Neustonic copepods (*Labidocera* spp.) discovered living residential in coral reefs

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Received: 13 July 2016 / Accepted: 17 October 2017

Abstract

Pontellid copepods are archetypical representatives of the neuston—the highly specialized community living in the top 5–10 cm of the ocean surface. Their deep blue pigmentation and large eyes are unique adaptations to surface irradiation and carnivory, but poor prerequisites for survival in the transparent waters beneath the sea surface. Here, we report the discovery of three reef-associated representatives of this group—*Labidocera bataviae* A. Scott, 1909; *L. pavo* Giesbrecht, 1889; and *Labidocera* sp.—living residential in coral reefs. We (1) document the presence of *Labidocera* spp. for two separate coral reefs on two expeditions to Papua New Guinea, (2) describe their migration behavior and substrate preference, and (3) quantify the effects of benthic reef community composition on their abundance. All life stages of *Labidocera* spp. were 43 to 94 times as abundant at the reef sites as in offshore sites. Although pontellids are generally considered non-migrators, *Labidocera* spp. showed discernible diel vertical migrations: living in reef substrates during the day, emerging into the water column at night (sometimes more than once), and returning to the substrate at dawn. *Labidocera* spp. showed a pronounced substrate preference for coral rubble, microalgae, and turf, over branching coral, massive boulder coral, and sand.

Keywords

Copepods
Neustonic
Residential
Coral reef
Pontellidae

Communicated by P. Martinez Arbizu

Introduction

Copepods are microscopic crustaceans that constitute the bulk of zooplankton. Most copepods drift with the currents; however, some copepods are demersal or live residential to a localized area and are able to maintain their position within a given area by seeking refuge in substrates (Alldredge and King 1977), swimming against currents (Genin et al. 2005), swarming behind seafloor structures to prevent being swept away (Hamner and Carleton 1979), or sometimes utilizing the ebb and flow of tides to stay within a coastal region (Kimmerer et al. 1998; Chew et al. 2015). Copepods that live residential to specific benthic environments emerge only temporarily into the water column, typically during the night (Ohlhorst 1982; Mauchline 1988), taking advantage of the sheltering darkness to forage for food while avoiding visual predators (Zaret and Suffern 1976; Alldredge and King 1985). During the day these copepods may live amongst or above the substrate (Alldredge and King 1977), swarm in the hyperbenthic layer above the seafloor (Carleton and Hamner 2007;

Carleton and McKinnon 2007), or hide in crevices (Hsiao et al. 2013). Different copepod species are associated with sand flats (Youngbluth 1982; Ohtsuka et al. 1996), kelp beds (Hammer 1981), seagrass beds (Walters and Bell 1994), lagoons (Jacoby and Greenwood 1988), mangroves (Sorokin and Sorokin 2010), and coral reefs (Emery 1968; Sale et al. 1978; McKinnon 1991; Heidelberg et al. 2004; Fukuoka et al. 2015). Zooplankton abundance associated with substrata is often patchy and changes with the seasons (McWilliam et al. 1981; Lewis and Boers 1991).

Relatively little is known about the behavior and life histories of copepods living in coral reefs, even though they are pertinent for coral health, fisheries production, and nutrient cycling within reefs (Ikeda et al. 1982; Hamner et al. 1988; Carleton 1993; Donelson et al. 2010; Ferrier-Pagès et al. 2011). Some holoplanktonic groups (i.e. pelagic throughout their life) include representatives also known to inhabit coral reef environments and behave like typical reef zooplankton. Taxa with such high behavioral flexibility include members of the genera *Acartia* Dana, 1846, and *Oithona* Baird, 1843 (Emery 1968; Heidelberg et al. 2004; Alvarez-Cadena et al. 2014). For neustonic copepods, living in the top 5–10 cm of the sea surface, such behavioral plasticity is so far unknown.

Little is known about the family Pontellidae and their role in coral reefs. Of the pontellid copepod genera, *Calanopia* Dana, 1853, are known to live within reefs (Clarke 1934; Heidelberg et al. 2004; Nakajima et al. 2008; Pessoa et al. 2014). Most other pontellid genera are considered either oceanic or neritic and also neustonic (Silas and Pillai 1973; Conley and Turner 1985). The genus *Labidocera* Lubbock, 1853, has large eye lenses for scanning (Land 1988), and their morphology is adapted for sea surface dwelling, as they are highly pigmented (Herring 1965), an adaptation to reduce the effects of damaging ultraviolet radiation and to hide from surface predators (Hansson et al. 2007; Hunt et al. 2010; Mojib et al. 2014). The pigment specific to pontellid copepods is a blue carotenoprotein (Zagalsky and Herring 1972), and they are able to adjust their level of pigmentation depending on risks in their immediate environment (Hansson 2000). Those copepods with high carotenoid pigment content that protects against UV radiation are generally non-migrators because they no longer need to swim away from potential damage caused by light in the surface layer (Hairston 1976).

Pontellid copepods are capable of escaping predators by jumping into the air (Gemmell et al. 2012). Although neustonic, pontellids can be further divided into categories based on their migration behavior; for example, some pontellids stay permanently in the top 10 cm (termed 'euneustonic', e.g. *Labidocera detruncata* Dana, 1849; *Pontella securifer* Brady, 1883), some species migrate diurnally within the top 30 cm, sometimes slightly deeper (termed 'facultative neustonic', e.g. *Labidocera acuta* Dana, 1849; *L. minuta* Giesbrecht, 1889; *Pontella fera* Dana, 1849; *P. kieferi* Pesta, 1933; *P. princeps* Dana, 1849), and a few species live in deeper waters but portions of their populations occasionally reach the neuston (termed 'pseudoneuston', e.g. *Calanopia elliptica* Dana, 1849, and *C. minor* A. Scott, 1909; [Matsuo and Marumo 1982]).

Labidocera Lubbock, 1853, represents the largest genus in the family, with several species distributed throughout the Indo-Pacific (Boxshall and Halsey 2004; Hirabayashi and Ohtsuka 2014). These neustonic copepods are often used as indicator species of different water masses, inshore–offshore boundaries, biogeographical boundaries, and seasons (Sherman 1962; Silas and Pillai 1973; Turner and Collard 1980; Matsuo and Marumo 1982; Jeong et al. 2009). Despite the obvious neustonic physical adaptations in the genus, the present study shows three *Labidocera* species living residential within coral reefs. The objectives of this study were to (1) document the presence of *Labidocera* spp. in two Papua New Guinea coral reefs, (2) compare *Labidocera* spp. abundance between reef and offshore waters, (3) assess life stage composition (copepodites C2, C3, C4 and C5, and adult males and females) at two separate reefs and for two expeditions, (4) determine migration patterns and substrate preferences, and (5) examine the impacts of reef composition on their abundance.

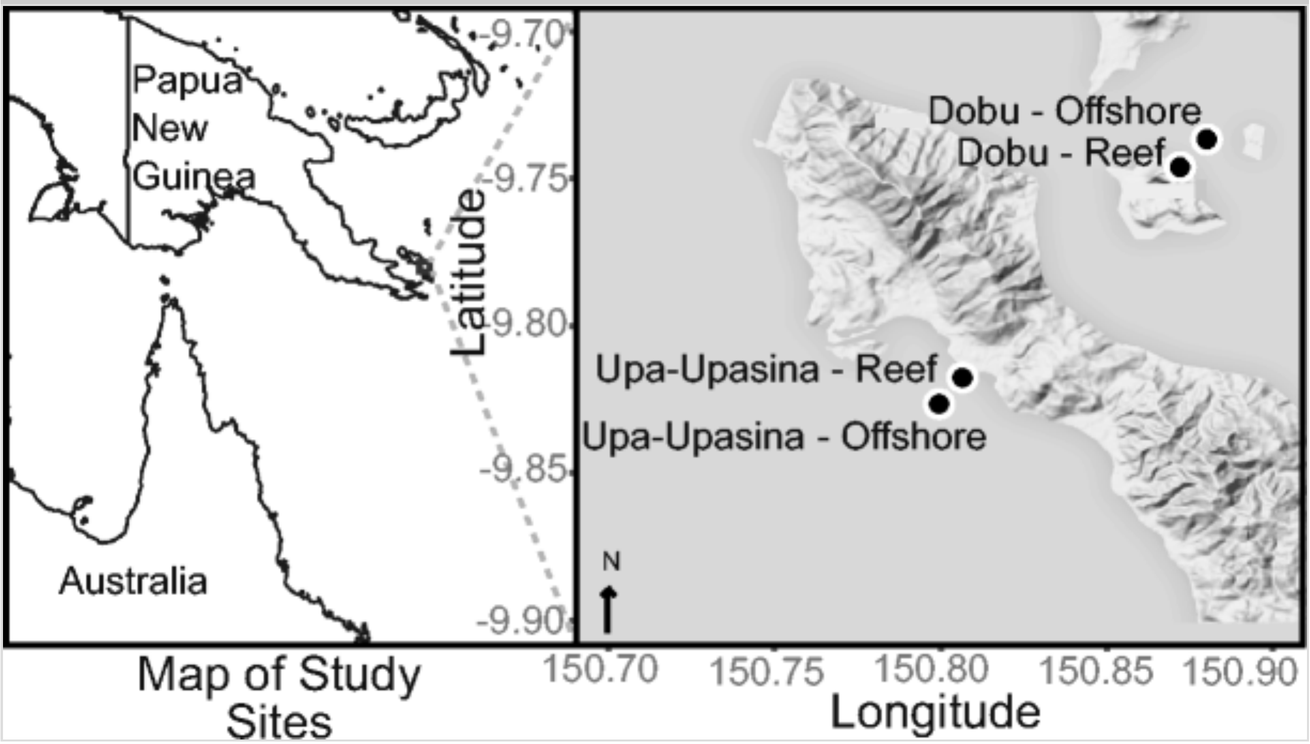
Materials and methods

Study site

Pontellid copepods were collected from tropical coral reefs that fringe the two sites, Dobu and Upa-Upasina, and in adjacent offshore waters approximately 500 m from the reef sites in Milne Bay Province, Papua New Guinea. Dobu and Upa-Upasina reef sites are 10.7 km apart and are separated by the large Normanby and Dobu islands (Fig. 1). Both sites were sampled on two expeditions (24 May to 5 June 2013 and 22 March to 20 April 2014) on board the M/V *Chertan*. During all collection times, the currents were longshore and weak (<0.03 m s^{-1}) and wave heights were 0.1–0.45 m (Smith et al. 2016). The two sites are located near natural CO_2 seep sites as previously described in ocean acidification studies on marine communities (Fabricius et al. 2011; Fabricius et al. 2014; Allen et al. 2016). In the present study, however, copepods were collected only from the control coral reefs away from the seep sites, unaffected by CO_2.

Fig. 1

Map of two reefs and offshore sites



Field sampling

The abundance of *Labidocera* was compared to the abundance of other pontellid genera present (*Calanopia* and *Pontella* Dana, 1846). Abundance was further compared between offshore and reef sites via horizontal net tows using a Nansen net (70-cm aperture diameter, 100-µm mesh size). Each horizontal net tow was conducted along a shore-parallel transect approximately 30 m in length at a speed of ~1 knot, with the volume of water recorded using a calibrated Hydro-Bios digital flowmeter attached to the center of the Nansen net aperture. The newly purchased flowmeter was calibrated by the manufacturer (Hydro-

Bios) based on distance traveled through water per revolution of the flowmeter's impeller. The calibration factor of 0.3 was supplied by Hydro-Bios and used to calculate the distance of each net tow, which was later used to calculate the total volume of water sampled. Three replicate horizontal net tows were collected at an offshore site and reef site between 2100 and 0200 hours on several consecutive nights of two separate expeditions (8 nights at Upa-Upasina and 2 nights at Dobu in 2013, and 6 nights at Upa-Upasina and 3 nights at Dobu in 2014). The reef sites were in shallow (2–3 m) waters, with the net towed approximately 0.5–1.0 m above the coral and approximately 1.5 m below the sea surface. The offshore sites were also towed approximately 1.5 m below the sea surface, where seafloor depth was 50–70 m.

During the second expedition, horizontal night tows were additionally collected over the course of 24-h cycles to observe the migration patterns of *Labidocera* spp. Samples were collected over the reef at Upa-Upasina every 2 h during dark hours (between 0630 and 0630 hours), and every 3 h during daylight hours. Samples were collected for four separate 24-cycles over the course of a month, with approximately one cycle per week (25–26 March 2014, 4–5 April 2014, 13–14 April 2014, and 18–19 April 2014). Sunset, sunrise, moonset, and moonrise times, along with percent moon illumination, were obtained from open source data provided by the Astronomical Applications Department, U.S. Naval Observatory (http://aa.usno.navy.mil/data/).

In an attempt to fully understand the substrate preference of *Labidocera* spp. during the second expedition, emergence tents of 100-μm mesh size were deployed for 5 nights over areas dominated by different substrate types at Upa-Upasina Reef. The pyramid-shaped tent dimensions were 1 m × 1 m × 1 m (length x width x height), similar to Porter and Porter (1977). Detachable cod-ends at the top of the tent had a light (3 lm) affixed inside to attract zooplankton. The emergence tents (nine per day) were deployed during daylight hours (between 1500 and 1700 hours), and the cod-ends were retrieved after nightfall once the plankton had time to emerge (between 2000 and 2100 hours). Emergence tents were placed over patches of reef substrates dominated by coral rubble, branching coral, or massive boulder coral (three emergence tents per substrate type). To be defined as any one of the main substrate categories, the base of the emergence tent, i.e. the quadrat, had to be dominated by at least 50% of that particular substrate. The quadrat was never 100% covered by any one category, so a photo was taken of each quadrat, and post-field image analysis later calculated the percent coverage of substrate types including coral rubble, branching coral, and massive boulder coral, with additional categories of sand, macroalgae, and turf. Although it was not possible to hermetically seal the emergence tents given the natural rugosity of the coral reef framework, we took great care to tie the tents close to the seafloor, leaving negligible gaps. A study that examined the difference between sealed and unsealed emergence traps found no significant difference in the abundance of specimens captured by the two types of emergence tents (Robichaux et al. 1981).

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All samples collected with each method were preserved in 4% formalin buffered with sodium borate and stored for further analysis.

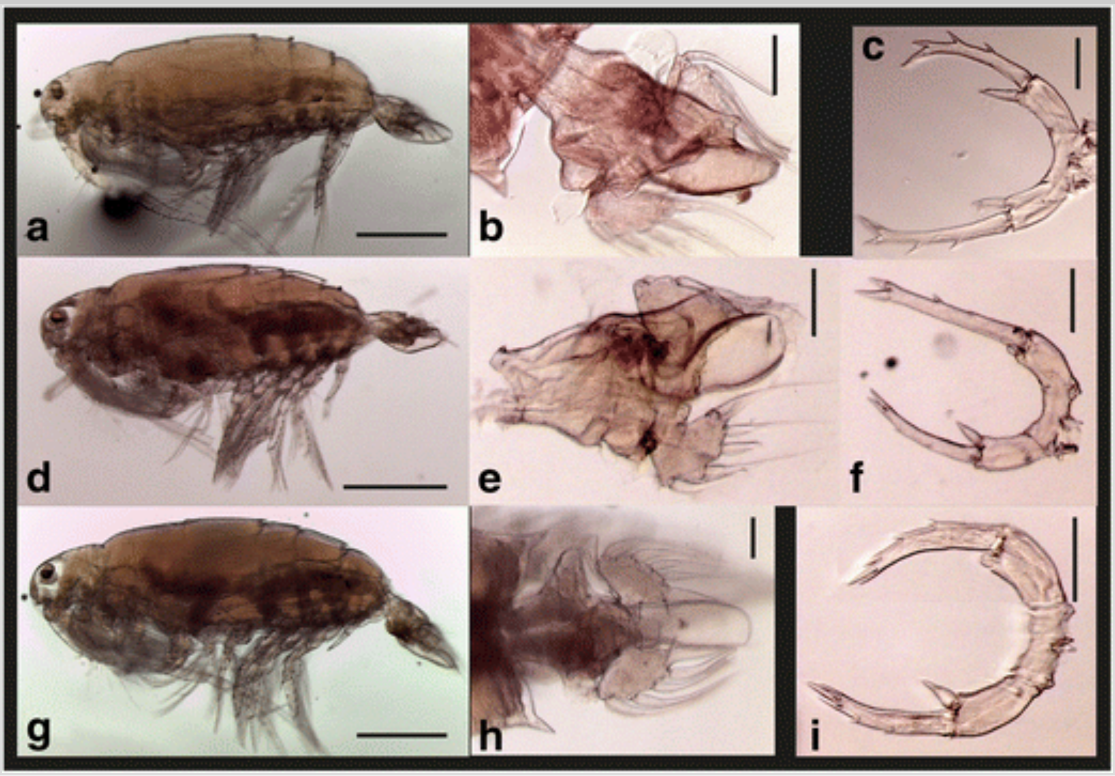
Laboratory analysis

All samples collected were sub-sampled with a Folsom plankton splitter, and half of each original sample was counted microscopically for pontellid copepods. Pontellidae were categorized into the dominant genera (*Labidocera*, *Calanopia*, *Pontella*, and other Pontellidae). *Labidocera* specimens were predominant within the reef, and thus were identified to species (for the adults) and life stage. Life stages were recorded for copepodite stages C2, C3, C4, C5 female, C5 male, and adult males and females. *Labidocera* spp. copepodite stage C1 was not present in the samples. Also, copepod nauplii were low in abundance and were not distinguished by genus or species, and thus were not analyzed in the present study. In addition, although adult *Labidocera* spp. were identified to species, the species were later grouped together for all statistical analysis, because the copepodites of all three species could not be distinguished reliably due to their similar sizes and morphologies.

Labidocera spp. specimens were identified according to the descriptions by Scott (1909), Mulyadi (2002), and Hirabayashi and Ohtsuka (2014). *Labidocera bataviae* A. Scott, 1909, constituted 70% of the *Labidocera* genus group, with scattered occurrences of *L. laevidentata* (Brady, 1883), *L. pavo* Giesbrecht, 1889, and a species possibly new to science (*Labidocera* sp.). While *L. laevidentata* was easily recognizable due to its cephalic hooks (Brady 1883; Mulyadi 2002), it contributed less than 1% to *Labidocera* abundance and was removed from further analysis. The other three species were of the same size and morphologically closely related, with the adults differing only in the shape of the fifth swimming leg and the structure of the urosome (Hirabayashi and Ohtsuka 2014). Copepod length is known to differ by sex and life stage, with adult males averaging 1.95 mm in length and adult females 2.05 mm (Mulyadi 2002). Photographs of the copepod, urosome, and fifth swimming leg of adult female *L. bataviae*, *Labidocera.* sp., and *L. pavo* can be found in Fig. 2. Note: prior to preservation, all copepods in Fig. 2 were dark blue in color. The two described species, *L. bataviae* and *L. pavo*, have both been documented as coastal, but have also been found in surface waters 10–40 km offshore tropical Pacific islands (<1% of present pontellids) (Sherman 1964). They belong to the *pavo* species group within the *L. detruncata* (Dana, 1849) species complex and are morphologically closely related (Hirabayashi and Ohtsuka 2014). The unidentified species also belongs to the *pavo* group.

Fig. 2

Photos of the three *Labidocera* species. *Labidocera bataviae* (female): **a** habitus, **b** urosome, **c** swimming leg 5 (P5). *Labidocera* sp. (female): **d** habitus, **e** urosome, **f** P5. *Labidocera pavo* (female): **g** habitus, **h** urosome, **i** P5. Scale bars = a, d, g: 500 µm (lower right); b, c, e, f, h, i: 100 µm (upper right)



Statistics

All statistical analyses were computed in R, version 3.2.2 (R Development Core Team, 2015). Generalized linear models (GLMs) were used to determine whether there were significant differences in abundance between offshore and reef, expeditions (first vs. second), or sites (Upa-Upasina vs. Dobu) for *Labidocera* spp., and for the other pontellid genera present (*Calanopia* sp., *Pontella* sp., or other Pontellidae). GLMs were also used to determine whether *Labidocera* spp. abundance correlated with percent cover of the different substrate types (coral rubble, branching coral, massive boulder coral, sand, macroalgae, and turf) and date. Data distributions were chosen for each GLM, and diagnostics of model stability (leverage, Cook's and DFBETAs) were calculated (Cohen and Cohen 2008). All model stability checks indicated that no influential cases or outliers existed in the data. Analysis of variance (ANOVA) was applied to the optimal GLMs.

Results

Comparison of reef versus offshore abundance

Pontellids of the genus *Labidocera* occurred in high abundance over the reefs at both Upa-Upasina and Dobu, and those of the genus *Calanopia* were also present at both reefs, albeit in lower abundance (Fig. 3). *Labidocera* spp. and *Calanopia* sp. abundance was consistently greater at the reef than in offshore waters, despite variations in abundance between dates and expeditions (Fig. 4). Results from the GLM confirm that *Labidocera* and *Calanopia* were both more abundant over the reef and more varied in abundance by expedition, with *Labidocera* abundance also differing between sites; meanwhile, none of the factors (reef vs. offshore, expedition, or site) affected the abundance of *Pontella* or 'other pontellids' (Table 1). For all pontellid genera, no significant difference in abundance ($p > 0.05$) was found for the interactions between the variables (reef vs. offshore, expedition, or site).

Fig. 3

Abundance of pontellid genera at offshore and onshore sampling locations at two separate coral reefs in Papua New Guinea

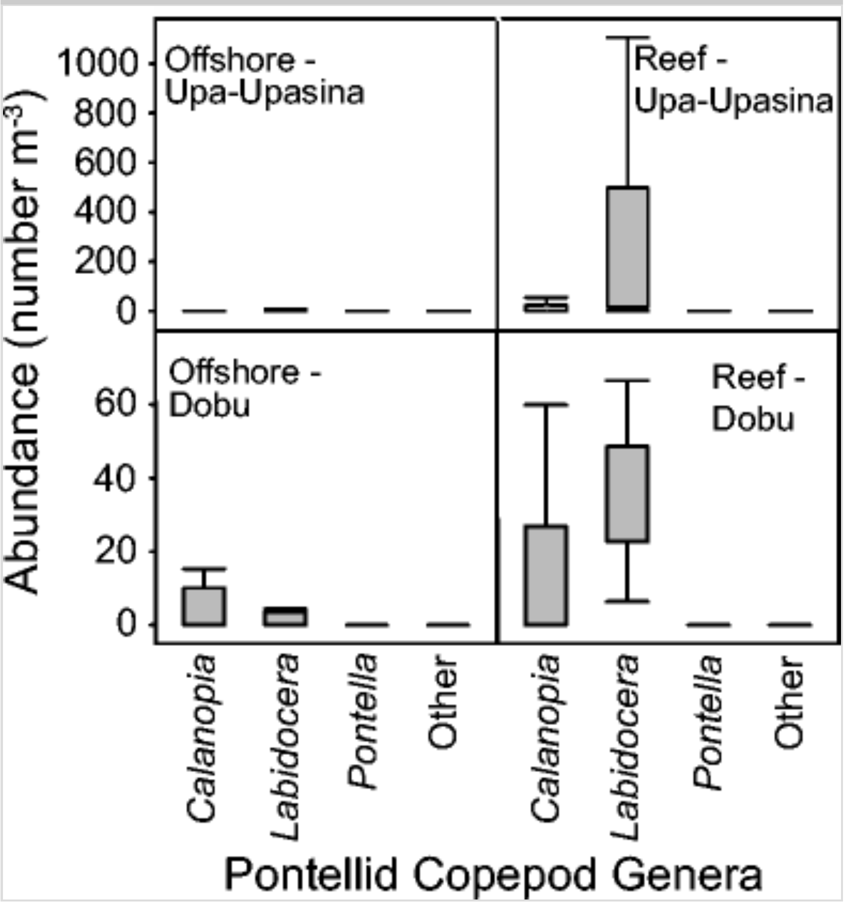


Fig. 4

Copepod abundance over the reef (circles) compared to offshore (triangles) for the two pontellid genera *Labidocera* and *Calanopia* at Upa-Upasina and Dobu over 19 nights from two expeditions

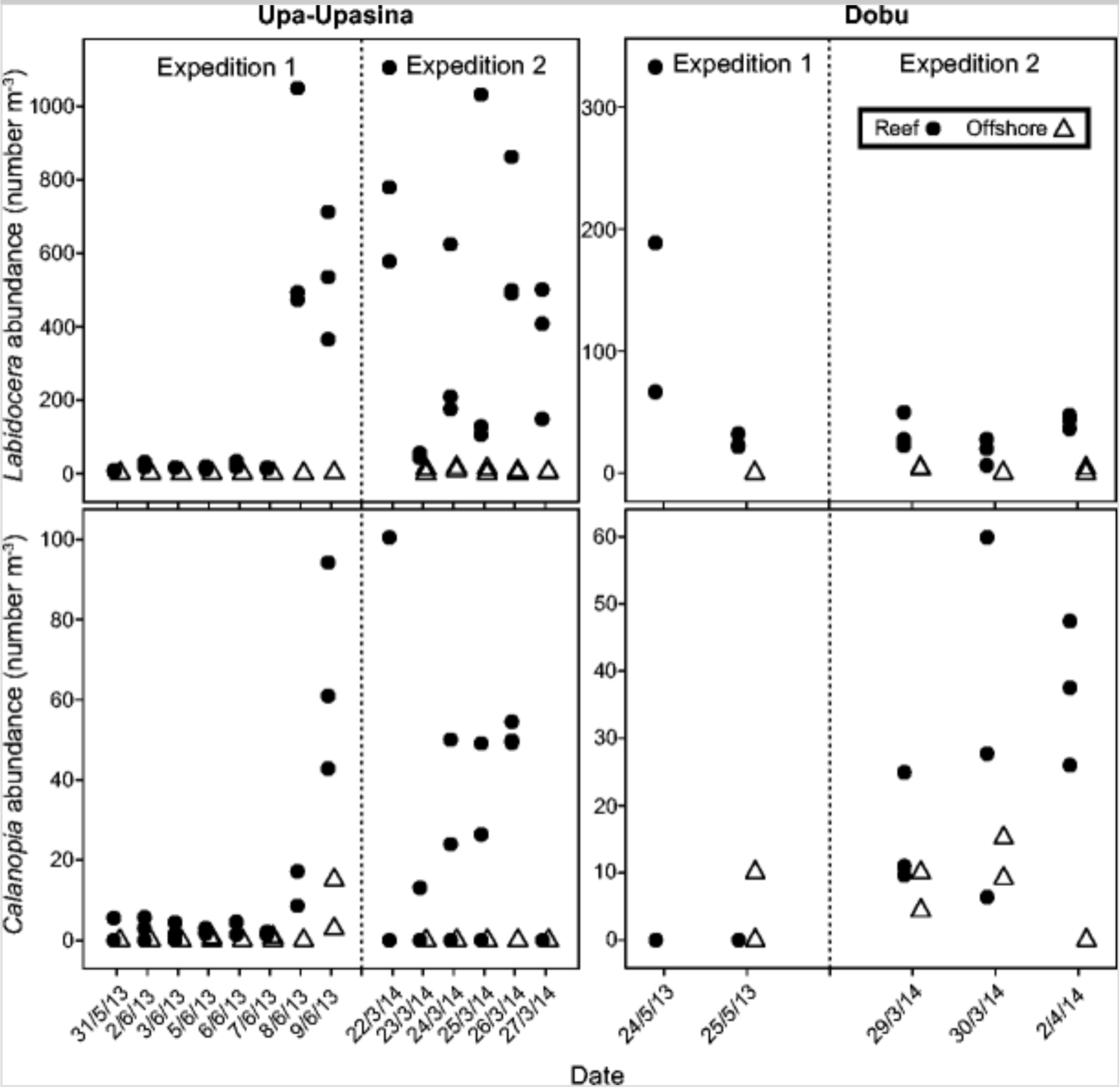


Table 1

Results from generalized linear models examining the differences in abundance of various pontellid genera in response to reef (reef vs. offshore), expedition (1 vs. 2), or site (Upa-Upasina vs. Dobu)

Pontellid genus	Reef–Offshore		Expedition		Site	
	X^2	*p*	X^2	*p*	X^2	*p*
Labidocera	1510.4	<0.001	151.7	<0.001	204.7	<0.001
Calanopia	240.2	<0.001	63.3	<0.001	0.1	0.746
Pontella	0.81	0.371	2.74	0.102	0.07	0.794

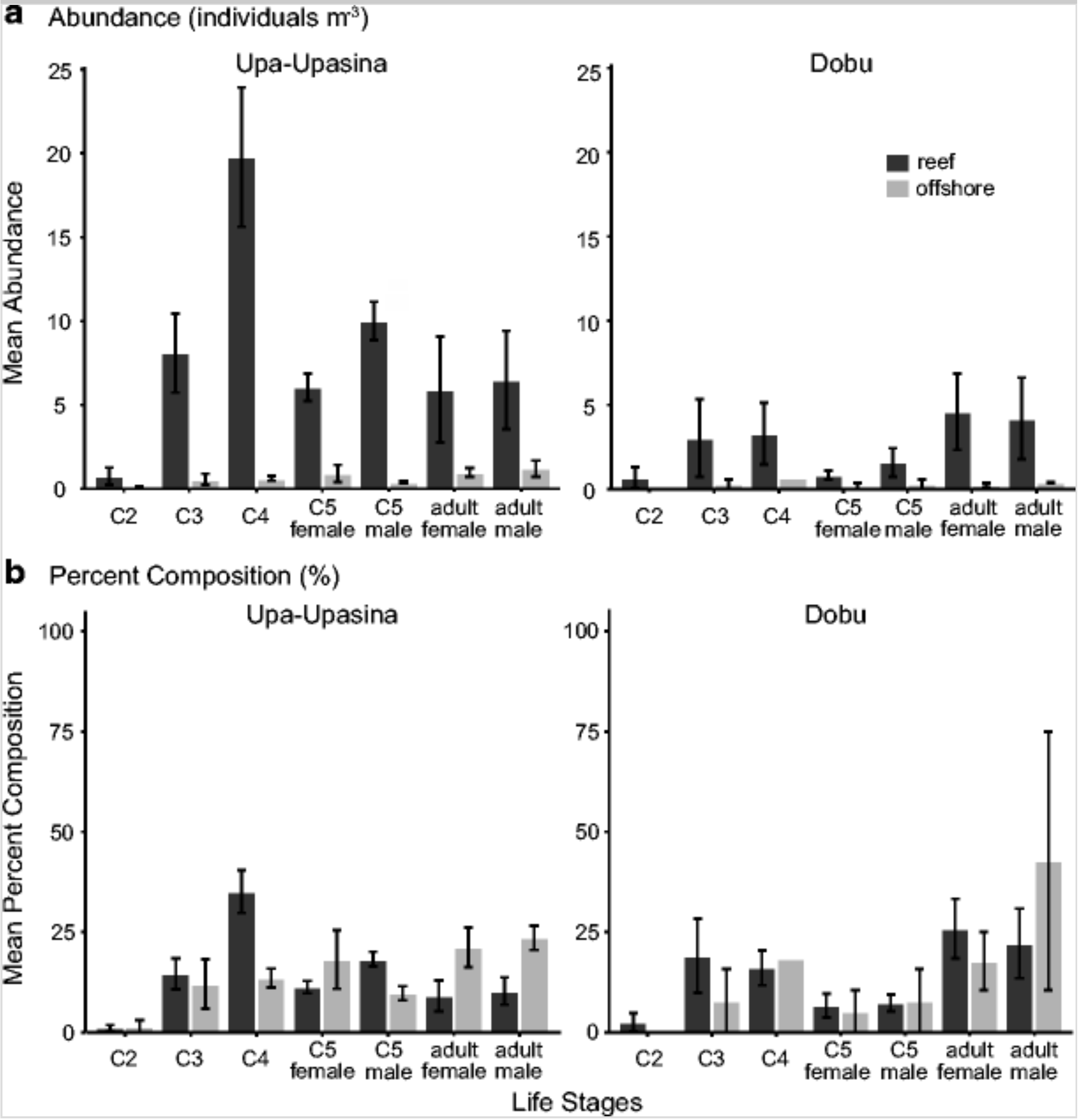
Other pontellids	1.87	0.989	0.14	0.711	0.19	0.668

Two-way and three-way interactions did not significantly affect the abundance of any pontellid genera ($p > 0.05$). *Df* = 1 for all analysis

All *Labidocera* spp. copepodite stages were more abundant over the reef, and no particular life stage was more likely to be advected offshore than any other (Fig. 5).

Fig. 5

The **a** abundance (individuals m^{-3}) and **b** percent composition of each life stage of *Labidocera* spp. collected from nocturnal horizontal tows at Upa-Upasina and Dobu study sites during the second expedition. Stage composition is compared between samples collected over coral reefs (dark gray) and several hundred meters offshore from the fringing reef crests (light gray). Life stages exclude the nauplii stages and the first copepodite stage (C1), but include copepodite stages C2, C3, C4 and C5 and the adults

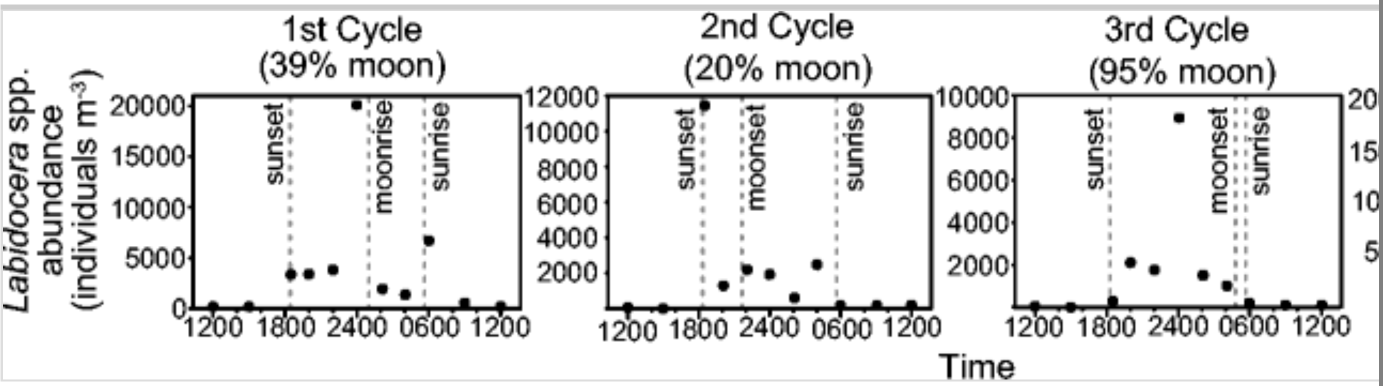


Diurnal migration patterns

Diurnal migration patterns were observed for *Labidocera* spp. at Upa-Upasina over the reef for four separate 24-h cycles within a 1-month period (Fig. 6). *Labidocera* spp. remained amongst the substrate during the day and emerged into the water column after dusk, returning to the substrate at dawn. A second emergence often occurred in the middle of the night (between 0000 and 0200 hours). The exact migration patterns and abundance differed between the four cycles, and there was no distinct pattern that coincided with moonlight level.

Fig. 6

Diurnal migration patterns of *Labidocera* spp. abundance over Upa-Upasina reef collected via horizontal tows



Substrate preferences

Substrate preference was analyzed for *Labidocera* spp. at Upa-Upasina reef. Results from a multi-factor GLM reveal that *Labidocera* spp. abundance, collected via emergence tents placed over patches of coral reef substrates, increased along with the percent cover of coral rubble (ANOVA, $F_{(1,36)} = 4.45$; $p = 0.04$), macroalgae (ANOVA, $F_{(1,32)} = 7.2$; $p = 0.04$), and turf (ANOVA, $F_{(1,31)} = 12.2$; $p = 0.009$). The cover of branching coral (ANOVA, $F_{(1,35)} = 3.27$; $p = 0.08$), massive boulder coral (ANOVA, $F_{(1,34)} = 3.72$; $p = 0.06$), and sand (ANOVA, $F_{(1,33)} = 3.64$; $p = 0.07$) did not significantly affect *Labidocera* spp. abundance (Fig. 7). Although macroalgae and turf never dominated a quadrat (<20% of cover), they proved a suitable substrate for *Labidocera* spp. to reside within. When separated into the three dominant substrate categories, coral rubble appears to be the substrate of choice for all life stages of *Labidocera* spp. at Upa-Upasina Reef, versus branching coral and massive boulder coral (Fig. 8). Additionally, the number of *Labidocera* spp. present was significantly different between sampling days during the substrate preference collection period (ANOVA, $F_{(1,27)} = 33.6$; $p < 0.001$).

Fig. 7

Labidocera spp. abundance at Upa-Upasina Reef as a function of percent cover of six substrate types: coral rubble, branching coral, massive boulder coral, sand, macroalgae, and turf. A single multi-factor generalized linear model (GLM) revealed which substrata types had an influence on *Labidocera* spp. abundance, and the GLM results ($F_{(\mathrm{df},\mathrm{df})}$ and p values) are included in each plot. The solid line represents the linear regression between percent cover of each substrate and *Labidocera* spp. abundance, while the dashed lines mark the 95% confidence intervals

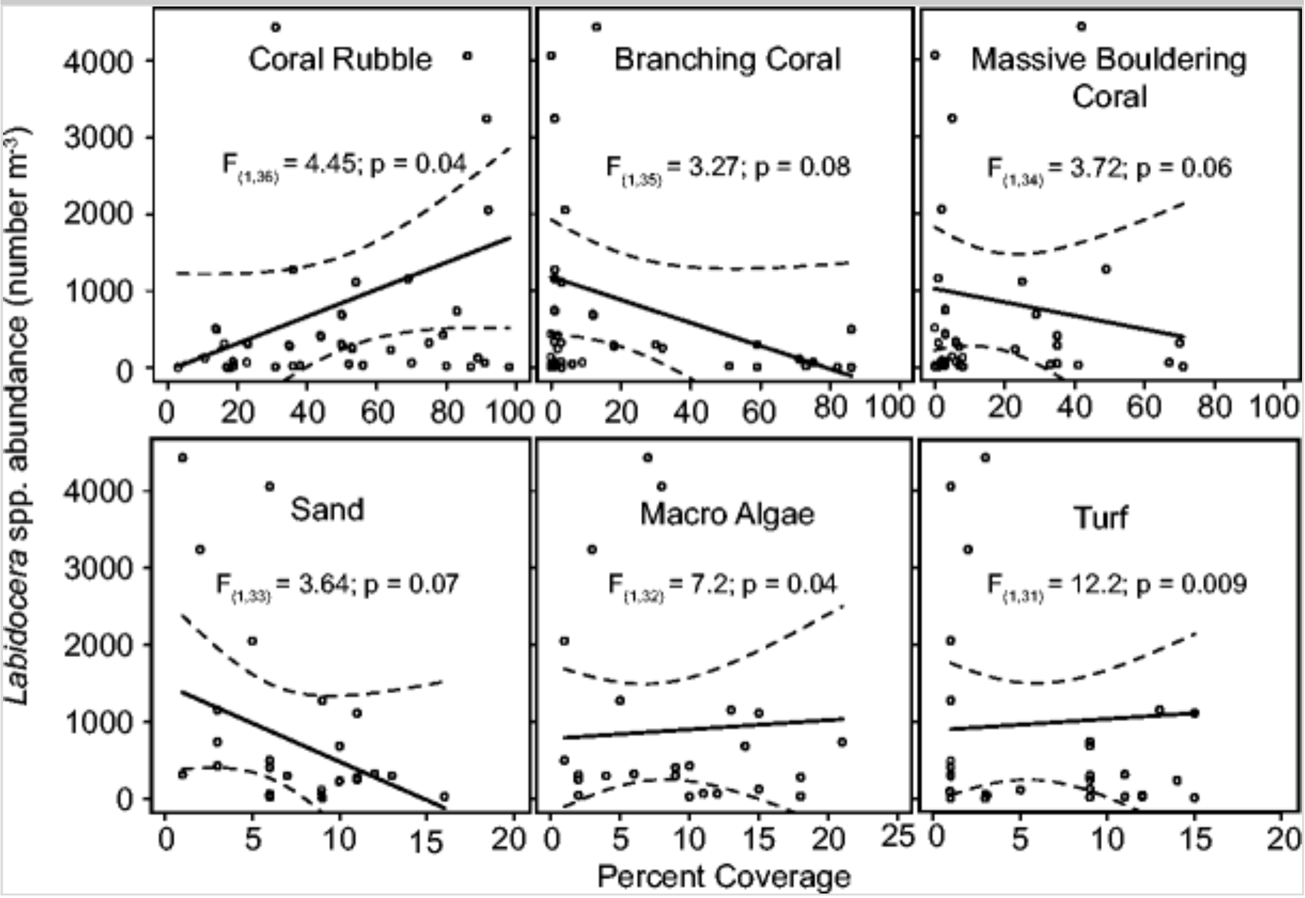
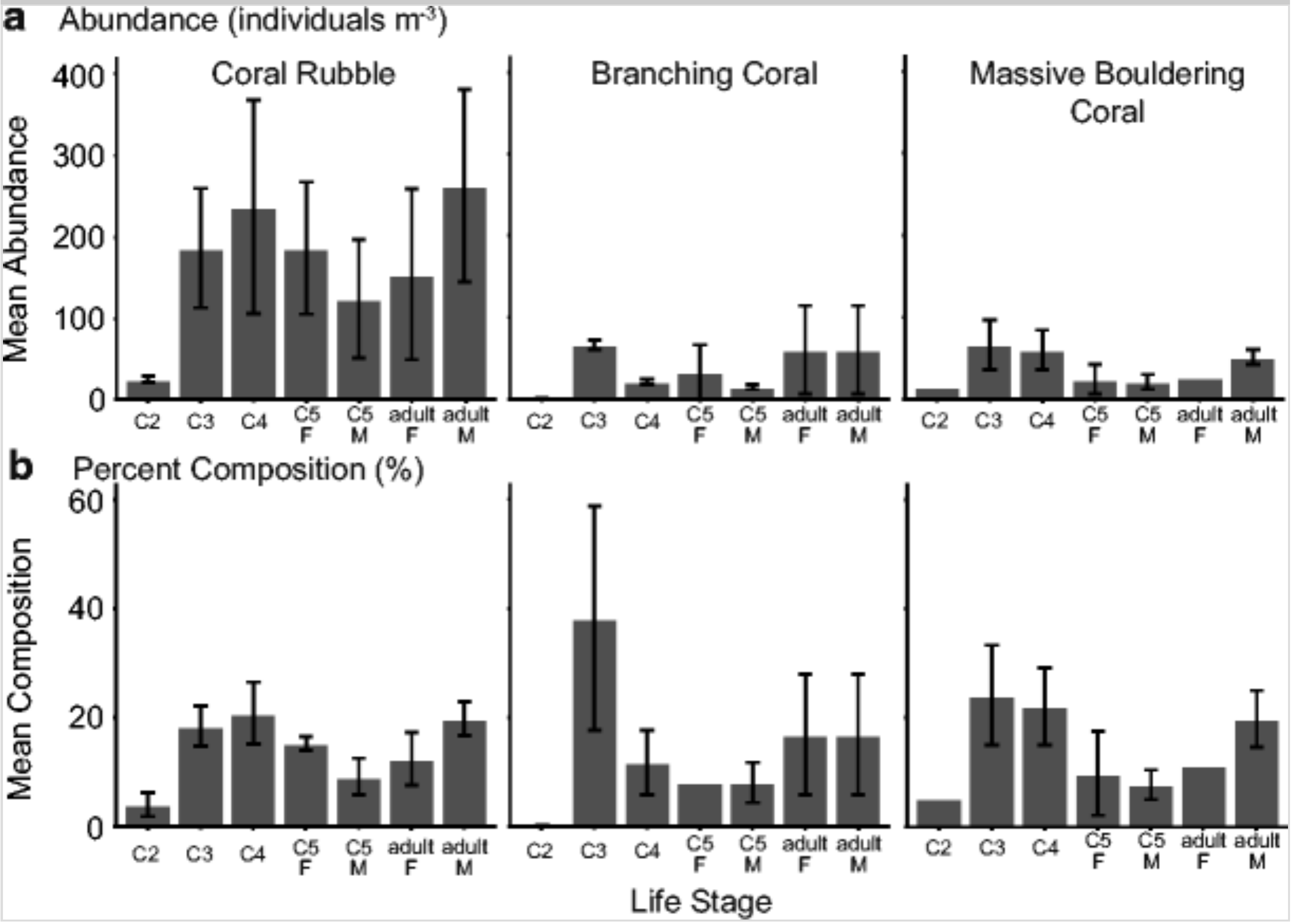


Fig. 8

The **a** abundance (individuals m^{-3}) and **b** percent composition of each life stage for *Labidocera* spp. for samples collected with emergence tents. The stage composition only represents *Labidocera* spp. from Upa-Upasina Reef for the three major substratum categories (coral rubble, branching coral, massive boulder coral)



Discussion

This study provides evidence that *Labidocera* spp. are able to live residentially within coral reefs, in contrast to previous studies from the Indo-Pacific region reporting *L. bataviae* and *L. pavo* as neustonic (Cohen and Forward 2002; Hirabayashi and Ohtsuka 2014). Greater abundance of all life stages of *Labidocera* spp. was observed over two reefs than in offshore waters. Evidence from fringing reefs in Papua New Guinea provide more detailed information on the ability of *Labidocera* spp. to live residentially within coral reefs, including observations on their diurnal migration patterns and associations with different substrate types.

All life stages (copepodite stage C2 through adulthood) captured in net tows and emergence tents were more abundant in the water over the reefs. Interestingly, no life stage seemed more vulnerable to export. Juvenile copepods are weaker swimmers than adults (van Duren and Videler 1995), and yet the juvenile *Labidocera* spp. were not disproportionally found offshore, although nothing is known about the nauplii or copepodite stage C1, since nauplii abundance was low and copepodite stage C1 was absent in the samples. Copepodite stage C2 was also minimally present (Figs. 4 and 7). Perhaps the low abundance of the younger life stages is due to lack of migration into the water column, a behavior exhibited by the youngest life stages of another demersal copepod *Pseudodiaptomus* as a mechanism for avoiding visual predators (Fancett and Kemmerer 1985).

Labidocera spp. unexpectedly exhibited diurnal migration within the reefs. Despite previous evidence suggesting that *Labidocera detruncata*, the same complex group that *Labidocera* spp. from this study belong to, are non-migrators (Matsuo and Marumo 1982; Cohen and Forward 2002), *Labidocera* spp. residing in coral reefs instead exhibited behavior common in other reef-associated zooplankton (Ohlhorst 1982; Alldredge and King 1985). Different species of zooplankton migrate in slightly different patterns (Ohlhorst 1982), but in general they emerge into the water column at dusk to forage and escape predation by nocturnal planktivorous fish and heterotrophic corals that extend their polyps at night (Porter 1974; Hobson 1991). At dawn they return to the substrate to avoid visual detection by fish (Hobson 1973).

Labidocera spp. emerged at dusk and often underwent a second emergence in the middle of the night, but this migration pattern was not obviously related to the lunar cycle. From other studies in coral reefs, residential zooplankton emergence patterns appear to depend in part on circadian rhythms and the lunar cycle (Alldredge and King 1980; Ohlhorst 1982; Madhupratap et al. 1991; Yahel et al. 2005).

The second emergence of *Labidocera* spp. may be explained as an attempt to maintain their position within the reef. In estuarine areas, certain copepod species will migrate when tides shift and currents are low, allowing them to maintain their position in a bay and not be swept away (Kimmerer and McKinnon 1987; Ueda et al. 2010). Although *Labidocera detruncata*, the same species complex that *Labidocera* spp. in this study belong to, generally do not migrate diurnally, and instead remain at the surface, diurnal migration within the top 30 cm of the Kuroshio current has been observed for other *Labidocera* species (Matsuo and Marumo 1982). Furthermore, *Labidocera euchaeta* Giesbrecht, 1889, *Labidocera jaafari* Othman, 1986, and *Labidocera pectinata*

Thompson & Scott, 1903, were all found to exhibit diurnal migration in a mangrove estuary in Malaysia (Chew et al. 2015), illustrating the ability of some *Labidocera* species to change their behavior within a mangrove. *L. pavo* has also been observed swarming and nocturnally migrating, sometimes with the tide, in subtropical waters near Japan (Ueda et al. 1983; Saigusa and Oishi 2000; Saigusa et al. 2003). Other pontellid copepods, specifically *Anomalocera ornata* Sutcliffe, 1949. also migrate, but with juveniles migrating normally and adults exhibiting reverse vertical migration patterns (Tester et al. 2004). As seen in this study, *Labidocera* spp. also begin to exhibit diurnal migration behavior within a coral reef ecosystem, and triggers for migration include changes in light.

Once sunlight dawned and *Labidocera* spp. returned to the substrate, they preferred to live in association with coral rubble, macroalgae, and turf, even though macroalgae and turf covered only a small percentage of the area within the emergence tents. Macroalgae and turf are home to many harpacticoid copepods (Logan et al. 2008; Kangtia et al. 2014), and are an important link in providing food for coral reef fishes (Logan et al. 2008; Kramer et al. 2013). However, less is known about calanoid copepods living within macroalgae. Furthermore, calanoid copepods are known to live amongst coral rubble, but often have a greater preference for living near branching coral in parts of the Great Barrier Reef (Alldredge and King 1977).

The percent cover of branching coral did not influence *Labidocera* spp. abundance within the Papua New Guinea reefs. In some coral reefs, branching corals have a higher number of zooplankton (e.g. decapod larvae, shrimp, calanoid and harpacticoid copepods) associated with them because the increased structural complexity offers more hiding places (Alldredge and King 1977; Porter and Porter 1977; Jacoby and Greenwood 1989). In contrast, branching corals have a larger surface area of stinging tentacles that can capture copepods and other zooplankton (Houlbrèque and Ferrier-Pagès 2009).

The percent cover of massive boulder coral also had no impact on *Labidocera* spp. abundance. Other calanoid copepods such as *Acartia* have been observed swarming around massive boulder corals, sometimes even mimicking the shape of the coral rock as a means of avoiding predators and also for maintaining their position within reefs by hiding from currents (Hamner and Carleton 1979).

Different copepod species prefer different substrates for seeking refuge, and although other copepod species may like to hide around branching coral or massive boulder coral, *Labidocera* spp. did not like either and instead preferred to live within the coral rubble and, when present, in macroalgae and turf.

In order for *Labidocera* spp. to make behavioral changes in their migration patterns and living preferences, there must be some advantages over remaining non-migratory and oceanic. Increased flexibility in plankton behavior is a reflection that these copepods are highly evolved, and yet there are several unknowns about reef-dwelling copepods. For example, the moment in time when *Labidocera* spp. populate a specific reef is unknown. *Labidocera* development is temperature-dependent and in tropical waters the growth from nauplii to adulthood is between 14 and 15 days (Gibson and Grice 1977). Within a single year, several generations of *Labidocera* spp. may have lived in association with coral reefs at both Upa-Upasina and Dobu. Despite the knowledge gaps, all evidence suggests that *Labidocera* spp. have adapted their lifestyle to living residential within coral reefs, and their abundance suggests an important food source sustaining reef trophodynamics.

Acknowledgements

Special thanks to Obedi Daniel, Robin (‘Lei’) Luke, Julia Strahl, Sam Noonan, Alfred Sauwa, and crew members from the M/V *Chertan* for field assistance. This project was funded in part by the Erasmus Mundus-funded MARES Joint Doctoral Programme on Marine Ecosystem Health & Conservation (FPA 2011-0016), the Great Barrier Reef Foundation’s ‘Resilient Coral Reefs Successfully Adapting to Climate Change’ Program in collaboration with the Australian Government, the BIOACID Phase II Programme of the German Science Ministry BMBF (Grant 03F0655B), and the Australian Institute of Marine Science.

Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

References

Alldredge AL, King JM (1977) Distribution, abundance, and substrate preferences of demersal reef zooplankton at Lizard Island lagoon, Great Barrier Reef. Mar Biol 41:317–333. https://doi.org/10.1007/BF00389098

Alldredge AL, King JM (1985) The distance demersal zooplankton migrate above the benthos: implications for predation. Mar Biol 84:253–260. https://doi.org/10.1007/BF00392494

Alldredge AL, King JM (1980) Effects of moonlight on the vertical migration patterns of demersal zooplankton. J Exp Mar Bio Ecol 44:133–156. https://doi.org/10.1016/0022-0981(80)90150-1

Allen R, Foggo A, Fabricius K et al (2016) Tropical CO_2 seeps reveal the impact of ocean acidification on coral reef invertebrate recruitment. Mar Pollut Bull. https://doi.org/10.1016/j.marpolbul.2016.12.031

Alvarez-Cadena JN, Suarez-Morales E, Gasca R (2014) Copepod assemblages from a reef-related environment in the Mexican Caribbean Sea. Crustaceana 71:411–433

Boxshall GA, Halsey SH (2004) An introduction to copepod diversity, volume 2. Ray Society, London

Brady GS (1883) Report on the Copepoda collected by H.M.S. challenger during the years 1873-1876. Rep Sci Results Voy Chall Zool 8:1–142

Carleton J, Hamner W (2007) The hyperbenthic plankton community: composition, distribution, and abundance in a coral reef lagoon. Mar Ecol Prog Ser 336:77–88. https://doi.org/10.3354/meps336077

Carleton JH (1993) Zooplankton and coral reefs: an overview. South Pacific Underw Med Soc 23:102–107

Carleton JH, McKinnon AD (2007) Resident mysids: secondary production, consumption, and trophic role in a coral reef lagoon. Mar Ecol Prog Ser 336:89–98. https://doi.org/10.3354/meps336089

Chew L-L, Chong VC, Ooi AL, Sasekumar A (2015) Vertical migration and positioning behavior of copepods in a mangrove estuary: interactions between tidal, diel light and lunar cycles. Estuar Coast Shelf Sci 152:142–152. https://doi.org/10.1016/j.ecss.2014.11.011

Clarke GL (1934) The diurnal migration of copepods in St. Georges harbor, Bermuda. Biol Bull 67:456–460

Cohen JH, Forward RB (2002) Spectral sensitivity of vertically migrating marine copepods. Biol Bull 203:307–314. https://doi.org/10.2307/1543573

Cohen Y, Cohen JY (2008) Statistics and data with R: an applied approach through examples. John Wiley & Sons Ltd., Chichester, West Sussex, UK

Conley WJ, Turner JT (1985) Omnivory by the coastal marine copepods *Centropages hamatus* and *Labidocera aestiva*. Mar Ecol Prog Ser 21:113–120. https://doi.org/10.3354/meps021113

Donelson J, Munday P, McCormick M et al (2010) Effects of elevated water temperature and food availability on the reproductive performance of a coral reef fish. Mar Ecol Prog Ser 401:233–243. https://doi.org/10.3354/meps08366

Emery AR (1968) Preliminary observations on coral reef plankton. Limnol Oceanogr 13:293–303. https://doi.org/10.4319/lo.1968.13.2.0293

Fabricius KE, De'ath G, Noonan S, Uthicke S (2014) Ecological effects of ocean acidification and habitat complexity on reef-associated macroinvertebrate communities. Proc R Soc B biol Sci 281:20132479. Doi: 20132479

Fabricius KE, Langdon C, Uthicke S et al (2011) Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations. Nat Clim Chang 1:165–169. https://doi.org/10.1038/nclimate1122

Fancett MS, Kemmerrer WJ (1985) Vertical migration of a demersal copepod *Pseudodiaptomus* as a means of predator avoidance. J Exp Mar Bio Ecol 88:31–43

Ferrier-Pagès C, Hoogenboom M, Houlbrèque F (2011) The role of plankton in coral trophodynamics. Springer Science

Fukuoka K, Shimoda T, Abe K (2015) Community structure and abundance of copepods in summer on a fringing coral reef off Ishigaki Island, Ryukyu Islands, Japan. Plankt Benthos Res 10:225–232. doi: https://doi.org/10.3800/pbr.10.225

Gemmell BJ, Jiang H, Strickler JR, Buskey EJ (2012) Plankton reach new heights in effort to avoid predators. Proc R Soc B Biol Sci 279:2786–2792. https://doi.org/10.1098/rspb.2012.0163

Genin A, Jaffe JS, Reef R et al (2005) Swimming against the flow: a mechanism of zooplankton aggregation. Science 308:860–862. https://doi.org/10.1126/science.1107834

Gibson VR, Grice GD (1977) The developmental stages of *Labidocera aestiva* wheeler, 1900 (Copepoda, Calanoida)

Hairston NC (1976) Photoprotection by carotenoid pigments in the copepod *Diaptomus nevadensis*. Proc Natl Acad Sci U S A 73:971–974. https://doi.org/10.1073/pnas.73.3.971

Hammer RM (1981) Day-night differences in the emergence of demersal zooplankton from a sand substrate in a kelp forest. Mar Biol 62:275–280. https://doi.org/10.1007/BF00397694

Hamner WM, Carleton JH (1979) Copepod swarms: attributes and role in coral reef ecosystems. Limnol Oceanogr 24:1–14

Hamner WM, Jones MS, Carleton JH et al (1988) Zooplankton, planktivorous fish, and water currents on a windward reef face: Great Barrier Reef, Australia. Bull Mar Sci 42:459–479

Hansson L-A (2000) Induced pigmentation in zooplankton: a trade-off between threats from predation and ultraviolet radiation. Proc R Soc London B 267:2327–2331. https://doi.org/10.1098/rspb.2000.1287

Hansson L-A, Hylander S, Sommaruga R (2007) Escape from UV threats in zooplankton: a cocktail of behavior and protective pigmentation. Ecology 88:1932–1939. https://doi.org/10.1890/06-2038.1

Heidelberg KB, Sebens KP, Purcell JE (2004) Composition and sources of near reef zooplankton on a Jamaican forereef along with implications for coral feeding. Coral Reefs 23:263–276. https://doi.org/10.1007/s00338-004-0375-0

Herring PJ (1965) Blue pigment of surface-living oceanic copepod. Nature 4966:103–104

Hirabayashi T, Ohtsuka S (2014) A new species of *Labidocera* (Copepoda, Calanoida, Pontellidae) collected from Okinawa, southwestern Japan, with establishment of five indo-West Pacific species groups in the *L. detruncata* species complex. Zookeys 447:21–34. https://doi.org/10.3897/zookeys.447.8171

Hobson E (1991) Trophic relationships of fishes specialized to feed on zooplankters above coral reefs. Ecol fishes coral reefs Acad press … 69–95

Hobson ES (1973) Diel feeding migrations in tropical reef fishes. Helgolander Wissenschaftliche Meeresuntersuchungen 24:361–370. https://doi.org/10.1007/BF01609526

Houlbrèque F, Ferrier-Pagès C (2009) Heterotrophy in tropical scleractinian corals. Biol Rev 84:1–17. https://doi.org/10.1111/j.1469-185X.2008.00058.x

Hsiao Y-H, Dahms H-U, Hwang J-S (2013) Ecology of swarming in the planktonic copepod *Dioithona sp.* (Crustacea: Copepoda). J Nat Hist 47:739–751. https://doi.org/10.1080/00222933.2012.724717

Hunt ME, Scherrer MP, Ferrari FD, Matz MV (2010) Very bright green fluorescent proteins from the pontellid copepod *Pontella mimocerami*. PLoS One 5:3–10. https://doi.org/10.1371/journal.pone.0011517

Ikeda T, Hing Fay E, Hutchinson S, Boto G (1982) Ammonia and inorganic phosphate excretion by zooplankton from inshore waters of the Great Barrier Reef, Queensland. I. Relationship between excretion rates and body size. Mar Freshw Res 33:55. https://doi.org/10.1071/MF9820055

Jacoby CA, Greenwood JG (1988) Spatial, temporal, and behavioral patterns in emergence of zooplankton in the lagoon of Heron Reef, Great Barrier Reef, Australia. Mar Biol 97:309–328. https://doi.org/10.1007/BF00397762

Jacoby C, Greenwood J (1989) Emergent zooplankton in Moreton Bay, Queensland, Australia: seasonal, lunar, and diel patterns in emergence and distribution with respect to substrata. Mar Ecol Prog Ser 51:131–154. https://doi.org/10.3354/meps051131

Jeong HG, Suh HL, Jeong SB et al (2009) *Labidocera* species (Copepoda: Pontellidae) in waters of the Tsushima warm current with notes on their genital structure and zoogeography. Zool Stud 48:508–523

Kangtia P, Dahms H, Song SJ, Myoung J (2014) On the occurrence of a new species of benthic copepod, Zaus wonchoelleei (Harpacticoida, Harpacticidae), in a macroalgal habitat from Tongyong, Korea. Proc Biol Soc Washingt 127:585–602

Kimmerer WJ, Burau JR, Bennett WA (1998) Tidally-oriented vertical migration and position maintenance of zooplankton in a temperate estuary. Limnol Oceanogr 43:1697–1709. https://doi.org/10.4319/lo.1998.43.7.1697

Kimmerer WJ, McKinnon AD (1987) Zooplankton in a marine bay II. Vertical migration to maintain horizontal distributions. Mar Ecol Prog Ser 41:53–60. https://doi.org/10.3354/meps041053

Kramer MJ, Bellwood DR, Bellwood O (2013) Emergent fauna from hard surfaces on the Great Barrier Reef, Australia. Mar Freshw Res 64:687–691. https://doi.org/10.1071/MF12284

Land M (1988) The functions of eye and body movements in *Labidocera* and other copepods. J Exp Biol 391:381–391

Lewis JB, Boers JJ (1991) Patchiness and composition of coral reef demersal zooplankton. J Plankton Res 13:1273–1289. https://doi.org/10.1093/plankt/13.6.1273

Logan D, Townsend KA, Townsend K, Tibbetts IR (2008) Meiofauna sediment relations in leeward slope turf algae of Heron Island reef. Hydrobiologia 610:269–276. https://doi.org/10.1007/s10750-008-9442-9

Madhupratap M, Achuthankutty CT, Nair SRS (1991) Estimates of high absolute densities and emergence rates of demersal zooplankton from the Agatti atoll, Laccadives. Limnol Oceanogr 36:585–588. https://doi.org/10.4319/lo.1991.36.3.0585

Matsuo Y, Marumo R (1982) Diurnal vertical migration of pontellid copepods in the Kuroshio. Bull Plankt Soc Jap 29:89–98

Mauchline J (1988) The biology of Calanoid copepods. Academic Press

McKinnon AD (1991) Community composition of reef associated copepods in the lagoon of Davies Reef, Great Barrier Reef, Australia. Bull. Plankt. Soc. Japan 467–478

McWilliam PS, Sale PF, Anderson DT (1981) Seasonal changes in resident zooplankton sampled by emergence traps in One Tree Lagoon, Great Barrier Reef. J Exp Mar Bio Ecol 52:185–203. https://doi.org/10.1016/0022-0981(81)90036-8

Mojib N, Amad M, Thimma M et al (2014) Carotenoid metabolic profiling and transcriptome-genome mining reveal functional equivalence among blue-pigmented copepods and appendicularia. Mol Ecol 23:2740–2756. https://doi.org/10.1111/mec.12781

Mulyadi (2002) The calanoid copepods family Pontellidae from Indonesian waters, with notes on its species-groups

Nakajima R, Yoshida T, Othman BHR, Toda T (2008) Diel variation in abundance, biomass and size composition of zooplankton community over a coral-reef in Redang Island, Malaysia. Plankt Benthos Res 3:216–226. https://doi.org/10.3800/pbr.3.216

Ohlhorst SL (1982) Diel migration patterns of demersal reef zooplankton. J Exp Mar Biol Ecol 60:1–15

Ohtsuka S, Fosshagen A, Soh HY (1996) Three new species of the demersal calanoid copepod Placocalanus (Ridgewayiidae) from Okinawa, southern Japan. Sarsia 81:247–263. https://doi.org/10.1080/00364827.1996.10413623

Pessoa VT, Melo PAMC, Melo Junior M, Neumann-Leitao S (2014) Population dynamics of *Calanopia americana* Dahl F., 1894 (Copepoda, Calanoida) in a reef environment in tropical Brazil. Trop Oceanogr 42:24–32

Porter JW (1974) Zooplankton feeding by the Caribbean reef-building coral *Montastrea cavernosa*. Proc Second Int Coral Reef Symp 1:111–125

Porter JW, Porter KG (1977) Quantitative sampling of demersal plankton migrating from different coral reef substrates. Limnol Oceanogr 22:553–556

Robichaux DM, Cohen AC, Reaka ML, Allen D (1981) Experiments with zooplankton on coral reefs, or will the real demersal plankton please come up? Mar Ecol 2:77–94. https://doi.org/10.1111/j.1439-0485.1981.tb00092.x

Saigusa M, Oishi K (2000) Emergence rhythms of subtidal small invertebrates in the subtropical sea: nocturnal patterns and variety in the synchrony with tidal and lunar cycles. Zool Sci 17:241–251. https://doi.org/10.2108/zsj.17.241

Saigusa M, Okochi T, Ikei S (2003) Nocturnal occurrence, and synchrony with tidal and lunar cycles, in the invertebrate assemblage of a subtropical estuary. Acta Oecol 24:191–204. https://doi.org/10.1016/S1146-609X(03)00034-1

Sale PF, McWilliam PS, Anderson DT (1978) Faunal relationships among the near-reef zooplankton at three locations on Heron Reef, Great Barrier Reef, and seasonal changes in this fauna. Mar Biol 49:133–145.

https://doi.org/10.1007/BF00387113

Scott A (1909) The Copepoda of the Siboga expedition. Part 1. Free-swimming, littoral and semi-parasitic Copepoda. E.J. Brill, Leydon

Sherman K (1962) Pontellid copepod distribution in relation to surface water types in the central North Pacific. Limnol Oceanogr 8:214–227

Sherman K (1964) Pontellid copepod occurrence in the central South Pacific. Limnol Oceanogr 9:476–484

Silas EG, Pillai P (1973) The calanoid copepod family Pontellidae from the Indian Ocean. J Mar Biol Assoc India 15:771–858

Smith JN, De'ath G, Richter C et al (2016) Ocean acidification reduces demersal zooplankton that reside in tropical coral reefs. Nat Clim Chang 6:1124–1129. https://doi.org/10.1038/nclimate3122

Sorokin YI, Sorokin PY (2010) Plankton of the central Great Barrier Reef: abundance, production and trophodynamic roles. J Mar Biol Assoc United Kingdom 90:1173–1187. https://doi.org/10.1017/S0025315410000597

Tester PA, Cohen JH, Cervetto G (2004) Reverse vertical migration and hydrographic distribution of *Anomalocera ornata* (Copepoda: Pontellidae) in the US South Atlantic bight. Mar Ecol Prog Ser 268:195–203. https://doi.org/10.3354/meps268195

Turner JT, Collard SB (1980) Winter distribution of pontellid copepods in the neuston of the eastern Gulf of Mexico continental shelf. Bull Mar Sci 30:526–530

Ueda H, Kuwahara A, Tanaka N, Azeta M (1983) Underwater observations on copepod swarms in temperate and subtropical waters. Mar Ecol Prog Ser 11:165–171. https://doi.org/10.3354/meps011165

Ueda H, Kuwatani M, Suzuki KW (2010) Tidal vertical migration of two estuarine copepods: Naupliar migration and position-dependent migration. J

Plankton Res 32:1557–1572. https://doi.org/10.1093/plankt/fbq078

van Duren LA, Videler JJ (1995) Swimming behavior of developmental stages of the calanoid copepod Temora Longicornis at different food concentrations. Mar Ecol Prog Ser 126:153–161

Walters K, Bell SS (1994) Significance of copepod emergence of benthic, pelagic, and phytal linkages in a subtidal seagrass bed. Mar Ecol Prog Ser 108:237–250. https://doi.org/10.3354/meps108237

Yahel R, Yahel G, Berman T et al (2005) Diel pattern with abrupt crepuscular changes of zooplankton over a coral reef. Limnol Oceanogr 50:930–944. https://doi.org/10.4319/lo.2005.50.3.0930

Youngbluth MJ (1982) Sampling demersal zooplankton: a comparison of field collections using three different emergence traps. J Exp Mar Biol Ecol 61:111–124

Zagalsky PF, Herring PJ (1972) Studies on a carotenoprotein isolated from the copepod, *Labidocera acutifrons*, and its relationship to the decapod carotenoproteins and other polyene-binding proteins. Comp Biochem Physiol Part B Comp Biochem 41:397–415

Zaret TM, Suffern S (1976) Vertical migration in zooplankton as a predator avoidance mechanism. Limnol Oceanogr 6:804–813