

## 11 Climate change and non-native species in the North Atlantic

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### 11.1 Introduction

Species introduced to regions outside their native ranges as the result of human activities are known as “non-native species” (Shine *et al.*, 2000; Carlton, 2001). Non-native species that are known to affect native biodiversity in the ecosystem within which they become established, and/or have a negative economic effect on human society, are referred to as “invasive species” (Eno *et al.*, 1997; Shine *et al.*, 2000; Olenin *et al.*, 2010). However, Carlton (2002) has noted that, in marine systems, no quantitative boundaries have been placed on the criteria by which species are designated as invasive.

Many novel anthropogenic pathways for the introduction of marine species to new areas have arisen during the past century, and the speed and frequency of global shipping activities has also increased. As a result, non-native species introductions have become increasingly common along the Atlantic coasts of Europe and North America (Carlton and Geller, 1993; ICES, 2007b), and are now being reported on a regular basis (Pederson *et al.*, 2005; Arenas *et al.*, 2006; Mathieson *et al.*, 2008). Although we focus here on species that have been transported by human activities (e.g. the movements of ships and shellfish) to the North Atlantic, we note that human-mediated alterations to the environment (e.g. climate change) have led, or will lead, to invasions of species previously absent from the North Atlantic, either from the north, through newly created Arctic corridors, or from the south. For example, Therriault *et al.* (2002) and Reid *et al.* (2007) document the arrival of the North Pacific diatom *Neodenticula seminiae* in the North Atlantic, whereas Sorte *et al.* (2010) summarize global examples of marine range shifts in general.

This section deals with the impacts of climate change that have already been observed for non-native species, and predicts the likely consequences of continued large-scale pervasive warming and ocean acidification for future invasions. The implications of regional-scale processes that include extreme weather events, storm frequencies, wave exposure, and the introduction and spread of species outside their natural distributional ranges in the North Atlantic are also discussed.

Although it has been suggested that a rise in records of non-native species may, in part, also be attributed to increased awareness and reporting by both scientists and amateur naturalists, it is often possible to distinguish new sightings from new invasions by a careful examination of the historical record in order to determine the probability of a species having been previously overlooked (Carlton and Geller, 1993). Moreover, the well-known decline in available expert systematists in many regions of the world means that a very large number of invasions among smaller and taxonomically difficult marine taxa are not reported, leading to a considerable under-reporting of the scale of invasions (Carlton, 2009).

The geographic scope of this section covers the Northwest and Northeast Atlantic and the North and Baltic seas, but excludes the Mediterranean. The focus on near-coastal marine and brackish-water benthic species reflects the lack of information currently available for non-native species in offshore benthic or pelagic communities. Exceptions include a compound sea squirt (*Didemnum vexillum*), which has been

found to 80 m depth, forming extensive mats on the pebble gravel substrata of Georges Bank, smothering infauna, and potentially affecting fishing and aquaculture (Valentine *et al.*, 2007; Bullard *et al.*, 2007). Another is the American comb jelly (*Mnemiopsis leidyi*), a planktonic species that, during the past decade, has been recorded both in the North Sea, the Skagerrak, the Kattegat, and the southern Baltic, and can cause a substantial reduction in zooplankton populations. There is, however, no apparent connection between its appearance in northern Europe and climate change, and Eurasian populations appear to have originated from two geographically different areas in North America (Reusch *et al.*, 2010). Information is also available for the red king crab (*Paralithodes camtschaticus*), which was intentionally introduced into the Barents Sea for commercial purposes but has spread beyond the country of introduction to new areas. Its subsequent expansion on the shelf north of Norway is not linked to climate change (ICES, 2005b).

The pelagic realm is briefly discussed, addressing non-native plankton. Occasional rare records (vagrants), for which there is no evidence of a reproducing population (Lusitanian species in the Northeast Atlantic, or cryptogenic species and micro-organisms that may be complexes and whose histories remain debated), are not included. For harmful algal bloom (HAB) species, there is no good evidence of species being introduced by human vectors into Northeast Atlantic waters. Any link in their occurrence to climate change is weak at best (Don Anderson, pers. comm.; Scholin *et al.*, 1995). For example, all of the *Alexandrium* problems off the northeast coast of North America, and the *Karenia brevis* blooms in the Gulf of Mexico, which occasionally extend along the Atlantic coast, are natural occurrences that may be attributable to storms or widespread coastal blooms; it is clear that, in most cases, there are records of the presence of the species that pre-date more recent outbreaks, in the latter case for centuries. However, in a recent review, Hallegraeff (2010) suggested that a number of responses to climate change can be expected from HAB taxa in future, which may reduce existing blooms in some areas and cause the development of new blooms in other areas where they are not currently a problem. Any response may be even more complicated; Masseret *et al.* (2009), using molecular analysis, have demonstrated that the toxic dinoflagellate *Alexandrium catenella* exhibits great intraspecific diversity. It is evident that it is not possible to clearly define speciation and migration patterns with the techniques currently available, and that this situation may apply broadly to the taxonomic status of native and non-native HAB species and other micro-organisms.

## 11.2 Colonization and impacts of non-native species

The history and vectors of many non-native introductions in the North Atlantic are detailed in previous ICES reports. (e.g. ICES, 1999, 2004b, 2007b; see also Rilov and Crooks, 2009). Major anthropogenic pathways and transportation vectors of non-native marine species include shipping (via water, sediment in ballast tanks and ballasted cargo holds, hull fouling, sea chests, seawater pipe systems, anchor systems, and other hard surfaces), aquaculture, mariculture, recreational fishing, marine recreation, aquaria, the live seafood trade, education and research activities, the construction of canals, and the movement of structures such as drilling platforms, dry docks, pontoons, and log booms (ICES, 2005b). The initial sites of introduction and colonization of non-natives within the marine environment are often within man-made features, such as ports, marinas, and aquaculture or mariculture facilities (Pederson *et al.*, 2005; Minchin, 2006), making near-coastal and brackish waters particularly susceptible to invasions. Marine and estuarine invasions are the subject of research and recording programmes throughout the North Atlantic (e.g. the Global

Invasive Species Database (GISD) of the International Union for the Conservation of Nature (IUCN); the North European and Baltic Network on Invasive Alien Species (NOBANIS; <http://www.nobanis.org/about.asp>); the Marine Invader Tracking Information System (MITIS); the Non-Indigenous Species Database Network (NISbase; <http://invasions.si.edu/nemesis/merge/spsearch.jsp>); the Non-indigenous Aquatic Species Database (NAS) of the US Geological Survey; and the Delivering Alien Invasive Species Inventories for Europe (DAISIE; <http://www.europe-alien.org/>; ended in 2008)).

The impact of non-native species on existing marine communities is both species-specific and regionally variable. Non-natives may act as dominant ecological engineers, competitors, and/or predators, leading to the alteration of the structure, functioning, and composition of some marine communities/habitats (Olenin *et al.*, 2007). They may, on occasion, also enhance population sizes of previously present species (Kochmann *et al.*, 2008; Rilov and Crooks, 2009) and provide substrate for additional non-native colonization. Such introductions can, therefore, result in both negative and positive changes within marine ecosystems (Olenin and Leppäkoski, 1999; Wallentinus and Nyberg, 2007).

To date, there has been no direct evidence to indicate that non-native species cause extinctions in recipient coastal communities. Few studies are sufficiently long term to facilitate the tracking of post-invasion demographic trajectories over extended periods, and there is limited study of potential extinctions among smaller marine taxa (J. T. Carlton, pers. comm.). Numerous studies since the 1950s demonstrate that species such as the Australasian barnacle *Austrominius modestus* (= *Elminius modestus*) became established in Europe during World War II and thereafter. Initial studies predicted that it would outcompete native cirripedes (Crisp, 1958), but at many natural shores throughout northern Europe where it became established, abundance subsequently declined to levels comparable with native co-occurring barnacles in most open-coast habitats (Southward, 1991; Harms, 1999; Mieszkowska *et al.*, 2005). Most recently, experimental studies indicate that it is outcompeting *Semibalanus balanoides* and *Balanus crenatus* in northern Europe in areas of lower salinity and embayments (Witte *et al.*, 2010).

### 11.3 Climate change in the North Atlantic

The marine climate of the North Atlantic has oscillated between warmer and cooler phases during the 20th century, with an incremental trend of increasing temperatures associated with global warming since the mid-1980s (see Section 3; Figure 3.4). In addition, changes to seawater chemistry (e.g. acidification; see Section 5), oceanic and coastal currents, and land–sea interactions, as well as biological aspects (including benthic–pelagic coupling, productivity, and eutrophication), may all have implications for established non-natives and their potential future colonizations. Recent climate-driven changes in geographic distributions and the relative abundance of native species of both warm- and cold-water origins have focused on regions of biogeographic transition between temperate and boreal waters (see Section 8). If climate change is a major driver of shifts in non-native species, it is likely that some of the first effects will also be seen at these boundaries.

Both global and regional climate models predict a continuation of the current warming trend throughout the 21st century, with the extent of warming depending on the emission scenario used in the models of the Intergovernmental Panel on Climate Change (IPCC, 2007a; see also Murphy *et al.*, 2009, and the US National

Oceanic and Atmospheric Administration (NOAA) National Weather Service Climate Prediction Center, [http://www.cpc.noaa.gov/products/precip/cwlink/climatology/.](http://www.cpc.noaa.gov/products/precip/cwlink/climatology/))

#### 11.4 Impacts of climate change on non-native species

Successful climate-driven invasions will depend upon a change in local or regional environmental conditions driving the system to a different environmental state (Walther, G. R., *et al.*, 2009). As a result of this alteration in climate, some native species will fail to adapt to their surrounding environment, whereas others will be able to take advantage of these altered climatic regimes. Climate change has not been a major driver of recent colonizations, but it exerts, and is likely to continue to exert, direct and indirect impacts on both native (see Section 8) and non-native marine species once successfully introduced. Recent patterns of response by non-native species are difficult to attribute to climate warming alone because of a paucity of both ecological and physiological data (Occhipinti-Ambrogi, 2007).

This section provides some examples of climatic impacts observed to date, with a relative assessment of confidence ascribed to each. The species have been selected on the grounds that:

- 1) the current ranges of established, reproducing populations are well known and the species are not thought to be cryptogenic;
- 2) the species are taxonomically well described and defined, i.e. there is little or no debate on whether two or more species are being mistakenly discussed under another synonym;
- 3) the biology and ecology is well understood, with sufficient peer-reviewed literature on key life-history attributes to assess impacts of potential future environmental shifts on distribution, reproductive output, or phenologies;
- 4) the species have already exhibited an impact (environmental, economic, societal, or otherwise) where they have become established.

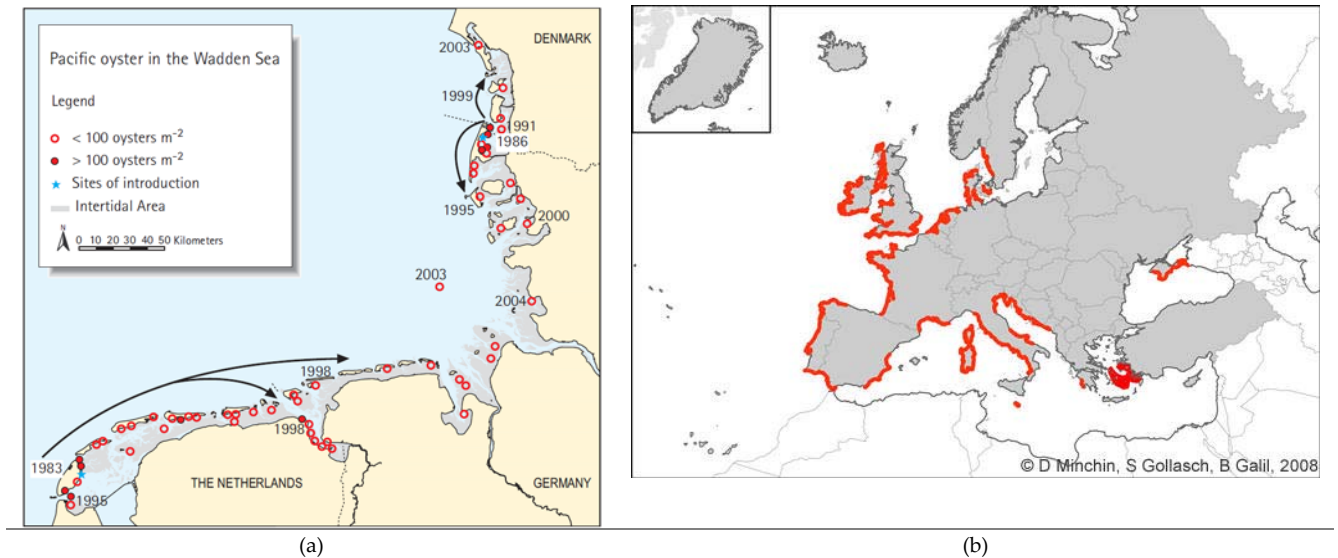
##### 11.4.1 High confidence

###### **Pacific oyster (*Crassostrea edulis*)**

The Pacific oyster (*Crassostrea gigas*) has become established on natural shores in western Europe since its deliberate introduction in the 1970s from farmed stocks in British Columbia and Japan (Figure 11.1). *Crassostrea gigas* (as *C. angulata*) was introduced from Portugal to the UK in 1926, but populations declined rapidly when importation ceased (Utting and Spencer, 1992). In 1965, the then Ministry of Agriculture, Fisheries and Food granted licences for the importation of *C. gigas* to the UK after physiological tests revealed that this species required higher temperatures than those experienced at that time in UK waters (18–23°C over a prolonged period) in order to successfully recruit (Mann, 1979; Utting and Spencer, 1992). Wild spatfall and successful localized recruitment first occurred in the vicinity of oyster farms in southwestern England and North Wales after the unusually warm summers of 1989 and 1990 (Spencer *et al.*, 1994).

In the Wadden Sea, mean monthly sea temperatures exhibited increased deviations of 1–3°C from long-term means during the summers of 1994, 1997, 2001, 2002, and 2003 (Diederich *et al.*, 2005), consistent with observed higher European shelf sea temperatures (see Section 3, Figure 3.4). Enhanced spatfall was observed in Schleswig-Holstein during these periods and may have contributed to an increased spread of feral populations of *C. gigas* in the Danish Wadden Sea (Nehls and Büttger,

2007). Similar invasions of natural habitats have taken place along the Atlantic coastline of Europe up to Scandinavia as temperatures warmed sufficiently to allow successful recruitment (ICES, 2009b; Wrange *et al.*, 2010). Additional factors, including changes in the composition/availability of food, may affect juveniles and adult reproductive outputs, thereby accounting for some of the variability observed at different locations (Gosselin and Qian, 1997). Laboratory experiments indicate that declining rates of calcification, resulting from increasing concentrations of  $p\text{CO}_2$ , are less pronounced for oysters than for other bivalves, but these results have yet to be confirmed for wild populations (Gazeau *et al.*, 2007).



**Figure 11.1.** (a) *Crassostrea gigas* in the Wadden Sea. Blue stars indicate introduction sites (Texel, in the Netherlands, and Sylt, in Germany). Years indicate first records of settlement. Circles refer to mean Pacific oyster abundance in 2003 (from (Reise *et al.*, 2005); (b) European distribution from DAISIE ([http://www.europe-aliens.org/pdf/Crassostrea\\_gigas.pdf](http://www.europe-aliens.org/pdf/Crassostrea_gigas.pdf)) and Sharma (2010).

In the northeastern US, attempts to grow *C. gigas* have been unsuccessful. Environmental conditions at the proposed locations were not suitable, and the benefits were insufficient to justify replacing the cultivation of the native species *C. virginica*. The public strongly opposed its introduction (Calvo *et al.*, 1999).

**Impacts.** *Crassostrea gigas* now forms extensive reefs in Europe (Figure 11.2) and may outcompete native species, including mussels and other sessile rocky fauna (Nehls and Büttger, 2007; ICES, 2009b). However, it may also facilitate localized increases in biodiversity on soft substrata, where it stabilizes the sediment and creates a three-dimensional biogenic habitat (Mieszkowska, unpublished data), thereby having a positive impact within some systems. In contrast, there has been a negative socio-economic impact where reefs of sharp oyster shells have formed on public sandy beaches (ICES, 2009b). Spat from natural populations are used by growers as a seed source in southeastern England (Syvret, 2008), and fisheries are also sustained by natural spatfalls in France and the Netherlands (Maggs *et al.*, 2010).



Figure 11.2. *Crassostrea gigas* forming a dense natural reef across the entire intertidal zone, Pornic, northern France. (Source: Graham Ledwith.)

#### 11.4.2 Medium confidence

##### ***Codium fragile* subsp. *fragile***

The task of attributing spread and proliferation of non-native species is further complicated by the potential for geographic differences in genotypes, expressed as adaptation to local thermal conditions. One such example is the non-native macroalga *Codium fragile* subsp. *fragile* (formerly subsp. *tomentosoides*), a green alga that is native to the western Pacific (Chapman, 1999). This species is now found on both sides of the Atlantic. It is considered to be a nuisance species in the Northwest Atlantic, but despite being found from northern Norway (by the 1970s) to Portugal, it has not aggressively colonized coastal habitats in the Northeast Atlantic, where it is usually in low abundance and cannot be readily distinguished from native species of *C. fragile* (Chapman, 1999). In the Northwest Atlantic, in contrast, *C. fragile* subsp. *fragile* is the only alga of this genus present, and has a marked impact on ecosystems because it is not a preferred food for herbivores and is in competition with other seaweeds so it can alter habitat extensively.

*Codium fragile* subsp. *fragile* was first reported in Europe in the 1800s, in the US in 1957, and, more recently, in Canada in 1991, with introduction attributed to shipping and aquaculture. Within Europe, the species has the potential to colonize more locations within its present range because its distribution is currently patchy. Although it can survive below-freezing temperatures, its temperature and salinity requirements necessitate prolonged periods for growth and gametogenesis. Its success in establishing in shallow estuaries and embayments in northern areas (e.g. Scandinavia and Prince Edward Island), but not in surrounding open seas, suggests it may be temperature-limited. However, the potential evolution of cold-adapted genotypes of *C. fragile* subsp. *fragile* may expand the colonization repertoire of this species. For example, as early as the 1970s, evidence revealed a divergence in the temperature tolerances of *C. fragile* subsp. *fragile* populations in Maine and populations farther south (Malinowski, 1974; Carlton and Scanlon, 1985). The predictive models of Burrows *et al.* (2009) forecast increased site occupancy and related impacts for *Codium* spp. (both native and non-native species) in the UK with rising sea temperatures of 0.4–3.3°C by 2080.

**Impacts.** The alga can attach to commercial shellfish (e.g. oysters and scallops) to the extent that harvesting is seriously impaired (Coulautti *et al.*, 2006; ICES, 2007b). In the US, *C. fragile* subsp. *fragile* has a negative socio-economic impact because it washes ashore in such abundance that bathing beaches are closed during peak summer periods until the alga is removed from the affected areas (J. Pederson, pers. obs.). It has also successfully occupied areas where eelgrass (*Zostera marina*) has died back and may prevent its re-establishment. As a species that is present all year in New England, *C. fragile* subsp. *fragile* serves as a stepping stone for several non-native species, such as the bryozoan *Membranipora membranacea*. In the UK, the invading *C. fragile* replaces native *Codium* species (Reid *et al.*, 2009a), although it is likely to enhance local biodiversity because of the number of epiphytes it supports (C. Maggs, pers. comm.).

#### **Manila clam (*Ruditapes philippinarum*)**

The Manila clam (*Ruditapes philippinarum*) is another bivalve that was introduced into the North Atlantic for aquaculture. At the time, thermal thresholds for reproduction were considered to be greater than the regional summer seawater temperatures (Laing and Utting, 1994). The culture of *R. philippinarum* began in Europe during the cooler 1970s and 1980s. Only recently has this species formed self-sustaining populations in the wild, which are now of sufficient size to sustain small commercial fisheries in Poole Harbour, southern England (Jensen, A. C., *et al.*, 2004). These introductions have been linked to rising summer temperatures (Laruelle *et al.*, 1994; Caldow *et al.*, 2007). Latitudinal variation in the timing and reproductive activity of *R. philippinarum* is positively related to temperature gradients, and there is growing evidence that the colonization ability of the species is enhanced in warmer locations.

**Impacts.** In the Brittany region of France, *R. philippinarum* has a greater capacity to colonize than the native conspecific *R. decussatus* owing to its prolonged reproductive period (Laruelle *et al.*, 1994). With warming seawater temperatures, *R. philippinarum* also outcompetes other functionally similar native venerid clams where it becomes established.

#### **Slipper limpet (*Crepidula fornicata*)**

The slipper limpet (*Crepidula fornicata*) is native to Atlantic North America. Established introductions occurred in southeastern England in the late 1800s as *C. fornicata* spat escaped from imported *Crassostrea virginica* stocks, and individuals were transported via ship hulls. Spreading throughout inlets in southeastern England during the 1900s, its distribution until recently was confined mainly to the south and southeast coasts (Crouch, 1894; Fretter and Graham, 1981; Maggs *et al.*, 2010). Minimum winter temperatures may be important in limiting the ability to develop extensive populations in northern Europe (Minchin *et al.*, 1995; Thieltges *et al.*, 2004). *Crepidula fornicata* now occurs from southwestern Norway to Spain. It was reported at a few sites on the Atlantic seaboard of Scandinavian countries between the 1930s and 1960s, but the populations were not sustained, possibly because of cold winters. Self-sustaining populations now exist, coinciding with recent warming in the Northeast Atlantic and supporting the view that climate change has been responsible for this relatively recent northern range extension that has occurred more than a century after its initial introduction (Nehls *et al.*, 2006).

**Impacts.** *Crepidula fornicata* is a filter-feeder that occurs intertidally and subtidally on rocky shores, on soft bottoms attached to shells, and in association with oyster and mussel culture operations. It competes with other filter-feeding organisms and



modifies habitat by creating extensive three-dimensional hard substrate for the attachment of epizoics.

Hundreds of thousands of tonnes of *Crepidula* occur in some areas, such as Mont-St Michel Bay in northern France (Gouletquer *et al.*, 2002). The occurrence of *C. fornicata* in large numbers results in competition for food and a consequent reduction in native biodiversity. In addition, the high biomass leads to the accumulation of faeces and pseudofaeces, thus increasing the deposition of mud, which smothers native habitats and species, and can prevent the settlement of oyster spat, resulting in a severe reduction in their productivity (Barnes *et al.*, 1973). The excreta contain enhanced levels of biogenic silicate that may stimulate diatom growth and thus reduce the potential for the production of harmful algal blooms (Ragueneau *et al.*, 2002).

### **Styela clava**

*Styela clava* is an Asian solitary tunicate (sea squirt; Figure 11.3). Detection in southwestern England in 1952 (Carlisle, 1954) was followed by observations of a subsequent spread along the south coast of England and Wales, and across into France by 1968 and to Ireland by 1972 (Minchin and Duggan, 1988). It is continuing to spread northward in both Europe and North America and is now found on both sides of the North Atlantic from Norway (A. Jelmert and F. Moy, pers. comm.), Denmark, Ireland, and the UK to Portugal (DAISIE), and from New Jersey, USA, to Prince Edward Island, Canada. Spawning is thought to take place once water temperatures reach 15°C (<http://www.jncc.gov.uk/page-1722>). Transmission is via shipping, the hulls of vessels, and movement of molluscan stock, but successful establishment requires suitable temperatures. This information supports the theory that its introduced range is temperature-limited, but other studies suggest that high temperatures experienced in the wild can also constrain growth (Davis and Davis, 2009). There are insufficient experimental and field data to confirm the driving role of climate change in range expansions to date.



**Figure 11.3.** *Styela clava* from Queen Anne's Battery Marina, Plymouth, UK. (Source: John Bishop, Marine Biological Association of the UK.)

**Impacts.** *Styela clava* is a fouling organism, which grows on oysters and mussels, and can colonize artificial substrate and natural rock. Around Prince Edward Island, Canada, it is one of several tunicates that have a negative impact on mussel aquaculture by competing for food. In addition, as the ascidians grow, their additional weight may cause the mussel culture ropes to sink into anoxic sediment below the cultivation sites (Thompson and MacNair, 2004). High densities of *S. clava*



may be found in marinas on pontoons, buoys, boat hulls, and other structures (Figure 11.4). Within man-made areas, such as marinas and harbours, it may increase local biodiversity by providing a biogenic habitat that facilitates subsequent settlement by other species (Figure 11.5), which, in the Northwest Atlantic, are frequently introduced species (J. Bishop, pers. comm.; <http://www.jncc.gov.uk/page-1722>).



Figure 11.4. *Styela clava* with epibionts from Queen Elizabeth II Marina, St Peter Port, Guernsey, UK. (Source: sealordphotography.net.)



Figure 11.5. Photograph of *Styela clava* covering mussel "socks", a buoy, and portions of the rope. (Source: Arsenault *et al.*, 2009; open access image.)

### 11.4.3 Low confidence

Climate change has been suggested as the primary driver of range expansions into higher latitude areas of the North Atlantic for several species, including the Chinese mitten crab (*Eriocheir sinensis*; Ojaveer *et al.*, 2007), harpoon weed (the alga *Asparagopsis armata*), Japanese wireweed (*Sargassum muticum*), and wakame (*Undaria pinnatifida*; Figure 11.6); for reviews see ICES (2007a, 2007b); Reid *et al.* (2009a). The common saltmarsh cord-grass (*Spartina anglica*) is a nuisance and is ranked among the world's worst 100 non-native species by the IUCN; flowering and seed formation is enhanced by mild winters and warm summers in Scandinavia (Nehring and Adsersen, 2006) and the Wadden Sea (Loebl *et al.*, 2006). All of these species were introduced via human vectors, but the delay in expansion after their initial invasion, coupled with recent rapid extensions of their introduced region, suggest that warmer temperatures may be promoting their spread.



Figure 11.6. The basal fertile parts of the brown alga *Undaria pinnatifida* attached to floating pontoons in Plymouth, UK. (Source: Dan Minchin.)

### 11.5 Community- and regional-level impacts

The effects of climate change and non-native species have been implicated in the decline and even collapse of several marine systems (Harris and Tyrrell, 2001; Stachowicz *et al.*, 2002b; Frank *et al.*, 2005). In the Gulf of Maine, USA, an epifaunal marine community, dominated by mussels, sponges, hydroids, and native ascidians, has shifted to a non-native-dominated community within a 30-year period. The shifts in species diversity and dominance resulted from a greatly diminished population of mussels, which provided secondary substrate to the seasonally abundant non-native ascidians that are the dominant species (Dijkstra and Harris, 2009).

Both rising winter temperatures and biotic interactions appear to play a role in the observed changes in community structure. Many ascidians recruit early, settle, and grow quickly, preventing other species from settling until they senesce, usually with the onset of cold weather; this makes the community vulnerable to invasions the next season (Dijkstra and Harris, 2009). Chemical compounds that may deter predation and prevent secondary settlement may also be involved (Pisut and Pawlik, 2002). It has been suggested that warm winter temperatures favour some non-native ascidian species, probably because they originate in areas where environmental regimes are typified by mild winter seasons that facilitate their continued dominance of primary habitat space (Stachowicz *et al.*, 2002a, 2002b; Stachowicz and Byrnes, 2006). These results must be approached with caution, however, because one of the species classed as non-native cannot be demonstrated to originate outside the region, and because the small number of study species and limited size of the study area make inferences problematic at the wider scale. For example, the sea squirt *Didemnum vexillum* survives at low temperatures throughout the Northwest Atlantic and may persist subtidally as large colonies on the bottom of Georges Bank for several years before regressing with the onset of colder conditions, with a resumption of growth again as temperatures rise (S. Gallager, P. Valentine, and J. Pederson, pers. obs., 2008).

In a recent study, Sorte *et al.* (2010) compared the range shifts of native species and non-native introductions using field and laboratory studies and field observations to assess impacts. Of the 109 species identified as meeting their criteria, 75% of species shifts were polewards and 70% were probably the result of climate change. Other researchers have also reported higher rates for native marine species compared with native terrestrial species, suggesting that they are responding more quickly to climate

warming (Parmesan and Yohe, 2003; Mieszkowska *et al.*, 2005; Beaugrand *et al.*, 2009). A slightly higher average rate of spread was derived for non-native species (Sorte *et al.*, 2010), but there was no demonstrable link between this expansion rate and climate change. In addition to rising temperature, species interactions and other environmental variables modulate the expansion of both native and non-native species.

Invasion of brackish waters in the Baltic Sea by the predatory cladoceran *Cercopagis pengoi*, most probably in the ballast water of shipping, may affect the ecosystem by lengthening food chains; this species is now an important food source for some fish species (Gorokhova, 2004; Vanderploeg *et al.*, 2002). There is no indication that the spread of this species is linked to climate change. Another cladoceran, *Penilia avirostris*, invaded the southern North Sea in the early 1990s and rapidly increased in numbers in autumn as a consequence of exceptionally high sea temperature (Johns *et al.*, 2005). The dormant resting eggs facilitate the distribution of these two species, which are likely to extend their ranges farther with rising temperature.

### 11.6 Predicted impacts

Climate change is likely to affect the introduction and spread of non-native species, the persistence of established non-native species, and the sensitivity of non-native species to direct and indirect impacts. Direct effects may include the removal of physiological constraints; new colonizations by species of warm-water affiliation, and persistence of founder populations, all of which will be facilitated by warmer climatic regimes in the North Atlantic, particularly in boreal/temperate regions (Carlton, 2000; Hulme, 2005). Some native and established non-native species from tropical/subtropical latitudes are also predicted to be driven polewards as temperatures become too warm for their survival and climatic regimes become suitable for the extension of their northern range boundaries. The thermal range of the region to which a species is native will determine thermal tolerances upon translocation, although local adaptation is to be expected in successful establishments. The impacts are likely to be manifested as increases in abundance, density, and distribution, and may be mediated by factors such as an extended breeding season, increased reproductive output, and increased survival.

In contrast, introduced species originating in cooler waters may be less likely to successfully colonize new regions if the thermal regime continues to rise above their upper pejus limits (*pejus* meaning “becoming worse”), beyond which the ability of animals to increase aerobic metabolism is reduced, or if low temperature thresholds for reproduction are not reached. Cold-water non-native and native species are likely to suffer in the warmer, lower-latitude parts of their introduced range as population abundance declines and local extirpation results in a northward retreat to cooler waters at higher latitudes.

Second-order results of changing abundance or new invasions will probably result in either further reductions or increases in the establishment of non-natives (J. T. Carlton, in prep.). Any increase in the abundance of native or established non-native species within a community can lead to fewer opportunities for new invasions through increased competition or predation. Similarly, increased competition and predation from increased numbers of resident non-native species, thermophilic native species, or new invasions, could result in a reduction in the abundance and distribution of already established non-native species (particularly susceptible may be cold-tolerant invaders, weakly competitive thermophilic non-natives, and susceptible non-native prey). Indirect climatic effects, such as shifts in the timing and

extent of primary production, may also affect the success of non-natives through changes in food provision (known as the match–mismatch hypothesis; Cushing, 1972, 1990) and the lack of, or reduction in, predators within the native community (known as the prey-release hypothesis; Edwards and Richardson, 2004). Native species have co-evolved with predators and competitors and may be less successful in new environments (Sorte *et al.*, 2010). Conversely, non-native species often arrive with few parasites or are less susceptible to native predators (Coulautti *et al.*, 2004; Torchin and Mitchell, 2004) and have life-history characteristics that favour their establishment, spread, and survival (Nyberg and Wallentinus, 2005).

Encompassed within the North Atlantic are warm and cold temperate marine biogeographic provinces, which are also subjected to environmental influences from subtropical areas, such as the Mediterranean and the Gulf Stream in the south, and boreal conditions deriving from the Arctic. Climate-driven change within the marine systems of the North Atlantic have often been recorded in the region of these major biogeographic breakpoints, where species of warm- and cold-water origins overlap and reach their respective limits of distribution (Mieszkowska *et al.*, 2006; Beaugrand *et al.*, 2009). Information on the ecological and biological mechanisms underpinning these changes in native species provides a basis for the prediction of the responses of non-natives from different thermal provinces within the major biogeographic regions.

If temperatures in Arctic waters, as predicted by models, continue to increase, environmental conditions may favour the introduction, survival, and establishment of non-native species from adjacent regions and between ocean basins. Seasonal transportation by ships in the Arctic is expected to increase significantly in the 21st century, owing to reduced sea ice, but Arctic voyages are expected to be overwhelmingly regional and not trans-Arctic by 2020 (Arctic Council, 2009; Bambulyak and Frantzen, 2009). Viability of the Arctic sea route will depend on the available navigable window and the extent and distribution of sea ice during summer/autumn in the 21st century (Somanathan *et al.*, 2009), as well as on a considerable reduction in the currently imposed fees for ice-breaking (Liu and Kronbak, 2010). Ballast-water treatment will be required by 2016 (but implementation may be slow for many ships), so impacts from non-native biota may be tempered, although hull fouling will continue to be an important route of transmission (Minchin and Gollasch, 2003).

Temperature is not the only environmental variable influenced by climate that will affect organisms. Ocean acidification may also affect the success of non-native species. A shift in the carbonate chemistry of seawater as a result of increased atmospheric concentrations of carbon dioxide is already occurring in the oceans (Doney *et al.*, 2009). This emergent field of research has demonstrated the deleterious effects of a reduction in the pH of seawater on general health, physiological processes, and the ability of calcareous species to form calcium carbonate structures such as shells oroliths (see Section 5). Currently, there is no field evidence that indicates any impacts from ocean acidification on natural populations or non-natives in the North Atlantic, but it is likely that the scenarios of a pronounced reduction in pH within the 21st century (Caldeira and Wickett, 2003; Blackford and Gilbert, 2007), in combination with elevated temperatures, may result in severe reductions in the fitness of marine species (Findlay *et al.*, 2009), including non-natives.

All of the above phenomena may result in important alterations to the structure and functioning of native marine communities, potentially disrupting key ecological processes and affecting the supply of goods and services to society. Additional

climatic factors, such as storm intensity and wave height, in addition to acidification, will also affect the role that non-native species play in ecosystem structure and functioning. Climate change may result in enhanced opportunities for non-native species (Figure 11.7) at each stage (introduction, colonization, establishment, and impact) of the invasion process (Maggs *et al.*, 2010), as well as for range-expanding native species.

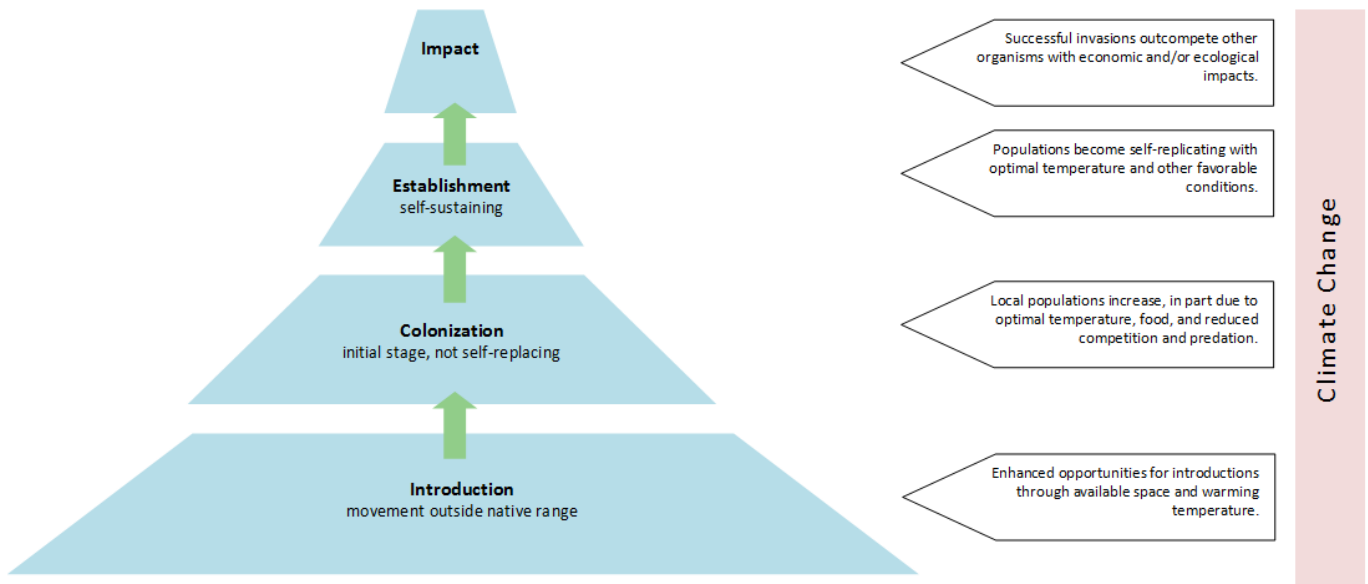


Figure 11.7. Stages in the sequential transitions of a successful invasion process. (Modified from Maggs *et al.*, 2010, and Walther, G. R., *et al.*, 2009.)

### 11.7 Future directions

Understanding the complexities of the impacts of multiple climate drivers on the invasion process requires an integrated approach, combining experimental and observational studies, which is currently not available for most invasions. One major challenge to documenting change is the need for data from many sampling sites over extended periods. This can be overcome to some extent by improving integration between research and monitoring projects across the Atlantic under a single umbrella. The Global Invasive Species Programme (GISP; closed March 2011) has applied an integrative approach by the centralized gathering of studies and information on non-native species from terrestrial, freshwater, and marine habitats (Wittenberg and Cock, 2001). This desk-based study highlights the problems currently facing countries with respect to the arrival of, and colonization by, non-native species, and it has produced a toolkit to assist nations in tackling invasive species problems. Such an approach demonstrates that international collaboration and integration of research programmes, including complementary standardized methodologies and data storage, centralized data archiving, data sharing, and dissemination to a wide international audience, can be achieved within a single, structured framework.

The new European Marine Strategy Framework Directive (MSFD) is a legislative framework for an ecosystem-based approach to environmental management that includes invasive species as a descriptor, with a requirement that “Non-indigenous species introduced by human activities are at levels that do not adversely alter the ecosystems” (Olenin *et al.*, 2010). Monitoring programmes and corrective measures

have to be put in place to achieve “Good Environmental Status” by 2020. Potential increases in the spread of invasive species resulting from climate change, and the difficulty of sampling and controlling ballast-water treatment, will make it difficult to achieve the deadline of 2020. Furthermore, the 2004 International Convention for the Control and Management of Ships' Ballast Water and Sediments is still awaiting signature, so the spread of new species via shipping is likely to continue for some time.

In July 2010, the US adopted recommendations for an ocean policy that identifies coastal and marine spatial planning (CMSP) as a framework for meeting the goals of protecting, restoring, and maintaining coastal and ocean resources, and the Great Lakes. The CSMP effort is designed to integrate a wide range of services, including identifying impacts of invasive species and adopting methods for their control and prevention (<http://www.whitehouse.gov/administration/eop/ceq/initiatives/oceans>).

Canada supports an ocean policy that focuses on healthy coastal and ocean ecosystems and, in addition, supports the Canadian Aquatic Invasive Species Network (CAISN), with the goal of providing scientific information to “influence the implementation of government policy, ensuring the regulation of preventive measures to minimize the spread of AIS in Canada’s aquatic ecosystems” ([http://www.nserc-crsng.gc.ca/Partners-Partenaires/Networks-Reseaux/CAISN-CAISN\\_eng.asp](http://www.nserc-crsng.gc.ca/Partners-Partenaires/Networks-Reseaux/CAISN-CAISN_eng.asp)).

Non-native micro-organisms and their potential invasive impacts are the most under-researched sector and must also be included in future non-native research programmes. In the past, their study and provenance have been complicated, owing to difficulties in determining their taxonomic status, but advances in molecular science are allowing progress in this field.

Long-term data on the presence and abundance of non-native species collected over large regions are necessary in order to determine what, when, how, where, and why colonization events occur, and to assess invasion risks across the North Atlantic. In addition, another option for increasing resources and gathering data on selected non-native species, especially near the limit of observed physiological ranges, is to employ “citizen scientists” to gather data (see box below). If networks of amateur naturalists are coordinated by professional organizations involved with the recording programmes for non-native species, and a robust quality assurance procedure is implemented, then citizen scientists provide a far larger network of observers and recorders than can be achieved within the scientific community alone.

## 11.8 Conclusions

The arrival of non-native species into the North Atlantic has, with rare exceptions, been independent of climate change until recently. However, evidence indicates that a few non-native species have expanded their range in response to rising temperature, although demonstrating the effects of climate change on the spread of non-native organisms in marine environments (cf. in terrestrial and aquatic habitats), and independent of spread during the invasion process, remains a challenge. Most of the studies in marine ecosystems focus on invertebrates and algae. A lack of techniques for defining speciation of native and non-native HABs and micro-organisms limits the understanding of impacts in the pelagic realm. Nevertheless, HAB species, one of the best-studied groups in the plankton, are not considered to be spread by humans and are only weakly associated with climate change.

Prior to the creation of *ICES Code of Practice* (ICES, 2005a) several non-native species were introduced to areas on the assumption that local temperatures were too low for reproduction and growth. For example, *Crassostrea gigas* and *Ruditapes philippinarum* are organisms that failed to reproduce well in areas that formerly experienced a colder climate and/or winter, but do so now. For example, the introduction of *Undaria pinnatifida* was based on an optimal temperature for growth rather than the range of temperature within which it survives. Determining a link between climate change and impacts may be tempered by the physiological responses of organisms; for example, *Codium fragile* subsp. *fragile* is a warm-water species that has adapted to cold waters and spread beyond its historically introduced range in the US.

Long-term community studies indicate that some non-native species appear to be benefiting from warmer temperature in the North Atlantic, with a shift in previously static distributions and an increase in the speed of range expansions. Compared with terrestrial species, marine species appear to be responding faster to climate change. In future, thermophilic non-native marine species are predicted to increase in biomass, density, and distribution within the temperate and southern boreal regions of the North Atlantic as warming continues, with the caveat that some native species will also increase and may retard the rate of change in non-native species. New invasions that would previously have been inhibited by temperature are also likely to increase in number.

As some species are driven northwards by rising temperatures, others in northern latitudes may experience local extirpation as temperatures become too high. Climate change may result in new pathways for the arrival of non-native species into the North Atlantic, with or without shipping as the vector of spread. Rising temperature and subsequent ice melt within the Northwest Passage will present a new route for vessel traffic and species migration through Arctic corridors.

At present, there is no evidence of any effects from ocean acidification on non-native species, but projected reductions in ocean pH are expected to affect many of them, with unknown consequences for their success, growth, or expansion/contraction.

Although there are several new national and regional policies and efforts directed at the prevention of new introductions, on-the-ground monitoring and enforcement of regulations remain understaffed and underfunded. An understanding of the role of anthropogenic influences as well as that of climate change is key to unravelling the primary drivers with respect to each species and invasion event. This information is essential to the development of the next generation of predictive ecological models which, by incorporating phenological responses and reproductive shifts to climate-driven environmental changes, can improve our understanding of the risks of non-native species in a changing environment. New tools are needed to translate the data collected from field studies and experimental observations, to identify species and country/region of origin through molecular probes, and to assess maps of past and present distributions, with information on vectors of spread, in order to identify which non-native species are enhanced or perturbed by climate change. Use of citizen scientists will benefit long-term studies for selected species and support scientific and taxonomic studies of non-native species and climate change.

More information is needed on the physiological responses of non-natives within their introduced range, together with knowledge of their potential for genetic adaptation. This will help us to understand why non-natives become an invasive problem in some areas but not others, and allow improved predictions of the scale of future impacts of established non-native species in response to increasing



temperatures and decreasing pH levels in the North Atlantic. Only then will it be possible to prioritize confidently the invasive species that should be removed, and to implement the best methods to ensure biosecurity within coastal regions of the North Atlantic.

Climate change and non-native introductions are two primary drivers of change within marine ecosystems, but tend to be studied in isolation. At present, there is insufficient information available to allow the quantitative assessment of the responses of non-native species to climate change, or to attribute climate change as a causal driver in many colonizations. An increase in detected arrivals of non-natives, coupled with an acceleration of the impacts of climate change on native species and communities, requires an integrative approach in order to document interactions between these two drivers and subsequent alterations to native biodiversity.

#### **Expanding non-native species surveys using citizen scientists**

The detection of new non-native species arrivals has been improved by using naturalists, students, college field classes, and divers (Lodge *et al.*, 2006; J. T. Carlton and J. Pederson, pers. comm.). In the US, the use of citizen scientists to assist with collecting data is not new, and it has been successful in terrestrial and aquatic environments and, more recently, in marine ecosystems (Delaney *et al.*, 2008; Crall *et al.*, 2010). Several New England non-governmental organizations and state-led initiatives have recruited citizen scientists to help identify the presence, abundance, and spread of non-native species in the New England region and to supplement observations by researchers and agencies (Salem Sound Coast Watch, Massachusetts Coastal Zone Management; <http://massbay.mit.edu/mitis/index.php>). The data provide valuable information on the spread of selected species, such as the seaweed *Grateloupia turuturu* and the sea squirt *Didemnum vexillum*. These data can be used to support policy decisions and the development of plans for managing non-native species. A citizen-based project enlisted over 1000 participants to assess the distribution of the Asian shore crab (*Hemigrapsus sanguineus*), the European green crab (*Carcinus maenas*), and native crab species from Long Island Sound to Maine (Delaney *et al.*, 2008).

The Marine Biological Association of the UK runs the “Alien Invaders and Climate Change Indicators” schools project in the UK. This project engages schoolchildren in the search for and recording of non-native species and promotes awareness of climate change within the national curriculum (<http://www.marlin.ac.uk/>).

A UK-wide Marine Aliens project is monitoring seven species within marinas and ports, namely: two brown algae, wakame (*Undaria pinnatifida*) and Japanese wireweed (*Sargassum muticum*); the green alga *Codium fragile* subsp. *fragile*; Chinese mitten crab (*Eriocheir sinensis*); Japanese skeleton shrimp (*Caprella mutica*); leathery sea squirt (*Styela clava*); and a colonial sea squirt (*Perophora japonica*). Several other species are also being monitored: the slipper limpet (*Crepidula fornicata*); zebra mussel (*Dreissena polymorpha*); Pacific oyster (*Crassostrea gigas*); Australasian barnacle (*Austrominius modestus*); a Pacific bryozoan, *Tricellaria inopinata*; the southern hemisphere solitary sea squirt *Corella eumyota*; and the compound sea squirt *Botrylloides violaceus*. Marine Aliens is a research project but also has recruited “alien detectives” to assist with the surveys in relation to climate change. Results are entered into the MarLIN website (<http://www.marlin.ac.uk/rml.php>).

Canada has launched an Invasive Alien Species Partnership Programme (IASPP) to encourage and fund amateur enthusiasts in the recording of non-native species

(<http://www.ec.gc.ca/eee-ias/default.asp?lang=En&n=A49893BC-0>). Transport Canada Marine, the Ontario Federation of Anglers and Hunters, and the Ontario Ministry of Natural Resources have joined forces to produce an information CD for recreational boaters entitled "Stop the Spread of Aquatic Invasive Species".

Although citizen monitoring programmes are not a substitute for bio-invasion research, the data provide the much-needed observations, over time and in numerous locations, that are required to document range expansions and to understand the relationships of such changes to climate variability. The efficiency and scientific validity of the data are supported from appropriately designed and executed citizen monitoring programmes (Delaney *et al.*, 2008).

### **Acknowledgements**

The authors thank the ICES Working Group on Introductions and Transfers of Marine Organisms (WGITMO), Marine Biodiversity and Climate Change Project (MarClim), UK Marine Climate Change Impacts Partnership, UK Marine Aliens Project, Don Anderson, Andrea Locke, Christine Maggs, and John Bishop for advice and information included in this section, and John Bishop, Graham Ledwith, and Richard Lord for use of photographic images.