Densities of the endolithic bivalve *Lithophaga lessepsiana* (Vaillant, 1865) in *Pocillopora damicornis*, Solitary Islands Marine Park, northern NSW, Australia

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Abstract

The Solitary Islands Marine Park is positioned in a transition zone between tropical and temperate regions and consequently supports a range of taxa with different biogeographic affinities. Driven by variable influence of the East Australian Current, there is increasing representation of tropical taxa along a cross-shelf gradient (inshore to offshore). Patterns in the population of the endolithic bivalve *Lithophaga lessepsiana* were examined by sampling host corals (*Pocillopora damicornis*) across the cross-shelf gradient and were more broadly contextualised by comparisons with samples from Heron Island. Contrary to predictions based on studies on low latitude reefs, where densities are higher close to shore, these increased with increasing distance from the coast. Densities were almost an order of magnitude higher at Heron Island than in the Solitary Islands Marine Park. These patterns indicate that factors other than nutrient load and temperature primarily determine *L. lessepsiana* densities over the scales of this study. These are likely to include larval supply, colony morphology and availability of larval settlement sites within individual coral colonies.

Key words: bioerosion, boring bivalve, colony morphology, cross-shelf gradient, high latitude reefs, Bivalvia, Mytilidae

Introduction

Scleractinian corals are a dominant feature of benthic communities in northern NSW (Veron *et al*. 1974; Harriott *et al*. 1994). Within the Solitary Islands Marine Park (SIMP), there is a gradient of increasing coral richness and cover across the shelf (Harriott *et al*. 1994). While nearshore reefal habitats are dominated by macroalgae, they nevertheless support sometimes extensive patches of coral-dominated communities (Smith and Simpson 1991; Smith *et al*. 2008). The patterns displayed by corals have recently been confirmed for reef fish with increasing tropical representation with distance from shore (Malcolm *et al*. 2010a, b). Similar patterns are emerging in current studies of molluscan communities, with nearshore assemblages dominated by large herbivorous taxa and offshore assemblages by a diverse mix of taxa, many of which have tropical affinity (Smith 2001, 2011; Harrison and Smith, unpublished data). These patterns are explained, at least in part, by the greater influence of the East Australian Current (EAC) offshore (Malcolm *et al*. in press), which provides a source of recruits of tropical biota (Booth *et al*. 2007) offshore, and the fact that many molluscs have specific habitat preferences which include association with scleractinian corals. One specific group of such molluscs are the endolithic date mussels (Mytilidae: Lithophaginae).

Coral-boring bivalves of the genus *Lithophaga* Röding, 1798 are commonly found associated with a wide variety of coral species (Soliman 1969; Kleemann 1980). Because of their capacity to bore into, and in most cases weaken, coral skeletons (Scott and Risk 1988), lithophagine bivalves are an important contributor to bioerosion in many reef environments (Soliman 1969; Sammarco 1996; Glynn 1997; Clark and Morton 1999; MacDonald and Perry 2003). *Lithophaga lessepsiana* (Vaillant, 1865) (= *L. simplex* Iredale, 1939; Lamprell and Healy 1998) is common in the

SIMP where it occurs in association with *Pocillopora damicornis* (Linnaeus, 1758), one of the dominant coral species in local coral communities (Veron *et al*. 1974; Smith and Simpson 1991; Harriott *et al*. 1994) (Fig. 1). Larvae of this species appear to settle preferentially on the growing tips of branches (Mokady *et al*. 1992) and corrode skeletal material using alkaline secretions (Loya 1991). Although abundant within the SIMP, *L. lessepsiana* has not been recorded further south in the nearshore coastal habitats of eastern Australia (but has been recorded from Lord Howe Island and Elizabeth Reef—I. Loch, Australian Museum, pers. comm.).

FIGURE 1. A specimen of *Lithophaga lessepsiana* in its coral host *Pocillopora damicornis* at North West Solitary Island.

Although there have been considerable recent advances in our understanding of the processes that limit coral reef development at high latitudes, data for some key processes remain scant (Harriott and Banks 2002). In an attempt to synthesise the available data Harriott and Banks (2002) proposed a qualitative biophysical model and listed 20 mechanisms that potentially contribute to the lack of

accretion of corals to form true reefs at high latitude sites. While most of these mechanisms were supported by previously published data from both experimental studies and surveys, the assumption that rates of bioerosion may be greater at high latitudes was supported only by anecdotal observations on the strength of attachment of coral colonies at sites in the SIMP (Harriott and Banks 2002). In an effort to partially address this lack of data on rates of bioerosion, this paper reports on densities of endolithic lithophagine bivalves inhabiting colonies of *Pocillopora damicornis* sampled over a cross-shelf gradient in the SIMP, and from Heron Island. Although this evaluation covers only one of the many organisms responsible for bioerosion in corals (Hutchings 1986), it nevertheless provides the opportunity to examine predictions made by previous workers that higher nutrient levels (and consequently higher planktonic production) and lower water temperatures, such as those found in high latitude sites, can lead to increased densities of endolithic bioeroders (Highsmith 1981; Hallock and Schlager 1986; Glynn 1997). While these two factors have repeatedly been shown to be primary contributors, bioerosion rates are also affected by additional factors such as hydrographic regime (Tribollet *et al.* 2002) and sedimentation (Hutchings *et al.* 2005). In addition, a number of studies have demonstrated considerable spatial and temporal variation in bioerosion rates even within a site (Kiene and Hutchings 1994; Pari *et al.* 2002; Hutchings *et al.* 2005).

Based on the majority of other studies examining macroborers of corals (Risk *et al.* 1995; Holmes *et al.* 2000; Hutchings and Peyrot-Clausade 2002), it might be predicted that: i) densities of *L. lessepsiana* will be higher at nearshore than offshore sites within the SIMP; and ii) densities within the SIMP as a whole will be higher than those occurring within the same coral host at a low latitude site. These hypotheses were tested during this study.

Materials and methods

Ten replicate samples of *P. damicornis* were collected from leeward reefs at six sites across a nearshore-offshore gradient within the SIMP. Sites ranged from 0.5–11 km from the coast (Fig. 2). All samples were taken from the same narrow depth range (8–10 m) and were randomly selected from the full range of colonies available within a 30 x 30 m area at each site. Within one month of sampling at the SIMP, a similar number of colonies were sampled from a similar depth range at a leeward site at Heron Island (approx. 23°S).

Prior to collection, the dimensions of each colony (length, width and height) were recorded. Samples were collected by first covering them in a plastic bag and using a hammer and chisel to dislodge the base of the colony from the substratum. Where possible, samples were removed with the base intact. On the few occasions where this was not possible, any obvious *L. lessepsiana* protruding from basal remnants were also collected. Samples were bleached and all *L. lessepsiana* removed from the skeleton. Following dissection, the volume of the coral rubble was measured using water displacement and *L. lessepsiana* abundances were converted to densities per 10 ml of coral skeleton.

A sample of lithophagine bivalves collected from *P. damicornis* at Spilt Solitary Island was confirmed to be *L. lessepsiana* by staff at the Australian Museum (Kasey 1996) and these were used as reference specimens for comparison. Three lots of specimens (from North Solitary, Split Solitary and Muttonbird islands) were subsequently deposited as vouchers at the Australian Museum (C.468223, C.468224, C.468225, respectively).

Observations of the colony shape and morphology during sampling suggested that colonies from nearshore sites within the SIMP were generally flattened with a few robust, erect branches while those from offshore sites, while still robust, had a more erect and branched growth form. In contrast, Heron Island colonies were finely branched and complex. In order to examine these morphological differences and the effect they may have on densities of *L. lessepsiana*, the ratio of displacement volume:theoretical volume (using the length, width and height measurements and assuming that colony shape approximates a hemisphere) was calculated for each colony. This provided a measure of the degree of infilling of the colony space by the branches.

Two sets of analyses were performed using ANCOVA with the volume ratio of each replicate colony as the covariate (to take the degree of infilling into consideration in comparison of densities): i) a one-way analysis in which bivalve densities were compared along the cross-shelf gradient in the SIMP; ii) a one-way analysis comparing mean densities between the SIMP (pooled across sites) and Heron Island. Data were logarithmically transformed prior to analysis to improve homoscedasticity. *Post hoc* tests were performed for the first analysis using Tukey's test.

Results

There was an obvious increase in *L. lessepsiana* density at offshore sites in the SIMP (Fig. 3A). Patterns for the volume ratio were not as clear. While the lowest values were recorded close to shore, and the two highest values at sites between 5–8 km offshore, values at North Solitary (~11 km from shore) were lower and similar to those at Woolgoolga Reef (0.5 km from shore) (Fig. 3B). The results of ANCOVA indicated that volume ratio partly determines *L. lessepsiana* densities with a significant effect returned for the regression between the two variables ($F = 1.85$, df = 1, $P = 0.049$). The analysis also indicated a highly significant difference in densities among sites ($F = 7.25$, df = 5, 51, $P < 0.001$) with *post hoc* contrasts revealing two homogeneous subsets of sites: i) nearshore and mid-shelf sites (Muttonbird Island, Woolgoolga Reef, Split Solitary Island and North West Solitary Island); and ii) offshore sites (South Solitary Island and North Solitary Island). As might be expected from the obvious differences in the means (Fig. 3A), the second analysis showed that densities at Heron Island were significantly greater than those in the SIMP ($F = 160.63$, df = 1, 68, $P < 0.001$).
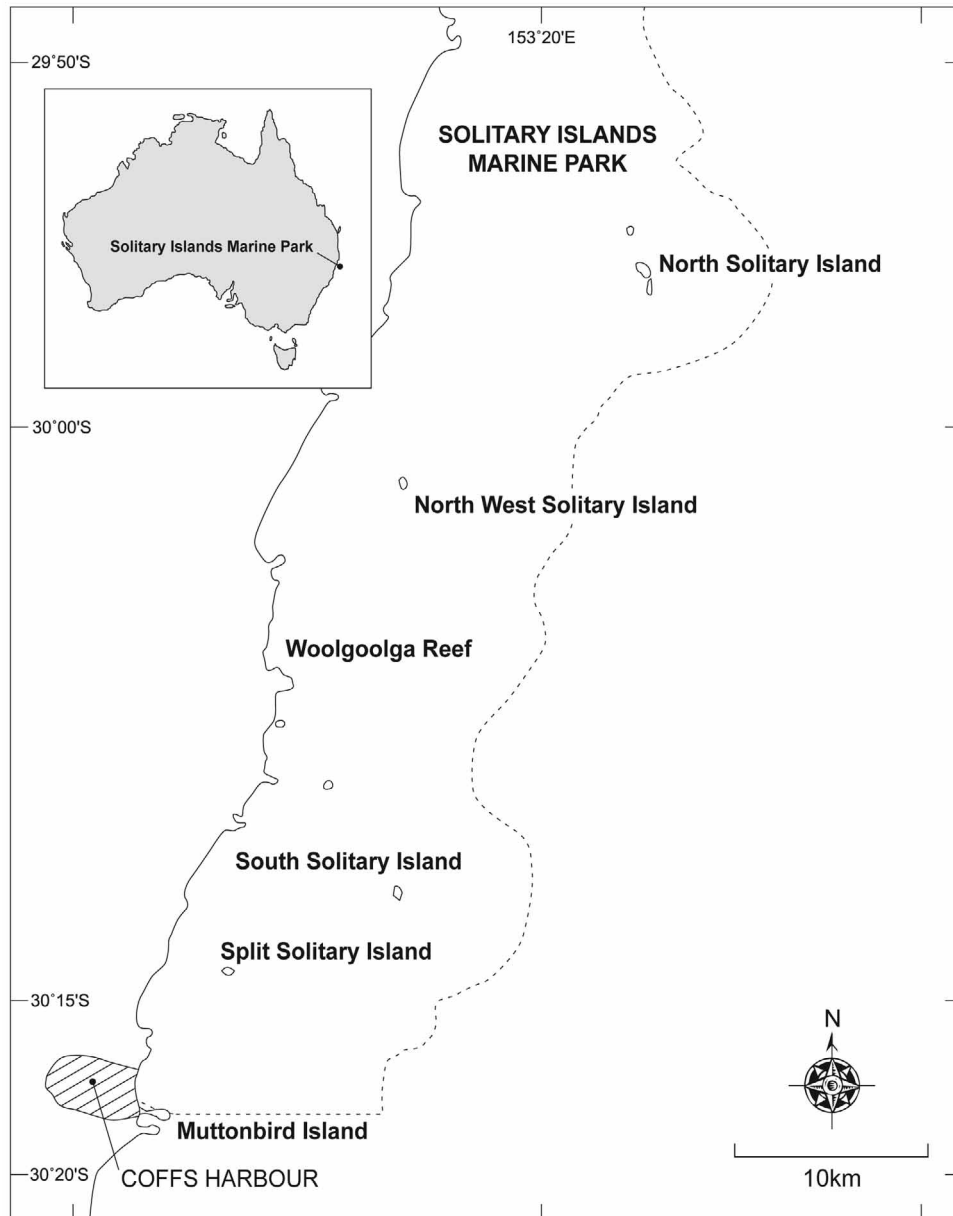
FIGURE 2. Map of the east coast of Australia and the Solitary Islands Marine Park showing the location of sampling sites.

Discussion

These results contrast strongly with most other published studies. In general, bioerosion by macroborers has been found to be higher in macroalgal-dominated habitats that are close to sources of terrestrial runoff and experience increased nutrient loading (Holmes *et al*. 2000; Chazottes *et al*. 2002), or where there is appreciable reef degradation (Fonseca *et al*. 2006). Two main gradients were evaluated here—a nearshore-offshore one at the same latitude, and a high latitude-low latitude one. In each case, trends in *L. lessepsiana* density were totally contrary to predictions. Thus, the lowest densities were recorded at nearshore sites in the SIMP that have higher nutrient loads than offshore sites (Smith *et al*. 1994) and densities at Heron Island, where waters are typically more oligotrophic, were almost an order of magnitude greater than densities averaged across the high latitude sites. Clearly, factors other than nutrient load are contributing to these observations.

Morphology of coral colonies had a significant effect on densities within this study and this is hypothesised to be due to the reduced number of growing tips in the robust, flattened colonies that typify many colonies in the SIMP. It has been speculated that larval recruitment of *L. lessepsiana* occurs at the growing tips of coral branches (Mokady *et al*. 1992). This mechanism was supported by Kasey (1996) who determined the age of all specimens of *L. lessepsiana* in a large colony of *P. damicornis* from Split Solitary Island and found that age was significantly inversely correlated to distance from the base of the colony. For this reason, it can be hypothesised that robust colonies with few branches would offer fewer suitable settlement sites for larvae and thus support fewer *L. lessepsiana* than colonies with the same displacement volume but a more branched morphology (i.e. higher volume ratio).

Although unlikely to explain much of the variation observed in the study, an artefact of the volumetric component of the method needs to be highlighted. That is, densities were calculated per 10 ml of skeleton. Clearly, where infection rates are higher, more coral skeleton will have been removed by the process of bioerosion and so estimates of *L. lessepsiana* density in these colonies will be overestimated.
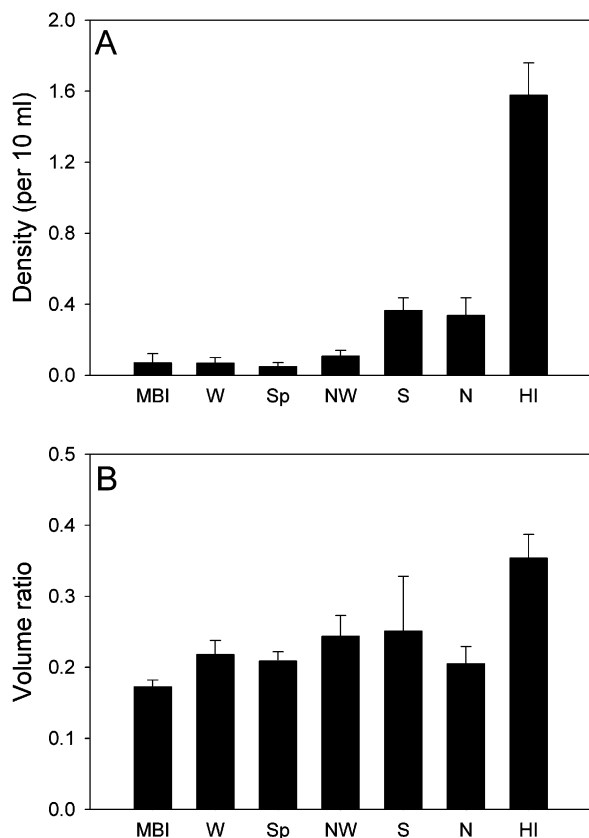
FIGURE 3. A. Mean (±SE) *Lithophaga lessepsiana* densities per 10 ml of host (*Pocillopora damicornis*) skeleton from each sampling site. **B**. Mean (±SE) volume ratio of coral colonies sampled from each site. MBI = Muttonbird Island (0.78 km from shore), W = Woolgoolga Reef (0.50 km from shore), Sp = Split Solitary Island (2.45 km from shore), NW = North West Solitary Island (5.2 km from shore), S = South Solitary Island (7.65 km from shore), N = North Solitary Island (11.15 km from shore), HI = Heron Island.

A number of additional factors may potentially contribute to the patterns evident in this study; however, due to a lack of data on important processes within the SIMP, these remain speculative. Firstly, Mokady *et al.* (1993) demonstrated that *L. lessepsiana* larvae require a minimum of four weeks to attain competency and can delay metamorphosis for up to four months. Given the demonstrated abundance of *L. lessepsiana* within the region, it is likely that local populations are able to successfully reproduce but also that larvae may be carried away from their source location before metamorphosis can occur (Wilson and Harrison 1998). At nearshore sites, the current direction is often northward from cooler, southern localities (Chidgey 1987; Smith *et al.* 1994; Malcolm *et al.* 2011)

where the host coral becomes progressively less abundant (Veron 1986; Harriott *et al.* 1999; Smith *et al.* 2008); larval supply is therefore likely to be low (also note that, while *P. damicornis* occurs as far south as Sydney (Veron 1986), data on the presence or absence of endolithic borers from southern localities are lacking). In contrast, the outer islands are regularly bathed by warm-water eddies from the southward flowing East Australian Current which are likely to carry a greater supply of larvae (Booth *et al.* 2007). Although these eddies reach nearshore sites, the frequency of contact with subtidal reefs increases offshore (Malcolm *et al.* 2011). In this model, *L. lessepsiana* densities reflect the putatively differential supply of larvae across the shelf. This larval-supply hypothesis has also been used to tentatively explain the greater number of tropically-affiliated coral and fish species occurring at the outermost island in the Solitary Islands group, North Solitary Island (Harriott *et al.* 1994; Malcolm *et al.* 2010b).

The reasons for the very large differences between densities in the SIMP and those at Heron Island are similarly likely to be due to a number of different factors, many of which can only be speculated upon (e.g., larval supply, differences in wave energy influencing settlement rates). Unfortunately, even where processes can be expected to differ between the two localities, they do not help to explain the observed patterns. For example, *P. damicornis* has a low growth rate in the SIMP (Harriott 1999) suggesting that, like other species of coral at high latitudes, skeletal density may be higher at this location than at low latitude sites (Harriott 1997; Spinaze *et al.* 1997). Intuitively, this observation would appear to support the observed lower densities of *L. lessepsiana* in the SIMP (i.e., more difficult for boring bivalves to become established in denser skeletal material). However, both Highsmith (1981) and Schönberg (2002) have demonstrated that bioerosion rates may actually be positively correlated with coral density, albeit primarily for bioeroding sponges. Interpretations are further complicated by the fact that skeletal densities and porosities of *P. damicornis* at Split Solitary Island have been found to be highly variable (statistically significantly so) even amongst neighbouring colonies (Spinaze *et al.* 1997).

Acknowledgements

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