

Prey selection of corallivorous muricids at Koh Tao (Gulf of Thailand) four years after a major coral bleaching event

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Abstract

Corallivorous *Drupella* (Muricidae) snails at Koh Tao are reported to have extended their range of prey species following a major coral bleaching event in 2010. Populations of their preferred *Acropora* prey had locally diminished in both size and abundance, and the snails had introduced free-living mushroom corals in their diet. Although the coral community largely recovered, the *Drupella* population grew and reached outbreak proportions. For this study, corallivorous muricids at Koh Tao were studied more intensively to examine their identities, distribution and prey choice four years after the bleaching event. *Drupella rugosa* was identified as the major outbreak species and occurred at densities > 3 m⁻² in depth ranges of 2-5 and 5-8 m. The density of *D. rugosa* was related to the live coral cover, *Acropora* colony density, and depth. Resource selection ratios revealed that species of *Acropora*, *Psammocora* and *Pavona* corals were attacked more frequently than would be expected based on their availability. Strikingly, fungiid corals were now avoided as prey in the recovered coral community, despite them being part of the preferred diet directly after the bleaching. Although *D. rugosa* showed a clear prey preference, it appears to be plastic by changing with prey availability. The muricids *Drupella margariticola* and *Morula spinosa* occurred in much lower densities and were less often associated with corals. Snails of the opportunistic corallivore *D. margariticola* usually co-occurred in *D. rugosa* aggregations, although they also formed feeding aggregations by themselves. Whether *M. spinosa* generally associates with corals as a corallivore or a scavenger has yet to be determined. Molecular analyses did not reveal cryptic speciation among snails sampled from different coral hosts and also no geographic variation. The present study also showed that corallivory is more common among *D. margariticola* and *M. spinosa* than previously known.

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Introduction

Coral reefs host a wide array of life forms. Next to providing substrate and shelter to invertebrates (Patton, 1994; Stella *et al.*, 2011; Hoeksema *et al.*, 2012a) and fish (Bos and Hoeksema, 2015, references herein), corals also serve as a food source for diverse opportunistic and obligate corallivores (Robertson, 1970; Glynn, 1990; Gittenberger and Hoeksema, 2013). Scleractinian coral-feeding lineages have evolved multiple times among the gastropod families Architectonicidae, Epitoniidae and Muricidae (Robertson, 1970; Glynn, 1990; Barco *et al.*, 2010). The large family Muricidae Costa, 1776 encompasses the entirely corallivorous subfamily Coralliophilinae Chenu, 1858 (Oliveiro and Mariottini 2001; Barco *et al.*, 2010), the possibly opportunistic coral-feeding *Morula spinosa* (Adams and Adams, 1853) (Yokochi, 2004) and *Ergalatax junionae* Houart, 2008 (Saledhoust *et al.*, 2011), and the genus *Drupella* Thiele, 1925, which also holds a number of corallivorous species (Claremont *et al.*, 2011a). Although the genus *Drupella* represents only a fraction of all corallivorous species, they have a reputation for their ability to degrade coral reefs on a large scale (Turner, 1994).

On account of molecular analyses, at least four obligate corallivorous *Drupella* species are distinguished, *i.e.*, *D. cornus* (Röding, 1798), *D. eburnea* (Küster, 1862), *D. fragum* (Blainville, 1832) and *D. rugosa* (Born, 1778), and one species complex that exhibits opportunistic corallivory, *i.e.*, *D. margariticola* (Broderip, 1833) (Taylor, 1980; Johnson and Cumming, 1995; Claremont et al., 2011a). While most related muricids are scavengers and predators of other molluscs, the radula of obligate corallivorous *Drupella* is altered for feeding effectively on coral tissue (Fujioka, 1982). The opportunistic feeding by *D. margariticola* on the other hand, is suggested to happen after co-occurring *D. rugosa* snails have initiated feeding on a coral prey since their own feeding apparatus is less suited for that purpose (Morton and Blackmore, 2009; Claremont et al. 2011a).

Drupella snails predominantly occur in small aggregations that prey on the same coral colony at night, but retreat to the underside or between branches of the colony during the day (Boucher, 1986; Hoeksema et al., 2013). Such aggregations seem to occur because individual snails are attracted to conspecifics (Morton et al., 2002; Schoepf et al., 2010), and to compounds that are secreted by stressed or damaged corals (Morton et al., 2002; Kita et al., 2005). Furthermore, aggregations of different species combinations have also been reported (Cumming, 1999; Morton and Blackmore, 2009), although those species may show different reef habitat preferences based on wave exposure and depth (Turner, 1994; Cumming, 1999). Other than common feeding aggregations, some large accumulations of *Drupella* are thought to be closely related offspring resulting from massive reproduction events (Baird, 1999; Cumming, 1999, 2009). Recruits of the same cohorts usually form large feeding aggregations, in which individuals show a common history of settlement and growth (Johnson et al., 1993).

Destructive outbreaks of *Drupella* have been witnessed throughout the Indo-Pacific since the 1980s. These outbreaks (usually > 3 individuals m⁻²) can be compared to the extensively studied corallivorous sea star *Acanthaster planci* (Linnaeus, 1758), which can cause severe damage when occurring in high densities (Glynn, 1990; Cumming, 2009; Scott et al., 2015). Such outbreaks occur frequently and cause secondary mortality by succeeding earlier stressful events on reefs (Antonius and Riegl, 1998). These events are either natural or human-induced and can be related to coral bleaching (Baird, 1999; Hoeksema et al., 2013), destructive fishing (McClanahan, 1994), deteriorating water quality (Plass-Johnson et al., 2015), diving tour-

ism (Guzner et al., 2010), nutrient enrichment (Al-moghrabi, 1997), siltation (Moyer et al., 1982), and storm damage (Boucher, 1986; Ayling and Ayling, 1992). The *Drupella* species that have been reported to occur in elevated densities are *D. fragum* (Moyer et al., 1982; Fujioka and Yamazato, 1983), *D. cornus* (Ayling and Ayling, 1987; Antonius and Riegl, 1998; Turner, 1994) and *D. rugosa* (Moyer et al., 1982; Cumming, 1999). In his review, Cumming (1999) concluded that only populations of *D. fragum* and *D. cornus* have attained persistent, considerable densities in outbreak situations. Densities were found of up to 5.1 individuals m⁻² for *D. fragum* in Japan (Fujioka and Yamazato, 1983) and 18.5 individuals m⁻² in for *D. cornus* in West Australia (Ayling and Ayling, 1987).

Prey choices of *Drupella* spp. have been documented in numerous normal and outbreak populations. Prey selection is complex and affected by relative abundance of coral taxa (Morton and Blackmore, 2009), although strong preferences for certain prey taxa and coral growth forms have been observed (Schoepf et al., 2010; Al-Horani et al., 2011). Most of the assumptions on this subject do not take relative availability of coral taxa into account, with exception of some papers on *D. cornus* (Turner, 1994; Schoepf et al., 2010). Results from most studies revealed a strong preference for acroporids (*Acropora* spp., followed by *Montipora* spp.) and some pocilloporid and poritid genera (Moyer et al., 1982; Fujioka and Yamazato, 1983; Turner, 1994; Al-Moghrabi, 1997; McClanahan, 1997; Cumming, 2002; Morton and Blackmore, 2009; Schoepf et al., 2010; Al-Horani et al., 2011). Many other taxa are mostly witnessed to be less commonly attacked or wholly avoided. Preferences are thought to depend on coral protein content and morphological complexity, both of which are high in *Acropora* (Keesing, 1990). Prey selection was also seen to differ within *D. cornus* age groups, with juveniles preferring structurally complex prey species that provide shelter (Forde, 1992; McClanahan, 1997; Schoepf et al., 2010). In some areas, *Drupella* prey preference is reported to differ from the above cited reports, due to a different coral assemblage composition or a lack of *Acropora* prey. *Drupella cornus* has been reported to favour corals of other genera at the periphery of its distribution range, such as *Porites* in Kenya (McClanahan 1997), and *Pocillopora* and *Porites* in Hawaii (Robertson 1970). A study by Morton et al. (2002) found that *D. rugosa* snails still preferred *Acropora* spp. despite their low abundance in the reefs of Hong Kong, which are primarily dominated by massive corals. So although their diet varies

according to the coral fauna composition, *Drupella* snails still maintain a dominant preference for *Acropora*. Prey shifts have also been documented after the preferred prey becomes less available. For instance following coral death by bleaching (Zuschin and Oliver, 2003; Hoeksema *et al.*, 2013) or even as direct consequence of predation by *Drupella* itself (Forde, 1992; Shafir and Gur, 2008).

One of such prey shifts to less preferred stony corals was documented for Koh Tao (Gulf of Thailand) following a mass coral bleaching event in 2010, related to elevated sea surface temperatures (Hoeksema *et al.*, 2013). The bleaching caused coral mortality throughout the Gulf of Thailand and adjacent areas, thereby locally decreasing diversity and abundance of various coral species (Yeemin *et al.*, 2012). However, some coral species were more susceptible to bleaching than others (Hoeksema and Matthews, 2011; Guest *et al.*, 2012), and some reefs at Koh Tao showed relatively fast recovery (Hoeksema *et al.*, 2012b), whereas local bleaching could still be noticed (or perhaps again) in some corals in February 2011 (Hoeksema and Matthews, 2015). Furthermore, the reefs around Koh Tao are increasingly subjected to sediment run-off from deforestation and development, pollution from the growing settlement on the island, as well as pressure from fishing and tourism-related activities (Weterings, 2011). *Acropora* colonies were specifically affected by bleaching and were further degraded by feeding *Drupella* (Hoeksema *et al.*, 2013), of which the population density doubled between 2009 and 2014 (unpublished data). Subsequently, *Drupella* aggregations started to form on less preferred prey, after the preferred prey species diminished. Peculiarly, many feeding aggregations moved to mushroom species (Fungiidae) co-occurring in large assemblages, which are usually avoided (Hoeksema *et al.*, 2013). Fungiids were still being preyed upon by *Drupella* in 2013 (Kim, 2013).

The present study looks into the *Drupella* population at Koh Tao four years after the 2010 bleaching

event. The population size and its distribution over sites and depths were measured for the muricids *D. rugosa* and *D. margariticola*, as well for the poorly studied *Morula spinosa*. Coral prey choice and microhabitat use were assessed to show ontogenetic and interspecific differences. Furthermore, molecular analyses were performed to investigate genetic differences of snails based on prey choice and geography. Seen in the light of the previous events that changed Koh Tao's reef community, along with the role of *Drupella* therein, the *Drupella* prey choice and its plasticity and potential ecological impact are discussed.

Material and methods

Molecular species identifications

Drupella and *Morula* snails were sampled to verify their identification at (sub)species level in order to examine if there is any geographic or prey-related cryptic speciation. Care was taken to include diverse within-species morphologies, which were stored on a > 70% alcohol solution. All specimens were obtained from Chalok Baan Kao, except for some *D. rugosa* from Sairee Beach found on *Fungia fungites* (Linnaeus, 1758). Sequences of muricid species and outgroups based on analyses by Barco *et al.* (2010), Claremont *et al.* (2011a), for *Drupella*, and Claremont *et al.* (2013) for *Morula* were downloaded from the NCBI GenBank sequence database (<http://www.ncbi.nlm.nih.gov/Genbank>; Appendix I).

The extraction of DNA was performed with, and according to the manufacturer's protocol of, the DNEasy Blood and Tissue Kit (QIAGEN, Venlo, The Netherlands). The mitochondrial genes cytochrome c oxidase subunit I (COI) and 12S rRNA (12S) were amplified through the use of primers previously designed to work on muricids (Table 1). The most rewarding reaction mix consisted of 1 μ L 10-100 \times diluted DNA, 0.2 μ M (1 μ L) of both the F and R primer,

Table 1. Primers used for amplification of markers 12S and COI of all muricid snail species.

Primer	Direction	Sequence	Reference
12S-I	F	TGC CAG CAG YCG CGG TTA	Oliverio and Mariottini (2001)
12S-III	R	AGA CGA CGG GCA ATT WGT AC	Oliverio and Mariottini (2001)
COIF	F	CTA CAA ATC ATA AAG ATA TTG G	Claremont <i>et al.</i> (2011b)
COI-MUR	R	ACA ATA RGA GAA ATT ATW CCA AA	Claremont <i>et al.</i> (2011b)

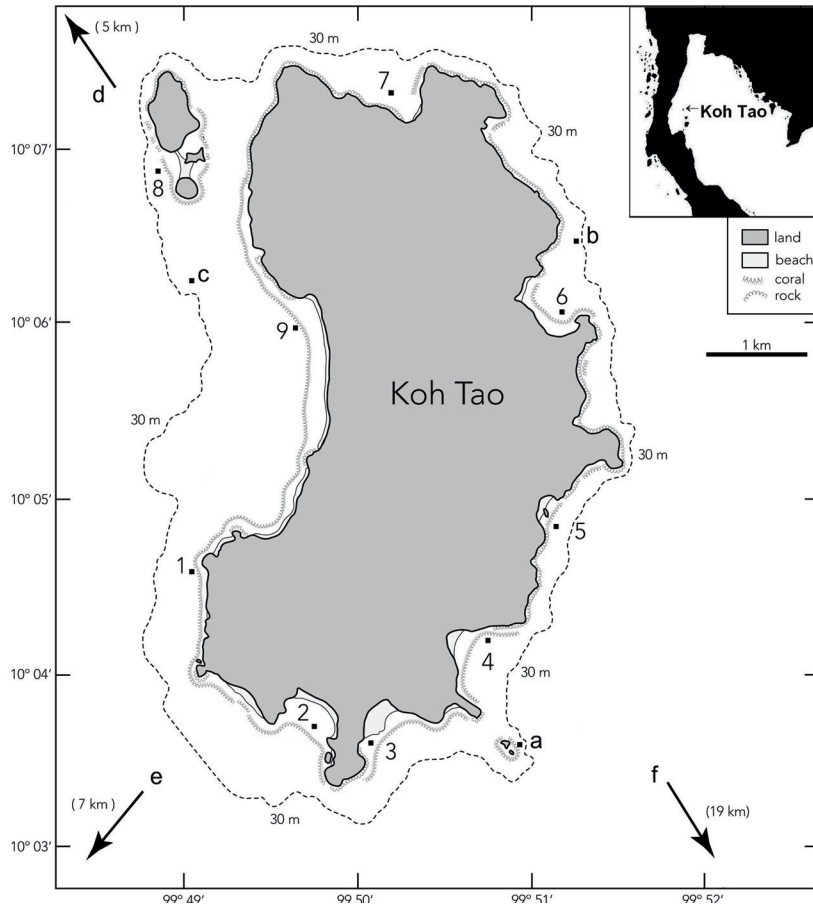


Fig. 1. Map of Koh Tao with transect sites at reef flats and slopes (numbers) and inspected outcrops and pinnacles (letters): 1) Had Sai Nuan, 2) Chalok Baan Kao, 3) Taa Chaa, 4) Aow Leuk, 5) Tanote, 6) Hin Wong Bay, 7) Mango Bay, 8) Twins, 9) Sairee, a) Shark Island, b) Hin Wong Pinnacle, c) White Rock, d) Chumphon Pinnacle, e) Southwest Pinnacle and f) Sail Rock. After Chansang *et al.* (1999) and Hoeksema *et al.* (2012).

2.5 μL dNTPs, 2.5 μL 10 \times NH_4 reaction buffer (Bio-line), 2 and 1.6 μM (1 and 0.8 μL) MgCl_2 for COI and 12S respectively, 0.2 μL Q-solution (QIAGEN) and 1 unit (0.2 μL) Taq polymerase. To reach a total reaction mixture volume of 25 μL the appropriate amount of MQ H_2O was added. The optimal PCR procedure for COI consisted of 5 min of initial denaturation at 95°C and 65 cycles of 40 s at 94°C, 40 s at 54°C for annealing and 60 s at 72°C for primer extension, followed by a final extension of 5 min at 72°C. The 65 cycles for 12S consisted of 60 s 60°C and 50 s at 72°C. The PCRs ran on a MyCycler™ Thermal Cycler (Bio-Rad). Sanger sequencing was performed by BaseClear (Leiden, The Netherlands).

Sequences were assembled and edited with Geneious version 6.1.6 (Drummond *et al.*, 2013). When indistinct peaks occurred in the forward and reverse sequences nucleotides were labelled as N. Sequences were aligned with the Geneious alignment function. The model of molecular evolution was selected for the

dataset of both markers under Akaike's Information Criterion with jModelTest version 0.1.1 (Posada, 2008). When substitution models were not available in the phylogenetic software package, one that was and had the lowest AIC was selected. Bayesian inference (BI) analyses were performed with MrBayes version 3.2.2 (Ronquist *et al.*, 2012). Branches that showed less than 50% posterior probability (PP) in the consensus tree were collapsed. The calculated MrBayes PP support values were obtained after 5,000,000 generations were sampled every 1,000 generations and a burn-in proportion of 25% was discarded.

Field survey

The study area encompassed nine sites around Koh Tao (Fig. 1), including some sites previously surveyed by Hoeksema *et al.* (2013), which consisted mostly of reef flats and gradually declining slopes. Fieldwork was conducted April - June 2014 during daytime. A sufficient

number of replicate measurements were required to study *Drupella* densities because of their possible clumped distributions (Cumming, 1999). A total of 31 belt quadrats of 1×10 m² were laid out, covering an area of 310 m². One to four quadrats were measured per depth range per site. A distinction was made between shallow (2-5 m depth, 18 total) and slightly deeper (5-8 m depth, 13 total) quadrats that were laid out haphazardly within areas with high hard coral abundance. Use of belt quadrats is recommended when densities of corals and coral-associated fauna are measured at different depths (e.g. Dai and Yang, 1995; Oigman-Pszczol and Creed, 2006; Gittenberger and Hoeksema, 2013).

The substrate composition within quadrats was estimated (m²), and consisted of the categories sand, rubble (including dead coral), rock, anthropogenic trash, sponge, algae, soft coral, healthy hard coral, recently killed coral and bleached coral. Coral colonies were included if at least half of the colony cover fitted inside the quadrat. All scleractinian corals were considered potential prey for corallivores and were thus included. Since Cumming (1999) observed that *Drupella* snails tend to avoid small coral colonies (Ø < 10 cm), these were not taken into account except when preyed upon. For all corals the following data was recorded: identity at genus level, size as maximum diameter measured (cm) and growth form (B, branching/arborescent; Bu, bushy/caespitose; C, corymbose; D, digitate; E, encrusting; F, foliose; L, laminar; M, massive; R, solitary/ mushroom; S, submassive; T, tabular). For the names of coral genera identified during the present study, recent relevant taxonomic studies were used that were based on phylogenetic analyses (Wallace *et al.*, 2007; Stefani *et al.*, 2008; Gittenberger *et al.*, 2011; Arrigoni *et al.*, 2014; Huang *et al.*, 2014).

For each muricid species, individuals were counted within each quadrat, depending on whether their prey coral was also mostly situated inside the quadrat (> 50%). Snail specimens could be identified in the field through characteristics described by Fujioka (1982) and supporting illustrations (e.g. Johnson and Cumming 1995). Inspection of the shell aperture was needed when shells were overgrown by crustose coralline algae. Snail size, based on shell length, was determined per size class as defined for *D. cornus* by Turner (1994) and Schoepf *et al.* (2010): juveniles (< 10 mm (recruits), 10-19 mm), adults (20-29 mm, > 29 mm). The size was measured for snails that could be sampled without causing damage to the coral and it was estimated for individuals that could not be caught.

Statistics

The density of muricids and its variation over depth was analysed through both Mann-Whitney-Wilcoxon tests and linear regression. The distribution of age groups over depth and substrates were compared through Chi-squared tests. Distribution over reefs in general for *D. rugosa* was investigated with linear regressions and generalized linear models. Median snail group sizes on coral colonies and among age groups were compared through Kruskal-Wallis tests and investigated further through Mann-Whitney-Wilcoxon tests. Statistical analyses were performed in RStudio (R Development Core Team 2010).

Prey preferences were assessed for *D. rugosa* through resource selection functions (Manly *et al.*, 1993). This was done by estimating the selection ratio (ω_i) for all potential prey genera and growth forms and the associated Bonferroni corrected 95 and 99% confidence interval with the formulas:

$$\omega_i = o_i / a_i \quad \text{and} \quad Z_{\alpha/2k} \sqrt{[o_i(1-o_i)/(u_i a_i^2)]}$$

where o_i is the proportion of occupied colonies of coral genus i among all occupied colonies of all genera, a_i is the proportion of available colonies of coral genus i among all available colonies of all genera, $Z_{\alpha/2k}$ is the critical value of a standard normal distribution upper tail area of $\alpha/2k$, k is the total number of coral genera in the analysis and u_i is the total number of coral colonies of all genera that are occupied. The confidence interval suggested that a prey was attacked less than expected from its relative availability when below 1 and more than expected from its relative availability when above 1. When the confidence interval encompassed 1, the prey species was not considered attacked significantly less or more than could be expected from its relative abundance. In addition to the resource selection of all *D. rugosa*, selection of juveniles and adults was calculated as well. The functions were applied according to Schoepf *et al.* (2002), although coral genera were taken into account, not species. All present scleractinian genera were included, as they were all considered potential prey species. This approach widens the resulting confidence intervals, making it less likely to find significant deviations from expected colony occupations. When availability of a coral genus was considered too low to be representative (< 7 colonies), such a genus was omitted from the analysis. Colonies of < 10 cm in diameter were also omitted from the analysis.

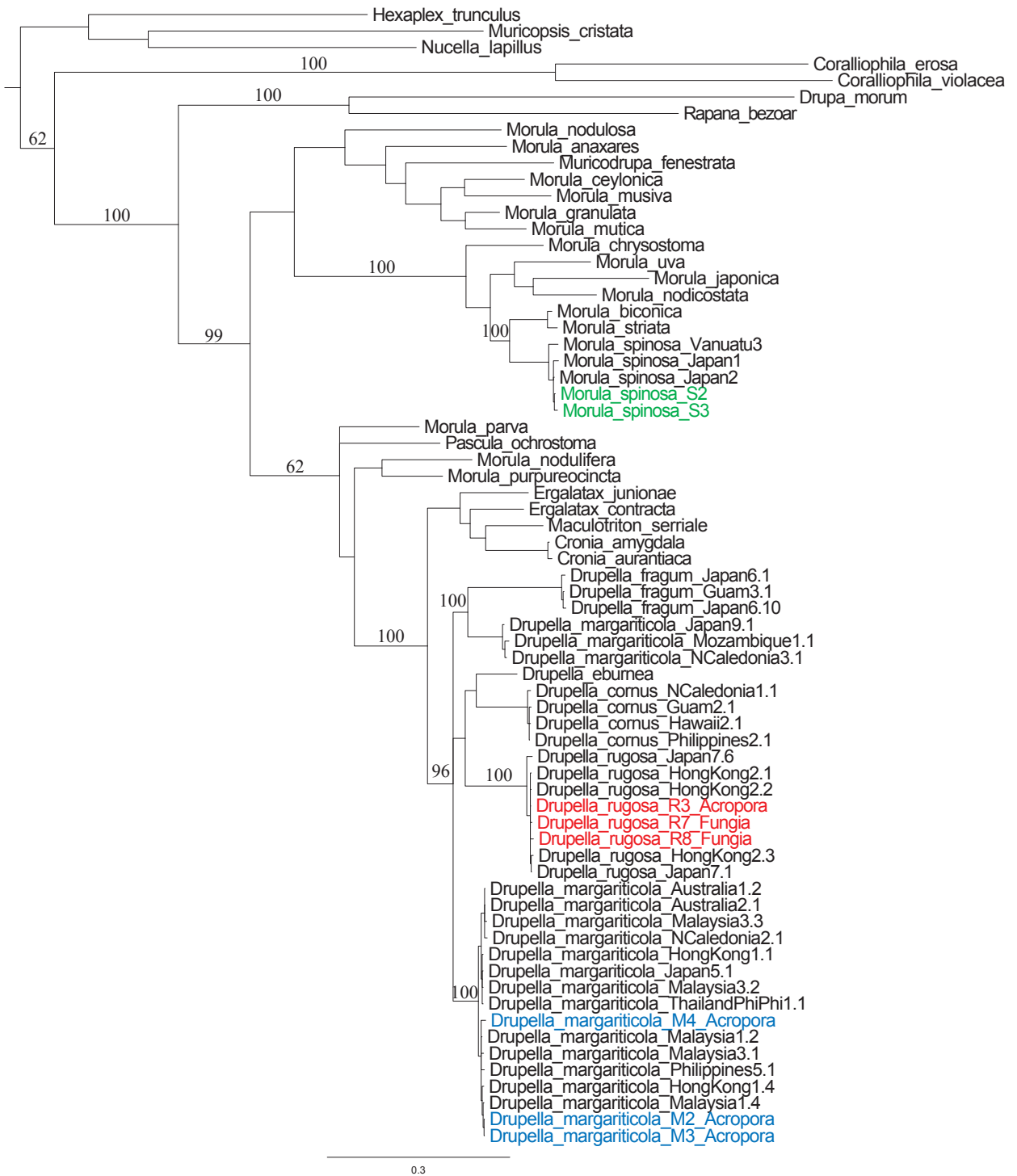


Fig. 2. Phylogeny of Muricidae with *Coralliophila* as muricid outgroup based on a Bayesian inference (BI) analysis of a two-locus molecular dataset (mitochondrial COI and 12S), with emphasis on on *Drupella* and *Morula* diversity. Values above branches are Mr-Bayes posterior probabilities as percentages. Specimens from Koh Tao are labelled R3, R7, R8 (*D. rugosa*), M2, M3, M4 (*D. margariticola*), S2 and S3 (*M. spinosa*). The coral prey from which a specimen was obtained is mentioned if applicable. The scale bar indicates the number of substitutions per site.

Species	1	2	3	4	5	6	7	8	9
<i>D. rugosa</i>	2.7 0.83	2 0.57	1.3 13.6	4.1 0.83	7.85 1.4	1.8 -	4 -	3.6 -	1.2 -
<i>D. margariticola</i>	0.03 0.17	0.07 0.1	0.2 0.05	1.34 0	0.25 0	0.03 -	0 -	0 -	0 -
<i>M. spinosa</i>	0.27 0.1	0.53 0.03	0.2 0	0.2 0	0.05 0.4	0.03 -	0.2 -	0.2 -	0 -

Table 2. Density (indiv. m⁻²) of *Drupella rugosa*, *D. margariticola* and *Morula spinosa* in transects at nine sites (Fig. 1) and two depth ranges: dark = 2-5 m, white = 5-8 m. Densities are the mean of 1-4 transects. Large aggregations of recruits have been omitted.

Since the analysis does not take *D. rugosa* group size into account, the mean group size per coral genus was compared with the results afterwards. Furthermore, when noting presence/absence (use/non-use) it can be difficult to demonstrate if the host coral is also used as prey (Boyce *et al.*, 2002). This seems less problematic for *Drupella* snails, which feed and rest on the same colony, directly linking presence to use and justifying the use of this method.

Results

Species identifications

After optimizing PCR conditions, both primer pairs worked on all muricids. The product size was approximately 720 for COI and 540 for 12S, and ultimate sequence sizes used for analysis were respectively 701 and 569 resulting in a concatenated analysis of 1270 characters based on 69 taxa. The models that were chosen were HKY+I+G for COI and GTR+I+G for 12S. The individual trees showed clear grouping of species in both *Drupella* and *Morula* (PP > 95%), although COI was more useful in resolving relationships within *Drupella* and 12S was more useful in resolving relationships in *Morula*.

The analysis produced well-defined groups with the two markers (Fig. 2). All species from this study fell within clear groups with their conspecifics (PP = 100%). *Morula* appeared polyphyletic as is currently being addressed (Claremont *et al.*, 2013), while the genus *Drupella* was well-defined. The *D. margariticola* samples were part of the 'Continental' clade of the species complex and, just as the coral eating specimens from Hong Kong, could not be distinguished from regions from which their coral feeding behaviour has not been documented. Furthermore, no distinction could be observed between *D. rugosa* specimens taken from *Acropora* and *Fungia* corals.

Distribution of muricids

The total of muricid individuals found within the 31 quadrats was 1249, consisting of 1145 *Drupella rugosa*, 60 *D. margariticola* and 40 *Morula spinosa* snails. Two quadrats were excluded from prey choice analyses due to minor uncertainties in the data and three large recruitment aggregations were left out of the mean site density calculation to prevent over-estimation. *D. rugosa* snails were found in every 10-m² belt quadrat in which their number varied from one to 168 (Table 2). The average density (\pm SE) for *D. rugosa* calculated from all site densities was 3.17 \pm 0.69 indiv. m⁻² in shallow areas and 3.45 \pm 1.54 indiv. m⁻² in slightly deeper areas. *D. margariticola* occurred in relatively small numbers (shallow: 0.21 \pm 0.07 indiv. m⁻², deep: 0.06 \pm 0.03 indiv. m⁻²) and *M. spinosa* occurred in even lower densities (shallow: 0.17 \pm 0.06 indiv. m⁻²; deep: 0.12 \pm 0.05 indiv. m⁻²) and generally did not seem as restricted to coral reef habitat as *Drupella*. All species were rare at pinnacles, with 0-2 individuals observed per dive. Related corallivores, *e.g.* other species of *Drupella* and Coralliophilinae, were not recorded at Koh Tao within and outside this study.

Although numbers of all three muricid species generally decreased with depth and were hardly seen below 8 m depth, no significant differences were found between medians of the shallow and slightly deeper quadrats (*D. rugosa*: W = 11, p = 0.147; *D. margariticola*: W = 20, p = 0.147; *M. spinosa*: W = 16.5, p = 0.460). Linear regressions based on the average depth of quadrats also showed slight negative trends that were insignificant (*D. rugosa*: p = 0.358; *D. margariticola*: p = 0.148; *M. spinosa*: p = 0.161). However, the distribution of juveniles and adults varied significantly over depth for *D. rugosa* (X² = 2610.57, p < 0.0001, Fig. 3) and *M. spinosa* (X² = 2.96, p < 0.0001), but not for *D. margariticola* (X² = 49.50, p = 0.085). Juveniles were more abundant in shallow quadrats whereas adults were more abundant in the deeper quadrats.

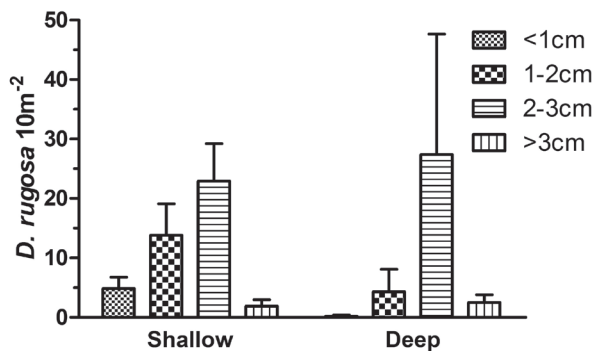


Fig. 3. Mean density (+SE) of *Drupella rugosa* per size class in shallow (3-5m) and deep (5-8m) transects.

All species and their age groups were most abundant on stony coral than on any other substrate (Fig. 4). The total number of individuals on living coral was highest for *D. rugosa* (95%) and *D. margariticola* (82%), which otherwise occurred on coral rubble. Relatively fewer *M. spinosa* snails were found on live coral substrate (65%), and they were also encountered on rock, rubble and sand. Substrate occupation differed between juveniles and adults only in *D. rugosa*, for which juveniles were found proportionally more on live coral (*D. rugosa*: $X^2 = \text{Inf.}$, $p < 0.0001$; *D. margariticola*: $X^2 = 1.28$, $p = 0.258$; *M. spinosa*: $X^2 = 0.04$, $p = 0.842$). *D. rugosa* were predominantly found on larger coral heads (> 10 cm diameter) (Fig. 5).

A significant positive correlation was found for *Drupella* density and healthy stony coral cover ($r = 0.118$, Adj. $R^2 = 0.199$, $p < 0.01$). When the numerical transect variables were analysed in a generalized linear model to explain *D. rugosa* distribution, the simplest significant model under a quasi-poisson link function consisted of *Acropora* density ($p < 0.01$), depth ($p < 0.01$), and rubble ($p < 0.05$). The proportion of the variance that could be explained with this model is 0.56, which is quite low.

Some *D. rugosa* aggregations consisted of high numbers of recruits or juveniles and sometimes a few adults on the coral colony margin. These were all found on digitate, tabular and bushy *Acropora* colonies. All were found on different sites between 2 and 4 m depth and contained up to ~100 individuals. Three large aggregations of recruits (55, 56 and 96 individuals in size) were found within quadrats, which is three aggregations per 310 m², or roughly one per 100 m².

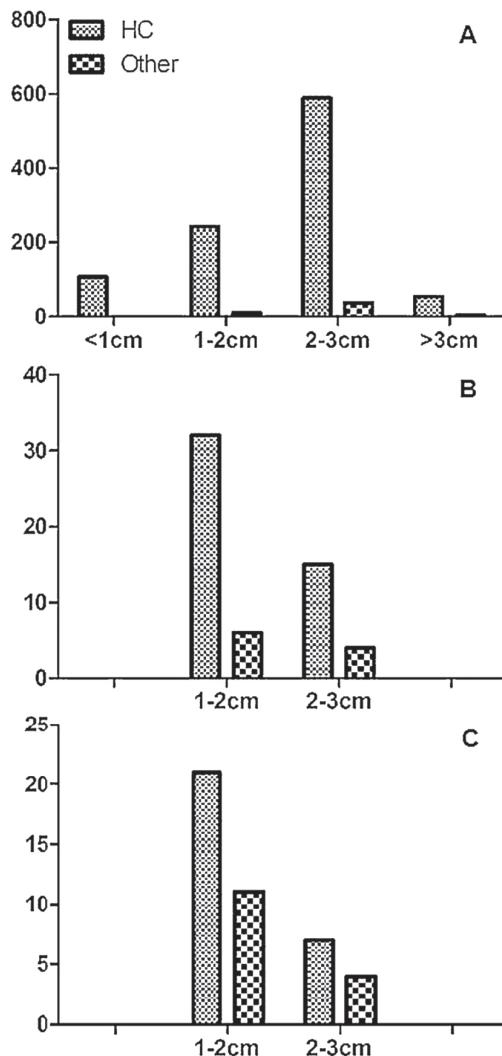


Fig. 4. Total numbers of snail individuals per size class found on stony coral (HC) and other kinds of substrate for A) *Drupella rugosa*, B) *D. margariticola* and C) *Morula spinosa*.

Prey choice

A total of 2714 coral colonies belonging to 33 genera were observed within the belt quadrats. The total number of coral colonies occupied by muricid snails was 235 for *Drupella rugosa*, 17 for *D. margariticola* and 25 for *Morula spinosa* (Table 3). Specimens of the opportunistic corallivore *D. margariticola* were found commonly, but not exclusively, together with those of *D. rugosa* (eight out of 17 colonies). Some *M. spinosa* snails were also found within a *D. rugosa* aggregation (four out of 25 colonies). The mean number of indi-

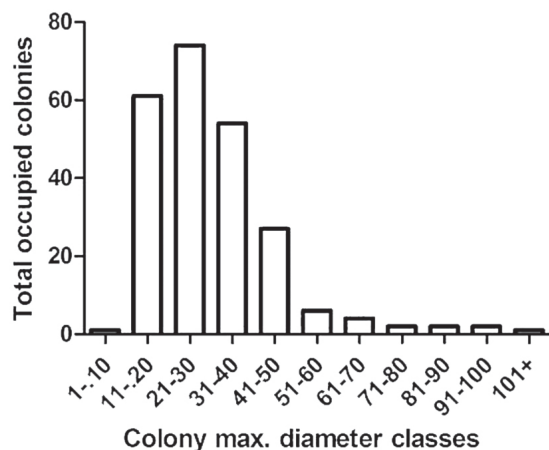


Fig. 5. Total number of coral colonies occupied by *Drupella rugosa* per colony size class based on maximum diameter (cm). Only one of the 235 occupied colonies fell within the 1-10 cm colony size range.

viduals per colony was 4.2 ± 0.6 for *D. rugosa*, 2.8 ± 0.8 for *D. margaritica* and 1.1 ± 0.1 for *M. spinosa*. Group size did not differ between *D. rugosa* juveniles and adults in general ($W = 5186$, $p = 0.337$), although the aggregation size on different coral groups did vary: juveniles $W = 7.74$, $p = 0.038$; adults $W = 14.29$, $p = 0.001$ (Fig. 6).

The resource selection ratios revealed differences in prey selection between *D. rugosa* juveniles (including recruits) and adults (Table 4). Corals of only a few genera were preyed upon by juvenile snails. *Acropora* corals were favoured by both juvenile and adult snails, although adult *D. rugosa* were absent on corymbose, digitate or tabular colonies. All *Acropora* growth forms had high occupation rates and mean abundances of snails per occupied colony. *Psammocora* corals had the highest occupation rate and also strikingly higher mean group size of occupants than those of the other genera, with the exception of *Acropora*. *Psammocora* was significantly selected for by snails of all size classes. Colonies of *Goniopora*, *Montipora* (S), *Platygyra* and *Porites* (B and S) were attacked by adult snails as expected from their abundance. *Pocillopora* corals were ignored by juveniles and used less than expected by adults. The abundant *Pavona* colonies were occupied more than expected by adult muricids and less than expected by juveniles. Strikingly, the 612 fungiid corals were devoid of snails and were only very rarely noted to be preyed upon outside the quadrats.

Table 3. Coral taxa and number of colonies > 10 cm found within the belt quadrats.

Family	Genus	Colonies	
Acroporidae	<i>Acropora</i>	513	
	<i>Astreopora</i>	1	
	<i>Montipora</i>	90	
Agariciidae	<i>Gardinoseris</i>	9	
	<i>Pavona</i>	999	
Diploastreidae	<i>Diploastrea</i>	13	
Euphylliidae	<i>Euphyllia</i>	1	
	<i>Galaxea</i>	9	
Fungiidae	<i>Ctenactis</i>	64	
	<i>Cycloseris</i>	7	
	<i>Danafungia</i>	12	
	<i>Fungia</i>	266	
	<i>Herpolitha</i>	25	
	<i>Lithophyllon</i>	162	
	<i>Pleuractis</i>	61	
	<i>Podabacia</i>	2	
	<i>Polyphyllia</i>	2	
	<i>Sandalolitha</i>	11	
	Lobophylliidae	<i>Lobophyllia</i>	17
		<i>Symphyllia</i>	7
		Merulinidae	<i>Dipsastrea</i>
<i>Echinopora</i>	26		
<i>Favites</i>	37		
<i>Goniastrea</i>	10		
<i>Hydnophora</i>	3		
<i>Leptoria</i>	7		
<i>Merulina</i>	8		
<i>Platygyra</i>	17		
Poritidae	<i>Goniopora</i>		49
	<i>Porites</i>		151
Pocilloporidae	<i>Pocillopora</i>	86	
Psammocoridae incertae sedis	<i>Psammocora</i>	25	
	<i>Leptastrea</i>	3	

Prey preference by *D. margaritica* snails followed that of co-occurring *D. rugosa*. When separate from their congeners, *D. margaritica* individuals were still observed to feed on corals of the same genera, although it is not known whether they initiated feeding on the coral while it was healthy or when it was already damaged or diseased. The coral genera selected by *D. margaritica* snails and the percentage of attacked colonies were *Acropora* (1.8%, B: 0.8%, Bu: 4.1%), *Montipora* (1.1%, S: 1.8%) and *Pavona* (0.7%). Only one or two *M. spinosa* individuals were found together on the same coral colony, and prey choice generally followed that of *D. rugosa*, although they were found relatively less commonly on *Acropora*. The coral genera selected by *M. spinosa* individuals and the percentage of colonies occupied by them were

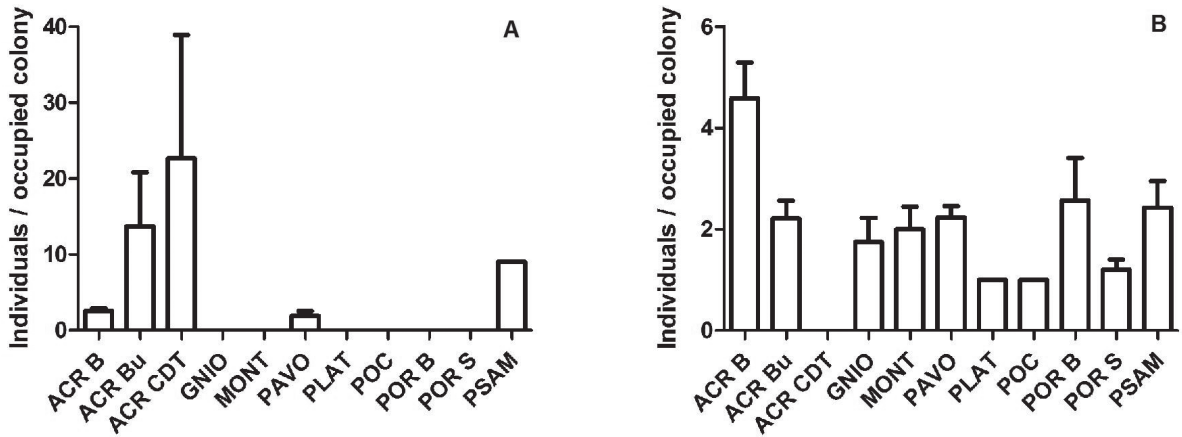


Fig. 6. Mean (+SE) group size of A) juvenile and B) adult *Drupella rugosa* on corals belonging to various genera and their growth forms: *Acropora* (B = branching/ arborescent, Bu = bushy/ caespitose, CDT = corymbose/ digitate/ tabular), *Goniopora*, *Montipora*, *Pavona*, *Platygyra*, *Pocillopora*, *Porites* (B = branching S = submassive), *Psammocora*.

Genus	Occupation (%)	Juveniles	Adults	All	Mean group size ±SE
<i>Acropora</i>	21.1	**	**	**	6.21 ± 1.15
B	22.1	**	**	**	4.85 ± 0.69
Bu	19	**	**	**	8.20 ± 3.54
CDT	23.1	**		NS	22.67 ± 16.29
<i>Ctenactis</i>					
<i>Cycloseris</i>					
<i>Danafungia</i>					
<i>Diploastrea</i>					
<i>Dipsastrea</i>					
<i>Echinopora</i>					
<i>Favites</i>					
<i>Fungia</i>					
<i>Galaxea</i>					
<i>Gardinoseris</i>					
<i>Goniastrea</i>					
<i>Goniopora</i>	8.2		NS	NS	1.75 ± 0.48
<i>Herpolitha</i>					
<i>Leptoria</i>					
<i>Lithophyllon</i>					
<i>Lobophyllia</i>					
<i>Merulina</i>					
<i>Montipora</i>	5.6		NS	--	2.00 ± 0.45
S	9.1		NS	NS	2.00 ± 0.45
EFL					
<i>Pavona</i>	9.6	--	**	*	2.40 ± 0.23
<i>Platygyra</i>	5.9		NS	NS	1
<i>Pleuractis</i>					
<i>Pocillopora</i>	1.2		--	--	1
<i>Porites</i>	7.9		NS	NS	2.00 ± 0.52
B	10.1		NS	NS	2.57 ± 0.84
S	6.1		NS	NS	1.20 ± 0.20
<i>Psammocora</i>	28	NS	**	**	3.71 ± 1.32
<i>Sandalolitha</i>					
<i>Symphyllia</i>					

Table 4. Overview of prey choice by *Drupella rugosa* through resource selection ratios of all, juvenile and adults occupied coral colonies. The occupation is in percentage of all colonies of that genus (and growth forms). The resource selection ratios with Bonferroni corrected 95 and 99% CI's are calculated to show in which proportion groups are used as would be expected from their availability. They were preferred at $p < 0.05$ (*) or $p < 0.01$ (**), avoided at $p < 0.01$ (--), not used significantly more or less than expected (NS) or remained unused.

Acropora (0.4%, Bu 1.4%), *Goniastrea* (10%), *Goniopora* (4.1%), *Montipora* (3.3%, S: 5.5%), *Pavona* (1.3%), *Porites* (1.7%, S: 1.2%) and *Psammocora* (12%).

Discussion

Corallivorous muricids have been studied before in relation to changes in prey choice and their distribution at Koh Tao (Hoeksema *et al.*, 2013). The present study allows a comparison of the muricid species composition with other situations in which muricids co-occurred in different geographic and ecological settings. The co-occurrence of coral feeding *Drupella rugosa* and *D. margaritica* has been extensively described for Hong Kong (*e.g.* Taylor, 1980; Morton and Blackmore, 2009). *D. rugosa* has been reported to reach high densities in co-occurrence with other *Drupella* species with high ecological impact on the Great Barrier Reef (Cumming, 1999). It is also known to co-exist with the muricid corallivorous snail *Coralliophilla violacea* (Kiener, 1836) (= *C. nerotoidea* (Gmelin, 1891)) (Fujioka and Yamazato 1983; Schuhmacher, 1992; McClanahan, 1994; Al-Moghrabi, 1997). The latter species has been reported to occur as individuals and in aggregations (Oren *et al.*, 1998; Chen *et al.*, 2004) but was not observed at Koh Tao. The extent of the diet of *Morula spinosa* has not consistently been defined despite its wide Indo-Pacific distribution (Taylor, 1978; Yokochi, 2004; Titlyanov and Titlyanova, 2009).

Implications for muricid (sub)species

Molecular characterization of the corallivorous muricids of Koh Tao shows that all species fall neatly within the expected existing groups of widely sampled muricid species. The two marker dataset produced a satisfactory tree with strong branch support. For *Drupella rugosa*, variation in shell morphology was noted. Nevertheless, no molecular basis was found to distinguish the variation, as was also found when Johnson and Cumming (1995) tested for *D. fragum* and *D. rugosa* hybrids. Moreover, no prey-related cryptic speciation seems to occur in *D. rugosa*, although data on this subject is preliminary and specimens from different prey should be more thoroughly sampled. Host-associated differentiation is already known from a selection of Caribbean and Indo-Pacific coralliophillines (Johnston *et al.*, 2012; Simmonds *et al.*, 2012), although this may not be the case and otherwise harder to prove for *Drupella*, owing to their cryptic and adaptive prey choice.

The sampled *D. margaritica* were part of the ‘Continental’ clade in which corallivory was already known to occur (Claremont *et al.*, 2011a). The theory that all snails belonging to this clade could potentially feed on coral tissue is supported by this study and possibly far more widespread than currently documented. Coral consumption by *Morula spinosa* has formerly been documented for Japan (Yokochi, 2004) and now for Thailand. The coral feeding individuals do not differ genetically from conspecifics and thus the same applies, implying that this widespread species may feed on corals in other locations. Moreover, more muricid taxa could be able to opportunistically feed on corals than is currently known, as it has only recently been discovered for *M. spinosa* (Yokochi, 2004) and *Ergalatax junionae* (Saledhoust *et al.*, 2011).

Distribution and habitat

Among *Drupella* species, *D. rugosa* was the first to catch attention because of its potential to cause damage to coral reefs (Moyer *et al.*, 1982). Afterwards, *D. cornus* and *D. fragum* outbreaks were observed with mean densities higher than 3 indiv. m⁻² (reviewed in Cumming, 2009). The density of > 3 *D. rugosa* m⁻² at Koh Tao for both shallow and deep quadrats during an ongoing outbreak is in line with the documented outbreaks of their congeners. A number of indicators for problematic *Drupella* populations are also in line with an outbreak (Cumming, 2009), since 9% of all coral colonies were preyed on and large aggregations of juveniles (50–100 indiv.) were frequently encountered. For *D. margaritica* local mean densities of approximately 5 indiv. m⁻² were found in Hong Kong (Morton and Blackmore, 2009), which was up to 1.3 indiv. m⁻² at Koh Tao. Regarding the distribution of *M. spinosa* the highest mean local density in the present study measured was 0.5 indiv. m⁻². Earlier reports on the occurrence and distribution of this species did not give quantitative data (Taylor, 1978; Yokochi, 2004). Concerning the density of populations of both *D. margaritica* and *M. spinosa* it is not known whether these have grown over previous years and it is not established in what density they occur under normal circumstances.

Since the 2010 mass bleaching event in the Gulf of Thailand, stony coral cover had declined and coral reef communities had changed (Chavanich *et al.*, 2012; Yeemin *et al.*, 2012). The reefs of Koh Tao were also affected by bleaching and other detrimental effects (Hoeksema and Matthews, 2011; Weterings, 2011; Hoeksema *et al.*, 2013), and as such *Drupella* snails

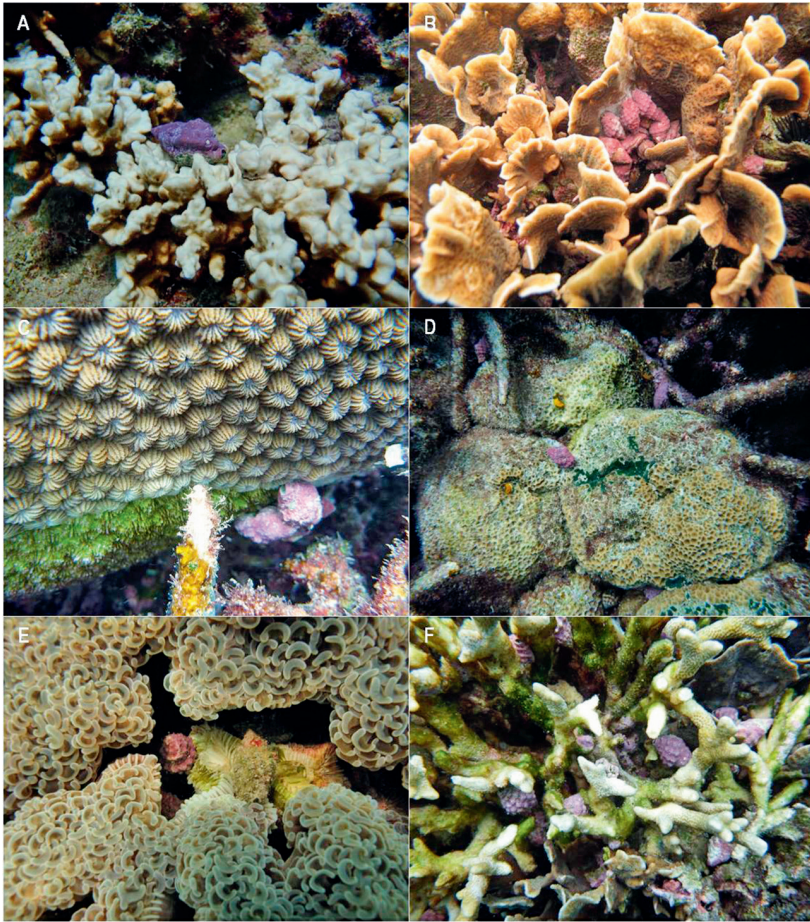


Fig. 7. *Drupella rugosa* aggregations feeding on coral colonies from a variety of families. A: *Psammocora contigua* (Psammocoridae), B: *Pavona* sp. (Agariciidae), C: *Diploastrea heliopora* (Diploastreidae), D: *Goniastrea* sp. (Merulinidae), also with a single *Drupella margariticola* individual, E: *Euphyllia ancora* (Euphyllidae) F: *Porites digitata* (Poritidae).

were able to thrive and more than double their relative abundance between 2009 and 2014 (unpublished data). Although some variation over sites occurs, a very high difference in occupation was noted among different habitats around Koh Tao. This was also described for Lizard Island (Great Barrier Reef), where *D. rugosa* occurs mostly on sheltered slopes, and *D. cornus* and *D. fragum* mostly occupy exposed reef crests (Cumming, 1999). Most reefs around Koh Tao are built on gentle slopes with moderate wave action, which appears ideal for *D. rugosa*. The pinnacles and rocky outcrops around Koh Tao (see Fig. 1) are exposed to stronger wave action and currents. Their steep slopes show low coral cover and therefore *Drupella* snails were rare.

The present results show a preference for high *Acropora* densities (see also Cumming, 2009), large colony sizes (see also Cumming, 2009; Schoepf et al., 2010) and a high cover of rubble and dead coral on which individuals dwell when not on a living colony. A high healthy stony coral cover was also preferred, al-

though indications of correlations with unhealthy reef sites have been found before in Hong Kong (Morton et al., 2002) and Koh Tao (unpublished data). No single variable was able to appropriately explain *Drupella* distribution and the generalized model could only explain part of the variation in the data. A negative correlation of *Drupella* density with depth was found in earlier years for *D. rugosa* at Koh Tao (unpublished data), but this correlation was not significant in the present study. This is presumably due to the wide 3-m intervals (2-5 and 5-8 m) within which quadrats were laid out and the high densities found below 5 m depth at Taa Chaa. The drivers for the distribution of *Drupella* species remain unclear, although various aspects have also been discussed in previous studies, such as depth (Schoepf et al., 2010), habitat (Cumming, 1999), substrate cover and coral communities (e.g. Cumming, 1999; Morton and Blackmore, 2009; Schoepf et al., 2010), reef status, and anthropogenic reef use (e.g. McClanahan, 1994; Morton et al., 2002).

The distribution of *D. margaritica* and *M. spinosa* seemed less dependent on coral cover owing to their relatively high occupation of other substrata and their ability to feed on other prey. *M. spinosa* was more commonly found on sandy substrates and isolated outcrops than *Drupella* spp. Juveniles of *D. rugosa* were found more in shallow areas and juveniles of all species were more abundant on stony coral, although this was not significant for *D. margaritica*. In general there appeared to be different habitat and prey requirements for juvenile snails as compared to the adults.

Scleractinian prey preferences

A high prey preference for *Acropora* spp. was found for *D. rugosa*, although there were differences in occupation rate and aggregation size for juveniles and adults on different species (and growth forms), which was also revealed through resource selection functions for *D. cornus* (Schoepf *et al.*, 2010). The present study also points out that *Montipora* is occupied less than can be expected from its availability and only by fairly small aggregations. This is even more so for *Pocillopora* species, which were generally observed to be one of the main prey species at Koh Tao in earlier years. In contrast, other studies point out that *Drupella* species, and *D. rugosa* in particular, often prey on *Montipora* and *Pocillopora* corals (*e.g.* Boucher, 1986; Baird, 1999), although there are many observations that do not take their relative abundance into account. The newly discovered preference for the relatively rare *Psammocora contigua* (Esper, 1794) is remarkable, whereas the preference of adult *D. rugosa* for *Pavona* spp. may be related to their abundance at Koh Tao. Compared to the coral community seen in Hong Kong (Morton and Blackmore, 2009), massive and encrusting corals do not dominate Koh Tao reefs and where local *Acropora* abundance is low, other genera with branching (*Porites*), foliose (*Pavona*) or submassive/foliose (*Psammocora*) growth forms are selected as second-choice prey of *D. rugosa*. Furthermore, the coral genera preyed on by *Drupella* snails within quadrats only represented a portion of the available prey. Predation on other taxa was observed in the same and previous years (Hoeksema *et al.*, 2013), although most of those occurrences are rare. Coral genera that *D. rugosa* has been observed to feed upon on Koh Tao reefs were *Acropora*, *Alveopora*, *Ctenactis*, *Diploastrea*, *Euphyllia*, *Favites*, *Fungia*, *Galaxea*, *Goniastrea*, *Goniopora*, *Hydnophora*, *Leptoria*, *Lithophyllon*, *Lobophyllia*, *Merulina*, *Montipora*, *Pavona*, *Platygyra*,

Pleuraetis, *Psammocora*, *Pocillopora*, *Porites*, *Sandalolitha* (examples in Fig. 7).

The present study shows that fungiids, which were abundant in transects, were avoided by *Drupella*. After the 2010 bleaching event, *Drupella* at Koh Tao were witnessed to feed on fungiid corals in large aggregations after nearby *Acropora* colonies had died (Hoeksema *et al.*, 2013). This was the first ever description of *Drupella* feeding on fungiids in high numbers. Although this was unusual, it was not entirely unexpected as *Drupella* diet is plastic and these corals also host various groups of parasitic molluscs (Gittenberger and Gittenberger, 2011; Hoeksema *et al.*, 2012b; Gittenberger and Hoeksema, 2013). Kim (2013) reported that *Fungia fungites* at Koh Tao was still being preyed upon by large aggregations of adults in 2013. This was remarkable since fungiids quickly recovered from bleaching (Hoeksema *et al.*, 2012a, 2013), and were not likely to be more vulnerable to predation. In the Java Sea, where massive coral bleaching was observed in 1983, neither mushroom corals nor other corals were reported as being under attack by *Drupella* (Brown and Suharsono, 1990; Hoeksema, 1991), although it was already known that secondary disturbances by predators after bleaching may occur (Glynn, 1988). Similarly, muricid predators of octocorals in Brazil also became more noticeable four years after the latter suffered from bleaching in 2010 (Dias and Gondim, 2016). The delayed shift of *Drupella* back to the preferred *Acropora* could be on account of a delayed recovery of the *Acropora* assemblages at Koh Tao and a co-occurring colony size and density refuge.

Drupella margaritica occurred in fairly low densities around Koh Tao. They were able to form small coral feeding aggregations separate from *D. rugosa*, although they occasionally co-occurred. This suggests that *D. margaritica* was able to initiate feeding by itself, although it is currently unknown whether it only occurs on already damaged colonies. They attacked corals of the common genera *Acropora*, *Montipora* and *Pavona*. Considering its low density around the island and relatively small size, *D. margaritica* is not expected to pose significant problems for coral reef communities as its large and numerous relatives. Nevertheless, its ability to initiate attacks on coral colonies and the proportion of corals in its diet might have been underestimated before. The first record of *D. margaritica* as opportunistic coral predator came from Hong Kong, where it co-occurred with *D. rugosa* (Morton *et al.*, 2002; Morton and Blackmore, 2009). The present observation at Koh Tao is its second record as a

corallivore, even though the species is known to have a widespread Indo-Pacific distribution. Its dietary preferences may previously have remained unnoticed because of its usually low population densities.

It is still unclear how *Morula spinosa* is able to feed on scleractinians, and they may be better described as coral scavengers than corallivores. Individuals have been found on damaged colonies of coral genera similar to those occupied by *D. rugosa*, whereas they have also been found on non-coral substrate and in non-reef habitats. Only one or two individuals occurred together and rarely in co-existence with *Drupella* aggregations. This indicates that they are able to feed on coral tissue, but not as intensively as *Drupella* snails. Coral damage by *M. spinosa* has been reported before, although this does not seem to be substantial (Yokochi, 2004), and mainly opportunistically on damaged or stressed corals (Titlyanov and Titlyanova, 2009). Their presence on a coral also does not always coincide with clear feeding scars and as such their presence could also mean that they associate with their host for other reasons. The main portion of its diet may consist of other molluscs, polychaetes, cadavers and other food sources many related predatory muricid species are known to feed on (see Taylor, 1978; Barco *et al.*, 2010).

Local and widespread ecological implications

The outbreak densities of the *Drupella rugosa* population at Koh Tao were restricted to certain depths at reef

flats and gentle slopes which occur much around the coastline. The population has grown despite removal efforts (unpublished data), and can have harmful effects on the already stressed reefs (Weterings, 2011; Lamb *et al.*, 2014). Effects on reef health and the coral community by *D. margariticola* and *Morula spinosa* are expected to be negligible according to their low numbers and non-obligate feeding on corals. This is mostly in line with earlier descriptions of coral predation by these muricids (Morton and Blackmore, 2009; Yokochi, 2004). Although coral prey selection based on their relative abundance was not calculated for Hong Kong, occupation instances have been witnessed to differ between *D. rugosa* at Koh Tao and Hong Kong on account of differences in coral communities. Both examples of *D. rugosa* populations are unique regarding their prey choice in different coral communities (this study, Morton *et al.*, 2002; Morton and Blackmore, 2009; Hoeksema *et al.*, 2013) and climatic regimes (Morton and Blackmore, 2009; Tsang and Ang, 2015).

Juveniles of *D. rugosa* were found to prefer *Acropora* species with caespitose/digitate/tabular growth forms (Fig. 8), on which they form large feeding aggregations through which the colony ultimately perishes. This is in line with earlier notes on juveniles preferring *Acropora* both as a food source and as a sheltered habitat (Forde, 1992; McClanahan, 1997; Schoepf *et al.*, 2010). Branching *Psammocora contigua* corals showed more aggregations of adult *D. rugosa* than expected and also a single juvenile aggregation.

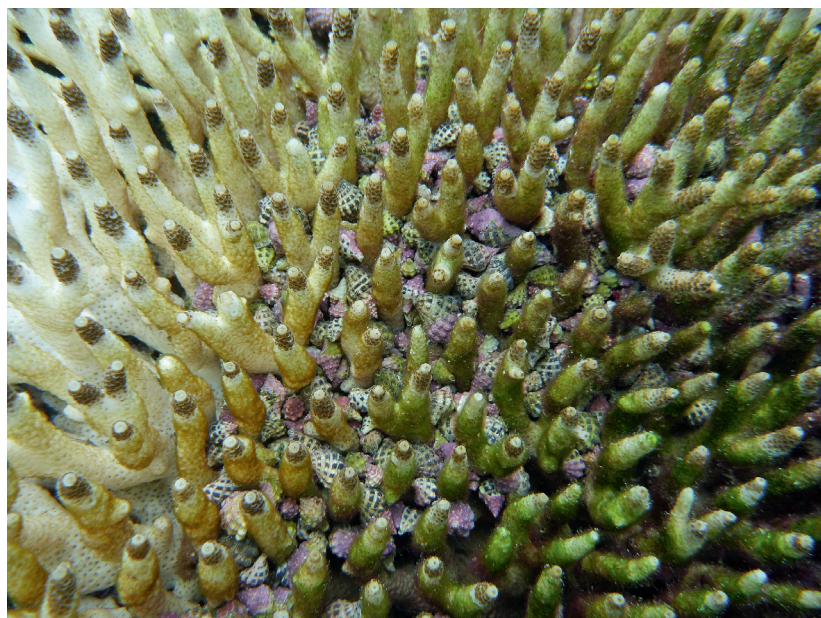


Fig. 8. Typical feeding pattern of *Drupella rugosa* recruits on acroporid corals. Many 0-2 cm snails are grouped together in a cryptic manner between *Acropora* sp. branches and a clear zonation is revealed of dead, recently killed and living coral.

P. contigua and caespitose/digitate/tabular *Acropora* spp. were found to be relatively rare within transects. Their branches were in general brittle and commonly mechanically damaged and affected by some bleaching. Their fragile state within the local coral community along with continued high predation pressure by *Drupella* snails could have detrimental effects for these specific groups. Nevertheless, there are indications that coral species are able to escape feeding *Drupella* through small (< 10 cm) colony size refuge (Cumming, 2009), depth refuge (> 8 m), and a low relative availability. They may also benefit from the possible ability of *Drupella* to adapt to community changes and from its dietary shifts involving less preferred prey species that are in high abundance for elongated periods of time (Hoeksema *et al.*, 2013). *Drupella* populations were observed to diminish living reef cover in many different habitats and coral communities (Moyer *et al.*, 1982; Ayling and Ayling, 1992; McClanahan, 1994; Al-moghrabi, 1997; Antonius and Riegl, 1998), and change the coral community structure (Forde, 1992; Shafir and Gur, 2008; Hoeksema *et al.*, 2013). Long-term monitoring should indicate whether *Drupella* outbreaks may be able to change the coral community so that certain coral species become locally endangered or extinct.

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Appendix

GenBank accession numbers for 12S and COI sequences. Accession numbers beginning with EU were first published by Claremont *et al.* (2008), FM by Oliverio and Modica (2010), FN by Barco *et al.* (2010), FR by Claremont *et al.* (2011), GU by Zou *et al.* (2011), HE by Claremont *et al.* (2013), and HQ by Zou *et al.* (2011). Field collection numbers and Naturalis Biodiversity Center collection numbers (RMNH) are listed for new sequences with GenBank accession numbers KT343581 through KT343595.

Genus	Species	12S	COI	Remarks
<i>Coralliophila</i>	<i>erosa</i>	FR853977	FR853815	
<i>Coralliophila</i>	<i>violacea</i>	FR853978	FR853816	
<i>Cronia</i>	<i>amygdala</i>	FR853984	FR853822	
<i>Cronia</i>	<i>aurantiaca</i>	FR853983	FR853821	
<i>Drupa</i>	<i>morum</i>	FN677394	FN677405	
<i>Drupella</i>	<i>cornus</i>	FR853988	FR853825	
<i>Drupella</i>	<i>cornus</i>	FR853979	FR853817	
<i>Drupella</i>	<i>cornus</i>	FR854005	FR853842	
<i>Drupella</i>	<i>cornus</i>	FR853993	FR853830	
<i>Drupella</i>	<i>eburnea</i>	FR853991	FR853828	
<i>Drupella</i>	<i>fragum</i>	FR854007	FR853844	
<i>Drupella</i>	<i>fragum</i>	FR854047	FR853884	
<i>Drupella</i>	<i>fragum</i>	FR854048	FR853885	
<i>Drupella</i>	<i>rugosa</i>	FR854011	FR853848	
<i>Drupella</i>	<i>rugosa</i>	FR853997	FR853834	
<i>Drupella</i>	<i>rugosa</i>	FR853998	FR853835	
<i>Drupella</i>	<i>rugosa</i>	FR853990	FR853827	
<i>Drupella</i>	<i>rugosa</i>	FR853992	FR853829	
<i>Drupella</i>	<i>rugosa</i>	-	KT343584	R3, RMNH.5003980
<i>Drupella</i>	<i>rugosa</i>	KT343592	KT343585	R7, RMNH.5003982
<i>Drupella</i>	<i>rugosa</i>	KT343593	KT343586	R8, RMNH.5003983
<i>Drupella</i>	<i>margariticola</i>	FR853985	FR853823	corallivorous
<i>Drupella</i>	<i>margariticola</i>	FR854020	-	corallivorous
<i>Drupella</i>	<i>margariticola</i>	FR854015	FR853852	crassulnata
<i>Drupella</i>	<i>margariticola</i>	FR854023	FR853860	typical
<i>Drupella</i>	<i>margariticola</i>	FR854026	FR853863	typical
<i>Drupella</i>	<i>margariticola</i>	FR854027	FR853864	typical
<i>Drupella</i>	<i>margariticola</i>	FR854037	FR853874	typical
<i>Drupella</i>	<i>margariticola</i>	FR854038	FR853875	typical
<i>Drupella</i>	<i>margariticola</i>	FR854039	FR853876	typical
<i>Drupella</i>	<i>margariticola</i>	FR854043	FR853880	typical
<i>Drupella</i>	<i>margariticola</i>	FR854012	FR853849	typical
<i>Drupella</i>	<i>margariticola</i>	FR854044	FR853881	typical
<i>Drupella</i>	<i>margariticola</i>	FR854024	FR853861	oceanic
<i>Drupella</i>	<i>margariticola</i>	FR853987	EU391587	oceanic
<i>Drupella</i>	<i>margariticola</i>	FR854058	FR853895	oceanic
<i>Drupella</i>	<i>margariticola</i>	KT343589	KT343581	M2, RMNH.5003984
<i>Drupella</i>	<i>margariticola</i>	KT343590	KT343582	M3, RMNH.5003985
<i>Drupella</i>	<i>margariticola</i>	KT343591	KT343583	M4, RMNH.5003986
<i>Ergalatax</i>	<i>contracta</i>	FR854045	FR853882	
<i>Ergalatax</i>	<i>junionae</i>	FR854046	FR853883	
<i>Hexaplex</i>	<i>trunculus</i>	AM712298	AM712604	
<i>Maculotriton</i>	<i>seriale</i>	FR854056	FR853893	
<i>Morula</i>	<i>anaxares</i>	HE583775	EU391584	
<i>Morula</i>	<i>biconica</i>	HE583792	-	
<i>Morula</i>	<i>ceylonica</i>	HE583780	HE584015	
<i>Morula</i>	<i>chrysostoma</i>	HE583793	HE584021	
<i>Morula</i>	<i>granulata</i>	FN677383	EU391585	
<i>Morula</i>	<i>japonica</i>	HE583795	HE584023	
<i>Morula</i>	<i>musiva</i>	HQ833881	GU188266	
<i>Morula</i>	<i>mutica</i>	FN677379	FN677418	
<i>Morula</i>	<i>nodicostata</i>	HE583796	HE584024	
<i>Morula</i>	<i>nodulifera</i>	HE583827	HE584048	
<i>Morula</i>	<i>nodulosa</i>	HE583778	HE584013	
<i>Morula</i>	<i>parva</i>	HE583811	HE584034	
<i>Morula</i>	<i>purpureocincta</i>	HE583831	HE584050	
<i>Morula</i>	<i>spinosa</i>	HE583798	HE584025	
<i>Morula</i>	<i>spinosa</i>	HE583799	HE584026	

Appendix. Cont.

Genus	Species	12S	COI	Remarks
<i>Morula</i>	<i>spinosa</i>	HE583797	-	
<i>Morula</i>	<i>spinosa</i>	KT343594	KT343587	S2, RMNH.5003987
<i>Morula</i>	<i>spinosa</i>	KT343595	KT343588	S3, RMNH.5003988
<i>Morula</i>	<i>striata</i>	HE583800	HE584027	
<i>Morula</i>	<i>uva</i>	HE583804	HE584029	
<i>Muricodrupa</i>	<i>fenestrata</i>	FN677378	FN677419	
<i>Muricopsis</i>	<i>cristata</i>	FN391981	FN651943	
<i>Nucella</i>	<i>lapillus</i>	FN651876	FM999169	
<i>Pascula</i>	<i>ochrostoma</i>	FR854002	FR853839	
<i>Rapana</i>	<i>bezoar</i>	FN677376	FN677421	