

*Living on the edge: the sponge fauna  
of Australia's southwestern and  
northwestern deep continental margin*

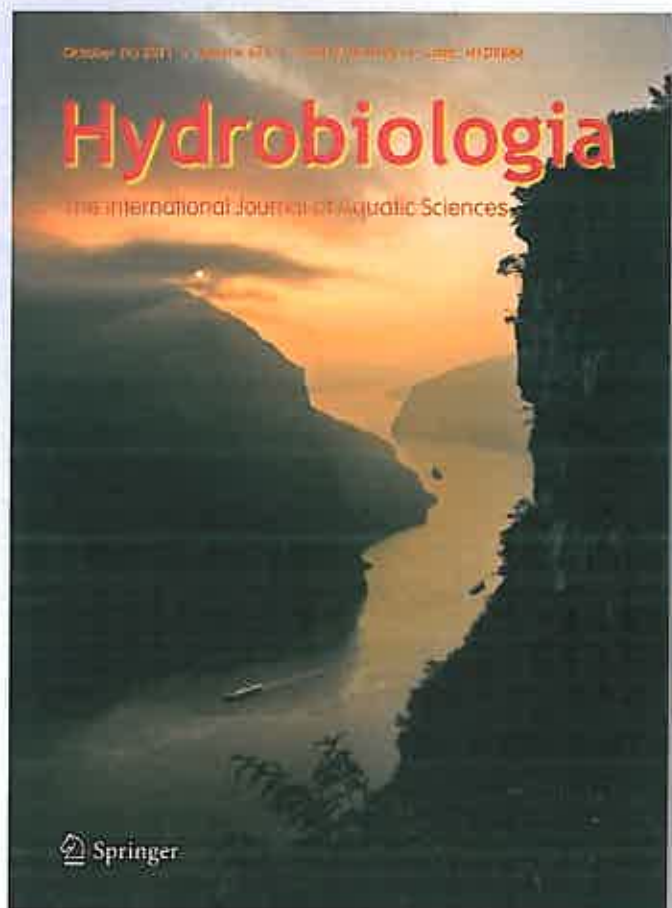


*Jane Fromont, Franziska Althaus, Felicity  
R. McEnnulty, Alan Williams, Mark  
Salotti, Oliver Gomez & Karen Gowlett-  
Holmes*

**Hydrobiologia**  
The International Journal of Aquatic  
Sciences

ISSN 0018-8158

Hydrobiologia  
DOI 10.1007/s10750-011-0845-7



 Springer

16p

**Your article is protected by copyright and all rights are held exclusively by Springer Science+Business Media B.V.. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your work, please use the accepted author's version for posting to your own website or your institution's repository. You may further deposit the accepted author's version on a funder's repository at a funder's request, provided it is not made publicly available until 12 months after publication.**

## Living on the edge: the sponge fauna of Australia's southwestern and northwestern deep continental margin

Jane Fromont · Franziska Althaus · Felicity R. McEnulty ·  
Alan Williams · Mark Salotti · Oliver Gomez ·  
Karen Gowlett-Holmes

Received: 24 February 2011 / Accepted: 30 July 2011  
© Springer Science+Business Media B.V. 2011

**Abstract** This first assessment of sponges on Australia's deep western continental margin (100–1,100 m) found that highly species-rich sponge assemblages dominate the megabenthic invertebrate biomass in both southwestern (86%) and northwestern (35%) areas. The demosponge orders Poecilosclerida, Dictyoceratida, Haplosclerida, and Astrophorida are dominant, while the presence of the order Agelasida, lithistid sponges, and the Verongida are noteworthy in providing contrasts to other studies from the deep temperate Australian margin. Most sponge species appeared to be rare as two-thirds were present in only one or two samples—a finding consistent with studies of the shallow Australian sponge fauna. The Demospongiae and Calcarea had similar

distribution and abundance patterns being found in the greatest numbers in the south on the outer shelf and shelf edge in hard substrates. In contrast, the Hexactinellida were more abundant at deeper depths and in soft substrates, and were more common in the north. Although the environmental factors that influence sponge distributions on the western margin cannot be completely understood from the physical covariates analyzed in this study, the data suggest depth-related factors, substrate type, and current regimes are the most influential. Incompletely documented historic demersal trawling may partly account for the lower sponge biomass found in the north. The potentially high importance of sponges to benthic ecosystems, as well as the potential for high impacts on sponges by bottom trawling, indicates that maintaining healthy sponge assemblages should be an important consideration for marine conservation planners. Successful management will need to be underpinned by additional research that better identifies the ecological roles of sponges, and their distributions over local and broad environmental scales.

**Electronic supplementary material** The online version of this article (doi:10.1007/s10750-011-0845-7) contains supplementary material, which is available to authorized users.

Guest editors: M. Maldonado, X. Turon, M. A. Becerro & M. J. Uriz / Ancient animals, new challenges: developments in sponge research

J. Fromont (✉) · M. Salotti · O. Gomez  
Western Australian Museum, Locked Bag 49,  
Welshpool DC, WA 6986, Australia  
e-mail: jane.fromont@museum.wa.gov.au

F. Althaus · F. R. McEnulty · A. Williams ·  
K. Gowlett-Holmes  
CSIRO Wealth from Oceans Flagship, Hobart Marine  
Laboratories, PO Box 1538, Hobart, TAS 7000, Australia

**Keywords** Continental margin · Porifera ·  
Diversity · Western Australia

### Introduction

Continental margins host some of the highest species diversity in the oceans (Grassle & Maciolek, 1992).

Deep benthic diversity is often enhanced by the presence of habitat-forming biota (Buhl-Mortensen et al., 2010), with deep sea sponge assemblages recognized as forming complex structural living space for large numbers of species from many taxa (Buhl-Mortensen et al., 2010; Howell et al., 2010). The potentially high ecological importance of deep sea sponges is indicated by their roles in coral reef ecosystems; these are suggested by Rützler (2004) to include habitat provision, predation, space competition, chemical defense, primary production, nutrient cycling, nitrification, food chains, bioerosion, mineralization, and cementation of substrates.

Western Australia encompasses one-third of Australia's coastline and has a topographically and oceanographically diverse continental margin. Emergent paleo-coastlines are a feature of the deep continental shelf in northern areas, and the south below 31°S; large rocky banks occur in the central west around the Houtman Abrolhos, while coarse sediments are found in the south around Point Hillier and Bald Island. The deeper margin includes small seamounts, rocky banks and plateaus, and many submarine canyons including large features off Kalbarri, Two Rocks, and Perth (Williams et al., 2010). The deep margin is influenced by complex oceanography (Ridgway & Condie, 2004; Waite et al., 2007): the Leeuwin Current, a warm, oxygen poor, low salinity, tropically originating current flows southward from Ningaloo along the shelf and shelf edge to a depth of ~250 m; at greater depths, the upper continental slope from 250 to 400 m is influenced by the northward flowing cool, oxygen-rich, Leeuwin Undercurrent, and the deep upper slope greater than 400-m depth by Antarctic Intermediate waters.

Despite the massive area and environmental complexity of Western Australia's deep margin, there was little information available of its benthic biodiversity, and there were no systematic surveys of its sponge fauna deeper than diving depths (~30 m) before 2005. This situation changed after two wide ranging surveys of benthic epifauna in 2005 and 2007 that collected sponges from depths between 100 and 1,100 m between latitudes 12°S to 36°S. Results from the first survey provided a regional scale account of habitat heterogeneity and megabenthos biodiversity based on distribution patterns of sponges, crustaceans, molluscs, echinoderms, ascidians, and corals

(Williams et al. (2010)). A species checklist of those taxa was presented by McEnulty et al. (2011) and photographic information collected during the 2005 survey has been used to evaluate the potential of geomorphic features to act as surrogates for benthic biodiversity distributions (Althaus et al., 2011). The faunal data from the 2007 survey had not previously been used for analyses of biodiversity distributions.

This article presents the first integration of data from the two surveys by examining the sponge fauna of the outer continental shelf, shelf edge and continental slope adjacent to the southwestern and northwestern coasts of Australia (36°S to ~12°S, 112°E to 124°E). The article has two primary aims: first, to document the diversity and abundance of sponges on the continental margin, and second, to examine environmental influences on sponge distribution patterns. Our findings are also discussed in the context of biodiversity conservation planning on Australia's western continental margin.

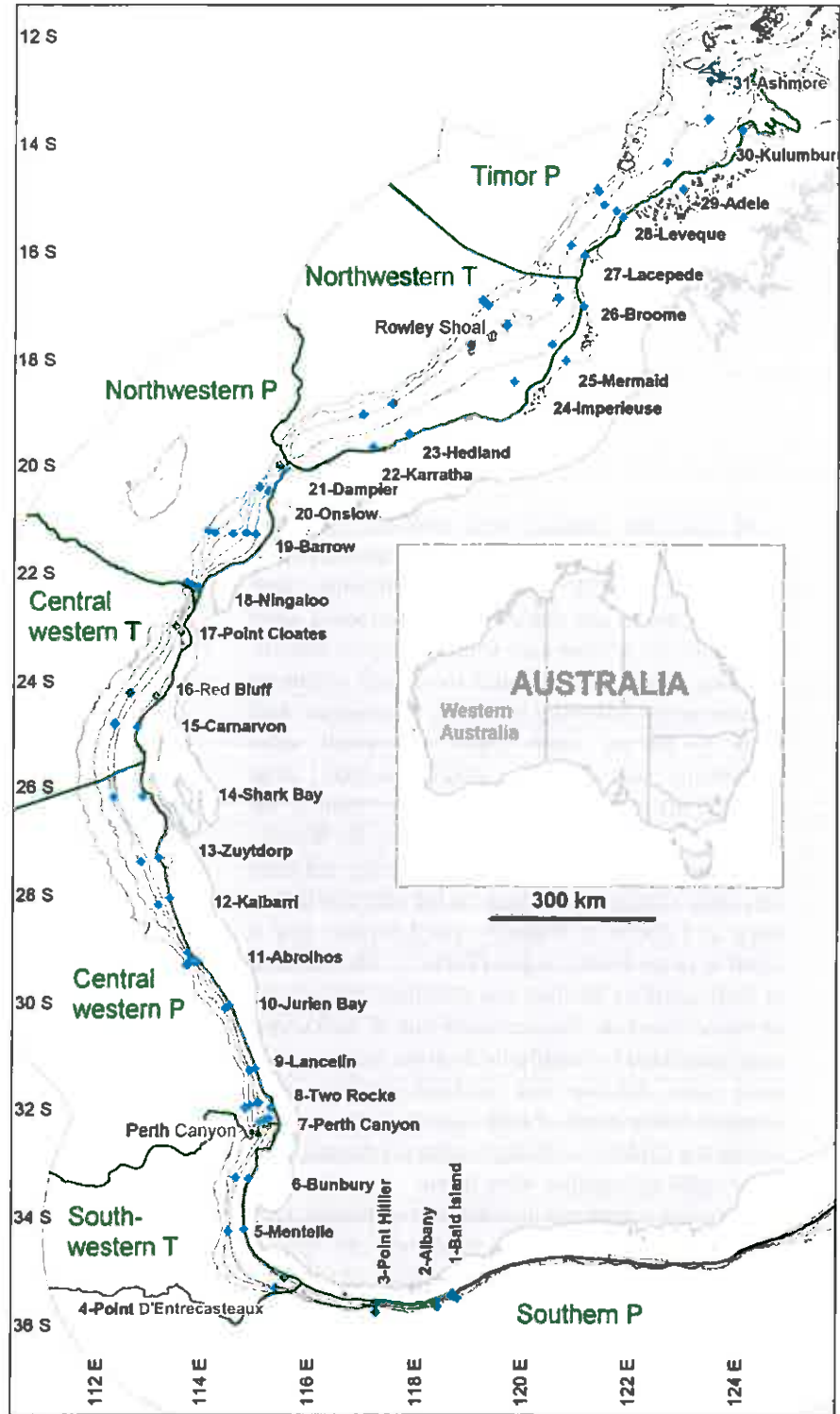
## Methods

### Field collections

Sponges were collected along with other benthic marine invertebrates on two surveys on *RV Southern Surveyor* in 2005 and 2007 (SS200510 and SS200705). The 2005 survey sampled Australia's southwestern margin (~22°S to 36°S); the 2007 survey continued the sampling program along the northwestern margin (12°S to 22°S). The field design detailed below was chosen to sample at four nested hierarchical spatial scales: biogeographic provinces, bathomes (ecologically meaningful depth zones), geomorphic features, and substrates (Williams et al., 2010; Althaus et al., 2011).

Samples were collected systematically at sites located at one degree longitudinal or latitudinal intervals off Australia's western continental margin, following the coastline from Bald Island to Ashmore Reef. The sites ranged in latitude from 12°S to 36°S and longitude from 112°E to 124°E (over 3,400 km of margin). One additional site at the Perth Canyon was included as a geological feature of special interest, resulting in 31 sites being surveyed (Fig. 1). This sampling approach was designed to position sampling

**Fig. 1** Map of the study region showing the 31 sites, depth contours (100, 200, 400, 700, and 1000 m), and provincial scale bioregions (Commonwealth of Australia, 2005). *Diamonds* indicate the average location of samples taken by study site and bathome (ecologically meaningful depth zones). The locations of the Perth Canyon and the Rowley Shoals are shown. *T* transition zone and *P* province



locations within each of the four biogeographic provinces and the three transition zones adjacent to Australia's western coastline that have been designated

in the national marine bioregionalization scheme (Commonwealth of Australia, 2005) (boundaries are shown in Fig. 1).

**Table 1** Number of samples taken over two surveys by gear type: (a) for each bathome (ecologically meaningful depth zones after Last et al., 2010); and (b) for each substrate type

Total number of samples:	Depth (m)	Sherman sled	Beam trawl	McKenna trawl	Total
<b>(a) Bathome</b>					
Outer shelf	~ 80–150	39	25	4	68
Shelf-break	150–250	6	12	3	21
Upper slope (shallow)	250–500	14	54	3	71
Upper slope (deep)	500–800	3	10	2	15
Mid-slope (shallow)	800–1,100	9	15		24
Mid-slope (deep)	1,100–1,500	1	1	1	3
<b>(b) Substrate</b>					
Hard		44	17	4	65
Mixed		17	19	1	37
Soft		11	81	8	100

At each site, samples were collected from two ecologically meaningful depth zones (bathomes sensu Last et al., 2010): the outer continental shelf (~ 100 m depth) and shallow upper continental slope (~ 400 m). At selected sites within each province, the sampling design was extended to include additional samples at the following bathomes: continental shelf break (~ 200 m), deep upper continental slope (~ 700 m), and shallow mid-continental slope (~ 1,000 m). Additional samples were taken at the northwestern offshore atolls comprising the Rowley Shoals (at sites Imperieuse and Mermaid), and three very deep samples were taken on the mid-continental slope at 1,200 m at Ningaloo and Leveque, and at 1,500 m in the Perth Canyon (Table 1). The substrate of each sampling location was classified as hard, soft or mixed based on visual examination of backscatter maps generated by multibeam acoustic surveys of the same areas. Separate soft and hard substrates were sampled within depths if both types were present at a survey site (Table 1). Owing to time constraints, only a few replicate samples were taken.

Sampling equipment included two epibenthic samplers with 25-mm stretched-mesh net cod ends to collect the megabenthos. The Sherman sled (Lewis, 1999, 2009) was used for sampling hard substrates; and a modified version of the French Institute de Recherche pour le Développement (IRD) designed and CSIRO modified light beam trawl (Forest, 1981; Lewis, 2010) was used for sampling mainly soft substrates (Table 1). At one site (Lacepede), a demersal fish trawl (McKenna trawl) was also used.

Geolocation of samples was based on the ship's GIS. The tow track and distance were derived from dynamic GIS mapping and the duration of bottom contact. Tow direction and duration were dependent on the roughness and topography of the substrate. In general, tows were along depth contours and of about 20-min duration (but were less for samples when the sled was full of catch within 5–10 min). Images and basic descriptions of gear types can be found at <http://www.cmar.csiro.au/research/seamounts/epibenthic.htm>.

#### Shipboard and laboratory processing

The total sponge catch was weighed for each sample and sponges were separated into morphospecies and weighed to the nearest gram to give a species weight for each sample. Voucher specimens were labeled with a field number and name and photographed with a scale bar and label to record live color. Details were recorded on field datasheets. Voucher specimens were preserved in 75% ethanol, and some large specimens were frozen. Specimens were identified by examining classical taxonomic characters including morphological, skeletal, and spicule features. Spicule preparations and skeletal slides were made for each specimen as per the methods outlined in Fromont et al., (2008). Specimens of the class Demospongiae except for the lithistids were identified to a species level operational taxonomic unit (OTU), and given a species code. Specimens of the classes Calcarea and Hexactinellida were confirmed in the laboratory and

recorded at class level. The Calcarea and lithistids are being identified in separate studies. All the specimens have been lodged in the collections of the Western Australian Museum. Specimens smaller than 5 g (less than the 25 mm mesh size of the epibenthic samplers) were not identified but have been retained at the WA Museum pending future study.

#### Data preparation

Data were analyzed at the class level: Demospongiae, Calcarea, Hexactinellida, and the dominant class Demospongiae (excluding the lithistids) were analyzed at species level. The biomass (wet catch weight) was standardized to  $\text{g m}^{-2}$  based on the area sampled (mouth width \* tow distance) for each sample. The McKenna trawl samples from a single site were not comparable in sampling effort, and were excluded from the statistical analyses.

#### Analyses

Analyses at class level were based on sponge biomass, averaged across all the samples by site and bathome. Univariate contrasts in the distribution over the three substrate types (hard, mixed, and soft) were made with the non-parametric Kruskal–Wallis test. Species accumulation curves, based on the non-lithistid demosponge species, were produced for each province in Primer-e v6 (Clarke & Gorley, 2006), using 999 permutations. To make the curves comparable, they were scaled to the total area sampled in each province.

For multivariate analyses, the standardized biomass data at class and species-level were square-root transformed to reduce the effect of dominant taxa. The Bray–Curtis dissimilarity between samples was visualized in a non-metric multi-dimensional scaling (nMDS) ordination (Clarke, 1993), and the differences between a priori groups of provinces and bathomes was tested using analysis of similarities (ANOSIM—Clarke, 1993). The relationship of the multivariate community structure, at class and at species level, with the environmental covariates (described below) was examined using distance-based linear models (DIST-LM). This method models the relationship between the multivariate data cloud (Bray–Curtis dissimilarity of biological data) and multiple predictor variables (environmental covariates) based on a multivariate

regression (Anderson et al., 2008). In case a relationship between the covariates and the biological data was found, distance-based redundancy analysis (dbRDA) was used for graphical representation of these results (Legendre & Anderson, 1999). The environmental covariates were superimposed onto the dbRDA plot as vectors whose direction and length are related to their partial correlation with the dbRDA axes (i.e. the role they played in generating them), creating a biplot (Clark et al., 2010).

Environmental covariate data for each sample's location were extracted from three databases: (1) Geoscience Australia—MARS modeled sediment data (<http://www.ga.gov.au/oracle/mars/index.jsp>); (2) CSIRO Atlas of Regional Seas—an interpolated oceanographic dataset (CARS 2006—<http://www.marine.csiro.au/~dunn/cars2006/>; Dunn & Ridgway, 2002; Ridgway et al., 2002); and (3) SeaWiFS—satellite seasurface data (<http://oceancolor.gsfc.nasa.gov/SeaWiFS>). Twenty-eight covariates were tested: depth, latitude, longitude (from survey data), aspect, slope, carbonate content, percentage of gravel, sand and mud (MARS), mean and variability (intra-annual standard deviation—SD) of oxygen ( $\text{O}_2$ ), salinity, temperature, nitrates ( $\text{NO}_3$ ), phosphates ( $\text{PO}_4$ ) and silicates (Si) at sampling depth (CARS), and mean and variability (intra-annual standard deviation—SD) of SeaWiFS surface measures of productivity (Chlorophyll *a*), turbidity (K490), irradiation, and sea surface temperature (SST).

## Results

### Overview of sponge collection

In total, 202 samples were taken over six depth zones (bathomes); 72 with the Sherman sled, 117 with the beam trawl and 13 with the McKenna trawl (Table 1). Seventy-five samples did not contain sponges, and these were predominantly deep bathomes and soft substrates. Sherman sleds were predominantly used on hard substrata (61%) and beam trawl and McKenna trawl on soft substrata (69% and 62% respectively, Table 1).

Porifera dominated the entire invertebrate catch by biomass; in the southwestern survey (SS200510), sponges accounted for 86% of the total catch weight

(see McEnnulty et al., 2011), and in the northwestern survey (SS200705), they accounted for 35%—followed by echinoderms (30%) and cnidarians (20%).

The largest Demospongiae specimen collected was an individual of the genus *Biemna* that weighed 37 kg and was collected at 200-m depth off Point Hillier in the southern province. The largest single catch of *Calcarea* was more than 1,700 individuals (total weight 850 g) taken from 400-m depth at Two Rocks in the central western province. In total, 941 kg of sponges and more than 4,600 individuals were collected from the 127 samples containing sponges (Table 2). The Sherman sled collected the majority of the sponge samples (758 kg, ~78%), followed by the beam trawl (177 kg, ~18%), and the McKenna trawl (42 kg, ~4% of the total catch, Table 2). The sled collected the majority of the Demospongiae (78%) and *Calcarea* (63%) and the McKenna trawl collected the least (4 and 0%, respectively), whereas the beam trawl collected most of the Hexactinellida (63%) (Table 2). The McKenna trawl samples were not comparable to the beam trawl and sled samples in sampling effort, and thus were excluded from the statistical analyses.

#### Distribution of sponge classes

Sponges were collected in all biogeographic provinces and transition zones sampled but predominantly from the outer shelf and shelf break bathomes; glass sponges (Hexactinellida) were sampled to 1,000-m depth on the mid slope (Fig. 2; Table 3). Most of the sponge biomass (averaged by sampling effort) was collected in the southern province and southwestern

transition zone on the outer shelf and shelf break (197 g m<sup>-2</sup>, Fig. 2). High biomass of sponges was also seen in the central western (50 g m<sup>-2</sup>) and north western provinces (15 g m<sup>-2</sup>). Lower biomass occurred in the other three biogeographic regions (~9 g m<sup>-2</sup>; Fig. 2; Table 3).

The Demospongiae (including lithistids) comprised the majority (98.31%) of the sponge biomass collected (Table 2) and were found principally in the outer shelf and shelf break bathomes (Table 3) in the southernmost temperate provinces (Fig. 2a). Only very low abundances were detected in the central western transition zone. In general, demosponge biomass decreased with decreasing latitude, with the exception of the northwestern province, in particular at Ningaloo and Onslow (sites 18 and 20), but also at Imperieuse (site 24) in the northwestern transition zone, and at Adele (site 29) in the Timor province (Fig. 2a). Within the total 90 samples that contained demosponges, their biomass was significantly higher in hard (mean = 22.25 g m<sup>-2</sup>) than on soft (mean = 0.220 g m<sup>-2</sup>) or mixed (mean = 6.182 g m<sup>-2</sup>) biotopes (Kruskal–Wallis test: 67.91,  $P < 0.0001$ ).

The lithistid demosponges were only collected in the northwestern and central western provinces and transition zones; they were not found south of Perth Canyon (site 7) at 32°S latitude (Fig. 2a). The largest biomass of lithistids was collected from site 20 at Onslow in the north western province (Fig. 2a). In total, 26 samples collected lithistids.

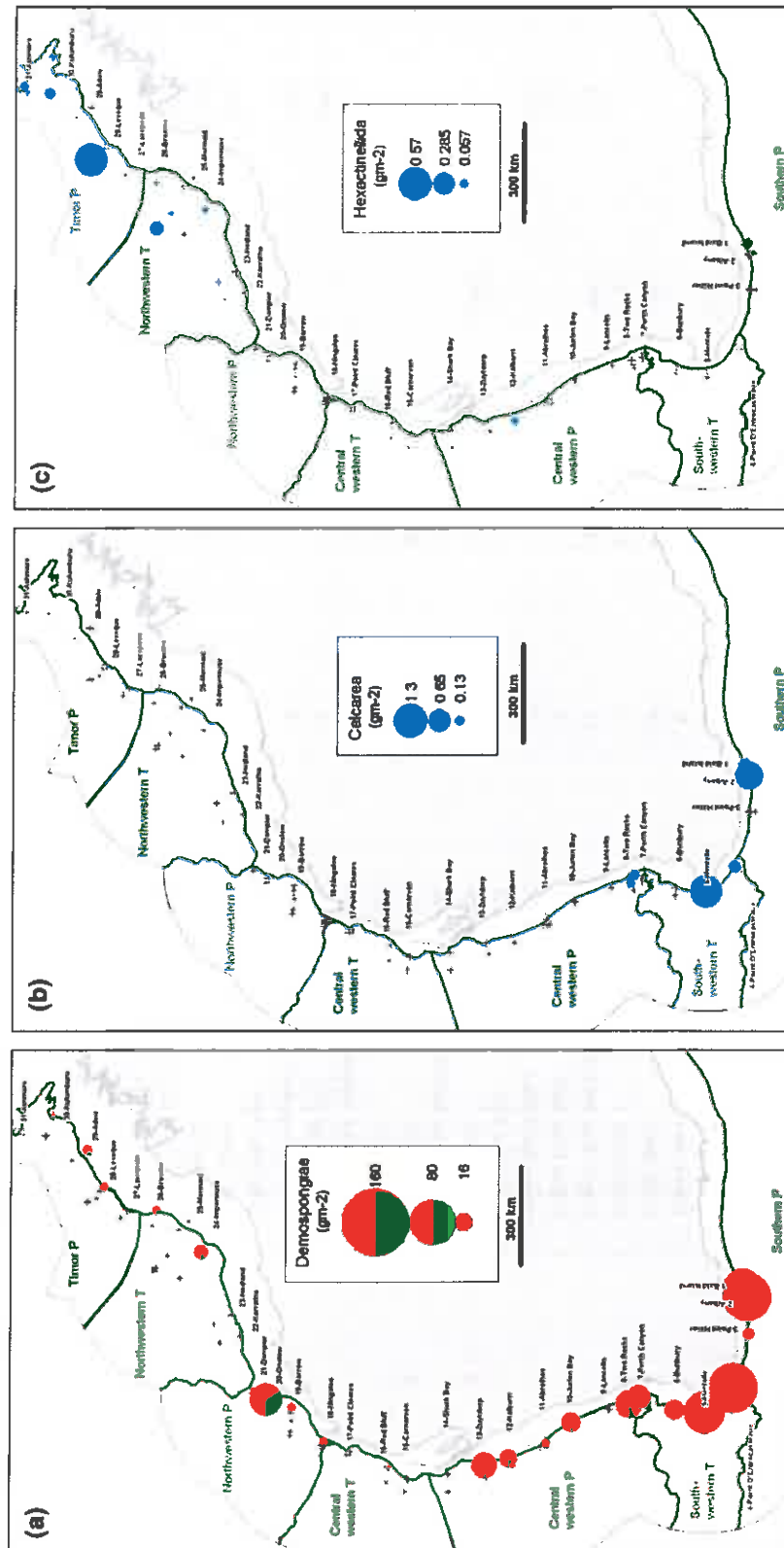
The *Calcarea* comprised a very low proportion (0.36%) of the sponge biomass collected in the study (Table 2). Most of the biomass of this class was

**Table 2** Number of individuals and catch weights of sponges sampled by Class; also shown is the catch weight by gear type

	No. of stations	No. of individuals	Total catch weight (kg)	% of total weight	Sherman sled (kg)	Beam trawl (kg)	McKenna trawl (kg)
Porifera total	127	4,657	976.687		758.124	176.532	42.042
Demospongiae total	119	2,521	960.174	98.31	753.425	166.930	39.820
Lithistids	27	122	35.702	3.66	31.907	3.757	0.038
Other	92	2,399	924.472	94.65	721.518	163.173	39.782
Calcarea	17	1,883	3.557	0.36	2.192	1.365	0.000
Hexactinellida	47	131	12.829	1.31	2.470	8.147	2.222
Unidentified	10	122	0.127	0.01	0.037	0.090	0.000

The Demospongiae are separated into lithistids and other (all other Orders); the latter were identified to species for all samples





**Fig. 2** Map of Australia's western coast showing the 31 sites and the provincial scale bioregions (Commonwealth of Australia, 2005). Graded circles show the averaged biomass of a Demospongiae (subdivided to show the proportion of lithistids), b Calcareia, c Hexactinellida collected at each sampled site-bathome combination; the plus-symbol indicates site-bathome combinations where no biomass of the respective classes was recorded

**Table 3** Averaged standardized biomass ( $\text{g m}^{-2}$ ) for the three sponge classes by province and bathome (including an indicative depth)

Province (S to N)	No. of sites	Bathome	Indicative depth (m)	No. of samples	Demospongiac ( $\text{g m}^{-2}$ )	Calcarea ( $\text{g m}^{-2}$ )	Hexactinellida ( $\text{g m}^{-2}$ )
SP	3	Outer shelf	100	7	83.84	0.31	
		Shelf-break	200	5	13.72	0.12	
		Upper slope shallow	400	6	1.30		0.02
		Upper slope deep	700	4	0.02		0.01
		Mid-slope shallow	1,000	11	0.13	0.49	
SWT	3	Outer shelf	100	3	99.26		
		Upper slope shallow	400	6	0.01		
		Outer shelf	100	14	15.74	0.01	
CWP	8	Shelf-break	200	3	34.38	0.02	
		Upper slope shallow	400	15	0.63	0.02	0.01
		Upper slope deep	700	3			0.01
		Mid-slope shallow	1,000	5			0.00
		Mid-slope deep	1,200	1			
		Outer shelf	100	7	1.65	0.00	
		Upper slope shallow	400	6	0.00		
NWP	4	Outer shelf	100	14	14.18		
		Shelf-break	200	4	0.97		
		Upper slope shallow	400	10	0.01		
		Upper slope deep	700	4			0.00
NWT	5	Mid-slope shallow	1,000	4			0.00
		Mid-slope deep	1,200	1			0.00
		Outer shelf	100	13	4.81		0.01
		Shelf-break	200	6	0.02		0.00
		Upper slope shallow	400	18	0.01		0.01
		Upper slope deep	700	3			0.00
		Mid-slope shallow	1,000	2	0.00		0.12
		Mid-slope deep	1,200	1			
		Outer shelf	100	10	2.44		0.01
		Shelf-break	200	3	0.00		0.01
Timor P	5	Upper slope shallow	400	10	0.35		0.03
		Upper slope deep	700	1			0.02
		Mid-slope shallow	1,000	2	0.00		0.57
		Mid-slope deep	1,200	2			

Number of sites and samples collected also provided

SP Southern province, SWT southwestern transition, CWP central western province, CWT central western transition, NWP northwestern transition, NWT northwestern transition, Timor P Timor province

collected in the southern province and southwestern transition zone on the outer shelf and shelf break (Fig. 2b) on hard (10) or mixed (4) substrates. Two upper slope (soft substrate) samples contained *Calcarea*. This class was not collected north of 24.5°S latitude at Carnarvon (site 15) in the central western transition zone. In total, 17 samples collected *Calcarea* which were significantly more commonly sampled in hard (mean = 0.0667 g m<sup>-2</sup>) and mixed (mean = 0.0124) than on soft (mean = 0.0003 g m<sup>-2</sup>) substrates (Kruskal–Wallis test: 8.164,  $P = 0.017$ ).

The Hexactinellida represented only 1.31% of the sponge biomass collected (Table 2). This class was collected in the southern and central western provinces with none being collected in the southwestern or central western transition zones (Fig. 2c). A low biomass of glass sponges was also collected from site 18 at Ningaloo in the northwestern province. North of this province, glass sponge biomass increased with decreasing latitude with most glass sponge biomass being collected in the tropical Timor province, in particular at Leveque (site 28). In total, 42 samples collected Hexactinellida with the majority being collected from soft substrates in the shallow upper shelf and deeper slope (27 samples), with fewer from hard substrates in the outer shelf to mid-slope bathomes (9 samples), and from mixed substrate in the shelf break to mid-slope bathomes (6 samples). Glass sponges were found at shallower depths on hard substrates in lower latitudes but the general trend was for them to be collected from soft substrates on the slope bathomes (Fig. 2c). Statistically, there were no significant differences in the distribution of the Hexactinellida over the three substrates—mean<sub>hard</sub> = 0.0086 g m<sup>-2</sup>; mean<sub>mixed</sub> = 0.0304 g m<sup>-2</sup>; mean<sub>soft</sub> = 0.0086 g m<sup>-2</sup> (Kruskal–Wallis test: 4.334,  $P = 0.115$ ).

Analysis of similarity of the distributions of the sponge classes detected a significant difference between the bathomes across provinces  $R = 0.442$ ,  $P = 0.001$ , in particular the outer shelf and shelf-break differed strongly from the deeper bathomes. There were no significant differences between provinces across bathomes detected in the multivariate distribution of the sponge classes.

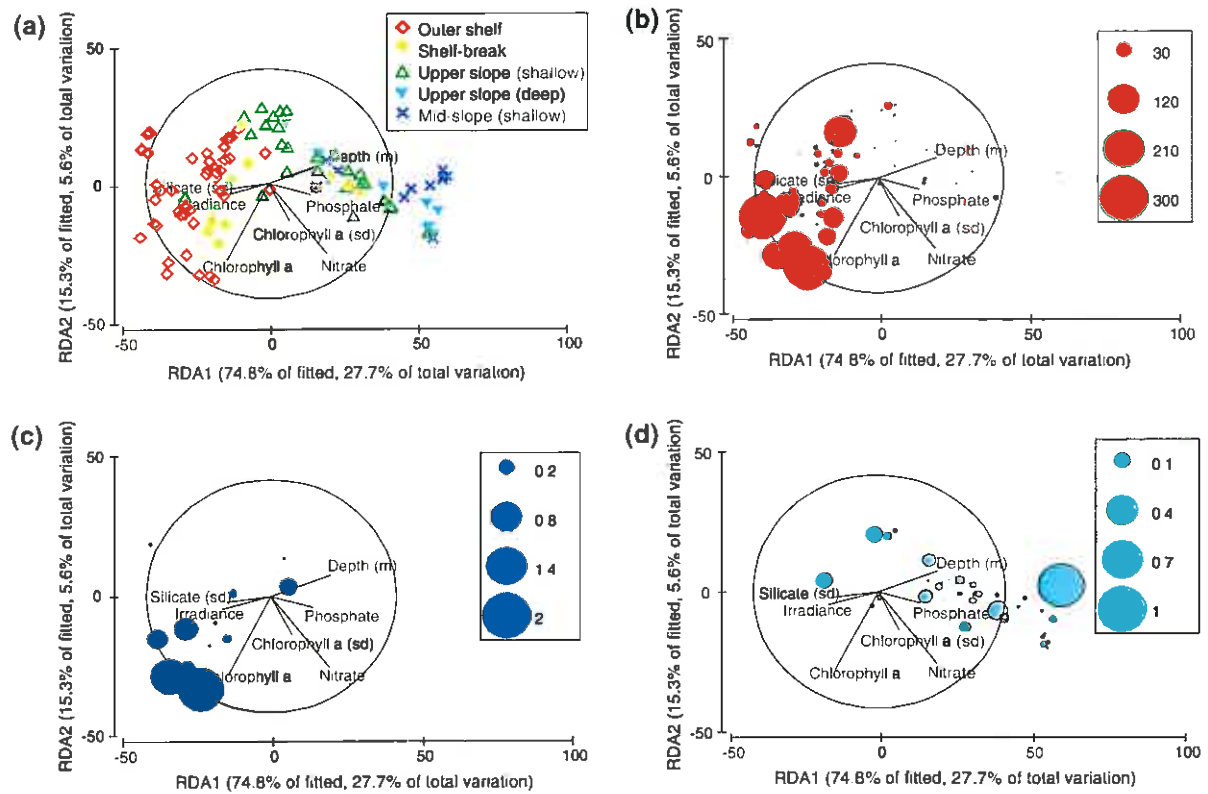
Seven of the 28 environmental variables considered in the DISTLM model account for 37% of the variance in the distribution of the three classes over the samples. Depth was the most influential

explaining 18% of the variation, the sequential addition of six other covariates accounted for the remaining 19%—nitrate (+4% of variance explained), phosphate (+4%), chlorophyll *a* (+2%), and variability (SD) in silicate (+2%), chlorophyll *a* (+2%), and irradiation (+1%). The marginal tests showed that in regard to single covariates, depth accounted for most of the variance (18%), followed by chlorophyll *a* (12%), silicate (11%), and nitrate (10%); the remaining covariates made less than 10% individual contributions. Figure 3a gives a visual impression of the distribution of the samples, coded by bathome, in the covariate space, with the first two dbRDA axes explaining 33% of the variance in the fitted data. The biplot also shows that depth is negatively correlated to the variability in silicates (SD) and to the irradiance (their vectors point in the opposite direction to the depth vector). Thus, the effect of each of these variables cannot be fully separated from the others. Depth showed little correlation to nitrate and variability in chlorophyll *a* (SD) (their vectors are near perpendicular to the depth vector).

Among classes, Fig. 3b shows that the Demospongiae distribution was clearly associated with decreasing depth and/or increasing variability in silicates, as measured by the standard deviation (SD), with the highest biomass in the shallowest depths where the silicates were the most variable and irradiance was the highest. A slight positive association with chlorophyll *a* can be seen in Fig. 3b. The distribution of the *Calcarea* (Fig. 3c) was very similar to the Demospongiae. In contrast, the Hexactinellida distribution (Fig. 3d) was associated with increasing depth with the highest biomass at deeper depths on the shelf break and upper slope, where silicate supplies were more constant—i.e., low silicate variability.

#### Demospongiae composition and distribution

The Demospongiae (excluding the lithistids) in the southwestern (SS200510) survey were identified to be 451 species in 141 genera, 51 families, and 11 orders (see McEnnulty et al., 2011). Of the 154 species collected and identified in the northwestern survey (SS200705), 72 had been collected in the south but have an extended range along the Western Australian coast as a consequence of this study, and 50 have extended depth ranges as a result of this



**Fig. 3** Sample distribution in relation to the first two dbRDA axes explaining 90.1% of the variance in the data. Samples are coded by a symbols for bathomes, and **b–d** bubbles graduated by the abundance of **b** Demospongiae, **c** Calcareia,

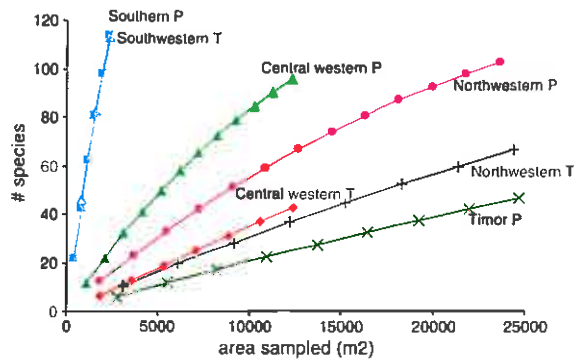
**d** Hexactinellida; the *lines* indicate the direction and influence of the relative covariates in the dbRDA space; the *circle radius* is equal to the unity vector

publication. The remaining 82 species were only found in the northern survey (see species list in supplementary material).

The order Poecilosclerida was the most speciose (110 species) followed by the Dictyoceratida (81), Haplosclerida (75), and Astrophorida (70 species). Of the demosponge species collected 205 (45.5%) were present in only a single sample (singletons), and 105 species (23.3%) were in two samples (doubletons). *Sarcotragus* Ng1 was the most widely distributed species, collected in 14 samples, from Bald Island to Dampier (sites 1–21). At the genus level, 25.5% of genera were only collected from a single sample and 14.9% were collected from two samples. The genus *Sarcotragus* was the most widely distributed (31 samples). The majority of species were relatively restricted in their distributions, however this result may in part be due to the lack of replication in the sample design, and the distance of 1° of latitude between sites.

Analyses of demosponge species composition were restricted to the sub-set of outer shelf samples in which they were highly abundant. Species accumulation curves by province (scaled to area sampled) showed that the demosponge species richness on the outer shelf generally decreased from south to north with the exception of the northwestern province that had higher richness than the central western transition zone (Fig. 4).

The nMDS ordination of the outer shelf sponge biomass data, after removal of two outlier samples, showed no clear separation into groups (e.g., provinces), although there is a slight latitudinal trend with the northernmost samples to the right of the graph (Fig. 5). This is confirmed by the significant, although low *R*-value of the ANOSIM comparing provinces  $R = 0.21$ ,  $P = 0.001$  (999 permutations). The two outlier samples excluded from both the nMDS and the ANOSIM each contained only one singleton species. DISTLM analysis of demosponge



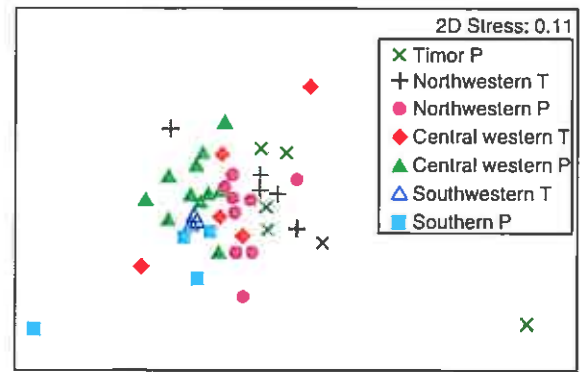
**Fig. 4** Species accumulation curves for demersal species collected on the outer shelf, by province (P)/transition zones (T) based on 999 permutations, scaled to the total area sampled

species showed that single covariates explained less than 4.5% of the variation in the data (the top three were SST 4.47%, latitude 4.43, and salinity 4.41%). Combining multiple covariates did not improve the model. Thus, the variation in the species-level demersal data could not be satisfactorily explained by the 28 covariates that were available for statistical analyses. The exclusion of singletons and doubletons did not fundamentally change the distribution patterns of the demersals, and thus did not improve the explanatory power of our environmental covariates.

## Discussion

### Composition and diversity of demersals

The most abundant and most speciose groups of sponges on Australia's western continental margin were the demersal orders Poecilosclerida, Dictyoceratida, Haplosclerida, and Astrophorida. These orders are known to be highly speciose in other locations including the Great Australian Bight (GAB) continental shelf (Sorokin et al., 2007), shelf edge canyons off Tasmania (Schlacher-Hoenlinger, unpublished sponge mudmaps from survey SS200404), and off the Bahamas between 30- and 922-m depths (Reed & Pomponi, 1997). Notable differences between the western margin and those from the GAB and Tasmania are the presence of the orders Agelasida, and lithistid sponges, and about 10 species of the Verongida—a group apparently absent in the GAB and represented by only one species off



**Fig. 5** nMDS ordination of the Bray-Curtis dissimilarities of the square-root transformed demersal species biomass data from the outer shelf off Australia's west coast; symbols indicating bioregional provinces (P) and transition zones (T) (Commonwealth of Australia, 2005). Two outlier samples were excluded (SS20705-141 & SS200705-171)

Tasmania (Table 4). Off the Bahamas, Reed & Pomponi (1997) found a high number of lithistids, Agelasida and Verongida, and fewer Dictyoceratida. In our study, the lithistids only occurred as latitudes decreased when fewer Dictyoceratida were also found, suggesting that these changes may be related to tropical environments which we sampled, but which were not present in the GAB and Tasmania which are temperate.

Mounting evidence supports the finding that sponge communities in shallow Australian waters consist of many rarely occurring species and few commonly occurring ones (Hooper & Kennedy,

**Table 4** Demersal orders, number of species present, and number of stations where they occurred

Order	No. of species	No. of stations recorded (summed for all species)
Agelasida	3	15
Astrophorida	70	182
Dendroceratida	2	2
Dictyoceratida	81	230
Hadromerida	31	79
Halichondrida	54	128
Haplosclerida	75	192
Homosclerophorida	4	11
Poecilosclerida	110	181
Spirophorida	9	22
Verongida	10	16

2002; Fromont et al., 2006; McQuillan, 2006, Fromont & Vanderklift, 2009). The study by Sorokin et al. (2007) and Schlacher et al. (2007) are the first reports of this phenomenon in Australian deepwater habitats. Sorokin et al. (2007) reported that 77% of the sponge species had limited distributions, with only 22% widely distributed; Schlacher et al. (2007) found on average only 10.3% of species were common to all five canyons, while 76% were spot endemics (= singletons). More than 68% of the species in this study were only found in one or two samples, thus further supporting the finding that sponges in deeper environments also have very limited distributions. This finding may be partly explained by low sampling replication within each site and depth zone, but replicated sampling in shallow diving depths did not decrease the high proportion of rare species (Fromont & Vanderklift, 2009).

Several theories exist to explain why sponge assemblages have numerous rare species and small-scale patchiness in species distributions. These include limited dispersal ability, specific microhabitat requirements, and exposure to episodic disturbance (see Fromont et al., 2006 and references therein).

High apparent rarity of species, in particular in poorly sampled environments, is not uncommon, but the replicate sampling necessary to distinguish rarity from patchiness or sampling efficiency is often lacking (Williams et al., 2010). Examples are known for most marine and terrestrial communities (Gray et al., 2005), indicating that the causal factors can be expected to be complex and variable between taxa.

#### Factors influencing sponge distributions

Sponge assemblages in the study area were characterized by high biomass and high species richness. The Demospongiae were most abundant on the outer shelf and shelf edge (~100 and ~200 m depth) where the majority of substrate types sampled were hard (Althaus et al., 2011). Most species of Demospongiae and *Calcarea* attach to hard substrates, and the availability of hard seabed as a factor influencing sponge distribution was confirmed to be significant in analyses. Relatively high sponge biomass usually occurred where the continental shelf was relatively narrow with a steep edge, for example, at Albany, Ningaloo, and Onslow (see Fig. 1).

Depth was the most influential of the 28 environmental covariates in models of the distribution of the three sponge classes. There was also a latitudinal trend (although not statistically significant) with higher biomass of Demospongiae in the southwestern regions compared to higher biomass of Hexactinellida in the tropical northwestern regions. More than 60% of the variation in the distribution of these classes was unexplained by the covariates we used in the DISTLM model. This is partly explained by the lack of replicate sampling. However, factors such as current dynamics that are not accounted for in the model, are assumed to also influence sponge distributions along this margin.

The Leeuwin Current and a deeper undercurrent dominate the oceanography of the shelf and shelf edge. The Leeuwin Current flows most strongly and continuously for 6 months of the year to ~200-m depth along the shelf and shelf break in the southwest where sponge biomass was high, and is weaker in the central western region above Shark Bay (Feng et al., 2010) where sponge biomass was lower. The average current speed is  $0.4 \text{ m s}^{-1}$  (Ridgway & Condie, 2004) with a maximum flow of  $0.64\text{--}0.68 \text{ m s}^{-1}$  southward from below Shark Bay (Hanson et al., 2007). This fast flow may increase particle encounter for suspension feeding organisms. Although the Leeuwin Current is oligotrophic, sponges are efficient filter feeders reported to filter between 60 and 900 times their volume per hour (Jimenez & Ribes, 2007 and references therein). They have high retention efficiencies of picoplankton and can take up dissolved organic matter, including carbon, nanoplankton and microplankton (Jimenez & Ribes, 2007 and references therein), as well as free-living bacteria and other particles to ~0.1- $\mu\text{m}$  diameter, with a near 100% retention of particles (Riisgard & Larsen, 2010).

The transport of nutrient poor water via the Leeuwin Current, and consequent low associated pelagic primary productivity appears inconsistent with the high abundance of seagrass beds and macroalgal communities reported in shallow coastal waters (Lourey et al., 2006 and references therein), and the high sponge biomass we found on the outer shelf and shelf edge in the southernmost regions of the study area. Low dissolved nitrate concentrations and a low N-to-P ratio suggests that primary producers in this region may be primarily nitrogen limited

(Lourey et al., 2006). Recent studies suggest that nitrification associated with sponges appears to be a general feature in oligotrophic zones (Jimenez & Ribes, 2007) and future studies examining the excretion products of the high sponge biomass in this region may provide some explanation for the observed nutrient budget imbalance.

Silicate concentrations in the Leeuwin Current are highest at its source with a gradual decrease as it travels south. This could be attributed to biological uptake, although silicate kinetics have not been studied to date (Lourey et al., 2006). Although the role of diatoms would be important in any uptake study, the high biomass of sponges we reported here may be an additional sink for silicates. Maldonado et al. (2010) suggest a diatom-driven loop may appropriately represent silicate cycling in the open ocean, but may not realistically reflect the situation on some continental shelves with substrates densely populated by siliceous consuming sponges. Hexactinellid sponges lay down more silica per unit biomass than many demosponges (Hogg et al., 2010), and this might in part account for the higher incidence of glass sponges in shallow depths in the north—at the source of the Leeuwin current.

The distribution of the *Calcarea* mirrored the distribution of the *Demospongiae*—being the highest in biomass in the southwest on the outer shelf and shelf break (100–200-m depth). However, their distribution did not extend northward, and no specimens were collected above Carnarvon at 24.5°S. A similar pattern has been found in shallow coastal sites along the Western Australian coast with higher abundance of *Calcarea* in the south than in northern tropical waters (Fromont unpublished data). No details are currently available on calcium carbonate budgets in northwest Australia but calcareous sponges may not compete well with reef-building scleractinian corals which dominate in shallow tropical seas.

Demosponge biomass was low in the central western and northwestern transition zones and the Timor province. Although our analyses did not find any strong correlation between sponge distribution and environmental variables aside from depth and substrate hardness, other factors are believed to have contributed to this pattern. In general, regions where demosponge biomass was low have a wider shelf compared to areas where biomass was high—although the central western province had a high

sponge biomass and a wide shelf area. The central western transition zone is influenced by high salinity outflows from Shark Bay, and is where the Leeuwin Current decelerates and flows shallower at ~50-m depth (Woo et al., 2006) compared to the central western province where sponge biomass and current flow are higher and deeper respectively.

Hexactinellida were found to have the opposite distribution pattern to the *Demospongiae* and *Calcarea* as they mostly occurred at depths greater than 300 m on the upper slope, and increased in biomass in the tropical provinces, where they were also collected at shallower depths (~100 m). The Leeuwin undercurrent flows northward below the Leeuwin current at 250–600 m depth with an average velocity of  $0.1 \text{ m s}^{-1}$  (Meuleners et al., 2007). In general, the glass sponges in the southwest were found in the path of the Leeuwin undercurrent in deeper waters.

#### Conservation of sponge biodiversity

Although recently trawled areas were avoided by our sampling, the removal of sponges by historical demersal trawling, which was not accurately mapped, cannot be ruled out as a contributor to the low sponge biomass observed in the northern part of our study area. The outer shelf was trawled up to the 1990s, intensively in the north western transition zone and, to a lesser extent, in the Timor province. It can be inferred from demersal trawl bycatch records that sponge biomass must have been substantially reduced over large areas, although the exact distribution of trawl fishing was not accurately recorded. The catch rate of epibenthic fauna (primarily sponges, alcyonarians and gorgonians) was  $\sim 500 \text{ kg h}^{-1}$  up to  $\sim 2,600 \text{ kg h}^{-1}$  in 1963, but reduced to less than  $300 \text{ kg h}^{-1}$  by 1979 (Sainsbury, 1987). Subsequent modeling (NWSJEMS, 2007) suggested that depletion rates of epibenthic fauna are rapid and recovery times can be slow (potentially more than 20 years). We found high biomass of demosponges at Onslow, where the steep shelf break is inaccessible to trawling activities and creates a natural refuge area. Sponge richness is also known to be high in shallow waters inshore of these areas, for instance, in the Dampier Archipelago (Fromont et al., 2006) and off Port Hedland (Fromont, unpublished data) where demersal trawling has not occurred. The importance of structural benthic fauna to creating habitats for fishes is

demonstrated here by the associated change in fish community structure. Large commercial fishes (species of *Lethrinus* and *Lutjanas*) that are associated with structured habitats, accounted for 40–60% of the catch in the early fishing years when sponge bycatch was high (Sainsbury, 1987). A significantly reduced bycatch of structural benthic fauna by the mid-1980s was accompanied by a shift to dominance by small fishes associated with open unstructured habitats, *Nemipterus* and *Saurida*, on the same fishing grounds. Trawling effects vary with gear type, so that lighter ground-gear has been reported to remove fewer sponges. Wassenberg et al. (2002) found that the less flexible and larger sponges are more likely to be dislodged, with a removal rate of 13.8% per tow using a McKenna demersal trawl, a significantly smaller proportion than reported by Sainsbury (1987) of 89% removal of sponges by demersal pair trawlers in the northwest of Australia. Wassenberg et al. (2002) suggested the biggest gap in our current understanding of these impacts is knowledge on the rate of recovery of sponges. More recently large, habitat-forming deep-water sponges have been found to be particularly slow-growing (Hogg et al., 2010), but more studies are required to fully understand the turnover of these important assemblages.

The high proportions of apparently rare species within broadly distributed taxa—including sponges—will require careful management outside any designated marine protected areas, as well as inside them (Williams et al., 2010). It will be important to compare species richness across major taxonomic groups to determine where individual marine areas will efficiently conserve benthic invertebrate biodiversity across taxa. Data for sponges illustrates the importance of adequately representing outer shelf and shelf break habitats in marine reserves on the western Australian margin because demosponges and *Calcarea* have few representatives in slope depths. It is also important to determine whether hard outer shelf areas support high diversity of other taxa in addition to sponges. This has been examined for higher taxa in the southwestern margin by Williams et al. (2010) who noted that mollusc, echinoderm, and sponge species richness increased with increasing substrate hardness. Hard substrates are largely confined to the shelf (61% of observations), whereas soft substrates were recorded in 78% of observations in depths greater than 200 m (Althaus et al., 2011).

Apart from substrate type, depth, and historic fishing, we found few factors that explained the distribution of sponges. Recent analyses by Huang et al. (2011) found depth to be the most important contributing factor in some models, with bottom-water temperature and variables that describe bottom-water nutrient status, such as nitrates and chlorophyll, being important in some cases. They conclude that these factors could be useful surrogates for the distribution of sponge assemblages at the regional scale. Maldonado & Uriz (1999) noted that fragmented habitats, characteristic of the deep sea, often appear to produce discrete, spatially separated populations. We found fine scale patchiness of the sponge communities examined here which appear to be largely related to substrate type and depth. Broad regional scale analyses are not sensitive to fine scale changes in species composition in these sponge assemblages. The lack of understanding of the function and role of deep sponge assemblages in the ecological processes of the marine environment off Western Australia suggest that more study is required to underpin conservation planning.

**Acknowledgments** The funding for this project was provided by the CSIRO Wealth from Oceans Flagship and the Australian Government Department of Environment Water Heritage and the Arts, with the assistance from the Australia's Marine National Facility. Some authors (FA, FM, and AW) were supported through the National Environment Research Programme (NERP), an Australian Government initiative, and in particular by the NERP Marine Biodiversity Hub. Special thanks are due to the Master and the crew of the Marine National Facility vessel FRV Southern Surveyor (surveys SS200507, SS200510 and SS200705) who assisted with the collection of data at sea, the scientific personnel on-board who were responsible for sorting and preserving the invertebrate catches, and all those responsible for organizing sample transport and curation. Among the many staff from the CSIRO who assisted and contributed to this project, we would like to specifically thank the following: Mark Lewis, Rudy Kloster, Nic Bax, Bruce Barker, Gordon Keith, Tony Cracknell, Tanya Gorenc, Mirosław Ryba and Pamela Brodie; and Sue Horner and Gavin Dally (Museum and Art Gallery of the Northern Territory).

## References

- Althaus, F., A. Williams, R. J. Kloster, J. Seiler & N. J. Bax, 2011. Evaluating geomorphic features as surrogates for benthic biodiversity on Australia's western continental margin. In Harris, P. (ed.), *Seafloor Geomorphology as*



- Benthic Habitat: GeoHab Atlas of Seafloor Geomorphic Features and Benthic Habitats. <http://geohab.org/atlas.html>. Accessed on 9 Aug 2011.
- Anderson, M. J., R. N. Gorley & K. R. Clarke. 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E, Plymouth, UK: 214 pp.
- Buhl-Mortensen, L., A. Vanreusel, A. J. Gooday, L. A. Levin, I. G. Friede, P. Buhl-Mortensen, H. Gheerardyn, N. J. King & M. Raes. 2010. Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. *Marine Ecology – An Evolutionary Perspective* 31: 21–50.
- Clark, M. R., F. Althaus, A. Williams, E. Niklitschek, G. M. Menezes, N.-R. Hareide, P. Sutton & C. O'Donnell. 2010. Are deep-sea demersal fish assemblages globally homogenous? – insights from seamounts. *Marine Ecology – An Evolutionary Perspective* 31(Suppl. 1): 39–51.
- Clarke, K. R., 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18(1): 117–143.
- Clarke, K. R. & R. N. Gorley, 2006. PRIMER-e v6: User Manual/Tutorial. Primer-E, Plymouth.
- Commonwealth of Australia, 2005. National Marine Bioregionalisation of Australia. Department of the Environment and Heritage, Geoscience Australia, CSIRO Marine Research. National Oceans Office. Canberra, ISBN 1-877043-61-3.
- Dunn, J. R. & K. R. Ridgway, 2002. Mapping ocean properties in regions of complex topography. *Deep-Sea Research Part I-Oceanographic Research Papers* 49: 591–604.
- Feng, M., D. Slawinski, L. E. Beckley & J. K. Keesing, 2010. Retention and dispersal of shelf waters influenced by interactions of ocean boundary current and coastal geography. *Marine and Freshwater Research* 61: 1259–1267.
- Forest, J., 1981. Compte rendu et remarques générales (texte bilingue)/Report and general comments (bilingual text). Résultats des campagnes MUSORSTOM, 1. Mémoires ORSTOM (Office de la Recherche Scientifique et Technique Outre-Mer): 91 pp.
- Fromont, J. & M. A. Vanderklift, 2009. Porifera (sponges) of Mermaid Reef (Rowley Shoals), Scott and Seringapatam Reefs, Western Australia. *Records of the Western Australian Museum. Supplement* 77: 89–104.
- Fromont, J., M. A. Vanderklift & G. A. Kendrick, 2006. Marine sponges of the Dampier Archipelago, Western Australia: patterns of species distributions, abundance and diversity. *Biodiversity and Conservation* 15: 3731–3750.
- Fromont, J., K. L. Usher, D. C. Sutton, S. Toze & J. Kuo, 2008. Species of the sponge genus *Chondrilla* (Demospongiae: Chondrosida: Chondrillidae) in Australia. *Records of the Western Australian Museum* 24(4): 469–486.
- Grassle, J. F. & N. J. Maciolek, 1992. Deep-sea species richness – regional and local diversity estimates from quantitative bottom samples. *American Naturalist* 139: 313–341.
- Gray, J. S., A. Bjoergesaeter & K. I. Ugland. 2005. The impact of rare species on natural assemblages. *Journal of Animal Ecology* 74: 1131–1139.
- Hanson, C. E., S. Pesant, A. M. Waite & C. B. Pattiaratchi, 2007. Assessing the magnitude and significance of deep chlorophyll maxima of the coastal eastern Indian Ocean. *Deep-Sea Research Part II-Topical Studies in Oceanography* 54: 884–901.
- Hogg, M. M., O. S. Tendal, K. W. Conway, S. A. Pomponi, R. W. M. van Soest, J. Gutt, M. Krautter & J. M. Roberts. 2010. Deep-Sea Sponge Grounds: Reservoirs of Biodiversity, UNEP-WCMC Biodiversity Series No. 32. UNEP-WCMC, Cambridge, UK.
- Hooper, J. N. A. & J. A. Kennedy. 2002. Small-scale patterns of sponge biodiversity (Porifera) on Sunshine Coast reefs, eastern Australia. *Invertebrate Systematics* 16: 637–653.
- Howell, K. L., J. S. Davies & B. E. Narayanaswamy, 2010. Identifying deep-sea megafaunal epibenthic assemblages for use in habitat mapping and marine protected area network design. *Journal of the Marine Biological Association of the United Kingdom* 90: 33–68.
- Huang, Z., B. Brooke & J. Li, 2011. Performance of predictive models in marine benthic environments based on predictions of sponge distribution on the Australian continental shelf. *Ecological Informatics* 6: 205–216.
- Jimenez, E. & M. Ribes, 2007. Sponges as a source of dissolved inorganic nitrogen: nitrification mediated by temperate sponges. *Limnology and Oceanography* 52: 948–958.
- Last, P. R., V. D. Lyne, A. Williams, C. R. Davies, A. J. Butler & G. K. Yearsley, 2010. A hierarchical framework for classifying seabed biodiversity with application to planning and managing Australia's marine biological resources. *Biological Conservation* 143: 1675–1686.
- Legendre, P. & M. J. Anderson, 1999. Distance-based redundancy analysis: testing multi-species responses in multifactorial ecological experiments. *Ecological Monograph* 69: 1–24.
- Lewis, M., 1999. CSIRO-SEBS (Seamount, Epibenthic Sampler), a new epibenthic sled for sampling seamounts and other rough terrain. *Deep-Sea Research I* 46: 1101–1107.
- Lewis, M., 2009. Sherman the epibenthic sled for rough terrain (CSIRO Marine and Atmospheric Research paper: 029). CSIRO Marine and Atmospheric Research, Canberra, ACT: 15 pp.
- Lewis, M., 2010. The CSIRO 4m Beam Trawl (CSIRO Marine and Atmospheric Research Paper 033). CSIRO Marine and Atmospheric Research, Hobart, Tas: 17 pp.
- Lourey, M. J., J. R. Dunn & J. Waring, 2006. A mixed-layer nutrient climatology of Leeuwin Current and western Australian shelf waters: seasonal nutrient dynamics and biomass. *Journal of Marine Systems* 59: 25–51.
- Maldonado, M. & M. J. Uriz, 1999. Sexual propagation by sponge fragments. *Nature* 398: 476.
- Maldonado, M., A. Riesgo, A. Bucci & K. Rutzler, 2010. Revisiting silicon budgets at a tropical continental shelf: silica standing stocks in sponges surpass those in diatoms. *Limnology and Oceanography* 55: 2001–2010.
- McEnulty, F. R., K. L. Gowlett-Holmes, A. Williams, F. Althaus, J. Fromont, G. C. B. Poore, T. D. O'Hara, L. Marsh, P. Kott, S. Slack-Smith, P. Alderslade, & M. V. Kitahara. 2011. The deepwater megabenthic invertebrates on the western continental margin of Australia (100–1100 m depths): composition, distribution and novelty. *Records of Western Australian Museum Supplement* 80: 1–189.

- McQuillan, L., 2006. Species richness, density and cover of sponges on temperate reefs in Western Australia. Unpublished MSc thesis, Edith Cowan University.
- Meuleners, M. J., C. B. Pattiaratchi & G. N. Ivey, 2007. Numerical modelling of the mean flow characteristics of the Leeuwin Current System. *Deep-Sea Research Part II-Topical Studies in Oceanography* 54: 837–858.
- North West Shelf Joint Environmental Management Study, 2007. CSIRO and Department of the Environment of Western Australia: 40 pp.
- Reed, J. K. & S. A. Pomponi, 1997. Biodiversity and distribution of deep and shallow water sponges in the Bahamas. In *Proceedings of the Eighth International Coral Reef Symposium*, Panama, June 24–29, 1996: 1387–1392.
- Ridgway, K. R. & S. A. Condie, 2004. The 5500-km-long boundary flow off western and southern Australia. *Journal of Geophysical Research-Oceans* 109: 18 pp.
- Ridgway, K. R., J. R. Dunn & J. L. Wilkin, 2002. Ocean interpolation by four-dimensional least squares – application to the waters around Australia. *Journal of Atmospheric and Oceanic Technology* 19: 1357–1375.
- Riisgard, H. U. & P. S. Larsen, 2010. Particle capture mechanisms in suspension-feeding invertebrates. *Marine Ecology-Progress Series* 418: 255–293.
- Rützler, K., 2004. Sponges on coral reefs: a community shaped by competitive cooperation. In Pansini, M., R. Pronzato, G. Bavestrello & R. Manconi (eds), *Sponge Science in the New Millennium*. Officine Grafiche Canessa, Rapallo, Genova: 85–148.
- Sainsbury, K. J., 1987. Assessment and management of the demersal fishery on the continental shelf of northwestern Australia. In Polovina, J. J. & S. Ralston (eds), *Tropical snappers and groupers – biology and fisheries management*. Westview Press, Boulder, CO: 465–503.
- Schlacher, T. A., M. A. Schlacher-Hoenlinger, A. Williams, F. Althaus, J. N. A. Hooper & R. Kloser, 2007. Richness and distribution of sponge megabenthos in continental margin canyons off southeastern Australia. *Marine Ecology-Progress Series* 340: 73–88.
- Sorokin, S., J. Fromont & D. Currie, 2007. Demosponge biodiversity in the benthic protection zone of the Great Australian Bight. *Transactions of the Royal Society of South Australia* 131: 192–204.
- Waite, A. M., P. A. Thompson, S. Pesant, M. Feng, L. E. Beckley, C. M. Domingues, D. Gaughan, C. E. Hanson, C. M. Holl, T. Koslow, M. Meuleners, J. P. Montoya, T. Moore, B. A. Muhling, H. Paterson, S. Rennie, J. Strzelecki & L. Twomey, 2007. The Leeuwin current and its eddies: an introductory overview. *Deep-Sea Research Part II-Topical Studies in Oceanography* 54: 789–796.
- Wassenberg, T. J., G. Dews & S. D. Cook, 2002. The impact of fish trawls on megabenthos (sponges) on the north-west shelf of Australia. *Fisheries Research* 58: 141–151.
- Williams, A., F. Althaus, P. K. Dunstan, G. C. B. Poore, N. J. Bax, R. J. Kloser & F. R. Mcenulty, 2010. Scales of habitat heterogeneity and megabenthos biodiversity on an extensive Australian continental margin (100–1100 m depths). *Marine Ecology – An Evolutionary Perspective* 31: 222–236.
- Woo, M., C. Pattiaratchi & W. Schroeder, 2006. Summer surface circulation along the Gascoyne continental shelf, Western Australia. *Continental Shelf Research* 26: 132–152.