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Restriction of sponges to an atoll lagoon as a result of reduced environmental quality

Ingrid S.S. Knapp [a], Gareth J. Williams [b], José Luis Carballo [c], José Antonio Cruz-Barraza [c], Jonathan P.A. Gardner [a], James J. Bell [a,*]

[a] CMEER, School of Biological Sciences, Victoria University of Wellington, P.O. Box 600, Wellington, New Zealand
[b] Scripps Institution of Oceanography, Centre for Marine Biodiversity and Conservation, La Jolla, CA 92083, USA
[c] Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México (Unidad Académica Mazatlán), Av. Joel Montes Camarena s/n, P.O. Box 811, Mazatlán (SIN) 82000, Mexico

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ABSTRACT

The lagoon at Palmyra Atoll in the central Pacific was subject to major military modifications during WWII and now the dominant fauna on the lagoon's hard substrate are sponges, not corals. In this study, we quantified the physical and biological factors explaining the variation in sponge distribution patterns across 11 sites to determine the potential for the sponges in the lagoon at Palmyra to invade the surrounding reef systems. Significant differences in sponge assemblages were found among all but three sites. For all the models we examined the strongest environmental relationships were found for variables related to sedimentation/turbidity and food/habitat availability. Our findings suggest that the sponges in Palmyra's lagoon are likely to be restricted to this habitat type where they are associated with conditions resulting from the earlier heavy disturbance and are unlikely to spread to the outer reef environments unless there is a dramatic decline in environmental quality.

1. Introduction

Coral reefs are highly diverse ecosystems providing numerous ecological and economic benefits (Barbier et al., 2011). Despite their importance, coral reefs are experiencing major anthropogenic pressure (Bellwood et al., 2004; Hoegh-Guldberg, 2011; Pandolfi et al., 2003) to the extent that no remaining reefs can be considered pristine. Anthropogenic alterations to marine environments often change the structure and function of the ecosystem by reducing species diversity, reducing light levels, modifying substrate type and availability, and increasing sediment loading and nutrient pollution (Cranfield et al., 2004; Fabricius, 2005; Rogers, 1990). When such disturbances are extreme, complex ecosystems can be rapidly transformed to simple ones and become characterized by reduced biological diversity (Rapport and Whitford, 1999). Furthermore, modifications and the removal of native fauna often make habitats more susceptible to colonization by non-indigenous species (NIS) (Mooney and Cleland, 2001; Olyarnik et al., 2009; Stachowicz et al., 1999), as well as inadvertently creating conditions and providing a substrate that is preferential to the NIS over the existing biota (Byers, 2002; Tyrrell and Byers, 2007).

Many atolls in the central Pacific Ocean have a long history of human colonization, and are characterized by degraded lagoon systems with low levels of water exchange and high levels of turbidity (Maragos et al., 2008; Maragos, 1993). These environments have experienced major changes to their original state and many such lagoons now support a number of non-indigenous species (Coles et al., 2001; deFelice et al., 1998; Knapp et al., 2011). Given that many of these introductions are thought to have occurred in recent times (past 50–100 years) through increased shipping traffic, there is concern that such introductions to lagoon systems as the point of incursion may lead to a later invasion of non-lagoon reef systems. While such invasions have not yet been widely reported (but see Knapp et al., 2011), it is possible that such species are still in an establishment phase. Therefore, it is important to understand the factors influencing the distribution patterns of species within degraded lagoons to determine their potential to invade outer reef systems.

Palmyra Atoll, situated 1930 km south of the Hawaiian archipelago, is considered a near-pristine atoll system and represents a biodiversity hotspot in the central Pacific Ocean (Maragos and Williams, 2011). However, although the outer reefs at Palmyra are characterized by a high cover of calcifying organisms and abundant predatory fish (Sandin et al., 2008), the dominant benthic fauna on the hard substrate in the lagoons, where extensive habitat modifications occurred (Collen et al., 2009), is sponges. The lagoon complex at Palmyra was subject to much modification during WWII (Dawson, 1959), including extensive dredging and construction that removed the fauna in the lagoons (Anon, 1947); coral diversity in the lagoon is now low (Williams et al., 2008). In addition, the military modifications reduced the water flow between

* Corresponding author.
E-mail address: james.bell@vuw.ac.nz (J.J. Bell).

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Table 1
Table of environmental (Env.), biological (Biol.) and categorical (Cate.) predictor variables and mean sponge cover for all species and target species used in the DistLM analysis. * = colineating variables not included in the final model. Values in bold denote the maximum or minimum mean values. Minimum numbers are not in bold if more than one site has the same value. n/a = not applicable, var. = variability (+1 SD) and Av. = availability.

Predictor	Code	Type	Units	Sites: Sa ●	St ▲	RW ■	P ◆	D ▼	C △	SC ▽	Q ✚	EI ✕	CE ✱	TP ○	Min	Max	Range	Mean
Temperature*	Temp	Env.	°C	28.57	28.71	28.63	28.50	28.11	28.79	28.95	28.98	28.93	**29.10**	**27.51**	27.51	29.10	1.58	28.62
Temperature var.	Temp var.	Env.	°C	0.59	0.66	0.32	**0.18**	**0.71**	0.33	0.27	0.39	0.24	0.36	0.35	0.18	0.71	0.53	0.40
Chlorophyll-*a**	Chl-*a*	Env.	$\mu g\ l^{-1}$	0.19	0.20	0.42	0.71	0.18	0.41	**0.14**	0.30	**0.78**	0.33	0.26	0.14	0.78	0.65	0.36
Chlorophyll-*a* var.	Chl-*a* var.	Env.	$\mu g\ l^{-1}$	**0.11**	0.14	0.24	0.22	0.13	0.24	0.18	0.11	**0.33**	0.11	0.13	0.11	0.33	0.22	0.18
Turbidity	Turb	Env.	STU	1.06	1.03	0.99	1.61	0.97	1.50	1.04	**0.68**	1.01	1.09	**5.97**	0.68	5.97	5.29	1.54
Turbidity var.	Turb var.	Env.	STU	0.32	0.33	0.33	1.00	0.56	**0.26**	0.31	0.30	0.50	0.31	**2.05**	0.26	2.05	1.79	0.57
Salinity	Sal	Env.	psu	**34.80**	34.60	34.61	34.21	34.45	34.49	34.10	**34.06**	34.24	34.30	34.62	34.06	34.80	0.74	34.41
Salinity var.	Sal var.	Env.	psu	0.23	0.24	0.14	**0.06**	0.22	0.25	0.14	0.18	0.06	**0.33**	0.15	0.06	0.33	0.27	0.18
Water flow*	Flow	Env.	$m\ sec^{-1}$	**0.0408**	0.0096	0.0024	0.0028	0.0060	0.0367	0.0034	0.0039	**0.0003**	0.0038	0.0024	0.0003	0.0408	0.04	0.01
Water flow var.	Flow var.	Env.	$m\ sec^{-1}$	**0.0422**	0.0185	0.0099	0.0133	0.0138	0.0363	0.0124	0.0145	**0.0031**	0.0133	0.0128	0.0031	0.0422	0.04	0.02
Total particulate matter*	TPM	Env.	$g\ m^{-2} day^{-1}$	32.81	54.40	**21.19**	42.70	81.28	60.36	49.95	65.55	105.22	53.07	**157.2**	21.19	157.2	135.97	65.79
Total particulate matter var.*	TPM var.	Env.	$g\ m^{-2} day^{-1}$	5.52	6.78	5.66	17.99	17.93	11.33	9.16	20.34	73.36	**5.09**	**121.63**	5.09	121.63	116.54	26.80
Percentage organic matter	PCOM	Env.	% in sediment	12.97	**11.14**	13.72	**15.25**	11.45	13.81	14.51	12.16	11.44	14.02	11.23	11.14	15.25	4.11	12.88
Percentage organic matter var.	PCOM var.	Env.	% in sediment	**1.27**	5.92	3.31	2.56	4.14	5.68	3.13	2.76	2.93	**7.38**	4.41	1.27	7.38	6.11	3.95
Av. of coarse sand	C. sand	Env.	proportion (%)	**41.37**	35.30	21.09	29.01	**11.10**	33.40	22.13	22.63	36.49	33.38	25.20	11.10	41.37	30.27	28.28
Av. of medium sand*	M. sand	Env.	proportion (%)	24.42	24.72	17.70	28.08	20.58	22.02	27.10	12.76	23.29	**35.50**	**11.01**	11.01	35.50	24.49	22.47
Av. of fine sand*	F. sand	Env.	proportion (%)	30.50	28.94	30.25	35.20	**43.97**	35.02	40.93	35.89	**26.94**	29.82	36.35	26.94	43.97	17.03	33.98
Av. of silt	Silt	Env.	proportion (%)	3.71	11.03	**30.95**	7.71	24.34	9.55	9.84	28.72	13.28	**1.29**	27.44	1.29	30.95	29.66	15.26
Av. of hard substrate	Hard sub.	Env.	proportion (%)	18.6	**44.1**	**12**	37.3	25.4	30.9	27.4	33	35.8	31.1	35	12.00	44.10	32.10	30.05
Av. of soft substrate	Soft sub.	Env.	proportion (%)	**73.80**	53.10	**43.70**	51.80	61.70	55.60	57.90	59.90	57.90	60.90	56.10	43.70	73.80	30.10	57.49
Angle	Slope	Cate.	sloped *vs.* horizontal	2	2	2	2	1	2	2	2	2	1	2	n/a	n/a	n/a	n/a
Mean cover																		
All species	n/a	n/a	%	30.83	31.96	17.73	26.58	23.08	30.53	24.99	**33.10**	30.39	31.67	**15.77**	15.77	33.10	17.33	26.97
Haliclona caerulea	n/a	n/a	%	0.12	**1.88**	1.01	0.23	1.44	0.00	0.02	0.01	0.00	0.55	1.69	0.00	1.88	1.88	0.63
Gelliodes fibrosa	n/a	n/a	%	0.00	0.27	0.06	1.15	0.00	0.62	**1.98**	0.00	0.00	0.00	0.00	0.00	1.98	1.98	0.37
Iotrochota protea	n/a	n/a	%	18.90	**20.61**	7.25	17.37	4.63	7.35	11.75	17.29	**3.92**	3.97	8.47	3.92	20.61	16.69	11.05

the lagoons and altered sedimentation distribution patterns (Collen et al., 2009; Dawson, 1959; Maragos, 1993), with residual effects to the reefs still evident today (Williams et al., 2010, 2011). It has been proposed, because of its shape, that the pre-war lagoon at Palmyra might have been similar to Millennium Atoll's lagoon (pers. comm. Jim Maragos), which is dominated by *Acropora* spp., but also characterised by abundant cover of crustose coralline algae, turfing algae and the giant clam *Tridacna maxima* (Barott et al., 2010). A large number of *T. maxima* shells and many dead coral microatolls remain in Palmyra's lagoon supporting this suggestion. The military modifications at Palmyra therefore most likely resulted in a decline in species diversity and change to the structure of the community, potentially making the lagoon system more vulnerable to NIS and led to the current environmental conditions, where sponges are the dominant benthic fauna on hard substrates. However, since sponges were not surveyed prior to the military modifications at Palmyra, we cannot completely rule out that sponges were a major component of the earlier biota in the lagoon.

Sponges are often understudied and overlooked despite performing range of important functional roles in coral reef ecosystems, particularly resulting from their filtering activities, competitive ability and complex relationships with other organisms (Bell, 2008; Wulff, 2001). Furthermore, where sponges occur in high enough densities they can have considerable impacts on benthic and pelagic ecosystems (e.g. Peterson et al., 2006). It is currently unknown how many of the sponge species in the lagoons at Palmyra are native to the atoll, although two non-indigenous sponge species have been reported (Knapp et al., 2011). Given the generally limited dispersal potential of sponges (Maldonado and Young, 1996) and the geographically isolated nature of Palmyra Atoll, it is likely that many of the sponges found in this disturbed environmental are non-native.

Several features of the sponges at Palmyra are of particular concern from a conservation and management perspective, and are potentially problems for other atoll systems where sponges are an abundant component of lagoon fauna. Firstly, sponges are usually top spatial competitors and have the ability to overgrow other reef organisms (Bell, 2008). Secondly, the filtering activity of sponges has the potential to impact the water column (e.g. nutrient and particulate removal). Therefore, changes to sponge abundance in the lagoon or an increase in the distribution range of sponges at Palmyra have the potential to alter overall community structure and ecosystem functioning (Bell, 2008). However, the recent surveys found no common sponge species between the lagoon and outer atoll reefs where sponges are rare suggesting that abiotic and biotic factors might be restricting the sponges to the lagoons. Despite this, sponges may still be in an 'establishment' phase given most of the sponges in the lagoon are likely to have arrived relatively recently (last 70 years since major military occupation or at most 200 years since Palmyra's discovery) compared to the likely age of the atoll and lagoon formation (as a result of sea level rise during the early Holocene; approximately 10,000 years ago).

In general there is a paucity of studies that have examined sponge assemblage diversity, abundance and ecology in the central Pacific Ocean (e.g. Bell and Carballo, 2008; Knapp and Bell, 2010), with little known about the environmental parameters driving the sponge assemblages in these coral reef ecosystems. Previous studies from many different geographic locations have shown that spatial variation in sponge distributional patterns and abundance