

REVIEW ARTICLE

Quantitative trends in sponge ecology research

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Keywords

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Abstract

It is almost dogmatic that sponges are one of the most relevant groups in benthic marine communities, a statement generally based upon their diversity and abundance in natural communities. But beyond their conspicuousness, do we really know the role that sponges play in nature? Using a series of productivity indicators, this review evaluates the relevance of sponge research to the general scientific community, particularly the contribution of sponge ecology to the broader science of ecology. The relevance of sponge research ranked second out of eight taxonomic groups. Ecology accounted for most of the sponge research output but it ranked poorly compared to the relative importance of the ecological literature in the remaining taxonomic groups. Sponge ecology focused primarily on the species level of organization even though the relevance of these studies fell well below expected. This review suggests that the ecological relevance of sponges is insufficiently supported by ecological data and would benefit from better scientific support. Sponge ecology has the opportunity to contribute to the broader science of ecology in numerous topics where sponge research may be particularly relevant. Broader ecological contributions will help verify the ecological relevance that the great diversity and abundance of sponges suggest.

Why sponge ecology?

Bearing pores. A simple description to define an apparently simple but fascinating group of organisms: sponges. The Phylum Porifera (from Latin *porus* 'pore' and *fero* 'to bear') includes the simplest and most primitive metazoans (Schutze *et al.* 1999), lacking most of what we commonly associate with the animal kingdom. The pores on the surface lead to a framework of canals and chambers of varying complexity that forms the aquiferous system, which distributes water throughout the sponge body to accomplish basic physiological functions (Bergquist 1978). Dating from the Precambrian era (Finks 1970; Li *et al.* 1998), sponges have evolved into a diverse and abundant group in aquatic environments worldwide, particularly in marine habitats (Sarà & Vacelet 1973; McClintock *et al.* 2005). It is generally accepted that sponges are an ecologically relevant group in marine benthic communities.

Sponges are highly diverse and abundant in many systems, contribute to community organization and functioning through a variety of biotic interactions, and play a role in ecosystem processes such as primary production, nutrient cycling or bioerosion (Sarà & Vacelet 1973; Becerro *et al.* 1997; Diaz & Rützler 2001; Rützler 2004; Wulff 2006a). Also, sponges are sessile organisms and rely primarily on their larvae for dispersion (Maldonado & Uriz 1999; Maldonado 2006). This brings to the ecological scene an array of colonization, habitat, biogeographic, and evolutionary approaches that are further enhanced by the development of molecular tools (Duran *et al.* 2004a,b; Duran & Rützler 2006; Calderon *et al.* 2007). Although this brief list is far from being exhaustive, the areas of sponge research with ecological implications loom large.

We, as researchers with a strong appreciation for sponges, may be biased about the role of sponges in nature. Not only that. We may also be biased about the

output of sponge research, which seems to draw little attention from those with interests other than sponges. For example, the Canadian Journal of Zoology publishes a series of virtual symposia on the biology of neglected groups. One of this series covered the Phylum Porifera in 2006 (Saleuddin & Fenton 2006). The concept of sponges as a neglected group i) contrasts with the apparent abundance of literature on sponges and ii) casts doubt on the rigor of some general assumptions, such as the important role of sponges in natural systems. What do we really know about the role of sponges in the organization and functioning of benthic communities? Is sponge research in good health? Can we evaluate the impact of sponge research? Is sponge ecology contributing to general ecological theory or mainly restricted to studies of local habitats? Are there any emerging areas? A comprehensive trend analysis of sponge research showed emerging topics, including a steady increase in the number of publications on sponge ecology since the 1970s (Sarà 2004). There is no further analysis on this trend or a more recent review on sponge ecology, but giving the increasing number and diversity of ecological studies on sponges, an analysis of the available literature seems timely.

This study quantifies and analyses the trends in sponge research to identify areas of relevant activity, to quantify their impact on the scientific community, and to evaluate the contribution of sponge research to ecology. It is by no means an exhaustive review on the multiple disciplines enclosed by ecology nor does it aspire to be. Readers are referred to the numerous reviews published in the last 2 years for more exhaustive compilations on particular areas of sponge research such as disease (Webster 2007), microbiology (Taylor *et al.* 2007b), ecological interactions (Wulff 2006a), larval ecology (Maldonado 2006), paleontology (Pisera 2006), systematics, phylogeny, and evolution (Boury-Esnault 2006; Manuel 2006; Reiswig 2006), or cellular biology, embryogenesis and mineralization (Uriz *et al.* 2003; Leys & Ereskovsky 2006; Pomponi 2006; Uriz 2006; Wiens & Müller 2006). Other reviews that also include information on sponges are cited below.

Reference Sampling and Analysis

Quantifying research trends is far from an easy task. Reviewing all ecological literature on sponges is a real challenge. Fortunately, the introduction of the citation index database facilitates monitoring literature and generating statistical reports, especially since it has become accessible through the worldwide web (Garfield 1964, 1970). The Thompson ISI web of knowledge (Institute for Scientific Information®, <http://isiwebofknowledge.com>) compiles the Science Citation Index® and other quantitative tools of interest for researchers. The Science Citation

Index Expanded database covers research publications from 1945 up to the present and allows for detailed analysis of research publications as a function of year, subject categories, and other variables. I used this database as a source to evaluate research on sponges.

Does research on sponges differ from research on other taxonomic groups? To answer this question I selected eight groups of plant and animals with a similar number of known species and compared their major research areas and overall impact in the scientific community. I searched (1945–2006 timespan) for the Latin name of each taxonomic group to avoid selecting unwanted publications as a result of multiple accepted common names. The terms (with approximate number of known species within brackets) are Porifera (7000), Anthozoa (6000), Echinodermata (6000), Bryozoa (4000), Opisthobranchia (5000), Rhodophyta (5000), Odonata (5000), and Euphorbiaceae (6000). This list includes common sessile and vagile benthic groups as well as terrestrial plant and animal outgroups for further comparison. I used the total number of publications, total number of citations, average number of citations per publication, and the H index to compare groups and categories within groups. The total number of publications is a measure of productivity but provides no information on the relevance of the publications. The total number of citations evaluates the impact of the published work, but may be inflated by a single or a few articles with an unusually high number of citations that do not represent the impact of the remaining research. The number of citations per paper allows comparison of areas that have been researched over a varying number of years (*e.g.* scientists of different ages) but it is biased by productivity. The H index is the number of publications with citations equal or greater than H (Hirsch 2005). Quoting Hirsch, 'A scientist has index h if h of his or her N_p papers have at least h citations each and the other $(N_p - h)$ papers have $\leq h$ citations.' The H index is an unbiased indicator of the relevance of research outputs and it is therefore very appropriate to compare quantitatively the relevance of multiple areas of research (Hirsch 2005). The overall scientific impact of two research areas with similar H indexes is similar (even if they differ in total number of publications or citations), while higher H values denote greater relevance (Hirsch 2005).

The Science Citation Index Expanded database at Thompson ISI® provides results as a function of Subject Categories, which allows quantitative evaluation of the research output of such categories. The number of categories is large. Although labels are very intuitive and self-explanatory, readers are encouraged to look at the webpage (Subject Category Scope Notes, Journal of Citations Reports®) for detailed information on what is covered by each category. The total number of subject

categories for the eight taxonomic groups used in this study was 92. I pooled subject categories for 13 topics, which include one or more subject categories. Some subject categories were very minor and were not considered in the analysis. Rather than the actual number of publications for each subject category, I used percentage to allow for better comparisons between taxonomic groups and topics. Subject categories are non-exclusive, so any single publication may be included in multiple subject categories. Accordingly, if we add up the number of publications (or percentages) in each category we obtain a number larger than the true number of publications (*i.e.* percentages larger than 100%). The total percentage for every taxonomic group after adding up all percentages in each subject category varied between 130% and 180%. The 13 topics are: paleontology, behavior, biology (subject areas: biology and reproductive biology), morphology (anatomy and morphology, cell biology, developmental biology, microscopy), molecular biology (biochemistry and molecular biology, genetics and heredity), physiology, ecology (agronomy, ecology, entomology, limnology, marine and freshwater biology, oceanography), diversity (biodiversity conservation, environmental sciences), microbiology (biotechnology and applied microbiology, microbiology), taxonomic specialty (zoology, plant science), chemistry (analytical, applied, medicinal, multidisciplinary, organic, inorganic and nuclear, pharmacology and pharmacy, toxicology), multidisciplinary, and evolution. The total percentage for every taxonomic group after adding up all percentages in each topic varied between 120% and 170%, so the information lost by the significant reduction from categories to topics appears negligible.

Many ecological publications use the common 'sponge' name rather than the more formal Porifera. For a detailed evaluation of the ecological aspects of sponge research I therefore searched for (*sponge OR porifera*) AND *ecolog**. The use of the wildcard allowed searching word variants such as 'ecology, ecological, or ecologically'. This combination specifically targeted publications related to sponge ecology, since a simple consideration of any 'ecological implication' in the title, abstract, or keywords resulted in the selection of the publication. However, this type of search strategy is bound to leave out relevant publications. For example, the paper by Mariani *et al.* (2006) investigates the dispersal strategies of several sponge species, nicely integrating life history, water dynamics, and community organization. The paper has been published in *Oecologia* and has clear ecological implications. Yet, the title, keywords, and abstract do not include the word 'ecology' (or any variant) so it was not selected by my search and it is not included in my analysis. The articles I analyse in this review are exclusively those selected by my

search strategy. The criteria used for my search strategy are simple, easy to reproduce, and equal for all fields or taxonomic groups. This makes results comparable and prevents bias due to my own research preferences or area of expertise. The timespan used for this search was from 1945 to 2006 and I recorded the total number of publications, total number of citations, average number of citations per publication, and the H index.

Specificities of Sponge Research

Porifera ranked third after a quantitative evaluation of the research output of the eight taxonomic groups considered in this comparison. Porifera ranked first for the highest average number of citations for each publication, second for the H index (tied with Echinodermata), and fifth for total number of publications and citations (Table 1). Only Rhodophyta (ranked first in total number of publications, citations and H index, and ranked sixth in average number of citations) and Echinodermata (ranked second in total number of publications and citations, and ranked fourth in average number of citations and H index) were ranked above Porifera in this general quantitative ranking (Table 1). The high H index showed by Porifera was particularly relevant because it was attained with the lowest number of publications compared to Echinodermata and Rhodophyta (two- and threefold higher than the number of publications on Porifera, respectively). Although not particularly abundant, publications on Porifera seem to have a very strong impact on the scientific community.

Within this comparison, Porifera research ranked first in the morphology and evolution topics and it was top second in the molecular biology and chemistry topics (Table 2). At the opposite end, behavior and ecology ranked sixth and seventh, respectively (Table 2). Averaging rankings for all topics, Porifera was ranked second

Table 1. Total number of publications (n) total number of citations (cites), average citations per publication (avg), and index H for each of the taxonomic groups searched in the Science Citation Index Expanded database from 1945 to 2006.

taxonomic group	n	cites	avg	H
(1) Rhodophyta	3778	34 632	9.17	53
(2) Echinodermata	2322	22 118	9.53	49
(3) Porifera	1188	13 851	11.66	49
(4) Odonata	1643	15 201	9.25	51
(5) Euphorbiaceae	1979	16 389	8.28	46
(6) Anthozoa	665	7306	10.99	38
(7) Opisthobranchia	717	7170	10	34
(8) Bryozoa	953	7271	7.63	36

Taxonomic groups sorted by descending rank.

Table 2. Percentage of publications (ranking for each topic shown within brackets in italics) for each of 13 topics and eight taxonomic groups searched in the Science Citation Index Expanded database from 1945 to 2006.

taxonomic group	topic												
	Paleo	Behav	Biol	Morpho	MolBiol	Physio	Ecol	Div	Micro	Tax	Chem	Multi	Evol
(1) Anthozoa	4.2 (3)	0.2 (4)	12.3 (1)	9.6 (2)	13.5 (3)	2.0 (2)	53.2 (5)	2.9 (7)	3.2 (3)	20.0 (6)	4.7 (4)	5.0 (1)	5.1 (3)
(2) Porifera	3.9 (4)	0.1 (6)	8.0 (3)	16.7 (1)	17.0 (2)	0.7 (5)	46.6 (7)	4.7 (4)	3.5 (2)	24.7 (4)	7.5 (2)	3.2 (4)	7.7 (1)
(3) Echinodermata	8.2 (2)	0.1 (5)	11.2 (2)	9.4 (3)	8.2 (4)	1.9 (3)	64.5 (4)	6.1 (3)	0.9 (6)	24.0 (5)	3.3 (5)	2.9 (5)	3.5 (6)
(4) Odonata	2.1 (5)	7.0 (1)	4.3 (6)	3.0 (6)	6.3 (6)	2.4 (1)	64.8 (3)	8.5 (2)	0.5 (7)	20.0 (7)	1.0 (8)	4.0 (2)	4.9 (4)
(5) Euphorbiaceae	1.0 (6)	0.2 (3)	1.6 (7)	0.6 (8)	17.4 (1)	0.2 (7)	18.8 (8)	3.4 (6)	1.7 (4)	50.2 (3)	46.6 (1)	2.7 (6)	6.5 (2)
(6) Opisthobranchia	0.6 (8)	2.6 (2)	6.1 (4)	6.1 (4)	6.0 (7)	0.7 (4)	69.2 (2)	3.5 (5)	0.4 (8)	54.4 (2)	1.5 (7)	0.8 (8)	4.3 (5)
(7) Bryozoa	18.3 (1)	0.0 (8)	6.1 (5)	3.3 (5)	2.5 (8)	0.3 (6)	52.4 (6)	11.4 (1)	1.6 (5)	18.7 (8)	2.2 (6)	3.7 (3)	2.9 (7)
(8) Rhodophyta	0.8 (7)	0.1 (7)	1.4 (8)	1.2 (7)	6.5 (5)	0.1 (8)	78.7 (1)	1.9 (8)	7.8 (1)	61.5 (1)	5.5 (3)	1.6 (7)	2.9 (8)

See text for the Thompson ISI[®] subject areas included in each topic.

Paleo, paleontology; Behav, behavior; Biol, biology; Morpho, morphology; MolBiol, molecular biology; Physio, physiology; Ecol, ecology; Div, diversity; Micro, microbiology; Tax, taxonomic specialty; Chem, chemistry; Multi, Multidisciplinary; Evol, evolution.

(Table 2). Pooling all groups, the most productive topics were ecology, zoology and molecular biology, and the least productive were physiology, behavior and microbiology (Table 2). Looking exclusively at Porifera, ecology, taxonomic specialty and molecular biology accounted for most publications (46.6%, 24.7% and 17%, respectively). Publications on behavior (0.1%), physiology (0.7%), and multidisciplinary (3.2%) were the least abundant (Table 2).

Sponge Ecology to the Arena

A total of 353 publications met the sponge ecology requirements of the search (see Reference sampling above). Five papers were totally unrelated to the objective of this study and were discarded. The remaining 348 articles totaled 4673 citations, which showed a dramatic trend to increase over the years that cannot be matched by the number of publications (Fig. 1). The number of publications showed a moderate increase in the early 1990s that leveled out at about 10 publications per year, then doubled in the late 1990s and early 2000s, and has tripled in the last 4 years (Fig. 1). The H index of these publications was 32. Of the 348 publications, 36 were reviews. These reviews accounted for over 20% of the citations (1052) and had an H index of 16. There was over a twofold increase in the average number of citations for each review compared with regular articles (29.2 *versus* 13.2).

The 348 publications were contributed by a total of almost 800 authors, and only 133 researchers had multiple contributions (two or more publications). The number of researchers with more than 10 contributions was just six.

Publications on sponge ecology covered a great variety of research areas. The 348 publications on sponge ecology represented over 30 subject categories in the Thompson

Record count

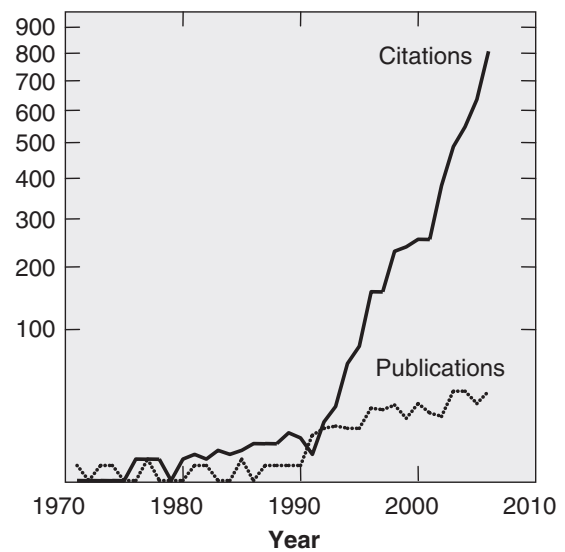


Fig. 1. Evolution of the number of publications (dot line) and citations (solid line) on sponge ecology found in the web of Science Citation Index Expanded database from 1945 to 2006. Search strategy: (sponge OR porifera) AND ecolog*.

ISI[®] web of knowledge (Table 3). However, almost 50% of the 348 records belonged to the Marine & Freshwater Biology subject category (Table 3). Barely 27% of the publications belonged to the Ecology category.

The 348 publications on sponge ecology were cited by more than 3100 publications that represented over 90 subject categories. This large number of subject categories indicates that sponge ecology is widely cited by research areas outside the sponge ecology field and is a powerful demonstration of the impact of sponge ecology on other scientific disciplines. A goodness of fit (Sokal & Rohlf

Table 3. Number of publications (n), percentage of the total 348 publications on sponge ecology (%), total number of citations (cites), average citations per publication (avg), and index H for each subject category.

subject category	n	%	cites	avg	H
marine & freshwater biology	157	45.1	2256	14.37	23
ecology	95	27.3	1113	12.94	20
oceanography	50	14.3	1049	20.98	16
zoology	30	8.6	227	7.57	9
biochemistry & molecular biology	25	7.1	238	9.52	10
paleontology	25	7.1	187	7.48	8
environmental sciences	22	6.3	118	5.36	7
geology	17	4.9	141	8.29	6
pharmacology & pharmacy	15	4.3	311	20.73	10
evolutionary biology	13	3.7	118	9.08	7
chemistry, medicinal	12	3.4	200	16.67	9
geosciences, multidisciplinary	12	3.4	98	8.17	7
fisheries	11	3.1	51	4.64	4
multidisciplinary sciences	10	2.8	224	22.4	7
biodiversity & conservation	9	2.5	60	6.67	5
biotechnology & applied	9	2.5	135	15	5
microbiology					
microbiology	9	2.5	330	36.67	9
plant sciences	9	2.5	166	18.44	7
biology	7	2.0	39	5.57	3
chemistry, applied	7	2.0	103	14.71	5
geography, physical	7	2.0	57	8.14	5
chemistry, organic	6	1.7	99	16.5	5
limnology	6	1.7	33	5.5	3
chemistry, multidisciplinary	5	1.4	50	10	5
genetics & heredity	4	1.1	38	9.5	2
toxicology	4	1.1	75	18.75	3
cell biology	3	0.8	59	19.67	2
microscopy	3	0.8	23	7.67	2
water resources	3	0.8	8	2.67	2
anatomy & morphology	2	0.5	62	31	2
engineering, environmental	2	0.5	1	0.5	1
behavioral sciences	1	0.2	11	11	1
developmental biology	1	0.2	12	12	1
physiology	1	0.2	5	5	1
veterinary sciences	1	0.2	0	0	0

1995) showed significant differences in the proportion of publications in specific subject categories between the 348 published articles on sponge ecology and the publications that cited them ($G = 53.542$, $df = 5$, $P < 0.001$). The proportion of articles on sponge ecology cited by the Biotechnology and Applied Microbiology, Organic Chemistry, and Microbiology subject categories approximately doubled the proportion of articles on sponge ecology published in the same categories (Fig. 2). Contrastingly, the proportion of articles published on sponge ecology exceeded those cited in the Ecology, Marine and Freshwater Biology, and Paleontology subject categories (Fig. 2).

The Thompson Journal of Citation Reports[®] showed 112 journals belonging to the Ecology subject category.

These journals were sorted by descending impact factor and classified into two groups of 56 journals. The top and bottom groups contained the high and low impact factor journals, respectively. I used a goodness-of-fit test to quantify whether the 95 articles published on sponge ecology in this subject category deviated from what was expected under the assumption of equal probability to publish in any journal. The high impact factor ecological journals published significantly more articles on sponge ecology than the low impact factor journals ($G = 48.571$, $df = 1$, $P < 0.001$, Fig. 3). However, the top 20 ecological journals are deficient in sponge ecology, whereas journals below rank 30 published more publications than expected (Fig. 3). Also, only three of the articles published in the top 20 ecological journals focused specifically on sponges (Thacker *et al.* 1998) or their associated flora and fauna (Palumbi 1985; Duffy 1996) and the remaining articles were not intended to specifically provide information on sponge ecology. Overall, the 348 articles were published in 146 journals. Most journals had occasional publications on sponge ecology and the top 5 and 10 journals account for over 25 and 35 of all publications, respectively (Table 4). Five of the top 10 journals focused on marine biology, two on chemical ecology/natural products, and one on aquatic biology, zoology, and paleontology (Table 4).

Trends in Sponge Ecology versus Trends in Ecology

Ecology is a vast science that includes numerous disciplines and approaches. In an attempt to understand why sponge ecology fails to be included in top ecological journals and to test whether or not sponge ecology deviates from general ecological research, I searched for all the articles with the wildcard *ecolog** in the journal *Trends in Ecology and Evolution (TREE)*. Besides being a journal particularly appropriate to analyse trends in ecology, it is also the journal with highest impact factor in the ecology subject category of the Science Citation Index database. A total of 661 out of the 3345 TREE articles (from 1986 to June 2007) met the criteria. I quantified and ranked the keywords of these 661 articles by abundance and used the most relevant keywords to search in the Science Citation Index Expanded database for the TREE and sponge ecology articles containing each particular keyword. I then quantified the number of papers and used goodness-of-fit to test for relative differences between both groups (TREE *versus* Sponge Ecology) (Sokal & Rohlf 1995).

A highly noticeable trend was the decrease in number of sponge ecology and TREE articles with increasing levels of ecological organization from species to ecosystem

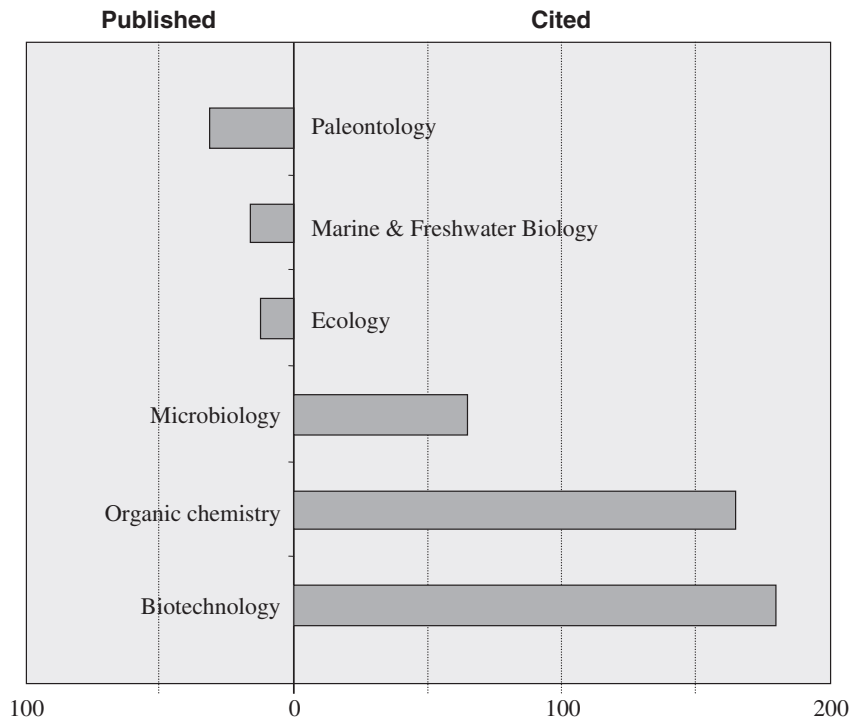


Fig. 2. Relative proportion (percentage) of articles on sponge ecology published (published/cited) or cited (cited/published) within the Biotechnology and Applied Microbiology (Biotechnology), Organic Chemistry, Microbiology, Ecology, Marine and Freshwater Biology, and Paleontology subject categories found in the ISI® web of knowledge Science Citation Index Expanded database. The proportion of sponge ecology articles published or cited in the remaining categories were approximately equivalent, i.e. the relative value did not deviate from 1. Bars to the left show higher proportion of sponge ecology papers published than cited, whereas the opposite is true for categories with bars to the right.

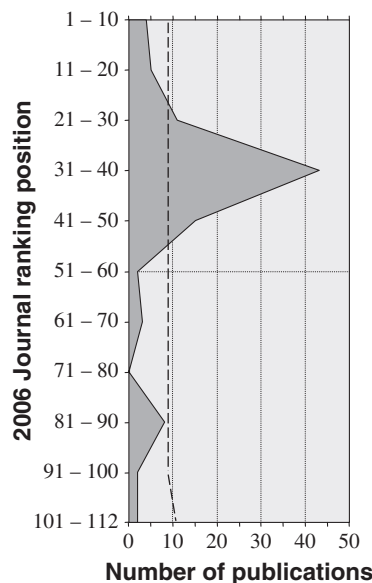


Fig. 3. Distribution of the 95 sponge ecology articles included in the Ecology category in the Thompson ISI® web of knowledge as a function of the impact factor of the journals. The 112 journals are ranked with descending impact factor (one highest impact factor) and grouped in categories of 10 journals (12 in the bottom group). Dashed line is the number of publications expected under the assumption of equal probability of publishing the 95 sponge ecology articles in any journal.

Table 4. Number of publications (n), percentage of the total 348 publications (%), and cumulative percentage (cum) in the top 10 journals publishing on sponge ecology according to the Thompson ISI® web of knowledge.

journal	n	%	cum
<i>Marine Ecology Progress Series</i>	27	7.7	7.7
<i>Marine Biology</i>	24	6.9	14.6
<i>Hydrobiologia</i>	14	4.0	18.6
<i>Marine Ecology PSZN and Evol. Persp.</i>	14	4.0	22.7
<i>Journal of Experimental Marine Biology and Ecology</i>	13	3.7	26.4
<i>Journal of Chemical Ecology</i>	10	2.8	29.3
<i>Bulletin of Marine Sciences</i>	8	2.3	31.6
<i>Facies</i>	7	2.0	33.6
<i>Canadian Journal of Zoology</i>	6	1.7	35.3
<i>Journal of Natural Products</i>	6	1.7	37.0

($G = 76.438$, $df = 3$, $P < 0.001$, Fig. 4). Compared to the TREE trend, sponge ecology doubled the proportion of articles at the species level while halved the population and ecosystem levels (Fig. 4). It is unclear whether these differences are a consequence of a holistic *versus* reductionist approach to ecology, approaches which have traditionally confronted each other in the history of ecology and continue to generate debate (Smith & Smith 2001; Schizas & Stamou 2007), but the autoecological

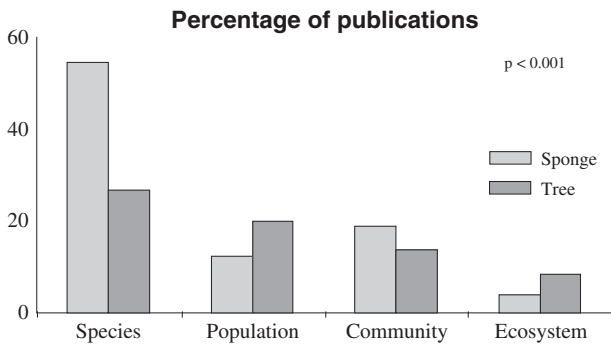


Fig. 4. Percentage of publications with the criteria species, population, community, and ecosystem in sponge ecology (sponge) and in the journal *Trends in Ecology and Evolution (TREE)*. Significant differences tested with goodness of fit. See text for details.

perspective noticeably dominated research on sponge ecology. Beyond the actual number of publications, the H index of this particular area of sponge ecology was well below the number expected for such a large number of publications, and clearly deviated from the trend found with the remaining sponge ecology and TREE articles of an increase in the H index with increasing number of publications ($R = 0.978$, $df = 6$, $P < 0.001$, Fig. 5).

Compared with the ecological articles in TREE, sponge ecology had a lower proportion of articles dealing with conservation, dispersal, dynamics, evolutionary ecology, extinction, life-history, physiology and resistance, and a higher proportion of articles on growth, patterns and predation ($G = 53.542$, $df = 7$, $P < 0.001$, Fig. 6). The proportion of articles containing the remaining keywords was equivalent in both groups.

Is Sponge Research 'Ecologically' Relevant?

Reviews are essential tools to keep up with the continuously expanding production and accumulation of informa-

Fig. 5. Scatterplot with number and H index of the publications with the criteria species (spp), population (pop), community (com), and ecosystem (eco) in sponge ecology (sponge) and in the journal *Trends in Ecology and Evolution (TREE)*. Note the low H index for the large number of papers on sponge ecology at the species level, which was not included in the regression analysis. Dashed lines are 95% confidence intervals.

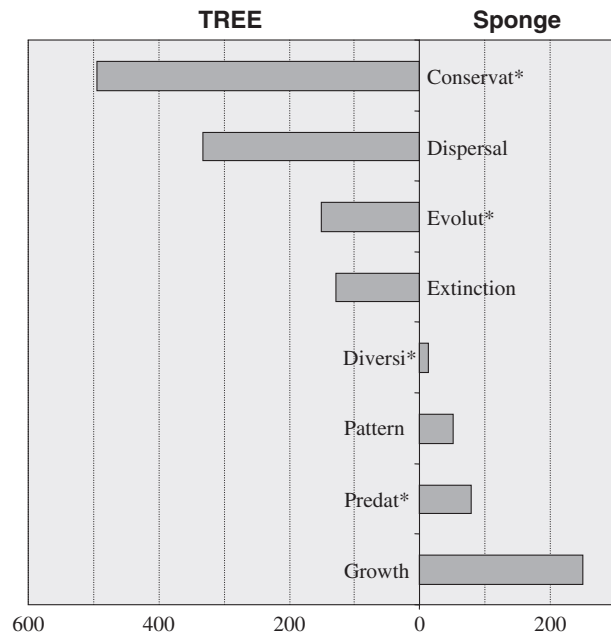
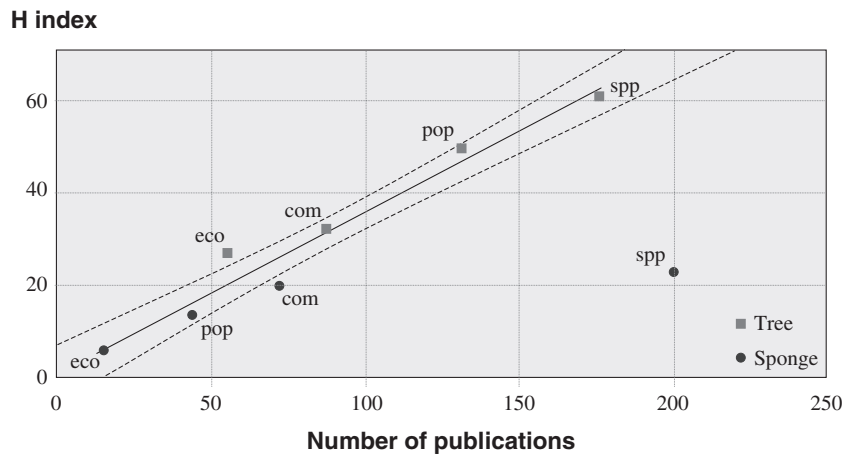


Fig. 6. Relative proportion (percentage) of articles of publications with the criteria conservat*, dispersal, evolut*, extinction, diversi*, pattern, predat*, and growth in sponge ecology (sponge) and in the journal *Trends in Ecology and Evolution (TREE)* found in the ISI® web of knowledge Science Citation Index Expanded database. See text for details. The proportion of articles with the remaining keywords was approximately equivalent in sponge ecology and TREE, i.e. the relative value did not deviate from 1. Bars to the left show a higher proportion of papers in TREE than in sponge ecology containing the specific keyword, whereas the opposite is true for categories with bars to the right.

tion in any given research area. But beyond the critical evaluation and synthesis of existing knowledge, reviews are also necessary to identify areas that have been overlooked and need further information, to detect new emerging areas, or to 'simply' become aware of the evolution of

established research areas. A quantitative analysis of published information provides opportunities to improve our research approach and to take full advantage of the existing literature in the field. This study quantitatively analysed the published information on sponges (Porifera) gathered within the Science Citation Index Expanded database. Although the overall impact of sponge research was quite strong, sponge ecology in particular showed some limitations and had a lower impact than other areas with a similar number of publications. This quantitative analysis highlights some overlooked research areas that could help improve our understanding of sponge ecology and, as a consequence, could have broader scientific implications.

Using multiple indicators of productivity, the research output generated by the Phylum Porifera ranked among the top eight taxonomic groups. These groups included some of the most representative marine benthic groups as well as terrestrial animal and plant groups for further reference. The impact of Porifera research, as evaluated by the H index, was mostly relevant as sponge research is not particularly productive. Although ecology accounted for most publications within Porifera, sponges ranked near the bottom of this particular field. The low number of publications in sponge ecology may be a consequence of the low number of researchers truly devoted to sponge ecology. Over 80% of the researchers contributed with a single publication compared with less than 1% who contributed more than 10 publications. This discrepancy suggests that sponge ecology is stimulating enough to draw the attention of a large number of researchers but lacks the appeal to make them establish a long-term commitment to this discipline. As sponges are considered an ecologically relevant group in marine communities (Sarà & Vacelet 1973; McClintock *et al.* 2005), the relatively lower effort to understand sponge ecology looks particularly worrisome and suggests that research on sponge ecology has significant room for quantitative and qualitative growth.

Overall, research on sponge ecology has a strong impact on the scientific community as suggested by the high number of subject categories that cited publications on sponge ecology. Biotechnology and Applied Microbiology, Organic Chemistry, and Microbiology categories cited sponge ecology research profusely compared with the proportion of sponge ecology articles published in those same categories. This deviation between the number of publications published and cited may suggest a great demand for information on sponge microbial ecology that these particular topics cannot meet. Although sponge microbial ecology is rapidly expanding, there are many areas where this field is still in its infancy (Taylor *et al.* 2007b). The prospects for increasing interest in the ecological perspectives of microbial–host associations are high but their biotechnological implications loom even

larger and may fuel both fundamental and applied research. For example, research on natural products chemistry has led to the isolation of abundant secondary metabolites from sponges (Blunt *et al.* 2007). Although we know only a fraction of the ecological roles of these compounds (Paul *et al.* 2006), sponge chemical ecology is well positioned and has clearly profited from the natural products field (and *vice versa*). Similarly, fundamental and applied interests in microbiology will be mutually beneficial and this review clearly shows that applied fields extensively cite research on sponge ecology.

On the other side of the coin, sponge ecology had a lower impact than expected in the Marine and Freshwater Biology, Ecology, and Paleontology subject categories. Somehow, research on sponge ecology remains relatively unnoticed in areas where its contribution should be large. This deficiency in citations of sponge ecology suggests that the research carried out in sponge ecology deviates from the demands of the broader audience within the Ecology, Marine and Freshwater Biology, and Paleontology categories. Many sponge ecology publications are aimed at the species level and their impact on the scientific community was below what is expected for such a large number of publications. In contrast, publications on sponge ecology at higher levels of ecological organization fell within the expected range of impact and proved the comparatively higher relevance of sponge ecology when studies are broader in focus.

Further evidence suggests that sponge ecology adds little to broader ecological issues of interest to the general ecological audience. The 20 top ecological journals were clearly deficient in sponge ecology, with just three articles specifically aimed at sponge ecology. Sponge ecology seems mostly to address benthic ecologists and marine zoologists as the bulk of publications reached marine-oriented journals. Most research was published in journals positioned above the average impact factor for the Ecology category, which can be interpreted as a sign of quality. However, it may also suggest that sponge ecology research falls outside the scope of the top ecological journals or fails to meet their standards. This study clearly shows that sponge ecology is in need of research on conservation and dispersal, which are well represented in the journal *Trends in Ecology and Evolution*. The increasing global awareness for conservation issues offers new challenges to marine ecology. Sponge ecology has overlooked this global environmental concern despite massive sponge mortalities worldwide (Gaino *et al.* 1992; Gammill & Fenner 2005; Wulff 2006b). This field may become more relevant as we gain an understanding of the local and global causes of sponge decline and their consequences at the community and ecosystem levels. Also, dispersal capacity is a critical trait to consider in conservation as it

directly relates to habitat connectivity and gene flow. Despite the literature available on larval ecology, the consequences of larval dispersal on the structure and dynamics of sponge populations remain largely uninvestigated (Maldonado 2006); moreover, larval ecology is a field with important theoretical and applied implications.

As stated earlier, sponges are traditionally considered an important component of benthic communities and the small contribution of sponge studies to broader ecological issues is surprising. Sponges have a great potential to alter coastal ecosystems. Because of their great abundance, impressive filtering capacity, heterogeneous diet, and complex bacterial associations, sponges could play a significant role both in depleting organic matter from the water column and in providing nutrients to planktonic primary producers (Diaz & Ward 1997; Jimenez & Ribes 2007). The study of biogeochemical cycles and energy flows are areas with strong ecological traditions where sponges could contribute significantly, yet they have been overlooked (Maldonado *et al.* 2005; de Goeij & van Duyl 2007).

Sponges can also play a major role in the organization and functioning of benthic communities. Their outstanding plasticity is matched by the production of secondary metabolites that confer many benefits on sponges in their biotic interactions (Paul & Puglisi 2004). As interactions are at the soul of ecology, sponges provide great opportunities to advance fundamental ecological concepts such as the role of biotic interactions in community organization. An excellent review of the ecological interactions of marine sponges is available (Wulff 2006a). Predatory–prey interactions in sponges have received considerable attention and may structure tropical and Antarctic communities (Pawlik 1998; McClintock *et al.* 2005), but not temperate ones (Wulff 2006a). This may suggest that, compared with other trophic interactions (*e.g.* herbivory), sponge predation is not a reliable source of community organization. Data on competition for space in sponges is far less abundant, yet competitive aspects mediated by multiple factors seem to alter community organization regardless of latitude (Dayton 1979; Turon *et al.* 1996; Thacker *et al.* 1998; Wulff 2005). Sponges also show many mutualistic relationships and the role of positive associations in structuring communities is receiving increasing attention (Cardinale *et al.* 2002; Bruno *et al.* 2003). There are unique opportunities with sponges to quantify the positive and negative interactions involved in space acquisition and maintenance, an area that warrants further research in marine benthic ecology.

Sponges are also well positioned for investigations of the ecology and evolution of host–symbiont interactions. Sponges contain complex microbial communities that we are just beginning to understand (Grozdanov & Hentschel 2007). For example, cyanobacterial populations in

sponges are restricted to 26 of the 72 demosponge families (Diaz & Ward 1999) and may confer both benefits and detriments on their hosts (Rützler 1988; Unson *et al.* 1994; Becerro *et al.* 2003; Erwin & Thacker 2005; Thacker 2005). Although benefits must surpass detriments for a putative symbiotic interaction to evolve, our understanding of the contribution of microbial symbionts to host ecology and evolution is in its infancy. Sponges are an invaluable system to study host–symbiont interactions and there is already progress in these directions (Taylor *et al.* 2007a).

Overall, sponge research successfully combines long-established lines of investigation with the implementation of modern techniques and will continue to make significant contributions to the advancement of science. This review shows that sponge ecology is an area that can grow to cover fundamental aspects of the science of ecology and highlights some areas where the specific characteristics of sponges make them particularly relevant. Moving forward into the broader ecological arena will focus more attention on sponges and bring them to the level of scientific prominence that their ecological diversity and abundance warrant and deserve.

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References

- Becerro M.A., Uriz M.J., Turon X. (1997) Chemically-mediated interactions in benthic organisms: the chemical ecology of *Crambe crambe* (Porifera, Poecilosclerida). *Hydrobiologia*, **355**, 77–89.
- Becerro M.A., Turon X., Uriz M.J., Templado J. (2003) Can a sponge feeder be a herbivore? *Tylodina perversa* (Gastropoda) feeding on *Aplysina aerophoba* (Demospongiae). *Biological Journal of the Linnean Society*, **78**, 429–438.

- Bergquist P. (1978) *Sponges*. University of California Press, Berkeley, CA.
- Blunt J.W., Copp B.R., Hu W.P., Munro M.H.G., Northcote P.T., Prinsep M.R. (2007) Marine Natural Products. *Natural Product Reports*, **24**, 31–86.
- Boury-Esnault N. (2006) Systematics and evolution of Demospongiae. *Canadian Journal of Zoology*, **84**, 205–224.
- Bruno J.F., Stachowicz J.J., Bertness M.D. (2003) Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution*, **18**, 119–125.
- Calderon I., Ortega N., Duran S., Becerro M., Pascual M., Turon X. (2007) Finding the relevant scale: clonality and genetic structure in a marine invertebrate (*Crambe crambe*, Porifera). *Molecular Ecology*, **16**, 1799–1810.
- Cardinale B.J., Palmer M.A., Collins S.L. (2002) Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature*, **415**, 426–429.
- Dayton P.K. (1979) Observations of growth, dispersal and population dynamics of some sponges in McMurdo Sound, Antarctica. In: Levi C., Boury-Esnault N. (Eds), *Biologie des spongiaires. Colloques Internationaux Centre National de la Recherche Scientifique* (France), **291**, 271–282.
- Diaz M.C., Rützler K. (2001) Sponges: an essential component of Caribbean coral reefs. *Bulletin of Marine Science*, **69**, 535–546.
- Diaz M.C., Ward B.B. (1997) Sponge-mediated nitrification in tropical benthic communities. *Marine Ecology Progress Series*, **156**, 97–107.
- Diaz M.C., Ward B.B. (1999) Perspectives on sponge-cyanobacterial symbioses. *Memoirs of the Queensland Museum*, **44**, 154.
- Duffy J.E. (1996) Eusociality in a coral-reef shrimp. *Nature*, **381**, 512–514.
- Duran S., Rützler K. (2006) Ecological speciation in a Caribbean marine sponge. *Molecular Phylogenetics and Evolution*, **40**, 292–297.
- Duran S., Giribet G., Turon X. (2004a) Phylogeographical history of the sponge *Crambe crambe* (Porifera, Poecilosclerida): range expansion and recent invasion of the Macaronesian islands from the Mediterranean Sea. *Molecular Ecology*, **13**, 109–122.
- Duran S., Pascual M., Estoup A., Turon X. (2004b) Strong population structure in the marine sponge *Crambe crambe* (Poecilosclerida) as revealed by microsatellite markers. *Molecular Ecology*, **13**, 511–522.
- Erwin P.M., Thacker R.W. (2005) Incidence and importance of photosynthetic symbionts in shallow-water sponge communities. *Integrative and Comparative Biology*, **45**, 992–992.
- Finks R.M. (1970) The evolution and ecological history of sponges during Paleozoic times. In: Fry W.G. (Ed.), *The Biology of the Porifera*. Academic Press, London: 3–22.
- Gaino E., Pronzato R., Corriero G., Buffa P. (1992) Mortality of commercial sponges: incidence in two Mediterranean areas. *Bollettino di Zoologia*, **59**, 79–85.
- Gammill E.R., Fenner D. (2005) *Disease threatens Caribbean sponges: report and identification guide*. Available at: <http://www.reefbase.org> (accessed on September 2007).
- Garfield E. (1964) “Science Citation Index” – a new dimension in indexing. *Science*, **144**, 649–654.
- Garfield E. (1970) Citation indexing for studying science. *Nature*, **227**, 669–671.
- de Goeij J.M., van Duyl F.C. (2007) Coral cavities are sinks of dissolved organic carbon (DOC). *Limnology and Oceanography*, **52**, 2608–2617.
- Grozdanov L., Hentschel U. (2007) An environmental genomics perspective on the diversity and function of marine sponge-associated microbiota. *Current Opinion in Microbiology*, **10**, 215–220.
- Hirsch J.E. (2005) An index to quantify an individual’s scientific research output. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 16569–16572.
- Jimenez E., Ribes M. (2007) Sponges as a source of dissolved inorganic nitrogen: nitrification mediated by temperate sponges. *Limnology and Oceanography*, **52**, 948–958.
- Leys S.P., Ereskovsky A.V. (2006) Embryogenesis and larval differentiation in sponges. *Canadian Journal of Zoology*, **84**, 262–287.
- Li C.W., Chen J.Y., Hua T.E. (1998) Precambrian sponges with cellular structures. *Science*, **279**, 879–882.
- Maldonado M. (2006) The ecology of the sponge larva. *Canadian Journal of Zoology*, **84**, 175–194.
- Maldonado M., Uriz M.J. (1999) Sexual propagation by sponge fragments. *Nature*, **398**, 476.
- Maldonado M., Carmona M.C., Velásquez Z., Puig M.A., Cruzado A., López A., Young C.M. (2005) Siliceous sponges as a Silicon sink: an overlooked aspect of benthic-pelagic coupling in the marine Silicon cycle. *Limnology and Oceanography*, **50**, 799–809.
- Manuel M. (2006) Phylogeny and evolution of calcareous sponges. *Canadian Journal of Zoology*, **84**, 225–241.
- Mariani S., Uriz M.J., Turon X., Alcoverro T. (2006) Dispersal strategies in sponge larvae: integrating the life history of larvae and the hydrologic component. *Oecologia*, **149**, 174–184.
- McClintock J.B., Amsler C.D., Baker B.J., van Soest R.W.M. (2005) Ecology of Antarctic marine sponges: an overview. *Integrative and Comparative Biology*, **45**, 359–368.
- Palumbi S.R. (1985) Spatial variation in an alga-sponge commensalism and the evolution of ecological interactions. *The American Naturalist*, **126**, 267–274.
- Paul V.J., Puglisi M.P. (2004) Chemical mediation of interactions among marine organisms. *Natural Product Reports*, **21**, 189–209.
- Paul V.J., Puglisi M.P., Ritson-Williams R. (2006) Marine chemical ecology. *Natural Product Reports*, **23**, 153–180.
- Pawlik J.R. (1998) Coral reef sponges: do predatory fishes affect their distribution? *Limnology and Oceanography*, **43**, 1396–1399.

- Pisera A. (2006) Palaeontology of sponges – a review. *Canadian Journal of Zoology*, **84**, 242–261.
- Pomponi S.A. (2006) Biology of the Porifera: cell culture. *Canadian Journal of Zoology*, **84**, 167–174.
- Reiswig H.M. (2006) Classification and phylogeny of Hexactinellida (Porifera). *Canadian Journal of Zoology*, **84**, 195–204.
- Rützler K. (1988) Mangrove sponge disease induced by cyanobacterial symbionts: failure of a primitive immune-system. *Diseases of Aquatic Organisms*, **5**, 143–149.
- Rützler K. (2004) Sponges on coral reefs: a community shaped by competitive cooperation. *Bollettino dei Musei e degli Istituti Biologici dell'Università di Genova*, **68**, 85–148.
- Saleuddin A.S.M., Fenton M.B. (2006) Biology of neglected groups: Porifera (sponges). *Canadian Journal of Zoology*, **84**(2), 143–356.
- Sarà M. (2004) Sponge peculiarities and their impact on general biology at the threshold of 2000. *Bollettino dei Musei e degli Istituti Biologici dell'Università di Genova*, **68**, 149–159.
- Sarà M., Vacelet J. (1973) Ecologie des démosponges. In: Grassé P.P. (Ed.), *Traité de Zoologie (Anatomie, Systematique, Biologie)*. Masson, Paris: 462–576.
- Schizas D., Stamou G. (2007) What ecosystems really are: physico-chemical or biological entities? *Ecological Modelling*, **200**, 178–182.
- Schutze J., Krasko A., Custodio M.R., Efremova S.M., Müller I.M., Müller W.E.G. (1999) Evolutionary relationships of Metazoa within the eukaryotes based on molecular data from Porifera. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **266**, 63–73.
- Smith R.L., Smith T.M. (2001) *Ecology and Field Biology*. Benjamin Cummings, San Francisco, CA.
- Sokal R.R., Rohlf F.J. (1995) *Biometry: The Principles and Practice of Statistics in Biological Research*. W.H. Freeman and Company, New York.
- Taylor M.W., Hill R.T., Piel J., Thacker R.W., Hentschel U. (2007a) Soaking it up: the complex lives of marine sponges and their microbial associates. *The ISME Journal*, **1**, 187–190.
- Taylor M.W., Radax R., Steger D., Wagner M. (2007b) Sponge-associated microorganisms: evolution, ecology and biotechnological potential. *Microbiology and Molecular Biology Reviews*, **71**, 295–347.
- Thacker R.W. (2005) Impacts of shading on sponge-Cyanobacteria symbioses: a comparison between host-specific and generalist associations. *Integrative and Comparative Biology*, **45**, 369–376.
- Thacker R.W., Becerro M.A., Lumbang W.A., Paul V.J. (1998) Allelopathic interactions between sponges on a tropical reef. *Ecology*, **79**, 1740–1750.
- Turon X., Becerro M.A., Uriz M.J., Llopis J. (1996) Small scale association measures in epibenthic communities as a clue for allelochemical interactions. *Oecologia*, **108**, 351–360.
- Unson M.D., Holland N.D., Faulkner D.J. (1994) A brominated secondary metabolite synthesized by the cyanobacterial symbiont of a marine sponge and accumulation of the crystalline metabolite in the sponge tissue. *Marine Biology*, **119**, 1–11.
- Uriz M.J. (2006) Mineral skeletogenesis in sponges. *Canadian Journal of Zoology*, **84**, 322–356.
- Uriz M.J., Turon X., Becerro M.A., Agell G. (2003) Siliceous spicules and skeleton frameworks in sponges: origin, diversity, ultrastructural patterns, and biological functions. *Microscopy Research and Technique*, **62**, 279–299.
- Webster N. (2007) Sponge disease: a global threat? *Environmental Microbiology*, **9**, 1363–1375.
- Wiens M., Müller W.E.G. (2006) Cell death in Porifera: molecular players in the game of apoptotic cell death in living fossils. *Canadian Journal of Zoology*, **84**, 307–321.
- Wulff J.L. (2005) Trade-offs in resistance to competitors and predators, and their effects of the diversity of tropical marine sponges. *Journal of Animal Ecology*, **74**, 313–321.
- Wulff J.L. (2006a) Ecological interactions of marine sponges. *Canadian Journal of Zoology*, **84**, 146–166.
- Wulff J.L. (2006b) Rapid diversity and abundance decline in a Caribbean coral reef sponge community. *Biological Conservation*, **127**, 167–176.