The effects of traditional gathering on populations of the marine gastropod *Strombus luhuanus* linne 1758, in southern Papua New Guinea

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Summary. Little is known of the response of mollusc populations to predation by humans, particularly for tropical species. In this paper, we examine the effects of human predation on populations of the gastropod *Strombus luhuanus* in Bootless Inlet, Papua New Guinea, by documenting both the population biology of the shellfish and the shell-gathering practices of traditional and contemporary human groups. *Strombus luhuanus* occurs in local colonies and individuals of each sex from different colonies differed significantly in size. Sexual maturity is reached within two years after settlement, at which time the shell length stabilises at about 35–60 mm, and the shell lip thickens. There was also significant between-colony variation in density (8.35–23.39 individuals/m^2), and colonies differed in the depth range of their distributions and the frequency of human collection visits. Traditional gatherers rarely collected individuals which were buried or subtidal. Contemporary collectors used different collecting methods, and gathered subtidal populations to a depth of 2.5 m. Both traditional and contemporary collectors gathered only individuals greater than 30 mm shell length, and in the contemporary sample the probability of being gathered increased significantly with shell length. This was due to size-dependent burying, which was greatest among young juveniles and least among adults. The traditional sample contained fewer shells in the largest size category (>45 mm) and more in the smallest (<40 mm), but this difference largely represents the pooling of shells from different collecting locations rather than widespread juvenisation of colonies due to exploitation. Stromb population densities at collected sites in PNG far exceeded those in comparable uncollected sites in northeastern Australia. We conclude that *S. luhuanus* displays high resilience to all gathering practices used to date, as a consequence of both its size-dependent burying and partly subtidal distribution, which provide refugia from human predation.

Key words: *Strombus luhuanus* – Population biology – Human predation

In spite of a large body of ecological literature on foraging and predator-prey relationships, there is little information on the biological interactions of human predators with their prey, other than for managed species of fish and game.

This paper investigates the relationships between a tropical marine gastropod and human gatherers (both traditional and contemporary) in Papua New Guinea.

Currently, many species of tropical gastropod are heavily collected for food and/or the shell trade (Wells 1981; Carleton 1984; Shenoy 1984). The large numbers of shell-middens throughout the West Pacific and Caribbean provide extensive evidence of the historical importance of molluscs to pre-western human populations (Meehan 1982; Beaton 1985; Swadling 1976, 1977a, b; personal observations). However, little is known about the response of mollusc populations to collection pressures of any intensity.

The Strombid gastropod, *Strombus luhuanus* Linne 1758 is one of the most important shellfish traditionally and currently gathered in parts of Papua New Guinea (PNG) (Swadling 1977a, b; Poraituk and Ulijaszek 1981) and elsewhere in the Indo-Pacific region (Northern Australia, Catterall and Poiner 1987; Torres Strait, Poiner and Harris, in press; Bismarck Archipelago, Kirch 1987, personal communication; Fiji, L. Zann, personal communication). Traditionally, with other molluscan flesh, it probably provided a dependable source of protein when other animal foods were scarce (Allen 1977; Swadling 1976, 1977a, b). The present report forms part of a wider study of the population biology of *S. luhuanus* in Papua New Guinea and in eastern Australia.

Study areas

Studies of *Strombus luhuanus* populations are being conducted at two geographical localities: Heron Island, Australian Great Barrier Reef (Latitude 23°26′S; Longitude 151°57′E) and Bootless Bay, neat Port Moresby, Papua New Guinea (Latitude 9°32′S; Longitude 147°41′E). The present study was mainly conducted at Bootless Inlet (Fig. 1). Bootless Inlet forms part of the Port Moresby Lagoon, which is enclosed by a barrier reef. It is a relatively shallow (<40 m deep) body of water approximately 10 km long (north-south) and 8 km wide (east-west). The area has a complex bathymetry with numerous islets, shoals and reefs. The physical oceanography of the area has been summarized by Brouns and Heijs (1985). The area has marked seasonality in temperature, salinity, rainfall and wind regimes. The dominant climatic features are related to seasonal wind events, with rainfall (annual average of 1145 mm) restricted to the north-western monsoon in the austral summer (December to February) and a dry period
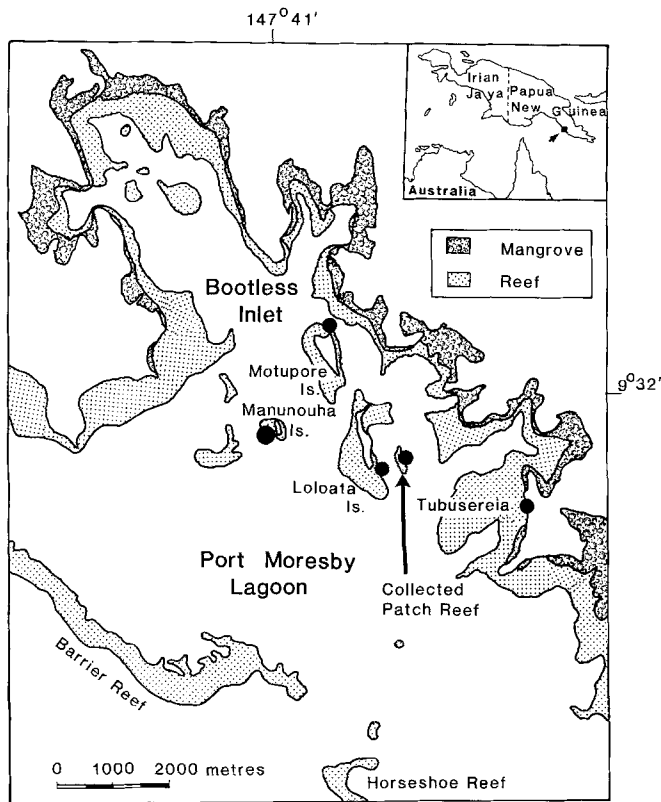
147°41'

Fig. 1. Bootless Inlet, PNG, showing study locations

during the winter (May–October) south-east trades. Mean monthly water temperature ranges from 24.9° C (August) to 31.6° C (February) and tidal amplitude for the area is 2.8 m (Brouns and Heijs 1985).

The study was sited on a cluster of three continental islets (Motupore, Loloata and Manunouha) within Bootless Inlet, each with a narrow fringing reef (Fig. 1). The bottom substrates of the fringing reefs are made up of varying proportions of sand, live coral boulders, dead coral boulders and other coral detritus; macroalgae and filamentous algae may be present in variable densities. Areas with a relatively high sand cover usually support multispecific seagrass beds, similar to those described by Johnstone (1979) and Brouns and Heijs (1985). *Strombus luhuanus* occurs mainly in the sandier areas within the seagrass beds.

At each locality, we chose several study sites, in areas where *Strombus luhuanus* was known to occur. The sites referred to in this paper are four sites for which reliable data are available over 30 to 36 months. The names and habitat characteristics of each site are: (1) Motupore Sand Spit: intertidal and subtidal sand bank of 100% deep sand; (2) Loloata reef: reef flat and subtidal slope of approximately 80% sand, 20% coral boulders and other rubble; (3) Collected Patch Reef: reef flat, of approximately 70% coarse sand, 30% coral and other rubble; and (4) Manunouha Island: subtidal slope of 100% coarse sand (Fig. 1). All sites support multispecific beds of the seagrasses *Halodule uninervis, Thalassia hemprichii, Cymodocea serrulata, Cymodocea rotundata, Syringodium isoetifolium, Halophila ovalis,* and *Enhalus acoroides.*

Motupore Island, Manunouha Island and Loloata Island have been the shellfish gathering grounds for several Motu villages for at least the past 500 years (Allen 1977).

At the time of writing they were primarily exploited by the people of the village of Tubusereia which is located on the western side of Bootless Inlet (Fig. 1). A large shell midden on Motupore Island, recently excavated by Drs. L. Groube and J. Pernetta (University of Papua New Guinea, PNG) and previously excavated by Allen (1977) and Swadling (1976, 1977a, b) is dominated in most strata by *S. luhuanus,* suggesting that this species has been a prominent feature in the diet of local inhabitants.

Materials and methods

Sampling times

The stromb population characteristics at Collected Patch Reef were sampled once only (following the collection in February 1983). The other three study sites were each visited at least six times during the period September 1980 to July 1983, on a twice-yearly schedule, in summer (December–January) and in winter (June–July).

Population biology

Catterall and Poiner (1983a, b) describe in detail the methods used in collecting data on distribution, density and reproductive activity at each study site. These methods provided counts of all individuals in each of a large number of 0.5 m² quadrats along predetermined transect lines. Size-frequency distributions were then obtained by measuring individuals on land after collecting them during sampling. Shell length (the distance from the anterior edge of the anterior canal to the apex of the shell measured along the shell axis, Fig. 2) was measured to the nearest millimetre. The thickness of the outer lip was measured (to the nearest tenth of a mm) at the shoulder of the body whorl, with calipers inserted to a point level with the notch adjacent to the posterior canal (labeled 'posterior notch' in Fig. 2) in adults, or to a point level with the junction of the lip and the shell apex in juveniles (Fig. 2).

Strombus luhuanus has separate sexes, and live adults can be sexed by observation of their genitalia (penis or genital groove; Kuwamura et al. 1983) if the foot is protruded; this was usually done prior to measuring shell dimensions. Individuals can also be categorized into broad age-classes on the basis of shell characters (Catterall and Poiner 1983a, b). In the current study, adults and juveniles were separated in the field according to the presence (adults) or absence (juveniles) of a fluted and thickened (>0.05 mm) outer lip (Fig. 2). Measured adults were also distinguished from juveniles by the presence of obvious genitalia. Similar methods were used to measure population densities and size-frequency distributions of *S. luhuanus* at totally unexploited sites on the intertidal reef flat of Heron Island.

Growth

The pattern of shell growth was investigated using mark-recapture methods. Shells were tagged by shaving a small area on the spire (removing the periostracum and a small amount of the underlying shell) and fixing a small numbered plastic disc to the shaved area with a waterproof glue (Bostik Clearstik). Because of low recapture rates in the field, samples of individuals were also held in roofless field cages on the Heron Island intertidal reef flat. These measured 2 × 2 m, and were constructed from plastic mesh
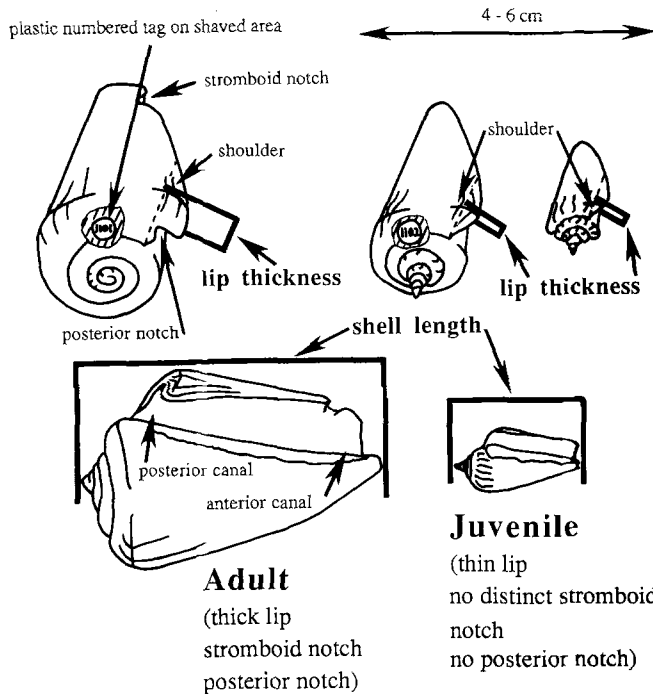
Fig. 2. *Strombus luhuanus* shell form of adults and juveniles, shell characters measured, and positioning of numbered shell tag
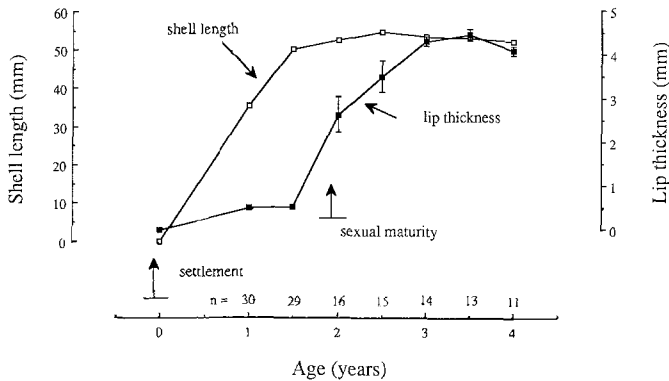

Fig. 3. The shell growth pattern of *Strombus luhuanus*. The curve shows the means and standard errors of shell length and shell lip thickness, of tagged individuals maintained in field enclosures on Heron Island, Measurements were taken initially in December 1981 (one year post-settlement, and then in June and December (or the following January) of each of 1982, 1983, and 1984. The sample sizes are shown above the bottom axis

(Nylex, 8 mm) fixed to a framework of 20 mm PVC pipes, with the lower walls buried into the substrate so that the cage bottom consisted of the normal field substrate. Strombs in these cages survived well over several years, although those in similar cages subtidally in PNG suffered high levels of predation by marine organisms.

Collecting practices

Information on current and traditional collecting practices was gathered primarily from the people of Tubusereia, using two different methods. The first method consisted of informal interviews with both old people (traditional collectors) and contemporary collectors. The following informa-

tion was obtained during interviews: age and sex of collectors; time of day or tide for collecting; collecting seasons; frequency; reason for collecting trips; collecting methods; and collecting sites.

The second method involved accompanying a contemporary family group on a collecting expedition, during which the collecting methods were observed in detail using SCUBA. A subsample of the catch was then aged, sexed and measured. The collected site was subsequently revisited on the same day, and the population sampled by the methods described earlier, to provide estimates of both its density and size composition after collection, and the portion of the population collected.

Midden sample

Allen (1977) describes the methods for the excavation and collection of samples of *S. luhuanus* from the Motupore Island midden. For the present study, three random subsamples of 100 shells selected from levels 6, 12 and 18 of excavation square N21/II were pooled to form a representative sample. These data were kindly provided by Dr. P. Swadling. All shells in the sample were categorized as either adults or juveniles according to the presence (adults) or absence (juveniles) of a fluted and thickened (>0.05 mm) outer lip (Fig. 2). Shell length was measured to the nearest millimetre.

Results

Life cycle, growth and burying

The following summary of reproductive events is based on unpublished observations during the years 1981–1986 at several localities in PNG and eastern Australia. *Strombus luhuanus* breeds mainly in spring and summer, from August to March. Large numbers of eggs (100000 to 200000) are laid in a long gelatinous string to which many sand grains are attached. This egg string is wound back on itself to form a flattened curved cylindrical egg mass approximately 4–5 cm long and 1 cm in diameter which lies on the substratum. The eggs hatch (after one week or less) into pelagic veliger larvae. The larvae metamorphose after an unknown period, probably of 2–3 weeks duration (Berg 1976; Brownell 1977).

The pattern of shell growth for a cohort of individuals one year after settlement and subsequently maintained in two field enclosures on the Heron Island reef flat is shown in Fig. 3. The density in each enclosure was maintained at high levels (approximately 15 individuals/m²). Between 18 months and two years after settling, the strombs could first be sexed from their external genitalia, at which time their shells stopped increasing in length (Fig. 3). At about the same time, the shell lips started to thicken, and continued to do so until about three years after settlement (Fig. 3). After this neither length nor lip thickness increased further.

Thus juveniles could be distinguished from sexually mature individuals (adults) on the basis of their unthickened (<0.5 mm) shell lips, irrespective of the shell length. Younger juveniles could be distinguished from older (1–2 years) juveniles on the basis of shell length, and younger adults (2–3 years) could also be separated from those more than three years postsettlement on the basis of the lip thickness.

Table 1. *Strombus luhuanus*: within and between colony comparisons of the shell length (mm) of males versus females from three of the PNG sites sampled in February 1982 (2 way-ANOVA, X = mean, SD = standard deviation, N = sample size)

Reef	Males			Females		
	X	SD	N	X	SD	N
Motupore sand spit	45.2	3.46	80	46.5	3.40	64
Manunouha Island	37.5	4.01	35	38.6	4.10	27
Loloata Island	40.4	3.48	53	41.7	3.94	70

ANOVA					
Source	df	SS	MS	F	p
Sex	1	117.3	117.3	8.68	0.004
Site	2	3201.9	1601.0	118.40	0.000
Sex × Site	2	3.4	1.8	0.12	0.880
Error	323	4368.0	13.5		
Total	328	7690.6			

Young *S. luhuanus* individuals (< 30 mm) spend a large proportion of the time buried. As they grow to maturity less time is spent buried, although even adults spend some time buried (Catterall and Poiner 1987). The proportion of the population buried frequently increases during adverse weather conditions (Catterall and Poiner 1983a, b, 1987).

Distribution and density

Strombus luhuanus frequently occurs in local aggregations or colonies which are relatively dense with discrete boundaries (Catterall and Poiner 1983a, b). Four types of aggregation have been described: mixed age-class colonies, juvenile colonies, mating aggregations, and clusters (Catterall and Poiner 1983a, b). The former two are termed colonies, because they persist over time (juvenile > 18 mo; mixed

age-class > 7 yr) and exhibit some coordinated movements (Catterall and Poiner 1983a). Mixed age-class colonies are the most commonly encounted and vary in size (500–5000 m²) and density (0.5–30/m²).

All four of the PNG study sites described earlier contained mixed age-class colonies. Within a colony females were significantly larger than males, and individuals of each sex from different colonies differed significantly in size (Table 1).

A comparison of the mean total densities (all age and sex classes for the summer of 1983) for the mixed age-class colonies at all four PNG study sites reveals significant between-colony variation in density (Table 2). Colonies also differed in the depth range of their distributions and the frequency of contemporary collection visits (Table 2). For example, the Manunouha Island site (a popular anchorage for visitors from the city of Port Moresby) had the highest densities of strombs at all study sites from 1980 until the summer of 1983 when it underwent intensive collecting of adults and the population decreased from 27.2/m² to 11.11/m² (Table 2) to one dominated by juveniles. In contrast, the Loloata Island site in our experience was never collected and we did not meet any person from Tubusereia who knew of its existence. Motupore Island Sand Spit was rarely collected because of the presence of the long seagrass *E. acoroides* and its proximity to the University of PNG's Research Centre located on the Island. The Collected Patch Reef is relatively close to Tubusereia and was probably the most intensively collected of the four sites (Fig. 1; Table 2).

Gathering

Traditional practices

The results of the interviews with the traditional (older) collectors (N = 9) suggested that the primary collectors were female. Collecting occurred during the day-time on an ebbing tide, year round, although there was some recognition of 'good' collecting periods, for example the winter (June

Table 2. *Strombus luhuanus*: depth range (m below MHW) and the degree of current collecting of the four mixed age colonies studied at Bootless Inlet, PNG, with a comparison (ANOVA, Sokal and Rohlf 1981) of total densities (No/m² in 1 m² units) among colonies (all ages and sexes), in February 1983 and February 1982 for Manunouha Island (X = mean, SD = standard deviation, N = sample size). Only 1983 data were used in the ANOVA

Reef	Density (No/m²)			Depth		Current collecting
	X	SD	N	max	min	
Motupore Sand Spit	12.20	12.55	10	3.5	0.5	little
Manunouha Island 82	27.21	14.33	85	9.0	1.5	exploited
Manunouha Island 83	11.11	15.96	90	9.0	1.5	exploited
Loloata Island	23.39	17.80	90	4.0	1.0	none
Collected Patch Reef	8.35	4.27	20	2.0	1.0	exploited

ANOVA					
Source	df	SS	MS	F	p
Sites	3	8374.1	2791.4	10.97	0.000
Within sites (error)	206	52674.4	255.7		
Total	209	61048.5			

Table 3. *Strombus luhuanus*: a comparison of the frequency of size classes collected by contemporary gatherers at the Collected Patch Reef with that of the resident population. The resident and gathered samples differed significantly in size over all length classes (contingency $X^2 = 85.4$, df = 6, $P < 0.001$). For large shells only, the resident and gathered samples also differed significantly (contingency $X^2 = 9.79$, df = 2, $P < 0.01$) and the component proportions (bracketed) differed significantly (tests of proportions, $P < 0.05$) for the size-classes 35–39 mm and ≥ 45 mm

| | Shell length (mm) | | | | | | | | | |
| | Small | | | | | Large | | | | |
Group	<20	21–24	25–29	30–34	Total	35–39	40–44	≥45	Total	Grand total
Resident	27	30	4	1	62	12 (0.11)	70 (0.63)	29 (0.66)	111 (1.00)	173
Gathered	0	0	0	2	2	8 (0.04)	101 (0.54)	78 (0.42)	187 (1.00)	189

and July) day-time low tides corresponding with the solstice. Each family group probably collected 2–3 times/week although the number collected and the frequency of collection increased during times when there was a shortage of fish. There was no forward planning, and decisions to collect were made on a day to day basis. Collecting trips were primarily for *S. luhuanus* but collecting also occurred during fishing trips with the men. Collecting was for home consumption. There was no marketing and little exchange.

Strombus luhuanus were gathered by walking and wading, following the tide as it ebbed. Occasionally, the collectors dived for shellfish but the gathering depth rarely exceeded 1m. Known sites were checked to find a 'good one' although the criterion for 'good one' was vague. A selected site was then collected for periods of up to several weeks. The people interviewed were vague about site selection and the number of times a selected site was gathered. Collectors preferred to gather from sites with short seagrass species (< 30 cm) rather than sites supporting dense stands of the long-leafed (0.5 to 1.3 m) seagrass *E. acoroides*.

Mainly surface strombs were collected and collectors did not distinguish between males and females. Thin lipped animals were recognized as juveniles, but individuals were not rejected by collectors on the basis of lip thickness.

Current practices

Interviews. The results of the interviews ($N = 46$) with the contemporary collectors suggest that gathering techniques had changed in recent times. Many of the inhabitants of Tubusereia were in paid employment in the near-by city of Port Moresby, and a monetary economy had been established. Population densities and unemployment rates in the region were both relatively high at the time of the study. Men and boys now frequently collected shellfish, and it was no longer regarded as principally a women's activity. Contemporary collectors, especially the younger men, collected subtidal as well as intertidal shellfish by free-diving using plastic swimming goggles to a maximum depth of 2.0–2.5 m. The area accessible to gatherers had increased due to the widespread use of outboard motors. However, some mixed aged colonies or parts of colonies still appeared to be unknown to many gatherers (for example, the studied Loloata Reef colony, Fig. 1), and several colonies extended below the usual maximum collecting depth (Table 2).

Quantitative data on the frequency of collecting trips was difficult to collect. Discussions with one extended family group of 27 people (15 adults) suggested they consumed

at least one *S. luhuanus* meal per week. From the interviews with the extended family-group and others from Tubusereia, there was little doubt that *S. luhuanus* was a common and valued feature of the current diet of the people of Tubusereia.

Collecting Expedition. The Collected Patch Reef site had been harvested for four days prior to our visit. During the collecting expedition six collectors gathered 1100 individual *S. luhuanus* in 45 minutes. This fed the family of 27 people at least twice. This collection had no visible impact on surface densities. The collectors gathered *S. luhuanus* by swimming down to the bottom, quickly gathering individuals into a plastic bag held in one hand and then returning to the surface for a breath of air. This procedure was repeated until the plastic bag was full, at which time the collectors returned to the boat where the catch was accumulated.

The underwater observations suggested that there was no selectivity by the contemporary collectors as they did not appear to discriminate between small and large individuals, or thin- and thick-lipped individuals, although they reported that they could discern between them underwater. Neither was there evidence of size selection whilst sorting of the accumulated catch. There appeared to be no discrimination between surface adults and surface juveniles, but buried individuals were not collected.

Effects of collecting

Gathered strombs. There was a significant difference between the size-structure of the resident stromb population and that segment of the population gathered by the contemporary collectors (Table 3). Although large numbers of juveniles less than 30 mm were present in the resident population none of these were collected (Table 3). Even when only the largest three size-classes were considered, the probability of being gathered increased significantly with increasing length (age) of strombs (Table 3). Possible reasons for these differences are: (1) larger strombs were less likely to be buried; (2) larger strombs were more visible; (3) larger strombs were less likely to be rejected.

Size-dependent burying may be related to age, and the data permit further tests of this relationship (Table 4). The probability of strombs being buried at the Collected Patch Reef was high for all ages, but varied significantly among ages, being greatest among young juveniles and least among adults (Table 4). Furthermore, within the larger shell

Table 4. *Strombus luhuanus*: a comparison of the the probability of being buried in relation to age at the Collected Patch Reef site. The buried and surface samples differed significantly in size (contingency $X^2 = 20.10$, df = 2, $P < 0.001$) and the component proportions differed significantly (tests of proportions, $P < 0.001$)

| Group | Shell length (mm) | | | |
	<30 (tiny juveniles)	≥30 (thin-lip juveniles)	≥30 (thick-lip adults)	Total
Buried	61 (0.42)	37 (0.25)	49 (0.33)	147 (1.00)
Surface	0 (0.00)	3 (0.14)	18 (0.86)	21 (1.00)

Table 5. *Strombus luhuanus*: a comparison (Chi-squared contingency analyses) of age and size in relation to the risk of being gathered at the Collected Patch Reef site (larger (>30 mm) strombs only). In each cell the proportionate representation of each lip class in each of the shell length totals is presented in parenthesis (NS = nonsignificant)

| Group | Shell length (mm) | | | |
	30–39	40–44	≥45	Total
Resident sample				
thick-lip (adult)	3 (0.23)	41 (0.59)	24 (0.83)	68 (0.61)
thin-lip (juvenile)	10 (0.77)	29 (0.41)	5 (0.17)	44 (0.39)
Total	13 (1.00)	70 (1.00)	29 (1.00)	112 (1.00)

Test of resident table (length versus lip): $X^2 = 12.64$, df = 2, $P < 0.005$

Group	30–39	40–44	≥45	Total
Gathered sample				
thick-lip (adult)	8 (0.80)	86 (0.85)	69 (0.88)	163 (0.86)
thin-lip (juvenile)	2 (0.20)	15 (0.15)	9 (0.12)	26 (0.14)
Total	10 (1.00)	101 (1.00)	78 (1.00)	189 (1.00)

Test of gathered table (length versus lip): $X^2 = 0.44$, df = 2, NS

Tests within each length class (sample versus lip)

X^2	5.24	13.92	0.21
p (df = 1)	<0.05	<0.001	NS

length-classes there was a significant difference in the proportion of thin- and thick-lipped individuals when the resident population was compared to the gathered sample (Table 5). Among the resident strombs, the proportion of adult individuals increased significantly with shell length. In contrast, most gathered strombs (80–90%) were adults (thick-lipped), irrespective of shell length. For each of the two size-classes where a large proportion of juveniles were present (<45 mm), adults were significantly more likely than juveniles to be gathered. This is consistent with the increasing proportion of juveniles present in the smaller size classes, and their greater probability of being buried (Table 4), showing that larger strombs were more likely to be collected because they were less likely to be buried.

The other possibilities that larger strombs were more visible and/or less likely to be rejected cannot be tested with our data, but neither the underwater observations of the contemporary collectors, nor the interviews with the contemporary and traditional collectors suggest any support for these hypotheses.

Midden samples. We can test whether prehistoric gathering processes (represented by the midden sample) were similar to contemporary gathering processes by comparing the contemporary sample with the midden sample. With respect to the length frequencies of shells gathered, the shell midden sample is similar to that of the contemporary sample in that there was also a virtual absence of shells less than 30 mm (gathered 0% of 189; midden 0.02% of 300; contingency $X^2 = 2.65$, df = 1, ns). However, when the size frequencies of larger shells were considered in more detail there were some significant differences. In both samples (shells ≥35 mm: gathered $N = 189$; midden $N = 293$), most shells were in the 40–44 mm length category (gathered 53%; midden 49%). However the midden contained significantly fewer shells in the largest size category (shells ≥45 mm: gathered 41%; midden 18%; test of proportions, $P < 0.001$), and significantly more in the smallest category (shells <40 mm: gathered 5%; midden 32%; test of proportions, $P < 0.001$). Therefore, there was a significant difference between gathered and midden samples across these shell lengths (contingency $X^2 = 61.13$, df = 2, $P < 0.001$).

There are three possible reasons for these differences: (1) the midden represents collections from several populations, including those with small adults; (2) the midden includes shells gathered at times of year when populations had more juveniles and subadults; and (3) the midden samples are from populations which had been exploited so heavily that they contained mainly juveniles, and the contemporary population was less heavily exploited. The second and third explanations require that relatively more of the midden shells be juvenile, except for the largest size class.

We can test whether the midden sample has a consistently high proportion of adults (as for the contemporary gathered shells from a single population) by comparing the proportion of thick- and thin-lipped individuals within each of the larger size classes (Table 6). The two larger size-classes of midden shells were both significantly more likely to be juveniles than those from the contemporary gathered sample (Table 6). This difference was greatest for the largest size class, and furthermore within the midden the proportion of adults decreases with increasing shell size (Table 6). This discounts hypothesis (2) since it is at variance with the usual occurrence of a larger proportion of adults in the larger shell length categories within any given stromb colony (for example, Table 5), as a result of the species' typical growth pattern (Fig. 3). It also contradicts the simplest form of the third hypothesis that midden shells were small because they were mainly from heavily exploited populations which were dominated by juveniles. On the other hand, the total proportion of juvenile shells across all size classes was higher in the midden sample than in the contemporary sample (Table 6).

The following scenario accounts for this pattern. The midden shells represent the pooling of gathered shells from several different collecting locations. The prehistoric Motu clans collected most intensively in the immediate vicinity of their camp (i.e. on Motupore Is.). The unexploited stromb population there is intrinsically not very dense (Table 2), which is probably due to habitat constraints, and the adult strombs there are large (Table 1). Repeated collecting removed most adults, although the burying habits and subtidal occurrence of juveniles and adults would ensure that a moderate number escaped gathering up to the time of reproduction. Local reproduction continued and

Table 6. *Strombus luhuanus*: a comparison (Chi-squared contingency analysis) of age and size in relation to the risk of being gathered (larger (>30 mm) strombs only) for the contemporary (Collected Patch Reef) and prehistoric (midden) samples. In each cell the proportionate representation of each lip class in each of the shell length classes is presented in parenthesis. (NS = non-significant)

| Group | Shell length (mm) | | | |
	30–39	40–44	≥ 45	Total
Gathered sample				
thick-lip (adult)	8 (0.80)	86 (0.85)	69 (0.88)	163 (0.86)
thin-lip (juvenile)	2 (0.20)	15 (0.15)	9 (0.12)	26 (0.14)
Total	10 (1.00)	101 (1.00)	78 (1.00)	189 (1.00)

Test of gathered table (length versus lip): $X^2 = 12.64$, df = 2, $P <$ 0.005

Midden sample				
thick-lip (adult)	78 (0.76)	59 (0.41)	11 (0.20)	148 (0.49)
thin-lip (juvenile)	24 (0.24)	85 (0.59)	43 (0.80)	152 (0.51)
Total	102 (1.00)	144 (1.00)	54 (1.00)	300 (1.00)

Test of midden sample (length versus lip): $X^2 = 52.2$, df = 2, $P <$ 0.001

Tests within each length class (sample versus lip)

X^2	0.02	46.15	59.15
p (df = 1)	NS	<0.001	<0.001

larval recruitment did not change greatly. During the centuries of exploitation, the strombs gathered from the Motupore fringing reef were mainly juveniles, but of relatively large shell length. However, other collecting trips were made by boat to nearby islands (e.g. Manunouha Is., Fig. 1), where populations of very high densities occurred (Table 2), but in which the adults were small (Table 1). These were not regularly or heavily exploited so as to remove most adults. Hence, many adults in the 30–44 mm size range were gathered during these occasional but high-yield trips.

Discussion

The impact of the exploitation by traditional societies of animal populations is poorly documented and poorly understood. Some reports have stressed that traditional Pacific societies may practice voluntary restraint to ensure a sustained long-term supply of essential resources; through both an accumulated understanding of local natural history, and a conservation ethic which is encoded in many aspects of the regional culture (e.g. Johannes 1978, 1982).

An alternative view is that much of the apparent balance between traditional societies and their resources may be a result of many vulnerable species having gone extinct soon after a particular human group colonized an area, with most remaining prey species persisting by virtue of some biological properties which make it difficult for that particular culture to deplete them (Christensen and Kirch 1986; Catterall and Poiner 1987). For example, over 30% of the Hawaiian non-marine bird and mollusc fauna went extinct within the span of prehistoric human tenure (Kirch 1982; Olsen and James 1982). In New Zealand there is evidence of over exploitation of shellfish by prehistoric humans (Anderson 1979), whose hunting and habitat modifi-

cation also probably contributed to the extinction of a number of bird species (Diamond and Veitch 1981). Over-exploitation may be due to an absence of a encoded conservation ethic, or if it is present at the time of colonization, it may not be effective with respect to the new environment (Kirch 1982).

Effects of exploitation on Strombus luhuanus

Strombus luhuanus is an important traditional food resource of the Motu villagers of the Papua New Guinea coast near Port Moresby (Swadling 1976, 1977a, b; Allen 1977). It is also eaten by other Papua New Guinea peoples (G. Smith, personal communication; O. Crimp, personal communication), Torres Strait Islanders (Poiner and Harris, in press; Hinton, no date on book), Pacific Islanders (L. Zann, personal communication) and is common in northern Australian aboriginal middens (Catterall and Poiner 1987).

Bootless Inlet, near Port Moresby, has been continuously occupied for at least the past 500 years (Allen 1977). Excavations of a large shell midden on one of the islands of Bootless Inlet, Motupore Island, have demonstrated that *S. luhuanus* has been continuously exploited for the entire occupation period (Allen 1977). It is the dominant shellfish in the midden, throughout all strata, both in numbers and estimated flesh weight (Allen 1977; Pernetta, personal communication). Midden pottery and its pattern of change through the strata suggested constant occupation of the area and thus exploitation of the shellfish (Allen 1977).

Currently Bootless Inlet is the shell gathering area of the people of Tubusereia (population approx. 3000) who still collect and eat this species. In spite of this gathering, the densities of *S. luhuanus* at collected sites in Bootless Inlet (Table 2) far exceed the densities (No/m^2 in 1 m^2 units, all age-classes pooled) recorded in the summer of 1983 at three uncollected Heron Island mixed age-class colonies (colony 1: mean = 1.15, standard deviation = 1.06, $N = 34$; colony 2: mean = 0.21, standard deviation = 0.38, $N = 30$; colony 3: mean = 5.22, standard deviation = 2.60, $N = 12$) and Lizard Island (Latitude 14°40′S; Longitude 145°38′E) colony (mean = 3.92, standard deviation = 3.63, $N = 25$) on the Great Barrier Reef, Australia. The density and distribution data suggest that contemporary gathering practices were having little long-term effect on the gross population densities of *S. luhuanus*. *Strombus luhuanus* in Bootless Inlet have so far proved resilient to human exploitation.

The results of our study are consistent with the observations of Hinton (1982), who estimated that over a 2 year period on Yule Is. (Latitude 8°50′S; Longitude 146°30′E), Gulf of Papua, an average of 100 people collected 85 *S. luhuanus* (2 plastic buckets) each per day over 300 days of the year (this implied about 5 million strombs per year). Hinton (1982) reported that the species remained common at the end of that period.

Mechanism of resilience to exploitation

Traditional gatherers rarely collected individuals which were buried, subtidal or less than 30 mm in shell length (approximately one year old). More recently the depth range (and area) accessible to collecting has increased with the adoption of free-diving using plastic goggles. However, buried (mainly juvenile) individuals still escaped being gathered (Tables 4–6), and there were still some colonies or parts

of colonies either too deep for collection by free-divers or not known as collecting areas (Table 2). Several studies (reviewed in Catterall and Poiner 1987) have found that individual shellfish less than 30 mm (maximum dimensions) were likely to be rejected by traditional gatherers but above this threshold the sizes collected reflect the available distribution rather than strong size selection. For *S. luhuanus* in the present study, juveniles less than 30 mm may be rejected, but juveniles greater than 30 mm were also protected because of burying (not rejection). Adults and juveniles were also protected because of the depth ranges of the colonies (Table 2) which allows successful reproduction and recruitment.

Thus both the size and age-dependent burying and the partly subtidal distribution provide refugia which buffer the stromb populations from human predation. For *S. luhuanus*, the data from both traditional and recent collectors suggest that there has never been a well developed conscious conservation ethic towards this species. Rather, *S. luhuanus* displays a high resilience to the described styles of exploitation. *Strombus luhuanus* has the ability through juvenile burying, subtidal distribution, and the existence of unexploited populations, to maintain recruitment and growth to maturity at high densities when locally exploited by traditional gatherers. However, heavily gathered populations would exhibit shifts in their age-distributions to domination by juveniles and subadults (Tables 5 and 6); such shifts have been documented by Swadling (1977a, b) for some heavily gathered contemporary *S. luhuanus* populations. We suggest that historically, despite relatively heavy collecting pressures, there has been no shortage of *S. luhuanus*, due to this combination of biological traits. There has therefore been no pressure to develop traditional management strategies (Johannes 1978, 1982).

For another strombid species, the introduction of new fishing technologies and the opening of markets has lead to a shift from resilience to recruitment overfishing (May 1984), or even potential collapse. The opening of a lucrative export market, the introduction of SCUBA diving technology and intensive collecting of whole populations have recently lead to dramatic declines in stocks of the previously common strombid *S. gigas* in many parts of the Caribbean (Brownell and Stevely 1981). The use of SCUBA equipment gives collectors access to the subtidal and buried components of populations, thus removing two of the three factors which bestowed resilience on the *S. luhuanus* populations described in the present study. Recruitment of pelagic marine larvae is notoriously variable (Lasker 1981; Sale 1982) and the potential for recruitment from other areas is lessened if there is widespread collecting.

To examine the effects of human gathering on any species two sets of information should be gathered and analysed: (1) a set of the most important parameters which define the exploitation techniques; and (2) a set of the most important biological parameters of the exploited species or population. From these two data sets the resilience of a species to past and present collecting pressures can be assessed. Furthermore, it may be possible to predict the effects on traditional mollusc resources of changing technologies associated with novel collecting practices (Catterall and Poiner 1987).

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