;0.001</td>
<td>20 85 15</td>
<td>+ Sand patch density 1 0.020</td>
<td>- Sand patch size 1 0.026</td>
<td>+ Sand mound density 2 0.016</td>
<td>- Sand mound size 4 &lt;0.001</td>
</tr>
<tr>
<td>Halodule uninervis shoot density (5)</td>
<td>0.024</td>
<td>7 60 40</td>
<td>- Sand patch density 3 0.047</td>
<td>+ H. ovalis shoot density 11 &lt;0.001</td>
<td>+ H. uninervis shoot density 1 0.020</td>
<td>- Sand patch size 1 0.026</td>
</tr>
<tr>
<td>Enhalus acoroides shoot density (6)</td>
<td>0.027</td>
<td>3 83 17</td>
<td>- Depth 2 0.007</td>
<td>- Sand patch density 1 0.020</td>
<td>- Sand patch size 1 0.026</td>
<td>+ Sand mound density 2 0.016</td>
</tr>
</tbody>
</table>

Note: Separate stepwise regressions included the following covariables as predictors of the dependent variables, but altogether explained much less variance than that accounted for by ANOVA: (1) sediment skewness (+) in place of H. uninervis shoot density; (2) sand patch density (-) and C. rotundata shoot density (+) in place of T. hemprichii shoot density; (3) sand patch density (+) and mud content (-); (4) mean grain size (-) and sediment skewness (+); (5) burrow opening density in place of sand patch density; and (6) mud content (-) and sediment sorting (-).
Vertical profiles of sediment properties
The profiles of undisturbed seagrass sediments were clearly different between Sites 5 (Silaki) and 12 (Rufina). Mean grain sizes were between 1.0 and 1.5 $\phi$ in Site 5 while the bed sediment in Site 12 was more heterogeneous, i.e., $\mu$ between 0.1 and 1.25$\phi$, and with coarser grains from 12 cm and deeper. Both burrowing alpheid and thalassinidean shrimps altered sediment texture but the effect of the shrimps was significant only in Site 5 (2-way ANOVA, $p < 0.005$), where the redistribution of coarser grain sizes was evident (Fig. 5). The vertical heterogeneity of the bed substrate in Site 12 appeared to obscure the effect of the shrimps in redistributing coarse grains in the upper 10 cm and in consolidating fine fractions in deeper sediments (2-way ANOVA, $p > 0.05$; Fig. 5).

Organic matter (OM) content in the undisturbed seagrass sediments was statistically similar for both sites and averaged ~40 ± 2 mg•g DW$^{-1}$. Alpheid shrimps increased OM only slightly (41 ± 1.3 mg•g DW$^{-1}$) while thalassinidean shrimps significantly raised OM content by 20% (50 ± 1 mg•g DW$^{-1}$, Fig. 6, a; 2-way ANOVA, $p < 0.001$). Total N profiles (as NH$_4$-N) had significant differences between the sites and concentrations were reduced by up to two-fold at the top 10 cm of shrimp-disturbed sediments (Fig. 6, b). In Site 5, shrimp disturbance seemed to keep nitrogen levels lower (0.24 ± 0.01 mg NH$_4$-N•g DW$^{-1}$) than in the undisturbed sediments (0.33 ± 0.01 mg NH$_4$-N•g DW$^{-1}$) (Tukey’s HSD, $p < 0.017$). Nitrogen was significantly higher in the top 10 cm layer than deeper in the...
Figure 4. Bolinao-Anda region (I) – Distributions of burrowing shrimp disturbance marks with sampling depth in (a) seagrass meadows and (b) unvegetated substrata.
undisturbed seagrass sediments of Site 12 (Tukey’s HSD, \( p < 0.017 \); Fig. 6, b); shrimp disturbance only reduced nitrogen levels on the top 10 cm of the sediments by 20-73% and by 4-36% at deeper than 10 cm, but did not affect overall profiles. Nitrogen levels of disturbed sediments in Site 12 also exhibited a positive linear relationship with OM \((y = 0.003x - 0.002, r^2 = 0.35, p < 0.001)\), with low levels associated with alpheid shrimps and the high ones with the thalassinidean shrimps. The sites also differed in total phosphorus concentrations, which were higher in Site 12 \((3.75 \pm 0.12 \text{ mg g}^{-1} \text{ o-PO}_4 \text{ g DW}^{-1})\) (Fig. 6, c) than in Site 5 \((3.02 \pm 0.01 \text{ mg g}^{-1} \text{ o-PO}_4 \text{ g DW}^{-1})\) (3-way ANOVA, \( p < 0.05 \)), and shrimp disturbance did not influence either concentration or distribution of phosphorus in the sediments (3-way ANOVA, \( p > 0.05 \)) (Fig. 6, c).

**Discussion**

The primary agents of readily observable disturbance in the seagrass beds studied were alpheid shrimps, *Alpheus macellarius*, which associated with at least two species of prawn goby *Cryptocentrus* (Palomar et al. 2004), i.e., the blue-speckled prawn goby *C. octafasciatus* Regan, 1908 and the Singapore prawn goby *C. singapurensis* (Herre, 1936). The observed restricted distribution imposed by vegetation suggests the animal’s food habit, thus, leaf clipping is an apparent behaviour for *A. macellarius* on the meadows (Nacorda et al., Chapter 3, this Thesis). Outside the seagrass beds, other distinct *Alpheus–Cryptocentrus* combinations were noted. Examples of such pairs frequently reported in sandy substrates within the region include *A. bellulus* Miya and Miyake, 1969 – *Cryptocentrus cinctus* (Herre, 1936), *A. bellulus–Cryptocentrus* sp. 1, *A. djiboutensis* De Man, 1909 – *C. caeruleomaculatus* (Rupell, 1830), and *A. djiboutensis–C. singapurensis* (Nakasone and Manthachitra 1986, Manthachitra and Sudara 1988). Densities of burrow openings were less than those reported by Bradshaw (1997) from reefal sediments of Phuket.

The next important disturbance agents were pooled as a distinct taxon group, the thalassinidean shrimps, in view of the difficulty in obtaining specimens for identification, and because we assumed that the relative effects on the meadows are
independent of the exact species. Hence, their distribution was not restricted to the vegetated substrates and the shrimps were common at greater depths below the depth limit of seagrass beds and in non-vegetated lagoon bottoms of the Bolinao-Anda region. The sand mound densities we found on seagrass and bare substrates correspond to the range of ‘low-’ and ‘medium-density areas’ reviewed by de Vaugelas (1985) and are within the range observed in shallow backreef lagoons (Roberts et al. 1981) and reefal sediments (Bradshaw 1997). We did not find any significant correlation between the densities of these two dominant burrowing shrimps, suggesting that other factors than interspecific competition for space may operate to constrain their densities. In addition, the observed variation was considerable.

Hydrodynamics appeared to influence the occurrence of burrowing shrimps. The disturbance of alpheid and thalassinidean shrimps was a constant feature of developed meadows with benign to mid-range hydrodynamics. Beds exposed to higher water movements have less or with shifting coarse sediments, e.g., where _Thalassodendron ciliatum_ occurs (Bandeira 2002) or where a dense mix of species is closely integrated on hard bottoms. Seagrasses were observed to adapt to such environments by allocating considerable resources to vertical growth (Duarte et al. 1996), growing longer rhizome internodal distances (Nathaniel et al. 2003) and maintaining higher belowground biomass, which could be unsuitable for shrimp bioturbation (Townsend and Fonseca 1998). However, when disturbance exposes large gaps within these beds, e.g., the 1,200 m²-gap of thin sediments in Bolinao in 1999 (Olesen et al. 2004), we observed burrowing alpheid shrimps to immediately emerge and transport sediments to the surface (pers. obs). The animals seemed opportunistic – these were smaller than usually found in other beds and their burrow openings were densely packed (up to 40 m⁻²), perhaps until the large gap completely became revegetated. In other relatively wave-exposed areas of meadows (e.g., Sites 3 and 18), bioturbation pits of the thalassinidean shrimp _Corallianassa_ sp. were evident. These ghost shrimps do not actively rework the sediment and use their burrow openings to catch drifting seagrass/detrital fragments and store them as cache (Griffis and Suchanek 1991, Dworschak et al. 2006).

Water clarity emerged as a significant factor for densities of _A. macellarius_ disturbance (sand patches, burrow openings). The abundance of _A. macellarius_ in

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**Figure 5.** Vertical distribution profiles of mean grain size $\mu$ (as $\phi \pm$ SEM) in undisturbed (▲) and shrimp-disturbed sediments of Sites 5 (Silaki) and 12 (Rufina) (Bolinao-Anda region).
clear-water meadows is linked to their prawn gobies’ camouflage and ability to perceive risk factors (e.g., predation) in the lighted environment (Karplus 1987). Because this view of the ambient environment becomes limited in turbid waters, the gobies could be trading-off hiding with the perceived risky emergence at the sediment surface. Also, since sediment type in silty beds are less compact and resuspend easily, shrimp burrows could be expectedly unstable and the openings would easily be filled up with sediments. These may cause the animal partners to stay hidden from view and the shrimp spending more burrow reconstruction and maintenance time rather than extending the burrows or harvesting seagrass leaves, at least until conditions become more favorable for emergence at the surface.

Figure 6. Vertical distribution profiles of (a) organic matter, (b) inorganic nitrogen (as NH₄-N), and (c) inorganic phosphorus (as o-PO₄) contents in the undisturbed and shrimp-disturbed sediments of Sites 5 and 12 in the Bolinao-Anda region. Data are means ± SEM.
The significant correlations of shrimp gap attributes with sediment and seagrass parameters explained only 1 to 3% of variability in the ANOVAs (Table 3). However, the significant relationship between sand patch density and number of seagrass species, despite large variation in the data (Table 4), offers a mechanism by which small colonizing species are maintained in mixed meadows (Duarte et al. 1997). As much as 14% of the meadow on average represents an open space for *Halophila ovalis*, noticeable on the sand mounds and capable of fast clonal expansion (Vermaat et al. 1995, Rasheed 2004). Once recolonized, the unconsolidated sediments become stabilized (Fonseca 1989), hence, prepared for subsequent colonizers, and the new vegetation becomes functional, e.g., as food, refuge from predators, and habitat (Bell and Westoby 1986). This series of processes for fast colonizers was thought to minimize ecosystem function losses due to frequent small-scale disturbance (Duarte 2000). Sediment burial reduces the cover and productivity of seagrasses (e.g., at >10 mounds m⁻², Roberts et al. 1981; but see also Chapter 5, this Thesis) but was also shown to elicit species-specific responses to cope with such disturbance, e.g., increased vertical growth, branching, and shoot densities (Duarte et al. 1997). *Cymodocea nodosa* grew upwards from rhizomes buried after the passage of sand waves (Marbá et al. 1994) while *Zostera novazelandica* moderated the effect of high sediment turnover activity by *Callianassa filholi* by higher above-ground plant growth during the warmer months (Berkenbusch et al. 2000).

Bioturbation by burrowing shrimps, as an example of case 4 allogenic engineering (Jones et al. 1994), has major consequences on local bed sedimentology and geochemistry, interface processes, the fate of benthic communities, and, eventually, on the rhizosphere of seagrass beds. Larger grain sizes were more prominent in the upper 10 cm section of sediments than deeper in the shrimp-disturbed cores (Fig. 5). Both types of shrimps rearrange large grains differently: thalassinidean shrimps bury such fractions whereas alpheid shrimps bring them to the surface (Bradshaw and Scoffin 2001). Rearrangements in the sediment framework results in redistribution and continual transfer of sediment organic matter and nutrients, which affects biogeochemical redox processes (Schulz 2000). The reworked but unconsolidated sediments are subject to resuspension (Aller and Dodge 1974, Rowden et al. 1998) and the associated benthos may either be enhanced (e.g., for bacteria; Gilbert et al. 1998) or diminished due to smothering and/or burial, e.g., for diatoms, meiofauna (Suchanek and Colin 1986, Branch and Pringle, 1987), and macrofauna (Posey et al. 1991, Berkenbusch et al. 2000). The presence of complex burrows that open to the sediment-water interface provides oxygenation of the sediments (Forster and Graf 1992) and bioventilation redistributes oxygen and nutrients to the water column (Koike and Mukai 1983, Waslenchuk et al. 1983, Murphy and Kremer 1992, Forster 1996). Oxygenation alleviates the moderately reducing conditions of the sediments (Terrados et al. 1999) and disturbance could be a mechanism to diffuse oxygen from seagrass roots (Hemminga 1998, Pedersen et al. 1998, Frouin 2000), hence, help accelerate organic matter degradation (Ziebis et al. 1996).

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References


Nacorda, H.M.E., Stamhuis, E.J., and Vermaat, J.E. Chapter 4: Burrows and behaviour of the snapping shrimp Alpheus macellarius, Chace, 1988, in different seagrass substrates. (this Thesis)


Chapter 3

Aboveground behavior of the snapping shrimp *Alpheus macellarius*, Chace, 1988, and its significance for leaf and nutrient turnover in a Philippine seagrass meadow

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Abstract

The aboveground behavior of the snapping shrimp *Alpheus macellarius*, Chace, 1988, was studied in a shallow clear–water seagrass meadow off Bolinao, NW Philippines. The shrimp’s activity pattern was analyzed from short video records taken every hour on sampling visits during the dry and wet months. *Alpheus macellarius* actively moved sediment (frequency = 77 h⁻¹), often surveyed its burrow opening (21 h⁻¹), stacked up rubble (17 h⁻¹), and occasionally harvested seagrass leaves (9 h⁻¹) during the dry months. Time allocated for these aboveground activities was only 12% of its daily active period of 9 hours during daylight; *A. macellarius* was in its burrow during the remainder of daytime. During the wet months, the shrimp’s activity rates and corresponding time allocations were reduced by at least 34% that of the dry months and its within-burrow period consequently increased by 5%. Overall, sediment moving and harvesting activities of *A. macellarius* contributed frequent disturbance to the meadow: an individual shrimp remobilized, on average, ~300 g dry weight (DW) of sediment d⁻¹ (range, wet to dry months = 204 to 346 g d⁻¹), which projects to 112 kg y⁻¹, and harvested 0.8 g DW of


leaves $d^{-1}$ (range = 0.2 to 1.1 g $d^{-1}$), or a total of 291.3 g $y^{-1}$. The estimated sediment-reworking rate falls within a considerable range of 0.8 to 1.4 kg $m^{-2} d^{-1}$ during the wet and dry months, for an average shrimp density of 2 $m^{-2}$, and, correspondingly, the estimated leaf harvesting rate of 0.4 to 2.3 g $m^{-2} d^{-1}$ represents moderate herbivory, equivalent to 12 to 42% of leaf production, respectively.

Keywords: Alpheidae, bioturbation, burrowing, herbivory

Introduction

Diverse faunal assemblages inhabit the different physical compartments of seagrass meadows for refuge and food (McRoy and Helfferich 1977, Leber 1985, Larkum et al. 1989). These assemblages account for the complex trophic hierarchy in seagrass meadows, together with large transient species like dugongs, green turtles, and waterfowl (Jacobs et al. 1981, Thayer et al. 1984, Lanyon et al. 1989, Preen 1995). Direct herbivory of seagrass leaves forms a significant pathway in this trophic hierarchy (Valentine and Heck 1999), which may have been underestimated in the past (Klumpp et al. 1989, Hemminga et al. 1991, Duarte and Cebrián 1996, Cebrián et al. 1997). The list of herbivores includes animals of broad size ranges and the smaller ones may contribute substantially to total herbivory, e.g., sea urchins *Lytechinus variegatus* (Lamarck) (Heck and Valentine 1995) and snapping shrimps of the genus *Alpheus* (Alpheidae, Caridea) (Stapel and Erftemeijer 1997).

Burrowing is a more prominent activity of these alpheid shrimps than leaf harvesting, and their active bioturbation features showcases of classical ‘ecological engineering’ (Jones et al. 1994). This bioturbation behavior, well described for the thalassinid shrimps (Thalassinidea), has been shown to affect plant dynamics (Suchanek 1983, Valentine et al. 1994, Duarte et al. 1997) which, in turn, contributed to either the fragmentation (Townsend and Fonseca 1998) or, conversely, the maintenance of meadows (Duarte et al. 1997). In Philippine meadows, the snapping shrimp *Alpheus macellarius*, Chace, 1988, is responsible for “crenate mounds” (*sensu* Dworshack and Ott 1993) or sand patches that may outnumber the sand volcanoes/ mounds of thalassinid shrimps (Nacorda et al., Chapter 2, this Thesis), and for clipped shoots within the vicinity of the sand patches. Burrowing and leaf harvesting make alpheid shrimps potentially important bioturbation agents as well as grazers, but their significance remains uncertain because a quantification of their behavior so far is lacking. In this paper, we describe the aboveground behavior of *A. macellarius*, and derive estimates of its importance for sediment reworking and leaf herbivory in the relatively pristine and well-studied seagrass meadow off Bolinao (NW Philippines).

Methods

Behavioral observations were carried out in the shallow and pristine meadow of mixed seagrasses located in Silaki off Santiago Island, Bolinao (NW Philippines; 16°26.42 N, 119°55.72 E; Fig. 1) during the El Niño year of 1998 (June-July, September-October), the following year’s dry months (April-May 1999) and in October 1999 (wet). The meadow is part of the 27 km² of seagrass vegetation that
covers 84% of the reef flat surrounding Santiago Island (McManus et al. 1995), has clear overlying water, is exposed to frequent wave disturbance, and its seagrass community of 9 species is dominated by *Thalassia hemprichii* (Ehrenberg) Ascherson (Rollon and Fortes 1991, Vermaat et al. 1995). Sand patches and mounds (volcanoes) are frequent within this dense meadow, and, on average, measured 30% (maximum = 52%) and 8% (maximum = 32%) of the bed, respectively (Nacorda et al., Chapter 2, this Thesis).

The snapping shrimp *Alpheus macellarius* in Silaki occurs with the blue-speckled prawn goby *Cryptocentrus octafasciatus* Regan, 1908. The shrimp’s body is typically dark green and its first abdominal somite is tinged orange. It carries its major cheliped extended, like most other alpheid shrimps, and the chela’s dactyl and plunger tips also have the orange coloration. Chace (1988) has placed *A. macellarius* as a member of the Brevirostris species group, which stands out from other species by the characteristics of its major and minor chela. The goby, on the other hand, approximates the color of the sand substrate, and the dark longitudinal bands and spots along its body help to discern its presence at the openings easily.

One day prior to video recording, a buoy marker was fixed in the middle of sand patches, then all openings with shrimps ~4 cm in length were selected within 1-m radius from the buoy and then marked by labeled wooden sticks. A stainless steel tripod was installed in place of the buoy upon return, in which an underwater videocamera system was secured. Observations of aboveground activity began at 0700H and proceeded until sundown (~1900H). Video recordings followed a focal sampling strategy, i.e., activity in a single opening was instantaneously recorded for 5 minutes from the shrimp’s first hour of emergence and every hour thereafter until neither shrimp nor goby guarding activity was observed to occur. Up to four openings were observed successively every hour. During interim recordings, sediment dumped by *A. macellarius* was collected on a low-form plastic tray (Fig. 2) installed at the burrow opening. Scoops from 10 dumping bouts were accumulated...
from every shrimp (n = 30) before the heap was collected into plastic bags. In the laboratory, these were oven-dried at 105°C to constant weight.

Shrimp behavior was described in terms of both structure and consequences (Martin and Bateson 1996). Structure was defined based on exclusive behavioral states (excluding the interaction behavior of the shrimp with its goby) identified from a preview of randomly selected videorecords then summarized in an ethogram. The sequence of states was transcribed using an electronic event recorder, and afterwards stored as ASCII data files in a PC utilizing a data transfer protocol (Stamhuis et al. 1996). Data transfers were performed after every 20 minutes of transcribing to allow for resets of the event recorder timer (to prevent memory overloading) and for observer rests (to prevent drifts due to fatigue).

Sequence records were subjected to zero-order Markov-chain analysis, which directly provided frequency and duration summaries for single behavioral states (Stamhuis et al. 1996). Characteristic single-state sequences were afterwards manually assigned into behavioral classes (= consequences) or specific activities, of which frequency and duration summaries were calculated. Values were all expressed as rates, i.e., numbers or time (in seconds) per hour. We pooled our 1998 (ENSO) dataset under one ‘dry’ period a posteriori, since our samplings were carried out during the climate window without the expected intermittent rains. Activity patterns within the observation hours were detected from plots of frequency and duration (y-axis) as a function of time (0800-1900H).

We applied repeated measures ANOVA to examine the effect of sampling period (between-subjects factor) on activity frequency and duration variables, which were obtained from the same shrimp individual every hour (within-subjects factor). We included data only for the time window common to all three sampling periods, i.e., between 1000 and 1600H. Results from the univariate approach of the within-subjects tests were used when the data complied with the test’s sphericity assumption (Mauchly’s W > 0.05), otherwise, results from the multivariate approach were utilized (Pillai’s Trace statistic) (sensu Potvin et al. 1990). Variables with significant effects were subsequently compared using simple contrasts (between-subjects) or Helmert contrasts (within-subjects, within- x between-subjects interaction). Finally, the significance of sediment moving and harvesting behavior was assessed from estimated rates of turnover and harvest biomass during the dry and wet months. The unit leaf biomass harvested was assumed as 50% of mean leaf weight, i.e., ~19 mg DW (Vermaat et al. 1995), and we incorporated a success rate of 75% in the calculations to account for the times the shrimps may have failed to secure their harvest into the burrow. Annual estimates were thereafter derived.
CHAPTER 3: ABOVEGROUND BEHAVIOR OF A. MACELLARIUS

Results

*Alpheus macellarius* was active during most of the observation period, emerging from its burrow at ~0900H and disappearing from view by ~1900H at the latest. Its goby partner, *Cryptocentrus octafasciatus*, emerged from the burrow earlier (~0700H) and was observed to extend its presence at the opening until past 1900H on quiet full moons. The shrimp’s ethogram consisted of 12 exclusive behavior states (Table 1, A) and typical successive states were categorized into four clearly identifiable behavioral sequences or activities (Table 1, B).

The shrimp’s aboveground bouts were all very short (bout length, Table 2) and the time interval between any of these bouts was 38 s (± 4 SEM), during which the shrimp was out-of-view (i.e., concealed in its burrow, accounting for 90±1% of its active period at daytime). The time allocated by *A. macellarius* for its aboveground

### Table 1. Behavioral states (A) and typical behavioral activities (B) of *Alpheus macellarius* observed in the seagrass meadow off Silaki, Bolinao (NW Philippines).

<table>
<thead>
<tr>
<th>Category</th>
<th>Description</th>
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<tbody>
<tr>
<td><strong>A. States</strong></td>
<td></td>
</tr>
<tr>
<td>1. Buldozer</td>
<td>Shovel and lift sediment with both major and minor chela</td>
</tr>
<tr>
<td>2. Carry</td>
<td>Walk with chela-load full of sediment; Walk with rubble or fragment clamped by minor chela</td>
</tr>
<tr>
<td>3. Dump</td>
<td>Drop carried sediment load at opening with slight push from the major chela</td>
</tr>
<tr>
<td>4. Drop</td>
<td>Let go of clamped rubble/ fragment at pile opposite the sediment dump site</td>
</tr>
<tr>
<td>5. Touch</td>
<td>Contact of antennae/ chela with seagrass or algae</td>
</tr>
<tr>
<td>6. Clamp</td>
<td>Hold rubble/ fragment/ leaf with minor chela</td>
</tr>
<tr>
<td>7. Pull</td>
<td>Drag clamped algal or other fragment into the burrow</td>
</tr>
<tr>
<td>8. Cut</td>
<td>Cut the clamped leaf/ fragment with plunger of major chela</td>
</tr>
<tr>
<td>9. Eat</td>
<td>Pick-up particles from sediments using pereiopods then bring to mouth one after another</td>
</tr>
<tr>
<td>10. Walk</td>
<td>Move forward on sediment without carrying anything on chela</td>
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<tr>
<td>11. Pause</td>
<td>Brief stop- body still but with antennal movements</td>
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<tr>
<td>12. Retreat</td>
<td>Walk backward on sediment without carrying anything on chela; Return to burrow tail first, e.g., after dumping sediment or cutting leaf/fragment; Disappear suddenly from view due to disturbance, e.g., approaching fish</td>
</tr>
<tr>
<td><strong>B. Activities</strong></td>
<td></td>
</tr>
<tr>
<td>1. Move sediment</td>
<td>Sequences of carrying sediment and dumping, sometimes with further bulldozing in between (carry-[buldozer]-dump-retreat)</td>
</tr>
<tr>
<td>2. Stack rubble</td>
<td>Sequences of carrying and dropping a piece of rubble or shell fragment, sometimes moving/transferring dropped material to a stable spot ([clamp]-carry-drop-retreat)</td>
</tr>
<tr>
<td>3. Survey</td>
<td>Sequences of walking and stopping at the opening (walk-pause), and sometimes approaching and ‘feeling’ seagrass then returning to and stopping at the opening (walk-touch-retreat-pause)</td>
</tr>
<tr>
<td>4. Harvest</td>
<td>Sequences of walking, touching, clamping, and cutting leaf or algae, and in some instances, clamped algae were merely pulled down into the burrow (walk-touch-clamp-[pull]-cut-retreat); the sequence ‘walk-pause-eat-retreat’ was subsumed under this functional class</td>
</tr>
</tbody>
</table>
Table 2. Frequencies, bout lengths, durations (both in seconds), and time allocations (% of total active period) of the activities of *A. macellarius* in the seagrass meadow off Silaki (Bolinao, NW Philippines). Frequency and duration values are average rates per hour (±SEM) pooled for 1 day in each sampling period. Superscripts denote significant ‘seasonal’ differences on frequency (lowercase) and duration (uppercase) data (simple contrasts, *p* < 0.05, following repeated measures ANOVA, Table 3).

<table>
<thead>
<tr>
<th>Sampling period</th>
<th>Variable</th>
<th>Activity</th>
<th>Move sediment</th>
<th>Stack rubble</th>
<th>Survey</th>
<th>Harvest</th>
<th>(Hidden)</th>
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<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Frequency</td>
<td>Duration</td>
<td>Bout length</td>
<td>% of time</td>
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<tr>
<td>Dry 1998</td>
<td>Frequency</td>
<td></td>
<td>72 ± 13</td>
<td>196 ± 45</td>
<td>2.6 ± 0.3</td>
<td>5.5 ± 1.3</td>
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<td>24^b± 8</td>
<td>78^a± 20</td>
<td>3.9 ± 0.5</td>
<td>2.2 ± 0.6</td>
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<td></td>
<td>22^b± 6</td>
<td>155^a± 42</td>
<td>7.2 ± 0.7</td>
<td>4.3 ± 1.2</td>
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<td></td>
<td>10 ± 6</td>
<td>59 ± 18</td>
<td>1.7 ± 0.5</td>
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<td></td>
<td>Duration</td>
<td></td>
<td>196 ± 45</td>
<td>155 ± 42</td>
<td>59 ± 18</td>
<td>3106 ± 102</td>
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<td></td>
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<td>78^a± 20</td>
<td>155^a± 42</td>
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<td>3106 ± 102</td>
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<td>3106 ± 102</td>
<td></td>
</tr>
<tr>
<td>Dry 1999</td>
<td>Frequency</td>
<td></td>
<td>81 ± 10</td>
<td>208 ± 40</td>
<td>2.5 ± 0.2</td>
<td>5.3 ± 1.1</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>12^ab± 3</td>
<td>38^a± 11</td>
<td>2.8 ± 0.4</td>
<td>1 ± 0.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>21^b± 3</td>
<td>104^a± 23</td>
<td>4.9 ± 0.4</td>
<td>2.6 ± 0.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>8 ± 1</td>
<td>52 ± 13</td>
<td>6.1 ± 0.8</td>
<td>1.3 ± 0.4</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>108 ± 11</td>
<td>3338 ± 58</td>
<td>33.5 ± 2</td>
<td>89.9 ± 1.6</td>
<td></td>
</tr>
<tr>
<td>Wet 1999</td>
<td>Frequency</td>
<td></td>
<td>51 ± 12</td>
<td>119 ± 26</td>
<td>2.6 ± 0.4</td>
<td>3.2 ± 0.8</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>7^e± 2</td>
<td>26^d± 10</td>
<td>3.8 ± 0.8</td>
<td>0.7 ± 0.2</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>10^a± 2</td>
<td>46^d± 16</td>
<td>4.6 ± 0.4</td>
<td>1.3 ± 0.4</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2 ± 1</td>
<td>69 ± 50</td>
<td>17 ± 8.5</td>
<td>1.6 ± 1.1</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>72 ± 11</td>
<td>3338 ± 58</td>
<td>53.5 ± 9.9</td>
<td>93.2 ± 4</td>
<td></td>
</tr>
<tr>
<td>Pooled</td>
<td>Frequency</td>
<td></td>
<td>70 ± 7</td>
<td>179 ± 23</td>
<td>2.6 ± 0.2</td>
<td>4.8 ± 0.6</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>14 ± 3</td>
<td>46 ± 9</td>
<td>3.4 ± 0.3</td>
<td>1.2 ± 0.2</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>18 ± 2</td>
<td>103 ± 18</td>
<td>5.5 ± 0.4</td>
<td>2.7 ± 0.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>7 ± 2</td>
<td>59 ± 15</td>
<td>10.5 ± 2.7</td>
<td>1.5 ± 0.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>102 ± 9</td>
<td>3279 ± 45</td>
<td>38.1 ± 4</td>
<td>89.8 ± 1.2</td>
<td></td>
</tr>
</tbody>
</table>

}\[9pt]\[
\text{SEM}\]
functions was altogether only 10% of its total active time (Table 2): moving sediment was displayed the most, followed by surveying, harvesting, and finally, stacking up rubble (Fig. 3). Carrying and retreat bouts accounted for >75% of the time for moving sediments and stacking up rubble, surveying mostly involved slow walks to the opening, and harvesting was mostly described by walking and subsequent cutting and pulling bouts.

All four behavioral sequences were regularly displayed by *A. macellarius* (Fig. 4). In 1998, activity commenced at 0900H and proceeded for 9 hours, and frequencies tended to increase towards midday (Fig. 4, top graphs). Patterns were not as apparent in 1999 (Fig. 4, middle and bottom graphs). Shrimp activity during the dry months started 1 h later (1000H) than previously recorded but still continued for 9 hours. Frequencies did not significantly differ from the previous sampling (*p* > 0.05, Tables 2, 3A), hence, pooled means may be utilized to represent activity on typical dry months: move sediment, 77 (± 8) h⁻¹; stack rubble, 17 (± 4); survey, 21 (± 3); and harvest, 9 (± 2). On the following wet period, shrimp activity was observed for 8 hours and frequencies were reduced by 34% for moving sediment, 52% for surveying, 78% for harvesting, and 59% for stacking up rubble (Table 2). The decrease in the frequencies for stacking and surveying activities was significant (*p* < 0.05, Tables 2, 3A).

Total duration of each aboveground activity followed the trends for frequencies (Fig. 4, Tables 2, 3B). Pooled daily allocations reach up to only 10 (± 2) and 7 (± 1)% during the dry and wet periods, respectively, or a range of ~2 to as much as nearly 30% on the dry months (Fig. 5) and only close to 10% on the wet month of 1999. On the other hand, the time spent by the shrimp in the burrow (‘hidden’) significantly increased during the wet period (1999), and was quite variable among observation hours (*p* < 0.05, Tables 2, 3B).
Figure 4. Frequencies (bars + SEM) and duration (filled circles ± SEM) of aboveground activities by *A. macellarius* from 0900 to 1800H during three sampling periods in the Silaki meadow (Bolinao, NW Philippines). No shrimp activity was observed between 0800 to 0859H and, hence, was omitted from the x-axis.
Table 3. Values of $F$ or approximate $F$ (*, converted from Pillai’s Trace statistic) from repeated measures ANOVA, which examined the effect of sampling period on the hourly frequency (A) and duration (B) of *A. macellarius* activities. Asterisks (*) denote significant effects ($\alpha = 0.05$); differences among sampling periods are given in Table 2. Legend: *, wet ’99 > dry ’98 (1100, 1400, and 1500H datasets) and dry ’99 > dry ’98 (1400 and 1500H).

<table>
<thead>
<tr>
<th>Variable / Factor</th>
<th>df</th>
<th>Move sediment</th>
<th>Stack rubble</th>
<th>Survey</th>
<th>Harvest</th>
<th>Hidden</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>A. Frequency</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Between-subjects test</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sampling period</td>
<td>2</td>
<td>2.043</td>
<td>4.604 *</td>
<td>4.715 *</td>
<td>1.669</td>
<td>-</td>
</tr>
<tr>
<td>Within cells (error)</td>
<td>18</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Within-subjects test</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hourly frequency</td>
<td>6</td>
<td>1.331</td>
<td>0.716 +</td>
<td>2.205 +</td>
<td>0.521 +</td>
<td>-</td>
</tr>
<tr>
<td>Hourly frequency x Sampling period</td>
<td>12</td>
<td>0.502</td>
<td>1.171 +</td>
<td>1.653 +</td>
<td>0.897 +</td>
<td>-</td>
</tr>
<tr>
<td>Within cells</td>
<td>108</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>B. Duration</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Between-subjects test</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sampling period</td>
<td>2</td>
<td>1.886</td>
<td>5.475 *</td>
<td>5.116 *</td>
<td>0.135</td>
<td>4.600 *</td>
</tr>
<tr>
<td>Within cells (error)</td>
<td>18</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Within-subjects test</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hourly duration</td>
<td>6</td>
<td>1.603</td>
<td>1.007</td>
<td>1.662</td>
<td>0.680 +</td>
<td>2.157 +</td>
</tr>
<tr>
<td>Hourly duration x Sampling period</td>
<td>12</td>
<td>1.117</td>
<td>1.322</td>
<td>1.502</td>
<td>0.751 +</td>
<td>2.436 +</td>
</tr>
<tr>
<td>Within cells</td>
<td>108</td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
</tbody>
</table>

A single full scoop of sediment carried and subsequently dumped by *A. macellarius* was 0.50 ± 0.03 g in dry weight. Results of subsequent calculation indicated weights of between 204 and 346 g of sediment moved per day, which, when projected over an area of 1 m$^2$ with 2 active shrimps, translates to between 0.8 and 1.4 kg of reworked sediments during the wet and dry months, respectively (Table 4A).

The shrimp harvested leaf fragments or full-length leaves of small seagrasses regardless of the species, and commonly nipped these at just above the substratum level in *Syringodium isoetifolium* (Ascherson) Dandy, past the ligula in *T. hemprichii*, past the sheath in *Cymodocea rotundata* Ehrenberg *et* Hemprich *ex* Ascherson, *C. serrulata* (R. Brown) Ascherson, and *Halodule uninervis* (Forsskål) Ascherson, or above the spathe in *Halophila ovalis* (R. Brown) Hooker f. Harvested leaf fragments ranged considerably in size because seagrass leaves elongate with age until maturity, are produced continuously, and are subject to sloughing and partial herbivory. Resulting estimates of specific harvest rates range, therefore, between 0.2 (wet months) and 1.1 g d$^{-1}$ shrimp$^{-1}$ (dry months) or between 0.4 and 2.3 g m$^{-2}$ d$^{-1}$.
The latter range represents a relocation of 8 to 42% of leaf production to the burrows. Generally, after all living fronds within its ‘working radius’ were harvested, *A. macellarius* would open new burrows close to its patch border under a canopy of shoots. Thereafter, we assume it to resume its dumping and harvesting bouts at similar rates. Hence, within a year, individual shrimps are projected to have reworked 112 kg of sediments and relocated 291.3 g of leaf material to their burrows.

**Figure 5.** Relative time allocation of *A. macellarius* for its aboveground activities from 0900 to 1900H on three sampling occasions in the clear-water seagrass meadow of Silaki, Bolinao (NW Philippines). Error bars are SEMs of the pooled activity totals.
Table 4. Estimates of the potential impact of sediment movement and leaf harvesting by *A. macellarius* in the seagrass meadow of Silaki (Bolinao, NW Philippines).

<table>
<thead>
<tr>
<th></th>
<th>Wet months</th>
<th>Dry months</th>
<th>Annual</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>A. Sediment movement</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Frequency, h⁻¹</td>
<td>51(a)</td>
<td>77(b)</td>
<td>70(a)</td>
</tr>
<tr>
<td>Number of hours aboveground per day</td>
<td>8</td>
<td>9</td>
<td>8.5</td>
</tr>
<tr>
<td>Daily dumping rate, d⁻¹</td>
<td>408</td>
<td>693</td>
<td>595</td>
</tr>
<tr>
<td>Σ weight dumped per shrimp (c)</td>
<td>204</td>
<td>346</td>
<td>298</td>
</tr>
<tr>
<td>(specific reworking rate, g d⁻¹)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of days</td>
<td>137(c)</td>
<td>228(c)</td>
<td></td>
</tr>
<tr>
<td>Estimated bulk of reworked sediment, kg (f)</td>
<td>27.9</td>
<td>79.0</td>
<td>112(g)</td>
</tr>
<tr>
<td>Sediment reworking rate, kg m⁻² d⁻¹(h)</td>
<td>0.8</td>
<td>1.4</td>
<td>1.2</td>
</tr>
<tr>
<td><strong>B. Leaf harvesting</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Frequency (h⁻¹)</td>
<td>2(a)</td>
<td>9(b)</td>
<td>7(a)</td>
</tr>
<tr>
<td>Frequency of successful harvests (i)</td>
<td>1.5</td>
<td>6.8</td>
<td>5.2</td>
</tr>
<tr>
<td>Daily harvest rate (d⁻¹)</td>
<td>12</td>
<td>60.8</td>
<td>44.6</td>
</tr>
<tr>
<td>Σ biomass harvested per shrimp (i)</td>
<td>0.2</td>
<td>1.1</td>
<td>0.8</td>
</tr>
<tr>
<td>(specific harvest rate, g d⁻¹)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Estimated total biomass of harvested leaves, g (g)</td>
<td>30.9</td>
<td>260.4</td>
<td>291.3(g)</td>
</tr>
<tr>
<td>Leaf harvesting rate, g m⁻² d⁻¹(h)</td>
<td>0.45</td>
<td>2.3</td>
<td>1.7</td>
</tr>
<tr>
<td>Relocated production (k)</td>
<td>8%</td>
<td>42%</td>
<td>31%</td>
</tr>
</tbody>
</table>

Notes: (a) from Table 2  
(b) pooled frequency for dry months  
(c) dry weight of single dump = 0.50 (± 0.03) g  
(d) days with rainshowers, tropical depressions, storms, and typhoons between May and October in Iba, (Zambales), Vigan (Ilocos Sur), and Dagupan (Pangasinan) – climate stations facing the South China Sea that were assumed to mirror the conditions in Bolinao; value represents the average for 1998 and 1999 (source: PAGASA, Quezon City, Philippines)  
(e) dry (no-rain) days between November and April in the 3 climate stations above, averaged for 1998 and 1999 (source: PAGASA, Quezon City, Philippines)  
(f) specific rate multiplied by number of days in column (then converted as appropriate); this estimate is for 1 shrimp individual  
(g) sum of values from wet and dry months  
(h) specific rate multiplied by 2 (±0.2) active shrimp individuals per m²  
(i) 75% of frequency per hour  
(j) daily harvest rate multiplied by 18.8 mg – represents 50% of mean leaf weight of all small seagrass species in the meadow for each successful harvest; leaf weights obtained from Vermaat et al. (1995)  
(k) expressed as % of mixed bed daily leaf productivity, i.e., 5.4 g m⁻² d⁻¹; extracted from Vermaat et al. (1995)

Discussion

Our observations across several seasons show that this alpheid is mainly engaged with burrowing/mining, and spends most of its time underground. The daily activity rhythm of *Cryptocentrus octafasciatus* and of *Alpheus macellarius* appears similar to the pattern reviewed by Karplus (1987) for other goby-shrimp associations. *Alpheus macellarius* allocated substantial time in maintaining the fragile structures of the burrow by its dumping and stacking bouts. Maintenance bouts also, consequently, present an assurance of the shrimp’s continued access to target
harvests at the sediment surface. For *C. octafasciatus* which is an omnivore (Froese and Pauly 2001) and which does not seem to actively participate in excavation bouts (‘endoecism’; Karplus 1987, Atkinson and Taylor 1991), dumping by *A. macellarius* delivers sediment with particulate organics which are usually filtered through their gills following a series of mouth grabs (Karplus 1987, pers. obs.).

The burrowing behavior of the presently studied alpheid causes substantial sediment reworking. Our estimate range of between 0.8 and 1.4 kg DW m$^{-2}$ d$^{-1}$ is modest compared to reworking rates reported for other thalassinidean shrimps in both tropical and temperate waters (from 0.8 to 12.1 kg m$^{-2}$ d$^{-1}$; Roberts et al. 1981, Suchanek 1983, Vaugelas 1985, Branch and Pringle 1987, Rowden et al. 1998, Berkenbusch and Rowden 1999) mainly due to differences in shrimp density. Further extrapolation from the quantities of sediment expelled to volume (density of wet sediment = 2.44 g/ml; burrow opening diameter = 4 cm; sediment water content = 34%, Kamp-Nielsen et al. 2002) leads to burrow lengths of 27 to 45 cm extended per day by an individual shrimp within an established burrow. These extensions exceed the tunnel length increases covered by *Callianassa subterranea* (3 cm d$^{-1}$; Stamhuis et al. 1997) or by burrowing terrestrial invertebrates, e.g., *Lumbricus terrestris* or *Aporrodetoa longa* (2 cm d$^{-1}$; Ligthart and Peek 1997). A significant part of the burrow may be ventilated substantially by the shrimp’s intermittent pumping behavior, e.g., as observed for *Alpheus mackayi* Banner and Banner (Gust and Harrison 1981). Ventilated burrows expand the sediment’s oxic zone (Andersen and Kristensen 1991, Frouin 2000) and may help counteract hypoxia in seagrass rhizomes and roots during periods of light reduction (*sensu* Hemminga 1998).

*Alpheus macellarius* harvested fresh seagrass leaves and never foraged on these materials at the sediment surface. Instead, the shrimp was observed to hoard the harvest belowground. This behavior seems to qualify for the ‘security hypothesis’ (Vander Wall 1990), which states that foraging areas (here the seagrass meadow) are less secure and that animals maximize security by returning to a refuge (i.e., burrows) to eat food items they have gathered. Our observations in an accompanying laboratory study revealed that *A. macellarius* usually inserted the leaves to the roof of its burrow then proceeded with its dumping or stacking bouts; while in the burrow, it consumed the stored fronds from the margins. We did not observe harvesting of leaf litter or sheaths, as has been documented for *A. edamensis* De Man, 1988 (Stapel and Erfemeijer 1997). There were, however, instances of particle feeding at the sediment surface, suggesting a preference for the smaller, organically-rich particulates over larger detrital items, akin to other deposit feeders (Taghon 1982, Karplus 1987). Overall, as a leaf hoarder, grazer, and deposit-feeder, *A. macellarius* does not appear to be resource-limited in the meadow.

The observed seasonality in shrimp activities is remarkable, and we speculate on its correlation with shifting monsoons. In addition, leaf harvesting varied substantially among seasons. Lower removal rates occurred during the wet months and coincided with the period of lower seagrass productivity (Vermaat et al. 1995, Agawin et al. 1997). At the shrimp’s harvesting rate, our estimate of relocated production of 8 to 42% overlaps with and well exceeds the herbivory attributed to the rabbitfish *Siganus fuscescens* (5 to 10%; Hernandez et al. 1990, Salita-Espinosa 1992) and may be as important as the grazing potential predicted for the sea urchin *Tripneustes gratilla* (24%; Klumpp et al. 1993) in the area. Harvesting per se, however, may not be detrimental to seagrasses: for example, partial defoliation was shown to enhance growth rates in defoliated shoots of *Thalassia testudinum* Banks

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ex König (Tomasko and Dawes 1989) and *T. hemprichii* (Chapter 5, this Thesis). Reallocation of carbohydrate reserves from the roots and rhizomes to the leaves may be induced (Hemminga 1998), hence, leaf growth rates may not be necessarily depressed (Cebrián et al. 1998). The potential food limitation by leaf availability can only be assessed on a larger bed- and longer time-scale, because the gaps, like territories, shifted positions with time (Bell et al. 1999, pers. obs.) as a result of simultaneous shrimp activity and seagrass recolonization. The gaps generated by the shrimps averaged 0.30 m² (± 0.03), which, similar to thalassinid mounds, may be rapidly recolonized by smaller seagrass pioneers of the meadow through clonal growth (Duarte et al. 1997). These pioneers, hence, may initiate a succession sequence, which is viewed as one of the mechanisms in the maintenance of mixed meadows (Hemminga and Duarte 2000). In addition, the transfer of leaf material to the burrows represents a process of nutrient conservation within the meadow, and must be included among the inputs that maintain mixed meadows (Hemminga et al. 1991).

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**References**


Chapter 4

Burrows and behavior of the snapping shrimp *Alpheus macellarius*, Chace, 1988, in different seagrass substrates

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Abstract

Burrowing alpheid shrimps occur commonly in seagrass meadows and as such, are presumed to respond to the various sediment environments in which seagrasses are found. To determine the effects of sediment type on seagrass-associated alpheid shrimps, we examined burrows and the burrowing behavior of *Alpheus macellarius*, Chace, 1988, in three bed substrates – sand, muddy sand, and sandy mud – in laboratory cuvettes. *Alpheus macellarius* immediately excavated into all the substrates at initiation of the experiment and successfully established the first burrows within 2 hours (sand) to 1 day (muddy sand, sandy mud). Burrowing effort was highest and tunnel lengths were most extensive in sand after 26 days (p < 0.05). After 37 days, shrimp activity in all substrates was observed to shift to considerable wandering and feeding (mainly particle ingestion) became conspicuous. Burrowing behavior, though reduced, remained significantly higher in sand than in the other two substrates (p < 0.05). Overall, soft sandy sediments presented greater support for the burrowing behavior of *A. macellarius*, which, with reinforcement from dense seagrass, probably accounts for higher burrow densities in sand in the field. Conversely, shrimp burrowing appeared limited and substituted by concealment...
strategies in terrigenous substrates. Hence, with less support from sparser vegetation in the field, burrow numbers were also reduced.

Introduction

Various decapod crustaceans are strongly associated with seagrass beds for shelter, refuge from predators, and food (Leber 1984, Zupo and Nelson 1999, Gallmetzer et al. 2005, Al-Maslamani et al. 2007). Shrimps and crabs, in particular, browse and burrow in sediments, which have known effects on the habitat fabric and on infaunal communities (‘ecosystem engineering’, sensu Jones et al. 1994, Levinton 1995, Berkenbusch et al. 2000, Berkenbusch and Rowden 2003, 2007). The significance of this disturbance in various meadows has been highlighted for the cryptic yet broadly studied thalassinidean shrimps (Thalassinidea) (Frey and Howard 1975, Ott et al. 1976, Suchanek 1983). Features of the burrows of these animals (i.e., the presence of pieces of seagrass or algae in the tiered galleries, chambers, and burrow lining/walls) and the conspicuous sediment mounds at the sediment surface were seen to provide indications of active sediment processing, which conform primarily to a deposit-feeding mode (Vaugelas 1985, Griffis and Suchanek 1991, Nickell and Atkinson 1995). The burrowing caridean shrimps, notably the Brevirostris group within the genus *Alpheus* (snapping shrimps) associated with gobiid fishes, constructed and maintained shallow burrows (Karplus 1987), which may become complex as gravel content increased (Palomar et al. 2005). These shrimps similarly exhibited a deposit-feeding mode (Karplus 1987, Palomar et al. 2005).

In mixed-seagrass species meadows of the tropics, bioturbation by these snapping shrimps was recently found to have direct negative effects on the growth of seagrasses (Stapel and Erftemeijer 2000). More recent field surveys in the Philippines have indicated that there can be differences in the numbers of burrow openings and bare sand patches of alpheid shrimps across the different sediment conditions covered by seagrass meadows (Nacorda et al., Chapter 2, this Thesis), which implied possible differences in the burrowing effort in different sediments. Seagrass biomass has been shown to decrease in silty sediments (Terrados et al. 1998) so that seagrass densities may also potentially contribute to the numbers of burrow openings and bare sand patches observed. *In situ* observations revealed that the shrimps frequently expelled sediment from their burrows and also harvested fresh seagrass leaves (Nacorda et al., Chapter 3, this Thesis; Palomar et al. 2005). However, the shrimps spent considerable time underground, which presents a gap in our knowledge of their full diel behavioral pattern. Therefore, the significance of much of the shrimp’s belowground activities has remained obscure so far.

Here we report on an extension of our previous field observations by determining the burrowing activity and documenting the behavior of *Alpheus macellarius* Chace, 1988, in three common types of seagrass substrata, using narrow-but-high, transparent cuvettes (sensu Stamhuis et al. 1996), allowing belowground behavior to be observed. We hypothesized that the range of substrate types suitable for seagrasses produced different effects on the behavior and burrowing success of *A. macellarius*, thus, we aimed to examine the influence of substrate type on shrimp activity pattern since substrate type may well affect the shrimps’ energy requirements for burrow construction, the subsequent construction time, the resulting burrow lengths and configurations (Griffis and Chavez 1988), and,
eventually, their spatial distribution in the meadows. We also expected that the alpheid shrimps, similar to thalassinideans, would spend their within-burrow periods (i.e., hidden from view in field conditions) mainly on further burrow work – extensions, maintenance – and feeding.

**Methods**

**Experimental set-up, field collections, and sampling**

A week before field collections, transparent glass cuvettes (45 cm width x 35 cm height x 2 cm depth; n = 12), were prepared and then completely submerged in seawater aquaria at the hatchery facility of the Bolinao Marine Laboratory (BML). Continuous aeration and flow-through seawater supply were provided to these units.

Soft sediments were collected from three seagrass sites within the siltation gradient of the Bolinao-Anda system (McManus et al. 1992, Terrados et al. 1998, Kamp-Nielsen et al. 2002): Site 1 – Silaki (carbonate sand; substrate type 1), Site 2 – Guiguiwanen (terrigenous muddy sand; substrate type 2), and Site 3 – Dolaoan (terrigenous sandy mud; substrate type 3) (Table 1, Fig. 1). Plant material was removed; the sediment was transferred to the cuvettes (with aeration turned off), and then allowed to settle up to a depth of 20 cm. Substrate types 1, 2, and 3 were arranged in a randomized complete block design (Gomez and Gomez 1984) to rid off bias during subsequent recordings of shrimp behavior. Seedlings (n = 10) of *Thalassia hemprichii* (Ehrenberg) Ascherson were planted in each cuvette. Plant density in the setups was chosen as a compromise of availability and observed natural densities (Vermaat et al. 1995, Rollon 1997). Spilled sediment was removed from each aquarium and then flow-through seawater was supplied until all aquaria were filled with clear water, and then sediment level in each cuvette was traced on clear plastic that was superimposed on the front wall of the aquarium. After tracing,

<table>
<thead>
<tr>
<th>Sediment type</th>
<th>Lucero</th>
<th>1 – Silaki</th>
<th>2 – Guiguiwanen</th>
<th>3 – Dolaoan</th>
</tr>
</thead>
<tbody>
<tr>
<td>TOM, %</td>
<td>4.9 (0.2)</td>
<td>5.8 (0.3)</td>
<td>5.2 (0.5)</td>
<td></td>
</tr>
<tr>
<td>MGS, φ</td>
<td>1.04 (0.1)</td>
<td>1.3 (0.03)</td>
<td>2.6</td>
<td>1.3</td>
</tr>
</tbody>
</table>

Wentworth’s grain size composition (%)

<table>
<thead>
<tr>
<th>Granules</th>
<th>Very coarse</th>
<th>Coarse sand</th>
<th>Medium sand</th>
<th>Fine sand</th>
<th>Very fine sand</th>
<th>Mud</th>
</tr>
</thead>
<tbody>
<tr>
<td>14.0 (1.8)</td>
<td>13.9 (1.1)</td>
<td>18.3 (1.6)</td>
<td>22.5 (1.3)</td>
<td>18.6 (1.4)</td>
<td>8.1 (1.3)</td>
<td>4.6 (0.8)</td>
</tr>
<tr>
<td>8.6 (0.6)</td>
<td>20.1 (0.3)</td>
<td>20.1 (0.3)</td>
<td>14.1 (0.2)</td>
<td>16.5 (0.3)</td>
<td>10.1 (0.3)</td>
<td>10.5 (1.0)</td>
</tr>
<tr>
<td>0.4</td>
<td>1.4</td>
<td>3.7</td>
<td>16.8</td>
<td>52.5</td>
<td>15.5</td>
<td>9.7</td>
</tr>
<tr>
<td>7.3 (4.1)</td>
<td>11.9 (2.0)</td>
<td>11.8 (2.4)</td>
<td>14.9 (1.0)</td>
<td>36.3 (4.0)</td>
<td>9.2 (1.5)</td>
<td>8.6 (1.9)</td>
</tr>
</tbody>
</table>
continuous aeration to the setups was resumed and then each aquarium was wrapped on all sides with black canvas and topped with nets after sundown to reduce the presumed influence of artificial light on animal behavior during nighttime and on the overgrowth of algae.

On a separate field visit, 12 naturally co-occurring pairs of the snapping shrimp *Alpheus macellarius* (total length = 4.2 ± 0.1 cm) and the blue-speckled prawn goby *Cryptocentrus octafasciatus* Regan, 1908 (total length = 3.9 ± 0.2 cm) were caught in Lucero (Table 1, Fig. 1), which is a shallow clear-water site with soft sandy sediment. The pairs were caught by inserting a shovel in the heap of sediments immediately outside a burrow opening (without collapsing the entrance), waiting for the animals to resume burrow guarding (goby) and sediment dropping bouts (shrimp), and then trapping the pair by hand in the sediment held by the shovel. These pairs were immediately brought to the hatchery facility, and temporarily held for three hours as separate pairs in containers provided with slow-flowing seawater.

Each alpheid shrimp was carefully introduced with its watchman goby to the cuvette (= Day 0), which was then immediately topped with a gravel-weighted net (mesh = 1 mm) to prevent the animals from escaping and not necessarily impede water flow. Simultaneously, shrimp behavior was recorded following a focal sampling rule (Altmann 1974, Martin and Bateson 1986), using a video camera mounted on a tripod and with the camera’s lens maintained at 50 cm distance from the aquarium continuously for 5 minutes. Later, this was reduced to 3 minutes because all sequences had been sufficiently sampled during that period. The development of burrows and changes in sediment levels were monitored after 2

---

**Figure 1.** Location of seagrass beds in Bolinao (NW Philippines) where sediment (X, 1-3) and shrimp and goby pairs (□) were collected. The cuvette setups were maintained at the Bolinao Marine Laboratory (BML).
hours (Day 0) and on Days 1, 2, 3, 7, 13, and 26. Configurations were traced on clear plastic (as above) and these traces were subsequently digitized.

The shrimp’s activity pattern was determined on Day 37, when burrow lengths remained the same. Our preliminary observations of shrimp feeding indicated that *A. macellarius* demonstrated no preference for any of the small seagrass species, seedlings of *E. acoroides* included. Thus, one day prior to filming, we replenished the lost seedlings (due to burial or consumption by the shrimp) by more readily available shoots (*n* = 10) of *Cymodocea rotundata* Ehrenberg et Hemprich ex Ascherson. The shrimps’ pre-disturbance activities were resumed following a short period of hiding (the state ‘retreat’) in response to disturbance (Nacorda et al., Chapter 3, this Thesis). Continuous minute video-records were taken for 3 minutes on each shrimp every hour during the day (from 1100 to 1800H) and at nighttime (from 1800 to 2400H; red light was used to facilitate filming).

The maintenance of the setups entailed the weekly removal of algae from the sides of both cuvettes and aquaria and the replacement of top-nets. During cleaning, water levels in the aquaria were ensured to be higher than the sediment level in the cuvettes to prevent the collapse of burrows. Water was subsequently replenished until clear and the flow-through supply was restored.

**Data analyses**

Shrimp behavior records were transcribed following an 18-state ethogram (Table 2, part A), with each state keyed in on an event recorder during videotape playback (Stamhuis et al. 1996). A type of Markov-chain sequence analysis tested the frequencies of typical behavioral state sequences (from duplets to sextuplets) within each record against the probability of the sequence to occur randomly (Stamhuis et al. 1996). From all significantly occurring sequences, those that were found in at least 5% of all the records for each sediment type were assigned into functional classes (= activities) (Table 2, part B). Frequencies (numbers per hour), bout lengths (seconds), and time allocations (percentage) for these classes were calculated.

A one-way ANOVA was used to examine the effect of substrate type (1, 2, and 3) on bout lengths and time allocations of shrimp activity observed on Day 0. Differences in shrimp behavior parameters on Day 37 (frequency, time allocation, bout length) attributed to the test substrates (between-subjects factor) and to time of day (day, night) (within-subjects factor) were assessed with repeated measures ANOVA. Results from the univariate approach of the within-subjects tests were used when the data complied with the test’s sphericity assumption (Mauchly’s *W* > 0.05), otherwise, results from the multivariate approach were utilized (Pillai’s Trace statistic; *sensu* Potvin et al. 1990). Simple contrasts were utilized (*α = 0.05*) to discriminate the substrates where between-subjects effects have been detected (*p* < 0.05). These statistical analyses were performed in SPSS Release 7.0 (SPSS Inc. 1995).

Burrow construction effort was gauged from tunnel lengths (*L*_tunnel, mm) measured from the sketches/stills, and from volumes of moved sediment (*V*_sediment, ml). The latter was calculated as the difference in the measured tunnel areas between two successive monitoring periods then multiplied by the cuvette thickness (= 2 cm). Burrowing velocities (cm tunnel length h⁻¹) were computed from total lengths every monitoring period divided by the number of hours between successive measurements. Cumulative means of total excavated length and the amount of
Table 2. Behavior of *Alpheus macellarius* observed in the laboratory-based cuvettes.

<table>
<thead>
<tr>
<th>Category</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. States</td>
<td></td>
</tr>
<tr>
<td>1. Bulldozer</td>
<td>Shovel and lift sediment with both major and minor chela</td>
</tr>
<tr>
<td>2. Carry</td>
<td>Walk with chela-load full of sediment, or with rubble/fragment clamped by minor chela, in both cases accompanied by pleopod movements during ascent towards the dump/drop site</td>
</tr>
<tr>
<td>3. Dump/Drop</td>
<td>Drop carried sediment load at entrance with slight push from the major chela; Pile/let go of clamped rubble or fragment at pile opposite the sediment dump site</td>
</tr>
<tr>
<td>4. Clamp</td>
<td>Hold rubble/leaf or fragment with minor chela</td>
</tr>
<tr>
<td>5. Excavate</td>
<td>Dig sediment with both chela and the first 2 pairs of pereiopods</td>
</tr>
<tr>
<td>6. Sweep</td>
<td>Fan pleopods fiercely, sometimes simultaneous with excavating or walking, resulting in loosened and suspended sediments/particulates</td>
</tr>
<tr>
<td>7. Tamp</td>
<td>Fix rubble in place; insert leaf/fragment into burrow wall or roof</td>
</tr>
<tr>
<td>8. Touch</td>
<td>Contact of antennae/chela with seagrass or goby</td>
</tr>
<tr>
<td>9. Pull</td>
<td>Drag clamped rubble/fragment into the burrow</td>
</tr>
<tr>
<td>10. Cut</td>
<td>Cut the clamped leaf/fragment with plunger of major chela</td>
</tr>
<tr>
<td>11. Eat</td>
<td>Hold leaf between both chela then bite from the leaf margin; pick-up grains/particles with from sediments using pereiopods then bring to mouth one after another; stoop cephalothorax then bite on sediment; or hang and bite on burrow wall</td>
</tr>
<tr>
<td>12. Walk</td>
<td>Move forward on sediment without carrying anything on chela</td>
</tr>
<tr>
<td>13. Pause</td>
<td>Brief stop; body still but with antennal movements</td>
</tr>
<tr>
<td>14. Retreat</td>
<td>Return to burrow tail first, e.g., after dumping sediment or cutting leaf/fragment, sometimes followed by silt-puffs from the buccal area; walk backward on sediment without carrying anything on chela</td>
</tr>
<tr>
<td>15. Turn</td>
<td>Change direction by doing a somersault</td>
</tr>
<tr>
<td>16. Ventilate</td>
<td>Fan pleopods slowly while sitting still (pause) or eating</td>
</tr>
<tr>
<td>17. Groom</td>
<td>Rub pereiopods; scratch carapace/pick into cephalothorax, pleopods, or telson using pereiopods</td>
</tr>
<tr>
<td>18. Swim</td>
<td>Ascend to swim in the water column, always with pleopod fanning; roam to the glass wall</td>
</tr>
<tr>
<td>B. Activities</td>
<td></td>
</tr>
<tr>
<td>4. Rest</td>
<td>State ‘pause’ with duration ( \geq ) 30 seconds</td>
</tr>
<tr>
<td>6. Groom</td>
<td>State ‘groom’; sequence ‘groom-pause’</td>
</tr>
<tr>
<td>7. Ventilate</td>
<td>State ‘ventilate’; sequence ‘pause-ventilate’</td>
</tr>
</tbody>
</table>

moved sediment for each substrate type were plotted against time (days), then were fitted to the saturation function:

\[
y = a \times (1-e^{-b \times t})
\]
with \( a \) as the maximum asymptotic length or volume, \( b \), as the increase parameter, and \( t \), time in days (Stamhuis et al. 1997). These parameters were estimated by the iterative least squares fitting procedure in Sigma-Plot v.8 (Jandel Scientific/SPSS, 2002).

**Results**

**Burrowing behavior and burrow development**

*Alpheus macellarius* immediately executed burrowing bouts in all substrates by swiftly digging in between the *Thalassia* seedlings or at the left/right border of the cuvettes. Burrowing was displayed the most (69 ± 4\% SEM; bout length = 15.5 ± 4.1 s; Fig. 2, a), and was represented by short duplet and triplet sequences in sand and chains of these sequences in the other substrates. Substrate type did not affect this initial burrowing behavior in terms of either time allocations or bout lengths (\( p > 0.05 \)). Apart from burrowing, the shrimps were also engaged in bouts of wandering (18 ± 4\%; bout length = 7.4 ± 0.7 s) and surveying (7 ± 2\%; bout length = 6.8 ± 4.1 s) or were observed at rest (6 ± 3\%; bout length = 41.3 ± 2.6 s) (Fig. 2, a).

The first burrow openings and short pits were excavated at high velocities either at an angle from or perpendicular to the sediment surface (Fig. 3). These were formed in sand within 2 h after introduction or by Day 2 in muddy sand and sandy mud. Tunnels were extended obliquely from these pits by excavating at much reduced velocities and this continued until new openings were created. There were 1-2 openings, positions of which were often shifted by the shrimps through excavations from the pits rerouted to the surface. Leaf harvesting and storing events

![Figure 2](image-url)
were observed directly when tracing the tunnels on transparencies, but did not occur sufficiently frequently to be quantified as behavioral bouts; clipped seedlings were observed to be completely buried already after 7 days.

The constructed burrows were simple and ranged from single J- or U-shapes to interconnected U’s in the two-dimensional cuvettes (Fig. 3). Tunnel widths were not regular (minimum \( \approx 2.0 \) cm but accommodated the sizes of the shrimps and gobies) and slight enlargements ('chambers') catered to convenient turns of both animals. In the case of burrow collapse, new segments were immediately made – *A. macellarius* excavated new pits either from the cuvette borders or into grooves, which then were extended as tunnels. After 26 days, excavations in sand produced the longest burrows and reached 54 ± 2 cm; those in muddy sand and sandy mud were shorter (42 ± 7 and 35 ± 1 cm, respectively; Fig. 4, a). The saturation equation explained over 85% of the variation in mean tunnel lengths \( p < 0.01 \) and predicted the mentioned maxima \( \alpha \), with \( b = 0.44 ± 0.06 \) (sand), 0.10 ± 0.04 (muddy sand), and 0.34 ± 0.03 (sandy mud). These maximum lengths also appeared to have been reached already within 1 week in sand and sandy mud (Fig. 4, a) and within 2 weeks in muddy sand.

Because of intense burrowing during the first few days, net volumes of sand displaced by *A. macellarius* were consequently larger compared with succeeding measurements. In all the substrates, however, shrimps were not only observed to execute bulldozing bouts from the burrows and expel sediments at the surface, but, often also remobilized only surface sediments. The estimated (net) maximum amount of remobilized sand was, hence, 699 ± 33 ml, which exceeded the maxima of either muddy sand (277 ± 6) or sandy mud (195 ± 19) after 26 days (Fig. 4, b). Curve fits similarly explained over 85% of the variation in the remobilized sediment volumes \( p < 0.01 \) with \( b = 0.34 ± 0.05 \) (sand), 0.68 ± 0.06 (muddy sand), and 0.43 ± 0.14 (sandy mud), and showed maximum tunnel volumes to have been reached within a week (Fig. 4, b).

**Shrimp activity pattern**

*Alpheus macellarius* evidently displayed seven activities (= functional classes) in the three test substrates on Day 37: feeding, grooming, and ventilating were added to the four classes displayed on Day 0 (Fig. 2, b). The shrimps apparently shifted their predominant activities to wandering (34.6 ± 1.3%; bout length = 9.4 ± 0.3 s) and feeding (24.1 ± 1.3%, bout length = 15 s). Active feeding on particles (75 ± 2% of pooled feeding events) was conspicuous; *A. macellarius* only sometimes consumed the hoarded leaves directly and exclusively within the burrow. Both feeding modes were accompanied by either ventilating or grooming bouts, and occurred within 10 and 20 seconds, respectively. Burrowing, i.e., bulldozing bouts in addition to moderate excavating and sweeping events (Table 2, part B), was exhibited for only 15.8 ± 1.1% – the activity may have ranked second in overall frequency but bout lengths became shorter to half the time observed at initiation (= 7.6 ± 0.3 s). Surveys of burrow walls/roofs were exhibited less (7.0 ± 0.7%; bout length = 7.1 ± 0.6 s) and periods of rest, as previously observed, were the least occurring behavior (1.8 ± 0.5%).

The control of substrate type on behavior was evident in the shrimps’ frequencies of burrowing, ventilating, and surveying activities. Burrowing and ventilating were significantly more frequent in sand than in sandy mud (Table 3A, Fig. 5, a) while surveying occurred considerably more often and with extended
periods in muddy sand compared with the other two test substrates (Table 3, A-C, Fig. 5, a-c). In addition to substrate effects, the shrimps exhibited notably more burrowing, grooming, and surveying bouts during the day than at night (Table 3B, Figure 3. Patterns of burrow excavation by *A. macellarius* depicted after initiation (2 h, Day 0) thru Day 26 in the three substrate types.)
Fig. 5, a and c). Periods of feeding and wandering, on the other hand, were particularly longer at night than at daytime (Table 3, B and C; Fig. 5, b and c).

Discussion

Burrowing emerged as the principal activity of *Alpheus macellarius* until the first burrow structure was successfully formed, suggesting that the purpose of such intense activity was concealment from the sediment surface. After the shrimps established a first simple hideout, they commenced with tunnel extension and maintenance routines with less intensity, or resolved burrow collapses with reconstruction bouts. This behavior continued up to 1 to 2 weeks, when maximum burrow lengths were achieved and when differences among substrate type became apparent. A similar pattern in the intensity of burrowing behavior with time was
Table 3. Mean squares (MS) and $F$-values from repeated measures ANOVA comparing day- and nighttime behavior of *A. macellarius* ($n = 4$) in three substrate types. $F$-values with asterisks are significant at $\alpha = 0.05$: * $p<0.05$, ** $p<0.005$, and *** $p<0.001$. Superscripts on the error MS in bout lengths (C, between-subjects effects) denote different df values: * $43$, ** $38$, * $67$, * $55$, * $38$, and * $23$.

<table>
<thead>
<tr>
<th>Variable/Source of variation</th>
<th>Burrow</th>
<th>Survey</th>
<th>Wander</th>
<th>Feed</th>
<th>Groom</th>
<th>Ventilate</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>A. Frequency (nos. per hour)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Between-subjects effects:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Error (within cells; df = 69)</td>
<td>8886.50</td>
<td>2432.80</td>
<td>5502.53</td>
<td>9656.59</td>
<td>931.22</td>
<td>2047.64</td>
</tr>
<tr>
<td>Sediment type (df = 2)</td>
<td>28030.93</td>
<td>11298.96</td>
<td>3113.30</td>
<td>23311.03</td>
<td>2.41</td>
<td>1047.24</td>
</tr>
<tr>
<td>Within-subjects effects:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Error</td>
<td>8015.28</td>
<td>2585.77</td>
<td>5117.76</td>
<td>9423.90</td>
<td>681.92</td>
<td>1732.57</td>
</tr>
<tr>
<td>Time of day (df = 1)</td>
<td>113784.52</td>
<td>79891.76</td>
<td>1105.78</td>
<td>13214.34</td>
<td>1.40</td>
<td>3395.16</td>
</tr>
<tr>
<td>Time of day * Sediment type</td>
<td>3080.85</td>
<td>2882.10</td>
<td>1727.91</td>
<td>5665.34</td>
<td>103.48</td>
<td>4979.83</td>
</tr>
<tr>
<td><strong>B. Time allocation (%)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Between-subjects effects:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Error</td>
<td>261.67</td>
<td>122.24</td>
<td>336.78</td>
<td>427.78</td>
<td>251.64</td>
<td>243.49</td>
</tr>
<tr>
<td>Sediment type</td>
<td>146.75</td>
<td>713.88</td>
<td>346.31</td>
<td>177.48</td>
<td>313.21</td>
<td>662.97</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Error</td>
<td>267.67</td>
<td>137.19</td>
<td>341.62</td>
<td>294.20</td>
<td>229.57</td>
<td>172.40</td>
</tr>
<tr>
<td>Time of day</td>
<td>2860.43</td>
<td>1886.48</td>
<td>3588.53</td>
<td>506.89</td>
<td>576.53</td>
<td>497.08</td>
</tr>
<tr>
<td>Time of day * Sediment type</td>
<td>96.76</td>
<td>150.66</td>
<td>113.39</td>
<td>52.78</td>
<td>95.42</td>
<td>0.55</td>
</tr>
<tr>
<td><strong>C. Bout length (seconds)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Between-subjects effects:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Error</td>
<td>154.49</td>
<td>114.50</td>
<td>451.89</td>
<td>464.10</td>
<td>248.62</td>
<td>463.51</td>
</tr>
<tr>
<td>Sediment type</td>
<td>8.74</td>
<td>376.22</td>
<td>291.34</td>
<td>283.63</td>
<td>589.12</td>
<td>187.57</td>
</tr>
<tr>
<td>Within-subjects effects:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Error</td>
<td>171.15</td>
<td>93.20</td>
<td>392.30</td>
<td>589.71</td>
<td>289.51</td>
<td>186.19</td>
</tr>
<tr>
<td>Time of day</td>
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<td>11.67</td>
<td>9475.62</td>
<td>3342.74</td>
<td>10.46</td>
<td>439.22</td>
</tr>
<tr>
<td>Time of day * Sediment type</td>
<td>234.99</td>
<td>97.29</td>
<td>279.69</td>
<td>153.89</td>
<td>148.40</td>
<td>90.06</td>
</tr>
</tbody>
</table>
Figure 5. The activity pattern of *A. macellarius* on Day 37: comparisons of measured behavior attributes (a – frequencies, b – bout lengths, c – time allocation) between time of day and among substrate types.
also found in *A. macellarius* observed for five days in outdoor tanks (Palomar et al. 1994, 1995). Burrow diameters appeared similar across the substrates in the constrained cuvettes, although in field conditions, these attributes may have apparent differences due to, e.g., the influence of tides and of exposure (Griffis and Chavez 1988).

The relatively firm and compact matrix of carbonate sand probably contributed to the shrimps’ early success in concealment (i.e., within 2 hours) despite the high energy allocated (= large volume of remobilized sediment) in the construction of the burrows. These burrows appeared comparatively stable, thus, presented an opportunity for the shrimps to engage in further burrowing to extend the tunnels so that, eventually, extensive lengths were attained at the end of 4 weeks (54 ± 2 cm). In tank conditions, relatively stable burrows that persisted for five days were observed in setups with 15 and 25% gravel, but that these were likely to collapse in the field because of wave action (Palomar et al. 2005). The interwoven rhizome-root compartment of the dense and mixed seagrass meadows on soft carbonate sand (aboveground and rhizome biomass 346 and 279 g DW m⁻², respectively; Vermaat et al. 1995) could provide additional reinforcement to the burrows. These meadows may, thus, be expected to sustain the relatively intense burrowing behavior of *A. macellarius*, which, in due course, would form sufficiently extensive tunnels and significantly more burrow openings aboveground (mean range 3 – 5 m², maximum = 15 m²; Nacorda et al., Chapter 2, this Thesis). In the experiment’s terrigenous substrates, the first (simple) burrows were constructed later and tunnels lengths attained at the end of the monitoring period were shorter – *A. macellarius* shifted its efforts to either belowground reconstructions/ new burrow initiation attempts, periods of inactivity once in relatively secure hiding, or to activities exclusively within the burrows (such as the relatively large amount of time spent surveying by shrimps in muddy sand sediments). The frequency of burrow openings in seagrass beds on terrigenous substrates is low (mean range < 1 to 4 m⁻²; maximum 10 m⁻² for sand; Nacorda et al., Chapter 2, this Thesis) and may be attributed to substrate instability and the limited stabilizing effect from the roots of the sparse seagrasses (from 172 to 492 shoots m⁻² in similar environments, Bach et al. 1998). All the leaves of the transplants were removed rapidly and hoarded in the burrows, similar to our observations in the field. The shrimps were also observed to fix buoyant leaves between rubble interstices to prevent dislodgement. Direct feeding on this secured cache was deferred for later, hence, passively subjecting the leaves to ‘gardening periods’ (Vander Wall 1990) that may improve the leaves’ food quality (Andersen and Kristensen 1991). On few occasions the shrimps were observed to directly utilize the fronds, *A. macellarius*, after defecation in the tunnels, contributed to the particulate organic matter pool of the sediment. This organic matter probably increased in digestibility and nutrient content (Thayer et al. 1984), and may be exploited as alternative food. Our observations revealed *A. macellarius* as primarily a deposit feeder, which directly accessed food by scratching/excavating sediments. The shrimp’s deposit feeding mode was clearly associated with burrowing, here represented by the behavioral states ‘scratch’ and ‘excavate’ (Table 2, part B), and was observed more frequently after the tunnels had been established and/or extended. The study also revealed that *A. macellarius* is, secondarily, a cryptic suspension feeder, with this feeding mode often occurring in the tunnels – the slow fanning movements of the shrimps’ pleopods (state ‘vent’) suspended detritus particles that were simultaneously caught then consumed. Gut content and stable
isotope analyses revealed *A. macellarius* as omnivores, whose diet was composed of largely seagrass and unidentified organic matter, and, to a lesser extent, algae, diatoms, spicules, and crustaceans (Palomar et al. 2004). Feeding behavior in the tanks suggested a deposit-feeding mode, however, and that suspension feeding via the burrow openings was not a vital means to obtain food but rather for burrow ventilation. Other shrimp species demonstrate combined feeding methods to compensate for nutritional deficits and satisfy energy demand (Thayer et al. 1984, Lopez and Levinton 1987, Nickell and Atkinson 1995, Stamhuis et al. 1998). For example, *Callianassa californiensis* and *C. gigas* are able to deposit-feed, utilize *Zostera*, and suspension-feed (Griffis and Chavez 1988), and *Upogebia omissa* filtered suspended particles and directly fed on the sediment, the latter as the main trophic mode (Coelho et al. 2000).

Feeding activity may, over time, limit the burrows’ relative stability (e.g., Suchanek 1983). In the field, this probability of unstable burrows would likely be delayed accordingly because of the sediment-stabilizing effect of seagrasses; *A. macellarius* would, however, continually and frequently rework its burrows and then resume with feeding, as was observed in the cuvettes. Further, the shrimps’ maintenance routines ensure tunnel stability and preclude tunnel collapse, i.e., during surveying, when walls are inspected and reinforced through tamping, and during sorting, when larger sediment grains are piled or inserted into the walls and tunnel roofs.

Prolonged periods of hiding, based on field observations, were apparent beyond sundown and when strong current episodes were detected at the sediment surface, largely associated with the goby’s response to light and water motion conditions at the immediate vicinity of the burrow openings (Karplus 1987). Biological threats – predation and competition – were seen to be anticipated by the goby and communicated to the shrimp prior to both animals’ retreat to the burrows for indefinite periods (Karplus 1987, Manthachitra and Sudara 1988). For *A. macellarius* and *C. octafasciatus*, which appear to be obligate partners (Palomar 2002), the latter was observed to remain within a guarding and communication radius of not more than 50 cm from the burrow opening as *A. macellarius* continued with its aboveground activities and maintained its proximity to the substratum. In the experimental setups, *A. macellarius* displayed more active burrowing (and subsequent grooming) and surveying at daytime and continued at night with less intensity; the shrimps also seemed to shift to more feeding and wandering at night. We consider the observed nighttime wandering and continued burrowing without associated feeding as indicators of habituation, especially given that chemical cues from predators and competitors were absent. We presume, however, that the shrimps would limit wandering to occur strictly within the tunnels to minimize the risk of being prey to e.g., eels (Pamintuan and Aliño 1994), and translate these bouts to activities within the goby’s ‘working’ radius aboveground or their belowground tunnels.

This study showed that three known mechanisms of bioturbation (cf. Andersen and Kristensen 1991) were used by *A. macellarius*, and feeding activity was closely associated to each: (1) shallow sediment mixing through bulldozing and sweeping bouts, (2) fecal material production after grazing on seagrass leaves, and (3) ventilation of the burrows through swift or controlled fanning of the pleopods. The control of sediment type on the burrowing behavior and burrows of *A. macellarius* was evident on the first and third mechanisms, which, together with density and the
type(s) of seagrass species and the degree by which the symbiotic partners interact in
the field, determines the shrimps’ spatial distribution within the various
environments occupied by seagrasses (Nacorda et al., Chapter 2, this Thesis). The
small-scale disturbance which A. macellarius populations impose within the top
shallow sediment compartment in seagrass meadows is likely to have a major impact
on the local environment – from the structure and distribution of biota (de Wilde

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Chapter 5

Growth response of the dominant seagrass
*Thalassia hemprichii* (Ehrenberg) Ascherson
to experimental shrimp disturbance

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Abstract

The effects of small-scale disturbance by burrowing shrimps (defoliation, shoot burial) on the growth patterns of the seagrass *Thalassia hemprichii* (Ehrenberg) Ascherson were examined in three manipulative experiments. Disturbance was applied *in situ* on apical shoots (Expt. 1) and on tank-grown seedlings (Expt. 2) and apparent shrimp activity was blocked *in situ* from seagrass plugs in exclosures (Expt. 3). Changes in leaf growth and rhizome elongation/ root growth rates were measured and compared after four short periods (4, 7 or 8, 14, and 25 or 28 days) in Expts. 1 and 2, while in Expt. 3, leaf growth rates of mature *T. hemprichii* shoots and shoot densities of coexisting species within the plugs were monitored for a year. In apical shoots, burial for at least 14 days induced accelerated leaf growth, while clipping and combined treatments had minimal effects on module growth. Clipping did not cause module growth differences with control seedlings. Burial, alone and combined with clipping disturbance, however, significantly and continuously decreased seedling growth. Exclusion from shrimp activity did not influence leaf growth rates of mature shoots. Both *T. hemprichii* growth and shoot densities of other coexisting seagrass species exhibited strong temporal variation as expected.
Our results show the tolerance of vegetative seagrass shoots (both early and late successional stages) to the small-scale disturbance imposed by burrowing shrimps. Seedlings also survived defoliation but were sensitive to burial events.

Keywords: plant response, disturbance, burrowing shrimps, bioturbation, Philippines, SE Asia

Introduction

Burrowing shrimps are important macrofaunal components of tropical seagrass ecosystems (Duarte et al. 1997, Nacorda et al., Chapter 2, this Thesis). In shallow multispecific SE Asian beds, these animals have been observed to rework impressive quantities of sediment (between 0.09 and 1.4 kg m$^{-2}$ d$^{-1}$) and also harvest living leaf material (between 0.4 to 2.3 g m$^{-2}$ d$^{-1}$ or 12 to 53% of daily biomass production) (Stapel and Erftemeijer 1997, Nacorda et al., Chapter 3, this Thesis). Sediment reworking generates topographic irregularities and gaps in the seagrass canopy, the dimensions and positions of which were found to vary over monthly time scales as the shrimps continually extended their tunnels and relocated their burrow openings and grazing grounds (Nacorda et al., Chapter 3, this Thesis). The harvesting of leaves directly transfers aboveground production to the burrows (Stapel and Erftemeijer 1997), where the material is fractionally consumed by the shrimps (Nacorda et al., Chapter 4, this Thesis) and/or stored as cache, which undergoes subsequent decomposition (Vander Wall 1990).

The present study focuses on the effects of these two aspects of shrimp behaviour on the common and often dominant seagrass *Thalassia hemprichii* (Ehrenberg) Ascherson. Leaf harvesting has modest to adverse effects on leaf growth (Cebrián and Duarte 1998, Cebrián et al. 1998, Valentine and Heck 1999) and sediment reworking inadvertently results in considerable shoot burial, which may either stimulate or depress seagrass performance (Marbá and Duarte 1994, Marbá et al. 1994, Duarte et al. 1997). We addressed the following questions in a series of three experiments: (a) does leaf clipping and burial increase leaf and rhizome/root growth in apical shoots and seedlings, and (b) does exclusion from shrimp activity benefit mature shoots and enhance densities of coexisting species? We also assessed whether these disturbance modes interacted in (a), thus, leaf clipping and burial were combined in an *in situ* factorial design.

For Expt. 1, we used undisturbed apical shoots on clonal rhizome runners (lateral meristems; Tomlinson 1974) to address the possible effects of shrimp behaviour on seagrasses established at the edge of bare, shrimp-occupied sand patches. For Expt. 2, we applied the factorial approach on young seedlings grown in an outdoor tank to quantify the sensitivity of newly established plants to shrimp behaviour. The third experiment, conducted *in situ*, was elevated beyond the scale of the shoots and employed experimental exclosures to block all shrimp activity. In this experiment, the effects on growth and shoot densities at the meter-scale in a mixed seagrass bed canopy were monitored over a longer period (up to 1 year). We did the field manipulations in a shallow, clear-water, and lush meadow off Lucero in Bolinao (NW Philippines) where apparent shrimp disturbance was moderate (Nacorda et al., Chapter 2, this Thesis).
CHAPTER 5: RESPONSES OF *Thalassia hemprichii* TO EXPERIMENTAL SHRIMP DISTURBANCE

Materials and Methods

### Experiment 1 – *In situ* leaf clipping and burial of apical shoots of *Thalassia hemprichii*

In August 1999, a total of 360 apical shoots (leaf lengths 33 ± 1 mm; leaf widths 5 ± 0.1 mm) were chosen at random within 40 m² of a mixed seagrass bed on the reef flat off Lucero, Bolinao (16° 24.85' N, 119° 43.48' E). The shoots were tagged, their leaves punched once with a needle below the leaf-sheath conjecture (Zieman 1974), and the lengths and diameters of their respective rhizome apices measured *in situ*. Treatments imposed (= modes of simulated shrimp disturbance) were applied only once on Day 0 on the marked and associated shoots and consisted of leaf clipping (leaves cut right above the needle mark in each shoot), burial at 2 and 5 cm, combined clipping and burial at 2 and 5 cm, and without manipulation (control). Shoots subjected to burial treatments were enclosed with PVC rings (diameter = 32 cm) that were fixed to the substrate prior to the actual burial using ambient mound sediments, i.e., material pumped out and/or dumped by burrowing shrimps. The setups were left in the field for fixed periods then 10 shoots per treatment were harvested after 4, 8, 14, and 25 days. In the laboratory, blades and rhizomes of the harvested shoots were immediately measured (leaf lengths, widths and growth increments, rhizome lengths and diameters), and the number of marked standing and new leaves were counted.

This experiment was conducted within the window of the rainy season when the zero-datum depth was 0.8 m (tidal range = 1.0 m), the overlying water remained relatively clear (total suspended solids = 2.5 ± 1.0 mg 1⁻¹), and temperature and salinity ranged between 29 and 32°C and 30 and 33 psu, respectively (Nacorda, unpubl. data). Surface water velocity during this period averaged 20 cm s⁻¹, which was typical of the rainy season (Rivera et al. 1997).

### Experiment 2 – *In situ* leaf clipping and burial of *T. hemprichii* seedlings

In December 1999, bed substrates and mound sediments were collected from four seagrass beds located along the major siltation gradient in Bolinao (Le Jeune 1995, Terrados et al. 1998, Kamp-Nielsen et al. 2002) – Lucero (clear water), Pislatan (16° 22.10' N, 119° 57.72' E), Rufina (16° 21.11' N, 119° 58.03' E), and Dolaoan (most silty; 16° 20.01' N, 119° 57.73' E). These sediments were separately stored; the bed substrates were rid of plants and decaying matter then set into black seedling pots (8 cm diameter x 10 cm height; n = 2 pots x 4 substrate types x 4 treatments x 5 harvest dates = 160 units prepared in total). Mature fruits of *T. hemprichii* were gathered from Lucero and allowed to dehisce naturally. Testae were removed from the seeds just before planting (n = 5 per pot). Pot units were organized randomly in an outdoor concrete tank (height = 50 cm up to brim) of the Bolinao Marine Laboratory, which continuously received filtered seawater in the daytime. Seeds were left to develop into seedlings for up to a month while algae and epiphytes were carefully brushed off from the units every other day.

Four pot units per substrate type (20 seedlings pooled) were randomly harvested on Day 30 for baseline module measurements – leaf lengths, leaf widths, and root lengths. On the same day, all leaves were marked with a needle hole at 1.3 cm from the base of the seedling then the three modes of simulated disturbance were applied. For the seedlings with the clipping treatments, the leaves were cut at 1.5 cm from the base. Pot units for the burial treatments were wrapped with canvass (2 height
from bottom = 15 cm) then filled up to brim (burial height = 5 cm) with the corresponding mound sediments from the source sites. All the pot units were rearranged randomly within the tank and then maintained as before. Two units per treatment per sediment type (32 units total) were collected on Days 33, 37, 44, and 58, corresponding to 3, 7, 14, and 28 days after the application of experimental disturbance. Post-disturbance sizes of leaves and roots and leaf growth increments were measured after each collection.

Experiment 3 – In situ blocking of shrimp disturbance in a *T. hemprichii* meadow

On March 2000, 18 experimental units were set up randomly within 400 m² of lush seagrasses in Lucero. These units measured 0.20 to 0.25 m² and consisted largely of mature shoots of *T. hemprichii* that were within the immediate vicinity of burrow openings and/or sand mounds. Thus, all the units have shrimp-disturbed and undisturbed sections, and on these sections. The units were divided into 3 treatments – excluded from shrimp disturbance, procedural controls, and unmanipulated controls. Each excluded unit (= seagrass plug) was sampled using a 50-cm diameter stainless steel corer. This gear was pushed down 20 cm deep into the sediment, stoppered, then slightly lifted as a fine-mesh nylon net cloth (850 µ opening) was slipped underneath it, after which the sediment plug was carefully released back into position. The nets, utilized to block further or potential shrimp activity, extended above the sediment surface (~50 cm) while semi-permanently tied to metal pegs in four corners. Procedural control plugs were similarly set up as the excluded units (but without nets) and were monitored to account for the possible negative effects of core sampling. Control units were simply delimited by metal pegs, into which a 50 x 50 cm quadrat could be directly fitted.

Shoots of all seagrass species in the units were counted. Complete shoots of mature *T. hemprichii* within and beyond 10 cm of an existing shrimp disturbance (n = 5) were also marked. Leaf growth rates were determined from the marked shoots based on *in situ* measurements of leaf lengths and widths. These and shoot densities of all species were monitored in the shrimp-disturbed (or previously disturbed, in the case of the net-excluded units) and undisturbed sections of each unit from March to August 2000 and in April 2001. Nets were periodically cleaned as these accumulated epiphytes and trapped drift algae through time.

Data analyses

Short-term responses of young shoots and seedlings were measured in terms of leaf growth (mm), rhizome elongation/ root growth (mm), and analyzed further as absolute leaf and rhizome growth rates (LAGR and RAGR, respectively, in mm² d⁻¹; Rollon 1998), root growth rates, and ratios of module growth (leaf: rhizome growth) and of growth rates (LAGR: RAGR). The overall effect of the disturbance modes and the durations on pairs of correlated dependent variables (Hair et al. 1998), i.e., (a) mean leaf growth and rhizome elongation (r for pooled data = 0.610, p < 0.001), (b) LAGR and RAGR (r = 0.242, p < 0.01), and (c) LAGR and root growth (r = 0.352, p < 0.01), were evaluated using multivariate analyses of variance (MANOVA). Subsequent MANOVAs were carried out to test for the effect of each independent variable – disturbance mode for each harvest time, and disturbance duration for each disturbance mode – on the pairs of dependent variables. Multivariate differences were based on Pillai’s criterion (α = 0.05) and where
significant probabilities were detected, post hoc comparisons (Tukey’s HSD) in univariate ANOVA were utilized to identify distinct groups. For the latter analyses, however, \( \alpha \) values were adjusted to 0.003 (comparisons of modes) and 0.008 (comparisons of duration) to maintain the experimentwise error rate at 0.05 (Sokal and Rohlf 1995, Hair et al. 1998). The variation in growth rate ratios was evaluated using the Scheirer-Rare-Hare extension of the Kruskal-Wallis test in lieu of the parametric two-way ANOVA (adjusted \( \alpha = 0.008 \)) (Sokal and Rohlf 1995).

For *T. hemprichii* in the field units (Expt. 3), leaf growth rates were similarly calculated as LAGR. Shoot densities and LAGR were compared using repeated measures ANOVA (Sokal and Rohlf 1995) with treatment (exclusion, procedural control, control) as the between-subjects factor and duration of disturbance as the within-subjects factor. The exclosure approach tested the effects of manipulation (exclusion procedure, exclusion of the shrimps) on densities of extant seagrasses.

Results from the univariate tests were used when assumptions of the analyses were met – homogeneous covariance matrices in the between-subjects test and homogeneity of variance in the within-subjects test. When data failed to meet these assumptions, results of multivariate tests (Pillai’s trace) were utilized. Post hoc comparisons (Tukey’s HSD) were carried out on parameters with significant treatment effects (\( \alpha = 0.017 \)).

**Results**

**Experiment 1 – Response of apical shoots to *in situ* leaf clipping and burial**

Under background conditions, leaf growth in apical shoots of *Thalassia hemprichii* increased by threefold after 25 days due to new and complete terminal shoots (mean rate 43 ± 5 mm\(^2\) d\(^{-1}\)). Rhizome growth increased by fourfold at 5 ± 0.5 mm\(^2\) d\(^{-1}\). Module growth continued under clipping and burial. The response from the leaves, in general, was greater than the response from rhizomes (Fig. 1, a and b). Module growth and absolute growth rates differed significantly in range depending on the mode and duration of the disturbance (Table 1A-1, B-1). The most pronounced differences were due to responses measured 25 days after the application of disturbance (Table 1A-3, 1B-2, 3). Differences in absolute leaf and rhizome growth rate ratios were only significant when disturbance durations were compared (Table 2A, B).

Leaf-clipped shoots maintained lower but steady leaf growth up to 14 days (15 ± 2 mm), and then showed comparable growth with control shoots after 25 days. Leaf growth rates in the disturbed treatments were generally lower than background rates up to Day 14, and then became comparable on Day 25. Leaf growth rates of buried shoots appeared to have accelerated from Days 7 to 25 (Fig. 1, a) while shoots under the combined treatment exhibited a similar range in leaf growth as undisturbed control shoots (Fig. 1, a). High growth rates were also evident in leaves of 2-cm buried shoots (both clipped and unclipped). In clipped shoots with 5-cm burial, leaf and rhizome growth rates slowed down continuously from 67 ± 6 to 40 ± 8 mm\(^2\) d\(^{-1}\) and from 8 ± 1 to 3 ± 0.5 mm\(^2\) d\(^{-1}\), respectively (Fig. 1, b). Rhizome extensions were similar for the control and disturbed shoots except those under 5 cm of burial and combined clipping and 2 cm-burial, which had longer lengths of 49 ± 7 and 42 ± 13 mm, respectively, on Day 25.
Figure 1. Young *Thalassia hemprichii*. Comparison of leaf growth rates (a, as LAGR) and rhizome elongation rates (b, as RAGR) (in mean mm$^2$ d$^{-1}$ ± SEM) between the experimentally disturbed (clipped, buried, clipped + buried) and undisturbed (control, gray lines) apical shoots for each disturbance period (3, 8, 14, and 25 days). (n=10 shoots disturbance mode$^{-1}$ period$^{-1}$)
CHAPTER 5: RESPONSES OF *Thalassia hemprichii* TO EXPERIMENTAL SHRIMP DISTURBANCE

**Table 1A.** Multivariate analyses of variance (Expt. 1). The effect of disturbance mode (clipping, burial, and clipping with burial) and disturbance duration (4, 8, 14, 25 days) on leaf growth and rhizome elongation rates in apical shoots of *T. hemprichii* in the field (*α* = 0.05). Superscripts indicate significant main effects - *p* < 0.05, **p** < 0.005, ***p** < 0.001 – in leaf (\(a\)), rhizome (\(b\)), or both parameters (\(c\)) from univariate F-tests.

<table>
<thead>
<tr>
<th>Dependent variable/ MANOVA design/ Source of variation</th>
<th>Pillai’s criterion</th>
<th>Approximate F</th>
<th>Hypothesized df</th>
<th>Error df</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean leaf growth, rhizome elongation (mm)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. Two-way factorial</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Duration of disturbance</td>
<td>0.795</td>
<td>29.011 *** c</td>
<td>6</td>
<td>264</td>
</tr>
<tr>
<td>Disturbance mode</td>
<td>0.173</td>
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<td>10</td>
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<tr>
<td>Duration x mode</td>
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<td>1.712 ** b</td>
<td>30</td>
<td>264</td>
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<td>2. One-way factorial: Main effect = disturbance duration</td>
<td></td>
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<tr>
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<td>Burial at 2 cm</td>
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<td>Burial at 5 cm</td>
<td>1.058</td>
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<td>6</td>
<td>38</td>
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<tr>
<td>Clipping + burial at 2 cm</td>
<td>1.048</td>
<td>7.711 *** c</td>
<td>6</td>
<td>42</td>
</tr>
<tr>
<td>Clipping + burial at 5 cm</td>
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<td>3.434 * a</td>
<td>6</td>
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<td>Control</td>
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<tr>
<td>4 days post-disturbance</td>
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<td>1.700</td>
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<td>25 days</td>
<td>0.486</td>
<td>2.055 *</td>
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<td>64</td>
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</table>

**Experiment 2 – Response of seedlings to *in situ* leaf clipping and burial**

After 30 days in the outdoor tank, the seedlings of *T. hemprichii* in all the substrates had 4 leaves and 3 roots on average (range = 2 to 6 and 1 to 7, respectively). Leaf material was produced at \(30 \pm 1 \text{ mm}^2 \text{ d}^{-1}\) while roots lengthened at \(6 \pm 0.2 \text{ mm} \text{ d}^{-1}\). Substrate type was not a significant factor in module growth (Pillai’s criterion = 0.121, *p* > 0.05).

Within the succeeding 28 days, seedlings displayed significant variation in overall module growth (Fig. 2, a and b), with both disturbance durations and modes particularly affecting leaf growth (Table 3A). In the clipped seedlings, the pattern in leaf growth followed that of the control, although rates appeared slightly lower from Day 37 (= Day 7 post-disturbance) and onwards (Fig. 2, a). Measured rates on Day 58, however, were similar to baseline values (Day 30 or Day 0 post-disturbance; Fig. 2, a). Seedlings with burial and combined treatments decreased leaf growth from Day 33 (\(20 \pm 2 \text{ and } 27 \pm 5 \text{ mm}^2 \text{ d}^{-1}, \) respectively) and by Day 44 (=Day 14 post-disturbance), some recovered seedlings were smothered and growth rates in both treatments became significantly depressed (\(7 \pm 3 \text{ and } 4 \pm 1 \text{ mm}^2 \text{ d}^{-1}\), respectively).
respectively). Such low rates continued until the end of the observation period (Fig. 2, a).

The response of the roots was not as considerable as the response of the leaves (Fig. 2, b) but the significant effects of disturbance mode and duration were still pronounced (Table 3B, C). Growth rates decreased continuously in the buried and in the combined clipped and buried seedlings, i.e., from 6 ± 0.3 to 2 ± 0.3 mm d⁻¹ (Fig. 2, b). In contrast (except for the drop on Day 37 or Day 7 post-disturbance) root growth of clipped seedlings was similar to that of the control (pooled mean = 5.2 ± 0.3 mm d⁻¹, Fig. 2, b).

**Experiment 3 – Response of excluded seagrasses to blocked shrimp activity**

Leaf growth rates of *T. hemprichii* in the excluded and procedural control units were similar with background rates ($p > 0.05$; Table 4, A; Fig. 3) regardless of the distance of the shoots from shrimp disturbance, but appeared strongly seasonal ($p < 0.001$, Table 4). Highest growth rates were found in March and April (169 ± 70 mm² shoot⁻¹ d⁻¹ maximum) and lowest in July (41 ± 6 mm² shoot⁻¹ d⁻¹ minimum) (Fig. 3).

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**Table 1B.** Multivariate analyses of variance (Expt. 1). The effect of disturbance mode (clipping, burial, and clipping with burial) and disturbance duration (4, 8, 14, 25 days) on absolute leaf growth (LAGR) and rhizome elongation rates (RAGR) in young *T. hemprichii* in the field ($\alpha = 0.05$). Superscripts indicate significant main effects ($p < 0.05$, **$p < 0.005$, ***$p < 0.001$) in leaf (*) or both leaf and rhizome parameters (**) from univariate *F*-tests.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Pillai’s criterion</th>
<th>Approximate $F$</th>
<th>Hypothesized $df$</th>
<th>Error $df$</th>
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<tbody>
<tr>
<td>LAGR, RAGR</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. Two-way factorial</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Duration of disturbance</td>
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<td>5.409 *** b</td>
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<td>Burial at 5 cm</td>
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<td>Clipping + burial at 5 cm</td>
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<td>Control</td>
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<tr>
<td>4 days post-disturbance</td>
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<tr>
<td>8 days</td>
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<td>1.168</td>
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<td>14 days</td>
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<tr>
<td>25 days</td>
<td>0.639</td>
<td>3.006 ** a</td>
<td>10</td>
<td>64</td>
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</table>

Notes: (a) leaf growth rates pooled from all distances; (b) leaf growth rates pooled from all times of day.
Table 2. Summary of non-parametric two-way analyses of variance (Scheirer-Rare-Hare extension of the Kruskal-Wallis tests) on ranked ratios of mean leaf growth and rhizome elongation (A) and LAGR and RAGR (B). Note: a computed as $\sum \Sigma SS / \Sigma df$ due to the presence of ties in the ranks, or b otherwise, as $[n(n+1)] / 12$; * significant at $\alpha = 0.008$

<table>
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<tr>
<th>Dependent variables/ Source of variation</th>
<th>Sum of Squares</th>
<th>df</th>
<th>Computed $H$</th>
<th>Critical $\chi^2$ $(\alpha = 0.05)$</th>
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<td>4.039</td>
<td>7.815</td>
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<td>2.884</td>
<td>11.070</td>
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<tr>
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<td>14.553</td>
<td>24.996</td>
</tr>
<tr>
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<tr>
<td><strong>B. LAGR: RAGR</strong></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Duration of disturbance</td>
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<td>7.815</td>
</tr>
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<td>5.278</td>
<td>11.070</td>
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<tr>
<td>Duration x mode</td>
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<td>8.859</td>
<td>24.996</td>
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<tr>
<td>Error (replicates)</td>
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<tr>
<td>Total</td>
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<td>155</td>
<td></td>
<td></td>
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<tr>
<td>Mean Square b</td>
<td>2093.500</td>
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</table>

Four other species occurred with *T. hemprichii* in the experimental units – *Halophila ovalis* (R. Br.) Hook, *Cymodocea rotundata* Ehrenb. and Hempr. ex Aschers., *Halodule uninervis* (Forssk.) Aschers., and *Enhalus acoroides* (L. f.) Royle. Except in *C. rotundata*, shoot densities varied significantly throughout the observation period ($p < 0.05$ for month; Table 4, B; Fig. 4). The negative effects of exclusion and core sampling on shoot densities were also apparent in some months ($p < 0.05$ for treatment; Table 4, B), since background densities appeared higher in most cases ($p < 0.017$, Tukey’s HSD).

**Discussion**

The modes of applied experimental disturbance elicited both positive and negative responses in shoots of *Thalassia hemprichii*. Leaf harvesting was not damaging while burial appeared to be beneficial to established shoots. The employed drastic clipping regime (>36%, cf. Cebrían and Duarte 1998), which was applied to mimic the leaf harvesting behaviour of burrowing alpheid shrimps, did not lead to shoot mortality or prolonged reduction in leaf and root growth of both apical shoots and seedlings. Single partial defoliation events were found to have little impact on leaf growth in this species (Cebrían and Duarte 1998) and its congener *Thalassia testudinum* (Tomasko and Dawes 1989a). This has been attributed to translocation processes of carbohydrates from the rhizomes (Dawes and Lawrence 1979; Tomasko and Dawes 1989b) and of leaf and root nitrogen (Valentine et al. 2004) to the affected shoots, where the basal meristem can simply continue producing new leaves.
Figure 2. *Thalassia hemprichii*. Comparison of leaf growth rates (a, mm seedling \(^{-1} \text{d}^{-1}\)) and root elongation rates (b, mm seedling \(^{-1} \text{d}^{-1}\)) between the experimentally disturbed and undisturbed seedlings (gray lines) from Days 30, 33, 37, 44, and 58 (corresponding to 0, 3, 7, 14, and 28 days post-disturbance). \(n = 10\) seedlings disturbance mode \(^{-1}\) period \(^{-1}\); different symbols denote sediment sources along the siltation gradient in Bolinao: LUC-Lucero (clear-water, carbonaceous sand), PIS-Pislatan, RUF-Rufina (silty, muddy sand), DOL-Dolaoan (most silty, sandy mud)
Table 3. Multivariate analyses of variance (Expt. 2). The effect of disturbance and disturbance duration (4, 7, 14, 28 days) on the correlated parameters (LAGR, root lengths) measured in *T. hemprichii* seedlings ($\alpha = 0.05$). Superscripts indicate significant main effects ($^{**}p < 0.005$, $^{***}p < 0.001$) in leaf ($\alpha$), root ($\beta$), or both measures ($\gamma$) from univariate $F$-tests.

<table>
<thead>
<tr>
<th>MANOVA design/ Source of variation</th>
<th>Pillai’s criterion</th>
<th>Approximate $F$</th>
<th>Hypothesized $df$</th>
<th>Error $df$</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Two-way factorial</td>
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<td></td>
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<tr>
<td>Duration of disturbance</td>
<td>0.236</td>
<td>13.420 $^{***} \beta$</td>
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<td>Disturbance mode</td>
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<td>Duration x mode</td>
<td>0.143</td>
<td>3.448 $^{***} \gamma$</td>
<td>18</td>
<td>802</td>
</tr>
<tr>
<td>B. One-way factorial: Main effect = disturbance duration</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Clipping</td>
<td>0.495</td>
<td>9.430 $^{***} \gamma$</td>
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<td>172</td>
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<tr>
<td>Burial (5 cm)</td>
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<tr>
<td>Clipping + burial</td>
<td>0.638</td>
<td>10.463 $^{***} \gamma$</td>
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<td>0.277</td>
<td>5.081 $^{***} \gamma$</td>
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<td>C. One-way factorial: Main effect = disturbance mode</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>3 days post-disturbance</td>
<td>0.419</td>
<td>8.044 $^{***} \gamma$</td>
<td>6</td>
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<td>7 days</td>
<td>0.520</td>
<td>8.669 $^{***} \gamma$</td>
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<td>14 days</td>
<td>0.484</td>
<td>9.905 $^{***} \gamma$</td>
<td>6</td>
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<tr>
<td>28 days</td>
<td>0.577</td>
<td>7.981 $^{***} \gamma$</td>
<td>6</td>
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</table>

Small-scale and short-term burial resulted in a different response in established shoots and seedlings by stimulating leaf growth by up to 2.6% in the former (mean range from 1.1 to 1.5%) but reducing growth by as much as 15% in the latter (mean range from 1.7 to 7.7%). The enhanced growth response agrees with previous observations of induced compensatory growth in apical shoots, i.e., that increased leaf production and longer new internodes were found (Gallegos et al. 1993, Marbá and Duarte 1994, Duarte et al. 1997) at intermediate burial levels for <2 months (cf. Vermaat et al. 1997). Rapid growth of seagrass leaves can be sustained by the translocation of reserve carbohydrates and nutrients (Terrados et al. 1997, Uy et al. 2001a), which are present in substantial quantities in the robust rhizomes of *T. hemprichii* (about 40% of the rhizome DW; Vermaat et al., unpubl. data), by reductions in the transport of leaf photosynthates to the rhizomes (Uy et al. 2001b) and possible reallocations of energy and resources from carbon assimilation to light harvesting, as was demonstrated for *T. testudinum* (Major and Dunton 2002). In contrast, the one month-old seedlings failed to recover, even at intermediate burial depths for short-term periods (Fig. 2), as their nutritional reserves were probably insufficient to meet the demand for increased leaf production that was necessary to counteract the negative effects of burial. This growth reduction was also apparent when burial was combined with one-time defoliation. Growth of established shoots under combined disturbance neither improved nor declined (Fig. 1, Table 1B-2) although the tendency towards recovery was apparent after 25 days in shoots buried in 2 cm of sediment. Carbohydrate reallocation to clipped shoots may have lasted about 25 days with 2 cm burial, but in clipped shoots with twice the burial depth, we presume that translocations may have proceeded considerably longer.
The ranges and the temporal pattern observed for leaf growth (Fig. 3, Table 4-A) and shoot densities of *T. hemprichii* vegetative shoots (Fig. 4, Table 4-B) were consistent with previous observations (Rollon 1998, Agawin et al. 2001). This emphasizes the significance of environmental forcing (cloudiness, rainfall, water turbulence, and total daily PAR) over species-specific traits. The increase in seagrass densities within the control plots was not observed in the enclosures. This indicates successful recruitment of vegetative shoots outside the exclosures and suggests that our barrier against shrimp activity may also have prevented clonal recruitment of most long-lived species. Shoots of *Halophila ovalis*, on the other hand, increased in numbers despite the barrier, and successfully colonized the disturbed section of the exclosures (Fig. 4), as expected for pioneer species (Brouns 1987, Clarke and Kirkman 1989, Duarte et al. 1997).

Small gaps in the canopy continuously created by burrowing shrimps, thus, become sites for fast clonal growth (Rollon et al. 1998, Rasheed 1999, Olesen et al. 2004), and, probably, for the recruitment of seedlings (Dumbauld and Wyllie-Echeverria 2003, Olesen et al. 2004). Although continued shrimp disturbance in these patches may limit the survival of these sexual recruits (Lacap et al. 2002, Balestri and Cinelli 2003, Rollon et al. 2003, Olesen et al. 2004), the gaps maintain small-scale heterogeneity in the landscape of shallow mixed beds, which allows for a suite of different species to coexist (Duarte et al. 1997) in a situation of continuous, small-scale recolonization (Rollon et al. 1998, Rasheed 1999, Olesen et al. 2004). The high sensitivity of *Thalassia* seedlings to both clipping and burial may be an important reason for the high mortality rates of these young recruits. Although massive seedling recruitment can sometimes be observed sometimes (Olesen et al. 2004), seedling densities are often very low. Activities of the often abundant alpheid shrimps are thus probable causes of seedling loss. This, and the availability of new bare habitat, may well have selected for a well-developed clonal expansion capacity in the suite of seagrass species present.

**Acknowledgments.** WOTRO, through Project WB84-413, provided funding for the study and the Marine Environment Resources Foundation, Inc. (MERF) granted a writing scholarship contract to HEN. We are grateful to Cris Diolazo, who helped in
Figure 4. Experiment 3 – changes in seagrass shoot densities in the undisturbed and disturbed sections of the experimental units from March to August 2000 and in April 2001.
Table 4. Repeated measures ANOVA (Expt. 3). The effects of exclusion and sampling procedure (\(a\)) and distance from shrimp disturbance (\(b\)) on leaf growth rates of *T. hemprichii* (A) and on seagrass densities (B) in the experimental units. The main effect of month (within-subjects factor) and the interaction terms were evaluated from results of the multivariate tests (\(c\) as Pillai’s trace). Significant \(F\)-values are (\(\alpha = 0.05\)) are indicated by asterisks: *\(p < 0.05\), **\(p < 0.005\), ***\(p < 0.001\)).

<table>
<thead>
<tr>
<th>Variables</th>
<th>Error (within replicates)</th>
<th>Treatment ((T, df=2))</th>
<th>Shoot location ((SL, df=1))</th>
<th>T x SL ((df=2))</th>
<th>Month, M</th>
<th>M x T</th>
<th>M x SL</th>
<th>M x T x SL</th>
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<td>((df=2))</td>
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<td><strong>A. LAGR, (mm^2/) shoot/ d</strong></td>
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<tr>
<td>MS</td>
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<td>0.82</td>
<td>0.23</td>
<td>0.01</td>
<td>0.46 ((df=5))</td>
<td>0.11 ((df=10))</td>
<td>0.05 ((df=5))</td>
<td>0.06 ((df=10))</td>
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<tr>
<td>(F)</td>
<td>1.10</td>
<td>0.30</td>
<td>0.10</td>
<td>14.45 ***</td>
<td>0.43</td>
<td>0.82</td>
<td>0.56</td>
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<tr>
<td><strong>B. Seagrass densities, nos./ 100 cm(^2)</strong></td>
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<tr>
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<tr>
<td>(F)</td>
<td>6.57 ***</td>
<td>2.23</td>
<td>5.18 **</td>
<td>13.71 ***</td>
<td>2.45 **</td>
<td>5.78 ***</td>
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<td>3.99 ***</td>
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<td>0.23</td>
<td>2.48 *</td>
<td>1.03</td>
<td>0.72</td>
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<td>0.07</td>
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<tr>
<td>(F)</td>
<td>0.67</td>
<td>2.24 *</td>
<td>0.30</td>
<td>0.82</td>
<td>2.45</td>
<td>0.82</td>
<td>1.79 *</td>
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</tbody>
</table>
the fabrication of the field corer, to staff, researchers, and volunteers at BML who assisted during experimental manipulations, field/ hatchery retrievals, and subsequent measurements for the duration of the study – Cris Ragos, Ronald de Guzman, Oytón Rubio Jr., Chà de Castro, Mimoy Silvano, Ronald Gijlstra, José Vos, Kat Villamor, Rex Montebon, Rómni Dizon, Makóy Ponce, Frank Wiegman, and Sheila Albasin. Dr. Dosette Pante explained patiently on the difficult details of multivariate statistics.

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Chapter 6

General discussion and conclusions

Because the footprint of man is now perceptible in all aspects of the state of the natural world, such that we accept that we are now in the Era of the “Anthropocene” (Crutzen and Stoermer 2000), there is much emphasis on quantifying the impact of global change on biological distributions, biodiversity, and ecosystem functions (Schulze and Mooney 1994, Chapin et al. 1997, Snelgrove 1999, Duarte 2000, Hughes 2000, Smith et al. 2000, Harley et al. 2006, Occhipinti-Ambrogi 2007). The discussion of Hughes (2000) however, recommended that these types of studies need to be grounded on sound monitoring of how existing natural perturbations already influence the behavior and life cycles of flora and fauna of interest. The series of papers compiled by Pickett and White (1985) on The Ecology of Natural Disturbance and Patch Dynamics and by Hobbie et al. (1994) are examples of good background as basis to study the effects of global change over and above natural disturbances. Changes in global climate are anticipated to greatly impact the world’s seagrasses (Short and Neckles 1999). The responses are predicted to be linked with hydrodynamics, which affects every aspect of the existence of seagrasses, the benthos in general (Koch et al. 2006), and the processes at various scales that affect clonal growth, and eventually, seagrass colonization and recovery from disturbance (Hemminga and Duarte 2000, Duarte et al. 2006). One focus of global change studies is watershed modification and sediment delivery to the coast and its consequences to coastal habitat distribution and health (e.g., Terrados et al. 1998, Kamp-Nielsen et al. 2002, Orth et al. 2006). Studies on the natural reworking of sediments in seagrass meadows have also developed from providing evidence of biotic interactions to the perspective of ecosystem engineering (e.g., Berkenbusch et al. 2000, Siebert and Branch 2006, Berkenbusch et al. 2007, Pillay et al. 2007).

This thesis covered one type of natural disturbance, small-scale, but ubiquitous in dense SE Asian seagrass beds. The work only barely scraped the surface of interactions that can be anticipated when an integrated approach to studying burrowing animals is coupled with analyses of associations with other fauna (mutualisms), the properties of the seagrass canopy and sediments, and the resultant seagrass and endofaunal distributions. The major issues addressed in the thesis are highlighted and integrated in this chapter, particularly describing the bioturbation of burrowing shrimps, the foraging of *Alpheus macellarius* and its mutualism with the species of the goby genus *Cryptocentrus*, the response of the dominant *Thalassia hemprichii* to their small-scale disturbance, and the implications of all these to large-scale seagrass dynamics. Finally, future directions are suggested.
Bioturbation by burrowing shrimps in seagrass meadows

Burrowing is a form of bioturbation, which mixes sediments and porewater and allows for frequent release of nutrients from belowground to the sediment surface, making them more readily available to benthic primary producers in general. This study showed that the burrowing shrimps *A. macellarius* (Caridea) and species of Thalassinidea are major agents of bioturbation in shallow Philippine seagrass meadows, mainly gauged from the size, abundance, and distribution of sediment gaps (Chapter 2). These animals are mainly engaged with burrowing or mining, with reworking rates of between 8 and 1.4 kg m\(^{-2}\) d\(^{-1}\) for *A. macellarius* (Chapter 3) and up to 12 kg m\(^{-2}\) d\(^{-1}\) for the thalassinidean shrimps. A potential follow-on study may assess the impact of these dominant burrowing shrimps to the environment based on other indicators. Meadows (1991b) has proposed indices of complexity (*C*), tortuosity (*T*), and activity (*A*), all morphological descriptions that may be tested and all independent of scale, so that impact and modification in terrestrial and aquatic habitats may be compared regardless of the sizes of animals involved. Moreover, the counterparts and functional roles in Philippine seagrass beds of temperate macrofaunal organisms that cause significant bioturbation, e.g., lugworms (Philippart 1994), crabs, and rays (Woods and Schiel 1997, Townsend and Fonseca 1998), remain to be assessed and evaluated at appropriate scales.

Burrowers both affect and are affected by mechanical properties of sediments (Dorgan et al. 2006). We showed in Chapter 4 that soft carbonate sand sediments present greater support for burrowing behavior and burrow complexity and, thus, concealment of *A. macellarius* than terrigenous seagrass substrates, where burrowing appears limited and substituted by concealment strategies, periods of inactivity, or within-burrow activities. The rhizome-root compartment of the dense and mixed seagrass bed often in soft carbonate sand also provides additional reinforcement to the burrows, and the beds, therefore, may be expected to sustain the intense burrowing behavior of *A. macellarius*. Hence, significantly more burrow openings were found (Chapter 2). The reduced diversity and densities of seagrasses in silty beds appear to offer less support to the burrowing behavior of *A. macellarius*, and, in parallel, the frequency of burrow openings was observed to be low (Chapter 2).

On the larger scale, hydrodynamics was important in constraining the spatial distribution of shrimp disturbance in the meadows, i.e., sediment gaps were more pronounced in sheltered than in open beds (Chapter 2). Hydrodynamics also influenced the periodicity of the aboveground activity of alpheid shrimps, which were found to be more prominent in the dry than during the wet months (Chapter 3). It would be interesting in future to quantify the flow properties and hydrodynamic forces operating at the sediment-water interface and within- and above the canopy that allow or restrict the aboveground activities of *A. macellarius* and, likewise, determine the distribution of faunal disturbance. Koch et al. (2006) discussed the increase of turbulence and mixing within canopies of less shoots or where seagrass patchiness is increased. In the studied seagrass habitats associated with the presence of rivers, water-column *K*\(_d\) was also high and the presence of shrimp gaps was observed to be limited (Chapter 2). High *K*\(_d\) may account for observed patchiness of seagrasses in the turbid areas visited and is also linked to sediments that are easily resuspended (e.g., Rollon 1998), and burrowing alpheid shrimps responded to these by spending more time hidden in their burrows. The *(in situ)* aboveground activity
GENERAL DISCUSSION AND CONCLUSIONS

of *A. macellarius* in these seagrass areas still needs to be established and compared with *A. macellarius* in clear-water beds.

**Trophic strategies of *A. macellarius***

Burrowing and the other mechanisms of bioturbation by *A. macellarius* are closely associated with its feeding (Chapter 4). Mound-forming thalassinidean shrimps are deposit feeders (Griffis and Suchanek 1991, Nickell and Atkinson 1995) and *A. macellarius* demonstrated a similar mode as its main feeding strategy (Chapter 4, this Thesis; Palomar et al. 2004) combined with grazing and suspension feeding (Chapter 4). *Alpheus macellarius* harvests seagrass leaves, hoards the harvest belowground (Chapter 3) and consumes these in its burrows (Chapter 4). Leaf harvesting appears to limit the shrimps’ distribution to seagrass-vegetated substrates (Chapter 2). Food hoarding, as an adaptive strategy, gains advantage for *A. macellarius* in the control of food availability in space and during environmental contingencies, e.g., when water movement is high (storms) or light is limiting (turbid) and emergence at the surface is perceived as risky. It also implies that the sediment surface of seagrass beds presents a risk for their foraging (‘security hypothesis’, Vander Wall 1990). Thus, because of its leaf hoarding behavior and ability to mix feeding strategies (grazing, deposit- and suspension-feeding; Chapter 4), *A. macellarius* demonstrates its fitness in a meadow that does not appear to be resource-limited. The potential food limitation by leaf availability can only be assessed, however, on a larger bed- and longer time-scale, because the gaps, like territories, shifts positions with time (Bell et al. 1999, pers. obs.) as a result of simultaneous shrimp activity and seagrass recolonization. Palomar et al. (2004) have cited the importance of seagrass leaves and detritus in the shrimp’s diet and included crustaceans and protozoans among the less frequently encountered food item in the guts. To strengthen this observation and resolve the shrimp’s preferential consumption of these food items, follow-on choice experiments may have to be conducted based on a larger sample size of subjects representing various seagrass environments. Further, studies that detail the functional morphology of feeding appendages and the digestive tract at various stages of the life history of *A. macellarius* may elucidate the importance of various food elements utilized in the seagrass beds; their activities would also provide indications of their bioturbation potential and impact to the system, as has been revealed for other large bioturbators (Tamaki 2004).

**The nonsymbiotic mutualism of *A. macellarius* and *Cryptocentrus* sp.**

Mutualisms are widespread in the tropics and important to many population and community characteristics (Boucher et al. 1982, Hay et al. 2004). Nonsymbiotic mutualisms, those in which two species are physically unconnected, can involve exchanges of benefits for nutrition, supply of energy, protection, and transport. Among marine animals, the burrow-sharing by gobies and shrimps appears such a non-symbiotic mutualism, probaly strongly embedded through natural selection (Migita and Gunji 1996). About 13 species of the burrowing shrimp *Alpheus* are known to be associated with gobiid fishes (Karplus 1987) while at least 18 species...
of Cryptocentrus are associated with alpheid shrimps (Karplus 1987, FishBase 2004, Nelson 2004). It is known that shrimp gobies primarily serve as watchman (using the vicinity of the burrow opening as post), may be instrumental in displacing the openings (Karplus et al. 1974), and do not participate in burrow construction (endoecism, Atkinson and Taylor 1991). Communication between partners is mainly tactual (Preston 1978) – gobies flick their tails to signals during emergence to the surface (initially at 70 to 400 lux – Karplus et al. 1974) or retreat to the burrows while shrimps use their antennae. Retreats and subsequent hiding were seen as response to low light levels (Karplus 1987), high water motion conditions (Chapter 3), and perceived biological threats at the sediment surface. In the clear-water meadow, C. octafasciatus remained within a guarding radius of not more than 50 cm from the burrow opening to maintain its communication distance with A. macellarius while the latter continued with its aboveground activities (Chapter 3). The interactions in situ of A. macellarius and C. singapurensis, the shrimp’s frequent partner in silty sediments (Palomar 2002), and the effects of such substrate and light conditions on the partners’ communication radius and their mutualism in general, remains to be studied.

**Shrimp disturbance and Thalassia hemprichii**

Although burrowing shrimps rework a substantial amount of sediments (Chapter 3), only moderate effects were observed on the dominant seagrass T. hemprichii. Specifically, both early and mature stages of vegetative T. hemprichii displayed tolerance to short-term burial (Chapter 5). The leaf harvesting mode of A. macellarius, which represents single and partial defoliation events, had little impact on leaf growth (Cebrián and Duarte 1998, Chapter 5). Seedlings were able to survive partial defoliation but were sensitive to burial events (Rollon et al. 2003, Olesen et al. 2004, Chapter 5), which may be an important reason for the high mortality rates of recruits. Longer-term shoot burial induced species-specific responses, e.g., increased vertical growth, branching, and shoot densities, to cope with the disturbance (Marbá et al. 1994, Duarte et al. 1997, Berkenbusch et al. 2000). For a period of 1 year, the vegetative shoots of T. hemprichii were able to sustain leaf growth but did not increase shoot density by branching in exclosures without shrimp (Chapter 5). The exclusion of such disturbance was beneficial only to Halophila ovalis, which increased its densities in the plots, compared with other accompanying species. We can only surmise that the overall positive effect of the bioturbation on T. hemprichii shoots outweighs the negative impact to the sensitive seeds, since the presence of burrowing shrimps persists and is, in fact, common in thriving tropical mixed-species seagrass meadows.

**Small-scale disturbance and large scale dynamics**

Burrowing animals and their burrows, both in the terrestrial and aquatic realms, modify the environment in a number of forms. Meadows (1991a) outlined what was known before the 1990s of their environmental impacts on soil fertility, aeration and water infiltration, sediment chemistry, pollutant retention and release, early
diagenesis, microbial activity, erosion and stability, landscapes, sediment turnover and reworking, and the development of plant and animal communities and associations. The small-scale disturbance that burrowing shrimp populations impose on the sediment compartment in seagrass meadows has a major impact on the local environment. In Chapter 2, we showed that burrowing shrimps altered the vertical profiles of sediment properties and reduced the nitrogen content of sediments – proof that the animals are of local (and global) importance. In coastal habitats, burrowing populations are assumed to prevent anoxia and hence, system collapse, primarily through (1) sediment oxygenation (ventilation), (2) the channeling of food particles to bacterial and macrobenthic production, and (3) the speed-up of mineralization and nutrient release from the sediment (de Wilde 1991, Frouin 2000). The latter may also account for enhanced mineralization in the root zone preferentially in the more often nutrient-limited Philippine seagrasses (Agawin et al. 1996). Leaf harvesting constitutes only moderate herbivory (12-42%, Chapter 3) and represents a translocation of material for microbial action and a process of nutrient conservation within the meadow (Stapel and Erftemeijer 2000). The presence of gaps in the meadows may be more important in the process of mixing within- and above-canopy waters of the beds (e.g., Granata et al. 2001), including dissolved nutrients and propagules therein, thus altering the “skimming flow” of water in homogeneous meadows (Koch et al. 2006). The sediment gaps (sand mounds) may be eroded preferentially (gap-widening) and particles be suspended and transported (Roberts et al. 1981, Suchanek, 1983, Rowden et al. 1998, Bouma et al. 2007). These gaps form a pattern of spatial habitat heterogeneity at scales of 10-100 m, increasing internal edge length in the meadow, and thus enhancing habitat availability for invertebrates and fish.

Conclusions and future directions

This thesis showed that bioturbation from burrowing shrimps is a main feature of lush seagrass beds of finer, autogenous, and carbonaceous sands. Its impact on the mineralization of nutrients may be important, as reworking helps to facilitate their availability to seagrasses. On terrigenous sediments, bioturbation, although less intense, may alleviate reducing conditions of sediments by ventilation/irrigation events in the burrows. The burrowing shrimps may well be instrumental in maintaining a small-scale heterogeneity (i.e., relative to the shrimps) in seagrass patches and in larger, mixed-species beds, constantly creating sediment gaps that are colonized by fast pioneers, e.g., Halophila ovalis, and then facilitating a sequence of succession in the gaps. Established seagrasses are able to exert tolerance to burial and leaf defoliation, but to which recruits could be limited.

Alpheus macellarius was first described in a taxonomic monograph by Chace (1988), based on material from Cebu and Leyte (Philippines). Our examination of its behavior progressed from quantifying visible activities in situ and then justifying the subsequent outdoor observations with the considerable time the shrimps spent within their burrows. As we make generalizations of the shrimps’ bioturbation, advanced research by physical engineers has begun to look at the physics of the loud sound from alpheid snapper claws (A. heterochaetis; Versluis et al. 2000). The snapping sound is caused by the collapse of the cavitation bubble that is formed during a pressure drop below vapor pressure, which occurs when high velocity water
jet is produced by the fast claw closure following the cocking of the claw in the open position. More recently, the role of water current signals by alpheid shrimps during social interactions was described (Herberholz and Schmitz 2001). Probably new perspectives are there at hand, as technology becomes more capable of unfolding the unknowns of alpheid shrimps.

As economically valuable coastal systems in the tropics, seagrass habitats have yet to gain further due legislation and conservation measures by linking burrowing shrimps, as engineers, to ecosystem function and biodiversity (e.g., Boogert et al. 2006). Also, since bioconstruction and bioturbation are involved in most faunal community relationships in the sediment (Reise, 2002), the interactions between burrowing shrimps and biotic sympatrics may also have to be elucidated to clarify their potential key role in the meadows, considering issues of both spatial and temporal scales (sensu Hastings et al. 2007). Current criteria for the zoning of seagrass ecosystems in the Philippines being tested, e.g., combinations of high canopy cover on bottom, seagrass species richness, and/or apparent significance to dugongs and turtles (PCSD 2007, Nacorda et al. 2008), show that specific core zones recommended are also frequently characterized by disturbance from burrowing shrimps. These critical areas are, thus, clear examples of disturbance-mediated and diverse habitats worthy of well-deserved protection.

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Samenvatting

Bodembewonende garnalen en zeegrasdynamiek in ondiepe kustwateren rond Bolinao (NW Filippijnen)

Natuurlijke verstoringen dragen bij aan de dynamiek van zeegrasvelden. Het doel van dit promotie-onderzoek was het effect te kwantificeren van kleinschalige verstoringen door algemeen in Filippijnszeegrasvelden voorkomende pistoolgarnalen (*Alpheus macellarius*) en spookgarnalen¹ (*Thalassinidea: Callianassidae*). De blinde pistoolgarnalen leven paarsgewijs in zelfgegraven tunnelstelsels in symbiose met een grondeltje (*Cryptocentrus spec.*). Ze knippen zeegrasbladeren af en slaan deze op in ondergrondse voorraadkamers. Zowel het intensieve grondverzet (bioturbatie) als het oogsten van bladmateriaal zou van belang kunnen zijn voor het omringende zeegrasveld. Spookgarnalen graven burchten bestaande uit meerdere U-vormige gangen, met één of meerdere vulkaanachtige uitmondingen. Ze leven van organisch materiaal in het sediment door dat te zetten met hun monddelen of filteren gesuspendeed materiaal uit het water wat door de burcht wordt opgepompt. Uitgegraven of anderszins verwerkt sediment wordt naar het bodemoppervlak gelegd. Dit proefschrift behandelt achtereenvolgens (a) de ruimtelijke verspreiding van deze twee typen gravende garnalen in zeegrasvelden langs een sedimentatiegradient bij Bolinao (Luzon, NW Filippijnen; hoofdstuk 2); (b) het boven- en ondergrondse gedrag van pistoolgarnalen (hoofdstuk 3 en 4); en (c) de gevolgen van grondverzet en bladoogst door pistoolgarnalen op de groei en uitbreiding van verschillende soorten zeegras.

Beide groepen bodembewonende garnalen komen algemeen voor in de zeegrasvelden rond Bolinao en elders op de Filippijnen. Met name in beschutte velden op fijn, zandig sediment zijn de dichtheden hoog. Bioturbatie door *Alpheus* resulteerde in meer open plekken in het zeegrasveld (15% ± 1% van het oppervlak, 102 ± 5 plekken per 100 m²) dan die door *Callianassa* (5% ± 1%, 52 ± 7 plekken per 100 m²). Beide garnalen-groepen beïnvloeden de verticale verdeling van de korrelgrootte, organische stof en stikstof. *Alpheus* stapelt grof materiaal aan het oppervlak, als een soort tunneldak, terwijl *Callianassa* fijn bodemmaterial concentreert tussen de 10 en 20 cm diepte. Beide groepen halverden de stikstofconcentraties in de bovenste 10 cm van de bodem. *Alpheus* besteedde slechts 12% van de tijd bovengronds buiten het gangenstelsel. Dan werd zeegrasblad geoogst of het gangenstelsel gerepareerd. In de natte moessontijd was dat nog minder (8%). De garnaaltjes verwerkten gemiddeld 1.1 kg m⁻² d⁻¹ sediment en oogsten 11.4 g blad m⁻² d⁻¹. Dit laatste komt neer op 27% van de dagelijkse zeegrasproductie, een aanzienlijke hervorming van plantaardige productie naar de bodem. In kleine cuvetten (45 x 2 x 35 cm, L x B x H) met koraalzand en zeegras in het lab begon *Alpheus* direct te graven. Binnen twee uur was de primaire tunnel afgerond en konden ze zich verbergen. Vervolgens ging het graafwerk door, afgewisseld door voets-, verkennings- en foerageergedrag (zowel suspensiefilteren, zeegras oogsten als sedimentopname). Overdag werd minder tijd

¹ Van *Callianassa* is ons geen Nederlandse naam bekend, zie bijvoorbeeld [www.kreeftengarnalen.nl](http://www.kreeftengarnalen.nl) of [www.imv.uit.no/crustikon](http://www.imv.uit.no/crustikon). We hebben spookgarnaal letterlijk uit het Engelse ghost shrimp vertaald.
bovengronds besteed dan’s nachts. In behandelingen met fijn terrigeen slib werd veel minder gegraven dan in koraalzand; de dieren verstopten zich voornamelijk in korte tunneljjes. Dit bevestigt de in het veld waargenomen habitatvoorkeur van deze pistoolgarnaalsoort.

Uit de experimenten die het effect van het garnaalgedrag op zeegras (*Thalassia hemprichii*, in deze regio meestal een dominante soort) bleek dat de planten weinig hinder hadden van de kleinschalige verstoringen. Apicale scheuten reageerden op veertien dagen durende begraving met versnelde blad- en stengelgroei. Afknippen van de bladschijven of een combinatie van begraven en knippen hadden slechts minimale gevolgen op de blad- en wortelstokgroei. Kiemplanten van *Thalassia* overleefden experimentele ontblanding maar bleken erg gevoelig voor begraving: de groei verminderde aanvankelijk tot slechts een derde van de controlegroep. Tenslotte bleek uit een dertien maanden durend *in situ* experiment waarbij pistoolgarnalen uitgesloten werden dat daar geen meetbaar effect was op de dichtheid en groei van de meeste aanwezige soorten zeegras. Slechts één soort, de kleine, snel groeiende maar kort levende *Halophila ovalis* nam gedurende enige tijd sterk toe in dichtheid, met een maximum na vijf maanden.

Resumerend kan geconcludeerd worden dat de twee algemeenste groepen in de bodem gravende garnalen van de tropische zeegrasvelden in Zuid-Oost Azië met name grote hoeveelheden sediment verplaatsen. Daarmee beïnvloeden ze ook de verticale verdeling in het sediment van korrelgrootte, organische stof en stikstof. Indirect zorgen ze er ook voor dat ongeveer een derde deel van de nutrienten dat in het bladmateriaal vastgelegd is niet door afslag uit het zeegrasveld verdwijnt, maar via mineralisatie in het sediment weer beschikbaar komt voor het zeegras. De pistoolgarnalen zijn het sterkst gebonden aan het zeebras omdat ze de bladeren oogsten. Zowel het graafwerk als de herbivorie hebben echter nauwelijks effect op de groei en overleving van de uitgebreide klonale rhizoomnetwerken van het zeebras. Wel wordt waarschijnlijk de recrutering en groei van kiemplanten negatief beïnvloed. Dit wordt vermoedelijk gecompenseerd door een effectieve vegetatieve vermeerdering.
Buód

Mga naghuhukay na hipon at dinámika ng mga lináng ng damong-dagat sa Bolinao (H-K Pilipinas)

May kontribusyon ang mga panggayari sa kalikasan sa dinámika ng mga lináng ng damong-dagat. Layunin ng tesis na ito na tsahin ang halagang mga pangyayari sa kalikasan sa dinámika ng mga lináng ng damong-dagat sa Pilipinas. Ang mga espesipikong layunin nitong pag-aaralan ay mailarawan ang spatial na distribusyon ng pagbabagong likhâ na mga naghuhukay na hipon sa isang siltation gradient at ang bunga nito sa mga vertikal na katangian ng latag ng sediment, ang masukat ang gawí ng naghuhukay na mga hipong alpheid, at mabatíd ang mga epekto ng panandaliang pagtatapal abangan sa dahon ng dominanteng damong-dagat na Thalassia hemprichii Ehrenberg (Ascherson).

Ang mga bukana ng hukay at mga patláng ng sediment ay nakaaran sa mga lináng at iniúugnay sa hipong caridean na Alpheus macellarius, Chace, 1988, o sa mas malaki at mas malalim maghukáy na species ng Thalassinidea. Sa mga lináng na ligtás-sa-alon ay mas madalas at malaki ang mga patláng hambing sa mga lantád na lináng; mas laganap din ang hukay at tumpók ng sediment na likhâ ng hipon sa mga lináng na may malinaw kaysa malabong tubig. Ang mga pagbabagong likhâ ng A. macellarius ay natuklasáng mas higít kaysa likhâ ng mga hipong thalassinidea, sa kalahatán, at ang distribusyon ng mga hipong alpheid ay kadalisang limitado lamang sa latag na may halaman ang pabahay. Ang latag ng buhangin na kaugnáy at binabago ng A. macellarius ay sumakop sa 15 ± 2% ng mga lináng (sa eskaladong dami na 102 ± 5 bawat 100 m², cf. larawan sa pabalat) samantalang ang tumpók ng buhangin ng hipong thalassinidea ay matatagpuán sa 5 ± 1% (sa dami na 52 ± 7 bawat 100 m²). Binago ng mga naghuhukay na hipon sa magkakabiháng paraán ang mga vertikal na katangian ng sediment—inilipat ng A. macellarius ang malaking bahagi ng malalaking butil sa 10 cm rabaw, samantalang tinipon ng hipong thalassinidea ang mga pinong butil mula 10 pababa hanggang 20 cm ng sediment, at nagtumpók ito ng organikong materyal. Gayunmán, ang dalawáng uri ng hipon ay nagpapababa sa nitrohéno ng sediment ng 20-73% sa rabaw na saray at ng 4-46% sa lahim na higit sa 10 cm.

Base sa aktwal na obserbasyon ng nasa rabaw-na-lupang gawí ng A. macellarius, ang mga hipon ay nagpakita ng aktibong pagrebasé ng sediment at okasyonál na pag-ani ng dahon ng damong-dagat sa lináng na malinaw ang tubig sa panahon ng tag-init. Ang ginugol ng mga hipon para sa ganitong nagkakita ng aktibong pagrebasé sa sediment ay 12% lamang ng kaniláng aktibong yugtô at sila ay nasa kani-kaniílang lunggá sa butál ng bawat araw. Sa panahon ng tag-ulân, nabawasan ang nasa rabaw-na-lupang gawí nila hindi babahá sa 34% at ang panahon nila sa loob ng 15 m nga dumás ng 5% bilang buhangin nito. Sa karaniwan, kaya ng A. macellarius ay nagmagsalintang alang ang kinalaláng bilis ng pagrebasé sa sediment (0.8 hanggang 1.4 kg kada 1 m² kada araw); para sa karaniwang dami ng hipon na 2 indibidwal kada 1 m², at ang bilis ng pag-ani nito ng dahon ay kumakatawan naman sa katamtamang herbivory (tuyóng timbang) ng sediment bawat araw (o 112 kg bawat taon), at umani ng 0.8 g DW ng dahon bawat araw (o 291.3 g bawat taon). Mahalaga at dapat isaalang-alang ang kinalaláng bilis ng pagrebasé sa sediment (0.8 hanggang 1.4 kg kada 1 m² kada araw) para sa karaniwang dami ng hipon na 2 indibidwal kada 1 m², at ang bilis ng pag-ani nito ng dahon ay kumakatawan naman sa katamtamang herbivory.
(0.4 hanggang 2.3 g kada 1 m² kada araw), katumbas ng 12 hanggang 42% ng produksiyón ng dahon.

Ang mga sumunód na obserbasyón sa laboratoryo na sumuri sa papél ng uri ng sediment—buhangin, maputik na buhangin, at mbabuhang putik—sa gawi ng *A. macellarius* ay nagpakita na nagsimulá agad ang mga hipon sa paghuhukáy sa oras na magkaroon ito ng kontak sa mga substrate. Sa substrate na buhangin, nagaganap na maaga ang pagtatagá ng hipon (may unang lunggá na sa loob ng 2 oras) sa kabila ng masikap nilang paghuhukáy, at nagawá rin ang ekstensibong habá ng lunggá. Narawasan ang paghuhukáy ng hipon at malinaw na nakita ang paglalaboy nito pagkaraan ng ikalimáng linggo ng obserbasyón. Litaw na litaw na rin ang kanyang panginginain—pangunahin ang pagkain ng partikél, paminsan-minsang pagkaing-suspensiyón, at pagngatngat sa dahon ng damong-dagat. Ang gawí na paghuhukáy, paglilinis ng sarili, at pagsisisyasat ay kapansin-pansin sa araw samantala ang paglaboy at pasinginain ay tumátagal hanggang gabi. Gayunman, ang paghuhukáy ay nanatiling mas malimit sa buhangin kaysa dalawa pang uri ng substrate. Sa kalahatán, ang malambot at carbonate na buhangin sediment, kaysa ng pagbilián na makapal na mga damong-dagat, ay ay mas mataas na damas na mga hipon sa araw na damong-dagat, at maagud na naglabay at pagtatabás sa buhangin ng *A. macellarius* at kaugnay ito ng naobserbahang mas mataas na damas na mga substrate na sa mga halip na may kasama ng kalihán ng damong-dagat, at kalibhasán ng naobserbahang mas mataas na damas na mga substrate.

Ang serye ng manipulatibong eksperimento pangunahin sa damong-dagat na *T. hemprichii* ay nagbigay ng patunay sa toleransi o hindi pag-indá ng mga usbóng sa toleransi o hindi pag-indá ng mga usbóng sa damong-dagat na *Halophila* lang ang napagyaman, partikular pagkaraan ng 21 linggo sa loob ng 13-buwang tagál ng eksperimento, at kapwa ang pagtubò ng *T. hemprichii* at dami ng usbóng ng ibang kasamang *species* ng damong-dagat ay nagpakita ng malakás na pagbabagong temporal tulad ng inaasahan. 

Sa madaling sabi, naipakita ng tesis na ito na ang dalawáng uri ng naghuhukay na hipon—ang *alpheid* at ang *thalassinidean*—na karaniwan sa mga lináng ng damong-dagat, ay may kakayahang maglabag na maring sediment at magdulot ng halagang epekto sa depth gradient ng organikong materyal, laki ng butil, at nitroheno. Ang mga hipon *alpheid* lamang ang may mahigpit na kasama ng *Halophila* lang ang napagyaman, partikular pagkaraan na 21 linggo sa loob ng 13-buwang tagál ng eksperimento, at kapwa ang pagtubò ng *T. hemprichii* at dami ng usbóng ng ibang kasamang *species* ng damong-dagat ay nagpakita ng malakás na pagbabagu-bagong temporal tulad ng inaasahan.
Kabuowan

Mga orang nin ampamotbot at dinamika sa bakas ran taretek sa Bolinao (H-K Pilipinas)

Main kontribusyon a pangyayadi sa paligid tamo sa dinamika sa bakas ran robot sa baybay o taretek. Say rabay nan mangyadi nin sitin tesis ket keketen nay importansa nin daedaekleng ni paninili ni gawa nin orang nin ampamotbot, bilang saya nin tagatagda sa mobilidad nan sedimento tan saya asalik sa pagkamain, pagpapaalawang, tan say abaw nin bakas sa linang nan robot sa taaw taretek sa Pilipinas. Say espesipikong importansya nan sitin pagaadal ket pigaw maipakit a spatial nin distribusyon nin pamabayoy nin bakas nin saray orang nin ampamotbot sa sayan siltation gradient tan say epeko nan siti sa vertical nin kabistawan sa kama nan sedimento, tan masukat a ugali nan ampangubot nin orang a alpheid, tan para matandaan a epeko nin anted nin panabon tan pangalap sa bulong sa pardon nin pamatubo nin dominanten robot sa baybay Thalassia hemprichii Ehrenberg (Ascherson).

Say adapan obot tan patiagn nan sedimento ket kasabyan sa linang tan manikoneksyon ra sa orang caridean nin Alpheus macellarius, Chace, 1988, o sa mas alaki tan mas ararem mamotbot a klase nan Thalassinidea, itaw sa linang nin protektado sa daluyon ket mas pirmi nin alaki a patiagn kompara sa konran nakaliwa nin linang; mas pirmi et a ubot tan tumpok nin sedimento nin gawa nan orang nan orang sa linang nin malinaw kompara sa malabo nin ranom. Sa kabuowan gawa nan A. macellarius ket nadiskubre ran bas abaw diyan sa gawa nan orang nin thalassinidean, sa kabuowan, tan say distribusyon ran orang alpheid ket karamiwan limitado tamo sa latag nan buyangin nin kaugnay tan sihinyan nan A. macellarius ket sumakop na 15 ± 2% nan linang (sa eskaldon kabawan na 102 ± 5 sa barang 100 m², cf. retrato sa pabalat) bale say tumpok nan buyangin nin orang thalassinidean ket makit sara sa 5 ± 1% (sa kabawan nin 52 ± 7 bawat 100 m²). Sihinyan ran orang nin ampangubot sa ambo pareho nin praan a vertikal; nin katangian nan sedimento – nialis nan A. macellarius a alakin parte nin alalakin butil sa 10 cm rabaw, bale si orang a thalassinidean ket pinikakalamo moy pinon butil mangibwat sa 10 pakayupa anggan 20 cm nan sedimento, tan nagtumpok yaet nin organiko nin material. Wanin man, saray ruwa nin klase tan orang ket ampat makayupa saran in nitrogeno nan sedimento ni 20-73% sa babo nin saray tan 4-46% sa rarem nin sobra sa 10 cm.

Base sa aktuwal nin obserbasyon sya in iti sa babo gawa nan A. macellarius, saray orang ket ampamakit saran in aktibong pagrebase nan sedimento tan mataleg nin pangalap nin ulo nin taretek sa linang nin malinaw a ranom sa tiyempon mamot. Sa gawa ran orang saw anti nin aktibidades ket 12% tamo a aktibon odas tan sara ket itaw sara sa ubot ra sa butal nin bawat awro. Sa tiyempon rapek, mankaglata a iti sa babo nin gawa ra nin kai kumayupa sa 34% tan say odas ra sa rarem ubot ra ket umatagay nin 5% bilang epeko nn siti. Kasabayan, kaya nan A. macellarius magrebase nin ~300 g DW (tuyo nin timbang) nin sedimento bawat awro (o 112 kg bawat taon), tan mangalap nin 0.8 g DW nin bawat awro (o 291.3 g bawat taon). Importante tan dapat biyan alang-alang a kalkuladong kapaspasan nin pagrebase sa sedimento (0.8 anggan 1.5 kg bawat 1 m² bawat awro), tan say kapaspasan nin pangalap nan bulong ket nankumatawan namaet sa katamtaman.
herbivory (0.4 anggan 2.3 g bawat 1 m² bawat awro), katumbas nan 12 anggan 42% nan produksyon nin bulong.

Saraytin obserbasyon sa laboratoryo nin nag-adal sa papel nin klase nin sedimento – buyangin, matupa nin buyangin, tan mabuyangin nin tupa – sa gawa nan A. macellarius ket man-ipaket nan timmarana tempor a pamumutbot ran orang sa odas nin magkamain saran in kontak sa substrate. Sa substrate nin buyangin, nangyadi nin masakbay a pag-adl nan orang (main unan ubot na sa loob nin ruway odas) sa kabila nin maseseg ran pang-ubot, tan nagawa ran anron ubot. Naglatan a pangubot ran orang ran talainan nin nakit a pikadaw ra mayadi a ikaliman linggo nan obserbasyon. Makit ni maong a mangangan ra, muna a pangan nin partikel, matalag a pangan ran in suspensyon, tan sa pangangangngat ran bulong nan tarektek o robot baya.bay. Say gawa ran in pangungubot, panglinis ran in lalaman ra, tan pag ikot-ikot ra ket madlaw sa awro balè say pamamasyar tan pangan ra ket umteng anggan yabi. Balè, say pangungubot ra ket mas pirmi sa mabuyangin diyan sa ruwa et nin sakalakon substrate. Sa kabuowan, say malumbo tan ma-carbonate nin buyangin sedimento, kalamo sa pagbilaan nin makubpal nin tarektek, ket main mas atagay nin suporta sa gawa ran pangungubot nin A. macellarius tan wanin et a naobserbawan nin mas atagay nin kabawan ra sa lugar nin wanta sa aktuwal nin kaligiran.

Say serye nin manipulatibong eksperimento nauna sa robot baybay nin T. hemprichii ket nami nin patunay sakasaw o kai pag-inda ran usbong nan tanaman sa daekleng nin paninili nan amangubot a orang. Say minsanan nin kasrep sa ubot sa eteng nin kai kumayupa sa 14 awro ket makapangkayat nin paspas a pagtubo nin bulong sa usbong nin iti sa apex, wanin man say pamumutol sa bulong tan say kombinasyon nin man-gaw en sa eksperimento ket main minimum a epekto sa katubo nin bulong o sa suwi na. Nalampasan ran lamang nin binhi a manabo nin bulong bale sentitibo sarayti sa pagkatabon ra sa ubot – kai sara guminwa nin sakalako sa pagtubo ran binhi, no kai pamumutol tamo, balè say katubo ket tuloy et a kumayupa bana sa pagkatabon, bukod et yayti o karngan sa pamumutol. Kai makaimpluwensya a eksklusyon nin saray aktibidades nan orang sa kapaspasan nin katubo nin bulong ran matua nin usbong. Siti tamo si kabawan nan Halophila a nagpayaman, particular mayadi a 21 linggo sa loob nan 13 bulan eteng nn eksperimento, tan saray kapwa katubo ran T. hemprichii tan kabawan nin usbong nin raruma nin species nan robot-baybay o tarektek ket namakit nin maksaw nin pisili-sili nin temporal tulad nin man-asahan.

Sa adanin irgo, naipakit nn tesis nin siti a say ruwa nin klase nin amangubot a orang – say alpheid tan thalassinidean – nin pirmin makit sa linang ran taretek, ket magwa ran magkakakalamo nin abaw sedimento tan mami nin importanten epekto sa depth gradient nan organikong material, kalakian nan butil, tan nitrogeno. Bale, main mahigpit a kaugnayan ran orang alpheid sa taretek, bilang nin pangangan ra sa sayti tan say panglat nin 12 anggan 42% nin primara produksyon, kai ra markadon mankaapektuwan a establecido tan clonal nin lainan ran robot baybay o taretek. Sa posiblen maapektuwan sarayti ket say pangalap nin bikoy tan binhi sa negatibo nin pamamaraan, bale magwa nin kasa nin grabe o duka nin epekto sa establecido kaligiran nan pagbaliwan nin saraytin orang.
About the Author

Hildie Maria Estacio Nacorda was born on 20 April 1966 in Lucena City (Quezon), The Philippines. She finished secondary school in 1983 at the Quezon National High School and then pursued a degree in Fisheries (major in Inland Fisheries) at the University of the Philippines in the Visayas (UPV). In 1987, she worked as a research assistant at the UPV College of Fisheries–Institute of Fisheries Development and Research (IFDR) and then as research associate at the Marine Science Institute (MSI) from 1988 to 1996 for a number of soft bottom community studies led by Prof. Helen Yap. Her M.Sc. in Marine Biology was granted by MSI–University of the Philippines in Dili man in 1996, with a thesis titled “Macroinfaunal communities of a tropical sandy reef flat”, which was based on research work carried out under the framework of the ASEAN-Australia Project on “Living Coastal Resources”. In 1997, WOTRO (Netherlands Foundation for the Advancement of Tropical Research) awarded her a fellowship grant to pursue PhD research under Dr. ir. Jan Vermaat on the project “Effects of burrowing crustaceans on sediment and seagrass dynamics along a silation gradient” (WB84-413), which is a sandwich scheme in Environmental Science and Technology at the UNESCO-IHE. This PhD thesis integrates several studies that assessed the impact of burrowing shrimps on seagrass dynamics in shallow-water meadows.

PUBLICATIONS


*Front cover:*
Puerto Princesa City, Palawan, Philippines – aerial photo of the seagrass meadow along the coast of Honda Bay, showing the extent of biological disturbance (as sand gaps/ discontinuities).
(Photo credit: B.S. Albasin)
The persistence of seagrass meadows depends on vegetation processes and the plants’ continuous response to various disturbances. Disturbance events cause discontinuities in the landscape (because the plants get dislodged) and affect vegetation processes as a negative response to sediment redistributions, eutrophication, and light reduction. In benign seagrass environments where biological disturbance is prominent, discontinuities in the landscape are also conspicuous though small, e.g., those caused by burrowing shrimps. Their bioturbation is known to affect plant dynamics, seagrass patch expansion, the benthos, processes at the sediment-water interface, and the export of organic matter.

This study examined the role of small-scale disturbance by burrowing shrimps and its interaction with seagrass performance against a changing background of anthropogenically altered sediment dynamics. It established that the two types of burrowing shrimps – the alpheids and thalassinideans – both common in the seagrass beds, redistribute considerable quantities of sediment with significant substrate effects on depth gradients of organic matter, grain size, and nitrogen. The alpheids have a tight connection to the seagrass, i.e., they feed on it removing about 12 to 42% of primary production, but these do not necessarily affect the established clonal stands. The shrimps potentially deter seed and seedling growth and recruitment through burial, but this probably does not have a severe impact on the established stands that these shrimps inhabit.