Spatial distribution and temporal shifts in the biology of the commercial sea cucumber Holothuria whitmaei [Echinodermata: Holothuroidea], Ningaloo Reef, Western Australia

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Three components of the biology of the aspidochirote sea cucumber Holothuria whitmaei were investigated at Coral Bay, Ningaloo Reef, in Western Australia: 1) spatial distribution, 2) temporal changes in behaviour, and 3) reproduction biology. The spatial distribution of specimens was typical of that reported in the literature. Individuals maintained distinct preferences for outer reef habitats, particularly the outer reef flat and reef slope, at average densities of 19.3–27.1 ind ha$^{-1}$. The distribution of specimens within these habitats was heterogeneous, with up to 40% of the population being significantly aggregated, particularly at the leading edge of the reef flat perpendicular to the prevailing current. Densities within these aggregations typically exceeded 100 ind ha$^{-1}$. Two biological advantages of species aggregations were hypothesised: 1) species aggregations enhance the probability of achieving fertilisation, a process that may be impeded under typical densities; and 2) large deposits of detrital matter, an important food source for holothurians, may accumulate within these zones.

Temporal changes in the behaviour of H. whitmaei were inferred to be important with respect to feeding and reproduction. Activity of H. whitmaei was low in the morning (average max. 3.7 cm h$^{-1}$) but increased significantly through the afternoon (average max. 31.6 cm h$^{-1}$). During periods of enhanced activity, between 16.7% and 47.7% of specimens were observed on open sand, at a distance of at least one body length from the nearest coral. Contrasting results were obtained during periods of relative inactivity, when up to 23.3% of individuals were positioned beneath shelter (and thus hidden from view). Seasonal changes in activity were also apparent, with late afternoon rates of activity being significantly higher in April (31.6 cm h$^{-1}$) than in January and August (17.3 and 15.71 cm h$^{-1}$, respectively).

Regression analysis investigating the effects of water temperature, light intensity and sediment egress on rates of activity, found that the effect of these variables explained only a portion of the variation in activity (in the range 9–56%). The April increase in activity is hypothesised to be a function of reproductive activity; specifically, the strong correlation between gonad somatic index and late afternoon rates of activity ($r = 0.9$) reflects seasonal aggregation prior to spawning. Although energetically expensive, it is suggested that such behaviour may increase the frequency of gamete fertilisation, a process that may be impeded under typical population densities, and in habitats characterised by rapid (and unidirectional) water movement.

Like most tropical aspidochirote holothurians, reproduction in H. whitmaei is achieved via broadcast spawning; however, in contrast to most aspidochirote, western Pacific and eastern Indian Ocean populations of H. whitmaei spawn over an extended period during the cooler months (April–October); a pattern congruent with that observed in New Caledonia. Gonad maturation in Ningaloo Reef (eastern Indian Ocean) specimens conformed to the Tubule Recruitment Model (TRM), a developmental process whereby distinct tubule cohorts of varying gametogenic status are recruited progressively to the gonad basis. A feature of the reproductive biology of this species was also the potential for asynchronous maturation among individuals; that is, although the majority of specimens sampled at any one time maintained roughly similar stages of gonadal development, smaller numbers were sampled containing gonads at odd stages of development. Such findings may result from sampling isolated individuals that were located too far from conspecifics to receive pheromone signals, cues known to entrain synchronous gonad development in some holothurians.

The bioturbation contribution of H. whitmaei, although highly variable on a temporal scale, was found to be low in comparison with more abun-
dant coral reef dwelling holothurians such as *Holothuria atra* and *Stichopus chloronotus*. Nevertheless, *H. whitmaei* makes contact with high percentages of sediments simply by crawling, and may therefore contribute to the productivity of coral reefs by transferring dissolved inorganic nutrients directly to the benthos. The maintenance by *H. whitmaei* of highly specific patterns of distribution may have significance for trophic level cascades in the outer reef zone, particularly where this species is present in higher densities (>100 ind ha$^{-1}$).

The findings of this study, apart from highlighting the spatial and temporal biological attributes that may have facilitated feeding and reproductive success (particularly in outer reef environments), also emphasised the importance of biological knowledge to the management of sea cucumber fisheries. This study highlighted the need for further research to ascertain both the importance of species aggregations to population recruitment, and of the actual densities required to achieve high rates of gamete fertilisation. Such knowledge may help ultimately to identify suitable habitats for inclusion in marine protected areas (MPAs).

Photos (a) and (b) showing the same *Holothuria whitmaei* specimen marked for identification during the behavioural component of the study. Numbers were scratched into the dorsal tegument of each specimen to a depth of approximately 1–2 mm, such that the underlying white flesh (photo a) was clearly visible beneath the contrasting dark skin. The marks healed quickly to form a scar that was then visible for a period of up to three weeks (Photo b). Scale bars represent 18 cm and 15 cm, in Photos (a) and (b), respectively.