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The influence of habitat on post-settlement processes, larval production and recruitment in a common coral reef sponge

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ABSTRACT

Population dynamics in marine sessile invertebrate communities are linked to both pre- and post-settlement processes. For species possessing low-dispersing, non feeding larvae, population demographics and distributions are primarily regulated by larval production and post-settlement effects. This study assessed the effect of temperature, photoperiod, rainfall and habitat on post-settlement mortality, growth, asexual reproduction (fission), larval production and recruitment in the abundant Great Barrier Reef brooding sponge *Carteriospongia foliascens*. The study was conducted over 24 months at two locations characterized by distinct hydrodynamics (wave height). Location-specific differences in growth, body size and fecundity for *C. foliascens* were attributed to water movement, with a higher wave height range corresponding to higher abundance of larger, more reproductive individuals. The positive effects of hydrodynamics on growth and larval production also translated to higher recruitment levels highlighting a stock-recruitment relationship in this species. *C. foliascens* showed no evidence of fission, and exhibited fluctuating growth trajectories in all size classes investigated. Decreasing growth variability corresponded with increasing size, reflecting growth trajectories for species having indeterminate growth. Results presented in this study highlight the importance of habitat characteristics for post-settlement processes, larval production and recruitment in low dispersing sessile invertebrate species, such as brooding sponges.

1. Introduction

The term "recruitment" is broadly defined as the addition of new individuals to populations after successfully reaching an arbitrary life stage (e.g. juveniles, Connell, 1985; Caley et al., 1996). The supply, survival and growth of new settlers to reach recruitment size and sexual maturity is therefore key to population maintenance and persistence (Cowen and Sponaugle, 2009; Pineda et al., 2009, 2010). For marine sessile invertebrates, temporal and spatial variability associated with both pre-settlement and post-settlement stages contribute to population heterogeneity. (Connell, 1985; Fraschetti et al., 2003; Stoner, 1990; Thorson, 1966).

Primary recruitment limitation (*sensu* Fraschetti et al., 2003), involving pre-settlement processes of production, supply, survival, dispersal, habitat selection and settlement of motile life stages, such as larvae, can shape population abundance and distribution patterns (Hughes et al., 2000; Jenkins, 2005; Pineda et al., 2010). Post-settlement processes subsequently contribute to secondary recruitment limitation (*sensu* Fraschetti et al., 2003), further structuring populations (e.g. abundance, distribution and individual body size) through mortality, growth and asexual reproduction. Biotic factors that could influence the mortality, growth and reproduction of sessile marine invertebrates include fission, fragmentation, predation, grazing, food availability and competition (Maldonado and Uriz, 1999; Penin et al., 2011; Tremblay et al., 2014; Vermeij and Sandin, 2008; Zilberberg et al., 2006b). In addition, abiotic factors such as habitat surface topography, temperature, light quality and eutrophication could also influence post-settlement processes (Fabricius, 2005; Nozawa and Harrison, 2007; Tremblay et al., 2014; Walters and Wethey, 1996). While mortality at the early post-settlement phase (e.g. juvenile) is usually very high (>90% for marine invertebrates, Gosselin and Qian, 1996; Wilson and Harrison, 2005), size-dependent survival (where larger individuals have higher survival) has been demonstrated (e.g. in scleractinian corals, Penin et al., 2010; Dmitriew, 2011; Guest et al., 2014).

The growth of ectotherms is significantly influenced by temperature. While higher ambient temperatures generally correspond to higher growth rates for conspecifics due to associated increases in metabolic rates (Brockington and Clarke, 2001; Gooding et al., 2009; Watson et al., 2014), anomalous temperatures exceeding the thermal tolerance

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of a species can lead to negative growth and death (Cebrian et al., 2011; De'ath et al., 2009). In addition, photoperiod and light quality are important for taxa that associate with photosynthetic symbionts, and rely on supplemental autotrophic nutrition for energetics, somatic growth and reproduction (Erwin and Thacker, 2008; Harland and Davies, 1995; Hawkins and Klumpp, 1995; Jantzen et al., 2008; López-Legentil et al., 2011; Muscatine and Hand, 1958; Wilkinson, 1983; Wooldridge, 2010). For species occupying intertidal zones and inshore reefs, sub-lethal stressors, including reduced salinity and eutrophication from terrestrial run-off can lead to increased investment in physiological maintenance with concomitant effects on growth and reproduction (Fabricius, 2005; Whalan et al., 2007b).

Sponges (Phylum Porifera) are conspicuous components of aquatic environments, playing significant evolutionary and functional roles (Bell, 2008; de Goeij et al., 2013; Srivastava et al., 2010). Despite their ecological importance and an increased research focus to ascertain how they will respond to a changing climate (summarized in Bell et al., 2013), information on sponge population demographics and dynamics is limited. On the Great Barrier Reef (GBR), sponges in the family Thorectidae can represent up to 80 % of total sponge numbers and biomass (Wilkinson, 1988). Being photosynthetic, these sponges are capable of acquiring up to 50 % of their nutrition from cyanobacterial symbionts, while releasing a proportion of the captured carbon to the environment, thereby contributing to reef nutrition (Webster et al., 2012; Wilkinson, 1983, 1988). Light intensity (at different depths) is also thought to influence distribution, growth and morphology of the highly abundant Thorectidae species, *Carteriospongia foliascens* (Abdul Wahab et al., 2014c; Wilkinson and Evans, 1989).

Carteriospongia foliascens occurs on the intertidal reef flats of inshore sectors of the GBR. This species is reproductive all year round, and larvae potentially self-recruit to natal habitats based on relatively short larval competency periods, low dispersal potential and the capacity to settle to non-specific settlement cues (Abdul Wahab et al., 2014a, b). This study aims to investigate processes involved in larval production and the limitation of secondary recruitment of *C. foliascens* over 24 months, by quantifying the effects of seawater temperature, photoperiod (daylight hours) and rainfall on fecundity, recruitment, growth and mortality of intertidal populations at two bays (separated by ca. 10 km), within the Palm Islands group, central GBR. These two bays were selected based on differences in their size (4 km across for Juno Bay and 1 km across for Little Pioneer Bay) and hydrodynamic features (Bannister et al., 2007), while maintaining similar extrinsic environmental parameters (i.e. photoperiod and rainfall). To investigate the effects of substrate and asexual reproduction on growth dynamics in this species, changes in substrate composition and presence of fission were monitored. In addition, growth of *C. foliascens* juveniles from settlement through the first two years of life in aquaria was quantified to investigate early growth trajectories. Lastly, an index of larval productivity (population sexual productivity index; PoSPi) was quantified for Juno Bay over 12 months to investigate how habitat and demographics contribute to *C. foliascens* fecundity and larval production when compared to published PoSPi data for Little Pioneer Bay over the same period (Abdul Wahab et al., 2014b).

2. Materials and methods

2.1. Study sites and sampling regime

Ten permanent quadrats (1 m x 1 m) were haphazardly established on the reef flats (ca. + 50 cm from the tidal datum) of Juno Bay, Fantome Island (18°41.405'S, 146°31.272'E), central Great Barrier Reef (GBR) and Little Pioneer Bay, Orpheus Island (18°36.989'S, 146°29.832'E) where *Carteriospongia foliascens* naturally occurred in July 2011, three months before the first sampling period in October 2011 (Abdul Wahab et al., 2014c). Each quadrat consisted of 1 – 5 adult sponges at the start of the study (October 2011). Quadrats were photographed every three months over 24 months to assess changes in substrate composition, recruitment (i.e. new individuals), survival and growth in the months of January, April, July and October.

2.2. Environmental parameters

The study sites were selected based on differences in modelled wave energy data reported by Bannister et al. (2007), which showed a two-fold increase in wave height at Juno Bay (range: 0.4 m – 0.8 m) compared to Little Pioneer Bay (range: 0 m – 0.4 m). Environmental parameters relevant to the energetics and growth of phototrophic, intertidal invertebrates were measured. Sea temperatures were monitored *in situ* using temperature loggers (HOBO®) deployed adjacent to sponges at both Juno Bay and Little Pioneer Bay over the entire duration of the study. Mean monthly photoperiod was sourced from Geoscience Australia (http://www.ga.gov.au) and total monthly rainfall data from the Bureau of Meteorology (BOM, http://www.bom.gov.au).

2.3. Substrate composition, adult survival and recruitment

Photographs were assessed using the image processing and analysis program ImageJ (National Institutes of Health, USA) to quantify proportion (%) of the substrate occupied by bare sand, bare coral rubble (i.e. free of other macro-invertebrates and macroalgae), *C. foliascens*, live hard coral, live soft coral, fleshy macroalgae and other sponges. The presence or absence of new individuals and existing individuals from previous sampling events were assessed at each sampling month by meticulously screening the substrata. A gridded 1 m x 1 m portable quadrat was employed to systematically record sponge position within each permanent quadrat.

2.4. Assessment of sponge growth

2.4.1. From larval settlement to 2 years old

To maximise individual survival for the assessment of growth from larval settlement to 2 year old juveniles, *C. foliascens* parenchymella larvae were settled and grown on surfaces of a High Density Polyethylene (HDPE) raceway (length – 585.0 cm, width – 71.0 cm, depth – 54.5 cm) at Orpheus Island Research Station (Abdul Wahab et al., 2014a). Fourteen reproductive female sponges were collected from Little Pioneer Bay and Juno Bay in October 2011 and maintained in the raceway for six weeks. The raceway received flow-through 10 μm filtered seawater sourced 60 m off the reef crest, 480 m away from the research station. As *C. foliascens* trickle spawn during the day, over a duration of weeks to months (releasing up to ca. 800 larvae sponge^{-1} day^{-1}), and larvae are negatively phototactic and settle non-specifically to surfaces within hours from release, larvae were expected to settle unassisted to the walls and floor of the raceway (Abdul Wahab et al., 2014a). Adult sponges were removed from the raceway after six weeks. The raceway received minimal maintenance (i.e. cleaning) and received constant water flow (ca. 1440 l h^{-1}) and water exchange (ca. 63% volume h^{-1}) over the two years growth period to maintain food supply and ambient water temperature. Daylight intensity within the raceway and in the field (adjacent to adult sponges) were logged using portable light loggers (HOBO®) to compare artificial and natural light conditions *in situ*. To observe early morphological development of *C. foliascens* recruits (within a week), additional larvae ($n \approx 50$) were settled onto 100 mm sterile Petri dishes to aid visualization under a dissecting microscope. Petri dishes were maintained in the same experimental raceway described previously for a week.

Two year old *C. foliascens* juveniles possessing both fan and cup morphologies were haphazardly scraped off the walls and floors of the raceway using a scalpel blade, and preserved immediately in 4% phosphate buffered formaldehyde. Volume (mm^3) of *C. foliascens* juveniles ($n = 32$) was quantified using water displacement in a 100 ml graduated cylinder. Distilled water, maintained at 22.25 °C, was used for all volume