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## Seasonality of asexual reproduction in *Holothuria (Halodeima) atra*, *H. (H.) edulis* and *Stichopus chloronotus* (Holothuroidea: Aspidochirotida) on the Great Barrier Reef

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**Abstract** Asexual reproduction by fission was monitored for 18 mo in populations of *Holothuria (Halodeima) atra*, *H. (H.) edulis* and *Stichopus chloronotus* on three nearshore fringing reefs and one midshelf reef in the Great Barrier Reef. Fission in *S. chloronotus* occurred exclusively between March and October, with a peak value of 31% recently divided individuals in one population in July. *H. atra* showed a similar pattern, with maxima of between 16 and 26% from May to July. In *H. edulis*, asexual reproduction occurred only between March and July, with a maximum of 17% recently divided individuals in March. Fission rates of *H. atra* and *S. chloronotus* in winter were significantly higher than in all other seasons. For *H. atra*, at least 76% of all individuals at Fantome Island were estimated to undergo fission per year, whereas only 9% undergo fission on the midshelf reef. Highest annual fission rates (43%) for *S. chloronotus* were found in a dense population on Great Palm Island. The lower-density midshelf reef population exhibited comparatively lower annual fission rates (19%). About 24% of *H. edulis* undergo fission each year. Annual fission rate and population density were positively correlated in the four populations of *S. chloronotus* and *H. atra* studied.

### Introduction

Cloning by asexual reproduction is common in many sessile marine invertebrates, especially in colonial animals (Jackson 1985). In contrast, mobile mega-fauna

rarely exhibit asexual reproduction, the major exception being the echinoderms (Emson and Wilkie 1980). Transverse fission in aspidochirotide holothurians has been reported for six *Holothuria* species (Crozier 1917; Deichmann 1922; Bonham and Held 1963; Harriott 1980) and two *Stichopus* species (Harriott 1980). On the southern section of the Great Barrier Reef (GBR), fission has been observed in *H. atra*, *H. edulis*, *S. chloronotus* and *S. horrens* on Heron Island (Harriott 1980). Fission products of the first three species are frequently observed on nearshore fringing reefs and midshelf reefs in the central section of the GBR (Uthicke 1997). *H. atra* and *S. chloronotus* are the most abundant holothurian species on the reef flats of the GBR (Harriott 1980; Hammond et al. 1985; Uthicke 1994), whereas *H. edulis* is more abundant in deeper water of the fore-reef area (Uthicke unpublished data). In several populations of *H. atra*, asexual reproduction is the main means of population size-maintenance (Ebert 1978; Chao et al. 1994). Seasonal fluctuations in fission frequency were reported for *H. atra* (Harriott 1982; Conand 1989, 1996) and *H. parvula* (Emson and Mladenov 1987). Chao et al. (1993) were the first to demonstrate that *H. atra* has a distinct seasonal periodicity, with a peak activity between July and September in Taiwanese populations; no information on fission periodicity of *H. edulis* and *S. chloronotus* is available.

In this investigation, asexual reproduction of *Holothuria atra*, *H. edulis* and *Stichopus chloronotus* was monitored for 18 mo on several reefs of the GBR to determine the seasonality of fission, spatial differences in fission frequency and the proportion of the populations reproducing by fission.

### Materials and methods

#### Study sites

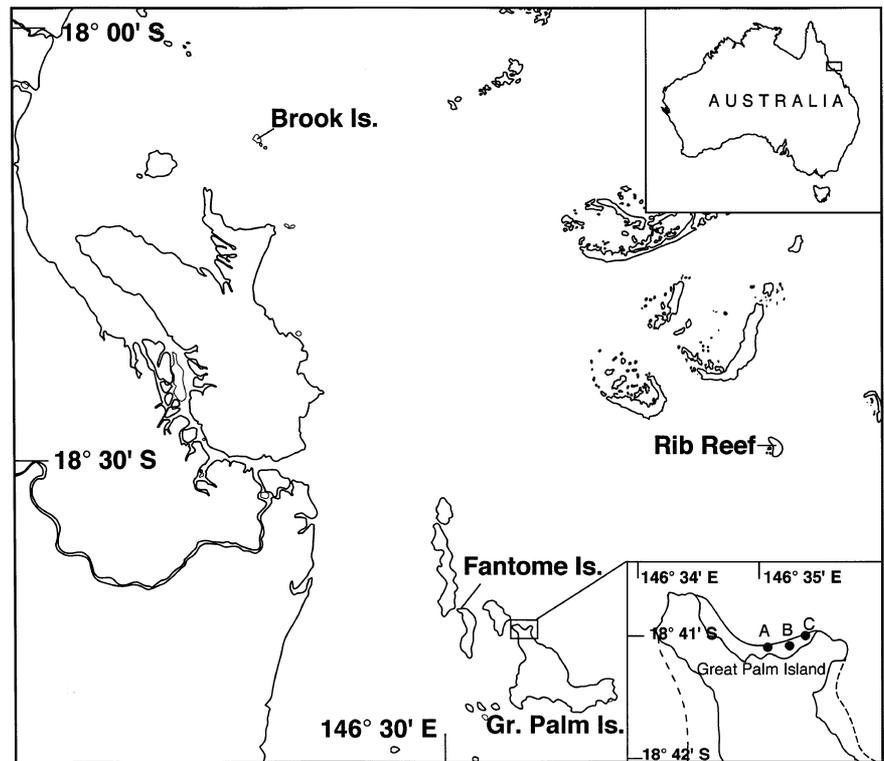
*Holothuria (Halodeima) atra* (Jaeger, 1833) occurs in water of 0.5 to 3 m depth at Brook Island, Fantome Island, Great Palm Island (Location B: Fig. 1) and Rib Reef (Fig. 1). All these reefs are lo-

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**Fig. 1** Locality map of study area (lower insert shows detailed map of Cannon Bay, Great Palm Island and Locations A, B and C)



cated in the central section of the GBR, Australia. The former three sampling sites are nearshore fringing reefs and the latter is a typical midshelf reef. *Stichopus chloronotus* (Brand, 1835) occurs at the same depth as *H. atra* at three locations on the reef flat of Great Palm Island (Locations A, B, C: Fig. 1) and on Rib Reef. One population of *H. (H.) edulis* (Lesson, 1830) occurs at 12 to 15 m on sediments in the fore-reef area off Location C of Great Palm Island. The shallow sites on the nearshore reefs were visited on a regular basis (every 4 to 8 wk) between March 1995 and August 1996; the deep population of *H. edulis* and the populations on the midshelf reef were monitored less frequently.

#### Frequency of asexual reproduction and spawning observations

Between 100 and 400 *Holothuria atra* and *Stichopus chloronotus* were examined for external signs of asexual reproduction at each location and each sampling date. A minimum of 60 *H. edulis* were examined. Individuals with either a fresh wound or with a healed wound and no regenerated anus or mouth were regarded as recently divided (Chao et al. 1993). The number of intact individuals and recently divided specimens was recorded. In February 1995, 30 *H. atra*, 20 *H. edulis* and 45 *S. chloronotus* were collected and maintained in 1000-litre outdoor tanks with flowing natural sea water. The occurrence of fission and spawning in these individuals was recorded throughout 1995.

#### Holothurian densities

Between May and August 1995, population density was estimated on one occasion at each site using transect methods. Depending on the size of the area surveyed and on holothurian abundance, two different transect sizes were used. On Rib Reef (number of transects,  $n = 9$ ) and Location B on Great Palm Island ( $n = 8$ ),  $50 \times 2$  m ( $100 \text{ m}^2$ ) belt transects were used to estimate abundances. On Brook Island ( $n = 20$ ), Fantome Island ( $n = 20$ ), Locations C ( $n = 10$ ) and A ( $n = 20$ ) on Great Palm Island and for the deep population of *Holothuria edulis* ( $n = 10$ ),  $10 \times 2$  m ( $20 \text{ m}^2$ ) transects were used.

#### Data analyses

The monthly frequency of fission products is expressed as the proportion of the total population which has recently undergone fission, with each fission product regarded as a single individual. Confidence intervals for these proportions were calculated for each sample date and reef, by the formula of Hald (1952) (see Lorenz 1992). This method assumes that each individual has a certain probability to be either a recently divided or an intact individual and provides asymmetric confidence intervals (95%) for binomial distributions.

For statistical analyses, percentage data of *Holothuria atra* and *Stichopus chloronotus* were arcsine-transformed and subjected to a two-factor analysis of variance (ANOVA) for each species, with reefs and seasons both regarded as fixed factors. Monthly observations were grouped into seasons (summer: December to February; autumn: March to May; winter: June to August; spring: September to November) since there was no within-month replication on a single reef. Observations from Rib Reef and for *H. edulis* had to be excluded from these analyses since sampling for these was less regular. The Tukey–Kramer test (TK) was chosen as a post hoc test for comparisons of means to allow for unequal sample size (Day and Quinn 1989) resulting from the unbalanced design.

The total annual fission rate was modelled by subtracting the proportion of individuals which had divided each month ( $= 0.5 \times$  percentage of fission products) from a hypothetical starting population comprised only of intact individuals. In the case of the months that were not sampled, the mean of two adjacent observations was assumed. This model assumes that the individuals counted as recently divided resulted from asexual reproduction within that month and would not be recounted on the following observation date. Although recently fissioned individuals of all three species did not completely regenerate in aquaria, initial wound-closure and regeneration of a mouth or anus took a maximum of 4 wk (Uthicke unpublished data). This information and the rapid decline in fission rate after the peaks indicate that the assumption that fission products are not recounted on subsequent sampling dates is a conservative one. Whether the individuals ac-

tually regenerate much faster in the field and more individuals than counted have divided, thus leading to higher annual fission rates, is not known. Hence, the calculated annual fission rate is considered to represent a minimum.

**Results**

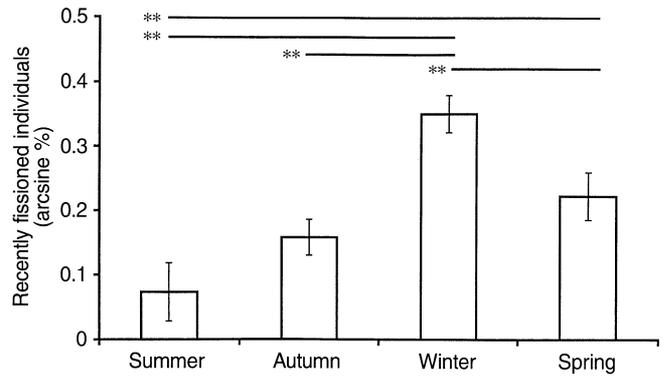
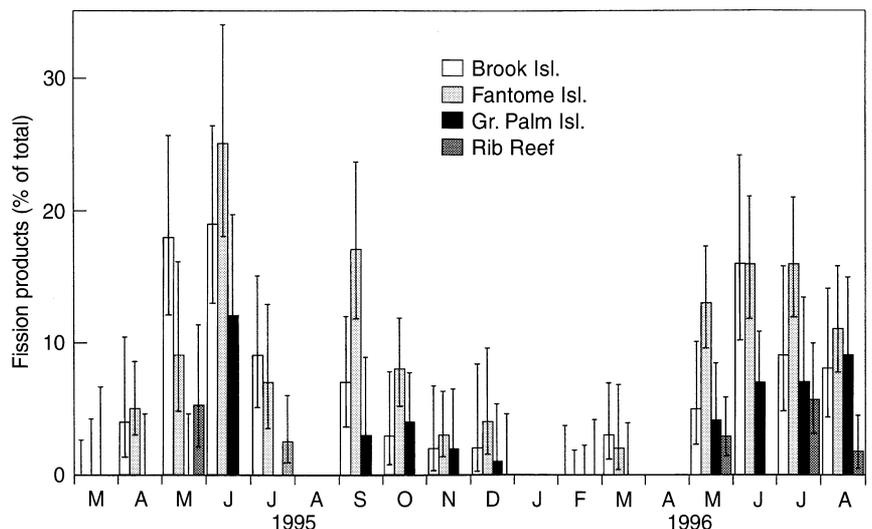
Frequency of division

The percentage of *Holothuria atra* produced by a recent fission event showed the same seasonal pattern for all the reefs examined (Fig. 2). In 1995 and 1996, asexual reproduction peaked in June, although in 1996 high values were also recorded between May and August. Recently divided individuals were found in all samples except in March 1995 and February 1996. The highest incidence of fission was encountered on Fantome Island, followed by Brook Island. Both the populations on Great Palm Island and Rib Reef showed considerably lower percentages of recent fission products. The ANOVA results for *H. atra* (Table 1) revealed significant differences in frequency of asexual reproduction between the three nearshore reefs and between the seasons. The low values on Great Palm Island were significantly different from those on Brook Island (TK test:  $p < 0.1$ ) and Fantome Island (TK test:  $p < 0.05$ ). Asexual reproduction in the winter season was significantly higher compared to all other seasons (Fig. 3).

**Table 1** *Holothuria atra*. Results of two-factor ANOVA on occurrence of recently fissioned individuals on three reefs in four seasons. Raw data were arcsine-transformed (*MS* mean square)

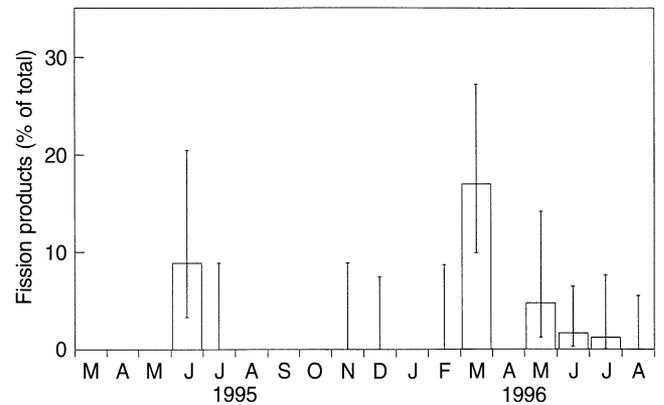
Factor	( <i>df</i> )	MS	<i>F</i>	<i>P</i>
Reef	(2)	0.038	3.48	0.043
Season	(3)	0.136	12.32	< 0.001
Reef × season	(6)	0.004	0.35	0.907
Error	(32)	0.011		

**Fig. 2** *Holothuria atra*. Frequency of fission products over course of 18 mo (error bars represent 95% confidence intervals for proportions)



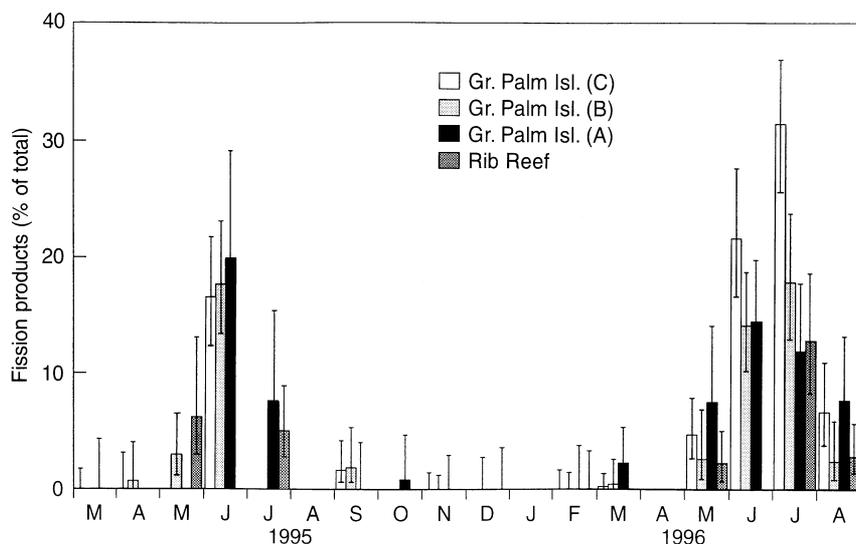
**Fig. 3** *Holothuria atra*. Frequency of recently fissioned individuals for the factor season (see ANOVA in Table 1); raw data were arcsine-transformed (horizontal lines indicate significant differences between two means determined by Tukey–Kramer comparison of means; \*\* significant difference at  $p < 0.05$ ; error bars represent  $\pm 1$  SE of the mean)

Asexual reproduction in *Holothuria edulis* at Great Palm Island was first observed in June 1995 (Fig. 4); before this, monitoring of this population had been ir-



**Fig. 4** *Holothuria edulis*. Frequency of fission products over course of 18 mo (error bars represent 95% confidence intervals for proportions)

**Fig. 5** *Stichopus chloronotus*. Frequency of fission products over course of 18 mo (error bars represent 95% confidence intervals for proportions)



**Table 2** *Stichopus chloronotus*. Results of two-factor ANOVA on occurrence of recently fissioned individuals on three locations at Great Palm Island in four seasons. Raw data were arcsine-transformed

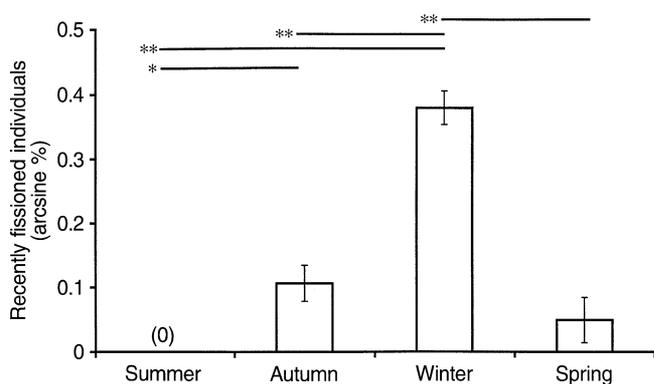
Factor	(df)	MS	F	P
Location	(2)	<0.001	0.027	0.974
Season	(3)	0.266	25.878	<0.001
Location × season	(6)	0.005	0.526	0.783
Error	(23)	0.010		

regular and no evidence of fission had been detected. All fission products of *H. edulis* found in June had regenerated by July. In 1996, asexual reproduction peaked in March and subsequently declined until no recently fissioned individuals were evident in August. Asexual reproduction of this species was not observed between August and March.

Asexual reproduction in *Stichopus chloronotus* was first detected in April 1995 and March 1996 (Fig. 5). Fission in this species was most common in June and July, and no signs of recent fission activity was detected between November and February. During the 1996 fission season, the highest incidence of asexual reproduction was found in July in Location C at Great Palm Island, and the lowest on Rib Reef. In the 1995 fission season, lowest values were observed on Rib Reef, and the three sites at Great Palm Island had fission activities on the same level. ANOVA detected no significant difference in asexual reproduction between the three locations at Great Palm Island (Table 2). However, the seasonal differences were highly significant and values of asexual reproduction were significantly higher in winter compared to all other seasons (Fig. 6).

**Aquarium observations**

The spawning period in *Stichopus chloronotus* preceded the fission season in 1995. On 20 and 21 February 1995,



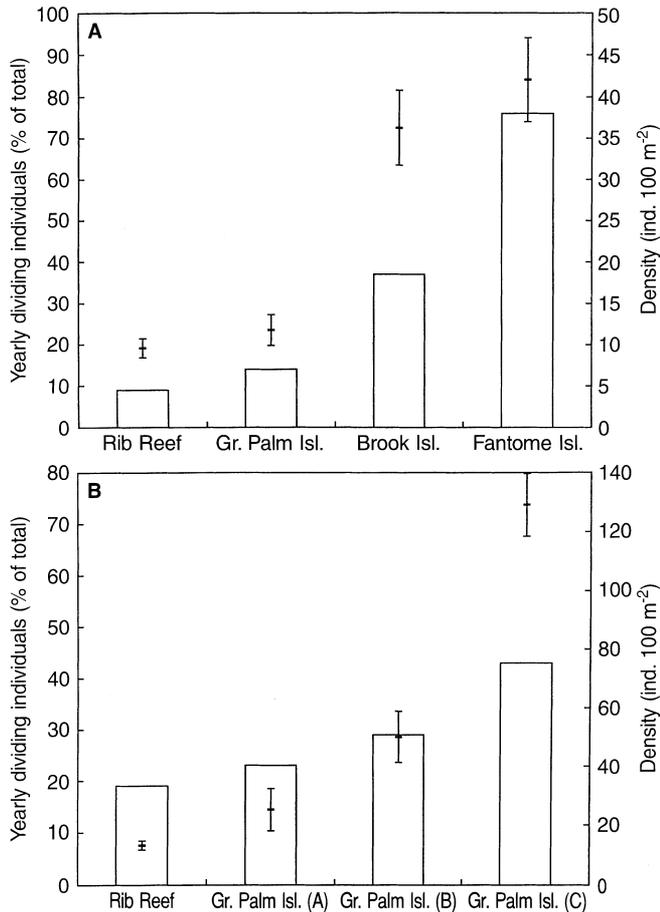
**Fig. 6** *Stichopus chloronotus*. Frequency of recently fissioned individuals for factor season (see ANOVA in Table 2), raw data were arcsine-transformed (horizontal lines indicate significant differences between two means determined by Tukey–Kramer comparison of means; \* significant difference at  $p < 0.1$ ; \*\* significant difference at  $p < 0.05$ ; error bars represent  $\pm 1$  SE of the mean)

16 individuals spawned between 18:30 and 20:00 hrs in the aquaria. A second spawning event comprising 9 individuals was observed 1 mo later (20 and 21 March), indicating a potential lunar influence. No spawning was observed after the full moons of the following months. Microscopic examination of the spawn from each single individual showed that all individuals which spawned were male.

During the 1995 fission period, 28 of the 45 *Stichopus chloronotus* held in aquaria divided. Only three *S. chloronotus* divided between the two spawning events. Most fission activity occurred in April and May. The last division event in 1995 occurred just before 8 July.

Three individuals of *Holothuria edulis* divided in the aquaria between May and August. Fission in *H. atra* was not observed in the aquaria, although individuals originated from Fantome Island, which had the highest incidence of recent fission.

Fission in *Holothuria atra* and *H. edulis* was observed on several occasions in the field, and exhibited the typ-



**Fig. 7** *Holothuria atra* (A) and *Stichopus chloronotus* (B). Estimates of annual magnitude of asexual reproduction modelled from regular observations on fission frequency (histograms) and holothurian population density (horizontal dashes) (error bars represent  $\pm 1$  SE for density estimates)

ical “twisting and stretching” mode (Emson and Wilkie 1980). The process of asexual reproduction was not observed for *Stichopus chloronotus*. In the aquarium, the fission products of this species were usually found in the morning, indicating that asexual reproduction is nocturnal and takes a maximum of 12 h.

#### Calculated annual fission rate and population densities

The estimated annual fission rate for *Holothuria atra* (Fig. 7A) showed similarly low values at Great Palm Island (14%) and Rib Reef (9%). This value was nearly three times higher at Brook Island (38%), and at Fantome Island a minimum of 76% of all individuals divide each year. The density estimates for *H. atra* (Fig. 7A) reflect the extent of asexual reproduction. The lowest population density (10 individuals 100 m<sup>-2</sup>) was observed at Rib Reef. The highest population density (42 individuals 100 m<sup>-2</sup>) was observed at Fantome Island, where annual fission rate was highest.

The population of *Holothuria edulis* at Great Palm Island had a density of 45 individuals 100 m<sup>-2</sup> and an estimated annual fission rate of 24%.

In *Stichopus chloronotus* (Fig. 7B), the relation between annual fission rate and density was similar to that observed for *Holothuria atra*. The lowest population density was at Rib Reef (13 individuals 100 m<sup>-2</sup>), and was correlated with the lowest value for asexual reproduction (19%). The second lowest values were observed at Location A at Great Palm Island followed by Location B. Location C showed exceptionally high densities (129 individuals 100 m<sup>-2</sup>), and at least 43% of the population underwent asexual reproduction per year.

## Discussion

Asexual reproduction in *Holothuria (Halodeima) atra* and *Stichopus chloronotus* displayed a distinct seasonal pattern, with significantly higher values in winter than in all other seasons. Although no statistical analyses could be performed for *H. (H.) edulis*, the observational data for this species suggest that the seasonal pattern is similar to that of the two other species; peak values for all species occurred between May and July. In Taiwan, the fission peak for *H. atra* occurs slightly later, in August and September (Chao et al. 1993). A high incidence of asexual reproduction for this species was observed during the same months on Heron Island, GBR (Harriott 1982) and in New Caledonia (Conand 1989) as in Taiwan. In Reunion (West Indian Ocean), high fission rates occurred between October and January and June to July (Conand 1996). However, with the exception of the fission rates from Taiwan and the present study, all reported fission rates have maintained a relatively high level, even outside the fission peak. One year of observations is not sufficient to describe seasonally recurring fission patterns. Physical disturbance, such as emersion during low tides (Conand 1989) and high temperatures (Bonham and Held 1963) have been suggested to trigger fission in *H. atra*. Fission on the GBR coincides with periods of low water-temperature. Emersion was never observed, even at the lowest tides. Since fission in *H. atra* seems to occur during the same months in the southern and northern hemisphere, Chao et al. (1993) excluded average water temperature as a factor controlling its periodicity, and suggested that it might be triggered by the coincidence of extreme low tides and midday temperatures. In the present study area, lowest low tides in winter occur in the daytime, but 2 to 3 h after midday, and exceptionally high water temperatures were never observed during this period (Uthicke unpublished data). Furthermore, the tide cycles at Heron Island used to substantiate Chao et al.’s theory showed lowest spring tides of similar height (max. difference = 30 cm: Australian National Tide Tables 1996) during the day and night throughout the year. Thus, on Heron Island there are no differences between low tide levels in winter, and high water

temperature during low tides is more likely to occur during summer. However, the observation that *H. atra* never underwent fission in aquaria in the absence of tidal signals may support the theory that tides have some unknown influence on fission frequency.

Nutrients such as bacteria, detritus and diatoms for sediment-feeding holothurians are generally less abundant during the cold season in the study area (Uthicke unpublished data). Thus, a potential advantage of asexual reproduction in the winter may be that cessation of feeding during regeneration results in decreased metabolic expenditure. Most holothurians lose their respiratory organs (respiratory tree) during fission (Uthicke 1997). In winter, oxygen availability can be higher due to colder water. This may reduce oxygen-exchange problems associated with the loss of the respiratory tree.

Although Harriott (1980) noted that *Holothuria edulis* and *Stichopus chloronotus* reproduce asexually, there is no published information on fission rates in these species. Tidal influence as a trigger seems unlikely for the deep population of *H. edulis*, since at depths between 12 and 15 m even a tidal range of ~2 m constitutes no drastic change to the environment. For both *Holothuria* species, the cycles of asexual and sexual reproduction seem uncorrelated. Gonads in all stages of development were found in several anterior sections of these species (Uthicke 1997). *H. edulis* in the GBR spawns all year round, whereas *H. atra* has a peak in gonad index in May/June and December/January (Harriott 1985). Hence, at least some of the asexually reproducing individuals of both species are also sexually mature. In contrast, *S. chloronotus* in the GBR has a spawning season between November and March (Franklin 1980; Uthicke unpublished data). Most individuals in both the aquaria and the field, started asexual reproduction after the spawning season was over. Gonads were never found in recent fission products, but in older anterior sections the gonads had started to develop (Uthicke 1997). It is likely that *S. chloronotus* that undergo fission in winter will spawn the following summer.

The estimates of the annual fission rate emphasise that asexual reproduction is an important means of population-size maintenance for all species on all reefs studied. At least 76% of all individuals of *Holothuria atra* at Fantome Island and up to 41% of *Stichopus chloronotus* at Great Palm Island undergo fission each year. These values correspond well to the 48 to 54% annual rate of division at one location in New Caledonia (Conand 1989). Using data from Guam (Doty 1977), Heron Island (Harriott 1982) and Enewetak Atoll (Ebert 1978), Ebert (1983) calculated that individuals of *H. atra* in some populations might even divide more than once per year.

The calculated differences in annual fission rate for *Holothuria atra* between reefs are corroborated by the significant differences in fission rates between reefs revealed by ANOVA. However, the same analyses failed to confirm differences in fission rate in locations on Great Palm Island for *Stichopus chloronotus*. The popu-

lation densities for *H. atra* and *S. chloronotus* seemed to be directly related to the annual fission rate in the respective populations; populations with high holothurian densities were also characterised by a high annual fission frequency. It is not clear which of the two parameters is cause and which is effect. It may be that some populations have a higher genetic predisposition to cloning and thus generate higher densities. The alternative explanation, that an optimum population density is pre-set by abiotic and biotic parameters such as food- and space availability at a certain reef, and the rate of asexual reproduction simply serves to keep population size at this level, seems more biologically and ecologically reasonable. Conand (1996) reported on high fission rates in *H. atra* at a eutrofied station with a dense holothurian population compared to a more pristine station where no fission occurred and population densities were lower. It may well be that increased nutrient input leads to higher food availability for sediment feeders due to higher benthos productivity (Uthicke and Klumpp 1997). Thus, the carrying capacity may be enhanced and a denser holothurian population may be sustained. Total organic carbon values and bacterial numbers are higher in sediments of Brook Island and Fantome than in Great Palm Island (Uthicke unpublished data), probably due to their proximity to the mainland. These values are likely to be even lower on Rib Reef. Thus, the high fission rates and densities of *H. atra* at the former two islands may be the result of a higher nutritional value of the sediment. However, further investigations comparing more stations on a nearshore/offshore gradient are necessary to substantiate this hypothesis.

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