Movement and growth of the coral reef holothuroids *Bohadschia argus* and *Thelenota ananas*

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ABSTRACT: Tropical sea cucumbers are among the largest mobile invertebrates on coral reefs and are widely regarded as sedentary. Mark-recapture methods provide empirical estimates of movement and growth but have often been unsuccessful with sea cucumbers. We applied a new photographic mark-recapture technique to measure rates of short-term displacement (over a few days), long-term displacement (over 2 yr) and growth of *Bohadschia argus* and *Thelenota ananas* on the Great Barrier Reef, Australia. Recapture rates were 50–100% in the short-term study and 50–77% in the long-term study. In the short-term studies in 2010 and 2012, average movement rates ranged 2–8 m d^{-1} for *B. argus* and 5–9 m d^{-1} for *T. ananas*. Long-term movement averaged 15–47 m over 2 yr, with some individuals displacing less than 5 m and several others moving more than 100 m. Our study shows that some tropical sea cucumbers can be highly mobile, and many appear to display home ranging. Growth rates were positive yet modest for smaller individuals, but many of the large individuals lost weight over the 2 yr study. Classical growth models indicated that *B. argus* attain an average maximum size in 15–20 yr, and the empirical data on growth show that they can lose or gain weight thereafter. Hence, longevity appears to be at least several decades. The 2 species are slow growing, and the negative growth in large individuals undermines previous estimates of growth and longevity based on size-frequency data.

KEY WORDS: Sea cucumber · Displacement · Behaviour · Echinoderm · Photographic identification · Mark-recapture · Marine invertebrate

INTRODUCTION

Movement and displacement of marine animals

Studies on movement of marine animals form a basis for understanding life-history processes, population dynamics, and the likely success of conservation and resource management strategies (Chapman & Kramer 2000, Pittman & McAlpine 2003, Grüss et al. 2011). Mobility provides animals with opportunities for foraging, finding mates for reproduction and accessing new areas for shelter and colonisation. On the other hand, high mobility of animals will increase their chance of spillover from within marine reserves to adjacent fishing grounds, where they can be harvested (Sale et al. 2005, Grüss et al. 2011), and diminishes the effectiveness of restoration strategies for reef invertebrates such as broodstock aggregation (Bell et al. 2008).

Both mark-recapture and tracking approaches have been used to assess movement rates in coral reef invertebrates, and some groups have remained relatively unstudied due to constraints of tagging or identification of individuals. Movement rates of marine animals are known to vary according to factors including the species, site, sex (Quinn & Brodeur 1991, O'Malley & Walsh 2013), body size and season (Hesse 1979). Movement rates can be just 1–2 m d^{-1}

for relatively sedentary coral reef invertebrates such as certain holothuroids (Conand 1989, Graham & Battaglene 2004), echinoids (Hammond 1982, Stimson et al. 2007) and gastropods (Clarke & Komatsu 2001). Other coral reef invertebrates, such as queen conch, are highly mobile, displacing several hundred metres, or more, per year (Hesse 1979). Similarly, spiny lobster and slipper lobster mostly displace on average 0.1–1 km yr^{-1} (O'Malley & Walsh 2013).

Growth of echinoderms and sea cucumbers

Growth estimates are essential to stock assessment models (e.g. Punt et al. 2013) and are one of a suite of life-history parameters used to predict a stock's response to fishing (Winemiller & Rose 1992, King & McFarlane 2003, Plagányi et al. 2015). Mark-recapture methods are well documented for sea urchins, albeit with some sources of error in measurement of growth (Rogers-Bennett et al. 2003, Ebert 2013). Conversely, mark-recapture studies on holothuroids are notoriously difficult because their extensible bodies make length alone an unreliable measure of size (Ebert 1978, Uthicke & Benzie 2002, Purcell et al. 2009), and the classical tagging methods have variable or poor success. Tags that involve piercing the body wall can adversely affect growth of holothuroids (Conand 1991), and individuals often shed physical tags quickly (Conand 1991, Purcell et al. 2006, 2008, Cieciel et al. 2009, Rodríguez-Barreras et al. 2014). Marks scratched on the body wall of holothuroids induce short-term trauma and do not last long enough for growth studies (Shiell 2006). Photographs have been used as a tool for examining short-term movements of some holothuroids that are externally identifiable (Raj 1998, Purcell & Eriksson 2015) and could be a valuable non-invasive tool for studies of growth.

Numerous growth models have been fitted to echinoderm growth data (see Ebert 2013 for a review), and classical models developed for finfish may inadequately describe growth over the animal's life (Rogers-Bennett et al. 2003, Flores et al. 2010). Echinoderms typically display considerable individual variation in growth, preventing unambiguous selection of a single model (Rogers-Bennett et al. 2003). The most appropriate growth model for a given dataset will probably depend on the number of observations and coverage of critical growth periods (Rogers-Bennett et al. 2003, Ebert 2013).

Growth rates of holothuroids under natural conditions in the wild have sometimes been estimated indirectly through modal progression analysis (Shelley 1985, Conand 1988) or models using size-frequency data (Herrero-Pérezrul et al. 1999, Poot-Salazar et al. 2014). However, this approach can be undermined for populations consisting mostly of adults and consequently exhibiting stable modal and mean sizes over time (Uthicke et al. 2004). Nonetheless, this indirect method of modal progression analysis indicated that smaller holothuroid species probably have much faster growth to a maximum adult size than large holothuroid species (Conand 1988). Two of the few studies to empirically estimate growth in tropical sea cucumbers were on the coral reef-dwelling black teatfish *Holothuria nobilis* (now *whitmaei*, in the Pacific and Southeast Asia) using genetic fingerprinting for mark-recapture (Uthicke & Benzie 2002, Uthicke et al. 2004). In those studies, very large individuals did not grow at all or shrank in size over the observation periods. There have been no further estimates of sea cucumber growth based on empirical data from mark-recapture studies.

Sea cucumbers on coral reefs

Sea cucumbers are one of the largest mobile coral reef invertebrates, with the widely distributed *Thelenota ananas* and *T. anax* reaching >60 cm in length and >4 kg in weight (Conand 1989, Purcell et al. 2012b). They play important roles in coral reef ecosystems by bioturbating sediments, recycling nutrients, acting as hosts for symbiotic biota and prey to a range of predators, and potentially buffering seawater from ocean acidification at local scales (Purcell et al. in press). They are fished either for export or subsistence consumption in almost all countries in the tropical Indo-Pacific and Caribbean (Toral-Granda et al. 2008), and 11 tropical species are currently threatened with extinction as a result of overfishing (Conand et al. 2014, Purcell et al. 2014).

Information on the biology and ecology of sea cucumbers is crucial for developing regulations for fisheries management and conservation (Purcell 2010). For example, growth and/or mortality rates are used in stock assessment models to derive catch quotas for harvests (Aumeeruddy et al. 2005, Plagányi et al. 2015). Movement rates are integral to planning the effective sizes of marine reserves (Purcell & Kirby 2006). Such data can also indicate a predisposition to demographic Allee effects through the encounter rates of potential mates at low population densities (e.g. Stoner & Ray-Culp 2000).

Tropical sea cucumbers have often been regarded as sedentary creatures (Conand & Byrne 1993, Bruck-

ner et al. 2003, Purcell 2010, Eriksson & Byrne 2015), giving an impression that they are sluggish and displace only short distances. The ecology of holothuroids varies greatly among species, and certainly some species are quite sedentary (Purcell et al. 2012b). Movement studies on tropical holothuroids have generally followed individuals at short intervals for periods of 1 d or less (Hammond 1982, Graham & Battaglene 2004, Purcell & Kirby 2006, Purcell & Eriksson 2015). A long-term movement study of *Actinopyga echinites* and *A. mauritiana* using external T-bar tags found that many individuals moved less than 10 m over 1 yr, although searches did not go far beyond the release sites and the tagging stressed the animals (Conand 1991). By scratching numbers on the outer body wall of *H. whitmaei*, Shiell & Knott (2010) found slow movement rates of 1.6 to 4.4 m d^{-1} and multiplied those rates by the number of days in a year to equate to a total potential distance covered annually.

Study aims

In the present study, we examined the movement and growth of *Bohadschia argus* (Holothuriidae) and *T. ananas* (Stichopodidae) at 2 coral reef sites at Lizard Island in the northern part of the Great Barrier Reef, Australia, using a new photographic mark-recapture technique. These 2 species are conspicuous and diurnally active, and both have external features that could potentially distinguish individuals over time. Both species are large compared to most

tropical holothuroids, and *B. argus* and *T. ananas* are important to fisheries catches in the central-western Pacific and Indo-Pacific, respectively (Purcell et al. 2012b). We aimed to photographically mark individuals of both species at 2 sites and relocate the animals after a few days to examine short-term movements and to relocate some after 2 yr to examine long-term movement and growth. The study provides empirical estimates of movement and growth of the 2 species, which are the first reported for *B. argus*.

MATERIALS AND METHODS

Study sites

The movement and growth studies were conducted at 2 semi-sheltered coral reef sites at Lizard Island in the northern part of the Great Barrier Reef, Australia (Fig. 1), which is within a no-take marine reserve. The sites were chosen on the basis of accessibility in variable sea conditions and reasonable abundances of the 2 study species. The Palfrey Lagoon site is a relatively shallow, semi-sheltered reef lagoon with soft sediments, patches of coral rubble and hard reef with branching corals. At this site, *Bohadschia argus* and *Thelenota ananas* were found mostly on coral rubble and sand or on the sandy reef flat. Mermaid Cove is sheltered from the dominant southeast trade winds, and the reef slopes descend to a sandy reef base at 6–8 m depth. At that site, most of the *B. argus* were found on the reef slope, whereas *T. ananas* were found on both the slope and sandy base of the reef.

Average seawater temperature (which might affect rates of movement and feeding) at the sites during the day was 27°C in 2010 and 26°C in 2012. Sea conditions during the field work in both years were moderately choppy. At both sites, we affixed several permanent markers, comprising stainless steel bolts with short cords and numbered sub-surface buoys, to the reef structure. Geographic waypoints of the markers were taken with a handheld GPS.

Location of animals and initial marking and photographs

The first study of short-term displacements was done from 27 to 31 October 2010, and the second was done from 9 to 14 October 2012. The studies of long-term displacements and growth examined changes over that 2 yr period. In both short-term studies, we searched soft-bottom and hard-bottom areas at both
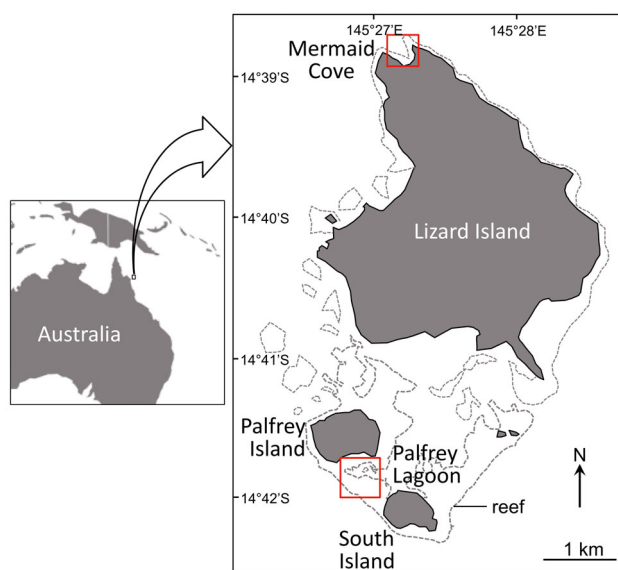

Fig. 1. Lizard Island showing locations of the 2 study sites, Mermaid Cove and Palfrey Lagoon (red squares)

sites for individuals of either species. Any individual encountered was photographed with a digital camera at the anterior end *in situ*. Body length and width (at centre of body) of the animals were measured to ±0.5 cm *in situ* with a ruler above the animals without touching them. Measurements of *T. ananas* excluded the papillae protruding from their body wall. We recorded time at each measurement and measured the water depth at each animal with an electronic depth gauge, which was later standardised to zero tidal datum using tide data. We then measured the distance of the animal to 1 or 2 nearest permanent markers to the nearest 1 cm with a measuring tape, and the bearing with a compass. Measuring to 2 markers allowed more options for later calculating displacements to a common marker.

For the purpose of a separate study (S. W. Purcell et al. unpubl. data), half of the *B. argus* and all of the *T. ananas* at both sites were injected *in situ* with a fluorochrome solution after initial measurements to the permanent markers. The injection was made through the dorsal body wall, animals were not moved or lifted from the substratum for the procedure and none of the animals eviscerated.

Relocation of animals

To verify that the *B. argus* retains its colour patterns, 2 specimens were photographed *in situ* and were then captured and held in flow-through aquaria at the Lizard Island Research Station with other reef organisms. One year later, the animals were released into the wild (not the study sites) and re-photographed (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m551p201_supp.pdf).

In both 2010 and 2012, we returned to the sites 1 to 5 d after initial marking of the sea cucumbers and repeated the photographing, measurement and geographic positioning (in relation to permanent markers) of individuals of the 2 species. For these follow-up searches, a broader area (by ~10 m in every direction) was searched around the initial core area where animals were first photographed in an attempt to find and re-photograph all of the photographed animals. Thus, more individuals were photographed in the follow-up searches than were initially photographed.

In 2012, we also conducted extensive broad searches for the 2 species on snorkel of the surrounding reef habitat to a distance of up to 360 m. All encountered individuals were photographed and measured, as described, and their geographic positions marked with a handheld GPS. Waterproof sheets

with photographs of the originally photographed animals were used underwater to help relocate previously photographed animals; nonetheless, we later rechecked the electronic versions of all photographs twice for matches.

Electronic versions of the initial photographs of the sea cucumbers were matched visually with recapture photographs. Sea cucumber bodies are highly flexible, and even the anterior ends that we photographed could be contorted to varying degrees, obviating the use of facial recognition software to match the photos. We relied on the unique spotting patterns in *B. argus* (Fig. S2 in the Supplement) and the orientations of papillae in *T. ananas* (Fig. S3 in the Supplement). Only completely certain matches were used. We did this by matching the orientations of at least 10 spots in *B. argus* or 10 papillae in *T. ananas*, which gives a confidence of identification of at least 99.8 % (i.e. misidentification rate = 0.5^9).

At the end of study in 2012, the lengths and widths of the sea cucumbers within the core study sites were re-measured *in situ*, as described, and they were removed from the water. After a draining period of 5 min on the deck of a boat, to expel a majority of the seawater from their bodies (see Skewes et al. 2004), the animals were weighed to ±5 g using an electronic balance and then returned to the sea. Basal area of each animal was later calculated using the formula of an ellipse.

Estimation of growth

Growth was estimated only for individuals re-identified in 2012, comprising 59 % of initially photographed individuals in 2010. *In situ* measurements of body length and width and *ex situ* measurement of body weight were used to construct non-linear relationships between length or basal surface area and body weight for both species, pooling data between sites (see 'Statistical analyses') (Fig. 2). Where individuals were weighed directly, we used those weights for analyses. Weights of sea cucumbers in 2010, and weights of animals not weighed empirically, were estimated using the fitted equations based on basal area of the animals.

Calculation of movement rates

Data on distances and bearings to common permanent markers allowed the determination of short-term movement rates (explained below) of animals
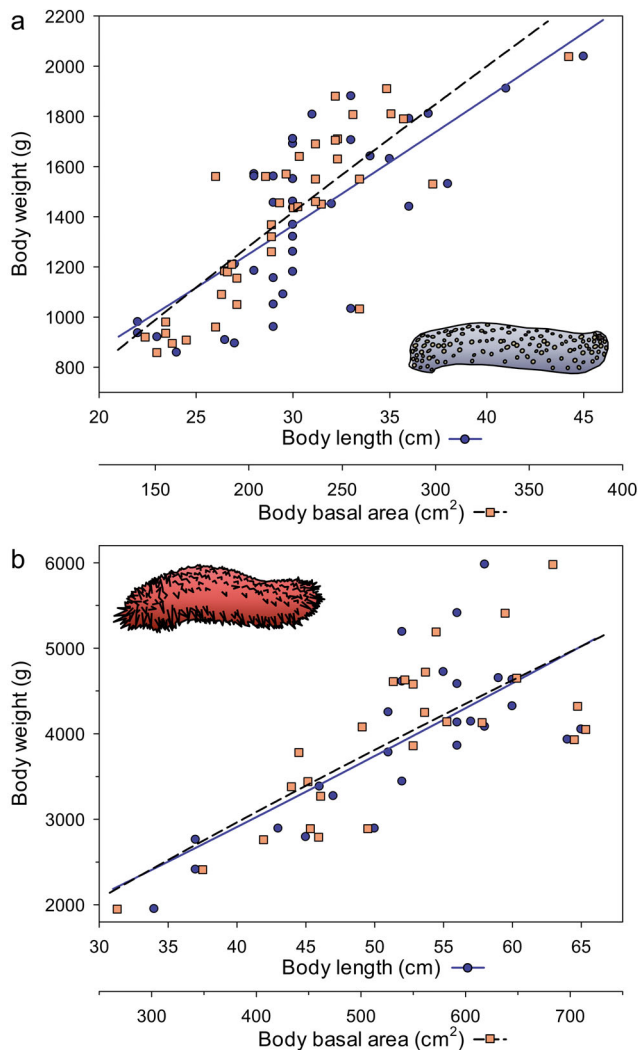
Fig. 2. Non-linear relationships between body length (blue dots and solid blue lines; upper *x*-axes) or body basal area (orange squares and dashed black lines; lower *x*-axes) and body weight (g) for (a) *Bohadschia argus* and (b) *Thelenota ananas*. Relationships are based on the standard growth function ($y = ax^b$) for both data sets for both species. The best fit for both species was with body basal area. *B. argus*: weight = $10.775 \times$ basal area$^{0.902}$; *T. ananas*: weight = $19.161 \times$ basal area$^{0.848}$; weight (in g) and basal area (in cm^2) are based on the equation of an ellipse

using the law of cosines (Appendix). Movement distances were converted to rates by dividing by the number of days, and fraction thereof, between initial photographs and photographs at time of relocation.

For long-term movement, we used 2 methods to calculate distances displaced. If relocated animals were within the study areas in 2012 and measured to a same marker as in 2010, movement was estimated as described. Otherwise, movement was estimated by georeferencing the starting (2010) positions in Google

Earth and measuring distance to waypoints of relocated animals marked by GPS, or georeferenced positions from alternate permanent markers, in 2012.

Statistical analyses

Using DataFit-9 software, relationships based on the standard growth function ($y = ax^b$) were determined for both species for (1) length vs. weight and (2) basal area vs. weight. Data were pooled between sites for both *B. argus* (n = 39) and *T. ananas* (n = 26) to provide general models for conversions of basal area (from measurements of length and width) to estimated weight. The relationships between weight and depth of occurrence for both species were tested using linear regression.

A 2-way ANOVA first tested whether injections of fluorochromes affected short-term displacements of *B. argus*. Site and fluorochrome injection were fixed factors, and depth and estimated body weight were covariates. That analysis indicated no significant effect of the injections on movement rates ($F_{1,20} = 0.745$, p = 0.40), so data on injected and non-injected animals were pooled for subsequent tests. Two-way ANOVAs tested the difference in short-term (per day) displacements (square root transformed) between sites and years (both fixed factors) for species separately, with depth of first sighting and estimated body weight as covariates. Levene's test verified homogeneity of variances.

Long-term displacements clearly differed between species, and formal tests of those differences were unnecessary. The relationships between the long-term displacements and depth of initial occurrence in 2010 for both species were tested with linear regression. Multiple linear regression was used to test the relationships between the relative weight gain of individuals (proportion of initial body weight) and their initial (estimated) body weight, depth at first sighting and site.

Recapture data for *T. ananas* lacked replication (n = 8) for modelling growth, so we provide descriptive results for that species. Growth of *B. argus* over the 2 yr study was modelled using the generalised von Bertalanffy, Gompertz and logistic growth functions. A generalized version of the von Bertalanffy model with a power transformation is the Richards function, and the weight at age *t* can then be modelled as:

$$W_t = W_\infty \left[1 - b \cdot \exp(-kt) \right] \qquad (1)$$

where *W* is the weight of the animals, *k* is the rate constant and *d* is the power parameter. When the

time at liberty (T) is a constant (2 yr in our case), $K =$ $\exp(-kT)$ also becomes a constant. Growth rate becomes zero when body weight achieves W_∞. The power-transformed weight, $(Wt)^{1/d}$, follows the von Bertalanffy curve if the power parameter d is known. Suppose W_1 is the initial body weight and W_2 is the weight at recapture. According to the well-known Faben's equation, we have:

$$W_2^{1/d} - W_1^{1/d} = \left(W_\infty^{1/d} - W_1^{1/d}\right)\left(1 - e^{-kT}\right) \quad (2)$$

Rewriting the equation gives:

$$W_2 - W_1 = -W_1 + \left[W_1^{1/d} + \left(W_\infty^{1/d} - W_1^{1/d}\right)\left(1 - e^{-kT}\right)^d \right] \quad (3)$$

Values of d of 1, −1 or infinity produce the von Bertalanffy, logistic or Gompertz models, respectively. Therefore, we estimated W_∞ (average maximum weight) and k separately using each of the 3 models.

For the Gompertz model ($d = \infty$), we can write the limiting case as:

$$W_2 - W_1 = -W_1 + W_\infty \left(W_1 / W_\infty\right)^{\exp(-kT)} \quad (4)$$

Francis' (1995) model reparameterised the traditional growth parameters to be more biologically meaningful with respect to growth and has been applied to another tropical holothuroid (Uthicke & Benzie 2002, Uthicke et al. 2004). The parameters (W_∞, k) can be re-expressed as g_1 and g_2 in the non-linear regression to obtain the estimates of growth rates at user-specified body sizes, y_1 and y_2, near the lower and upper ends of the data range (Francis 1995). Here, 1000 and 1800 g were specified as the initial body weights y_1 and y_2. The equations to estimate growth rates at those 2 body weights are:

$$g_1 = -y_1 + \left[y_1^{1/d}D + W_\infty^{1/d}(1-D) \right]^d \quad (5)$$

$$g_2 = -y_2 + \left[y_2^{1/d}D + W_\infty^{1/d}(1-D) \right]^d \quad (6)$$

in which $D = e^{-k}$. Vice versa, we can also obtain $W_\infty^{1/d}$ and k from these Francis parameters (g_1 and g_2). Specifically, $W_\infty^{1/d} = c_1/c_2$, where:

$$c_1 = 1800^{1/d}\left(1000 + g_1\right)^{1/d} - 1000^{1/d}\left(1800 + g_2\right)^{1/d} \quad (7)$$

$$c_2 = \left(1000 + g_1\right)^{1/d} - 1000^{1/d} + 1800^{1/d} - \left(1800 + g_2\right)^{1/d} \quad (8)$$

and

$$K = \exp(-k) =$$
$$\left[\left(1800^{1/d} - 1000^{1/d}\right) \div \left\{ \left(1800 + g_2\right)^{1/d} - 1000^{1/d}\left(1000 + g_1\right)^{1/d} \right\} \right]^{-T} \quad (9)$$

where T is the time at liberty in years. The modest replication for *B. argus* (n = 28) caused convergence problems, preventing estimation of d, a parameter

describing curvature in the model (Francis 1995). Therefore, we calculated growth rate estimates g_1 and g_2 at several fixed values of d.

Age at body weight curves were constructed from parameters of each of the 3 classical growth models based on the equation:

$$\text{age} = -\left[\log\left\{ 1 - \left(W^{1/d} - 1\right) \div \left(W_\infty^{1/d} - 1\right)\right\} \right] \div K \quad (10)$$

For the Gompertz model, we have:

$$\text{age} = -\left[\log\left\{ 1 - \log(W) \div \log(W_\infty)\right\} \right] \div K \quad (11)$$

RESULTS

Validation of photo-identification method

The 2 individuals of *Bohadschia argus* kept in aquaria for 1 yr showed almost imperceptible changes in spotting pattern (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m551p201_supp.pdf). None of the spots disappeared or appeared after 1 yr, and spots remained in the same orientations to one another.

Matching of individuals in photographs after 2 yr was relatively easy for *B. argus*, as the spot patterns were distinctive and either changed very little or not at all over that period (Fig. S2 in the Supplement). In a few individuals, a small number of new spots had appeared or disappeared by 2012, but the vast majority of spots remained unchanged in size and orientation to one another. Matching of photos of *Thelenota ananas* between 2010 and 2012 was often difficult because the long papillae could be variably retracted at the time of the photograph, the gonopore (a pimple-like bump sub-dorsally at the anterior end of the body, from where gametes are released) offered the only reference point by which to orientate papillae and was often obscured, and some individuals grew additional papillae over the 2 yr (Fig. S3 in the Supplement). We posit that we relocated many *T. ananas* but could not re-identify them confidently based on photographs, especially where papillae were numerous and unbranched.

Estimation of weight from length and width measurements

B. argus were slightly larger and *T. ananas* smaller at Mermaid Cove compared to Palfrey Lagoon, but there was broad overlap in sizes between sites (Table 1). For both species, the relationships between

Table 1. Means (±SD in parentheses) for short-term displacements, body length and estimated weight of the 2 species at the 2 sites in both years. Sample sizes are given for sea cucumbers initially photographed (n_p) and relocated (n_r) days later

Site	Year	n_p	n_r	Displacement rate (m ind.$^{-1}$ d^{-1})	Body length (cm)	Estimated weight (kg)
Bohadschia argus						
Palfrey Lagoon	2010	16	14	1.9 (1.4)	32 (6)	1.3 (0.3)
	2012	33	29	5.7 (3.1)	32 (6)	1.4 (0.3)
Mermaid Cove	2010	16	13	8.1 (5.1)	36 (2)	1.6 (0.2)
	2012	10	9	4.4 (2.7)	31 (4)	1.5 (0.2)
Thelenota ananas						
Palfrey Lagoon	2010	2	2	9.3 (1.3)	64 (6)	5.1 (0.2)
	2012	1	1	4.6 (0)	57 (0)	4.4 (0)
Mermaid Cove	2010	12	6	9.2 (5.2)	53 (5)	3.8 (0.7)
	2012	16	13	5.5 (3.0)	52 (7)	3.6 (0.6)

placement rates were variable and averaged 2–9 m d^{-1} across species and sites (Table 1). Across both sites and years, *B. argus* displaced 0.5–16.8 m d^{-1}, averaging 5.1 m d^{-1}, and *T. ananas* displaced 1.6–19.2 m d^{-1}, averaging 6.8 m d^{-1}. Short-term displacements by *B. argus* differed significantly between sites depending on the year (interaction $F_{1,58}$ = 23.11, p < 0.001). Those of *T. ananas* did not differ significantly between sites or years (p > 0.05). In both tests, neither body weight nor depth significantly affected displacement rates across the range of measured values (p > 0.05).

measures of both body size and weight were highly significant (p < 0.001). For *B. argus*, body weight was explained better by body basal area (adj. r^2 = 0.68) than body length (adj. r^2 = 0.54). Likewise for *T. ananas*, body basal area provided a better fit to estimating body weight (adj. r^2 = 0.57) than when using body length alone (adj. r^2 = 0.52). Hence, we used the modelled relationships with body basal area to estimate body weight. Across years and sites, *B. argus* tended to be heavier as depth increased (F = 26.9, p < 0.001), but this was not the case for *T. ananas* (F = 0.36, p = 0.55).

Short-term movement

Overall, 82 % of animals photographed at the start of field studies in 2010 and 2012 were relocated and re-photographed 1–5 d later (Table 1). Short-term dis-

Table 2. Mean (±SD in parentheses) long-term displacements of the 2 study species at the 2 sites. Sample sizes are given for sea cucumbers photographed in 2010 (n_p) and the number relocated in 2012 (n_r). Individuals photographed in 2010 include those photographed at the start and end of the short-term movement study (days later) that year

Site	n_p	n_r	Displacement (m ind.$^{-1}$)
Bohadschia argus			
Palfrey Lagoon	22	17	45.5 (38)
Mermaid Cove	20	11	47.2 (46)
Thelenota ananas			
Palfrey Lagoon	3	2	15.4 (1)
Mermaid Cove	12	6	31.3 (18)

Long-term movement

At both sites, we relocated in 2012 at least half of the individuals of both *B. argus* and *T. ananas* that had been photographed in 2010 (Table 2). A couple of individuals of both species that were photographed in 2010 and lost in the follow-up search days later were subsequently found in 2012.

Movement distances of relocated *B. argus* were similar between sites, averaging 46 and 47 m over the 2 yr study (Table 2). Although *T. ananas* had larger body sizes, movements averaged just 15 and 31 m at the 2 sites. Notably, variability in movement rates was generally quite high (Table 2, Fig. 3). Several *B. argus* were found in 2012 within 5 m from where they had been photographed in 2010, while several others were relocated more than 100 m away. For *B. argus*, long-term movement distance was not significantly related to initial body weight (p = 0.72), depth of initial occurrence (p = 0.13) or site (p = 0.55). Likewise for *T. ananas*, long-term movement distance was not significantly related to initial body weight (p = 0.79), depth of initial occurrence (p = 0.63) or site (p = 0.99).

Animals displaced in various directions, with no common direction for either species at either site (Fig. 3). Some animals that had been in deeper waters (~6–7 m) in 2010 moved to shallower waters (~3–4 m) by 2012, and vice versa. At Palfrey Lagoon, the search area far exceeded the distance of the furthest relocated animal, but at Mermaid Cove, one animal was found near the limit of our search area (Fig. 3). At Palfrey Lagoon, the 2 relocated *T. ananas* were originally found 3 m from one another and were only 30 m from each other 2 yr later.
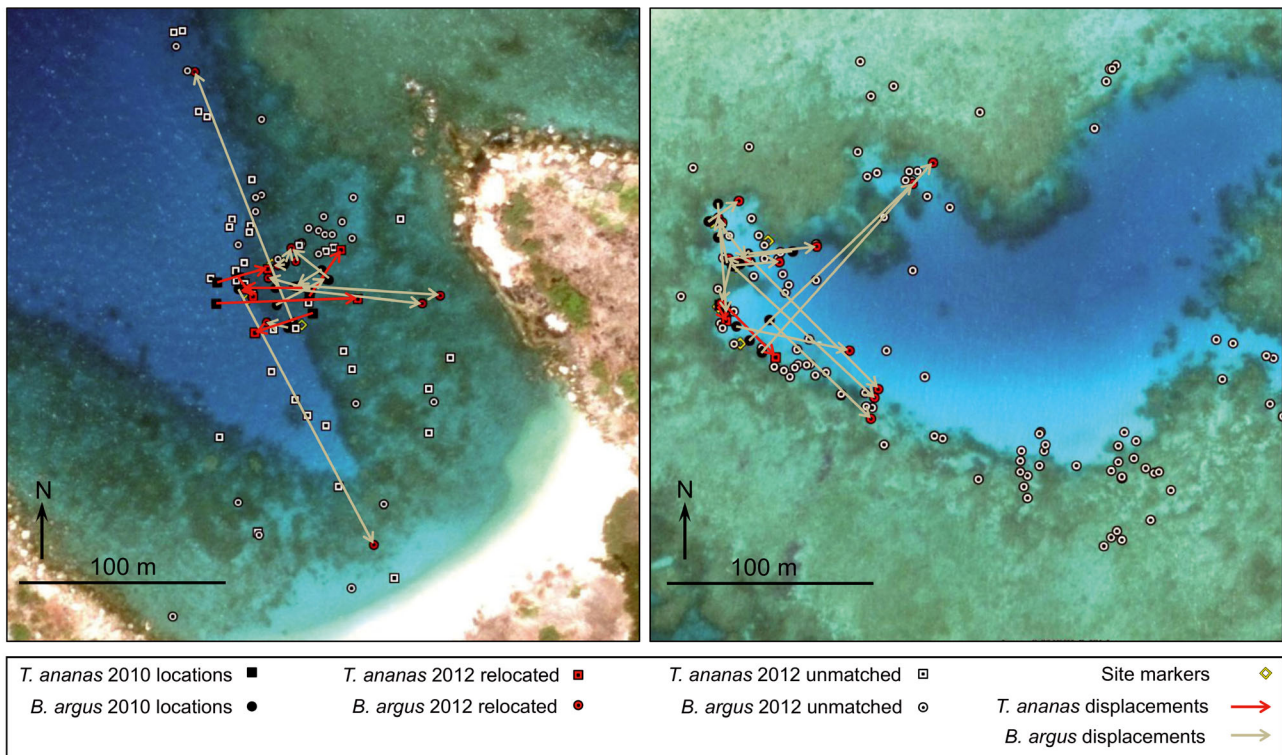
Fig. 3. Aerial photographs of the 2 study sites showing superimposed long-term displacements of animals over the 2 yr study period at Mermaid Cove (left) and Palfrey lagoon (right). Unmatched individuals were those located in 2012 that could not be confidently matched to individuals in 2010. Locations of another 14 unmatched *Bohadschia argus*, 5 to 110 m to the east of the photograph of Palfrey lagoon, are not shown

Growth

Growth over the 2 yr study was highly variable among individuals for both species (Table 3). On average, *B. argus* gained 7% body weight at Palfrey Lagoon and 5% body weight at Mermaid Cove. On average, *T. ananas* lost 10 and 6% body weight at those sites, respectively (Table 3). The individual *T. ananas* with the greatest weight loss (1790 g, from direct weights) measured 17 cm shorter and 2.5 cm narrower in 2012 compared to 2010 and, indeed, appeared thinner in the recapture photograph (Fig. S4 in the Supplement). Across the 2 sites, weight loss occurred in 8 of 28 recaptured *B. argus* and 4 of 8 recaptured *T. ananas* over the 2 yr period, and both sites for both species had individuals that lost weight.

Growth was not significantly related to initial depth of occurrence for either species (p = 0.99 and p = 0.23). Growth over the 2 yr was significantly negatively (linearly) related to initial (estimated) body weight for *B. argus* (p < 0.001) but not for *T. ananas* (p = 0.55). *B. argus* <1.3 kg consistently gained weight over the 2 yr, whereas individuals above this size either gained or lost weight. The relationship between initial body weight and the change in weight of *B. argus* over the 2 yr was similar among the von Bertalanffy, Gompertz and logistic models (Fig. 4). The models concurred that zero growth occurred around 1550 to 1580 g (Table 4), which can be considered the average maxi-

Table 3. Means (±SD in parentheses) for initial length, weight, and growth rates of the 2 study species over the 2 yr study period based on re-identified individuals

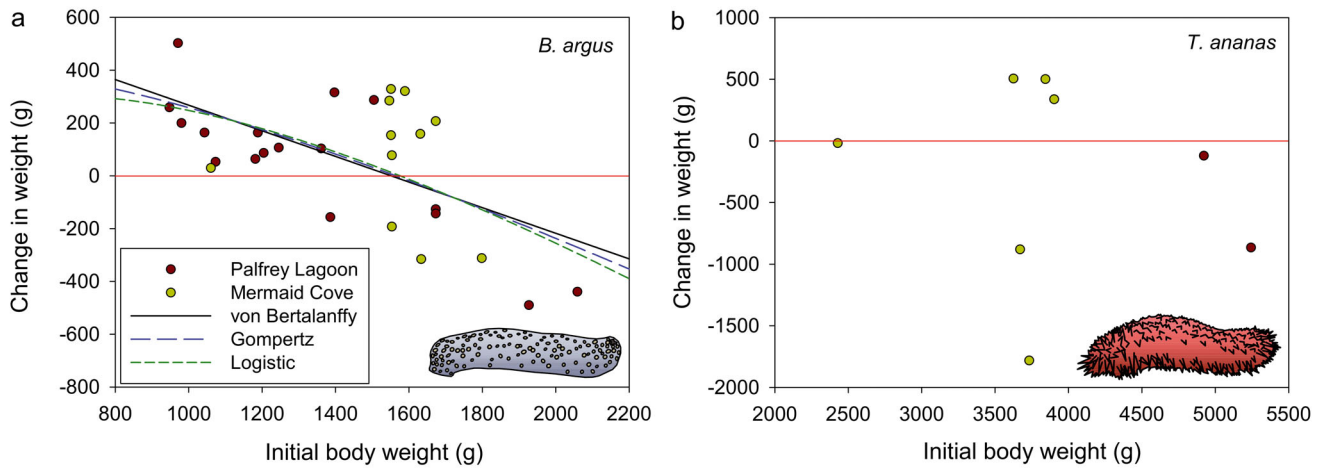| Site	n	Initial length (cm)	Initial estimated weight (g)	Growth (g)	Relative growth (% of body wt)
Bohadschia argus					
Palfrey Lagoon	17	31 (6)	1342 (333)	56 (259)	7 (19)
Mermaid Cove	11	36 (3)	1558 (182)	67 (240)	5 (15)
Thelenota ananas					
Palfrey Lagoon	2	63 (8)	5083 (228)	−493 (527)	−10 (10)
Mermaid Cove	6	47 (8)	3533 (552)	−223 (924)	−6 (25)

Fig. 4. Initial (estimated) body weight vs. the relative weight gain over 2 yr for (a) *Bohadschia argus* and (b) *Thelenota ananas*. The von Bertalanffy, Gompertz and logistic growth models are fitted for *B. argus*. Relationships fitted to data on *T. ananas* using the 3 growth models were unreliable owing to the limited replication. Red horizontal lines are at the point of zero growth

Table 4. Parameter estimates from 3 classic growth models for *Bohadschia argus*, pooled across sites. K is a growth parameter, W_∞ is the average maximum weight in grams and d is the power parameter. Parameter estimates from Francis' (1995) growth model, g_1 and g_2, are also derived (annualised growth rates for 1000 and 1800 g; see Eqs. 5 & 6)

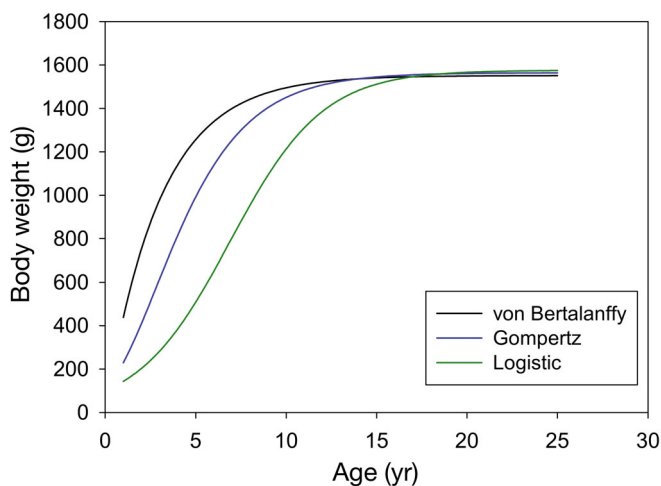| Model	K	W_∞	g_1 (g yr^{-1})	g_2 (g yr^{-1})
von Bertalanffy ($d = 1$)	0.33	1552	156	−70
Logistic ($d = -1$)	0.39	1576	134	−79
Gompertz ($d = \infty$)	0.36	1564	145	−75

Fig. 5. Relationships between predicted age and body weight, reconstructed from parameter estimates from the von Bertalanffy, Gompertz and logistic growth models for *Bohadschia argus* up to the average maximum body size. Once animals attain the average maximum size, they can lose or gain weight in subsequent years

mum weight (W_∞) for *B. argus* at Lizard Island at the time of the study. Over the 2010–2012 study period, all 3 models show negative growth in animals larger than that size. K, the estimated proportional annual growth rate, varied from 0.33–0.39 among the 3 classical growth models (Table 4). Francis' (1995) model produced slightly variable estimates of growth rates for 1000 and 1800 g *B. argus*, depending on the value of the curvature parameter d (Table 4). Growth tended to be roughly 130–160 g yr^{-1} at body size 1000 g and −70 to −80 g yr^{-1} at body size 1800 g.

Age-at-weight curves for *B. argus*, constructed from parameter estimates from each of the classical growth models, reiterate the trend in the mark-recapture data that smaller animals exhibited much faster growth (Fig. 5). At growth rates measured in this study, *B. argus* are estimated to attain average maximum size at around 15 to 20 yr old, depending on the growth model. After reaching the average maximum size, the growth models do not account for the fact that some large individuals can lose weight and probably subsequently regain weight. Positive and negative growth of individuals after the average maximum size infers that longevity in *B. argus* is in the range of several decades or more.

DISCUSSION

Movement of sea cucumbers

Our study shows that over short temporal scales, both species were very mobile and displaced appreciable distances in the space of a few days. Short-

term movement rates for *Bohadschia argus* were in the range of 2–8 m d^{-1} and for *Thelenota ananas* averaged 5–9 m d^{-1}. These movement rates are mostly higher than reported for the coral reef holothuroid *Actinopyga mauritiana* from Solomon Islands (3 m d^{-1}) (Graham & Battaglene 2004) and similar to those of *Holothuria mexicana* and *Isostichopus badionotus* from Jamaica (4–6 m d^{-1}) (Hammond 1982). Thus, not all holothuroids can be characterised as sedentary.

Most of the animals that we relocated after 2 yr had not displaced very far. At outer reef flat sites in New Caledonia, Conand (1991) also found limited long-term movement of *A. echinites* and *A. mauritiana.* Our long-term data indicate both home-ranging and nomadic behaviours (see Quinn & Brodeur 1991, Grüss et al. 2011), since some animals kept within the initial core study areas while others moved away. Hence, the animals moved relatively fast on a daily basis, but many of them are not displacing far over long temporal scales. Our study sends a caution to extrapolating long-term movements of animals from data taken over short temporal scales, highlighting the value of a multi-scale approach (Pittman & McAlpine 2003). This finding has also been illustrated in tropical lobsters, which are highly mobile yet often move limited distances in the long term owing to site fidelity (O'Malley & Walsh 2013).

Movement directions appeared random within the populations with an absence of coordinated directional movement, as found in other mobile coral reef invertebrates such as queen conch (Hernandez-Lamb et al. 2012) (but see Hesse 1979 for 1 exception) and spiny and slipper lobster (O'Malley & Walsh 2013). Many other tropical holothuroids have also been shown to have random foraging movements (Hammond 1982, Conand 1991, Graham & Battaglene 2004, Purcell & Kirby 2006), which explains how the long-term displacements of our 2 species were not hundreds of times greater than daily movement rates.

About one-third to one-half of the individuals photographed in 2010 were not relocated or confidently matched with photographs of animals in 2012. Some of the animals were probably either buried in sand (for *B. argus*) or hidden in reef structures where we could not find them, or they were not confidently matched with the photographic method (especially *T. ananas*). At Mermaid Cove, others could have moved beyond the limits of our search area, so the long-term displacements at that site are probably underestimated. The close proximity of the 2 *T. ananas* at Palfrey Lagoon, which persisted 2 yr later, is curious. We speculate whether such associations could represent long-term pairing, and such behav-

iour would improve the chance of mates finding one another at low densities (see Bell et al. 2008).

Growth

Negative growth has been shown for *H. whitmaei* on the Great Barrier Reef (Uthicke & Benzie 2002, Uthicke et al. 2004). Negative growth implies resorption of tissue, probably in response to stress. For example, Conand (1991, 1993) tagged 7 holothuroid species with T-bar tags and released them on inner reef flat, reef slope and outer reef flat sites in New Caledonia. Five of the 7 species lost weight, owing to stress induced by the tags. Tropical holothuroids in captivity often lose weight due to stocking densities and sub-optimal conditions (Morgan 2000, Purcell et al. 2012a, Robinson et al. 2015, Kumara & Dissanayake in press), and temperate holothuroids are known to lose weight during seasonal aestivation (Qin et al. 2009, Wang et al. 2015). Apparent weight loss of some individuals in our study could be explained by potential differences in gonad development between sampling events, i.e. spawning could have occurred earlier in 2012, producing negative growth estimates. Earlier spawning in the season would be likely if water temperatures were warmer in 2012, but average monthly surface seawater temperatures were actually 2°C cooler for the 3 mo leading up to the measurements in 2012 compared with temperatures recorded in 2010 (AIMS 2013), so the data at hand do not lend support to such a hypothesis for weight loss.

The growth relationships presented here must be interpreted in context. Our model for growth in *B. argus* indicates that animals above 1600 g lose weight, but in reality, they must gain weight in some years to attain this weight threshold. We surmise that once holothuroids attain a large size (e.g. 1600 g in *B. argus*), they may gain or lose weight depending on various environmental factors. Negative growth of larger individuals could simply be attributed to less favourable conditions for growth (e.g. water temperatures or environmental factors that affect food supply) during the 2010–2012 study period compared to previous years. Smaller individuals are likely to have positive growth rates, which slow as they get larger. This overall picture of holothurian growth is supported by Uthicke & Benzie (2002) and Uthicke et al. (2004), who reported that small *H. whitmaei* displayed positive growth, medium-large individuals displayed zero growth and large individuals lost weight. What is clear from our study is that estimates of age of tropical sea cucumbers from modelling of

length or weight data are unreliable at adult body sizes. The potential for weight loss in fully grown individuals cannot be accounted for in age-at-size models and thus will undermine estimates of their age. Past estimates of holothuroid age based on size-frequency data (e.g. Conand 1988, 1989) must be regarded as underestimates.

Growth modelling indicated that *B. argus* attains an average maximum size at around 15–20 yr, corresponding to the size at which growth becomes zero. As we did not find small individuals for the mark-recapture study, and data from captive-rearing indicate that young juvenile sea cucumbers exhibit slower absolute growth rates than predicted from the models here (c.f. Purcell & Kirby 2006), age at maximum size is probably somewhat underestimated. Our study suggests that some tropical holothuroids can lose and regain weight from one year to another, depending on environmental conditions. An alternative hypothesis is that after attaining a full growth adult size, the animals shrink due to senescence. In any case, the animals are likely living at least a couple of decades, and perhaps much longer, concurring with findings by Uthicke et al. (2004) for *H. whitmaei*.

The classic growth models used here, including Francis' reparameterised model, do not take account of individual variability. To incorporate individual growth variability, one would need to allow parameters (W_∞, K, or Francis' g_1 and g_2) to vary among individuals. Distributional assumptions or moment assumptions on these random variables would have to be specified in the model, and extra parameters would need to be estimated (Wang et al. 1995). However, in our case, relatively small sample sizes prevented such complex models. Considering that individual variability can lead to 5 to 10% underestimation in the models (Wang & Thomas 1995), more work is needed to further examine growth trajectories in holothuroids.

Implications for fisheries management and conservation

Most of the large tropical holothuroids are exploited throughout the tropics (Purcell et al. 2012b). Marine reserves must be appropriately sized to avoid boundary effects and significant spillover of animals into fishing grounds (Sale et al. 2005, Purcell & Kirby 2006). Nomadic animals will receive lower conservation benefits from marine reserves than those moving within a home range (Grüss et al. 2011). Our study indicates that many individuals in holothuroid popu-

lations remain within small home ranges and would be well protected even by small reserves. On the other hand, nomadic individuals can potentially displace more than 100 m and would be likely to disperse beyond the boundaries of small reserves during their lives. Reserves to protect most of the adults from capture should therefore be in the order of hundreds of hectares rather than just a few hectares.

The high movement rates in the short term, with site fidelity in the long term, are good news for restocking programs (Bell et al. 2008). First, high mobility of both species infers high likelihood of potential mates finding one another in spawning seasons. Mate finding is considered a critical limitation to recovery of populations fished to low density (Purcell et al. 2013). Second, site fidelity of many of the individuals suggests that artificially created breeding groups should persist over long time frames, validating the rationale for broodstock aggregation as a restocking approach.

Generally among animals, growth rates are related to mortality rates and are negatively related to longevity. Shrinkage in some of the large animals in a population will cause underestimates of growth, mortality rates and longevity, which are used to develop management measures such as rotational harvest strategies (Plagányi et al. 2015) and catch quotas (see Aumeeruddy et al. 2005). Our findings of slow growth in *B. argus* and *T. ananas* suggest that these large coral reef holothuroids might be longer lived and have lower mortality rates than previously estimated.

Limitations of the study

Habitat types and reef configuration may have restricted long-term displacements, as both sites were in habitats partially bounded by shallow reef and land. At Palfrey Lagoon, long-term movements of the sea cucumbers might have been confined by the shallow reef flat and reef configuration. This could explain why *T. ananas* moved twice as far over the 2 yr at Mermaid Cove. We surmise that movement rates could be greater in unbounded habitats, which could be examined in future studies.

The photographic identification proved a breakthrough for mark-recapture, but we had trouble confidently matching many of the photos of *T. ananas*. Also, sometimes *B. argus* can bury in sand, so we may have overlooked buried individuals. That some non-relocated individuals in 2010 were subsequently relocated in 2012 shows that incomplete recovery of photographed animals can be partly attributed to hiding behaviours or incomplete efficacy of our searches.

We did not revisit sites in different seasons due to financial limitations. Movement behaviour of tropical invertebrates is known to vary seasonally (e.g. Stoner & Sandt 1992), so the short-term movement rates of *B. argus* and *T. ananas* reported here could be higher or lower at other times of the year. Future studies could examine seasonal variation in the movement of holothuroids. For species with uniquely marked individuals (e.g. *Astichopus multifidus*, *B. marmorata*, *H. fuscogilva*, *H. lessoni*, *H. nobilis*, *I. badionotus*), our study provides the methodological template for such research.
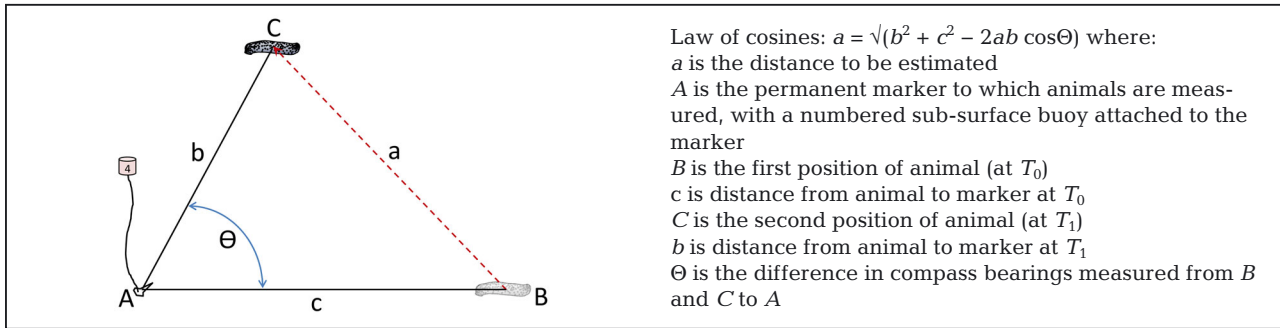
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Appendix. Law of cosines applied to measure holothurid movement rates

Law of cosines: $a = \sqrt{(b^2 + c^2 - 2ab \cos\Theta)}$ where:
a is the distance to be estimated
A is the permanent marker to which animals are measured, with a numbered sub-surface buoy attached to the marker
B is the first position of animal (at T_0)
c is distance from animal to marker at T_0
C is the second position of animal (at T_1)
b is distance from animal to marker at T_1
Θ is the difference in compass bearings measured from B and C to A