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The invasive biology of the talitrid amphipod *Platorchestia platensis* in North West Europe

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Abstract

The talitrid amphipod Platorchestia platensis (Kröyer, 1845) is an invasive species which has been spreading along European coasts over the last 150 years. This paper will review what is known of the distribution of *P. platensis* to date, before discussing potential distribution methods, evaluating potential management strategies and providing a perspective on the future distribution of this species. Despite *P. platensis* having worldwide distribution, very little is known about its invasive history. It has been established that the most likely methods of dispersal for *P. platensis* are on currents and in ballast water, though further research is needed. Although dispersal on currents is unavoidable, heating ballast water provides a cheap, effective and environmentally friendly solution. Predictions of the future distribution of *P. platensis* can be made using demographic models or by studying genetic diversity and evolutionary changes for understanding the potential for colonisation, geographic patterns of invasion and the potential for evolutionary responses to novel environments.

Key words: *Platorchestia platensis*, invasive, Amphipoda, North West Europe, current transport, ballast water management.

Introduction

An invasive species can be defined as a non-indigenous species which adversely affect the ecosystems they invade economically, environmentally or ecologically, whose introduction causes or is likely to cause economic or environmental harm, reducing biodiversity (ISAC, 2006). In the past 40 years the rate of introductions and associated risks of biotic invaders have increased enormously because of human population growth, rapid movement of people and alteration of the environment. In addition to this, more goods and materials are being traded among nations than ever before, creating increased opportunities for unintentional introductions (Bryan, 1996; USBC, 1998). These marine invasive species restructure the food web, introduce diseases, compete with and prey on native organisms and destroy populations of commercially-valuable native species. This paper will focus on the invasive, semi-terrestrial talitrid (*Crustacea: Amphipoda*) *Platorchestia platensis* as current literature suggests it has spread along the European coast outcompeting native species, reducing the diversity of amphipods in this ecosystem. This results in excess strandline as *P. platensis* do not break down the wrack as efficiently, negatively affecting aesthetics and tourism whilst altering the balance of nutrients available for use by other organisms in the intertidal ecosystem.

This paper will review what is known of the distribution of *P. platensis* to date. This will be done by discussing the species origin and its invasive history, before critically evaluating potential distribution methods of the invasion, suggesting potential management strategies to minimise dispersal and provide a perspective on the likely future distribution of this species.

Origin

Originally found in Uruguay, it is unclear whether *P. platensis* originated from here as the site is close to the international port of Buenos Aires, which played an essential role as the main connecting port for goods between the New World and Europe (www.nileguide.com). *P. platensis* is therefore a cryptogenic, cosmopolitan species distributed both in temperate and tropical regions around the world (Behbehani & Croker, 1982); North Western Europe (Dahl, 1946), South America (Stebbing, 1906)**,** Bermuda (Kunkel, 1910), India (Chilton, 1921), Hawaii and other Pacific Islands (Stephensen, 1935), extended to the Swedish west coast (Backlund, 1945; Dahl, 1946; Karlbrink, 1969) Japan (Ruffo, 1949; Morino, 1978), the Canary Islands (Andersson, 1962), Atlantic coast of Canada and the USA and the West Indies (Bousefield, 1973), Korea (Jo, 1988) Israel (Morino & Ortal, 1995), Uruguay (Serejo & Lowry, 2008) and Poland (Spicer & Janas, 2006).

Invasion

In the last 100 years anthropogenic introduction of alien species in freshwater, estuarine and coastal areas has become an increasing problem (Carlton, 1989) often resulting in the competitive displacement of native species (Nichols *et al*., 1990; Pinkster, *et al*. 1992; Cohen *et al*., 1995). *P. platensis* has been found to co-exist with *Orchestia gammarellus* often out competing it (Backlund, 1945; Dahl, 1946; Persson, 2001; Bock, 1967) by enduring lower salinities (Persson, 2001), up to 30% water loss (Morritt & Spicer, 1998) and is a more active jumper than *O. gammarellus* so is probably better at escaping from predators (Karlbrink, 1969). *P. platensis* also has a higher rate of reproduction due to a longer period of reproduction, higher rates of development and larger broods for females (Dahl, 1946). Classically, factors like resource exploitation, interference competition, predation and hybridisation have been proposed as mechanisms causing exclusion or displacement. Dick *et al.* (1993) have suggested that differential cannibalism and mutual predation have caused replacement of an indigenous freshwater amphipod. However, the outcome of the interactions between introduced and native species may also be balanced by environmental factors, giving different results in different areas (Dick *et al*., 1997; Dick & Platvoet, 2000). Despite this invasive species having worldwide distribution very little is known about its invasive history (Iwasa, 1939; Backlund, 1945; Dahl, 1946; Persson, 2001) and it is unclear as to the methods of invasion. Below the potential transport methods and management strategies for each will be critically discussed before presenting a holistic view of the factors affecting future distribution of this species in North West Europe.

Potential transport methods

As with many terrestrial and semi-terrestrial amphipods, dispersal capacity is naturally low (Friend & Richardson, 1986) although unlike other *Talitridae*, *P. platensis* has been observed in a variety of habitats; wrack beds, pebbly shores, sandy shores, estuaries, salt marshes, beneath dead leaves on the upper shore (Persson 2001; Karlbrink, 1969) and in coastal defences on the upper shore (Spicer, 2010) which increase the chances of secondary dispersal by different means. The main natural vectors known to mediate passive dispersal of aquatic invertebrates are waterfowl (Green & Figuerola, 2005), wind (Vanschoenwinkel *et al.,* 2008a), amphibians (Bohonak & Whiteman, 1999), aquatic insects (Van de Meutter *et al.,* 2008), mammals (Vanschoenwinkel *et al.,* 2008b; Waterkeyn, unpublished data), water connections (Michels *et al.,* 2001; Hulsmans *et al.,* 2007) and human-mediated dispersal which includes all means of transport of pets, livestock, human equipment and food (Wichmann *et al.,* 2008).

Previous research on human dispersal of aquatic invertebrates focused primarily on ship-mediated vectors (Ruiz *et al.,* 2000; Havel & Shurin, 2004; Bailey *et al.,* 2005; Panov & Ca´ ceres, 2007) ignoring other human activities such as management and maintenance of ponds, lakes, ditches and streams, recreational activities in and around water bodies (hiking, swimming, etc.) and research. Waterkeyn, *et al.,* (2010) demonstrates that dispersal via footwear and motor vehicles may also play a major role in the dispersal of aquatic invertebrates. This section will discuss the major potential transport methods, these being dispersal by currents, ballast water, wild bird migration and livestock transportation.

Current carried wrack

Karlbrink (1969) stated that *P. platensis* ‘clings tenaciously to anything floating and this behaviour may be responsible for its secondary dispersal’. As labelled on Figure 1 the most likely route of transport for *P. platensis* from Oresund Bay along the Swedish coast to Southern Norway and along the German and Swedish coasts in to the Baltic Sea is by currents. These currents could carry *P. platensis* floating on rafts of seaweed along the coast (Stock & Beimbaum, 1994). Karlbrink (1969) found that southerly currents dominate for most of the year in the Baltic Sea hampering the dispersal of *P. platensis* northward along the Swedish Baltic coast. This was expanded upon by Persson (2001) who mapped the distribution of *P. platensis* demonstrated in Figure 2. However, this theory does not account for Wildish & Lincoln’s (1979) finding of *P. platensis* in the Thames Estuary, United Kingdom, nor

Hartog's (1963) findings in the Dutch Wadden Sea, Netherlands, as the North Seas currents do not flow south westwards from Scandinavia.

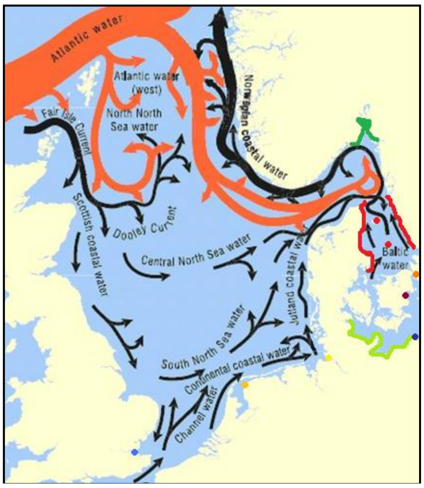

Figure 1: The distribution of *P. platensis* around North West Europe chronologically from dark red (1860), through red (1940), dark orange (1960), orange (1960), yellow (absence of *P. platensis* 1960), light green (1967), dark green (1980), light blue (1977 and 2010) to dark blue (2005). See Appendix 1 for more information. Currents weighted for magnitude of transport. Adapted from: www.safetyatsea.se [Last accessed: 15/11/10 1454].

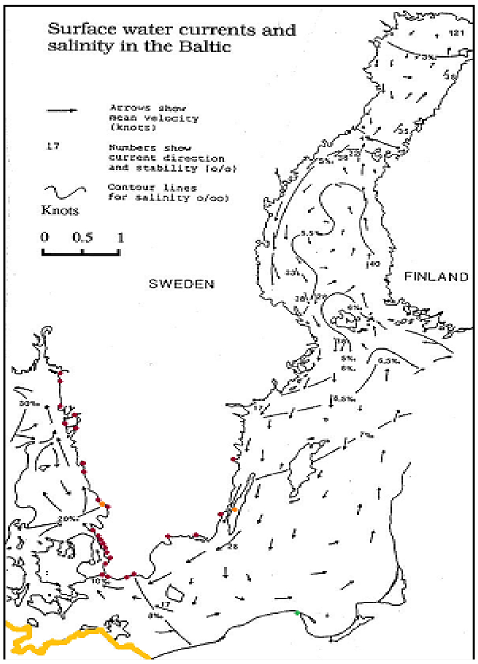

Figure 2: The distribution of *Platorchestia platensis* in the Baltic Sea. Points coded: Red shows the distribution of *P. platensis* 1995- 1996 in Sweden (Persson, 2001), Orange shows the limits of *P. platensis* distribution found by Karlbrink (1969), yellow shows the presence of *P. platensis* on the German Baltic coast (exact locations unknown), (Dahl, 1946; Wolff, 2005; Bock, 1967) and green shows the presence of *P. platensis* in Poland (Spicer & Janas, 2006). Adapted from: www.balticuniv.uu.se [Last accessed: 05/01/11 1742].

Ballast water

Karlbrink (1969) also said that ballast water is the most likely vector of transport, which would be the most logical transport method to the Dutch Wadden Sea and the Thames Estuary (see Fig. 1) as both these sites are in close proximity to international ports. Ocean going ships carry seawater as ballast that is taken on in port and released at subsequent ports. Most taxa with a planktonic phase in their life cycle have been found in ballast water, as were all major marine habitat and trophic groups (Carlton & Geller, 1993). Presence of taxonomically difficult or inconspicuous taxa in these samples suggests that ballast water invasions are already pervasive (Carlton & Geller, 1993). The high salinity tolerance of *P. platensis* is thought to have allowed it to survive ballast changes both mid ocean and in coastal waters (Lacey, unpublished). Persson (2001) demonstrated that *P. platensis* had an LT50 value (mean time taken for 50% of population to die) of 15-22 days in low salinity of 0.5ppt, showed no mortality after 5 days in high salinity of 51ppt and had an LT50 value of 117 hours in 35ppt. For example, in the Dutch Wadden Sea, the port of Gemeente Harlingen, a site where *P. platensis* is present, has a large fishing fleet, many inter-island ferries and numerous container ships (see Fig. 3) which deliver 1 million tonnes of commodities annually (www.harlingen.nl) which could unknowingly transport *P. platensis*. However, although this method would provide a clear link between primary and secondary sites of *P. platensis*, further research is needed into whether *P. platensis* is present further east along the Dutch coast to support or refute this theory.

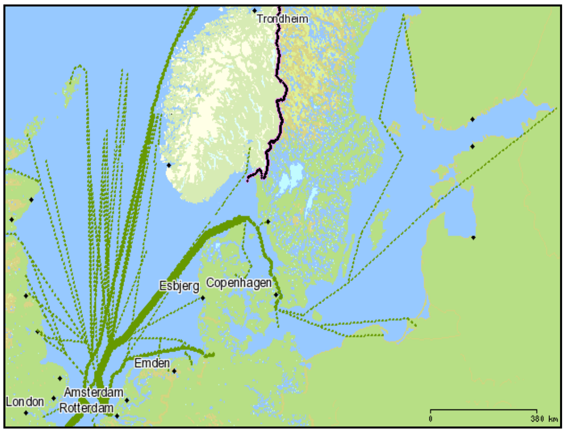

Figure 3: Shipping routes in the North Sea and Baltic Sea. The green lines of different thickness represent the usage of the routes per year (thick: 201-588 ships, medium: 51-200 ships and thin: 0-50 ships). Available [online]: http://maps.safetyatsea.se/ [Last accessed: 07/01/11 15:52].

Wild birds

Green and Figuerola (2005) said birds may have a major role in the expansion of exotic species. Frisch *et al.* (2007) found that many species present widespread distributions consistent with dispersal by migratory water birds, indicating that bird-mediated passive transport of aquatic invertebrates is a frequent process in the field, both via endozoochory (internal) and ectozoochory (external) transport. Northward dispersal of aquatic propagules by endozoochory during spring migration is a frequent process in the northern hemisphere (Green *et al.,* 2002). Dahl (1946) stated that amphipods leap onto birds, seeking protection among the feathers and get dispersed passively along migratory routes. A similar view is held by Segerstrale *et al.* (1954) as cited by Hurley (1968).

Although Darwin pioneered the study of long-distance dispersal (LDD) of aquatic invertebrates via water birds, it remains in its infancy and the characteristics of the dispersed and the disperser species that facilitate such transport remain largely un-investigated (Figuerola & Green, 2002). A handful of recent studies have quantified internal and external transport in the field, confirming that a variety of long distance migrants carry invertebrates both internally and externally. These studies show that variation in the morphology of vectors influences the frequency and size of propagules transported, and suggest that more invertebrate groups disperse via birds than was previously thought (Green & Figuerola, 2005; Frisch *et al.,* 2007). Green *et al.,* (2005) carried out the most extensive field demonstration to date that invertebrates can disperse readily, via gut passage through birds. We expect that the spatial and temporal scales at which dispersal limitation constrains geographical ranges, species richness and genetic structure of invertebrates depends partly on the density of migratory birds using the area.

Livestock

P. platensis could either be ingested by or transported on grazing livestock which are then transported elsewhere by land or sea and/or defecate elsewhere allowing secondary dispersal (Spicer, 2010). Vanschoenwinkel (2008b) demonstrated that large mammals such as wild boar can act as dispersal vectors of aquatic invertebrates at a local scale and suggest that external transport may be quantitatively more important than internal transport. As wallowing (mud bathing) is common in many terrestrial mammals, this mode of dispersal may be quite widespread.

Potential management strategies

Based on past experiences management strategies have been tried and tested for optimum results for minimum cost. In this section, potential management strategies for the future restriction of the dispersal of invasive species, in this case the amphipod *P. platensis* will be discussed.

Currents

The dispersal of invasive species on ocean currents or circulation gyres cannot be managed other than to monitor rates of dispersal and the success of secondary populations along the coastline. One management strategy would be to remove strandline from beach. However, this may have a much greater impact than the arrival of the invasive species as nutrients key to other organisms would be removed from the intertidal ecosystem.

Ballast Water

The accelerating rate of dispersion of exotic aquatic species on a global scale has prompted a need to develop methods to treat ballast water which are fully effective, safe, practicable, financially viable and environmentally friendly. Treatment options that have been trialled include ballast exchange at sea (Rigby & Hallegraeff, 1994), sterilisation with hydrogen peroxide (Ichikawa *et al.,* 1992, Bolch & Hallegraeff, 1993), electric shock (Montani *et al.,* 1995), de-oxygenation (Mountfort, 1997), high speed microfiltration (Cangelosi, 1997) and heat treatment (Bolch & Hallegraeff, 1993, Yoshida *et al.,* 1995).

Of these options, ballast water exchange is only partially effective (Hallegraeff & Bolch, 1992) and there are no efficient monitoring protocols within the shipping industry other than the inspection of ship log books which can be falsified. Most forms of chemical treatment would lead to unacceptable environmental problems wherever the water was discharged. Moreover, hydrogen peroxide which degrades in to innocuous water and oxygen. It has also been ruled out as it is too expensive, costing £320, 620 per ship per trip (Rigby *et al.,* 1993). Similarly, electric shock treatment, envisaged to be applied to ballast water outlets (Montani *et al.,* 1995), has been discarded as an option as laboratory experiments showed it was local heat generation and/or free chlorine, and not electricity that were responsible for mortality (Hallegraeff *et al.,* 1997). De-oxygenation of ballast tanks would not kill dinoflagellate cysts nor many benthic marine invertebrates (Mountfort, 1997), while research to apply high speed microfiltration to ballast water may not be successful for dinoflagellates or their cysts because of limitations imposed by the 50 and 100pm screens used (trials with 20pm screens suffer from clogging) (Cangelosi, 1997).

In contrast, heating ballast water may provide an effective environmentally friendly solution. It would involve a once-only cost to modify ship engineering designs, would indiscriminately eliminate a wide range of marine organisms (without the need for monitoring of target organisms in ballast water), and would not pose any environmental hazards as associated with chemical treatment, nor create any ship's safety hazards as posed by mid-ocean ballast water exchange (Rigby *et al.,* 1993). A careful assessment of various waste heat sources on the BHP bulk carrier 'Iron Whyalla' has confirmed the practicability of this approach, and a pilot heat treatment plant was successfully trialled onboard in April 1997, achieving temperatures of 37-38.4ºC after 24-30 hours (Rigby *et al.,* 1997). The precise physiological mechanism underlying the effectiveness of this comparatively mild heat treatment is not completely understood, but mortality is most likely due to a loss of cellular organisation rather than protein inactivation or disruption of membrane integrity (Brock & Madigan 1994).

Wild Birds

There is a particular need for more quantitative studies of LDD by birds that will enable modellers to assess its role in maintaining invertebrate biodiversity among increasingly fragmented wetlands and in the face of climate change, as well as in the spread of invasive species (Green & Figuerola, 2005). Much more systematic fieldwork and reanalysis of the existing data sets (e.g. from diet studies) are needed before the relative roles of various water bird species as dispersers can be fully assessed (Green *et al.,* 2002).

Livestock

The research on livestock as vectors of secondary dispersal of marine invertebrates by endozoochory and/or ectozoochory is sparse. Therefore until further research has been carried out to assess the extent to which grazing of livestock in the intertidal zone affects the transport of invasive species such as the amphipod *P. platensis* to other areas, no management strategy can be enforced. Once this has been done it may be viable to restrict grazing in areas where invasive species such as *P.*

platensis is present or rinse livestock prior to transportation in order to remove mud from coats and feet which carry flora and fauna propagules (Vanschoenwinkel *et al.,* 2008b), including those of invertebrates such as *P. platensis*.

Future distribution patterns

It is important to study and predict the spatial and temporal distribution patterns of invasive species in order to guide management decisions regarding where to allocate resources for detection and prevention. Unfortunately, traditional invasion paradigms are derived exclusively from terrestrial studies so a new conceptual framework is needed to understand aquatic invasions (Ricciardi & MacIsaac, 2000).

Contributions from the field of population biology hold promise for understanding and managing invasiveness; invasive species also offer excellent opportunities to study basic processes in population biology. Life history studies and demographic models may be valuable for examining the introduction of invasive species and identifying life history stages where management will be most effective. Evolutionary processes may be key features in determining whether invasive species establish and spread. Studies of genetic diversity and evolutionary changes should be useful for understanding the potential for colonisation and establishment, geographic patterns of invasion and range expansion, lag times, and the potential for evolutionary responses to novel environments, including management practices. The consequences of biological invasions permit study of basic evolutionary processes, as invaders often evolve rapidly in response to novel abiotic and biotic conditions and native species evolve in response to the invasion (Sakai *et al.,* 2001). Quantitative methods can now also be used to predict which species are probable invaders (Kolar & Lodge, 2001). Although restricted to few taxa, studies reveal clear relationships between the characteristics of releases and the species involved, and the successful establishment and spread of invaders. These promising quantitative approaches should be more widely applied to allow us to predict patterns of invading species more successfully (Kolar & Lodge, 2001).

In the case of *P. platensis* it has been established that the most widespread methods of dispersal are on currents and in ballast water. Without a better knowledge of the bird species which act as vectors to *P. platensis* and their migration patterns or transport routes of livestock, it is difficult to predict how these will affect the future distribution of the invasive species in question.

Currents

Using current strength and direction data from The Baltic University Programme (www.balticuniv.uu.se) and a European Union funded project called the Interreg North Sea Region (www.safetyatsea.se/), rough predictions can be made as to where *P. platensis* could spread to (see Fig. 4). However, this does not necessarily lead to successful colonisation of a secondary population.

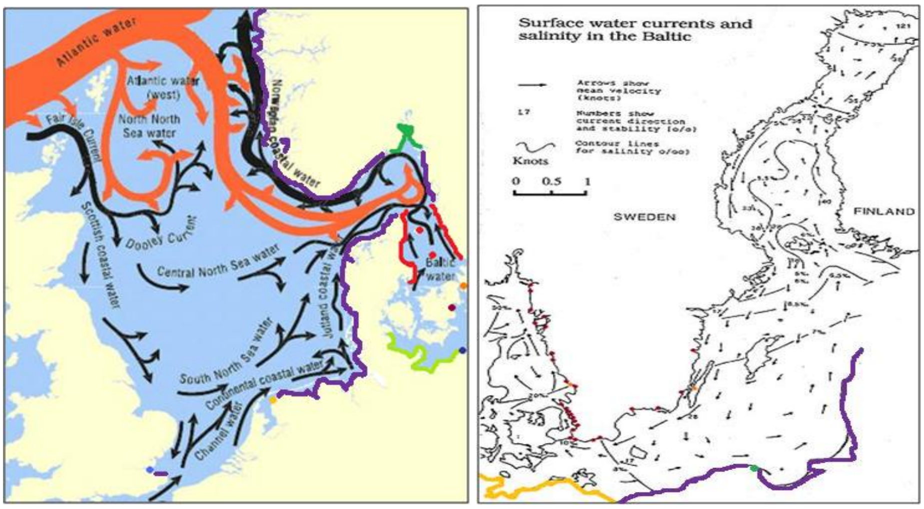

Figure 4: Showing currents weighted for magnitude of transport, distribution of *P. platensis* around North West Europe chronologically from dark red to dark blue with except purple lines showing the possible future distribution of *P. platensis* in the North Sea (left) and Baltic Sea (right). Left: Adapted from: www.safetyatsea.se/webedit_images/2979_original.gif [Last accessed: 15/11/10 1454]. Right: Adapted from: www.balticuniv.uu.se [Last accessed: 05/01/11 1742].

Ballast water

Ballast water transport is hard to predict, however studies such as that carried out by MacIsaac *et al.,* (2002) demonstrate the use of invasion models in the Great Lakes, Canada to explore long distance invasions mediated by the discharge of contaminated ballast water by ships. These aquatic invasion models can then be used to develop models with predictive capabilities in forecasting the spread of *P. platensis.* In the North Sea and Baltic Sea there are numerous shipping routes (see Fig. 3), any of which could inadvertently transport invasive species in their ballast water.

Climate change

In addition to this environmental factors such as climate change causing sea level rise could result in the local extinction of *P. platensis* in many areas around North West Europe (see Fig. 5). *P. platensis*, as already discussed, is an intertidal amphipod so would be vulnerable to this. Figure 6 shows the heights of sea level rise in North West Europe based on the model SRTM30 PLUS v. 2.0, which corresponds closely to the current distribution of *P platensis*. This could be because the beaches *P. platensis* favours are more dissipative with a lower gradient for easier access and less energy expenditure to reach the spring strandline.

Climate change also leads to increased frequency and magnitude of storm events, displacing *P. platensis* higher up the shore. This can lead to increased genetic diversity as demonstrated in Japan where *P. platensis* was displaced up shore and evolved into a new species, *P. japonica* (Spicer, 2010). To conclude, increased storminess and sea level rise will both alter the distribution of *P. platensis* populations but on different time scales.

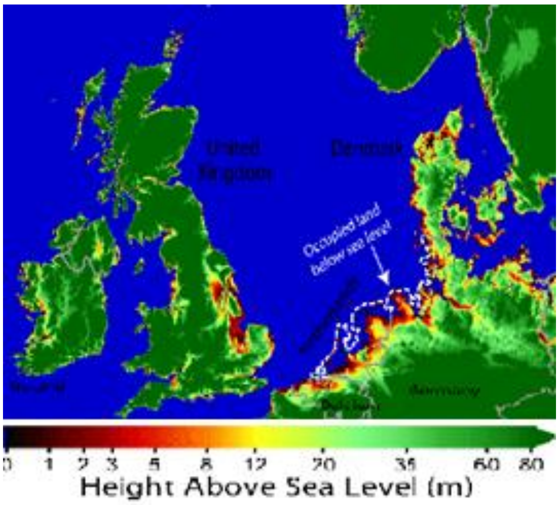

Figure 5: Map showing the areas of coastline in the North Sea which will be affected by sea level rise. Available [online]: www.globalwarmingart.com/wiki/File:North_Sea_Sea_Level_Risks_png [Last accessed: 22/11/10 1652]

Conclusion

Despite this invasive species having worldwide distribution very little is known about its invasive history (Iwasa, 1939; Backlund, 1945; Dahl, 1946; Persson, 2001) and the methods of dispersal are unclear. It has been established that the most widespread methods of dispersal for *P. platensis* are on currents and in ballast water. However, further research needs to be carried out to gain a better understanding of their transport processes. Although dispersal on currents is unavoidable, heating ballast water with waste heat onboard provides a cheap, effective, environmentally friendly solution. Predictions of the future distribution of *P. platensis* can be made using demographic models for examining the introduction of invasive species, using data such as current strength and direction, shipping routes and predicted sea level rise. Studies of genetic diversity and evolutionary changes could also be useful for understanding the potential for colonization and establishment, geographic patterns of invasion and range expansion, lag times, and the potential for evolutionary responses to novel environments, including management practices (Ricciardi & MacIsaac, 2000; Sakai *et al.,* 2001).

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