

The role of
***Neaxius acanthus* (Thalassinidea: Strahlaxiidae) and its burrows**
in a tropical seagrass meadow, with some remarks on
***Corallianassa coutierei* (Thalassinidea: Callianassidae)**

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Meinen Eltern (wem sonst...)

Abstract	6
Zusammenfassung	8
Abstrak	10
Abbreviations	12
1 Introduction	13
1.1 Thalassinidean shrimp	13
1.1.1 Taxonomy	13
1.1.2 Morphology	13
1.1.3 Distribution	15
1.1.4 Ecology	16
1.2 Outline of the thesis	21
2 Material and methods	23
2.1 General remarks	23
2.2 Study area	23
2.2.1 The Spermonde Archipelago	23
2.2.2 Bone Batang island	25
2.3 Study object	28
2.3.1 The burrowing shrimp <i>Neaxius acanthus</i> and <i>Corallianassa coutierei</i>	28
2.4 The monitoring of burrow openings of <i>Neaxius acanthus</i> in permanent transects	29
2.5 Burrows of driftcatching thalassinideans in the seagrass bed	29
2.5.1 <i>In-situ</i> polyester resin casting of thalassinidean burrows in the seagrass bed	29
2.5.2 The burrow lining of <i>Neaxius acanthus</i> and <i>Corallianassa coutierei</i>	30
2.5.3 Burrow water properties for <i>Neaxius acanthus</i>	31
2.6 Morphometric properties and individual weight in <i>Neaxius acanthus</i>	34
2.7 Observations of the behaviour of <i>Neaxius acanthus</i>	35
2.7.1 <i>In-situ</i> observation of <i>Neaxius acanthus</i> in the burrow entrance	35
2.7.2 Observation of <i>Neaxius acanthus</i> in aquaria	36
2.7.3 Quantification of a potential grazing effect of <i>Neaxius acanthus</i> on seagrass	38
2.7.4 Burrow openings of <i>Neaxius acanthus</i> as detritus traps	38

3. Results	39
3.1 The monitoring of burrow openings of <i>Neaxius acanthus</i> in permanent transects	39
3.2 Burrows of driftcatching thalassinideans in the Bone Batang seagrass meadow	41
3.2.1 The burrow structure of <i>Neaxius acanthus</i> and <i>Corallianassa coutierei</i>	41
3.2.2 The burrow lining of <i>Neaxius acanthus</i> and <i>Corallianassa coutierei</i>	48
3.2.3 Burrow water properties for <i>Neaxius acanthus</i>	50
3.3 Morphometric properties and individual weight in <i>Neaxius acanthus</i>	52
3.4 Observation of the behaviour of <i>Neaxius acanthus</i>	54
3.4.1 <i>In-situ</i>	54
3.4.2 In aquaria	54
3.4.3 Seagrass density and biomass decrease in the proximity of the opening	63
3.4.4 Burrow openings of <i>Neaxius acanthus</i> as traps for leaf detritus	63
3.5 General observations	63
4 Discussion	66
4.1 Permanent transects	66
4.1.1 The population density of <i>Neaxius acanthus</i> in relation to seagrass cover	66
4.1.2 Population composition, growth and recruitment for <i>Neaxius acanthus</i>	68
4.1.3 Residency and states of thalassinidean burrows in permanent transects	69
4.2 The burrows of <i>Neaxius acanthus</i> and <i>Corallianassa coutierei</i>	70
4.2.1 The burrow structure of <i>Neaxius acanthus</i> and <i>Corallianassa coutierei</i>	70
4.2.2 Commensals in burrows of <i>Neaxius acanthus</i>	71
4.2.3 The burrow lining of <i>Neaxius acanthus</i> and <i>Corallianassa coutierei</i>	73
4.2.4 Abiotic factors in water from burrows of <i>Neaxius acanthus</i>	74
4.4 Behaviour	76
4.4.1 The intake of seagrass detritus into burrows of <i>Neaxius acanthus</i>	76
4.4.2 The behavioural properties of <i>Neaxius acanthus</i>	77
4.4.3 The impact of <i>Neaxius acanthus</i> on the seagrass surrounding its burrow opening	79
4.5 General observations made in the study site	79
4.6 Outlook	80
Appendix	81
Acknowledgements	82
References	84
Eidesstattliche Erklärung	92

Abstract

In this thesis an attempt was made to describe the impact of a population of the driftcatching burrowing shrimp *Neaxius acanthus* on its habitat, a tropical seagrass meadow.

By monitoring burrow openings in permanent transects from September 2005 to January 2006 it was found that average opening density is higher in an area with dense seagrass cover compared to an area with sparse cover. Mean opening diameter was not measured in September but remained unchanged from October (18 mm) to January (18 mm). At least 75% of all burrows were found to be inhabited by pairs. Openings were found open only 65% of the time, the remaining time they are closed or replaced by small expulsion mounds.

The burrow of *N. acanthus* is made up of a vertical to sub vertical shaft leading from the single opening to a large basal chamber which is located at about 45 cm depth and contains gravel and seagrass debris. All walls with an inclination of more than 45° are covered by a thick brown lining composed of small sediment grains and fragments of multicellular plants.

The occurrence of the goby *Austrolethops wardi* as a commensal of *N. acanthus* is described for the first time. Furthermore a bivalve species, two species of tube-building polychaetes and an amphipod species were found as commensals. A palaemonid shrimp species can frequently be found in the burrow entrance. At low tide, small crabs and juvenile fish belonging to the genera *Dischistodus* and *Apogon* seek refuge in the entrance which then represents a little tidal pool.

The burrow of *Corallianassa coutierei*, a co-occurring driftcatching callianassid, resembles a deep U. One opening is always non-functional and blocked with sediment. A chamber containing coarse sediment was found halfway down the functional shaft, at the deepest point several chambers filled with gravel and seagrass debris branch off. The walls are covered by a thin lining composed of fine sediment grains.

Water content, organic content and the silt fraction are higher in the burrow lining of both species compared to the surrounding sediment. This effect is more marked for *N. acanthus*.

Water quality measurements in the water column, sediment pore water from depths between 1.5 and 45 cm and inside burrows of *N. acanthus* showed that the ammonium concentration in the burrows is comparable to the values measured at 45 cm sediment depth. Reactive phosphate concentrations in the burrow are much higher than measured elsewhere. The values measured for oxygen and pH are in between those measured in the sediment and the water column.

Individuals of *N. acanthus* show a sexual dimorphism in the major cheliped. Burrow diameter and carapace length are correlated. The relation between carapace length and WW, DW and AFDW is different for males, females carrying eggs and females without eggs.

Records of the behaviour of animals in the burrow entrance were made *in-situ*. The entrance was found to be always “guarded” by one of the inhabitants. On average 1.920 g DW opening⁻¹ d⁻¹ of leaf detritus was caught by the shrimp observed. This represents more than 50% of the primary production measured in the same area.

The observation of the behaviour of shrimp in narrow aquaria filled with sediment showed that during burrow construction and maintenance only little sediment is brought to the surface. Small grains are sieved out of sediment which is stirred up with the anterior appendages. These grains are then mixed with a sticky substance secreted by the animals and tamped into the burrow walls. Additional fine sediment is gained by mining in the surroundings of the basal chamber.

By the definition of five behavioural classes containing 12 behavioural states it could be shown that the animals spend most time on construction, followed by resting, locomotion, grooming and feeding. No differences were found between day and night time activity. Offered seagrass leaves were cut into pieces and later worked into the burrow walls.

Shrimp were observed to be highly aggressive towards individuals of the same gender but would immediately accept a new burrow inmate of the opposite gender.

In cores taken around burrow openings of *N. acanthus* seagrass shoot density and biomass was found to decrease by about 50% compared to cores taken away from openings.

By deploying litter traps the passive intake of leaf detritus into burrows of *N. acanthus* could be quantified to be about 1.386 g DW opening⁻¹ d⁻¹. Shrimp activity therefore increases the intake by 39%.

Zusammenfassung

Diese Arbeit stellt einen Versuch dar, den Einfluss einer Population von *Neaxius acanthus*, einem Driftmaterial fangenden grabenden Krebs auf sein Habitat, eine tropische Seegraswiese zu beschreiben.

Durch die Überwachung von Bautenöffnungen in permanenten Transekten von September 2005 bis Januar 2006 konnte gezeigt werden, dass die Anzahl der Bautenöffnungen in einem Gebiet mit dichter Seegrasbedeckung grösser ist als in einem Gebiet mit spärlicher Bedeckung. Der durchschnittliche Öffnungsdurchmesser wurde im September nicht erfasst, blieb aber von Oktober (18 mm) bis Januar (18 mm) unverändert. Mindestens 75% der Bauten werden von Paaren bewohnt. Die Öffnungen waren zu 65% offen, ansonsten waren sie verschlossen oder durch Sedimentauswurfshügel ersetzt.

Der Bau von *N. acanthus* besteht aus einem senkrechten bis schrägen Schaft, der nach unten in eine grosse, mit Kies und Seegras gefüllte Kammer mündet. Alle Wände mit einer Steigung von mehr als 45° sind mit einer dicken braunen Auskleidung aus kleinen Sedimentkörnern und Bruchstücken mehrzelliger Pflanzen bedeckt.

Das Auftreten der Grundel *Austrolethops wardi* als Kommensale von *N. acanthus* wird das erste Mal beschrieben. Weiterhin wurden eine Muschelart, zwei Arten von röhrenbildenden Polychaeten und eine Amphipodenart als Kommensalen gefunden. Eine palaemonide Garnele kann ebenfalls regelmässig in der Bautenöffnung gefunden werden. Bei Niedrigwasser suchen kleine Krabbenarten und juvenile Fische der Gattungen *Dischistodus* und *Apogon* in der Bautenöffnung, welche dann einen kleinen Gezeitentümpel darstellt, Schutz.

Der Bau von *Corallianassa coutierei*, einem mit *N. acanthus* koexistierenden Driftmaterial fangenden Callianassiden, gleicht einem tiefen U. Eine der beiden Öffnungen ist immer nichtfunktional und mit Sediment verschlossen. Auf halber Höhe des funktionalen Schaftes liegt eine mit Kies gefüllte Kammer, am tiefsten Punkt zweigen mehrere mit Kies und Seegras gefüllte Kammern ab. Die Wände sind mit einer dünnen Auskleidung aus feinen Sedimentkörnern bedeckt.

Wassergehalt, organischer Gehalt und die Schlickfraktion sind grösser in den Bautenauskleidungen beider Arten als im umgebenden Sediment. Dieser Effekt ist deutlicher für *N. acanthus*.

Messungen der Wasserqualität in der Wassersäule, im Porenwasser des Sediments in Tiefen von 1,5 bis 45 cm und in Bauten von *N. acanthus* zeigten, dass die Ammoniakkonzentration in den Bauten mit der des Sediments in einer Tiefe von 45 cm vergleichbar ist.

Die Konzentration an reaktivem Phosphat in den Bauten ist höher als anderswo. Die für Sauerstoff und pH gemessenen Werte liegen zwischen denjenigen für Sediment und Wassersäule.

Individuen von *N. acanthus* zeigen einen Sexualdimorphismus der grösseren Schere. Es gibt eine Korrelation zwischen Bautendurchmesser und Carapaxlänge. Die Korrelation zwischen Carapaxlänge und Nassgewicht, Trockengewicht und aschefreiem Trockengewicht ist für Männchen, eiertragende Weibchen und Weibchen ohne Eier verschieden.

Das Verhalten der Tiere im Bauteneingang wurde *in-situ* beobachtet. Der Eingang wurde immer von einem der Bewohner „bewacht“. Durchschnittlich 1,920 g Trockengewicht Öffnung⁻¹ d⁻¹ an Blattdetritus wurden von den beobachteten Krebsen gefangen. Das entspricht mehr als 50% der Primärproduktion in diesem Gebiet.

Bei der Beobachtung des Verhaltens von Tieren in schmalen sedimentgefüllten Aquarien konnte festgestellt werden, dass während der Konstruktion und Instandhaltung des Baues nur wenig Sediment an die Oberfläche gebracht wird. Kleine Körner werden aus Sediment, welches mit den vorderen Fortsätzen aufgewirbelt wird, ausgesiebt. Diese Körner werden dann mit einer klebrigen Substanz, die von den Tieren ausgeschieden wird, vermischt und in die Wand gestopft. Zusätzlich wird feines Sediment in der Umgebung der unteren Kammer abgebaut.

Durch die Definition von fünf Verhaltensklassen in denen 12 Verhaltenszustände enthalten sind wurde gezeigt, dass die Tiere die meiste Zeit mit Konstruktion verbringen, gefolgt von Inaktivität, Fortbewegung, Putzen und Fressen. Es wurde kein Unterschied in der Tag- und Nachtaktivität gefunden. Angebotenen Seegrassblätter wurden zerrissen und später in die Wand eingearbeitet.

Die Krebse verhalten sich höchst aggressiv gegenüber Geschlechtsgenossen, neue Baubewohner des anderen Geschlechtes werden aber sofort akzeptiert.

Um Bautenöffnungen von *N. acanthus* herum wurde eine Abnahme von Seegrassprossdichte und Seegrassbiomasse um etwa 50% festgestellt.

Durch den Einsatz von Detritusfallen wurde der passive Eintrag von Detritus in Bauten von *N. acanthus* auf etwa 1,386 g Trockengewicht Öffnung⁻¹ d⁻¹ geschätzt. Die Aktivität der Krebse erhöht den Eintrag demnach um 39%.

Abstrak

Dalam thesis ini diteliti pengaruh populasi udang *Neaxius acanthus* yang berliang di padang lamun dengan cara makan *driftcatching* terhadap habitatnya.

Dengan metode transek permanen dipantau 188 bukaan liang di 9 transek mulai bulan September 2005 s/d bulan Januari 2006 dan ditemukan bahwa rata-rata kepadatan bukaan di daerah penutupan lamun yang besar lebih tinggi dibandingkan dengan penutupan lamun kecil, yaitu 3 bukaan m⁻² dibandingkan 1 bukaan m⁻². Diameter rata-rata bukaan tidak diukur pada bulan September tetapi tidak berubah antara bulan Oktober (18 mm) dan bulan Januari (18 mm). Paling sedikit 75% dari jumlah liang dihuni oleh udang-udang secara berpasangan. Liang-liang ditemukan terbuka 65% dari waktunya dan sisanya ditutupi sedimen atau diganti dengan bukit-bukit kecil (*expulsion mounds*).

Liang-liang dari spesies *N. acanthus* terdiri dari terowongan vertikal (atau miring sedikit) dengan kedalaman kurang lebih 45cm yang menghubungkan permukaan sedimen dengan goa tinggal yang berisi kerikil karang dan serasah lamun. Semua dinding terowongan dengan inklinasi diatas 45° diselimuti dengan semacam lapisan tebal berwarna cokelat yang terbuat dari butir-butir sedimen halus yang dicampur dengan fragmen-fragmen tumbuhan multiseluler. Komensalisme antara ikan gobi *Austrolethops wardi* dan *N. acanthus* pertama kali dipublikasikan di dalam tesis ini. Selain itu satu spesies kerang, dua spesies cacing tabung (Polychaetes) dan satu spesies amphipod ditemukan hidup secara komensalis. Spesies udang palaemonid juga sering ditemukan di mulut liang. Pada pasang surut kepiting dan ikan-ikan kecil dari genus *Dischistodus* dan *Apogon* mencari perlindungan di muka bukaan liang-liang yang pada waktu itu berfungsi sebagai kolam pasang surut kecil.

Spesies simpatis *Corallianassa coutierei* yang juga hidup dari menangkap serasah lamun yang terapung atau melayang di dalam air memiliki liang yang mirip dengan huruf 'U'. Salah satu bukaannya selalu tertutup dengan sedimen. Pada setengah jalan dari terowongan yang sedang berfungsi ditemukan goa berisi sedimen kasar dan pada bagian paling bawah dari terowongan terdapat cabang-cabang yang menuju ke beberapa goa yang berisi kerikil karang dan fragmen lamun. Seluruh bagian dinding liang dan goa diselimuti dengan lapisan tipis dari butiran-butiran sedimen halus.

Kandungan air, bahan organik dan sedimen halus lebih tinggi pada lapisan dinding liang dari kedua spesies tersebut dibandingkan dengan sedimen disekitarnya, tetapi efek tersebut lebih jelas pada spesies *N. acanthus*.

Kandungan amonium dari air yang terdapat dalam liang-liang *N. acanthus* memiliki jumlah yang hampir sama dengan kandungan yang terdapat dari sedimen disekitarnya sedalam 1,5 sampai 45 cm. Kandungan fosfat jauh lebih tinggi di dalam liang-liang. Kandungan oksigen dan nilai pH di dalam liang lebih rendah dibandingkan dengan perairan disekitarnya, tetapi lebih tinggi daripada kandungan oksigen dan nilai pH yang terdapat di dalam sedimen.

Jantan dan betina dari spesies *N. acanthus* dapat dibedakan dari perbedaan bentuk (dimorfisme) capitnya. Ditemukan korelasi antara diameter liang dengan panjang karapaks. Korelasi antara panjang karapaks, berat basah, berat kering dan berat dari analisis abu ditemukan adanya perbedaan untuk jantan, betina dan betina yang sedang bertelur.

Perilaku dari hewan-hewan yang terdapat di mulut liang dipantau secara *in situ*. Pada tiap-tiap bukaan liang ditemukan selalu dijaga salah satu penghuninya. Udang jantan ditemukan menghabiskan waktu lebih banyak untuk kegiatan tersebut dibandingkan dengan udang betina. Rata-rata $1,920\text{g DW bukaan}^{-1}\text{d}^{-1}$ detritus lamun ditangkap oleh seekor udang. Hal ini menunjukkan lebih dari 50% produksi primer dari lamun yang telah diukur pada daerah yang sama.

Di akuarium sempit berisi sedimen, telah diamati bahwa untuk penggalian dan perawatan sebuah liang jumlah sedimen yang digali dan dibawa ke permukaan hanya sedikit. Butir-butir sedimen halus disaring dari sedimen yang diaduk dengan apendiks-apendiks anterior kemudian dicampur dengan sekret yang lengket untuk selanjutnya ditempelkan di dinding-dinding liangnya. Selain itu, udang-udang tersebut juga mencari sedimen halus tambahan secara aktif dari sekitar bagian bawah dari goanya.

12 kategori kegiatan ditetapkan dan waktu yang dihabiskan untuk masing-masingnya diukur. Dengan peringkasan kegiatan-kegiatan tersebut kedalam 5 kategori utama bisa ditemukan bahwa waktu yang dihabiskan oleh hewan-hewan itu paling banyak untuk konstruksi, kemudian istirahat, lokomosi, *grooming* dan makan.

Eksperimen paksaan dilakukan dengan menambah jumlah udang ke dalam akuarium. Udang-udang tersebut ternyata agresif sekali terhadap individu yang berjenis kelamin sama tetapi segera menerima udang dari jenis kelamin lainnya.

Kepadatan tegakan dan biomassa lamun di sekitar liang-liang *N. acanthus* ditemukan berkurang sekitar 50% dibandingkan dengan sampel-sampel lamun yang tidak terpengaruh. Dengan metode jebakan serasah (*litter traps*) ditemukan bahwa jumlah detritus daun lamun yang memasuki liang-liang spesies *N. acanthus* secara pasif kurang-lebih $1,386\text{ gDW bukaan}^{-1}\text{d}^{-1}$; Dengan demikian, pemasukan detritus secara aktif bertambah hanya 39% dari total detritus yang masuk.

Abbreviations

AFDW	ash-free dry weight
approx.	approximately
cm	centimetre
comm.	communication
conc.	concentrated
d	day
°C	degrees Celsius
DI	deionised water
DW	dry weight
Fig.	Figure
h	hour
l	liter
lab	laboratory
Mxp.	Maxilliped
m	metre
mm	millimetre
min	minute
obs.	observation
%	per cent
‰	per mille
pers.	personal
pic.	picture
s	second
Tab.	Table
WW	wet weight
USP	unspoiled

1 Introduction

1.1 Thalassinidean shrimp

1.1.1 Taxonomy

The Thalassinidea (Latreille 1831), a group of shrimp- and lobsterlike decapods, are mainly burrowers, only some live in corals or sponges (Dworschak 2000). A total number of about 556 species (Dworschak 2005) is known. Common names include shrimp lobsters, mud lobsters, mud shrimp and ghost shrimp.

Their position within Decapoda as a sister taxon to Anomura + Brachyura as proposed by Scholtz & Richter (1995) is confirmed by Ahyong & O'Meally (2004).

The monophyly of a taxon Thalassinidea has often been disputed but is supported by the most recent and most comprehensive morphological and molecular cladistic analysis (Poore 1994 (morphological), Tudge & Cunningham 2002 (molecular), Ahyong & O'Meally 2004 (morphological and molecular)). Morphologically, it is based largely on a setose lower margin of pereopod 2 (Poore 1994).

Internal relationships are likewise disputed. Three “superfamilies” are recognized by Poore (1994): Thalassinoidae and Callianassoidea, more closely related to each other than Axioidea. Callianassoidea sensu Poore (1994) contain Callianassidae, Upogebiidae and Laomediidae. More recent studies produced different results, with Strahlaxiidae (Poore 1994) (as representatives of Axioidea) being placed as a sister taxon to Callianassidae on the first of two branches. On the second branch, Laomediidae and Thalassinidae, the single family within Poore's Thalassinoidae, are more closely related to each other than to Upogebiidae (Tudge & Cunningham 2002, Ahyong 2004 & O'Meally). A recent study on the morphology of the gastric mill (Sakai 2005) reflects these findings.

1.1.2 Morphology

Poore (1994) contends that “the primitive thalassinidean had the general habitus shown by modern axiids, upogebiids, laomediids or thalassinids rather than by callianassids”. The latter are shown to have more morphological adaptations to their burrowing lifestyle.

The comparison of the habitus of *Neaxius acanthus* (Milne-Edwards 1878) (Strahlaxiidae) and *Corallianassa coutierei* (Nobili 1904) (Callianassidae) shall give an impression of the variations encountered within Thalassinidea, their taxonomic placement is given in the appendix:

The lobsterlike habitus of *N. acanthus* is a good example for the more basal type (Fig. 1 A). The rostrum is well developed, the carapace rigid and almost as long as the pleon, the animals are fully pigmented, have round chelae which cannot be positioned besides the carapace and a digitiform propodus and dactylus of Mxp. 3 and pereopods 2 to 5.

C. coutierei represents the more specialised type (Fig. 1 B). The rostrum is inconspicuous or fully reduced, the body elongate, the carapace short with hinged lateral plates which facilitates the ventilation and cleaning of the gills, the animals show little or no pigmentation, have laterally compressed chelae which can be positioned besides the carapace inside the burrow and laterally compressed distal segments of Mxp. 3 and pereopods 2 to 5.

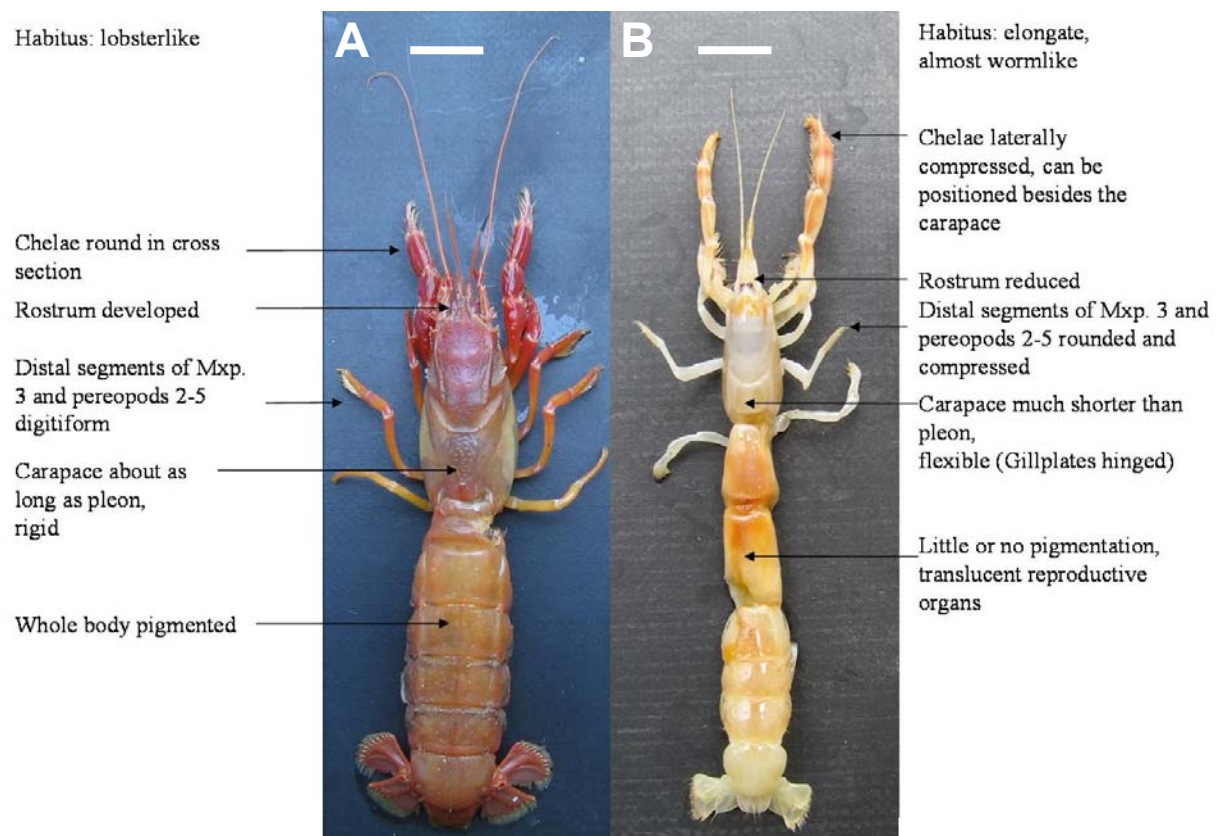


Fig. 1: Female specimen of *Neaxius acanthus* (A) and *Corallianassa coutierei* (B), showing general lobsterlike traits and their modifications as morphological adaptations to a burrowing lifestyle, respectively. Scale bars are 1 cm.

1.1.3 Distribution

Thalassinidean shrimp occur worldwide in marine and brackish waters, with higher species numbers in low latitudes than in high latitudes (Dworschak 2000). Especially Upogebiidae, Thalassinidae, Strahlaxiidae and Callianassidae almost exclusively live in intertidal to very shallow waters (Dworschak 2000).

The tropical strahlaxiid *Neaxius acanthus* has been reported from New Caledonia (*Axia acanthus* in Milne-Edwards 1878), Papua New Guinea (*Eiconaxius taliliensis* in Borradaile 1900 and *Eiconaxius acanthus* in De Man 1896), Indonesia (*Eiconaxius acanthus* in De Man 1896), the Mariana islands (Holthuis 1953), Mauritius (*Axius (Neaxius) acanthus* var. *mauritanus* in Bouvier 1915), the Comores (*Axius acanthus* var. *mauritanus* in Fourmanoir 1955), Northern Australia (*Axius (Neaxius) acanthus* in Poore & Griffin 1979), Taiwan (Kensley 2000), Japan (Sakai 2005), the Philippines (Dworschak, pers. comm.) and probably also the Seychelles (*Neaxius* sp. in Farrow 1971), suggesting a typical indopacific distribution (Fig. 2). Mukai & Sakai (1992) state that *N. acanthus* var. *mauritanus* is not distinguishable from *N. acanthus*.

Corallianassa coutierei is known from Djibouti, Hawaii, the Philippines, Tahiti, Fiji island, the Maldives, Indonesia and Madagascar (Sakai 1999) as well as from the Marquesas islands (Ngoc-Ho 2005) (Fig. 2). Nobili (1904) first described the species as *Callianassa coutierei*, while de Man (1905) described its junior synonym *Callianassa placida*. De Saint Laurent (1973) and de Saint Laurent & Le Loeuff (1979) placed the two species under *Callichirus*. Manning (1987) erected the new genus *Corallianassa* which included both species. In 1992 Manning established the new taxon *Corallichirus*, but only *Callichirus placidus* was placed in it. Sakai (1999) considered both species as synonyms and assigned them to the genus *Glypturus* (Stimpson 1866). Whereas Ngoc-Ho (2005) accepts the synonymy of *Callianassa coutierei* and *Callianassa placida*, Tudge, Poore & Lemaitre (2000), Ngoc-Ho (2005) and Dworschak (pers. comm.) reject the placement in *Glypturus*.

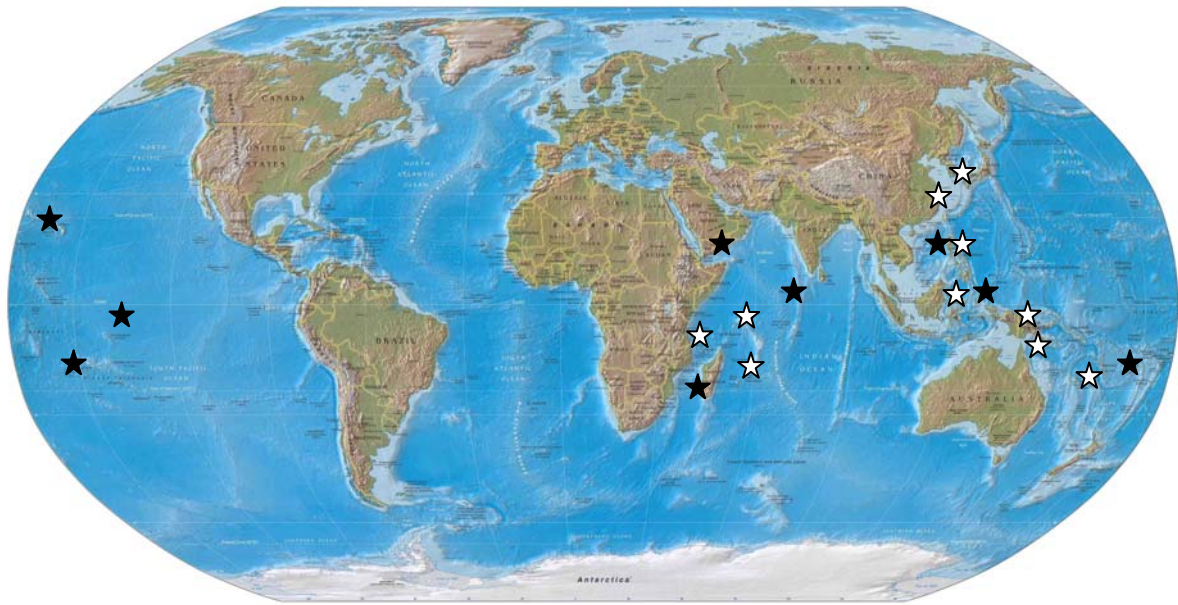


Fig. 2: Physical map of the world. White asterisks mark reports of *Neaxius acanthus*, whereas black asterisks represent *Corallianassa coutierei* (after www.lib.utexas.edu).

1.1.4 Ecology

The self-constructed burrows are an intrinsic part of the life of thalassinidean shrimp. By the construction of burrow casts using polyester or epoxy resins it has been possible to understand many aspects of the ecology of these cryptic animals. An overview on the burrow architecture of various members of the taxon is given by Dworschak (1983), Griffis & Suchanek (1991) and Nickell & Atkinson (1995).

I Upogebiidae:

Suspension feeders like Upogebiidae construct simple U- or Y-shaped burrows without big sediment expulsion mounds (Fig. 3A). The shallow burrows provide efficient paths for an unidirectional filtration flow (Griffis & Suchanek 1991).

II Axiidae, with special regard to the state of knowledge on *Neaxius* spp.:

Axiidae generally seem to construct simple vertical shafts with only one opening and, due to low sediment reworking rates, do not produce surface mounds in shallow water sedimentary areas. So far, they have attracted little attention (Buchanan 1963 on *Calocaris macandreae*, Pemberton, Risk & Buckley 1976 on *Axius serratus*, burrows of this species reach at least 2,5 m down what represents the deepest bioturbation known to date). Their feeding modes in general remain enigmatic, *Axiosis serratifrons* has been shown to feed on detrital seagrass (Abed-Navandi & Dworschak 2005).

In Farrow (1971) a description of the burrow morphology of *Neaxius* sp. (probably *N. acanthus* according to distribution data) in the Seychelles can be found. The burrows were found to have a single opening, followed by several swollen chambers linked by a succession of sub vertical shafts which ends in a large basal chamber at approx. 45 cm depth. A thick brown burrow lining “apparently” composed of macerated eel-grass blades is mentioned (Fig. 3B).

Besides *N. acanthus*, the taxon *Neaxius* comprises *N. glyptocercus* (von Martens 1868) with reports from Australia, *N. vivesi* (Bouvier 1895) with reports from the Gulf of California and, as recent additions, *N. frankeae* (Lemaitre 1992) from the pacific coast of Columbia and *N. trondlei* (Ngoc-Ho 2005) from the Marquesas islands.

Berill (1975) gives an account of the burrowing, aggressive and early larval behaviour of *N. vivesi*. It is noted that individuals defend their burrows against intruders but are helpless if driven out. Big burrows are inhabited by pairs.

Burrows of the same species were counted by Leija-Tristan (1994), a maximum density of 9 burrows m⁻² each of which is inhabited by a pair is given.

In Farrow (1971) the bivalve *Erycina* sp. is described as a commensal in the burrows of *Neaxius* sp. (*N. acanthus* ?), carrying individuals of the mesogastropod *Capulus* sp. as secondary commensals. *Neaxius* sp. is assumed to be a suspension feeder. The inhabitants are found to live in pairs, one of which can be seen hovering in the entrance and seizing drifting particles.

An active capture and introduction of plant debris is also reported for *N. acanthus* by Abed-Navandi, Koller & Dworschak (2005).

Mukai *et al.* provide an estimation of oxygen consumption and ammonium excretion by a population of *N. acanthus* in a Papua New Guinean seagrass bed (*Axius acanthus* in Mukai *et al.* 1989).

Notes on its morphology and quantitative characteristics can be found in Mukai & Sakai (1992).

The occurrence of *N. acanthus* on Barrang Lompo island, Spermonde Archipelago, Indonesia and their population density estimated from counts of burrow openings is briefly mentioned in Erftemeijer, Drossaert & Smekens (*Axius acanthus* in Erftemeijer, Drossaert & Smekens 1993).

In contradiction to Leija-Tristan (1994), Berill (1975) and Farrow (1971), both Mukai *et al.* (1989) and Erftemeijer, Drossaert & Smekens (1993) equate shrimp number with the number of burrow openings.

III Callianassidae, with special regard to the state of knowledge on *Corallianassa* spp.:

Many callianassidae are deposit-feeders and intersperse the sediment with a maze of tunnels and chambers to guarantee maximum sediment exploitation. The burrow is linked to the surface by a U-shaped connection. One is an inhalant and the other an exhalant opening through which fine sediment particles are pumped to the surface. This way the animals produce large sediment expulsion mounds, the inhalant opening is situated at the base of a funnel (Fig. 3C).

Due to the high sediment turnover rates of deposit-feeding callianassid species, larger grains and shells tend to accumulate in depths of about 30 to 50 cm, while the smaller fraction ends up at the surface. A bulky literature has been built up on species showing this behaviour which, in many cases, has been shown to have dramatic effects on the sedimentology and geochemistry of the seabed:

Koike & Mukai (1983) showed that burrows of *Callianassa japonica* and *Upogebia major* have about the same oxygen consumption and ammonium excretion as the surrounding sediment surface and the effects are thus doubled in a given area. Colin, Suchanek & McMurtry (1986) studied water pumping and particulate resuspension by *Callianassa* sp.. Suchanek *et al.* (1986) proved that bioturbation by *Callianassa* sp. leads to the accumulation of fine-grained sediment particles at the surface. Branch & Pringle (1987) measured that the impact of *Callianassa kraussi* on the sediment averages a 59% turnover to a depth of 30 cm

over a month. Abu-Hilal, Badran & de Vaugelas (1988) show that trace elements in the mucus-rich and metal-reacting burrow lining of *Callichirus laurae* (junior synonym of *Glypturus armatus*, see Sakai 1999) reach 85 to 250 times the concentration measured in the seagrass bed at the surface. Ziebis *et al.* (1996) give an account of the geochemical impact of the burrows of *Callianassa truncata* caused by the biopumping of oxygen and detrital particles down to 80 cm sediment depth. Rowden, Jones & Morris (1998) report on sediment resuspension by *Callianassa subterranea*, a maximum contribution to the lateral sediment transport of $7 \text{ kg m}^{-2} \text{ month}^{-1}$ is estimated. Berkenbusch & Rowden (1999) estimate sediment turnover by *Callianassa filholi* to be $96 \text{ kg DW m}^{-2} \text{ year}^{-1}$. Bird, Boon & Nichols (2000) measured higher microbial activity in the burrow lining of *Biffarius arenosus* compared to the surrounding sediment. Webb & Eyre (2004) assume that by the impact of *Trypaea australiensis* total sediment porewater exchange rates increase 5-fold compared to uninhabited sediments.

Subsequently, the whole benthic community can be markedly influenced by natural populations of callianassid thalassinideans. Examples are the detrimental effects of *Callianassa* (*Glypturus*) *acanthochirus*, *Callianassa* (*Corallianassa*) *longiventris*, *Callianassa rathbunae* and *Callianassa quadracuta* on seagrass communities (Suchanek 1983), of *Callianassa californiensis* on sedentary species (Posey 1986), of *Callianassa japonica* on polychaetes (Tamaki 1988), of *Callianassa filholi* on benthic macrofauna (Berkenbusch, Rowden & Probert 2000) and of *Callianassa californiensis* on seagrass (Dumbauld & Wyllie-Echeverria 2003).

In contrast, Harrison (1987) shows that *Callianassa californiensis* decreases in response to an expanding seagrass bed and Dittmann (1996) shows that meio- and macrofaunal densities are lower in *Callianassa australiensis* exclusion sites.

A special burrow type is constructed by the Caribbean *Corallianassa longiventris* (Milne-Edwards 1870), characterised by the absence of permanent expulsion mounds and the presence of chambers filled with seagrass debris which is actively captured by the animals at the burrow entrance (Griffis & Suchanek 1991, Dworschak, Koller & Abed-Navandi 2005). The burrow is described as a simple, deep U, between 80 and 150 cm deep with only one functional opening. Chambers branch off below the functional opening at a depth of between 14 and 52 cm and from the deepest part of the U (Dworschak, Koller & Abed-Navandi 2005) (Fig. 3D).

Abed-Navandi, Koller & Dworschak (2005), Abed-Navandi & Dworschak (2005), Dworschak & Ott (1993) and Dworschak, Koller & Abed-Navandi (2005) provide a detailed description of the food sources, nutritional ecology, burrow structure, burrowing and feeding behaviour of *C. longiventris*:

In a stable-isotope study, *C. longiventris* was shown to mainly use detrital seagrass leaves as a food source, followed in importance by the burrow wall. The content of essential amino acids was found to be higher in seagrass leaves stored in the burrow compared to surface detrital leaves. The behaviour of *C. longiventris* is shown to be strikingly similar to the one displayed by the Atlantic *Callianassa subterranea*, which is described in detail by Stamhuis *et al.* (1996).

To my knowledge, no studies on the ecology of *C. coutierei* exist so far.

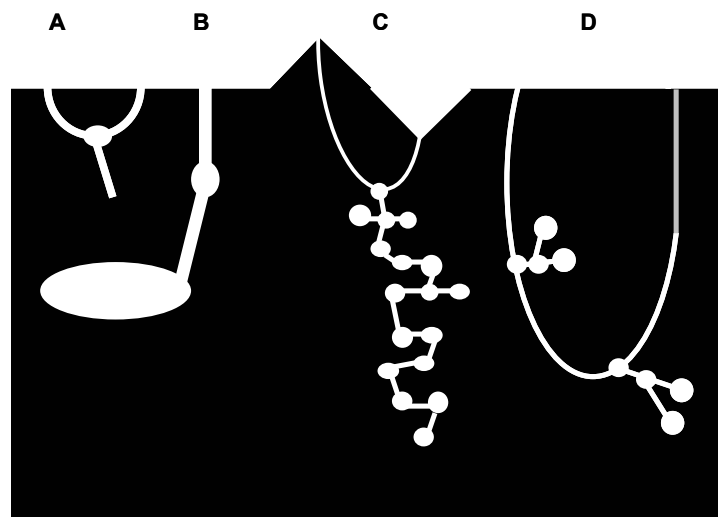


Fig. 3: Variations in burrow morphology encountered within Thalassinidea. Sketches not drawn to scale. (A) Filter feeders like Upogebiidae construct simple U- or Y-shaped burrows (B) *Neaxius* sp. as a representative of Axiidae constructs simple vertical burrows with a basal chamber (C) Deposit-feeding species like many Callianassidae intersperse the sediment with a maze of tunnels and chambers, excess sediment is pumped out of the burrow and forms an expulsion mound, an other opening lies within a funnel. (D) Driftcatching species like *Corallianassa longiventris* maintain chambers filled with seagrass debris, one opening is always non-functional and blocked with sediment. (A) after Dworschak (1983), (B) after Farrow (1971), (C) after Ziebis *et al.* (1996), (D) after Dworschak, Koller & Abed-Navandi (2005).

1.2 Outline of the thesis

In this thesis an attempt is made to describe the role of a population of *Neaxius acanthus* in its habitat, a tropical seagrass meadow.

To determine

- whether the number of burrows and individuals of *N. acanthus* depends on or influences seagrass density
- whether burrow openings of *N. acanthus* are permanent structures or change position
- the growth rate of individuals of *N. acanthus*

a number of permanent transects was set up at the study site. Monthly records of the number of burrow openings, their position, diameter and gender of inhabitant were made.

To find out about

- shape, size and inhabitants of burrows of *N. acanthus* and *Corallianassa coutierei*, a co-occurring callianassid decapod with a similar lifestyle

a number of burrows of both species was cast *in-situ* using Polyester resin.

To prove that

- water content, organic content and grain size composition are different in the burrow lining of both species compared to the surrounding sediment

these factors were analyzed.

It was assumed that

- ammonium, reactive phosphate and oxygen content as well as the pH in burrows of *N. acanthus* is different from the values measured in the pore water of the surrounding sediment and the water column

so water quality measurements had to be made.

The questions whether in *N. acanthus*

- burrow diameter and carapace length are correlated
- male and female individuals can be separated *in-situ* because of major cheliped dimorphism
- there is a relation between carapace length and weight

could be answered by measuring morphometric properties and individual weight on a number of fixated specimen.

To determine for *N. acanthus*

- the amount of floating detritus caught
- the burrowing behaviour
- differences in the behaviour at day and night time
- what happens to the detritus caught
- whether there is inter- or intrasexual aggression

observations were made *in-situ* and in narrow aquaria filled with sediment and put with live seagrass plants.

To test

- a potential grazing effect of *N. acanthus* on seagrass around the burrow entrance
- seagrass shoot density and leaf, leaf sheath and rhizome biomass were determined in cores taken around and away from burrow openings.

Finally

- the amount of floating debris falling passively into open burrows
- was estimated using detritus traps.

2 Material and methods

2.1 General remarks

The terms shrimp and prawn seem to be deliberately interchangeable, especially in a commercial and culinary context; a confinement of the word prawn to dendrobranchiate decapods seems to be reasonable to avoid confusion. Pleocyemate decapods are commonly referred to as shrimps, crabs, lobsters and crayfish. Problems arise with members of the Thalassinidea having common names as diverse as lobster shrimps (used for Axiidae), ghost shrimp and mud shrimp (used for Callinassidae and Upogebiidae, respectively) and mud lobsters (used for Thalassinidae). The species *Neaxius acanthus* is a “slow prawn”, whereas its close relative *N. glyptocercus* is the “red mud lobster” (www.marine.csiro.au/caab). In this thesis all thalassinid decapods will therefore be referred to by their scientific name or by the relatively neutral term “shrimp”.

Prior to ANOVA, data were transformed to achieve normal distribution according to the recommendations given in Sachs (1984).

2.2 Study area

2.2.1 The Spermonde Archipelago

The Spermonde Archipelago (Fig. 4) is situated in the Makassar Strait off the west coast of South Sulawesi, Indonesia. The islands lie on a broad carbonate platform and are separated from open marine settings by a discontinuous barrier reef on the western side of the shelf. The shelf depth gradually increases with distance from the main land to reach a maximum of 60 m just east of the barrier. Maximum tidal amplitude in the area is 1.2 m and sea surface temperature is 28.5°C, whereas salinity is about 33‰ (Renema 2001). The coral reefs surrounding all the islands create sheltered conditions favourable for the growth of seagrasses. About 30,000 inhabitants used to live on the 24 islands and in approx. 25 coastal villages ten years ago (Pet-Soede *et al.* 1995). Today, 5000 people live on Barrang Lompo island alone (inofficial number, Barrang Lompo local, pers. comm.).

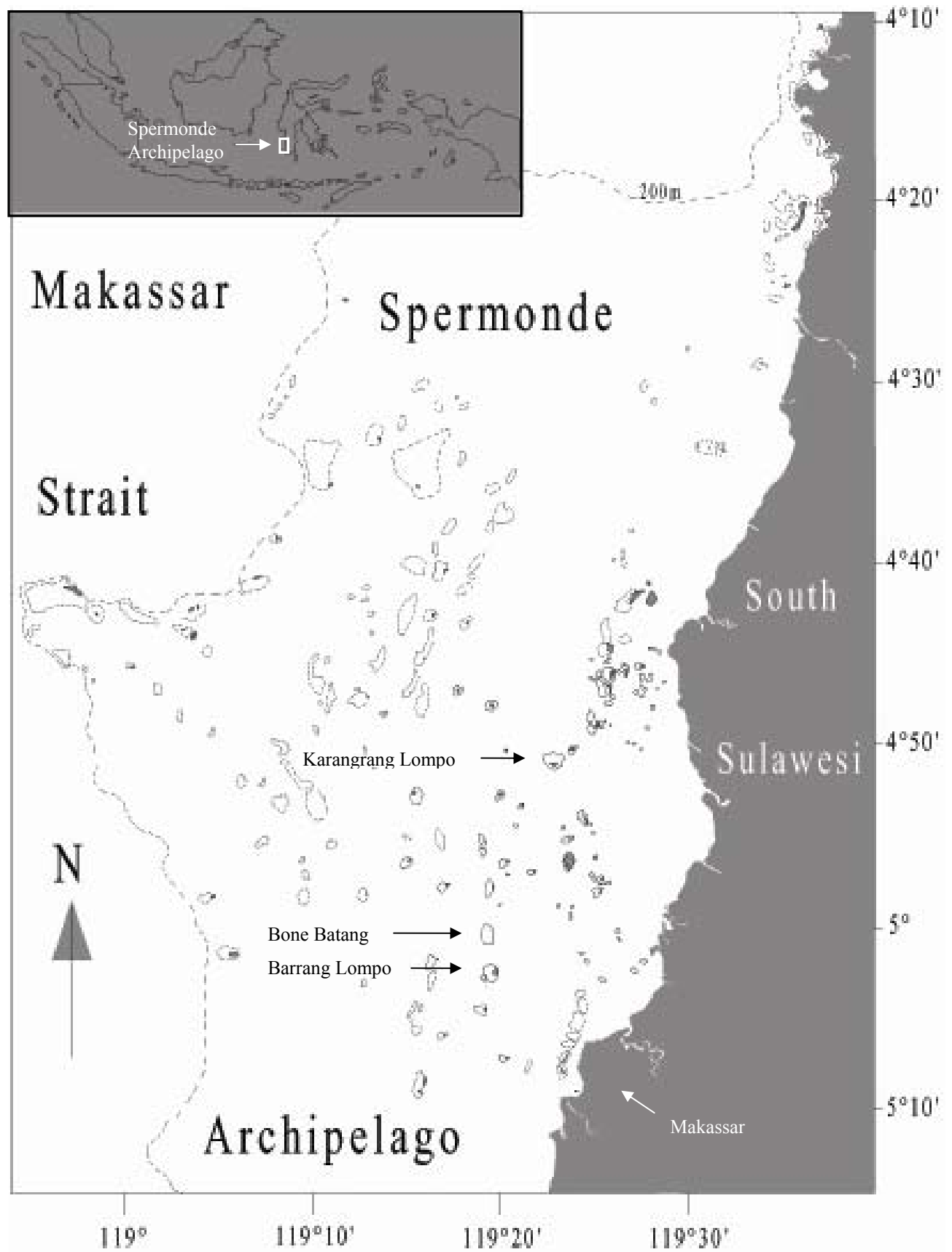


Fig. 4: The Spermonde Archipelago and its position in the Indonesian Archipelago (inset); dashed lines represent submerged reefs and the 200 m isobath, the position of some of the islands and the province capital Makassar is indicated (after Stapel (1997)).

2.2.2 Bone Batang island

Bone Batang island ($5^{\circ}1' S$, $119^{\circ}19'30''E$) (Fig. 5) is situated just east of the 30 m isobath and about 12 km to the northwest of the province capital Makassar. It is enclosed by a submerged coral reef. Bone Batang literally means “a good place to stop and eat” in Makassar language (Massang, pers. comm.), indicating that it has been used as a reliable source of seafood for a long time.



Fig. 5: Aerial view of Barrang Lompo (BL), Bone Batang (BB), Pajenekeng (P) and Gontosua (G) island. Note that Bone Batang island is lacking terrestrial vegetation (after www.advancedaquarist.com).

Although being nothing more than an unpopulated sand flat, Bone Batang is visited by several vessels daily. The activities of the visitors, most of which are fishermen from nearby populated Barrang Lompo island, include catching fish and molluscs for food, collecting ornamental fish and invertebrates for sale and removing sand for building purposes. The latter might have contributed to the recent shrinking of the island which is reported to have had trees (Moka, pers. comm. with Vonk) and even buildings (Barrang Lompo local, pers. comm.) just a decade ago, but today it is completely submerged at high tide. Bone Batang is also not being spared of illegal fishing methods; a number of violations of fishery laws (fishing with explosives, fishing with cyanide and collection of endangered *Tridacna* sp.) could be observed during the study period.

The reef flat in the south eastern part of Bone Batang island (Fig. 6) was chosen as study area. It is covered by a mixed inter- to subtidal *Thalassia hemprichii* (Ehrenberg) Ascherson / *Cymodocea rotundata* (Ehrenberg & Hemprich ex Ascherson) / *Halodule uninervis* (Forsskål) Ascherson seagrass bed, interspersed with patches of *Enhalus acoroides* (L. f. Royle). *Halophila ovalis* (R. Brown) Hooker f. also occurs, mainly at the edge of the seagrass meadow and on sandy patches located in between it.



Fig. 6: Map of Bone Batang Island. All fieldwork was done in the seagrass meadow in the south eastern part of the reef flat, the position of the permanent transects is indicated by dots (after Christianen (2006)).

The area can be separated into a densely (north) and a sparsely (south) vegetated part with shoot density being 3355 ± 95 (SE) and 2520 ± 90 (SE) m^{-2} , respectively (outside patches dominated by *Enhalus acoroides*, Vonk, unpubl.) (Tab. 1).

Tab. 1: Average (AV) total seagrass density and density per species \pm standard error (SE) (number of shoots m^{-2}) (after Vonk, unpubl.).

	Total seagrass		<i>Thalassia hemprichii</i>		<i>Halodule uninervis</i>		<i>Cymodocea rotundata</i>	
	AV	SE	AV	SE	AV	SE	AV	SE
Dense	3355	± 95	724	± 33	1735	± 88	783	± 35
Sparse	2520	± 90	766	± 36	1276	± 87	414	± 31

It is bordered by an intertidal sandflat to the northwest, by a subtidal sandflat with a high density of *Callianassa* expulsion mounds to the north and by sparse patches of corals situated on a sandy slope which gradually drops to the shelf bottom to the east, south and southwest.

The tidal regime on Bone Batang island, for which no tide chart is available, closely corresponds to the one on Karangrang Lompo island (Vonk, pers. comm.).

As predicted by the tide chart, extremely low tidal levels coincide with the hours of intense solar radiation around noon from September to November each year (Stapel 1997). This causes a large scale burn off of the intertidal seagrass population but no large scale mortality of benthic fauna was recorded, sea urchins and sea stars migrate to the subtidal parts or, when

trapped in small pools, cover themselves completely to prevent overheating (Stapel 1997, Vonk, pers. comm.). All permanent transects were set up in the subtidal areas to avoid the direct impact of this phenomenon on the results.

Commercially valuable holothurians (locally known as Teripang) seem to be absent now and have obviously been replaced by other echinoderms such as *Proteraster* sp., a development which has taken place on virtually all Indonesian reef flats (Tomascik *et al.* 1997). Due to the severe anthropogenic impact, large seagrass grazers like the dugong and green sea turtles are nowadays almost extinct in the Spermonde Archipelago (pers. obs.).

Pelagic grazers like rabbit fish (Siganidae) can still be observed. Another conspicuous bony fish frequently encountered in and around seagrass beds is the bream *Pentapodus trivittatus* (Bloch 1791). Individuals of this species will always stay close to the researcher in the field, especially if sediment is stirred up. They eat invertebrates from the sediment and the activity of the researcher gives them opportunities to find more prey (Vonk, pers. comm.).

In contrast to the seagrass beds surrounding nearby Barrang Lompo island (seemingly dominated by *Callianassa* expulsion mounds and *Alpheus* burrows) and off the small fishing village of Puntondo on the mainland (little crustaceans, high numbers of synaptid holothurians), Bone Batang island seems to have its own special macrozoobenthos community. Due to their large size and high abundance three components here readily stand out from the rest: several species of *Pinna* bivalves (*P. bicolor* (Gmelin 1791) and *P. muricata* (Linnaeus 1758)), the sea urchin *Tripneustes gratilla* (Linnaeus 1758) and the burrowing shrimp *Neaxius acanthus* (Milne-Edwards 1878). Besides *N. acanthus*, a variety of other crustaceans construct burrows in the study area: various species of stomatopods, amongst them the large *Lysiosquilla maculata* (Fabricius 1793), alpheid shrimp (the most numerous probably being *Alpheus edamensis* (de Man 1888) associated with gobies *Cryptocentrus* sp. and *Amblyeleotris* sp.) and at least two more thalassinideans: *Corallianassa coutierei* (Nobili 1904) and one or more unidentified callianassid species responsible for large (height up to 20 cm) expulsion mounds.

2.3 Study object

2.3.1 The burrowing shrimp *Neaxius acanthus* and *Corallianassa coutierei*

Unlike most thalassinideans which are never seen unless they are dug out, the orange to pink *Neaxius acanthus* seems to spend a lot of time sitting in the opening of its burrow and even stretches out its claws in order to catch floating debris, mainly detached seagrass leaves which



Fig. 7: Two openings of burrows of *Neaxius acanthus* in the Bone Batang seagrass bed.

are then transported below the sediment surface. As soon as the observer casts a shadow on it an individual will usually venture to the opening. The opening itself (diameter approx. 2 cm) is a conspicuous feature of the bottom, being perfectly circular and leading to a vertical shaft with black lining, contrasting with the white carbonate sediment (Fig. 7). Openings are usually surrounded by a spot of 10 cm diameter lacking vegetation; this spot also tends to form a shallow funnel (approx. 2

cm deep). Expulsion mounds as observed around openings of burrows of alpheidids and callianassids seem to be absent.

Another thalassinidean present in the Bone Batang seagrass meadow is the callianassid *Corallianassa coutierei* with brightly yellow claws. Like *N. acanthus*, it also ventures to the entrance of its burrow in order to catch floating seagrass leaves. Openings of *C. coutierei* are likewise perfectly circular (diameter approx. 1 cm). The burrow lining is grey instead of brown. It seems to be less abundant than *N. acanthus*.

2.4 The monitoring of burrow openings of *Neaxius acanthus* in permanent transects

Nine permanent transects were set up in the seagrass meadow covering the south western part of the Bone Batang reef flat. Each transect measured 15 x 1 m and was defined by four wooden poles which were left in the sediment throughout the study period. These poles served as anchor points for a ladder built of 2 ropes to which 16 sticks made of split bamboo were tied. The ropes and the bamboo sticks thus defined 15 quadrants measuring 1 x 1 m each. All burrow openings within these 9 transects which could doubtlessly be ascribed to *Neaxius acanthus* (because an individual of this species was at least seen once in the opening) were then marked with smaller bamboo sticks (approx. 30 cm) which were planted into the sediment next to each opening. State (open / closed / expulsion mound) was recorded monthly. Position, inhabitant (male / female / couple) and diameter were likewise recorded monthly for open burrows only. To cover an approx. equal number of openings in the densely and the sparsely vegetated area two transects were maintained in the dense and seven in the sparse seagrass bed.

The ladder was only tied to the poles for the duration of the counting to keep disturbance at a minimum (Fig. 8).

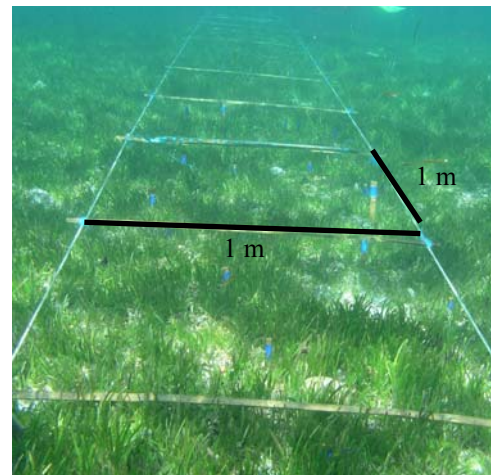


Fig. 8: Transect ladder in the seagrass bed. Bamboo sticks mark the position of each burrow opening (pic.: Vonk)

2.5 Burrows of driftcatching thalassinideans in the seagrass bed

2.5.1 *In-situ* polyester resin casting of thalassinidean burrows in the seagrass bed

Polyester resin and catalyst / hardener (trade name unknown, distributed by Toko Ocean Fiberglass, Jalan Irian 89, Makassar, Sulawesi, Indonesia) were used to cast burrows of *Neaxius acanthus* and *Corallianassa coutierei*. The two components were mixed in a ratio of approx. 100:1 allowing a processing time of approx. 30 min before hardening set in. The casts were dug out 1 to 2 days later to allow for complete hardening.

Only complete and semi complete casts were used for the subsequent measurements. A cast was considered complete if no parts of it were left at the study site and semi complete if not all burrow structures were reflected because of water blockage. All casts recovered were



Fig. 9: A Polyester cast recovered from a burrow of *Corallianassa coutierei*, presented for photographic documentation.

cleaned of coral gravel and sediment and all organisms trapped in the resin were recorded and, if possible, specified. A sketch showing the position of all animals trapped in the resin was made for each cast. The cleaned casts were photographed (Fig. 9) showing their maximum horizontal and vertical extension which was then quantified from the photographs using Adobe Photoshop 7.0. All casts were covered with adhesive tape without creating any overlaps or gaps. The surface area was then estimated from the length and width of the tape used. Finally all casts were weighed to estimate their volume. The weight / volume ratio for resin + catalyst was determined by weighing six 1 ml subsamples of a 100:1 mixture.

2.5.2 The burrow lining of *Neaxius acanthus* and *Corallianassa coutierei*

A total of 18 sediment cores was taken from the study area, six of which included the upper part of burrows of *Neaxius acanthus* and another six which included the upper part of burrows of *Corallianassa coutierei*. Core diameter was 156 mm and core depth was 30 cm. Cores including burrow linings were split and as much lining as possible was separated from the surrounding sediment (Fig. 10). Sub samples of the six cores containing sediment only were taken from the surface as well as from 15 and 30 cm depth. All animals and plant fragments visible without magnifying devices were sorted out of all 30 samples. Samples were then weighed wet. This later allowed for the subtraction of the weight of the salt contained in the water. After drying for 48 h at 70°C DW and following combustion at 500°C for 4 h in a muffle furnace AFDW were determined.

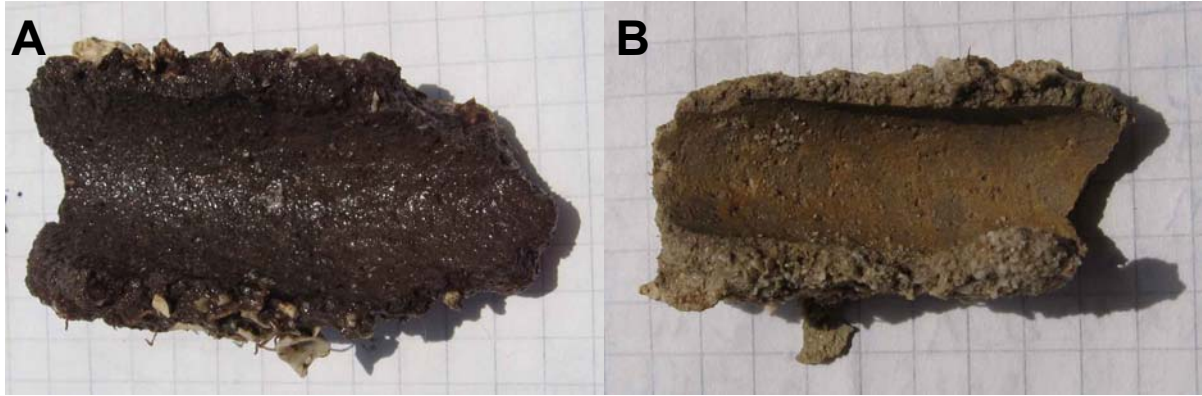


Fig. 10: Burrow lining of *Neaxius acanthus* (A) and *Corallianassa coutierei* (B); both species produce a coherent lining which can be easily distinguished and separated from the surrounding sediment. Squares measure 5 mm.

The 30 samples were subjected to washing two times in tap water and once in distilled water before they underwent drying at room temperature. Grain size composition was analyzed using a series of sieves measuring 2000, 1000, 500, 250, 125 and 63 μm after shaking for 10 min on test sieve (JEL 200 T, J. Engelmann AG, 67059 Ludwigshafen). The relative weight of all seven fractions was calculated using Microsoft Excel.

2.5.3 Burrow water properties for *Neaxius acanthus*

Six stations (Fig. 11) which had already been implanted into the Bone Batang seagrass meadow by Vonk in May 2004 were used to extract water for the analysis of oxygen content, pH, salinity and the macronutrients ammonium and reactive phosphate.

Three stations were positioned in the dense and three in the sparse part of the seagrass bed. Each station was equipped with five pore water samplers (Rhizon 10 cm soil moisture sampler, Eijkelkamp Agrisearch Equipment) buried in the sediment at depths of 1.5, 4.5, 7.5, 10.5 and 13.5 cm. A wooden pole had been placed close to each set of pore water samplers to facilitate recovery. Pore water from between 0 to 3, 3 to 6, 6 to 9, 9 to 12 and 12 to 15 cm could be pulled into a 50 ml syringe through a thin tube.

12 more pore water samplers were added to the setup, two were placed in 30 and 45 cm depth within 2 m distance of each of the old stations. The new pore water samplers were left undisturbed for several weeks before water for the analysis was extracted.

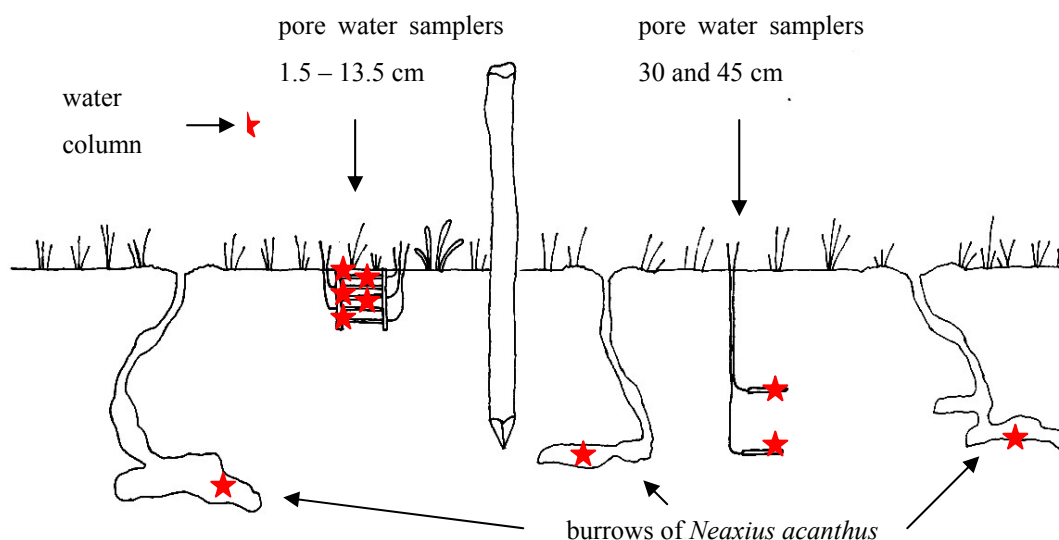


Fig. 11: Line drawing of one of the stations used for the extraction of pore water and burrow chamber water. Each replicate sample is indicated by an asterisk. Three replicates each were taken in the dense and in the sparse area, but only a total of three replicates in the water column (half asterisk).

When not in use, the tubes leading to the surface were closed with cable ties and protected against fish bites by covering them with a piece of tube.

When retrieving water, the first few ml were rejected since they represent water from inside the pore water sampler and the hose. In addition, water from the water column was collected at three random points scattered between the stations. The delicate pore water samplers could not be introduced into the burrows because the inhabitant shrimp would damage them. Water was therefore obtained using a tube of 1 m length connected to a 50 ml syringe which was pushed into an open burrow as deep as possible, a few ml were then extracted and rejected before the syringe was filled completely. Three open burrows next to each station were covered for each set of measurements (Tab. 2).

Tab. 2: Number of replicates (n) for water quality measurements. Bold letters represent data provided by Vonk. Two sediment moisture samplers (at 4.5 and 10.5 cm depth) were defect. Salinity was not measured for all samples.

	Water column	Sediment depth in cm							Burrow chamber
		1.5	4.5	7.5	10.5	13.5	30	45	
Ammonium	3	6	5	6	5	6	6	6	18
Phosphate	3	6	5	6	5	6	6	6	18
Oxygen	3	6	5	6	5	6	6	6	18
pH	3	6	5	6	5	6	6	6	18
Salinity	3	5	4	5	4	5	6	6	17

Measurements of oxygen content, pH and salinity were made immediately aboard the boat by carefully opening the syringes and introducing the adequate sensor heads (CellOx 325 for oxygen, SenTix 21 for pH and TetraCon for salinity, all connected to a WTW Multi 340i Multimeter) into the samples. The multimeter was calibrated prior to the measurement of Oxygen and pH.

Water samples for ammonium and phosphate measurement were stored on ice until arrival in the lab. The water from the burrow chambers was filtered through sediment moisture samplers before further treatment.

Ammonium and reactive phosphate values for the water column and sediment porewater between 0 and 15 cm depth were provided by Vonk.

Chemical analysis of water samples:

- Ammonium

For the ammonium determination the following reagents were used (after Solorzano 1969):

1. 10 g of C_6H_5OH (phenol) dissolved in 100 ml of 95% (v/v) ethyl alcohol USP.
2. Sodium nitroprusside solution. 0.5%. 1 g of $Na_2Fe(CN)_5NO \cdot 2H_2O$ dissolved in 200 ml of DI.
3. Alkaline solution. 100 g of $Na_3C_6H_5O_7 \cdot 2H_2O$ (trisodium citrate) and 5 g of NaOH (sodium hydroxide) dissolved in 500 ml of DI.
4. Sodium hypochlorite solution. Reagent grade NaClO (sodium hypochlorite) (>1.5N).
5. Oxidizing solution. 100 ml of Alkaline solution (3.) mixed with 25 ml of sodium hypochlorite solution (4.).

53.5 g of NH_4Cl were dissolved in DI to a final volume of 500 ml. A calibration line was generated using a blank and doublet concentrations of 1, 2, 5 and 20 μmol .

0.2 ml of phenol-ethanol solution, 0.2 ml of sodium nitroprusside solution and 0.5 ml of oxidizing solution were added to 5 ml of sample in a test tube and mixed well. The test tubes were left in the dark overnight and absorbance was measured at 620 nm the next morning in a 5 cm cell.

- Reactive phosphate

For the determination of reactive phosphate the molybdate method of Murphy & Riley (1962) was used. It requires the following reagents:

1. Ammonium molybdate solution: 15 g of $(\text{NH}_4)_6 \text{Mo}_7\text{O}_{24} \cdot 4\text{H}_2\text{O}$ dissolved in 500 ml of DI.
2. Sulfuric acid solution: 140 ml of conc. H_2SO_4 added to 900 ml of DI.
3. Ascorbic acid solution: 27 g of $\text{C}_6\text{H}_8\text{O}_6$ (ascorbic acid) dissolved in 500 ml of DI.
4. Potassium antimonyl-tartarate solution: 0.34 g of $\text{K}(\text{SbO})\text{C}_4\text{H}_4\text{O}_6$ dissolved in 250 ml of DI.
5. Mixed solution: 100 ml of (1.), 250 ml of (2.), 100 ml of (3.) and 50 ml of (4.).

136.1 g of KH_2PO_4 were dissolved in DI. 10 ml of sulphuric acid solution (2.) was added. The mixture was then diluted to a final volume of 500 ml. This resulted in a concentration of 2 mmol PO_4 / l . A calibration line was generated using a blank and doublet concentrations of 0.5, 1, 2, 5 and 10 μmol .

0.5 ml of the mixed solution were added to 5 ml of sample. Absorbance was measured after 15 min at 885 nm.

2.6 Morphometric properties and individual weight in *Neaxius acanthus*

Individuals of *Neaxius acanthus* were caught underwater by luring them close to the entrance with a seagrass leaf and then blocking their retreat with a metal spike. Animals were then carefully flushed out of the sediment and immediately fixated in 4% Formol + seawater.

In the lab animals were sexed according to presence (female) or absence (male) of pleopods 2. Total length (tip of rostrum to end of telson), carapace length (tip of rostrum to posterior end of dorsal margin), length of the propodus of major and minor cheliped were measured to the closest 0.5 mm using a sliding calliper. Presence or absence of eggs on female pleopods or well developed ovaries inside female pleon was determined. Further on WW, DW and AFDW were determined for propodus + dactylus of major and minor cheliped each and for the rest of each animal separately to the closest 0.01 g. The position of the major cheliped (left or right) was recorded for each individual.

Burrow diameter was measured to the closest 0.5 mm using a sliding calliper before capture.

Morphometric measurements were performed on a total of 66 individuals, (40 male and 26 female). Burrow diameter was recorded before capture for 30 out of these 66 individuals (16 male and 14 female), and for 45 out of these 66 individuals (24 male and 21 female) DW and AFDW were determined. Total length was measured on 21 out of 66 individuals (16 male and 5 female).

For three male and three female individuals, N, C and protein content were determined. The dry material (48 hours at 70° C) was homogenized in a ball mill (Retsch MM 301) for 30 s. Ca. 5 µg (between 2 and 8) of the homogenized material were weighed into silver cups. One drop of distilled water was added to each cup, followed by the addition of 2M HCl to exclude inorganic carbon until the reaction stopped. The content of the cups was then dried overnight at 60 °C.

Analysis for C and N was done with a NC Sediment analyzer (Thermo Finnigan Flash 1112 series). Protein content was calculated following the method of Kjeldahl.

2.7 Observations of the behaviour of *Neaxius acanthus*

2.7.1 *In-situ* observation of *Neaxius acanthus* in the burrow entrance

Six randomly chosen open burrows in the densely vegetated area were marked with bamboo sticks and the entrance was monitored for 15 min for each burrow on three different days. Care was taken by the observer not to cast a shadow on the entrance and not to break off any seagrass leaves upstream of the entrance observed. A distance of at least 1 m to the animal



Fig. 12: A male *Neaxius acanthus* catching a *Thalassia*-leaf.

observed was kept. The time the entrance was “guarded” by male or female shrimp and the time it was unattended was measured to the closest 30 s using a stop watch. The length of all seagrass fragments caught by the animals (Fig. 12) was estimated by assigning fragments to four size classes (0 to 1, 1 to 3, 3 to 5 and >5 cm). A ruler was therefore placed next to the opening but out of sight of the shrimp for the duration of the observation.

Fragments similar in length to the ones caught by the shrimp in the *in-situ* observation experiment were picked from a bucket filled with leaf detritus and dry weight was determined cumulated for each day of observation. Leaves were not cleaned of epiphytes and no separation between seagrass species was made.

2.7.2 Observation of *Neaxius acanthus* in aquaria

Six narrow aquaria (internal dimensions 49 (length) x 49.5 (height) x 4.5 (width) cm) were built from glass slates (thickness 5 mm) and set up in the facilities of the hatchery, Barrang Lompo island. Sediment from the Bone Batang seagrass meadow was filled into each aquarium to a height of approximately 35 cm. Living seagrass plants were put into all aquaria. The uppermost layer of sediment was therefore stabilized by seagrass rhizomes as in the study area.

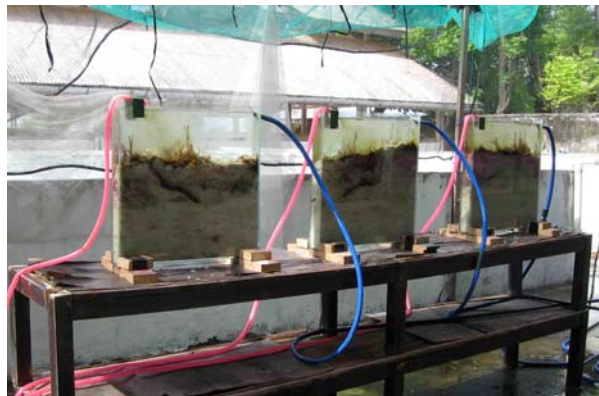


Fig. 13: Three of the six aquaria used for the observation of behaviour.

All aquaria were individually supplied with running unfiltered sea water. Sediment was allowed to settle for two weeks before the introduction of animals. Observations were only made on animals which had already constructed a burrow consisting of at least a more or less vertical shaft and a chamber big enough to turn around inside the burrow (Fig. 13).

I Single individuals:

The first set of observations was on single animals (one female and three male individuals) each of which was observed for 15 min at noon (between 11 and 13 o'clock), in the evening (between 17 and 19 o'clock), in the night (between 23 and 1 o'clock) and in the morning (between 5 and 7 o'clock) for two days. 12 behavioural states had been defined before. Their

duration was measured to the closest s using a stop watch. The behavioural states were integrated in 6 behavioural classes one of which was the time the animals were not visible.

II Burrow dynamics:

Before the behaviour was observed, a sketch of the outline of each burrow was drawn every six hours for two days. The state of the opening (open / closed) was also recorded with each set of observations.

III Leaf processing by single individuals:

A new seagrass leaf was placed next to the opening every 5 min and all behaviour related to the leaves was recorded for 15 min. This was done with the same individuals as in the first set of observations.

IV Encounters:

Four encounters were enforced by putting new shrimp into each aquarium. The newcomers would quickly try to descend into the existing burrows. Any behaviour following these encounters would be recorded following the first contact. Encounters were female 1 (resident) + female A (newcomer), male 1 (resident) + female B (newcomer), male 2 (resident) + male A (newcomer) and male 3 + female C (newcomer).

V Time allocation in pairs:

The time allocation of two pairs in relation to the burrow opening was recorded for 15 min on three days.

VI Leaf processing by pairs:

A new seagrass leaf was placed next to the opening of the two pairs every 5 min and all behaviour related to the leaves was recorded for 15 min.

2.7.3 Quantification of a potential grazing effect of *Neaxius acanthus* on seagrass

Two sets of cores were taken from the dense part of the Bone Batang seagrass bed. The first set consisted of 4 cores including an opening of a *Neaxius acanthus* burrow in their center and another four taken randomly but excluding openings and the funnel surrounding them. Core diameter was 156 mm. The second set consisted of 6 cores including and 6 cores excluding an opening. The sampling core had a diameter of 109.5 mm for the second set. Coring depth was 20 cm for both sets.

In the lab all seagrass leaves, leaf sheaths, rhizomes, flowers and seeds were sorted according to species (*Thalassia hemprichii*, *Halodule uninervis*, *Cymodocea rotundata*, *Enhalus acoroides* and *Halophila ovalis*). Roots were discarded. All leaf bearing shoots were counted for the three most dominant species *Thalassia hemprichii*, *Halodule uninervis* and *Cymodocea rotundata*. Leafs were cleaned of epiphytes with a blade. Leaf sheaths were washed in tap water to remove adhering sediment particles. All plant parts were then washed in distilled water to remove excess salt. Before drying for 48 h at 70 °C, the washed material was placed on absorbent paper for several minutes. All dried material was weighed to closest 0.01 g.

2.7.4 Burrow openings of *Neaxius acanthus* as detritus traps

All open burrows within two transects (15 m² each) in the densely vegetated area were equipped with pieces of PVC tubing of 10 cm length. The tubes were closed off at one end using cloth tape and inserted into the opening until the open end was flush with the sediment surface (Fig. 14). On three different days the tubes were left in the openings for approx. 3 h. All leaf detritus “caught” in the tubes was then sorted out and weighed cumulated for each transect after drying at 70°C for 48 h. Only detritus from tubes which were neither cut open by the shrimp nor completely filled with sediment was used to calculate for overall detritus entrapment. Three different sizes of tubes were used: 12.5, 15 and 17 (internal) and 14.5, 17 and 19 mm (external) diameter to effectively close burrows of different diameters.

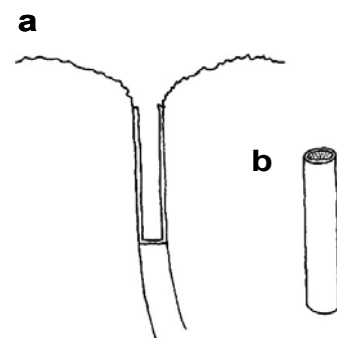


Fig. 14: A detritus trap as deployed in the field (a) and in lateral view (b).

3. Results

3.1 The monitoring of burrow openings of *Neaxius acanthus* in permanent transects

A total of 89 openings was monitored in the densely and 99 in the sparsely vegetated area. Average density of burrow openings was found to be about 3 openings m^{-2} (ranging from 0 to 9) in the dense and about 1 opening m^{-2} (ranging from 0 to 5) in the sparse area.

Opening density is positively correlated with seagrass density (factors: dense or sparse, variants: opening density m^{-2} ; ANOVA $F(1, 133) = 46.354, p < 0.01$).

Seagrass density has no influence on mean opening diameters (factors: dense or sparse, variants: diameter (mm); ANOVA $F(1, 119) = 0.575, p > 0.05$ for October). The mean diameter remained unchanged from October (18 mm) (Fig. 15) to January (18 mm) (factors: October, January, variants: diameter / mm; ANOVA $F(1, 255) = 0.004, p > 0.05$). A comparison of the openings < 15 mm produces the same result.

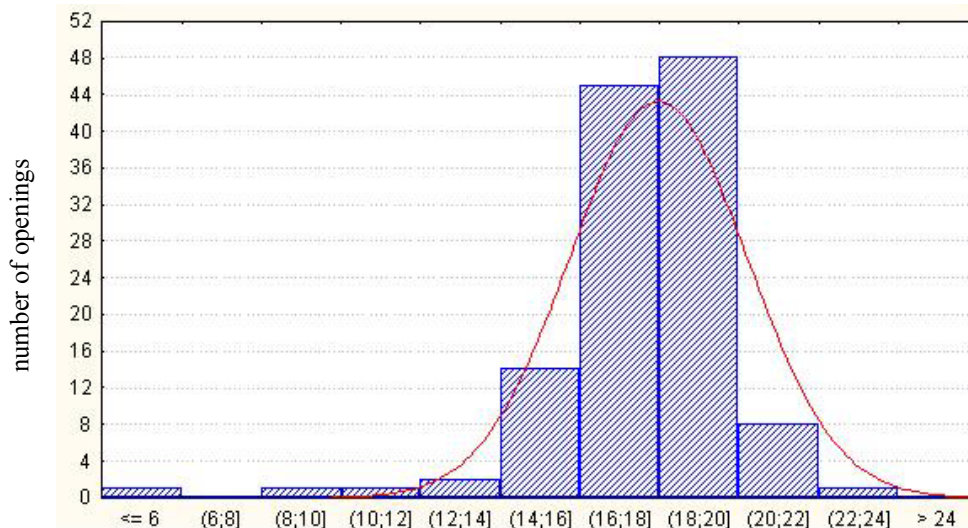


Fig. 15: Frequency of burrow diameters (open burrows only) as encountered in October 2005 in a total of 9 permanent transects covering 135 m^2 of the Bone Batang seagrass meadow.

The absolute position of all burrows marked in August did not change until January. Some openings were only discovered during the course of the monitoring; it is here assumed that they were closed during the first counting and thus overlooked. 76 and 73% of all burrows were found to be occupied by at least two shrimp of different gender in the dense and the sparse area, respectively. In 8 and 3% only male and in 6 and 9% only female individuals

could be seen in the opening. In 10 and 14% of the openings the gender (and as a consequence of this the minimum number) of the inhabitants could not be determined.

These burrows measure on average 8 mm and are thus significantly smaller (factors: pair, male, female, unidentified, variants: diameter / mm; ANOVA $F(3, 117) = 20.118, p < 0.001$) than the burrows where the gender of the inhabitants was identified (mean diameter 18 mm).

On average 65% of the openings were found open, on average 26% were found closed and on average 5% of the openings were found to have been replaced by expulsion mounds (Fig. 16) in the dense and the sparse area, respectively. The remaining 4% represent overlooked burrow openings.

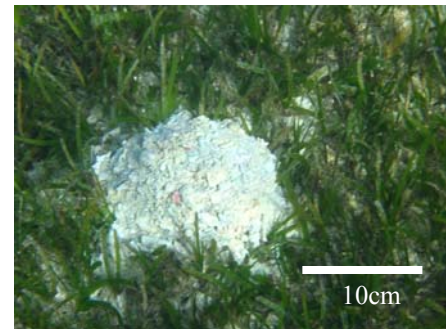


Fig. 16: A small sediment expulsion mound was from time to time found to have replaced an opening of a burrow of *Neaxius acanthus*.

The percentage of open burrows is not dependent on the month of the counting (factors: (September, October, November, December, January) * (open, closed, expulsion mounds, overlooked), variants: % open, closed, expulsion mounds, overlooked; ANOVA $F(12, 20) = 1.2316, p > 0.05$) and not influenced by seagrass density (factors: (dense, sparse) * (open, closed, expulsion mounds, overlooked), variants: % open, % closed, % expulsion mounds, % overlooked; ANOVA $F(3, 32) = 4.1268, p < 0.05$; Tukey HSD post-hoc for dense vs. sparse all $p > 0.05$).

The number of visible openings therefore is mostly lower than the actual number. Closed openings are indistinguishable from the sediment surface, the expulsion mounds produced by *N. acanthus* are never higher than 5 cm (Fig. 17).

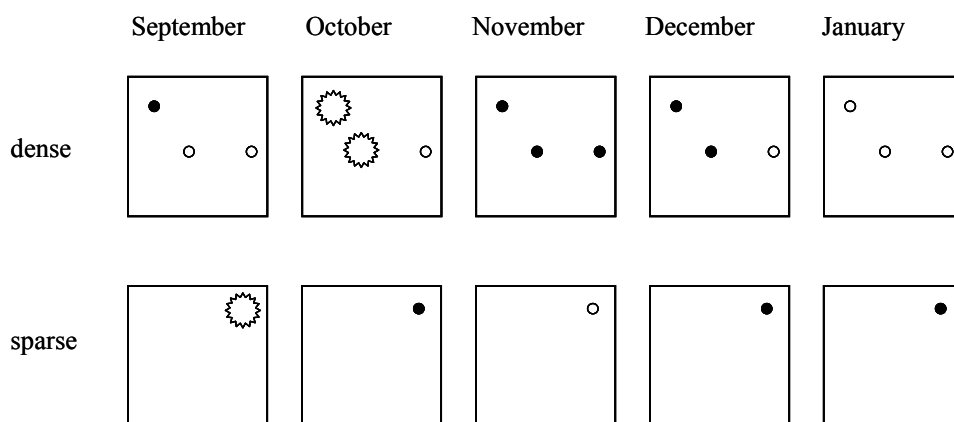


Fig. 17: A representative 1 m² from the dense (3 openings of *N. acanthus*, upper row) and the sparse (1 opening, row below) area as encountered in September, October, November and December 2005 and January 2006 (left to right). No new burrows occurred in 5 months and no openings changed position. Closed burrows (open circles) are indistinguishable from the sediment surface and expulsion mounds (asterisks) replace openings occasionally. The number of open burrows (black dots) seems to be different every month.

3.2 Burrows of driftcatching thalassinideans in the Bone Batang seagrass meadow

3.2.1 The burrow structure of *Neaxius acanthus* and *Corallianassa coutierei*

Three complete and two semi complete casts of burrows of *Neaxius acanthus* (Fig. 18) and three complete casts of burrows of *Corallianassa coutierei* (Fig. 19) were recovered from the study site.

The single opening of burrows of *N. acanthus* is usually situated in a shallow funnel-shaped depression (diameter about 10 cm and depth about 2 cm). Aggregations of coral rubble, mainly dead *Acropora* sp. fragments, around the opening are common. The following vertical to sub vertical shaft is cylindrical to just below the initial funnel and lined with a thick (several mm to 1 cm) brown material. Light microscopy reveals a composition of a mixture of fine sediment particles and fragments of multicellular plants. Between one and three swollen chambers lie between the opening and the large basal chamber from which short, finger-like protuberances extend into the surrounding sediment. Floor areas with an inclination of less than about 45° are not lined. This locally allows the penetration of resin into the surrounding sediment. The more distant parts of the basal chamber are often filled with fragments of seagrass leaves or a mixture of the latter with sediment. Casts of burrows of *N. acanthus* were found to contain one or two shrimp (if two shrimp were found they were of different gender). In addition to the shrimp, a diverse community of cohabitants was found, consisting of up to 8 individuals of a yet unidentified clam species (similarities to *Erycina*, *Lentidium*, *Corbulomya* and *Pomatocorbula* sp., all Myoidae: Lentidiinae) (Fig. 22B) and up to two specimen (male and female) of a small bony fish which was identified as the goby *Austrolethops wardi* (Whitley 1935) (Teleostei: Gobiidae) (Fig. 22A). Amphipods and polychaete burrows (two species of tube-building polychaetes, one of them probably *Spirorbis* sp. (Spirorbinae) as found on the tail fans of some individuals) were also found associated with the casts (Fig. 22 C to F). Shaft diameter is from 15 to 18 mm. The maximum vertical extension of the five burrows cast ranged from 39 to 63 cm whereas the maximum horizontal extension ranged from 37.5 to 65.5 cm. The surface area was between 1273 and 3105 cm² and the volume was from 1182 to 4083 cm³. A general reconstruction of the burrow of *Neaxius acanthus* showing all inhabitants is shown in Fig. 20.

The upper most part of the burrow of *C. coutierei* is similar to that of *N. acanthus* except for the funnel being slightly steeper.

The subsequent vertical to sub vertical shaft shows a grey lining. A star shaped crossing consisting of several blind tunnels opening out in an extension of the shaft is situated halfway down in all three casts. From the deepest part, a comparable extension of the shaft diameter branches into several, sometimes bifurcate tunnels extending in all directions. These branches end in swollen extensions containing clusters of seagrass debris. One of the casts has two openings; the subsequent shafts meet at the chamber halfway down. The other two show long tunnels originating from the basal crossing which are not completely filled with resin. In one of the casts made of burrows of *C. coutierei* an individual was found clogging the run and was in this way preventing the resin from entering the tunnel. The inhabitants of the other two casts could not be found trapped in the resin. The diameter of the cylindrical part was between 7 and 11 mm. Maximum vertical and horizontal extension was from 42.5 to 96 cm and 27 to 31.5 cm, respectively. The values for surface and volume are 308 to 1048 cm² and 76 to 413 cm³. A reconstruction of a typical burrow of *Corallianassa coutierei* showing all features is given in Fig. 21.

An overview of the dimensions of all burrows and the animals trapped in the resin is given in Tab. 4.

Tab. 4: Dimensions and inhabitants of five burrows of *Neaxius acanthus* and three burrows of *Corallianassa coutierei*.

species	shaft diameter (mm)	maximum extension (cm)		surface area (cm ²)	volume (cm ³)	number of animals trapped				
		vertical	horizontal			inhabitant	shrimp	fish	clam	amphipods
<i>Neaxius acanthus</i>	15	43	54	1506	1347	2	0	4	0	0
	16	63	65,5	1416	1182	1	2	8	1	0
	16.5	51	37.5	1429	1290	1	0	5	0	0
	17.5	39	71	1273	1209	2	1	5	0	0
	18	53	55.5	3105	4083	2	1	7	1	2
<i>Corallianassa coutierei</i>	7	42,5	27.5	308	76	1	0	0	0	0
	10.5	69	31.5	633	216	0	0	0	0	0
	11	96	27	1048	413	0	0	0	0	0

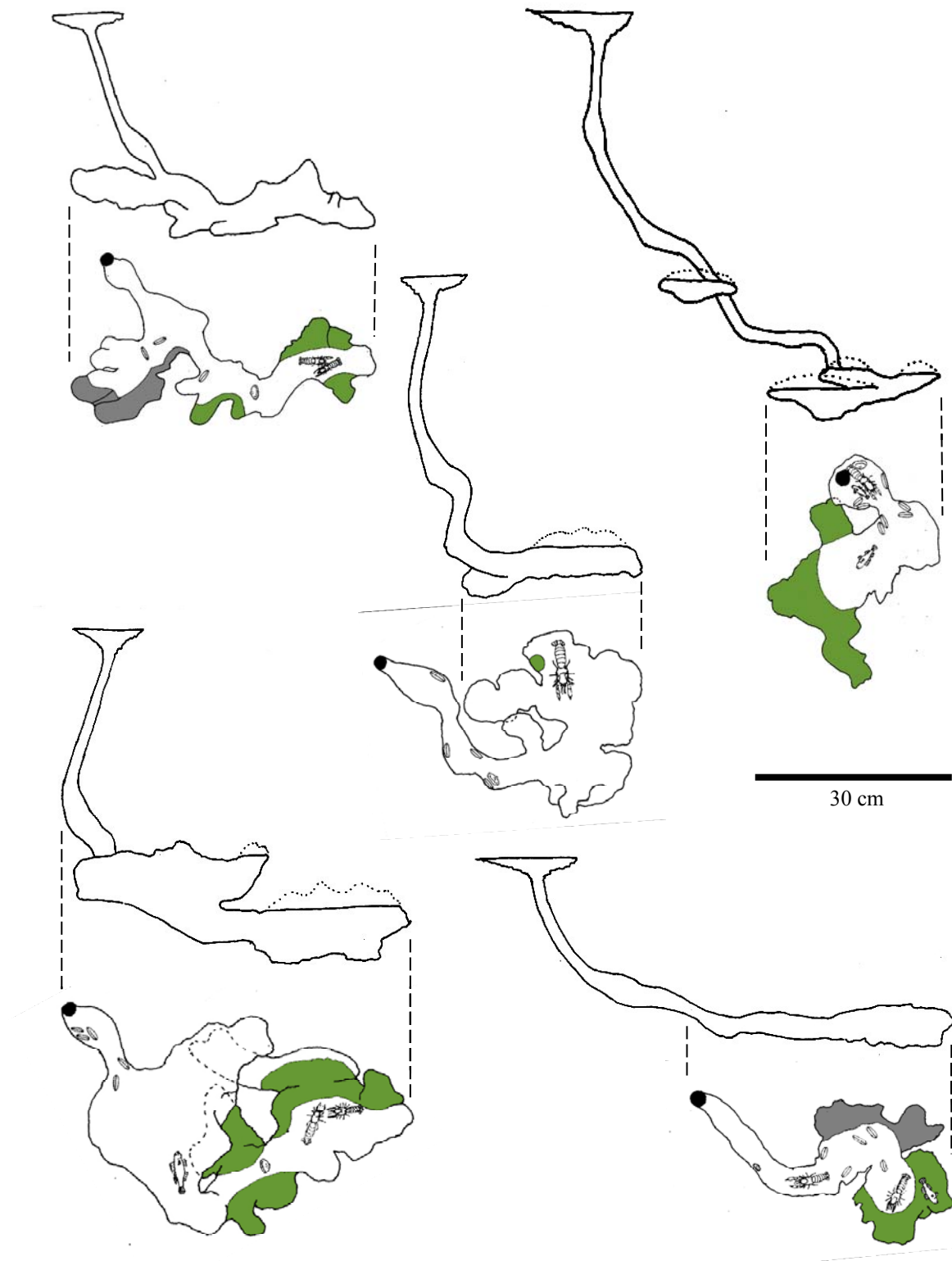


Fig. 18: Line drawing of the shape of five casts recovered from burrows of *Neaxius acanthus*; all are orientated showing their maximum vertical and horizontal extension. Dotted lines indicate sections not completely filled with resin due to water blockage.

A projection of the corresponding basal chamber is shown below as viewed from above, respectively. Dotted lines here represent overlapping parts. Grey areas indicate gravel only and green areas indicate a mixture of seagrass and gravel enclosed in the resin. The position and orientation of inhabitant shrimp, commensal bivalves and commensal fish as trapped in the resin is shown.

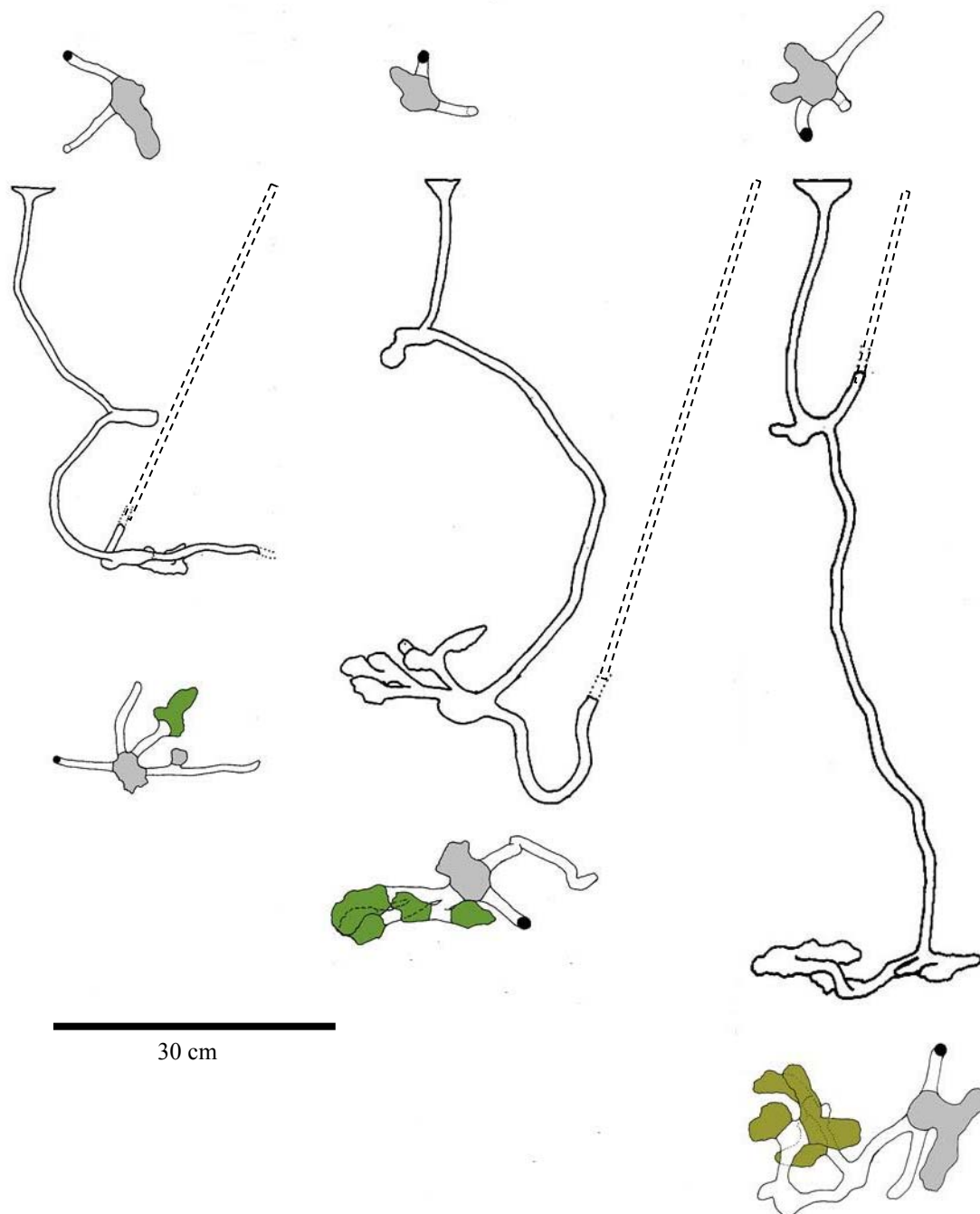


Fig. 19: Line drawing of the structure of three burrows of *Corallianassa coutierei*. The maximum vertical and horizontal extension is shown.

A projection of the chambers as viewed from above (the chamber halfway down above, the basal chamber below the sideview) is given. Accumulations of gravel are shaded grey whereas a mixture of seagrass and gravel is shaded green. All burrows probably had a second, non-functional opening which was filled with sediment (dashed lines).

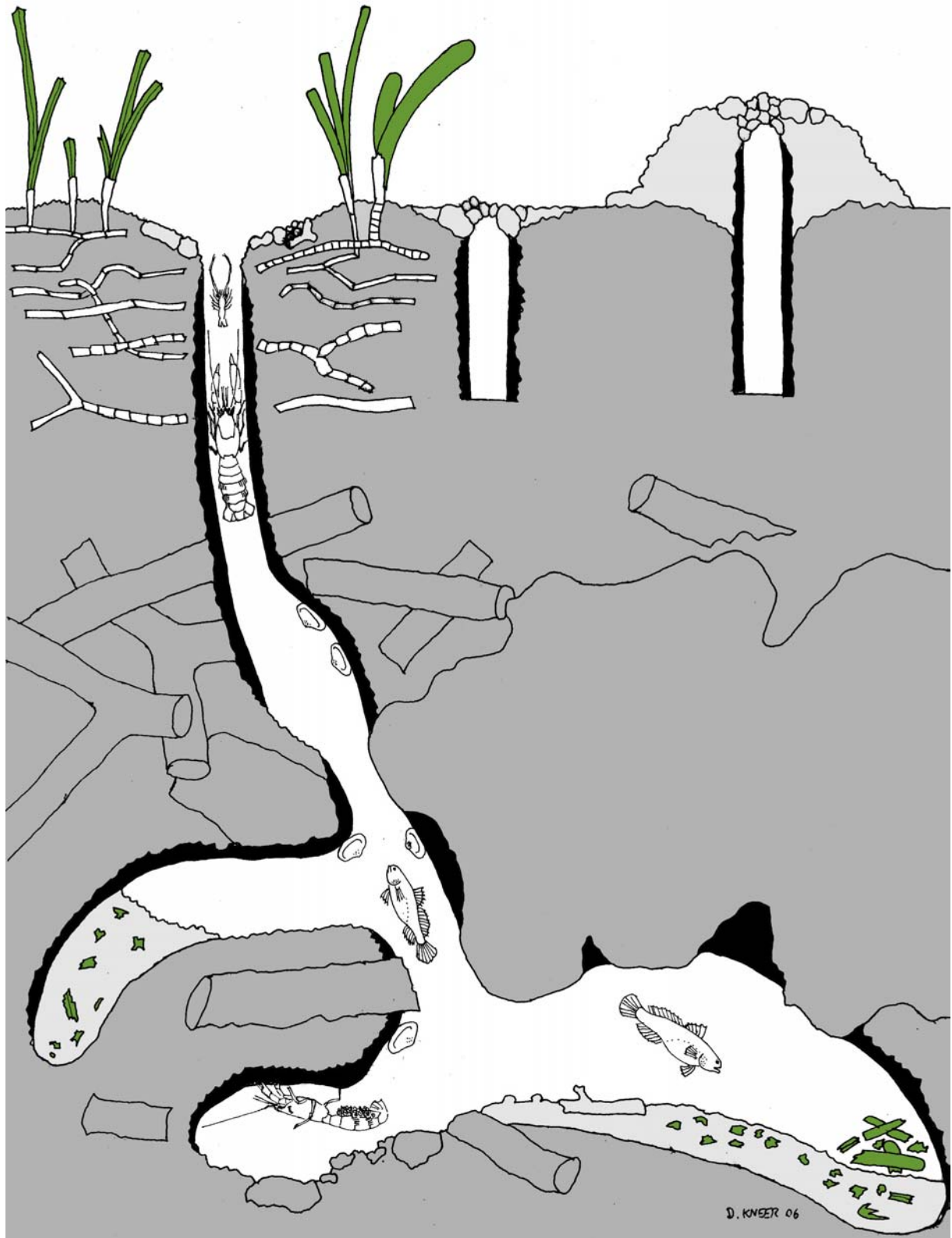


Fig. 20: Reconstruction of a burrow of *Neaxius acanthus* based on five polyester resin casts and the observation of the burrowing behaviour in aquaria. Three potential states of the entrance are shown: open, closed and replaced by an expulsion mound. The upper layer of the sediment in the study area is typically interspersed with seagrass rhizomes whereas *Acropora*-gravel and coral boulders are found deeper down. Black represents the burrow lining with a high silt fraction, grey indicates surrounding sediment and light grey indicates coarser sediment which has already been sorted by the shrimp. A palaemonid shrimp is shown in the entrance above the male shrimp whereas the female shrimp is shown tamping sediment into the roof of a freshly dug tunnel. Commensal clams are typically positioned where the shaft merges into the basal chamber whereas the position of the mobile gobies could not be derived from the resin casts and needed to be guessed for this reconstruction.

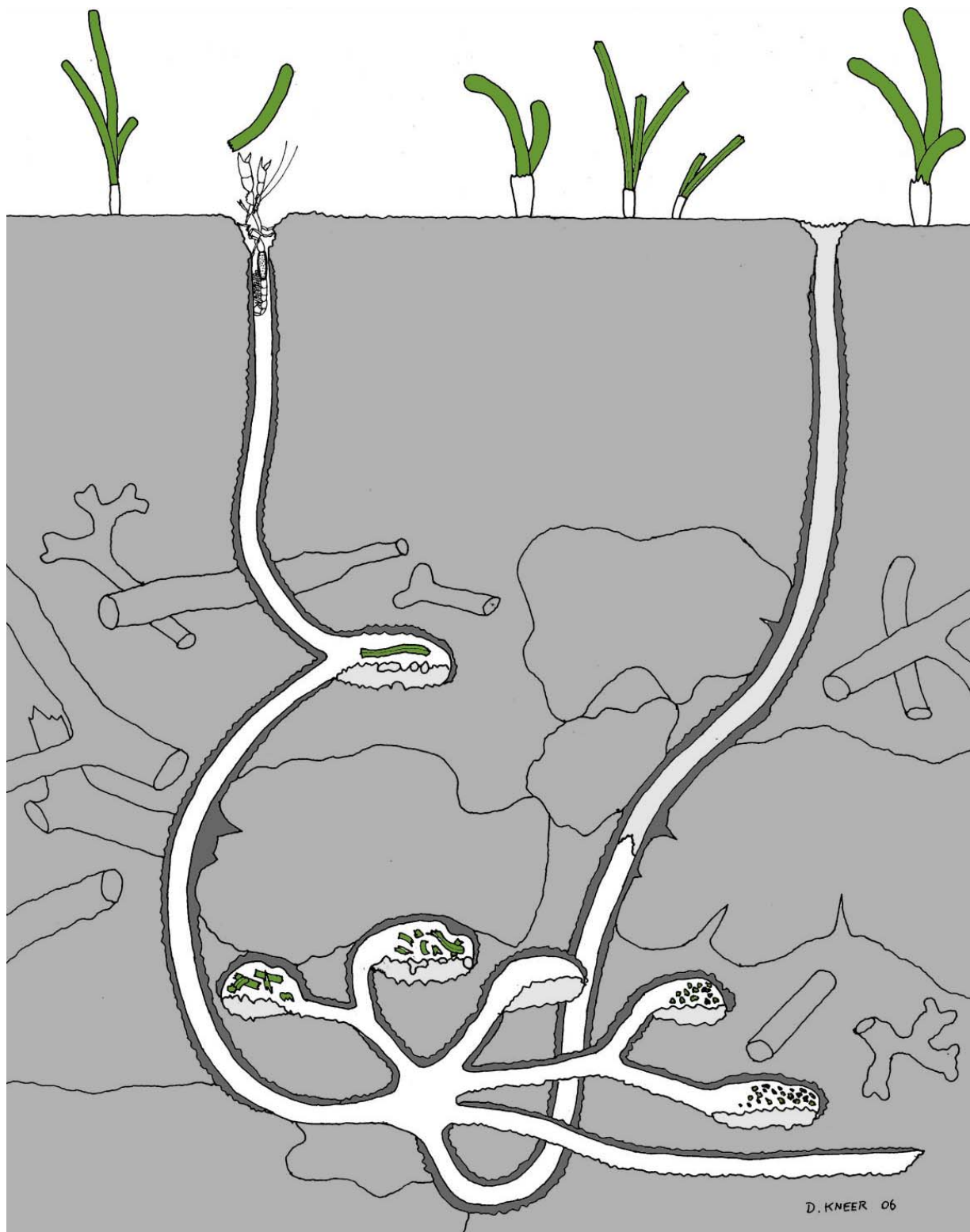


Fig. 21: Reconstruction of a burrow of *Corallianassa coutierei* based on three polyester resin casts and data on *Corallianassa longiventris* in Dworschak, Koller & Abed-Navandi (2005). Seagrass rhizomes are not shown. The deeper sediment layers are interspersed with *Acropora*-gravel and coral boulders. Most burrows of *C. coutierei* probably have two openings one of which is non-functional and filled with sediment. The inhabitant is shown trying to catch a piece of floating debris which will first be transported to the chamber halfway down. Later the debris will be transported to the deeper chambers and be reduced to increasingly smaller pieces (left to right). Blind tunnels are occasionally dug into the surrounding sediment when the animal is mining for small sediment particles. These tunnels are later refilled. Light grey represents coarse sediment which has already been sorted, grey indicates untouched sediment and dark grey represents the burrow lining. No commensals were found with *C. coutierei*.

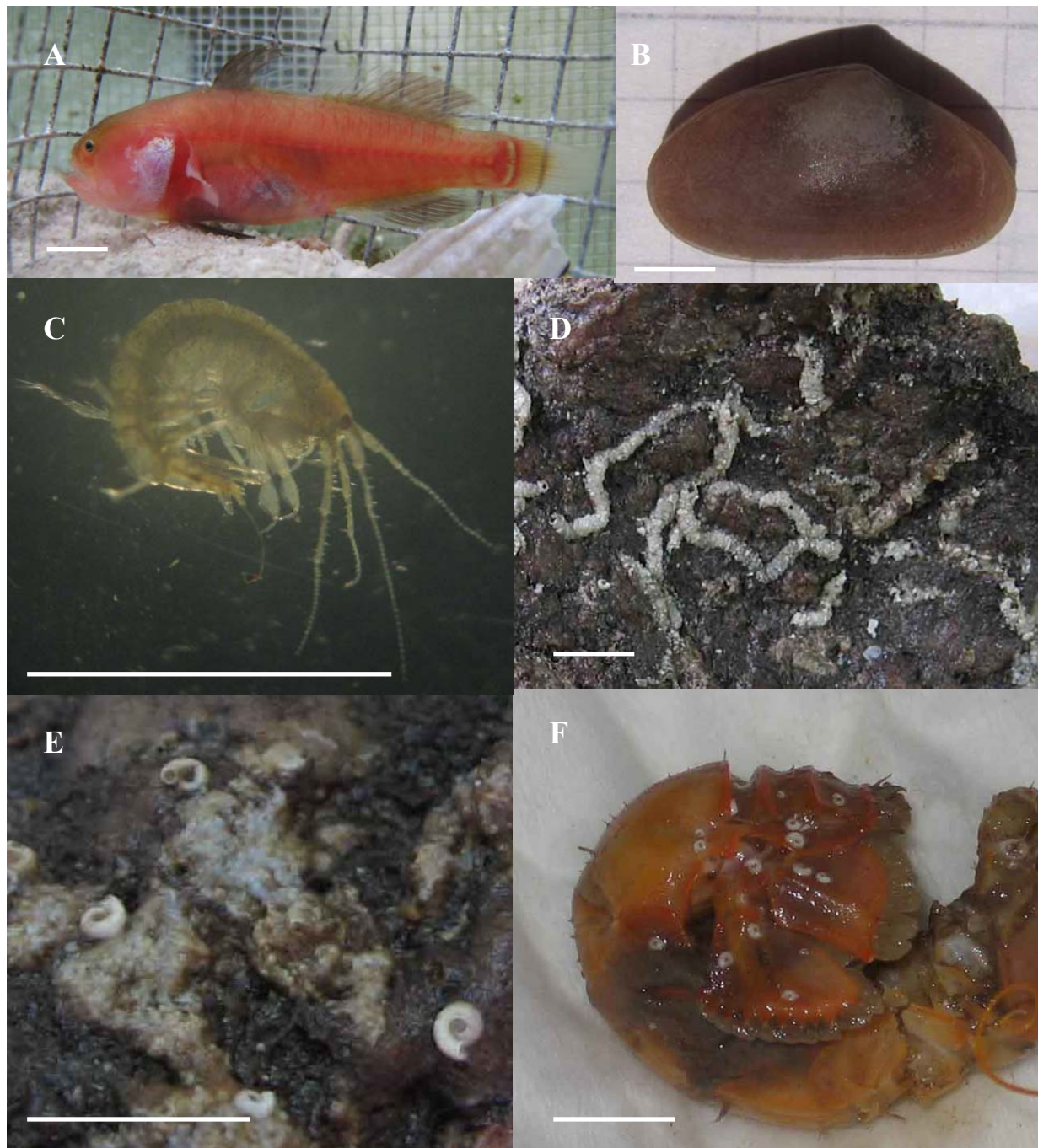


Fig. 22: (A) A live specimen of *Austrolethops wardi* caught from a burrow of *N. acanthus*, (B) Up to eight specimen of a previously unidentified clam species were found in burrows of *N. acanthus*, (C) a commensal Amphipod species, (D) Tube-building polychaete worms dwell on the burrow lining of *N. acanthus*, (E) & (F) another tube-building polychaete species is found on the burrow lining and growing on the tail fan of individuals of *N. acanthus*. All scale bars represent 5 mm.

3.2.2 The burrow lining of *Neaxius acanthus* and *Corallianassa coutierei*

I Water and organic content

ANOVA was not possible due to high in-group variation even after arcsin / root-transformation.

No differences in water and organic content were found between surrounding sediment samples from different depths. The water content as difference between wet and dry weight was greatest for the lining of *Neaxius*-burrows (87% / DW), followed by the lining of *Corallianassa*-burrows (52%) compared to the sediment with a water content of 26% (Fig. 23A). The same applies for the loss on ignition (LOI; difference between dry weight and ash free dry weight) which represents the organic content of a sediment (LOI 16% / DW for *Neaxius*, 5% for *Corallianassa* and 3% for sediment) (Fig. 23B).

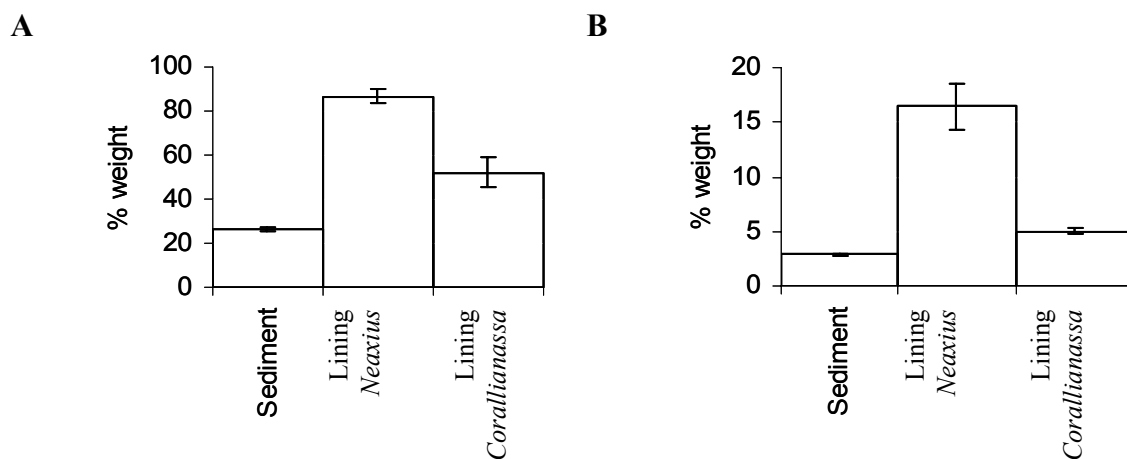


Fig. 23: (A) Water content of surrounding sediment, burrow lining of *N. acanthus* and *C. coutierei* as % weight water / DW ; (B) Organic carbon content of surrounding sediment, burrow lining of *N. acanthus* and *C. coutierei* as % LOI / DW. Bars represent standard errors.

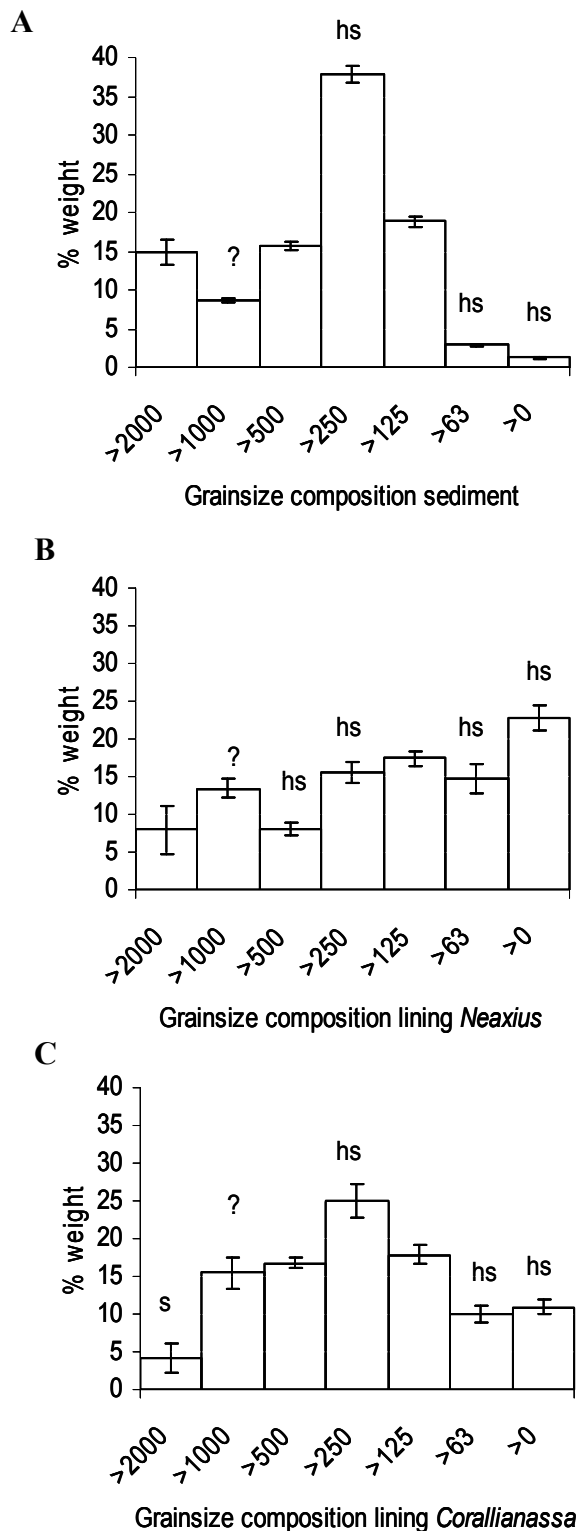


Fig. 24: Grainsize composition as % weight of the inorganic fraction; letters indicate significant (s) or highly significant (hs) differences between samples; (A) Grainsize composition of sediment from the Bone Batang seagrass meadow, cumulated for surface sediment and sediment from 15 and 30 cm depth (B) Grainsize composition of the lining of *Neaxius*-burrows (C) Grainsize composition of the lining of *Corallianassa*-burrows.

II Grain size

The silt fraction in the surrounding sediment shows much smaller percentages than in the burrow lining of *N. acanthus* and *C. coutierei*. A 19- and 9-fold increase in percentage of grains $<63 \mu\text{m}$ was found, respectively, compared to the surrounding sediment.

The grain size class between 63 and 125 μm show a 5-fold higher percentage for *N. acanthus* and a 3-fold higher value for *C. coutierei*. The fraction between 1000 and 2000 μm shows an about 2-fold increase in the lining of both species. All other fractions are underrepresented in the lining compared to the surrounding sediment.

Following arcsin-root (x/n) – transformation, ANOVA was possible for all fractions except grains $>1000 \mu\text{m}$ (factors: surface sediment, sediment 15 cm, sediment 30 cm, variants: >2000 , >1000 , >500 , >250 , >125 , >63 , >0 ; ANOVA $F(28, 69.928) = 10.259$, $p < 0.01$). No differences were found between surrounding sediment samples from the surface, 15 and 30 cm depth. *Neaxius*-lining shows a decrease of the fraction $>500 \mu\text{m}$ (Tukey HSD post-hoc, $p < 0.01$) compared to the surrounding sediment. *Corallianassa*-lining shows a decrease of the fraction $>2000 \mu\text{m}$ (Tukey HSD post-hoc, $p < 0.05$). The lining of both species shows a significant increase of the fractions >250 and $>0 \mu\text{m}$ (Tukey HSD post-hoc, all $p < 0.01$) (Fig. 24).

3.2.3 Burrow water properties for *Neaxius acanthus*

The ammonium data had to be log-transformed to achieve normal distribution. Ammonium concentration in sediment pore water and the water column is not dependent on vegetation cover (dense or sparse) but on sampling depth (factors: (dense, sparse, water column) * (water column, burrow, different sediment depths), variants: values; ANOVA $F(7, 43) = 2.4936$, $p < 0.05$) (factors: water column, burrow, different sediment depths, variants: values; ANOVA $F(8, 51) = 6.818$, $p < 0.01$). Burrow water significantly differs from the upper ten cm of sediment and the water column (Tukey HSD post-hoc, $p < 0.05$ for all depths except < 0.01 for 4.5 cm depth) (Fig. 25A).

The reactive phosphate data were also log-transformed to achieve normal distribution. Vegetation cover has no influence on concentrations of reactive phosphate; values only depend on sampling site (water column, sediment pore water, burrow water), burrows show a highly significant increase in reactive phosphate concentrations (factors: (dense, sparse, water column) * (water column, burrow, different sediment depths), variants: values; ANOVA $F(7, 44) = 0.476$, $p > 0.05$) (factors: water column, burrow, different sediment depths, variants: values; ANOVA $F(8 / 52) = 20.390$, $p < 0.01$) (Fig. 25B).

Oxygen concentrations showed too much in-group variation to allow ANOVA but burrow water oxygen values seem to be in between those for water column and sediment. Sediment pore water shows a gradual decrease in oxygen saturation with increasing depth but is still oxygenated at 45 cm depth (Fig. 25C).

The pH data were root-transformed to achieve normal distribution. pH values of both burrow and water column differ from the rest, again no significant influence of vegetation cover on the values measured could be found ((factors: (dense, sparse, water column) * (water column, burrow, different sediment depths), variants: values; ANOVA $F(7, 44) = 0.205$, $p > 0.05$) (factors: water column, burrow, different sediment depths, variants: values; ANOVA $F(8, 52) = 39.918$, $p < 0.01$) (Fig. 25D).

Salinity was found to be 33‰ in all samples.

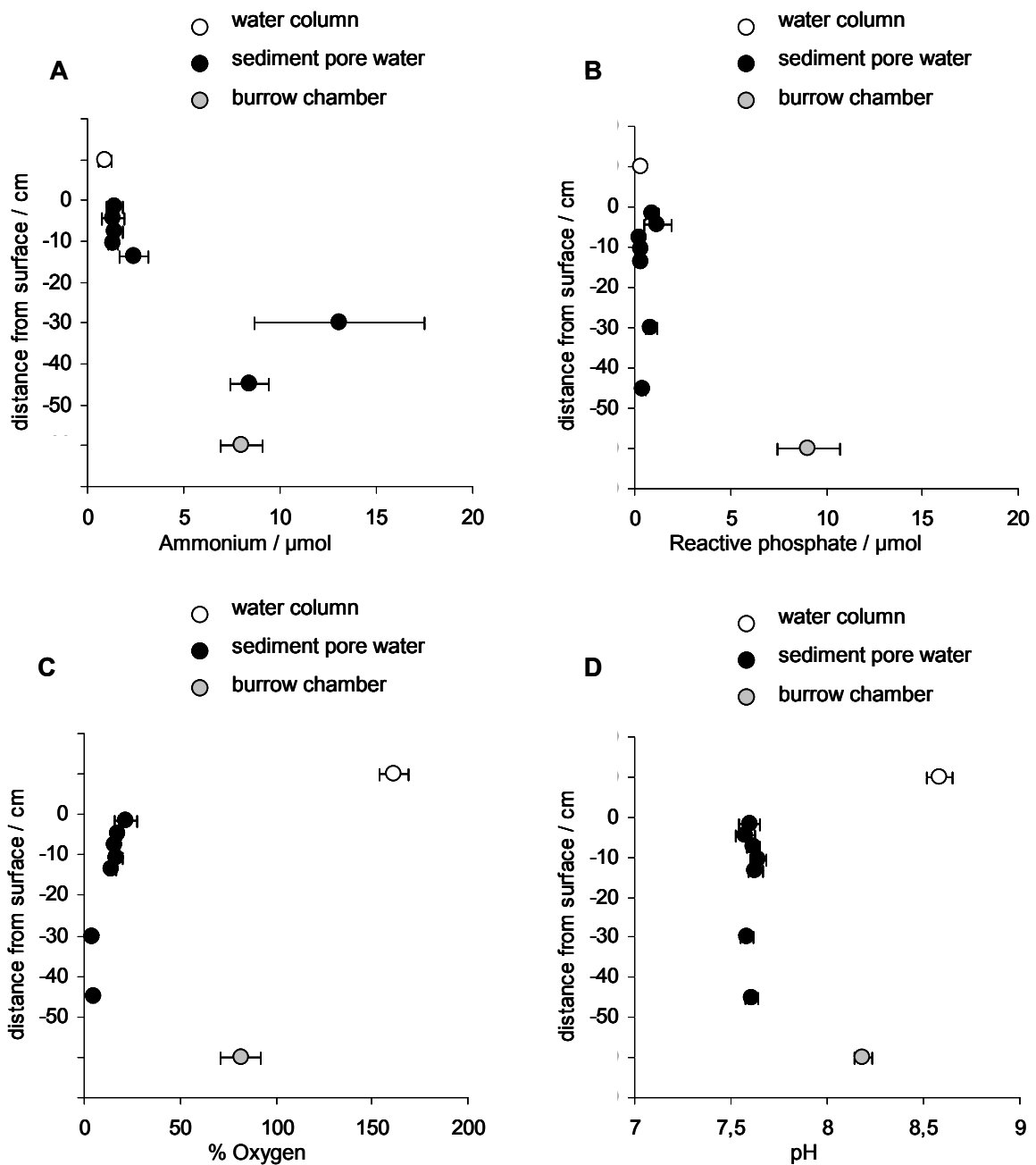


Fig. 25: Abiotic factors as measured in burrows of *N. acanthus* compared to sediment pore water and water column in the Bone Batang seagrass meadow. Bars represent standard errors. (A) Ammonium concentration in the water column, in sediment pore water and *Neaxius*-burrows; (B) Reactive phosphate values measured in the water column, in sediment pore water and *Neaxius*-burrows; (C) Oxygen values in % saturation measured in the water column, in sediment pore water and *Neaxius*-burrows; (D) pH values measured in the water column, in sediment pore water and *Neaxius*-burrows.

3.3 Morphometric properties and individual weight in *Neaxius acanthus*

The carapace length of individuals of *Neaxius acanthus* is correlated to the diameter of the burrow inhabited, the correlation was found to be better for male individuals (male: $y = 1.190x + 4.123$, $R^2 = 0.872$ ($n = 16$), female: $y = 0.741x + 12.897$, $R^2 = 0.663$ ($n = 14$)) (Fig. 26). Large specimen (carapace length >15 mm) were found to be sexually dimorphic with females possessing a relatively shorter carapace compared to total length than males (male: $y = 0.354x + 2.648$, $R^2 = 0.840$ ($n = 16$); female: $y = 0.254x + 7.512$, $R^2 = 0.699$ ($n = 5$)) (Fig. 27A). *N. acanthus* was found to possess a major and a minor cheliped: one claw was always slightly (females) or markedly (males)

longer and bulkier than the other one. Male major chelipeds in general were longer (male: $y = 0.384x^{1.157}$, $R^2 = 0.667$ ($n = 39$); female: $y = 0.312x + 4.962$, $R^2 = 0.643$ ($n = 25$)) (Fig. 27B) and heavier (male: $y = 0.000004x^{3.555}$, $R^2 = 0.5496$ ($n = 39$); female: $y = 0.011e^{0.089x}$, $R^2 = 0.705$ ($n = 25$)) (Fig. 27C) than female major chelipeds. The differences were greater for big individuals. About 50% of all male and all female individuals carried the major cheliped on their right side.

The ratio between carapace length and body wet weight was the same for males and females which carried eggs on their pleopods (male: $y = 0.0003x^{3.074}$, $R^2 = 0.899$ ($n = 40$); female carrying eggs: $y = 0.0003x^{3.080}$, $R^2 = 0.889$ ($n = 14$)), females without eggs were lighter ($y = 0.470e^{0.095x}$, $R^2 = 0.741$ ($n = 12$)) (Fig. 27D).

Body dry weight increases with increasing carapace length, the sequence from heavier to lighter was male over female with eggs to female without eggs (male: $y = 0.0002x^{2.804}$, $R^2 = 0.855$ ($n = 24$); female with eggs: $y = 0.174e^{0.085x}$, $R^2 = 0.584$ ($n = 12$); female without eggs: $y = 0.006x^{1.679}$, $R^2 = 0.788$ ($n = 9$)) (Fig. 27E).

The sequence for ash-free dry weight is the same for big individuals, whereas the ranking for smaller individuals is altered to female with eggs over female without eggs to male (male: $y = 0.00007x^{2.874}$, $R^2 = 0.806$ ($n = 24$); female with eggs: $y = 0.007x^{1.467}$, $R^2 = 0.523$ ($n = 12$); female without eggs: $y = 0.128e^{0.077x}$, $R^2 = 0.407$ ($n = 9$)) (Fig. 27F).

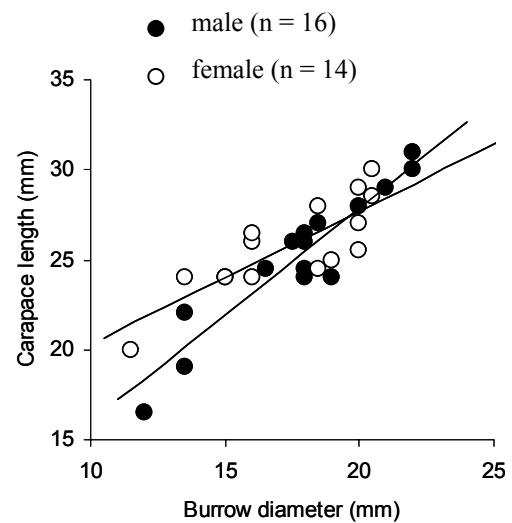


Fig. 26: The relation between burrow diameter and carapace length for male and female specimen of *Neaxius acanthus*.

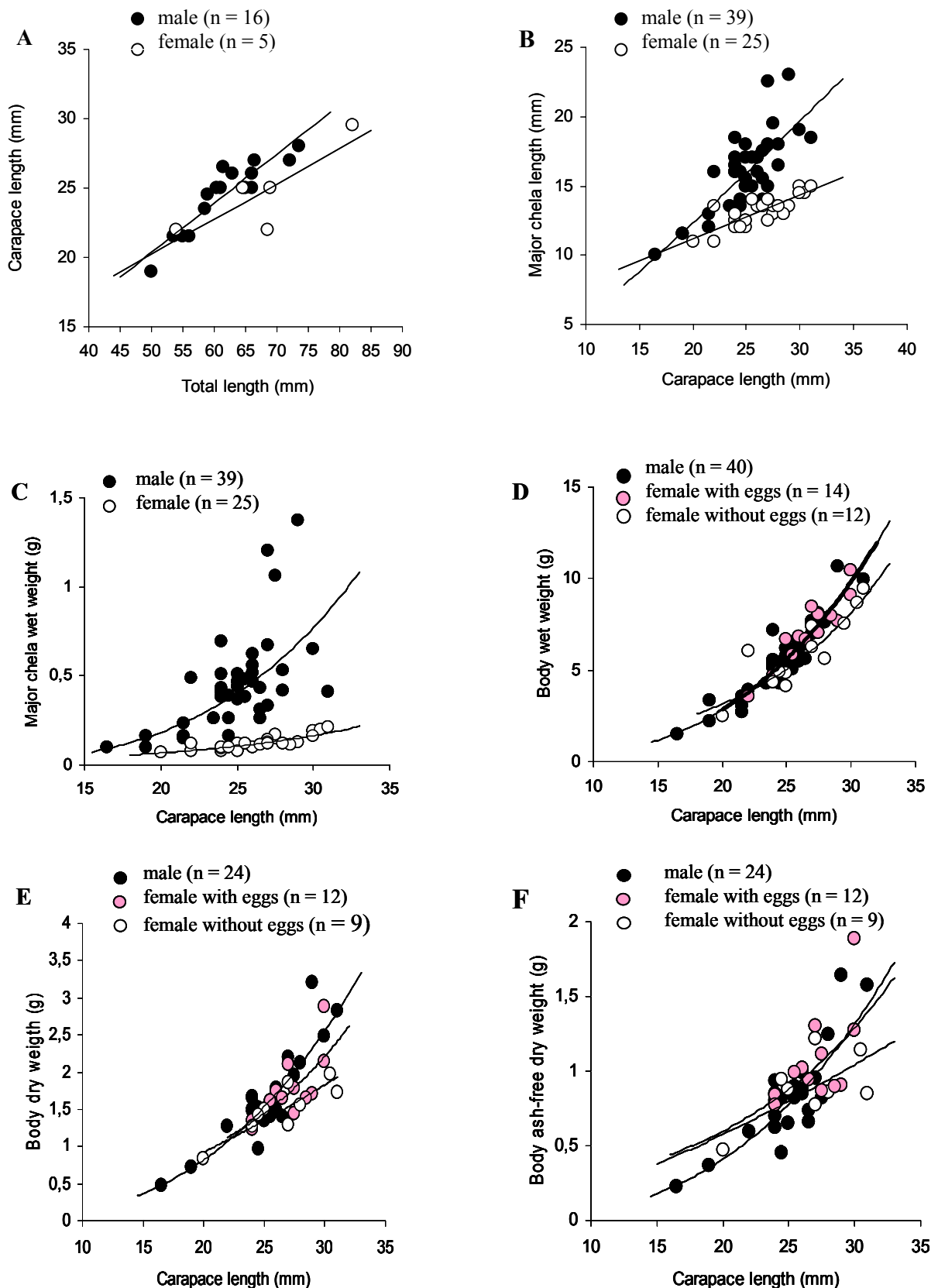


Fig. 27: (A) The relation between total length and carapace length. The abdomen is more pronounced in big female individuals, (B) Big male individuals possess a larger major chela (propodus), (C) Major chela wet weight (propodus + dactylus) is markedly higher for big male individuals, (D) The relation between carapace length and body wet weight is the same for male individuals and females carrying eggs, (E) Body dry weight is higher for big male individuals than for females carrying eggs, which in turn show a higher value than females without eggs, (F) Body ash-free dry weight is higher in small female individuals, big males show about the same value as females carrying eggs, which is more than for female individuals without eggs.

Assuming that 88% of the burrows contain a male and 88% contain a female individual (meaning 75% pairs) this equals a total of 4.4 g AFDW m⁻² in the dense and 1.5 g AFDW m⁻² in the sparse area if the relations established here are integrated into the frequency of diameters. Dry weight can be assumed to be 8.3 or 2.8 g m⁻², respectively. N, C and protein were found to be 3.7, 18.3 and 22.8% of shrimp DW, the population of *N. acanthus* on Bone Batang thus represents 0.3 and 0.1 g N, 1.5 and 0.5 g C and 1.9 and 0.6 g protein m⁻² in the dense and the sparse area, respectively.

3.4 Observation of the behaviour of *Neaxius acanthus*

3.4.1 *In-situ*

All six burrows chosen were inhabited by couples. In 61 ± 6 (SE) (0 to 100) % of the time, the male shrimp was observed at the burrow entrance. Female shrimp were visible 38 ± 6 (SE) (0 to 100) % of the time. Openings were unattended 1 ± 0 (SE) (0 to 7) % of the time.

On average 2 ± 0 (SE) (0 to 5) leaves were caught in 15 min. Of the resulting total of 30 leaves, two measured between 0 and 1, seven between 1 and 3 and six between 3 and 5 cm. The remaining 15 leaves measured more than 5 cm.

An estimation of the biomass (leaves + epiphytes) transported in the burrows resulted in 1.920 ± 1.364 g DW opening⁻¹ d⁻¹.

3.4.2 In aquaria

All animals introduced into the aquaria immediately started excavating a new burrow. The animals first created a depression in the ground by picking up sediment with the anterior appendages and then walking either backwards and dropping it, rotating and dropping it or performing a somersault followed by a half roll and dropping it. As soon as the depression had grown to a more or less vertical tunnel big enough to accommodate the whole animal it would slide into it tail first and tamp the sediment around the entrance.

To enlarge the hole, the animals left it, turned around, dove into it head first and picked up more sediment from the end of the tunnel which was then brought up by walking backwards

and carrying the load and then deposited around the opening or tamped into the burrow wall. From time to time, the animals bulldozed the sediment which accumulated around the opening to the side. At a depth of about 15 cm the animals created a chamber which was high and / or wide enough to permit the somersault and / or the rotation. Thereafter, only little sediment was deposited around the entrance. Most sediment gained by digging was either deposited on the floor or tamped into the walls. The entrance was only approached headfirst and animals never again ventured out of it. As a result of tamping, all parts of the burrow except for floor areas with an inclination of less than about 45° became lined.

Digging was only successful if the sediment offered was stabilized by seagrass rhizomes and / or big rubble parts. Whereas all animals that had created a burrow lived until the experiment was stopped animals that failed to create a burrow died within hours or days.

Burrows excavated in aquaria all showed a circular embankment of excavated sediment around the opening. The embankment was also lined from the inside. For periods which lasted between hours and days the openings were blocked with sediment, shells or boulders. By transporting new sediment to the entrance and pushing it into the block a small expulsion mound grew. When reopening the burrow, the upper parts of the embankment were flattened by bulldozing excess sediment down their sides. Each burrow constructed in the aquaria had only one opening. Interestingly, closed openings are immediately closed again and open burrows are immediately reopened by their inhabitants if they are experimentally opened or filled, respectively.

I Single individuals:

All behaviour observed in the burrows could be ascribed to one of the 12 behavioural states listed below:

1. **Tamping / Sticking:** maxillipeds 3 and pereopod 2 perform tamping movements on sediment which is secured by pereopods 1 and 3. This state is typically performed on sediment gained by “stirring” or “digging”. The animal is only supported by pereopods 4 and 5, when “tamping / sticking” head down only by pereopods 4. A sticky substance is secreted from maxillipeds 3 and / or pereopods 2, both of which are stabbed into the burrow wall to a depth of several mm. “Tamping / sticking” is only done on burrow walls and roof, never on the floor. While “tamping / sticking”, food particles may also be ingested.

2. **Cleaning:** pereopods 4 are predominantly used to clean setal rows on pereopods 2, whereas maxillipeds 3 are used to clean the antennae. Pereopods 5 clean the ventral side of the carapace. “Cleaning” is mostly done in a big chamber which is high enough to allow the animal to stand on pereopods 1 and the tail fan and form an arch, the typical posture when cleaning.
3. **Carrying:** pereopods 1 (sides) and 2 (bottom) form a basket, the load is secured with maxillipeds 3 on top. Setal rows on pereopods 1 and 2 close the gaps. Is mostly done while walking forwards or backwards.
4. **Stirring:** pereopods 2 performs movements from lateral to central while maxillipeds 3 move from anterior to posterior. There is a smooth transition between gentle and vigorous stirring; the latter includes lateral to central movements of pereopods 1 (Fig. 28). Frequently leads to carrying sediment on pereopods 2 or pereopods 1 and 2. “Stirring” can also be performed while slowly walking forwards or backwards. Vigorous stirring will cause the front end of the animal to disappear behind a cloud of particles. “Stirring” probably serves for filtering out particles of a certain size and weight and may often lead to the ingestion of particles. It might also serve for brushing particles of smooth surfaces like shell fragments and burrow walls.
5. **Scratching:** like “Stirring” but performed on a glass wall or shell fragment.
6. **Digging:** maxillipeds 3 and pereopods 1 and 2 are stabbed into the sediment and withdrawn by a movement of maxilliped 3 towards posterior and a movement of pereopods 1 and 2 towards central / posterior. This results in a small pile of sediment being loaded on pereopods 2.
7. **Resting / Waiting:** no movements except for the beating of the scaphognathite and pleopods 3 – 5 (breathing). This activity is almost exclusively performed when sitting just beneath the entrance.
8. **Turning:** changing the direction of locomotion by performing a forward somersault followed by a half roll along the body axis or by rotating 180°.



Fig. 28: Anterior end of a female *N. acanthus* stirring; this action serves in sorting sediment.

9. **Walking:** moving forwards or backwards on pereopods 2 – 5. Individuals were observed carrying sediment or objects while walking in both directions.
10. **Bulldozing:** pushing sediment which is not lifted up by appendages in front of the carapace.
11. **Feeding:** manipulating small amounts of sediment or seagrass leaves in front of the mandibles. Feeding probably also occurs while “stirring” and “tamping / sticking”.
12. **Manipulating objects:** activities like trying to lift up a stone, working a shell fragment out of or into the ground or cutting seagrass leaves.

Walking was ascribed to stirring or carrying if it co-occurred with these activities. Likewise, feeding often had to be ascribed to stirring.

Walking was most frequently displayed (49 times h⁻¹) but lasted only 10 s on average. It is followed in frequency by tamping / sticking (33 times, 28 s), stirring (21 times, 14 s), resting (19 times, 62 s), being invisible (14 times, 15 s), digging (12 times, 9 s), carrying (11 times, 10 s), turning (10 x, 5 s), cleaning (4 times, 29 s), bulldozing (4 times, 7 s), scratching (3 times, 18 s), feeding (2 times, 20 s) and manipulating objects (2 times, 13 s). If the behavioural states are listed according to their average duration, the sequence is the following: resting, cleaning, tamping / sticking, feeding, scratching, being invisible, stirring, manipulating objects, walking, carrying, digging, bulldozing and turning.

Based on these findings, five behavioural classes were defined:

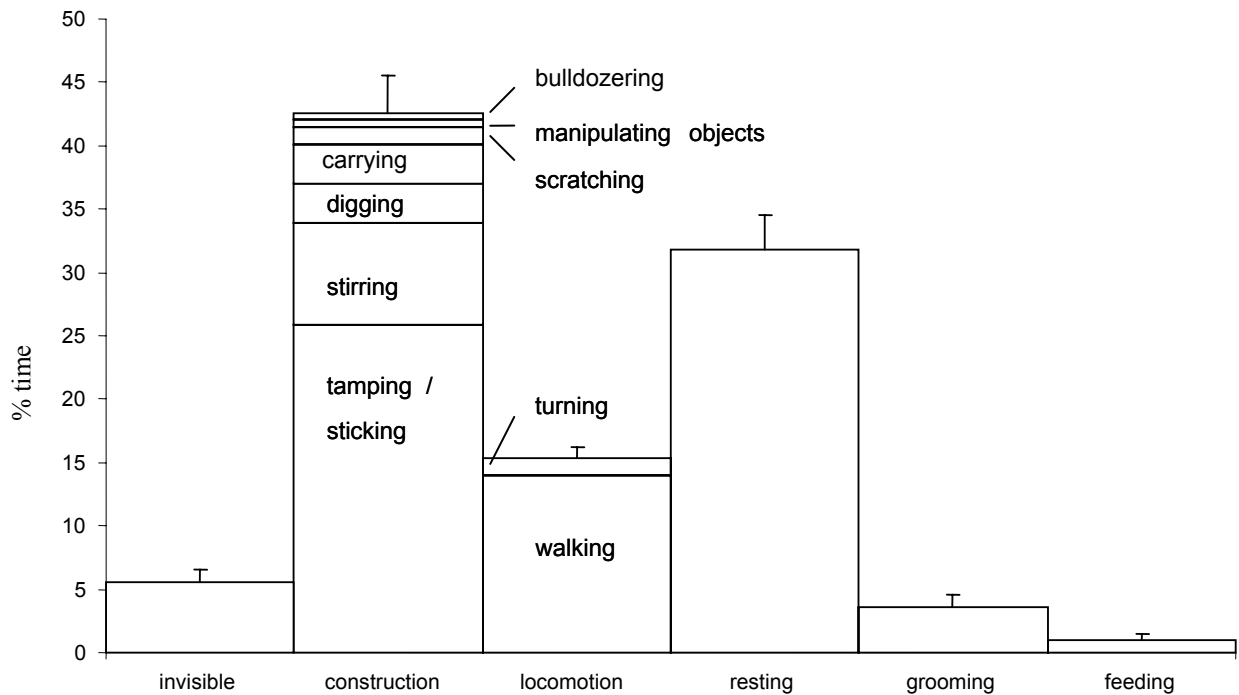
1. **Construction:** contains tamping / sticking, bulldozing, scratching, stirring, carrying, manipulating objects and digging.
2. **Locomotion:** contains walking and turning. Walking while carrying or stirring is ascribed to construction.
3. **Resting:** contains resting / waiting.
4. **Cleaning:** contains cleaning.
5. **Feeding:** contains feeding.

ANOVA was not possible due to high in-group variation even after arcsin / root-transformation. No differences were, however, found in the time budget according to the behavioural classes at any time of the day.

Animals were invisible 6 ± 1 (SE) (between 0 and 19), engaged in construction 43 ± 3 (SE) (between 9 and 70), engaged in locomotion 15 ± 1 (SE) (between 6 and 28), resting 32 ± 3 (SE) (between 6 and 63), cleaning themselves 4 ± 1 (SE) (between 0 and 26) and exclusively feeding 1 ± 0 (SE) (between 0 and 9) % of the time ($n = 32$) (Fig. 29A). 39 ± 4 (SE) % of the time was spent at the entrance where the animals were mainly resting (81% of the total time

spent resting), followed by construction (28% of the total time spent on construction, construction as performed in the entrance is almost exclusively tamping / sticking) (Fig. 29B).

A



B

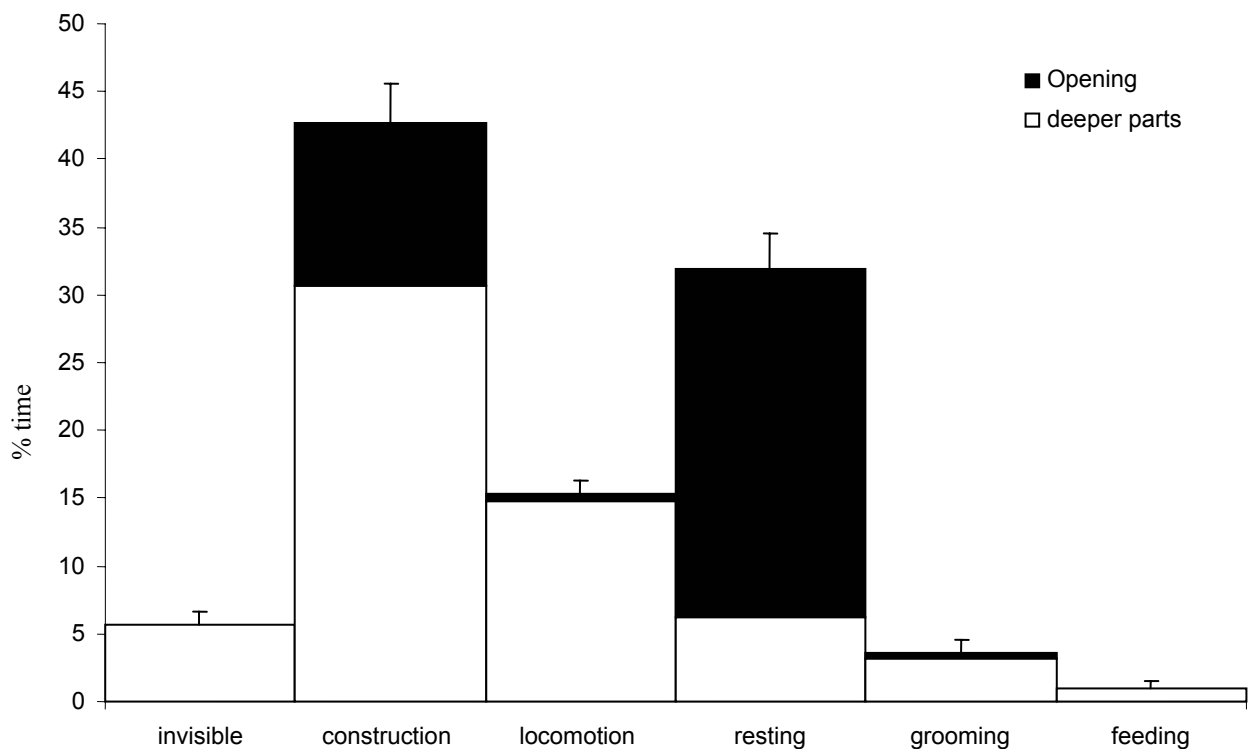


Fig. 29: (A) Time budget of single Individuals of *Neaxius acanthus* heltered in aquaria as estimated from 32 observations a 15 min on 4 animals; (B) Time sharing between activity at the opening and in the deeper parts of the burrow. Most behavioural components are displayed below the surface; when in the opening animals are mainly inactive, the remaining time is almost exclusively spent on tamping / sticking. Bars represent standard errors.

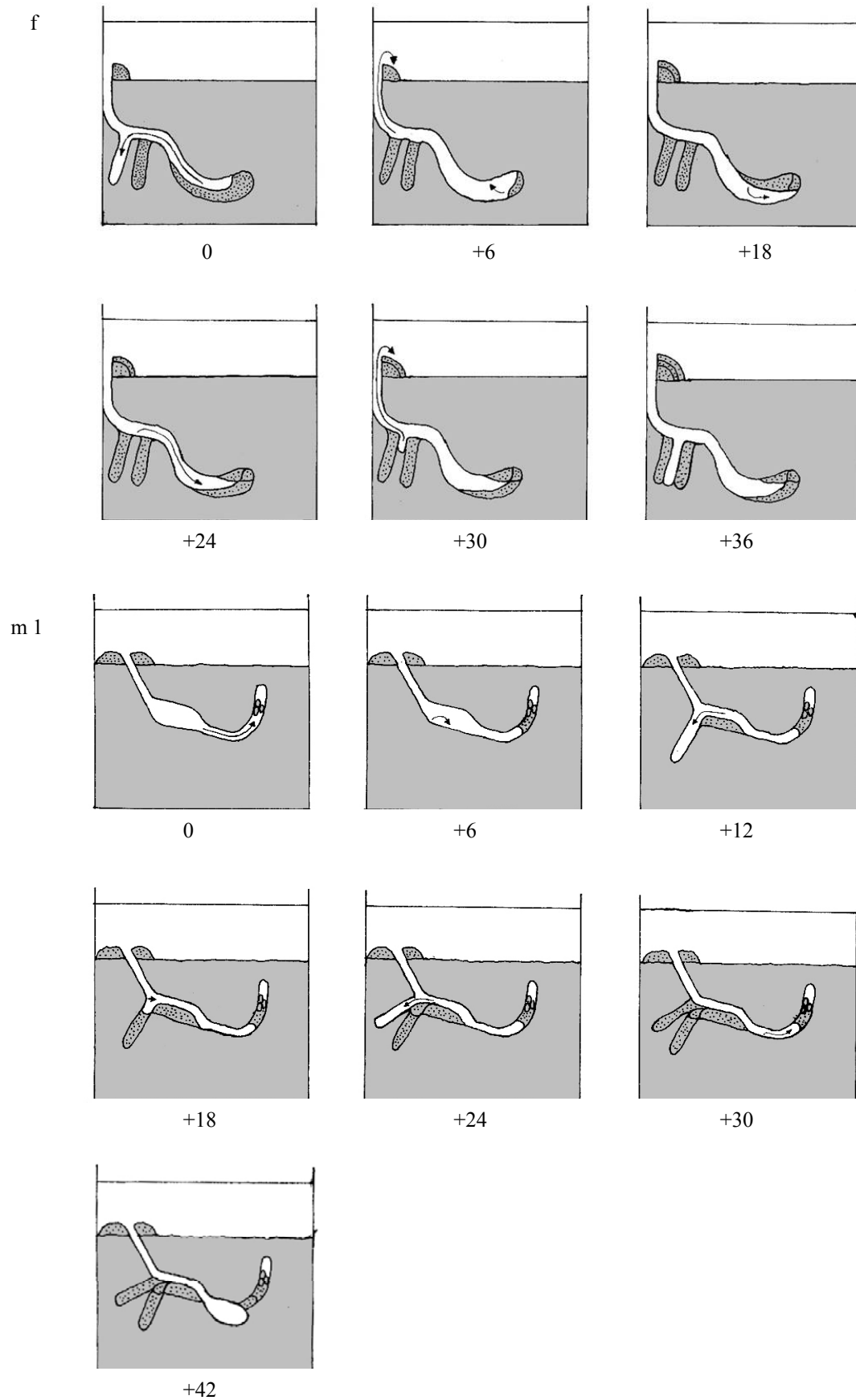


Fig. 30: Dynamics of the burrow of a female (f) and a male (m1) individual within 6 h spanning a total of 42 h. Dotted areas represent sediment which has already been moved by the animal. Arrows indicate the movement of sediment at the moment the sketch was drawn. If no changes occurred within 6 h the corresponding sketch is not shown here.

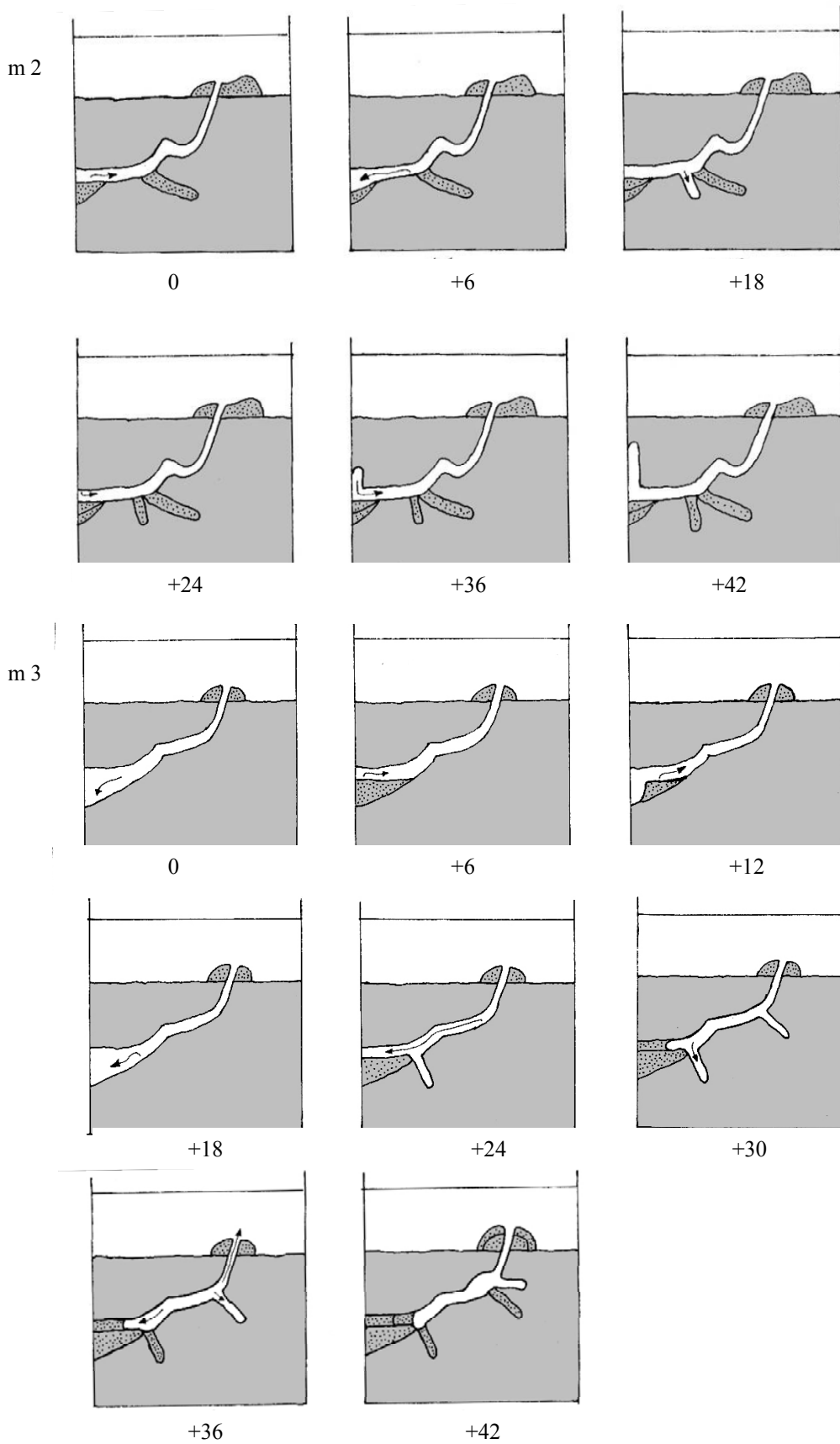


Fig. 31: Dynamics of the burrow of two male individuals (m2 and m3) within 6 h spanning a total of 42 h. Dotted areas represent sediment which has already been moved by the animal. Arrows indicate the movement of sediment at the moment the sketch was drawn. If no changes occurred within 6 h the corresponding sketch is not shown here.

II Burrow dynamics:

A sketch of the outline of four burrows was drawn every six h spanning a total of 42 h. The general shape made up of a vertical shaft and a horizontal chamber was found to remain unchanged during the observation period but finger like extensions of the basal chamber were continuously being dug into the surrounding sediment. These blind tunnels of about 10 cm length never lasted for more than two consecutive observations before they were refilled by the animals. New extensions were always built where no tunnel had been before. The sediment excavated when digging such a new tunnel was dropped on the chamber floor and later used to fill an old tunnel. Two of the animals were observed depositing small amounts of sediment around the openings (Fig. 29, Fig. 30).

III Leaf processing in single individuals:

In contrast to the *in-situ* observation, some leaves were not immediately accepted. Leaf processing typically started by grasping the leaf with Mxp. 3 and pereopods 1 and 2. Leaves were then either rolled into a ball or directly transported below where the animals manipulated them with their mouthpart (this was sometimes done while performing tamping / sticking or stirring) or ripped them into pieces with alternating movements of pereopods 1. This ripping movement greatly resembled the way a pair of scissors is used to cut a large piece of cloth. The leaf fragments were scattered on the burrow floor (because the animals moved while ripping on the leaves) and ultimately either became buried (by pushing them into the sediment at the end of blind tunnels or actively placing sediment over them) or worked in the burrow wall by tamping / sticking. Leaf manipulation always alternated with construction, cleaning and resting.

IV Encounters:

One of the encounters between a male (resident) and a female (newcomer) shrimp led to a short (several s) tackling with the claws. The newcomer then walked past the resident and immediately performed behaviour which is here referred to as “construction”. From thereon, both shrimp generally avoided contact. When walking past one another in a narrow chamber, the partners seemingly ignored each other. The other intersexual encounter was similar, except for the fact that there was no tackling.

In contrast, the two intrasexual encounters were characterized by aggressive behaviour: The new female shrimp retreated from the burrow when it was first attacked by the resident but stayed close to the entrance. The resident almost jumped out of its burrow to reach it with its claws. The newcomer entered again and both shrimp then fought for about ten min.; phases where both rested with their claws interlocked alternated with phases of pushing and / or pulling and tackling. The newcomer then turned around, left the burrow and started digging its own hole at the other end of the aquarium. The two female shrimp were not lacking appendages or were otherwise damaged after the fight.

After a short phase of tackling, the two male shrimp also interlocked their claws for about a minute and a half. When the resident shrimp started pushing a vigorous fight broke out which lasted for about a minute before the resident lost both pereopods 1. It then made the roof in front of him collapse to form a barrier between itself and the newcomer. Later it removed the block, walked past the newcomer, turned around and again made the roof collapse. About an hour then passed while the newcomer was busy pushing against the barrier while the resident continued to build it up by adding new sediment to it. This was interrupted by phases of resting and construction. Two hours after the initial contact, the resident had been driven out of his burrow and started digging a new one.

V Time allocation in pairs:

As an outcome of the encounters experiment two burrows were inhabited by pairs. One partner typically remained inactive at the entrance while the other was mainly engaged in construction. The latter mostly initiated the exchange by positioning itself behind the shrimp in the entrance and touching its tail fan and / or pleopods with antennae 2. The shrimp in the entrance then walked backwards, turned around and started construction in the deeper parts of the burrow while the other walked up to the opening and remained there in an inactive state.

VI Leaf processing in pairs:

Offered seagrass leaves were treated as by single individuals; the shrimp that had caught the leaf started processing it but the other would also pick up fragments which had been dropped and would process them.

3.4.3 Seagrass density and biomass decrease in the proximity of the opening

ANOVA was not possible due to high in-group variation. On average shoot number, leaf biomass, leaf sheath biomass and rhizome biomass of *Thalassia hemprichii*, *Halodule uninervis* and *Cymodocea rotundata* decrease by about 50% in the proximity of the burrow opening; this decrease is more prominent if a smaller core diameter is chosen (Fig. 32).

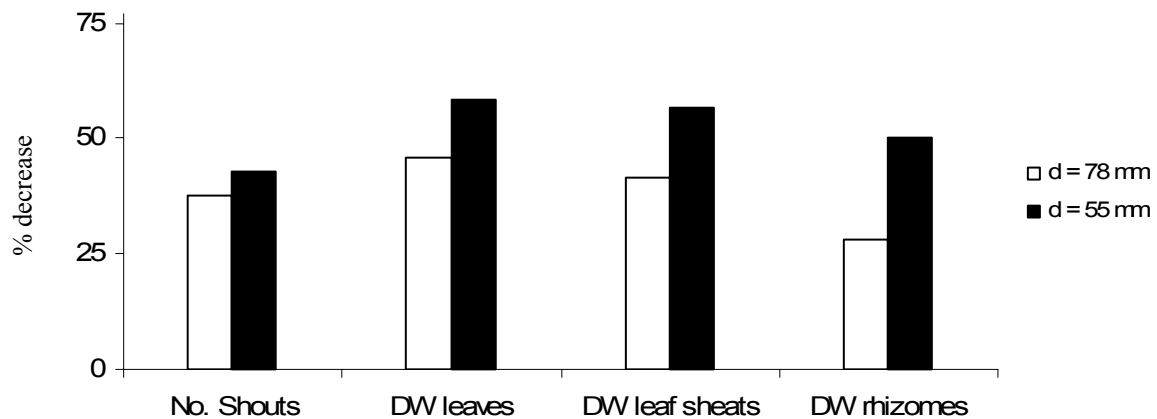


Fig. 32: % decrease in shoot number and leaf, leaf sheath and rhizome biomass within 78 and 55 mm distance (radius) from burrow openings of *Neaxius acanthus*.

3.4.4 Burrow openings of *Neaxius acanthus* as traps for leaf detritus

On average 1.386 ± 0.177 g (SE) DW opening⁻¹ d⁻¹ were caught in the detritus traps.

The amount of litter caught actively by the shrimp was estimated to be 1.920 ± 1.364 (SE) g DW opening⁻¹ d⁻¹.

Shrimp activity therefore increases the intake of detritus by 0.543 g DW d⁻¹ or 39%.

3.5 General observations

The colouration in *Neaxius acanthus* can be anything from bright pink to pale orange. As observed in one case in an aquarium, freshly moulted individuals are pink; thereafter, the colour gradually fades to orange. The apparent density of coverage with hairs, especially on chelipeds, antennae, pleopods and pleon was also found to be subject to considerable variation (Fig. 33). Light microscopy revealed that this is caused by particles sticking to the

hairs. Whether these particles represent sediment grains or epibionts could not be determined due to the fixation method.

The shrimp gut was found to contain a mixture of fine sediment particles and fragments of multicellular plants.

A single inspection of the study area was made at night time using a flashlight. No individuals of the burrowing shrimp *N. acanthus* or the commensal goby

Austrolethops wardi were observed outside the burrow. Many shrimp were seen in the entrance and stretching out their claws just like during daytime.

Two more species of thalassinidean shrimp were found in the Bone Batang seagrass meadow: two specimen of *Callianidea typha* (Milne-Edwards 1837) and three specimen of *Calliastina* cf. *novaebritanniae* (Borradaile 1900) (Fig. 34A). The latter is probably responsible for some of the expulsion mounds found to the north of the seagrass meadow (Fig. 34B). The majority of the mounds, however, are probably caused by another callianassid species, maybe *Glypturus armatus* (Milne-Edwards 1870) which is very hard to catch (Dworschak, pers. comm.).

One or two individuals of an unidentified palaemonid shrimp species (probably *Periclimenes* sp.) (Fig. 34D and E) could frequently be observed sitting in the burrow entrance just above - or on the carapace of - the *N. acanthus* individual waiting below the entrance. From time to time these cleaner shrimp had to quickly escape from being grasped by an individual of *N. acanthus* but would remain in the burrow opening. At low tide the burrow entrance represents a little tidal pool. In this situation other animals were occasionally observed seeking a refuge in there: several species of small crabs (Brachyura) (Fig. 34C) and juvenile fish, probably *Dischistodus* sp. (Pomacentridae) and *Apogon* sp. (Apogonidae).

Three individuals of *N. acanthus* placed outside their burrows were immediately but without success attacked by unidentified fishes of about the same size as their own. Seconds later, an individual of the bream *Pentapodus trivittatus* (Bloch 1791) (Fig. 34F) would appear on the scene. The bony fish which is hardly twice the size of the shrimp first swallowed the posterior end and broke off the claws by repeatedly trashing its head against the sediment. The claws were then ingested by individuals of the cigar wrasse *Cheilio inermis* (Forsskål 1775). *Pentapodus trivittatus* was also observed swallowing the commensal clams if they were dug out.



Fig. 33: *Neaxius acanthus*, a male individual. The woolly appearance is caused by particles, maybe epibionts, sticking to the hairs (source: www.flmnh.ufl.edu).

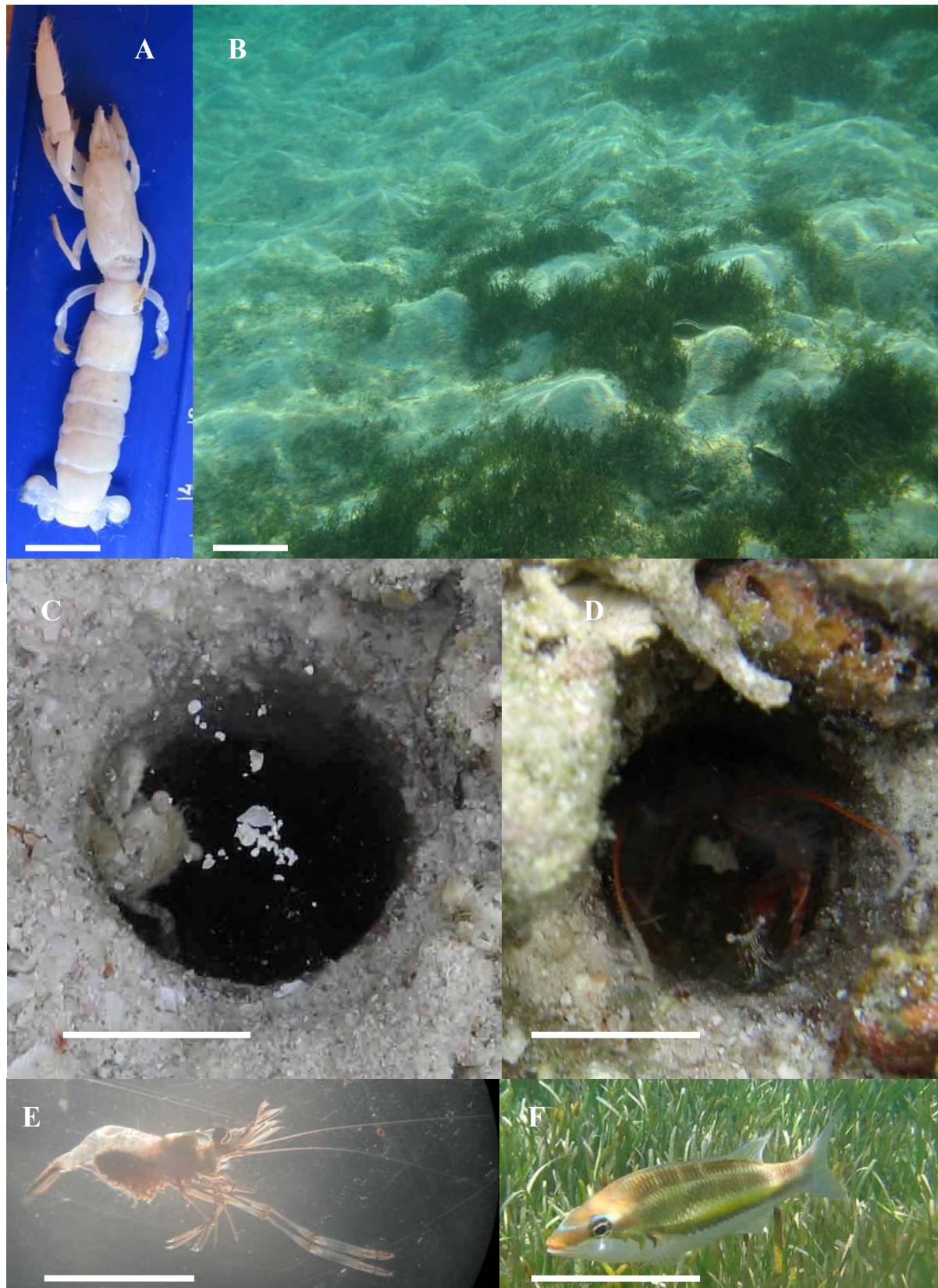


Fig. 34: (A) *Calliixina cf. novaebritanniae* (Callianassidae) may be responsible for some of the expulsion mounds encountered to the North of the study site (B). (C) At low tide mall crabs can be seen seeking refuge in burrow openings of *Neaxius acanthus*. (D) A palaemonid shrimp is sitting just above a female *Neaxius acanthus*. (E) The same palaemonid shrimp in lateral view (E) The bream *Pentapodus trivittatus* has been observed swallowing individuals of *Neaxius acanthus* placed outside their burrows. Scale bars are 1 cm for (A), (C), (D) and (E) and 10 cm for (B) and (F).

4 Discussion

In this thesis an attempt was made to describe the role of a population of *Neaxius acanthus* in its habitat, a tropical seagrass meadow on Bone Batang island, Indonesia. *N. acanthus* co-occurs with the less abundant *Corallianassa coutierei* which has a similar lifestyle: both species can be observed catching floating leaf detritus passing their burrow openings.

The data resulting from a 5-month observation of the same 188 burrows of *N. acanthus* in a total of 135 m² in 9 permanent transects will be discussed in chapter 1.

A discussion of the burrow morphology of *N. acanthus* and *C. coutierei* as derived from polyester resin casts will follow. The unique properties of the burrow lining of both species compared to the surrounding sediment are also highlighted in chapter 2. Data gathered on ammonium, reactive phosphate, oxygen and pH in burrows of *N. acanthus*, the surrounding sediment and the water column are also discussed here.

Data on morphometric properties and individual weight were collected on 66 fixated specimen of *N. acanthus*. The results are discussed in chapter 3.

Chapter 4 will deal with various aspects of the behaviour of *N. acanthus* as observed *in-situ* and in aquaria, completed by a discussion of the function of the burrow opening as a detritus trap and decreasing seagrass shoot density and seagrass biomass around the latter. Some suggestions are made on the food resources of *N. acanthus*.

In chapter 5 some general observations made in the study site are highlighted.

The discussion closes with chapter 6, which represents an outlook.

4.1 Permanent transects

4.1.1 The population density of *Neaxius acanthus* in relation to seagrass cover

With about 3 openings m⁻² in the densely and 1 opening m⁻² in the sparsely vegetated area (1.75 and 5.25 individuals, respectively, assuming that 75% of the burrows are inhabited by pairs), the population density of *N. acanthus* is lower than the densities reported for some callianassid species (a mean 200 m⁻² for *Callianassa kraussi* in Branch & Pringle 1987, 120 m⁻² for *Callianassa truncata* in Ziebis *et al.* 1996, 22 m⁻² for *Callianassa subterranea* in Rowden, Jones & Morris 1998).

Pemberton, Risk & Buckley (1976) report an average density of 9 ind. m⁻² for *Axius serratus*. This species is closer related to *N. acanthus* and might be more representative because it is larger than the callianassid species mentioned before.

The densities given for *N. acanthus* in the literature are comparable to the densities observed in the sparse seagrass area. It must be considered that Mukai *et al.* (1989) and Erfteimeijer, Drossaert & Smaekens (1993) which both arrive at approx. 1 opening m⁻² have neither considered that a certain percentage of openings may be closed nor that burrows are mostly inhabited by pairs. The maximum density for *N. vivesi* is 9 m⁻² in Leija-Tristan (1994), the same number was measured here.

A dense seagrass cover in general might be unsuitable for most thalassinidean species and thus prevents their colonisation (Harrison 1987). It must be considered, however, that the species referred to in Harrison (1987) needs to sort large quantities of sediment when feeding. Accordingly, mound-building thalassinideans on Barrang Lompo island seem to be restricted to the upper intertidal which is unsuitable to seagrass due to long air exposure times (pers. obs.). On the other hand, the distribution of seagrasses and deposit-feeding thalassinideans in the Spermonde Archipelago could depend on the rubble content of the sediment. Unstable sediments with low rubble content probably do not suit seagrasses but favour sediment turnover by deposit feeders.

Since the burrows constructed by *N. acanthus* are very voluminous (up to 4 l) another factor restricting population densities to about 9 burrows m⁻² might simply be space.

N. acanthus seems to have no large-scale detrimental effects on seagrass density, the decrease in seagrass shoot density and seagrass biomass is restricted to the direct surroundings of the openings. The highest density of openings measured was 9 m⁻², even in this quadrant only an about 25% decrease of seagrass is caused by the shrimp (see the discussion of its grazing effects). Seemingly, the density of *N. acanthus* depends on seagrass density and not the other way round. Plausible reasons for this dependence might be the availability of floating detritus which is higher in areas of high seagrass production and the stabilising effect of seagrass rhizomes on the sediment. Without these conditions *N. acanthus* might not be able to construct its burrow. It was observed that the density of openings of *N. acanthus* decreases rapidly at the edge of the seagrass meadow. No openings were found at more than a few m distance from the edge. Aquarium observations also indicate that *N. acanthus* is unable to construct a new burrow in the absence of stabilizing rhizomes or large pieces of coral gravel.

4.1.2 Population composition, growth and recruitment for *Neaxius acanthus*

Burrows inhabited by pairs were not significantly bigger than burrows which were seemingly inhabited by single shrimp. This indicates that animals find their partners early and probably stay together in the same burrow for the rest of their lives. It must be assumed that the percentage of burrows inhabited by pairs is even higher (maybe close to 100%) than suggested in this study. The gender of the inhabitants of small burrows could not be determined in the field. The fact that most burrows of *N. acanthus* are inhabited by pairs has been overlooked by some researchers who equate shrimp number with the number of openings (Mukai *et al.* 1989, Erftemeijer, Drossaert & Smekens 1993). At the relatively low population densities observed, pair-bonding is an effective way to ensure reproduction (Shimoda *et al.* 2005).

Opening diameters, which have been shown to depend on the carapace length of the inhabitant shrimp, seem to be normally distributed. No changes occurred in population composition between October and January. The same pattern applies if only the smaller sized burrows are compared. It must be assumed that individuals of *N. acanthus* grow very slowly and that there is little recruitment, at least in the time of year when the permanent transects were monitored. Predation also seems to be an unlikely event under natural circumstances. It must be noted here that the related species *Calocaris macandreae* was found to live as long as 10 years and single annual moults were assumed (Buchanan 1967). The life history of *N. acanthus* might be subject to similar circumstances. It must, however, be considered that Mukai *et al.* (1989) measured an average diameter of only 15 mm for a population of *N. acanthus* in Papua New Guinea. This may have been caused by measuring at another time of the year than in this study, but unfortunately the month the measurements were made is not given by Mukai *et al.* (1989). Another reason for this difference might be that in the present study diameters are overestimated because the uppermost part of the shaft can be slightly funnel-shaped. Despite this, the general size distribution pattern proposed in the Papua New Guinean study is reflected here.

The monitoring of the permanent transects showed that there are little or no losses to predation. This might be different for smaller individuals which could be flushed out of the ground by stingrays (Harada & Tamaki 2003). Stingray feeding pits are visible in the Bone Batang seagrass meadow and stingrays were observed foraging in the seagrass meadow.

4.1.3 Residency and states of thalassinidean burrows in permanent transects

Burrows of *N. acanthus* are obviously permanent constructions; at least the single opening does not change position. This implies that such behaviour is not necessary because the animals do not frequently have to access new feeding opportunities at the surface; they seem to rely on floating debris. It was observed that *N. acanthus* is capable of constructing a new opening within hours if the original one is experimentally blocked, but this does not seem to happen under natural circumstances.

The burrow openings are frequently closed or replaced by expulsion mounds. Estimations of population densities based only on the counting of open burrows will therefore always underestimate the actual number of shrimp in a given area (Mukai *et al.* 1989, Erfteimeijer, Drossaert & Smekens 1993) or assume population fluctuations each time the same transect is counted.

The expulsion mounds produced by *N. acanthus* are no permanent structures. There is no frequent addition of new material as in deposit-feeding species, so they tend to get flattened by wave and current action soon after their construction (pers. obs.).

The frequent closing of the burrow opening might simply be made for excluding predators in times of little wave and current action and subsequently low detritus intake, as well as keeping certain conditions inside the burrow or preventing excess intake of leaf material. It might also merely be an artefact when the animals are ejecting sediment and gravel.

Burrow openings of *Corallianassa coutierei* are probably closed most of the time (90% for *C. longiventris* in Dworschak, Koller & Abed-Navandi 2005). In accordance with the observation made by Dworschak, Koller & Abed-Navandi (2005) *C. coutierei* on Bone Batang island opens its burrow in response to wave action or sediment disturbance. This makes sense since more water movement means more floating detritus. The frequency of open burrows of *C. coutierei* was found to be only 0.1 m⁻², but the actual population density might be much higher (around 2 m⁻²). This number was estimated locally when large amounts of sediment were stirred up when burrow casts were dug out.

4.2 The burrows of *Neaxius acanthus* and *Corallianassa coutierei*

4.2.1 The burrow structure of *Neaxius acanthus* and *Corallianassa coutierei*

The occurrence of accumulations of gravel around openings of *N. acanthus* probably results from the expulsion of sediment and gravel. While smaller grains are quickly dispersed by wave and current action which are especially high in the intertidal and shallow subtidal area, larger gravel parts (up to larger size than that of the animals) stay where they have been deposited.

All burrows of *N. acanthus* cast in the Bone Batang seagrass meadow only have one opening, this is the same for all burrows of Axioidea in the literature (Pemberton, Risk & Buckley 1976, Dworschak 2003). The two openings mentioned in Griffis & Suchanek (1991) for *Neaxius* sp. are a misinterpretation of Farrow (1971). This is further corroborated by the observation of the digging behaviour in aquaria; only one male individual in a preliminary experiment changed the position of the opening but no two openings were functional at the same time.

It could be observed in aquaria that the bulbous extensions in diameter of the vertical shaft allow both shrimp to turn or to pass each other.

The situation is different for *C. coutierei* where a second opening filled with sediment was found in the process of digging out the casts. This is also in line with the findings of Dworschak, Koller & Abed-Navandi (2000) for *C. longiventris*. The presence of a chamber halfway down is also plausibly explained by Dworschak, Koller & Abed-Navandi (2005): it is made for the storage of sediment used to block the opening in times of no surface activity and for temporary storage of seagrass which is later brought to the deeper chambers.

Special blind tunnels have also been observed for *C. coutierei*. Like for *N. acanthus*, they probably represent “mining operations” when the animals search for silty sediment to line their burrow walls.

4.2.2 Commensals in burrows of *Neaxius acanthus*

A diverse community of commensals belonging to nine different species has previously been reported for *Callianassa californiensis* (Mac Ginitie & Mac Ginitie 1968): the goby *Clevelandia ios*, three species of crabs (*Scleroplax granulata*, *Pinnixa franciscana* and *Pinnixa schmitti*), two species of copepods, the polynoid worm *Hesperonoë complanata*, the clam *Cryptomya californica* and the shrimp *Betaeus ensenadensis*.

The bivalve *Phacoides pectinatus* lives in the surrounding sediment and only protrudes its siphon into the burrow lumen of *Axianassa australiensis* (Felder 2001). Another bivalve, *Pseudophytina rugifera* lives attached to pleopods of the filter-feeding *Upogebia pugettensis* and thus must be considered a parasite (www.rosario.wwc.edu).

The spacious burrows of *N. acanthus* were found to contain at least five species of commensals:

The bivalve species found in this study is probably the same as reported in Farrow (1971), although the secondary commensals (gastropods) were not found. It lives attached to the burrow lining. Live specimen were observed climbing up the walls of the transportation jars, probably by the help of byssus threads (Fig. 35). Since it is considered unlikely that *N. acanthus* is a suspension feeder (no such behaviour observed in aquaria, burrow shape with only one opening does



Fig. 35: The commensal bivalve found in all burrows of *Neaxius acanthus* is capable of climbing up vertical plastic walls. In its natural habitat it lives attached to the burrow lining.

not permit continuous water flow, no adequate filtering devices in the form of long and fine seta present), it is also unlikely that the clam species is a parasite. *N. acanthus* has been observed ejecting empty shells of this bivalve species out of its burrow, it can therefore be assumed that it would also eject live specimen if they had detrimental effects.

The commensal goby *Austrolethops wardi* has so far only been described as living among coral rubble (www.fishbase.org). This interpretation might have been caused by the sampling methods (dredges, corers or grabs) used by previous authors (Ahnelt, pers. comm.). In being laterally compressed, *A. wardi* is different from other commensal gobies living with thalassinid or alpheid shrimp (Mac Ginitie & Mac Ginitie 1968, Karplus 1987, Ahnelt, pers. comm.). This unusual feature might be of benefit only in the especially spacious burrow

produced by *N. acanthus*. Further observations may show to what extent *A. wardi* depends on *N. acanthus*: it might be a real commensal or even a symbiont that reduces the number of amphipods which feed on the leaf material brought into the burrow by *N. acanthus*. It can also be assumed that *A. wardi* reproduces inside the burrow, probably by temporarily occupying a side branch as observed for other symbiotic gobies (Ahnelt, pers. comm.). One goby or a pair of gobies might also need to cover several burrows to satisfy their dietary needs (Ahnelt, pers. comm.).

Only few amphipods were found in the resin casts but high numbers were observed leaving the burrow following the introduction of sodium hypochlorite. It must therefore be assumed that most amphipods were not visible in the resin due to their small size. The amphipods probably benefit from the dead leaf material brought into the burrow by the host shrimp. Unless these amphipods are specified, it cannot be said whether they represent one or more species and whether they also occur outside the burrow.

Two species of commensal tube-building polychaetes were found attached to the burrow lining of *N. acanthus*, one of the species was also occasionally found on the tail fans of individuals of the host shrimp. Like the bivalve species, they both probably benefit from elevated bacterial numbers in the burrow water caused by the dead material decomposing inside the burrow.

The palaemonid shrimp species observed in the burrow opening might not be a real commensal since these animals tend to leave the burrow if disturbed. They might just benefit from the burrow lining with its high organic content. Palaemonid shrimp have also been observed in burrows and on individuals of stomatopod malacostracans (Debelius 1999).

The small crab species and the juvenile fish occasionally observed in the burrow opening likewise might not be real commensals since they were only observed seeking refuge in the burrow at low tide, they might otherwise be independent of *N. acanthus*.

In contrast, the limited space available inside burrows of *C. coutierei* probably does not suit macroscopic commensals.

4.2.3 The burrow lining of *Neaxius acanthus* and *Corallianassa coutierei*

The higher water content measured in the burrow lining of *N. acanthus* and *C. coutierei* compared to the surrounding sediment is likely to be caused by plant fragments which have been worked into it by the shrimp. No microscopic observation was made on the lining of *C. coutierei* but Dworschak, Koller & Abed-Navandi (2005) report that *C. longiventris* incorporates its faecal pellets which still contain a certain amount of leaf fragments into the burrow walls. The same might also be true for *N. acanthus* since no accumulations of faecal pellets were observed in the aquaria, indicating that they end up somewhere else.

The elevated organic content of the lining material is reflected in the higher content of fine material (silt fraction) and is caused by plant fragments as well as faecal material of shrimp and their commensals.

In addition elevated silt content in the lining of both species implies effective sediment sorting. *N. acanthus* probably spends a considerable effort in mining for fine sediment grains; at least this would be a plausible explanation for the fact that this species continuously digs short protuberances into the surrounding sediment which are refilled after a short time. This behaviour is thought not to be shown only in aquaria since all burrow casts also show these protuberances.

It can be assumed that a representative burrow has a surface area of 1500 cm², about 50% of which is covered by a lining with an average thickness of 3 mm. The lining therefore has a volume of 750 cm² * 0.3 cm = 225 cm³. The silt fraction in 1 ml lining has a weight of 0,366 g, this results in 82 g for the whole burrow. The volume of sediment handled during the excavation (approx. 1.5 l for a normal burrow) contains, however, only 40 g of silt. This implies that in addition to the sediment handled during the construction of the burrow, at least another 1.5 l of sediment have to be processed assuming 100% sorting efficiency, which is highly unlikely. In addition, the lining is in many places thicker than the 3 mm used in this calculation. It cannot be ruled out that there is a certain influx of silty sediment into the burrow by sedimentation. Still it seems to be plausible that individuals of *N. acanthus* spend a lot of their time on mining for untouched sediment. This is in line with the observation that new tunnels are mostly dug where no tunnel has been before. During the life history of a single burrow, most sediment in its surroundings might be handled by the shrimp at least once; a total volume of 10 l sediment might be sorted over time.

Ultimately, the fine sediment grains are mixed with small pieces of seagrass debris and a sticky substance secreted by the shrimp. This mixture is tamped into the burrow walls.

Dworschak (2003) suggests that mucus secreted from tegumental glands in Mxp. 3 and pereopods 2 and 3 of *Pestarella candida* and *P. tyrhenna* is used to stabilise the burrow wall. Besides its stabilizing effect, the mixture might serve as a nutritional source to the shrimp. The burrow lining of both species might be a place of elevated microbial activity (Branch & Pringle 1987). In aquaria, individuals of *N. acanthus* frequently walked slowly along the lined shafts and performed a gentle stirring movement which might serve in brushing bacteria off the walls. They were also observed to systematically clean the glass plates of the aquaria from algal covers.

4.2.4 Abiotic factors in water from burrows of *Neaxius acanthus*

Sediment ammonium shows a gradual increase with increasing sediment depth. The peak at 30 cm depth is caused by two extraordinarily high values, eventually caused by decaying infauna. The other values measured at 30 cm are in between those for 13,5 and 45 cm depth. Burrow water ammonium concentrations are about the same as measured at 45 cm in the sediment, it must be considered, however, that ammonium is transformed into nitrate and nitrite in the presence of oxygen (Asmus, pers. comm.). The oxygen values measured in the burrow water indicate that there is no lack of oxygen. This process of nitrification was firstly described for coral reef systems by Webb & Wiebe (1975), who reported a net export of nitrogen from a windward reef of Enewetak (Webb & Wiebe 1975, D'Elia & Wiebe 1990). Therefore it must be assumed that there is a high production of ammonium to maintain the levels measured, with the decaying seagrass debris, the shrimp and its commensals being potential sources.

Phosphate levels in the burrow water are much higher than those measured in the sediment and the water column. Since phosphate is effectively absorbed by carbonate sediments (De Kanel & Morse 1978, D'Elia & Wiebe 1990) this highlights the role of the burrow of a phosphate source.

With about 20% saturation in the upper sediment layers sediment pore water oxygen is remarkably high. It must be considered, however, that seagrass roots actively pump oxygen into their surroundings (Vonk, pers. comm.). Still, the presence of oxygen at 45 cm depth is remarkable and can only be explained by the very coarse sediment with its low organic fraction and the very high oxygen content in the water column caused by the high production of the seagrass cover. The concentrations in the burrow are in between those measured in the

water column and in the sediment. They are above the levels which are commonly considered hypoxic (Asmus, pers. comm.).

pH values like wise are in between those in the sediment pore water and the water column.

In total, the shrimp seem to maintain a moderate exchange of water.

4.3 Morphometric properties and individual weight of *Neaxius acanthus*

Carapace width was not measured; male individuals seem to possess, however, a carapace which is wider than a female carapace of the same length. This might explain why carapace length is shorter for males caught from burrows with smaller diameters. It would also plausibly explain why the correlation between burrow diameter and carapace length is better for male individuals. For bigger females the pleon tends to be more pronounced and might be the reason why burrows of larger diameters are inhabited by male and female shrimp of comparable carapace lengths.

The findings of this study closely reflect the burrow diameter / carapace length ratio established by Mukai *et al.* (1989) for *Neaxius acanthus* in Papua New Guinea.

The major chela was much bigger in big male individuals than in females. The higher variation encountered in male major chela length and weight may be due to the fact that males which are more aggressive than females lose their chelae more frequently. In addition, chelae in small males probably grow proportional to carapace length. They do so in females for their whole lives. Only with the onset of sexual maturity, which might not be at the same size for all male shrimp, they start to grow exponentially.

The correlations between carapace length and WW, DW and AFDW are generally less precise than they are for male individuals. This is likely due to the lower number of replicates and / or the grade of maturity of the ovaries.

The total biomass of *N. acanthus* in the seagrass meadow is not particularly high compared to the biomass of some mud-flat inhabitants but still quite respectable for a tropical ecosystem (Alongi 1989, Boucher & Clavier 1990, Baird *et al.* 2004).

4.4 Behaviour

4.4.1 The intake of seagrass detritus into burrows of *Neaxius acanthus*

Even without the surface activity of the shrimp the burrow opening of *N. acanthus* acts as a detritus trap due to its funnel-like shape. The estimated catch rate of 1.386 g DW for the opening alone and 1.920 g DW if corrected for shrimp activity is within the ranges reported by Stapel (1997) for *Alpheus edamensis* and Abed-Navandi, Koller & Dworschak (2005) for *Corallianassa longiventris*: The same activity for both day and night is here proposed since no difference was observed in the activity between day and night in the aquaria. The single night inspection of the study site likewise indicated no differences in day and night activity.

Stapel (1997) arrives at 1.46 g DW living leaves and 0.43 g DW leaf litter (together 1.89 g or 53% of the assumed daily production of 3.53 g) being transported below the sediment surface by alpheid shrimp in a *Thalassia hemprichii*-dominated seagrass meadow on Barrang Lompo island.

Abed-Navandi, Koller & Dworschak (2005) assume a daily catch rate of 132 mg assuming 10% surface activity per day for *Corallianassa longiventris*. This equals 1.32 g d⁻¹ assuming 100% surface activity as in this study. It must be noted that the openings observed by Abed-Navandi, Koller & Dworschak (2005) are positioned outside the seagrass meadow.

On average 3 openings of *N. acanthus* m⁻² were found in the dense seagrass area, and 65% are kept open at a given time, implicating that there are 2 active openings m⁻² all the time. The value of 1.920 g DW was not corrected for epibionts growing on the seagrass blades but it is reasonable to assume that they do not contribute more than 20% of the total weight (50% on rare occasions, Asmus pers. comm.). Therefore it can be assumed that at least 3 g DW opening m⁻² d⁻¹ are brought underground by the activity of *N. acanthus*. The production in the dense seagrass area was calculated to be about 5.3 g DW m⁻² d⁻¹, about 1g m⁻² d⁻¹ of which is removed by the grazing activity of the sea urchin *Tripneustes gratilla* (Vonk, unpubl.). It can thus be said that by the activity of *N. acanthus* more than 50% of the primary production are removed in the dense seagrass area. Considering the combined activity of *N. acanthus* and *T. gratilla*, only about 1.3 g DW m⁻² d⁻¹ are “left” for other grazers like the pelagic rabbit fish (Siganidae), for decomposition at the surface and for the current driven export of dead material out of the seagrass meadow.

It must be considered that the dense seagrass area where these observations were made may receive leaf detritus from other areas because a certain fraction of the leaf detritus produced is

still positively buoyant and thus out of reach for the shrimp. The positively buoyant fraction can get lost for the ecosystem. In Stapel (1997) an export of roughly 10 % of the primary production of a seagrass meadow in the Spermonde Archipelago is estimated.

All in all, the estimated production of $5.3 \text{ g DW m}^{-2} \text{ d}^{-1}$ might not be sufficient to explain the intake measured. On the other hand, the values measured might be overestimates because wave action was particularly high on some of the days the experiments were run. In the course of the year, the intake might thus be lower.

The tropical seagrass meadow on Bone Batang island still seems to be characterized by a very efficient utilization of the primary production which is unparalleled in temperate seagrass meadows (Baird *et al.* 2004).

4.4.2 The behavioural properties of *Neaxius acanthus*

I General:

The behavioural states of *N. acanthus* show remarkable similarities to the ones observed on *Callianassa subterranea* by Stamhuis *et al.* (1997) and *Corallianassa longiventris* and *Pestarella tyrrhanea* by Dworschak, Koller & Abed-Navandi (2005). It is sound to assume that the burrow-dwelling lifestyle of thalassinideans requires that a fixed amount of time is spent on construction.

II Burrowing:

It could be shown that even large-sized *N. acanthus* are capable of quickly constructing a new burrow in aquaria. Under natural circumstances, however, a shrimp driven out of or leaving its burrow would be quickly consumed by predatory fish. It is therefore assumed that the animals never venture out further than observed when catching floating detritus, e.g. with the abdomen still inside the shaft. By performing a series of tail flicks, the animals are able to reach the deepest part of their burrows within seconds at any sign of real danger. As observed many times in the study site and in aquaria, they venture to the opening rather than away from it if there is a disturbance or a shadow at the entrance. This certainly is an adaptation to their driftcatching habit.

III Feeding:

When observing thalassinid decapods it is difficult to determine whether an individual is actually feeding or merely manipulating objects or sediment because the mouthparts are always obscured by other appendages (Stamhuis *et al.* 1997). Since the behavioural relative *Corallianassa longiventris* seems to feed mainly on detrital seagrass, followed in importance by the burrow wall (Abed-Navandi, Koller & Dworschak 2005), a similar nutrition is assumed for *N. acanthus*. The finding that a lot of the seagrass brought into the burrows is not consumed directly but rather cut into pieces and worked into the burrow walls strongly indicates that *N. acanthus* actively creates conditions favourable for bacterial growth. Through this “microbial gardening” activity the nutritional value of seagrass debris could be enhanced.

Suspension feeding as proposed by Farrow (1971) is ruled out.

IV Aggressive behaviour:

Many callianassid species show a ritualized aggressive behaviour (Shimoda *et al.* 2005). This goes along with a solitary lifestyle, high population densities and a sexual dimorphism in the major cheliped which is even more marked than for *N. acanthus*. In contrast, high intrasexual aggressiveness is associated with a less distinct sexual dimorphism in the major cheliped in many decapods (Shimoda *et al.* 2005).

Fatal combats have been reported for *N. vivesi* (Berill 1975). The high level of intrasexual aggression is understandable considering the burrow-sharing behaviour of pairs in *Neaxius* spp. (Shimoda *et al.* 2005).

It is assumed that individuals of *N. acanthus* recognize the gender of individuals of the same species by olfactory clues since no recognition display was noted.

The maximum number of shrimp in a single burrow is effectively limited to two due to the high level of intrasexual aggression. It is conceivable that fights might even lead to the death of individuals if they are driven out of their burrows or become buried. Male individuals with their larger claws obviously are more aggressive than female individuals. In case of a repeated disturbance, the male individual usually stays close to the entrance or even replaces the female. It can be assumed that male *N. acanthus* with their large claws and series of spines on rostrum, the anterior half of the carapace and on the exopods of antennae 2 cannot be

extracted out of the burrow entrance by most predators. The function of the male as the more “daring” of the partners is underlined by the observation that only male individuals in the study site were lacking claws.

4.4.3 The impact of *Neaxius acanthus* on the seagrass surrounding its burrow opening

A decrease of about 50% in both shoot density and seagrass biomass was measured within a 55 mm radius around each open burrow. Although individuals of *N. acanthus* were observed pulling on and breaking off living leaves within the reach of their claws it is here assumed that this decrease is rather caused by the fact that individuals of *N. acanthus* frequently bulldoze sediment and coral gravel radially away from their openings and thereby cover living seagrass plants in the proximity of the openings.

Assuming that shrimp influence reaches no further than between 13 and 14 cm away from the opening (the value reached when drawing a logarithmic regression line using leaf biomass (which was most severely reduced) and setting the value for 9 mm from the centre of the opening to 100% decrease) still only an area of about 17% m⁻² is affected at the average density of 3 openings m⁻¹ in the densely vegetated area.

With the additional assumption that seagrass shoot density and biomass decrease by about 50% in the affected areas only a total decrease of between 8 and 9% m⁻² can be postulated.

It is thus safe to say that *N. acanthus* does not largely affect its habitat by consuming live seagrass plants.

Its influence is much more prominent when it comes to the relocation of dead leaf material into the sediment.

4.5 General observations made in the study site

The woolly appearance of some of the *Neaxius acanthus* from the Bone Batang seagrass meadow may be caused by bryozoan ectosymbionts belonging to the genus *Triticella*. A comparable symbiont is described for *Calaocaris macandreae* (Axioidea) in Buchanan (1963) and for the paddle crab *Ovalipes catharus* (Portunidae) in Gordon (1999). Further microscopic studies might clarify this question.

4.6 Outlook

Although appearing at relatively low densities compared to some callianassid (in mudflats) and alpheid shrimp (Ziebis *et al.* 1996, Stapel 1997) *N. acanthus* seems to have a profound effect on its habitat.

On the one hand, the species relies on seagrass for its nutrition and because of the sediment-stabilizing effect of the rhizomes. On the other hand it might play a key role in nutrient cycling by either speeding up or slowing down the release of nutrients from detritus.

By providing a habitat for many commensals *N. acanthus* adds to the diversity in its habitat.

It remains an unsolved question whether the driftcatching behaviour of *N. acanthus* and *C. coutierei* represents a rather ancient (Dworschak, Koller & Abed-Navandi 2005) or derived state within thalassinideans. The reliance on surface material for nutrition might be a special adaptation of deposit-feeders to survival in nutrient-poor carbonate sediments (Wiese, pers. comm.). This is further corroborated by the observation that the gross burrow morphology of both species dealt with in this study is largely influenced by evolutionary background rather than behaviour.

Other questions of interest for further studies might be

- year-round observation of burrow residency, the growth of burrow openings and the leaf intake into these openings
- the nutritional value of and the microbial activity in the burrow lining
- stable-isotope studies and aquarium observations to find out about the food web inside burrows of *N. acanthus* and the role of the commensals.

Appendix

Systematic position:

Animalia

Arthropoda

Crustacea (Brünnich 1772)

Malacostraca (Latreille 1802)

Eumalacostraca (Grobber 1892)

Eucarida (Calman 1904)

Decapoda (Latreille 1802)

Pleocyemata (Burkenroad 1963)

Thalassinidea (Latreille 1831)

Axioidea (Huxley 1879)

Axiidae (Huxley 1879)

Strahlaxiidae (Poore 1994)

Neaxius (Borradaile 1903)

Neaxius acanthus (Milne-Edwards 1878)

Callianassoidea (Dana 1852)

Callianassidae (Dana 1852)

Callichirinae (Manning & Felder 1991)

Corallianassa (Manning 1987)

Corallianassa coutierei (Nobili 1904)

(after: Integrated Taxonomic Information System, National Museum of Natural History, Washington, D.C., <http://www.itis.usda.gov>).

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Ort, Datum

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