

No taxonomy needed: Sponge functional morphologies inform about environmental conditions

Christine Hanna Lydia Schönberg^{a,b,c,d}

^a Australian Institute of Marine Science, Indian Ocean Marine Research Centre, Crawley, WA 6009, Australia

^b College of Marine Science, National Sun Yat-sen University, Kaohsiung City 80424, Taiwan

^c Oceans Graduate School and UWA Oceans Institute, Indian Ocean Marine Research Centre, The University of Western Australia, Crawley, WA 6009, Australia

^d Marine Invertebrates, Aquatic Zoology, Western Australian Museum, Welshpool, WA 6106, Australia

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ABSTRACT

The need to study sponge communities in comparatively inaccessible habitats led to a sponge classification system that relies on the strictly functional interpretation of traditional sponge morphologies. The aim is to deliver a standardised approach that can optionally be based on imagery and can be applied across all oceans and to any water depth. The system is designed to recognise community-level changes across time and space. The functional context allows a basic interpretation of environmental conditions and may thereby inform on the reasons for observed differences in prevailing morphologies. In terms of growth form sponges appear to respond most strongly to the flow regime and to sediments. Strong turbulent flow will favour low-relief, morphologically simple sponges that are often structurally reinforced and well attached, such as crusts and simple-massive forms. Laminar flow selects for two-dimensionally erect, vertically flattened, usually flexible sponges that are aligned broadside to the current, inhalant openings (ostiae) pointing upstream, and exhalant openings downstream (oscula). Flow strength is generally inversely related to number of erect sponges, to body height (except in globular sponges), oscular diameter, branch number and branch complexity. Where flow conditions reduce or limit access to water exchange and nutrients, sponges tend to separate in- and exhalants in cup-like forms, reach into the water column as erect and even stalked forms, and in cases of extreme nutrient limitation the community will consist predominantly of carnivorous sponges. Globular and fistular sponges are usually abundant where the substrate is dominated by sediments, and where sediment deposition or movement is high. Fine sediments will often exclude sponges with much horizontal surface area. Based on these insights, the proposed scheme uses four basic morphologies: functional 1 – crusts, 2 – massives, 3 – cups and 4 – erect sponges. These are further divided into sponges that function as 1 – true crusts, endolithic-bioeroding, and creeping sponges, 2 – simple-massive, globular massive, composite-massive, and fistular sponges, 3 – cups, tubes, and barrels, and 4 – one-dimensionally, two-dimensionally and three-dimensionally erect forms, stalked, and carnivorous sponges.

1. Introduction

Marine environments in Western Australia (WA) and elsewhere are subjected to continuous and pronounced anthropogenic pressures. Global change incurs widespread bleaching and benthic mortality (Thomson et al., 2011; Abdo et al., 2012; Moore et al., 2012; Depczynski et al., 2013; Short et al., 2015; Lafratta et al., 2017; Le Nohaïc et al., 2017; Garrabou et al., 2019; Gilmour et al., 2019). Commercial fisheries cause significant damage by removing and killing more than the targeted species, with cascading consequences (e.g., Sainsbury et al., 1993; Moran and Stephenson, 2000). Moreover, infrastructure in WA is rapidly expanding into marine environments, by coastal development and urbanisation (e.g., Kullmann, 2014), in-

and offshore industries (e.g., Cambridge and McComb, 1984; May, 1992; Brocx and Semeniuk, 2017) and growing tourism (Hercov, 1999; Collins, 2008; Strickland-Munro et al., 2016). Many of these developments require coastal restructuring and associated environmental assessment. Traditionally, benthic monitoring assessed sediment, infauna, seagrass and macroalgae, coral and some motile macroinvertebrates or those with importance for fisheries and tourism, but if sponges were surveyed at all, they were commonly grouped without further resolution or listed under “others” (e.g., Bremner et al., 2003; Chabanet et al., 2005; Currie and Isaacs, 2005; Emslie et al., 2008; Edgar and Stuart-Smith, 2009). Therefore, our knowledge on sponges and other filter feeders is still rudimentary in this context (e.g., Fig. 4 in Costello et al., 2010; Tab. 1 in Schönberg and Fromont, 2012;

E-mail address: cschoenberg@mail.nsysu.edu.tw.

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Kirkendale et al., 2019). This situation is changing, however. Sponges are increasingly recognised and assessed as key benthic organisms with significant biological importance in many marine habitats, and for their ecological roles and bioindicator functions (e.g., Wulff, 2001; Przeslawski et al., 2008; Powell, 2011; Kenchington and Hutchings, 2012; Carroll et al., 2014; Althaus et al., 2015). This led to repeated recommendations for consistent inclusion of sponges in monitoring programs (Wulff, 2001; Bell et al., 2006, 2017; Bell, 2007a; Berman et al., 2013; Schönberg, 2015a). At this stage, however, widely contrasting reports on the status of sponge communities exist and further highlight the need for more generally applicable, large-scale surveys that include sponges (e.g., Gaino et al., 1992; Pérez et al., 2000; Wulff, 2006a, 2006b; Stevely et al., 2010; Wulff, 2013; Bell et al., 2018).

Mounting evidence attests to extraordinary and highly diverse sponge habitats around Australia's coasts (Hooper et al., 1999; Alvarez et al., 2002; Hooper et al., 2002; Hooper and Kennedy, 2002; Hooper and Ekins, 2004; Ward et al., 2006; Pitcher et al., 2007; Sorokin et al., 2007, 2008; Sutcliffe et al., 2010; Barnes et al., 2013; Przeslawski et al., 2013, 2014, 2015; Currie and Sorokin, 2014), and especially along WA's coasts (Fromont, 2004; Fromont et al., 2006, 2011, 2016; Fromont and Vanderklift, 2009; Heyward et al., 2010; Williams et al., 2010; Schönberg and Fromont, 2012; Fromont and Sampey, 2014; Schönberg et al., 2015). However, sponge species identification is often seen as being difficult (e.g., Knowlton, 2000; Schönberg and Beuck, 2007), and full taxonomic assessment lags behind the sampling effort (e.g., Pitcher et al., 2007; Hooper et al., 2013). Sponge taxonomy strongly relies on expensive physical samples for spicule and skeleton analysis, processes that commonly require a large time and salary investment and not always lead to reliable identifications (e.g., Ashok et al., 2018; Marlow et al., *in press*). Many of the above studies thus employed the use of operational taxonomy units (OTUs), when sponges were taxonomically *distinguished* within the frame of a given study, but not fully *identified*. This means that meaningful comparisons can be made *within* a given study, but not usually *between* studies (e.g., Schönberg and Fromont, 2012; Hooper et al., 2013).

At other times, only underwater imagery is available to analyze sponge communities. WA field conditions do not readily facilitate physical sampling, especially not with SCUBA divers in the water. The occurrence of large sharks (e.g., Gibbs and Warren, 2015; McAuley et al., 2016), crocodiles (e.g., Mawson, 2004; Caldicott et al., 2005) and dangerous sea jellies (e.g., Gershwin, 2005), extreme tidal currents in the north (e.g., Wilson et al., 2011; McInnes et al., 2016; Gruber et al., 2017), sites with high turbidity (e.g., Semeniuk, 1993; Lafratta et al., 2017) and hazards due to expanding industrial activity and ship traffic (e.g., Blakeway et al., 2013; Wilson et al., 2019) restrict diving opportunities that would enable representative tissue sampling for reliable sponge taxonomy. The use of autonomous or towed camera equipment is often preferred to capture still and video imagery at no risk for divers and as a means to survey larger areas in less time, thus potentially creating larger datasets (e.g., Barrett et al., 2010; Althaus et al., 2015). In consequence, surveys conducted with towed cameras became increasingly common, and requests for sponge identifications from underwater imagery developed into a persistent issue. However, due to a high level of morphological plasticity within many species (e.g., Hill, 1999; Duran and Rützler, 2006; López-Legentil et al., 2010; DeBiasse and Hellberg, 2015) and at the same time a large potential for similar habits and morphology in different species (e.g., Solé-Cava and Boury-Esnault, 1999; Schönberg, 2002a; Schönberg et al., 2005, 2006; Xavier et al., 2010; Leal et al., 2016; Mote et al., 2019), sponges can neither be reliably identified from images that lack finer detail, nor without experts with local knowledge and earlier reference samples. This is especially true in areas such as WA, where many sponge identifications are OTUs and where respective biologies remain largely unexplored. Further, until recently no guides or *in situ* reference images existed for live WA

sponges that were matched to skeletal characters and thereby linked to confirmed taxonomy at the species level.

However, even without taxonomy, imagery can still allow spatial and temporal comparison of sponge assemblages by recognising and describing patterns within a community or at a given point in time, i.e. via frequency of different sets of morphologies or growth forms before and after an impact or across environmental gradients. Sponge morphologies were previously mainly investigated for other reasons, predominantly in the context of taxonomy (e.g., van Soest, 1989; Chombard and Boury-Esnault, 1999) or with a mathematic or computational interest (e.g., Kaandorp, 1991; Kaandorp and de Kluijver, 1992; Becerro et al., 1994; Abraham, 2001; Kaandorp et al., 2008). Yet some studies used morphologies for community assessment (e.g., Lawler and Osborn, 2008), and some discussed form and function as a reflection of or response to environmental conditions (e.g., de Laubenfels, 1936; Wilkinson, 1988; Wilkinson and Cheshire, 1989; Schmahl, 1990; Aerts and van Soest, 1997; Aerts, 2000; Bell and Barnes, 2000a; 2000b; 2000c; Gerovasileiou et al., 2017; Bell et al., 2002b). Therefore, the strategy of characterising sponge communities through predominant morphologies is not new. Yet hitherto used approaches, terminologies and classification systems varied widely or were not clearly defined, thus preventing comparison across different studies (Suppl. 1). Most authors appear to uniformly use the terms “encrusting”, “repent” or “globular”, but beyond that the terminology is inconsistent and sometimes confused. Depending on the study, massive sponges may or may not include cups and branching morphologies, and sometimes they are part of the category “upright”. The term “lobate” has been widely implemented for massive and branching sponges alike but was never adequately defined and appears to refer to very different morphologies (e.g., Swearingen III and Pawlik, 1998; Barnes and Bell, 2002; Kefalas et al., 2003; Neves and Omena, 2003). A more uniform approach to sponge morphologies would be desirable, as well as a better understanding of the biological context that selects for certain growth forms. Bell (2007b) proposed implementing field surveys by investigating sponge biodiversity, as well as their growth forms with respect to function. However, the format of this particular proposal involved 39 different morphologies, a number that may be somewhat impractical for environmental assessment in general. Moreover, the functional roles to be assessed at this level of detail require prior knowledge about the sponges' biologies and may thus be unsuitable for use by a wide range of agencies. Despite some studies that evaluated the ecological potential of looking at sponge growth forms (e.g., Schönberg et al., 2005; Bell, 2007b; de Voogd and Cleary, 2007, 2009; Gerovasileiou et al., 2017), the science community has not yet widely employed the interpretation of sponge morphologies with the general aim of generating further information about prevailing habitat conditions. Yet sponges respond to their environments, and a predominance of certain growth forms can yield information about their functions and about environmental conditions that select for them (e.g., de Laubenfels, 1936; Bell and Barnes, 2000a; Schönberg and Fromont, 2012; Schönberg, 2016a). This insight has led to the proposal for a standardised classification scheme defining sponge growth forms explicitly in the context of ecological function, providing a tool to characterise sponge assemblages and a proxy for environmental conditions (Schönberg and Fromont, 2013, 2014; Althaus et al., 2014, 2015; Suppl. 2). To date, this concept has only been employed for surveys in Australia (e.g., Schönberg and Fromont, 2012; Carroll et al., 2014; Przeslawski et al., 2014; Althaus et al., 2015; Bewley et al., 2015; Abdul Wahab et al., 2017, 2018; James et al., 2017; George et al., 2018). These studies relied on earlier versions of the scheme that were later changed and adjusted, or the scheme was at times incorrectly used, misunderstanding some of the

concepts (see details in Suppl. 1). As the proper application of it and its underpinning have not before been explained in detail, the purpose of the present paper is to formally introduce the concept of sponge functional growth forms as a globally compatible tool in environmental assessment. The paper provides sufficient detail and examples for the scheme to be used in widely differing contexts.

2. Material and methods

The present concept or classification scheme of using functional sponge morphologies for benthic surveys grew over a number of years. Known sponge growth forms and related terminologies were reviewed using pertaining literature (e.g., Boury-Esnault and Rützler, 1997; and further references listed in Suppl. 1). Around 300 publications were screened, and relevant information was extracted and synthesised for patterns in sponge functional morphology and their bioindicator value (Suppl. 2). Originally the focus lay on marine demosponges and on imagery of shelf sponge communities between the intertidal and ca. 200 m water depth, mostly from sites around the northern half of Australia between Perth and Townsville. This focus was gradually expanded. New or revised definitions and terms were created for sponge morphologies that were not yet clearly described, and resulting concepts evaluated during fieldwork in WA and on the Great Barrier Reef. Emerging categories and functional interpretations were further developed during discussions with international colleagues familiar with sponges *in situ* in different oceans, but also with non-sponge experts as potential users and with people who have long-term experience with surveys conducted by underwater imagery.

Examples for sponge taxa fitting various morphologies were assembled. Formats and validities of any species name used in the publication and the [supplementary material](#) were checked in the World Porifera Database (van Soest et al., 2020) and itemised together with the most common growth form per species as Suppl. 3.

Various environmental or anthropogenic factors were considered that may have an impact on sponge morphologies and that may select for certain growth forms (for further details see Suppl. 2); they were here considered for horizontal substrates only for clearer pattern recognition and standardisation, but some of the listed factors also create community patterns on inclined, vertical or inverted substrates:

1. Hydrodynamics (flow structure and strength, mixing)
2. Sedimentation (turbidity, sediment deposition, abrasion)
3. Nutrients (gradients, anthropogenic eutrophication)
4. Physical damage (storms, human activity through fisheries or construction)
5. Substrate type (hard, sandy, muddy bottom)
6. Biological interaction (predation, competition, symbiosis)
7. Illumination (photosynthetic ability, UV damage; exposed/covered location)
8. pH (ocean acidification)
9. Temperature (climate, season, climate change, heat events)
10. Bathymetry (a product of pressure, hydrodynamics, illumination, sedimentation)
11. Salinity (gradients, freshwater influx)
12. Oxygenation (saturation state)

According to Petchey and Gaston (2006) and their thoughts on the methodologies in the assessment of functional diversity, the appropriateness, relative importance and prediction value of the above factors was evaluated after extracting relevant reports from the literature (Suppl. 2). Thereby, factors 1 and 2 were generally judged to exert the most influence on sponge growth forms, and that certain sponge morphologies appear to be indicative of environmental conditions governed by them. Factors 3–7 are also thought to be able to affect sponge morphology to some degree, but these are less well understood. It is not known whether and how the rest of the listed factors may select for predominant sponge growth forms

and to what extent they may covary with other factors, but whatever information became available was listed as part of Suppl. 2. Factor 1 was here regarded as one of the strongest drivers (e.g., Hiscock, 1983; Carballo et al., 1996; 2008; Barnes and Bell, 2002; Bell, 2007b) and was more closely considered by comparing possible effects of

- i. stagnant water *versus* high energy flow,
- ii. persistent *versus* acutely disruptive flow, and
- iii. laminar flow such as caused by tides or by seabed structures causing a channel effect *versus* chaotic and turbulent flow such as from crashing waves.

As a result, the development of the classification scheme was mostly based on factors 1 and 2 as the key drivers. And in addition, flow conditions were assessed in further detail. Related patterns apparent in the main sponge morphologies were summarised and specifically set in the context of their function within a given environment and in view of the ecology of sponges. Based on this, a range of “functional morphologies” were distinguished for sponges at different levels of resolution for scoring. These morphologies were again tested and adjusted as part of ongoing fieldwork in WA and on the Great Barrier Reef (e.g., Heyward et al., 2010; Schönberg and Fromont, 2012; at that time based on 6 different morphologies) and by consulting the literature (Suppl. 1–2). During a sponge classification workshop held by the University of Western Australia during the 2013 World Sponge Conference this pilot scheme was first made available to the public and tested by a range of potential users from different countries (Schönberg et al., 2016; the system then relied on 4 principal morphologies and 12 sub-categories). The workshop participants were asked to score a number of underwater images to assess whether the chosen morphologies sufficed to describe common sponge growth forms and whether different users with experience from different benthic habitats would reliably recognise the same forms. The scheme was then further edited, which resulted in 4 basic, overarching morphologies that can be scored to finer resolution as 14 or 21 categories to also include sponge classes beyond the Demospongiae and from other sites than Australia. Finally, definitions were created and used for recommendations for surveys and monitoring purposes, and CAAB numbers were allocated to different categories (Codes for Australian Aquatic Biota; <http://www.marine.csiro.au/data/caab/>). These numbers create consistency by making it possible to match the same groups across different resolution levels and over time in cases for which terminology was changed or the scheme was rearranged compared to earlier versions (e.g., in the CATAMI image classification scheme; <http://catami.github.io/>). The present classification scheme for sponges is now published so it can become more widely available and to be tried and fine-tuned at global scale, in marine and freshwater environments, across the entire bathymetric scale and in all climates.

3. Results and discussion

3.1. A sponge classification scheme by functional morphologies: Definitions in the ecological context

The present classification scheme is structured in several cascading levels of resolution to suit the needs of different users (Table 1). The coarsest differentiation employs 4 basic functional morphologies: functioning as crusts, as massive forms, as cups and as erect forms, each category being further subdivided (Figs. 1–3). Where the sponge morphologies are to be applied as a proxy for environmental conditions, they need to be strictly scored in the context of function, and their resolution should distinguish 14 different morphologies or more, as explained below (including the morphologies numbered at integer-level in Table 1). The maximum of distinguished morphologies was consciously kept to a manageable number at the finest resolution, and a total of 21 different forms is here explained. However, it is very unlikely that all categories occur at any given site at the same time, so the number

Table 1

The tabulated structure and hierarchy of the classification system based on sponge functional morphologies. There are four basic forms: functioning as encrusting, massive, cup-like and erect (in frames). These are subdivided into some further morpho-functions for finer scoring as indicated by numbering. When using the scheme in order to resolve for environmental conditions, it is recommended to assess sponge morphologies with a resolution of a minimum of 14 separate categories (categories in the first column, numbered by integers). As numbering, terms and group-allocations changed during the development of the system, allocated CAAB numbers (Codes for Australian Aquatic Biota) generate consistency when matching various assessments. CAAB numbers recently added for adjustments made with this publication are marked with an asterisk (and earlier versions can be compared to this one in Suppl. 1). The colour scheme in the PDF version of blue – red – green – yellow for the groups encrusting – massive – cup-like – erect and their subgroups is carried through the rest of the paper in the electronic version, but is not displayed in hardcopy. Example images for the different categories are provided in Figs. 1–3 and Suppl. 4–6.

1.-2. CRUST-LIKE in function CAAB 10 000901		
1. Encrusting <i>sensu lato</i> *CAAB 10 000922	1.1. True crusts, crusts <i>sensu stricto</i> CAAB 10 000902	1.1.1. Thin crusts *CAAB 10 000923 1.1.2. Thick crusts *CAAB 10 000924
	1.2. Endolithic-bioeroding CAAB 10 000921 (= “alpha” and “beta” bioeroders)	
2. Creeping, repent CAAB 10 000917		
3.-6. MASSIVE in function CAAB 10 000903		
3. Simple-massive CAAB 10 000904		
4. Globular-massive, balls CAAB 10 000905		
5. Composite-massive, meshes and dense clusters * CAAB 10 000925		
6. Fistular, cryptic-massive, endosammitic CAAB 10 000908 (incl. “delta” bioeroders)		
7.-9. CUP-LIKE in function CAAB 10 000909		
7. Cups CAAB 10 000910	7.1. Tabular “cups” CAAB 10 000920 7.2. Incomplete “cups”, curled fans CAAB 10 000918 7.3. Complete, apically wide cups, vases CAAB 10 000919	
8. Tube-like forms, “narrow cups” *CAAB 10 000926	8.1. Chimneys, proper tubes CAAB 10 000911 8.2. Amphoras, sack-like sponges, bladders *CAAB 10 000927	
9. Barrels, “massive cups” CAAB 10 000907 (incl. some “gamma” bioeroders)		
10.-14. ERECT in function CAAB 10 000912		
10. One-dimensionally erect, simple erect CAAB 10 000916		
11. Two-dimensionally erect *CAAB 10 000928	11.1 Erect-laminar, flabellate CAAB 10 000913 11.2 Erect-palmate CAAB 10 000914 11.3 Erect-reticulate *CAAB 10 000929	
12. Three-dimensionally erect, branching CAAB 10 000915		
13. Stalked CAAB 10 000906		
14. Carnivorous *CAAB 10 000930		

handled during fieldwork will usually remain well below 20. Of course, there are intermediate morphologies and functions, and the environmental context should rigorously be applied as the predominant factor to decide the scoring result. As an aid to facilitate such decisions, a basic layman’s key was added in form of a flow chart for scoring (Table 2), but further details are explained below.

3.1.1. Sponges functioning as crusts (CAAB 10 000901; Fig. 1A)

Definition: Sponges that function as a crust *sensu lato* combine encrusting sponges in the wider sense with creeping sponges. They have a very low profile and extend in a layer parallel to the substrate. Their area is significantly larger than their height, and they have a paucity of three-dimensional or vertical structure in comparison to horizontally extending tissue. In- and exhalant openings are on the same plane, as the body shape does not allow distinct separation of them, but they may be arranged in different groups, e.g. in rows or in patchily distributed clusters. More example images are figured in Suppl. 4–5.

Functional context: Sponges functioning as crusts have the lowest profile of all listed forms and do not experience much drag by flow (Denny et al., 1985). They are anchored across a proportionally very large area due to their shape, which makes them very resistant to damaging water movement (Bell and Barnes, 2000a; Wulff, 2006a; Gochfeld et al., 2020). The more damaging the local flow regime is, the less three-dimensional structure and the more flattening can be seen in sponges (de Laubenfels, 1936; Bell and Barnes, 2000a; except in balls, see Suppl. 2). Fully attached encrusting sponges will thus be best equipped to persist in environments frequently exposed to unpredictable and/or high-energy hydrodynamic conditions such as at exposed coasts where waves break, and they will be more likely to survive storm events, experiencing less damage than other morphologies (Bell and Barnes, 2000a; Wulff, 2006a). However, when occurring on horizontal surfaces, the shape of encrusting sponges creates a high risk of being smothered by sediment deposition, i.e. they could quickly become entirely covered by sediment. Many crusts do not normally tolerate fine sediments unless

they have particle-repellent mechanisms (Lawler and Osborn, 2008; Schönberg, 2016b) or can actively clean their surfaces (e.g. Könnecker, 1973). Alternatively, sponges functioning as crusts can find refuge on vertical or inverted surfaces (e.g., Bell and Barnes, 2000a; 2000b; 2000c). When occurring on e.g. vertical substrate, however, their presence will no longer inform on sediment pressures and can only be used as proxy for the flow regime. Overall, predominance of crusts generally implies strong, mostly turbulent, potentially damaging flow that resuspends and removes sediments from their surfaces. Due to their favourable filtration : surface ratio (Bibiloni et al., 1989) they can also exist in flow-reduced, nutrient-poor habitats if sedimentation is low, but

encrusting sponges appear to be more common in exposed coastal settings, and most occur to roughly –200 m water depth (de Laubenfels, 1936; Maldonado and Young, 1996; Mendola et al., 2008; Schönberg and Fromont, 2012). Where they are reported to occur deeper than –200 m, they are usually found on inclined, vertical or inverted surfaces where they do not experience sedimentation (e.g. see Fig. 8 and Video 5 in Santín et al., 2018).

Subgroups: Category 1 – Encrusting sponges in the wider sense, *sensu lato* (CAAB 10 00922) divide into the categories 1.1 – true crusts, i.e. encrusting sponges *sensu stricto* (CAAB 10 000902) and 1.2 – endolithic, bioeroding sponges (CAAB 10 000921). The true crusts are

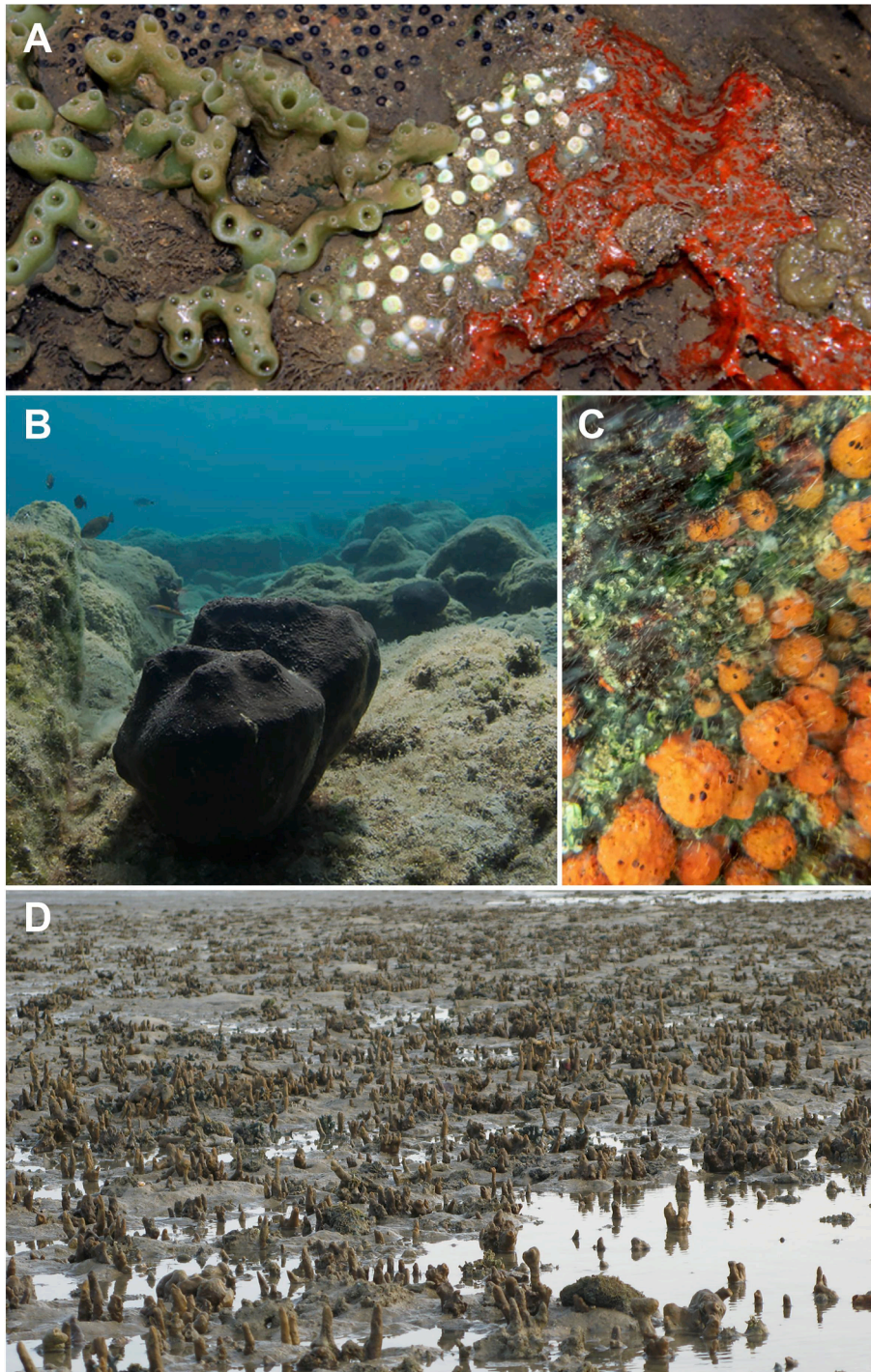


Fig. 1. Examples of sponge functional morphologies in environments that select for certain growth forms – communities functioning as encrusting or massive. A – Creeping (left, green) and encrusting (right, red) sponges often occur in areas with turbulent flow, in this case in the Mumbai intertidal, likely due to waves in shallow water. Creative commons photograph by Pradip Patade (2019). B – Simple-massive sponges such as these eastern Mediterranean *Spongia (Spongia) officinalis* can occur in a wide range of conditions that do not tend to the extreme, but due to the mixed in- and exhalant openings sufficient flow is needed to wash away the exhaled water. Photograph by Thanos Dailianis©, with friendly permission. C – Ball-shaped sponges such as *Tethya* spp. can occur in clear and turbid waters, usually in strong flow conditions, here in the exposed intertidal of southern New South Wales. Photograph by Paul Whittington© (2019), with friendly permission. D – Fistular sponges such as the pictured *Spheciospongia* cf. *inconstans* at Singapore often live endopsammic, i.e. mostly buried in sediment. Fistular sponges are usually indicative of moving sediment and high sediment deposition rates. Photograph by Swee-Cheng Lim©, with friendly permission. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

thin crusts (CAAB 10 000923; Fig. 1A) and thick crusts (CAAB 10 000924). Thin crusts have a tissue thickness of very few mm and best represent the traditional understanding of encrusting sponges. They display the best-defined functional traits and are the most reliable proxies for high-energy environmental flow conditions. They are those that usually predominate at sites with strong, damaging, unpredictable hydrodynamic conditions that exclude more delicate or vulnerable morphologies (Schmahl, 1990; Bell and Barnes, 2000a). Thick crusts or low cushions of few mm to around 1 cm in thickness have similar properties with regards to flow as thin crusts, but their often slightly more convex form or slightly raised papillae render them a little less vulnerable to sedimentation. The definition how thick a crust should be to fall into either thin or thick crusts varies between publications (e. g., in Bell and Barnes, 2003 thick crusts are > 2 mm thick) and may require quantitative research for a better characterisation of the categories. There may be a trade-off between flow-resistance and growth rate, as some thickly encrusting sponges have been found to grow faster than thinly encrusting sponges (Ayling, 1983). Examples for thin crusts are e.g.: Timeidae, *Plakortis simplex*, *Spirastrella* spp., *Terpios* spp., *Merlia* spp., *Halicnemis patera*, *Hymedesia (Stylopus) coriacea*, *Clathria (Microciona) aceratoobtusata*. Examples for thick crusts are e.g.: *Spirastrella* spp., *Placospongia* spp., *Acanthoclada prostrata*, *Phorbas fictitius*, *Crambe crambe* (see also Suppl. 5.1). Please note that some of the species listed as examples may sometimes belong to more than one morpho-functional category and may display a range of morphologies depending on conditions.

Due to their sheltered position and good attachments, insinuating sponges that grow into existing cracks (e.g. *Mycale laevis*), grooves and depressions should probably be counted into the encrusting sponges like the endolithic bioeroders, but at times they can be functionally closer to creeping forms (e.g. some small *Haliclona* spp.) and decisions should be made on case-to-case basis. When using sponge growth forms as environmental proxies, the functional context needs to be strictly more important for scoring than their mere shape. If crusts develop erect structures such as in *Polymastia* or *Ciocalypa* spp. and become partially buried in sediment, they rather function as fistular than as encrusting sponges. Thin crusts can occasionally adopt the function of thick crusts or even massive sponges if they grow over rounded stones or rocks that give them an overall convex shape, in which case they should be scored according to this functional context, not as thin crust. Crusts growing around erect or massive structures are counted according to the shape they then inherit: e.g. as simple-erect if they coat a whip-like gorgonian, as stalked or erect-branching if they coat a stalked or tree-like structure, and as simple-massive when coating most of a rock – these crusts are no longer restricted to the boundary layer environment and stop functioning like crusts in terms of flow conditions (Fig. 4A-C). Conveniently, this approach facilitates standardisation when scoring sponges from imagery without taxonomic knowledge – the visual impression will deliver the right answer.

Category 1.2 – Papillate (“alpha”) or sheet-like (“beta”) endolithic, bioeroding sponges (CAAB 10 000921) are a special category within the crusts. Within the substrate they erode, some species can be relatively three-dimensional, but where they are exposed to the environment, they experience conditions like a crust. They can usually withstand the same extreme flow regimes as thin crusts and appear to be resilient to storm damage, grow faster and are often more common and more diverse at sites with good hydrodynamic mixing (Schönberg, 2001; Schönberg and Burgess, 2013; Schönberg unpubl. data). However, they cannot colonise just any kind of hard substrate and depend on calcium carbonate or organic substrate with a high content of calcium carbonate (Schönberg, 2002b, 2008). In this way they are bio-indicators for the presence of calcium carbonate materials. Their upper surfaces bear both, in- and exhalant openings in close proximity, although these can occasionally form groups, fields or lines. Papillate sponges that inhabit flat, horizontal pieces of substrate can at times separate inhalants (bottom surface) from exhalants (upper surface;

Schönberg pers. obs. for a *Cliona celata* complex sponge from the central Great Barrier Reef), but this is uncommon. Tolerance of being covered by a sediment layer varies with species and sediment properties, with finer sediments being more damaging (Siebler et al., 2013; Schönberg pers. obs.). However, due to erect spicules embedded in their ectosome all clionaid species have a velvety surface that appears to be particle-repellent so that they are tolerant to sedimentation (Schönberg, 2015b). Like true crusts, endolithic sponges may sometimes be scored in a different functional context, e.g. if they inhabit the entire skeleton of a massive coral they should be scored as simple-massive (Fig. 4C), if they fully penetrate a branching coral, they become erect-branching. They may often simply be mistaken as true crusts, which will not change their functional context or the scoring result for environmental conditions. Widely distributed examples are: *Cliona* spp., *Pione* spp., *Cliothesa* spp. and tetractinellid bioeroders (see also Suppl. 5.1).

Category 2 – Creeping or repent sponges (CAAB 10 000917; Fig. 1A) hug the substrate, but they form a horizontal branching or meandering network or patchy crusts that are often weakly attached. Therefore, they commonly function as hybrids at the crust-branching interface and can develop erect portions. Like other crusts, creeping sponges can quickly be smothered if sediments were to build up around them, but by developing erect parts they can escape the suffocating layer. Depending on the size and the frequency of the erect parts and the degree of burial, creeping sponges may alternatively be scored as erect-branching or fistular. However, creeping sponges still have a much larger attachment area than erect-branching ones and may not commonly be endosammitic like fistular ones. The adaptation of creeping sponges to survive in unpredictable, high-energy hydrodynamic conditions appears to rely less on firm attachment or direction of growth and more strongly on either being more elastic due to high spongin content or due their fast growth rates and their high capacity to fragment, heal, re-attach and regenerate. These are functions commonly found in “ropy” or creeping sponges (Wulff, 1990, 2006a). Creeping sponges are not usually as dependent on firm, hard substrate as other encrusting sponges, as some can extend over rubble or even sediments, which they bind (e.g. Carter, 1882 for *Callyspongia (Cladochalina) tenerrima*, *Mycale (Mycale) laevis* and *Spongia (Spongia) officinalis* (Fig. 1B, 5A–D); Biggs, 2013 for *Niphates erecta* and *Aplysina* spp.). They are overall more variable in their ecological requirements, functions and forms than many of the other listed morphologies. As a consequence, they can occur in diverse and less predictable environments and can adjust to different prevailing conditions, such as different substrate types. Further examples of creeping sponges are e.g.: *Agelas conifera*, *Callyspongia (Callyspongia) fallax*, *Clathria (Thalysias) virgultosa* (Fig. 7D), *Haliclona (Gellius) cymaeformis*, *Hyrtios erectus*, *Pseudoceratina purpurea*, *Petrosia (Petrosia) ficiformis*, *Petrosia (Strongylophora) strongylata* (see also Suppl. 5.2).

3.1.2. Sponges functioning as massive forms (CAAB 10 000903; Fig. 1B-C)

Definition: Compact massive sponges are very roughly as wide as high. Sponges functioning as massive very often, but not always, have most of their body mass as one coherent piece of tissue. However, they can also be amorphous and irregular in shape or can be composed of merged subunits that overall form a common mass. Most massive sponges do not distinctly separate in- and exhalants on different surfaces. Therefore, barrels are here excluded from the category “massive”: While their body shape and mass suggest they belong to the “massives”, one of their most important functions manifests in separated in- and exhalant surfaces and more strongly relates to the cup-like sponges (Fig. 5F-G). Further examples are displayed in Suppl. 4–5.

Functional context: As an entire group, functionally massive sponges are not as good bioindicators as are other morphologies, and they commonly occur across a relatively wide range of environmental conditions. Jackson (1979) confirmed this impression through calculations using approximated parameters: The massive “growth form represents a series of adaptive compromises for almost all shape parameters

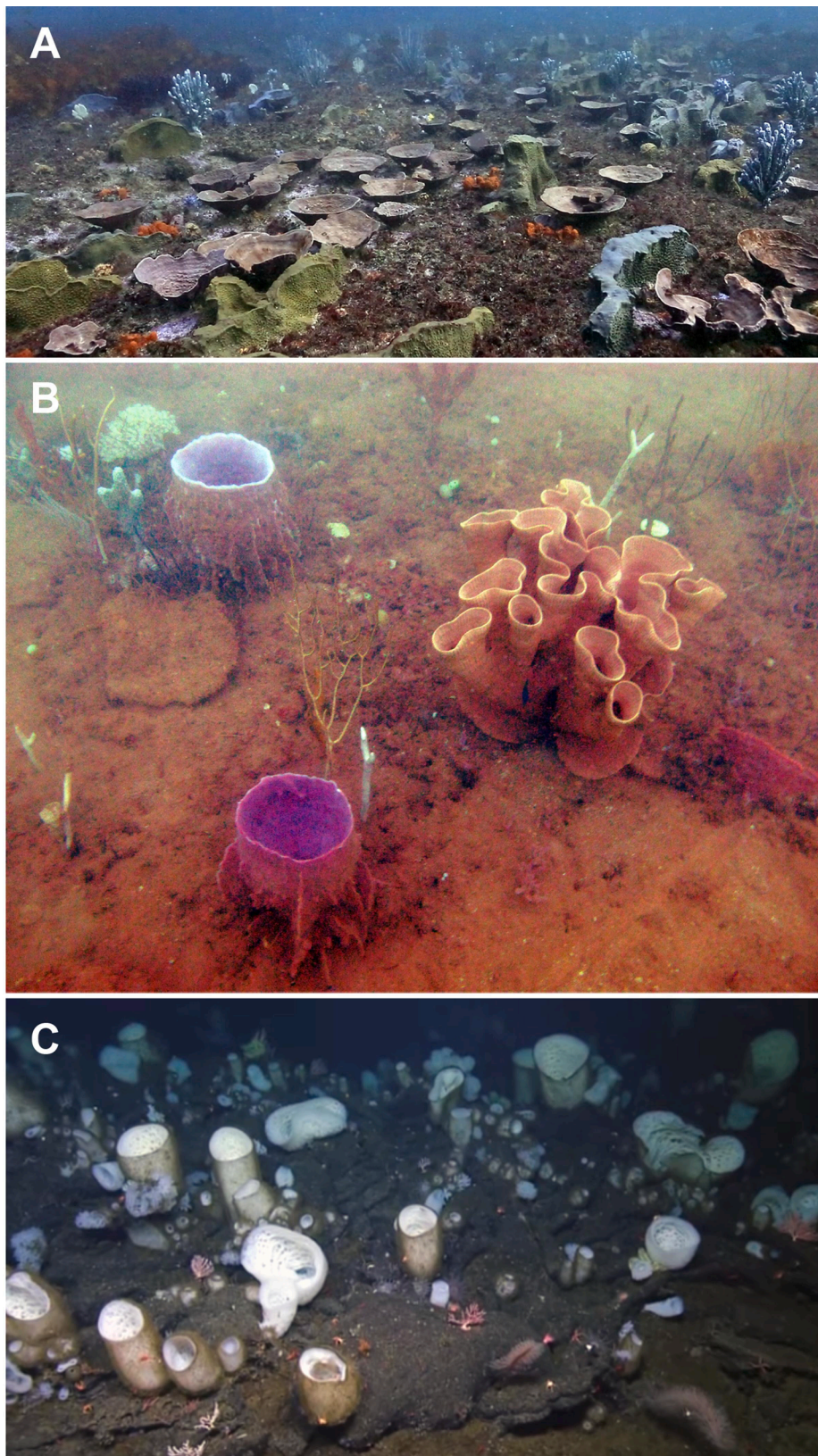


Fig. 2. Examples of sponge functional morphologies in environments that select for certain growth forms – cup-like communities. A – A sponge community that is strongly dominated by wide cups mingling with erect sponges at Bare Island (Sydney, E Australia) in –22 to –24 m suggests reduced sedimentation pressure and benign flow conditions. Image extracted from video by Thierry Rakotoarivelo© (2019), with friendly permission. B – *Xestospongia testudinaria* barrels with separate in- and exhalant areas were conspicuous in a filter feeder community in –11 m in the Pilbara (NW Australia) that was characterized by fine sediments and high turbidity and sedimentation rates. *Ianthella basta* on the right was curled into tubes and chimneys. C – A glass sponge community in –860 m at Socorro Island at the Revillagigedo Archipelago (Mexican E Pacific). The dominant sack-like morphology suggests reduced flow conditions. Screenshot from video by Ocean Exploration Trust© (2017), with friendly permission from Nautilus Live, Ocean Exploration Trust.

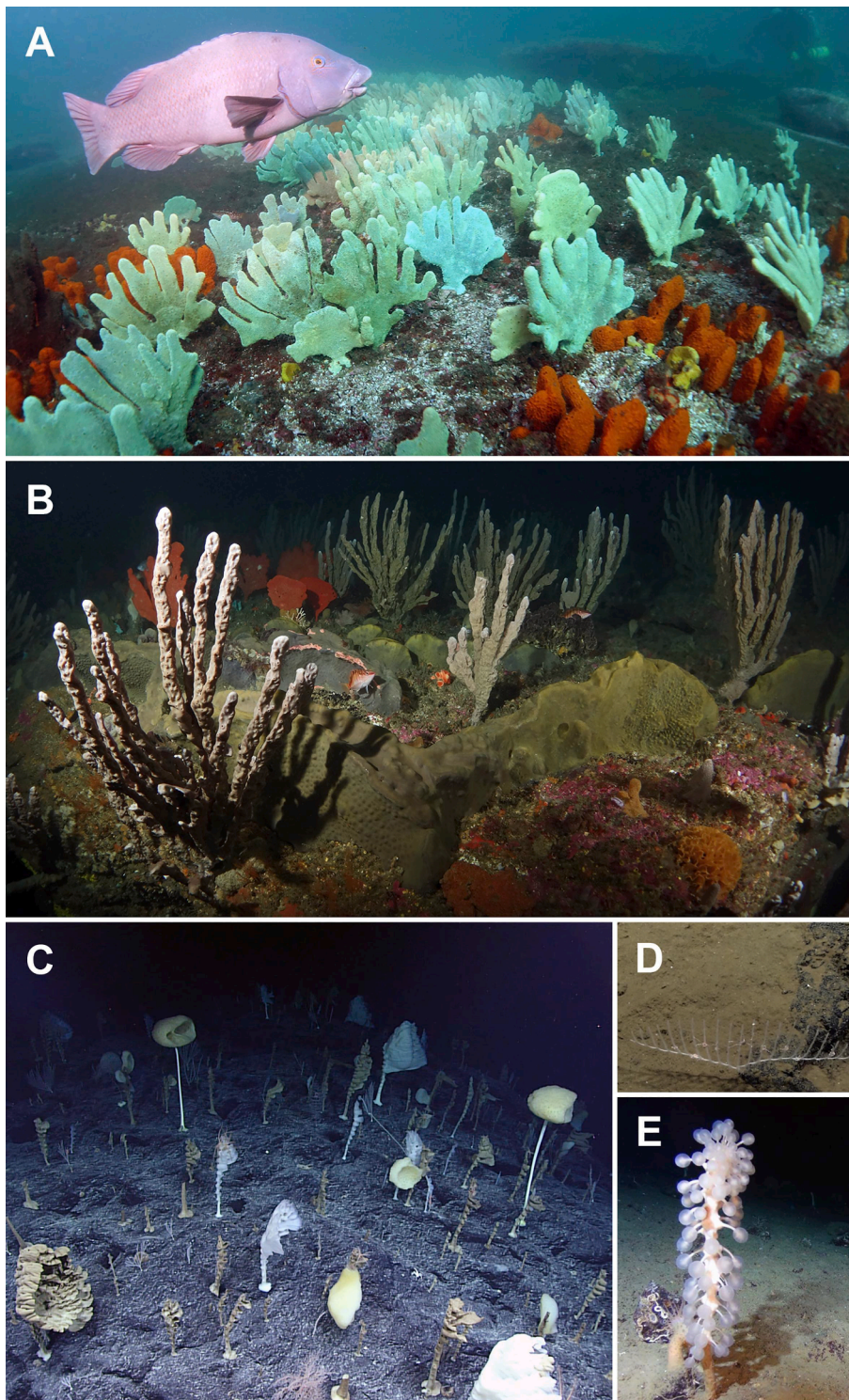


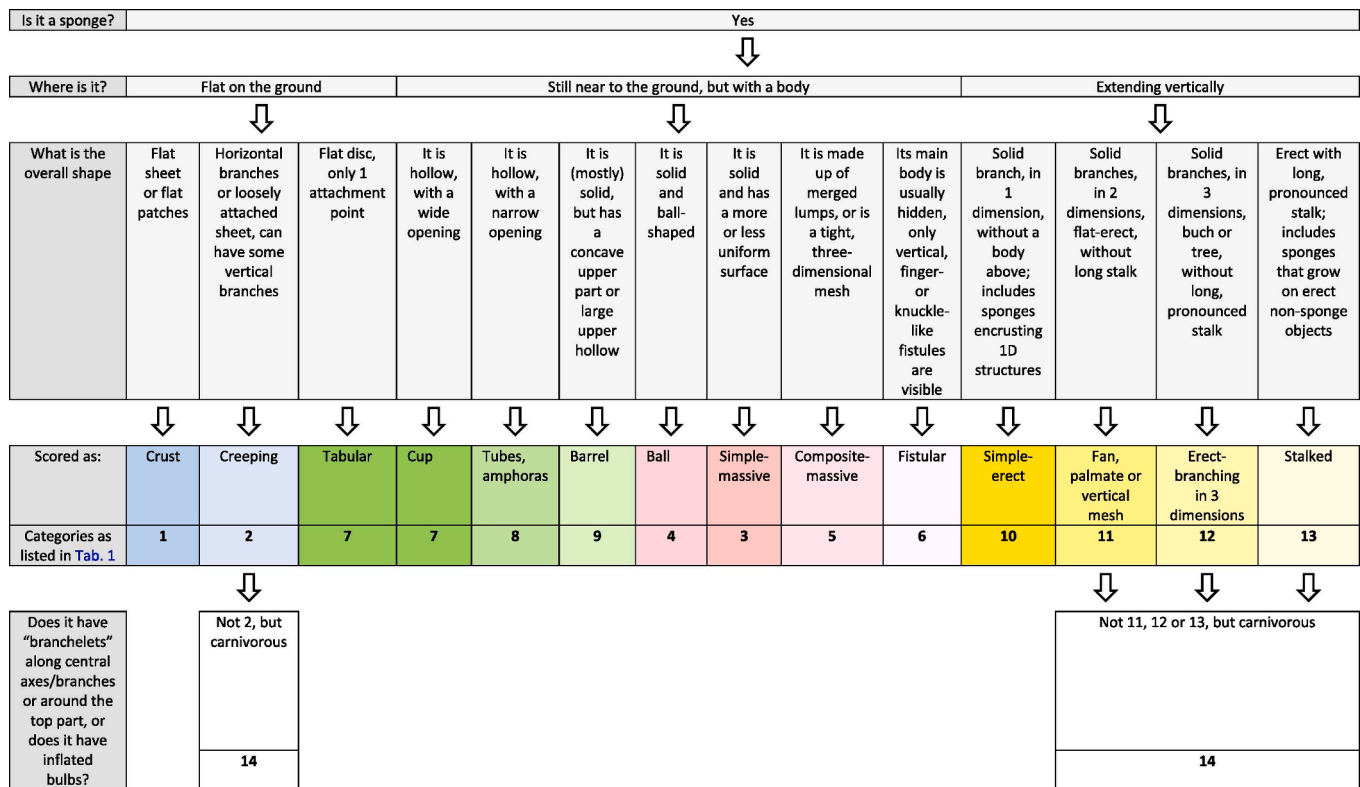
Fig. 3. Examples of sponge functional morphologies in environments that select for certain growth forms – communities with erect sponges. A – Palmate, two-dimensionally erect sponge community at Bare Island, Sydney, E Australia, that imply predominantly laminar flow in the right-left direction of the photograph. B – Mostly three-dimensionally erect-branching sponges in Sydney Harbour suggest reduced flow conditions. The prevailing currents may be mostly laminar, as two-dimensional sponges appear scattered in between. Creative commons photographs A and B by [John Turnbull \(2014\)](#), with friendly permission. C – Delicately stalked glass sponges at Ridge Seamount of Johnston Atoll in ~2360 m, with their convex sides pointing into the main current, presumably a current with low flow speeds. In this depth currents are usually strongly reduced, and sponges have to reach far into the water column. Screenshot of a video by [NOAA Office of Exploration and Research \(2017\)](#), creative commons. D – The carnivorous harp sponge *Chondrocladia* (*Symmetrocladia*) *lyra*, Hadal Wall at the Mariana Trench. Screenshot of a video by [NOAA Office of Exploration and Research \(2016\)](#), creative commons. E – The carnivorous ping-pong tree sponge *Chondrocladia* (*Chondrocladia*) *grandis* off Baffin Island, Canada. [NOAA Office of Exploration and Research \(2015\)](#), creative commons. Presumably, both sponges occurred in areas with little access to food suitable for filter feeding, thus specialising in carnivory.

considered.” He reasoned that massive and encrusting forms together will likely only dominate if food and other staple resources are in abundant supply and disturbance levels are low, so that sessile organisms of a more simple form can outcompete more erect forms. However, it may in fact be the other way around, i.e. that erect forms persevere under more restricted conditions, but more observations are needed. Different species will prefer different flow conditions, and most massives would require enough flow to quickly remove their wastewater as they either do not bundle their exhalant stream, or do not do this very well (e.g. *Rhopaloeides odorabile* was more abundant at high-flow sites on the Great Barrier Reef; [Bannister](#)

[et al., 2007](#)). Most massive sponges are not overly fragile, and some robust sponges can withstand turbulent flow without damage (e.g., [Bell and Barnes, 2000a](#)). Yet their structure can fail in strong currents, and they can be fragmented or detached during storm surges, depending on their shape and attachment area, and breaking waves select against them. Massive sponges have significant area in form of upper surfaces that will collect some sediment, but usually they grow up from the bottom far enough to avoid smothering and have a significant amount of vertical or sloped surface that will remain sediment-free, or have erect fistules that can reach through layers of sediment. Massive sponges appear to have commonly a

Table 2

Decision flow chart or layman key for scoring the 14 sponge functional morphologies that can be used as a proxy for environmental conditions. The scoring context needs to be strictly functional.



bimodal bathymetric distribution, with a shallower, upper-shelf group and a deeper group that reaches beyond the shelf edge (Maldonado and Young, 1996; Schönberg and Fromont, 2012), an observation that presently remains unexplained and may need to be better matched with morphologic traits.

Subgroups: Category 3 – Simple-massive sponges (CAAB 10 000904; Fig. 1B) are best suited to mid-range environmental conditions. They are not well adapted to survival in stagnant water, because their in- and exhalants are not as clearly separated as e.g. in barrels (Fig. 5). This simultaneously means that the oscules are usually scattered, which makes their exhalant stream weaker than in sponges with oscular grouping (Fry, 1979). Without sufficient flow, they would risk to re-inhale their own wastewater (Bidder, 1923; Fry, 1979), however, some sponges can apparently choose which particular oscules to use depending on existing currents (Patterson et al., 1997). Moreover, depending on the ambient flow, simple-massive sponges can have more spread-out or more apically grouped exhalants (Fig. 5A-D). Violent hydrodynamic conditions can dislodge massive sponges (Wulff, 1999, 2006a), especially if they have a low spongin content. Once unattached their survival potential is low, unless larger fragments are stabilised (Wilkinson and Thompson, 1997; Bell and Barnes, 2001a; Wulff, 2006a). Simple-massive sponges are usually bulky enough not to be entirely smothered at sites with high sedimentation rates, but their upper surfaces can become sediment-covered and may develop anoxic parts or pockets that collect so much sediment that it becomes embedded in the sponge (Schönberg, 2016a; Hoffmann et al., 2004 Schläppy, pers. comm.). They do not usually tolerate soft sediments (Lawler and Osborn, 2008) and can be comparatively vulnerable to diseases (Wulff, 2006b; Abdo et al., 2008). In general, simple-massive sponges will do best in low-sedimentation, coarse-sediment environments with rocky outcrops

for settlement, and with moderate to strong, predictable flow (e.g., Carballo et al., 1996). Examples are e.g.: *Asteropus niger* (Fig. 7E), *Petrosia* (*Petrosia*) *ficiformis*, *Fascaplysinopsis reticulata*, *Hyrtios cavernosus* (Fig. 7B), *Rhopaloeides odorabile*, *Spongia* (*Spongia*) *officinalis* (Fig. 1B, 5A-D; see also Suppl. 5.2).

Category 4 – Balls or globular sponges (CAAB 10 000905; Fig. 1C) occur in a large variety of conditions, some of which would be harmful to other sponge morphologies. For example, spirophorine balls are common at high energy sites with turbulent flow, are drag-resistant or nestle in concave parts of the substrate that reduce hydrodynamic pressures, and some have a high potential for regeneration after physical damage (Schmahl, 1990; Denny, 1994; Barnes, 1999; Siebler et al., 2013 – but Wulff, pers.comm.: balls commonly regenerate slower than other morphologies). Some astrophorine balls have been found under reduced flow conditions, however (Cleary and de Voogd, 2007). Unlike the other growth forms, balls become smaller and flatter in low flow and are larger at exposed sites (McDonald et al., 2002; Meroz-Fine et al., 2005; Lawler and Osborn, 2008). Especially tetractinellid balls are known for their resistance to sedimentation, and many species maintain an external crust of sediments and algae or agglutinate coarse materials that adhere to their surfaces (Schönberg, 2016a). Unlike many other sponges, many balls can tolerate fine sediments, high sedimentation rates, turbid water and even week-long burial in sediment (Rice, 1984 for *Cinachyrella apion*; Bell and Barnes, 2000b for *Tethya aurantium*; van Soest and Rützler, 2002 for the Tetillidae; de Voogd and Cleary, 2007). Yet some ball-shaped sponges have also been reported to prefer or to require clear water (e.g., Carballo et al., 1996 for *Tethya aurantium*). Like barrels, some globular sponges spatially separate incurrent ostiae from excurrent oscula, with the inhalants on their lateral surfaces and the exhalants downstream or apically concentrated. However, as balls with mixed, as

well as with separated openings both occur in clear and turbid waters, and at high-energy and flow-reduced sites, their most important functions seem to be related to their drag-reducing shape and mode of attachment, rather than to their feeding and gas-exchange strategies. As presently no clear patterns can be reported, future observations may help fine-tune the functional niches of this category or possible subgroups. Nevertheless, based on what we presently know about the functional ecology of globular sponges, they should probably best be scored as a single group, and no attempt should be made to distinguish them into simple-massive and barrel-like sponges according to the distribution of their ex- and inhalants until we better understand their environmental requirements. Typical balls are relatively small sponges that are situated close to the substrate and the boundary layer. Their function will change if they grow on erect structures and are situated much higher in the water column. In that case they may be scored as functioning like stalked sponges (Fig. 4D). Examples for balls are e.g.: *Tethya* spp. (Fig. 1C), globular astrophorine sponges such as *Stelletta clavosa*, spirophorines such as *Cinachyra* spp., *Cinachyrella* spp. (Fig. 7H), but also small-bodied, globular sponges such as some *Suberites* spp. (see also Suppl. 5.2).

Category 5 – Composite-massive sponges (CAAB 10 000927) are those that by their overall shape resemble and behave like a massive sponge under the prevailing conditions, but they are really mounds of mesh-like, reticulate or clathrate sponges such as *Clathria* spp. or composed of closely merged subunits such as tightly clustered branches or densely joined thick fans that are arranged in three dimensions (Fig. 4E). Overall, they largely function like simple-massive sponges in that they do not usually have a clear separation of in- and exhalants, but clathrate sponges are more delicate and more vulnerable in strong currents, and due to an increased surface rugosity clustered sponges would likely accumulate more sediment than simple-massive sponges. They also have an increased surface area compared to simple-massive sponges, which may enhance their feeding efficiency. Examples are e.g.: *Acanthella pulcherrima*, *Agelas dispar*, *Dragmacidon reticulatum*, *Ircinia felix*, *Stylissa massa*.

Category 6 – Fistular sponges (CAAB 10 00908; Fig. 1D – called cryptic-massive in earlier versions), mostly the so-called endopsammic sponges, are sediment specialists with high bioindicator value (e.g., de Laubenfels, 1936; Rützler, 1997; Cerrano et al., 2002; Schönberg, 2016a, and references therein). They are well suited to environments with high sedimentation rates and moving sediments and are adapted to being covered by or being partly or almost entirely buried in sediment. Many are also tolerant to intertidal environments where the sponges' upper parts may become exposed to air (e.g., Schönberg, 2000; 2001 for *Siphonodictyon mucosum*; Vinod et al., 2009 for *Spheciospongia inconstans*; see also Fig. 1D; Lim et al., 2008; Schönberg and Lim, 2019 for *Spheciospongia* spp. and *Coelocarteria singaporensis*). In most cases their main body can best be described as massive, sometimes as encrusting to cushion-shaped, but for their ecological function it is more important that they have raised, elevated or erect, knuckle, wart- or finger-like parts or pronounced fistules on their upper surface, or sometimes strongly collared, extended oscules that reduce the risk of sediment entering the aquiferous system. Exhalant fistules are hollow or contain large canals. If inhalants are vertically extended, they can be more compact and may be terminally closed and appear solid in cross section, with much more narrow canals. Fistular sponges usually have basal or endolithic root-like tissue extensions (e.g., Schönberg and Tapanila, 2006; Schönberg, 2016a, and references therein), and other anchoring adaptations on their lower half that include incorporation of fragments and sediment, attachment to or inhabiting buried pieces of rock (summary in Schönberg, 2016a). The convex or erect parts of fistular sponges provide the same function as for other erect sponges, as they avoid a build-up sediment on their surfaces and prevent occlusion and smothering of important parts of the sponges' aquiferous system. These sponges can further develop a polar morphology to separate in- and exhalants so that either mostly occur on the elevated parts or on the main part of the sponge body (e.g., Fry and Fry, 1979; Rützler, 1997;

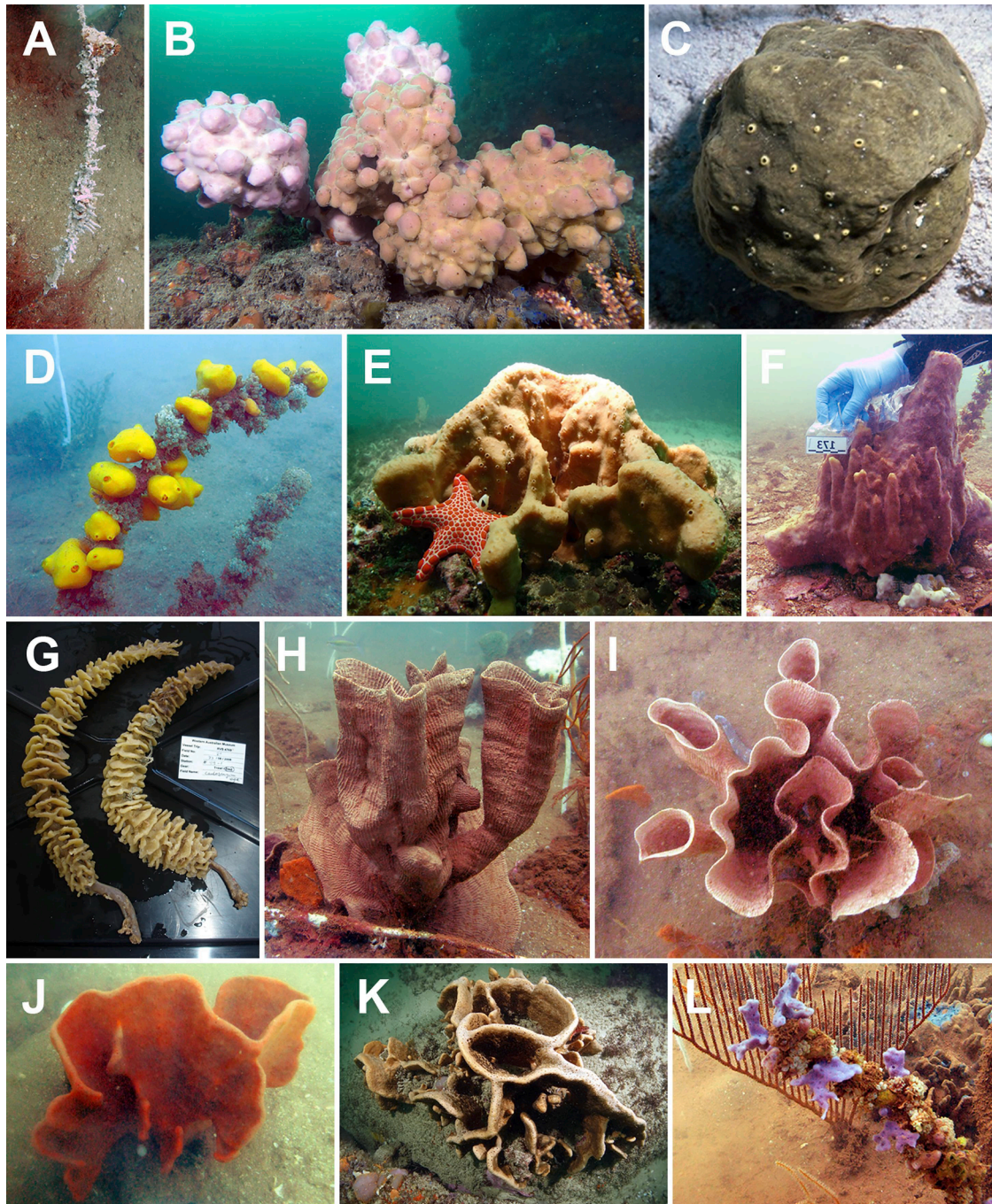
Schönberg, 2016a). Some fistular species such as *Tentorium papillatum* can keep their surfaces sediment-free (Barthel and Gutt, 1992). Sedimentation, as well as starvation can induce formation of erect parts and processes in sponges that do not normally display fistule-like structures, such as in some Suberitida, Haplosclerida and Poecilosclerida (Stone, 1970; Jones, 1994; Cummings et al., 2020). Even if the sponge is not embedded in sediment, occurrence of fistule-like structures is thus a good indicator of locally permanent or temporally elevated sedimentation rates (Fig. 4F). Fistular sponges combine elements of massive and erect sponges, but the main body mass of many species can occur both, on top of the substrate, wedged in between substrate or buried in sediment (e.g., Schönberg and Lim, 2019), and they often have longer and more pronounced fistules in the latter case (e.g., warty or hillocky to fistular in *Spheciospongia* spp.; Fig. 1D, Suppl. 5.3H, I, N, P, Schönberg pers. obs.). For scoring, endopsammic or sediment-dwelling specimens only showing fistules above the substrate differ from branching or palmate sponges by their “branches” (fistules) being more horizontally distributed and rising from the massive or crustose sponge body, rather than originating from a stem. In endopsammic sponges that are largely hidden in the sediment, the fistules can look like separate, simple-erect sponges rising from the bottom. Typical examples of fistular sponges include *Oceanapia* spp., *Ciocalypa* spp., *Coelocarteria* spp., *Polymastia* spp., larger species of the genus *Siphonodictyon*, and some *Spheciospongia* spp. (Schönberg, 2016a).

The unattached, disc- or inverted cup-shaped sponge *Xenospongia patelliformis* is here regarded as an unusual member of this category (Fig. 6). While it does not have pronounced fistules, Sarà (2002) described its upper surface as “minutely tuberculate or conulose” and as having “small rounded tubercles and oscules on slight prominences”. Moreover, the upper side is convex (Fig. 6A-B; Fig. 9A in Sutcliffe et al., 2010), so that the sloped, hispid surface may allow sediment to roll off (Fig. 6A; Schönberg, 2015b). The sponge lives on sandy bottoms and rests on the rim of the convex disc, which is fringed with megascleres extending from the sponge and prevent the sponge from sinking into the substrate (Fig. 6D-E). At the same time the lower, inner, concave surface is weighed down by embedded sand grains to 2/3 of the sponge's thickness (Sarà, 2002; Sutcliffe et al., 2010), presumably to prevent the sponge from being flipped over by currents. By having raised oscules on the central part of the upper, concave side (Fig. 6B), and by incorporating sediment for anchoring (Fig. 6A, C, E), this sponge thus matches basic morphological patterns of fistular sponges, as well as the function of being highly adapted to sediment-dominated environments. Despite the flat body of this sponge, this interpretation may be supported by other weakly attached or unattached, sediment-dwelling sponges with spicule fringe that also have fistules, such as e.g. *Polymastia grimaldii* and *Polymastia hemisphaerica* (Plotkin et al., 2018). *X. patelliformis* occurs in shallow, sandy environments with variable oxygen saturation (Sutcliffe et al., 2010).

3.1.3. Sponges functioning as cups and cup-like forms (CAAB 10 000909; Fig. 2)

Definition: Cup-like sponges have a concave upper surface. Most can efficiently separate their in- and exhalant openings, with inhalants on the outer or lower surface, and exhalants on the upper, inner surface (Bergquist, 1978; Fry, 1979; Trammer, 1979). This separation may not always be complete, but it is generally more strongly pronounced than in other sponge morphologies (Fig. 7). Cup-like sponges commonly have a roughly cylindrical (tubes and barrels) or inverted-cone symmetry (cups) and a small to medium attachment area. Sponges with hollow bodies and wide apical diameters are here combined as cups and are distinguished from tube-like hollow sponges or “narrow cups” with narrow apical diameter, and from barrels with filled bodies and a convex apical depression. Additional example images are provided in Suppl. 4–5.

Functional context: Cup-like sponges can occur in more flow-reduced, oxygen- or nutrient-poor environments than other morphologies with comparatively low profile (e.g., Schmahl, 1990), because



(caption on next page)

Fig. 4. Situations in which sponge morphologies should be scored by function, i.e. possibly in a different context than for most traditional approaches. A – This *Chondropsis* sp. coats a whip-like structure and should be scored as one-dimensionally erect or simple-erect as it is no longer restricted to the boundary layer. It has small branches or tubes, but for the overall habit these seem to be of subordinate importance. B – The encrusting cf. *Darwinella australiensis* commonly coats the stalked giant sea tulip *Pyura spinifera*. In this way the sponge attains the overall morphology of the ascidian and should be scored as “stalked” itself as it reaches into higher levels of the water column. C – The endolithic-bioeroding sponge *Cliona caribbaea* in “beta” morphology would usually be part of the encrusting sponges, but in this particular case it inhabits a rounded piece of calcium carbonate and should be scored as simple-massive, with in- and exhalant openings mingling on the same surface. D – This *Plakortis* sp. settled on the upper part of an erect structure and has no living tissue closer to the substrate surface. It should be scored as “stalked” instead of “ball” or “simple-massive”. E – This sponge consists of laminar portions that have no main direction and are robust and densely merged. It cannot inform on prevailing currents, and due to the compact appearance, it should best be counted as “composite-massive”. F – This *Sphecospongia* sp. is fistular, even though in this case it is not buried in the sediment. G – *Caulospongia* spp. have a central axis and tiers of plate-like, tabular to more convoluted elements. They are three-dimensionally arranged in the water column and are best scored as erect-branching, unless they become very narrow and dense or develop a longer stalk, in which case they may function more like a simple-erect or a stalked sponge if the basal part is long. H-I – *Ianthella basta* is commonly perceived as a fan-shaped, erect-laminar sponge, but it often forms pronounced tubular structures that would potentially concentrate the exhalant stream, whereas in an erect-laminar sponge this would not occur. It might thus better be scored as a tubular sponge. J – This *Axinella* sp. is composed of several laminar parts that are mostly in one plane, and it can probably still be scored as erect-laminar. If the structure were more complex, but still loosely arranged, this sponge could possibly be scored as three-dimensionally branching. K – While this sponge mostly consists of laminar parts, they are not aligned in one plane. Due to its central portion, it is partly cup-like, due to the outer elements partly three-dimensionally branching. Considering the rigid appearance and the orientation that is not governed by flow conditions and seeing the sediment caught in some of the compartments, this particular sponge should probably be counted as a cup, as composite-massive if it were more densely arranged. L – This partly-branching, partly-laminar *Haliclona* sp. settled on the upper parts of a gorgonian and should thus be scored as “stalked”. A, D, F, H-I, J, L – Sponges in –12 to –14 m, Pilbara near Onslow, NW Australia. B, E, K – Photographs from SW Australia by John Turnbull© (2020), with friendly permission. C – Photograph from the Bahamas by Sven Zea©, with friendly permission (Zea et al., 2014). G – Specimens from the Carnarvon Shelf near Point Cloates, NW Australia, ca. –60 m.

spatial separation of their in- and exhalants reduces the risk of re-inhalation of their own wastewater (Bidder, 1923; Bergquist, 1978; Fry, 1979). The link to nutrient-poor, clear waters may explain that cup-like sponges with a large proportion of near-horizontal surface can often be photosymbiotic (e.g., Wilkinson, 1988). However, unless they have a high spongin content (Wulff, 1995), their morphology is not as suitable for strong, unpredictable flow regimes, because they can become detached or broken. And while damaged sponges or basal pieces that may remain attached to the substrate will often grow back, the dislodged sponge body or fragments are less likely to reattach and survive (Wilkinson and Thompson, 1997; Bell and Barnes, 2001a; Gilliam et al., 2009). To some degree cup-like sponges can tolerate sedimentation, because the upper surfaces bear the exhalants. By apically concentrating the exhalant flow, finer sediments that fall onto the concave exhalant areas or into a cup may be washed away, while the coarser particles may collect but still allow oxygenation and flow away from the sponge (Fig. 8; Swierts et al., 2018). In this as in other cases within the Porifera, coarser materials are usually less stressful or detrimental than fine sediments (Pronzato et al., 1998; Schönberg, 2016b).

Subgroups: Category 7 – Cups (CAAB 10 000910) include tabular or table-like sponges, incomplete and complete cups. Their widest diameter is usually expressed by the apical rim.

Category 7.1 – Tables (CAAB 10 000920) are very shallow cups that have a near horizontal, flat shape but are not crusts. They have a short central stem or small attachment area to hold them in place, but they are otherwise unattached. Due to this small attachment and despite having a low profile, they can become dislodged in high energy flow regimes, and they would typically inhabit areas with moderate to strong, but predictable flow patterns. Stagnant water would not be supportive of tabular sponges, as their large upper surface could quickly be covered in sediments. Multiple table-like structures stacked in tiers along an upright axis in a single sponge such as in *Caulospongia* spp. are at the interface between tabular sponges (horizontal surfaces) and three-dimensional erect-branching sponges (increased structure, reach into the water column; Fig. 4G). In this case the three-dimensionally distributed body and the erect-branching function in combination are more important and the sponge should be scored instead as erect in three dimensions. Where the branch-like structure is very close to the central axis and the sponge is long and slim, it can instead be scored as simple-erect (e.g. as in Fig. 4A). Examples for simple tabular sponges include e.g.: flat *Cymbastela* spp. in the Demospongiae, and *Bathydorus* spp. and *Docosaccus* spp. in the Hexactinellidae.

Category 7.2 – Incomplete cups or curled fans (CAAB 10 000918) are an intermediate form between erect-laminar sponges and cups or tables

and cups. They may in part be incompletely curled fans or cups with parts missing. In fact, some dictyoceratid cups such as *Carteriospongia foliascens* can display the whole spectrum between a tabular sponge, cup and a fan (Fig. 9). While incomplete cups largely function like a wide cup, they are not entirely closed, which means that sediments collecting within can trickle out or possibly be washed out more easily (Fig. 9E-G). Examples include e.g.: *C. foliascens*, *Phakellia ventilabrum*.

Category 7.3 – Complete, wide cups (Fig. 2A) are basally fully closed and entirely hollow and concave sponges in which the apical diameter is usually the largest one. They can be more funnel-, more goblet- or more cup-shaped, but they all have a small to medium basal attachment area, e.g. as a short stem. We need more information about the distribution of ostiae and oscula in wide cups as they do not always seem to be as clearly separated as in other cup-like sponges, or they are not always separated in the same way. The exhalants are mostly scattered across the inner, concave surface of wide cups, but in *Carteriospongia foliascens* some of the oscules may also be found on outer surfaces (Fig. 8B). Some *Cymbastela* spp. were reported with reverse separation, i.e. with inhalants on the concave inner surface and exhalants on the lower convex surface of the cup, or with both types of openings on the inner, concave surface (Hooper and Bergquist, 1992; Hall and Hooper, 2019). In such cases, sediments that collect in the cup cannot effectively be washed out by the exhalant flow (Fig. 9A, C-D), and there would be a high risk of inhaling fine sediments into the aqueous system. Sediments can build up at the bottom of such cups and cause anoxia and tissue death (Fig. 3I-J in Schönberg, 2016b), so that some cup-shaped sponges may develop a basal or lateral hole and start to function as an incomplete cup (Fig. 9E), or other organisms grow on the concave surface of the sponge, further reducing water exchange (Fig. 9D). *Cymbastela* spp. have a surface spicule palisade that creates particle-repellent conditions (Schönberg, 2015b), and many cup-like sponges can shed adhering particles with a mucus veil (Fig. 8G, I, K), but overall, hollow cups are not well-suited for high rates of sedimentation. This is especially true if the sponges are photosymbiotic, such as e.g. the cyanosponges *C. foliascens* or *Cymbastela* spp. (e.g., Wilkinson, 1988; Roberts et al., 2006; Schönberg, 2016b). Many photosynthetic sponges develop morphologies with proportionally more horizontal surface to maximise the area exposed to light, and being covered with sediments would reduce the primary production by shading. Therefore, these sponges are usually less abundant at turbid sites with high sedimentation rates of fine sediment, and more common at clear-water, more nutrient-poor sites with coarser sediments (Wilkinson, 1988; Wilkinson and Cheshire, 1989; Wilkinson and Evans, 1989). Examples for complete, wide cups include e.g.: *Axinella infundibuliformis*, *Cliona patera* (or it can be stalked), *Ircinia campana*, *Echinodictyum mesenterinum*. Some species can produce cups stacked inside of

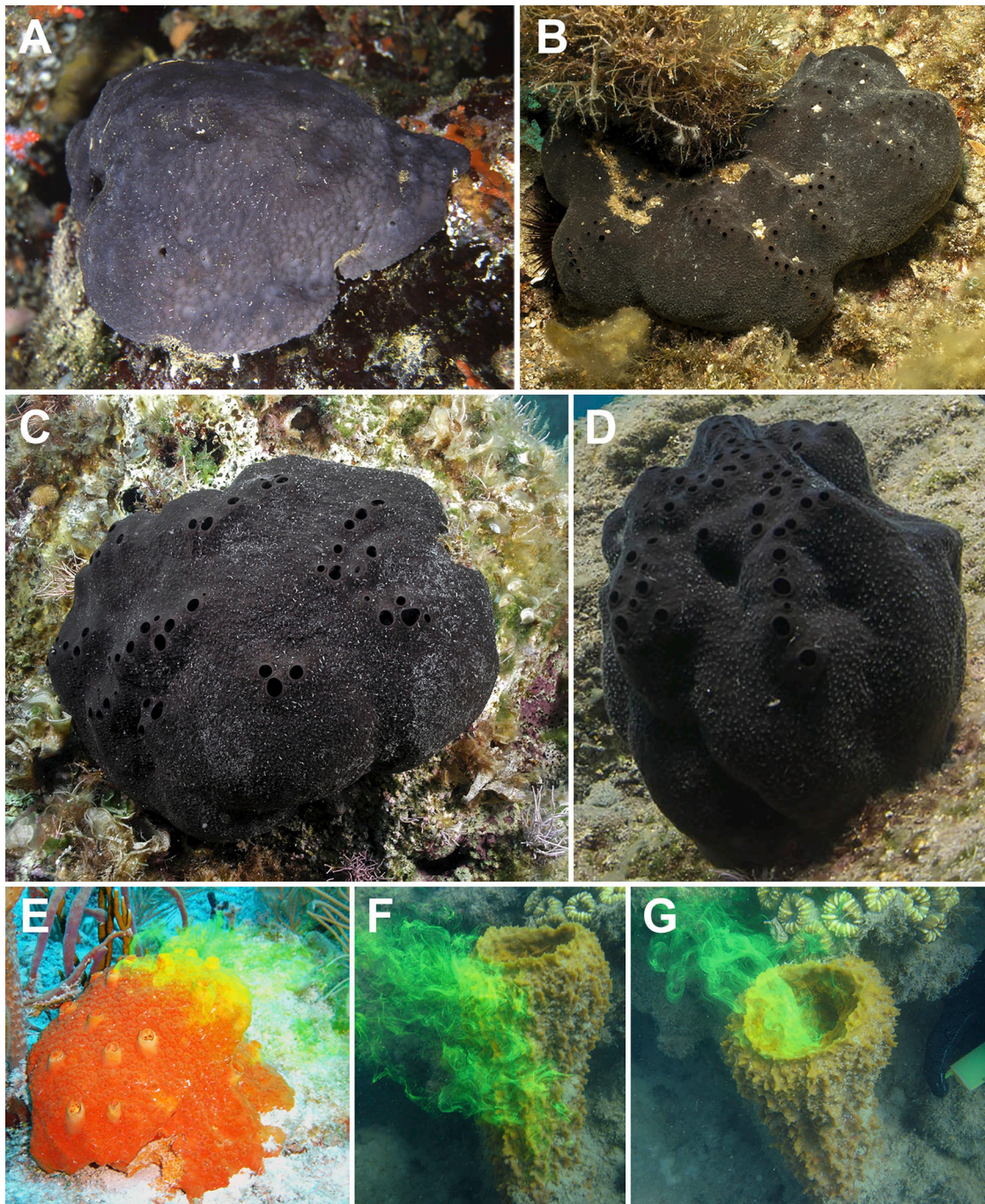


Fig. 5. The simple-massive sponge *Spongia (Spongia) officinalis* in the Mediterranean as an example for mixed or patchier oscular grouping that can be more concentrated at the apex of the sponges (A-D), compared to the here functionally simple-massive sponge *Clathrodictyon delitrix* with relatively evenly mixed in- and exhalants (E) and the barrel *Xestospongia testudinaria*, in which ostiae and oscules are on different body surfaces (inhalant phase: F, exhalant phase: G). The *S. officinalis* individuals are not exactly to scale, but the distribution and location of the oscules, their more pronounced oscular collars, their diameter and the more vertical growth of the sponge in D suggests that this site had the lowest flow and was likely the most oligotrophic, requiring this sponge to separate in- and exhalants more clearly than in the other specimens and to reach higher into the water column. Oscular grouping results in spatially combining the flow of separate exhalant openings, creating a stronger jet that carries wastewater further way from the sponge (Fry, 1979). In *C. delitrix* in –13 m at Looe Key, Florida exhalants are distributed across the entire surface, but in this case the water is predominantly exhaled from the top of the sponge, creating a morphologically less clearly defined and more behaviourally realised separation (E). In *X. testudinaria* in –4 to –5 m at Orpheus Island, Great Barrier Reef a clear separation exists between lateral inhalants on the outer surface (F) and apical, grouped oscules producing a single, exhalant stream spatially separated from the inhalants (G). A – Photograph by Roberto Pronzato©, with friendly permission. B-D – Photographs by Thanos Dailianis©, with friendly permission. The passage of the water was made visible by the use of fluorescein dye in E-G.

cups (e.g. *Cymbastela marshallae*) or spiral cups (*Carteriospongia* sp. LG 1, p. 100 in Goudie et al., 2013) – these still function as complete cups.

Category 8 – Narrow cups or tube-like forms (CAAB 10 000926), i.e. tubes and chimneys (CAAB 10 000911; Fig. 2B) and sack- or amphora-like forms (CAAB 10 000927; Fig. 2C), are extreme forms of cup-like sponges. In cross section they are hollow along most of their body. Proper tubes have apical openings that have a diameter similar to the tube or body diameter, while sack- or amphora-like forms are barrel-shaped, but hollow sponges, with apical openings that are smaller than the maximum sponge diameter. In both morphologies the exhalant stream is strongly bundled by a single exhalant opening, situated apically. Thereby, narrow cups are best adapted to and protected from moderate sedimentation pressure (Krautter, 1998; Bell, 2004) and have never been reported to accumulate sediments in their lumens. Nevertheless, we need more data to better understand the ecological role of tube-shaped sponges. As in erect sponges, most of their surfaces are vertical and do not collect significant amounts of sediments. Nevertheless, they are usually reported from clear waters (Suppl. 2), and the tubular *Aplysina aerophoba* grew faster when sedimentation was excluded (Wilkinson and Vacelet, 1979). If one sponge individual is formed by several tube-like structures arranged in a group, it may function more like an erect-branching or an erect-palmate sponge when in clear-water environments, or more like a battery of narrow cups if sedimentation is high. However, the tubular shape is such a specialised morphology that it may usually be best to score it as tube-like sponge, as long as the oscular opening is similar to or smaller than the diameter of this part of the sponge. Some sponges such as *Ianthella basta* form erect-laminar morphologies when they are small, but can grow into large tube systems and should then be counted under “narrow cups” (Fig. 2B, 4H-I). The Atlanto-Caribbean has many examples of tubular sponges and only few are known from Australia: *Callyspongia* (*Cladochalina*) *aculeata*, *Agelas tubulata*, *Aplysina fistularis*, *Liosina paradoxa*, *Pipestela candelabra*, *Echinochalina* (*Protophilaspongia*) *isaaci*. The glass sponge *Euplectella aspergillum* would be a good example from the Hexactinellida, even though the apical exhalant opening is covered by a delicate spicule mesh. Examples for amphora-like demosponges include e.g.: *Mycale* (*Arenochalina*) *laxissima*, *Theonella swinhoei*, glass sponges such as *Rossella* spp., *Anoxycalyx* (*Scolymastra*) *joubini*, wide specimens of *E. aspergillum*, and calcareous sponges such as *Sycon* spp.

Category 9 – Barrels (CAAB 10 000907; Fig. 2C) embody a special form of cup-like sponges. While they have a massive appearance due to their overall shape and tissue distribution that fills most of their body, their main function is driven by the cup-like separation of in- and exhalants (Fig. 5E-F). The exhalants are located on a concave apical portion that creates a similar, bundled exhalant stream as in narrow cups, but here the jet is slimmer than the apical opening and less well defined than in tubular forms. The inhalants are situated on the outer, lateral surface. The sponges can be more conical, more barrel-shaped or more globular, but often quite large. They can commonly tolerate reduced flow and high rates of sediment deposition, and fine sediments. Some barrels are photosymbiotic cyanosponges. Classic examples for barrels are e.g. larger *Xestospongia* spp. (Fig. 2B, 8, 5F-G), *Ircinia strobilina*, *Sphaciospongia vesparium* and *Geodia neptuni*.

3.1.4. Sponges functioning as erect forms (CAAB 10 000913; Fig. 3)

Definition: Erect sponges have a very small attachment area; their main body is in the water column, and in considerable distance from the substrate and the boundary layer. These sponges are predominantly vertical and have minimised their horizontal surface areas. Oscules and ostiae are not usually as clearly separated as in the cups (Fry, 1979). They can be situated on vertical surfaces, on branch apices or in a line along a ridge or the top of a branch. However, they can be mostly divided between the two prevailing surfaces on vertically flattened, fan-shaped sponges, with the exhalants mostly facing downstream. Further examples for erect sponges are depicted in Suppl. 4–5.

Functional context: Due to their height and small attachment area, erect sponges can be vulnerable to fragmentation, detachment and

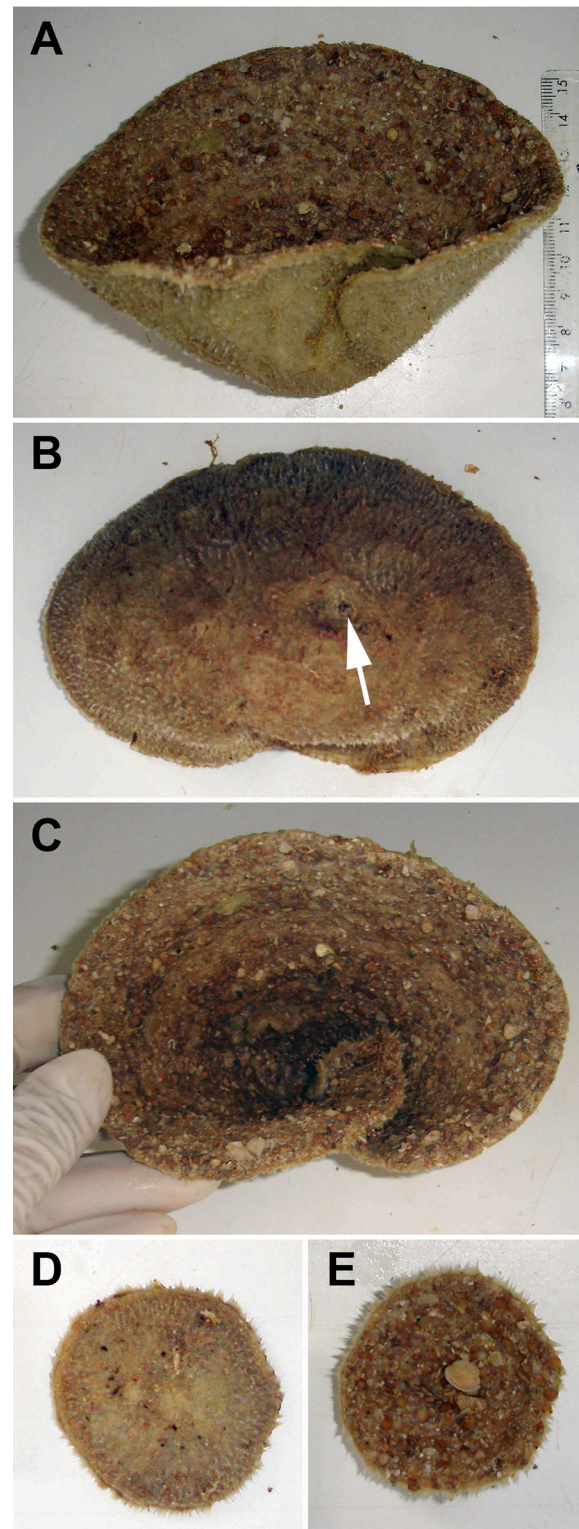


Fig. 6. *Xenospongia patelliformis* is an unattached sponge highly adapted to sandy environments. A – Sideview: When dredged up and without context, larger individuals can easily be mistaken for a cup. B – However, the sponge rests unattached on the substrate convex side up. Note that the sponge is quite conical and thus not prone to burial. The arrow points to the large apical osculum. C – The lower side contains densely embedded particles to weigh the sponge down. D-E – A smaller individual is flat and disc-shaped, D – upper surface, E – lower surface (D-E are at 1.5x the size of A-C). The sponges were sampled on sandy bottom in –66 m off Point Cloates, Carnarvon Shelf in NW Australia (Schönberg and Fromont, 2012).

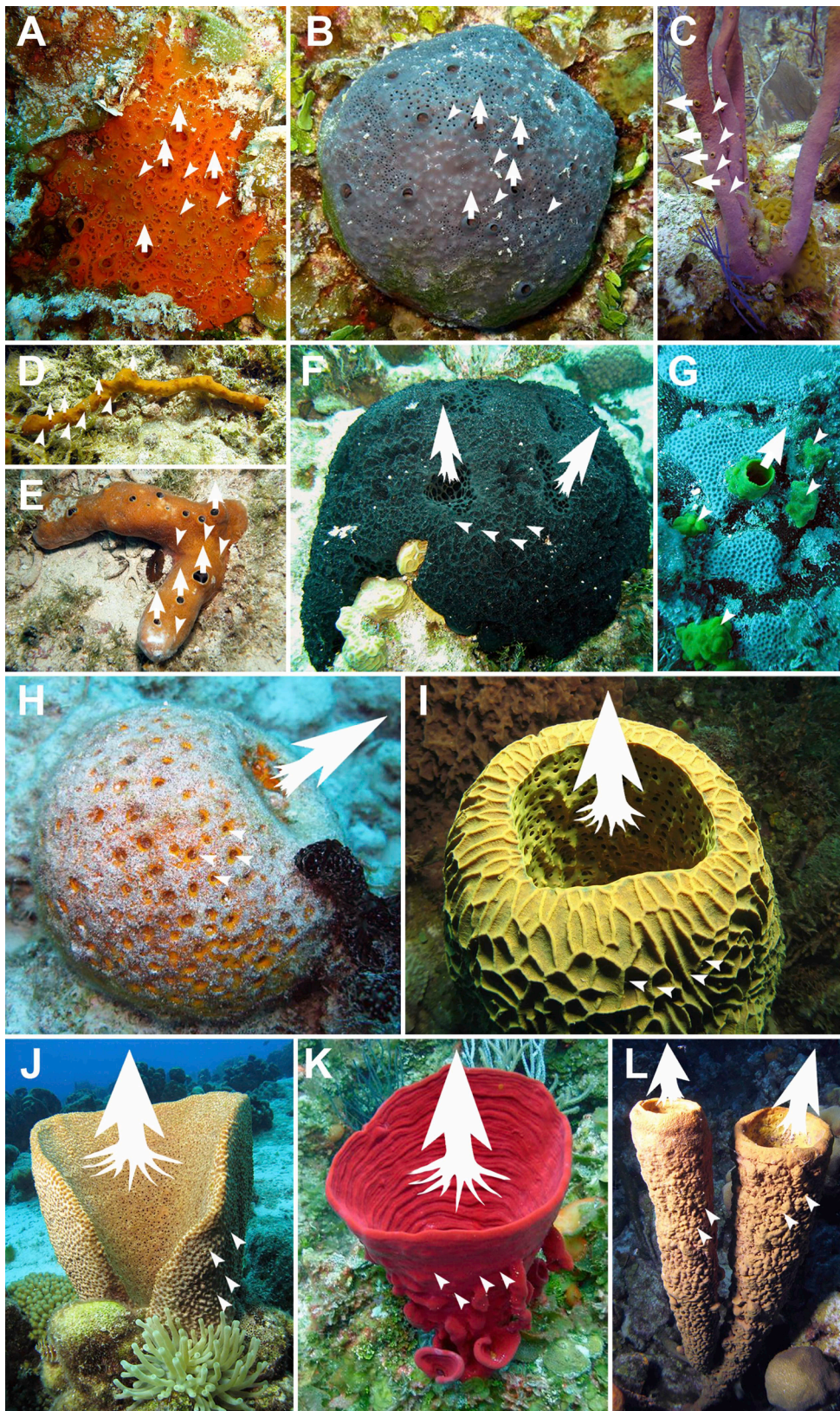


Fig. 7. Examples of the spatial distribution of in- and exhalants in different growth forms of sponges. A-D have fully mixed in- and exhalant openings and rely on external currents to carry off used exhaled water and provide enough flux of fresh oxygenated and nutritious water. In E, oscules are all located apically but still on the same surface as the inhalants, and in F they are grouped in patches to better bundle exhalant jets. In G entry and exit points are situated on the tops of fistules, thus somewhat better separated, despite being on the same plane. H-L are examples for cup-like sponges that are assumed to take up water through pores on their lateral sides and eject it from concave surfaces on the inside of the “cup”. Depending on the oscule and “cup” diameters, the exhalant flow can be bundled as a strong jet, carrying the wastewater well away from the sponge, even at low ambient flow speeds. A – Encrusting *Placosphaera micraster*, Bahamas (J. Pawlik; see taxonomic remarks on [Zea et al., 2014](#) re genus name). B – Simple-massive *Hyrtios cavernosus*, Bahamas (S. Zea). C – Erect-branching *Aplysina archeri*, Bonaire (J. Pawlik). D – Creeping *Clathria (Thalysias) virgultosa*, Bahamas (S. Zea). E – Creeping *Neopetrosia subtriangularis*, Bahamas (S. Zea). F – Simple-massive *Asteropous niger*, Bahamas (S. Zea). G – Fistulate *Siphonodictyon coralliphagum*, Bahamas (S. Zea). H – Globular *Cinachyrella kuekenthali*, Bahamas (S. Zea). I – Barrel or cup-like *Verongula reisi*, Martinique (J. Pawlik). J – Here incomplete cup *Ircinia campana*, Curaçao (J. Pawlik). K – Cup *Cribrachalina vasculum*, Bahamas (J. Pawlik). L – Tubular *Aplysina cauliformis*, Bahamas (S. Zea). Photographs from [Zea et al. \(2014\)](#), creative commons, individual photographers as indicated in brackets.

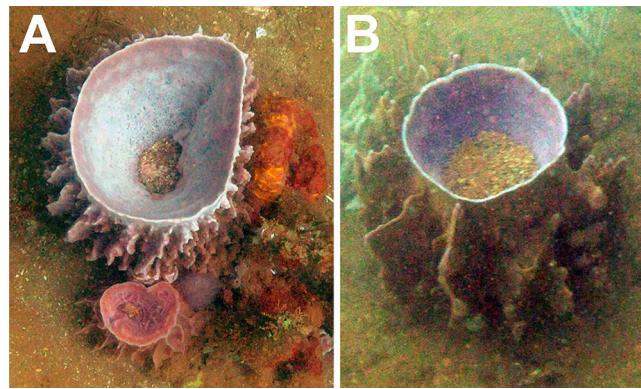


Fig. 8. Sediment deposition in cup-like sponges. A-B – Barrel-shaped *Xestospongia testudinaria* in 12–14 m at Onslow on the Pilbara coast, NW Australia. The sponges discharge an exhalation stream from the upper and inner, concave surface. While this habitat was characterized by fine, mud-like sediment, a high turbidity and high sedimentation rates, the grains remaining in the concave parts of the barrels were coarse, the exhalant water having washed out the fine material.

removal due to strong flow, waves or storm surges, unless they have a high spongin content that makes them flexible (e.g., Jackson, 1979; Wulff, 1995; Fig. 10). However, some branching sponges have a high survival rate after fragmentation and can quickly re-attach and regenerate (Wulff, 1985, 1991, 2006a), which can result in similar before-after-storm counts. Disregarding acute events such as storms, erect sponges commonly occur in habitats with benign or predictable flow regimes and become simpler with decreasing exposure and increasing sedimentation (Abraham, 2001; Bell et al., 2002a; Lawler and Osborn, 2008). Mixing of the water column and renewal of nutrients and oxygen is lower near the substrate surface (Mendola et al., 2008), and erect sponges reach up into the water column to maximise feeding by bringing inhalant openings into water away from the boundary layer, avoiding the more depleted layers close to the substrate, and enhancing ventilation and waste removal (Bidder, 1923; Jackson, 1979; Jones, 1994). Sponges situated at a higher level of the water column grow faster than those closer to the substrate surface (McLean and Lasker, 2013). With the exception of balls, sponges develop larger heights at sites with less water movement than at more exposed sites (Lawler and Osborn, 2008). Erect morphologies are more resistant to sediment deposition, clogging and smothering as their predominantly vertical surfaces and some apical arrangement of oscules prevent particle build-up (Bell, 2004; Divine, 2011). Erect sponges can occur in highly turbid habitats with high levels of suspended particles and high sedimentation rates, while most of the other morphologies do not tolerate such conditions as well (Lawler and Osborn, 2008).

Subgroups: Category 10 – One-dimensional or simple-erect sponges (CAAB 10 000916) are significantly higher than wide and do not branch or only to an insignificant amount. These are whip-like or columnar sponges (not tubular structures such as fistules). In cross section they are solid. Literature providing information about the environmental conditions simple-erect sponges occur in is scarce (Suppl. 2), but high sedimentation pressure appears to induce branch reduction in three-dimensionally branching sponges (Bell et al., 2002a), and simple-erect sponges are sedimentation-tolerant. Whips and rope-like sponges often contain much spongin and are flexible, while columnar sponges are usually more reliant on their inorganic skeleton. This would mean that whips can likely tolerate high energy environments, but columns would rather be found in less exposed situations with reduced flow and in that respect may function more like simple-massive sponges. However, both reach up high into the water column, and the ambient nutrient conditions may thus be limited. Examples include single branches of usually three-dimensionally erect-branching species e.g.: rope sponges such as *Aplysina fulva*, *Haliclona koremella*, *Clathria (Thalysias) procera*.

Category 11 – Two-dimensionally erect sponges (CAAB 10 000928; Fig. 3A, 10) are erect-laminar or fan-shaped, erect-palmate or branching in one plane, and erect-reticulate or erect meshes in one plane. All three

are strong bioindicators for laminar currents, in which they arrange themselves at right angle to the main flow direction.

Category 11.1 – Erect-laminar sponges (CAAB 10 000912; often also called flabellate or foliaceous sponges, Suppl. 1) have erect morphologies with a simple, vertically flattened body and a comparatively small attachment area and include forms such as fans, blades and spatulas. The blade can have short fissures or a few holes, but the overall body form is mostly intact. Erect-laminar sponges of significant height are commonly flexible and have a high spongin content, and they bend when larger flow speeds are reached, e.g. in strong tidal currents (Fig. 10A; Schönberg and Fromont, 2012). They stand at right angle to prevailing directional flow (de Laubenfels, 1936; McDonald et al., 2003; Schönberg and Fromont, 2012), thereby maximizing the yield of nutrients. In places such as channels, where the currents predominantly proceed in only one direction, the in- and exhalants can become mostly separated, i.e. most of the inhalants would face into the flow, and most of the exhalants would be on the downstream side of the sponge's blade (de Laubenfels, 1936). Where this occurs, the most efficient separation of in- and exhaled water is achieved (Bidder, 1923; Bergquist, 1978). De Laubenfels (1936) observed that many erect-laminar sponges do not change their morphology to colonise other flow regimes, but only occur in laminar flow. Examples include e.g.: *Ianthella flabelliformis* (Fig. 10A), *Stylissa flabelliformis*, *Clathria (Thalysias) costifera* and *C. (T.) placenta*. If laminar sponges lose their two-dimensionality by having multiple blades arranged in different directions, they no longer reflect laminar flow conditions and can become functionally more like composite-massives if densely merged or erect-branching if loosely arranged (Fig. 4J-K).

Category 11.2 – Erect-palmate sponges (CAAB 10 000914; Fig. 3A, 10B) are sponges with branches oriented in one plane like fingers on an open hand. The branches can be and are often flattened, but do not have to be. Palmate sponges very much function like the other two-dimensional sponges, except that they experience less drag. Many palmate sponges also have a high spongin content and bend in the currents, but they commonly have a more rigid consistency, when spongin is reinforced with inorganic spicules. Examples include e.g.: *Trikenion flabelliforme*, *Ectyoplasia tabula*, *Reniochalina stalagmitis*, *Clathria (Thalysias) major*, *C. (T.) spinifera* and *Ernstilla lacunosa* (Fig. 10B).

Category 11.3 – Erect-reticulate (CAAB 10 000929; Fig. 10C) sponges are vertical meshes in one plane, i.e. when an erect-laminar sponge has many holes or when the sponge consists of branches that reconnect to form a flat, vertical lattice. They function like the other two-dimensional sponges, but due to their composition of inorganic and organic skeleton they are often firmer and thus rely on the gaps to reduce the drag caused by currents. Examples include e.g.: *Axinella australiensis*, *Iophon minor*, *Echinodictyum pulchrum*, *Clathria (Clathria) hjorti*, *C. (C.) multipes*, *Clathria (Thalysias) coppingeri* (Fig. 10C).

Category 12 – In three-dimensionally, erect-branching sponges (CAAB 10 000914; Fig. 3B) branches are longer than wide and arranged

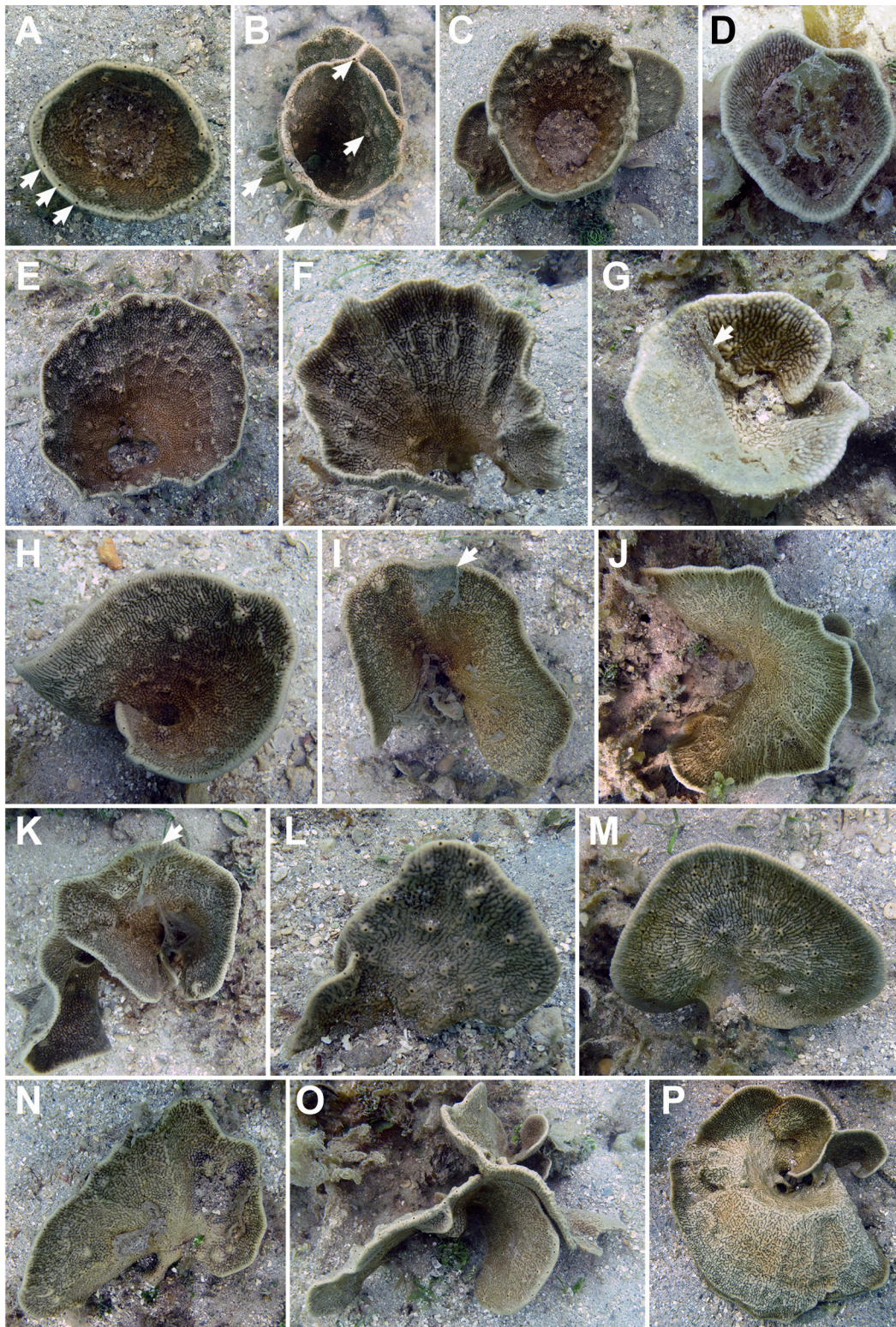


Fig. 9. Examples for different morphological expressions in the same sponge species, ranging from cup- to fan-like forms in *Carteriospongia foliascens* in –1 to –3 m in the Palm Island Group, central Great Barrier Reef. A-D – Complete cups, partially with additional structure (B-C) and commonly collecting sediments that cannot easily be washed out (A, C) so that they sometimes become substrate for other organisms (D). Please note the widely spaced, small oscules predominantly on the rim and on the inside of the cup in A (arrows). Ex- and inhalants are not completely separated between inner and outer surfaces in *C. foliascens* (B, arrows). E-G – Slightly incomplete cups may have resulted from necrosis after sediment accumulation, or from spongivory or other damage. H-K – Intermediate stages between incomplete cups and erect-laminar forms. L-N – Erect-laminar morphologies. O – A composite-laminar form in three dimensions functioning more like an erect-branching than a fan-shaped sponge. P – A fan horizontal to the substrate can be scored as tabulate. Arrows in G, I and K denote mucus veils in sponges that slough off material to clean their surfaces.

fascicularly (bush-like, merging out from a common base at the substrate) or arborescently (tree-like, merging out from a common, short stem that can bear in- and exhalants, and having a more complex branching pattern). Oscules and ostiae are mostly mixed and scattered across the sponges' surfaces and can reach down to the short stem, but in some species the oscules can be arranged in lines along the branches (Fry, 1979). This branching pattern may most commonly develop as a response to reduced water mixing and limited access to nutrients near the substrate, and the predominant sponges stretch into the water column to reach enhanced flow and nutrient conditions. In erect-branching sponges their number of secondary branching and total branch number increases with flow (Lawler and Osborn, 2008). Due to their more fragile morphology, three-dimensionally branching sponges are usually excluded from areas with strong and turbulent flow and only start in at deeper depths, where those flow regimes become more benign (e.g., Bell and Barnes, 2000a). However, they can be more resistant to disease, due to slower spread within an infected branching sponge relative to an infected massive or encrusting sponge, or recover faster after mortality events due to high tolerance to fragmentation and fast regrowth rates and may at least temporarily become dominant after disturbance (Wulff, 2006a, 2006b, 2006c). Groups or clusters of fan-like or tube-like composite structures can occasionally be scored as erect-branching if their function within the given environment is more strongly governed by the erect growth, sediment and food conditions than by flow conditions. If such clusters become very dense and well-merged, they may be scored as composite-massive sponges. Where branching sponges have settled on an erect structure in considerable distance from and without connection to the substrate, they should be scored as stalked (Fig. 4L). Examples include e.g.: *Pararhaphoxya sinclairi*, *Raspailia* (*Raspaxilla*) *topsenti*.

Category 13 – Stalked-erect sponges (CAAB 10 000906; Fig. 3C) represent a very specialised morphology. They have a clear separation of a basal stalk-like portion that does not normally contain any obvious ostiae or oscules, and an apical part that represents the main body with all the functional parts. Short stems differ from stalks in that the former can contain functional parts. The elevated body can exhibit different forms and can be globular or even cup-like, as long as it is clearly removed from the substrate and the boundary layer by a largely “inactive” stalk, which can mostly consist of spongin or of inorganic skeleton – or it can be a foreign object the sponge settled on (Fig. 4D, L). This is one of the most extreme adaptations to poor nutrient conditions, and many deep-sea sponges display this morphology as this environment is depauperate of the typical food sources of shallow water environments (e.g., Leinfelder et al., 1996; Krautter, 1998). Stalked sponges can occur in areas with different substrates, and if there is fine sediment, the stalk is also a good means to remove the sponge from the deleterious mud. Stalked glass sponges often turn their convex side with the inhalant pores into the current and the wide concave side with the exhalants points downstream so that the wastewater is more easily carried away (Bergquist, 1978; Tabachnick, 1991; Janussen pers. comm.). Bidder (1923) said about such hexactinellid sponges: “In the great depths where they live, an unchanging current sweeps slowly from the poles to the equator. They have but to spread a net across it. [...] Such an organism becomes a mere living screen between the used half of the universe and the unused half.” Some morphologies can be quite complex and may communicate between branching or palmate and stalked morphologies, depending how far more complex structures reach down the stalk, e.g. *Chonelasma* spp. Examples for demosponges include e.g.: *Tethycometes radicata*, *Podospongia virga*, *Stylocordyla chupachups*, *Rhizaxinella* spp., *Clathria* (*Thalysias*) *fusterna*, and e.g. *Hyalonema* spp., *Bolosoma* spp., *Caulophacus* spp. for glass sponges.

Category 14 – Carnivorous sponges (CAAB 10 000930; Fig. 3D-E) mostly occur in nutrient-limited deep water or occasionally in caves and are the most extreme adaptation to food limitation in sponges (Hajdu and Vacelet, 2002). Their habitats are generally unsuitable for filter feeding or so oligotrophic that these sponges have reduced or abandoned their aquiferous system and instead rely on velcro-like surfaces with protruding

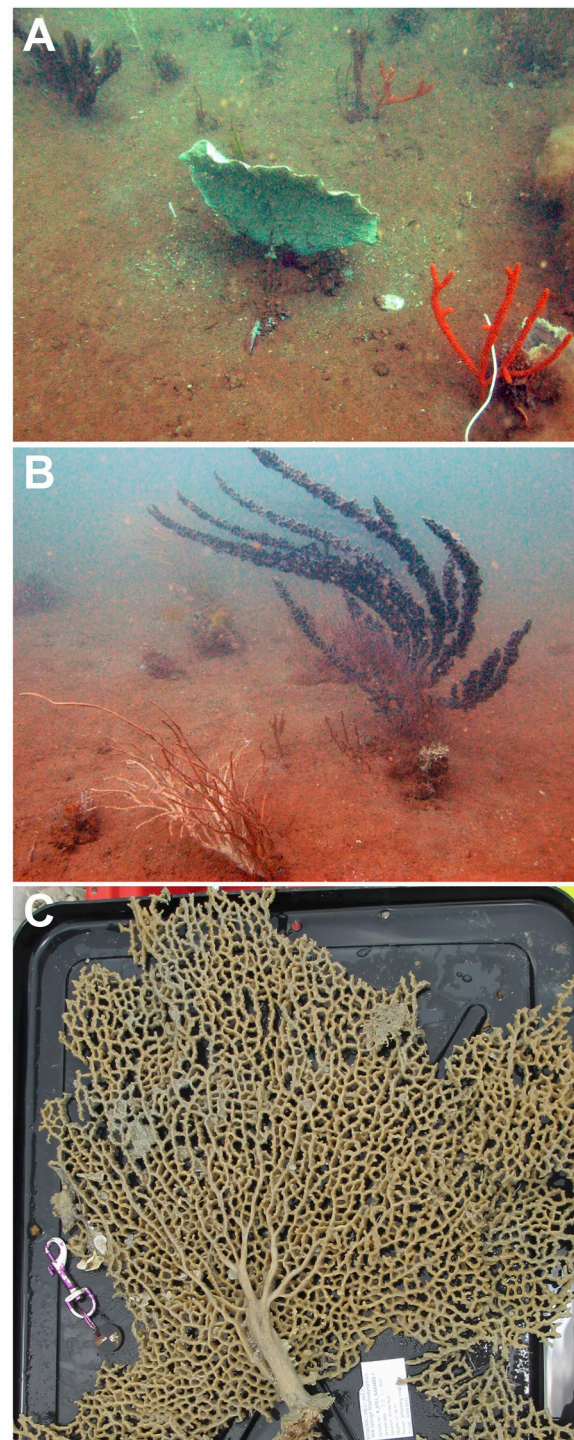


Fig. 10. Examples of two-dimensionally erect sponges typical for habitats with strong tidal currents in NW Australia. A – *Lanthella* cf. *flabelliformis* (light blue-green blade), and B – the palmate *Ernstilla lacunosa* in –12 to –14 m at Onslow. Both species have an exclusively organic skeleton (spongin). Note that the other branching organisms in this habitat were also usually two-dimensional and arranged at right angle to the predominant flow direction created by tidal currents in the area. The orange branching sponges would be either *Axos* or *Clathria* spp., sponges with inorganic and organic skeleton, but with a high content of the latter. C – A benchtop photograph of the erect-reticulate *Clathria* (*Thalysias*) *coppingeri* with spicular skeleton and a high spongin content, from –24 m at southeast Montgomery Reef, Kimberley, northern Australia. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3

Dominant sponge morphologies in relation to prevailing environmental conditions and the strongest environmental drivers. All major environmental factors below covary to some extent (Jackson, 1979), and they change along the same axis downwards in the table. The observations for sponge functions relate to horizontal substrate and are here supported by a few key publications. The terminology for morphologies follows the present concept. Details and further references are provided in Suppl. 2. *In situ* examples are provided by Figs. 1-3.

Environmental factor	Expected predominant sponge morphologies	Ecological implications
Hydrodynamic regime (see e.g. Wulff, 2006a; Schönberg and Fromont, 2012)		
Strong, turbulent flow	Firmly attached <u>encrusting</u> , <u>simple-massive</u> , and some <u>ball-shaped</u> sponges (Fig. 1A-C), with comparatively low profile, large attachment area and relatively small size, at times reinforced by a high skeleton content; oscules may be comparatively small.	Drag, acceleration and lift can break and dislodge any sponge with high profile, delicate consistency and weak attachment. Having a small, compact size, a firmer tissue : skeleton composition and a low profile is thus a survival strategy. The strong flow regime and good mixing do not require a clear separation of in- and exhalant openings, and oscules can remain small due to good mixing of the water column.
Strong, laminar flow	Often flexible, <u>two-dimensionally erect</u> sponges (Fig. 3A) with a high spongin content, as well as some ridge-like <u>simple-massive</u> sponges dominate (Fig. 3B); they will orient themselves at right angle to the flow. <u>Fistular</u> sponges can also be common in laminar flow (Fig. 1D).	Erect forms are thought to extend vertically into faster flow regimes to gain better access to food and to eliminate waste products. Flat shapes at right angle to the flow optimize this effect, creating eddies. When having a small attachment : body area, flexibility safeguards against dislodgement. The peak flow regime does not require a clear separation of in- and exhalants, but some sponges exhibit a separation by having most exhalants placed at the surface facing prevailing downstream currents or on apical ridges.
Moderate, predictable flow	Morphologies may be diverse but may increasingly include erect components apart from morphological complexity. <u>Cup-like</u> , <u>erect</u> and <u>massive</u> sponges are usually common in medium to low flow, as well as a more pronounced separation of in- and exhalants. <u>Encrusting</u> forms become uncommon. With flow reduction oscular diameter and <u>erect</u> specimen height increase (Fig. 5A-D), but <u>balls</u> become smaller or flatter, and branch number, branch width and branching complexity are reduced in <u>erect</u> sponges.	Erect forms are thought to escape the flow-reduced boundary layer by reaching into faster flow regimes to gain better access to food and to eliminate waste products, which encrusting sponges cannot, unless they develop erect structures such as fistules, or they grow on vertical surfaces. With diminishing flow sponges separate in- and exhalant openings to reduce the risk of re-inhaling food- and oxygen-depleted water and waste products (esp. in cup-like morphologies). Moreover, with reduced flow sedimentation increases, and horizontal body surfaces are of disadvantage, and large, apical exhalant structures of advantage to concentrate the exhalant jet and to blow sediments away.
Low-flow, stagnant or nutrient-poor conditions, sediment fine and soft where present	<u>Erect</u> , and especially <u>stalked</u> forms predominate (Fig. 3C), or carnivorous sponges as an extreme (Fig. 3D-E). Otherwise sponges may develop erect structures on their surfaces. In stalked glass sponges, the body often has a concave side (facing downstream) and a convex side (facing into the prevailing current; Fig. 3C).	Erect structures extend the reach into flow regimes beyond the boundary layer to gain better access to food and oxygen, and to eliminate waste products that are carried away by remaining currents. Stalked forms represent an extreme by significantly separating and elevating the bulk of their body mass from the substrate and the boundary layer. This also removes the body from soft, fine sediments that are most deleterious to sponges. Exhalants may be placed on surfaces facing downstream to maximize the removal of the exhaled water. Where food supply becomes limiting to filter-feeding, carnivorous sponges occur.
Substrate type (see e.g. Schönberg, 2016a, 2016b)		
Prevailing rocky, hard bottom	All sponge morphologies can be found on rock, but <u>crusts</u> and <u>simple-massive</u> sponges usually dominate (Fig. 1A-B). If the hard substrate is calcium carbonate, <u>endolithic-bioeroding</u> sponges may be abundant (Fig. 4A).	Most sponges can only settle on firm substrate, and bedrock would be the safest. If the habitat is characterised by bare rock, it is likely an exposed site where sediments cannot easily settle. In such an environment, low-relief morphologies with a large attachment area and forms that reduce risk of scouring will prevail (see above).
Prevailing sandy bottom	<u>Endosammic</u> , <u>fistular</u> (Fig. 1C) or <u>endolithic-bioeroding</u> sponges will be dominant, and some <u>creeping-ramose</u> sponges may occur. All of these are likely to have oscules in apical positions, most typically on elevated, fistular structures.	Sandy ground is suggestive of a milder flow regime than for rocky bottom but offers less suitable substrate to colonise. Sponge larvae often settle on small stones, shells or other fragments, and can later anchor themselves within the substrate by agglutinating more such material, or by including sand and particles into their tissues and by growing root-like extensions. Sand may shift and move and may cover organisms living in this area, and fistule-like structures will prevent smothering.
Prevailing muddy bottom	<u>Fistular</u> and <u>erect</u> sponges are most dominant (Fig. 1C, 3).	With even less water movement, fine sediment will settle out, which is overall more harmful to sponges than coarse sediment and may clog the aquiferous system after being inhaled and can cause anoxia and necrosis where tissue becomes covered for longer time. In such an environment all sponges will have erect or convex components that emerge from the mud (fistules) or elevate them above the fine sediments (various erect forms, incl. stalks).
Water clarity, sedimentation (e.g. Wilkinson, 1988; Wilkinson and Cheshire, 1989; Wilkinson and Evans, 1989)		
Clear, nutrient-poor water	Many sponge morphologies can occur in clear water, but <u>cup-like</u> morphologies may be most common (Fig. 2A). <u>Crusts</u> may also prevail (Fig. 1A).	Clear water relates to a reduced nutrient load, which requires sponges to separate their in- and exhalant streams to maximize the feeding success, or they supplement their nutrition by photosymbiosis, and many photosymbiotic sponges are wide cups with much horizontal surface exposed to light. Crusts can survive without becoming smothered by sediment.
Turbid water	<u>Globular</u> (Fig. 1C), <u>erect-laminar</u> , <u>erect-palmate</u> (Fig. 3A), and <u>erect-branching</u> sponges will be common (Fig. 3B), as well as some <u>cup-like</u> sponges (Fig. 2B).	Turbid water suggests reduced flow and fine sediments, which selects for erect morphologies to reduce the amount of surface area on which sediment can settle. Cup-like morphologies commonly have exhalants on their upper surfaces, which reduces the risk of inhaling sediment (e.g. barrels).
High sedimentation rate	<u>Fistular</u> sponges will occur (Fig. 1D). Sponges with otherwise unornamented surfaces may develop erect or convex portions. <u>Barrels</u> and <u>tubular</u> sponges can occur (Fig. 2B). <u>Crusts</u> may survive on vertical surfaces.	The best-adapted sponges will be those that can live buried in the sediment and that have fistules and erect or convex structures that emerge from the substrate. As above, sponges that can keep their upper surfaces clean by washing sediments away with a strong apical exhalant stream are also well adapted.

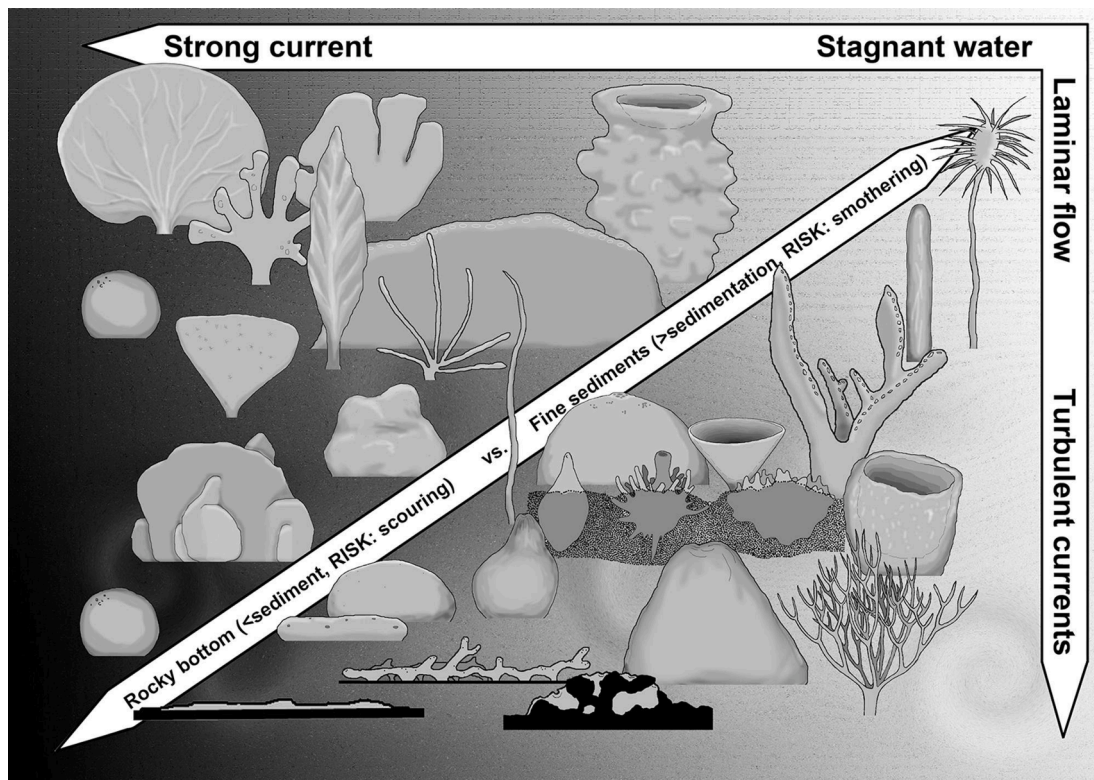


Fig. 11. Proposed distribution of different sponge morphologies in a continuum of different environmental conditions according to the present understanding of their functions as summarised in Table 3 (see also Suppl. 2).

spicules that trap e.g. little arthropods that are then engulfed by sponge tissue and digested (Vacelet and Boury-Esnault, 1995). The morphologies of carnivorous sponges can be very variable among taxa but are often delicate and mostly stalked or erect-branching in different patterns, with fine, ray-like branchelets extending comb- or bottle brush-like from their axes for prey capture (e.g., Vacelet, 2006, 2007, 2008; Lee et al., 2012; Vacelet, 2020). Carnivorous sponges may be confused with other erect sponge morphologies (palmate, branching, stalked). This may not much change the outcome of the interpretation of environmental conditions, however, as long as these extreme forms of erect morphologies are understood as an adaptation to oligotrophy or reduced flow. Carnivorous sponges are here listed as a separate morphology, because they represent the strongest deviation from the basic physiological functions in sponges, but they may respond to subtle ambient flow conditions with two- and three-dimensionality as do other erect sponges. Carnivorous sponges such as *Abyssocladia* spp., *Cladorhiza* spp. and *Chondrocladia* spp. belong into the family Cladorhizidae (Fig. 3D-E).

3.2. Application of the sponge classification scheme based on functional morphologies

The proposed classification scheme will enable science and management to quantify sponges widely and consistently for environmental surveys of the marine benthos. Traditionally, surveys that aim to detect differences or changes in biologic communities relied on the quantification of biodiversity via taxonomy or by assessing trophic guilds (e.g., Bremner et al., 2003). However, limitations to resources or expertise or by hazardous environments can prevent easy access to such information. Instead, recent environmental surveys increasingly include other observations accessed with different means. They look into the link between biota and their ecosystems and generating quantitative data about the

community structure, its function, ecosystem health and environmental conditions (e.g., Bremner et al., 2003; Petchey and Gaston, 2006; Saito et al., 2015; Zawada et al., 2019). The proposed sponge classification scheme caters for the same outcome: morphologic and functional diversity can be used as a proxy for taxonomic community diversity, even if based only on imagery (Lauder, 1990; Bell and Barnes, 2001b; 2002; Bell, 2007a; Giribet, 2015; Hadi et al., 2015; Gerovasileiou and Voultsiadou, 2016). In addition, the scoring structure is designed to explain dominant functional traits of the sponges, which can in turn inform on disturbance or functional shifts, as has been done in similar benthic groups (e.g., Alvarez-Filip et al., 2011; Álvarez-Noriega et al., 2016). Moreover, strongly predominant morphologies can act as surrogates for prevailing environmental conditions (Table 3, Suppl. 1). Similar insights have earlier been realised and applied for very different benthic assemblages and taxa, e.g. for corals (e.g., Denis et al., 2017), polychaetes (e.g., Bonsdorff and Pearson, 1999), fishes (e.g., Bellwood et al., 2019) and macroalgae (e.g., Balata et al. 2011), and sponge surveys based on the present scheme can yield comparable data (e.g., Bell et al., 2017). As long as a standardised system is used, such data can provide a wide range of spatial and temporal context and can fit into the CATAMI classification system (<http://catami.github.io/>) and other monitoring or classification systems such as e.g. proposed by Gutt (2007) or Makowski et al. (2009).

According to the present observations, hydrodynamic and sediment conditions appear to be the strongest selective forces for certain sponge morphologies (Fig. 11) and may have the most impact on sponge functions, which is in agreement with earlier results (e.g., Carballo et al., 1996; 2008). With the exception of carnivorous sponges, all physiological functions in sponges rely on the pumping of water through their aquiferous system: the inhalant water carries food, oxygen and sperm into the sponges, the exhalant water releases waste and sexual products (e.g., Reiswig, 1970; Fry, 1979; Weissenfels, 1992; Nickel et al., 2006;

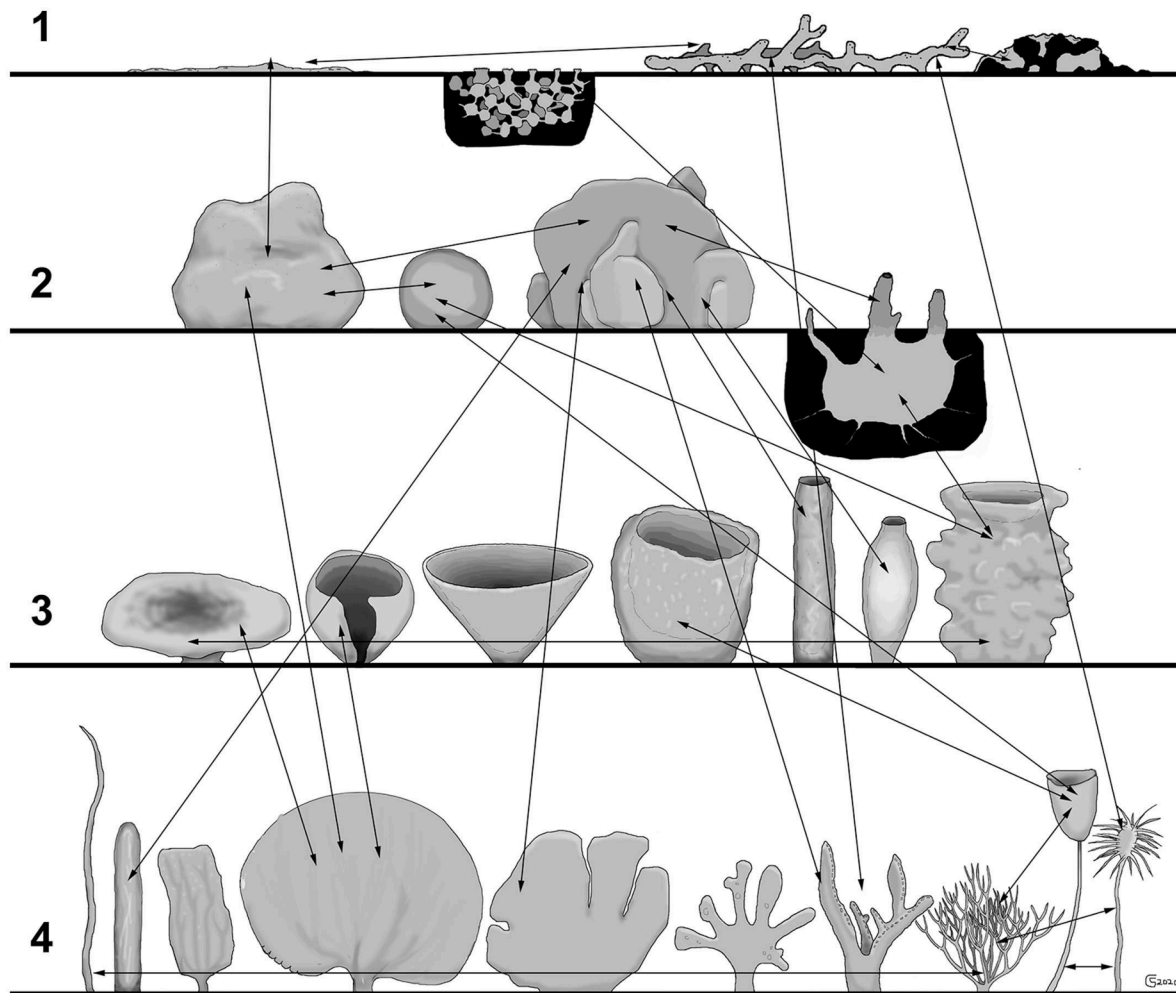


Fig. 12. Common interrelationships between sponge morphologies – many forms can express intermediate shapes. Arrows connect morphologies that are not depicted next to each other but can still merge into each other or develop intermediate shapes. From top to bottom and left to right: 1 – Functional crusts (crusts, endolithic bioeroding, creeping, insinuating), 2 – functional massives (simple, globular, composite, fistular), 3 – functional cups (table, incomplete, complete-infundibuliform, complete-vasiform, tubular, amphorate, barrel), 4 – functional erect forms (1D: whip, column, 2D: spatulate, flabellate, flabellate to palmate, palmate, 3D: thickly branching, thinly branching; stalked; carnivorous). Within the cup-like forms and within the 1D to 2D erect forms all hybrid forms are possible.

Bell, 2007b; Schläppy et al., 2007). Water movement is thus vitally necessary to bring new supplies to the sessile organisms and to carry away the expelled materials. At the same time, sediments may exert a risk of occlusion and clogging of the aquiferous system, especially finer sediments (Schönberg, 2016b). In sponges, the hydrodynamic environment will therefore impact on almost every aspect of life. Where ambient water movement becomes too violent or turbulent, sponge morphological diversity becomes reduced due to the damaging effect on the more fragile growth forms, and sponges with a large attachment area such as crusts and massive forms will be favoured (Bell and Barnes, 2000a; Fig. 1A–C). In moderate flow with less mixing, separation of in- and exhalants will occur (Figs. 2, 5, 7). In environments characterised by finer sediments, erect forms dominate that stretch into the water column, either to reach fresh supplies, or to lower the proportion of horizontal tissue area to minimise effects of sedimentation (Bell and Barnes, 2000a; Fig. 3). Two-dimensionally erect sponges are a distinctive group to indicate laminar flow (Lawler and Osborn, 2008; Fig. 3A). Carnivorous sponges are a very specialised group that no longer relies on the aquiferous system, and their occurrence suggests food limitation (Fig. 3D–E). Flow conditions will have further, indirect impacts on sponges, e.g. by affecting the presence and quality of sediments, turbidity and sedimentation. Fistular, endoposammic sponges are

specialists that tolerate burial in sediments by stretching parts of their bodies vertically into the water column or develop convex, knuckle-shaped portions, parts that remain free of sediment deposition (Bell and Barnes, 2000a; Fig. 1D). In this way, sponge morphologies and environmental conditions are clearly linked, and ecological information relates most often to the hydrodynamic conditions.

There are some constraints to the present scheme, however, and the functional context is always very important. The surrogate information about environmental conditions here discussed only becomes available from sponges growing on horizontal surfaces. Where they grow on vertical surfaces or underneath ledges, they experience other flow regimes than their morphologic equals on open horizontal ground. On vertical and inverted surfaces they would also escape sediment deposition, and where they grow underneath stones, they cannot attain larger and more complicated growth forms. Sponges in such microhabitats are also less recognisable, less visible or even invisible on imagery. Apart from this, encrusting sponges have been identified as superior space competitors (Jackson, 1979; Aerts and van Soest, 1997). However, it has also been argued that at sites with much live cover and high pressure of space competition, sponges with small attachment area or fast-growing species such as commonly found in creeping forms may emerge in favour of other morphologies (Hadi et al., 2015) – which is another theory that

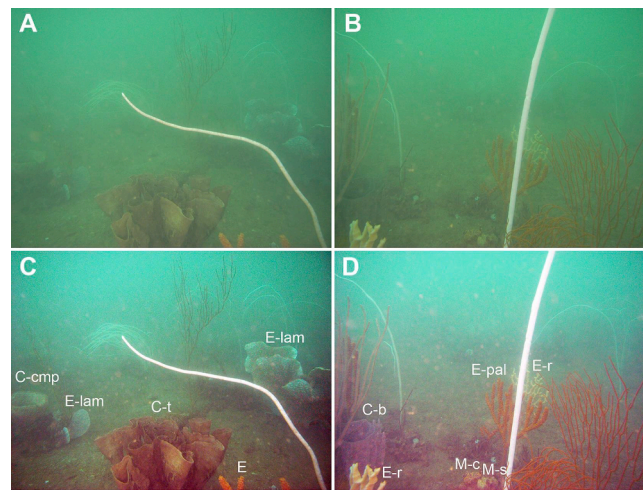


Fig. 13. Assessment of underwater imagery in turbid environments can be very difficult either through lack of contrast or by backscatter of light reflecting off suspended particles (A, B; here forward image capture, rather than downwards, in –10 to –15 m, Onslow, NW Australia). Image enhancement can bring out more details (C, D) and allows scoring of more forms than apparent on A-B; forms indicated above each sponge: *C-b* – barrel (*Xestospongia testudinaria*), *C-cmp* – complete cup, *C-t* – tubular sponge (*Ianthella basta*), *E* – erect (in this case it is likely palmate, but cannot conclusively be evaluated as it is mostly cut off), *E-lam* – two-dimensionally erect-laminar (*Ianthella* sp.), *E-pal* – two-dimensionally erect-palmate (cf. *Axos* sp.), *E-r* – two-dimensionally reticulate-erect (cf. *Echinodictyum pulchrum*), *M-c* – composite-massive, *M-s* – simple-massive. Digital enhancement can render underwater imagery quite grainy, and it is at the expense of an increased effort. Examples for scoring from images that were obtained with the camera pointing downwards are given in Suppl. 6.

may require more evidence. Environmentally driven selection for certain morphologies will be more strongly expressed and will generate clearer form dominances when the drivers are few and strong, with visible effects not being diluted by antagonistic factors (Jackson, 1979).

It also needs to be understood that the proposed sponge morphologies are not static, and not always immediately obvious. There are morphologic continua and intermediate forms that can make unambiguous scoring difficult (Fig. 12). Also, the ecological context can change the functional setting for each morphology (Fig. 4), as was explained above during the definition of the functional morphologies. Moreover, the factors here considered as selective forces for the sponge morphologies are acting at the survival or growth level, not so much at the level of settlement and establishment as has also been discussed by e.g. Jackson (1979). These early phases of community formation and maintenance also play a role and may further complicate the situation and can lead to temporal successions of morphologies. Jackson (1979) proposed that in such a succession, disturbance creates newly available substrate, which should first be colonised by creeping and encrusting forms. Under good conditions and reduced disturbance, the community should then move towards massive forms, into which he included cups. Should food become limited, the community would then or alternatively tend towards erect forms. While the present proposal is well supported by published field observations (Suppl. 2), further confirmation and more quantitative cause-response evaluations should be pursued using experimental settings.

The concept of scoring sponges by their functional morphologies was originally devised to enable quantitative assessment of sponge communities when physical sampling is impossible. It is based on a number of different impulses and principles, which have advantages and disadvantages, more strongly leaning towards advantages:

- + Imagery allows access to habitats where hazardous local conditions prevent safe diving and thus preclude direct observations (water depth, hydrodynamic conditions, wildlife, visibility; Althaus et al., 2015).
- + *In situ* imagery can greatly enhance and augment already available ecological and taxonomic information beyond traditional out-of-context bench top observations (e.g., Fig. 6), even if it will never replace measured data, taxonomic analysis and voucher collections (e.g., Garrouste, 2017; Newcomer et al., 2019).

- + Assessing sponge communities through imagery can significantly shift costs from fieldwork to the office and time expense from sampling and species analyses to data evaluation (Bell, 2007a; Althaus et al., 2015; Bell et al., 2017). Thereby larger areas can be surveyed in less time than by physical collection, thus producing larger, more complete and more generally applicable datasets. This is especially important for taxa that are as patchily distributed as sponges (e.g., Barnes et al., 2006, 2013).
- + The proposed approach readily fits into published and tried Australian classification schemes including other biota and geomorphological features (Last et al., 2010; Althaus et al., 2015), and can be fitted into non-Australian schemes (e.g. Gutt, 2007; Makowski et al., 2009). These schemes are suitable for marine habitats globally.
- + Monitoring programs often rely on simple approaches in accordance with resources and means, and they commonly depend on assistance by non-experts. The simple nature and the detailed images and explanations for the present scheme remove the necessity of specialist participation and allow non-expert involvement, e.g. citizen scientists, as long as they can recognise sponges and distinguish them from other organisms (Bell, 2007a; Gerovasileiou and Voultsiadou, 2016; Gerovasileiou et al., 2017).
- + Imagery can be more versatile than specimen collections, in that imagery and derived data are retained and can be revisited at different times and used for different purposes and formats than originally intended; by standardization and character annotation, resulting datasets can be reformatted and amended at any time without data loss or confusion of scored groups (Althaus et al., 2015).
- + Imagery represents a means of non-destructive sampling for organisms of which we know little with respect to survival, regeneration potential and their conservation status at global scale or at the community level (Bell et al., 2015; Schönberg, 2016b).
- + By employing a standardised approach, growing knowledge collecting from the scheme's use will be comparable across different studies and will increasingly improve our approaches to benthic surveys comparing sponge communities across spatial and temporal scales, and will enable before-after-impact assessment (in contrast to data from references in Suppl. 1).
- + Characterising sponge communities by dominant morphologies facilitates recognition and matching of functionally similar

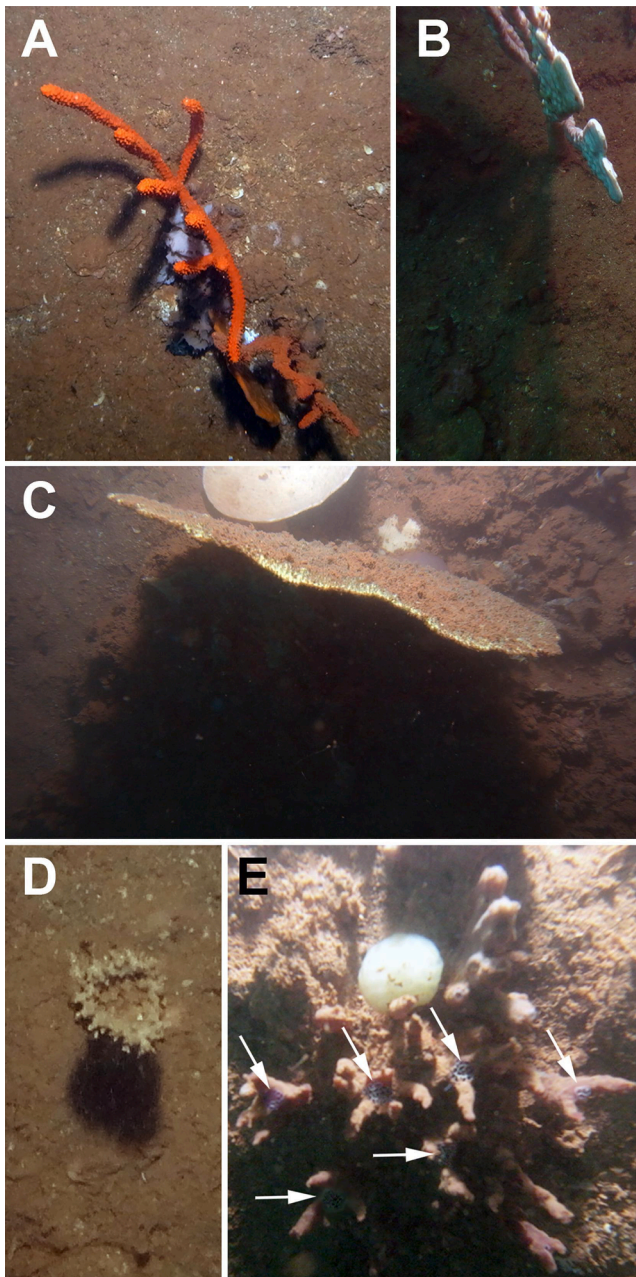


Fig. 14. Imagery from towed equipment with downward capture generates a haphazard selection of objects that are often only partially in the frame. These objects then appear reduced in bulk or shape due to the angle of view. The shadow and other details can at times be used to access more information or to better interpret the images (images were here rotated 180° for a more intuitive angle – the light source of the towing gear usually projects the shadows forwards). A – From above this sponge looks like a creeping sponge, but the shadow shows that it is erect and palmate (cf. *Axos* sp.). B – There large shadow confirms the form of the partial palmate sponge. C – Erect-laminar sponges or fans usually appear as slim bands in the images, but the shadow reveals that it has a large vertical area (*Ianthella* sp.). D – The large shadow suggests this is a stalked sponge, not just a low-relief cup (cf. *Aplysinopsis* sp. or cf. *Echinodictyum clathroides*). E – At first glance this individual looks like a three-dimensionally branching sponge, but after image enhancement and when zooming in, oscular fields can be seen where the branches meet (arrows), revealing that this is an endopasmmic sponge with branching fistules (*Oceanapia* sp.).

assemblages between different situations and validates the method (Bell et al., 2006).

- + With the proposed classification scheme, imagery can be explored in a functional context even without physical samples, at times creating more meaningful data beyond a mere specimen count and allowing interpretation of environmental conditions (de Laubenfels, 1936; Schönberg and Fromont, 2013, 2019). In comparison to taxonomy-only biodiversity assessments, scoring biological traits or ecological functions can occasionally generate stronger information to distinguish benthic assemblages, the habitat, or a level of disturbance at a finer scale (Bremner et al., 2003; Bell et al., 2017). Multimetric approaches in benthic surveys are thought to provide better insights into ecosystem function and cause-response relationships where community changes can be detected (Saito et al., 2015; here: organismic diversity and function *versus* ambient conditions).
- + A deeper understanding of morphology-related traits is vitally important in palaeoenvironmental reconstruction using fossilised sponges (Trammer, 1979; Leinfelder et al., 1996; Krautter, 1998; Giribet, 2015). Present, imagery-derived knowledge will support respective efforts.
- Sponge species cannot usually be identified from imagery, and occasionally resulting taxonomic information will remain superficial without physical samples.
- While imagery can be a means for data collection where physical sampling is impossible, vouchers and reference collections are still absolutely necessary (e.g., Suarez and Tsutsui, 2004). Classification and data extraction from images are heatedly being discussed and thought to lower the scientific diligence and data quality, as well as removing lasting opportunities arising from reference collections (e.g., Cerfaco et al., 2016; Grandcolas, 2017; Orrico, 2017; Thorpe, 2017; Newcomer et al., 2019).
- Lack of physical samples can also limit deeper insights into the sponges' biology in general (Homberger, 1988). Where samples can be taken, this approach should be preferred for traditional biodiversity assessments and to acquire additional biological data, e.g. whether sponges are photosymbiotic or when they are reproductive. Therefore, using the scheme we generate knowledge with respect to community status and shifts, but we may not always understand the reasons for the observations or physiological consequences down the line.
- Underwater imagery can only work with organisms that can still be adequately focused during the image assessment to recognise the phylum and the morphology. Respective datasets will thus be biased towards larger, conspicuous individuals. Communities that mainly consist of cryptic or small individuals such as on Carnarvon Shelf, NW Australia (Bell et al., 2006; Schönberg and Fromont, 2012) cannot be comprehensively surveyed in this way. Smaller, less obvious species are generally more easily overlooked (Bell, 2007a).
- Image quality and angle can be an obstacle for reliable scoring. In particular, images taken in turbid waters may not allow enough resolution, even after image enhancement (Fig. 13A-D). The vertical angle that is often used in towed image capture, and sponges being only partially captured per frame can also cause problems. However, at times such obstacles can be overcome by local knowledge, by assessing the sponge's shadow (Fig. 14A-D) or by looking for characteristic, group-specific details (Fig. 14E).
- Classification and scoring accuracy from images may be lower than in a traditional taxonomy analysis (Lawler and Osborn, 2008 reached 77% overall accuracy), and bias may be introduced by accuracy levels varying from morphology to morphology (Lawler and Osborn, 2008: 56-80%). This is the reason why a standardised approach and well-illustrated instructions are vital.

Since the publication of earlier versions (Schönberg and Fromont, 2013, 2014, 2019; Althaus et al., 2015), this sponge classification scheme based on functional morphology has been applied during a number of benthic surveys in Australia (e.g., Schönberg and Fromont, 2012; Fromont et al., 2013; Carroll et al., 2014; Przeslawski et al., 2014; Bewley et al., 2015; James et al., 2017). However, as the use has not previously been explained in detail, some studies led to inconsistent or erroneous application. For example, an unpublished trial version in which the groups were not yet settled was prematurely used and published (e.g., Przeslawski et al., 2013). Further, in their photo catalogue Abdul Wahab et al. (2017) mostly identified erect-palmate (2D) forms as erect-branching (i.e., as 3D), and some barrels or fistular sponges were listed as simple-massive, which would each reflect different responses to environmental conditions and might have led to the inaccurate interpretation of environmental conditions or would have been inappropriate for comparisons. However, this was not the aim for the photo catalogue, and the inaccurate application of the present classification scheme is of little consequence in this particular case. In contrast, George et al. (2018) specifically employed this scheme to test the usefulness of sponge functional morphologies as environmental proxies, but the authors did not follow the proposed terminology and grouping, and the functional properties were incorrectly applied (see their Table 1 *versus* the present Tables 1–3). They erroneously identified sponges with small attachment area as resistant to turbulence (stalked and tabular forms). They stated that currents would select for encrusting, as well as for foliaceous (erect-laminar, 2D) morphologies, but the latter form was lumped with erect-branching forms (3D). While parts of the reasoning are correct, predominance of either of the three forms would reflect different flow regimes: turbulent flow selects for encrusting, laminar flow for two-dimensionally erect sponges such as fans and palmate forms, while reduced flow often results in the occurrence of three-dimensionally branching sponges. George et al. (2018) implied that sponges respond to turbidity by expanding their horizontal area to preferably form massive and cup-like morphologies. However, such sponges are more vulnerable to sediment deposition, and turbidity and sedimentation would likely rather select for erect morphologies. Moreover, the locations for their imagery and the locations for the environmental data measurements did not match, thus making the whole effort futile. In consequence, the authors did not find good correlations between their observations of the growth forms of sponge and environmental conditions and arrived at erroneous conclusions, e.g. that flow has no impact on sponge morphologies and that they are all roughly equally tolerant to adverse conditions such as heat stress and storm damage. Another disadvantage inherent to previous approaches is that as a rule the choice of used morphologies included only sponge forms that were commonly present but did not consider what was absent and why (Suppl. 1). Where a set of morphologies is not considered from start, it may become overlooked. Final datasets can only provide a good understanding of the assemblages' functions if the investigators not only list dominant morphologies, but also consider which forms are missing, and why.

4. Conclusions

The present publication maintains that sponges can and will respond to certain environmental conditions with phenotypic changes (branch patterns, oscular diameters), or selective pressures will establish a dominance of certain sponge growth forms represented by different species. The most influential factors in this context appear to be flow and sediment conditions. Both factors impact directly on the most important function in sponges: the way they pump water through their bodies and the physiological processes that are supported by this. Future studies may fine-tune the proposed categories and identify whether there are further environmental conditions that have a direct effect on sponge morphologies and how they contribute to the community structure in some yet unknown way. For the time being, the proposed classification scheme provides a valuable tool that can be used across sponge taxa, oceans and bathymetry, enabling standardised data acquisition comparable between approaches

with widely different motives and purposes.

Declaration of Competing Interest

The author declares that she has no known competing financial interest or personal relationship that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2021.107806>.

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