ABSTRACT: The population ecology of the tropical bêche-de-mer sea cucumber *Stichopus herrmanni* (curryfish) was investigated on One Tree Reef, a no-take protected area in the Great Barrier Reef Marine Park. The size class frequency and density of this species at several sites were determined over 2 years: 2009 and 2011. There was a spatial separation of populations that differed in size and density, but these parameters did not change over the 2 yr of the study, indicating stable population metrics. The spatially heterogeneous population pattern has relevance for fisheries management, as current size limits protect animals with low fecundity that occur in shallow habitat, but make it legal to remove 85% of large, fecund animals in deeper areas. Data for 4 *S. herrmanni* populations were used to address 2 theories on the potential drivers of population structure: (1) adult migration and (2) phenotypic plasticity in growth with respect to habitat conditions. While connectivity through adult migration appears possible, the size structure and location of some populations indicate that population features are determined by post-recruitment growth in the habitat. The latter likely plays a major role in population dynamics and terminal growth of *S. herrmanni*. There was no day-night difference in density at fixed transects, indicating that data obtained in daytime surveys was representative. A frequency distribution profile of density data from manta tows is presented as an alternative to using mean density as an assessment indicator in sea cucumber fisheries. *S. herrmanni* showed a noticeable affinity for reef features, an important finding for improved resolution of spatial planning in management.

KEY WORDS: Sea cucumber · Bêche-de-mer · Echinoderms · Population ecology · Fisheries management · Coral reefs

INTRODUCTION

How populations of benthic marine invertebrates are distributed, interact and change over time and space are related to complex ecological processes (Cowen & Sponaugle 2009, Uthicke et al. 2009). Identification of protected areas and spatial planning in management is made difficult by the lack of understanding of these processes (Andrew & Mapstone 1987, Nagelkerken et al. 2000, Sale et al. 2005, Orensanz et al. 2005, Crowder & Norse 2008, Purcell 2010). Very little is known about the temporal dynamics of adult sea cucumber populations and how these dynamics are related to spatial distribution. That the ‘supply-side’ of holothuroid ecology is so poorly studied undermines the understanding of regulation of adult populations (Grosberg & Levitan 1992), spatial links and habitat connectivity (e.g.
Nagelkerken et al. 2000) and associated relationships in population dynamics (Gillanders et al. 2003). Thus it is difficult to apply an ecosystems approach (i.e. Purcell 2010) to a broader context of fisheries management (Berkes 2011). Mapping population metrics along spatial and temporal scales, as undertaken here with *Stichopus herrmanni*, increases our understanding of population dynamics of commercial species and assists in assessing their distribution patterns and ability to persist in response to harvest pressures.

Aspidochirotid sea cucumbers are ubiquitous and conspicuous components of coral reef ecosystems, and despite an increase in research attention due to their importance as a fishery resource for production of bêche-de-mer (dried body wall) for Chinese consumers, their ecology is poorly understood (Purcell et al. in press). These holothurians have been called the ‘vacuum cleaners’ of the reef (Samyn & Tallon 2005), capturing their importance in the food web as epibenthic feeders that function in the nutrient regeneration pathway (Uthicke 2001). They have an ecological role in promoting growth of seagrass and sediment microalgae, predominantly through their nitrogenous waste compounds (Uthicke 2001, Wolkenhauer et al. 2010). Common coral reef aspidochirotids ingest enormous quantities of sand, playing a key role in bioturbation and turnover of sediments (Uthicke 1999, Mangion et al. 2004). The carbonate sand that they ingest is partially dissolved in the gut and the faecal casts that they deposit increase ambient alkalinity, potentially enhancing calcification in corals and providing a buffer against the negative effects of ocean acidification (Schneider et al. 2011).

Sea cucumbers are particularly vulnerable to overfishing due to their ease of collection, simple low-cost processing methods and high commercial value (Conand & Byrne 1993, Friedman et al. 2011, Purcell et al. 2011). Evidence from surveys and fisheries landings indicate that recovery of sea cucumber populations post-harvest can take decades, depending on Allee effects (e.g. low spawner density) and other variables that are not understood (Friedman et al. 2011). Aspidochirotids have a larval phase of weeks to months (Smiley 1986, Hu et al. 2010). Seagrass habitat is an important recruitment site and adult habitat for sandfish *Holtthuria scabra* (Mercier et al. 2000). In some areas, curryfish and teatfish species (e.g. *H. whitmaei, H. fuscosilva*) recruit into shallow soft sediment and seagrass habitats, followed by ontogenetic migration into deeper water (Conand 1993, Reichenbach 1999, Byrne et al. 2004, Shiell 2004). In other reef areas where seagrass is not present, coralline algae and associated bacterial films are likely to provide suitable habitats for larval settlement (Keesing et al. 1993, Mercier et al. 2000). These and other cryptic habitats are known to be important substrates for settlement and metamorphosis for echinoderm larvae (Johnson et al. 1991, Swanson et al. 2012), with subsequent growth and migration to the adult habitat. For other echinoderms there is little or no post-settlement cross-habitat migration; instead, population demography (e.g. maximum adult size) depends on environmental parameters (e.g. food and hydrodynamics) (Levitan 1989, Edwards & Ebert 1991, Byrne et al. 1998, Ebert et al. 1999).

Sea cucumbers are commercially harvested on the Great Barrier Reef (GBR), Australia, by the East Coast bêche-de-mer fishery (ECBDMF) (DEEDI 2010). This fishery is managed under a rotational zoning scheme (DEEDI 2011), although a substantial portion of the catch (~70%) is not managed by this scheme (SEWPaC 2011). The ECBDMF is a multi-species fishery that includes 19 species for which there are few or no baseline ecological data (DEEDI 2010). The curryfish *Stichopus herrmanni* (formerly known as *Stichopus variegatus*) is a key species in the fishery. This species is usually listed as a low to medium value species, but due to improvement in processing, *S. herrmanni* has recently become an important target species in the ECBDMF (Roelofs 2004, DEEDI 2010). *S. herrmanni* is harvested under the commercial ‘curryfish’ group (DEEDI 2011), which is also the common name for the cryptic species complex including *S. occelatus* and *S. vastus* (Byrne et al. 2010). Between 2006 and 2009 a total of 136 000 individual *S. herrmanni* were harvested in the fishery (DEEDI 2011), roughly equivalent to 150 t of gutted weight (using the per piece gutted weight of 1.14 kg reported by Roelofs 2004).

*Stichopus herrmanni* is an abundant tropical Pacific species inhabiting sandy sediments, fragmented coral structures, coral rubble habitat, and seagrass beds between depths of 0 and 30 m (Conand 1993, Desurmont 2003). In the southern GBR *S. herrmanni* occurs in high densities in association with coral habitat (Eriksson et al. 2010a) (Fig. 1). In this study, the ecology and population dynamics of *S. herrmanni* were investigated on One Tree Reef (OTR) in the Capricorn Bunker Group in the southern GBR. Data on density and size distribution of 4 populations of *S. herrmanni* (defined as populations as their gametes are unlikely to meet due to distance and reef topography), were analysed to determine spatial trends in population metrics over time. One Tree
Reef is a platform reef located entirely within a no-take zone of the GBR Marine Park (GBRMP). For decades this reef system has been a ‘Scientific Research Zone’ and has thus been protected from fishing. It is the only reef system in the GBRMP where the entire reef system has full protection. This reef has supported high density populations of *S. herrmanni* (i.e. Eriksson et al. 2010a) for decades, providing an ideal situation to investigate population dynamics and habitat utilization of this species on an unfished reef. This study therefore provides baseline population profiles as reference for nearby areas in the Capricorn Bunker Group where the fishery is operating. The data generated for *S. herrmanni* were used to address 2 theories as to the potential drivers of population size class structure: (1) adult migration and (2) phenotypic plasticity in growth with respect to habitat conditions.

**MATERIALS AND METHODS**

**Study site**

Populations of *Stichopus herrmanni* were studied at 4 sites at OTR (23° 30’ S, 152° 05’ E) from May 2009 to May 2011 (Fig. 2, Table 1). The reef contains One Tree Reef.
Tree Island (OTI), a small coral cay of 4 ha in the southeastern corner. The reef is situated 20 km from the continental shelf edge, 70 km from the Queensland coast, and is surrounded by water ~60 m deep (Marshall & Davies 1982). It consists of a coralline algal rim, coral flat, sand flat and an enclosed lagoon sheltered by continuous reef.

The survey area, 'Shark Alley', was divided into 2 sites representing 2 habitats (Fig. 2, Table 1). Site A was shallower (0.4 to 1.5 m) with scattered and continuous 'pie-crust' reef structures dominated by coral and crustose coralline algae interspersed with sandy substrate. Site B was deeper (1 to 5 m). This was a sand substrate adjacent to a reef wall that reaches the ocean surface. Sites A and B are ~150 m apart. Site C was just inside the reef rim (3 to 6 m depth) and was a mixture of rubble, coral and sand habitat. Surveys at Sites A to C were done by snorkel or walking in shallow water. Additional data were collected at Site D, the outside reef slope in deeper water (6 to 10 m) by SCUBA. Sites C and D are separated by the barrier reef wall that reaches the ocean surface at low tide. Sampling was carried out at each site as detailed below. All statistical analyses described here and below were performed in R version 2.9.2.

**Spatial and temporal population metrics**

Population density was determined using a targeted transect sampling technique. Transects (40 × 1 m, n = 12 per site, May 2009 and May 2011) were laid out following sand substrate between and around reef features at Site A, and similarly following the contour of the reef wall at Site B. Sampling was conducted on 2 occasions (May 2009 and May 2011). Density data from the 2 sites and within the sites over time were analysed using a 2-factor ANOVA with site (i.e. Site A or B) and time (i.e. May 2009 or May 2011) as fixed factors. The density data deviated from normal distribution, as determined by Bartlett’s test, so data were log transformed to achieve homogeneity of variance and fulfill requirements of ANOVA. The correlation of the model and the effect size (partial eta-squared) were calculated.

The length of each *Stichopus herrmanni* encountered was taken along the centerline of the animal using a flexible tape measure, without lifting or otherwise disturbing the individual. *S. herrmanni* that were stuck in reef features or otherwise deemed difficult to measure (e.g. horseshoe-shaped) were not sampled. Measurements were taken randomly while snorkeling or walking in shallow water and diving in the deeper water off the reef. To avoid sampling the same animal twice, care was taken to start at one point and then move across to a set end point. Length data were obtained at Site A on 3 occasions (May 2010, October 2010 and May 2011) and at Site B on 4 occasions (May 2009, December 2009, October 2010 and May 2011). Sites C and D were sampled on 1 occasion each, in May 2011 and Jan 2011 respectively. Sampling effort focused on the 2 Shark Alley sites, with the other sites sampled as weather conditions allowed. Length data over time and among sites were compared using a Kruskal-Wallis test.

To determine whether there was increased activity of *Stichopus herrmanni* at night, 6 transects (40 × 1 m) were fixed in the coral reef habitat at Site B. The transects were re-surveyed during 5 consecutive days and nights in December 2010. Transects were surveyed at midday and midnight regardless of tide. Each transect was set as a replicate and was tested for differences in day and night observations using Welch’s pairwise *t*-test.

**Manta tows**

The manta board technique outlined by English et al. (2003) was used to survey larger areas of the lagoon. This method is also applied to survey reef flats for other bêche-de-mer species (Uthicke & Benzie 2000, Shiel & Knott 2010), to assess habitat utilization and distribution patterns (Eriksson et al. 2012), and for more general abundance censuses of conspicuous sea cucumbers (e.g. Purcell et al. 2009). An area of 300 × 2 m was covered at walking speed (~2.5 km h⁻¹). The distance and speed was calibrated by a surveyor in the boat using a handheld GPS. A total of 24 manta tows were performed following the contour of reef features in the lagoon, consequently providing a census of 1.4 ha of benthos. Some tows unintentionally deviated from 300 m; for example, transects can be cut short if habitat rapidly changes. Therefore, the actual distance was calibrated using the logged route in the program MapSource®. Observations were extrapolated against the total calibrated area of each transect to calculate a density measure (individuals ha⁻¹). Data were plotted as a frequency distribution to determine the density profile of the reefs’ population. This measure has been suggested for capturing the spatial distribution of other sedentary/sessile invertebrates that tend to occur in spatially complex patterns (i.e. Orensanz et al. 1998). A linear model was applied to the distribu-
tion to derive correlation and slope, providing a baseline of population structure.

**Distance from reef feature**

The distribution of individuals in relation to the reef wall at Site B was mapped using 40 m transect lines. Twelve transect lines were placed in sequence perpendicular to the reef feature, and the distance from the reef wall on the transect line was noted for every animal counted within 1 m of the transect line. A linear regression model was applied to the data to describe the relationship between frequency of observations and distance from reef feature.

**RESULTS**

**Spatial and temporal population metrics**

Density of *Stichopus herrmanni* in Shark Alley was significantly influenced by site ($F_{1,1} = 59.22, p < 0.001$) but not by year ($F_{1,1} = 0.46, p = 0.499$), and there was no interaction between these factors ($F_{1,1} = 0.01, p = 0.998$) (Table 2). The model had a good correlation ($R^2 = 0.58$). The mean ± SE density over the 2 yr was $0.18 \pm 0.03$ ind. m$^{-2}$ at Site B and $0.03 \pm 0.01$ ind. m$^{-2}$ at Site A, illustrating that Site B had considerably higher density of *S. herrmanni* than Site A throughout the 2 yr, and that the density within these populations remained stable between the 2 sampling occasions (Fig. 3).

Length distribution was unimodal at all sites. *Stichopus herrmanni* were larger at Site B (mean ± SD = 346 ± 49 mm, n = 796) than at Site A (272 ± 38 mm, n = 173) ($H = 480.74, df = 160, p < 0.001$). However, there was no change in length over time at Site A ($H = 0.40, df = 2, p = 0.818$) or at Site B ($H = 5.87, df = 3, p = 0.118$). Thus, the size frequency distribution within these populations remained stable between the 2 sampling occasions. There was no increase in size over time in either of the sampled populations (Fig. 4a). The smallest individual encountered was 110 mm long, found at Site A. This indicates that juveniles were not evident in the populations, or else were too cryptic to locate.

The animals on the inside of the reef rim at Site C were shorter (mean ± SD = 365 ± 46 mm, n = 201) than those measured on the outside reef slope at Site D (397 ± 59 mm, n = 39) ($H = 11.84, df = 1, p < 0.001$) (Fig. 4b).

Pairwise comparisons of the fixed transects showed that there was no difference in day and night observations of *Stichopus herrmanni* ($p = 0.23$ to $0.67$), indicating that there was no nocturnal increase in activity (Fig. 5).

**Manta tows**

The mean ± SE density of *Stichopus herrmanni* within the lagoon was $172 \pm 51$ ind. ha$^{-1}$. *S. herrmanni* were widespread, with occurrence observed in 21 of the 24 transects (84.5%). Density records in transects varied (Fig. 6) and the relationship between frequency of observations and density was

<table>
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<tr>
<th>Source of variation</th>
<th>df</th>
<th>MS</th>
<th>$F$</th>
<th>$p$</th>
<th>Partial eta-squared</th>
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<td>Site</td>
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<td>19.72</td>
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<tr>
<td>Year</td>
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<td>0.15</td>
<td>0.46</td>
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</tr>
<tr>
<td>Site × year</td>
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<td>0.991</td>
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better explained by a second order polynomial model \( (R^2 = 0.72, F_{2,20} = 25.44, p < 0.001) \) than a linear model \( (R^2 = 0.38, F_{1,21} = 12.86, p = 0.002) \), indicating a fairly homogenous distribution with some occasional very dense aggregates. While most transects had less than 100 ind. ha\(^{-1}\), 25% of the records were higher than 200 ind. ha\(^{-1}\) and one was over 1100 ind. ha\(^{-1}\).

Almost 80% of individuals located were within 10 m of the reef wall, illustrating that *Stichopus herrmanni* exhibited a strong skewed distribution with a higher density of individuals near a reef feature (Fig. 7). A second order polynomial relationship \( (R^2 = 0.92, F_{2,5} = 25.85, p = 0.002) \) was a better fit for the data than a linear one \( (R^2 = 0.66, F_{1,6} = 11.87, p = \)
ties could intuitively support a theory of ontogenetic
mals with different sizes occurring at different densi-
growth plateauing at larger sizes as a response to
sub-adults have rapid growth to adulthood, with
are unknown, but it is possible that juveniles and
situ the juvenile stage. The growth rates of juveniles
mented as ‘considerable’ (sensu Hu et al. 2010)
tively stable over time. Growth rates of similar spe-
from the unfished OTR system suggest that
rather than adult migration, these populations may
be characterized by local recruitment, and the
growth trajectory post-settlement may depend on
habitat features. This pattern is well demonstrated
for sea urchins where post-settlement growth is de-
termined by habitat hydrodynamics and food avail-
ability (Ebert et al. 1999). Interestingly, for Holothu-
atra, Lee et al. (2008) noted a striking plasticity
in growth, with a 300% increase in body size follow-
in growth, with a 300% increase in body size follow-
creasing translocation to areas with high food content and
lower competition. Thus for H. atra, and perhaps also
S. herrmanni, individuals and populations may reach
a growth plateau to match habitat carrying capacity
with regard to density and adult modal size. Based on
our findings, it seems that S. herrmanni recruit into
unidentified settlement substrates within the reef
matrix and then migrate to adjacent sand habitats.
We suggest that while adult migration may occur at a
mesoscale as a response to habitat properties (e.g.
food content), recruitment processes (e.g. larval sup-
ply or presence of suitable settlement substrate), and
the carrying capacity of habitats are the main drivers
of the observed patterns.

Population structure complexity and the curryfish
size limit in ECBDMF

Despite the statement that ‘full exploitation of cur-
ryfish will not be permitted however until sustainable
yield estimates can be developed through scientifi-
cally rigorous resource assessments’ (DEEDI 2010),
this is the first study of Stichopus herrmanni on the
GBR, and ~150 t of S. herrmanni has already been
extracted since 2006. The ECBDMF currently has a
minimum size restriction of 35 cm for S. herrmanni
(DEEDI 2011). This size limit is compliant with the best knowledge of size at sexual maturity of this species from populations in New Caledonia, where Conand (1993) studied this species in detail, but it is not hinged on the size distribution of animals in harvested populations. The set size limit would make it legal to remove 2% of the population at Site A, 53% of the population at Site B and 85% of the population on the reef slope at Site D. So while smaller individuals in shallower habitats may be protected, populations of larger, fecund S. herrmanni in deeper habitats may be nearly entirely removed. Conand (1993) found a relative fecundity of 9000 oocytes g⁻¹ drained weight, suggesting that reproductive output increases with size. Whether this is a linear relationship is not clear, and a study on the relationship between size and reproductive output of this species is needed to better assess the impact of removing the larger individuals.

The spatial separation of populations of Stichopus herrmanni characterized by different densities and mean lengths, as found here, coupled with difficulty in understanding how they are connected and how their physiological traits and growth trajectories are related to habitat, are barriers to gauging whether the use of a size limit is a suitable management tool for this species. For reference, based on a slow growth rate, Uthicke et al. (2004) argued that removal of more than 5% of the virgin stock of Holothuria whitmaei would be considered overfishing. This indicates that even though we believe that S. herrmanni is a faster growing species than H. whitmaei (based on aquaculture research, Hu et al. 2010), the current legal harvest is very likely inappropriate.

**Resource appraisals and target species ecology**

Our findings illustrate the importance of ecologically relevant spatial definition of stocks for assessment and management. In resource appraisals, population density of commercial sea cucumbers is commonly presented and analyzed using mean density, with limited reference to spatial scales of populations (e.g. Purcell et al. 2009, Eriksson et al. 2010b). As illustrated here by sampling with manta tows, the use of mean density as a measure over the spatial scale of OTR would potentially simplify a markedly heterogeneous spatial distribution and mask local variation in population structure, as has been shown in appraisals of shellfish (Orensanz et al. 1998). Thus, a population density profile may be better suited to improving resolution in analysis of appraisal data. For example, it is likely that fishing would target the denser patches of Stichopus herrmanni first, which would be immediately visible in the histogram and interquartile range of the population density profile. Future studies should focus on the sensitivity and applicability of this measure in sea cucumber fisheries in order to improve resolution in analysis and sensitivity to change compared to commonly used indicators such as mean density.

We included an investigation of day and night activity of Stichopus herrmanni, because some members of the curryfish group are nocturnal (e.g. *S. monotuberculatus* and *S. horrens*) (Byrne et al. 2010). This was required to establish that surveys of *S. herrmanni* during the day would not bias our study. For other species that have cryptic behavior (e.g. nocturnal or burying), appraisal methodology must relate to the ecology of the species. For example, manta tow is only suitable for conspicuous species in shallow habitat (Eriksson et al. 2012).

**Habitat utilization and spatial planning in management**

*Stichopus herrmanni* at OTR exhibited an affinity to reef features, similar to *Holothuria whitmaei* on Ningaloo reef (Shiell & Knott 2008), indicating that sand areas adjacent to coral and coral rubble features are key habitat variables for predicting the distribution of this species. Fishing zones for bêche-de-mer species in Queensland are currently not dependent on habitat parameters (DEEDI 2011); consequently, the potential abundance or productivity capacity of the fishing zones is not considered. This is a barrier to analyzing the spatial organization of the fishery, interpreting catch from zones and developing relevant quotas. The reference trigger, which is set at 50 t per year, has not been exceeded for this species in the ECBDMF (DEEDI 2009, 2010). However, because no baseline studies exist, the relationship between the available stock and harvestable habitats is unclear. A definition of fishing area in relation to suitable habitat for *S. herrmanni* and other target species is needed to support ecologically relevant catch and effort analysis from zones in the GBR fishery. With evidence emerging that this coral-associated sea cucumber provides significant levels of nutrients to support productivity and contributes to reef resilience (Schneider et al. 2011), the GBR bêche-de-mer fishery requires further assessment to gauge its impact and sustainability.
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