Biological Synopsis of the Lacy Crust Bryozoan (*Membranipora membranacea*)

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BIOLOGICAL SYNOPSIS OF THE LACY CRUST BRYOZAN
(*Membranipora membranacea*)

by

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ABSTRACT

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Lacy Crust is a white and/or grey marine bryozoan which may also be
known colloquially as Coffin Box. It is an epiphyte, forming encrusting sheets on
species of algae that it depends upon for support but not nutrition. Lacy Crust
forms thin, lacy, mat-like colonies of connected zooids, which have spines for
protection from predation. Colonies are typically found from the intertidal zone to
10 metre depths.

Native to the North Pacific Ocean from Alaska to Baja California, and
throughout the temperate Northeast Atlantic Ocean, Lacy Crust is a spatially
disjunct and cryptic species. Populations in both the northern and southern
hemispheres occur in the USA, Canada, Japan, Australia, New Zealand, Chile,
South Africa, and western Europe. Non-native populations occur along the
western North Atlantic coastline from Long Island Sound, USA to northern
Newfoundland, Canada.

Heavy encrustations of Lacy Crust can be found on native species of kelp,
which often leads to defoliation during periods of intense wave action. Synergistic
interactions between Lacy Crust and an invasive green alga *Codium fragile* ssp.
have caused devastation of native kelp beds in some regions. These will likely
impact populations of associated species such as lobsters that depend on kelp
beds for food and habitat.

1.0. INTRODUCTION

Marine ecosystems are being impacted at an accelerated rate from human-induced species introductions (Ruiz et al. 2000). The ability to assess and mitigate effects on ecosystems is often difficult due to the lack of knowledge of the ecosystem prior to invasion, the behaviour, physiology, and population dynamics of the invasive species is often poorly understood, and patterns and mechanisms of invasion are lacking (Scheibling and Gagnon 2009). Assessing the risk of potential aquatic invasive species is one of the mandates for Fisheries and Oceans Canada's Centre of Expertise for Aquatic Risk Assessment (CEARA). Lacy Crust, or Coffin Box, (*Membranipora membranacea*) has been identified as a species of concern and a biological synopsis is a first step in the process.

Native to the Northeast Atlantic, and the North Pacific, Lacy Crust was first recorded on the Northwest Atlantic in the Gulf of Maine in 1987 (Schultz 2010) and in Mahone Bay and St. Margaret's Bay in Nova Scotia in 1992 (Scheibling et al. 1999) where it became the dominant epiphyte on kelps within two years (Berman et al. 1992). Species with a dispersive phase are likely to be successful invaders because they are easily picked up in ballast water (Ricciardi and Rasmussen 1998). Lacy Crust has a dispersive larval phase (Yoshioka 1982) and has been found in ship ballast in eastern Canadian ports (Simard et al. 2011). It is also known to raft on dislodged kelp (Schwaninger 2008) and has been found encrusted on drift plastic (Aliani and Molcard 2003). The combination of a short reproductive cycle, fast growth rates, and the absence of predators and competitors will contribute to the invasive success of Lacy Crust (Pratt 2008, Saunders and Metaxas 2009a, Saunders et al. 2010).

Lacy Crust forms heavy encrustations on native species of kelp (Dixon et al. 1981), which often leads to defoliation during periods of intense wave action (Scheibling et al. 1999). Synergistic interactions between Lacy Crust and an invasive green alga, *Codium fragile* ssp., have caused displacement of native kelps (Scheibling and Gagnon 2009). Field observations indicate that recurring

seasonal outbreaks of coffin box have devastating effects on native kelp populations (Scheibling et al. 1999, Saunders & Metaxas 2008, Scheibling and Gagnon 2009, Saunders et al. 2010). Populations of sea urchins and American lobster (*Homarus americanus*) that depend on kelp beds for food and habitat may be impacted (Lambert et al. 1992, Chapman et al. 2002).

A biological synopsis of Lacy Crust, including its description, distribution, biology, natural history, and known impacts are presented in this report. Areas where information is lacking are identified.

1.1. NAME AND CLASSIFICATION

Kingdom: Animalia
Phylum: Ectoprocta
Class: Gymnolaemata
Order: Cheilostomata
Family: Membraniporidae
Genus and Species: *Membranipora membranacea* (Linnaeus 1767)
Original Combination: *Flustra membranacea* Linnaeus 1767
Junior synonyms: *F. teleacea, M. serrilamella, M. villosa* (Yoshioka 1982)
Common English Name (Canada): coffin box
Other English Names: lacy-crust bryozoan, lacy bryozoan, sea mat
French Name (Canada – Quebec): croûte de dentelle, Membranipore

M. membranacea is a disjunct and cryptic species complex. There are populations in the Pacific and Atlantic oceans and in the northern and southern hemispheres (Yoshioka 1982, Schwaninger 2008, Arkema 2009).

1.2. DESCRIPTION

Lacy Crust is a marine, epiphytic bryozoan. It forms thin, lacy, mat-like colonies that reach one mm in height. A colony is made up of individual zooids that are each approximately 0.42 x 0.13 mm (Schultz 2010), although there is variability. Each zooid is surrounded by calcified walls shaped in rectangular

boxes, hence the name coffin box. Each box has fine spines, giving Lacy Crust a rough texture. Spines protect the zooids from predation by nudibranchs (Yoshioka 1982). In a colony, zooids abut each other on all sides, so that it completely covers its substrate (Pratt 2005). A frontal membrane covers the space between the side walls with a lophophore, or feeding tentacle. Some zooids, known as towers, have frontal membranes that project upwards in a column (Schultz 2010). The white to grey colonies form encrusting sheets on algal substrates such as kelp, often covering kelp blades that are meters in length (Pratt 2005). Colonies usually inhabit areas from the deepest kelp forest up to the intertidal zone (Rowley 2004, Pratt 2008, Schultz 2010).

Bryozoans are often difficult to distinguish and identify, even for experts (Meinkoth 1981). Lacy Crust demonstrates ecophenotypic variation in the North Pacific (Yoshioka 1982). *M. membranacea* is characterized by an insignificant smooth or finely serrate cryptocyst. *M. villosa* (a junior synonym) has a finely serrate cryptocyst with many cuticular spines on the frontal membrane and lateral margin. *M. serrilamella* (a junior synonym) has a strongly serrated, spinous cryptocyst. This variation is partly induced by its nubibranch predators (Dick and Mawatari 2004).

A native bryozoan, the hairy sea-mat (*Electra pilosa*), may be confused with Lacy Crust. Both form white sheets on marine alga, but the hairy sea-mat forms star-shaped colonies with hairy extensions and small oval-shaped individuals (DFO 2011).

1.2 GENETICS

The plasticity and paucity of identifying characteristics in *Membranipora* makes its taxonomy difficult. The simple zooids have few characters with which to distinguish species and/or phenotypic plasticity (Yoshioka 1982, Harvell and Grosberg 1988). Other bryozoan species appear to offer more reliable morphological characters to determine taxonomic differences (Jackson and Cheetham 1990).

Three species of bryozoan were originally described in the North Pacific native range based on morphology: *M. serrilamellq*; *M. villosa*; and, *M. membranacea* (Osburn, 1950). Yoshioka (1982) determined that these three species occurring together on brown macroalgae from the west coast of North America were eco-phenotypic variants, and that the morphological difference in the spines of the zooids were induced by nudibranch predators. Populations from more distant locations were also described as different species including *M. isabelleana* from Chili, *M. serrilamella* from Japan and the Northeast Pacific, and *M. hyadesi* from Chile and Argentina. These were also later determined to be indistinguishable from *M. membranacea* (Schwaninger 2008). Studies conducted on population differences between the North Atlantic and Northeastern Pacific also concluded that there were distinct populations based on details of zooid morphology (Dick et al. 2005).

Schwaninger (2008) reconstructed the phylogeographic history of the cosmopolitan coffin box using mtDNA cytochrome oxidase 1 (COI) sequences. Maximum parsimony, maximum likelihood, and Bayesian genealogies revealed three deep clades in the North Pacific and one monophyletic clade each in the southeast Pacific (Chile), southwest Pacific (Australia/New Zealand), North Atlantic, and southeast Atlantic (South Africa). The three morphs proved to be genetically indistinguishable at the allozyme level.

Strong support of the clades suggest that long-distance dispersal events, across oceans in the same climate zone, and across the tropics, are rare events even given the adaptations for dispersal and colonization of coffin box. Over a long enough period of time, coffin box has adapted to disperse and colonize while being transported to suitable habitats around the world. Limited long-range dispersal has resulted in some genetic differentiation among subpopulations (Saunders pers. comm. 2012).

2.0. DISTRIBUTION

2.1. NATIVE DISTRIBUTION AND ABUNDANCE

Lacy Crust is native to the North Pacific Ocean from Alaska to Baja, California (Meinkoth 1981), and throughout the temperate Northeast Atlantic Ocean (Gordon and Hayward 2011). It inhabits coastal areas from the low tide line down to the limit of kelp forests (Schultz 2010). Colonies vary in size and may consist of up to tens of thousands of zooids, covering kelp blades many metres in length (Pratt 2005). Competition for substrate is often fierce and rapid occupation (several mm per day) of areas often occurs (Rowley 2004). Intense predation in its native range episodically occurs by specialized nudibranchs, which may reduce their abundance (Yoshioka 1982). However, large abundances of nudibranchs are seen only on occasion in Nova Scotia (Saunders pers. comm. 2012). Food supply and warm water during the growth stage in summer and autumn contribute to a greater abundance of zooids, hence larger colonies (Saunders and Metaxas 2009b). In summer, colony size in high population densities is approximately 62% smaller than one grown at low densities (Harvell et al. 1990).

2.2. NON-NATIVE DISTRIBUTION (EXCLUDING CANADA)

Lacy Crust was first recorded in the Gulf of Maine in 1987 and within the first few years became the dominant epiphyte on kelp (Berman et al. 1992). It now occupies coastal bays of Maine, Massachusetts, New Hampshire, Rhode Island and Connecticut in the USA (O'Connell and Fuller 2012).

Lacy Crust is a spatially disjunct and cryptic species complex, with populations in both the Pacific and Atlantic coasts, in each of the northern and southern hemispheres including USA, Canada, Japan, Australia, New Zealand, Chile, South Africa, and western Europe.

2.3. NON-NATIVE DISTRIBUTION AND ABUNDANCE IN CANADA

Lacy Crust was first discovered in Nova Scotia in the early 1990s. In 2003, it was observed in the Gulf of St. Lawrence, Quebec. It is now established in Quebec, New Brunswick, Nova Scotia, and Newfoundland (Schultz 2010).

In Nova Scotia, the peak abundance in colony size occurs in August. Settler abundance is highest in early autumn at depths between 8 and 12 meters (Saunders and Metaxas 2008). Larval abundance varies temporally and spatially and is influenced by water column stratification, with larvae occurring in higher abundances in the higher, shallower, fresher layer above the pycnocline (Saunders and Metaxas 2010)

3.0 BIOLOGY AND NATURAL HISTORY

3.1. LIFE CYCLE

Egg production in Lacy Crust occurs in the spring (Rowley 2004). The planktonic larvae, known as cyphonautes, remain in the water column for about four weeks (Yoshioka 1982) and then settle in late summer on the proximal ends of kelp (Seed and O'Connor 1981). In Nova Scotia, the cyphonautes begin to settle in May through July, but peak settlement occurs during September and October (Saunders and Metaxas 2007). Settlement is defined as the movement of larvae from plankton to benthos, and subsequent metamorphosis. Once settled, the larva metamorphoses into a pair of sessile filter-feeding zooids, known as ancestrula. Settlement is an important process in the biphasic life histories of many marine invertebrates. However, there is a lack of knowledge regarding the behavioural mechanisms of finding and attaching to a substrate for Lacy Crust (Matson et al. 2010).

In native populations, colonies are usually reproductive 40 days after settlement (Harvell and Helling 1993). Sperm is transferred from male to female via the water column (Temkin 1994). Sperm enters the female ITO (which is a tubular secondary sexual structure formed by the basal fusion of the two distomedial tentacles) and fusion of egg and sperm occurs shortly after ovulation (Temkin 1994). Fertilized eggs are released into the water column (Yoshioka 1982). Approximately 1% of the colony overwinters to provide eggs for the next spring (Saunders and Metaxas 2009b). Overwintering colonies commence new

growth when the water warms (Menon 1972). Fecundity, growth rate, and survival increase with increasing colony size (Pratt 2005).

Zooids are able to replicate by asexually budding to form sheet-like colonies (Berman et al. 1992). Growth of colonies occurs during increasing seasonal temperature (spring to fall) (Saunders et al. 2010). Peak coverage of kelp occurs in autumn (Saunders and Metaxas 2008), then colonies senesce.

3.2. AGE AND GROWTH

The growth of bryozoan colonies into very large plates is advantageous, as there is an increase in fecundity and survival, however, growing large must outweigh any disadvantages (Pratt 2005). The growth of a coffin box colony is indeterminate, as it continues to expand peripherally with the production of new buds (Harvell et al. 1990, Harvell and Helling 1993). Overgrowth of the colony at the periphery rarely, if ever, happens as growth ceases when it comes in contact with another coffin box colony (Harvell et al. 1990). Dense assemblages are therefore populated with many, smaller individual colonies. The mean colony size in high population density situations is approximately 62% smaller than those grown in low densities (Harvell et al. 1990).

Growth rate is positively correlated to increased temperature (Menon 1972) (within the range 6–18ºC) and size of colony (Saunders and Metaxas 2009b). Rate of regeneration of a colony in spring is also temperature dependent, with no capacity to regenerate at extreme temperatures. A colony that has degenerated during the winter regenerates in the spring with the onset of increasing temperatures. Regeneration of a colony begins at the periphery and moves toward the centre (Menon 1972). In Nova Scotia, most colony growth occurs from March to September (Saunders and Metaxas 2009a). Along the coastline of Santa Barbara, California, growth rates varied such that greatest increases in colony size occurred when average temperatures were the coolest and current speeds were intermediate (Arkema 2009).

3.3. REPRODUCTION

Zooids of Lacy Crust reproduce both asexually and sexually. Asexual reproduction involves budding at the periphery to form sheet-like colonies (Berman et al. 1992). Once colonies reach a minimum of 15 zooids, crowding by conspecifics may trigger the onset of sexual reproduction. Normally only the largest colonies reproduce sexually, however, crowding may also cause smaller colonies to reproduce (Harvell and Grosberg 1988). Production of gametes is proportional to the size of the colony as the entire surface of the colony produces eggs (Yoshioka 1982b). Although most bryozoans brood their offspring, the female coffin box releases fertilized eggs into the water column (Yoshioka 1982).

Sexual reproduction involves sperm being transferred from male to female zooids via the water column (Temkin 1994). Spermatozoa adhere together in aggregations of 32 or 64, known as spermatozeugmata. These pass through the distomedial tentacles of the male zooid and into the exhalant feeding currents with tail ends leading (Temkin and Bortolami 2004). The motility of the spermatozeugmata is dependent upon the generation of waveforms from within (Temkin and Bortolami 2004). Maternal zooids have synchronous development of groups of oocytes, with up to 25 ovulated at one time (Temkin and Bortolami 2004). Maternal zooids likely need more sperm than most bryozoans and this would explain the aggregations of spermatozoa. The transfer of spermatozeugmata from male to female zooids occurs in the water column. Spermatozeugmata enter headfirst into the ITO of the female (Temkin 1994). The fusion of egg and sperm occurs during or shortly after ovulation (Temkin 1994). Coffin box zooids can be simultaneously hermaphroditic, where zooids produce both oocytes and spermatozeugmata at the same time (Temkin 1994). The ITO regulates the entrance of spermatozeugmata and the release of oocytes but it does not act as a filter to prevent self-fertilization (Temkin and Bortolami 2004).

3.4. PHYSIOLOGICAL TOLERANCES
3.4.1. Temperature
The metabolic rate of ectothermic organisms is directly affected by temperature. Shorter development times and increased growth rates are both

associated with higher temperatures (Arkema 2009). Temperature regulates many life-history characteristics such as growth, development, and reproduction in ectothermic organisms (Trudgill et al. 2005).

Little is known about the large scale spatial patterns in larval settlement of Lacy Crust in Nova Scotia, or along the Atlantic coast of North America (Saunders and Metaxas 2007). This information would be useful to determine the factors responsible for initiation of outbreaks of coffin box. Temperature fluctuations may indicate changing water masses due to tides, upwellings or downwellings. In California, a link between temperature and upwellings, with abundance and transport of coffin box has been suggested (Yoshioka 1982).

Severity of outbreaks of coffin box is dependent on warm sea temperatures (Saunders and Metaxas 2007, 2008, Scheibling and Gagnon 2009). In Nova Scotia, Saunders and Metaxas (2008) predicted that variability in temperature during summer and autumn were important. They expect outbreaks to occur during years when summer and autumn water temperatures are warmer, with the most pronounced outbreaks during years where water is warmer from winter through to autumn. In Nova Scotia, Scheibling and Gagnon (2009) proposed that warm sea temperature in late summer and fall accelerates colony growth on kelp blades, and is the key determinant of the severity of coffin box outbreaks. This contradicts the findings of Saunders and Metaxas (2007, 2008) that propose higher winter and spring temperatures are most important for outbreaks due to the effects on timing and recruitment. Results by Scheibling and Gagnon (2009) were later supported by modelling work by Saunders et al. (2010).

Both laboratory and field studies have shown that growth of Lacy Crust is directly related to temperatures between 6 and 18°C in its native range (Menon 1972) and in Nova Scotia (Saunders et al. 2010). In Maine, Lacy Crust lives with temperatures up to 18°C in summer and down to 2°C in winter.

Annual ocean temperature increased continuously between 1992 and 1999 along coastal Nova Scotia and with it, the severity and frequency of coffin box outbreaks (Scheibling and Gagnon 2009).

3.4.2. Flow rate

Sessile animals require particulate food suspended in the water column (Eckman and Okamura 1998). These animals depend on flow to deliver food and remove waste. Ambient-flow conditions are key to the feeding success of *M. membracacea* (Larsen and Riisgård 2002, Pratt 2004). Flow rate affects the size and growth of coffin box colonies. A field experiment in California showed that sites with too slow (0 to 5 cm per second) or too fast (> 20 cm per second) flow speed had comparatively low cover of coffin box colonies due to poor feeding success (Arkema 2009). Maximum feeding success occurred at intermediate flow rates (10 to 12 cm per second) and colonies showed growth rates that were 2 – 5 times greater (Arkema 2009). Lophophores functioned well at flows <14 cm per second, were retracted at flows between 14 and 18 cm per second, and were bent at flow speeds >20 cm per second (Eckman and Duggins 1993). Particulate capture by zooids is increased significantly by turbulent rather than laminar flow; turbulence plays a fundamental role in suspension feeding (Eckman and Okamura 1998).

Zooids tend to become miniaturized with increased flow. They become less elongate with smaller lophophores having fewer tentacles and a shorter distance between excurrent jets (Okamura and Partridge 1999). This demonstrates that coffin box is adaptive to different environmental regimes and has the ability to change its morphology accordingly. Okamura and Partridge (1999) suggest that these morphological changes are the result of phenotypic plasticity and not selection for colonies with particular morphologies.

3.5. FEEDING AND DIET

Flow rates and food acquisition are vital in determining distribution, feeding, abundance, morphology, growth, and survival of coffin box and other sessile, suspension-feeding invertebrates (Pratt 2008, Arkema 2009). *M. membracacea* is often found in a wide range of flow rates in nature as it is very effective at capturing food particles even at relatively high flow rates (Pratt 2008).

This leads to rapid growth of the colony. Understanding how flow rates affect feeding in bryozoans helps predict their effectiveness as an invasive species (Pratt 2008).

Some zooids in a colony are modified for feeding and have a crown of ciliated feeding tentacles, called a lophophore, which generates current. Zooids that are capable of feeding also have a movable part, or polypide, that holds the digestive system. Feeding zooids are arranged in different patterns within a colony and coordinate the feeding currents depending on the size of the colony (Okamura 1984). Pratt (2008) determined that coffin box exhibits a unimodal feeding response as described by Wildish and Kristmanson (1997).

Large encrusting bryozoan colonies have an advantage over smaller ones for feeding success. Colonies with eight or more zooids showed higher success in feeding than single zooids (Pratt 2005). Large colonies of close-set zooids synchronize currents that benefit the whole colony, although feeding flow to individuals in the middle of a crowded colony appears to be reduced leading to a scarcity of food (Grunbaum 1997). Zooids that are close together have significantly faster incurrent velocities than those that are isolated or spaced far apart (Eckman and Okamura 1998). Isolated zooids re-filter more water than those close together demonstrating that the benefits of increased zooid integration outweigh the consequences of intrazooid competition (Eckman and Okamura 1998, Pratt 2004). However, colonies with tightly-packed lophophores and exhalant chimney jets appear to have stronger, more coordinated feeding currents that reach further into the food rich water column (Okamura and Partridge 1999); hence, a higher feeding rate than those that are smaller with more scattered lophophores (Larsen and Riisgard 2002, Pratt 2004). Conducting transplant experiments along the Santa Barbara coastline, California, Arkema (2009) determined that feeding was most successful in coffin box at intermediate ambient flow speeds of 10-12 cm per second.

There are many factors that influence the capture of food particles by coffin box including environmental conditions such as flow speed (Okamura and Partridge 1999), characteristics of the food particle (Grunbaum 1997), shape and

size of the colony (Okamura and Partridge 1999, Pratt 2008), recruitment (Yoshioka 1982), and competition from neighbours (Harvell et al. 1990). Still unclear is the relationship between feeding success and water velocity (Pratt 2008), colony shape (Grunbaum 1997), and competition (Harvell et al. 1990).

In the native range of Lacy Crust on North America's Pacific coast, the species is kept in check through grazing by specialist nudibranchs and fishes (Yoshioka 1982). Grazing has not been observed by fishes in Nova Scotia, however, recently the generalist nudibranch *Onchidoris muricata* has been observed on coffin box (Saunders pers. comm. 2012) and it is known to graze on the native *E. pilosa* (Saunders and Metaxas 2008). Lacy Crust also produces long, energetically-costly spines in response to the nudibranch *Doridella steinbergae* (Lyengar and Harvelle 2002). Although many nudibranchs in the lab occasionally triggered the production of spines in Lacy Crust, its primary predator, *D. steinbergae* triggered the highest response (Lyengar and Harvell 2002).

3.6. HABITAT

Lacy Crust prefers shallow subtidal waters down to 10 meters. It is an epiphyte, growing on algae, particularly native species of kelp, where it forms heavy encrustations (Scheibling and Gagnon 2009). It may also be associated with rocks, boat hulls, and other surfaces. Kelp provide high space availability, but are dynamic; whereas, non-kelp algae provides lower space availability, but is more stable (Yorke and Metaxas 2010). Kelp provides space during the seasonal peak in abundance; however, non-kelp refuges may preserve smaller populations during off-peak (York and Metaxas 2010). Yoshioka (1982) stated that the limiting factor for coffin box is space availability on kelp blades. Coffin box coverage on kelp in Nova Scotia was generally 0% in late spring, increased significantly in August and September, peaked in October through December, then declined during the winter (Saunders and Metaxas 2009a). Higher overwintering occurred on the kelp species *Laminaria digitata* and *Agarum clathratum* than on *Saccharina longicruris* in Nova Scotia (Saunders and

Metaxas 2009a). These results are similar to those found in Maine (Harris and Jones 2005). These overwintering colonies likely provide larvae for the first settlement in May and June (Saunders and Metaxas 2007).

There is little published literature on the habitat requirements of larval coffin box. The main mechanism in invertebrate larval distribution is ocean currents (Daigle and Metaxas 2011). In southern California, larvae were more abundant below the thermocline when the water was warm and stratified (Yoshioka 1982). However, in Nova Scotia, larvae were in higher abundances in the higher, shallower, fresher layer above the pycnocline (Saunders and Metaxas 2010). In Washington, larvae exhibited different searching behaviours when choosing a substrate for settling. When given a choice of two algae *Nereocystis luetkeana* or *Mazzaella splendens*, the larvae exhibited fine-scale active search behaviours on the preferred habitat of N. *luetkeana.* Little search behaviour was exhibited near the unpreferred *M. splendens* (Matson et al. 2010).

3.7. BEHAVIOUR AND MOVEMENT
3.7.1. Larval dispersal

Lacy Crust has planktotrophic larvae, meaning they are planktonic-dispersing larvae deriving their nourishment from consuming plankton. This larval stage lasts two to four weeks, but has been known to last two months (Yoshioka 1982). The earliest larvae are released from the parent colony in late spring, likely from overwintering colonies (Menon 1972). Others are released throughout the summer and remain in the water column until settlement (Seed and O'Connor 1981). Lacy Crust has a relatively continuous distribution in Nova Scotia, indicating that its spread is mostly from larval dispersal (Watanabe et al. 2009). Larvae have been found tens of km offshore. Cyphonautes start to settle in May with peak settlement occurring in September and October (Saunders & Metaxas 2007). At Friday Harbor, Washington, coffin box larvae that settled early in the season lived longer (Harvell et al. 1990).

Larvae were found to be more abundant below the thermocline when the water was warm and stratified in summer months (Yoshioka 1982). In California,

a link between temperature and upwellings, with abundance and transport of coffin box cyphonautes has been suggested (Yoshioka 1982).

Successful invaders frequently have a dispersive phase in their life cycle allowing them to be easily transported in ballast water (Ricciardi and Rasmussen 1998). The dispersive larval phase of Lacy Crust has been found in ship ballast in eastern Canadian ports (Couture and Simard 2007).

3.7.2. Settlement

Settlement is defined as the movement of larvae from plankton to benthos, and subsequent metamorphosis (Saunders and Metaxas 2007). This is considered a critical stage in Lacy Crust life history (Harvell et al. 1990). The thermal integral (growing degree day) was found to explain most of the variation in settlement abundance (Harvell et al. 1990). When choosing a substrate for settling, larvae exhibited different searching behaviours. When given a choice of two algae *Nereocystis luetkeana* or *Mazzaella splendens*, the larvae exhibited detailed, active search behaviours on the preferred habitat of *N. luetkeana.* Little search behaviour was exhibited near the less preferred *M. splendens* (Matson et al. 2010). In the laboratory, a chemical cue for settlement may be released by the kelp (*Saccharina longicruris*) that may induce Lacy Crust cyphonaute to settle (Seed and O'Connor 1981).

In Nova Scotia, settlement of coffin box larvae is not necessarily uniform among kelp species (Saunders and Metaxas 2009a). Earlier and higher settlement of larvae on the numerically dominant kelp (*Saccharina longicruris)* indicates larger colonies and an increase in loss of kelp in autumn (Saunders and Metaxas 2007, 2008). Further studies on the mechanisms regulating settlement and the relationship between large-scale oceanographic events and coffin box larval supply in its native and introduced regions are warranted (Saunders and Metaxas 2007).

4.0. IMPACTS ASSOCIATED WITH INTRODUCTIONS

4.1. IMPACTS ON THE ECOSYSTEM

As with many invasive species, lack of predators, and only few competitors in the introduced range contribute to the success of Lacy Crust. A combination of a short reproductive cycle, fast growth rates, ability to reach large sizes, and adaptations to disperse and colonize in suitable habitats around the world also contribute to its invasive success (Pratt 2008, Schwaninger 2008, Saunders et al. 2010). Colonies of coffin box are now playing dominant roles in their invaded ecosystems, and drastically altering community composition (Lambert et al. 1992, Harris and Tyrrell 2001). This shift in species composition in the ecosystem may have implications for populations of sea urchins and lobster that depend on kelp beds for food and habitat (Chapman et al. 2002). Knip and Scheibling (2007) found however, that the sea urchin (*Strongylocentrotus droebachiensis*) showed no discrimination toward kelp fronds encrusted with coffin box. Coffin box provides nitrogen and calcium for urchins, enhancing the nutritional value of encrusted kelp. This results in increased somatic and gonadal growth for the sea urchin (Levin et al. 2002).

Changes in winter and spring temperature had the most pronounced effects on the timing and abundance of colonies, while changes in summer temperature had the most pronounced effect on colony size and coverage on kelp blades. Outbreaks of this species will increase in frequency and intensity if temperatures warm as a result of climate change, which will cause defoliation of kelp beds and facilitate the invasion of other nonindigenous benthic species (Saunders et al. 2010).

The epiphytic coffin box forms large encrusting colonies on algae, particularly the kelp *Saccharina longicruris*, blocking light that is needed for photosynthesis. The presence of coffin box colonies impacts the survival of the host and exacerbates the natural seasonal cycle of kelp bed decline in autumn (Scheibling and Gagnon 2009). Growth rates and nutrient uptake are affected (Levin et al. 2002) as is spore release (Saier & Chapman 2004). Some epiphytic fauna that excrete ammonium as a waste product are associated with macroalgae, such as kelp, that can absorb and use ammonium for growth.

However, Hepburn et al. (2012) did not find conclusive evidence to suggest there was a flow of nitrogen between coffin box and kelp *M. pyrifera* in winter when a close association exists between the two.

Larger, older colonies of coffin box degrade kelp tissue underneath to a point where the algae completely senesces. Lesions occur on kelp after prolonged encrustation that cause greater weakening of blades than just encrustation; therefore tissue strength appears to decrease with increasing duration of coffin box coverage (Krumhansl et al. 2011). Encrusted kelp becomes brittle and breaks during periods of strong wave action (Lambert et al. 1992, DFO 2011). Partial or complete removal of kelp blades results in a decrease in kelp canopy. However, blades may regenerate the following spring providing the basal meristem remains intact (Johnson & Mann 1988). Kelp loss in Nova Scotia was relatively low when cover of coffin box was <25% but was high when cover was >50%. This indicates a low resilience of kelp to moderate and severe infestations (Scheibling and Gagnon 2009). A complete removal of blades with only stipes and holdfasts remaining results in a loss of the meristematic region, which leads to the inability of blade regeneration and eventual rotting of the algae (Scheibling et al. 1999, Scheibling and Gagnon 2009).

Defoliation has a pronounced ecological effect in kelp forests (Saunders and Metaxas 2008). Large kelp forests have been destroyed in the Gulf of Maine due to Lacy Crust. Some kelp species are more susceptible to coffin box infestations than others, for reasons that are unclear (Saunders and Metaxas 2009a). In the laboratory, larval coffin box were induced to settle on the kelp *S. longicruris* suggesting that there may be a chemical cue released by the kelp to induce settlement (Saunders and Metaxas 2009a). The ability of upstream exploration by coffin box larvae may allow them to track waterborne chemicals to specific settlement sites (Abelson 1997). When coffin box was first discovered at the Isles of Shoals, New Hampshire, USA, it was primarily covering the kelp species *S. longicruris*, *Laminaria* spp. and less frequently on *Agarum clathratum.* Shortly thereafter, it was seen growing on the algae *Desmarestia aculeata.* In 2000, coffin box occurrence was as follows: *Codium fragile* (76%); *A. clathratum*

59%; and, *S. longicruris* 7% (Harris and Tyrrell 2001). In Nova Scotia, a similar study in 2005 noted that during the peak in abundance in autumn, coffin box cover was consistently highest on *L. digitata* due to colonies attaining larger sizes. Lowest abundance occurred on *A. clathratum.* In 2006, defoliation of the kelp bed occurred primarily from a decrease in *S. longicruris*, and to a lesser extent, *A. clathratum.* A loss of *L. digitata*, was not observed and in fact increased in abundance at one location (Saunders and Metaxas 2009).

Lacy Crust is also known to occur on the native brown algae species *Fucus evanescens* and the introduced *F. serratus* (Yorke and Metaxas 2010)*.* Although kelp is able to sustain losses in autumn from defoliation it often re-grows in winter and spring, whereas fucoid algae has slower growth rates (Chapman 1991).

Lacy Crust is known to facilitate the introduction of other introduced benthic species because of its negative impact on kelp beds (Saunders and Metaxas 2009a). Once kelp beds are defoliated, monospecific strands of invasive green algae *Codium fragile* replace the kelp and become established (Scheibling et al. 1999, Saunders and Metaxas 2008). The synergistic interactions of these two introduced species results in mass defoliation of native kelp beds in the western North Atlantic by mid-November, followed by the colonization and establishment of *C. fragile* (Scheibling and Gagnon 2009, DFO 2011). Once established in dense meadows, *C. fragile* prevents re-colonization by kelp and becomes the dominant canopy forming seaweed (Scheibling and Gagnon 2009).

Codium fragile is able to chemically defend against herbivory (Lyons and Scheibling 2007). It also has a lower nutritional value as compared to kelp, and its consumption reduces the gonadic and somatic growth of the sea urchin *Strongylocentrotus droebachiensis* (Schmidt and Scheibling 2007). Species such as sea urchins and American lobster may be negatively impacted by the invasive coffin box and subsequent invasion of *C. fragile* (Chapman et al. 2002, Scheibling and Gagnon 2009)*.*

4.2. COMPETITION

Interactions between Lacy Crust and other epiphytic bryozoans occur on the western North Atlantic. *Electra pilosa,* although not proven to be native, is often considered to be because of its long-term presence and integration into subtidal communities (Yorke and Metaxas 2011). This bryozoan also occurs on kelp and other algae in the region. The proportional abundance of coffin box is higher than that of *E. pilosa* on kelp, however, it is lower on fucoids. The growth rate of *E. pilosa* is higher on fucoids than on kelps (Yorke and Metaxas 2011). Where space is not limited on kelp species, the large colony size and fast growth of Lacy Crust ensure its success and competitive dominance. Factors that may limit its success are reduced space availability, such as on smaller fucoids. Mechanisms of co-existence may exist between the invasive bryozoan coffin box and the native bryozoan *E. pilosa*. Incorporating this co-existence into further invasion research may reveal the resilience of some native communities (Yorke and Metaxas 2011).
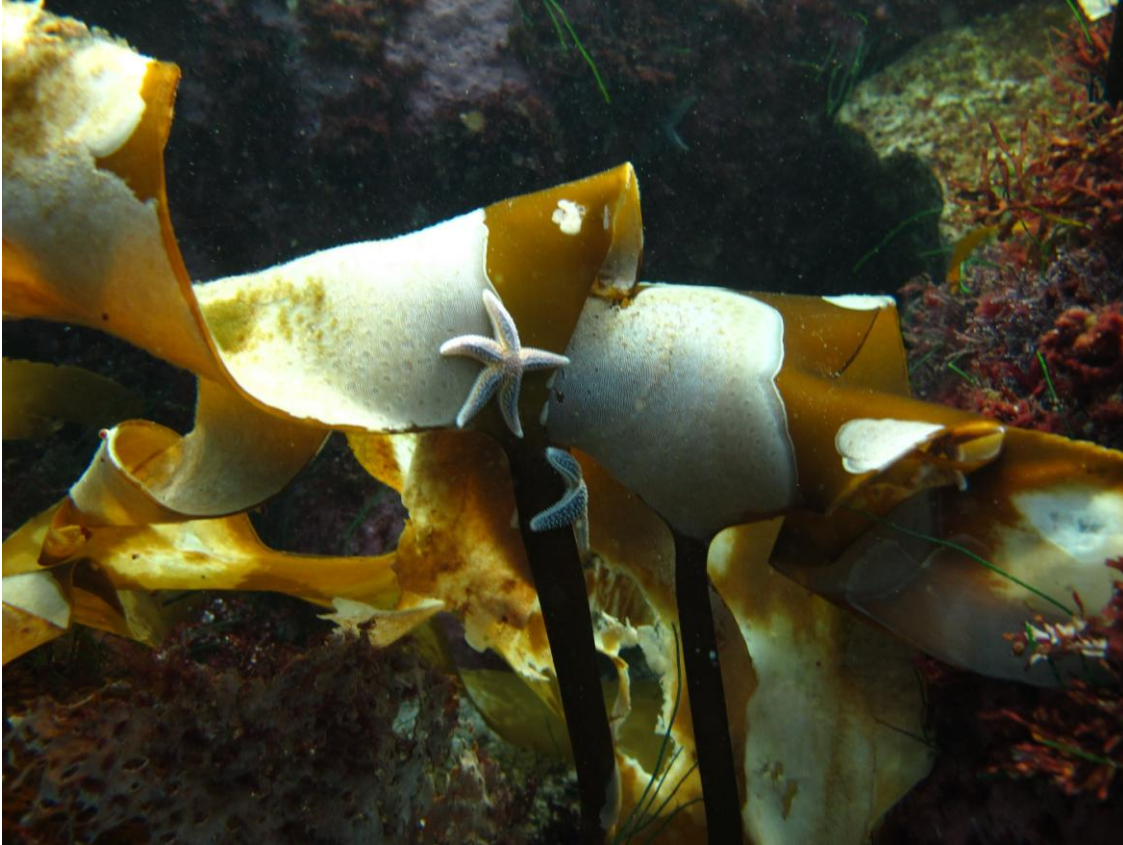
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Figure 1. Lacy Crust/Coffin Box bryozoan (*M. membranacea*). (Photo credit: Megan Saunders, University of Queensland).

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