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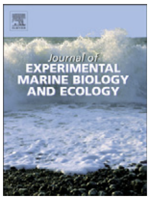

Host-use patterns and factors influencing the choice between anemone and urchin hosts by a caridean shrimp

Nicolas C. Ory [a,b,*], Dudgeon [b], Martin Thiel [c,d]

[a] The Swire Institute of Marine Science, The University of Hong Kong, Pokfulam Rd., Hong Kong, China
[b] School of Biological Sciences, The University of Hong Kong, Pokfulam Rd., Hong Kong, China
[c] Facultad Ciencias del Mar, Universidad Católica del Norte, Larrondo 1281, Coquimbo, Chile
[d] Centro de Estudios Avanzados en Zonas Áridas (CEAZA), Coquimbo, Chile

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ABSTRACT

Small marine decapods often associate with other invertebrates in order to gain protection from predators. However, the factors that influence host choice by symbionts, such as shrimps, are poorly understood but may have important implications for the distribution and abundance of these mesoconsumers. In Hong Kong, the rhynchocinetid shrimp *Rhynchocinetes brucei* uses two alternative hosts: an urchin (*Diadema setosum*) and an anemone (*Entacmaea quadricolor*). We examined the association between *R. brucei* and its anemone and urchin hosts in the field and laboratory, investigating host choice and host fidelity. Underwater surveys on shallow rocky reefs in Hong Kong revealed that shrimps were rarely found outside refuges, such as crevices and holes, unless they were associated with anemones and urchins. Shrimps were more frequently associated with urchins than with anemones, although anemones were more abundant within the survey area. Host-choice experiments in the laboratory confirmed that, when given a choice, shrimps avoided open areas and associated with anemones, urchins or artificial refuges. Shrimps overwhelmingly chose urchins over artificial refuges, but did not show any clear preference for anemones over refuges. When offered a choice, shrimps displayed fidelity for their original host species (i.e. the host with which they were associated when collected from the field), suggesting that they imprinted upon the host. Host-imprinting may allow symbionts to efficiently relocate their original host species after separation (e.g. following nocturnal foraging trips) thereby, perhaps, reducing the risk of predation. However, host preference by *R. brucei* was facultative because shrimps would associate with an unfamiliar host when their original host was unavailable. This flexibility may allow shrimps to respond to local variability in host abundance.

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1. Introduction

Predation pressure is considered to be one of the most important forces driving the evolution of symbiotic associations in decapods, and it has been frequently suggested that anemone (Baeza and Stotz, 2003; Fautin et al., 1995; Wirtz and Diesel, 1983) or urchin (Hartney and Grorud, 2002; Randall et al., 1961) hosts provide protection from predators. Symbiotic associations, i.e. two species 'living together' (sensu De Bary, 1879; see also Paracer and Ahmadjian, 2000; Baeza and Stotz, 2003; Bauer, 2004), are widespread in a variety of habitats (e.g. Grutter and Irving, 2007; Secord, 2002). These associations can be facultative or obligate, and have positive effects on the fitness of at least one member of the association by reducing predation risk or physical stress, or enhancing access to food (Bruno and Bertness, 2001; Grutter and Irving, 2007). Although the implications of symbiotic associations for community structure still need to be clarified (Brooker et al., 2008; Lafferty, 2013; Stachowicz, 2001), there is evidence that, by reducing competition or predation on the associated species, such interactions contribute towards assemblage resilience (Chapin et al., 2000) and increase species diversity (Hacker and Gaines, 1997).

Refuge availability and predation intensity both appear to influence the benefits of symbioses (Bertness and Callaway, 1994; Bruno et al., 2003), and the distribution and abundance of prey species often reflect spatial variability in predation risk and habitat complexity (reviewed by Barbosa and Castellanos, 2005). The presence of relatively large, sessile or slow moving benthic organisms that can be used as a refuge from predators may allow prey to persist in homogeneous habitats with low complexity (such as sandy bottoms or barren rocky reefs; Eggleston et al., 1997; Ryer et al., 2004) that they would not otherwise have occupied (Bruno and Bertness, 2001; Grutter and Irving, 2007). For example, the abundance of the goby *Lythrypnus dalli* on rocky reefs in southern California is enhanced by the presence of the urchin *Centrostephanus coronatus* (Diadematidae) which is used as a refuge by the fish (Hartney and Grorud, 2002).

The degree of host specificity varies among symbiont species: some alpheid shrimps for example, associate with up to six different sponge

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[*] Corresponding author at: The Swire Institute of Marine Science, The University of Hong Kong, Pokfulam Rd., Hong Kong, China. Tel.: +852 28092179; fax: +852 28092197.
E-mail address: nory@hku.hk (N.C. Ory).

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species in Caribbean waters (Macdonald et al., 2006), whereas the damselfish *Dascyllus trimaculatus* associates with eight different anemone species (Fautin and Allen, 1992). The factors that influence symbiont preferences among host species are poorly understood (Sotka, 2005), although they have important consequences for symbiont fitness (De Bruyn et al., 2010). Symbionts may associate preferentially with the most abundant host species because they are easier to locate or are closer to each other than scarce hosts, thereby reducing predation risks experienced when moving between hosts (Roughgarden, 1975; Thiel and Baeza, 2001). Hosts in dense aggregations may provide especially effective protection, which may facilitate the establishment of a symbiotic association (Grutter and Irving, 2007).

Symbionts should preferentially associate with host species that offer them maximum benefits; for example, amphipods associated more often with the more structurally complex of two macroalgae host species as it offered better protection from predators (Zamzow et al., 2010). Nonetheless, host choice is likely to reflect optimization between potential benefits (e.g. refuge provision) and costs, which may include restrictions on foraging areas or access to potential mates (Bertness and Callaway, 1994; Callaway, 2007; Roughgarden, 1975). For example, many marine invertebrates will not leave the protection of their hosts to search for mates when predation risks are high (Knowlton, 1980; Thiel and Baeza, 2001). While the trade-offs between the benefits and costs of symbioses will vary depending on the species involved, if circumstances permit, symbionts should always associate with host species that provide both effective protection and access to food (Baeza and Stotz, 2003; Baeza and Thiel, 2003; Jeffries and Lawton, 1984).

Host-preferences have mainly been studied among different morphotypes of the same (Baeza and Stotz, 2003) or similar host species (e.g. sea anemones: e.g. Fautin and Allen, 1992; Briones-Fourzán et al., 2012; urchins: e.g. De Bruyn et al., 2010), but rarely among hosts of taxonomically-distant groups (but see Baeza and Thiel, 2003) that are likely to provide contrasting benefits to symbionts. Preferences for mobile hosts (e.g. urchins) relative to those with limited mobility (e.g. anemone) have seldom been compared (Hayes, 2007, but see Baeza and Thiel, 2003), although movement patterns of hosts are likely to have important consequences for symbiont distribution (Bell, 1984).

Symbiont preferences for particular host species may be enhanced by 'host imprinting' (sensu Immelmann, 1975), and various studies have demonstrated fidelity of small invertebrates for anemones (Baeza and Stotz, 2003; Mascaró et al., 2012), urchins (De Bruyn et al., 2011) or limpets (Ocampo et al., 2012). The ability to recognize chemical or physical cues from specific hosts may allow symbionts to relocate the host after foraging, moulting or mating and may prevent association with unfamiliar hosts, such as anemones, which could attack naïve individuals (Brooks and Rittschof, 1995; Melzer and Meyer, 2010). However, even if host fidelity is beneficial for a symbiont, it may be reversible, allowing the symbiont to respond to changes in its environment (Derby and Atema, 1980). For example, a symbiont could change to associate with an alternative host if the abundance of the preferred host declines (Reeves and Brooks, 2001).

Small marine decapods are commonly associated with echinoderms, anemones or other invertebrates that they may use as a refuge from predators as well as a source of food or a mating site (Bauer, 2004; Jonsson et al., 2001; Wirtz, 1997). We used the rhynchocinetid shrimp *Rhynchocinetes brucei* (Caridea) as a model symbiont to investigate host preferences. Rhynchocinetid shrimps play an important role in shallow barren reef communities both as epibenthic predators (Dumont et al., 2009; Dumont et al., 2011) and as food for predatory fishes (Medina et al., 2004; Ojeda and Fariña, 1996; Ory et al., 2012). *R. brucei* is common in shallow (5 to 30 m depth) rocky reefs in the tropical eastern Pacific from Hong Kong to the Great Barrier Reef (Bruce, 1986; Chase, 1997; Okuno, 1994). Preliminary field observations in Hong Kong (NCO, personal observations) indicated that *R. brucei* associates with the long-spined sea urchin *Diadema setosum* (Diadematidae) and the sea anemone *Entacmaea quadricolor* (Actiniidae). Associations with these hosts appear facultative as the shrimp is sometimes observed inside small holes, crevices or, more rarely, in open areas in the absence of urchin or anemone hosts.

The present study compared the preference of *R. brucei* for anemone and urchin hosts, and examined what factors influence the association. Underwater surveys were carried out to examine how shrimps were influenced by the availability of small holes or crevices in the substratum or the presence of potential hosts, and whether shrimp abundance would vary between host species or be influenced by host aggregations. We predicted that hosts would provide refuges for shrimps allowing them to occupy habitats they would not have occupied otherwise, i.e.where alternative refuges, such as holes and crevices, are not available. Accordingly, laboratory experiments were conducted to compare shrimp preferences between both host species, or artificial refuges that mimic holes or crevices in the reef, relative to areas lacking refuges. In addition, we tested the hypothesis that the shrimp would exhibit host fidelity and prefer to associate with the host from which they were collected in the field, but would associate with an alternative host when the preferred host was unavailable.

2. Materials and methods

2.1. Sampling site

All in situ observations and experiments were conducted at a semi-sheltered bay of the South Ninepin Island (N 22°14′48, E114°20′15) in Hong Kong SAR, southern China (Fig. 1). The study site was a 200 × 50 m shallow (5–8 m deep) gently-sloping rocky reef, delimited by a steep barren bedrock shore and by sand at its lower margins (8–9 m water depth). Studies were conducted in the hot and wet season between June and mid-September 2012 when water temperatures varied from 28 to 30 °C, salinity was 32.7 to 34.2 psu and visibility (Secchi disc depth) ranged from 2.9 to 4.4 m (www.epd.gov.hk).

The reef comprised boulders of various sizes (see below), overgrown by red crustose coralline algae (Rhodophyta), encrusting sponges and barnacles (*Balanus trigonus*, Balanidae). Patches of sand or consolidated bedrock covered ~10% of the study site (see below). The anemone *E. quadricolor* and the sea urchin *D. setosum*, which are used as hosts by *R. brucei*, were both abundant, and preliminary observations suggested that the main predatory fishes at the site were groupers, *Cephalopholis boenak* and *Epinephelus fasciatomaculosus* (Serranidae), and the scorpaenid *Sebastiscus marmoratus*.

2.2. Shrimp–host associations in the field

The effects of host species (*E. quadricolor*, *D. setosum*), degree of host aggregation (aggregated, not aggregated), substratum type and refuge availability (presence, absence) on the presence and abundance of *R. brucei* were quantified from direct SCUBA observations. Surveys were conducted on four occasions at four week intervals over the study period, between 10 h and 16 h. During each survey, two 150 m transect lines were laid at a depth of 5 to 8 m, parallel to the shore and 10 m apart from each other. Starting from the shoreward end of each transect line, the first anemone or urchin seen within a 2.5 m belt on each side of the transect line was examined for the presence of shrimp, which were then counted (see below). The survey continued until at least 15 aggregated hosts (i.e. two or more conspecific host individuals in physical contact with each other: Bernstein et al., 1981) and 15 isolated individuals of each of the two host species were surveyed along the transect. All shrimps on the open surfaces of the reef (i.e. surfaces lacking refuges), or at the entrance of refuges (i.e. holes or crevices in the reef with an aperture size of <5 cm; see Ory et al., 2012), were also counted.

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