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Modelling habitat associations of the common spider conch in the Cocos (Keeling) Islands

L. M. Bellchambers[1,*], J. J Meeuwig[2], S. N. Evans[1], P. Legendre[3]

[1]Department of Fisheries, Western Australian Fisheries and Marine Research Laboratories, North Beach, Western Australia 6920, Australia
[2]School of Animal Biology and Centre for Marine Futures, Oceans Institute, The University of Western Australia, Crawley, Western Australia 6009, Australia
[3]Département de Sciences Biologiques, Université de Montréal, Montréal, Québec, Canada H3C 3J7

ABSTRACT: The type and configuration of benthic habitats can influence community structure of marine fauna and the effectiveness of management actions, such as spatial closures. We quantified the relationship between the distribution and density of *Lambis lambis*, an exploited marine gastropod, and available benthic habitats at the Cocos (Keeling) Islands. We used 3 modelling approaches to develop a model of the density of *L. lambis* as a function of habitat: conventional polynomial regression, Moran's eigenvector maps (MEM) and variance partitioning. Distribution and abundance of *L. lambis* was not uniform throughout the lagoon. Both the amount and configuration of habitat influenced *L. lambis* density; the highest densities were associated with moderate levels of hard macroalgae and submassive corals, and the lowest densities with seagrass and relict coral. These results illustrate that incorporating information on the distribution and patchiness of preferred habitats is essential to ensure that appropriate habitats are included in the design and implementation of long-term monitoring programs and management tools such as spatial closures.

KEY WORDS: *Lambis lambis* · Habitat associations · Spatial ecology

INTRODUCTION

Knowledge of the spatial distributions of marine populations is fundamental to understanding their ecology and has direct relevance to fisheries and conservation management (Freeman & Rogers 2003, Bellchambers et al. 2010, Harper et al. 2010, Bejarano et al. 2011). The recognition that fisheries and conservation management should encompass the protection of habitats is increasing, as the amount and configuration of habitat can influence the faunal communities it supports (Bellchambers et al. 2010, Moore et al. 2010). The first step in this process is to develop a good understanding of the relationship between the density of the exploited species and the spatial distribution of available habitat types (Harper et al. 2010, Moore et al. 2010, Bejarano et al. 2011). Previous studies have illustrated that the abundance and distribution of marine molluscs, e.g. *Strombus gigas,* is determined by the availability of preferred habitats (Stoner & Waite 1990, Tewfik & Béné 2000, Tewfik & Guzman 2003).

The common spider conch *Lambis lambis* is another strombid gastropod that is harvested by artisanal fisheries. It is found throughout the Indo-Pacific from Tonga to the east coast of Africa. A number of studies have reported the distribution of *L. lambis* (Abbott 1961); however the basic biology and ecology of the species is largely unstudied. Remains of *L. lambis* from Lene Hara Cave, East Timor, date back to ca. 35 000 years before present (YBP), showing a long history of capture in the Indo-Pacific (O'Connor et al. 2002). *Lambis lambis*, known locally as gong gong, is regarded as a delicacy by the Malays of the Australian territory of the Cocos (Keeling) Islands in the Indian Ocean, where it is extensively fished using artisanal techniques. Although how long the Cocos Malays have

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*Email: lynda.bellchambers@fish.wa.gov.au

been collecting *L. lambis* is not known, surveys indicate that collecting only became popular in the last 2 decades (Lincoln-Smith et al. 1993). The fishery is currently unregulated, but new fishing guidelines are being introduced. Whether these new guidelines will ensure the sustainability of the Cocos (Keeling) Islands *L. lambis* fishery remains uncertain.

Lambis lambis shares similarities with *Strombus gigas*, which has been severely overfished throughout the tropical and subtropical waters of the Caribbean; diverse stock management regulations have been in place in Caribbean nations since the 1970s (Theile 2003). Factors that contribute to the sensitivity of *L. lambis* to over-fishing include probable late maturation, shallow water habitat, slow movement, and tendency to aggregate in shallow water for spawning. Previous studies have suggested that the distribution and abundance of *S. gigas* are dependent on the distribution of the habitats used by the species, as well as on the processes that are inherent to their life cycle such as recruitment, migration and mortality (Stoner & Waite 1990, Stoner 2003). Assessing the sustainability of fishing and management practises on *L. lambis* at the Cocos (Keeling) Islands requires an understanding of its distribution and density in relation to available habitats. The extent and location of these habitats in relation to the fishing community can also provide information on patterns of exploitation and assist in implementing management strategies such as temporal and spatial closures.

In this study, we used several modelling approaches to explore the relationships of *Lambis lambis* density within the lagoon at the Cocos (Keeling) Islands with both habitat and distance to the main fishing village. We used (1) conventional polynomial regression, (2) Moran's eigenvector maps (MEM) that quantify underlying spatial structure through the production of spatial eigenfunctions and then (3) variance partitioning to combine the habitat variables with the MEM spatial eigenfunctions such that variation in *L. lambis* density can be apportioned between habitat variables and the underlying spatial structure of the sampling design. The use of these 3 statistical modelling approaches allowed us to develop a model of the density of *L. lambis* as a function of habitat and, more importantly, to understand the way in which the underlying spatial structure combines with habitat to determine the density of *L. lambis* within the lagoon.

MATERIAL AND METHODS

The Cocos (Keeling) Islands are located in the Indian Ocean (12° 12′ S, 96° 54′ E)(Fig. 1). The group is comprised of 2 separate coral atolls, consisting of 27 islands. The southern atoll consists of 26 islands surrounding a shallow lagoon, 2 of which are inhabited by a total population of ~600 people.

In 2008, the density of *Lambis lambis* in these islands was surveyed at 67 sites. Sites were chosen by dividing the lagoon into 40 squares of 1 by 1 geographical minutes. In each, up to 3 random sampling sites were located. At each of the sampling sites, surveys were conducted by divers on snorkel or SCUBA along 2 parallel belt transects 100 m long and 2 m wide, ~10 m apart. The total number of *L. lambis* and the percent cover of each habitat type (Table 1) were recorded along the 100 m transect. In this study only adult *L. lambis* were recorded, as juveniles are cryptic and buried in the sand. The ±SD of *L. lambis* were calculated for each site from the 2 replicate transects. Mean percentage cover for each habitat class was similarly calculated from the 2 replicate transects.

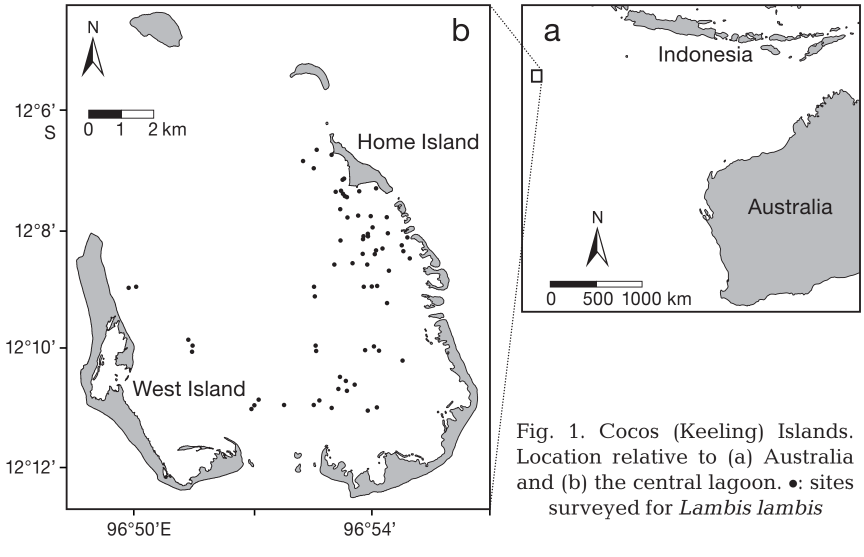

Fig. 1. Cocos (Keeling) Islands. Location relative to (a) Australia and (b) the central lagoon. •: sites surveyed for *Lambis lambis*

Modelling density using polynomial regression. *Lambis lambis* density was transformed as $\log_{10}(x + 1)$ given the positive skew in the data and the presence of many zero values. Habitat data were centred by subtracting the value for each site from the mean value across all 67 sites for each habitat class (Legendre & Legendre 1998). The second and third order monomials were then calculated using the R function *poly* which provides orthogonal monomials (R Development Core Team 2009). Polynomials allow the statistical model to account for nonlinear responses of the dependent variable in regression models (Legendre & Legendre 1998), which is appropriate for

Table 1. *Lambis lambis*. Descriptive statistics for (a) individual counts and distribution from inhabited island and (b) habitat variables along transects. Habitat genera are not a comprehensive list but represent the dominant components of each habitat type. Massive corals were defined as those solid and similar in shape in all directions, while submassive coral were less than, or not quite, solid and similar in shape in all directions. Hard macroalgae: algae that had a brittle or mineralised appearance

Variable	Dominant characteristics	Mean	SD	Min.	Max.
(a) Species density and distribution					
No. of individuals per 200 m^2		13.5	22.9	0.0	109
Minimum distance (m)		3368	2392	268	7777
(b) Habitat variables (% coverage)					
Sand		37.1	22.1	1.3	98.1
Sand and rubble		6.5	10.7	0.0	35.0
Rubble	Limestone rubble	5.9	9.5	0.0	40.0
Seagrass	*Thallasia* sp., *Thalassodendron* sp.	6.3	14.3	0.0	90.6
Macroalgae	*Hydroclathrus* sp., *Padina* sp., *Caulerpa* sp.	13.3	16.7	0.0	73.8
Hard macroalgae	*Acanthophora* sp.	11.8	13.1	0.0	56.3
Filamentous algae		4.6	7.6	0.0	35.6
Massive coral	*Porites* sp., *Pavona* sp., *Favia* sp.	3.0	5.3	0.0	23.1
Branching coral	*Acropora* sp.	4.5	9.9	0.0	40.6
Submassive coral	*Favia* sp., *Pocillopora* sp., *Favites* sp., *Porites* sp.	5.2	7.4	0.0	31.9
Relict coral	Old eroded limestone reef	1.7	4.3	0.0	25.0

habitat modelling. Minimum distance to the fishing village was used untransformed in models. Forward selection of explanatory variables in linear regression, with permutation tests, was carried out using the function *forward.sel* of the 'packfor' R-language package (version 0.0-9, 2007, http://r-forge.r-project.org/R/?group_id=195) with $p \leq 0.10$ to ensure eventual consideration of variables nearly significant at the usual $p \leq 0.05$ level. The regression R function *lm* was used to test the relationship between *L. lambis* density and distance to village as well as the degree to which inclusion of distance with the selected habitat variables improved model fit. Goodness-of-fit was assessed by the adjusted R^2 (R^2_{adj}) to control for varying numbers of variables within the models (Ohtani 2000).

Modelling density using MEM analysis. MEM eigenfunctions represent a spectral decomposition of the spatial relationships among the sampling locations at all scales, given the sampling design. Effectively, they are a series of sinusoidal waves with decreasing period representing the distances between sampling locations arranged as a straight line (Borcard & Legendre 2002). They provide a relative measure of the spatial scale over which the response variable varies, with large periods indicating variation at larger spatial scales and short periods indicating variation at smaller spatial scales (Borcard & Legendre 2002). They can be used to model the spatial structure of single response variables, as in the present study, or multivariate (multi-species) data tables, thus allowing the underlying spatial structure to be separated from the influence of environmental variables, such as the habitat variables in this study. The types of MEM variables computed in the present study were formerly called principal coordinates of neighbour matrices (PCNM, Borcard & Legendre 2002, Borcard et al. 2004, Dray et al. 2006). The relationship between the log of *Lambis lambis* density and the spatial location of the sampling sites was tested using the function *quickPCNM* from the 'PCNM' R-language library (version 1.9, 2009, http://r-forge.r-project.org/R/?group_id=195). As there was no significant linear trend in the response data, the data was not detrended prior to MEM analysis. A set of 17 MEM eigenfunctions modelling positive spatial correlation was used for modelling. Forward selection was used again through the R function *forward.sel* with $p \leq 0.10$ to determine which of the MEM eigenfunctions were correlated with the log of *L. lambis* density.

Combining habitat variables with MEMS. The selected habitat variables and all MEMs were combined into a single model so that the variation of the overall model could be partitioned between the environmental and spatial explanatory tables (Borcard et al. 1992, Peres-Neto et al. 2006) using the *varpart* function of the community ecology R-language package 'Vegan' (version 1.15–2, 2009, http://CRAN.R-project.org/package=vegan). Such variation partitioning is used to assess the contribution of environmental variables independent of underlying spatial structure as well as reducing the probability of a Type 1 error when assessing environmental variables alone, when spatial autocorrelation is present (Peres-Neto & Legendre 2010). Correlations between the selected habitat variables and the MEMs selected by *forward.sel* were evaluated using the R function *cor* in order to identify the spatial scales at which habitat categories vary. The predicted distribution of *Lambis lambis* based on the combined model of habitat variables and MEM was then generated.

Table 2. Results of forward selection indicating the change in the coefficient of determination (R^2) after accepting new habitat variables in the environmental model, as well as the cumulative and adjusted R^2, and statistical results for the additional effect of the newly accepted variables. Order refers to whether the variable is a first or second order polynomial and sign refers to the direction of the relationship

	R^2 (%)	R^2_{cum} (%)	Adj R^2_{cum} (%)	F	p	Order	Sign
Hard macroalgae	18.8	18.8	17.5	13.9	0.002	2nd	+
Submassive coral	10.6	29.5	27.1	8.9	0.004	2nd	+
Seagrass	5.8	35.2	31.9	5.2	0.039	1st	–
Relict coral	6.4	41.6	37.5	6.3	0.012	1st	–

RESULTS

Lambis lambis were observed at 51 of the 67 sites (82%) and ranged in abundance from 0 to 109 individuals in an area of 200 m^2 (mean ± SE = 13.5 ± 2.9 SE ind. per 200 m^2; Table 1). Habitats were dominated by sand, sand and rubble, or rubble, which collectively comprised 51.3% of the surveyed areas (Table 1), with any given site having a mix of habitat types. Algae and seagrass were less common, covering 29.7 and 6.3% of the area respectively. Live coral covered ~12.7% of the area, with relict coral contributing a further 1.7%. The mean distance between the surveyed sites and the main village from which most fishing for *L. lambis* occurs was 3.4 km, and it ranged from 268 m to 7.8 km (Table 1).

Lambis lambis density was predicted by 4 of the first and second order habitat monomials (Table 2). The relationship between *L. lambis* density and hard macroalgae and submassive coral was quadratic with peak densities occurring at moderate values of these 2 habitat variables. *L. lambis* density was also linearly and negatively related to both seagrass and relict coral. Combined, these 4 variables accounted for 41.6% of the variation in *L. lambis* density (Table 2). There was no relationship between *L. lambis* density and distance to the village either when distance was considered alone ($p = 0.84$) or included in the habitat model ($p = 0.61$).

Lambis lambis density was also spatially structured. The MEM analysis identified 4 MEMs out of the 17 possible eigenvectors, accounting for 37% of the variation in *L. lambis* density (Table 3). These MEMs captured spatial structure at a relatively coarse scale (MEM 4) as well as at moderate (MEM 9) and finer scales (MEMs 12 and 13), but not at the coarsest (MEMs < 4) or finest (MEMs > 13) scales modelling positive spatial autocorrelation.

The variance in *Lambis lambis* density explained by both the selected habitat variables and MEMs and adjusted for the number of variables was 51%. Variance portioning indicated that nearly half (~21%) of the variation was explained jointly by the habitat variables and the MEMs. Habitat-related processes independent of spatial location accounted for 17% of the adjusted variability, while spatial location independent of habitat accounted for 13% of the adjusted variability in the log of *L. lambis* density. The shared 21% of the variation reflects the correlation between the habitat variables and the MEMs. Relict corals were correlated with MEM4 and MEM9 and as such occurred at relatively coarse and moderate scales. Submassive corals were only correlated with MEM9 and as such appeared spatially structured at a moderate scale. Hard macroalgae was correlated only with MEM12 and thus appeared to be spatially structured at a moderate scale. Seagrass, which had the weakest relationship with *L. lambis* density (Table 2), was distributed at a moderate spatial scale (MEM9) but was the only habitat variable to be correlated with the relatively fine-scaled MEM13 (Table 4). This combined model accounted for the greatest amount of variation in *L. lambis* density and allowed us to predict the relative density of *L. lambis* across the lagoon (Fig. 2).

Table 3. Results of forward selection indicating the change in the coefficient of determination (R^2) after accepting a new Moran's eigenvector map (MEM) eigenfunction in the spatial model, as well as the cumulative and adjusted R^2, and statistical results for the additional effect of the newly accepted variables

MEM	R^2 (%)	R^2_{cum} (%)	Adj R^2_{cum} (%)	F	p
V4	11.5	11.5	10.0	7.8	0.008
V12	10.1	21.6	18.9	7.6	0.007
V9	9.6	31.2	27.6	8.1	0.008
V13	5.8	37.0	32.6	5.2	0.021

Table 4. Correlations between the selected habitat variables and Moran's eigenvector map (MEM) eigenfunctions. $^{**}p \leq 0.001$, $^{*}p \leq 0.05$

MEM	Seagrass	Hard macroalgae	Submassive coral	Relict coral
V4	0.035	0.168	−0.142	0.484**
V9	0.290**	0.094	0.232*	0.223*
V12	−0.119	−0.214*	−0.089	0.064
V13	0.250**	0.077	−0.008	0.009

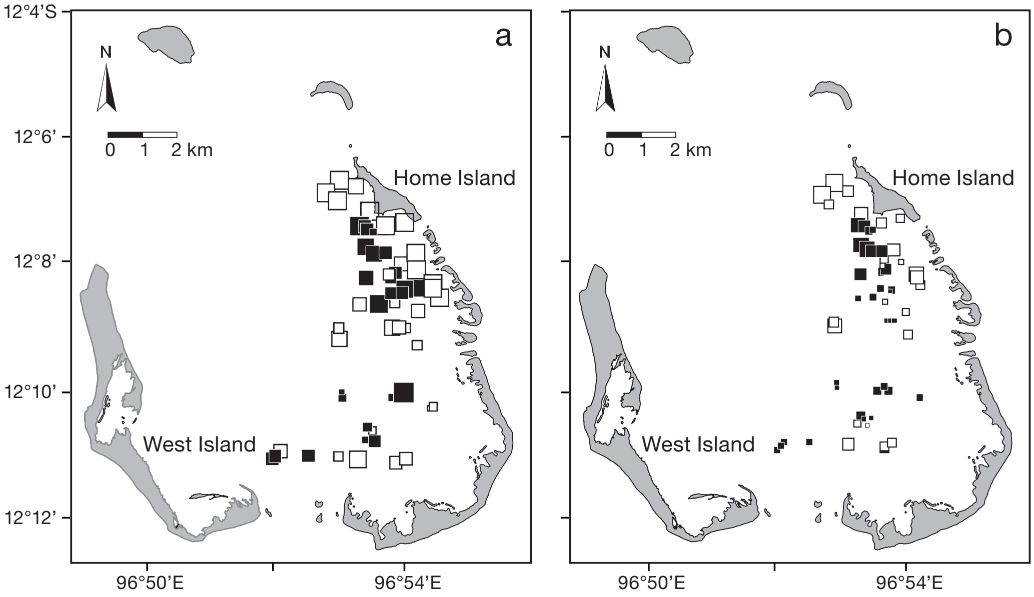

Fig. 2. *Lambis lambis.* (a) Observed and (b) predicted densities of *L. lambis* from the combined model. Square sizes are proportional to the associated values of positive (black) and negative (white) densities

DISCUSSION

The distribution of *Lambis lambis* was not uniform throughout the lagoon at Cocos (Keeling) Islands. Peak *L. lambis* densities were associated with moderate values of hard macroalgae and submassive corals and negatively correlated with seagrass and relict coral. The highest densities of *L. lambis* were observed in the northeastern part of the lagoon where the habitat consisted of sand, macroalgae and hard macroalgae, while the lowest densities occurred in shallow, sand-dominated areas and also in seagrass. The centre of the lagoon is unsuitable habitat for *L. lambis* as it is dominated by branching coral, *Acropora* sp.

No previous studies on habitat associations of *Lambis* sp. exist; however, a number of studies have shown that the density of various strombids is correlated to habitat (Torres Rosado 1987, Tewfik & Béné 2003, Tewfik & Guzman 2003). Densities of adult *Strombus gigas* were highest in algal plains and seagrass habitats in both the Turks and Caicos Islands (Tewfik & Béné 2003) and at Bocas del Toro in Panama (Tewfik & Guzman 2003) while the highest densities in La Parguera, Puerto Rico, were in rubble habitats (Torres Rosado 1987). Densities of the milk conch, *S. costatus*, at the same locations in Panama (Tewfik & Guzman 2003) and Puerto Rico were highest in rubble habitats (Torres Rosado 1987). These studies illustrate that habitat plays an important role in determining the distribution and abundance of strombids throughout their geographic range.

In our study, *Lambis lambis* density was negatively correlated with seagrass, a surprising result given the importance of seagrass as a habitat and food source for other strombids (Stoner & Waite 1990, Stoner & Waite 1991). However the majority of seagrass at Cocos (Keeling) is in the southeastern part of the lagoon, an area that is exposed for prolonged periods at low tide and has patches of anoxic sediment. In addition, a previous study suggested that *L. lambis* may feed on fine red algae rather than on seagrass (Younge in Abbott 1961); therefore a negative correlation with seagrass appears reasonable. *L. lambis* may also be associated with macroalgae and hard macroalgae for shelter; most of the *L. lambis* counted were at least partially concealed by the macroalgae and could only be located by touch. *L. lambis* were also observed clustered around the edges of submassive corals (e.g. *Porites*) where they were inconspicuous.

The distance of the survey sites from Home Island, the island on which the Cocos Malay population resides, did not have a significant correlation with the density of *Lambis lambis*. In isolation this result may indicate that fishing pressure does not affect density as much as habitat type; however several other confounding factors need to be considered. (1) The Cocos Malay population tends to practice a system of rotational fishing where they fish an area intensively and then move to another once the density of *L. lambis* declines. Given the relatively small size of the lagoon (~100 km^2), this practice tends to spread fishing effort across the lagoon rather than concentrating it close to Home Island. (2) Most families own at least 1 boat, and fishing from boats is extremely popular as it provides easy access to most fishing and collecting areas throughout the lagoon, so not just areas close to Home Island are harvested (Lincoln-Smith et al. 1993).

The inclusion of spatial structure in the habitat modelling process greatly improved the predictive capacity of the model. Also, it provided an understanding of the relationship between habitat variables and the underlying spatial structure and how the habitat variables contributed to explaining *Lambis lambis* density. In the present study, density variation seemed to be determined by spatial scales operating at moderately broad to moderately fine levels. The lack of broad-scaled MEM variables in the spatial model suggests some habitat heterogeneity within the lagoon, whereas the lack of very fine-scaled MEMs reflects a relatively open system where highly patchy microhabitats do not develop. This result also indicates that the sampling design did not allow the detection of very fine-scaled patterns resulting from population-level processes

Approximately 56 % of the variance explained by the environmental variables is shared by the selected spatial MEM eigenfunctions, indicating that these habitats occur largely at the intermediate scales modelled by the selected MEM variables. However, the selected habitat variables account for ~35 % of the explained variance independently of underlying spatial structure. This relatively high level of independence suggests that the distribution of these habitats may also reflect autonomous biotic interactions such as settlement and growth of the biota forming them.

However, 49 % of the variation in *Lambis lambis* density remains unexplained. This unexplained variation might reflect autonomous biological characteristics of *L. lambis* such as their propensity to aggregate, unmeasured environmental variables that are important descriptors of *L. lambis* habitat, or patterns in the settlement of the recruits. Aggregation in strombids is well known, although the causes and advantages are not fully understood (Catterall & Poiner 1983, Stoner & Ray 1993, Ray & Stoner 1994). Aggregation of *Strombus gigas* is a common phenomenon in important nursery areas (Stoner & Ray 1993), while *S. luhuanus* frequently occurs in local aggregations with discrete boundaries (Catterall & Poiner 1983). Personal observations of *L. lambis* at Cocos Keeling would also suggest that aggregation is a common phenomenon in this species. Had the sampling been denser spatially, we would expect the spatial model to contain very fine-scaled significant spatial variation resulting from the aggregation behaviour of *L. lambis* or other neutral processes acting at the population level (Alonso et al. 2006).

When Cocos Malays began collecting *Lambis lambis* is not known, but Gibson-Hill (1946) does not mention conch collection in his description of fishing activities in this area, which suggests that it is a relatively new fishery. Lincoln-Smith et al. (1993) estimated that between 40 000 and 55 000 *L. lambis* were collected annually, weighing between about 2.2 and 3.2 t (meat without shells). However, these estimates should be treated with caution because they are based on the impressions of the local community and have not been independently validated. Fishing for *L. lambis* occurs for about 10 d a month at low tide, usually in the morning (Parks Australia pers. comm.). Typically, between 200 and 1000 *L. lambis* are collected, if available. Up to several thousand are collected for special events such as the conclusion of Ramadan or weddings (Parks Australia pers. comm.). Large areas in the south and west of the lagoon are not presently fished for *L. lambis.* Similarly, because *L. lambis* are collected by wading and not by free or SCUBA diving as with other strombids (Tewfik & Guzman 2003), areas that contained unexploited populations of *L. lambis* were thought to exist, particularly in deeper water. Deep-water refuges have been found in other strombid populations such as for *Stombus luhuanus* on the south coast of Papua New Guinea where overfishing has occurred in shallow water but deep-water populations have not been affected (Poiner & Catterall 1988). However our results suggest that densities of *L. lambis* in the unfished areas were low due to unsuitable habitat, i.e. sand and seagrass, while deeper water areas (>2 m) generally displayed low densities of *L. lambis* due to the lack of hard macroalgae. These findings correlate with previous descriptions of the marine habitats of the Cocos (Keeling) Islands that indicate the majority of macroalgae habitats are located in the shallow eastern portion of the lagoon (Williams 1994). Given the relationship between *L. lambis* and macroalgal habitats, the location of these habitats within the lagoon and the predominately shallow nature of the lagoon, the finding that few adult *L. lambis* are found in deeper waters (>2 m) is not surprising. However, while no refuge areas for adult *L. lambis* appeared to be present in the lagoon, juveniles are believed to live embedded in the sand until sexually mature, thus only the adult stage is ever harvested (Hender et al. 2001).

Spatial closures have been one of the most effective management tools for protecting queen conch populations (Tewfik & Béné 2000). Spatial closures can protect spawning stocks at high densities and can be an important source of larvae and new recruits to exploited areas (Tewfik & Béné 2003). In the Bahamas, the density of *Strombus gigas* was 31 times greater in no-take zones than in unprotected areas outside the park (Stoner & Ray 1996). However the effectiveness of spatial closures for *S. gigas* depended on protecting critical habitats such as spawning sites and nursery grounds. Appeldoorn (1997) suggested that *S. gigas* stocks are largely dependent on self-recruitment, making the preservation of local stocks that much more important for sustainable management. Implementation of management measures to ensure sustainability of *Lambis lambis* populations at the Cocos (Keeling) Islands are especially important as it is an isolated atoll and sources of larvae from other areas are unlikely (Berry 1989). Spatial or temporal closures may be the simplest and most effective management measure for *L. lambis*, but an essential first step is to understand the relationship between the distribution and density of *L. lambis* and its preferred habitat. Given the results of this study, any spatial closures in this location would need to include intermediate levels of macroalgae and submassive coral. The fine to medium spatial scales of habitat classes that influence the distribution of *L. lambis* suggest that a number of moderately sized spatial closures would be required to support the recovery of *L. lambis* populations at the Cocos (Keeling) Islands.

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