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Interactions between benthic molluscs in a Sulawesi mangal, Indonesia: the cerithiid mud-creeper *Cerithium coralium* and potamidid mud-whelks, *Terebralia* spp.

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The sediment surface within the *Osbornia* belt of a mangal on Pulau Hoga, Tukang Besi Islands, Sulawesi, Indonesia, is dominated *inter alia* by deposit-feeding gastropod molluscs at a mean density of some 230 ind m^{-2} although, unusually, species of *Cerithidea* do not occur. Densities of the two most numerous species, the potamidid mud-whelk *Terebralia sulcata* and the *Cerithidea*-like cerithiid mud-creeper *Cerithium coralium*, are inversely correlated, although the species occurred together in 42% of quadrat samples. Within and beyond the normal range of field densities of each species (*C. coralium* mean 153 m^{-2}; *T. sulcata* mean 75 m^{-2}) there was no evidence of intraspecific depression of feeding rate, as assessed by the production of faecal pellets, although this was significantly reduced in the occasional very high density aggregations of *C. coralium* ($>$1100 m^{-2}). The presence of the larger *T. sulcata* did appear to have a strong inhibitory effect on feeding in *C. coralium*; the converse, however, could not be demonstrated. Abundances of *Terebralia palustris* and *C. coralium* were also inversely correlated where the two co-occurred.

INTRODUCTION

Potamidid mud-whelks or 'horn shells' are the dominant sediment-dwelling prosobranch molluscs of mangals (Macnae, 1968), *Terebralia* and *Telescopium* occurring throughout the Indo-West-Pacific and the many species of *Cerithidea* dominating this habitat across the whole of the tropics, as well as being prominent in equivalent saltmarsh and mudflat habitats in warm-temperate areas. In contrast, cerithiid gastropods, although closely related to potamidids (Boss, 1982), are very poorly represented in mangrove faunas (Houbrick, 1985, 1992; Tomascik et al., 1997). Two cerithiids, however, are characteristically associated with mangals in the central Indo-Pacific. *Clypeomorus pellucida* (Hombron & Jacquinot) (=*Cerithium patulum* Sowerby) climbs up the aerial roots of mangroves (Frith et al., 1976; Houbrick, 1985) in a manner equivalent to species of the nominate subgenus of *Cerithidea*, e.g. *C. decollata* (Linn.) (Cockroft & Forbes, 1981), and *Cerithium coralium* Kiener inhabits the sediment surface (Houbrick, 1992) similarly to species in the subgenus *Cerithideopsilla* (Brandt, 1974), which it closely resembles and with which it can easily be confused (Houbrick, 1992). These cerithiids often occur in the absence of *Cerithidea* spp. (Abe, 1937; Whitten et al., 1987) and appear to take their place, whilst in some sites they occur sympatrically, e.g. *Cerithium coralium* with *Cerithidea cingulata* (Gmelin) (Vohra, 1971; Vermeij, 1973; Houbrick, 1992). Although competition within and between such species has on occasion been inferred (Vohra, 1971), it has never been demonstrated. Branch & Branch (1980), however, have shown that intraspecific competition does occur in the mangrove littorinid *Bembicium*, and Fratini et al. (2000) have demonstrated interspecific competition for leaves between the grapsid crab *Neosarmatium* and adults of the potamidid *Terebralia palustris*.

The Tukang Besi Islands off the southern tip of Sulawesi Tenggara, Indonesia, are classic examples of raised limestone islands with series of elevated fossil coral terraces (van Bemmelen, 1949; Tomascik et al., 1997), one such terrace being located intertidally on the north coast of Pulau Hoga. As seen elsewhere in Indonesia (van Steenis, 1958; Soemodihardjo et al., 1977; Soemodihardjo & Kastoro, 1977), this coral terrace supports a fully marine mangal, and its associated mudflats contain a rich deposit-feeding epifauna of ocypodid crabs and potamidid mangrove mud-whelks, together with the cerithiid *Cerithium coralium* in abundance. This report describes an investigation into some potential competitive interactions within and between the unusual mangrove cerithiid *C. coralium* and the more typical and more widespread potamidid *Terebralia*.

MATERIALS AND METHODS

The study mangal, near the village of Furake (Global Positioning System determined co-ordinates 123°46′22″E 5°27′34″S), comprises a seaward zone of *Rhizophora* and *Sonneratia*, a landwards fringe dominated by *Ceriops*, and in many areas a thick intervening band of *Osbornia*. Epifaunal gastropod populations were censused on the extensive areas of bare calcareous silt that very thinly overlies the raised coral terrace within this *Osbornia* belt. Pulau Hoga lies within the 1.4×10^6 ha Wakatobi Marine National Park. Fieldwork was carried out between June and August 2001, with some additional observations in July 2002.

Population densities of the two numerically dominant gastropods, *Terebralia sulcata* (Born) and *Cerithium coralium*, were assessed using a series of $>$200 quadrat samples (0.25 m side-length) along transects through the inhabited areas, a quadrat typically being dropped blindly every five

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paces. The snails enclosed within the quadrats were also used to provide information on population structure via measurement of shell height by vernier calipers (reported below correct to the nearest 0.5 mm). Densities in an adjacent region of sympatric *C. coralium* and *Terebralia palustris* (Linn.) were assessed in a similar series of >100 quadrats.

Measurement of the faecal output of the two numerically dominant gastropods, *T. sulcata* and *C. coralium*, was adopted as a proxy for their feeding rates and was carried out using the same basic methodology as in earlier studies of the temperate mud-snails *Hydrobia ulvae* (Pennant) and *H. knysnaensis* (Krauss) (Barnes, 2001, 2002). Faeces were collected in the field from units of 25 individual snails by immediately transferring each snail from the sediment surface to a 55-mm diameter plastic container with some 10 mm depth of local seawater. After one hour the snails were removed, returned to their original location, and the containers were sealed, for eventual transport to the laboratory for counting of the faecal pellets under a binocular microscope. Snails were collected only from within a single visually uniform region of mudflat, from areas of standing water, during daylight high tides and from within 0.0625 m^2 quadrats placed so as to enclose areas in which the desired test field population densities of *T. sulcata* and/or *C. coralium* were located. These densities were selected so as to represent the whole available range of abundance of each species separately and in combination. Containers in which the faeces of *T. sulcata* had been produced in large clumps rather than separately, rendering counting problematic, were discounted, and in cases where the faecal pellets were broken, the number of (pointed) ends were counted and the resulting total divided by two to yield the faecal count. The number of snails at a given population density from which faeces were collected was selected so as to allow for such discounting, preliminary analysis indicating that a total of 20 would yield 98% confidence. In respect of both the full range of *Cerithium* population density (M=12.93; df=7) and that of *Terebralia* (M=8.41; df=4), Bartlett's tests for homogeneity of variances were satisfied at $P>0.05$ and the faecal data were therefore subjected to analysis of variance (ANOVA).

RESULTS

Mean population densities were: *Cerithium coralium* 153 m^{-2} (SE 17), maximum 848 m^{-2}; *Terebralia sulcata* 75 m^{-2} (SE 7), maximum 464 m^{-2}. Overall gastropod density was 229 m^{-2} (SE 16) with a maximum encountered of 912 m^{-2}. The two species were present together in 42% of the quadrats, but their numbers were strongly inversely correlated (Kendall correlation $\mathcal{Z}$ -9.0; $P<0.0001$) (Figure 1). The sampled populations of both species mainly comprised large juveniles and small adults, 93% of the *C. coralium* being between 16 and 28 mm in shell height (N=215), and 90% of the *T. sulcata* being between 23.5 and 38.5 mm shell height (N=264). On the basis of their estimated volumes, one modal *T. sulcata* is equivalent to three modal *C. coralium*. Adulthood in both species can be determined from shell morphology: the smallest adult *Cerithium* was 16.5 mm high and the largest juvenile was 25 mm; *T. sulcata* became adult at ~22 mm.

Two other potamidids also occurred within the *Osbornia* belt: *Telescopium telescopium* (Linn.) rarely, and *Terebralia palustris* in local abundance slightly to landwards of the zone dominated by *T. sulcata*, where present *T. palustris* attaining a mean density of 73 m^{-2} (SE 6). *Telescopium* was largely restricted to permanent pools of water in depressions in the coral terrace, in which *Terebralia palustris* also occurred, although the latter was mainly found in shallow tidal streams, where it was sympatric with *C. coralium* (*Cerithium* occurring there at the same density—154 m^{-2} (SE 19)—as when sympatric with *T. sulcata*). As in sympatry with *T. sulcata*, the numbers of *T. palustris* and *C. coralium* within individual 0.0625 m^2 areas were inversely correlated (Kendall correlation $\mathcal{Z}=-2.7$; P=0.007), although both occurred together in 60% of quadrats. Elsewhere, adults of *T. palustris* have been reported to occur in a different microhabitat to the juveniles, in association with their specific diet of fallen mangrove leaves (Nishihira, 1983; Houbrick, 1991; Fratini et al., 2000), on to which they can home using olfactory cues (Fratini et al., 2001). On Hoga, however, none could be found on fallen leaves and all of the very few adults present were in the same habitat as the juveniles. The most widespread and species-rich potamidid genus *Cerithidea* was absent.

In the absence of *T. sulcata*, there was no significant difference in the numbers of faecal pellets produced by *Cerithium coralium* at population densities ranging from 96 m^{-2} (below mean local field abundance) through to 944 m^{-2} (well above it) (ANOVA F=0.97; P=0.44) (Figure 2). Over this range, a mean 76 (SE 2) pellets were produced in the hour after collection. Neither in the absence of *C. coralium* was there any significant difference in those produced by *T. sulcata* over a field abundance range of 32 m^{-2} (below local mean field density) to 656 m^{-2} (well above it) (ANOVA F=2.14; P=0.08) (Figure 3), producing a mean 176 (SE 5) pellets. The higher densities of these ranges lie outside the maxima recorded by the population

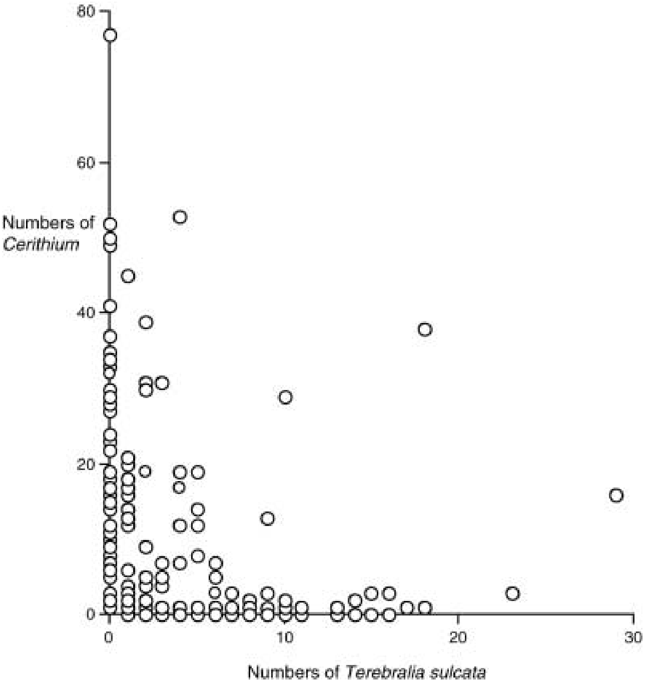

Figure 1. Numbers of *Cerithium coralium* and of *Terebralia sulcata* present together within the same 0.0625 m^2 of a mudflat in the *Osbornia* zone of a mangal on Hoga.

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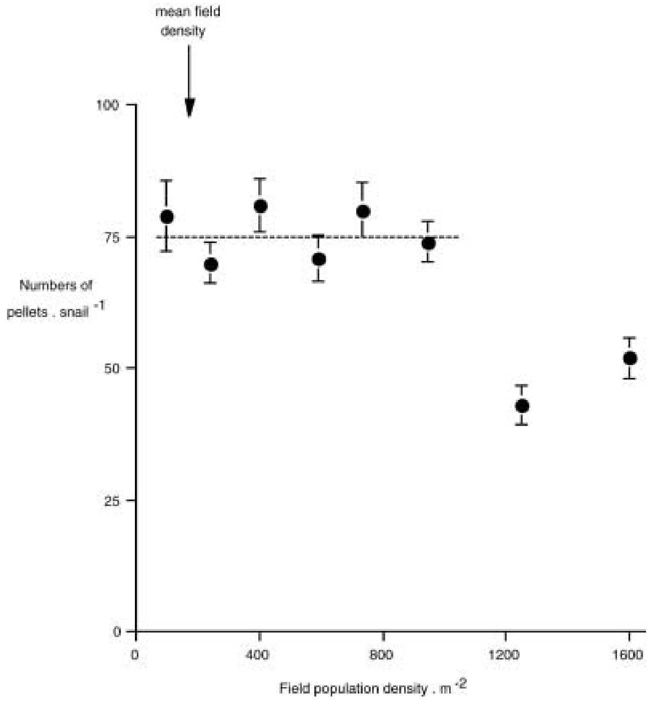

Figure 2. Numbers of faecal pellets produced by individual *Cerithium coralium* in the field in relation to ambient population density on a mudflat in the *Osbornia* zone of a mangal on Hoga. Data points are means ±SE from ~25 snails from each population density.

density survey, and were found only as a result of scouring the region for abnormally high local concentrations. In the two highest such aggregations of *C. coralium* observed, equivalent to 1248 and 1600 m^{-2}, faecal production per snail did fall significantly (ANOVA $F=8.70$; $P\leqslant0.0001$) (see Figure 2).

The presence of even small numbers of *T. sulcata* in the same 0.0625 m^2 area as unit density of *C. coralium* (211 ind m^{-2}; SE 6) was associated, however, with a significant depression of *Cerithium* faecal production (ANOVA $F=33.84$; $P<0.0001$), down to a minimum of some 42% of the 'standard value'. Although there was a significant continued fall in *Cerithium* egestion as the numbers of sympatric *Terebralia* present increased (regression ANOVA $F=11.00$; $P=0.001$) (Figure 4), its scale was relatively minor and the magnitude of the drop was less than the initial effect of the presence or absence of *T. sulcata*. The fall in faecal production, however, did occur over ranges of total snail density well within the density range within which there was no intraspecific declines (Figures 2 & 3), maximum snail density being equivalent to 560 *Cerithium*-equivalents m^{-2} (112 *T. sulcata* + 224 *C. coralium*). Any potential converse effect of *C. coralium* on *T. sulcata* was difficult to investigate because of the rarity in the field of large numbers of both species together. A small sample size test, equivalent to 112 *Terebralia* and 208 *Cerithium* m^{-2} did yield the lowest observed faecal production of *T. sulcata*, but the numbers of faeces were not significantly different from those produced by 112 *T. sulcata* in the absence of any *Cerithium* (ANOVA $F=3.00$; $P=0.09$).

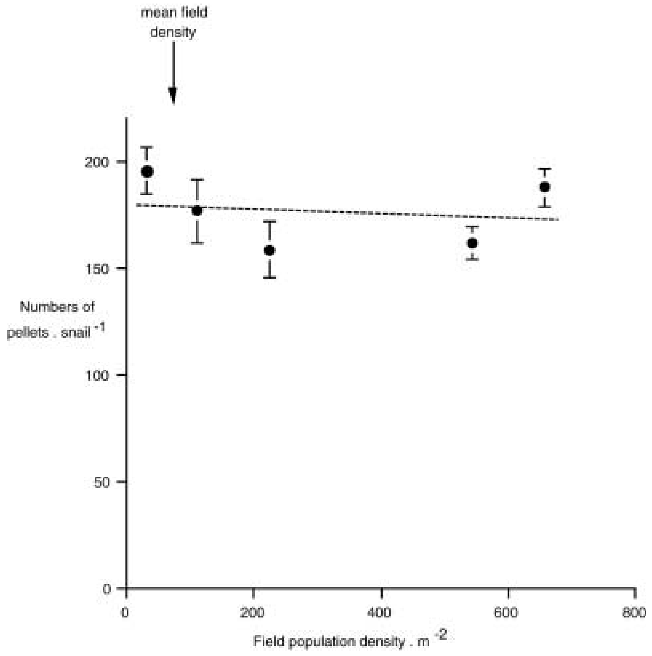

Figure 3. Numbers of faecal pellets produced by individual *Terebralia sulcata* in the field in relation to ambient population density on a mudflat in the *Osbornia* zone of a mangal on Hoga. Data points are means ±SE from ~25 snails from each population density.

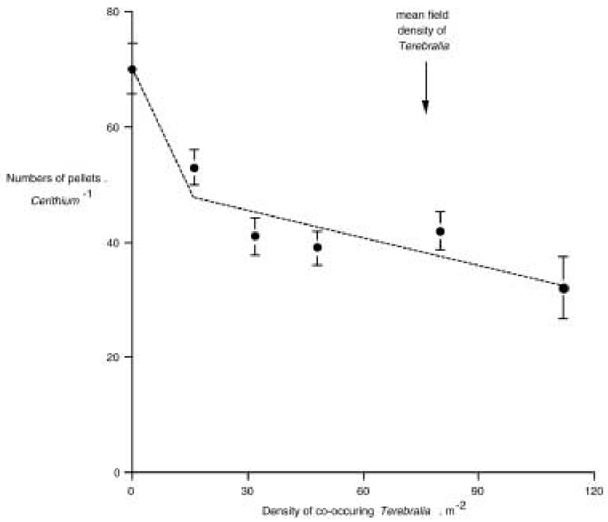

Figure 4. Numbers of faecal pellets produced by individual *Cerithium coralium* in the field at a density of 211 (±6) m^{-2} in the *Osbornia* zone of a mangal on Hoga when in the presence of from 16 to 112 m^{-2} *Terebralia sulcata* in the same 0.0625 m^2 area. Data on egestion by *Cerithium* at the same population density but in the absence of *Terebralia* (from Figure 2) have been included for comparison. Data points are means ±SE from ~25 *Cerithium* from each sympatric *Terebralia* density.

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DISCUSSION

Terebralia sulcata is a hardy, generalist mud-whelk that inhabits a wide range of intertidal substrata (Houbrick, 1991), there consuming diatoms, macroalgae, vascular plants and detritus (Yipp, 1980). It or the closely related *T. semistriata* (Mörch) can dominate the density and biomass of mangal mudflat molluscs (Wells, 1986), although they may tend, as in the present study as well as in the Bay of Rest, Western Australia (Wells, 1980), to occur lower on the shore than their congener *T. palustris*. Both in the Bay of Rest (Wells, 1980) and on Hoga, they were also more common on well-draining regions, whereas *T. palustris* occurred in semi-permanent shallow pools on the mudflat surface. *Cerithium coralium* is a typically estuarine species (Houbrick, 1992) although on Hoga it occupied a fully marine habitat. There it occurred in equal abundance in both the microhabitat types preferred by *T. sulcata* and *T. palustris*. *Cerithium coralium* is the only species in its genus to occur in association with mangroves and like *T. sulcata* it also occurs on a range of substrata from soft mud to muddy sand (Houbrick, 1992) and contains in its gut microalgae (especially diatoms), macroalgae, and vascular plant material (Yipp, 1980). On the raised Hoga terrace, the living epipelic photosynthesizers supporting these gastropods occur beneath the very thin layer of sediment on the surface of the platform. The geographical distributions of *T. sulcata* (Houbrick, 1991) and *C. coralium* (Houbrick, 1992)—as well as the *Osbornia* with which they are associated on Hoga (Spalding et al., 1997)—are also all very similar. The ecological overlap between *C. coralium* and *Terebralia*, especially *T. sulcata*, is therefore very high, and considerable potential for interaction is likely to be present.

The precise nature of any interaction was not investigated, and it is possible that the *Cerithium* were reacting not to the *Terebralia* themselves but to some microhabitat feature that correlated with the presence and abundance of these mud-whelks. Three observations suggest that their response was not to a habitat feature: the visual uniformity of the mudflat microhabitat sampled; the changing patchwork of *Cerithium* and *T. sulcata* abundance observed (equivalent to those seen on temperate mudflats; Barnes, 1998); and the insensitivity of *Cerithium* egestion rates to their precise location within the habitat that can be read from Figure 2. Work on temperate mud-snails, however, has shown the marked effects of physical interference—that of one snail 'bumping' into another—on egestion rate in *Hydrobia* (Levinton, 1979), and equivalent inhibition of *Hydrobia* by the larger *Ilyanassa* (Levinton, 1985; Levinton et al., 1985) and of *Ilyanassa* by the introduced *Littorina littorea* Linn. (Brenchley & Carlton, 1983). The effects in the tropics demonstrated above on unit population density of *Cerithium* by even small numbers of the larger *Terebralia* are consonant with the above interspecific models from the temperate zone. The results of the intraspecific series of faecal counts are also consonant with those of Barnes (2001) on *Hydrobia ulvae* (although cf. Levinton, 1979).

Although cerithiids may occur in the same habitat as potamidids (Abe, 1937; Whitten et al., 1987; Houbrick, 1992), there is evidence from other studies that their precise distributions and/or centres of maximum abundance do not overlap much (Vohra, 1971; Whitten et al., 1987). The interspecific effects of *T. sulcata* on *Cerithium* may explain why this is so, and may also account for the relative infrequency with which *C. coralium* has been recorded; Tomascik et al. (1997), for example, do not mention it in their list of 278 gastropods associated with mangrove forests in Asia and Oceania (including the 180 species recorded from Indonesia). It would be particularly interesting to examine interactions between *C. coralium* and species of *Cerithidea*—with which *Cerithium coralium* is generally similar in size, shape and preferred habitat—in the light of the observations that *C. coralium* occupies regions of the shore normally frequented by *Cerithidea* and that the latter, effectively omnipresent genus seems unaccountably to be absent from those shores on which *Cerithium coralium* is especially abundant. It may also be relevant that, as seen in other characteristically estuarine species (Barnes, 1999), the occurrence of *C. coralium* in a somewhat atypical fully marine habitat is consistent with a release from interspecific competition. The necessary studies, however, still wait to be undertaken.

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