Alien Species Alert: Didemnum vexillum Kott, 2002: Invasion, impact, and control
Alien Species Alert: *Didemnum vexillum* Kott, 2002: Invasion, impact, and control

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1 Introduction

*Didemnum vexillum* Kott (2002) is a high-impact, globally-invasive, colonial tunicate species that is native to Japan (Lambert, 2009; Stefaniak et al., 2012). It is generally a temperate cold-water organism, and its introduced range currently includes New Zealand, the Netherlands, France, Ireland, United Kingdom, Spain, Italy, and both the west and east coasts of the United States and Canada (Lambert, 2009; Stefaniak et al., 2012; Tagliapietra et al., 2012; Ordóñez et al., 2015, Vercaemer et al., 2015). Like other invasive tunicates, *D. vexillum* has the capacity to reproduce rapidly, outcompete native species, deteriorate environmental integrity, and cause significant economic harm (Lambert, 2005; Blum et al., 2007; Daniel and Therriault, 2007; Langyel et al., 2009; Cordell et al., 2013). For these reasons, this document aims to increase awareness of *D. vexillum*, with a focus on identification, natural history, current global distribution, potential impacts, and prospects for management and control where introductions occur.
2 Identification and taxonomy

Identification of *Didemnum vexillum* Kott (2002) (Table 2.1) is challenging due to the vast number of species within the genus *Didemnum*. The inability to confidently confirm identification of *D. vexillum* led researchers to use the “umbrella” name *Didemnum sp. A*; therefore, both *Didemnum vexillum* and *Didemnum sp. A* were used interchangeably prior to 2009. Genetic analyses have been used to demonstrate that samples of *Didemnum sp. A* and *D. vexillum* from Europe, the east and west coasts of North America, Japan, and New Zealand were the same species (Stefaniak *et al.*, 2009). Ongoing work to develop genetic primers may also assist future detection of invasive ascidians, such as *D. vexillum* (Stewart-Clark *et al.*, 2009, Vercaemer *et al.*, 2015). A comprehensive record of historical geographical spread and identification of this species was completed by Lambert (2009).

Table 2.1. The taxonomic statue of *Didemnum vexillum*.

<table>
<thead>
<tr>
<th>Phylum</th>
<th>Chordata</th>
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<tbody>
<tr>
<td>Class</td>
<td>Asciidiacea</td>
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<tr>
<td>Order</td>
<td>Aplousobranchia</td>
</tr>
<tr>
<td>Family</td>
<td>Didemnidae</td>
</tr>
<tr>
<td>Genus</td>
<td>Didemnum</td>
</tr>
<tr>
<td>Species</td>
<td><em>Didemnum vexillum</em> Kott, 2002</td>
</tr>
</tbody>
</table>

*D. vexillum* can form encrusting mats or lobate masses, depending on the environment. Each colony is composed of morphologically and genetically identical individuals, termed zooids, which are enclosed in a common tunic (Figure 2.1A). Colonies can vary in colour, but most are tan, cream, or yellow and can cover both non-living and living substrates (Kott, 2002; Lambert, 2009). The species can settle on and overgrow other sessile animals, such as other ascidians, bivalves, marine grasses, and seaweeds (Figure 2.1B; Carmen and Grunden, 2010). *D. vexillum* has also been observed overgrowing itself, fusing with other parts of the colony surface and forming thick sponge-like masses (Kott, 2002). Colonies tend to form mats on hard substrates and any other surface where currents are strong (Figure 2.1C), but hang in lobate clumps off structures such as wharves or kelp blades where currents are weaker (Figure 2.1D). These clumps tend to form long tendrils that easily break off living tissue which floats away, settles, and grows into new colonies, thus leading to further dispersal (Lambert, 2009; Valentine *et al.*, 2009). Outgrowths from the surface of the colony may occur from colony overlap or result from overgrowing 3-dimensional structures of other substrates (Kott, 2002). The gelatinous tunic itself is colourless. However, the colony gets its colour from the yellow gut loop, eggs, and embryos and from the white calcareous spicules, which are unevenly distributed throughout the tunic surface (Kott, 2002; Lambert, 2009). Additionally, the spicules can be used to distinguish *D. vexillum* from other *Didemnum* spp. and are stellate in shape, with 9–11 pointed rays in optical transverse sections, ranging in size between and within a colony, but generally measuring 20–30 µm (Kott, 2002; Lambert, 2009).
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Figure 2.1. Tunic surface patterns of *Didemnum vexillum*. (A) Marine Biological Laboratory dock, Woods Hole, MA, USA, 24 July 2007; (B) Marine Biological Laboratory dock, Woods Hole, MA, USA, 24 July 2007; (C) Rye Harbor State Park intertidal, Rye, MA, USA, 29 July 2007; (D) Massachusetts Maritime Academy floating dock, Bourne, MA, USA, 25 July 2007 (Photo: G. Lambert).

At the colony surface, the zooids form irregular groups each with a 6-lobed oral siphon opening at the surface of the tunic (Figure 2.2). Dark meandering lines are visible around zooid groups where spicules are absent (Figure 2.1A,C). Scattered throughout the colony are the common cloacal cavities where the atrial openings of the zooids discharge digestive waste and gametes at the tunic surface (Berrill, 1935; Van Name, 1945; Kott, 2002). The zooids of *D. vexillum* are small in size, measuring 1–2 mm (Kott, 2002; Daniel and Therriault, 2007; Lambert, 2009) with two body parts, a posterior yellow abdomen containing the digestive and reproductive organs, and the colourless anterior thorax, which contains the branchial sac (Figure 2.2). In the abdomen, the post-pyloric part of the gut is long and flexed ventrally, forming a double loop. There are about nine coils of the vas deferens surrounding the single spherical-to-oval-shaped testis, and a single oocyte at a time maturing in the ovary, which lies almost behind and under the gut loop. The number of coils in the vas deferens and orientation of the internal organs is critical in the accurate identification of *D. vexillum* (Figure 2.2; Kott, 2002; Lambert, 2009). Crescent-shaped, dense, white, lateral organs of the thorax filled with new spicules are visible in newly settled and developing individual oozoids (Valentine et al., 2009), as well as in the zooids of mature colonies. The branchial sac of each individual zooid has four rows of stigmata; the first row contains 8 or 9 stigmata per side (Kott, 2002).
Larval characteristics also play a crucial role in the accurate identification of *D. vexillum* (Lambert, 2009). Larvae can often be found within the tunic beneath the zooids during the reproductive season. Key features of *D. vexillum* larvae include 6 pairs of lateral ampullae and three adhesive papillae (Figures 2.2 and 2.3).
Figure 2.3. Brooded unhatched *D. vexillum* larva, Whangamata, New Zealand. Scale bar: 200 µm (Photo: G. Lambert).
3 Biology/Ecology

3.1 Natural history

3.1.1 Habitat

*D. vexillum* is a successful fouling organism because of its ability to grow on many natural and artificial structures (see review in Daniel and Therriault, 2007) and can thrive in both coastal and offshore environments in depths ranging from <1 to 65 m (Valentine et al., 2007a,b; Kleeman, 2009). In coastal habitats, *D. vexillum* is found clinging to the undersides of wharves, boats, and other artificial substrates, in addition to natural surfaces, such as rocks or living organisms, usually in locations where colonies are protected from wave action, predation, sedimentation, and deposited fecal matter (Bullard et al., 2007; Coutts and Forrest, 2007; Osman and Whitlatch, 2007). *D. vexillum* can engineer habitats by utilizing resources and space and is a well-known nuisance, due to its ability to rapidly foul harbour facilities, vessel hulls, and aquaculture equipment (Blum et al., 2007; Valentine et al., 2009). In offshore environments, such as Georges Bank in the Northwest Atlantic, huge masses of colonies have been observed by underwater ROVs, covering more than 230 km² on benthic substrates (Valentine et al., 2007a). However, shifting sandy substrates appear to limit colony formation in this area.

3.1.2 Feeding

Only the adult stages of ascidians are active filter feeders, whereas larval stages (which have a very short duration) obtain energy from an egg yolk (Cloney, 1978; Tyree, 2001). Like all other ascidians, *D. vexillum* is a ciliary-mucus feeder that relies primarily on phytoplankton for nutrients, but it also feeds on small particulate matter and suspended bacteria (Millar, 1971; Lambert, 2005). Factors such as the amount of food in the water, particle size, filtering capacity (which increases with the size of the colony), and time spent filtering all affect feeding rates (Millar, 1971; Tyree, 2001). For these reasons, actual filtering capacity for colonial ascidians is difficult to determine and remains unknown (Daniel and Therriault, 2007).

3.1.3 Environmental tolerances

Like other invasive species, *D. vexillum* can tolerate wide ranges of environmental parameters, including temperature and salinity (Lambert, 2005; Valentine et al., 2007b, 2009). Like most ascidians, *D. vexillum* colonies are rarely found in salinities less than 25 psu (Millar, 1971; Lambert, 2005), and colony die-offs have been observed at salinities below 20 psu (Bullard and Whitlatch, 2009). In fact, Bullard and Whitlatch (2009) showed that optimal growth of *D. vexillum* colonies occurs at higher salinities (26–30 psu) compared to medium and low salinities (i.e. 15–28 psu, 10–26 psu). Valentine et al. (2007b) demonstrated that *D. vexillum* colonies can survive temperatures ranging from −2 to 24°C, and fluctuations of up to 11°C in one day. While survival is not an issue within this wide range, *D. vexillum* thrives best within a narrower temperature range (14–20°C; Valentine et al., 2009), which may vary among colonies from different locations and exposed to different climates (Fletcher et al., 2013a). For example, colonies grow more rapidly in water temperatures between 15 and 20°C than those grown in temperatures >21°C (McCarthy et al., 2007). Furthermore, recruitment generally occurs between 14 and 20°C, but continues into cooler temperatures towards the end of the season. Colonies have been observed to initiate both development and spawning at the start of the season (Millar, 1971; Valentine et al., 2009), making the lower temperature limit at the end of the spawning and larval-release season unclear. However, some data
suggest that recruitment ceases between 9 and 11°C (Kleeman, 2009; Valentine et al., 2009).

3.1.4 Predation

Colonies of *D. vexillum* thrive best when attached to shaded undersides of suspended objects, like boat hulls or floats. However, colonies can be preyed upon by chiton (Kleeman, 2009), sea urchins, and other echinoderms (Bullard et al., 2007; Lambert, 2009). Littorinid snails have been seen feeding on both dying, which they prefer, and live colonies (Valentine et al., 2007b; Carman et al., 2009; Lambert, 2009). Some research has studied the potential use of predation by organisms, such as the green sea urchin, to reduce localized populations (i.e. on suspended shellfish aquaculture), but predation rates are unlikely to be high enough to reduce populations or prevent further spread (Epelbaum et al., 2009).

3.2 Reproduction

3.2.1 Asexual reproduction

*D. vexillum* reproduces both sexually and asexually. Asexual reproduction occurs in two ways. The first is by budding of each zooid. Didemnid budding, or “pyloric budding”, is the formation of two buds near the middle or narrowing of the zooid body between thorax and abdomen. The anterior-most bud arises from the region of the oesophagus and forms a new abdomen; the posterior-most bud, which arises from the anterior of the abdomen, forms a new thorax (Van Name, 1945; Millar, 1971; Monniot et al., 1991). The new buds that are formed, called blastozooids, are genetically identical to their parent zooid (Monniot et al., 1991). Asexual reproduction by budding expands the colony size from the first recruit (the oozooid that forms from the settlement and metamorphosis of the tadpole larva). The second type of asexual reproduction involves the breaking off of pieces of the colony which float away, settle, and re-establish a sister colony from the fragments (Lambert, 2005; Valentine et al., 2009). The establishment of colonies can occur from very small fragments (Morris and Carman, 2012). At temperatures between 6 and 10°C, ca. 77% of *D. vexillum* fragments reattached to both plastic and eelgrass substrates in laboratory experiments (Carman et al., 2014).

3.2.2 Sexual reproduction

Sexual reproduction, unlike asexual reproduction, produces larvae to colonize new sites. Like all Didennidae, *D. vexillum* is hermaphroditic and ovoviviparous. Eggs in the ovary develop one at a time, with an average of 1–20 eggs produced per zooid (Berrill, 1950; Kott, 2001; Lambert, 2005), and development of mature eggs is linked to the presence of conspecific sperm in the environment, as is the case for *Diplosoma listerianum* and probably most or all other didemnids (Bishop et al., 2000a). Spawning appears to be linked to the period with maximum food availability (Lambert, 2005); the exact time of year and temperature vary with geographic location. During spawning, sperm are released from the atrial aperture of the zooid and leave the colony through the common cloacal openings. Sperm then enter the oral siphon of a different zooid in another colony (and possibly the cloacal openings) and eggs are then fertilized, probably before being released from the ovary into the tunic (Millar, 1971; Monniot et al., 1991; Bishop et al., 2000a; Kott, 2001). This form of broadcast spawning, where only sperm is released, is known as spermcast mating; it is likely that sperm may be stored and utilized on a first-in-first-out manner (Bishop et al., 2000b; Bishop and Pemberton, 2006). Larval brooding, which can take several weeks, occurs within the tunic and re-
sults in the release of free-swimming larvae (1.4 mm in length; Lambert, 2009). Research has shown that light exposure plays a large role in both spawning and the release of ascidian larvae, including *D. vexillum* (Svane and Havenhand, 1993; Fletcher and Forrest, 2011). Larvae are released from common cloacal apertures (Fletcher and Forrest, 2011) in response to light stimulation and often at dawn in nature (Olson, 1983; Svane and Young, 1989). Didemnid tadpole larvae are equipped with two sensory organs in their trunk called the statocyte and the ocellus. Upon release from the colony, these organs cause larvae to be positively phototactic (Grave, 1937; Berrill, 1955; Monniot et al., 1991) and negatively geotactic and swim towards the light (Millar, 1971; Cloney, 1982).

When larvae are ready to settle, they become positively geotactic and negatively phototactic and seek shaded areas, such as undersides of docks (Berrill, 1955; Millar, 1971; Olson, 1983; Monniot et al., 1991), rather than well-lit or completely dark environments (Fletcher and Forrest, 2011). Research has shown that larvae may attach to a substrate and initiate metamorphosis only minutes after release, but most larvae will successfully settle and begin metamorphosis within 24 h (Fletcher and Forrest, 2011). Like many ascidian larvae, *D. vexillum* may begin metamorphosis before attachment to a substrate, which may have implications for increased dispersal, as it extends the possible distance travelled before attachment (Millar, 1971; Feng et al., 2010; Fletcher and Forrest, 2011; Reid et al., 2016).

Metamorphosis transforms non-feeding mobile tadpole larvae into sessile feeding juveniles (Cloney, 1982). Cloney (1982) has explained in detail the process of metamorphosis. Following metamorphosis, new *D. vexillum* recruits have a colourless tunic, free of spicules, a pale yellow digestive system, and a black statocyte and ocellus. Just days after settlement, the lateral organs of the thorax become white with the production of calcium carbonate spicules, which then move out into the tunic (Valentine et al., 2009). Further colony expansion occurs through asexual budding, which can occur within two weeks of settlement, but is dependent on environmental conditions (Fletcher and Forrest, 2011).

### 3.2.3 Reproduction and growth

The success of the species as an invader is, in part, due to its impressive capacity for growth and reproduction (Kott, 2002; Bullard and Whittlatch, 2009; Lambert, 2009). *D. vexillum* colonies in New England exhibited 6- to 11-fold increase in size in only 15 d (Valentine et al., 2007b); however, it is difficult to determine the age of a colony because of regular degeneration and regrowth of colonies during cold and warm seasons respectively (Millar, 1971; Tyree, 2001; Valentine et al., 2009). Like many other aspects of the life history of *D. vexillum*, colony growth and lifespan are greatly affected by season and changes in temperature, habitat, and other environmental variables (Millar, 1971; Lambert, 2005; Valentine et al., 2007b; Fletcher et al., 2013a). For example, growth rates slow or even stop during unfavourable conditions in colder months, while rapid colony expansion occurs during nutrient-rich and warmer months (Valentine et al., 2007b). Temperatures <0°C cause colonies to regress, but not necessarily die, while the maximum temperature for survival is likely >25°C, although temperatures >23°C may have adverse effects on a colony (McCarthy et al., 2007). During the warm season, highly variable temperatures likely inhibit the reproductive process and successful colonization (Valentine et al., 2009).

In New England, May–July is a regrowth period when surviving remnants of overwintered colonies begin asexual budding and expansion; in July–September during the
warmest seawater conditions (e.g. ca. 20°C), colonies experience rapid growth. The degree to which colonies degrade in cooler seasons influences the length of time required to regenerate, reproduce sexually, brood, and release larvae during the warm season (Valentine et al., 2009). Larvae are released at the end of their developmental period, as temperatures increase, but not when a specific temperature is reached. Recruitment occurs between 14 and 20°C, and is dependent on local environmental conditions (Valentine et al., 2009). While growth may continue beyond December in New England, a decline coincides with decreases in temperature (McCarthy et al., 2007; Valentine et al., 2007b). However, D. vexillum demonstrates a greater affinity or ability to grow in cooler temperatures, compared to other invasive ascidians, such as Botryoloides violaceus and Botryllus schlosseri (McCarthy et al., 2007). Dijkstra et al. (2007) also found that D. vexillum in the Gulf of Maine in 2003 and 2005 had the highest percent coverage in autumn and winter, while percent coverage of B. violaceus was greatest in summer and autumn.

Changes in habitat type can also influence growth cycles of D. vexillum. For example, colonies exhibited faster growth in open coastal habitats than in a protected marina, likely because of less competition with co-occurring species in the open habitat (Osman and Whitlatch, 2007). Further studies by Valentine et al. (2007b) show greater seasonal fluctuations in colony growth in a coastal tide-pool location than in subtidal habitats. In the more stable temperature regimes of deeper subtidal habitats, colonies degenerated less during the cold season, which led to a longer recruitment season than in shallow coastal locations (Valentine et al., 2009). While deep offshore colonies can exhibit more growth throughout the year, due to smaller temperature fluctuations, Bullard and Whitlatch (2009) compared growth at depths of 1, 2.5, and 4 m and found highest growth rates at 1 m. However, these differences may be due to differences in food availability at shallower depths, rather than changes in temperature.

While D. vexillum can withstand wide variations in salinity, this, like other environmental parameters, also affects colony growth. A controlled experiment carried out in the natural environment by Bullard and Whitlatch (2009) showed that higher salinity in the range of 26–30 psu (normal seawater salinity) results in higher growth than in 15–28 psu or 10–26 psu. In fact, colonies exposed to lower salinities experienced die-offs during this experiment.
4 Distribution

4.1 Native range

Deciphering the native and invasive distribution of an invasive ascidian is vital to effectively managing and controlling the species (Stefaniak et al., 2012). *D. vexillum* likely originated in Japan (Figure 4.1; Lambert, 2009; Stefaniak et al., 2009). The description of *D. vexillum* matches that of specimens identified as *D. pardum* (Nishikawa, 1990), the earliest of which was a museum sample collected in 1926 from Mutsu Bay in northern Japan (Lambert, 2009), where it is still common today (Lambert, 2009), as well as numerous other sites in Japan. Stefaniak et al. (2012) utilized the DNA sequence of two genes, cytochrome c oxidase subunit 1 (*co1*; mitochondrial) and THO complex subunit (*tho2*; nuclear) to determine the portion of the current distribution that was native. They demonstrated that Japan is the most genetically diverse region for *D. vexillum* (a typical test for determining endemicity), although there is possibly a wider native distribution.

While initial reports suggested that *D. vexillum* was spread with the importation of oysters and spat from Japan prior to the 1960s, this hypothesis was rejected because there were no reports of sudden appearance of this species prior to the 1970s (Lambert, 2009). It is more plausible that introductions occurred through shipping (either from fouling on boat hulls or in sea chests), while secondary spread within regions likely resulted from recreational boating activities (Lambert, 2009).

4.2 Invasive range

The invasive distribution includes New Zealand, the Netherlands, France, Ireland, United Kingdom, Spain, Italy, and both the west and east coasts of the United States and Canada (Figure 4.1). The invasive range is described by country and chronicles the first detection in the region (e.g. earliest European report is from the Netherlands). This does not always imply spread, but highlights the relatively recent introduction of this species in several regions and the potentially high risk for its spread to neighbouring areas or countries, if current biosecurity practices are not considered and controlled.

4.2.1 New Zealand

In New Zealand, *D. vexillum* was first detected in October 2001 on the North Island near Tauranga Harbour and Whangamata Harbour (Figure 4.2A; Kott, 2002; Kleeman, 2009; Lambert, 2009). This area is used largely by recreational boaters, and the colonies at the time dominated the community on 112 of 130 mooring posts and on some of the infrequently-used anchored boats (Kott, 2002). The description provided by Kott (2002) of these colonies would later be declared as the official species description of *D. vexillum* by Lambert (2009). Two months later, it was discovered in Shakespeare Bay, ca. 500 km south of its original detection site, after the movement of a heavily fouled barge (Coutts and Forrest, 2007). *D. vexillum* was subsequently detected on the seabed below the barge (Coutts and Forrest, 2007).

4.2.2 The Netherlands

The earliest European report of *D. vexillum* was in the Netherlands in 1991 by Ates (1998), who listed it as a range extension of *D. lahillei* in the Dutch Delta (Figure 4.2B; Gittenberger, 2007; Lambert, 2009; Gittenberger et al., 2014). Ates (1998) reported the species as “extremely dominant” in the Zijpe region (Eastern Scheldt estuary). By 2014, the species was confirmed in the Dutch Wadden Sea off Terschelling, Öudeschild, Texel, and Vlieland, as well as on oyster reefs near Terschelling and Texel (Gittenberger et al., 2014).
Figure 4.1. Map showing global native (blue) and invasive (red) geographic range of *Didemnum vexillum*. Potential Northern Hemisphere distribution range limits (in yellow) are based on current distribution.
4.2.3 France

The first record of *D. vexillum* in France may have been as early as 1968 in the Glénan archipelago (Lafargue, 1968), but was only confirmed in December 1998 in the port of Le Havre. Colonies were then found in 2002 on floating docks, at two additional harbours in northwest France (Figure 4.2B; Perros Guirec and Camaret-sur-Mer). In both instances, the species was originally identified as *D. lahillei* (Lambert, 2009). By 2005, the species had spread to new ports around the French Atlantic coast, including Brest and Concarneau (Stefaniak et al., 2009), and has remained prevalent (Valentine, 2003; Breton, 2005, 2014; Goulletquer, 2016). Due to regional shellfish stock movements, further spreading of the species is likely (FranceAgriMer, 2013). As the species is reported to be present in neighbouring countries in the Mediterranean (the Ebro delta in Spain and along the Italian Adriatic coast), its spread to the French Mediterranean coast is highly likely. Its environmental tolerance makes it possible for it to extend to the entire French coastline.

4.2.4 Ireland

The first record of *D. vexillum* in Ireland was in Malahide Estuary, north of Dublin on the east coast of the island in 2005 (Figure 4.2B; Minchin and Sides, 2006). Colonies were found overgrowing chains, ropes, pontoons, boat hulls, and fouling organisms, such as sabellid worms and mussels. Due to the extensive fouling by this species, it was assumed that the arrival was not recent. Some years later during a heavy rainfall event, all tunicates attached to the marina pontoons expired. In 2006, it was reported farther north in Carlingford Lough (Minchin, 2007), and additional surveys found *D. vexillum* on the west coast in 2007 in Clew Bay and Galway Bay associated with mussel longline cultivation and on oyster bags held on trestles. Along one shore, the tunicate was found to cover the sides of boulders and stones at low water spring tides. In Strangford Lough in Northern Ireland, it was found attached to the hull of an unused lightship serving as a yacht-club base. Both carpet and pendulous colonies were found (Minchin and Nunn, 2013).

4.2.5 United Kingdom

An established population of *D. vexillum* was found in September 2008 in Holyhead Harbour, north Wales (Figure 4.2B). Follow-up rapid assessment surveys in Wales showed that this was an isolated invasion (Griffith et al., 2009). Following several waves of eradication attempts within the harbour in 2009 and 2010, colonies re-established onto freshly treated surfaces (Holt and Cordingley, 2011). After further eradication attempts during the winters of 2010, 2011, and 2012, during which all surfaces were treated, no additional colonies were observed. In addition to the eradication, development of a decontamination berth was undertaken. Initial trials looked promising, but parts of the equipment were damaged during a winter storm. A self-cleaning rotating pontoon float was also developed (R. Holt, pers. comm.). Since then, populations have been found extending along the southern English coast (Plymouth, Kingswear, Lymington, Cowes, and Gosport) and farther east and on the north coast of Kent (Hitchin, 2012; Bishop et al., 2015). In 2010, *D. vexillum* was found in the Clyde at Largs Yacht Haven on the southwest coast of Scotland. In a follow-up survey, the species was found in three additional locations in close proximity to the yacht haven, including Fairlie Quay Jetty, Fairlie moorings, and Clydeport Jetty (Beveridge et al., 2011), but was not found in northern Scotland (Nall et al., 2015). To date, this is the most northerly record for *D. vexillum* in Europe.
4.2.6 Spain

*D. vexillum* was first reported in 2008 in northern and northwestern Spain (Figure 4.2B; Santander, Baiona, Moaña, Corme-Porto, and Gijón; Nagar et al., 2010). The range of *D. vexillum* in Spain expanded to the Mediterranean coastline in May 2012 on cultivated oysters in the Ebro Delta (Ordóñez et al., 2015).

4.2.7 Italy

The first reported *D. vexillum* population was in 2012 in the Venetian Lagoon (Figure 4.2B; Tagliapietra et al., 2012) and was later verified in five other locations inside the same lagoon (Venetian Arsenal, Certosa marina, San Nicolò, Sant’Andrea beacon tower, and Marina di Lio Grando) overgrowing various invertebrates and other ascidians, in addition to docks, pilings, and pontoons (Ordóñez et al., 2015).

4.2.8 Germany

Germany has a monitoring programme dedicated to locating new non-indigenous species, with several sampling stations in ports. To date, no *D. vexillum* has been detected, although it occurs in nearby countries.

4.2.9 United States

In the United States, established populations have been reported from both the west (Figure 4.2C) and east (Figure 4.2D) coasts. The first observed population on the northeast coast was in the late 1980s (although its identification was not confirmed until 2000) and on the west coast during the 1990s (Bullard et al., 2007). Rapid population expansion has led this species to become a dominant member of the subtidal community on both coasts (Bullard et al., 2007). During surveys conducted between 1998 and 2005 by Bullard et al., (2007), west coast populations ranged from several sites in Puget Sound, Washington and from Humboldt Bay to San Diego Bay in California (Figure 4.2C; Lambert, 2009). East coast populations extended from Eastport, Maine to Shinnecock Bay, New York (Figure 4.2D). Deeper subtidal populations also occur off the northeast coast, including Georges, Stellwagen, and Tillies banks, with coverage reaching 50–90% on Georges Bank (Bullard et al., 2007), marking the first detection of this species in an offshore habitat (Langyel et al., 2009). On Georges Bank, the species has been observed growing in continuous mats over an area covering 230 km², with coverage up to 90% and at depths between 45 and 65 m (Bullard et al., 2007; Valentine et al., 2007a). The northern-most distribution of *D. vexillum* in the United States is in coastal waters of Alaska, where it was first discovered in Whiting Harbor near Sitka on an oyster farm. This was the only site out of the 10 surveyed in the region where *D. vexillum* was detected. (Cohen et al., 2011; McCann et al., 2013).

4.2.10 Canada

*D. vexillum* has invaded both the west and east coasts of Canada (Figure 4.2C, D). The species is present in British Columbia on the west coast and Nova Scotia on the east coast. Established populations were first discovered in British Columbia in 2003, where colonies were found fouling mussel cages in Okeover Inlet; shortly thereafter, colonies were also detected in Deep Bay and Lemmens Inlet (Figure 4.2C). The species has since been detected in numerous locations on the east and west sides of the Strait of Georgia, including various inlets and harbours and along the south and west coast of Vancouver Island (Daniel and Therriault, 2007; Therriault and Herborg, 2007; Lambert, 2009). Coincidentally, as of 2009, the infestations are on or near Pacific oyster (*Crassostrea gigas*)
farms, which were originally imported from Japan (Lambert, 2009). Probably, however, the current infestations on oyster farms have resulted from movement of contaminated oysters from spawning and settlement bays in British Columbia to grow-out areas.

Although several rapid assessment surveys targeted at *D. vexillum* were conducted in southwest New Brunswick near Eastport, Maine in 2010 and 2012 (Martin et al., 2010; Sephton and Vercaemer, 2015) and southwest Nova Scotia in 2013 (Sephton and Vercaemer, 2015), no *D. vexillum* was detected at survey locations. *D. vexillum* was discovered by a recreational diver in October 2013 (although it may have been present as early as 2011) in Parrsboro, Nova Scotia, attached to rock substrate (Figure 4.2.D). This marked the northern-most population of this species on the east coast of North America (Moore et al., 2014). Rapid response surveys were conducted in the Minas Basin in the Bay of Fundy off Parrsboro in April 2014, and further sampling took place in May–August of the same year, during a scallop stock assessment in the Bay of Fundy and Scotian shelf (German Bank, northern Browns Bank, and eastern Georges Bank; Vercaemer et al., 2015). Extensive coverage of *D. vexillum* was found in the Minas Basin and Minas Channel and additional sites in the Bay of Fundy off Digby Gut and Yarmouth (Moore et al., 2014; Vercaemer et al., 2015). The introduction into the Bay of Fundy is likely from populations along the east coast of the United States, probably introduced to this new area through coastal vessel activity.

![Figure 4.2](image-url)  
Figure 4.2. Map showing invasive (red circles mark a station) geographic range of *Didemnum vexillum* by region. (A) New Zealand; (B) Europe; (C) North America west coast; (D) North America east coast.
Invasives biofouling species have created a range of complications for marine commercial activities and are considered one of the primary issues facing the marine aquaculture industry (Lambert, 2007). Shellfish aquaculture is particularly susceptible because operations create an array of multifaceted artificial substrates and are often positioned in protected embayments with significant food resources, creating optimal conditions for fouling organisms (Osman and Whitlatch, 1999; McKindsey et al., 2007). Solitary ascidians, such as *Styela clava* (clubbed tunicate) and *Ciona intestinalis* (vase tunicate) have had considerable impacts on shellfish aquaculture, increasing costs for production and processing (e.g. Carver et al., 2003; Thompson and MacNair, 2004; Ramsay et al., 2008) and negatively affecting meat yields and growth rates because of increased competition for resources (Daigle and Herbinger, 2009).

In New Zealand, the recent introduction of *D. vexillum* has threatened the green-lipped mussel (*Perna canaliculus*) industry in the Marlborough Sound region. Early income loss for the green mussel industry had been estimated to be more than NZD 800 000 over five years (Sinner and Coutts, 2003). Experiments by Fletcher et al. (2013a) demonstrated that early life stages of green-lipped mussels (i.e. 20–40 mm) are most vulnerable to fouling by *D. vexillum*, and impacts are mostly restricted to fouling-related displacement of spat, rather than to reduced growth and condition. Elsewhere, studies in northeast United States have shown that overgrowth by *D. vexillum* can lead to decreased growth rates (Auker, 2010). On the west coast of Canada, Pacific oysters fouled by *D. vexillum* were shown to have a lower condition index than oysters that underwent chemical or mechanical treatments to reduce fouling (Switzer et al., 2011). These impacts can also be the result of decreased water flow to shellfish, limiting access and creating competition for food resources.

Beyond artificial substrates, *D. vexillum* can readily foul natural substrates (Valentine, 2003; Valentine et al., 2007a). In addition to pebbles, cobble, and boulders, it can rapidly overgrow and out-compete species, such as other tunicates, hydroids, seaweeds, sponges, and various bivalves (Valentine et al., 2007a,b; Lengyel et al., 2009). In northeast United States, *D. vexillum* has been observed growing on eelgrass (Carman and Grunden, 2010; Carman et al., 2016), which may lead to reduced growth due to reductions in light transmission, as observed in eelgrass fouled by other invasive colonial ascidians (Wong and Vercaemer, 2012). Overgrowth by *D. vexillum* can decrease swimming ability in sea scallops (*Placopecten magellanicus*), which may limit their ability to escape predation and access food-rich habitats, which may ultimately affect growth and survival (Dijkstra and Nolan, 2011). Also, *D. vexillum* may affect recruitment of bay scallops (*Argopecten irradians*), as scallop larvae have been observed to avoid settlement on *D. vexillum* colonies (Morris et al., 2009).

Unlike other fouling invasive ascidians, *D. vexillum* can alter habitat complexity by forming extensive mats over cobble–pebble substrates (Mercer et al., 2009). Mercer et al. (2009) and McCann et al. (2013) found no substantial differences in benthic diversity between infested and non-infested areas; only subtle changes in community structure were observed, which included more deposit-feeders and infauna in fouled samples, possibly a result of decreasing foraging ability by larger predators. However, Lengyel et al. (2009) demonstrated that *D. vexillum* can significantly increase abundance of polychaete species. It has been speculated that such an altered benthic habitat community structure may negatively affect prey availability for benthic fish species (Lengyel et al., 2009). It might also have an impact on Atlantic herring (*Clupea harengus*) spawning.
grounds where eggs are laid on gravel, which can be localized in shallow coastal waters.
6 Prospects for further invasions

Factors leading to further spread of invasive ascidians include fragmentation of established colonies that result in local population intensification, combinations of anthropogenic and larval dispersal (local range expansions), and human-mediated transport (regional scales or greater; Wasson et al., 2001). Tadpole larvae of colonial ascidians are generally motile for only a few hours before settling, which tends to retain populations close to the site of origin, but leads to local intensification and usually limits further natural spread of the species (Berrill, 1950; Lambert, 2002). However, Fletcher et al. (2013b) consistently detected larval recruitment of D. vexillum 250 m away from the source, and models suggest that dispersal >1 km is theoretically possible. D. vexillum colonies that form long tendrils are susceptible to fragmentation from wave action and mechanical forces from vessels or equipment and can survive for extended durations of time (up to 30 days) to disperse and establish new populations (Figure 6.1; Bullard et al., 2007; Reinhardt et al., 2012). Furthermore, the colonization of seagrasses or macroalgae by D. vexillum can lead to rafting colonies, as seagrass shoots or algal fronds break and have the potential to travel farther than individual larvae (Worcester, 1994; Carman and Grunden, 2010; Fletcher et al., 2013b). While non-feeding tadpole larvae remain in the plankton for a very limited time and thus are not a factor for anthropogenic transport in ballast water, this may be a significant vector for the transport of colony fragments.

Artificial substrates, such as those in marinas, can provide a competitive advantage to non-indigenous fouling species over native species since native species may not be as evolutionarily adapted to colonize as wide an array of novel surfaces (Tyrrell and Byers, 2007). Closely spaced networks of harbours and other artificial substrates can act as dispersal strongholds and “stepping stones” for introduced ascidians (Wasson et al., 2001; López-Legentil et al., 2015).

As globalization accelerates, the risk of continued spread of non-indigenous species worldwide also increases (Ruiz et al., 1997, 2000; Cohen and Carlton, 1998). As ascidian larvae are non-feeding and generally short-lived, new introductions and spread of invasive ascidians, including D. vexillum, are expected primarily through human-mediated transport (e.g. fouled vessels and aquaculture gear; Figure 6.1; Kleeman, 2009; Lacoursière-Roussel et al., 2012; Roche et al., 2015). For example, recreational boating is considered a high-risk vector for primary introduction and secondary spread of non-indigenous ascidians, in part because it is a largely unregulated vector (Wasson et al., 2001; Clarke-Murray et al., 2011; Simard et al., 2016). The IMO (2011) has provided biofouling guidelines for commercial and recreational vessels, which could be strong management tools to avoid the future spread of this species, particularly when used as a basis for biosecurity protocols. Since TBT (tributyltin) was banned, anti-fouling coatings are less effective at limiting transport of non-indigenous species. Research continues on finding effective alternative antifouling coatings and treatments for vessels and gear. Enclosed seas, such as the Mediterranean, where yachting and recreational boating are increasing (Occhipinti-Ambrogi et al., 2016) are particularly exposed to the rapid spread of this ascidian. The October 2015 sighting in Crete (Greece) of putative colonies of D. vexillum (Aylin Ulman, pers. comm.) may confirm the eastward progression of this species. However, in-water encapsulation treatment methods provide novel attempts to limit transfer of fouling non-indigenous species on vessels at marine transportation hubs (Roche et al., 2015).
Figure 6.1. Growth patterns of *Didemnum vexillum*. (A) Pendulous growth on a yacht hull in 2006 (Photo: Damien Offer, Manager of Malahide Marina, Ireland); (B) Pendulous growth removed from a yacht hull in Malahide Marina, Ireland, June 2006 (Photo: Dan Minchin); (C) *D. vexillum* attached to cultivated mussels in Clew Bay, Ireland October 2008 (Photo: Fergal Guilfoyle); (D) *D. vexillum* overgrowing sabellid worms in Malahide Marina, October 2015 (Photo: Dan Minchin).

As management of long-established invaders is increasingly being questioned (Simberloff, 2014), prevention through the restriction of introduction pathways is the universally preferred management option. However, there are inherent challenges because of the high number and complexity of pathways combined with the openness of marine environments. The development of marine biosecurity strategies is critical for effective prevention, as well as preparedness and response to invasions. Without such rapid-response plans and the legal authority to implement them, the time to decide “what to do” limits the rapidness of any response (Kleeman, 2009; McKenzie et al., 2016). Furthermore, the risk of reinoculation from nearby sources, especially those where several countries share geographic boundaries (e.g. UK) is greater without widespread biosecurity protocols (Kleeman, 2009; Sambrook et al., 2014). With recent uncontrolled novel introductions and range expansions of *D. vexillum* in locations such as, but not limited to, Atlantic Canada (Vercaemer et al., 2015), Alaska (McCann et al., 2013), regions of Europe (e.g. Ates, 1998; Minchin and Sides, 2006, Griffith et al., 2009), and New Zealand (Forrest and Hopkins, 2013), further introductions and local population intensification are likely. For example, consequences of climate change, such as
the disappearance of summer Arctic sea ice, can lead to increased opportunities for shipping, mineral exploration, and other human developments and may greatly increase invasion prospects in the Arctic (Ruiz and Hewitt, 2009).
7 Prospects for control or management where introductions occur

Prospects for control and management of invasive species have gained an increasingly high profile with the introduction of numerous policies that address management of invasive species (IMO, 2004, 2011; Hewitt and Campbell, 2007). Thus far, examples showcasing the eradication of an established marine invasive species are rare (e.g., Anderson, 2005), but it is increasingly recognized that control or management efforts are worthwhile strategies, although the probability of success depends primarily on compliance with biosecurity protocols. Lessons learned from recent attempts to manage invasive ascidians (e.g., Coutts and Forrest, 2007; Kleeman, 2009; Rolheiser et al., 2012; McKenzie et al., 2016) and development of biosecurity measures, such as those in Australia requiring records of international vessel movement in and out of marinas, regular cleaning, and application of antifouling coatings (Sambrook et al., 2014) provide frameworks for future management of D. vexillum. Attempts to eradicate D. vexillum have proven unsuccessful in the long term because of, but not limited to, lack of sustained efforts, affordable control tools, stakeholder support, vector management, delayed responses, spatial distribution of species, and site topography (Coutts and Forrest, 2007; Sambrook et al., 2014). Regarding vector management, the IMO Ballast Water Management Convention and IMO Biofouling Guidelines could be strong management tools to avoid the future spread of this species (IMO, 2004, 2011).

A variety of methods have been tested to remove or control D. vexillum, including exposing the colonies to different chemical solutions, such as acetic acid, lime, chlorine, bleach, brine, freshwater, or desiccation (air drying). Most control options have been tested as potential solutions to mitigate growing concerns about invasive tunicate impacts in shellfish aquaculture. With this in mind, solutions must effectively remove biofouling organisms, but have limited or acceptable impacts on shellfish or other non-target organism survival and the environment (Locke et al., 2009). The use of lime solutions (3–4%) for 4–5 min effectively removed D. vexillum from Pacific oysters (Crassostrea gigas) without adverse impacts on oyster survival, growth, or condition, but multiple applications are suggested to attain 100% mortality in D. vexillum (Switzer et al., 2011; Rolheiser et al., 2012). Although the use of 5% acetic acid can be effective against D. vexillum even after 1 min, 5% acetic acid can also dramatically reduce the survival of oysters (Piola et al., 2010; Rolheiser et al., 2012; McCann et al., 2013). Furthermore, studies in New Zealand indicated that acetic acid, sodium hydroxide, and bleach are all effective at reducing fouling of D. vexillum on green-lipped mussel seed, but only 0.5% bleach resulted in 100% tunicate mortality with limited impact on seed mussels (Denny, 2008). The use of brine and freshwater did not reduce fouling after short (<10 min) exposures (Rolheiser et al., 2012), but longer-term exposures (4 h) effectively removed D. vexillum (McCann et al., 2013). A recent study designed and tested decontamination berths, which are based on the concept that a vessel can be positioned in an enclosed berth, seawater can be pumped out, and a chemical solution pumped in to treat non-indigenous species (Roche et al., 2015). This study suggests that treatments with acetic acid and sodium hypochlorite were equally effective at reducing fouling by D. vexillum, and the development of decontamination berths (or similar devices) can be useful to contain the spread of other non-indigenous species (Roche et al., 2015). This method may be particularly effective in killing organisms that have settled in sea chests, which are under the waterline and inaccessible except during dry-docking. Mechanical cleaning has proven effective (Switzer et al., 2011), but biological controls testing susceptibility of D. vexillum or other ascidians to various predators (e.g., urchin, sea star, crab, gastropod, periwinkles, and nudibranchs) are unlikely to limit biofouling by these species (Carman et al., 2009; Epaulbaum et al., 2009; Switzer et al., 2011).
Eradication of *D. vexillum* was attempted in Shakespeare Bay, New Zealand, in 2003, following its discovery and concerns for its likely spread to shellfish aquaculture sites in the region. The tunicate spread from a barge to the seabed beneath where it was moored and to nearby vessels and artificial structures (Coutts and Forrest, 2007). Coutts and Forrest (2007) documented the short-term removal success of *D. vexillum* by taking out and cleaning vessels, encapsulating pilings, barge hulls, and an artificial rock wall with plastic sheeting, and smothering the seabed with uncontaminated dredge spoil (Pannell and Coutts, 2007). After considerable biomass of *D. vexillum* re-established and spread, sustained regional control efforts occurred in 2006–2008 (Forrest and Hopkins, 2013). These sustained efforts had increased benefits in reducing risks of further vector reinfection and spread, but the termination of control measures due to very high costs again led to rapid biomass accumulation of *D. vexillum* (Forrest and Hopkins, 2013). Most recently, focus has shifted to biosecurity measures in an attempt to prevent further spread.

Following the discovery of *D. vexillum* in Holyhead Marina, north Wales in 2008, it was determined that eradication would be viable because of its limited natural dispersal potential and the consensus that the invasion was detected early (Kleeman, 2009; Sambrook et al., 2014). Based on previous knowledge gained from activities in New Zealand, wrapping, chemical application, and removal methods were scheduled when water temperatures were between 9 and 11°C. This timing was chosen because *D. vexillum* had been observed to cease recruitment at these temperatures (Valentine et al., 2009). However, this eradication attempt did not succeed partly because larvae continued to settle on panels in the marina until water temperatures fell below 9°C, which occurred 6 weeks after initiation of eradication activities (Sambrook et al., 2014). The difficulty in securing funding led to delays in a second eradication attempt until 2012, and although results were promising, the continued appearance of small colonies led to focusing on long-term containment (Sambrook et al., 2014).
Summary and conclusions

*Didemnum vexillum* has demonstrated the ability to be a highly invasive colonial tunicate with the capacity to reproduce rapidly, outcompete native species, deteriorate environmental integrity, and cause significant economic harm. Identification of *D. vexillum* Kott (2002) is challenging due to the vast number of species within the genus *Didemnum*. Increased taxonomic training in ascidian morphology is an important tool in early detection. In addition to traditional identification, ongoing work to develop genetic molecular tools may aid future detection of invasive ascidians for early detection and rapid response activities.

*D. vexillum* can engineer habitats by utilizing resources and is a well-known nuisance due to its ability to rapidly foul harbour facilities, vessel hulls, and aquaculture equipment. In offshore environments, colonies have been observed growing on benthic rocky substrates. Although *D. vexillum* has predators (e.g. chiton, sea urchins, other echinoderms, and littorine snails), predation is unlikely to be high enough to reduce populations or prevent further spread. The species’ success as an invader is partly due to its impressive capacity for growth and reproduction. *D. vexillum* colonies in New England exhibited a six- to 11-fold increase in size in only 15 d. Like many other aspects of *D. vexillum*, life history, colony growth, and lifespan are greatly affected by season, changes in temperature, and habitat, among other environmental variables. The consequences of climate change, such as the disappearance of summer Arctic sea ice, can lead to increased opportunities for shipping, mineral exploration, and other human developments, and may greatly increase invasion prospects in the Arctic and expand current temperature-limited ranges for this species.

*D. vexillum* likely originated in Japan; however, the invaded distribution now includes New Zealand, the Netherlands, France, Ireland, United Kingdom, Spain, Italy, and both the west and east coasts of the United States and Canada. Impacts include aquaculture (e.g. bivalve spat settlement displacement, decreased growth rates, lower condition index), overgrowth, and out-competition of species (e.g. seaweeds, sponges, bivalves), and reduced growth of overgrown eelgrass. Unlike other fouling invasive ascidians, *D. vexillum* can alter habitat complexity by forming extensive mats over cobble–pebble substrates, which may negatively affect prey availability for benthic fish species and Atlantic herring spawning grounds.

Factors leading to further spread of these invasive ascidians include fragmentation of established colonies resulting in local population intensification, combinations of anthropogenic and larval dispersal (local range expansions), and human-mediated transport, particularly as biofouling on vessel hulls (both commercial and recreational). As ascidian larvae are non-feeding and generally short-lived, new introductions and spread of invasive ascidians, including *D. vexillum*, are expected primarily through human-mediated transport (e.g. fouled vessels and aquaculture gear). For example, recreational boating is considered a high-risk vector for primary introduction and secondary spread of non-indigenous ascidians, partly because vessel biofouling (commercial and recreational) is a largely unregulated vector.

Attempts to eradicate *D. vexillum* have proven unsuccessful in the long term, because of, but not limited to, lack of sustained efforts, affordable control tools, stakeholder support, vector management, delayed responses, spatial distribution of species, and site topography. A variety of methods has been tested to remove or control *D. vexillum*, including exposing the colonies to different chemical solutions, such as acetic acid, lime, chlorine, bleach, brine, freshwater, or desiccation (air drying). Most control options have been tested as potential solutions to mitigate growing concerns of invasive
tunicates in shellfish aquaculture. With this in mind, solutions must effectively remove biofouling organisms, but have limited or acceptable impacts on shellfish or other non-target organism survival and the environment. A recent study designed and tested de-contamination vessel berths, which are based on the concept that a vessel can be positioned in an enclosed berth, seawater can be pumped out, and a chemical solution pumped in to treat non-indigenous species.

Prevention through the restriction of introduction pathways is the universally preferred management option for invasive species. However, there are inherent challenges because of the high number and complexity of pathways combined with the openness of marine environments. The IMO Ballast Water Management Convention (2004) and the IMO Biofouling Guidelines (2011) could be strong management tools to avoid the future spread of this species.

The development of marine biosecurity strategies and the legal frameworks to implement them are critical for effective prevention, as well as preparedness and response to invasions. Furthermore, the risk of reinoculation from nearby sources, including those where several countries share geographic boundaries, is greater without widespread, regional, biosecurity protocols.
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Alien Species Alert: Didemnum vexillum Kott, 2002: Invasion, impact, and control

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