

Review

A Review on Genus *Halichondria* (Demospongiae, Porifera)

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Abstract: Demosponges of the genus *Halichondria* Fleming (1828) are common in coastal marine ecosystems worldwide and have been well-studied over the last decades. As ecologically important filter feeders, *Halichondria* species represent potentially suitable model organisms to link and fill in existing knowledge gaps in sponge biology, providing important novel insights into the physiology and evolution of the sponge holobiont. Here we review studies on the morphology, taxonomy, geographic distribution, associated fauna, life history, hydrodynamic characteristics, and coordinated behavior of *Halichondria* species.

Keywords: demosponges; morphology; taxonomy; geographic distribution; holobiont; life history; hydrodynamics; coordinated behavior; model organism

1. Introduction

The genus *Halichondria* Fleming (1828) [1] (Demospongiae, Porifera; subgenera *Halichondria* and *Eumastia*) contains the most common marine sponge species of the North Atlantic [2], including the common “bread-crumbs” sponge *Halichondria* (*Halichondria*) *panicea* Pallas (1766) [3] and Bowerbank’s horny sponge *H. bowerbanki* Burton (1930) [4]. The most studied species, *H. panicea*, occurs in habitats covering a broad range of salinities, temperatures, turbidities, and flow conditions [5,6] and has been recorded in marine intertidal and sublittoral zones down to depths of more than 500 m [2]. *Halichondria panicea* provides substrate for many other marine organisms, including a large and varied associated fauna [7–9], symbiotic algae [10,11], and numerous bacteria [12,13]. The life histories of *Halichondria* spp. are characterized by different modes of asexual and sexual reproduction [14], with the latter revealing strong species- and habitat-specific adaptations [15–18]. *Halichondria* sponges are filter feeders capable of processing large volumes of seawater (up to six times their own body volume per minute [19]) and efficiently retaining small food particles [20], thus playing a key role in nutrient recycling of coastal marine ecosystems [8]. Modular arrangement of their leuconoid aquiferous systems [21,22] has made it possible to study the hydrodynamic properties of the sponge filter-pump, which may help to shed light on the evolution of complex filter-feeding systems in sponges (cf. [23]). Despite their apparently simple bauplan without a nervous or muscular system, *Halichondria* spp. show coordinated responses to changing environmental conditions, including phototactic responses of larvae [24], sponge body shape changes [25], and contractile behavior [22,26–28]. The detailed mechanisms underlying coordinated behavior in sponges are still unclear [29], but existing data for *Halichondria* points out the importance of cellular communication based on a neuronal-like ‘toolkit’ and could serve as a milestone towards an improved understanding of tissue organization in the first animals.

The vast majority of studies on *Halichondria* (a total of 11,100 research articles according to Google scholar) are based on *H. panicea* (36.4% of total research articles) with a focus on the biological and ecological aspects, whereas much fewer studies within these research



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fields have addressed other species, such as *H. bowerbanki* (4.0%), *H. melanadocia* Laubenfels (1936) [30] (1.5%), *H. moorei* Bergquist (1961) [31] (1.0%), or *H. semitubulosa* Lamarck (1814) [32] (0.2%, Table 1).

Table 1. Number of research articles on *Halichondria* Fleming (1828) based on genus- and species-level (cf. [33]) according to Google Scholar (Web of Science) along with the main Web of Science research categories (accessed on 6 July 2022).

Species	No. Articles	(%)	Web of Science Categories (%)
<i>Halichondria panicea</i>	4040 (229)	36.4	Marine Freshwater Biology (43.5), Ecology (19.2), Oceanography (16.2)
<i>Halichondria okadai</i>	2980 (96)	26.8	Organic Chemistry (39.6), Pharmacology Pharmacy (16.7), Biochemistry Molecular Biology (14.5)
<i>Halichondria</i> sp./spp.	1390 (73)	12.5	Organic Chemistry (34.3), Medicinal Chemistry (20.6), Pharmacology Pharmacy (20.6)
Genus <i>Halichondria</i>	723 (14)	6.5	Organic Chemistry (21.4), Pharmacology Pharmacy (21.4), Biochemistry Molecular Biology (14.3)
<i>Halichondria bowerbanki</i>	447 (10)	4.0	Ecology (50.0), Marine Freshwater Biology (40.0), Zoology (30.0)
<i>Halichondria japonica</i>	260 (20)	2.3	Biochemistry Molecular Biology (30.0), Organic Chemistry (20.0), Fisheries (15.0)
<i>Halichondria cylindrata</i>	173 (10)	1.6	Organic Chemistry (70.0), Medicinal Chemistry (30.0), Biochemistry Molecular Biology (10.0)
<i>Halichondria melanadocia</i>	169 (17)	1.5	Marine Freshwater Biology (52.9), Ecology (29.4), Anatomy Morphology (50.0)
<i>Halichondria moorei</i>	108 (2)	1.0	Marine and Freshwater Biology (50.0), Multidisciplinary Sciences (50.0)
<i>Halichondria sitiens</i>	89 (5)	0.8	Biodiversity Conservation (20.0), Biology (20.0), Ecology (20.0)
<i>Halichondria oshoro</i>	82 (2)	0.7	Microbiology (100.0)
<i>Halichondria magniconulosa</i>	67 (2)	0.6	Applied Chemistry (50.0), Medicinal Chemistry (50.0), Ecology (50.0)
<i>Halichondria semitubulosa</i>	25 (1)	0.2	Zoology (100.0)
<i>Halichondria cartilaginea</i>	19 (0)	0.2	-
<i>Halichondria genitrix</i>	19 (0)	0.2	-
<i>Halichondria albescens</i>	18 (0)	0.2	-
<i>Halichondria lutea</i>	18 (3)	0.2	Biochemistry Molecular Biology (66.7), Ecology (66.7), Evolutionary Biology (66.7)
<i>Halichondria coerulea</i>	14 (1)	0.1	Ecology (100.0), Marine Freshwater Biology (100.0), Oceanography (100.0)
<i>Halichondria glabrata</i>	14 (2)	0.1	Anatomy and Morphology (50.0), Biology (50.0), Food Science Technology (50.0)
<i>Halichondria diazae</i>	13 (0)	0.1	-
<i>Halichondria cebimarensis</i>	12 (1)	0.1	Ecology (100.0), Marine Freshwater Biology (100.0)
<i>Halichondria phakellioides</i>	12 (1)	0.1	Fisheries (100.0), Limnology (100.0), Marine Freshwater Biology (100.0)
<i>Halichondria attenuata</i>	11 (2)	0.1	Marine Freshwater Biology (50.0), Zoology (50.0)
<i>Halichondria contorta</i>	10 (1)	0.1	Zoology (100.0)
<i>Halichondria topsenti</i>	10 (0)	0.1	-
<i>Halichondria oblonga</i>	9 (0)	0.1	-
<i>Halichondria aspera</i>	8 (0)	0.1	-
<i>Halichondria cristata</i>	7 (0)	0.1	-
<i>Halichondria agglomerans</i>	5 (0)	0.0	-
<i>Halichondria flava</i>	5 (0)	0.0	-
<i>Halichondria kelleri</i>	5 (0)	0.0	-
<i>Halichondria migottea</i>	5 (0)	0.0	-
<i>Halichondria osculum</i>	5 (1)	0.0	Medicinal Chemistry (100.0), Pharmacology Pharmacy (100.0)
<i>Halichondria colossea</i>	4 (0)	0.0	-
<i>Halichondria marianae</i>	4 (2)	0.0	Marine Freshwater Biology (50.0), Zoology (50.0)
<i>Halichondria prostrata</i>	4 (0)	0.0	-
<i>Halichondria tenebrica</i>	4 (0)	0.0	-
<i>Halichondria capensis</i>	3 (0)	0.0	-
<i>Halichondria convolvens</i>	3 (0)	0.0	-
<i>Halichondria elenae</i>	3 (1)	0.0	Ecology (100.0), Marine Freshwater Biology (100.0)
Other species	316 (36)	2.1	Cell biology (100.0), Zoology (100.0)
Total	11,100 (532)	100.0	Marine and Freshwater Biology (27.3), Organic Chemistry (17.5), Ecology (12.8)

Other studies have explored the metabolite chemistry of *Halichondria*, mainly for the species *H. okadai* Kadota (1922) [34] (26.8%, Table 1), for undefined species (*Halichondria* sp./spp., 12.5%), or on a genus-level (6.5%), reflecting partially unresolved and still ongoing taxonomic revisions of *Halichondria* species [35]. Molecular biology, including studies on the sponge microbiome, has mainly been investigated on *H. okadai*, *H. japonica* Kadota (1922) [34] (2.3%), *H. cylindrata* Tanita & Hoshino (1989) [36] (1.6%), and *H. oshoro* Tanita (1961) [37] (0.7%). Few morphological studies exist for *H. melanadocia* and *H. glabrata* Keller (1891) [38] (0.1%), while research on the hydrodynamics of sponges has remained restricted to *H. panicea* and *H. coerulea* Berquist (1967) [39] (0.1%). Despite the relevance

of comparative studies on sponge cell biology, most *Halichondria* species have remained understudied (2.1%, Table 1). The aim here is to provide a compilation of studies concerning sponges in the genus *Halichondria* and point out existing knowledge gaps that may aid in future studies of these ecologically important demosponges.

2. Morphology, Taxonomy, and Distribution

The genus *Halichondria* is placed in the animal phylum Porifera, class Demospongiae, subclass Heteroscleromorpha, order Suberitida, and family Halichondriidae. Growth forms of *Halichondria* species include encrusting, massive, occasionally irregularly branching, or digitate sponges with smooth or papillate surfaces. An important morphological character to separate the two subgenera, *Halichondria* and *Eumastia*, is the absence or presence of short conical papillae on the sponge surface, respectively [2]. Members of the genus *Halichondria* typically form chimneys of variable size (up to 5 cm high) with conspicuous, relatively large oscula (2–4 mm in diameter). They are characterized by their firm but compressible texture and variable color, from olive-green (due to symbiotic algae) over orange-yellow to creamy-yellow [2] (cf. Appendix A, Figure A1). The siliceous spicule skeleton of *Halichondria* consists exclusively of oxeas or oxea derivatives in a wide size range, which are arranged in an ectosomal crust (200–300 µm thick) and appear scattered or in tight bundles in the choanosome along with spongin fibers [2,40]. While the functional cell morphology and number of cell types in *Halichondria* has remained largely unknown, 18 distinct cell types which comprise four major cell families, including contractile, digestive, and amoeboid-neuroid cells, have recently been described in the freshwater demosponge *Spongilla lacustris* [41].

Species identification is traditionally based on morphological characteristics, such as the shape and structure of the skeleton and the size and form of spicules [42], but several of these characters show strong intra-specific variation and are, therefore, of rather poor quality to distinguish species. For instance, a variety of growth forms are represented by *H. panicea*, ranging from thin encrusting (Figure A1a) to erect ramose (Figure A1b), which seems to depend on the intensity of ambient water currents [43] (cf. [44]). Moreover, an extensive overlap of spicule sizes in different species has been documented [2]. Molecular data used in phylogenetic studies includes complete mitochondrial genomes of several *Halichondria* species [45–47] and mitochondrial and ribosomal markers [48,49]. The classification of genus *Halichondria*, as defined in [2], is still in need of a major revision at an ordinal level [35,50], as classification based on morphology disagrees with phylogenetic analyses using molecular data. Overall, morphological, biochemical, and molecular characters applied in recent phylogenetic analyses seem to point out that *Halichondria* is nonmonophyletic [51–54].

To date, about 100 *Halichondria* species are accepted [33,55,56]. They occur in different types of marine habitats around the world, being widespread in European [4,11,57,58], American [2], and Brazilian coastal waters of the Atlantic [59], but also in parts of the Baltic Sea [60], the White Sea [61], and the Mediterranean Sea [62]. *Halichondria* species also occur in the North Pacific, including Alaska [63,64], Japan [65], Korea [42,66], and the South China Sea [67]. The closely related species *H. panicea*, *H. bowerbanki*, and other species in this complex may serve as a suitable model to illuminate possible speciation events due to their overlapping distribution in the North Atlantic, where *H. panicea* is mainly found in shallow, protected coastal regions of the eastern parts, and shows adaptation to frequent air exposure, while *H. bowerbanki* is most common in exposed habitats of the western parts, where it tolerates high levels of siltation [11]. A molecular study based on a part of the mitochondrial marker COI suggests that North East Pacific *H. cf. panicea* is genetically distant from and forms a sister group to a species complex consisting of European *H. panicea* and *H. bowerbanki* [53]. *Halichondria panicea* has also been reported from the Tropical Southwestern Atlantic, along with other species such as *H. magniconulosa* Hechtel (1965) [68], *H. cebimarensis*, *H. tenebrica*, *H. migottea*, *H. sulfurea* Carvalho & Hajdu (2001) [59] and *H. marianae* Santos et al. (2018) [69]. Common species in the Pacific Ocean

are *H. japonica* [65], *H. okadai*, *H. oshoro* [70], *H. gageoensis* and *H. muanensis* Kang & Sim (2008) [42], while *H. panicea* and *H. bowerbanki* have been reported from Alaska [63,64] and Korea [66], respectively. Revisions of the classification system should include more molecular data and more species and be used to reevaluate the morphological characters used in the traditional classification [50] (cf. [53,54]).

3. The Holobiont *Halichondria*

Halichondria spp. occur on a variety of inorganic and organic hard substrates, including mussel banks, small stones and rocks, and macroalgae [8,9,43,71]. The sponges themselves provide habitat for a diverse associated fauna and various symbiotic microorganisms. The associated epi- and endofauna of *H. panicea* include various Arthropoda such as skeleton shrimps (*Caprella* spp.) and copepods, but also molluscs, e.g., the scallop *Chlamys varia*, annelids, platyhelminths, and demersal fish that prey almost exclusively upon sponge epifauna [7–10]. Symbiosis with the dinoflagellate *Prorocentrum lima* has been documented in *H. okadai* [72,73], and *H. panicea* seems to harbor (intracellular) green algae [10,11]. However, many *Halichondria* species have not been investigated, indicating numerous other yet undiscovered symbiotic interactions, e.g., with dinoflagellates, cryptophytes, microalgae, and diatoms [73]. While the growth of pathogenic bacteria on *H. panicea* can cause sponge mortality under stagnant flow conditions [74], sponges harbor diverse microbial assemblages that contribute positively to host metabolism and defense [12,75,76]. *Halichondria* spp. are characterized as low microbial abundance (LMA) sponges with high variability in their bacterial diversity across species and environments [12,13,76]. While only 7 operational taxonomic units (OTUs) of microorganisms have been identified in *H. okadai* from Korea [77], about 500 OTUs were detected in *H. panicea* and *H. (Eumastia) sitiens* Schmidt (1870) [78] from the White Sea [76], respectively, and 1779 OTUs seem to be unique to *H. bowerbanki* from the mid-Atlantic region of the eastern United States [13]. The microbiome of *H. panicea* is dominated by a core taxon of Alphaproteobacteria within the class *Amylibacter* which has recently been named ‘Candidatus *Halichondriabacter symbioticus*’ [12,76,79–82]. Transmission of bacterial symbionts occurs in a mixed vertical (i.e., direct through reproduction) and horizontal mode (i.e., indirect through the environment) in *H. bowerbanki*; it is likely to vary across *Halichondria* species [13]. Metagenomics have revealed that distinct viromes with low similarity to known viral sequences are associated with *H. panicea* and *H. sitiens*, suggesting the existence of bacterial antiphage systems in sponges [76].

Halichondria sponges and their microbial symbionts produce a broad spectrum of mainly symbiont-derived bioactive metabolites [83] with cytotoxic or cell growth-inhibiting properties. Substances isolated from *Halichondria* sponges include halichondrin B and okadaic acid in *H. okadai* [72,84,85] or gymnostatins and dankastatins from an *H. japonica*-derived fungal strain [86] which may additionally serve *Halichondria* sponges as a defense mechanism against pathogens, predators, and biofouling [73,87]. Okadaic acid is a biotoxin known for its cyto-, neuro-, immune-, embryo-, and genotoxicity in marine animals [87–89] and has been suggested to protect the demosponge *Suberites domuncula* from bacterial and parasitic infections [87]. Epibiotic *H. panicea* can negatively affect the heart performance of blue mussels (*Mytilus edulis*), which may be due to the sponges’ release of excretory/secretory products. Such substances with cytotoxic properties and antimicrobial activity seem to benefit *H. panicea* in the competition for space and food across benthic fouling communities [90]. Neuroactive bacteria-derived compounds in *H. panicea* [73] suggest the relevance of symbiotic interactions for essential physiological processes such as coordinated behavior. The natural variability of sponge-microbe associations in *Halichondria* seems to provide a meaningful framework for modeling symbiotic interactions in metazoans (cf. [91]). In *H. bowerbanki*, for instance, changes in microbial communities after exposure to thermal stress have been documented [92], pointing out the relevance of future studies on sponges for assessing possible shifts in symbiont community composition and structure in response to global warming.

4. Life History

The life histories of *Halichondria* species typically include a reproductive period of 2–3 months in temperate regions [15,71,93]. *Halichondria* spp. are ovoviviparous and characterized by asynchronous gameto- and embryogenesis, while habitat-specific differences include successive hermaphroditism in White Sea populations of *H. panicea* and *H. sitiens* [18], simultaneous hermaphroditism in *H. panicea* and *H. bowerbanki* from the southwest coast of the Netherlands [16], incomplete gonochorism in *Halichondria* sp. from Mystic Estuary, US [15], or gonochorism in *H. panicea* from Kiel Bight, Germany [17]. In temperate regions, environmental parameters such as temperature and salinity drive the onset of sexual reproduction in *H. panicea* [17]. Differentiation of gametes from somatic cells has been observed in both *H. panicea* and *H. semitubulosa*, indicating the development of spermatozoa from choanocytes or archaeocytes, a process that may be species-dependent [62,94]. The larvae of *Halichondria* species are typically of parenchymella type and sometimes contain choanocyte chambers before settlement [24,95]. The release of *Halichondria* larvae seems to follow a light cue, being triggered by the onset of darkness in the temperate species *H. panicea* [96], while tropical *H. melanadocia* release larvae on exposure to light following a period of dark adaptation [24]. Phototactic responses of larvae range from positive to neutral to negative before settlement upon various hard substrates [24] (Figure A2a,b).

The growth of *Halichondria* sponges is dependent on temperature [70] and the concentration of available food, which mainly consists of bacteria and phytoplankton [97]. Pumping rates of *H. panicea* increase linearly with temperature and require relatively low energy demands for filtering large volumes of seawater [20,98], as expressed by F/R-ratios $\geq 15.6 \text{ L H}_2\text{O (mL O}_2\text{)}^{-1}$, which are comparable to other filter-feeding marine invertebrates [19]. In contrast, the energetic cost of growth is high in sponges [20,99], with exponential growth at a maximum rate of $4\% \text{ d}^{-1}$ in *H. panicea* under natural conditions [100]. The weight-specific growth of *H. panicea* is constant over sponge size, which has been pointed out as a unique feature among most other filter-feeding invertebrates, reflecting the modular organization of sponges [100]. A study of *H. panicea* from the Western Baltic Sea suggested that stored glycogen reserves fueled sexual reproduction and that the sponges degenerated in the end of the following year after reproduction [71]. Tissue regression and high mortality during the colder months of the year have also been reported for temperate *Halichondria* sp. from the Mystic and Thames estuaries, US [57,101] and for *Halichondria bowerbanki* from New England, US [102], respectively, while the longevity of *H. okadai* in Japanese waters may exceed 3 years when considering asexual reproduction, i.e., fission and fusion of sponge fragments [14]. *Halichondria panicea* is capable of rapid regeneration of damaged parts, as expressed in ≥ 3 -fold increased growth rates in response to predation [103] or during the reorganization of the aquiferous system in explant cuttings within approximately 6–10 days [22] (Figs. A2c-f), while other species, such as *H. magniconulosa*, seem to regenerate at slower rates [104]. Several *Halichondria* species, including *H. lutea* Alcolado (1984) [105], *H. magniconulosa*, and *H. melanadocia* have been recognized as important members of the Caribbean mangrove and coral reef communities, where they are preyed upon by fish [106,107]. *H. panicea* can also serve as a food source for hermit crabs, shrimp, large isopods (e.g., *Idothea* sp.), or the nudibranch *Archidoris montereyensis*, which may appear in such high density that it can eliminate large and long-lived sponge populations [63,64]. *Halichondria* sponges play an important role in nutrient recycling of coastal marine ecosystems due to their unique ability to retain small particles ($\leq 0.1 \mu\text{m}$) [20,108]. Regular tissue sloughing has been observed in *H. panicea* in response to sedimentation of organic material and settlement of small organisms on the sponge surface [109], along with seasonal remineralization of released *H. panicea* biomass following reproduction [8]. As the water pumping activity of *H. panicea* leads to an accumulation of pollutants, such as heavy metals, in direct proportion to ambient concentrations, their potential use as biomonitoring organisms has been proposed [40,110].

5. Hydrodynamics

As for other demosponges, the aquiferous system of *Halichondria* is leuconoid [21,40,111] and characterized by choanocytes organized in small spherical chambers which create a unidirectional flow of ambient water through a complex canal system [112,113]. The aquiferous elements of *Halichondria* act like a sieve for particles of variable size due to their aperture diameters (Figure A3a). As documented for *H. panicea*, they include numerous inhalant openings (ostia; 7–32 μm) through which seawater is drawn into incurrent canals (50–200 μm), finer incurrent canal branches (prosodi; 5 μm), and the prosopyles (1–4 μm) of choanocyte chambers (18–35 μm ; Figure A3b) [113]. Here, choanocytes retain small food particles $\leq 0.1 \mu\text{m}$ [20] on their microvilli collars (Figure A4a). Each choanocyte chamber of *H. panicea* contains about 40–120 choanocytes at an estimated choanocyte chamber density of 18,000 mm^{-3} [113]. Water leaves choanocyte chambers through an apopyle (7–17 μm ; Figure A4b) via excurrent canals (140–450 μm), which drain into an atrium (2.1 mm) from where the water exits the sponge in an excurrent jet through the osculum (1.2 mm) [113] (but see also [21]).

Each osculum represents a functional unit of aquiferous elements in a certain sponge volume (cf. Figure A2b–d), thus characterizing *Halichondria* sponges with multiple oscula as an array of several autonomous aquiferous modules [22,114,115]. The pumping rate of each aquiferous module is directly proportional to the density of choanocyte chambers in *H. panicea* [22], implying constant choanocyte densities for different *Halichondria* species. However, module size seems to determine the volume-specific pumping rates of *H. panicea*, which can reach a maximum of 15 $\text{mL min}^{-1} (\text{cm}^3 \text{ sponge})^{-1}$ in growing modules, as observed in single-osculum explants [26,27] (Figure A2c,d), while the modules in multi-oscula explants seem to pump at a lower maximum rate of 3 $\text{mL min}^{-1} (\text{cm}^3 \text{ sponge})^{-1}$ [22], probably due to a decrease in choanocyte chamber density with increasing module volume [116]. Based on the volume-specific pumping rate and choanocyte chamber density of *H. panicea*, the pumping rate per choanocyte chamber in a multi-oscula sponge can be estimated to $(3/18,000)/60 = 2.78 \times 10^{-6} \text{ mm}^3 \text{ s}^{-1} = 2778 \mu\text{m}^3 \text{ s}^{-1}$, and thus the pumping rate per choanocyte at an average of 80 choanocytes per chamber [113], to $(2778/80) = 35 \mu\text{m}^3 \text{ s}^{-1}$. This value is in range with a previous estimate of $(4.46 \times 10^{-6} \text{ mm}^3 \text{ s}^{-1}/95) = 47 \mu\text{m}^3 \text{ s}^{-1}$ for the demosponge *Haliclona permollis* [113,117] (their Table 1, respectively). A recent hydrodynamic model on the pump characteristics of leuconoid sponges assumed the presence of flagellar vanes along with a glycocalyx mesh which distally connects the microvilli collars of choanocytes, as has been shown for the freshwater sponge *Spongilla lacustris* [118,119], in order to deliver observed pump pressures [23]. These ultra-structural features of choanocytes have so far not been documented in *Halichondria* (cf. Figure A4a), pointing out the need for further studies on ultrastructure and hydrodynamic properties, which may provide valuable insight into the evolution of demosponge filter-pump systems (cf. [120]).

6. Coordinated Behavior

At least three different basic cell types are found in *Halichondria* species, including choanocytes, pinacocytes, and amoeboid (mesohyl) cells [24,121]. The coordinated behavior of sponge cells mediates the hydrodynamic and physical properties of the aquiferous system required for efficient filter feeding under different environmental conditions. Communication between motile cells is the basic principle underlying continuous tissue reorganization, regeneration, and microscale movements in sponges [122–125]—a topic which has, unfortunately, so far only been addressed by a few studies on *Halichondria* spp. Continuous tissue remodeling in *H. panicea*, as expressed by fusion, shape changes, and movement of sponges, has been observed in aquaria and intertidal rocky pools [25]. *Halichondria japonica* explants have been shown to fuse with explants of the same sponge, while they reject cells from other *H. japonica* sponges or from *H. okadai* [126]. Several types of mesohyl cells seem to be involved in this process of “self and nonself” recognition in *H. japonica*, including amoeboid archaeocytes, motile (granule-rich) gray cells, and collencytes [126].

Recent work on *H. panicea* points out the importance of cellular transport for the removal of inedible particles from the aquiferous system [27]. At the same time, sponge sandwich cultures may provide a suitable method (Figure A2e,f) for studying the cell types and mechanisms mediating capture, transport, and digestion/removal of edible and inedible particles (Figure A5).

Coordinated behavior further includes contraction of various parts of the aquiferous system, including the osculum [26], in- and excurrent canals, ostia and apopylar openings of the choanocyte chambers, resulting in reduction and temporal shut down of the water flow through single-ostium explants of *H. panicea* [27,28]. Contractile behavior is common among sponges and seems to follow species-specific cycles of distinct frequency and intensity [127–131] which can be expressed in asynchronous patterns across conspecifics in *H. panicea* [28,132]. Contractions can occur spontaneously in *H. panicea* explants under undisturbed conditions in the laboratory and can be induced by chemical messengers (γ -aminobutyric acid and L-glutamate) or by mechanical stimulation with inedible particles [28]. Coordinated contractions of different aquiferous modules in *H. panicea* explants with multiple oscula have been observed in response to external stimuli [22]. Peristaltic-like waves of contraction travel through the sponge, resulting in osculum closure at speeds of up to 233 nm s^{-1} in *H. panicea* ($15 \text{ }^\circ\text{C}$) [28]. Comparatively, observed contraction speeds of up to $12 \text{ }\mu\text{m s}^{-1}$ in the marine demosponge *Tethya wilhema* ($26 \text{ }^\circ\text{C}$) [129] and $122 \text{ }\mu\text{m s}^{-1}$ in the freshwater demosponge *Ephydatia muelleri* ($21 \text{ }^\circ\text{C}$) [131] seem considerably higher, emphasizing the need for future studies on the contraction kinetics of *Halichondria* species. During contractions, *H. panicea* shows reduced pumping activity [19,26,27], an associated decrease in respiration rates [132], and local internal oxygen depletion [133]. These physiological changes have been suggested as adaptations to variable environmental conditions, including food limitation [134], resuspension of sediment during storm events [135] (cf. [136]), seasonal changes in water temperature, changes in illumination period, spawning events of other sponge species [128], and facilitation of suitable habitat for specific symbiotic microorganisms [132,133]. Contractions may serve *Halichondria* sponges as an important mechanism to protect the sponge filter-pump in distinct aquiferous modules from clogging and damage and seem to be mediated by exo- and endopinacocytes [22,27,28,134,137], while the underlying cellular pathways have remained unclear. Previous studies have described contractile epithelial cells in sponges that function based on a ‘toolkit’ of neuronal-like elements, including sensory cilia, conduction pathways, and signaling molecules [41,134,138–140]. The pinacocytes of other demosponges exhibit actomyosin-based contractility [41,130,137,139,141,142], and myosin type II has been isolated from cells of *H. okadai* [143].

It is likely that communication between sponge cells in *Halichondria* is based on the extracellular spreading of chemical messengers [41,123,144], neuronal-like receptors [145], and cell contacts via cellular processes/membrane junctions [146–148]. As the abovementioned examples emphasize, cellular communication pathways require further attention in future studies. More detailed information on the functional cell morphology of *Halichondria*, as can now be accessed using whole-body single-cell RNA sequencing (cf. [41]), is needed to shed light on the principles underlying coordinated behavior in sponges. We encourage future work on the LMA demosponge *H. panicea* as a model organism to revisit functional coordination pathways with an integral perspective on the underlying morphological structures combining molecular, cytological, and physiological techniques.

7. Conclusions

Halichondria sponges are well-studied and the literature represents a strong base for our present understanding of the ecology and physiology of demosponges. Previous work has mainly focused on *H. panicea*, paving the foundations for modeling sponge-microbe interactions, hydrodynamics of the sponge filter pump, and cell communication in demosponges. We encourage future research to fill in present knowledge gaps regarding the functional cell morphology and filter-pump characteristics of *H. panicea*, along with comparative studies including other *Halichondria* species, to improve and verify existing models based on this ubiquitous demosponge genus.

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Appendix A

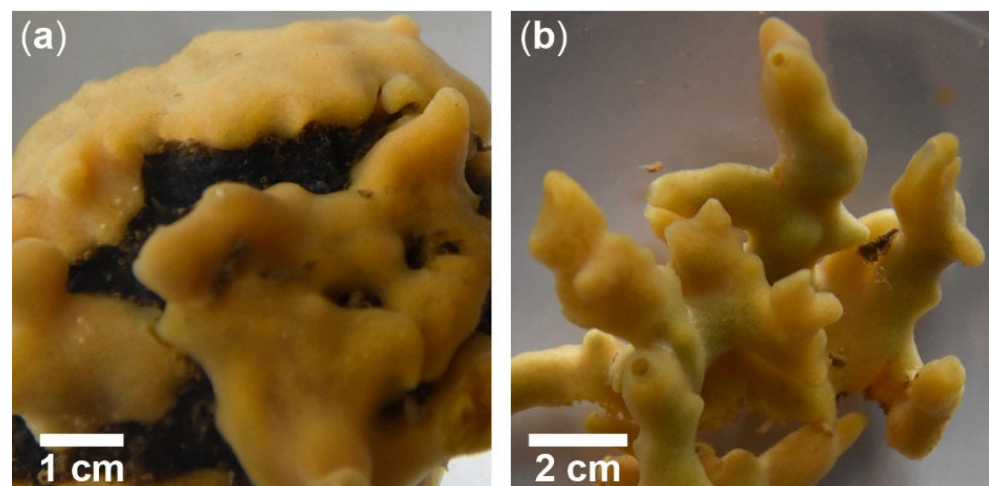


Figure A1. Growth forms of *Halichondria panicea* Pallas (1766) in the inlet to Kerteminde Fjord, Denmark (55°26′59″ N, 10°39′41″ E). (a) Growing on a piece of rope, collected in November 2020 and (b) with finger-shaped chimneys, found on wood in November 2020. Pictures: Héloïse Hamel.

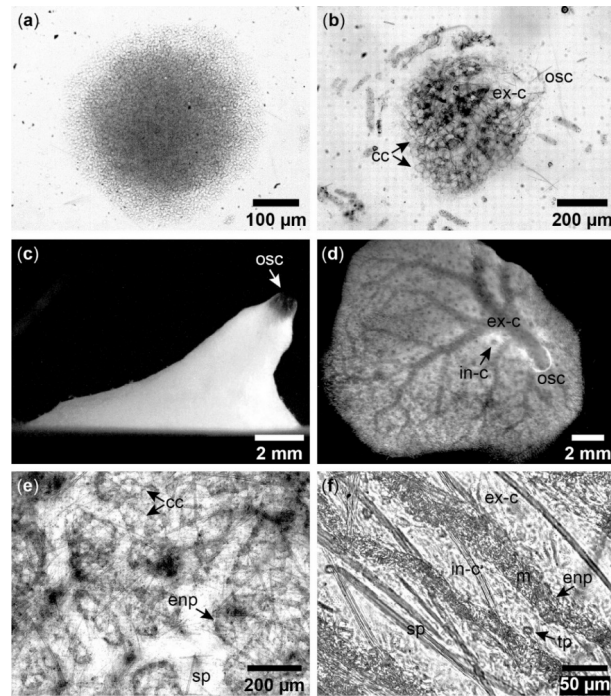


Figure A2. Aquiferous module formation in *Halichondria panicea*. (a) Sponge cells after larval settlement, (b) development of choanocyte chambers (cc), excurrent canals (ex-c) and an osculum (osc) in a juvenile sponge, (c) single-osculum explant (side-view), (d) explant (top-view) with visible incurrent (in-c) and excurrent canals (ex-c), (e) sandwich culture with choanocyte chambers (cc), spicules (sp), and endopinacoderm (enp) lining aquiferous canals, (f) sandwich culture after addition of edible particles (tp) for tracing water flow in the incurrent canal (in-c) which is separated from the flow in the excurrent canal (ex-c) by endopinacocytes (enp) and mesohyl (m).

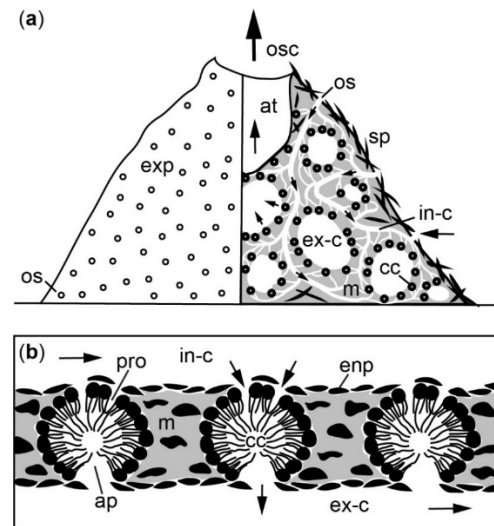


Figure A3. Schematic illustration of the aquiferous system in a functional module of *Halichondria panicea*. (a) Left: external surface with ostia (open circles), right: canal system with choanocyte chambers (black circles) and flow direction towards osculum indicated by arrows (b) water flow (arrows) through choanocyte chambers (cf. [111,117], their Figures 9d and 2b, respectively). Abbreviations: exp = exopinacoderm, os = ostium, in-c = incurrent canal, enp = endopinacoderm, pro = prosopyle, cc = choanocyte chamber, ap = apopyle, m = mesohyl, sp = spicule, ex-c = excurrent canal, at = atrium, osc = osculum.

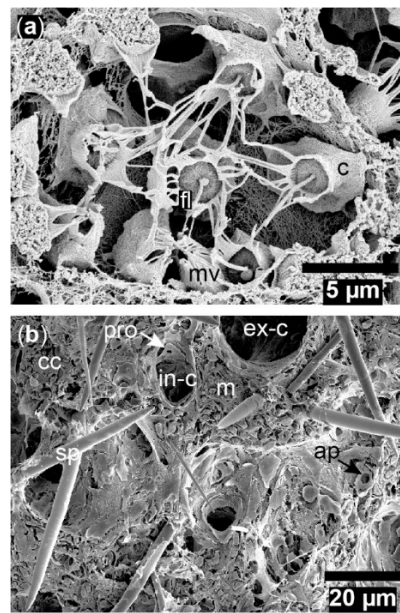


Figure A4. *Halichondria panicea*. SEM of cryo-fractured explants. (a) Choanocyte chamber with choanocytes (c) and their microvilli collars (mv) surrounding the flagellum (fl), (b) the fracture shows components of the aquiferous system with prosopyles (pro) and apopyles (ap) connected to incurrent (in-c) and excurrent canals (ex-c), respectively, embedded in mesohyl (m) with choanocyte chambers (cc) and spicules (sp).

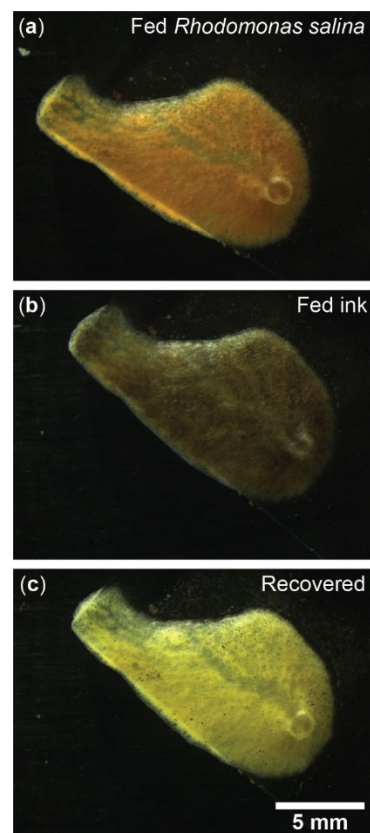


Figure A5. Exposure of *Halichondria panicea* to different particle types. Single-osculum explant (top-view) after (a) feeding on *Rhodomonas salina* (Cryptophyceae); note the red color originating from added algae, (b) exposure to inedible ink (Pelikan ScribtoI, 2×10^4 -fold diluted) for 1 h; note black color, and (c) recovery in particle-free seawater for 24 h. Pictures: Janni Magelund Degn Larsen.

References

- Fleming, J. *A History of British Animals: Exhibiting the Descriptive Characters and Systematical Arrangement of the Genera and Species of Quadrupeds, Birds, Reptiles, Fishes, Mollusca, and Radiata of the United Kingdom, Including the Indigenous, Extirpated, and Extinct Kinds, Together with Periodical and Occasional Visitors*; Bell & Bradfute: London, UK, 1828; pp. 506–524.
- Erpenbeck, D.; Van Soest, R.W. Family Halichondriidae Gray, 1867. In *Systema Porifera*, 1st ed.; Hooper, J.N.A., Van Soest, R.W.M., Willenz, P., Eds.; Springer: Boston, MA, USA, 2002; pp. 787–815.
- Pallas, P.S. *Elenchus Zoophytorum Sistens Generum Adumbrationes Generaliores et Specierum Cognitarum Succintas Descriptiones, Cum Selectis Auctorum Synonymis*; Fransiscum Varrentrapp: The Hague, The Netherlands, 1766; p. 451.
- Burton, M. Additions to the sponge fauna at Plymouth. *J. Mar. Biolog. Assoc. U. K.* **1930**, *16*, 489–508. [[CrossRef](#)]
- Hiscock, K.; Jones, H. Halichondria (Halichondria) bowerbanki Bowerbank's halichondria. In *Marine Life Information Network: Biology and Sensitivity Key Information Reviews*; Tyler-Walters, H., Hiscock, K., Eds.; Marine Biological Association of the United Kingdom: Plymouth, UK, 2007; pp. 1–14. [[CrossRef](#)]
- Hiscock, K. Halichondria (Halichondria) panicea breadcrumb sponge. In *Marine Life Information Network: Biology and Sensitivity Key Information Reviews*; Tyler-Walters, H., Hiscock, K., Eds.; Marine Biological Association of the United Kingdom: Plymouth, UK, 2008; pp. 1–16. [[CrossRef](#)]
- Forester, A.J. The association between the sponge *Halichondriapanicea* (Pallas) and scallop *Chlamys varia* (L.): A commensal-protective mutualism. *J. Exp. Mar. Biol. Ecol.* **1979**, *36*, 1–10. [[CrossRef](#)]
- Barthel, D. On the ecophysiology of the sponge *Halichondriapanicea* in Kiel Bight. 2. Biomass, production, energy budget and integration in environmental processes. *Mar. Ecol. Prog. Ser.* **1988**, *43*, 87–93. [[CrossRef](#)]
- Peattie, M.E.; Hoare, R. The sublittoral ecology of the Menai Strait: II. The sponge *Halichondriapanicea* (Pallas) and its associated fauna. *Estuar. Coast. Shelf Sci.* **1981**, *13*, 621–635. [[CrossRef](#)]
- Long, E.R. The associates of four species of marine sponges of Oregon and Washington. *Pac. Sci.* **1968**, *22*, 347–351.
- Vethaak, A.D.; Cronie, R.J.A.; Van Soest, R.W.M. Ecology and distribution of two sympatric, closely related sponge species, *Halichondriapanicea* (Pallas, 1766) and *H. bowerbanki* Burton, 1930 (Porifera, Demospongiae), with remarks on their speciation. *Bijdr. Dierkd.* **1982**, *52*, 82–102. [[CrossRef](#)]
- Knobloch, S.; Jóhannsson, R.; Marteinson, V. Bacterial diversity in the marine sponge *Halichondriapanicea* from Icelandic waters and host-specificity of its dominant symbiont “*Candidatus Halichondriabacter symbioticus*”. *FEMS Microbiol. Ecol.* **2019**, *95*, fiy220. [[CrossRef](#)]
- Sacristán-Soriano, O.; Winkler, M.; Erwin, P.; Weisz, J.; Harriott, O.; Heussler, G.; Hill, M. Ontogeny of symbiont community structure in two carotenoid-rich, viviparous marine sponges: Comparison of microbiomes and analysis of culturable pigmented heterotrophic bacteria. *Environ. Microbiol. Rep.* **2019**, *11*, 249–261. [[CrossRef](#)]
- Tanaka, K. Growth dynamics and mortality of the intertidal encrusting sponge *Halichondriaokadae* (Demospongiae, Halichondrida). *Mar. Biol.* **2002**, *140*, 383–389.
- Fell, P.E.; Jacob, W.F. Reproduction and development of *Halichondria* sp. in the Mystic Estuary, Connecticut. *Biol. Bull.* **1979**, *156*, 62–75. [[CrossRef](#)]
- Wapstra, M.; Van Soest, R.W.M. Sexual reproduction, larval morphology and behaviour in demosponges from the southwest of the Netherlands. In *Taxonomy of Porifera*, 1st ed.; Vacelet, J., Boury-Esnault, N., Eds.; Springer: Berlin/Heidelberg, Germany, 1987; pp. 281–307.
- Witte, U.; Barthel, D.; Tendal, O. The reproductive cycle of the sponge *Halichondriapanicea* Pallas (1766) and its relationship to temperature and salinity. *J. Exp. Mar. Biol. Ecol.* **1994**, *183*, 41–52. [[CrossRef](#)]
- Gerasimova, E.I.; Ereskovsky, A.V. Reproduction of two species of *Halichondria* (Demospongiae: Halichondriidae) in the White Sea. In *Porifera Research—Biodiversity, Innovation and Sustainability. Série Livros*, 1st ed.; Custódio, M.R., Ed.; Museu Nacional: Rio de Janeiro, Brazil, 2007; Volume 28, pp. 327–333.
- Riisgård, H.U.; Kumala, L.; Charitonidou, K. Using the F/R-ratio for an evaluation of the ability of the demosponge *Halichondria panicea* to nourish solely on phytoplankton versus free-living bacteria in the sea. *Mar. Biol. Res.* **2016**, *12*, 907–916. [[CrossRef](#)]
- Thomassen, S.; Riisgård, H.U. Growth and energetics of the sponge *Halichondriapanicea*. *Mar. Ecol. Prog. Ser.* **1995**, *128*, 239–246. [[CrossRef](#)]
- Vogel, S. Current-induced flow through the sponge, *Halichondria*. *Biol. Bull.* **1974**, *147*, 443–456. [[CrossRef](#)]
- Kealy, R.A.; Busk, T.; Goldstein, J.; Larsen, P.S.; Riisgård, H.U. Hydrodynamic characteristics of aquiferous modules in the demosponge *Halichondriapanicea*. *Mar. Biol. Res.* **2019**, *15*, 531–540. [[CrossRef](#)]
- Asadzadeh, S.S.; Larsen, P.S.; Riisgård, H.U.; Walther, J.H. Hydrodynamics of the leucon sponge pump. *J. R. Soc. Interface* **2019**, *16*, 20180630. [[CrossRef](#)]
- Woollacott, R.M. Structure and swimming behavior of the larva of *Halichondriamelanadocia* (Porifera: Demospongiae). *J. Morphol.* **1990**, *205*, 135–145. [[CrossRef](#)] [[PubMed](#)]
- Burton, M. Observations on littoral sponges, including the supposed swarming of larvae, movement and coalescence in mature individuals, longevity and death. *Proc. Zool. Soc. Lond.* **1949**, *118*, 893–915. [[CrossRef](#)]
- Kumala, L.; Riisgård, H.U.; Canfield, D.E. Osculum dynamics and filtration activity studied in small single-osculum explants of the demosponge *Halichondriapanicea*. *Mar. Ecol. Prog. Ser.* **2017**, *572*, 117–128. [[CrossRef](#)]

27. Goldstein, J.; Riisgård, H.U.; Larsen, P.S. Exhalant jet speed of single-osculum explants of the demosponge *Halichondriapanicea* and basic properties of the sponge-pump. *J. Exp. Mar. Biol. Ecol.* **2019**, *511*, 82–90. [CrossRef]
28. Goldstein, J.; Bisbo, N.; Funch, P.; Riisgård, H.U. Contraction-expansion and the effects on the aquiferous system in the demosponge *Halichondriapanicea*. *Front. Mar. Sci.* **2020**, *7*, 113. [CrossRef]
29. Abe, T.; Sahin, F.P.; Akiyama, K.; Naito, T.; Kishigami, M.; Miyamoto, K.; Sakakibara, Y.; Uemura, D. Construction of a metagenomic library for the marine sponge *Halichondriaokadai*. *Biosc. Biotechnol. Biochem.* **2012**, *76*, 633–639. [CrossRef]
30. Laubenfels, M.W. A discussion of the sponge fauna of the Dry Tortugas in particular and the West Indies in general, with material for a revision of the families and orders of the Porifera. *Publ. Carnegie Instit. Wash.* **1936**, *467*, 1–225.
31. Bergquist, P.R. A collection of Porifera from Northern New Zealand, with descriptions of seventeen new species. *Pac. Sci.* **1961**, *15*, 33–48.
32. Lamarck, J.B. Sur les polypiers empâtés. *Ann. Mus. Natl. Hist. Nat.* **1814**, *20*, 294–312.
33. Van Soest, R.W.; Boury-Esnault, N.; Hooper, J.N.; Rützler, K.; de Voogd, N.J.; de Glasby, B.A.; Hajdu, E.; Pisera, A.B.; Manconi, R.; Schoenberg, C.; et al. *Halichondria Fleming*, 1828. World Porifera Database. World Register of Marine Species 2020. Available online: <https://www.marinespecies.org/aphia.php?p=taxdetails&id=131807> (accessed on 6 July 2022).
34. Kadota, J. Observations of two new species of the genus *Reniera* of monaxonid sponges. *Zool. Mag.* **1922**, *34*, 700–711.
35. Erpenbeck, D.; Hall, K.; Alvarez, B.; Büttner, G.; Sacher, K.; Schätzle, S.; Schuster, A.; Vargas, S.; Hooper, J.N.A.; Wörheide, G. The phylogeny of halichondrid demosponges: Past and present re-visited with DNA-barcoding data. *Org. Divers. Evol.* **2012**, *12*, 57–70. [CrossRef]
36. Tanita, S.; Hoshino, T. *The Demospongiae of Sagami Bay*; Biological Laboratory, Imperial Household: Tokyo, Japan, 1989; p. 197.
37. Tanita, S. Two sponges obtained by the Training Ship 'Oshoro Maru' in the Eastern Behring Sea. *Bull. Fish. Sci. Hokkaido Univ.* **1961**, *11*, 183–187.
38. Keller, C. Die Spongienfauna des Rothen Meeres (II. Hälfte). *Z. Wiss. Zool.* **1891**, *52*, 294–368.
39. Bergquist, P.R. Additions to the sponge fauna of the Hawaiian Islands. *Micronesica* **1967**, *3*, 159–174.
40. Olesen, T.M.E.; Weeks, J.M. Accumulation of Cd by the marine sponge *Halichondriapanicea* Pallas: Effects upon filtration rate and its relevance for biomonitoring. *Bull. Environ. Contam. Toxicol.* **1994**, *52*, 722–728. [CrossRef] [PubMed]
41. Musser, J.M.; Schippers, K.J.; Nickel, M.; Mizzon, G.; Kohn, A.B.; Pape, C.; Ronchi, P.; Papadopoulos, N.; Tarashansky, A.J.; Hammel, J.U.; et al. Profiling cellular diversity in sponges informs animal cell type and nervous system evolution. *Science* **2021**, *374*, 717–723. [CrossRef]
42. Kang, D.W.; Sim, C.J. Two new sponges of the genus *Halichondria* (Halichondrida: Halichondriidae) from Korea. *Anim. Cells Syst.* **2008**, *12*, 65–68. [CrossRef]
43. Barthel, D. Influence of different current regimes on the growth form of *Halichondriapanicea* Pallas. In *Fossil and Recent Sponges*, 1st ed.; Reitner, J., Keupp, H., Eds.; Springer: Berlin/Heidelberg, Germany, 1991; pp. 387–394.
44. Bell, J.J.; Barnes, D.K. The influences of bathymetry and flow regime upon the morphology of sublittoral sponge communities. *J. Mar. Biolog. Assoc. U. K.* **2000**, *80*, 707–718. [CrossRef]
45. Wang, D.; Zhang, Y.; Huang, D. The complete mitochondrial genome of sponge *Halichondria* (Halichondria) sp. (Demospongiae, Suberitida, Halichondriidae). *Mitochondrial DNA B Resour.* **2016**, *1*, 512–514. [CrossRef]
46. Kim, H.; Kim, H.J.; Jung, Y.H.; Yu, C.; An, Y.R.; Han, D.; Kang, D.W. The complete mitochondrial genome of sponge *Halichondriaokadai* (Demospongiae, Suberitida, Halichondriidae) from Korea water. *Mitochondrial DNA B Resour.* **2017**, *2*, 873–874. [CrossRef]
47. Kim, H.; Kang, D.W.; Yu, C.; Jung, Y.H.; Yoon, M.; Kim, H.J. The complete mitochondrial genome of sponge *Halichondria* sp. (Demospongiae, Suberitida, Halichondriidae) from Dok-do. *Mitochondrial DNA B Resour.* **2019**, *4*, 1729–1730. [CrossRef]
48. Erpenbeck, D.; Breeuwer, J.; van der Velde, H.; van Soest, R. Unravelling host and symbiont phylogenies of halichondrid sponges (Demospongiae, Porifera) using a mitochondrial marker. *Mar. Biol.* **2002**, *141*, 377–386.
49. Erpenbeck, D.; Duran, S.; Rützler, K.; Paul, V.J.; Hooper, J.N.; Wörheide, G. Towards a DNA taxonomy of Caribbean demosponges: A gene tree reconstructed from partial mitochondrial CO1 gene sequences supports previous rDNA phylogenies and provides a new perspective on the systematics of Demospongiae. *J. Mar. Biolog. Assoc. U. K.* **2007**, *87*, 1563–1570. [CrossRef]
50. Morrow, C.C.; Picton, B.E.; Erpenbeck, D.; Boury-Esnault, N.; Maggs, C.A.; Allcock, A.L. Congruence between nuclear and mitochondrial genes in Demospongiae: A new hypothesis for relationships within the G4 clade (Porifera: Demospongiae). *Mol. Phylogenetics Evol.* **2012**, *62*, 174–190. [CrossRef]
51. Alvarez, B.; Crisp, M.D.; Driver, F.; Hooper, J.N.; Van Soest, R.W. Phylogenetic relationships of the family Axinellidae (Porifera: Demospongiae) using morphological and molecular data. *Zool. Scr.* **2000**, *29*, 169–198. [CrossRef]
52. Castellanos, L.; Zea, S.; Osorno, O.; Duque, C. Phylogenetic analysis of the order Halichondrida (Porifera, Demospongiae), using 3 β -hydroxysterols as chemical characters. *Biochem. Syst. Ecol.* **2003**, *31*, 1163–1183. [CrossRef]
53. Erpenbeck, D. A molecular comparison of Alaskan and North East Atlantic *Halichondriapanicea* (Pallas 1766) (Porifera: Demospongiae) populations. *Boll. Mus. Ist. Biol. Univ. Genova* **2004**, *68*, 319–325.
54. Erpenbeck, D.; Breeuwer, J.A.; Van Soest, R.W. Identification, characterization and phylogenetic signal of an elongation factor-1 alpha fragment in demosponges (Metazoa, Porifera, Demospongiae). *Zool. Scr.* **2005**, *34*, 437–445. [CrossRef]
55. Hooper, J.N.A.; van Soest, R.W.M. *Systema Porifera. A Guide to the Classification of Sponges*; Kluwer Academic/Plenum Publishers: New York, NY, USA, 2002; Volume 1, pp. 1–1101.

56. Alvarez, B.; Hooper, J.N. Taxonomic revision of the order Halichondrida (Porifera: Demospongiae) of northern Australia. Family Halichondriidae. *Beagle Rec. Mus. Art Galleries North. Territ.* **2011**, *27*, 55–84. [[CrossRef](#)]
57. Fell, P.E.; Lewandrowski, K.B. Population dynamics of the estuarine sponge, *Halichondria* sp., within a New England eelgrass community. *J. Exp. Mar. Biol. Ecol.* **1981**, *55*, 49–63. [[CrossRef](#)]
58. Picton, B.E.; Goodwin, C.E. Sponge biodiversity of Rathlin Island, Northern Ireland. *J. Mar. Biolog. Assoc. U. K.* **2007**, *87*, 1441–1458. [[CrossRef](#)]
59. Carvalho, M.D.S.; Hajdu, E. Comments on Brazilian *Halichondria* Fleming (Halichondriidae, Halichondrida, Demospongiae), with the description of four new species from the São Sebastião Channel and its environs (Tropical Southwestern Atlantic). *Rev. Bras. Zool.* **2001**, *18*, 161–180. [[CrossRef](#)]
60. Barthel, D. Population dynamics of the sponge *Halichondria* panicea (Pallas) in Kiel Bight. In *Marine Eutrophication and Population Dynamics: 25th European Marine Biology Symposium*; Colombo, G., Ed.; Olsen & Olsen: Fredensborg, Denmark, 1992; pp. 203–209.
61. Khalaman, V.V.; Komendantov, A.Y. Experimental study of the ability of the sponge *Halichondria* panicea (Porifera: Demospongiae) to compete for a substrate in shallow-water fouling communities of the White Sea. *Biol. Bull. Russ. Acad. Sci.* **2016**, *43*, 69–74. [[CrossRef](#)]
62. Gaino, E.; Lepore, E.; Reborja, M.; Mercurio, M.; Sciscioli, M. Some steps of spermatogenesis in *Halichondria* semitubulosa (Demospongiae, Halichondriidae). *Ital. J. Zool.* **2007**, *74*, 117–122. [[CrossRef](#)]
63. Knowlton, A.L.; Highsmith, R.C. Convergence in the time-space continuum: A predator-prey interaction. *Mar. Ecol. Prog. Ser.* **2000**, *197*, 285–291. [[CrossRef](#)]
64. Wulff, J. Ecological interactions and the distribution, abundance, and diversity of sponges. *Adv. Mar. Biol.* **2012**, *61*, 273–344.
65. Hoshino, S. Systematic status of *Halichondria* japonica (Kadota) (Demospongiae, Halichondrida) from Japan. *Boll. Mus. Ist. Biol. Univ. Genova* **2004**, *68*, 373–379.
66. Jeon, Y.J.; Sim, C.J. A new record of genus *Halichondria* (Demospongiae: Halichondrida: Halichondriidae) from Korea. *Anim. Syst. Evol. Diversity* **2009**, *25*, 137–139. [[CrossRef](#)]
67. Li, Z.; Hu, Y.; Liu, Y.; Huang, Y.; He, L.; Miao, X. 16S rDNA clone library-based bacterial phylogenetic diversity associated with three South China Sea sponges. *World J. Microbiol. Biotechnol.* **2007**, *23*, 1265–1272. [[CrossRef](#)]
68. Hechtel, G.J. A systematic study of the Demospongiae of Port Royal, Jamaica. *Bull. Peabody Mus. Nat. Hist.* **1965**, *20*, 1–103.
69. Santos, G.G.; Nascimento, E.; Pinheiro, U. Halichondriidae Gray, 1867 from the Northeastern Brazil with description of a new species. *Zootaxa* **2018**, *4379*, 556–566. [[CrossRef](#)]
70. Kim, H.S.; Park, B.J.; Sim, C.J. Marine sponges in South Korea (I). *Korean J. Syst. Zool.* **1986**, *11*, 37–47.
71. Barthel, D. On the ecophysiology of the sponge *Halichondria* panicea in Kiel Bight. I. Substrate specificity, growth and reproduction. *Mar. Ecol. Prog. Ser.* **1986**, *32*, 291–298. [[CrossRef](#)]
72. Kobayashi, J.; Ishibashi, M. Bioactive metabolites of symbiotic marine microorganisms. *Chem. Rev.* **1993**, *93*, 1753–1769. [[CrossRef](#)]
73. Lee, Y.K.; Lee, J.H.; Lee, H.K. Microbial symbiosis in marine sponges. *J. Microbiol.* **2001**, *39*, 254–264.
74. Hummel, H.; Sepers, A.B.; De Wolf, L.; Melissen, F.W. Bacterial growth on the marine sponge *Halichondria* panicea induced by reduced waterflow rate. *Mar. Ecol. Prog. Ser.* **1988**, *42*, 195–198. [[CrossRef](#)]
75. Hentschel, U.; Hopke, J.; Horn, M.; Friedrich, A.B.; Wagner, M.; Hacker, J.; Moore, B.S. Molecular evidence for a uniform microbial community in sponges from different oceans. *Appl. Environ. Microbiol.* **2002**, *68*, 4431–4440. [[CrossRef](#)]
76. Rusanova, A.; Fedorchuk, V.; Toshchakov, S.; Dubiley, S.; Sutormin, D. An interplay between viruses and bacteria associated with the White Sea sponges revealed by metagenomics. *Life* **2021**, *12*, 25. [[CrossRef](#)]
77. Jeong, J.B.; Kim, K.H.; Park, J.S. Sponge-specific unknown bacterial groups detected in marine sponges collected from Korea through barcoded pyrosequencing. *J. Microbiol. Biotechnol.* **2015**, *25*, 1–10. [[CrossRef](#)]
78. Schmidt, O. *Grundzüge einer Spongien-Fauna des atlantischen Gebietes*; Wilhelm Engelmann: Leipzig, Germany, 1870; pp. 1–88.
79. Wichels, A.; Würtz, S.; Döpke, H.; Schütt, C.; Gerdt, G. Bacterial diversity in the breadcrumb sponge *Halichondria* panicea (Pallas). *FEMS Microbiol. Ecol.* **2006**, *56*, 102–118. [[CrossRef](#)]
80. Steinert, G.; Rohde, S.; Janussen, D.; Blaurock, C.; Schupp, P.J. Host-specific assembly of sponge-associated prokaryotes at high taxonomic ranks. *Sci. Rep.* **2017**, *7*, 2542. [[CrossRef](#)]
81. Naim, M.A.; Morillo, J.A.; Sørensen, S.J.; Waleed, A.A.S.; Smidt, H.; Sipkema, D. Host-specific microbial communities in three sympatric North Sea sponges. *FEMS Microbiol. Ecol.* **2014**, *90*, 390–403. [[CrossRef](#)]
82. Strehlow, B.W.; Schuster, A.; Francis, W.R.; Canfield, D.E. Metagenomic data for *Halichondria* panicea from Illumina and nanopore sequencing and preliminary genome assemblies for the sponge and two microbial symbionts. *BMC Res. Notes* **2022**, *15*, 135. [[CrossRef](#)]
83. Sun, J.F.; Wu, Y.; Yang, B.; Liuc, Y. Chemical constituents of marine sponge *Halichondria* sp. from south China sea. *Chem. Nat. Compd.* **2015**, *51*, 975–977. [[CrossRef](#)]
84. Hirata, Y.; Uemura, D. Halichondrin-antitumor polyether macrolides from a marine sponge. *Pure Appl. Chem.* **1986**, *58*, 701–710. [[CrossRef](#)]
85. Tachibana, K.; Scheuer, P.J.; Tsukitani, Y.; Kikuchi, H.; Van Engen, D.; Clardy, J.; Gopichand, Y.; Schmitz, F.J. Okadaic acid, a cytotoxic polyether from two marine sponges of the genus *Halichondria*. *J. Am. Chem. Soc.* **1981**, *103*, 2469–2471. [[CrossRef](#)]
86. Amagata, T.; Tanaka, M.; Yamada, T.; Minoura, K.; Numata, A. Gymnastatins and dankastatins, growth inhibitory metabolites of a *Gymnascella* species from a *Halichondria* sponge. *J. Nat. Prod.* **2008**, *71*, 340–345. [[CrossRef](#)]

87. Prego-Faraldo, M.V.; Valdiglesias, V.; Méndez, J.; Eirín-López, J.M. Okadaic acid meet and greet: An insight into detection methods, response strategies and genotoxic effects in marine invertebrates. *Mar. Drugs* **2013**, *11*, 2829–2845. [[CrossRef](#)]
88. Fu, L.L.; Zhao, X.Y.; Ji, L.D.; Xu, J. Okadaic acid (OA): Toxicity, detection and detoxification. *Toxicon* **2019**, *160*, 1–7. [[CrossRef](#)]
89. Corriere, M.; Soliño, L.; Costa, P.R. Effects of the marine biotoxins okadaic acid and dinophysistoxins on fish. *J. Mar. Sci. Eng.* **2021**, *9*, 293. [[CrossRef](#)]
90. Khalaman, V.V.; Sharov, A.N.; Kholodkevich, S.V.; Komendantov, A.Y.; Kuznetsova, T.V. Influence of the White Sea sponge *Halichondriapanicea* (Pallas, 1766) on physiological state of the blue mussel *Mytilus edulis* (Linnaeus, 1758), as evaluated by heart rate characteristics. *J. Evol. Biochem. Physiol.* **2017**, *53*, 225–232. [[CrossRef](#)]
91. Pita, L.; Fraune, S.; Hentschel, U. Emerging sponge models of animal-microbe symbioses. *Front. Microbiol.* **2016**, *7*, 2102. [[CrossRef](#)]
92. Lemoine, N.; Buell, N.; Hill, A.; Hill, M. Assessing the utility of sponge microbial symbiont communities as models to study global climate change: A case study with *Halichondriabowerbanki*. In *Porifera Research: Biodiversity, Innovation and Sustainability; Série Livros*, 1st ed.; Custódio, M.R., Ed.; Museu Nacional: Rio de Janeiro, Brazil, 2007; Volume 28, pp. 419–425.
93. Fröhlich, H.; Barthel, D. Silica uptake of the marine sponge *Halichondriapanicea* in Kiel Bight. *Mar. Biol.* **1997**, *128*, 115–125. [[CrossRef](#)]
94. Barthel, D.; Detmer, A. The spermatogenesis of *Halichondriapanicea* (Porifera, Demospongiae). *Zoomorphology* **1991**, *110*, 9–15. [[CrossRef](#)]
95. Sokolova, A.M.; Pozdnyakov, I.R.; Ereskovsky, A.V.; Karpov, S.A. Kinetid structure in larval and adult stages of the demosponges *Haliclona aquaeductus* (Haplosclerida) and *Halichondriapanicea* (Suberitida). *Zoomorphology* **2019**, *138*, 171–184. [[CrossRef](#)]
96. Amano, S. Larval release in response to a light signal by the intertidal sponge *Halichondriapanicea*. *Biol. Bull.* **1986**, *171*, 371–378. [[CrossRef](#)]
97. Lüskow, F.; Riisgård, H.U.; Solovyeva, V.; Brewer, J.R. Seasonal changes in bacteria and phytoplankton biomass control the condition index of the demosponge *Halichondriapanicea* in temperate Danish waters. *Mar. Ecol. Prog. Ser.* **2019**, *608*, 119–132. [[CrossRef](#)]
98. Riisgård, H.U.; Thomassen, S.; Jakobsen, H.; Weeks, J.M.; Larsen, P.S. Suspension feeding in marine sponges *Halichondriapanicea* and *Haliclona urceolus*: Effects of temperature on filtration rate and energy cost of pumping. *Mar. Ecol. Prog. Ser.* **1993**, *96*, 177–188. [[CrossRef](#)]
99. Koopmans, M.; Martens, D.; Wijffels, R.H. Growth efficiency and carbon balance for the sponge *Haliclona oculata*. *Mar. Biotechnol.* **2010**, *12*, 340–349. [[CrossRef](#)]
100. Riisgård, H.U.; Larsen, P.S. Actual and model-predicted growth of sponges—with a bioenergetic comparison to other filter-feeders. *J. Mar. Sci. Eng.* **2022**, *10*, 607. [[CrossRef](#)]
101. Fell, P.E.; Parry, E.H.; Balsamo, A.M. The life histories of sponges in the Mystic and Thames estuaries (Connecticut), with emphasis on larval settlement and postlarval reproduction. *J. Exp. Mar. Biol. Ecol.* **1984**, *78*, 127–141. [[CrossRef](#)]
102. Hartman, W.D. Natural history of the marine sponges of southern New England. *Bull. Peabody Mus. Yale* **1958**, *12*, 1–155.
103. Knowlton, A.L.; Highsmith, R.C. Nudibranch-sponge feeding dynamics: Benefits of symbiont-containing sponge to *Archidoris montereyensis* (Cooper, 1862) and recovery of nudibranch feeding scars by *Halichondriapanicea* (Pallas, 1766). *J. Exp. Mar. Biol. Ecol.* **2005**, *327*, 36–46. [[CrossRef](#)]
104. Wulff, J. Regeneration of sponges in ecological context: Is regeneration an integral part of life history and morphological strategies? *Integr. Comp. Biol.* **2010**, *50*, 494–505. [[CrossRef](#)]
105. Alcolado, P.M. Nuevas especies de esponjas encontradas en Cuba. *Poeyana* **1984**, *271*, 1–22.
106. Wulff, J.L. Parrotfish predation on cryptic sponges of Caribbean coral reefs. *Mar. Biol.* **1997**, *129*, 41–52. [[CrossRef](#)]
107. Wulff, J.L. Sponge predators may determine differences in sponge fauna between two sets of mangrove cays, Belize barrier reef. *Atoll Res. Bull.* **2000**, *477*, 251–263. [[CrossRef](#)]
108. De Goeij, J.M.; Van Oevelen, D.; Vermeij, M.J.; Osinga, R.; Middelburg, J.J.; De Goeij, A.F.; Admiraal, W. Surviving in a marine desert: The sponge loop retains resources within coral reefs. *Science* **2013**, *342*, 108–110. [[CrossRef](#)]
109. Barthel, D.; Wolfrath, B. Tissue sloughing in the sponge *Halichondriapanicea*: A fouling organism prevents being fouled. *Oecologia* **1989**, *78*, 357–360. [[CrossRef](#)]
110. Hansen, I.V.; Weeks, J.M.; Depledge, M.H. Accumulation of copper, zinc, cadmium and chromium by the marine sponge *Halichondriapanicea* Pallas and the implications for biomonitoring. *Mar. Pollut. Bull.* **1995**, *31*, 133–138. [[CrossRef](#)]
111. Langenbruch, P.F.; Scalera-Liaci, L. *Structure of Choanocyte Chambers in Haplosclerid Sponges*; Smithsonian Institution Press: Washington, DC, USA; Woods Hole, MA, USA, 1985; pp. 245–251.
112. Haeckel, E. XXVII. On the Calcispongiae, their position in the animal kingdom, and their relation to the theory of descendance. *J. Nat. Hist.* **1873**, *11*, 241–262.
113. Reiswig, H.M. The aquiferous systems of three marine Demospongiae. *J. Morphol.* **1975**, *145*, 493–502. [[CrossRef](#)]
114. Fry, W.G. The sponge as a population: A biometric approach. *Symp. Zool. Soc. Lond.* **1970**, *25*, 135–162.
115. Fry, W.G. Taxonomy, the individual and the sponge. In *Biology and Systematics of Colonial Organisms: Proceedings of an International Symposium Held at the University of Durham*; Published for the Systematics Association; Academic Press: London, UK, 1979; Volume 11, pp. 39–80.

116. Riisgård, H.U.; Larsen, P.S. Filtration rates and scaling in demosponges. *J. Mar. Sci. Eng.* **2022**, *10*, 643. [[CrossRef](#)]
117. Larsen, P.S.; Riisgård, H.U. The sponge pump. *J. Theor. Biol.* **1994**, *168*, 53–63. [[CrossRef](#)]
118. Weissenfels, N. The filtration apparatus for food collection in freshwater sponges (Porifera, Spongillidae). *Zoomorphology* **1992**, *112*, 51–55. [[CrossRef](#)]
119. Mah, J.L.; Christensen-Dalsgaard, K.K.; Leys, S.P. Choanoflagellate and choanocyte collar-flagellar systems and the assumption of homology. *Evol. Dev.* **2014**, *16*, 25–37. [[CrossRef](#)]
120. Suarez, P.A.; Leys, S.P. The sponge pump as a morphological character in the fossil record. *Paleobiology* **2022**, *48*, 446–461. [[CrossRef](#)]
121. Evans, C.W. The ultrastructure of larvae from the marine sponge *Halichondria moorei* Bergquist (Porifera, Demospongiae). *Cah. Biol. Mar.* **1997**, *18*, 427–433.
122. Harris, A.K. Cell motility and the problem of anatomical homeostasis. *J. Cell. Sci.* **1987**, *8*, 121–140. [[CrossRef](#)]
123. Gaino, E.; Burlando, B. Sponge cell motility: A model system for the study of morphogenetic processes. *Ital. J. Zool.* **1990**, *57*, 109–118. [[CrossRef](#)]
124. Bond, C. Continuous cell movements rearrange anatomical structures in intact sponges. *J. Exp. Zool.* **1992**, *263*, 284–302. [[CrossRef](#)]
125. Lavrov, A.I.; Kosevich, I.A. Sponge cell reaggregation: Cellular structure and morphogenetic potencies of multicellular aggregates. *J. Exp. Zool. A. Ecol. Genet. Physiol.* **2016**, *325*, 158–177. [[CrossRef](#)]
126. Saito, Y. Self and nonself recognition in a marine sponge, *Halichondria japonica* (Demospongiae). *Zool. Sci.* **2013**, *30*, 651–657. [[CrossRef](#)]
127. Storr, J.F. Field observations of sponge reactions as related to their ecology. In *Aspects of Sponge Biology*; Harrison, F.W., Cowden, R.R., Eds.; Academic Press Inc.: New York, NY, USA, 1976; pp. 277–282.
128. Reiswig, H.M. In situ pumping activities of tropical Demospongiae. *Mar. Biol.* **1971**, *9*, 38–50. [[CrossRef](#)]
129. Nickel, M. Kinetics and rhythm of body contractions in the sponge *Tethya wilhelma* (Porifera: Demospongiae). *J. Exp. Biol.* **2004**, *207*, 4515–4524. [[CrossRef](#)]
130. Nickel, M.; Scheer, C.; Hammel, J.U.; Herzen, J.; Beckmann, F. The contractile sponge epithelium sensu lato—Body contraction of the demosponge *Tethya wilhelma* is mediated by the pinacoderm. *J. Exp. Biol.* **2011**, *214*, 1692–1698. [[CrossRef](#)]
131. Elliott, G.R.; Leys, S.P. Coordinated contractions effectively expel water from the aquiferous system of a freshwater sponge. *J. Exp. Biol.* **2007**, *210*, 3736–3748. [[CrossRef](#)]
132. Kumala, L.; Canfield, D.E. Contraction dynamics and respiration of small single-ostium explants of the demosponge *Halichondria panicea*. *Front. Mar. Sci.* **2018**, *5*, 410. [[CrossRef](#)]
133. Kumala, L.; Larsen, M.; Glud, R.N.; Canfield, D.E. Spatial and temporal anoxia in single-ostium *Halichondria panicea* demosponge explants studied with planar optodes. *Mar. Biol.* **2021**, *168*, 173. [[CrossRef](#)]
134. Leys, S.P. Elements of a ‘nervous system’ in sponges. *J. Exp. Biol.* **2015**, *218*, 581–591. [[CrossRef](#)]
135. Gerrodette, T.; Flechsig, A.O. Sediment-induced reduction in the pumping rate of the tropical sponge *Verongia lacunosa*. *Mar. Biol.* **1979**, *55*, 103–110. [[CrossRef](#)]
136. Bell, J.J.; McGrath, E.; Biggerstaff, A.; Bates, T.; Bennett, H.; Marlow, J.; Shaffer, M. Sediment impacts on marine sponges. *Mar. Pollut. Bull.* **2015**, *94*, 5–13. [[CrossRef](#)]
137. Nickel, M. Evolutionary emergence of synaptic nervous systems: What can we learn from the non-synaptic, nerveless Porifera? *Invertebr. Biol.* **2010**, *129*, 1–16. [[CrossRef](#)]
138. Jones, W.C. Is there a nervous system in sponges? *Biol. Rev.* **1962**, *37*, 1–47. [[CrossRef](#)]
139. Ludeman, D.A.; Farrar, N.; Riesgo, A.; Paps, J.; Leys, S.P. Evolutionary origins of sensation in metazoans: Functional evidence for a new sensory organ in sponges. *BMC Evol. Biol.* **2014**, *14*, 3. [[CrossRef](#)]
140. Leys, S.P.; Nichols, S.A.; Adams, E.D. Epithelia and integration in sponges. *Integr. Comp. Biol.* **2009**, *49*, 167–177. [[CrossRef](#)]
141. Bagby, R.M. The fine structure of myocytes in the sponges *Microciona prolifera* (Ellis and Solander) and *Tedania ignis* (Duchassaing and Michelotti). *J. Morphol.* **1966**, *118*, 167–181. [[CrossRef](#)]
142. Hammel, J.U.; Nickel, M. A new flow-regulating cell type in the demosponge *Tethya wilhelma*—Functional cellular anatomy of a leuconoid canal system. *PLoS ONE* **2014**, *9*, e113153. [[CrossRef](#)]
143. Kanzawa, N.; Takano-Ohmuro, H.; Maruyama, K. Isolation and characterization of sea sponge myosin. *Zool. Sci.* **1995**, *12*, 765–769. [[CrossRef](#)]
144. De Ceccatty, M.P. Coordination in sponges. The foundations of integration. *Am. Zool.* **1974**, *14*, 895–903. [[CrossRef](#)]
145. Perovic, S.; Krasko, A.; Prokic, I.; Müller, I.M.; Müller, W.E. Origin of neuronal-like receptors in Metazoa: Cloning of a metabotropic glutamate/GABA-like receptor from the marine sponge *Geodia cydonium*. *Cell Tissue Res.* **1999**, *296*, 395–404. [[CrossRef](#)]
146. Lieberkühn, N. *Über Bewegungserscheinungen der Zellen*; Band IX, N.G., Ed.; Elwert’sche Universitätsbuchhandlung: Marburg/Leipzig, Germany, 1870; pp. 9–22.
147. Galtsoff, P.S. The amoeboid movement of dissociated sponge cells. *Biol. Bull.* **1923**, *45*, 153–161. [[CrossRef](#)]
148. Loewenstein, W.R. On the genesis of cellular communication. *Devel. Biol.* **1967**, *15*, 503–520. [[CrossRef](#)]