RESEARCH PAPER

Human harvesting impacts on managed areas: ecological effects of socially-compatible shellfish reserves

**Shankar Aswani · Carola F. Flores ·
Bernardo R. Broitman**

Abstract We examined how human harvesting impacts on managed areas affect the abundance and size distribution of the edible mangrove shellfish *Anadara granosa* and *Polymesoda* spp. in the Roviana Lagoon, Solomon Islands. We tested two hypotheses: (1) in areas permanently and temporally closed to human exploitation, abundance and size distribution of these shellfish species is significantly greater than in sites open to exploitation and (2) moderate human disturbance of shell beds, particularly of *Polymesoda* spp., increases their abundance. Firstly, we studied perceptions of environmental states and processes coupled to foraging and management interventions to assess sociocultural influences on harvesting practices and ascertain the types of management regime that people would consider in a context where poaching and interloping are common practices. Secondly, we compared shellfish abundance and shell size from areas that were permanently protected, temporally reserved for communal harvest, and permanently open for exploitation. Thirdly, drawing from women's local knowledge, we measured the abundance of *Polymesoda* spp. in relation to mud compactness in quadrats across the three management regimes. Results showed that both species were significantly more abundant in permanent and temporally closed sites than in open sites. In the mud compactness study, however, while shell abundance was greater in moderately compacted quadrats, there was no statistical relationship between mud compactness and shell abundance within or across the three management regimes. Results suggest that even under the strong impacts of poaching, temporally closed areas have more clams than open areas and are as effective as areas that are permanently closed nominally. The results also suggest that human harvesting regimes can influence the effectiveness of

S. Aswani (✉)
Department of Anthropology, Rhodes University, Grahamstown 6140, South Africa
e-mail: s.aswani@ru.ac.za

S. Aswani
Department of Ichthyology and Fisheries Science (DIFS), Rhodes University, Grahamstown 6140, South Africa

C. F. Flores
Department of Anthropology, University of California, Santa Barbara, CA 93106-3210, USA

C. F. Flores
IGP Marine Science, University of California, Santa Barbara, CA 93106-3210, USA

B. R. Broitman
Centro de Estudios Avanzados en Zonas Aridas (CEAZA), Universidad Católica del Norte, Larrondo 1281, Coquimbo, Chile

local management decisions and thus are important when designing community-based conservation programs in the Solomon Islands and other Pacific Islands.

Introduction

Increasing human degradation of marine ecosystems has led to efforts to halt, ameliorate, or manage anthropogenic impacts with effective and holistic management tools. State-sponsored management initiatives that focus on protecting biodiversity and ecosystem function through strategies like no-take and/or large marine reserves or ecosystem-based management initiatives, are important for sustaining and fostering ecological services (Worm et al. 2006; Barbier et al. 2008; Levin and Lubchenco 2008). Many local communities in Southeast Asia and the Pacific Islands have begun to independently experiment, or in collaboration between communities and either external researchers, conservation or development agencies, with small and temporal closures as a means to deal with increasing marine resource scarcity (e.g., Cinner et al. 2006; Cohen and Foale 2013). These community-based marine closures often allow for the traditional harvest of resources either during set periods of time or according to the cultural, political, and economic needs of a given community (Cinner and Aswani 2007; Cohen et al. 2013).

Researchers have a limited understanding of the complexity of periodic management regimes because communal, socioeconomic, and cultural concerns associated with human-environmental interactions (such as differential foraging strategies during harvest periods) have been slowly incorporated into research plans. Thus, there are still gaps of information regarding the social and biological outcomes of these periodic closures, albeit case studies from the Solomon Islands (Aswani and Weiant 2004; Cohen and Alexander 2013), Vanuatu (Bartlett et al. 2009; Dumas et al. 2010), Papua New Guinea (McClanahan et al. 2006), Fiji (Tawake et al. 2001) and Eastern

Indonesia (Evans et al. 1997) suggest that under certain social and ecological circumstances (Daw et al. 2011), temporal community-based marine protected areas (MPAs) are biologically successful with higher abundance of the targeted species (Cinner et al. 2006; Jupiter et al. 2012), particularly in the case of gleaning invertebrates (Cohen et al. 2013). Research in this region also indicates that spatio-temporal closures are socially more acceptable than permanent reserves because they fulfill people's livelihood needs and fit local governance, socioeconomic, and cultural frames of reference (Cinner and Aswani 2007). Many questions remain, however, regarding the nature of human foraging effects on permanent and periodic closures, particularly for management of marine resources, such as invertebrates, which are fundamental to the livelihoods of maritime communities.

We investigated the effects of human foraging on the abundance and size distribution of the mangrove shellfish *Anadara granosa* and *Polymesoda* spp. (*Polymesoda* [*Geloina*] *expansa/erosa*). Gleaning is a critical subsistence activity on most shorelines in developing countries around the world and species from these genera are often ignored by studies on marine resource use and exploitation, but are extremely important for local subsistence users throughout the tropical Pacific (Meehan 1982; Broom 1985; Johannes and Hviding 2000; Muller 2003). First, we studied local patterns of use and environmental perceptions of these species to qualitatively evaluate household dependency on these shells, understand sociocultural influences on harvesting practices, ascertain the types of management regimes that people would consider, and aid our sampling design and the formulation of testable hypotheses about human foraging. Second, by drawing from the qualitative study on women's resource use and knowledge we asked: how do absent, periodic, and continuous human foraging of mangrove shell beds affect the size and abundance of shellfish populations? To quantitatively address local observations of the resource, we tested two hypotheses: (1) in areas permanently and temporally closed to human exploitation, abundance and size distribution of these species are significantly different from open sites, and (2) following women's' perspective that mud compactness influences clam abundance and that limited disturbance during harvests creates more favourable habitat for *Polymesoda* clams, we examined how moderate human disturbance of shell
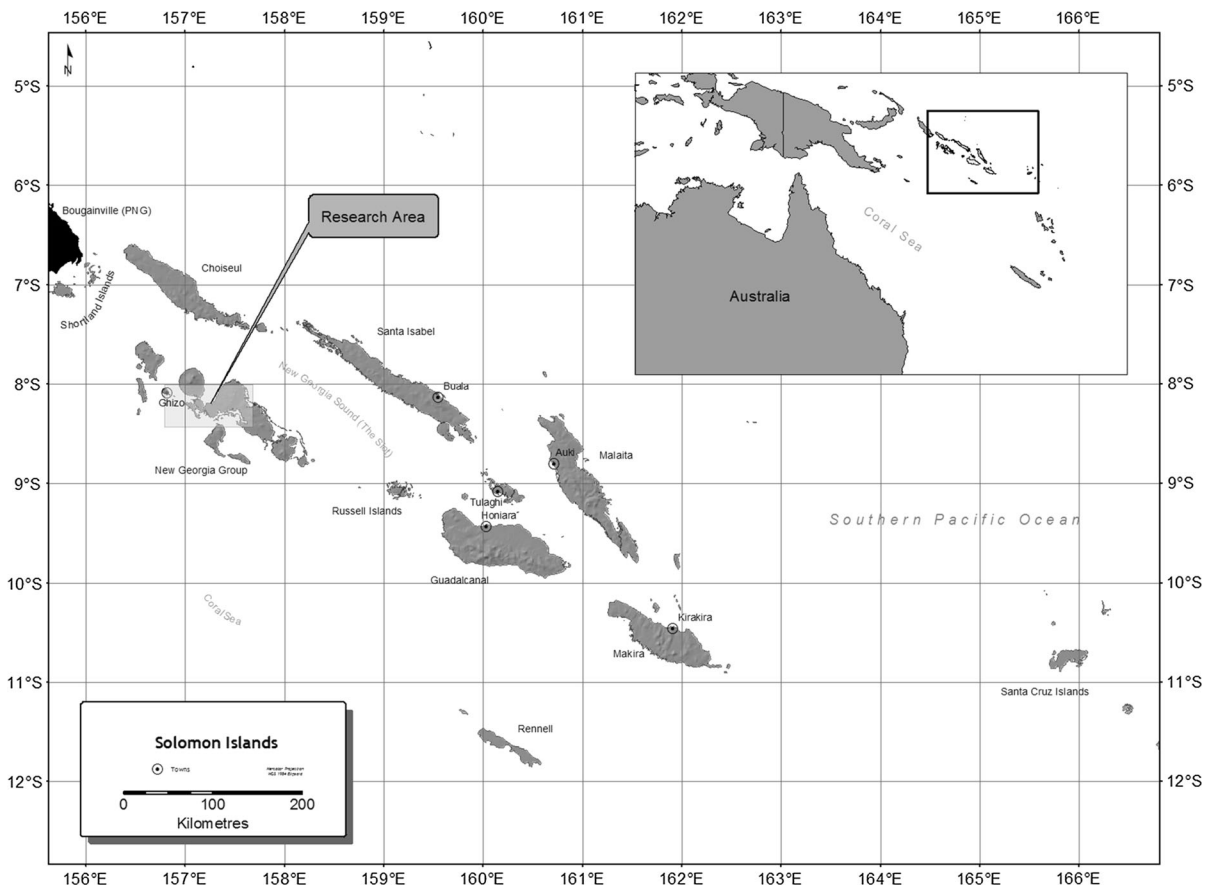
Fig. 1 The Solomon Islands

beds influences the abundance of shellfish, particularly *Polymesoda* spp., in temporal (seasonal) harvesting areas in comparison to fully closed or permanently open areas. To test these hypotheses, we compared clam abundance and shell size from traditional harvesting grounds with similar ecological characteristics (e.g., mangrove tree species, soil characteristics, etc.) around the Roviana Lagoon, Western Solomons Islands (Fig. 1), which were fully protected, reserved for periodic harvest, and unprotected from human exploitation. In sum, we aimed to assess which forms of management are biologically effective and socially acceptable for similar social and ecological contexts in the Solomon Islands where poaching and interloping in MPAs are common practices. More generally, our intention was to analyze management measures that are commonly employed across the Asia–Pacific region yet are rarely examined empirically (but see Cohen and Foale 2013).

Social and ecological context

The Roviana Lagoon in the Western Solomon Islands (Fig. 1) was formed by uplifted offshore coral islands that are characterized by rugged and notched limestone with numerous inlets, bays, carbonate-sand beaches, and moats. The lagoon includes a wide variety of aquatic habitats, including shallow reefs, outer reef drops, seagrass, mangroves, river estuaries, and freshwater swamps (Brookfield and Hart 1971). Human exploitation of marine resources is vital for both protein and income for coastal communities in the region, and the harvesting of marine invertebrates is mostly carried out by women and children. Women primarily exploit mangrove and outer barrier island intertidal flats for molluscs, with the former habitat being the most important for this activity. The main season for collecting inner-lagoon molluscs is between May and August, when diurnal low tide allows women

to enter the mangrove forests. Molluscs exploited in mangroves include blood cockles (*Anadara* spp.), mud clams (*Polymesoda* spp.), oysters (e.g., *Crassotrea rhizophorae*), Venus shells (*Gafrarium tumidum*), and mudwhelks (*Terebralia palustris*), among others (Aswani and Vaccaro 2008).

The main targets for shellfish communities in the Roviana Lagoons, however, are the mangrove blood cockle (*Anadara granosa*) and mud clams (*Polymesoda* spp.), with the latter representing possibly more than one species. The mud clams found in Roviana are likely *Polymesoda* (*Geloina*) *expansa* and/or *Polymesoda* (*Geloina*) *erosa*. These clam species are targeted because of their historic abundance, large size, accessibility, trade value, and due to their non-perishable qualities. Women, therefore, have remarkable ecological knowledge regarding their spatial and temporal distribution, spawning seasonality, feeding habits, and reasons for mass mortality, among other ecological factors (Aswani and Weiant 2004).

Biological studies of *A. granosa* include Broom (1985), Narashimham (1988), and Nakamura and Shinotsuka (2007), but these studies were conducted in the Philippines, Malaysia, Thailand, India, South Korea, Japan, and Indonesia and did not include the insular Pacific. For *Polymesoda* spp. (subgenus Geloina), some authors have reviewed the ecology of these bivalves in the Indo-Pacific region (Morton 1984; Clemente 2007; Clemente and Ingole 2011), but little is known about stock status in the Solomon Islands.

Despite the lack of scientific data on the actual status of these shellfish populations, we assisted local communities to establish a series of preventive-management measures to manage these invertebrate populations for food security, including temporal and permanent closure in the Baraulu and Nusa Hope Villages on the Roviana Lagoon in 1999 (see Aswani and Weiant 2004). The management sites were selected through a combination of locally driven assessments and social and ecological research of local habitats and associated management needs. Temporal and permanent closures were selected following a perceived decrease in shell size and abundance driven by fishing pressure, site preferences, and village proximities. Temporal closures, and their seasonal harvesting in particular, were established to conform to local social (e.g., death and feasting) and economic (e.g., cash for school fees) realities of the Baraulu and Nusa Hope communities. As of 2014, the

permanent and temporal closures were still operational in Nusa Hope but less so at Baraulu Village due to an ongoing religious conflict.

Women's daily and historical experience on clam harvesting, as has been noted for other fisheries (Shackeroff et al. 2011), can provide a historical perspective on recent changes and the current status of these invertebrates. Women's close contact with the environment has led them to recognize the ill effects of earthquake/tsunamis (McAdoo et al. 2009), logging, and human exploitation on mangrove invertebrates and coral communities. In this respect, indigenous ecological knowledge is crucial for understanding social, ecological, and economic factors that mediates between management and conservation purposes and local human foraging behavior (Berkes 2012).

Materials and methods

We studied Baraulu village Women's reliance and harvesting of *A. granosa* and *Polymesoda* species from known harvest areas around the Roviana Lagoon by measuring household dependency on these species for food security and income. We also qualitatively evaluated indigenous ideas of environmental states and processes of molluscs and perceptions of how management interventions impact the abundance and size distribution of edible mangrove clams. We collected this information not only for establishing a qualitative context about sociocultural influences on harvesting practices, household resource dependence, and the types of management regimes that people would consider, but also to formulate the sampling design and testable hypotheses about women's gleaning. Consequently, to examine the effects of management regimes on shellfish populations, we monitored abundance and size distribution of *A. granosa* and *Polymesoda* spp. across different management regimes and sampling years, as well as measuring the relationship between mud compactness and shellfish abundance for *Polymesoda* spp. across all management regimes.

Household shell resource dependence and perceptions

In August of 2006 and 2008, we used a systematic sampling design to randomly identify village households and their associated traditional kitchens for

interviewing and measuring livelihood dependency on these shell species. Household head women (and clam collector) from every third kitchen along a single track, were contacted for interviewing ($n = 25$ each year). "Kitchen" was used as the sampling unit because kitchens are both single- and multi-family units, within which all members share the responsibilities of providing and preparing food. We used structured and semi-structured questions in a household survey, and open-ended interviews with key informants to elicit household data regarding food procurement strategies, the use of mangrove invertebrates (Weiant and Aswani 2006), views regarding the management interventions, and perceptions of environmental states and processes of invertebrates.

Shell abundance and size distribution

We surveyed the effect of three management regimes on populations of *Polymesoda* spp. and *A. granosa* during successive sampling years (2008–2010). The first management regime is a permanently closed area (a marine protected area [MPA] established in 1999), the second are permanently open areas of regular clam collection, and the third management regime is a temporarily closed area that follows a local management regime allowing a few months of clam collection each year (usually between June and August) in preparation for special community-wide events when extra food supplies are needed (see Aswani and Weiant 2004 for further discussion).

We surveyed 16 locations during daytime low tides in August 2008, 2009, and 2010. The location of sampling areas (sites and quadrats) for clams followed local knowledge gathered through the interviews done in 2006 and 2008 to women clam collectors. Four locations corresponded to permanently closed areas, seven to permanently open areas, and five to temporarily closed ones (see temporal and permanent closures in Fig. 2). Our systematic field assessment of the natural conditions of traditional shellfish gathering locations included tidal elevation and water temperature (defined as limiting factor for clam distribution by Clemente 2007: 69). Tide fluctuations and water temperature were similar at all the sampled locations which indicated their similarities in ecological and geographical characteristics. The survey methodology was the same every year. At each survey location, we laid transects on the intertidal zone inside

and outside the mangrove canopy, the habitats for *Polymesoda* spp. and *A. granosa*, respectively. Transects were situated in the same area each year, but they were not fixed. For *Polymesoda* spp., a total of 21 m^2 were sampled per site: seven 12-m transects were placed every 3 m perpendicular from the low-tide edge toward the mangroves. One quadrat of 1 m^2 was surveyed with local research assistants at 0, 6, and 12 m along the transect collecting all live clams that were accessible (arm depth ~ 80 cm) inside the quadrats.

For *A. granosa*, a total of 5.25 m^2 were sampled per site; seven transects of 6 meters were placed every 3 m, also perpendicular to the shore. Three quadrats of 0.25 m^2 were surveyed with local research assistants at 0, 3, and 6 m along the transect collecting all accessible clams inside the underwater quadrats (~ 1 m depth). Before defining the sampling areas, we conducted interviews and pilot field surveys that indicated that individuals of both species were haphazardly distributed, which was confirmed by the lack of clam aggregations during our systematic sampling. Differences in quadrat size for each clam species was based on the logistic imposed by their natural habitats. While both species are buried in the mud, *Polymesoda* spp. occupies small cavities between the mangrove roots and *A. granosa* is buried underwater in open areas immediately outside the mangrove roots. Size distributions of living shells of *A. granosa* and *Polymesoda* spp. clams were established at the sampling site using a caliper and were classified by size class following earlier work where clams where classified by the size range identified and used by local people when harvesting clams (see Aswani and Weiant 2004; Weiant and Aswani 2006). For *Polymesoda* spp., class 1 grouped clams between 0 and 5.9 cm, class 2 between 6 and 7.9 cm, class 3 between 8 and 9.9 cm, and class 4 equal to or larger than 10 cm. For *A. granosa*, class 1 grouped clams between 0 and 2.9 cm, class 2 between 3 and 4.4 cm, class 3 between 4.5 and 5.9 cm, and class 4 equal to or greater than 6 cm. Size class was considered a fixed factor in ANOVA.

Mud compactness

We measured mud compactness inside mangrove habitats at each quadrat where *Polymesoda* spp. density was sampled to evaluate a relationship
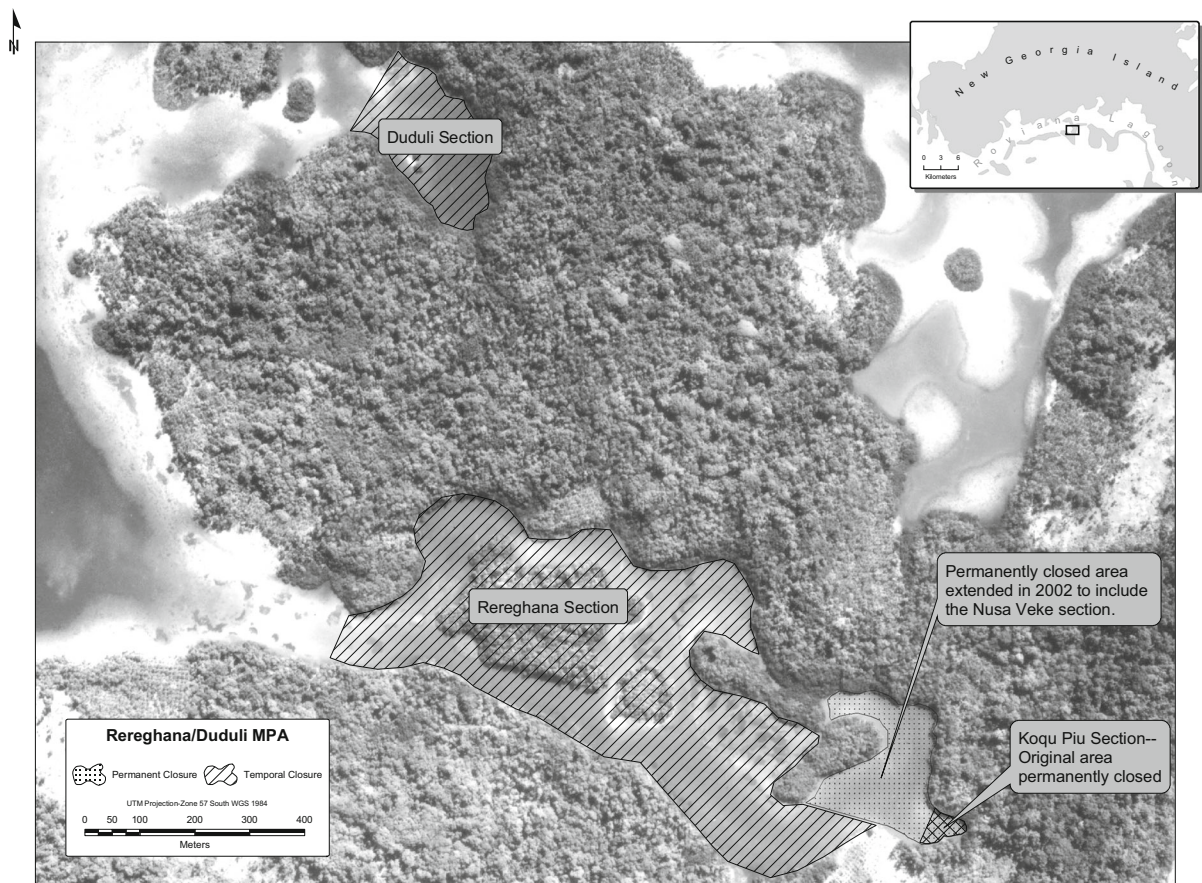
Fig. 2 Baraulu area permanent and temporal MPAs. All other areas in the image are permanently open for exploitation

between mud compactness and shellfish abundance. The measuring instrument consisted of two PVC pipes—a wider one and a thin one inside with a weight of one kilo attached on the upper end. The wider pipe was placed on the mud surface, and the thinner one with a measuring scale in centimeters was dropped inside the mud from a standard height (1 m) through the wider pipe using mud penetration by the thinner pipe as an indicator of mud compactness. Quadrats where the pipe sunk less than 5 cm were classified as highly compacted, between 5 and 15 cm defined as moderately compacted and more than 15 cm considered to be lightly compacted.

Statistical analysis

To test for differences in abundance and size distribution among management regimes, we used a 4-way, mixed-model, nested ANOVA with size class (4 levels: 1, 2, 3,

or 4), management (3 levels: closed, open, or temporal), year (3 levels: 2008, 2009, or 2010) as fixed and crossed factors, and site as a random factor, nested within management and year. The abundance of live clams was analyzed separately for each species. Denominators for F-ratios were obtained by equating the expected and observed mean squares (Zar 1999). Before conducting the ANOVA tests, we randomly selected 4 sites for each year and management regime to balance the data and the generality of our results did not depend on the particular choice of sites included. The Student–Newman–Keuls (SNK) test was used for post hoc unplanned comparisons. Cochran's tests revealed heterogeneity of variance in all analyses. Nevertheless, ANOVA is robust against heterogeneity of variance when total variance is partitioned in many subsets ($k = 144$) and the data set is balanced ($n = 21$) (Underwood 1997; Quinn and Keough 2002). In addition, we visually inspected homogeneity of variances and normal distribution of

errors by means of residuals-versus-fits and normal Q–Q plots', corroborating that heteroscedasticity was minimal. Analyses, therefore, were run on raw data. Nonparametric tests and regressions were carried out using MatLab while ANOVA were conducted in the R environment version 2.12.2. Finally, to analyze the relationship between mud compactness and *Polymesoda* abundance, we used a purely quadratic regression to test for a unimodal relationship between mud compactness and clam abundance.

Results

Household shell resource dependence and perceptions

Interviews done in 2006 ($n = 25$) showed that *A. granosa* and *Polymesoda* spp. clams were significant contributors to household food and income. Over 80 % of households stated that these molluscs were "very important" to their household diet and income. Over 90 % of households harvested *A. granosa* and *Polymesoda* spp. year-round and 75 % of households sold these invertebrates at the market. Of the households sampled, over 60 % sold these shells on a regular basis (≥ 3 times per week), and over 75 % of them stated that their sale was "important" or "very important" to their household operational income (Weiant and Aswani 2006). The average number of gleaning trips to permanently open areas was 2–3 times per week, and the number of bags collected (in 20 kg rice bags) during a typical gleaning trip (3–4 h) was around 1 bag of *A. granosa* and between 1 and 2 bags of *Polymesoda*. Results from interviews done in 2008 ($n = 25$) showed that while catches (number of bags collected per gleaning trip) were very similar to those of 2006 (0.8 bag of *A. granosa* and 1.5 bag of *Polymesoda* spp.); the average number of trips per week had decreased to one, indicating possible changes in preferences and livelihood dependency. Also, women interviewed in 2006 and 2008 said that they had to increase the time allocation and number of bags collected per gleaning trips during the "open" seasons of the temporal closures.

Results from the interviews done in 2006 and 2008 show that while 95 % of all women supported the temporal and permanent closed areas within the community-based MPA, 68 % of them acknowledged that poaching occurs periodically within the temporal and permanent closures, and that since 2008 poaching has increased (due to the death of an elder who was responsible for keeping the times of seasonal harvest). Another interesting point regarding the effect of human intervention on clam populations, particularly for *Polymesoda* spp., is the conviction that permanent closed areas are not good for clams. In fact only 50 % of all women would like to see another closed area established in the region.

Almost half of the interviewed women (49 %) said that the absence of people digging into the mud to collect clams hardens the mud, making it difficult for clams to breathe. The interviews yielded the notion that although human exploitation is identified locally as one of the main causes for the decrease in clam abundance, especially for *Polymesoda*, women clam collectors believe that total absence of human harvesting inside mangrove areas do not improve clam's habitat, abundance, or size. On the contrary, they think that areas permanently closed harden the mud making the mangroves unsuitable for clams to live and reproduce. As stated by an elder gleaner woman: "when we tramp the mud while gleaning, we soften it, and I think that this results in a better home for clams because in hard un-tramped mud we find many dead shells." Regardless of the veracity of this reasoning, this is what people perceive and is one of the factors that regulate their behaviour towards shellfish gathering. This perception result was important for formulating the testable hypotheses presented in this study regarding mud compactness and shell abundance. The open-ended interviews with various key informants also established that permanently closed areas may be perceived by local people as not worth looking after since there is not a direct benefit from them as there is from temporally closed areas, which are harvested during occasions of particular interest for the local community.

Shell abundance and size distribution

Over the 3-year sampling period (2008–2010), we counted a total of 939 *Polymesoda* spp. and 3,720 *A. granosa* individuals (0.31 ± 0.01 and 1.23 ± 0.04 living clams per m^{-2}, respectively). The size structure of both species showed positive skewness, but skewness in size structure of *Polymesoda* spp. was stronger than that of *A. granosa*. Management treatment had a significant effect on size structure of *Polymesoda* spp.
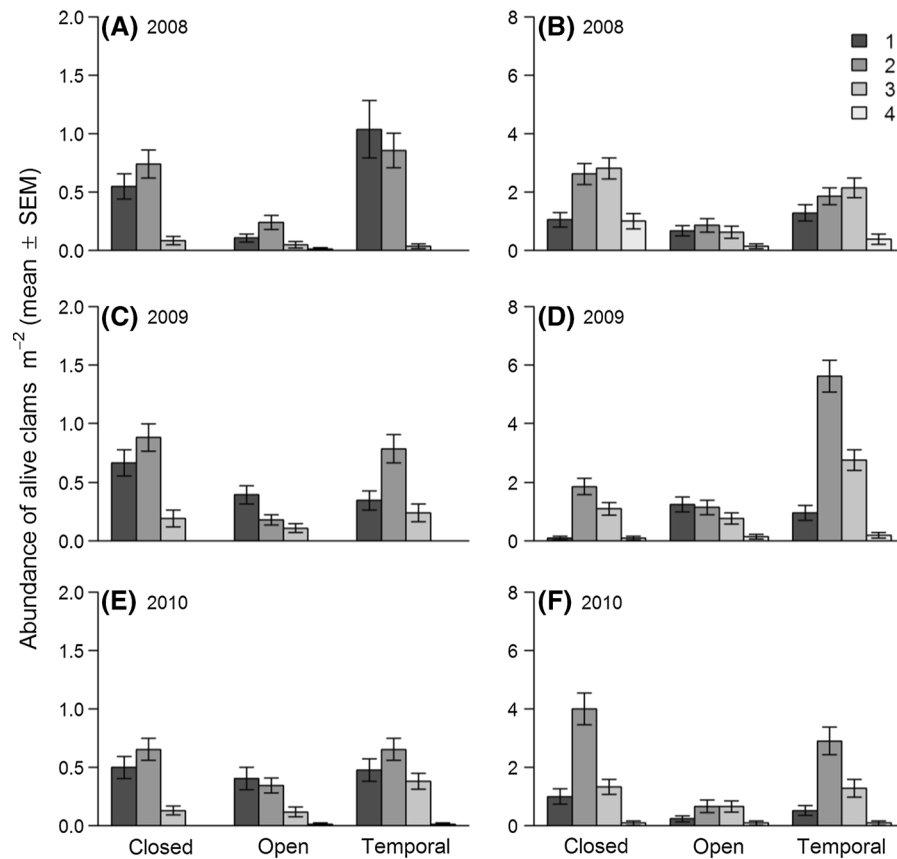
Fig. 3 Abundance per square meter of clams of *Polymesoda* spp. (graphs A, C and E) and *Anadara granosa* (graphs B, D and F) per each size and management area sampled around Roviana lagoon between 2008 and 2010. Values are given as mean ± standard error mean (SEM). Note that size classes shown are based on Aswani and Weiant 2004. For *Polymesoda* spp. : size 1 = clams between 0 and 5.9cm, size 2 = clams between 6 and 7.9 cm, size 3 = clams between 8 and 9.9 cm, and size 4 = clams equal or higher than 10 cm. For *Anadara granosa*: 1 = 0–2.9cm, 2 = 3–4.4 cm, 3 = 4.5–5.9 cm, and 4 = equal or higher than 6 cm

and *A. granosa*, which was indicated by a significant interaction between size class and management type (see Fig. 3; Table 1). We also found a significant effect due to sampling site. For *Polymesoda* spp., SNK tests conducted on data averaged across years and sites showed that significant differences between management treatments only occurred within size classes 1 and 2, and open management regimes corresponded with a significantly lower clam density than closed and temporal sites (SNK test, $p < 0.05$, Table 1). For *A. granosa*, the density of clams of size classes 2 and 3 was significantly lower in open sites than in closed and temporal areas (SNK test, $p < 0.05$). While there was significant amount of variance explained by sites, maximal densities of live clams were consistently

observed in sites under closed and temporal management (Table 1).

Mud compactness and *Polymesoda* spp. abundance

The relationship between mud compactness and *Polymesoda* spp. abundance across different management regimes showed that soil compactness was not significantly related to the number of clams found inside each quadrat nor to the different management regimes. However, for all three regimes, *Polymesoda* were more abundant in quadrats with mud compactness between 2 and 15 cm than in those between 20 and 40 cm. In fact, quadrats with moderate

Table 1 Four-way mixed-model nested ANOVA of the effects of size class (four levels: 1, 2, 3, or 4), management (three levels: closed, open, or temporal), year (three levels: 2008, 2009, or 2010), and site (four levels) on density of live *Polymesoda* spp. and *Anadara granosa* clams

Source	Cochran's test							F-ratio versus
	DF	*Polymesoda* spp. $C = 0.16$, *p* value **<0.001**			*Anadara granosa* $C = 0.037$, *p* value **<0.001**			
		MS	F-ratio	*p* value	MS	F-ratio	*p* value	
Size class = C	3	59.172	42.691	**<0.001**	651.010	20.896	**<0.001**	C × S (M × Y)
Management = M	2	16.619	7.382	0.003	312.440	5.794	0.008	S (M × Y)
Year = Y	2	0.019	0.008	0.992	18.590	0.345	0.712	S (M × Y)
C × M	6	4.499	3.246	**0.007**	93.280	2.994	**0.011**	C × S (M × Y)
C × Y	6	0.939	0.678	0.668	40.290	1.293	0.270	C × S (M × Y)
M × Y	4	2.075	0.922	0.466	117.600	2.181	0.098	S (M × Y)
C × M × Y	12	2.133	1.539	0.127	41.220	1.323	0.222	C × S (M × Y)
Site = S (M × Y)	27	2.251	4.303	**<0.001**	53.920	11.508	**<0.001**	Residual
C × S (M × Y)	81	1.386	2.649	**<0.001**	31.150	6.649	**<0.001**	Residual
Residual	2880	0.523			4.690			
Significant fixed effects	SNK test				SNK test			
	Size class				Size class			
C × M	1	**Open < Closed = Temp**			1	Closed = Open = Temp		
	2	**Open < Closed = Temp**			2	**Open < Closed = Temp**		
	3	Open = Closed = Temp			3	**Open < Closed = Temp**		
	4	Closed = Temp = Open			4	Open = Temp = Closed		

The post hoc SNK test is given under each ANOVA for significant fixed effects. Characters in bold denote significant differences at $\alpha = 0.05$
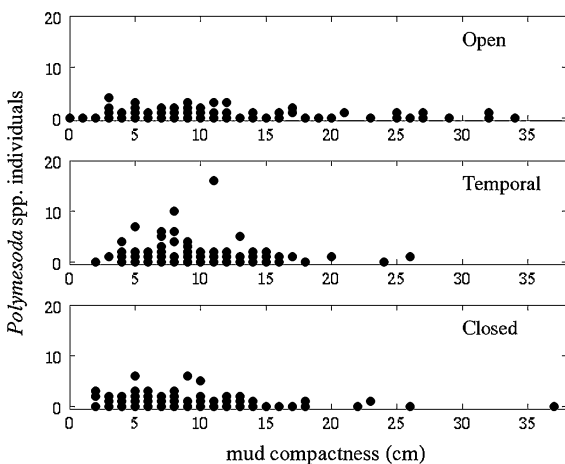
Fig. 4 Relationship between mud compactness (cm depth) and abundance of *Polymesoda* spp. per treatment (open, temporal and closed areas). *Each dot* corresponds to sampled quadrats with their soil compactness and number of clams standardized by m^2. *Dots overlap* representing more than one quadrat

compactness, or between 5 and 15 cm, had more live shells across all sampled areas (Fig. 4). Among the three management regimes, open areas had a higher number of quadrats with mud compactness between 20 and 40 cm, showing overall lower mud compactness in sites permanently open to human harvesting (Fig. 4).

Discussion

Does management regime make a difference in the abundance of *Polymesoda* species and *A. granosa*? Our results suggest that it does, as both permanent and temporal closures had more clams than open sites. The results also indicate that temporal/periodic closures, which are seasonally opened to human foraging, have at least the same effects that permanently closed sites, particularly for *Polymesoda* clams. The analysis of

local perceptions for clams, where intermediate disturbance of the mud around shell beds of *Polymesoda* spp. allows the clams to "breath" and "reproduce" and therefore increases their numbers, was inconclusive. No statistically significant relationship was found between mud compactness and *Polymesoda* abundance across management regimes. While this result does not support the hypothesis of an interdependent relationship between the abundance of targeted prey species and human foraging, it does not reject it either. *Polymesoda* abundance was higher in quadrats with moderate mud compactness across all regimes, and such similarities could be a product of human disturbance, in agreement with indigenous ecological knowledge.

Similar abundance of clams between temporally and permanently closed areas could result from poaching activities. While there is no quantitative evidence of widespread and systematic poaching in permanently or temporally closed areas, interviews and survey results suggest that some poaching occurs in these areas. Temporally closed areas seem to combine conservation goals and local needs, generating strong stewardship towards these areas, which may not happen with permanently closed ones. It is important to highlight that the three years of clam sampling were undertaken during the month of August, which corresponds to the end of the clam harvesting season of temporally closed areas (May–August) (Aswani and Weiant 2004). Thus, our surveys may actually underestimate the effect of temporal closure as abundances are still higher in these areas than in open sites. Similarly, the larger size classes missing from temporally closed areas could also be ascribed to a cumulative effect of the periods of open harvest over the course of the study.

The results of our case study allow us to support the hypothesis that both permanent and temporal closures have different clam abundance than open areas. Both closed regimes are more effective that open areas in maintaining relatively high clam density, although it cannot be ascertained whether or not higher density of shells has optimized yields (Cohen and Alexander 2013) or catch per unit effort (Jupiter et al. 2012). In several studies, human access to intertidal sites has been demonstrated to be strongly correlated with reductions in the number of large-size shellfish individuals (e.g., Castilla and Duran 1985; Keough et al. 1993). Our study shows that the managed areas

we monitored have a great number of small and medium/big size-class individuals and a low abundance of large individuals. Studies from other regions about size and reproductive maturity of *A. granosa* (e.g. Broom 1985) highlight that despite the fact that the age of maturity of this clam species is uncertain, it's sexual maturity may be attained at sizes between 48.3 and 52.5 mm. Broom's work (1985) also shows that population structure of this clam species, although variable, ranges from 20 to 63 mm. Despite the fact that the theoretical maximum size of *A. granosa* could be as large as 63 mm, clams larger than 53.3 mm are commonly low in natural populations. Finally, regarding growth rate of *A. granosa*, it takes approximately one year to grow 31.5 mm with a growth rate much faster during the second year reaching up to 49.5 mm. For *Polymesoda erosa*, the single study done about ecology and population dynamics of this mangrove clam species comes from India (Clemente 2007) and shows that the size for sexually mature individuals of this species goes from 35 to 40 mm. It also shows that population structure of *Polymesoda erosa* can vary from 1.5 to 102 mm with the majority of the clams between 70 and 80 mm. The growth rate of this species is 100 mm in approximately 4 years (Clemente 2007). Despite the fact that the cited study is not from the study area, and considering that there is no information available for size at maturity in *Polymesoda* spp. nor *A. granosa* at the Solomon Islands, data about growth rate from other regions is the only and more comprehensive reference for these species of mangrove clams. Based on this information, it can be said that permanently and temporally closed sites have higher number of sexually mature individuals of *Polymesoda* spp. (clams bigger than 35–40 mm. presented in size class 1 and 2) and *A. granosa* (clams bigger than 48.3–52.5 mm presented in size class 3) than open sites and therefore are biologically more effective. Also, despite the fact that the absence of the largest individuals of *Polymesoda* spp. (class size 4 with shells equal or higher to 10 cm) and the low abundance of large *A. granosa* in permanently closed sites may be due to poaching, and in the temporal closed sites may be due to harvesting during the lift of the ban, it is important to highlight that the abundance of clam sizes equal or bigger than 10 cm for *Polymesoda* spp. and equal or bigger than 5.3 cm for *A. granosa* are commonly low in the natural populations of these mangrove clam species. *Polymesoda* spp.

observed in local markets nearby are ∼7 cm long, suggesting a preference during harvesting (see photo in supporting material). As expected, sites sampled within open areas showed low abundance of clams in the size class comprising 7 cm and bigger (size class 2, 3 and 4) (Fig. 3). On the other hand, sites sampled within temporally and permanently closed areas had higher abundance of clams of size class 2 (6–7.9 cm), suggesting a greater availability of *Polymesoda* spp. individuals larger than 7 cm for harvesting in these areas.

It is possible that differences in densities and size distributions of invertebrates are related to hydrology, food availability, habitat quality, sediment composition, lack of predators (e.g., mud crabs) owing to human foraging, or other ecological or biophysical variables. If true, manipulative experiments would be required to understand the causes of observed differences (Rondinelli and Barros, 2010). Given the general similarities in habitat characteristics and distances between sampled sites, human predation seems to be the cause of the abundance and size distribution differences observed in this study. More data, however, is needed on physical and intertidal community characteristics among different management regimes and about rates of extraction from the three zoning types to evaluate this interdependent relationship between *Polymesoda* and *Anadara* clams and women collection. Overall, however, our results concur with other studies in the tropical Pacific showing that periodically-harvested reserves are well suited to manage fecund invertebrate species with relatively fast turnover rates (Cohen and Foale 2013). On the other hand, periodical harvesting may be less effective for highly mobile or slower growing taxa (Cohen et al. 2013; Dumas et al. 2010).

Our results did not support the local notion that mid-level human disturbance on *Polymesoda* mud flats creates differences in the abundance of clams between management regimes. However, the results did show that there was greater density of clams in quadrats with moderate mud compactness across all regimes, which could conceivably hold the local claim. This uniformity could be a result of human disturbance, given that some poaching occurs across all sites and that mud is tramped intermittently. Humans are among the top predators in intertidal and nearshore trophic food webs, and their selective predatory activities can cause subtle or profound changes to these communities (e.g.,

Castilla and Duran 1985; Keough et al. 1993). Nevertheless, more data will be needed on intertidal community characteristics among different management regimes to evaluate this interdependent relationship between *Polymesoda* clams and women collection.

Regardless of the scientific veracity of women's indigenous knowledge regarding mid-level disturbance and habitats enhancement, this idea shapes people collection activities and the opportunity to take clams from temporal areas makes people more amenable to look after their resources, which consequently can grow and reproduce thus preserving and reinforcing indigenous perception. Under this context, temporal closures work as a pressure release valve from the prohibition of harvesting in permanent closures, reducing widespread and systematic poaching in these last areas, allowing permanent closures to conserve ecosystems and their associated fauna. Thus, temporal closures work as a tool for resource management and conservation (see also Bartlett et al. 2009) while simultaneously fostering the maintenance of indigenous ecological knowledge and local harvesting strategies.

The results also have theoretical implications. In recent years socio-ecological systems approaches have gained prominence among social and natural scientists. These approaches argue that the separation of the social and ecological aspects of a system is inadequate because they are strongly coupled, highly complex, and evolving (e.g., Berkes et al. 2003; Folke et al. 2005). A limitation of current studies in this field, however, is the frequent lack of empirical and longitudinal data to test hypotheses related to social and natural interactions, vulnerability, and resilience. Furthermore, socio-ecological research is less sensitive at paying attention to the role of individuals in shaping social and ecological interactions or to the outcomes of individual actions in particular socio-ecological contexts at a fine spatial scale. As emphasized decades ago in human ecological studies (e.g., Smith 1981), researchers need to consider the foraging interaction between individual actors and their immediate environment before scaling up (Vayda 2009).

In addition, several management implications can be derived from our results that transcend the study area. Broadly speaking, we show that even if community-based-MPAs are opened seasonally and poached periodically, they can still provide effective protection for particular species of invertebrates

compared to unprotected sites. Periodically harvested areas can provide effective protection under relatively low human population densities and market integration, but in areas with high population density more stringent management regimes may be required to avoid resource overexploitation and to maintain the reproductive capacity of the targeted species (Cinner et al. 2006). We suggest that when MPAs are adapted to the local social and ecological context—through the creation of temporal closures that integrate people's ecological knowledge and community sociocultural needs (e.g., seasonal feasting)—MPAs can gain local acceptance, and these successes have been recorded for other temporal community-based MPAs in Oceania (McClanahan et al. 2006; Bartlett et al. 2009). For coastal communities in regions with similar social and ecological characteristics, spatio-temporal MPAs may be equally suited for shellfish management than permanent no-take marine reserves. However, more research has to be done to evaluate the effect of these spatio-temporal shellfish MPAs. In sum, in embracing adaptive management, it is not too farfetched to suggest that conservation practitioners and/or policy-makers can still protect shellfish resources by adapting to local conditions and allowing some human exploitation of managed conservation sites. An example comes from the Chilean artisanal fisheries and the positive conservation effects of implemented management exploitation areas (e.g., Gelcich et al. 2008). Management exploitation areas, open in certain moments around the year, have provided a way to engage fishers to participate and enforce limited access policies and also has been proposed as a system complement of no-take marine protected areas (MPAs) (Gelcich et al. 2007).

Despite the possible benefits of temporal closed areas, the role of no-take marine protected areas cannot be disregarded as scientific control locations and as untested centers of enhancing spawning, larval dispersal, and the export of adults to adjacent unprotected areas (Burgess et al. 2014). However, we want to emphasize that MPAs or any top-down, community-based, or co-management restriction of access to resources should be thought of in terms of interrelated social and ecological systems (Pollnac et al. 2010; Cinner 2011), and accommodate traditional foraging activities of artisanal fishers and their long-term ecological impacts. Successful temporary/periodic closures must arise from a comprehensive understanding of

local strategies and perceptions of marine resource use and ecological and oceanographic characteristics of the resource and its habitats. In the Roviana case, regardless of whether right or wrong, women's perceptions of natural and human effects on shellfish populations were essential to understanding the parameters they use for food acquisition and therefore for getting involved around management initiatives.

Conclusion

The Roviana Lagoon case study suggests that human foraging activities (fishing and gleaning) should not be strictly considered as livelihood activities, but also as a result of local perceptions of shellfish abundances and about what is best for the shellfish resources that humans exploit. The results of this paper suggest that (1) spatio-temporal/ periodic and permanent MPAs are suitable biological and social forms of resource management for the sampled shellfish species in the Solomon Islands and (2) natural seascapes are often products of human-environmental relationships that evolve through long-term human interactions between people and certain species. In general terms, then, we suggest that conservation practitioners need to consider the fine spatial scale of human-invertebrate ecological interactions (i.e., consider actor-level and intra- and inter-group behaviours) that occur in any given context as well as their linked local adaptive management responses. We also illustrate the relevance of integrating indigenous ecological knowledge and local foraging strategies (and their concomitant effects, whether real or perceived) into the design of temporal and permanent (i.e., no-take) marine reserves and also of adapting management responses to local conditions. Naturally, our conclusions need further investigation because human-environment interactions are usually very complex and relationships are rarely linear in the natural world. What is important to highlight is that participatory resource management approaches need to merge the biological goal of conserving ecological systems in a sustainable manner' (e.g., creating marine protected areas) with social and economic goals contextualized inside local community needs. Clearly, more participatory approaches to conservation need to be developed to achieve social and

ecological sustainability in the Solomons and elsewhere in the region with similar social and ecological characteristics.

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