INFAUNAL SAND-DWELLING MOLLUSCS AT HILA, AMBON, INDONESIA

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ABSTRACT

This study analyses a rich and diverse assemblage of benthic molluscs occupying an extensive sand patch on a fringing reef platform on Ambon Island, Maluku, Indonesia, with emphasis on species composition, abundance and trophic roles. The quantitative sample included 188 living molluscs, an average density of 42 m^{-2}. More than 70 % were gastropods; neogastropods dominated the assemblage with respect to diversity, abundance and, except for one large scaphopod, body size. The 30 gastropod species included 4 neotaenioglossans, 20 neogastropods, and 6 heterogastropods. Fourteen additional gastropod species were present but did not occur in the quantitative sample. Bivalves comprised 21 % and scaphopods 8 % numerically. Among the gastropods, *Oliva* was the dominant genus numerically; its four species comprised nearly one-third of the entire sample. *O. carneola* (56 individuals) was the commonest species in the quantitative sample. *Terebra* ranked second in abundance but first in diversity with 12 species, four of which were present in the quantitative sample. Predators dominated the assemblage, but knowledge of the specific trophic roles of most awaits further study.

INTRODUCTION

Despite the uniform appearance of large, subtidal areas of sand substratum, such habitats may harbour diverse assemblages of benthic molluscs. Prosobranch gastropods tend to be the dominant taxon on tropical sand flats, both numerically and with respect to individual size, and within this group the majority are often active predators (Taylor 1986). This is not only a modern phenomenon, because it is also true of some Cenozoic fossil assemblages from nearshore sedimenting environments (Stanton *et al.* 1981; Kohn & Arua in press).

This study analyses the species composition, abundance and trophic roles of molluscs in an extensive sand patch on a fringing reef platform on Ambon Island, Indonesia.

STUDY SITE AND METHODS

The site was located under and adjacent to the pier at the Hila Fisheries Station of Universitas Pattimura near Hila Village on the Leihitu Peninsula of Ambon Island, Maluku, Indonesia, and was studied 26-27 November 1996. An area of uninterrupted medium sand substrate of about 130 m^2 extends between about 74 and 82 m seaward of the high tide line. Its inshore boundary is a bench of rough reef limestone with sparse living coral. Offshore, living coral heads and soft corals begin and increase in density seaward. Parallel to the shoreline, sparse living coral heads occur on both sides of the approximately 16 m wide sand patch. The bottom slopes gently, from about -0.35 to -0.55 m with respect to tidal datum over the 8 m length.

Within this 130 m^2 area, 18 haphazardly placed 0.25 m^2 quadrates were sampled, for a total of 4.5 m^2. The sediment within each was shovelled into a large sieve of about 2 mm mesh. Because of the difficulty of shovelling accurately under water, the following standard procedure was adopted: Four shovelfuls of the surface layer of sand (about 8 cm deep), each starting at one corner of the quadrate, were sieved first, then four shovelfuls of the remaining sediment, also to a depth of about 8 cm, and finally one shovelful from the center of the quadrate. All molluscs remaining on the sieve, as well as any

observed on the surface of the quadrate were counted, identified to family or genus and assigned a descriptive field species name, and the data recorded on an underwater slate. The specimens were placed in screw-capped plastic vials of sea water and later fixed in 5 % formalin in sea water. Additional molluscs were collected when observed within the area but outside quantitatively sampled quadrates, *eg* at the ends of trails. These included several species that were not present in the quantitative samples, and they are treated separately in the Results section.

RESULTS

Faunal composition and diversity

The total sample comprised 244 living molluscs of 54 species; of these 188 of 40 species occurred in the quantitatively sampled quadrates (Tab. 1). More than 70 % of all the molluscs were gastropods, and prosobranchs dominated the assemblage with respect to diversity, abundance, and body size. All of the prosobranchs were caenogastropods, and in the quantitative sample 97 % (130/134) were neogastropods. In addition, 14 other species, all neogastropods, were observed in the vicinity of the quadrates (Tab. 1). Among the gastropods *Oliva* predominated numerically; two of its four species, *O. carneola* and *O. amethystina,* comprised nearly 40 % (77/188) of all molluscs in the quantitative sample. The family Terebridae was by far the most diverse with 15 species, 12 of them in the genus *Terebra*. Bivalves, represented by only 8 species, comprised 21 % of the sample and the two species of scaphopods, 9 %. One species dominated each of the latter classes; 70 % of the bivalves were *Callista florida*, and all but one of the scaphopods was *Antalis* sp. cf. *A. longitrorsum.*

Population density

The density of living molluscs over the 4.5 m^2 sampled was 42 m^{-2}. *Oliva carneola* was by far the most abundant species in the quantitative sample (12 m^{-2}), followed by *Callista florida* (6.2 m^{-2}), *O. amethystina* (4.7 m^{-2}), and *Antalis* sp. cf. *A. longitrorsum* (2.9 m^{-2}). All other gastropod species averaged less than 1 individual m^{-2}, and the total density of all terebrids, with four species in the quantitative sample, was 2.2 m^{-2}.

Size

Most of the molluscs sampled were strikingly small compared with the recorded adult size of their species (Tab. 1). The largest individuals of only seven species exceeded 30 mm in shell length: The single specimens of *Dentalium bisexangulatum* (57 mm), *Casmaria erinacea* (32 mm), *Oliva reticulata* (32 mm) and *Duplicaria raphanula* (42 mm), and the largest of three other terebrids, *Terebra jenningsi* (37 mm), *T. cerithina* (35 mm) and *T. anilis* (33 mm). As Tab. 1 indicates, these (and most others) are known to attain at least twice these lengths. Some species in the sample were even strikingly smaller. For example, the two *Terebra areolata* were only 13 and 19 mm long; adults of this species are known to attain 167 mm (Bratcher & Cernohorsky 1987). Overall the mean shell length of gastropods

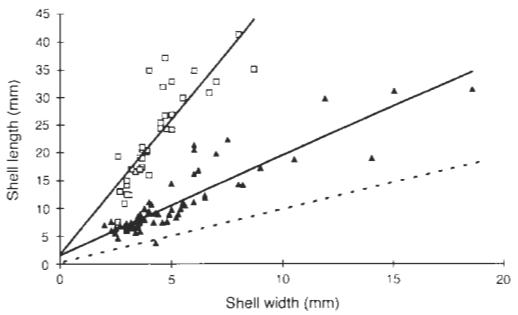

Fig. 1. Variation in shell shape and size of sand-dwelling gastropods on the fringing reef at Hila, Ambon, Indonesia. Squares represent members of the Family Terebridae (N=36); Length = 4.9 · Width + 1.7; R^2 = 0.70. Triangles represent members of all other gastropod families (N=76); Length = 1.8 · Width + 1.5; R^2 = 0.80. The dashed line represents shell length = shell width.

Table 1. Species composition, abundance, size, and functional feeding groups of molluscs inhabiting a large sand patch on the coral reef platform at Hila, Ambon, Maluku, Indonesia. The quantitative sample comprised a total area of 4.5 m^2. Functional feeding groups are designated as follows: D, Deposit feeder; H, Herbivore; O, Omnivore; P, Predator; Par, Parasite; S, Suspension feeder.

Species	No. in quantitive sample	No. in non-quantitive sample	Size range (mm)	Maximum reported adult size	Functional feeding group
GASTROPODA					
Polinices tumidus (Swainson, 1840)	1		19	50	P
Natica sp.	1		4		P
Cerithium sp.	1		6		D
Casmaria erinaceus (Linnaeus, 1758)	1		32	75	P
TOTAL NEOTAENIOGLOSSA	4				
Nassarius conoidalis (Deshayes, 1832)	1		9	30	O
Nassarius crenoliratus (Adams, 1852)	2		6	14	O
Nassarius sp.	1		5		O
Mitrella ligula (Duclos, 1840)	1		16	20	?
Anachis sp.	3		7-9		?
Oliva carneola Linnaeus, 1758	56	3	6-16	24	P
Oliva amethystina (Röding, 1798)	21		6-20	58	P
Oliva sidelia Duclos, 1835	1		9	23	P
Oliva reticulata (Röding, 1798)	1		32	48	P
Latirus noumeensis (Crosse, 1870)	2		8-10	22	P
Neocancilla papilio (Link, 1807)		1	23	60	P
Domiporta praestantissima (Röding, 1798)	5	2	8-15	55	P
Mitra mitra Linnaeus, 1758		1	30	170	P
Vexillum exasperatum (Gmelin, 1791)	2		7-20	26	P
Vexillum cithara Reeve, 1845		1	17		P
Vexillum sp. cf. *V. coronatum* (Helbling, 1779)	1		11		P
Inquisitor sterrhus (Watson, 1881)	2		21		P
Duplicaria raphanula (Lamarck, 1822)		1	42	64	P
Hastula albula (Menke, 1843)		1	11	40	P
Hastula strigillata (Linnaeus, 1758)	3	1	24-30	52	P
Terebra anilis (Röding, 1798)	3	1	14-33	88	P
Terebra areolata (Link, 1807)		2	13-19	167	P
Terebra argus Hinds, 1844		1	35	108	P
Terebra babylonia Lamarck, 1822		3	16-20	76	P
Terebra cerithina Lamarck, 1822		3	31-35	70	P
Terebra flavofasciata Pilsbry, 1921		1	22	35	P
Terebra funiculata Hinds, 1844	3	3	12-27	69	P
Terebra jenningsi Burch, 1965	1	2	32-37	80	P
Terebra paucistriata E.A. Smith, 1873		1	16	38	P
Terebra plumbea Quoy & Gaimard, 1833		1	17	25	P
Terebra undulata Gray, 1834		1	13	45	P
Terebra sp.	1		8		P
Conus arenatus Hwass, 1792		4	12-19	90	P
TOTAL PROSOBRANCHIA	114	34			
Pupa alveola (Souverbie, 1863)	4		6-9	13	P
Atys cylindrus (Helbling, 1779)	5		6-8	30	H?
Retusa sp. (?)	5		7-8		P
Turbonilla sp.	1		7		Par
Pyramidella terebella (Müller, 1774)	4		6-11	30	Par
Otopleura mitralis (A. Adams, 1856)	1		7	20	Par
TOTAL HETEROBRANCHIA	20				
BIVALVIA					
Callista florida (Lamarck, 1818)	28		3-11		S
Antigona sp.	1		5		S
Fulvia tenuicostata (Lamarck, 1819)	1		20	60	S
Cardiidae sp. undet.	6		4-7		S
Cardiidae? spp. undet.	2		10-12		S
Tellinidae spp. undet.	2		4-7		D
SCAPHOPODA					
Dentalium bisexangulatum Sowerby, 1860	1		57	78	P
Antalis longitrorsum (Reeve, 1843)	13		27-30	75	P

	Individuals in quadrats	Total individuals	Species in quadrats	Total species
TOTAL GASTROPODA	134	190	30	44
TOTAL BIVALVIA	40	40	8	8
TOTAL SCAPHOPODA	14	14	2	2
TOTAL MOLLUSCA	188	244	40	54

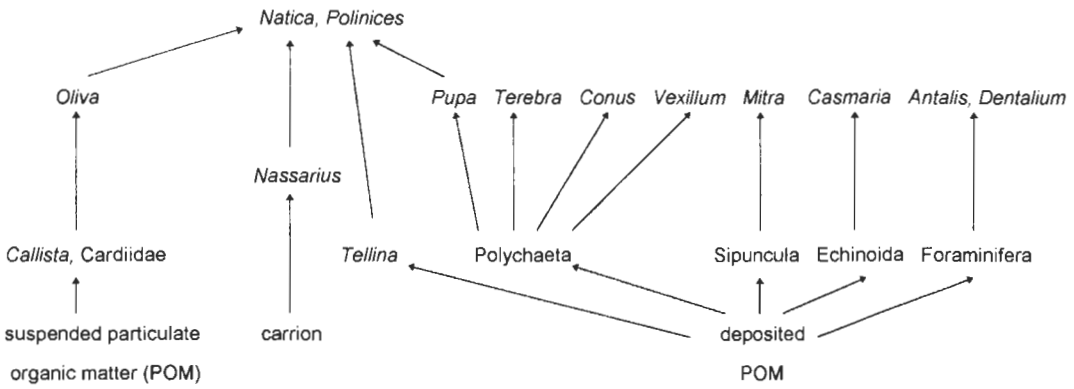

Fig. 2. Partial food web of the commonest infaunal sand-dwelling molluscs on the fringing reef at Hila, Ambon, Indonesia. Arrows point in the direction of energy flow.

was 38 % and the range, 9-80 % of maximum adult sizes recorded in the literature (Tab. 1).

Shape

Almost all species present have elongate shells; Fig. 1 shows that the mean length-width ratio is much greater than 1, and that it is greater (about 5) in the Family Terebridae than the other families present (about 2). Only one specimen, of an unidentified species of *Natica*, had a length width ratio < 1, *ie* below the dashed line in Fig. 1. Cain (1977, 1978) demonstrated a similar relationship for many gastropods in various environments, and it is especially pronounced in the motile, sand-plowing neogastropods that dominate the Hila assemblage.

Community structure

Predatory molluscs were the clearly dominant functional feeding group. Numerically they comprised 68 % of the sample (74 % counting the probably parasitic pyramidellids), and they included all of the largest animals (Tab. 1). The most important primary consumers present were bivalves. Most of these belonged to the families Veneridae and Cardiidae, whose members feed on organic particles in suspension. Only *Tellina* and the one cerithiid gastropod likely feed exclusively on deposited particulate organic matter. The four specimens of three *Nassarius* species belong to a family-group known for omnivory and including carnivores, herbivores, detritivores and scavengers (Britton & Morton 1993, 1994).

Although the diets of Olividae are poorly known, bivalves, foraminifera and carrion are the most frequently recorded food items. Most *Terebra* species prey on polychaetes; the genus *Hastula* includes specialists on the polychaete family Spionidae (Miller 1980). *Conus arenatus* preys on polychaetes mainly of the families Capitellidae, Maldanidae and Nereidae (Kohn & Nybakken 1975; Reichelt & Kohn 1985). *Vexillum* species also prey on polychaetes as well as gastropods (Taylor 1986), and all members of the Mitridae whose diets have been studied eat sipunculans exclusively (Kohn *et al.* 1997).

The Naticidae are the only known secondary carnivores among the molluscs collected, but one shell of the buccinid *Nassaria acuminata* had been drilled by a muricid, indicating the presence of this family. Heterobranch gastropods in the sample were much more frequently drilled by naticids (19 % of shells) than were prosobranchs (1.5 %). The sample contained an *Oliva carneola* shell and one of the turrid *Clavus* sp. with complete naticid drillholes. In addition, one *Domiporta praestantissima* was evidently the victim of successful durophagous preda-

tion, probably by a crab. Only one bivalve shell in the sample, an undetermined tellinid, was drilled, by a naticid.

Fig. 1 synthesises this information in a food subweb involving the molluscs of the Hila fringing reef sand areas. However, most of the data derive from studies of the same or related taxa from other geographic regions, and the figure can best serve as a model to guide future testing of trophic relationships in this type of habitat.

DISCUSSION AND CONCLUSIONS

The benthic infaunal assemblage of molluscs occupying extensive sand areas on coral reef platforms may be very rich with respect to both diversity and abundance. The 4.5 m^2 sampled in this study of a large sand patch on a fringing reef at Ambon, Maluku, Indonesia, harboured 40 species representing three molluscan classes, and a density of 42 individuals m^{-2}. At least 14 additional species were observed to occur in the same habitat. Predatory neogastropods, most prominently of the family Olividae, predominated, accounting for 53 % of species (60 % if parasitic species are included) and 68 % of individuals. At the present time, very limited knowledge exists of the specific trophic roles of most species. The extent to which the predators depend on molluscs lower in the food chain and the other invertebrates present remains unknown. The food subweb (Fig. 2) probably presents a roughly correct view of the trophic roles of the dominant molluscs but is offered as a model to be tested in future studies.

Most of the molluscs in the Hila sample had long and slender shells, with mean length-width ratios of 5:1 in the Terebridae and 2:1 in the other families. The large majority of these were neogastropods (Tab. 1), and as Cain (1977) demonstrated, most neogastropods (at least in the North American fauna he analyzed) have high-spired shells. Cain (1977) did not address the adaptive significance of this pattern, and the association of high-spired shells with burrowing has received only limited attention in subsequent studies (Cain 1978; Signor 1982; Cowie 1996). In the present study the overwhelming predominance of species with length-width ratios equal to or exceeding 2:1 is clearly associated with their habit of active burrowing in sand.

Most of the Hila molluscs were also much smaller than the adult sizes that their species are known to attain. Despite the fact that most values in the literature indicate maximum rather than typical adult lengths, the gastropods present averaged only 39 % (range 9-73 %) of recorded adult sizes. This suggests that the extensive sand area on the Hila fringing reef may serve as a nursery ground for gastropods, with a rich food supply for juveniles but a limited one for adults.

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