Gonad development and spawning of the Vulnerable commercial sea cucumber, *Stichopus herrmanni*, in the southern Great Barrier Reef

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Despite the important ecological roles of commercial bêche-de-mer holothuroids in coral reef ecosystems their reproductive biology is poorly studied, including on the Great Barrier Reef (GBR). We investigated reproduction of Stichopus herrmanni, *a commercially important species listed as Vulnerable, at One Tree Island, southern GBR. Gonad index, histology and spawning observations indicated an annual reproductive cycle with gamete release in the Austral spring and summer (November–February), as for populations of this species at a similar latitude in New Caledonia.* Stichopus herrmanni *releases gametes episodically, spawning multiple times during summer. Assimilation of spawning observations from OTI and elsewhere along the GBR and tropical Pacific revealed that gamete release by* S. herrmanni *is influenced by the lunar cycle, with spawning taking place around the new moon in summer. This species is an aggregative spawner with a behavioural change to attain elevated positions on the reef at dusk prior to spawning. After the spawning season, gametes remaining in the gonads are reabsorbed. Spent gonads completely lacked gametes. There was a quiescence in gonad development in winter with an absence of gonads in some specimens, indicating an aestivation-like period for reproduction. By late-winter (August) recovery stage gonads were distinguished by the initiation of gametogenesis, which coincided with increasing temperature and day length. Our findings contribute to the understanding of the reproductive biology of* S. herrmanni, *a consideration for future fisheries management in the protection of this Vulnerable species, especially with respect to the increasing global trade in bêche-de-mer.*

Keywords: Holothuroidea, reproduction, bêche-de-mer, curryfish, overfishing

INTRODUCTION

Aspidochirotid holothuroids are a conspicuous component of the macro-benthos of marine environments. As deposit feeders, they process vast quantities of sediment, and thus play an important role in the mineralization and cycling of nutrients in benthic habitats (Uthicke & Klumpp, 1998; Uthicke, 1999, 2001; Purcell *et al.*, 2016; Lee *et al.*, 2017). The release of nitrogenous waste by aspidochirotids can increase the productivity of benthic microalgae and seagrass systems, a particularly important functional role in oligotrophic coral reef ecosystems (Uthicke & Klumpp, 1998; Uthicke, 2001; Eriksson *et al.*, 2010; Wolkenhauer *et al.*, 2010; Purcell *et al.*, 2016; Wolfe & Byrne, 2017a, b). The digestion and dissolution of carbonate sands by tropical holothuroids can also influence local biogeochemistry by increasing local alkalinity, potentially buffering against ocean acidification and enhancing reef resilience (Hammond, 1981; Schneider *et al.*, 2011, 2013; Wolfe *et al.*, 2018).

Many holothuroid species are harvested for the lucrative dried seafood trade, with the dried body wall product (bêche-de-mer) highly prized in the Asian market (Purcell *et al.*, 2013, 2016; Eriksson & Byrne, 2015; Eriksson & Clarke, 2015). Many commercial species are in a perilous state of conservation with 16 species, largely from tropical regions, recently listed as Threatened with extinction by the International Union for Conservation of Nature (IUCN) (Purcell *et al.*, 2013, 2014; Conand *et al.*, 2014). At least 70% of the world's tropical holothuroid fisheries are considered exploited, over-exploited or depleted (Purcell *et al.*, 2013), with many species now locally extinct (Hasan, 2005; Anderson *et al.*, 2011; Branch *et al.*, 2013; Price *et al.*, 2013; Purcell *et al.*, 2014).

Despite the important ecological roles of commercial holothuroids in coral reef ecosystems and their commercial value, we have a limited understanding of their reproductive cycles and spawning periodicity. These animals are iteroparous and investigation of 11 Indo-Pacific species including some of the most commercially valuable (*Holothuria fuscogilva*, *Actinopyga mauritiana*, *Thelenota ananas*) indicates that they spawn annually during summer (Conand, 1981, 1993a, b; Conand *et al.*, 2002; Ramofafia *et al.*, 2003). Spawning during winter is also documented including for

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H. whitmaei (Conand, 1981, 1993a, b; Ramofafia *et al.*, 2000, 2001; Shiell & Uthicke, 2006; Asha & Muthiah, 2008). While less common, biannual spawning has been observed for *H. atra* in New Caledonia (Conand, 1993a, b). The timing of spawning can differ among geographically separated conspecific holothurian populations (Ramofafia *et al.*, 2003). *Holothuria scabra* spawns year round in equatorial regions (Ramofafia *et al.*, 2003), but spawns annually in higher latitude regions (Conand, 1993a, b). These differences in spawning within a species are largely restricted to populations separated by latitudinal (north-south) oriented differences (Shiell & Uthicke, 2006). Due to the threatened status of commercial sea cucumbers, globally, we need a better understanding of their reproductive biology as a key fishery biology trait.

The curryfish, *Stichopus herrmanni*, is an abundant Indo-Pacific sea cucumber distributed from East Africa to Australia and Indonesia, which inhabits sandy lagoons, seagrass and coral reef habitats between depths of 0–30 m (Conand, 1993a, b; Eriksson *et al.*, 2013; Wolfe & Byrne, 2017a, b). *Stichopus herrmanni*, a mid- to low-value bêche-de-mer species, has become a major harvest target as populations of higher value species continue to decline (Purcell *et al.*, 2013, 2014; Eriksson & Byrne, 2015). Between 2007 and 2011, curryfish catches along the Great Barrier Reef (GBR) Marine Park, increased at an average annual rate of 200% (Eriksson & Byrne, 2015). Overall fishing pressure has resulted in a 60–90% population decline over half of the species' global range (Conand *et al.*, 2014). *Stichopus herrmanni* is listed as Vulnerable to extinction by the IUCN (Purcell *et al.*, 2014; Eriksson & Byrne, 2015).

We investigated the reproductive biology of *S. herrmanni* at One Tree Island (OTI), southern GBR. Our current understanding of the reproduction of *S. herrmanni* is based on data obtained from a population in New Caledonia, where spawning over 5 years occurred in summer (Conand, 1993a, b). Thus far, the reproductive cycle of only two bêche-de-mer species has been determined for populations on the GBR; *H. whitmaei* spawns in winter and *H. atra* spawns in summer (Shiell & Uthicke, 2006; Lee *et al.*, 2008; Thorne *et al.*, 2012). We determined the timing of gonad development and gamete maturation for *S. herrmanni* using gonad histology and the gonad index method. We also compiled observations of spawning by *S. herrmanni in situ* at OTI and elsewhere along the GBR and the Indo-Pacific. We hypothesized that reproduction of this species at OTI would be similar to that observed in New Caledonia (Conand, 1993a, b), as OTI and New Caledonia exist at similar latitudes. Our goal was to identify the spawning period of *S. herrmanni* at OTI and where possible, elsewhere on the GBR, providing important new information for the curryfish fishery to facilitate development of sustainable fisheries practices for this key bêche-de-mer species.

MATERIALS AND METHODS

Stichopus herrmanni (120–600 mm length) were collected from the lagoon (2–4 m depth) at One Tree Island (OTI) (23°30′S 152°05′E), southern GBR. Due to permit restrictions (GBR Marine Park Authority Permit G13/36027.1.) on the total number of sea cucumber species allowed to be collected annually we used data from collections over many years (Jan 2009, 2016, Feb 2011, 2013, Apr 2012, May 2009, Jul 2009,

Aug 2015, Sep 2009, Oct 2013, Nov 2008, Dec 2009). We combined data per collection month across years. To determine the gonad index, *S. herrmanni* were dissected and the coelomic fluid drained. The gonad index was calculated as the weight % of the gonads relative to the combined drained body wall and viscera weights. Averages were taken per month. The seasonal temperature cycle of the lagoon was determined from a long-term monitoring programme (http://data.aims.gov.au/aiemsrtds/station.html?station=131). Average daily temperatures in OTI lagoon were combined to calculate monthly averages between 2008 and 2017 (N = 66–99 month^{-1}).

A portion of the gonad was fixed in Bouin's fluid and processed for routine wax histology. The gonad sections (7 μm thick) were stained in haematoxylin and eosin, and gonad histological condition was determined by microscopic examination. The gametogenic state of the gonads were scored in four stages: mature, partly spawned, post-spawned/spent and recovering, as in previous studies of sea cucumber gonad histology (Ramofafia *et al.*, 2001, 2003). Digital images of gonad sections were captured using an Olympus DP70 digital camera mounted onto an Olympus BX50 microscope. Maximum egg size in mature ovaries and the thickness of the gonad wall of testes and ovaries were determined using Image-J (NIH, Bethesda, MD, USA).

Observations of spawning of *S. herrmanni* with information of the date and time of gamete release were assimilated from personal and published observations collected at OTI, elsewhere along the GBR and at other locations in the Pacific (see Table 1). Data were assessed with respect to the lunar cycle. Based on the pattern that emerged (see Results), we undertook a targeted survey for spawning behaviour at OTI around the new moon in January 2017. On three days (28–30 January, 17:30–18:30 h) coinciding with the new moon (NM), NM + 1 day and NM + 2 days, the number of spawning individuals were counted in the first 18–20 individuals randomly encountered along two transects (10–20 m) along the reef edge at Shark Alley (0.5–3 m depth), OTI, on snorkel.

To determine whether the gonad index differed among months, these data were compared by one-way ANOVA, with month as the fixed factor. Percentage data were arcsine transformed before analysis using JMP 501 (Cary, NC, USA). As required for ANOVA, homogeneity of variance and normality was checked and confirmed for all data series (Quinn & Keough, 2003). *Post-hoc* Tukey's HSD tests were used to determine where significant differences lay.

RESULTS

Ovary histology

Mature ovaries *Stichopus herrmanni* had late stage oocytes (mean diameter: 94.3 ± 0.9 μm; N = 420) filling the lumen, each located in an individual follicle (Figure 1A, B). During the mature stage the ovary wall was at its minimal thickness (14.3 ± 1.5 μm; N = 120). Partly spawned ovaries were marked by loosely packed unspawned oocytes and the presence of aggregations of phagocytes in the lumen (Figure 1C, D). Overlapping generations of oocytes were present in mature and partly spawned ovaries with a renewal of gametogenesis evident along the germinal

Table 1. Observations of *Stichopus herrmanni* spawning on the Great Barrier Reef between 1987 and 2016, with indication of lunar cycle (NM = new moon). Data taken from: 1. Uthicke (1994); 2. Conand (1989); 3. Desurmont (2008).

Location	Date	Time	Moon phase	Observer
Little Broadhurst, GBR	23/10/1987	1645	NM	
Davies Reef, GBR	18/12/1990	1700	NM + 1	
	07/12/1991	1800	NM + 1	
	08/12/1991	2005	NM + 2	
	07/01/1992	2050	NM + 2	
Lizard Island, GBR	25/11/1992	1730	NM	B. Kerrigan
	26/11/1992	1740	NM + 1	S. Uthicke[1]
Heron Island, GBR	23/12/2016	1800	NM − 6	R. Sweetapple
One Tree Island, GBR	18/12/2009	–	NM + 1	H. Eriksson
	22/01/2015	1710	NM + 1	M. Kingsford
	19/02/2015	1800	NM + 1	K. Wolfe
	28/01/2017	1730	NM	K. Wolfe, M. Byrne
	29/01/2017	1730	NM + 1	K. Wolfe, M. Byrne
–	02/12/2013	–	NM	J. Gillespie
Noumea, New Caledonia	20/02/1980	–	NM + 4	C. Conand[2]
	07/01/2008	1730–1800	NM − 1	A. Desurmont[3]
	09/01/2008	1730–1800	NM + 1	A. Desurmont[3]

epithelium (Figure 1C, D). Fully mature and partly spawned gonads were observed in late spring and summer (Nov–Feb). The largest oocytes had a mean diameter of 101.1 ± 2.8 μm (N = 120) (Figure 1B).

Spent ovaries of *S. herrmanni* were largely empty and had a thick gonad wall (27.7 ± 2.0 μm; N = 120) (Figure 1E). Variable numbers of relict oocytes and phagocytes were present. It appears that the unspawned eggs were broken down and reabsorbed. Recovery stage ovaries had basophilic previtellogenic oocytes developing along the germinal epithelium (Figure 1F). As the oocytes developed they became increasingly eosinophilic, indicating vitellogenesis.

Testis histology

Mature testes were packed with basophilic spermatozoa (Figure 2A, B). Infolds of the germinal epithelium were absent and the wall of the testis was at its thinnest (7.0 ± 0.8 μm; N = 120). Partly spawned testes had fewer sperm in the lumen and an increase in the thickness of the gonad wall (Figure 2C, D). There was evidence of renewed spermatogenesis in partly spawned testes with developing sperm present along the re-appeared folds of the germinal epithelium. Spent testes were devoid of contents, with the exception of a few unspawned spermatozoa (Figure 2E) and the gonad wall was thick (24.1 ± 1.7 μm; N = 120) and had a wrinkled appearance. In recovery stage testes, developing sperm lined the germinal epithelium. The layer of developing sperm increased as the testis developed with invaginations of the germinal epithelium protruding towards the centre of the tubule, increasing the surface area of the germinal epithelium (Figure 2F).

Seasonal trends in histology and the gonad index

Gametogenesis of *S. herrmanni* showed a seasonal pattern (Figure 3). In both sexes, mature gametes were observed from late-spring (Nov, 25%) through summer (Dec, 80%; Jan, 5.6%; Feb, 64.7%). In summer, most *S. herrmanni* were

mature (Figure 3). Partly spawned individuals were also present in summer, especially in January (77.8%). Almost all *S. herrmanni* observed in autumn (April–May) and winter (July–Aug) had spent gonads. Recovery stage gonads were evident from August (55%) through to November (75%).

OTI lagoon has a distinct seasonal temperature cycle, with daily averages ranging from 25.2–29.4°C in the summer months (mean: Dec = 26.7°C, Jan = 27.3°C, Feb = 27.2°C), to 19.4–23.9°C in the winter months (mean: Jun = 22.3°C, Jul = 21.2°C, Aug = 21.2°C) (Figure 4). The annual mean daily temperature was 24.4°C (± 0.7), with an average range of 19.4–29.4°C across the year. The gonad index of *S. herrmanni* differed between months ($F_{8,59}$ = 10.16, $P < 0.0001$), in parallel with water temperature (Figure 4). Tukey's HSD tests revealed that the average gonad index was highest in January (8.26 ± 1.4%) and February (3.65 ± 0.5%) (Figure 4). Some *S. herrmanni* lacked identifiable gonads in the winter.

Spawning observations

Records from *in situ* observations (N = 13) show that *Stichopus herrmanni* spawns from late spring (Nov) through summer (Dec–Feb) near sunset (1730–1830) (Figure 5), typically around the new moon at several sites along the GBR from the southern (One Tree Island, Heron Island), central (Little Broadhurst Reef, Davies Reef), northern (Lizard Island) GBR, and also in New Caledonia (Table 1). One spawning observation was made ∼1 week before a new moon event in December 2016 (Table 1). As is typical of aspidochirotids, *S. herrmanni* adopts an erect posture during spawning (Figure 6A).

Observations of spawning by *S. herrmanni* were most frequently documented in January with additional observations in November, December and February (Figure 5). Overall, most spawning observations were recorded on the day following the new moon, as well as on the new moon and a day before the new moon. Of the months where spawning was recorded, February had the lowest number of spawning events, with only one event recorded on the day after a new
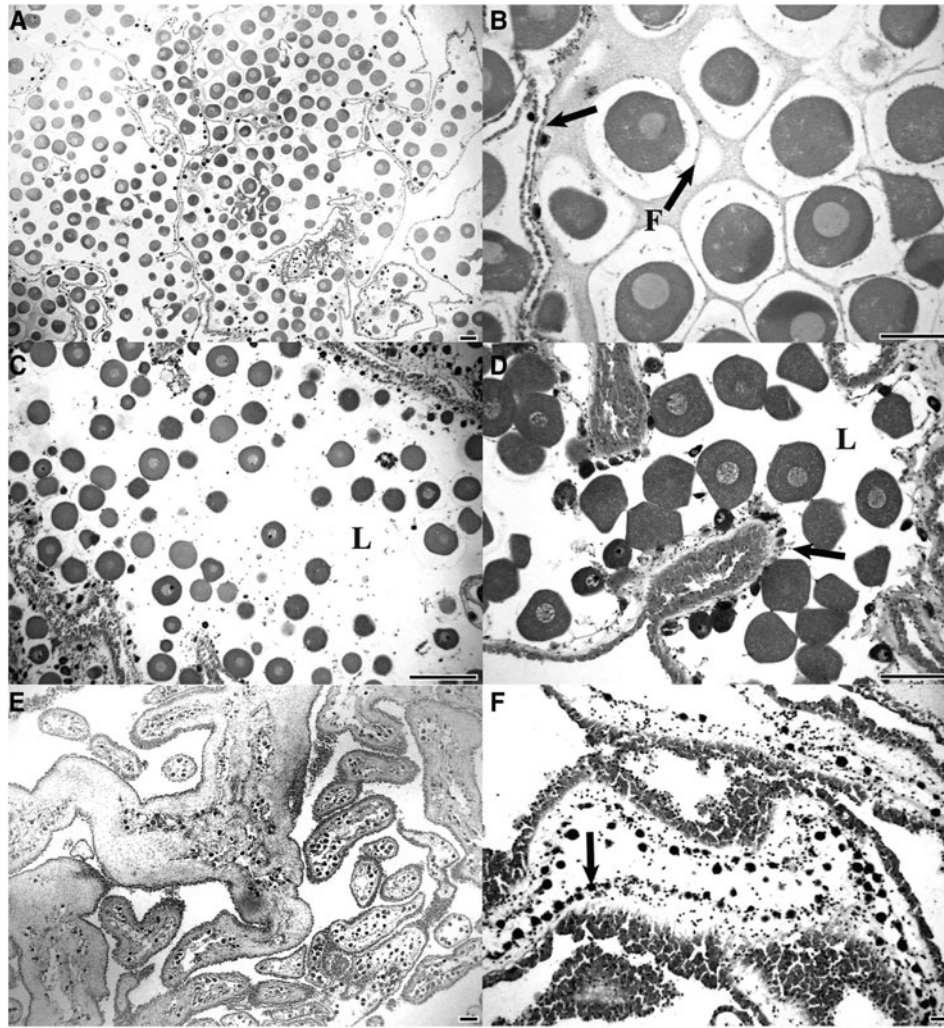
Fig. 1. Ovary histology of *Stichopus herrmanni*. (A, B) Mature ovary with the lumen filled with late stage oocytes within individual follicles (F). Note the thin gonad wall (arrow); (C, D) partly spawned ovary with oocytes scattered in the lumen (L) and early developing oocytes along the germinal epithelium (arrow); (E) spent ovaries with a few remaining oocytes and a thick wall; (F) recovering ovary with a new cohort of developing oocytes along the germinal epithelium (arrows) (scale bars = 200 μm).

moon. There was a single outlier observation, a report of spawning in late October (Table 1).

In the surveys conducted at OTI on 28–29 January 2017 (new moon and one day following) (Table 1), spawning was observed late afternoon of the NM (5/20 spawning) and NM + 1 (16/21 spawning). No spawning was observed on NM + 2 (Table 1). Males spawned before females. As sunset approached individuals were still in the process of moving to elevated positions (Figure 6A). Small fishes attacked the anterior end of spawning individuals and appeared to be consuming the released gametes (Figure 6B).

DISCUSSION

Stichopus herrmanni has an annual reproductive cycle at OTI, spawning from late spring through summer. This pattern, based on evidence from gonad index, gonad histology and spawning observations, is similar to that reported for this species in New Caledonia in a 5-year study (Conand, 1993a, b), at a similar latitude to the population investigated here. Summer spawning is reported for several tropical aspidochirotids, including other stichopodids (e.g. *Thelonata ananas*) and holothurids (e.g. *Holothuria atra*) (Conand, 1981, 1993a, b; Conand *et al.*, 2002; Ramofafia *et al.*, 2003). Although our data for elsewhere on the GBR is limited, the spawning observations suggest that *S. herrmanni* spawns during the summer in this region.

Stichopus herrmanni at OTI has an annual gametogenic cycle. Oocytes developed from late winter to summer with the fully grown oocytes evident from November, as also reported in New Caledonia (Conand, 1993a, b). The histological condition of the gonads indicated that spawning in *S. herrmanni* is partial with fully mature and partly spawned gonad tubules present throughout summer. Spawning observations also indicate that *S. herrmanni* has episodic gamete release (i.e. multiple spawning) through late-spring and summer. By April, the gonads were post-spawned and the remaining gametes appear to be reabsorbed. Resorption of unspawned gametes is a common feature of aspidochirotid and echinoderm gonads and is suggested to be associated with exogenous cues and/or an underlying endogenous rhythm (Eckelbarger & Young, 1992; Morgan, 2000; Ramofafia *et al.*, 2003). After the spawning period, the
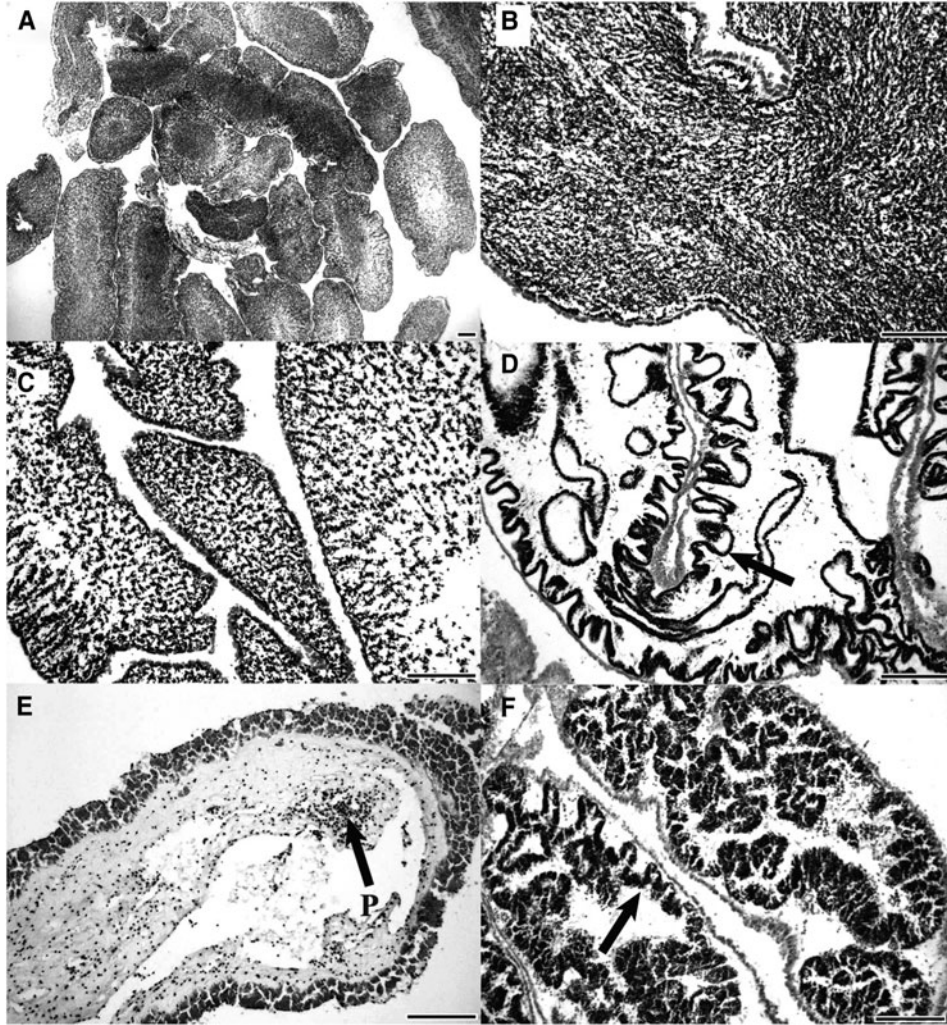
Fig. 2. Testis histology of *Stichopus herrmanni.* (A, B) Mature testis with the lumen filled with sperm; (C) partly spawned testis with sperm scattered in the lumen; (D, E) spent testis with an empty lumen. The folds of the germinal epithelium are evident (arrows) as are aggregations of phagocytes (P); (F) recovering testis with a new cohort of developing sperm along the folds of the germinal epithelium (scale bars = 200 μm).

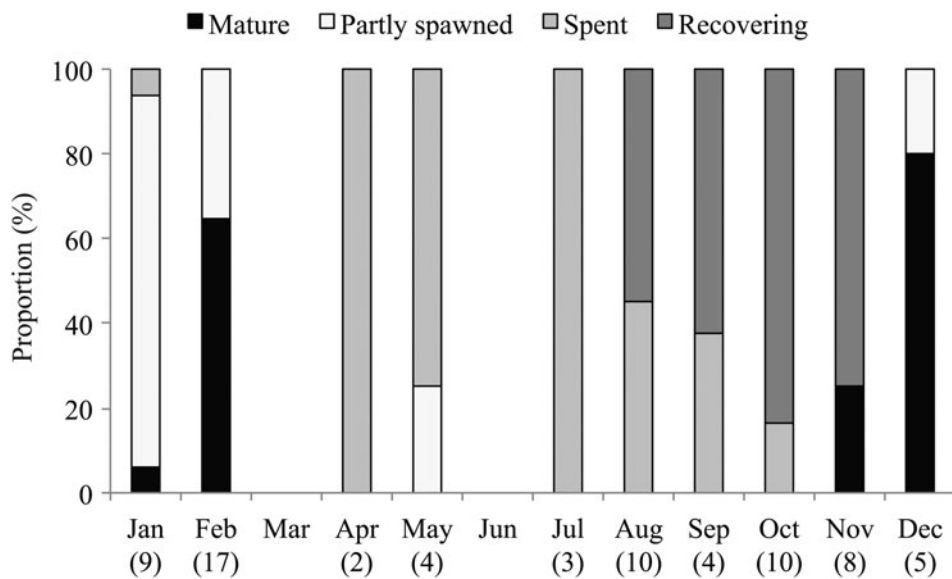**Fig. 3.** Histological condition of the gonads of *Stichopus herrmanni* (sample size in parentheses) across the seasons.
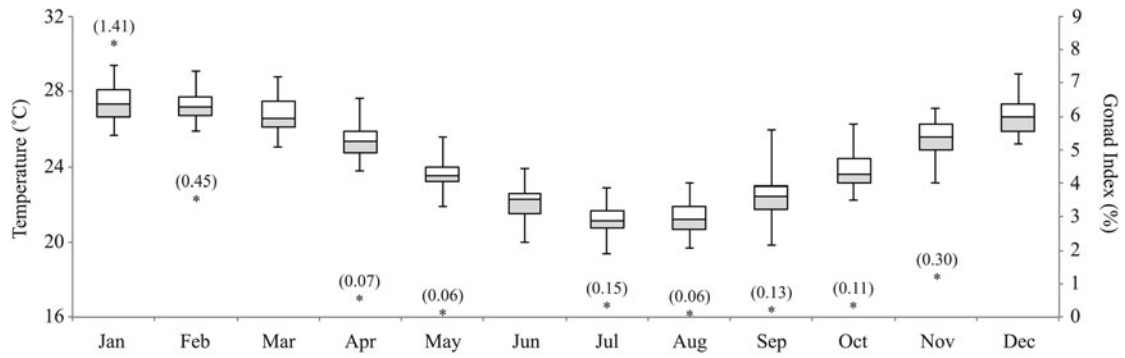
Fig. 4. Annual temperatures at One Tree Island lagoon (2008–2017) and gonad index for *Stichopus herrmanni* (sample size in parentheses).
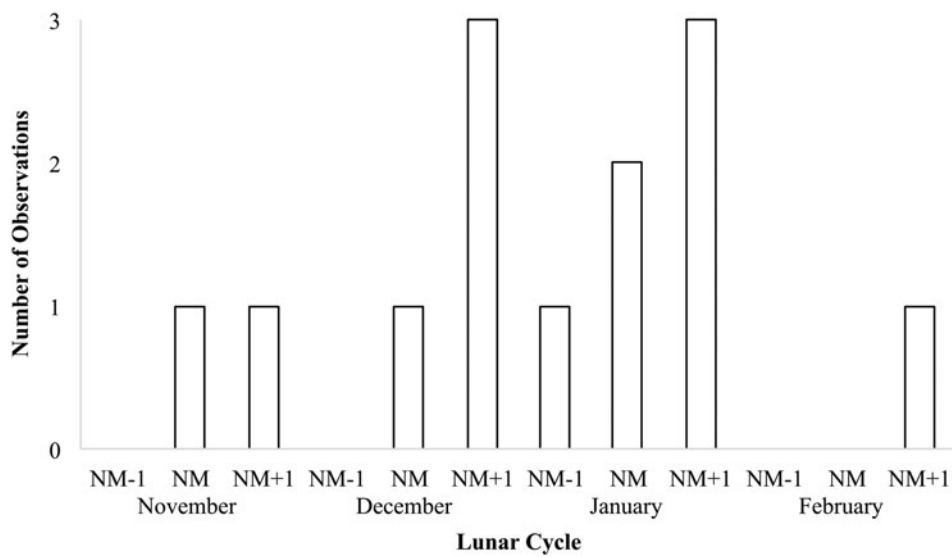

Fig. 5. Number of observations of spawning of *Stichopus herrmanni* on the Great Barrier Reef and New Caledonia with respect to lunar cycle (NM = new moon).
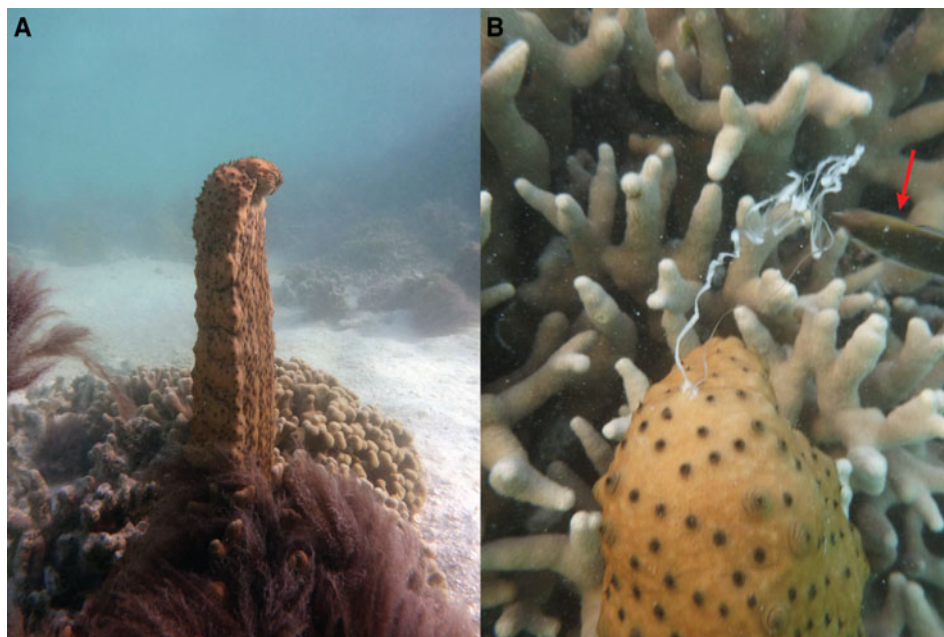

Fig. 6. Broadcast spawning behaviour of *Stichopus herrmanni* on One Tree Island, showing the (A) erect posture typical of spawning holothuroids and (B) sperm release. Spawning individuals attract fishes (arrow) to the released gametes.

gonads enter a spent/resting phase with little gametogenic activity for 6 months over winter (March/April to Sept/Oct) as also reported for *S. herrmanni* in New Caledonia (Conand, 1993a, b).

Temperature, salinity, photoperiod and food availability have been suggested to regulate the process of gametogenesis in sea cucumbers (Cameron & Fankboner, 1986; Conand, 1993a, b; Morgan, 2000; Hamel *et al.*, 2001; Conand *et al.*, 2002; Ramofafia *et al.*, 2003; Shiell & Uthicke, 2006). The gonads of *S. herrmanni* had minimum development in winter and were mature in summer, indicating gametogenesis is controlled by temperature and day length. In both temperate and tropical species, the early gametogenic phase appears to coincide with the cooler months and when days are shorter than nights, as suggested for *Actinopyga mauritiana*, *H. scabra*, *S. californicus*, *Thelenota ananas* (Cameron & Fankboner, 1986; Conand, 1993a, b; Ramofafia *et al.*, 2001). A resting phase in the winter, when the gonads are at their minimal size (or absent), is a feature described for temperate stichopodids, and is suggested to represent an aestivation-like cessation of activity due to cold conditions at high latitudes (Cameron & Fankboner, 1986). This phenomenon is also observed for tropical species, indicating that a quiescent gonad phase may be common among aspidochirotids (Morgan, 2000; Hamel *et al.*, 2001; Ramofafia *et al.*, 2003).

At OTI, *S. herrmanni* experiences distinct seasonal temperature fluctuations (~10°C), and the cold season might initiate an aestivation-like response in reproductive activity. However, *S. herrmanni* is abundant in equatorial locations where annual temperature flux is minimal. In these regions with minimal seasonal cues, continuous reproduction is predicted for echinoderms (Giese & Pearse, 1974) as occurs in equatorial populations of *H. scabra* (Ramofafia *et al.*, 2003). An assessment of the reproductive cycle of low latitude populations of *S. herrmanni* would provide insight into whether a gonadal resting phase is species-specific or varies with latitude (i.e. temperature-driven). In addition to the seasonal temperature cycle, day length and lunar cycle, which are fairly predictable among years, it would also be important to consider the influence of other environmental variables such as food availability and cyclones on reproduction of *S. herrmanni*.

The onset of gonad growth occurred in late-winter (August), correlating with increasing day length. There was an overlap in spent and recovering stages of gametogenesis in the gonads of *S. herrmanni* at OTI from August to October. Gonad maturation is reached by November at OTI and New Caledonia (Conand, 1993a, b), as temperature and day length increase. Summer spawning indicates that the small individuals observed in autumn (four months later) on nearby reefs are likely to be new recruits (Wolfe & Byrne, 2017b).

While gonad development and maturation appear to be entrained by a seasonal cycle, coinciding with the warmest temperatures and longest days, spawning and the behavioural change to move to elevated places such as coral bommies appears to be cued by the lunar cycle. This behavioural change brings individuals closer together, an aggregation-like response also observed in *H. scabra* (Morgan, 2000; Hamel *et al.*, 2001). At OTI, *S. herrmanni* began moving up coral bommies before dusk and spawning started soon after, between 1645 and 2050 h. It is likely that a more aggregated distribution and spawning continues into the night, as for *S. chloronotus* on the GBR (Babcock *et al.*, 1992). Observations

in the Solomon Islands indicate that *H. scabra* are normally scattered but progressively form pairs, trios and larger groups, peaking a few days before the new moon. Pheromones released by males have been shown to induce aggregation and spawning in *H. arguinensis* and sympatric holothuroids (Marquet *et al.*, 2018). Aggregative spawning is suggested to be an evolved strategy to increase fertilization rates and reduce predation of gametes through predator satiation (Babcock *et al.*, 1992). As for *S. herrmanni*, males spawn prior to females in other aspidochirotids (Babcock *et al.*, 1992; Morgan, 2000; Hamel *et al.*, 2001; Marquet *et al.*, 2018). Males release sperm over long periods in contrast to the short bursts of egg release by females (Babcock *et al.*, 1992).

The timing of spawning can differ among geographically separated conspecific holothurian populations (Ramofafia *et al.*, 2003). The tropical sea cucumber *H. scabra* spawns all year round in the Solomon Islands near the equator and annually in higher latitude regions, a disparity reflecting latitudinal (north–south) differences (see review, Ramofafia *et al.*, 2003). For *H. whitmaei*, spawning occurs in winter for western and eastern Australian populations at the same latitude, in the Indian and Pacific Oceans, respectively (Shiell & Uthicke, 2006). As *S. herrmanni* is such a widely distributed species in the Indo-Pacific, it remains to be determined if its reproductive cycle and spawning periodicity differs across oceans and latitude.

Successful reproduction of marine invertebrates requires individuals to be in close proximity (Pakoa *et al.*, 2014). Low population densities effectively reduce the chances of the successful fertilization, leading to reproductive failure – the Allee effect (Allee, 1938). Unlike several tropical holothuroids that can reproduce asexually (e.g. *H. atra*, Lee *et al.*, 2008), *S. herrmanni* only reproduces by sexual means. Weakened mating capacity of stocks due to overfishing leads to population declines and local extinctions with minimal population recovery, as observed for several commercial species (Uthicke *et al.*, 2004; Hasan, 2005; Purcell, 2010; Friedman *et al.*, 2011). Although the population density of *S. herrmanni* is particularly high on OTI (Eriksson *et al.*, 2013; Wolfe & Byrne, 2017a), which has been an unfished reef for decades, populations on reefs open to fishing are vulnerable to exploitation. There are no pre- or post-harvest data for any of the fished areas on the GBR, so the impact of removal of mature adults on reproductive success and the persistence of populations is not known. This is an urgent knowledge gap to address considering the Vulnerable status of *S. herrmanni* (Eriksson & Byrne, 2015).

Early research on the primary high-value target bêche-de-mer species on the GBR, *H. whitmaei*, prompted the closure of its fishery over a decade ago (Roelofs, 2004; Uthicke *et al.*, 2004). As populations of high-value species decline, low- to mid-value species are targeted leading to a sequential pattern of depletion across the Indo-Pacific (Purcell *et al.*, 2014; Eriksson & Byrne, 2015; Eriksson & Clarke, 2015). As a result, the mid-value curryfish, *S. herrmanni*, is now a major target species on the GBR (Eriksson & Byrne, 2015). It is likely that the commercial exploitation of *S. herrmanni* will mimic the patterns documented for previous target species if appropriate management strategies are not implemented (Eriksson & Byrne, 2015; Eriksson *et al.*, 2015). Based on our data, spawning closures could be considered. At present there are no constraints on fishing throughout the year for *S. herrmanni*. Importantly, this species

exhibits an ontogenetic migration within their recruitment reef (Eriksson et al., 2013; Wolfe & Byrne, 2017b). This connectivity between juvenile recruitment and adult habitats highlights the vulnerability of many marine species to overfishing (Gillanders et al., 2003; Grüss et al., 2011). However, there are no data available on S. herrmanni, and many other target commercial species, on fished reefs along the GBR.

Current approaches of bêche-de-mer fisheries are extremely exploitive and are not viable for holothuroid resources (Conand et al., 2014; Purcell et al., 2012, 2013, 2014; Eriksson & Byrne, 2015), prompting the suggestion that a paradigm shift in fisheries management is needed. Fisheries-independent information is necessary to understand the true status of the commercial fishery on the GBR, and elsewhere. This is particularly important with regard to the aggregative behaviour exhibited during spawning and the clear implications for negative Allee effects following unsustainable fishing practices.

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