Biological Synopsis of the Light-Bulb Tunicate (*Clavelina lepadiformis*)

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BIOLOGICAL SYNOPSIS OF THE LIGHT-BULB TUNICATE(*CLAVELINA LEPADIFORMIS*)

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Clavelina lepadiformis, commonly known as the light-bulb tunicate, is a colonial ascidian with a native habitat from the north-eastern Atlantic Ocean to the Mediterranean Sea. This species has many characteristics advantageous to successful establishment in non-native habitats, such as high growth and reproductive rates, and a wide tolerance of habitat characteristics. These traits have resulted in invasions of numerous coasts, including South Africa and the eastern United States, and have flagged the light-bulb tunicate as a possible invader of Atlantic Canadian waters. *C. lepadiformis* is not able to disperse over large areas naturally since they are sessile in adult form, and are short-living in larval form. Therefore, invasions are thought to be aided by human-mediated dispersal methods such as ballast water and hull fouling.

Invasive ascidians with these characteristics have proven harmful to the invaded habitat regarding reduced biodiversity. This biological synopsis is intended to summarize available information on its biological characteristics, distribution, and potential impacts.

RÉSUMÉ

Mackenzie, A.B. 2011. Biological synopsis of the light-bulb tunicate (*Clavelina lepadiformis*). Can. Manuscr. Rep. Fish. Aquat. Sci. 2967: iv + 15 p.

Clavelina lepadiformis, communément connue sous l'appellation de grande claveline, est un tunicier colonial dont la distribution d'origine s'étend du nord-est de l'océan Atlantique jusqu'à la mer Méditerranée. Cette espèce a plusieurs caractéristiques avantageuses lui permettant de s'introduire efficacement dans de nouveaux habitats non-indigènes, comme ses taux élevés de croissance et de reproduction ainsi que sa grande tolérance face aux caractéristiques des habitats envahis. Ces traits ont favorisé l'envahissement d'une multitude de littoraux de l'Afrique du Sud et l'est des États-Unis. La grande claveline est maintenant considérée comme un envahisseur potentiel des eaux canadiennes de l'Atlantique. *C. lepadiformis* est incapable de se disperser sur de grandes distances de part la sessilité de sa forme adulte et son stade larvaire éphémère. Par conséquent, les introductions sembleraient être facilitées par différents vecteurs anthropogéniques tels les eaux de ballast et la fixation à la coque des navires.

Les tuniciers envahisseurs ont eu des effets néfastes sur les habitats envahis en produisant une réduction de la biodiversité. Ce résumé de la biologie est réalisé dans le but de fournir un outil facilitant les efforts d'atténuation en résumant l'information disponible sur les caractéristiques liées à la biologie, à la distribution et aux impacts potentiels de l'introduction de *C. lepadiformis*.

1 INTRODUCTION

Aquatic invasive species (AIS) are a great threat to biodiversity. The light-bulb tunicate, *Clavelina lepadiformis*, has invaded South Africa and the eastern United States (Reinhardt et al. 2010). It forms dense aggregations that have the potential to outcompete native species and overgrow aquaculture operations (Reinhardt et al. 2010). *C. lepadiformis* has been flagged as a potential invader to Atlantic Canadian waters, with concerns raised regarding the environmental and economic repercussions (Locke 2009).

This biological synopsis is a review of the biological characteristics of the species and known effects of past invasions. Information regarding reproductive effort and life cycles are critical for early mitigation plans in uninhabited areas at risk of invasion.

1.1 NAME AND CLASSIFICATION

(from ITIS 2011)

Kingdom: Animalia
Phylum: Chordata
Subphylum: Tunicata
Class: Ascidiacea
Order: Enterogona
Suborder: Aplousobranchia
Family: Clavelinidae
Genus: Clavelina
Species: *Clavelina lepadiformis*

Common Name: Light-bulb tunicate

1.2 DESCRIPTION

Clavelina lepadiformis is a colonial ascidian with loosely attached individual zooids reaching 20 mm in length and 5 mm in diameter (Riley 2008; Picton and Morrow 2010). The zooids are clear with white, yellow, or pink bands around the endostyle, dorsal lamina, and the oral siphon, giving the species its light-bulb appearance (Riley 2008; Reinhardt et al. 2010; Picton and Morrow 2010) (Figure 1). Its transparent body makes it easy to observe its internal structures, such as the branchial sac, oesophagus, stomach, intestine, rectum, and atrial cavity (Ooishi 2010).

The individual zooids are housed in a common structure made of tunicin, a cellulose-like substance (Coleman 2008). Each zooid is joined to the tunic (or test) at the base, and functions independently using a branchial sac for respiration, an intestinal loop posterior to the branchial sac, gonads in the lower part of the intestinal loop, and a heart on the ventral side of the abdomen (Berrill 1950) (Figure 2). The branchial sac has 45 stigmata in transverse rows (Berrill 1950). The intestinal loop consists of an oesophagus, a square-shaped stomach, several sections of intestine and an anus that opens into the lower part of the atrial chamber (Berrill 1950). The heart is a short, straight tube (Berrill 1950). In all other Aplousobranchia families, the heart is V-shaped and horizontal (Kott 1969). The light-bulb tunicate is a hermaphrodite, with each zooid having both an ovary and a testis (Berrill 1950). The testis is adjacent to the compact ovary (Berrill 1950).

The light-bulb tunicate may be misidentified as *Diazona violacea,* which has similar markings, but can be distinguished by the extra white spots around the exhalent siphon of *D. violacea* (Picton and Morrow 2010).

2 DISTRIBUTION

2.1 NATIVE DISTRIBUTION

The light-bulb tunicate was first described in Atlantic waters in the eighteenth century (Tarjuelo et al. 2001) and is native from the Shetland Islands and Bergen, Norway, to the Bay of Biscay, the Mediterranean, and the Adriatic (Reinhardt et al. 2010). Millar (1966) reports specific coasts of its natural habitat, including the west and south coasts of Norway, the east coast of the British Isles, as well as Skagerrak, Kattegat, and the North Sea coasts.

2.2 NON-NATIVE DISTRIBUTION (EXCLUDING CANADA)

During the 1990s, this species was reported as present in the Azores and Madeira, Portugal (Reinhardt et al. 2010). A decade later, reports from the Knysna Estuary and Port Elizabeth, South Africa, stated that *Clavelina lepadiformis* had invaded and established (Reinhardt et al. 2010) (Figure 3). In 2009, populations were found in the northwest Atlantic (Connecticut) for the first time (Reinhardt et al. 2010).

2.3 DISTRIBUTION IN CANADA

There are currently no reports of *Clavelina lepadiformis* in Canadian waters, though Locke (2009) predicted *C. lepadiformis* to be a likely invader of Atlantic Canadian waters due to its past invasion history and native range encompassing large variability in environmental conditions (Reinhardt et al. 2010).

2.4 POTENTIAL VECTORS FOR INTRODUCTION

Clavelina lepadiformis has a short natural dispersal range since its larvae cannot feed and are only free-swimming for up to 3 hours. For the same reasons, young light-bulb tunicates are unlikely to survive transatlantic trips in ships ballast water. The most likely vector for introduction is therefore as hull fouling adults (Reinhardt et al. 2010). This is thought to be the case for transport to Portugal and South Africa (Reinhardt et al. 2010). It is possible that cryptic invasions of benthic invertebrates occur frequently without our knowledge due to the fact that individuals may not be distinguished from one another morphologically (Turon et al. 2003).

3 BIOLOGY AND NATURAL HISTORY

3.1 FEEDING AND RESPIRATION

Clavelina lepadiformis feeds on suspended particulate matter by actively pumping water through a mucus net lining the branchial basket (Petersen and Svane 2002). This active feeding method allows this species to thrive in very still water (Riley 2008). Water is pumped in through the inhalant siphon using cilia and the particles trapped in the mucus net are rolled into a food string and drawn into the oesophagus (Petersen and Svane 2002) (Figure 4). The mucus net is produced by the endostyle and consists of an elongate rectangular mesh with pore sizes 0.5 µm wide and 2 µm long (Petersen and Svane 2002).

Filtration rates are dependent on the area of the branchial basket as well as the length of the ciliary band (Petersen and Svane 2002). Larger animals are able to filter water at 150 cm^2/h, which means more food particles are available for consumption (Flood 1982). Flood (1982) attempted to measure the speed of feeding using latex spheres. Feeding speed is highly dependent on animal size, with animals 5.0–10.2 mm moving the food string into the oesophagus at 7 µm/s, and animals 21.6–31.2 mm feeding at 78 µm/s (Flood 1982). Flood (1982) calculated that animals 1.5–2.2 cm long produce 100 cm^2 of mucus per hour. Feeding rates may also depend on temperature since cilia beat slower at cooler temperatures (Flood 1982).

It is estimated that ascidians filter 10–20 litres of water for every millilitre of oxygen consumed, and that each millilitre of oxygen can combust 0.8 mg of food (Barrington 1965). This means that an individual requires 0.05 mg of organic material per litre of seawater filtered to maintain its respiration rate (Barrington 1965). When taking into account other requirements such as growth and reproductive investment, it is estimated that an individual requires 0.15 mg of food per litre of water (Barrington 1965). This is not an issue for many temperate waters. For example, the English Channel averages 1.6–1.8 mg per litre of particulate matter (Barrington 1965). Ascidians secrete ammonia as a waste (Barrington 1965). Waste is discharged through the anus (Moen and Svensen 2004).

3.2 REPRODUCTION AND DEVELOPMENT

Like most colonial ascidians, the light-bulb tunicate is a hermaphrodite that reproduces sexually and asexually (Riley 2008). Sexual reproduction occurs with internal fertilization, allowing 50–70 embryos in the atrial cavity at one time (Riley 2008).

Clavelina lepadiformis eggs are 0.26 mm in diameter (Berrill 1935a). Eggs are enclosed in a thick vitelline coat called the chorion, which sperm bind to in a species-specific manner during fertilization (Fukumoto 2000). The sperm are plesiomorphous, meaning that they have apical acrosomal vesicles and an elongated, cylindrical nucleus (Franzén 1992). Immature sperm have a spherical nucleus with granular chromatin, as well as several small mitochondria and ribosomes and some vesicles (Franzén 1992). During spermiogenesis, the nucleus elongates and the chromatin becomes dense

(Franzén 1992). When mature, the head of the sperm cell is 6 µm long and the tail flagellum is 36 µm long (Franzén 1992). The head houses a nucleus 0.5 µm in diameter consisting of tightly coiled chromatin fibres within a nuclear envelope (Franzén 1992). The acrosome is pear-shaped (300 nm x 200 nm x 40 nm; length, width, height) (Fukumoto 2000). It is believed that the acrosome participates in fusing gamete plasma membranes during fertilization (Fukumoto 2000). Acrosome differentiation in the light-bulb tunicate is similar to that seen in mammals (Fukumoto 2000).

C. lepadiformis sperm have some characteristics in common with the more primitive sperm of *Ciona intestinalis*. These include an elongated head (6 µm and 3 µm, respectively), a single mitochondrion close beside the nucleus, and the lack of a midpiece (Fukumoto 2000). However, *C. lepadiformis* has an elongated mitochondrion that spirals 1.5 times around the nucleus, while *C. intestinalis* has a compact, straight mitochondrion (Franzén 1992; Ooishi 2010). This is interesting because the colonial *C. lepadiformis* is an internal fertilizer, while the solitary *C. intestinalis* is an external fertilizer (Fukumoto 2000). Franzén (1992) suggests that these sperm commonalities may have evolved along with internal fertilization in ancestral ascidians, and that the sperm type was retained by solitary ascidians after secondarily developing external fertilization.

Berrill (1935b) studied the breeding season of light-bulb tunicates collected from Plymouth, England. He found the sexual breeding season began in July and ended in September, followed by senescence of the adult form, which exposed the basal mass (Berrill 1935b). This basal mass housed totipotent cells which are used to form asexual buds without involving the epicardium, which is unique to the family Clavelinidae (Berrill 1935a; Kott 1969). As long as the vessels in the stolon are attached to the zooids, bud development is inhibited, but once the totipotent cells are exposed, the basal mass becomes active and grows a new colony (Berrill 1935b). If the colony is damaged during high summer temperatures, there is a rapid development of new zooids, but the typical course of exposure occurs in low winter temperatures when growth is retarded (Berrill 1935b). Growth of the new colony gets a boost in the spring, and asexual budding can overlap with the sexual breeding season slightly (Berrill 1935b).

Berrill (1935a) observed *C. lepadiformis* development at 16°C, and found that gastrulation occurred 40–50 hours after fertilization. Sensory pigments were visible at 145 hours, and hatching occurred within 220 hours (Berrill 1935a). The free-swimming larvae then searched for suitable settlement substrate for up to 3 hours (Berrill 1935a). Pennati et al. (2009) examined the adhesive papillae and their role in settlement. Adhesive papillae of *C. lepadiformis* are complex, housing multiple cell types: mucus-secreting cells, supporting cells, and at least two types of neurons (Pennati et al. 2009). The authors found central neurons and peripheral ciliated neurons. It is thought that the central neurons may have chemo- or mechano-receptors that sense the substrate for suitable attachment sites. Once attached, the peripheral neurons are thought to be involved in the mechanism triggering metamorphosis (Pennati et al. 2009). This theory is compelling because serotonin was found in the peripheral neurons, which has been shown to play a role in such a mechanism in other ascidians (Pennati et al. 2009).

After settlement, metamorphosis occurs, allowing the organs to develop into adult stages. The heart becomes fully functional 40 hours after settlement, and the gut after 60 hours (Berrill 1935a).

3.3 LIFE CYCLE: GROWTH, GENERATION TIME, AND LONGEVITY

The life history of the light-bulb tunicate varies with the environment in which it lives. In general, it follows an annual cycle of asexual budding in the spring and sexual reproduction in the summer, followed by death of the adult zooids, leaving a basal mass to overwinter (Picton and Morrow 2010). Colonies of this species enter an inactive period after sexual reproduction when only the buds survive, but this period differs with region (Berrill 1935b). In the Atlantic populations, dormancy occurs during the winter and is called hibernation, while the opposite is seen in the Mediterranean populations, with dormancy occurring during the summer and is referred to as aestivation (de Caralt et al. 2002).

Life history characteristics may drastically differ between adjoining habitats with different conditions, such as the open water of the Mediterranean Sea and a harbour environment. de Caralt et al. (2002) examined such a situation, and found the open water population had one breeding season per year, producing larvae in the winter and spring, while the harbour population had several breeding cycles resulting in larvae being present over a broad stretch of time (November–June) (de Caralt et al. 2002). Outer population zooids were immature October–December, maturing February–March (de Caralt et al. 2002). The larvae were brooded within the test for 2 months then released, followed by senescence of the adults (de Caralt et al. 2002). Within the harbour, January had peak reproductive activity with the vast majority of zooids matured with gonads and/or mature larvae, with a second, smaller peak in April (de Caralt et al. 2002). After the breeding season, most zooids were immature and zooid density was lowest in July (de Caralt et al. 2002).

The abundance of *C. lepadiformis* is typically high, partially due to its high growth rate, growing from immature zooids to full size in two months (Riley 2008). Abundance in the outer population was an order of magnitude lower than the populations in the harbour which reached densities of 3900 zooids/m^2 (de Caralt et al. 2002). This finding is in agreement with the Howes et al. (2007) Nova Scotia study finding that recruitment of *Ciona intestinalis* varies with exposure, being highest in sheltered areas and lowest in exposed areas.

The zooids and larvae of the harbour population were significantly larger, and accumulated 6 times more copper and 8 times more lead, whereas the open water population produced more secondary metabolites (de Caralt et al. 2002). Copper was the most abundant metal in the harbour, reaching maximum concentrations October–December, and minimums April–July (de Caralt et al. 2002). Vanadium accumulation was low May–September and high December–January (de Caralt et al. 2002). The purpose of vanadium accumulation is not known, but could be used as a predator deterrent, an antimicrobial agent, or to deter fouling of the colony (de Caralt et al. 2002).

de Caralt et al. (2002) experimented with survivorship of colonies switched to the opposite habitat, and found that colonies from open water could survive in the harbour (30–50% survivorship after one month), but harbour colonies had 5% survival rates after one month in the open water.

3.4 HABITAT AND ENVIRONMENTAL TOLERANCES

The light-bulb tunicate inhabits shallow littoral areas down to 50 m, growing on natural or artifical hard substrates (Reinhardt et al. 2010). It is one of the most common ascidians in shallow rocky sublittoral habitats (Picton and Morrow 2010).

Harbour environments are well suited to *C. lepadiformis* growth due to their nutrient rich, low current waters providing food and abundant secure substrates for growing colonies (Tarjuelo et al. 2001). However, they also have higher pollution concentrations which can negatively affect growth (Tarjuelo et al. 2001).

The light-bulb tunicate can tolerate a wide range of habitats, from open coasts that are very exposed, to estuaries and enclosed bays that are extremely sheltered (Riley 2008). They can also tolerate typical seawater salinities of 30–40‰, to more variable estuary salinities of 18–40‰ (Riley 2008). The light-bulb tunicate is also capable of surviving in a wide range of temperatures and oxygen levels (Riley 2008).

3.5 ECOLOGY

Clavelina lepadiformis grows on hard substrates, including rocks, wharf pilings, docks, and boat hulls. This species has the potential to thrive on aquaculture sites because of the availability of hard substrates on which to settle and grow, with minimal competition or predation risk (Carman et al. 2010). Predators of the light-bulb tunicate include bottom-feeding fishes, carnivorous gastropods, starfishes, and flatworms such as *Prostheceraeus moseleyi* (Riley 2008). However, there are not many natural predators of ascidians due to their unpalatable production of secondary metabolites (de Caralt et al. 2002). These characteristics lead to the rapid dominance of the light-bulb tunicate by out-competing native species, and can result in decreased biodiversity.

There is evidence of marine succession, or the presence of one organism aiding the introduction of another organism to an area. Newly submerged surfaces are quickly covered by bacteria, diatoms, and other microorganisms which create a biofilm (Zardus et al. 2008). These biofilms produce biochemical cues that can attract invertebrate larvae to the site; such is the case with the ascidian *Phallusia nigra* (Zardus et al. 2008).

3.6 DISEASES AND PARASITES

There is little known about diseases caused by, or affecting, tunicates. However, there are reports of organisms parasitizing tunicates, such as the copepod *Enterocola hessei* inhabiting zooids of *Clavelina lepadiformis* (Ooishi 2010). This typically occurs with a single female, sometimes carrying 2 egg sacs with orange eggs, living in the zooid’s stomach and directing its cephalosome toward the oesophagus (Reinhardt et al. 2010) (Figure 5).

4 HUMAN USES

The light-bulb tunicate is often used as a model for the morphology and physiology of all ascidians (Tarjuelo et al. 2001). They may be useful as water quality indicators due to their capability of concentrating toxic substances, such as heavy metals and hydrocarbons, within their tissues (Tarjuelo et al. 2001). Most ascidians have also been found to be cytotoxic, possessing anti-leukemic properties (Teo and Ryland 1994).

5 IMPACTS ASSOCIATED WITH INTRODUCTIONS

5.1 IMPACTS ON THE ENVIRONMENT

Coastal and estuarine systems are susceptible to invasions of non-indigenous species due to the great variety and abundance of species transported to them, as well as the presence of urbanization stressors such as fisheries, recreational boating, and shipping (Altman and Whitlatch 2007; Harris and Dijkstra 2007). Colonial ascidians have the potential to become dominant over native coastal species within a short period of time (Vance et al. 2008). More information is needed regarding impacts of high ascidian abundance on water quality through eutrophication.

It is important to understand the factors that might facilitate the introduction of non-native species. Altman and Whitlatch (2007) examined disturbance as one of these factors. Disturbances on the seafloor expose spaces, which organisms may exploit for population expansion. Small scale disturbances are often driven by biological processes, such as predation, while large scale disturbances are often driven by physical processes, such as storms or human activities (Altman and Whitlatch 2007). Coastal systems are prone to both types of disturbances, making them particularly susceptible to invasion (Altman and Whitlatch 2007). *Clavelina lepadiformis* is known to be an opportunistic grower which can rapidly dominate disturbed habitats (Reinhardt et al. 2010).

The major threat to environmental health in invaded regions comes from the indirect consequences of biofouling. The aquaculture industry uses copper-treated nets to deter ascidian settlement and growth; however, this practice has broad ecological impacts. While copper is an essential nutrient for plant and animal growth, it is toxic in high concentrations (Hall and Anderson 1999). Copper accumulates in the aquatic ecosystem, with highest concentrations in marinas and harbours, followed by estuaries and, finally, open seas where concentrations are lowest (Hall and Anderson 1999). Seasonally, they found that copper concentrations increased during the summer months of June to August in marinas and harbours. Matthiessen et al. (1999) took similar readings in Essex and Suffolk, and found the ambient copper levels in coastal waters exceeded safety levels from 1992 to 1996.

5.2 IMPACTS ON OTHER SPECIES

The light-bulb tunicate forms dense aggregations that have the potential to overgrow and outcompete native species (Reinhardt et al. 2010). Ascidians such as *C. lepadiformis* are successful competitors for space due to their high growth rates and the presence of toxic metabolites (lepadin A) in their tissues (Tarjuelo et al. 2001). These toxic effects seem to be pronounced in *C. lepadiformis*, causing high mortalities in many invertebrates such as *Flustrellidra hispida* and *Spirorbis spirorbis* (Teo and Ryland 1994, 1995). These characteristics of invasive tunicates can have significant ecological impacts (Reinhardt et al. 2010).

5.3 IMPACT SUMMARY

Invasive tunicates can impact invaded regions in a variety of ways. Past invasions have decreased biodiversity due to competition for food and space, driving the decline of native species abundance.

6 CONSERVATION STATUS

Clavelina lepadiformis is not listed under the International Union for Conservation of Nature (IUCN) list of threatened species and is therefore considered to be without conservation status (IUCN 2011).

7 SUMMARY

The light-bulb tunicate is a colonial ascidian with fast growth rates and high reproductive output that can tolerate a wide variety of environmental conditions. These life history traits make it a successful invader to non-native habitats. Past invasions have had significant impacts on native species, reducing biodiversity. *Clavelina lepadiformis* has been flagged as a possible invader to Atlantic Canadian waters.

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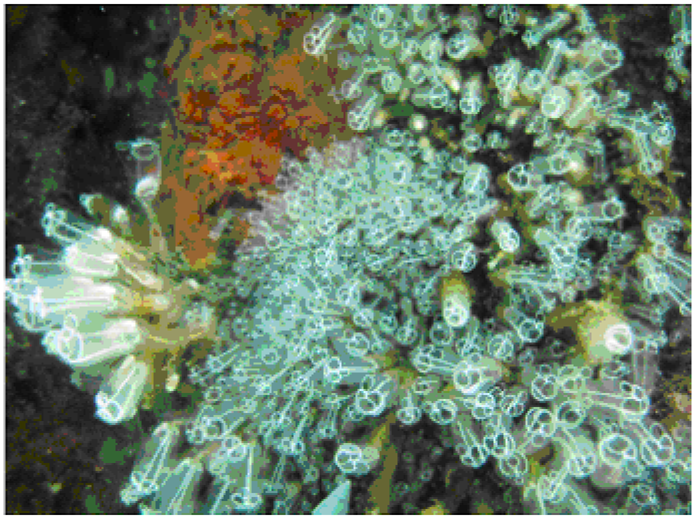

(Photo by J.F. Reinhardt)

Figure 1. *Clavelina lepadiformis*
(Reinhardt et al. 2010)
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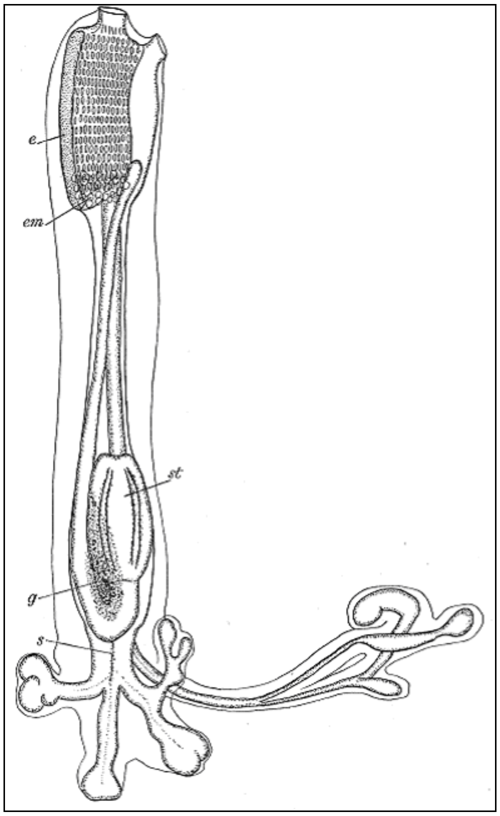

Figure 2. Individual *Clavelina lepadiformis* zooid
e - Endostyle; em - Embryos; g - Gonads; st - Stomach; s - Septum of vascular stolon
(Berrill 1935b)
(Reproduced with permission of the Royal Society of London)

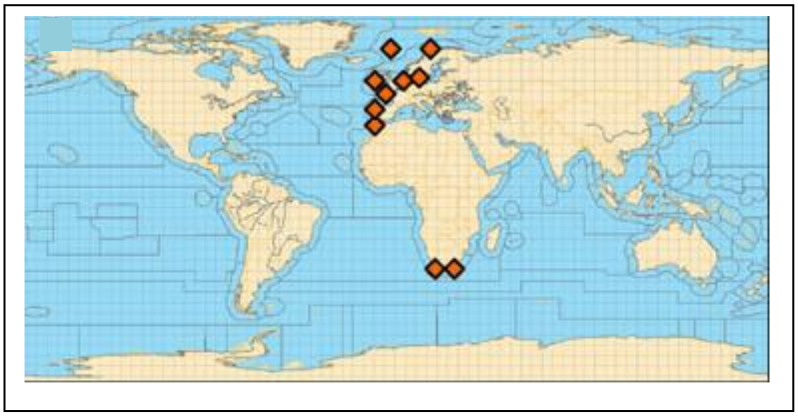

Figure 3. Worldwide distribution of *Clavelina lepadiformis*
(Locke 2009)
(Reproduced with permission from Aquatic Invasions)

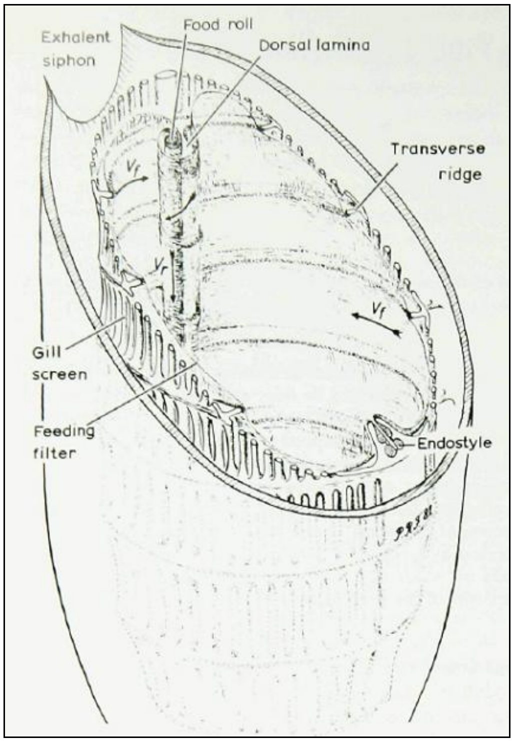

Figure 4. Branchial basket of *Clavelina lepadiformis* with the inhalant and upper half of exhalent siphon removed
(Flood 1982)
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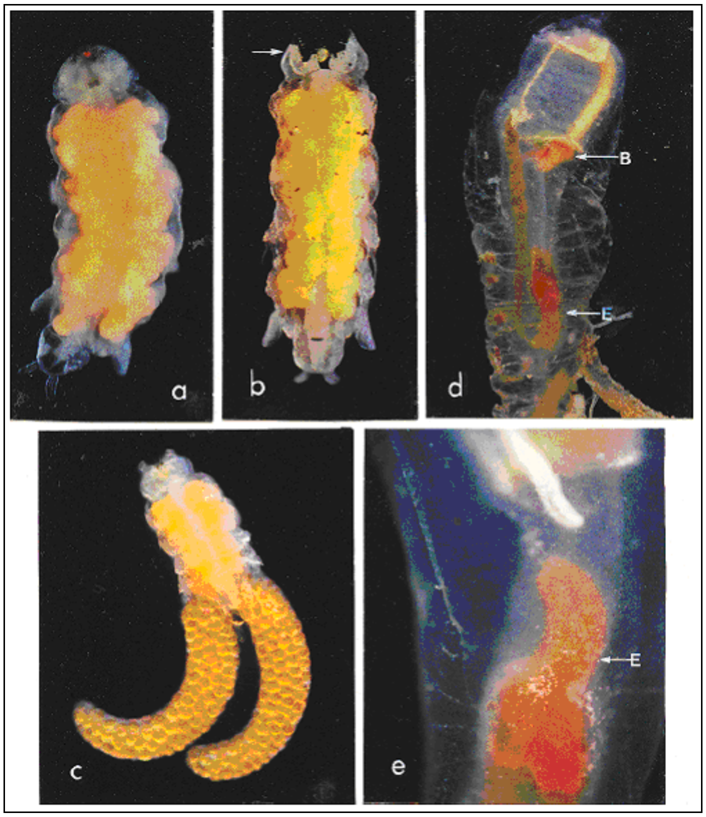

Figure 5. Macrophotos of *Enterocola hessei* females living inside *Clavelina lepadiformis*
(a-c) *Enterocola hessei* females; (d, e) *Enterocola hessei* females living inside *Clavelina lepadiformis*
a) Body form, dorsal; b) Body form, ventral; c) Female carrying 2 egg sacs; d) Zooid with *E. hessei* in stomach (arrow E), and female *Botryllophilus* in branchial sac (arrow B); e) Zooid with female *E. hessei* showing egg sacs in oesophagus and body in stomach (arrow E). Caption modified from original (Ooishi 2010)
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