**FEATURE ARTICLE**

Limited long-term movement and slow growth of the sea cucumber *Pearsonothuria graeffei*

Alison R. Hammond, Steven W. Purcell*

National Marine Science Centre, Southern Cross University, Coffs Harbour, NSW 2450, Australia

ABSTRACT: Sea cucumbers are heavily exploited worldwide, yet data are lacking on animal mobility and life-history parameters for fishery management and conservation planning. This study assessed movement and growth rates for a medium-sized holothuroid, *Pearsonothuria graeffei*, harvested throughout the Indo-Pacific. We used photographic mark–recapture to track long-term movements and growth for this species over 2 yr. Recapture rates were 67–72%. Movement rates averaged 9 m yr^{-1}, and many individuals were found in aggregations and recaptured there in 2 successive years. Growth was highly variable; small animals (<700 g) tended to gain weight while large animals (>700 g) tended to lose weight. Some individuals lost weight and then regained weight, while others gained weight and later lost it. Growth models estimated that *P. graeffei* approach their average maximum weight (769 g) in 7–12 yr and are slow-growing (growth coefficient = 0.17). Natural mortality (*M*; 0.48 yr^{-1}) was low, and estimated longevity was 18 yr. *P. graeffei* exhibits traits that heighten its vulnerability to overfishing: aggregation behaviour, low mobility, slow growth, a long lifespan and low *M*. The site fidelity and low mobility infer that a system of small reserves would effectively protect breeding populations and that emigration to new sites is very limited. This study provides the first published evidence from natural habitats that holothuroids can lose and later regain weight. Our empirical findings suggest that small- to medium-sized holothuroids might be slower growing and longer lived than previously believed, imploring a more conservative approach to conservation policy.

KEY WORDS: Holothuroidea · Echinoderm · Growth modelling · Longevity · Natural mortality · Mark–recapture · Marine invertebrate
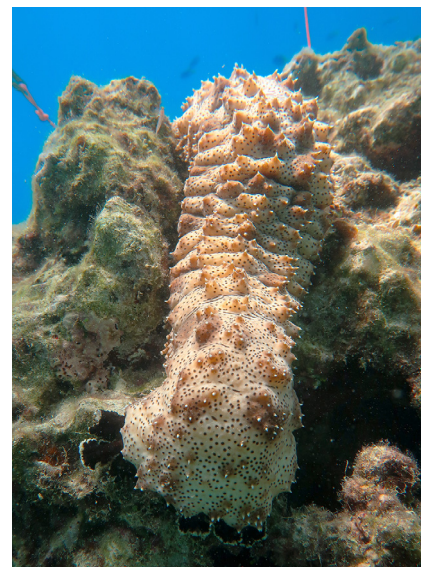
A 'flowerfish', *Pearsonothuria graeffei*, crawling down a reef slope at Lizard Island, Australia, where more than 100 of the animals were photographically marked.

Photo: A.R. Hammond

1. INTRODUCTION

1.1. Movement and growth in echinoderms

Studies on growth and movement patterns are integral to the development of effective conservation and fishery management strategies for exploited marine animals (Campana 2001, Nathan et al. 2008, Allen & Singh 2016). Knowledge of long-term movement patterns can inform plans for spatial management measures such as optimal sizing for no-take zones that protect breeding populations and rotational harvest areas (Taggart et al. 2008, Green et al. 2015). Likewise, age and growth parameters are

*Corresponding author: steven.purcell@scu.edu.au

used to formulate optimal harvesting rates, catch quotas, rotational closures, and time needed for stock recovery (Pauly 1983, Morales-Nin 1992). Movement and growth studies thus furnish key information for planning regulatory measures suited to certain species or groups.

Information on the movement and mobility of animals in natural habitats improves our understanding of population dynamics (Bell et al. 2008, Courchamp et al. 2008). Most echinoderms are broadcast spawners; therefore, successful fertilisation of gametes relies heavily on the proximity of mates in order to avoid Allee effects (Courchamp et al. 2008, Byrne & O'Hara 2017). In low densities, echinoderms with low mobility face a reduced likelihood of encounters with mates during the spawning season (Babcock et al. 1992, Bell et al. 2008). While high mobility provides animals with opportunities for spatial intermixing of populations and colonisation of new areas, highly mobile echinoderms are at increased risk of spillover out of marine reserves (Sale et al. 2005, Purcell & Kirby 2006).

Mark–recapture studies can reveal the movement potential and growth rates of echinoderms (e.g. Da Silva et al. 1986, Dumont et al. 2006, Purcell et al. 2016). Two large-bodied (i.e. commonly >1 kg) holothuroids, *Bohadschia argus* and *Thelenota ananas*, that forage on soft-bottom habitats were found to be capable of displacing 10s of m yr^{-1} (e.g. Purcell et al. 2016). Although some sea urchins can move considerable distances, others are highly sedentary, moving less than 20 cm in 3 wk (Lowe et al. 2015). Little is known of the long-term movement potential of small sea cucumbers (i.e. <1 kg) and those typical of hard reef surfaces. Similarly, while mark–recapture has shown that larger holothuroid species (i.e. >1 kg) are long-lived (Uthicke et al. 2004, Purcell et al. 2016), uncertainty remains about the longevity of smaller species that are also commercially targeted.

Long-term movement patterns have been characterised by animals' long-term displacements. These range from short movements within a home range to nomadic movements between locations and seasonal migrations (Grüss et al. 2011, Jonzén et al. 2011, Teitelbaum & Mueller 2019). Movement rates differ greatly among marine animals, contingent upon factors such as habitat type, resource availability, population density, season, trophic level, body size, and sex (Hammond 1982, Kramer & Chapman 1999, Sale et al. 2005, Frisch 2007). Giant triton snails can travel up to 234 m d^{-1} (Schlaff et al. 2020), greatly outpacing the 10 m d^{-1} movement rates of their prey, the crown-of-thorns starfish (Keesing & Lucas 1992). Al-

though often regarded as sedentary (Grantham et al. 2003), some sea cucumbers are surprisingly mobile, often moving more than 5 m d^{-1} (Siegenthaler et al. 2015, Purcell et al. 2016, Hammond et al. 2020).

1.2. Age and growth in holothuroids

The formulation of effective fishery management plans or recovery strategies relies heavily on estimating baseline parameters such as growth rate, natural mortality (M), and longevity (t_{max}) (Beverton & Holt 1959, Pauly 1980, Pine et al. 2003). The underlying tenant is that stocks with high t_{max} and low M are less resilient to exploitation and have reduced capacity to recover from depletion (Froese et al. 2000, Cochrane 2002, Hewitt et al. 2007).

Mark–recapture studies rely upon long-term tag retention and non-invasiveness of the tags or marking method. Physical tags and body etching have had poor retention with holothuroids and can interfere with behaviour and metabolism (Conand 1991, Shiell 2006, Wheeling et al. 2007, Rodríguez-Barreras et al. 2014). Genetic fingerprinting has good application for holothuroids (Uthicke & Benzie 2002) but is more expensive and sophisticated to apply (Purcell et al. 2006, Shiell 2006). Photographic mark–recapture methods have proven valuable for holothuroids with individually distinguishable colour or body patterns and have been applied to a few large-bodied species (i.e. adults mostly >1 kg) (Purcell et al. 2016, Hammond et al. 2020).

Growth increments in body size over a known period can be used to model life-history parameters. Field studies have shown that large-bodied tropical holothuroids (i.e. >1 kg) have slow or moderate growth rates and lifespans of at least several decades (Uthicke & Benzie 2002, Uthicke et al. 2004, Purcell et al. 2016). The first of those studies on *Holothuria whitmaei* used genetic fingerprinting (Uthicke et al. 2004), while the second study on *B. argus* and *T. ananas* used photographic mark–recapture (Purcell et al. 2016). Negative growth, or shrinkage, in holothuroids has been reported in several empirical mark–recapture studies (Uthicke & Benzie 2002, Uthicke et al. 2004, Purcell et al. 2016, Dumestre 2017). This phenomenon is also known for some other invertebrates, including planarians, cnidarians, and nemerteans (Hamner & Jenssen 1974, Oviedo et al. 2003, Hariharan et al. 2016). Standard fishery growth models assume positive growth increments and will underestimate t_{max} in the presence of negative growth.

1.3. Knowledge gaps for managing and conserving sea cucumbers

Over the past 2 decades, sea cucumber fisheries have spread like a contagion, serially over-exploiting stocks in all of the world's oceans (Anderson et al. 2011, Eriksson et al. 2015). The majority of tropical sea cucumber fisheries are ineffectively managed (Purcell et al. 2013), and 16 of the 90 or so commercially fished species are threatened with extinction (IUCN 2021). The lack of knowledge of life-history parameters of most of the commercially exploited sea cucumbers has contributed to resource mismanagement and has hampered conservation planning (Bruckner et al. 2003, Toral-Granda et al. 2008, Purcell et al. 2013). Early work on the abundant reef holothuroid *Holothuria atra* using chemical marking indicated relatively high rates of M (1.02) yet slow growth (growth coefficient, $K = 0.11$) (Ebert 1978). Further studies since then have yielded a range of estimates for M and the growth constant for various holothuroids (discussed later).

Our focal species, *Pearsonothuria graeffei*, is one of only a few small-bodied, commercially exploited sea cucumbers suitable for photographic mark–recapture. Widely distributed across the Indo-Pacific, this deposit-feeding holothuroid lives on hard coral reef surfaces in depths of up to 25 m (Purcell et al. 2012). It is fished heavily in low-income countries despite its low commercial value (Conand et al. 2013, Pakoa et al. 2013, Mustagfirin et al. 2021). This species can sometimes be found in aggregations (Idreesbabu & Sureshkumar 2017). They are predominantly active diurnally, and daytime movement rates from 51 individuals averaged 1.1 m h^{-1} in a short-term study at a coral reef in the Philippines (Wheeling et al. 2007).

1.4. Study aims

This study aimed to uncover long-term movement rates and life-history parameters of *P. graeffei*, which offers an example of a small-bodied holothuroid typical of hard reef habitats. We achieved this goal by photographically marking animals that were geo-referenced, measured and weighed, and then re-photographed and measured in the same way in 2 successive recapture years. By collecting data at several sites, we also assessed the extent of population mixing. A key objective of this study was to furnish data that could inform spatial management measures, fishery harvest strategies, and conservation measures.

2. MATERIALS AND METHODS

2.1. Study site

The study was conducted at Lizard Island (14° 40′ S, 145° 28′ E) in north-eastern Australia, within the Great Barrier Reef Marine Park. In the late 1800s, Lizard Island was the base for commercial sea cucumber fishing (DES 2021). Today, the lagoon and reefs around this island group are protected within a no-take marine park designated as a Scientific Research Zone (SR-14-2004), and the sea cucumbers have not been subject to harvesting for many decades. The southern lagoon, delimited by Palfrey and South islands, creates sheltered habitats amenable to *Pearsonothuria graeffei* populations.

2.2. Field methods

Fieldwork was undertaken around the same time each year over 3 yr: 21 February 2019, 24–26 February 2020, and 19–25 February 2021. As *P. graeffei* can be found in aggregations (the collective noun proposed as 'pickles' on some internet sites) of high abundance in shallower (2–8 m) areas of the lagoon between Palfrey and South Island, we chose this area as the study site. Broadscale searches identified the protected reef edges as the preferred habitat of *P. graeffei*.

In 2019, we recorded (method below) the first 25 animals located at the Palfrey Island site, which appeared to be the majority of animals at that site. In 2020, we recorded 34 animals at Palfrey Island and, after a broad search to find a second site with reasonable numbers of *P. graeffei*, we recorded the first 57 animals found at a second site near South Island. In 2021, we expanded the final recapture search area to maximise the chance of recapturing potentially nomadic animals. The search area extended 30–70 m from both sites and included the reef slopes and rubble substrata between the 2 sites (Fig. 1). For the 2021 survey, we recorded 139 individuals — again, all individuals that were encountered.

As *P. graeffei* camouflages against the reef and sometimes shelters within the reef matrix, searching involved checking crevices and holes within the reef while keeping an eye out for the characteristic string-of-beads faecal pellets, which might indicate the presence of a cryptic animal (Fig. 2a,b). For the 2019, 2020, and 2021 surveys, the same procedure was followed for photographing, measuring, and weighing the sea cucumbers. Two snorkellers searched for the
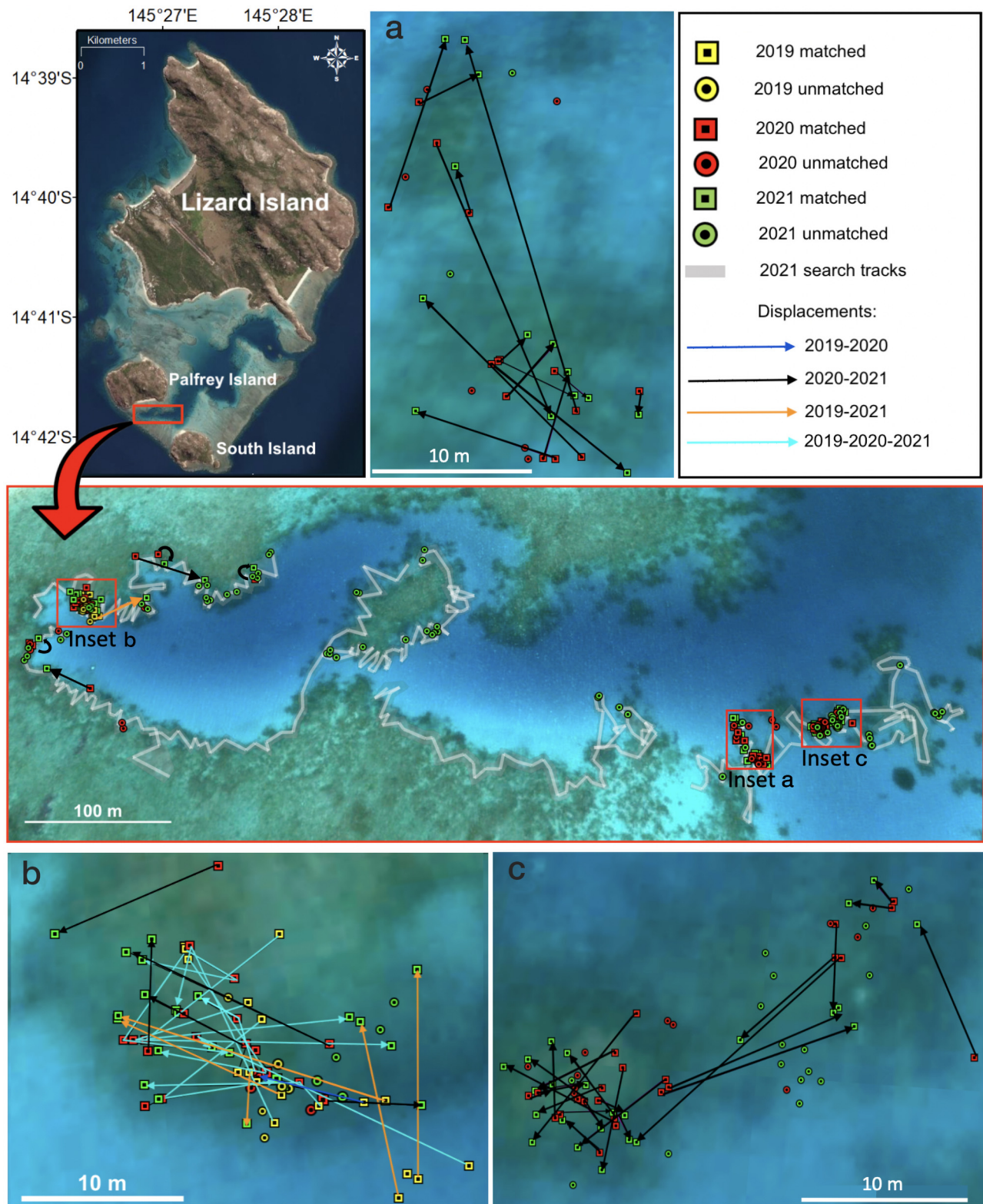
Fig. 1. Lizard Island, Queensland, study sites at (a,c) South Island lagoon and (b) Palfrey Island lagoon and locations and displacements of *Pearsonothuria graeffei* across 3 sampling periods (February 2019, 2020, 2021). Arrows are displacement distances of individuals photographically matched (square symbols); square symbols without displacement arrows denote animals that moved <1 m (i.e. symbols are overlaid on the same point). Curved black arrows in the middle panel denote animal displacements of only a few metres

Fig. 2. (a) *Pearsonothuria graeffei* showing mottled colouration that is well camouflaged against the coral rubble habitat that they frequently occupy, making sighting them difficult. (b) The tell-tale string-of-beads faecal pellets from *P. graeffei* indicate the presence of a cryptic or hidden animal

animals, and one of them towed a dive float with a handheld GPS unit, recording search tracks and animal locations. Dive watches were synchronised to the time on the GPS unit. Upon location of each animal, we positioned the GPS at the water's surface directly above the animal for 1 min and recorded the time to later match up with the time-synced GPS. The anterior end of each animal was then photographed and the lengths and widths (at body midpoint) of the animals were measured to ±0.5 cm *in situ* in an undisturbed state. We recorded the water depth at each sighting using a digital depth gauge (±0.1 m) and later corrected it to zero tidal datum. Animals were brought to the nearby boat in individual bags with labels and weighed using an electronic hanging balance (±10 g) after a 5 min draining period, which was carefully timed and recorded in each instance. That draining period allowed the animals to expel water from their body while minimising stress and is a standard procedure to reduce measurement error (following Skewes et al. 2004). Both field sites were in sheltered 'back-reef' habitats, although some light wind chop could cause 10−20 g variation in weight measurements using a hanging scale, corresponding to a 1−3% error in weight measurements relative to mean body weight. We then returned the animals to their original position on the reef, identified by a numbered marker and float.

2.3. Photographic mark−recapture method and matching

The tendency of *P. graeffei* to contort its body, even when undisturbed, made it untenable to use photo-identification software that requires fixed body reference points, as in marine megafauna (e.g. Flukebook, Sharkbook). Therefore, we undertook photo identification manually, matching the orientation of at least 10 white papillae, black spots, and/or black lines at the anterior end of each animal (Fig. A1 in the Appendix). Only animals matched with absolute certainty were considered recaptures. The only difficulties encountered in matching animals were those few animals handled through necessity (e.g. extracting from a crevice to photograph). Disturbed animals contracted their body and retracted their papillae, reducing or obscuring reference points for matching.

2.4. Long-term movement

The position of each animal, obtained from the corresponding time stamp on the GPS tracks, was entered into Google Earth Pro (v.7.3 Google, 2021), and displacement of recaptured animals was measured using the ruler function (±0.1 m). We marked 12 fixed positions on land with the same GPS unit and track settings. After returning to those positions and measuring the distances with the same method, the average accuracy was found to be 1.28 m. This measurement error is proportionally large for animal displacements of just a few metres and smaller with greater displacements.

Data from all recaptured animals were grouped by site (Palfrey or South Island lagoon) for initial analyses. ArcGIS Pro (v.2.4 ESRI, version 2021) density-based clustering identified major aggregations using the distance between neighbours and a reachability plot to separate clusters from noise. A minimum of 15 animals within a search distance of 45 m was considered a pickle.

An ANCOVA test using SPSS v.17 software (IBM) was used to examine mean annual displacement (ln transformed) across the 2 sites between 2020 and 2021 while accounting for water depth and initial animal body weight covariates. The natural log transformation addressed the non-normality of data due to a few animals that had moved long distances. Normality of data was checked using box-and-whisker plots, and homogeneity of variances was verified using Levene's test ($p > 0.05$). Residuals were checked for normality and outliers, and the assumptions were met. The relationship between annual displacement and animal size was investigated via nonlinear regression using Datafit™ software, applying the best-fitting 2-parameter model in order to avoid overfitting.

2.5. Growth

Growth was estimated for 69 animals. For 11 animals recaptured in both 2020 and 2021, we used data only for the 2020 recaptures in growth analyses to avoid pseudoreplication. Weight was used as the metric for assessing growth because of the flexible bodies of sea cucumbers. None of the animals weighed in this study eviscerated internal organs. In order to illustrate how annual growth increments (i.e. weight gained or lost) varied across different starting weights of animals, the 2 variables were plotted and the trend analysed with linear regression. We also separately plotted the weights of the 11 multiple re-captured animals to explore weight changes of those animals across 2019, 2020, and 2021 and applied simple trend smoothing to illustrate the responses.

Relative growth rates for individuals were determined from the change in body weight over time, standardised by the initial weight and time, using the equation:

$$\frac{W_2 - W_1}{W_1(t_2 - t_1)} \times 100 \tag{1}$$

where W_1 and W_2 are body weights at time t_1 and t_2. Relationships between growth rate and initial weight, depth, and displacement were also explored via nonlinear regressions using Datafit-9™ software.

To model growth rates, we first applied Fabens' equation in order to derive von Bertalanffy parameter estimates of asymptotic weight (W_∞) and growth coefficient (K). This was done by applying our data on the time at liberty (T), with growth increments determined from initial weight (W_1), and final weight (W_2):

$$W_2^{1/d} - W_1^{1/d} = (W_\infty^{1/d} - W_1^{1/d})(1 - e^{-KT}) \tag{2}$$

For the von Bertalanffy model, $d = 1$, which simplifies the equation. The parameters in Fabens' equation were given new symbols to be recognised in Datafit-9™ as:

$$y = (a - x_1) \times (1 - \exp(-b \times x_2)) \tag{3}$$

where y is the growth increment ($W_2 - W_1$), a is W_∞, x_1 is W_1, b is K, and x_2 is T. Values of W_∞ and K were used to plot size-at-age curves using the equation:

$$\text{age} = -\left\{\log[1 - (W \div W_\infty)^{1/d}]\right\} \div K \tag{4}$$

for the von Bertalanffy model and:

$$\text{age} = -\left\{\log[1 - (\log(W) \div \log(W_\infty))]\right\} \div K \tag{5}$$

for the Gompertz model (Purcell et al. 2016). t_{max} (Taylor 1958, Pauly 1984) was approximated by:

$$t_{max} \approx 3 \times K^{-1} \tag{6}$$

This simplified equation for t_{max} assumes that the animal age at zero weight (t_0) is zero. This is an approximation based on fishes in tropical waters (Pauly 1984), so caution is naturally needed when interpreting results for other taxa such as sea cucumbers.

Parameters were entered into the online FishBase life-history tool for elongate fishes, which yielded a standard error estimate (Froese & Pauly 2021). The value of M for the population was estimated using Pauly's (1980) empirical model:

$$\log M = -0.2107 - 0.0824 \log W_\infty + 0.6757 \log K + 0.4627 \log Tp \tag{7}$$

where Tp is the mean annual sea temperature (°C) at Lizard Island for 2020 (AIMS 2021). This model was used because it applies to data on animal weights and uses estimates for K and seawater temperature, which were both available. This model is founded on a general trend across most finfish whereby M correlates directly with environmental temperature (Pauly 1980), and it has been similarly applied for other holothuroids (Herrero-Pérezrul et al. 1999, Siddique & Ayub 2019).

3. RESULTS

In total, we photographically marked and measured animals on 255 occasions and recaptured animals on 80 occasions. For the 2020 and 2021 surveys, that translated to recapture rates of 67 and 72% of animals after 1–2 yr (Table 1). Six animals photographed in 2019 and not found in 2020 were relocated in 2021, while 11 animals photographed in 2019 were relocated in 2020 and 2021.

Table 1. Long-term displacement rates (mean ± SD) of *Pearsonothuria graeffei* at 2 sites at Lizard Island, Queensland. At Palfrey Island lagoon site, sea cucumbers were first captured in 2019 and then recaptured in 2020 and 2021. At South Island lagoon, sea cucumbers were first captured in 2020 and then recaptured in 2021. Sample sizes are given for animals photographed (n_p) and recaptured (n_r) 1–2 yr later

Site	Year of first capture	n_p	n_r	Recapture rate (%)	Displacement (m yr^{-1})
Palfrey Island lagoon	2019	25	18	72	8 ± 6
	2020	34	24	70	11 ± 14
South Island lagoon	2020	57	38	67	8 ± 7

Table 2. ANCOVA results for mean displacement rates (m yr^{-1}) (ln transformed) for *Pearsonothuria graeffei* from 2020–2021 and 2 sites at Lizard Island, Qld (n = 62). Water depth and body weight are covariates in the analysis

Source	df	SS	*F*	p
Site	1	0.022	0.043	0.836
Water depth	1	0.427	0.838	0.364
Body weight	1	34.599	9.017	0.004
Residual	58	29.581		

3.1. Long-term movement

For the 2020–2021 period, average movement rates were similar between the 2 sites, averaging (±SE) 9 ± 10 m yr^{-1}. Across all time periods, individual animal displacements ranged from 1 to 64 m yr^{-1} (Table 1). Displacement rates between 2020 and 2021 did not differ significantly between the 2 sites (Table 2). While depth did not appear to significantly affect long-term displacement, annual displacement distances increased with larger-sized animals (Table 2; $F_{1,78}$ = 9.73, p < 0.01, r^2 = 0.11). Density-based cluster analysis identified 3 distinct aggregations: 2 at South Island lagoon (Fig. 1a,c) and one at Palfrey Island lagoon (Fig. 1b), with no exchange of animals between aggregations in successive years. Individual *Pearsonothuria graeffei* outside these aggregations exhibited the highest displacement rates (mean ± SD: 25 ± 22 m). Nine of the 11 animals recaptured in 2020 and 2021 at the Palfrey Island site moved in a V-shaped trajectory, and all but one were found within 12 m (8 ± 5 m) of their location 2 yr earlier. Few of the recaptured animals had stayed in exactly the same place on the reef.

3.2. Growth

The average body weight of *P. graeffei* in 2021 was 697 g; the range for 2020 and 2021 was 150–1275 g.

In 2021, body lengths averaged 34 cm and ranged from 17 to 52 cm. Individual animal growth (by weight) across the 2 years and 2 sites was highly variable, with an average (±SD) annual relative growth rate of 2.6 ± 15.4%. More than half the animals exhibited apparent weight loss (Fig. 3). The individuals with the greatest weight gain and loss were located within the same aggregation at Palfrey Island lagoon in 2020 and relocated in 2021. The animal with the greatest relative weight loss (−39%) was the smallest, weighing 245 g in 2020 and dropping to 150 g in 2021. The animal's basal area more than halved, from 110 to 53 cm^2. Conversely, the animal with the greatest relative growth rate (46%) was also one of the smallest, increasing from 453 to 660 g. The change in basal area was not as pronounced, from 125 to 150 cm^2.

The annual weight increment tended to decline as a function of initial body weight, although the relationship was highly variable (regression: $F_{1,67}$ = 4.4,
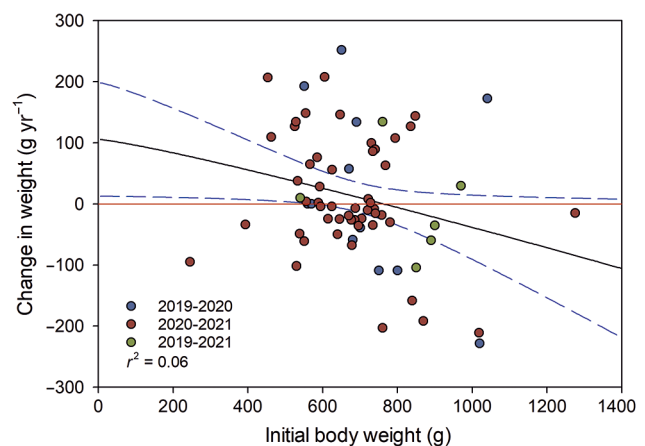

Fig. 3. Change in weight (growth increment) as a function of initial body weight of *Pearsonothuria graeffei* during the study (2019–2021) at Lizard Island, Queensland (n = 69). Red line: point of zero growth; black line: the best fit by linear regression; blue lines: 95% CIs. Points represent changes in weight for individuals weighed over the periods 2019–2020, 2020–2021, and 2019–2021 as indicated
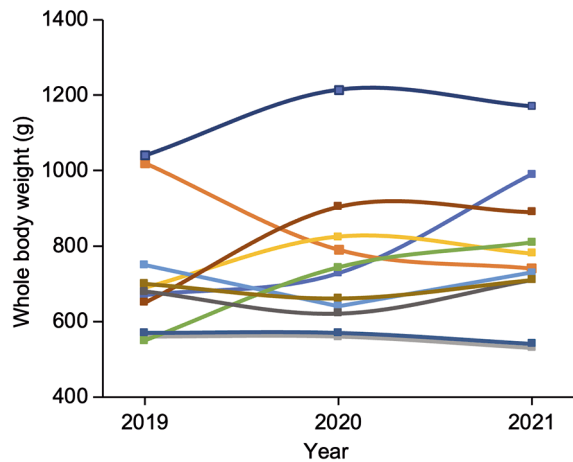
Fig. 4. Body weights of 11 *Pearsonothuria graeffei* identified across 3 sampling periods (February 2019, 2020, 2021) at Palfrey Island lagoon, Lizard Island, Queensland. Lines are smoothed trends among years
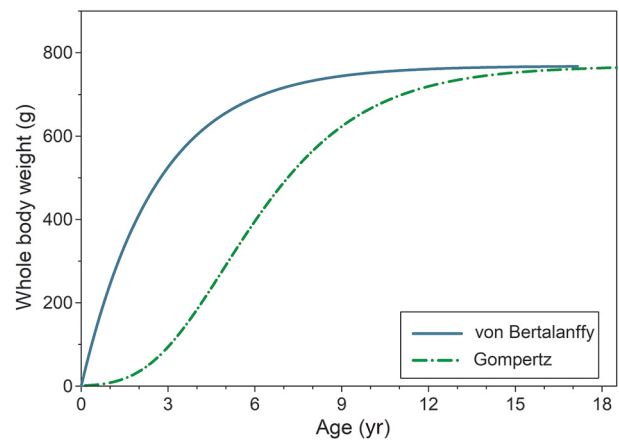

Fig. 5. Predicted age vs. body weight of *Pearsonothuria graeffei* at Lizard Island, Queensland, reconstructed using von Bertalanffy and Gompertz growth models. Note that these curves are constructed using the asymptotic weight and growth coefficient parameters derived from Fabens' equation which is itself based on the actual study data. Hence, no data can be plotted

p = 0.04, r^2 = 0.06). As a rough comparison, a majority of animals smaller than 700 g gained weight, while a majority of animals larger than 700 g lost weight (Fig. 3).

Of the 11 animals recaptured in both 2020 and 2021, weight fluctuated across the years inconsistently among individuals (Fig. 4). Some individuals gained weight in 2019, then lost weight in 2020 and vice versa, while others maintained a relatively consistent weight trajectory. Note that the measurement error was only 1–3% of the body weight of the animals and cannot account for the large weight gain and weight loss results, which were also corroborated by corresponding changes in body lengths.

The modelling from growth increments incorporated into Fabens' equation was statistically significant ($F_{1,67}$ = 4.43, p = 0.039). The model revealed an average (±SE) expected W_∞ of 769 ± 81 g for the Lizard Island population of *P. graeffei* — closely concurring with the point of zero growth in Fig. 3 — and a *K* of 0.17 ± 0.08. The constructed age-at-weight curves provide 2 growth scenarios: animals are predicted to approach the average maximum size at around 7 yr of age in the von Bertalanffy model and around 12 yr of age in the Gompertz model (Fig. 5). Under the von Bertalanffy model, an individual of 500 g would be about 3 yr old, while one of 700 g would be about 6 yr old. Those above 750 g are likely to be older than 8 yr. While the models assume continuing growth up until average maximum size, they do not account for the variability in growth shown in Fig. 4.

The rate of *M* for *P. graeffei* at Lizard Island was estimated to be 0.48 yr^{-1} based on Pauly's (1980)

model, using weight data. The value of t_{max} was then approximated to be 18 yr, with an asymmetric SE range of 12–37 yr.

4. DISCUSSION

4.1. Photographic mark–recapture

The non-invasiveness and low costs of photographic mark–recapture offer promise for future studies on holothuroid species with distinct external makings. The high recapture rates (67 and 72%) are comparable to those found for *Bohadschia argus* and *Thelenota ananas* (Purcell et al. 2016). Considering also that the animals occurred in aggregations and do not release Cuvierian tubules, which for *B. argus* is problematic for studies, these results signal *Pearsonothuria graeffei* as an ideal candidate for future studies. In contrast, Conand (1991) recaptured just 2–16% of *Actinopyga echinites* and *A. mauritiana* using physical tags over 1–2 yr, while Uthicke & Benzie (2002) recaptured 27–42% of *Holothuria whitmaei* (then described as *H. nobilis*) using genetic fingerprinting. Photographic marking avoids the issues with ejection of tags as seen in Conand's (1991) study. Recapture rates in our study are boosted by the apparent site fidelity of *P. graeffei* and the relative ease of matching the characteristic papillae and spots, which was somewhat problematic for photo-matching of *T. ananas* (Purcell et al. 2016).

We saw fresh fecal casts of *P. graeffei* in some places but could not locate the animals. Further, some animals photographically marked in 2019 were not found in 2020 but were recaptured in 2021. These observations show that cryptic/refuging behaviour played a role in some of the non-recaptures. Some animals may have died during the study and others might have moved beyond our search areas.

4.2. Long-term movement

Despite reports of *P. graeffei* being capable of substantial short-term movement (1.1 m h^{-1}: Wheeling et al. 2007), most animals in this study remained within small home ranges of around 8–11 m radius over annual timescales. This displacement range is more than 6 times greater than the average error of the GPS tracking methodology (mean: 1.28 m). The trend of tight home ranging is further underscored by data from the 11 animals relocated in both recapture years showing that they appear to move back towards the centre of the aggregations. However, a general trend of the animals moving at least a few metres suggests that either they venture far from refuges or show little fidelity to specific refuges within sites over the long term.

Using injected T-bar tags in New Caledonia, Conand (1991) found that 2 reef holothuroids, *A. echinites* and *A. mauritiana*, often moved less than 10 m during 1 yr. At 2 sites at Lizard Island, Australia, long-term movement of the large-bodied holothuroid *T. ananas* averaged 15 and 31 m in 2 yr (Purcell et al. 2016), which is also comparable to our data on *P. graeffei*. On the other hand, another large-bodied holothuroid, *B. argus*, in the same study had greater average displacements of 45 and 47 m over 2 yr, and several individuals were found more than 100 m away from the places where they were first captured (Purcell et al. 2016). At least some individuals of *Stichopus herrmanni*, another large-bodied species foraging on soft-bottom reef habitats, also exhibit long-term site fidelity (Wolfe & Byrne 2017). The site fidelity in *P. graeffei* suggests, from an ecological viewpoint, that small reef-dwelling holothuroids might not need large reserves to be well protected from exploitation. The findings of low mobility also imply that if harvested to low population density, finding mates could become difficult for individual *P. graeffei*, potentially inciting extirpation.

Similar average yearly displacements between sites and years (Table 1) and similar displacements of these sea cucumbers found in shallow and deeper waters give strength to generalizing our findings more broadly. The tendency of some larger animals (>700 g) to move longer distances (>12 m) could relate to their increased foraging requirements, as demonstrated for certain reef fishes (Grant 1997) and crown-of-thorns starfish (Keesing & Lucas 1992). Larger individuals might venture farther beyond social groups since they are (presumably) less vulnerable to predators, e.g. by size or chemical defences (Kramer & Chapman 1999). With this behaviour, individuals presumably avoid resource limitations (Kramer & Chapman 1999) as occurs in ophiuroids (Rosenberg et al. 1979), although we can only speculate at this stage.

Bare sand seemed to act as a natural barrier to movement, with no crossover of animals between the 2 reef patches at the South Island site. Some sea urchins and starfish are believed to be similarly constrained (Kriegisch et al. 2016, Pratchett et al. 2017). Seascape topography is thus a key consideration for predicting echinoderm movements on reefs (Eriksson et al. 2012, Tanita et al. 2022). Our study on *P. graeffei* indicates that some reef-dwelling holothuroids are unlikely to emigrate to repopulate disturbed or overfished areas as suggested for other benthic invertebrates (Pridmore et al. 1991, Cummings et al. 1995).

Habitat-use patterns of sea cucumbers can inform fisheries management planning (Eriksson et al. 2012, Tanita et al. 2022). While some holothuroids are found in flat habitats such as seagrass beds and sand-flats, others such as *P. graeffei* and *Actinopyga varians* occur mostly on topographically complex reef structures (Tanita et al. 2022). In this study, we observed *P. graeffei* mostly on complex reef outcrops and coral rubble substrata. Bare sand substrata away from hard reef appear to act as barriers to movement for such species. Natural borders between discrete areas of reef are advocated as boundaries of marine reserves for certain fish (Meyer & Holland 2005) and could also serve to reduce the dispersal of commercially harvested macroinvertebrates into unprotected areas.

4.3. Growth, longevity and mortality

Growth increments varied greatly among individuals in this study, and the majority (80%) of animals gained or lost up to 20% of their body weight in a year. We interpret these results cautiously because slight errors in measuring somatic weight can occur due to variable amounts of sediments in the digestive

tracts and small errors in weight readings taken on an anchored boat, although the latter error was only 1–3% of average body weight. Weight variability due to changing gonad size is likely limited, as sampling was undertaken at the end of the 4 mo spawning period for *P. graeffei* at Lizard Island (Uthicke 1994). *P. graeffei* gonads account for a maximum of 11% of whole-body weight, reducing as spawning season progresses (Mustagfirin et al. 2021).

Growth variability is a common phenomenon in sea cucumbers, influenced by factors such as food availability, stocking density (Battaglene et al. 1999, Slater & Carton 2007), and genetics (Liang et al. 2010). Growth variability is exacerbated by the ability of sea cucumbers to store large amounts of organic material (mainly proteins) in their body wall, to be reabsorbed during periods of nutrient deprivation (Prim et al. 1976), stress (Conand 1993), and possibly gametogenesis (Morgan 2000), resulting in shrinkage in weight and length.

The tendency of larger *P. graeffei* to shrink is consistent with mark–recapture studies on other holothuroids (Uthicke & Benzie 2002, Uthicke et al. 2004, Purcell et al. 2016, Dumestre 2017). Shrinkage of the body or test has been reported for some echinoderms and could be adaptive or a consequence of tissue resorption during periods of stress (Ebert 1996). While negative growth, or 'degrowth', has been reported for several other invertebrates, including planarians, cnidarians, and nemerteans (Hamner & Jenssen 1974, Oviedo et al. 2003, Hariharan et al. 2016), sea cucumbers are perhaps one of the only commercially fished animals displaying this phenomenon. We can understand that readers unfamiliar with these animals would turn to measurement errors or artefacts as likely explanations for negative growth increments.

Classic fisheries growth models do not account for this unusual trait. The asymptotic size-at-age curve generated from the estimates of K and W_∞ underestimates the age-at-maximum-size and t_{max}. Hence, while K in this study resulted in an approximated t_{max} of 18 yr, the lifespans of the animals could be several decades or more. Our finding pairs closely with longevity estimates determined for other tropical holothuroids (*H. whitmaei*, *B. argus*) based on mark–recapture (Uthicke et al. 2004, Purcell et al. 2016).

The estimated K (0.17) indicates that *P. graeffei* is relatively slow-growing, with a coefficient similar to those published for *Holothuria atra*, *T. ananas*, *A. mauritiana*, and *Isostichopus fuscus* and slower growing than *B. argus*, *Stichopus chloronotus*, and *S. vastus* (Table 3). The growth models suggest that individuals of *P. graeffei* attain 90% of their maximum size at about 7–12 yr of age.

Recaptures in 2 successive years in this study reinforce that weight change is variable and unpredictable among individuals. Some individuals gained weight, others lost weight, lost and regained weight, or gained and then lost weight in successive years. In subtropical waters, *Holothuria leucospilota* is known to undergo seasonal weight loss (Dumestre 2017). Our data provide the first evidence in the primary literature that tropical sea cucumbers can lose and later regain weight from year to year. The variable patterns of weight change among individuals imply that the circumstances of individuals play a large role in the process. In contrast, annual variations in food availability or environmental conditions would influence growth in a similar way across individuals at a site, which was not apparent.

Since the study populations were within a strictly controlled no-take scientific marine reserve and this

Table 3. Estimated life-history parameters reported for adult tropical and sub-tropical sea cucumbers in various regions. K: growth coefficient; ∞: asymptotic size (length or weight); M: natural mortality; ND: no data; GBR: Great Barrier Reef

Species	K yr^{-1}	∞ length or weight	M yr^{-1}	Region	Source
Actinopyga echinites	0.09	29.5 cm	0.64	New Caledonia	Conand (1989)
A. mauritiana	0.12	34 cm	1.45	New Caledonia	Conand (1989)
Bohadschia argus	0.33–0.39	1552–1576 g	ND	GBR, Australia	Purcell et al. (2016)
Holothuria arenicola	0.40–0.50	38.9 cm	0.85–1.02	Pakistan	Siddique & Ayub (2019)
H. atra	0.11	32.4 cm	1.02	Micronesia	Ebert (1978)
Isostichopus badionotus	0.20–0.70	ND	0.41–0.62	Mexico	Romero-Gallardo et al. (2018)
I. fuscus	0.18	36.1 cm	0.51	Mexico	Herrero-Pérezrul et al. (1999)
I. fuscus	0.21	42.5 cm	0.79	Galapagos	Ramírez-González et al. (2020)
Pearsonothuria graeffei	0.17	769 g	0.48	GBR, Australia	Present study
Stichopus chloronotus	0.45	34.2 cm	1.79	GBR, Australia	Conand (1988)
S. vastus	0.55	31.6 cm	0.30	Indonesia	Sulardiono et al. (2012)
Thelenota ananas	0.20	66.3 cm	0.50–0.63	New Caledonia	Conand (1988)

species is not exploited in Australia, the uncaptured animals could not be attributed to loss by fishing. We found that *P. graeffei* has a low rate of M compared with other sea cucumbers (Table 3). Potential reasons could include overestimation of M in earlier studies based on indirect methods or that *P. graeffei* might be less prone to predation due to its cryptic colouration, association with highly complex hard-reef structures, or defences against predation. Its defensive arsenal, which includes high levels of toxic saponins (Van Dyck et al. 2010) and cryptic colouring and behaviour, offers an explanation for this low rate of M. Indeed, the juveniles of this species have a colouration that mimics the stunning colouration of the toxic nudibranch *Phyllidia varicosa* (Putz et al. 2010).

Our study gives estimates of movement and life-history parameters from a holothuroid that is relatively small-sized among the commercially exploited species. Similarly sized holothuroids typical of hard reef surfaces, for which life-history data are lacking, include *A. lecanora*, *A. mauritiana*, *Apostichopus californicus*, *A. japonicus*, *Holothuria cinerascens*, *H. forskali*, *H. lubrica*, *H. sanctori*, and *Stichopus chloronotus*.

5. CONCLUSIONS

We present the first published evidence of the long-term persistence of sea cucumbers within dense aggregations. The potential benefits of such aggregations to sea cucumbers or the demography of their populations are not yet clear. At least in terms of movement behaviour, *Pearsonothuria graeffei* and the photographic mark–recapture method are good choices for further examination of this phenomenon.

This empirical study adds to the growing evidence that sea cucumbers can shrink after reaching a large body size. This phenomenon undermines age and longevity estimations using indirect methods (e.g. length–frequency analysis). Novel mathematical models that incorporate negative growth are sorely needed for further life-history studies on holothuroids.

P. graeffei exhibits many traits that are known in sea cucumbers to result in high vulnerability to overexploitation: aggregation behaviour, low mobility, slow growth, high longevity, and low natural mortality (Parrish 1999, Uthicke et al. 2004, Purcell et al. 2010, O'Hara & Byrne 2017). The animals appear to take up to a decade to reach a maximum body size, and they have a lifespan of several decades or more.

These biological traits are at odds with rotational harvest strategies with short (e.g. triennial) cycles. The findings also foreshadow that recovery of heavily fished populations is likely to be slow for certain species—even those that are relatively small-bodied. Indeed, the long timeframe for *P. graeffei* to reach maximum body size provides some explanation for why fishing moratoria have been variably effective across holothuroid species (Friedman et al. 2011). The evidence from this study implores a more conservative approach to conservation policy and more realistic inputs to harvest strategy models for comparable species.

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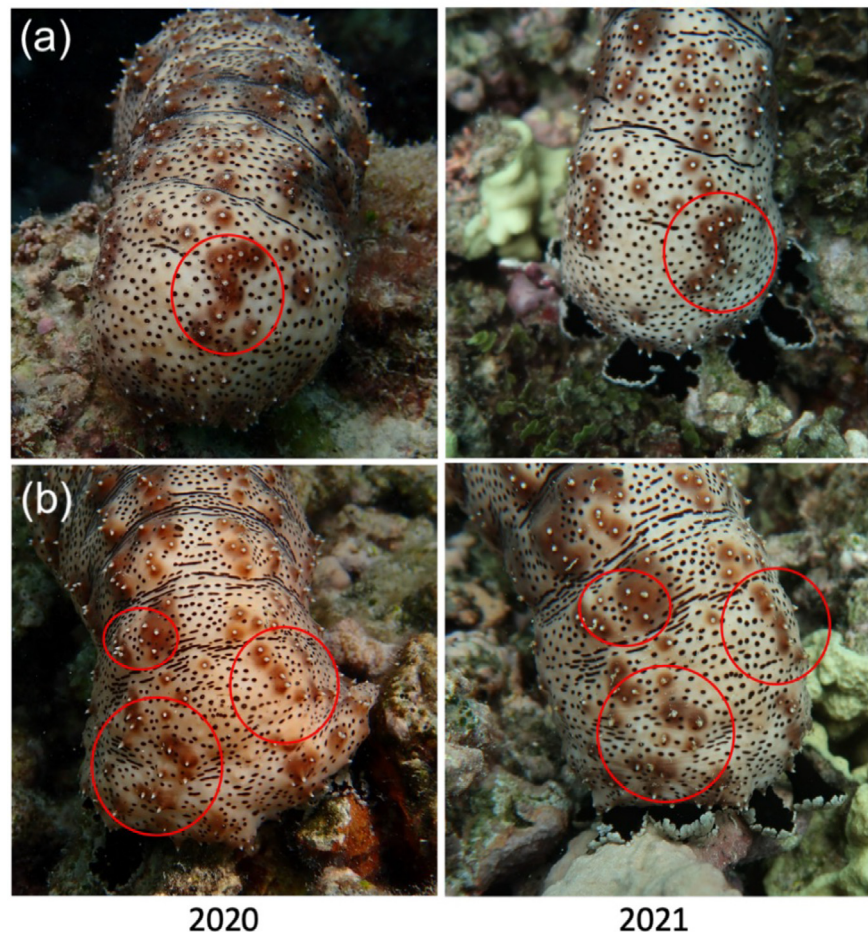
Appendix

Fig. A1. Examples of the photographic mark–recapture technique using the orientation of at least 10 white papillae, black dots and/or black lines to match 2 animals (a and b) from 2020 and 2021. Photos: (a,b) left: S. W. Purcell; (a,b) right: A. R. Hammond