Algal Spores

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The structure, production, dispersal and recruitment of algal spores is discussed in relation to their survival in a turbulent hydrodynamic environment. Spore settlement and adhesion to substrata are moderated by a range of environmental cues and signals.

Introduction

The algae are a very diverse, polyphyletic assemblage of oxygen-producing photosynthetic organisms, currently placed into nine divisions or phyla. Members of four of these divisions (Rhodophyta, Heterokontophyta, Chlorophyta and Chlorarachniophyta) produce spores, which we define here as cells that can reproduce independently (i.e. asexually) an individual of that species. We exclude cells that must fuse with another cell, as gametes do in sexual reproduction, and the zygotes that result from fertilization. Spores and other propagules play central roles in the reproduction of most multicellular algae, affecting their ecology, population genetics and biogeography. Fossils of the oldest taxonomically resolved eukaryote on record, the 1.2 billion-year-old red alga *Bangiomorpha pubescens*, exhibit astonishing well-preserved sporangia (the structures within which the spore arises), with released and germinating spores (Butterfield, 2000). Algal spores also impact on human activities by settling in abundance on artificial surfaces, resulting in biofouling, and in the mariculture of seaweeds, which are of increasing commercial importance globally.

The rhodophyte (red algal), heterokontophyte (including brown algal) and chlorophyte (green algal) lineages contain algae of highly diverse forms that occupy almost every available habitat – marine, freshwater, terrestrial and even aerial. They include the red, green and brown seaweeds, marine macroalgae individually visible to the naked eye, on which spore studies have largely focused. A wide range of life-history patterns, involving sexual and asexual reproduction, is exhibited by these groups. Many of these include independent diploid and haploid phases (haplodiploid life history) linked by fertilization and meiosis.

Algae and their spores exhibit enormous diversity. Spores can be classified in various ways such as whether meiosis takes place during their development (meiospores) or whether they are formed mitotically (mitospores), or according to function (e.g. parthenogenetic gametes) or motility (nonflagellate spore versus flagellate zoospore). Algal spores vary greatly in their levels of specialization, from relatively simple release of the contents of vegetative cells (e.g. nonmotile monospores in several groups) to

morphologically complex tetrasporangia, restricted to higher red algae. They also exhibit a wide range of sizes, from typically less than 10 μm in brown and green algae to up to 100 μm in diameter in some rhodophytes. Here, following a survey of spore occurrence among the algae, we take a functional approach, examining in turn the formation, release, survival, dispersal and settlement of spores.

Occurrence of Spore Types among Major Algal Groups

The three main spore-forming lineages, Rhodophyta, Heterokontophyta and Chlorophyta, are all members of the evolved 'crown' eukaryotes, but relationships among these groups are still controversial. Although they are often all attributed to the kingdom Protista (or Protoctista), there are many alternative schemes such as the placement of the Rhodophyta and Chlorophyta in the kingdom Plantae and the Heterokontophyta (including diverse groups such as water moulds) in the kingdom Chromista.

The Rhodophyta, comprising the classes Bangiophyceae and Florideophyceae, is unique amongst nonfungal eukaryotes in that its members entirely lack flagella or centrioles at any stage of their life histories. Members of the Bangiophyceae, which is both ancient and morphologically simple, reproduce by mitotic spores formed in various types of sporangia. In the best-known genus, *Porphyra*, which is commercially cultivated for nori, the blade-like haploid gametophytic phase gives rise after fertilization to a microscopic shell-boring diploid conchocelis phase. Meiosis takes place during germination of spores (conchospores) formed by the conchocelis phase. The two phases of this heteromorphic life history are so morphologically dissimilar that they could be linked only by studying it in culture. The more complex Florideophyceae (e.g. *Rhodochorton, Iridaea*) exhibit an enormous diversity of haplodiploid life histories. Some are isomorphic, i.e. haploid and diploid phases are morphologically closely similar if not identical, whereas others such as that of *Bonnemaisonia hamifera* are heteromorphic like *Porphyra*.

The cryptic phase, which may be either the gametophyte (unisexual or bisexual) or the sporophyte, is crustose, filamentous or boring, whereas the more conspicuous phase is erect, often resembling leaves or twigs. These intricate life histories display a wealth of mitotic spores formed in various ways, and specialized meiotic sporangia (tetrasporangia) that release four haploid tetraspores. Uniquely, in most Florideophycidae, the immediate product of fertilization is not the diploid sporophyte, but a hemi-parasitic diploid tissue surrounded by female nutritive tissue, collectively called the cystocarp (**Figure 1**). This stage, regarded as a mechanism compensating for the lack of motile sperm in the red algae, releases numerous ($30-10 000 +$) genetically identical diploid carpospores that give rise to sporophytes.

Four of the seven algal classes of the Heterokontophyta form spores. One class, the Bacillariophyceae (diatoms), which are unicellular organisms encased in a pair of silica shells (valves), has specialized nonflagellate auxospores. In the normal mode of cell division, the two valves separate, and a new valve is formed within each of the original valves, resulting in a progressive reduction in size. The auxospores function to restore the size of diatom cells before they become too small to survive. The Xanthophyceae, Eustigmatophyceae and Phaeophyceae (brown algae) all form flagellate zoospores displaying the characteristic heterokont paired flagella, one of which is short and smooth and points backwards when swimming, the other being forward-pointing, long and tinsel-like.

In the Phaeophyceae, meiospores or gametes are formed in single-chambered (unilocular) sporangia, and mitospores in many-chambered (plurilocular) sporangia. Both single-phase and haplodiploid life cycles are seen, and, as in

the red seaweeds, may be isomorphic or heteromorphic. Morphological phase is not necessarily linked to ploidy, as brown algal life histories are often highly plastic. For example, unfused gametes can develop into haploid thalli that morphologically resemble the diploid sporophytes. Parthenogenetic and sexual reproduction frequently occur in tandem, e.g. in the isomorphic species *Ectocarpus siliculosus*, influenced by environmental factors such as temperature. The kelps (Laminariales, including the genera *Laminaria* and *Macrocystis*) have an extremely heteromorphic life history, in which the diploid sporophytes are amongst the largest organisms on Earth (giant kelp, *M. pyrifera*, is up to 60 m in length). Meiospores formed by sori on the kelp blades germinate into minute few-celled gametophytes that exhibit *in situ* fertilization of the egg cell. Gametophytes are unisexual (i.e. male and female individuals are separate) so the survival of at least two meiospores is required for a new kelp sporophyte to develop. The order Fucales has a type of life history that is unusual in the algae, more resembling that of many animals. The only haploid stages are the gametes – fusion leads to zygotes (sometimes loosely termed spores) that develop directly into new diploid individuals.

Five of the 11 classes of the Chlorophyta form motile spores, bearing one or two pairs of isokont (morphologically similar) flagella. Of these, the best-studied group is the Ulvophyceae, which contains the common marine fouling genera *Ulva* and *Enteromorpha*. Spores are generally formed in sporangia that are relatively little-differentiated from ordinary vegetative cells. Every cell of the monostromatic, hollow thallus of *Enteromorpha*, apart from the rhizoid region, has the potential to produce 8, but sometimes 16, zoospores or gametes. *Enteromorpha* exhibits an isomorphic alternation of generations with haploid gametophytic plants producing either plus (female) or minus (male) biflagellate gametes. Diploid sporophytic plants, after meiosis, produce asexual, haploid, quadriflagellate, sometimes biflagellate, zoospores. Life histories are otherwise similar to those of the
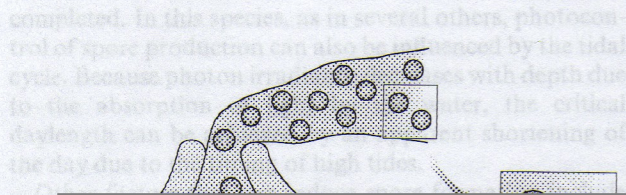
sporangia. Most such responses are observed in algae with heteromorphic life histories, probably because the two phases have different ecological susceptibilities and potentials. A typical example of an alga showing a short-day response is that of *Porphyra*, in which the conchocelis phase forms conchospores only when daylength reduces in the autumn. The photoperiodic response thus controls the seasonal development of the erect *Porphyra* phase. The conchocelis is shell-boring and can survive within barnacle shells even under severely desiccating conditions in the intertidal zone, whereas the blades require the damper, cooler, environment of late autumn and winter. Daylength is an early warning system, permitting the rapidly growing erect phase to be produced as early as possible under favourable or optimal environmental conditions.

Latitudinal ecotypes in photoperiodic responses for formation of tetrasporangia have been detected in the florideophyte red alga *Rhodochorton purpureum*. The critical daylength for the short-day response increases with the latitude of origin of cultured isolates, which ensures that spores do not form too early at southern latitudes where summer daylength is equivalent to the autumn daylength for northern isolates. Frequently the formation of sporangia also requires the temperature to be within a particular permissive range. At higher or lower temperatures, although the daylength is suitable, sporangium induction will not occur. Interaction between daylength and temperature results in a narrow reproductive 'window' in the Japanese red alga *Bonnemaisonia hamifera*. At other times, tetrasporangial formation is blocked by low temperature and/or long daylength. Outside its native range, the window can be entirely closed, so that meiosis does not occur and the life history is not completed. In this species, as in several others, photocontrol of spore production can also be influenced by the tidal cycle. Because photon irradiance decreases with depth due to the absorption of light by the water, the critical daylength can be achieved by an apparent shortening of the day due to the timing of high tides.

Other factors that can induce spore formation include nutrient levels (high or low) and biotic interactions. In members of the Ulvales, ectosymbiotic bacteria may play a part in regulating sporogenesis. The secretion of regulatory factors into the cell walls controls sporogenesis and spore release in *Ulva* (Stratmann *et al.*, 1996). A glycoprotein (M_r 1–4 × 10^4) inhibits sporulation; dilution of a swarming inhibitor of low M_r results in spore release.

Spore release in algae can be triggered by a huge range of factors, such as desiccation, grazing by invertebrates, abrasion and chemicals. Mucilage produced within the sporangia of red and brown algae and within the cystocarps of red algae is extruded during the release of the spores. Although the high viscosity of water minimizes the projectile effect of explosive spore release, it is sufficient at least to take the majority of spores out of the boundary layer, providing opportunities for dispersal. In red algae it is noteworthy that cystocarp openings frequently correspond to a Venturi tube (**Figure 1**), forcing the spores out rapidly.

Survival and Dispersal

Enormous numbers of spores are produced by seaweeds; a release rate of 5.3×10^5 zoospores per plant per day was estimated for *Enteromorpha linza*. Various seaweed species allocate 4–50% of annual biomass production to their reproductive effort; thus the potential for recruitment is clearly enormous. However, the great majority of the spores will not survive long enough to germinate. From an estimated 9×10^9 zoospores released annually by a single diploid sporophyte of the kelp *Laminaria longicruris*, about 0.1% survive to the microscopic gametophyte stage and an average of only one sporophyte will successfully establish in each square metre. Following release, spores become part of the plankton distributed throughout the water column or may swim or sink to the bottom. Spore traps and filtration of coastal seawater have revealed large quantities of macroalgal spores among the plankton, where they are assumed to be an important source of nutrients for grazing zooplankton. The many sources of mortality include attack by viruses or other pathogens, grazing by protists and invertebrates, and sinking out of the photic zone or on to unfavourable surfaces. Spores are typically 5–10% denser than water. Sinking speeds are affected by spore size and possibly also by the surrounding mucilage sheath that typically doubles the volume of the spore (**Figure 1**). The function of the mucilage sheath is poorly known, but speculations include roles in reducing pathogen attack and in the initial processes of spore attachment.

The distance over which spores can successfully colonize new sites depends on the time for which they remain competent (Reed *et al.*, 1992). Medium-range dispersal may be increased by transportation of fertile reproductive tissue by drift, and long-range dispersal occurs via the fouling communities on the hulls of ships and through discharge of ballast water. Since spores are photosynthetically active, survival may not be limited primarily by physiological constraints. *Enteromorpha* zoospores are observed to remain motile for up to 8 days and zygotes viable for over 6 weeks, thereby enhancing the chances of an enlarged area of colonization. Prolonged spore survival may account for the reported colonization by *Enteromorpha* of a newly formed (volcanic) substratum at a distance of 35 km from the nearest source of inoculum. Much evidence suggests that small opportunistic species like *Enteromorpha* have wider spore dispersal ranges than larger longer-lived algae. Although swimming zoospores of the giant kelp *Macrocystis pyrifera* photosynthesize and also utilize lipid reserves, they can swim for only 5 days.

However, when they stop swimming, they are still able to germinate – thus spores are not the only viable planktonic stage, with major implications for the dispersal ability of this keystone species (Reed *et al.*, 1992). Nutrients do not influence swimming behaviour or settlement rates of *Ectocarpus siliculosus* zoospores (Amsler *et al.*, 1999).

Settlement Cues

Following their release and subsequent dispersal, spores must re-enter the benthic boundary layer from which they then colonize the substratum via a range of surface location and attachment behaviours and mechanisms. 'Settlement' is the stage whereby the surface is located and surface contact is established. In many organisms, this stage is regulated by the perception of a range of chemotactic signals as well as physical and physico-chemical interactions with the substratum. Spore motility is of little relevance for dispersal, because the swimming abilities of spores are negligible in comparison with the speed of movement of the water in which they are swimming. The small size of spores means that water is highly viscous, comparable to a human swimming in tar. However, spore motility may be highly significant during settlement. Spore attachment data suggest that adhered spores are able to regulate density-dependent settlement in the exploitation of the substratum. Spore settlement is not directly related to the concentration of swimming spores, positive co-operativity occurring at low spore densities and negative cooperativity occurring at high spore densities (Callow *et al.*, 1997). Gregarious settlement, i.e. settlement of spores in groups, is also observed. This strategy enhances survival in a turbulent environment and ensures proximity of reproductive adults. Even red algal spores, which lack flagella, are able to move enough to influence their settlement sites. Video microscopy (**Figure 2**) has revealed that the spores of many red algae show continuous directional gliding at speeds of up to 2.2 μm s^{-1} (Pickett-Heaps *et al.*, 2001). Some are amoeboid or can squeeze actively through gaps. Although the mechanism of their motility is unknown, it may move spores out of the boundary layer and give spores a limited ability to optimize their site of germination.

Microtopography appears to play an important role in the selection of settlement sites. Field observations have led many authors to conclude that algae prefer to settle on roughened surfaces. Studies employing characterized substrata with a range of microfabricated topographies clearly show that swimming spores of *Enteromorpha* seek out and attach preferentially in the angle between valleys and ridges. The shape and scale of features on a surface determine where spores will colonize and in general, features of approximately the same size as the colonizing spore appear to be especially favourable. Settlement on
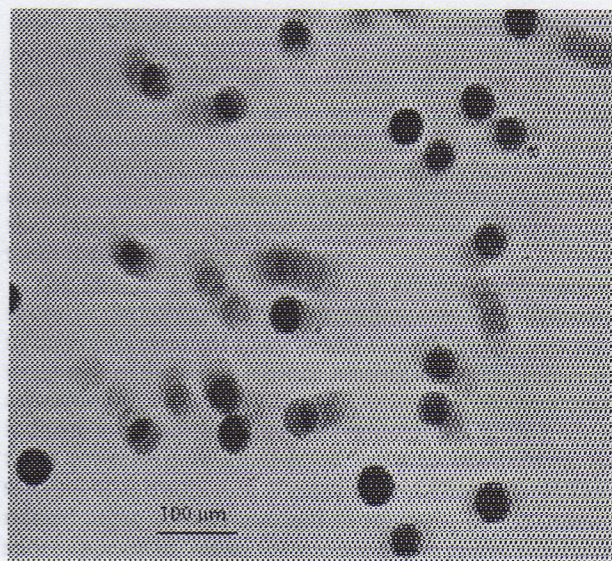
Figure 2 Carpospores of red alga (*Spyridia filamentosa*): superimposed montage of six images, each 4 seconds apart, showing spores moving at variable speeds, or stationary. (Reproduced from Pickett-Heaps *et al.*, 2001.)

rough substrata will provide a greater surface area for attachment and protect the spore from desiccation, wave action and predation. However, some red algal spores settle preferentially on or near the tips of small-scale surface projections, places that would not provide any of these benefits (Johnson, 1994). It seems likely that their observed 'preference' for high microtopography is a result of being released in long mucilage skeins. These are strong and sticky enough to be draped across adjacent projections without touching the intervening depression.

The ability of motile spores to detect and respond to environmental cues is particularly pertinent to their survival and the colonization of new substrata. The negative phototaxis displayed by many swimming spores guides them to areas of low irradiance where they will find places to settle, but the positive phototaxis shown by other spores is thought to aid dispersal by increasing the chances that they will be distributed up into the water column. Nonmotile spores are transported to settlement sites by water movement or sinking, but settlement and adhesion of both motile and nonmotile spores appear to be moderated by a whole range of signals.

Signals for settlement may be associated with the substratum (topographic, physico-chemical), biological (biofilms, basiphytes), chemical (diffusible attractive or inhibitory compounds) or hydrodynamic. In nature, it is likely that a number of cues all play a role in the settlement process. Some epiphytic algae are associated almost exclusively with a specific host, e.g. the obligately epiphytic red alga *Polysiphonia lanosa* on the fucoid *Ascophyllum*

nodosum, although little is known about possible recognition events that confer specificity.

Chemotactic responses mediated by secretion of pheromones by algal gametes are well known but little is known regarding the existence or nature of diffusible settlement cues in the algae. Brown and green algal spores can detect and respond to a variety of inorganic and organic nutrients, thereby ensuring settlement in a habitat nutritionally favourable for growth. *Enteromorpha* spores are attracted by fatty acids and it is possible that these and other compounds act as settlement cues in the natural environment. The diffusion of compounds from basiphytes has provided an explanation for the specificity or absence of epiphytic associations. Differences in the susceptibility to colonization by epiphytes has often been attributed to defense mechanisms, notably the secretion of inhibitory compounds such as phenols or furanones. Coralline red algae prevent overgrowth by epiphytes by producing allelochemicals, as well as by shedding their surface layers. The chemicals are released in the medium in culture studies, and suppress the development of *Laminaria* sporelings (Denboh *et al.*, 1997).

A limited number of studies have investigated spore settlement on different materials, but in most cases, the substrata have not been well defined or characterized. *Enteromorpha* and *Ectocarpus* spores settle preferentially on hydrophobic surfaces, and moreover, the spores appear to be able to 'sense' the best surface for settlement (see Amsler *et al.*, 1999; Callow *et al.*, 2000). Spores attach more readily to hydrophobic ('water-hating') surfaces, probably because such a surface more readily allows the exclusion of water molecules from the adhesive/substratum interface. However, spores appear to be more easily removed from hydrophobic than hydrophilic surfaces, which is consistent with much published data that shows weak strengths of attachment of a range of marine organisms to hydrophobic low-energy surfaces. The situation regarding the impact of the substratum in nature is complicated by the ubiquitous presence of microbial biofilm, which also moderates the settlement of algal spores. The presence of biofilm bacteria may influence spore settlement in a number of ways. Bacteria alter the topography of the surface as well as changing the physico-chemical properties of the substratum by altering its wettability (hydrophobicity) or by exposing different surface domains associated with extracellular polymeric substances (EPS). Some strains of bacteria can enhance or inhibit the settlement of algal spores. A variety of signal molecules may be involved, including homoserine lactones or secondary metabolites.

Adhesion of Spores

'Adhesion' comprises both initial (temporary) and primary (permanent) attachment, and secondary processes that result in consolidation of permanent attachment. While a number of studies have been concerned with the settlement phase, for example the responses of spores to light, thigmotactic and chemotactic stimuli, and the role of other surface properties such as surface free energy, we remain remarkably ignorant of the composition and physicochemical nature of adhesives used by different algae, how they bond to surfaces and how they consolidate attachment through 'curing' reactions.

The change from a motile to a permanently adhered spore, or the adhesion of a nonmotile spore, is fundamental to the colonization of a new substratum. Many papers refer to the role of flagella in surface-sensing and even temporary adhesion but video recordings of *Enteromorpha* zoospores indicate a role for the anterior region of the spore body in these processes. A number of features involved in the settlement and adhesion of zoospores of *Enteromorpha* and related algae are summarized in **Figure 3**. The swimming spore appears to 'sense' the surface via an apical papilla on which it rotates and it may, at this stage, become temporarily attached to the surface by means of a small deposit of secreted elastic material. Permanent adhesion is characterized by the discharge of the contents of Golgi-derived, adhesive-containing cytoplasmic vesicles as the cell contracts against the substratum and retraction of the microfilaments of the flagella inside the cell. The newly settled spore is surrounded by secreted 'adhesive' material and is devoid of the intracellular 'adhesive' vesicles present in the swimming spores. Commitment to permanent adhesion as evidenced by vesicle discharge is followed by exploitation of the surface by amoeboid-like, space-filling movements against the substratum and adjacent cells (Callow *et al.*, 1997). Synthesis and secretion of a cell wall begins immediately after discharge of adhesive vesicles. Similarly, in kelps, actively swimming spores can choose
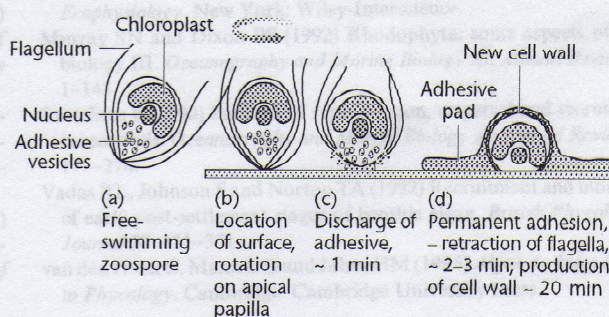
Figure 3   Summary of features involved in the settlement and adhesion of zoospores of *Enteromorpha* and other green algae. The swimming spore (a) appears to 'sense' the surface via an apical papilla (b) on which it rotates and may become temporarily attached to the surface by a small deposit of elastic material (c). Permanent adhesion (d) is characterized by the discharge of the contents of Golgi-derived, adhesive-containing cytoplasmic vesicles as the cell contracts against the substratum and retraction of the microfibrils of the flagella inside the cell. The newly settled spore is surrounded by secreted 'adhesive' material and has lost the intracellular adhesive vesicles of the swimming spores.

whether or not to settle and can terminate the settling process after contacting a surface (Reed *et al.*, 1992).

The properties of the adhesives in terms of spreading and curing underwater are crucial to successful colonization of substrata. However, much of the evidence on the composition of algal spore adhesives is circumstantial and based on methodologies such as histochemistry. These studies indicate that the permanent adhesives of green, brown and red algae are glycoproteins that 'cure' with time after discharge, thereby increasing the strength of attachment to the substratum. Some progress towards the molecular characterization of the spore adhesive of the green alga *Enteromorpha* has been made employing monoclonal antibodies (mAbs) to settled cells displaying adhesive. Immunolocalization methods were used to screen the resulting hybridomas for antibodies that recognize the contents of vesicles in unsettled spores and the secreted extracellular materials of adhered spores. The primary adhesive was shown to be a polydisperse, N-linked self-aggregating glycoprotein of approximately 110 kDa (Stanley *et al.*, 1999), which becomes progressively less soluble after settlement, presumably through crosslinking or 'curing' reactions. Atomic force microscopy imaging of the adhesive in its hydrated state reveals a swollen gel-like pad, approximately 1 μm thick, surrounding the spore body. Force measurements showed that freshly released adhesive has a maximum adhesion strength of $458\,\mathrm{mN\,m^{-1}}$ indicating a very sticky material. The adhesive had a compressibility similar to a 20% solution of gelatin but within minutes of release the adhesive undergoes a progressive 'curing' process, presumably by crosslinking, becoming less sticky and more compressible, assuming a consistency more like natural rubber.

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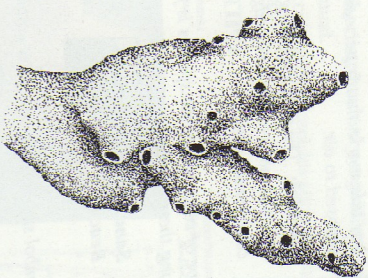# GUÍA DE INVERTEBRADOS MARINOS DEL LITORAL VALDIVIANO

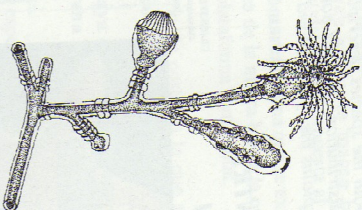### Guide to Marine Invertebrates of Valdivia

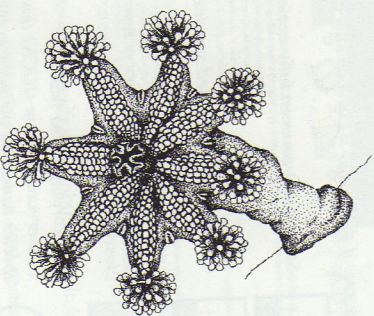CAROLINA ZAGAL R. • CONSUELO HERMOSILLA C.
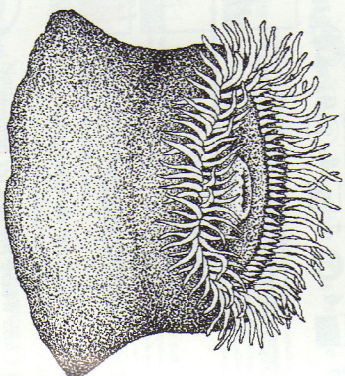Fotografías ALEJANDRO RIEDEMANN H.

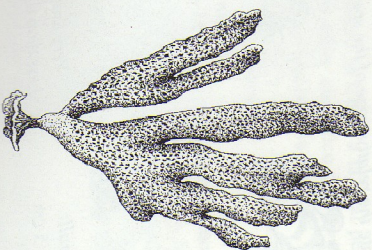# Clave taxonómica / Taxonomic key
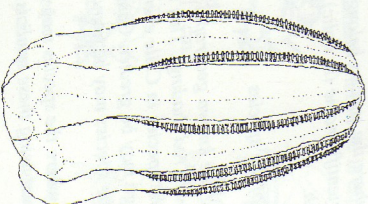
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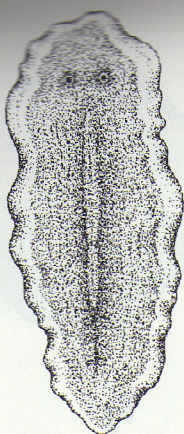
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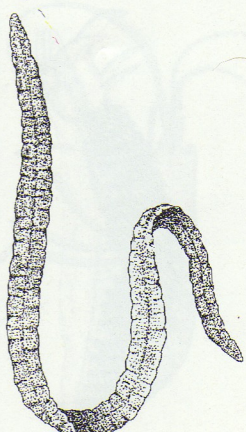
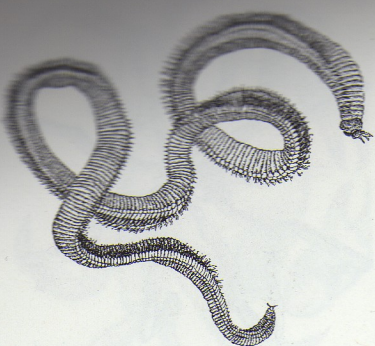Actinias / *Sea Anemones* Pag. 31

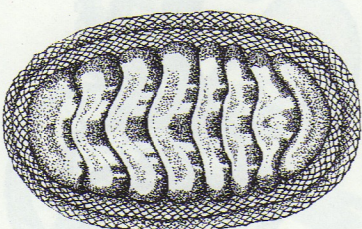Corales / *Corals* Pag. 34

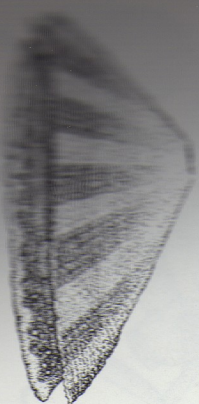Ctenóforos / *Comb Jellies* Pag. 37

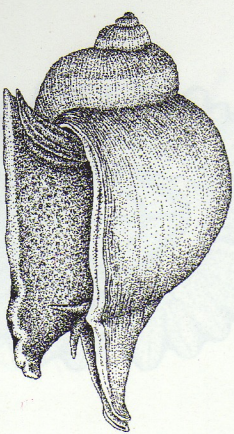Planarias / *Flatworms* Pag. 41

Nemertinos / *Ribbon Worms* Pag. 44

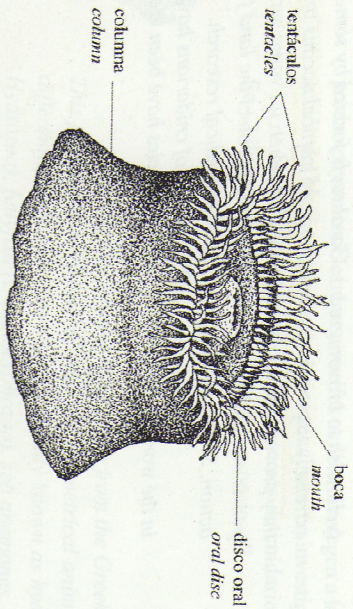Poliquetos / *Polychaete Worms* Pag. 48

Chitones / *Chitons* Pag. 60

Lapas / *Keyhole Limpets* Pag. 66

Caracoles / *Snails* Pag. 74

14

tentáculos
tentacles

columna
column

boca
mouth

disco oral
oral disc

Vista lateral de una actinia / *Lateral view of a sea anemone*

pólipos
polyps

ramas
branches

disco de fijación
attachment disc
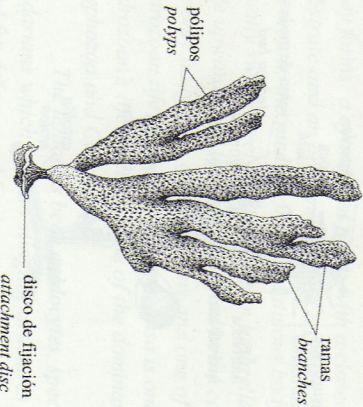
Vista lateral de un coral gorgonáceo / *Lateral view of a gorgonian* (Lophogorgia platyclados)

CLASE HYDROZOA
Sarsia sarsii
Hidrozoo
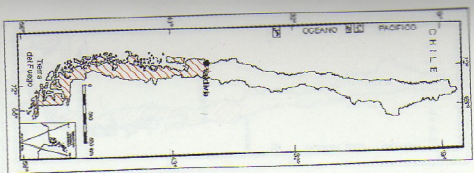
DESCRIPCIÓN: Hidrocaulo irregularmente ramificado de color rosado pálido. En los extremos de ca...
existe un **hidrante** ovoide sin **hidroteca**, con **tentáculos** cortos y delgados que terminan en esferas y g...
globosos de color rosado que generan las **medusas**.
TAMAÑO: Hasta 2 cm de altura.[241]
DISTRIBUCIÓN: Valdivia, Tierra del Fuego.[165]
HISTORIA NATURAL: Habita pozas **intermareales** junto al luche verde (*Ulva lactuca*), el alga roja
Gymnogongrus furcellatus y el carmínico (*Ceramium rubrum*). Evita el contacto directo con la luz solar...
común también, en caras invertidas de rocas y en sustratos vivientes (esponjas, choritos y briozoos).[86]
medusa de este hidrozoo se libera a fines de verano,[86] forma parte del **zooplancton** y es capaz de caza...
de su mismo tamaño (incluso **larvas** de crustáceos y peces) y soportar grandes variaciones de salinida...

DESCRIPTION: *Hydrocaulus* is branched, pail pink. The end of each branch has an ovoid **hydranth** w...
hydrotheca, with short slender **tentacles** that end in spheres and globose pink gonophores to produce...
DISTRIBUTION: Valdivia, Tierra del Fuego.[165]
SIZE: Height to about 2 cm.[241]
NATURAL HISTORY: *Inhabits **intertidal** rock pools with the Sea Lettuce (Ulva lactuca), and the red al...*
Gymnogongrus furcellatus and Ceranium rubrum. It avoids direct contact with sunlight. It is also com...
rocks and live substrates (sponges, mussels and bryozoans).[86] The medusa stage of this hydroid is relea...
*end of summer[86] and makes up part of **zooplankton** and it is capable of hunting animals of similar siz...*
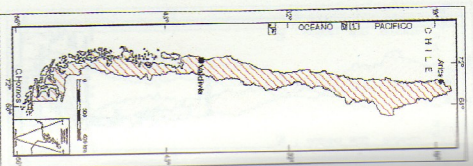*crustacean and fish **larvae**) and can withstand great salinity variations.[22]*

Phylum Mollusca
CLASE BIVALVIA
Mytilus chilensis
Chorito, Quilmahue

CLASS BIVALVIA
Mytilus chilensis
Chilean Blue Mussel, Common Mussel

DESCRIPCIÓN: Sus valvas presentan un **periostraco** de color negruzco a violáceo. La superficie externa de las valvas exhibe sólo estrías concéntricas de crecimiento. Se diferencia del choro zapato por poseer una **charnela** con numerosos dientecillos.
TAMAÑO: Longitud máxima 10.6 cm. [175]
DISTRIBUCIÓN: Arica - Cabo de Hornos, [124] Islas Malvinas. [25]
HISTORIA NATURAL: Habita la zona **intermareal** inferior alcanzando a 25 m de profundidad. [25] Forma parte de la fauna asociada al piure (*Pyura chilensis*). [247] Se alimenta filtrando **plancton** y **detritus** orgánico. Es depredado por el caracol rubio (*Xanthochorus cassidiformis*), [112] estrellas de mar, jaibas, centollas, el pato quetru no volador (*Tachyeres pteneres*) [143] y el hombre. El macho presenta **gónadas** de color amarillento y las hembras de color crema anaranjado. Presenta **fecundación** externa y desarrollo de una **larva** de vida libre. [175]

DESCRIPTION: Valves have a blackish to violet **periostracum**. The external surface of the valves has only concentric growth lines. It is distinguished from the giant mussel because it has a **hinge** with numerous small teeth.
SIZE: Maximum length is 10.6 cm. [175]
DISTRIBUTION: Arica to Cape Horn, [124] Falkland Islands. [25]
NATURAL HISTORY: It inhabits the lower **intertidal** zone to 25 m depths. [25] It makes up part of the fauna associated to the tunicate *Pyura chilensis* [247] and feeds by filtering **plankton** and organic **detritus**. It is preyed upon by the whelk *Xanthochorus cassidiformis*, [112] sea stars, crabs, kingcrabs, the Flightless Steamer Duck (*Tachyeres pteneres*) [143] and human beings. The male has yellowish **gonads** and the female's are cream to orange color. It has external **fertilization** with the development of free - swimming **larvae**. [175]

Phylum Mollusca
CLASE BIVALVIA
Perumytilus purpuratus
Choito maico, Chorito
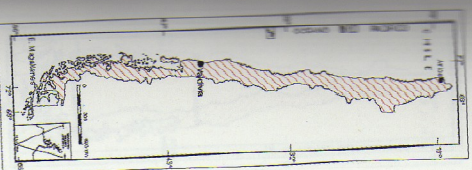
Phylum Mollusca
CLASS BIVALVIA
Perumytilus purpuratus
Mussel

DESCRIPCIÓN: Valvas pequeñas presentan un **periostraco** grueso de color violáceo a púrpura oscuro. La superficie externa de las valvas presenta estrías concéntricas y marcadas estrías radiales de crecimiento. La **charnela** presenta varios dientecillos.
TAMAÑO: Longitud máxima 3.0 cm. [173]
DISTRIBUCIÓN: Ecuador, [25] Arica - Estrecho de Magallanes (Chile), [124] Argentina. [25]
HISTORIA NATURAL: Habita la zona **intermareal** rocosa media, formando extensos bancos que quedan expuestos durante marea baja. Se alimenta filtrando microalgas y **detritus**. Es depredado por moluscos (el caracol con diente *Acanthina monodon*, el loco *Concholepas concholepas*, el caracol panal *Crassilabrum crassilabrum*), [49] la gaviota (*Larus dominicanus*) [49] el guarén (*Rattus norwegicus*) [162] y el hombre. Presentan **fecundación** externa con el desarrollo de una **larva** de vida libre. En la zona central de Chile, **desova** durante todo el año, con máxima intensidad entre primavera – verano. [173]

DESCRIPTION: Its small valves have a thick violet to dark purple **periostracum**. The external surface of the valves have marked radial and concentric growth lines. The **hinge** has many small teeth.
SIZE: Maximum length is 3.0 cm. [173]
DISTRIBUTION: Ecuador, [25] Arica to the Straits of Magellan (Chile), [124] Argentina. [25]
NATURAL HISTORY: It inhabits the **mid intertidal** rocky zone forming extensive banks which are exposed during low tide. It feeds by filtering microalgae and **detritus** and is preyed upon by mollusks (the whelks *Acanthina monodon*, *Crassilabrum crassilabrum* and the Chilean Abalone *Concholepas concholepas*), [49] the sea star *Heliaster helianthus*, the fish *Sicyases sanguineus*, the seagull *Larus dominicanus*, [49] the rat *Rattus norvegicus* [162] and human beings. In central Chile it sheds its **gametes** during the whole year with a maximum intensity during spring to summer. [173]