

Review

A review of the life history, invasion process, and potential management of *Clavelina lepadiformis* Müller, 1776: a recent invasion of the northwest Atlantic

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Abstract

The colonial tunicate *Clavelina lepadiformis* is a recent invader to the northwest Atlantic and has the potential to cause ecological and economic harm. This paper provides a review of the biological and ecological characteristics of *C. lepadiformis*, and hypothesizes the likely mechanisms of introduction, establishment and future expansion. The intent of this paper is to provide a consolidated source of information for marine ecosystem managers and provide a starting point for developing a management strategy, should one be desired. Although *C. lepadiformis* is not currently a management challenge because of the limited range of the invasion in North America; the similarities between *C. lepadiformis* and other tunicate invaders, and the proximity of incipient populations to boating, shipping, aquaculture, and energy infrastructure suggest future economic burden of this new invader. Other regions such as the west coast of North America and New Zealand may be at risk for invasion by *C. lepadiformis*.

Key words: invasive species; Long Island Sound; tunicate; ascidian; non-indigenous; management; marine invasion

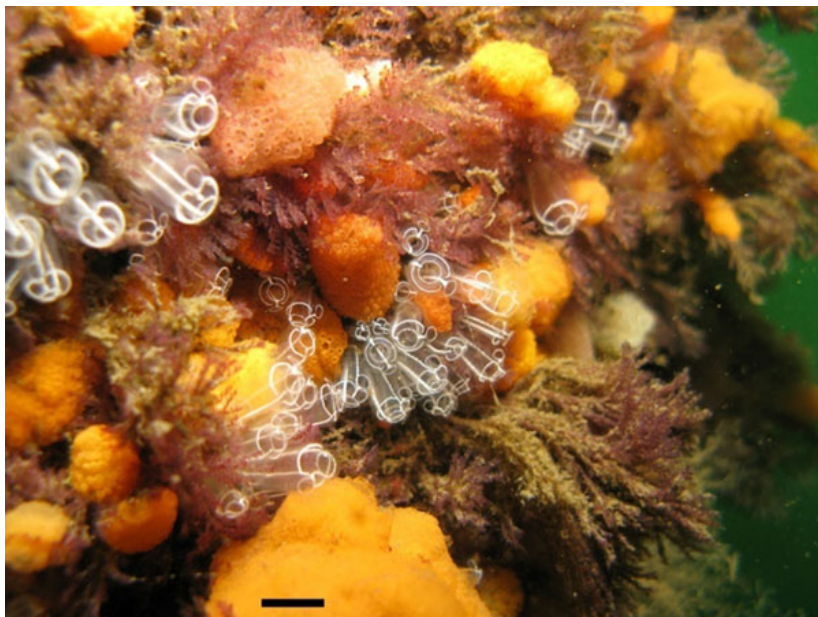
General background

Biological invasions, along with climate change, chemical pollution, and land use change, remain the most pressing threats to ecosystems (Millennium Ecosystem Assessment 2005). Invasive species were a contributing factor in more than 50% of animal extinctions included in the IUCN red list database. Only habitat destruction and direct harvesting contributed to more extinctions (Clavero and Garcia-Berthou 2005). Beyond extinctions, invasive species contribute to rapid changes in the character of ecosystems by causing lasting changes in food webs and ecosystem stability (Harris and Tyrell 2001; Dijkstra and Harris 2009). The economic costs of invasive species are just as dramatic. Some estimates put the cost of invasive species in the USA at over \$120 billion per year (Pimentel et al. 2005). Canada's direct costs from invasive species are \$187 million Canadian dollars with additional costs amounting to \$13.3

to \$34.5 billion Canadian dollars (Colautti et al. 2006). In Germany annual costs associated with 20 invasive species are between 100 and 265 million euro (Reinhardt et al. 2003). Although the USA federal government has enacted numerous laws and regulations to curb the onslaught of invasive species (USDA 2011), new species are still arriving.

The recent discovery of the non-indigenous tunicate *Clavelina lepadiformis* Müller, 1776 in Long Island Sound (USA) (Reinhardt et al. 2010) gives us an opportunity to review and assess the current status of applied marine invasive species ecology and to make recommendations for the management of *C. lepadiformis* for Long Island Sound. Long Island Sound is a highly populated estuary along the eastern seaboard of the USA, surrounded by the states of New York and Connecticut. Currently *C. lepadiformis* has been discovered in two distinct harbors, New London and Stonington, in Connecticut, USA. Here we review what is known about *C. lepadiformis* in

Figure 1. Photograph of *Clavelina lepadiformis* (clear tunic with white stripes) taken from Stonington Harbor, Connecticut on October 19, 2009. *C. lepadiformis* is nested in a matrix of other invasive species including *Botrylloides violaceus* and *Bugula neritina*. Scale bar is ~ 2 cm. Photograph taken by J. F. Reinhardt.



relationship to its recent invasion of the northwest Atlantic. We then consider the invasion process using *C. lepadiformis* as our case study and hypothesize various outcomes and environmental impacts. Thus, this review follows an outline that tracks the invasion process (and potential invasion process) of *C. lepadiformis* that was used by others (Hulme 2006; Lodge et al. 2006) and utilizes basic analyses from existing resources to provide preliminary assessments for a variety of key invasion parameters. Lastly, we briefly touch on management implications and options for the *C. lepadiformis* invasion. Given the recent nature of the *C. lepadiformis* invasion there are many questions that have not been answered and many questions that are currently unanswerable.

Life history of *Clavelina lepadiformis*

Natural populations of *Clavelina lepadiformis* are distributed in Europe from the Shetland Islands and Bergen, Norway in the north to the Bay of Biscay, the Mediterranean, Aegean and the Adriatic seas in the south (Berrill 1951). During the past 30-40 years *C. lepadiformis* has begun a global expansion; specifically *C. lepadiformis* was discovered in the Azores and Madeira, Portugal in the 1990s (Wirtz and Martins 1993; Wirtz 1998), was then found in

two separate South African bays (Robinson et al. 2005) and in South Korea (Pyo and Shin 2011), representing a significant jump in range, not merely a range expansion (Primo and Vazquez 2004). Currently the extent of *C. lepadiformis* in the northwest Atlantic is not known and has only been verified in New London and Stonington Harbor, Connecticut, USA (Reinhardt et al. 2010). The broad geographic range of *C. lepadiformis* is not only indicative of broad temperature tolerance but also tolerance to a broad range of salinities. A salinity tolerance of 14 psu to 35 psu allows *C. lepadiformis* to occupy fresh Norwegian fjords as well as highly saline Mediterranean embayments (Millar 1971). Existing databases were also used to map *C. lepadiformis* distribution (from Global Biodiversity Information Facility see Appendix 1 for full citation list; Shenkar et al. 2011).

Colonies of *C. lepadiformis* are limited to shallow littoral habitats (< 50 m) and occupy natural or artificial hard substrates such as rocky outcrops, piers, and wooden docks. Colonies are composed of distinct zooids (up to 6 cm in length) connected by a common basal test or stolon. Stolons can connect up to hundreds of zooids (see Figure 1). The thorax of *C. lepadiformis* is clear except for white, yellow or pink bands around the oral siphon and along the dorsal lamella (Berrill 1951). In natural bedrock communities in the United Kingdom,

C. lepadiformis is a conspicuous species often contributing highly (10%) to community similarity (Connor et al. 2004). In a multivariate analysis of environmental parameters using ascidians as bioindicators, Narnajo et al. (1996) classified *C. lepadiformis* as a transgressive species. Based upon a classification scheme derived from multivariate analysis:

Transgressive species are dominant in harbors and nearby zones with highly transformed substrates, low rate of water renewal and excess silting and suspended matter. These species can also be found in conserved areas although they never appear dominant. They are commonly typical of biofouling and categorized as pioneers and opportunists; they mainly adopt a solitary strategy and have large bodies and wide apertures that prevent clogging by suspended particles. Colonial forms are often sheet-like encrusting ascidians that grow quickly under favorable conditions and form irregular shaped colonies (Narnajo et al. 1996).

Colonial tunicates have multiple reproductive strategies reproducing both sexually and asexually. Zooids of *C. lepadiformis* are hermaphroditic and brood their larvae. Larvae are stored in individual zooids at the base of the atrial chamber. Once released larvae are viable for three hours. Other tunicates with larval survival times on this order tend to disperse <10 m (Shanks et al. 2003). Colonial tunicates become reproductive rapidly and have high reproductive output. Greater than 60% of all *C. lepadiformis* colonies had developing embryos or larvae when temperatures reached 12°C, which corresponded to June and July in Scottish waters (Millar 1958). Rates of juvenile survival are high, around 30%-50% in populations from Spain (de Caralt et al. 2002). Following settlement, formation of the oozoid is complete after 2 to 3 days (Berrill 1951). Reproduction also occurs via asexual budding. Buds are formed on the terminal ampullae along branching stolons. Stolons separated or isolated by some fragmentation process can also develop zooids. The complete budding and development process of a zooid takes 200 hr at 20°C (Berrill and Cohen 1936).

Zooids of *C. lepadiformis* typically have an inactive period during the winter months (hibernation) after sexual reproduction, during which time the zooids slough off (Berrill 1951). In Mediterranean populations, the inactive period (aestivation) occurs during the summer months (de Caralt et al. 2002). During the inactive

period the colonies survive in the form of stolons with ampullary buds. Following the inactive periods buds redevelop into zooids.

Adult colonies of *C. lepadiformis* are known to have cytotoxic alkaloids that serve as a predatory defense mechanism. However, the flatworm *Prostheceraeus villatus* is a specialist predator that can accumulate the alkaloids for its own defense (Kubanek et al. 1995). Experiments have shown that adults are unpalatable to a variety of generalist consumers from their native range. The larvae have a greater palatability and, likely, juvenile stages are more vulnerable to predation (Tarjuelo et al. 2002). This is similar to established communities of ascidians in southern New England, where control of populations are linked to predation on juvenile recruits by benthic invertebrate predators (Osman and Whitlatch 1998).

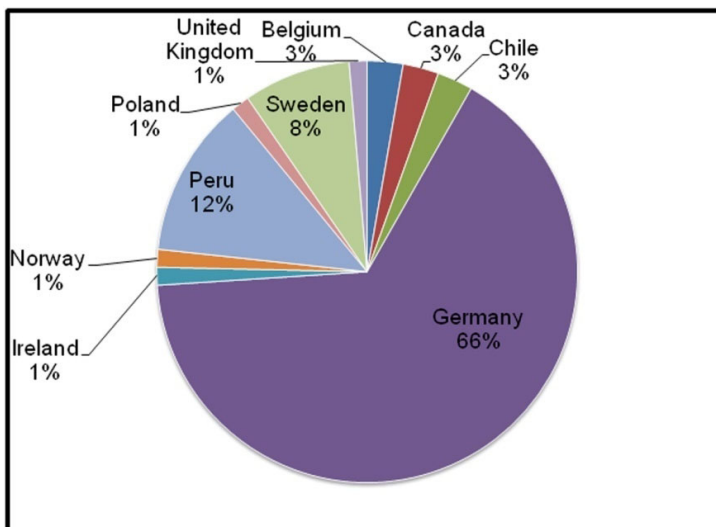
Invasion process and management

The typical invasion process includes the following steps; introduction, establishment, spread, and impact (Hulme 2006). There are specific management practices that can be used at each step along the invasion process. A successful invasion is often the result of a breakdown of management or ambivalence (lack of management).

Transport and introduction of Clavelina lepadiformis

Given the short dispersal distance of colonial tunicates, introduction by natural dispersal via larvae would be impossible. Likely anthropogenic vectors of marine invasion are ballast water, hull fouling or sea chest fouling, dredge spoils, aquaculture, imported live bait, aquarium trade, scientific research and intentional introductions (Lodge et al. 2006). The primary invasion of *C. lepadiformis* from its native habitat would preclude dredge spoils, aquaculture and bait trade as vectors. Also, it is unlikely that *C. lepadiformis* is sought after in the aquarium trade, even though this is a common vector for marine invasions (Lodge et al. 2006). During 1988 *C. lepadiformis* was used for scientific research in Woods Hole, Massachusetts, USA using flow-through tanks. Subsequent surveys of Eel Pond (where the outflow occurs) never turned up samples of *C. lepadiformis* (JT Carlton pers. comm.).

Figure 2. Shows the percentage of vessels originating at ports in foreign countries that arrived in New London Harbor from 1/1/2004 – 7/24/2008, the period when *Clavelina lepadiformis* may have been first introduced to New London Harbor (Data from National Ballast Information Clearinghouse 2011).



It is unknown in what order *C. lepadiformis* invaded New London and Stonington harbors; it is possible that invasions were either from independent vectors or colonization may be a secondary or post-border invasion. However, because New London is a substantially busier port, it makes it more likely to be the site of primary invasion. It is home to a US naval base, a US Coast Guard station, interstate ferry terminals, and a fishing fleet, as well as being a port for international shipping traffic and hundreds of recreational boaters. Stonington has a fishing fleet and recreational boaters. Between 2004 and 2008 there were 60 international vessels transiting directly from ports in the native range of *C. lepadiformis* (Belgium, Germany, Ireland, Sweden and the United Kingdom); the greatest number of foreign arrivals were from Germany (Figure 2, National Ballast Information Clearinghouse 2008). Although it may be impossible to know the exact dates of first introduction of *C. lepadiformis*, it seems reasonable to suggest that it occurred in the recent past (2000–2008) and that it was mediated by shipping. The probability of introduction is influenced by connectivity between habitats, modeled by the number of ship passages and the duration of transit (Drake and Lodge 2004), but also the duration of “the visit” is important if reproductive adults are on board. A longer stay in a foreign port of reproductive adults will increase propagule pressure. It is well known that ballast water from international shipping was a vector for thousands of taxa

(Carlton and Geller 1993), however the short larval duration would prevent *C. lepadiformis* from surviving in transit for more than a single day. Transportation of adults on the hull, within a sea-chest or some other interior structure may be more likely. Other solitary and colonial ascidians from the genera *Aplidium*, *Botrylloides*, *Didemnum*, and *Steyla* are transported internationally via this mechanism (Coutts and Dodgshun 2007). Hull fouling is often considered the most important vector for introduction or secondary spread for some tunicates (Therriault and Herborg 2008). In some marine systems hull fouling accounts for a greater percentage of invasions than other vectors including ballast water (Bax et al. 2003). The extent of international travel by recreational boaters in the area is unknown, but recreational boaters can transport adults that have either fouled the hull, intakes, pipes or other equipment. It is reasonable to conclude that introduction likely resulted from hull or sea chest fouling, and subsequent release of propagules.

Establishment of *Clavelina lepadiformis*

Following transport and introduction of a non-indigenous species to a new range, new populations either become established or the species is unable to survive. Survival of non-indigenous populations is limited by physical and biological properties of the invaded habitat as well as

environmental and demographic stochasticity. Factors that typically limit the distribution of ascidians are substrate, temperature, salinity, predators and turbidity. It is often presumed that the vast majority of introductions are unsuccessful in establishing populations (Veltman et al. 1996). Estimates for birds put successful invasions below 10% (Williamson and Fitter 1996). Studies have not been conducted to determine the likelihood of success in ascidian invasions.

At least 57 tunicate species have a history of invasion (Locke and Hanson 2009), and many other tunicates have characteristics of successful invaders, including *C. lepadiformis*. In addition, the harbors and marinas where tunicates dominate have many characteristics of highly invaded habitats. The continued development of coastal areas has increased the number of docks, marinas, groins, breakwaters on which tunicates can rapidly colonize (Lambert and Lambert 1998; Connell 2000). In harbors, boating traffic provides a constant disturbance, and seasonal removal of floating bocks and vessels provides great resource fluctuations and inhibits full successional development of fouling communities. Harbors are often in population centers with potentially high nutrient runoff, or sites of waste treatment facilities. Mixing caused by boat traffic in harbors may help keep food particles suspended in the water column, providing ample food supply to filter feeders (Monniot et al. 1985). Slower current speeds around dock structures may enhance the settlement and attachment of tunicate larvae (Monniot et al. 1985).

Comparing traits of *C. lepadiformis* to those frequently attributed to other invaders can give us a valuable understanding of the animal. Some characteristics of invasive species include self-fertilization, multiple reproductive strategies, phenotypic plasticity, genotypic variation, high growth rate, strong competitive ability, release from native pests and predators, strong association with anthropogenic influenced or disturbed habitats, large geographic ranges and broad ecological requirements (Table 1, Sax and Brown 2000; Sakai et al. 2001). Many of these “invasive” characteristics are shared with colonial tunicates including *C. lepadiformis* (Table 1, Lambert and Lambert 1998). Habitat characteristics that may allow invasions include geographic isolation, low species diversity (Stachowicz et al. 1999), high disturbance (Altman and Whitlatch 2007), resource fluctuations (Davis et al. 2000, Dunstan and Johnson 2007),

high resource availability including free space, high nutrient concentrations (Locke et al. 2007), absence of predators (Osman and Whitlatch 2004) and urbanized habitats (Connell 2000). Many of these characteristics are not mutually exclusive (Table 1). Some debate exists over whether there are generalizable characteristics of successful invasive species and heavily invaded habitats (Hayes and Barry 2008). Consideration of species and habitat characters should be done with caution and with a robust personal understanding of the system because invasive characteristics may be taxon- and habitat-specific (Hayes and Barry 2008).

Using information on regional connectivity and species biogeography, Locke and Hanson (2009) considered *C. lepadiformis* one of 17 tunicates likely to have a successful invasion of Atlantic Canada. Her analysis utilizes the first two stages of the invasion process to make predictions (1. transport and introduction and 2. establishment). This work provides a good analysis for the New England coast as well. The latitudinal range of *C. lepadiformis* extends from south of New England through to Canada (although water temperature may be a better indicator). The arrival of *C. lepadiformis* in New England is an unfortunate confirmation of Locke and Hanson’s (2009) prediction.

Spread of *Clavelina lepadiformis*

The spread of an invasive species is functionally analogous to an introduction; both spread and introduction requires dispersal to unoccupied habitats (Puth and Post 2005). Introductions typically refer to overseas dispersal while spread occurs on a regional level, and only after an introduction (Forrest et al. 2009). Because the spreading of an invasive can occur at much smaller dispersal distance, vectors that are unlikely to cause intercontinental introductions can spread an invasive species within a region. Likely vectors for regional spread *C. lepadiformis* include 1) recreational and commercial vessels, including inter-state ferries serving Fishers Island, Long Island and Block Island, and fishing vessels; 2) aquaculture operations, including exchange of seed between harbors, short-term storage and depuration practices (Wasson et al. 2001); 3) scientific research (Lodge et al. 2006); 4) larval dispersal; and 5) dispersal by fouled crabs, lobsters or snails (Bernier et al. 2009). However, the status of

Table 1. Evaluation of “invasive” characteristics of *C. lepadiformis* and known habitats that have been invaded in North America.

Species Characteristic	Source	<i>Clavelina lepadiformis</i>	Source
Self-fertilize	Reviewed in Sakai et al. 2001	Hermaphroditic	Berrill 1951
Multiple reproductive strategies	Reviewed in Sakai et al. 2001	Budding and sexual	Berrill 1951
Phenotypic Plasticity	Reviewed in Sakai et al. 2001	Unknown, likely not great	de Caralt et al. 2002
Genetic Variation	Reviewed in Sakai et al. 2001	Unknown in New England, high else where	Turon et al. 2003
High growth-rate	Reviewed in Sakai et al. 2001	Yes	Berrill 1951
Competitive ability	Reviewed in Sakai et al. 2001	Unknown	Berrill 1951
Release from native pests	Reviewed in Sakai et al. 2001	Release from specialist predator	Berrill 1951
Association with Disturbed habitat	Reviewed in Sakai et al. 2001	Yes	Narnajo et al. 1996
Large geographical ranges	Reviewed in Sax and Brown 2000	Yes, >20° Latitude	Berrill 1951
Broad ecological requirements	Reviewed in Sax and Brown 2000	Filter feeder, broad temperature and salinity range	Millar 1971 Wirtz 1993, Primo and Vazquez 2004
History of Invasion success	Reviewed in Sax and Brown 2000	Azores, South Africa, Spain	
Habitat Characteristics for Stonington and New London Harbors			
Isolated Habitat	Reviewed in Sax and Brown 2000	No	New London and Stonington Harbors are connected to other harbors by shipping, fishing and recreational boat traffic
High disturbance	Altman and Whitlatch 2007	Yes, boating traffic	High use harbors with multiple use. (Altman and Whitlatch 2007)
Resource fluctuations	Davis et al. 2000	Yes, seasonal space and nutrient	personal observation
High resource available	Locke et al. 2007	Space likely enhanced	Surface area enhanced by docks, boats, piers and other artificial structures
High nutrient concentration	Locke et al. 2007	Likely, nitrogen inputs/urbanized surrounding	New London, Thames River significant nitrogen inputs (Mullaney et al. 2002)
Absence of predators	Osman and Whitlatch 2004	Absence of Specialist	personal observation
Urbanized habitats	Connell 2004	Yes	Many piers and industrial structures

New London, Connecticut as an international shipping port means it may serve as a hub for further introductions. Other ports in North America may have a greater risk of invasion from New London than Europe because of shorter transit times and higher survivorship. Vessels from New London travel to other major ports in the United States, such as Boston, Baltimore and New York (National Ballast Information Clearinghouse 2011) and establishment in a major shipping port would greatly increase the potential for spread throughout North America.

The short larval lifetime of *C. lepadiformis* prevents the direct natural dispersal from one harbor to another. However, natural dispersal influences the spread of *C. lepadiformis* within a harbor. Harbors in New England typically have

substantial amounts of artificial substrates to colonize (Lambert and Lambert 1998). Unsuitable habitat such as soft or cobble sediments may isolate harbor populations. Such unsuitable habitats may serve as a natural barrier for the natural spread of *C. lepadiformis* (Forrest et al. 2009). Populations of *C. lepadiformis* that inhabit Mediterranean harbors had higher gene flow between harbors than they did with populations at the exterior of harbors (Tarjuelo et al. 2002; Turon et al. 2003), which suggests high connectivity between harbors facilitated by boat traffic; and the inability of natural dispersion to connect harbor populations with those outside of harbors. This means that it is unlikely for *C. lepadiformis* to spread from harbors without anthropogenic assistance (Tarjuelo et al. 2002; Turon et al. 2003). Having

multiple mechanisms of dispersal is a distinct advantage, as natural dispersal favors local persistence of populations, while human-mediated transportation favors colonization of new habitats. Natural dispersal might be best modeled by a diffusion model while human-mediated dispersal is better characterized by jump dispersal and puts extended tails on the natural dispersal kernel (Forrest et al. 2009).

Spread rates for most invasive tunicates, including rates for *C. lepadiformis*, are not known. Rates of spread for one colonial tunicate, *Botrylloides violaceus* Oka 1927, had an estimated spread rate of 114 km/yr but an observed spread rate of 16 km/yr (Grosholz 1996). In past invasions the spread of *C. lepadiformis* does not appear to be rapid. In 2005, at least four years post invasion, *C. lepadiformis* was still apparently restricted to two harbors along the South African coast. Its initial spread may have been caused by oyster aquaculture (Robinson et al. 2005). Future rates of spread are often difficult to assess during the early stages of an invasion because the transition from an establishment to invasion can often involve a lag phase (Mack et al. 2000). There are three general categories of lag: 1) lags caused by the nature of population growth, 2) lags related to favorable changes in environmental conditions; and 3) lags caused by changes in genetic factors (Crooks and Soule 2001). Alternatively, the lag phase may occur simply because information or knowledge of an invasive species is not observed (e.g. because monitoring in the marine environment is difficult) or disseminated in a timely manner. In practice the reasons lag phases occur are seldom known, but they can cause severe underestimation of the effects of non-indigenous species. Thus, when lag occurs past performance is not a guarantee of future performance for non-indigenous species. Also, rates of spread in one region may be difficult to generalize to other regions because of differences in environmental conditions, vectors and habitat heterogeneity among other factors (Hastings et al. 2005). Even under highly controlled conditions dispersal rates show high variability and prediction of rates of spread must be considered highly uncertain (Melbourne and Hastings 2009). Additionally, monitoring the spread of an invasion is difficult to accomplish with limited resources. While *C. lepadiformis* is an easily identifiable animal, identification of tunicates and other marine organisms often require specialized training.

Niche model

To address international and domestic (USA) spread potential for this species, we undertook an environmental niche model or species distribution model. Environmental data was taken from the Bio-ORACLE dataset (Tyberghein et al. 2012) from 70°N to 70°S and included the following variables: sea surface temperature (minimum, mean, maximum, and range), salinity (mean), dissolved oxygen (mean), chlorophyll A (minimum, mean, maximum, and range), and diffuse attenuation (minimum, mean, and maximum). The environmental data had a 5 arcmin resolution. To assess the relative suitability of habitats, we used MaxEnt version 3.3.3 (Phillips et al. 2006). MaxEnt is a machine-learning algorithm that utilizes presence only data to determine relative suitability of habitats from species point data (i.e., uses known locations or realized niche to predict likely habitats that a species might be able to inhabit or fundamental niche). Species observance records were taken from the combined database described previously 4340 distinct sample locations (with duplicates removed). The analysis was limited to within 300 km of the coast; we did this by applying a mask. There is little reason to include areas further from the coast, as they are often deeper than *C. lepadiformis* is thought to exist. By masking these areas we limit the area of “background” sampling to coastal habitats (Elith et al. 2011). There may be some sampling bias that exists between temperate and tropical regions, but we believe that temperate harbors and ports are relatively well sampled across developed nations, particularly within the native range (i.e., Europe). We used K-folds (with 5-folds) cross validation in order to evaluate model fit and present the model results as the median of all trials (Figure 3). The results of this analysis should not be over interpreted; these results provide an indication of areas that should keep a watch for *C. lepadiformis*. But, because of the broad extrapolation the accuracy may limit the models utility at local scales. Local conditions and factors have variability much smaller than captured by the BIO-ORACLE (Tyberghein et al. 2012) data set. Local conditions are likely a primary driver for invasive species persistence post-transport. Output represents the median log values of all 5 K-fold replications (Figure 3). A common interpretation of this output is that log values represent the likelihood of *C. lepadiformis* the species can persist in that locale.

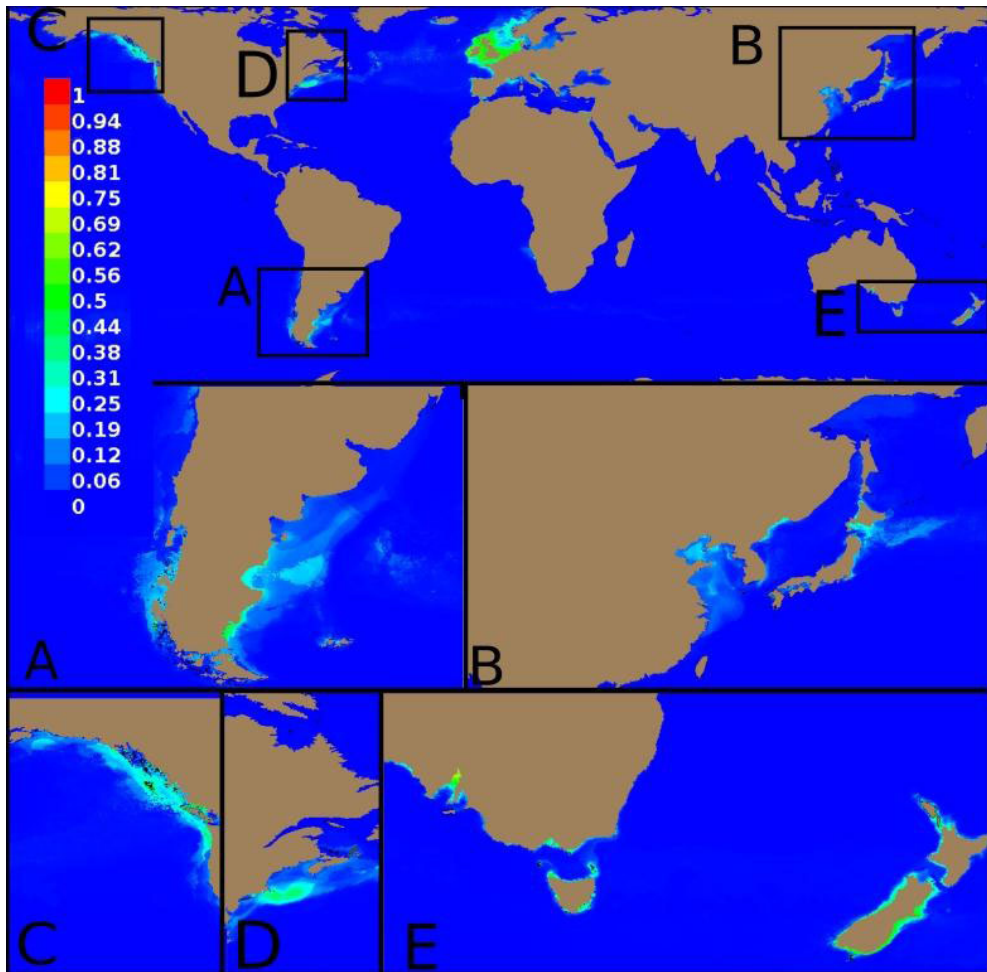


Figure 3. MaxEnt model results for potential future distributions of *Clavelina lepadiformis*. Predicted distributions are logistic outputs, from low values (blue, 0–0.2) through yellow orange and red (0.8–1.0). Brown indicates the land. Boxed areas correspond to frames in the lower half.

The MaxEnt species distribution model output suggests that possible future areas of *C. lepadiformis* expansion include the western United States and western Canada, South Australia, New Zealand, Japan, Korea and Argentina (Figure 3). Since our model was run the species was found in Korea (Pyo and Shin 2011), confirming the potential utility of this model.

Impacts of *Clavelina lepadiformis*

Following introduction, establishment and spread of a non-indigenous species there is potential for negative impacts on the native environment, ecology and economy. The known ecological and

economic impacts of species invasions are numerous. Invasive species can directly destroy habitat (Kizlinski et al. 2002), indirectly change habitat structure (Bertness 1984) or propel changes in ecosystem state (Harris and Tyrrell 2001; Dijkstra and Harris 2009). Global introductions have led to loss and homogenization of biodiversity (McKinney and Lockwood 1999), threaten ecosystem function (Kizlinski et al. 2002) and led to large-scale changes in food web structure (Byrnes et al. 2007). Non-indigenous species have directly led to loss of biodiversity through extinction or local extirpation (Fritts and Rodda 1998). However the role of invasive species in marine extinctions is equivocal. Marine extinctions appear to be less common than terrestrial ones (Simberloff 2000; Gurevitch

and Padilla 2004). Invasive species can have important human health implications either by directly causing disease or by serving as a vector. The total economic value of invasive species must consider both direct and indirect costs as well as non-use values such as existence value, bequest value and option values (Born et al. 2005). Many of these costs may be difficult to value; for instance a species may have minimal direct economic or ecological cost, however, a non-indigenous species may facilitate the invasion of another species which has more dramatic effects on economies or the environment (Simberloff and von Holle 1999). Of course, the cost of an invasive species may not be constant over time as exemplified by the lag effects.

Tunicates have direct economic cost because they rapidly foul hard substrates. Fouling creates costs for a variety of industries including shipping and power production. Hull fouling reduces fuel efficiency and the fouling of intake pipes can restrict the proper functioning of machinery. Ostensibly, most work has evaluated the costs of fouling on aquaculture. Fouling organisms can affect the growth and survivorship of a variety of aquaculture products including mussels, oysters, scallops and finfish. Tunicates and other fouling organisms can compete with shellfish for food, occlude net or cage openings reducing flow and reduce oxygen availability (Cronin et al. 1999). Overgrowth can decrease survivorship and the size of the product although the affects of tunicate overgrowth are inconsistent (Dalby and Young 1993). The typical management strategies include air drying and power washing aquaculture products and equipment, which are labor intensive and costly practices. Other methods of management and remediation are desperately need for aquaculturalists and are being developed (see Baker et al. 2011; Parent et al. 2011). Recent introductions of tunicates have put the livelihoods of shellfish farmers at risk and the current cost of treatment to remove tunicates of Prince Edward Island is estimated at CDN\$28 million (Edwards and Leung 2009).

In South Africa *C. lepadiformis* is already known to be associated with aquaculture facilities (Robinson et al. 2005); would the addition of another species of tunicate put additional strain on aquaculture operations in North America? Aquaculture operations already utilize management strategies (e.g. air drying) for fouling organism that would likely be

affective in removing *C. lepadiformis*. In Prince Edward Island bays one invasive tunicate replaced another as a dominant component of the fouling assemblage (replacement of *Steyla clava* Herdman 1881 with *Ciona intestinalis* Linnaeus, 1767; Ramsay et al. 2008). The threat of *C. intestinalis* is, however, considered much greater threat because of a 1) longer reproductive season 2) faster growth 3) tolerance of crowding and 4) *S. clava* does not settle on it (Ramsay et al. 2008). The risk of an additional fouling organism in the system is that the new species may not respond to current management practices and it may extend the length of time in which management must be used. Extending the period of active management would cut into profit margins and may provide additional dangers by having to operate during wintery conditions (Malinowski pers. comm.).

Management of *Clavelina lepadiformis*

The most effective strategy in the management of invasive species is to prevent introductions (Hulme 2006). Currently legislation is in place to limit the exchange of ballast water between international locations and US ports (USDA 2011), however, there is no regulation of hull fouling. Although management post invasion is less desirable, it is often necessary particularly when there is a health or economic cost.

There is a broad range of options available for invasive species management from eradication to complete ambivalence. Any management strategy should consider 1) expected impacts on environment and economy; 2) the technical possibilities and limitations of management; 3) risks of management; 4) likelihood of management success; and 5) public concern and stakeholder interest (Hulme 2006).

Eradication can be the most cost effective management technique assuming successful invasion (Baxter et al. 2008). Successful eradication, however, usually includes five main features: 1) early detection and management action; 2) sufficient long-term resources available; 3) existence of an agency with the ability to enforce cooperation; 4) significant knowledge of invader; and 5) energetic project leaders (Simberloff 2009). The environmental impact of those control and/or eradication measures must be deemed acceptable, even with likely ambiguity as to full extent of those environmental impacts. Eradication is often

dismissed as an unrealistic management option because of highly publicized eradication failures (Simberloff 2009) even though the number of successful eradications of marine invaders is growing. The eradication of the highly invasive *Caulerpa taxifolia* (M.Vahl) C.Agardh, 1817 is a highlight for proponents of eradication (Anderson et al. 2005). However, the only attempted eradication of a tunicate species (*Didemnum vexillum* Kott, 2002) that we are aware of has not been considered successful (Coutts and Forrest 2007). Colonial tunicates often inhabit inconspicuous areas, and may be difficult to detect. When detected eradication methods have not been perfected, or even adequately established. Even still, cost-benefit analyses and the precautionary principal strengthen arguments for eradication (Kriebel et al. 2001; Edwards and Leung 2009). There seems to be a tendency for the traditional scientist to prefer to study a new invader per se, rather than attempt eradication, thus the science and technological advancement of eradication may be hampered.

With only preliminary surveys of *C. lepadiformis* completed there is a high level of uncertainty in estimates of its range in the western North Atlantic. Our current understanding, however, suggests that *C. lepadiformis* is limited to two harbors on the coast of southern New England (Reinhardt et al. 2010). There is a significant amount of natural history information available for *C. lepadiformis* (Berrill 1951; Millar 1971). But although *C. lepadiformis* has a recent history of invasion (Wirtz 1998; Robinson et al. 2005) and was predicted to invade the western North Atlantic (Locke and Hanson 2009), a risk assessment has never been completed. It can be more difficult to take immediate action against an invader if a risk assessment was not completed prior to invasion because of the difficulty convincing people to allocate resources when the consequences are do not seem disastrous. With the hypothetical allocation of necessary resources *C. lepadiformis* would be a candidate for eradication because of 1) its recent and constrained invasion; 2) existing knowledge of the organism; and 3) the power in the Connecticut Department of Environmental Protection to destroy undesirable species (Connecticut General Statutes 2011). The likely limiting factor for eradication of *C. lepadiformis* is the availability of funding, particular if state and federal enforcement agencies are not given the appropriate funding to carry-out management

plans. Based on the results of our MaxEnt analysis (Figure 3), managers in other potential areas of introduction might consider *C. lepadiformis* as a potential invader and evaluate if a management strategy is warranted.

Current management strategies for invasive tunicates in Long Island Sound rest on the industries that are affected by them, and thus power plant operators, shellfish farmers and boat owners currently hold the burden of managing invasive fouling organisms. Management typically consists of use of antifouling materials (e.g., antifouling paints) and removal (e.g., power washing, scraping or cleaning) on an as needed basis. Such management efforts are uncoordinated and do not consider large scale management techniques. Coordinated management efforts for fouling organisms could have large financial incentive, but require initial capital investment and organization (Edwards and Leung 2009). The association of tunicates with artificial substrates assures economic impacts (at least in the form of removal by owners); no management is, therefore, not a viable option. An open meeting between government officials, scientist and stakeholders in Long Island Sound is necessary to move forward with management strategies for *C. lepadiformis* and other fouling organisms. Should the implementation of management fail in Long Island Sound, these locations are ideally located to spread to international ports of Boston and New York, which could result in further international spread of this species.

Summary and conclusions

The expansion of *C. lepadiformis* from its broad native European distribution to the Azores, Madeira, South Africa, the western North Atlantic, and now South Korea is a significant jump in distribution that has occurred over the last 30-40 years. Its colonial life history strategy contributes to its classification as a transgressive species (Naranjo et al. 1996). Reproduction typically occurs above 12°C in *C. lepadiformis*, and its corresponding reproductive phase duration in invaded areas is may also be dictated by temperature. Its inactive period is also temperature-linked, occurring when temperatures are too cold or too warm for aggressive growth. Ecological release also likely facilitates this species' invasion, as its specialist flatworm predator *Prostheceraeus villatus* is not known to be in invaded habitats.

It is reasonable to conclude that the introduction of *C. lepadiformis* to Connecticut likely resulted from hull or sea chest fouling, and subsequent release of propagules, and that this is the likely mode of introduction to other areas of the world. The MaxEnt species distribution model suggests that possible future areas of *C. lepadiformis* expansion include the western United States and western Canada, South Australia, New Zealand, Japan, Korea and Argentina (Figure 3), and since our initial run of this model, the species was found in Korea (Pyo and Shin 2011).

Given the propensity of non-native tunicate species to cause ecological and economic harm, a management strategy should be developed before there are substantial negative impacts. Eradication remains a viable option because of *C. lepadiformis* limited distribution. There is a great deal of uncertainty regarding the future impacts from *C. lepadiformis*. Certainly a monitoring program should be established in order to track the invasion process for this species. The lack of any coordinated response to this recent discovery represents a failure in invasive species management.

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References

- Altman S, Whitlatch RB (2007) Effects of small-scale disturbance on invasion success in marine communities. *Journal of Experimental Marine Biology and Ecology* 342: 15–29, <http://dx.doi.org/10.1016/j.jembe.2006.10.011>
- Anderson LW J, Tan W, Woodfield R, Mooney R, Merkel K (2005) Use of sediment bioassays to verify efficacy of *Caulerpa taxifolia* eradication treatments. *Journal of Aquatic Plant Management* 43: 1–9
- Baker M, Paetzold C, Quijón PA, Davidson J (2011) The use of food grade oil in the prevention of vase tunicate fouling on mussel aquaculture gear. *Management of Biological Invasions* 2: 15–25
- Baxter PWJ, Sabo JL, Wilcox C, McCarthy MA, Possingham HP (2008) Cost-effective suppression and eradication of invasive predators. *Conservation Biology* 22: 89–98, <http://dx.doi.org/10.1111/j.1523-1739.2007.00850.x>
- Bax N, Williamson A, Aguero M, Gonzalez E, Geeves W (2003) Marine invasive alien species: A threat to global biodiversity. *Marine Policy* 27: 313–323, [http://dx.doi.org/10.1016/S0308-597X\(03\)00041-1](http://dx.doi.org/10.1016/S0308-597X(03)00041-1)
- Bertness M (1984) Habitat and community modification by an introduced herbivorous snail. *Ecology* 65(2): 370–371, <http://dx.doi.org/10.2307/1941400>
- Bernier RY, Locke A, Hanson JM (2009) Lobsters and crabs as potential vectors for tunicate dispersal in the southern Gulf of St. Lawrence, Canada. *Aquatic Invasions* 4: 105–110, <http://dx.doi.org/10.3391/ai.2009.4.1.11>
- Berrill N (1951) Regeneration and budding in tunicates. *Biological Reviews* 26: 456–475, <http://dx.doi.org/10.1111/j.1469-185X.1951.tb01207.x>
- Berrill NJ, Cohen A (1936) Regeneration in *Clavelina lepadiformis*. *Journal of Experimental Biology* 13: 352–362
- Born W, Rauschmayer F, Bräuer I (2005) Economic evaluation of biological invasion - a survey. *Ecological Economics* 55: 321–336, <http://dx.doi.org/10.1016/j.ecolecon.2005.08.014>
- Byrnes JE, Reynolds PL, Stachowicz JJ (2007) Invasions and extinctions reshape coastal marine food webs. *PLoS ONE* 2 (3): e295, <http://dx.doi.org/10.1371/journal.pone.0000295>
- Carlton JT, Geller JB (1993) Ecological Roulette: The global transport of nonindigenous marine organisms. *Science* 261: 78–82, <http://dx.doi.org/10.1126/science.261.5117.78>
- Clavero M, Garcila-Berthou E (2005) Invasive species are a leading cause of animal extinctions. *Trends in Ecology and Evolution* 20: 110, <http://dx.doi.org/10.1016/j.tree.2005.01.003>
- Colautti RI, Bailey SA, van Overdijk CDA, Amundson K, MacIsaac HJ (2006) Characterised and projected costs of nonindigenous species in Canada. *Biological Invasions* 8: 45–59, <http://dx.doi.org/10.1007/s10530-005-0236-y>
- Connecticut General Statutes (2011) Chapter 490 §26-3
- Connor DW, Allen JH, Golding N, Howell KL, Lieberknecht LM, Northen KO, Reker JB (2004) The marine habitat classification for Britain and Ireland version 04.05 JNCC, Peterborough. <http://www.jncc.gov.uk/MarineHabitatClassification> (Accessed 7 December 2011)
- Connell S (2000) Floating pontoons create novel habitats for subtidal epibiota. *Journal of Experimental Marine Biology and Ecology* 247: 183–194, [http://dx.doi.org/10.1016/S0022-0981\(00\)00147-7](http://dx.doi.org/10.1016/S0022-0981(00)00147-7)
- Coutts ADM, Dodgshun TJ (2007) The nature and extent of organisms in vessel sea-chests: A protected mechanism for marine bioinvasions. *Marine Pollution Bulletin* 54: 875–886, <http://dx.doi.org/10.1016/j.marpolbul.2007.03.011>
- Coutts ADM, Forrest BM (2007) Development and application of tools for incursion response: Lessons learned from the management of the fouling pest *Didemnum vexillum*. *Journal of Experimental Marine Biology and Ecology* 342: 154–162, <http://dx.doi.org/10.1016/j.jembe.2006.10.042>
- Cronin ER, Cheshire AC, Clarke SM, Melville AJ (1999) An investigation into the composition, biomass and oxygen budget of the fouling community on a tuna aquaculture farm. *Biofouling* 13: 279–300
- Crooks JA, Soule ME (2001) Lag times in population explosions of invasive species: Causes and implications. In: Sandlund OT, Schei PJ, Viken A (eds), *Invasive Species and Biodiversity Management*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 103–125.
- Dalby JE, Young CM (1993) Variable effects of ascidian competitors on oysters in a Florida epifaunal community. *Journal of Experimental Marine Biology and Ecology* 167: 47–57, [http://dx.doi.org/10.1016/0022-0981\(93\)90183-O](http://dx.doi.org/10.1016/0022-0981(93)90183-O)
- Davis MA, Grime MA, Thompson K (2000) Fluctuating resources in plant communities: A general theory of invasibility. *Journal of Ecology* 88: 528–534, <http://dx.doi.org/10.1046/j.1365-2745.2000.00473.x>
- de Caralt S, Lopez-Legentil S, Tarjuelo I, Uriz MJ, Turon X (2002) Contrasting biological traits of *Clavelina lepadiformis* (Ascidiacea) populations from inside and outside harbours in the western Mediterranean. *Marine Ecology Progress Series* 244: 125–137, <http://dx.doi.org/10.3354/meps244125>

- Dijkstra JA, Harris LG (2009) Maintenance of diversity altered by a shift in dominant species: Implications for species coexistence. *Marine Ecology Progress Series* 387: 71–80, <http://dx.doi.org/10.3354/meps08117>
- Drake JM, Lodge DM (2004) Global hot spots of biological invasions: Evaluating options for ballast-water management. *Proceedings of the Royal Society B: Biological Sciences* 271: 575–580, <http://dx.doi.org/10.1098/rspb.2003.2629>
- Dunstan PK, Johnson CR (2007) Mechanisms of invasions: Can the recipient community influence invasion rates? *Botanica Marina* 50: 361–372, <http://dx.doi.org/10.1515/BOT.2007.041>
- Edwards PK, Leung B (2009) Re-evaluating eradication of nuisance species: invasion of the tunicate, *Ciona intestinalis*. *Frontiers in Ecology and the Environment* 7(6): 326–332, <http://dx.doi.org/10.1890/070218>
- Elith J, Phillips SJ, Hastie T, Dudik M, Chee YE, Yates CJ (2011) A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* 17: 43–57, <http://dx.doi.org/10.1111/j.1472-4642.2010.00725.x>
- Forrest BM, Gardner JPA, Taylor MD (2009) Internal borders for managing invasive marine species. *Journal of Applied Ecology* 46: 46–54, <http://dx.doi.org/10.1111/j.1365-2664.2008.01544.x>
- Fritts TH, Rodda GH (1998) The role of introduced species in the degradation of island ecosystems: a case history of Guam. *Annual Reviews in Ecology and Systematics* 29: 113–140, <http://dx.doi.org/10.1146/annurev.ecolsys.29.1.113>
- Grosholz ED (1996) Contrasting rates of spread for introduced species in terrestrial and marine systems. *Ecology* 77: 1680–1686, <http://dx.doi.org/10.2307/2265773>
- Gurevitch J, Padilla DK (2004) Are invasive species a major cause of extinctions? *Trends in Ecology and Evolution* 19: 470–474, <http://dx.doi.org/10.1016/j.tree.2004.07.005>
- Harris LG, Tyrrell MC (2001) Changing community states in the Gulf of Maine: Synergism between invaders, overfishing and climate change. *Biological Invasions* 3: 9–21, <http://dx.doi.org/10.1023/A:1011487219735>
- Hastings A, Cuddington K, Davies KF, Dugaw CJ, Elmendorf S, Freestone A, Harrison S, Holland M, Lambrinos J, Malvadkar U, Melbourne BA, Moore K, Taylor C, Thomson D (2005) The spatial spread of invasions: new developments in theory and evidence. *Ecology Letters* 8(1): 91–101, <http://dx.doi.org/10.1111/j.1461-0248.2004.00687.x>
- Hayes KR, Barry SC (2008) Are there any consistent predictors of invasion success? *Biological Invasions* 10: 483–506, <http://dx.doi.org/10.1007/s10530-007-9146-5>
- Hulme PE (2006) Beyond control: Wider implications for the management of biological invasions. *Journal of Applied Ecology* 43: 835–847, <http://dx.doi.org/10.1111/j.1365-2664.2006.01227.x>
- Kizlinski ML, Orwig DA, Cobb RC, Foster DR (2002) Direct and indirect consequences of an invasive pest dominated by eastern hemlock. *Journal of Biogeography* 29: 1489–1503, <http://dx.doi.org/10.1046/j.1365-2699.2002.00766.x>
- Kriebel D, Tickner J, Epstein P, Lemons J, Levins R, Loechler EL, Quinn M, Rudel R, Schettler T, Stoto M (2001) The precautionary principle in environmental science. *Environmental Health Perspectives* 109: 871–876, <http://dx.doi.org/10.1289/ehp.01109871>
- Kubaneck J, Williams DE, Dilip De Silva E, Allen T, Andersen RJ (1995) Cytotoxic alkaloids from the flatworm *Prostheceraeus villatus* and its tunicate prey *Clavelina lepadiformis*. *Tetrahedron Letters* 36: 6189–6192, [http://dx.doi.org/10.1016/0040-4039\(95\)01246-E](http://dx.doi.org/10.1016/0040-4039(95)01246-E)
- Lambert CC, Lambert G (1998) Non-indigenous ascidians in southern California harbors and marinas. *Marine Biology* 130: 675–688, <http://dx.doi.org/10.1007/s002270050289>
- Locke A, Hanson JM, Ellis KM, Thompson J, Rochette R (2007) Invasion of the southern Gulf of St. Lawrence by the clubbed tunicate (*Styela clava* Herdman): Potential mechanisms for invasions of Prince Edward Island estuaries. *Journal of Experimental Marine Biology and Ecology* 342: 69–77, <http://dx.doi.org/10.1016/j.jembe.2006.10.016>
- Locke A, Hanson J (2009) Rapid response to nonindigenous species. 3. A proposed framework. *Aquatic Invasions* 4: 259–273, <http://dx.doi.org/10.3391/ai.2009.4.1.26>
- Lodge DM, Williams S, MacIsaac HJ, Hayes KR, Leung B, Reichard S, Mack RN, Moyle PB, Smith M, Andow DA, Carlton JT, McMichael A (2006) Biological invasions: Recommendations for U.S. policy and management. *Ecological Applications* 16: 2035–2054, [http://dx.doi.org/10.1890/1051-0761\(2006\)016\[2035:BIRFUP\]2.0.CO;2](http://dx.doi.org/10.1890/1051-0761(2006)016[2035:BIRFUP]2.0.CO;2)
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications* 10: 689–710, [http://dx.doi.org/10.1890/1051-0761\(2000\)010\[0689:BICEGJ\]2.0.CO;2](http://dx.doi.org/10.1890/1051-0761(2000)010[0689:BICEGJ]2.0.CO;2)
- McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *TRENDS in Ecology and Evolution* 14(11): 450–453, [http://dx.doi.org/10.1016/S0169-5347\(99\)01679-1](http://dx.doi.org/10.1016/S0169-5347(99)01679-1)
- Millennium Ecosystem Assessment (2005) Ecosystems and human well-being: Biodiversity synthesis. World Resources Institute, Washington, DC
- Millar RH (1958) The breeding season of some littoral ascidians in Scottish waters. *Journal of Marine Biological Association* 37: 649–652
- Millar RH (1971) The biology of Ascidians. In: Russell, Yonge M (eds), *Advances in Marine Biology*, Number 9, Academic Press, New York, NY, USA, pp 1–100
- Monniot C, Monniot F, Labute P (1985) Les Ascidiées de (Polynésie française): relations avec le milieu naturel et apports intercontinentaux par la navigation. *Memoires du Museum National d'Histoire Naturelle* 7 (3): 481–495
- Melbourne BA, Hastings A (2009) Highly variable spread rates in replicated biological invasions: Fundamental limits to predictability. *Science* 325: 1536–1539, <http://dx.doi.org/10.1126/science.1176138>
- Mullaney JR, Schwarz GE, Trench ECT (2002) Estimation of nitrogen yields and loads from basins draining to Long Island Sound, 1988–1998. United States Geological Survey, Water Resources Investigations Report 02-4044
- Naranjo SA, Carballo JL, Garcia-Gomez JC (1996) Effects of environmental stress on ascidian populations in Algeciras Bay (southern Spain). Possible marine bioindicators? *Marine Ecology Progress Series* 144: 119–131, <http://dx.doi.org/10.3354/meps144119>
- National Ballast Information Clearinghouse (2008) NBIC Online Database. Electronic publication, Smithsonian Environmental Research Center and United States Coast Guard. Available from <http://invasions.si.edu/nbic/search.html> (Accessed 20 October 2011)
- Osman RW, Whitlatch RB (1998) Local control of recruitment in an epifaunal community and the consequences to colonization processes. *Hydrobiologia* 375–376: 113–123, <http://dx.doi.org/10.1023/A:1017000820646>
- Osman RW, Whitlatch RB (2004) The control of the development of a marine benthic community by predation on recruits. *Journal of Experimental Marine Biology and Ecology* 311: 117–145, <http://dx.doi.org/10.1016/j.jembe.2004.05.001>
- Parent M, Paetzold C, Quijon PA, Davidson J (2011) Non perforation with and without vinegar injection as a mitigation strategy against two invasive tunicates, *Ciona intestinalis* and *Styela clava*. *Management of Biological Invasions* 2: 27–38
- Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190: 231–259, <http://dx.doi.org/10.1016/j.ecolmodel.2005.03.026>

- Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52: 273–288, <http://dx.doi.org/10.1016/j.ecolecon.2004.10.002>
- Primo C, Vazquez E (2004) Zoogeography of the southern African ascidian fauna. *Journal of Biogeography* 31: 1987–2009, <http://dx.doi.org/10.1111/j.1365-2699.2004.01144.x>
- Puth LM, Post DM (2005) Studying invasion: have we missed the boat? *Ecology Letters* 8: 715–721, <http://dx.doi.org/10.1111/j.1461-0248.2005.00774.x>
- Pyo J, Shin S (2011) A new record of invasive alien colonial tunicate *Clavelina lepadiformis* (Ascidia: Aplousobranchia: Clavelinidae) in Korea. *Korean Journal of Systematic Zoology* 27: 197–200, <http://dx.doi.org/10.5635/KJSZ.2011.27.2.197>
- Ramsay A, Davidson J, Landry T, Arsenault G (2008) Process of invasiveness among exotic tunicates in Prince Edward Island, Canada. *Biological Invasions* 10: 1311–1316, <http://dx.doi.org/10.1007/s10530-007-9205-y>
- Reinhardt F, Herle M, Bastiansen F, Streit B (2003) Umweltforschungsplan des bundesministeriums für umwelt, naturschutz und reaktorsicherheit. Federal Environmental Agency of Germany
- Reinhardt JF, Stefaniak LM, Hudson DM, Mangiafico J, Gladych R, Whitlatch RB (2010) First record of the non-native light bulb tunicate *Clavelina lepadiformis* (Müller, 1776) in the northwest Atlantic. *Aquatic Invasions* 5: 185–190, <http://dx.doi.org/10.3391/ai.2010.5.2.09>
- Robinson TB, Griffiths CL, McQuaid CD, Ruis M (2005) Marine alien species of South Africa - status and impacts. *African Journal of Marine Sciences* 27: 297–306, <http://dx.doi.org/10.2989/18142320509504088>
- Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN, Weller SG (2001) The population biology of invasive species. *Annual Review of Ecology Evolution Systems* 32: 305–332, <http://dx.doi.org/10.1146/annurev.ecolsys.32.081501.114037>
- Sax DF, Brown JH (2000) The paradox of invasion. *Global Ecology and Biogeography* 9: 363–371, <http://dx.doi.org/10.1046/j.1365-2699.2000.00217.x>
- Shanks AL, Grantham BA, Carr MH (2003) Propagule dispersal distance and the size and spacing of marine reserves. *Ecological Applications* 13: 159–169, [http://dx.doi.org/10.1890/1051-0761\(2003\)013\[0159:PDDATS\]2.0.CO;2](http://dx.doi.org/10.1890/1051-0761(2003)013[0159:PDDATS]2.0.CO;2)
- Shenkar N, Gittenberger A, Lambert G, Rius M, Moreira Da Rocha R, Swalla BJ, Turon X (2011) World Ascidiacea Database. Available online at <http://www.marinespecies.org/ascidiacea> (Accessed 4 November 2011)
- Simberloff D (2000) No reserve is an island: Marine reserves and nonindigenous species. *Bulletin of Marine Science* 66: 567–580
- Simberloff D (2009) We can eliminate invasions or live with them. Successful management projects. *Biological Invasions* 11: 149–157, <http://dx.doi.org/10.1007/s10530-008-9317-z>
- Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: Invasional meltdown? *Biological Invasions* 1: 21–32, <http://dx.doi.org/10.1023/A:1010086329619>
- Stachowicz JJ, Whitlatch RB, Osman RW (1999) Species diversity and invasion resistance in marine ecosystems. *Science* 286: 1577–1579, <http://dx.doi.org/10.1126/science.286.5444.1577>
- Tarjuelo I, Lopez-Legentil S, Codina M, Turon X (2002) Defense mechanisms of adults and larvae of colonial ascidians: Patterns of palatability and toxicity. *Marine Ecology Progress Series* 235: 103–115, <http://dx.doi.org/10.3354/meps235103>
- Therriault TW, Herborg L-M (2008) Predicting the potential distribution of the vase tunicate *Ciona intestinalis* in Canadian waters: informing risk assessment. *ICES Journal of Marine Science* 65: 788–794, <http://dx.doi.org/10.1093/icesjms/fsn054>
- Turon X, Tarjuelo I, Duran S, Pascual M (2003) Characterising invasion processes with genetic data: An Atlantic clade of *Clavelina lepadiformis* (Ascidacea) introduced into Mediterranean harbours. *Hydrobiologia* 503: 29–35, <http://dx.doi.org/10.1023/B:HYDR.0000008481.10705.c2>
- Tyberghein L, Verbruggen H, Pauly K, Troupin C, Mineur F, De Clerck O (2012) Bio-ORACLE: a global environmental dataset for marine species distribution modeling. *Global Ecology and Biogeography* 21: 272–291, <http://dx.doi.org/10.1111/j.1466-8238.2011.00656.x>
- United States Department of Agriculture (USDA) National Invasive Species Information Center (2011) <http://www.invasivespeciesinfo.gov> (Accessed 7 December 2011)
- Veltman CJ, Nee S, Crawley MJ (1996) Correlates of Introduction Success in Exotic New Zealand Birds. *The American Naturalist* 147: 542–557, <http://dx.doi.org/10.1086/285865>
- Wasson K, Zabin CJ, Bedinger L, Diaz MC, Pearse JS (2001) Biological invasions of estuaries without international shipping: The importance of intraregional transport. *Biological Conservation* 102: 143–153, [http://dx.doi.org/10.1016/S0006-3207\(01\)00098-2](http://dx.doi.org/10.1016/S0006-3207(01)00098-2)
- Williamson MH, Fitter A (1996) The characters of successful invaders. *Biological Conservation* 78: 163–170, [http://dx.doi.org/10.1016/0006-3207\(96\)00025-0](http://dx.doi.org/10.1016/0006-3207(96)00025-0)
- Wirtz P (1998) Twelve invertebrate and eight fish species new to the marine fauna of Madeira, and a discussion of the zoogeography of the area. *Helgolander Meeresuntersuchungen* 52: 197–207, <http://dx.doi.org/10.1007/BF02908748>
- Wirtz P, Martins H (1993) Notes on some rare and little known marine invertebrates from the Azores- with a discussion of the zoogeography of the area. *Arquipelago Life and Marine Sciences* 11A: 55–63