Affinities of Sponges (Porifera) of the Marquesas and Society Islands, French Polynesia[1]

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Abstract: This article reports on a survey of sponges from the higher-island reefs and slopes of the Marquesas and Society Islands archipelagos, French Polynesia, recording presence/absence and an estimate of local abundance at 109 sites from six and eight islands within each archipelago, respectively. Sponge distributions within archipelagos were relatively homogeneous, showing some differential patterns in affinities between north-south islands, and approximately one-third of the fauna apparently endemic to these archipelagos, but between-archipelago comparisons showed large heterogeneity, with only four of the 75 species shared between both archipelagos. The fauna of the Marquesas Islands (with sites consisting mostly of rocky slopes) was dominated by species in order Poecilosclerida and showed a range of taxonomic diversity similar to that of the remote fauna of the Hawaiian Islands. By comparison, the sponge fauna of the Society Islands sites was dominated by species of order Dictyoceratida, reflecting predominance of coral reef and lagoon sites and associated phototrophic feeding strategies. Parsimony and multivariate statistical analyses comparing French Polynesian sponge faunas with others in the southwestern Pacific showed closest nested faunal similarities between the (Marquesas Islands + Society Islands), (((Tonga + Fiji) + Vanuatu) + New Caledonia), and (North Great Barrier Reef + South Great Barrier Reef) but no or very low similarity between more geographically isolated faunas such as Palau and the collective Great Barrier Reef.

French Polynesia is a large territory, consisting of 118 islands forming five archipelagos, with a land mass of only 1,467 km^2 scattered over 2.5 million km^2 of ocean (7°–28° South, 134°–155° West): Society (Leeward and Windward), Tuamotu, Austral, Marquesas, and Gambier Islands archipelagos. The area is reportedly characterized by poor biodiversity but with high levels of endemism for some groups, both terrestrial and marine.

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Some marine taxa have been surveyed extensively in French Polynesia, such as mollusks (391 species [Tröndle and van Cosel 2005]), corals (51 genera, 168 species [Richard 1985]), algae (Payri et al. 2000), and fishes. The Marquesas Islands appear in the top-ranked areas based on the percentage of biodiversity and endemism for Indo-Pacific coral-reef fishes (Allen 2008), with an endemism rate of 8.3% (Kulbicki 2007). Ascidians (tunicates) were reported from Moorea (Society Islands archipelago) and Tikehau and Rangiroa (Tuamotu archipelago) to have an exceptional rate (42%) of new species (Monniot and Monniot 1987), but virtually nothing has been reported on the sponge fauna to date. Kelly-Borges and Valentine (1995) reviewed the sponge fauna of Oceania and reported that, although no general comprehensive review has been conducted for the sponges of French Polynesia, there are a few isolated reports of species scattered throughout the literature; they cited five instances of sponges from the region. Calcareous "pharetronids" (*Lelapiella incrustans sphaerulifera*, *Lepidoleucon inflatum*, *Plectroninia radiate*, *and Murrayona phanolepis*) and the demosponge "sclerosponge" (*Astrosclera willeyana*) were reported from Moorea (Society Islands archipelago) and Takapoto (Tuamotu archipelago) by Vacelet (1977). A single species of Dictyoceratida (*Hyrtios eubama*) from Moorea and Tahiti (Society Islands archipelago) was investigated for antimicrobial compounds (Amade et al. 1982). Wörheide et al. (2002*b*) studied the distribution and dispersal in the Pacific of *Leucetta "chagosensis"* (a species complex that is not yet formalized within the Linnaean nomenclature) using molecular phylogenetics and included samples from Moorea (Society Islands archipelago) and Rangiroa (Tuamotu archipelago). The work presented here is part of an ongoing larger program to better understand the natural marine resources of French Polynesia, to document the sponge fauna of the region in both taxonomic and ecological contexts, and to look for new sources of marine natural products.

Here we report on the diversity of the sponge fauna of the Society and Marquesas Islands. The Society Islands consist of nine high volcanic islands surrounded by a barrier reef (except for Mehetia, the easternmost island, which is a current volcanic hot spot) and five lower or coralline islands (Figure 1). The Marquesas Islands (Figure 2) are among the most isolated islands in the world, lying 5,500 km from Central America, consisting of 11 islands largely without coral reef barriers (except for one sandy islet lining a coral reef, Motu One). Specifically these sites include Mehetia, Tahiti, Moorea, Tetiaroa (atoll), Huahine, Raiatea, Tahaa, and Bora Bora in the Society Islands (Figure 1); and Nuku Hiva, Ua Huka, Ua Pou, Hiva Oa, Tahuata, and Fatu Hiva in the Marquesas Islands (Figure 2).

MATERIALS AND METHODS

Sampling and Identification

The first survey consisted of two legs of a cruise dedicated respectively to the exploration of the Leeward Islands (8–21 August 2009) and Marquesas Islands (29 August–12 September 2009). This collection of sponges from the Society Islands was complemented with samples from northern Tahiti acquired from occasional dives, and from Tetiaroa Atoll and Mehetia Island in 2011 (see Table 1).

Collections were made using scuba during 260 dives around the Society Islands (67 sites) and 210 dives around the Marquesas Islands (39 sites) (see Table 1). Each site was described with a morphological profile and georeferenced GIS and ecological data, and where possible the fauna and flora present were assessed via an abundance metric ranging from 1 (poorly abundant) to 4 (richly abundant). Every effort was made to ensure the completeness of the sampling; however, the collection of cryptic species was beyond the scope of this study, and there has been an undisputed focus on macroscopic sponges in this collection. In situ and ex situ photographs of each sponge, together with their georeferenced and ecological data, and a gross morphological description of each specimen (its habit, surface characteristics, consistency, interior and exterior coloration),

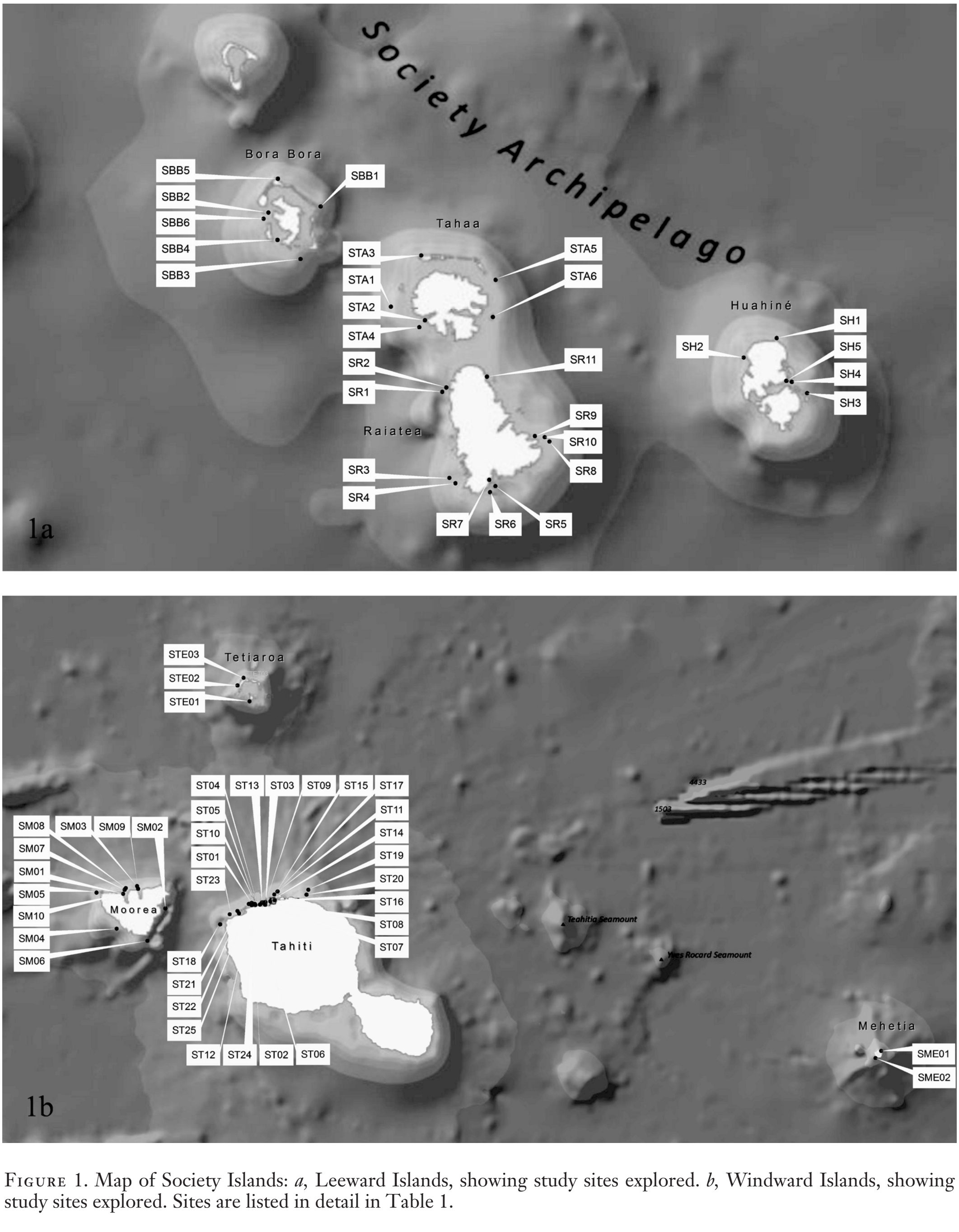

Figure 1. Map of Society Islands: *a*, Leeward Islands, showing study sites explored. *b*, Windward Islands, showing study sites explored. Sites are listed in detail in Table 1.

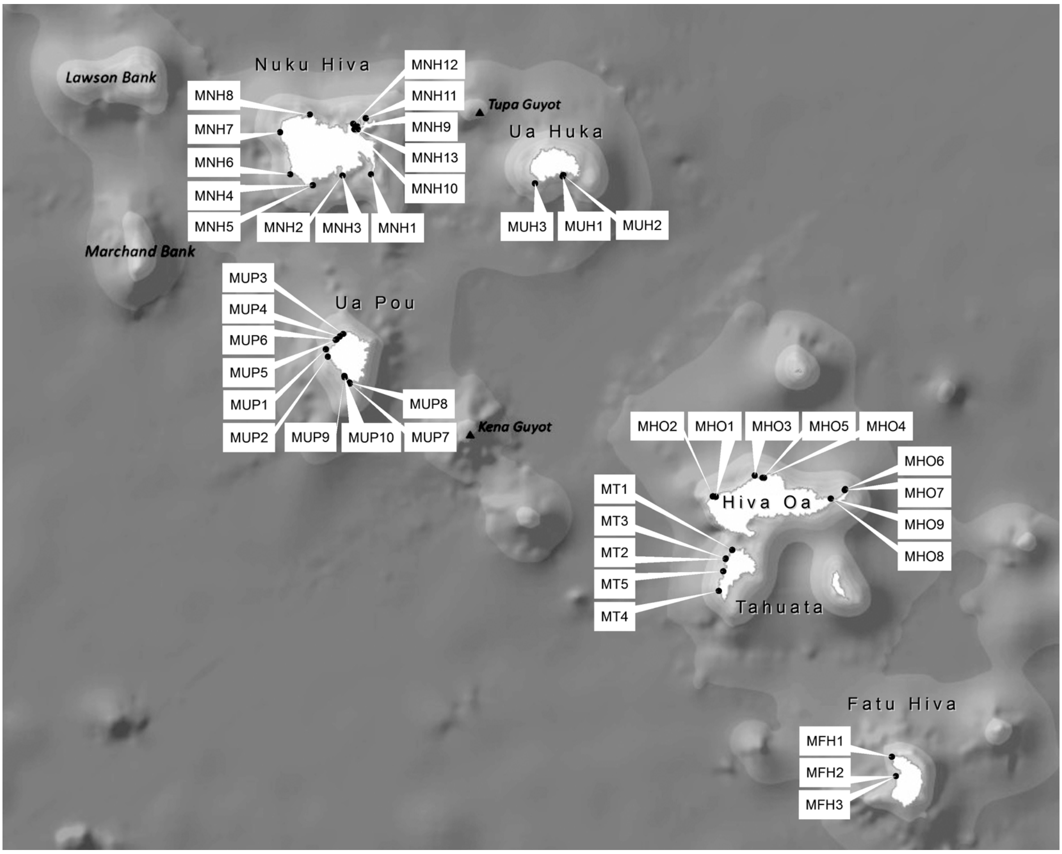

Figure 2. Map of Marquesas Islands, showing sites explored. Sites are listed in detail in Table 1.

following the protocol of Boury-Esnault and Rützler (1997), were captured in a field database, with a unique number identifier assigned to each specimen. This unique identifier accompanied every specimen throughout its processing from morphological examination to chemical analysis to ensure the integrity of the sample. Voucher samples (fragments of specimens used for chemical analyses) were preserved in 85% ethanol and further identified at Queensland Museum (QM) using traditional morphological data sets (see Hooper and van Soest 2002). Specimens were assigned to an OTU (morphospecies or operational taxonomic unit), and its characteristics were documented in an online summary description (or "mudmap" [see Appendix II in supplemental online material; also available at www.spongemaps.org]). This rigorous process ensured that every specimen acquired was assigned to an OTU (irrespective of whether it was a taxon recognized within the Linnaean classification) to enable unequivocal comparison across all collections as "same" or "different." Currently, these morphological hypotheses are being further tested through light and electron microscopy and also by independent molecular data sets for a large number of sponge specimens vouchered in QM collections (see the Sponge Barcoding Project, www.spongebarcoding.org). Barcoding sponge samples is a challenging and time-consuming process (Vargas et al. 2012), and compelling results may yet be years away;

in the interim, the OTUs presented here act as useful devices for the estimation of biodiversity.

Surveys included diverse biotopes: outer reefs, passes, inner reefs, fringing reefs, lagoons, bays, capes, and on different windward and seaward exposures. In the Marquesas Islands, weather conditions did not allow for exploration of eastern (windward) shores. Each island survey was terminated when the species accumulation curve reached an asymptote (i.e., when no more new species for that island were collected), except for Fatu Hiva, which was only explored in a cursory way due to time and weather constraints.

Faunal Comparisons

The collections of sponges from the Marquesas and Society Island archipelagos in French Polynesia were compared with other collections acquired from adjacent regions elsewhere in the southwestern Pacific Ocean using multivariate statistics and maximum parsimony analysis. These included all described and undescribed taxa (OTUs) held by the Queensland Museum from Fiji, Vanuatu, New Caledonia, the Great Barrier Reef (Australia), and Palau. The sponge fauna of the Great Barrier Reef (GBR) was divided into GBR North and GBR South, with beta-diversity (or species turnover) occurring at 19° S latitude, based on sponge bioregional distributions (Hooper and Ekins 2004), which have been confirmed by population genetics of the model species complex *Leucetta* "*chagosensis*" (Wörheide et al. 2002*b*).

A presence/absence matrix of sponge taxa (Appendix I in supplemental online material) was subjected to parsimony analysis of endemicity (PAE) (Rosen and Smith 1988). Parsimony analysis was completed using PAUP* (ver. 4.0b10) (Swofford 2002). We used a branch-and-bound search algorithm to search for maximum parsimony trees. A number of analyses were performed; characters were subjected to accelerated transformation and delayed transformation (ACCTRAN and DELTRAN options), and the GBR (North and South) character sets were included and excluded from analyses (because the size of the GBR sample sets was much larger than those from other geographical regions). Each permutation of the data set was tested using bootstrapping (1,000 replicates, branch-and-bound searching). Tree statistics were calculated for all trees to examine the fit of the data. All trees were unrooted.

The species matrix used for PAE was also analyzed using multivariate statistics (Minitab, ver. 16 [Minitab, Inc. 2009]). Factor Analysis explored the covariance of the data matrix, with four factors extracted using Principal Components Analysis, and the regions plotted against the first two factors. Cluster Analysis (Variables) generated a hierarchy of similarity among the regions; Ward linkage and Average linkage methods were used with distances from correlation coefficient distances in separate analyses. Results from the analyses were interpreted in relation to the geography of the southwestern Pacific Ocean.

RESULTS AND DISCUSSION

A total of 41 sponge species (or OTUs) was identified for the Society Islands (Table 2) and 38 for the Marquesas Islands (Table 3). Each species was assessed for abundance criteria for use in further qualitative (Figure 3) and quantitative (Figure 4) analyses. The sponge fauna of the Marquesas Islands archipelago shows partitioning broadly in agreement with the geophysical subdivision of the northern (Nuku Hiva, Ua Huka, Ua Pou) and southern islands (Hiva Oa, Tahuata, and Fatu Hiva) (Figure 2). Fifteen species were found only on the northern islands, and nine only on the southern ones (Table 2), with 12 taxa shared across the archipelago. The two island groups (Leeward and Windward Islands) of the Society Islands archipelago had similar faunas, containing 32 and 24 species, respectively. Sixteen species were common across both island groups, with seven of 32 species found only in the Leeward Islands, and seven of 24 found only in the Windward Islands. Tahaa and Raiatea are surrounded by single barrier reefs and lagoons and as such represent the largest set of reefs and lagoons of the

TABLE 1

List of Sites Explored in French Polynesia

Site[a]	Latitude (S)	Longitude (W)	Date	Island	Maximum Depth (m)
Society Islands: Leeward Islands					
SBB01	16°28,773′	151°41,287′	09/08/2009	Bora Bora	35
SBB02	16°29,332′	151°46,069′	09/08/2009	Bora Bora	20
SBB03	16°33,951′	151°43,132′	10/08/2009	Bora Bora	60
SBB04	16°31,824′	151°45,235′	10/08/2009	Bora Bora	20
SBB05	16°26,240′	151°45,208′	11/08/2009	Bora Bora	60
SBB06	16°29,893′	151°46,497′	11/08/2009	Bora Bora	16
SR01	16°45,715′	151°30,194′	12/08/2009	Raiatea	45
SR02	16°45,326′	151°29,827′	12/08/2009	Raiatea	26
SR03	16°53,602′	151°29,521′	13/08/2009	Raiatea	47
SR04	16°54,068′	151°28,984′	13/08/2009	Raiatea	27
SR05	16°54,351′	151°25,316′	14/08/2009	Raiatea	45
SR06	16°54,980′	151°25,820′	14/08/2009	Raiatea	31
SR07	16°53,759′	151°25,899′	14/08/2009	Raiatea	15
SR08	16°50,260′	151°20,399′	15/08/2009	Raiatea	62
SR09	16°49,754′	151°21,728′	15/08/2009	Raiatea	26
SR10	16°49,873′	151°20,825′	16/08/2009	Raiatea	54
SR11	16°44,331′	151°26,106′	16/08/2009	Raiatea	31
ST01	16°37,928′	151°34,888′	17/08/2009	Tahaa	60
ST02	16°39,186′	151°31,770′	17/08/2009	Tahaa	25
ST03	16°33,254′	151°32,101′	18/08/2009	Tahaa	57
ST04	16°39,817′	151°32,284′	18/08/2009	Tahaa	27
ST05	16°35,477′	151°25,309′	19/08/2009	Tahaa	60
ST06	16°38,882′	151°25,553′	19/08/2009	Tahaa	28
SH01	16°40,807′	150°59,639′	20/08/2009	Huahiné	58
SH02	16°42,596′	151°02,640′	20/08/2009	Huahiné	25
SH03	16°45,854′	150°56,857′	21/08/2009	Huahiné	60
SH04	16°44,812′	150°58,253′	21/08/2009	Huahiné	20
SH05	16°11,710′	150°58,749′	21/08/2009	Huahiné	28
Society Islands: Windward Islands					
ST01	17°31,013′	149°33,440′	19/11/2008	Tahiti	62
ST02	17°31,225′	149°33,220′	20/11/2008	Tahiti	31
ST03	17°30,889′	149°31,429′	21/11/2008	Tahiti	46
ST04	17°31,215′	149°32,222′	28/01/2009	Tahiti	17
ST05	17°31,149′	149°32,930′	29/01/2009	Tahiti	20
ST06	17°31,140′	149°32,985′	30/01/2009	Tahiti	30
ST07	17°31,244′	149°31,494′	02/02/2009	Tahiti	19
ST08	17°31,047′	149°31,472′	02/02/2009	Tahiti	27
ST09	17°30,901′	149°31,477′	04/02/2009	Tahiti	47
ST10	17°31,270′	149°32,863′	04/02/2009	Tahiti	27
ST11	17°29,380′	149°29,741′	20/03/2009	Tahiti	5
ST12	17°31,30′	149°33,40′	23/03/2009	Tahiti	11
ST13	17°30,907′	149°31,940′	25/03/2009	Tahiti	33
ST14	17°30,75′	149°30,75′	26/03/2009	Tahiti	19
ST15	17°29,795′	149°30,168′	27/03/2009	Tahiti	27
ST16	17°30,592′	149°30,146′	27/03/2009	Tahiti	6
ST17	17°29,352′	149°29,711′	25/05/2009	Tahiti	28
ST18	17°34,050′	149°37,907′	26/05/2009	Tahiti	44
ST19	17°29,122′	149°25,315′	27/05/2009	Tahiti	34
ST20	17°29,814′	149°25,593′	27/05/2009	Tahiti	17
ST21	17°32,140′	149°35,449′	28/05/2009	Tahiti	28
ST22	17°32,485′	149°35,205′	29/05/2009	Tahiti	24
ST23	17°32,615′	149°36,536′	30/07/2009	Tahiti	23
ST24	17°31,225′	149°33,220′	16/03/2011	Tahiti	36
ST25	17°31,131′	149°33,832′	17/03/2011	Tahiti	35
SM01	17°29,681′	149°51,717′	29/11/2010	Moorea	18
SM02	17°31,767′	149°45,722′	30/11/2010	Moorea	21

TABLE 1 (continued)

Site[a]	Latitude (S)	Longitude (W)	Date	Island	Maximum Depth (m)
SM03	17°28,600′	149°49,754′	30/11/2010	Moorea	22
SM04	17°34,682′	149°52,640′	01/12/2010	Moorea	26
SM05	17°29,528′	149°55,540′	01/12/2010	Moorea	25
SM06	17°36,41′	149°48,271′	02/12/2010	Moorea	32
SM07	17°29,121′	149°51,534′	03/12/2010	Moorea	38
SM08	17°28,905′	149°51,355′	03/12/2010	Moorea	39
SM09	17°28,982′	149°49,595′	04/12/2010	Moorea	20
SM10	17°29,681′	149°51,717′	04/12/2010	Moorea	19
SME01	17°52,109′	158°03,678′	26/04/2011	Mehetia	61
SME02	17°53,11′	148°04,454′	26/04/2011	Mehetia	30
STE01	17°02,258′	149°33,707′	26/04/2011	Tetiaroa	75
STE02	16°59,967′	149°35,440′	31/05/2011	Tetiaroa	30
STE03	16°59,454′	149°34,104′	01/06/2011	Tetiaroa	53
Marquesas Islands					
MNH01	08°55,977	140°01,178	28/08/2009	Nuku Hiva	55
MNH02	8°56,173	140°05,593	29/08/2009	Nuku Hiva	11
MNH03	8°56,173	140°05,593	29/08/2009	Nuku Hiva	11
MNH04	08°57,661	140°10,149	30/08/2009	Nuku Hiva	42
MNH05	08°57,466	140°10,149	30/08/2009	Nuku Hiva	24
MNH06	08°56,012	140°13,588	31/08/2009	Nuku Hiva	32
MNH07	08°49,513	140°15,118	31/09/2009	Nuku Hiva	24
MNH08	08°46,820	140°10,568	01/09/2009	Nuku Hiva	36
MNH09	08°03,295	140°48,627	01/09/2009	Nuku Hiva	32
MNH10	08°49,114	140°03,738	01/09/2009	Nuku Hiva	24
MNH11	08°47,372	140°02,003	02/09/2009	Nuku Hiva	34
MNH12	08°48,242	140°03,936	02/09/2009	Nuku Hiva	28
MNH13	08°49,115	140°03,202	02/09/2009	Nuku Hiva	22
MUH01	08°56,326	139°31,816	03/09/2009	Ua Huka	34
MUH02	08°56,067	139°31,727	03/09/2009	Ua Huka	24
MUH03	08°57,355	139°36,077	03/09/2009	Ua Huka	26
MUP01	09°22,823	140°08,144	04/09/2009	Ua Pou	42
MUP02	09°23,952°°°	140°07,838	04/09/2009	Ua Pou	28
MUP03	09°20,466	140°05,490	05/09/2009	Ua Pou	20
MUP04	9°20,835	140°05,987	05/09/2009	Ua Pou	23
MUP05	9°21,376	140°06,611	05/09/2009	Ua Pou	20
MUP06	9°21,322	140°06,448	05/09/2009	Ua Pou	23
MUP07	9°28,082	140°04,434	06/09/2009	Ua Pou	32
MUP08	9°27,952	140°04,471	06/09/2009	Ua Pou	30
MUP09	9°26,937	140°05,281	06/09/2009	Ua Pou	25
MUP10	9°27,092	140°05,280	06/09/2009	Ua Pou	25
MHO01	9°45,421	139°08,275	07/09/2009	Hiva Oa	21
MHO02	9°45,396	139°08,776	07/09/2009	Hiva Oa	43
MHO03	9°42,196	139°02,356	08/09/2009	Hiva Oa	40
MHO04	9°42,540	139°00,878	09/09/2009	Hiva Oa	22
MHO05	9°42,553	139°01,181	08/09/2009	Hiva Oa	28
MHO06	9°44,307	139°48,480	09/09/2009	Hiva Oa	49
MHO07	9°44,445	139°48,539	09/09/2009	Hiva Oa	35
MHO08	9°45,767	139°50,699	09/09/2009	Hiva Oa	20
MHO09	9°45,767	138°50,698	09/09/2009	Hiva Oa	27
MT01	9°53,589	139°05,805	10/09/2009	Tahuata	38
MT02	9°55,029	139°06,848	10/09/2009	Tahuata	28
MT03	9°54,933	139°06,780	10/09/2009	Tahuata	23
MT04	9°59,917	139°07,879	11/09/2009	Tahuata	58
MT05	9°56,917	139°07,203	11/09/2009	Tahuata	26
MFH01	10°25,360	138°41,334	12/09/2009	Fatu Hiva	31
MFH02	10°28,311	138°40,698	12/09/2009	Fatu Hiva	27
MFH03	10°28,323	138°40,675	12/09/2009	Fatu Hiva	27

[a] Sites are divided into groups for the Windward Islands and Leeward Islands (both Society Islands) and the Marquesas Islands. Sites are plotted onto maps and shown in Figures 3–4.

TABLE 2

List of Sponges (Porifera) from the Society Islands with Their Relative Abundance by Study Site

					Island Group										
					Windward Islands					Leeward Islands					
				Island	Bora Bora	Huahiné	Raiatea	Tahaa	Total	Mehetia	Moorea	Tahiti (NW)	Tetiaroa	Total	Grand Total
				Number of Sites	6	5	11	6	28	2	9	25	3	39	67
				Number of Species	12	12	22	13	24	5	12	19	12	21	41
Class	Order	Family	Genus	Species											
Calcarea	Clathrinida	Clathrinidae	*Clathrina*	sp. (OTU QM4850)			1				1	1			
				sp. (OTU QM4851)		1							1		
		Leucettidae	*Leucetta*	*chagosensis*	4	4	3	4			3	4	3		
				microrhaphis	2		1				2	1	2		
Demospongiae	Dictyoceratida	Dysideidae	*Dysidea*	*arenaria*								2	1		
				herbacea		1	1	1			4	4			
				frondosa				4							
				sp. (OTU QM0103)				4							
				sp. (OTU QM0229)	4						1				
				sp. (OTU QM1214)				4							
				sp. (OTU QM2669)	3		2								
				sp. (OTU QM4759)			4								
				sp. unidentified	2	1	1	1			2	3			
			Euryspongia	sp. (OTU QM4409)		4	4	3			1		1		
			Lamellodysidea	sp. (OTU QM2538)			2	3				4			
		Irciniidae	*Psammocinia*	sp. (OTU QM4758)	1		4								
		Spongiidae	*Coscinoderma*	sp. (OTU QM4176)			3								
			Spongia (*Spongia*)	sp. (OTU QM4763)				1				2			
		Thorectidae	*Dactylospongia*	*metachromia*									3		
			Hyrtios	sp. (OTU QM4761)			1								
			Smenospongia	sp. (OTU QM4760)			4								
	Hadromerida	Suberitidae	*Prosuberites*	sp. (OTU QM1680)	4						2	3	3		
	Halichondrida	Axinellidae	*Axinella*	sp. (OTU QM0353)			4								
			Phycopsis	sp. (OTU QM1640)								3	1		

	Dictyonellidae	*Stylissa*	*flabelliformis*								1	
	Halichondriidae	*Amorphinopsis*	sp. (OTU QM4757)	2	4							
		Epipolasis	sp. (OTU QM0452)						2			
		Halichondria	sp. (OTU QM4720)								4	
		Spongosorites	sp. (OTU QM4762)				3					
Haplosclerida	Chalinidae	*Haliclona*	sp. (OTU QM0854)	3		1	4					
			sp. (OTU QM2309)		4				3	2	2	
			sp. (OTU QM4386)	1	2	1	3					
			sp. (OTU QM4715)		1					2	4	2
	Phloeodictyidae	*Siphonodictyon*	sp. (OTU QM4700)		1	1					2	3
Spirophorida	Tetillidae	*Cinachyrella*	sp. (OTU QM2119)			4						
Verongida	Aplysinellidae	*Suberea*	sp. (OTU QM2093)			1						
			sp. (OTU QM2121)	1	4	4	4					
			sp. (OTU QM4728)						3	4	4	4
	Pseudoceratinidae	*Pseudoceratina*	sp. (OTU QM2872)								1	
			sp. (OTU QM4755)	1	1	4	1		2	1	2	1
			sp. (OTU QM4756)								1	

Note: Abundance is a qualitative measure: 4 indicates high abundance and 1 indicates rarity. Specimens are listed in alphanumeric order within a systematic scheme by higher rank.

Society Islands; these sites were also the best sources of sponges, harboring 26 of the 32 species in the Leeward Islands.

In contrast to these relatively homogeneous within-archipelago faunas, the taxonomic composition was very different between archipelago groups (especially at the ordinal level). Sponges belonging to order Dictyoceratida were predominant within the sites of the Society Islands, whereas sponges of order Poecilosclerida dominated the Marquesas Islands (Figure 3). These taxa were dominant both in their abundance and species diversity (Tables 2–3, Figure 4), reflecting differences in geomorphology and biotopes between the two island groups. The Society Islands are dominated by coral reefs, where dictyoceratid sponges are abundant (many phototrophic), whereas the Marquesas Islands are composed mostly of rocky slopes, where poecilosclerids predominate (all heterotrophic). Sponges of order Verongida are important components of the faunas in both these archipelagos (six species in the Society Islands, four species in the Marquesas Islands). The abundance of *Suberea ianthelliformis* in the Marquesas Islands is also noteworthy and similar to that observed previously in the Solomon Islands (Mani et al. 2011), which lie within the same latitude. The rocky slopes of the Marquesas offer deep faults and overhangs that are covered by a yet-undescribed species of calcareous sponge (*Leucaltis* sp.). These volcanic islands also contain underwater lava tubes, such as Ekamako, a cave on the southern coast of Nuku Hiva, which had an abundant cover of a lithistid sponge (*Microscleroderma* sp.).

Remarkably, only four species are shared between the Marquesas and Society Islands archipelagos, all of which are common throughout the Pacific (Table 4). *Leucetta "chagosensis"* is very common on Society Islands reefs, but only two specimens were found in the Marquesas. *Suberea* sp. (OTU QM2093) was often found with different gross morphological forms in the Marquesas and only once on the *Nordby* wreck in Raiatea (lagoon). *Epipolasis* sp. (OTU QM0452) was found on two islands in the Marquesas and once on the rocky island Mehetia of the

TABLE 3

List of Sponges (Porifera) from the Marquesas Islands with Their Relative Abundance by Study Site

				Island Group							
				Island	Nuku Hiva	Ua Huka	Ua Pou	Hiva Oa	Tahuata	Fatu Hiva	Grand Total
				Number of Sites	12	3	10	9	5	3	42
				Number of Species	19						38
Class	Order	Family	Genus	Species							
Calcarea	Clathrinida	Leucascidae	*Leucascus*	sp. (OTU QM4853)	4	4	4	4	4	4	
	Leucettida	Leucettidae	*Leucetta*	*chagosensis*				1		1	
	Leucosolenida	Grantiidae	*Leucandra*	sp. (OTU QM4854)					1		
Demospongiae	[Lithistida]	Scleritodermidae	*Microscleroderma*	sp. (OTU QM4852)	2						
	Chondrosida	Chondrillidae	*Chondrosia*	*corticata*	4						
	Dictyoceratida	Dysideidae	*Dysidea*	sp. (OTU QM2102)	1						
		Thorectidae	*Dactylospongia*	*elegans*	4		1		1	1	
			Fasciospongia	sp. (OTU QM4703)	2		2				
	Hadromerida	Suberitidae	*Suberites*	sp. (OTU QM3294)				1			
		Spirastrellidae	*Diplastrella*	sp. (OTU QM1362)			1				
			Spirastrella	sp. (OTU QM1142)	4	4	4	4	4	4	
				sp. (OTU QM4689)		1	3	4	2	2	
	Halichondrida	Axinellidae	*Phycopsis*	sp. (OTU QM1640)			4	3	2	4	
		Halichondriidae	*Ciocalypta*	sp. (OTU QM0857)	1						
			Epipolasis	sp. (OTU QM0452)	4		1				
			Topsentia	sp. (OTU QM4695)						2	
		Hymerhabdiidae	*Hymerhabdia*	sp. (OTU QM4743)	4						
	Haplosclerida	Petrosiidae	*Neopetrosia*	*exigua*						2	
			Petrosia (*Petrosia*)	sp. (OTU QM4710)	1						
			Xestospongia	sp. (OTU QM4688)	4						
		Phloeodictyidae	*Siphonodictyon*	sp. (OTU QM0331)			2				
	Poecilosclerida	Chondropsidae	*Batzella*	sp. (OTU QM2753)			2				
				sp. (OTU QM4713)					1		
			Phoriospongia	sp. (OTU QM1599)	4	4	4		2		
				sp. (OTU QM3715)			1	1	1		
				sp. (OTU QM3730)						2	
			Psammoclema	sp. (OTU QM0736)			2				
		Coelosphaeridae	*Coelosphaera* (*Coelosphaera*)	sp. (OTU QM4683)	3		4		3		
		Crambeidae	*Monanchora*	sp. (OTU QM4696)			1	3	2		

	Desmacellidae	*Microtylostylifer*	sp. (OTU QM0785)	1					
	Microcionidae	*Antho* (*Antho*)	sp. (OTU QM4699)				2	2	
	Mycalidae	*Mycale* (*Mycale*)	*grandis*				2		
		Mycale (*Zygomycale*)	sp. (OTU QM2635)	1					
Spirophorida	Tetillidae	*Cinachyrella*	sp. (OTU QM4680)	4	2	2	2	1	1
		Craniella	*abracadabra*			1		1	
Verongida	Aplysinellidae	*Aplysinella*	*rhax*	4	4	4	4	2	2
		Suberea	*ianthelliformis*				3	2	2
			sp. (OTU QM2093)	3		1	1	1	

Note: Abundance is a qualitative measure: 4 indicates high abundance and 1 indicates rarity. Specimens are listed in alphanumeric order within a systematic scheme by higher rank.

Society Islands, with only one specimen collected. *Ptilocaulis* sp. (OTU QM1640) is a very common sponge in the Marquesas, and also on the outer reef of Tahiti, but only one specimen was found on the outer reef of Tetiaroa atoll (Society Islands).

The taxonomic diversity from a similarly remote archipelago, such as the Hawaiian Islands (de Laubenfels 1950, 1954, 1957), indicates higher levels of endemism for sponges than for any other animal or plant group and also little affinity to the faunas of Asia or Australia. Sponge faunas of the Hawaiian, Marquesas, and Society Islands show close similarities in terms of the numbers of species, genera, and families distributed across each of the orders (Figure 5), even though there are very few (Marquesas versus Society Islands) or no shared species (Hawaiian Islands versus (Marquesas + Society Islands)) among these three archipelagos. In contrast, the sponge fauna of remote Clipperton Island (van Soest et al. 2011) is very different in its taxonomic composition from either the Marquesas or Society Islands faunas, and this comparison will be explored further pending the results of a more recent Tuamotu archipelago sponge survey.

In total, 14 (of 41) and 11 (of 38) species collected from the Society and Marquesas Islands archipelagos, respectively, had not previously been encountered from collections made elsewhere in the southwestern Pacific (putative “new species”). Only 20 species were shared between French Polynesia and other sites in the southwestern Pacific (Table 4). Parsimony analysis of endemicity (PAE) and multivariate analyses of these data showed similarity patterns between the Marquesas Islands, Society Islands, Tonga, Fiji, Vanuatu, New Caledonia, the Great Barrier Reef, and Palau that largely reflect their geographic proximity (and isolation) across the central and Southwest Pacific. Figure 6 shows an unrooted phylogram, inferred using PAE, that supports a close similarity between the faunas of the Marquesas and Society Islands (95% bootstrap support [BS]). Support for the relationship of this fauna with those of other sites in the southwestern Pacific, however, is, at best, equivocal; parsimony shows the fauna of

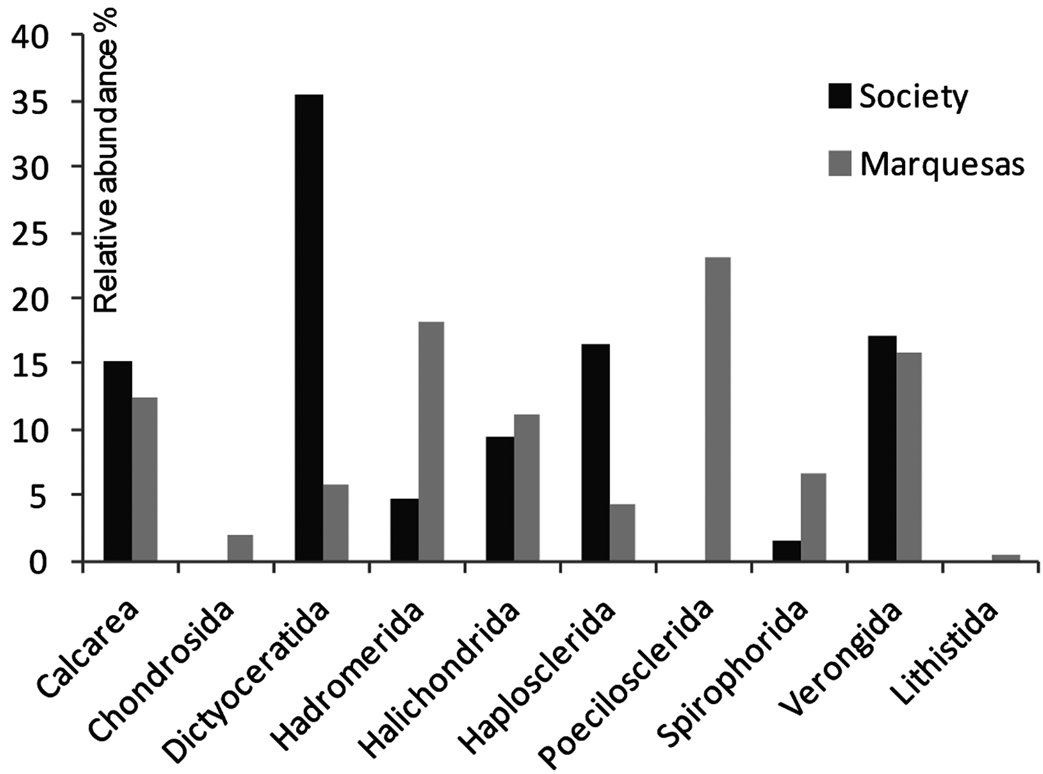

Figure 3. Comparison of quantitative abundance (%) of the sponge fauna of the Society and Marquesas Islands.

French Polynesia as similar to that of New Caledonia with only 53% BS. The paucity of shared species between the two French Polynesian archipelagos, and between other sites investigated in the Southwest Pacific, does not provide strong insight into their affinities, other than confirming high levels of apparent endemism, as demonstrated for other remote island groups in the Pacific Ocean, such as the Hawaiian Islands. It is interesting that the phylogram (Figure 6) indicates a strongly supported similarity among the faunas of the Great Barrier Reef (North and South) and faunas of Vanuatu and Fiji (98% BS), to the exclusion of other sites in the southwestern Pacific. The sample size for the collection records from the Great Barrier Reef is very large in comparison with those from other regions, and given the sensitivity of parsimony analysis to long branches, it could be that PAE is inadequate to test faunal similarities across the whole region.

Exploration of the data matrix using multivariate analyses allowed further interpretation of faunal relationships. Factor Analysis (Figure 7) emphasized the strong influence of the Great Barrier Reef data set on the analysis. The long vectors and different directions from the origin for the northern and southern Great Barrier Reef regions indicate that these faunas are very different. Reasons for these clear differences may be due to actual taxonomic composition but also collection bias (the Great Barrier Reef has been examined far more extensively and intensively as a source of sponges). The French Polynesian faunas are indicated as being similar, and distinct from all other faunas, as is the fauna of Palau. In the

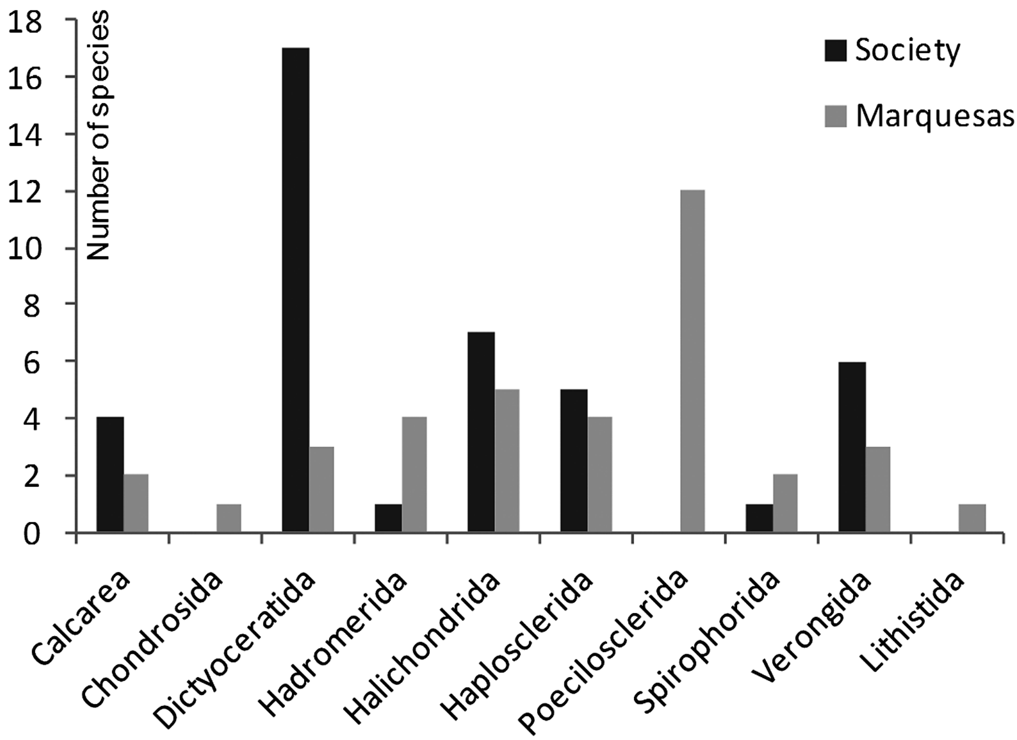

Figure 4. Comparison of species diversity (number of species) of the sponge fauna of the Society and Marquesas Islands.

quadrant that is positive for both factors, there is a cluster of regions spanning New Caledonia, Fiji, Tonga, and Vanuatu. Clustering of variables (= the geographical regions) repeats these relationships among the data sets, as illustrated by the hierarchical similarity among the faunas of the regions (Figure 8 and Tables 5 and 6).

Although both multivariate and PAE analyses demonstrate the closer relationship between the two French Polynesian archipelagos to each other than to other faunas, the cluster analysis further indicates that the faunas of Fiji, Tonga, and Vanuatu are slightly more similar to one another (57% similarity) than the faunas of the Marquesas and Society Islands archipelagos are to each other (53%) (see Table 6). The two French Polynesian archipelagos are as geographically isolated from each other as the island groups of Tonga, Fiji, and Vanuatu are from each other (Figure 8), and the comparable levels of similarity reflect this degree of geographical separation. Table 6 shows that the two faunal groups on the Great Barrier Reef (North and South) are comparatively dissimilar; the two faunas are most similar to each other but only with a level of similarity of 43%. This level of similarity is almost equivalent to the similarity between the French Polynesian fauna and the remainder of the Pacific island groups included in this investigation (similarity of 44%). The high degree of dissimilarity between the North and South faunas of the Great Barrier Reef reflects the action of the South Equatorial Current, which splits at the Great Barrier Reef (at ~19° S), as previously explained in Wörheide et al. (2002*a*,*b*, 2008) and Wörheide (2006). Although the influence of historical biogeography on the

TABLE 4

Species of Sponges from French Polynesia That Are Known from Other Sites throughout the Southwestern Pacific

Class	Order	Family	Genus	Species	Society Islands	Marquesas Islands	Fiji	GBR North	GBR South	New Caledonia	Palau	Tonga	Vanuatu
Calcarea	Clathrinida	Leucettidae	*Leucetta*	*chagosensis*	•	•	•	•	•				•
Demospongiae	Dictyoceratida	Dysideidae	*Dysidea*	*arenaria*	•		•	•	•	•	•		•
				sp. (OTU QM0103)	•						•		
				sp. (OTU QM1214)	•			•	•				
				sp. (OTU QM2102)		•	•						
			Euryspongia	sp. (OTU QM4409)	•								•
		Thorectidae	*Dactylospongia*	*elegans*		•		•	•		•		•
				metachromia	•		•						
	Halichondrida	Axinellidae	*Ptilocaulis*	sp. (OTU QM1640)	•	•	•	•	•		•		•
		Dictyonellidae	*Stylissa*	*flabelliformis*	•			•					
		Halichondriidae	*Epipolasis*	sp. (OTU QM0452)	•	•			•				
	Haplosclerida	Petrosiidae	*Neopetrosia*	*exigua*		•		•	•		•	•	•
		Phloeodictyidae	*Aka*	sp. (OTU QM0331)		•	•		•				
	Poecilosclerida	Chondropsidae	*Batzella*	sp. (OTU QM2753)		•						•	
			Phoriospongia	sp. (OTU QM3715)		•		•					
	Spirophorida	Tetillidae	*Cinachyrella*	sp. (OTU QM2119)	•								•
	Verongida	Aplysinellidae	*Suberea*	*ianthelliformis*		•		•	•				
				sp. (OTU QM2093)	•	•	•						
				sp. (OTU QM2121)	•								•
		Pseudoceratinidae	*Pseudoceratina*	sp. (OTU QM2872)	•								•

Note: Presence of the species at a location is denoted by a dot (•). Taxa common to both the Society and Marquesas Islands are shaded. Note that the Great Barrier Reef sites are divided into North and South bioregions and are listed as GBR North and GBR South.

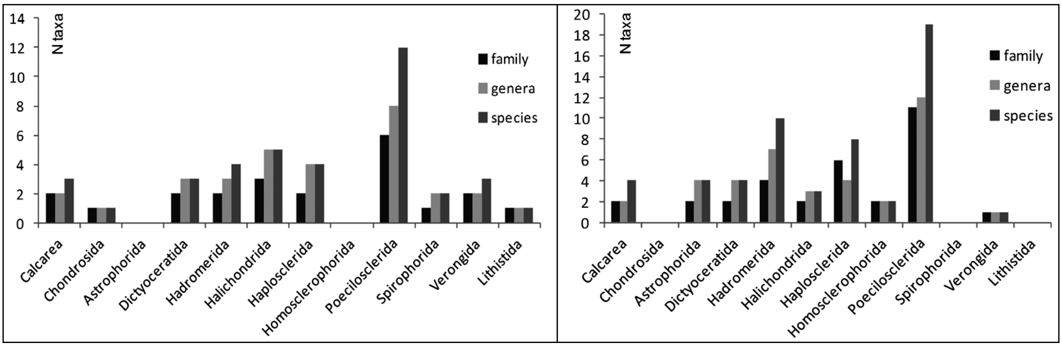

Figure 5. Comparison of the sponge diversity of the Marquesas Islands and the Hawaiian Islands. Estimates of the sponge diversity of the Hawaiian Islands are based on the records of de Laubenfels (1950, 1954, 1957). The graph on the left represents the Marquesas Islands, and on the right is the Hawaiian Islands.

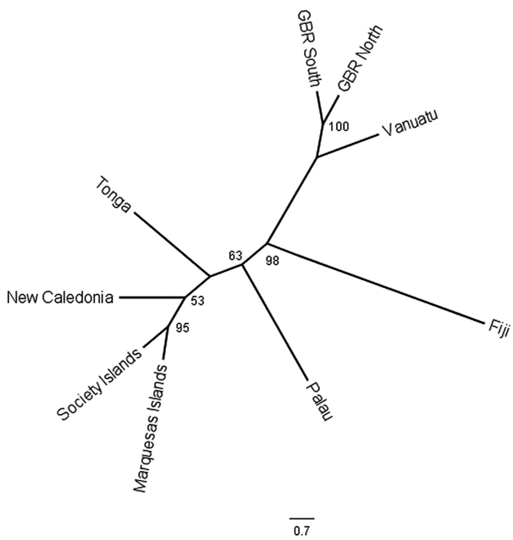

Figure 6. Maximum parsimony tree of shared similarities among the sponge faunas of the southwestern Pacific produced by PAE. Representation of the relationships is as an unrooted phylogram. Tree inferred using branch-and-bound searching and accelerated character transformations. Bootstrap values are presented on each node (*nreps* = 1,000). This tree is one of two equally parsimonious trees generated excluding uninformative characters, based on 516 parsimony informative characters. Tree statistics: (including uninformative characters): length = 2294, CI = 0.902, HI = 0.098; (excluding uninformative characters): CI = 0.697, HI = 0.302, RC = 0.604.

observed faunas discussed here cannot be discounted, these patterns of faunal similarities (summarized by the hierarchical clustering analysis [Tables 5 and 6]) largely reflect their geographic isolation and minimal genetic connectivity across the southwestern Pacific via the South Equatorial Current (Figure 8).

The absence of a strong relationship between the Great Barrier Reef fauna and that of geographically close Vanuatu and New Caledonia is consistent with the findings of Wörheide et al. (2002*a*,*b*, 2008) based on genetic studies of three different species of sponges across the Indo-West Pacific. Those authors noted that local populations of a particular species have very low levels of genetic diversity and population structure, and that their low genetic connectivity may be more heavily influenced by historical glaciations and the dispersal away from an Indonesian center than by present-day oceanic currents. Nevertheless, the influence of the South Equatorial Current is important in maintaining some level of genetic connectivity among the southwestern Pacific sponge populations (which otherwise lack a lecithotrophic planktonic larval stage that is capable of oceanic dispersal), and our analyses show a pattern of similarity among nested groups of isolated faunas, indicating that geographical proximity is an important factor influencing the similarity of faunas.

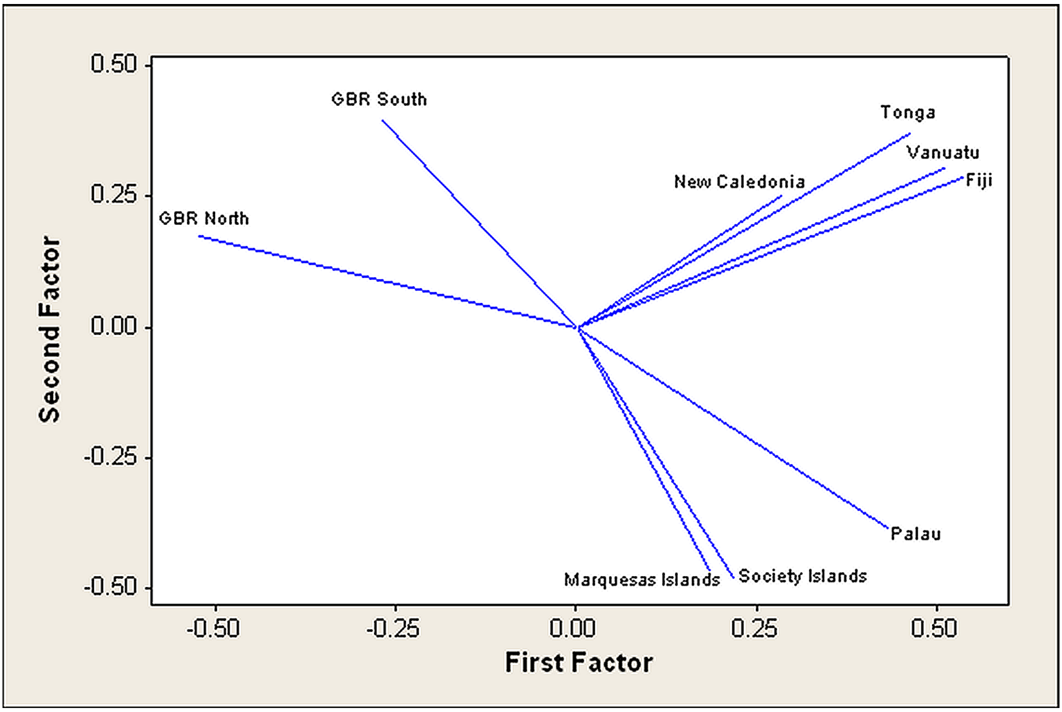

Figure 7. Factor Analysis of presence/absence data matrix for 2,070 species distributed in the southwestern Pacific. Graph shows vectors for each geographical region plotted against the first two factors extracted by Principal Components.

According to our analysis, the close sponge faunal partners are as follows: (Marquesas Islands + Society Islands), (((Tonga + Fiji) + Vanuatu) + New Caledonia), and (North GBR + South GBR). Hierarchical cluster analysis supports the negative correlation between geographic distance and faunal similarity, but the relationship of these groups with those of other regions (such as Micronesia [as represented here by the Palau data set] and the Great Barrier Reef) is much more difficult to assert with confidence. The results of the biodiversity survey presented here show levels of apparent endemism of approximately one-third of the sponge fauna in both the Marquesas and Society Islands. This observed level of apparent endemism (that is, as far as we are aware these species do not occur in other island groups), coupled with the dispersal and colonization barrier provided by the geographical isolation of the islands and historical patterns of dispersal eastward across the Pacific, likely accounts for the reciprocal similarity of the faunas of the two French Polynesian archipelagos to each other and to the exclusion of other regions in the southwestern Pacific.

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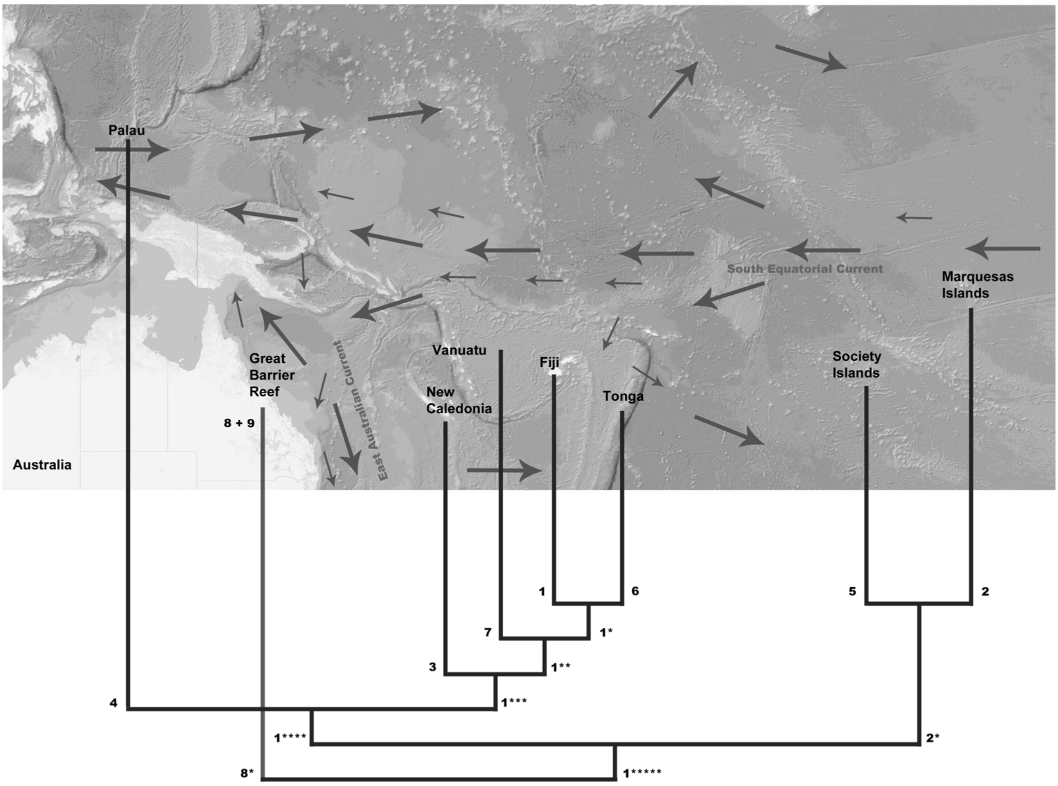

FIGURE 8. Map of the southwestern Pacific overlain with hierarchical relationships indicated by multivariate analysis (cluster analysis of variables) of the faunas of the regions. Major oceanic currents are overlain and indicated by arrows; these currents are redrawn from a map of ocean surface currents by Rick Lumpkin (NOAA/AOML) available at the Scripps Oceanography photostream on Flickr (www.flickr.com/photos/8581704@N02/sets/). Please note that the hierarchical representation is not to scale (for percentage similarities of the clusters, refer to Table 6).

TABLE 5

Matrix of Correlation Distances among the Variables Used in the Cluster Analysis (Variables = Locations)

	Fiji	Marquesas Islands	New Caledonia	Palau	Society Islands	Tonga	Vanuatu	GBR North	GBR South
Fiji	—	0.978	0.93723	0.961	0.969	0.851	0.852	1.081	1.046
Marquesas Islands	0.978	—	1.035	1.011	0.946	0.986	1.010	1.102	1.073
New Caledonia	0.937	1.035	—	1.040	1.023	0.975	0.942	1.124	1.070
Palau	0.961	1.011	1.040	—	1.015	0.946	0.969	1.202	1.169
Society Islands	0.969	0.941	1.023	1.015	—	1.027	0.969	1.111	1.088
Tonga	0.851	0.986	0.975	0.946	1.027	—	0.866	1.057	1.021
Vanuatu	0.852	1.010	0.942	0.969	0.9697	0.866	—	1.077	1.063
GBR North	1.081	1.102	1.124	1.202	1.111	1.057	1.077	—	1.130
GBR South	1.046	1.073	1.070	1.169	1.089	1.021	1.063	1.130	—

Note: GBR North and GBR South refer to the two groups of Great Barrier Reef taxa included in the study.

TABLE 6

Amalgamation Steps Completed during the Cluster Analysis of Variables

Step	*N* (clusters)	Similarity (%)	Distance	Clusters Joined	New Cluster	*N* (Observations in Cluster)
1	8	57	0.85078	1 — 6	1*	2
2	7	57	0.86180	1* — 7	1**	3
3	6	53	0.94067	2 — 5	2*	2
4	5	50	0.99898	1** — 3	1***	4
5	4	49	1.02388	1*** — 4	1****	5
6	3	44	1.12485	1**** — 2*	1*****	7
7	2	43	1.13044	8 — 9	8*	2
8	1	39	1.22825	1***** — 8*	1******	9

Note: Clustering was completed using the Ward Linkage method on the correlation distance matrix (Table 5). Legend for Clusters Joined: 1, Fiji; 2, Marquesas Islands; 3, New Caledonia; 4, Palau; 5, Society Islands; 6, Tonga; 7, Vanuatu; 8, Great Barrier Reef North; 9, Great Barrier Reef South. Note that after the first amalgamation step, the new cluster = 1*; asterisks are added sequentially to show the amalgamation of new clusters. Clusters (as in New Cluster) are marked on Figure 8.

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