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Research Article

Present distribution and possible vectors of introductions of the alga *Heterosiphonia japonica* (Ceramiales, Rhodophyta) in Europe

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Abstract

In order to trace the introduction history of the western Pacific species *Heterosiphonia japonica* to and within Europe, information on distribution pattern of the species in Europe, oyster import and shipping activity has been compiled and analyzed. Additionally survival of fragments of *H. japonica* during a simulated journey in ballast water from Asia (Korea) to Europe (France) has been observed. The species was first recorded in Europe near an oyster culture area in Brittany (France) in 1984. Since then, it has spread quickly in Europe. The first introduction into Europe and secondary dispersal in southern Europe has most likely been trough movement of the Pacific oyster *Crassostrea gigas*. However, survival of *H. japonica* in temperatures varying from 14 to 28 degrees during a simulated 28-days journey in ballast water was demonstrated, and an introduction by ships from the Pacific Ocean may thus be considered as possible. Spreading of the species in the North Sea area and Scandinavia is most likely due to transport by ships, e.g. as attached to ships hulls, as fragments in ballast water or entangled e.g. in fishing gear.

Key words: ballast water, *Heterosiphonia japonica*, introduced species, introduction vector

Introduction

Spreading of marine species across natural barriers by human–mediated means is an increasing problem. An overview published in 2006 reported a total of 664 non-indigenous marine species (NIMS), including brackish water species, in European and adjacent waters (Gollasch 2006). The highest rate of arrival of NIMS to European and adjacent waters is seen after 1950 (Gollasch 2006).

Reise et al. (1999) sorted the introductions of NIMS to the North Sea according to the most likely vector for introduction. Before 1940 more than half of the introductions to the North Sea probably were by ship, while more than half of the introductions most likely have been through aquaculture after 1940 (Reise et al. 1999). According to Gollasch (2006) the main vectors for introductions of marine species to European and adjacent waters have been ships (400 species), the Suez Canal (253 species) and aquaculture (251 species). Ships have carried boring organisms (wooden ships), organisms attached to their hull or associated with ballast sand or rock, or in the ballast water. Many NIMS have been intentionally introduced in order to cultivate the species, which has subsequently resulted in establishment of viable populations outside the cultivation areas. A great number of NIMS have also come to Europe associated with introduced species for cultivation. In particular, the extensive import of Pacific oysters has resulted in many NIMS in the North Sea (Reise et al. 1999; Maggs and Stegenga 1999).

Macroalgae constitute an important group of NIMS. According to Hewitt et al. (2007), the highest numbers of accidentally introduced macroalgae are found in the Mediterranean and in Australia and New Zealand waters (90 and 99, respectively), followed by the northeast Atlantic (38). Ballast water and aquaculture are considered to be important ways for introduction of macroalgae, in addition to hull fouling (Hewitt et al. 2007).

The first European observation of the Pacific red alga *Heterosiphonia japonica* Yendo was in France (Brittany) in 1984 (Verlaque and Cabioch, pers. comm.) (Annex 1, Figure 1). It is now widespread in Europe. Yendo (1920) described two varieties of the species from Japan; *Heterosiphonia japonica* f. *nipponica* with four pericentral cells and *Heterosiphonia japonica* f. *pacifica* which has four or five pericentral cells. According to Choi (pers. comm.) the former variety is the species present in Korea and Europe. Recent genetic studies show that *H. japonica sensu* Choi et al. (2002) most likely is misplaced in the genus *Heterosiphonia* (Choi et al. 2002). Spanish, French (Atlantic and Mediterranean) and Norwegian material of *H. japonica* has been shown to be genetically similar to *H. japonica sensu* Choi et al. (2002) from Korea (Bjærke 2004).

The vector for the introduction of *H. japonica* to Europe from Asia remains unknown, but imports of oysters from The Pacific to Europe has been suggested (Maggs and Stegenga 1999). *H. japonica* may e.g. have grown on oyster shells of half grown or adult oysters, or on empty shells on which oyster spat have been set. Here, two possible ways by which *H. japonica* may have spread to Europe from the West Pacific will be considered; import of oyster from the Pacific and transportation in ballast water. In addition, an attempt will be made to trace the subsequent spreading pattern and possible vectors for secondary spreading inside Europe.

Methods

Geographical survey of Heterosiphonia japonica

In order to trace the establishment of *H. japonica* in Europe information from different sources has been compiled: publications, responses to a request made through the ALGAE-L e-mail list, which reaches a great number of European phycologists (see http://www.seaweed.ie/), and information from other sources. Care was taken to ensure that all non-published information about distribution of *H. japonica* is correct; e.g. by only including verified registrations of *H. japonica*, or collecting preserved samples or pictures showing characteristic features of *H. japonica* from the information sources. Based on the collected information the time of first recordings and spreading of *H. japonica* in various countries in Europe have been established.

Assessment of introduction vectors of Heterosiphonia japonica

In order to examine oyster import from the Pacific as a possible vector for introduction of *H. japonica* to Europe, information about time periods and places for imports of Pacific Oysters (*Crassostrea gigas*) has been compiled. Also, transport of oysters within Europe as a possible vector for secondary introductions has been examined. The overview has been based on information from available publications.

Boat traffic to and within European waters was assessed as a possible alternative vector for the introduction of *H. japonica* to Europe, and for subsequent spreading within Europe. *H. japonica* may be transferred by boats in different ways, e.g. by ballast water, growing on the hull or e.g. ropes, or entangled in fishing nets. Ships are most likely to function as vector for introduction along busy traffic lines. In order to get an overview of boat traffic to and within European waters the web site Sailwx (http://www.sailwx.info/) was used, which collects weather reports from ships and stores positions. The collection of ship positions by this web site will account for about 2-3 % of the total boat traffic according to the web master of the web site. Positions may be under-reported close to harbours or along busy shipping areas.

In order to test survival of *H. japonica* under conditions resembling those in ballast water a laboratory experiment was conducted, simulating a journey from South Korea to Le Havre, France, through the Suez Canal. Fragments of uniseriate small side branches (pseudolaterals) of *H. japonica*, 1-2 mm long, were put in two round glass beakers (6 cm high and 10 cm wide) filled with natural seawater, with 25 fragments in each. In addition, two 5-7 cm long shoots of *H. japonica* were kept in seawater in two separate beakers. The shoots and fragments were kept in total darkness in a temperature-regulated room for 28 days, which would be a normal duration for a bulk boat from Korea to Le Havre (according to the APL Asia-Europe timetable for the CEX China Europe Express). The temperature in the room was gradually increased

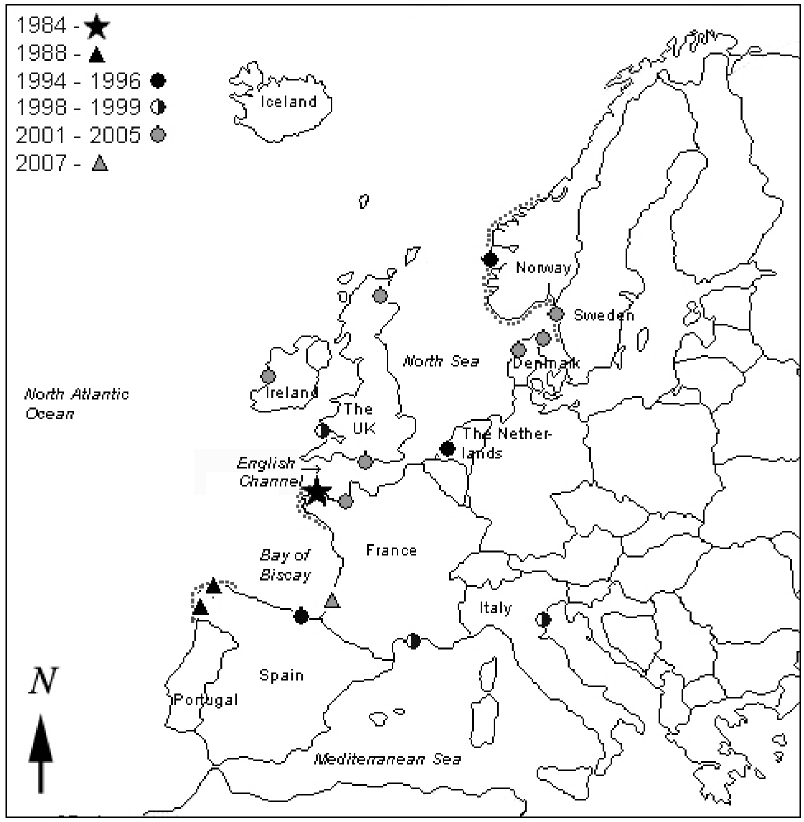

Figure 1. Sites of first observations of *Heterosiphonia japonica* in different countries of Europe. Symbols show year or time periods during which observations were made. The site of the first observation in Europe is shown by a star. Dotted lines show coast lines where more or less continuous distribution has been observed. A detailed description of localities is provided in Annex 1.

Table 1. Overview of main import events of exotic oysters to Europe (country or region) from the Pacific (origin). Year or period for imports is given, main periods in brackets. The information is compiled from: 1) Boudry et al. 1998; 2) O'Foighil et al. 1998; 3) Wolff and Reise 2002; 4) Ruesink et al. 2005 and references therein; 5) Grizel and Héral 1991; 6) Mann 1983; 7) le Borgne and Le Pennec 1983; 8) Drinkwaard 1999; 9) Nehring 2006.

Species	Country or region	Origin	Year (and main period)	Imported as	References
Crassostrea angulata (= *C. gigas*? 1), 2))	Portugal	Taiwan 1), 2)	< 1819	Probably growing on ship's hull	3)
Crassostrea gigas	Portugal	USA (west)	1977		4)
Crassostrea gigas	France, Mediterranean	Japan	1971-1976 (1971-1975)	Spat (cultchless or set on shells)	5)
Crassostrea gigas	France, Bay of Biscay	Japan	1971-1977 (1971-1975)	Spat (cultchless or set on shells)	5)
Crassostrea gigas	France, Brittany	Japan	1971-1976 (1971-1975)	Spat (cultchless or set on shells)	5)
Crassostrea gigas	France	British Columbia, Canada	1971-1975 (1971-1973)	Adult oysters	3), 5)
Ostrea denselamellosa	France	Korea	1982?		6)
Ostrea denselamellosa	France, Normandie	Japan	1982	Adult oysters	7)
Saccostrea commercialis	Italy	Australia	1985		4)
Crassostrea gigas	UK	Canada (west)	1926		4)
Crassostrea gigas	UK	USA (west)	1965-1979		4), 8)
Crassostrea gigas	Netherlands	Canada, USA (west)	1964-1981		4), 8)
Crassostrea gigas	Netherlands	Japan	1966		8), 9)
Crassostrea gigas	Denmark	USA (west)	< 1986		4)
Crassostrea gigas	Norway	USA (west)	1985		4)

from 18°C to 29°C during the first 14 days and thereafter gradually lowered to 14°C during the next two weeks, by following the temperature surface isolines of a random day in November (30 November 2006) through the ship's simulated journey. Data on isolines were achieved from the Space Science and Engineering Center, University of Wisconsin-Madison, USA (http://www.ssec.wisc.edu). The maximum change in temperature during a 24-hour period was 3 degrees throughout the experiment. When completing the experiment the survival of shoots and fragments of *H. japonica* was examined. Survival was estimated by degree of pigmentation. If fragments had a normal red pigmentation the tissue was considered to be alive. Surviving uniseriate fragments on the bottom were counted. Surviving thallus parts and uniseriate fragments were afterwards kept in culture (sterile seawater (33 PSU with no nutrients) in 14°C and a photon fluence rate of around 25 $\mu Em^{-2}s^{-1}$. Development was checked after 14 and 21 days, in order to see if normal growth occurred.

Results

Distribution of H. japonica in Europe

A survey of information on the first registrations of *Heterosiphonia japonica* in various countries in Europe is shown in Annex 1 and Figure 1. Some years after the first registration in Europe in 1984 (Bretagne, France) the species was found in Galicia (NW Spain, 1988). During 1994-1996 it was discovered in Zeeland, The Netherlands, on the southwest coast of Norway (Hordaland) and in the Bay of Biscay (Bilbao, Spain). During 1998 and 1999 it was found at two places in the Mediterranean, in the Thau lagoon in France and in the Venice lagoon in Italy, and it was also recorded in Wales, the UK. During 2001-2005 *H. japonica* was recorded in several places in the UK and Ireland, and also in Denmark and Sweden. The most recent recording (2007) is in the Bay of Biscay, from Arcachon, France. *H. japonica* has spread very rapidly around the Norwegian south coast since it was first recorded on the southwest coast (Figure 1). The species has spread along the coast of Galicia after 1988, and in France it has been found along the coast of Brittany (Annex 1, Figure 1). In Brittany it was recorded at 7 of 10 maërl beds during 2003-2005 (Annex 1). *H. japonica* has also spread southwards along the coast of west Sweden since 2002, while in the Mediterranean it has not been reported to spread outside the areas of the first registration in 1998 and 1999 (Annex 1). *H. japonica* may of course be present in many areas from where we have no reports. However, it is probably not yet present in Iceland (K. Gunnarsson, pers. comm.) or in south Spain (C. Pena-Martín, pers. comm.), and it is not mentioned in a recent overview of introduced marine species in Belgium (Kerckhof et al. 2007).

Gametophytic specimens are readily obtained in culture (Bjærke and Rueness 2004), but seem to be very rare in nature. Examinations of *H. japonica* samples in Norway have only shown vegetative or tetrasporophytic specimens (Husa and Sjøtun 2006). Gametophytes have been found in Roscoff, France (1984), Galicia, Spain (2004, 2005 and 2008) and in The Netherlands (2004) (Annex 1; M. Verlaque and J. Cabioch, pers. comm., H. Stegenga, pers. comm.). Gametophytic specimens from Galicia are placed in the SANT-Algae herbarium, University of Sanitiago de Compostela.

Oyster import as vector

Many of the sites of the first observation of *Heterosiphonia japonica* in Europe are situated near areas with oyster farming (Annex 1). In order to examine if the import of Pacific Oysters is a possible vector for introduction of *H. japonica* into Europe, information from Ruesink et al. (2005) and others about main introductions and import events were summarized (Table 1). The first introduction of *Crassostrea* into Europe may have taken place from Taiwan, as a fouling organism on ships's hull before 1819 (Wolff and Reise 2002). In more recent time, imports of Pacific Oysters from the west coast of the USA and Canada to Portugal, the UK, The Netherlands, Denmark and Norway have taken place between 1926 and 1986 (Table 1). In 1966 Pacific Oysters were imported from Japan to The Netherlands, and between 1971 and 1977 an extensive import of *Crassostrea gigas* took place from the Pacific to France. During 1971-1975 adult oysters were imported from British Columbia, Canada, and were directly planted in the sea at several places in France (Grizel and Héral 1991). During 1971-1977 large amounts of spat were imported from Japan to various places in France. The spat was partly cultchless and partly set on oysters or scallop shells (Grizel and

Héral 1991). The most extensive import took place to Marennes-Oléron during 1971-1975, but much was also imported to other areas in the Bay of Biscay, to Brittany, and to the Mediterranean (Grizel and Héral 1991). In addition, there were plans to import *Ostrea denselamellosa* to France from Korea in 1982 (Mann 1983), but only one record of such an import from Japan to Brittany in 1982 has been found (le Borgne and Le Pennec 1983). In 1982 the import of oysters to France from the Pacific stopped due to the discovery of a parasite in Japan (Wolff and Reise 2002).

An extensive transport of oysters for cultivation has also taken place within Europe (Ruesink et al. 2005). In order to investigate if such transport may have caused secondary introductions of *H. japonica* reports of oyster transfers within Europe from the 1970s and onwards were taken into consideration, since the first record of *H. japonica* in Europe is from 1984. Norway imported seed oysters and spat from Scotland (the UK) during 1976-1986 (Strand and Vølstad 1997), and Denmark has imported seed oysters from the UK, The Netherlands and France during the last 30 years of the last century (Nehring 2006). According to the overview and information summarized by Ruesink et al. (2005), Denmark also imported oysters from Germany in 1980, Ireland from France in 1993, The Netherlands from France during 1964-1981 and Portugal from France during 1990-1992. Spain has imported Pacific oysters from France since the 1980s (Ruesink et al. 2005; Iglesias et al. 2005). The import of oysters from France to The Netherlands was stopped in 1981 due to the discovery of a disease (Drinkwaard 1999).

Ships as vector

Transfer of *H. japonica* by ships, e.g. in ballast water, is an alternative to transport by oyster imports. When completing the experiment with survival of thallus parts in darkness and under temperature stress 86 % of the uniseriate pseudo-lateral fragments of *H. japonica* had normal pigmentation and were recorded as alive in one beaker, and 63 % in the other. One of the two main shoots was without normal pigmentation in any part, while the other had normal pigmentation in several side shoots when completing the experiment (Figure 2). The viability was confirmed by a resumption of growth in fragments after two weeks in culture conditions (Figure 2).

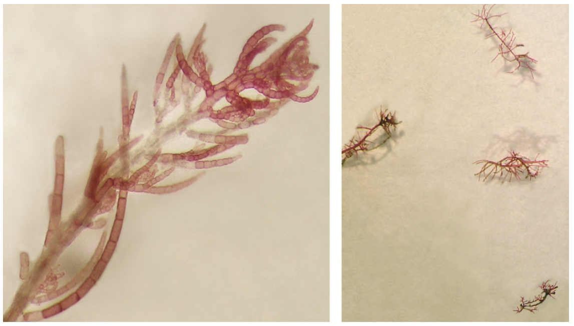

Figure 2. Left: photo of *Heterosiphonia japonica* after 28 days in darkness and under temperature stress. Right: the development of surviving uniseriate pseudolateral fragments of *H. japonica* two weeks after the experiment (Photograph by V. Husa).

Figure 3 shows reported positions of ships in the Mediterranean and eastern parts of North Atlantic during random months in 2005 and 2006, according to the Sailwx database. The patterns of the main traffic are similar during all months. A main shipping line extends from the Suez Canal and the Mediterranean, around Portugal and into the English Channel. The coast from Brittany and northwards through the English Channel is also a very busy shipping route up to Germany and Denmark. The coast of south Norway also represents a main shipping line, and the North Sea is in general busy, specially the south and southeast part. Some areas with relatively little traffic seem to be the Bay of Biscay, the waters around Ireland and the western and northern part of the UK. In the Mediterranean the busiest shipping lines appear to be on the Mediterranean coast of France and Spain.

Discussion

Introduction of H. japonica to Europe

In order to assess possible vectors involved in the introduction of a species it is crucial to know the donor region of the species in question. Outside Europe *H. japonica* is reported from Korea (Choi 2001), China, Japan, Russia, Alaska and California (according to references in the database AlgaeBase, Guiry and Guiry 2008). However, according to S. Lindstrom (pers.comm.), *H. japonica* is not present in north-west America. The north-west American *H. densiuscula* was called *H. japonica* for a period since Abbott (1972) considered these two

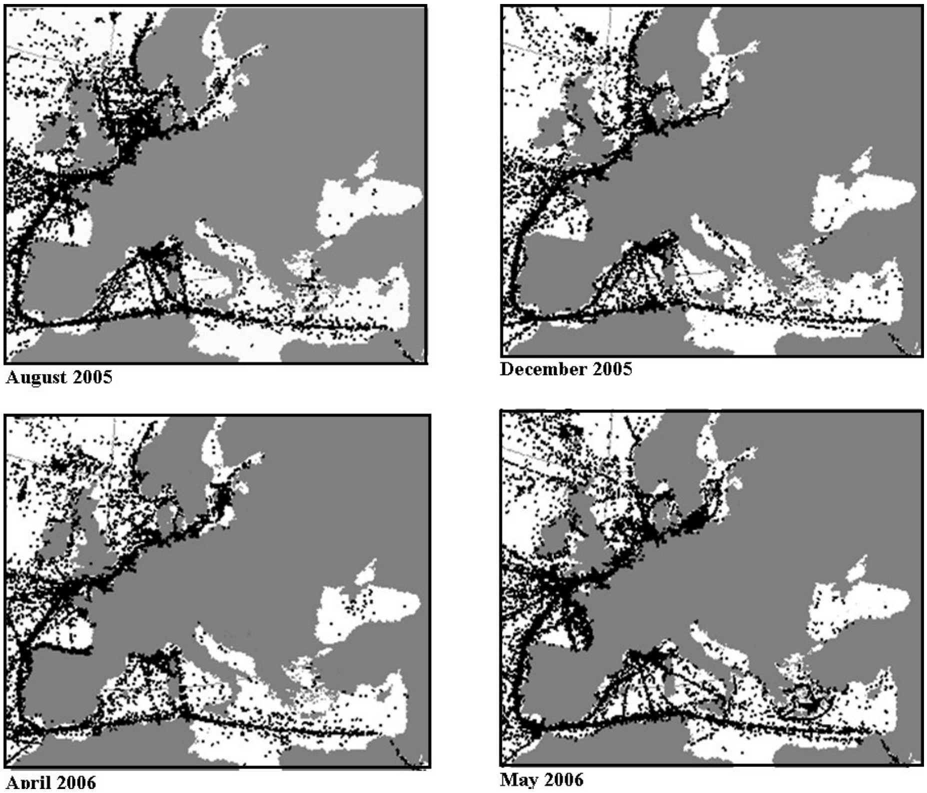

Figure 3. Data from the web page Sailwx showing positions of ships in European waters (see Figure 1 for names) during 4 random months in 2005-2006.

to be conspecific (S. Lindstrom, pers. comm.). *H. japonica* and *H. densiuscula* separate clearly from each other with regard to morphology (Choi 2001), and Choi (2001) regards these as two separate species. Since *H. japonica* is not present in British Columbia (Canada), the introduction to Europe of this species cannot have followed from the import of oysters from British Columbia to European countries, and the donor region of the European *H. japonica* must be the western Pacific (Korea, China or Japan). While European material of *H. japonica* was genetically similar to Korean material when analysed by using cox2-3 spacer (Bjærke 2004), no comparisons have been made between European and Chinese or Japanese material of *H. japonica*.

In order to assess the most likely vector for an introduction it is equally important to localize the first site of arrival. It is not known to what extent the reports of *H. japonica* from various parts of Europe actually reflect the time of establishment of this species in each area. Some areas have probably been more searched than others, and e.g. in France and South Europe there are several red algae with a similar habit as *H. japonica*, which may have made it difficult to spot the new species (Peña and Bárbara 2006). However, it is likely that the now reported first site of observation, Brittany in France, actually is the first site where *H. japonica* became established in Europe. Brittany was one of the main areas for import of oyster spat from Japan to Europe in the 1970s (Grizel and Héral 1991), and this import seems to be a very likely vector for the first introduction of *H. japonica* to Europe. There are several ways in which algae, like *H. japonica*, may have hitchhiked with imported oysters. Algal material may have been used as cover during transport. The oyster spat was transported to Europe partly set on shells, and a number of species may have survived transport growing on these shells. Some measures were taken to prevent introduction of new species to France, like immersion of the spat in fresh water for some time (Grizel and Héral

1991), but it is not known how efficient this was or how well this treatment was carried out. *H. japonica* was not registered in Brittany until several years after the main period of oyster import from Japan had stopped, but in some cases it takes time before introduced species build up large enough populations to become discovered.

Even though imports of oyster spat from Japan to France is a very likely vector for the introduction of *H. japonica* to Europe, we cannot rule out that the European *H. japonica* may have another donor region than Japan, or that there may have been multiple introductions of *H. japonica* from the western Pacific to Europe. The invasive kelp *Undaria pinnatifida* is an example of a species which may have spread with several vectors to different parts of the world (Voisin et al. 2006). In addition to its arrival in the Mediterranean with oysters (Voisin et al. 2006), *U. pinnatifida* has also probably spread to other parts of the world by ships (Wallentinus 2007). *H. japonica* may have spread in a similar way, by both oyster transfers and ships. The result of the experiment with survival during a simulated journey in ballast water shows that thallus parts and fragments of uniseriate pseudolaterals of *H. japonica* are capable of surviving in total darkness and under temperature stress for a considerable amount of time, at least as long as a journey by a bulk carrier takes from Korea to Le Havre. A high survival of *H. japonica* sporelings after 40 days in darkness was also observed by Bjærke and Rueness (2004). Survival of fragments and small thallus parts is sufficient for successful establishment of *H. japonica* at a site of arrival, since uniseriate pseudolateral branches of this species show great ability to regenerate at a variety of temperatures (Husa and Sjøtun 2006).

However, the experiment simulating a journey in ballast water only takes temperature stress and light deficiency for algal fragments in ballast water into consideration. Other types of stress, e.g. burial of algal fragments in sediments, variation in salinity or hypoxic or even anoxic conditions, may be more important than temperature and light in limiting transportation success of live algae by ballast water. On the other hand, Flagella et al. (2007) did not find the physical conditions in ballast tanks they sampled to be lethal for macroalgal species, and David et al. (2007) identified as many as 120 early macroalgal stages per litre ballast water in ships in a Mediterranean harbour.

Spreading of H. japonica in Europe

About 25 years after the first observation of *H. japonica* in Europe it is widespread in both south and north Europe. *H. japonica* is found in a variety of marine habitats, but does not tolerate much wave-exposure (Husa et al. 2004) and grows poorly at 15 psu or below (Bjærke and Rueness 2004). It grows abundantly as an epiphyte, on any type of solid substratum, or it can grow loose on soft substratum (Husa et al. 2004). Thus, there are few stretches along the European coasts where the physical conditions would be unfavourable for establishment, once the species has arrived.

H. japonica may spread naturally, by spores or fragments carried by currents, or it may spread by growing attached to loose buoys or other drifting items. However, *H. japonica* has spread over large areas in relatively short time in Europe. It has also spread countercurrent in some places, e.g. southwards and eastwards along the Norwegian and southwards along the Swedish west coast. This suggests that some direct human-mediated secondary spread of the species is most likely in these cases.

After the import stop of Pacific Oysters from Japan in 1982, oysters have frequently been transferred between many countries within Europe. *H. japonica* may have spread to Galicia (NW Spain) during the 1980s by ships or oyster transfers. Galicia is one of the main oyster cultivation areas in Spain, and Spain has been importing oysters from France from the 1980s onwards (Iglesias et al. 2005). The establishment of *H. japonica* in Ireland may possibly have been a result of oyster imports from France during the 1990s, since the site where it was found is close to an oyster farm, and in addition relatively little boat traffic connects Ireland with the English Channel and Spain. The oyster cultivation in the Mediterranean is likely to have caused the spreading of *H. japonica* between the Atlantic and the Mediterranean coasts, since the process of oyster cultivation in France involves frequent transfers of oysters between the Mediterranean and the Atlantic coast (Mineur et al. 2007b). In addition, one cannot rule out that *H. japonica* may have spread into the Mediterranean as a result of transport of other bivalves than oysters for cultivation (see e.g. Breber 1985).

H. japonica is reported to grow well in oyster beds in The Netherlands and in the Mediterranean (Haydar and Wolff 2003; Mineur et al. 2005). The fact that oyster beds represent a good habitat for *H. japonica* does not necessarily mean that oysters are the vector for introduction to the area, even though it cannot be ruled out in the cases where *H. japonica* has first been recorded in an area close to an oyster cultivation site. The first record of *H. japonica* in The Netherlands was in 1994 in an empty oyster farm, and it was suggested that oyster transfer was the vector of introduction (Maggs and Stegenga 1999). However, the import stop of oysters from France to The Netherlands as early as in 1981 (Drinkwaard 1999) makes oyster imports a less likely vector for the introduction of *H. japonica* to The Netherlands. *H. japonica* can also have spread naturally northwards along the coast from Brittany, but the fact that it is not recorded in Belgium suggests that there has been a vector involved for the spreading to the North Sea.

An alternative to transport with oysters in the North Sea is transport of *H. japonica* by other types of shellfish or by ships. The coasts around the North Sea, specially the south and southeast part including the western part of the Baltic Sea have busy shipping lines. The fact that *H. japonica* is not yet recorded in the Baltic Sea, other than along parts of the Swedish west coast, is probably due to a lethal salinity limit of 10 psu to the species (Bjærke 2004). The spreading of *H. japonica* along the Norwegian southwest coast and along the Swedish west coast is most likely facilitated by boat traffic, since this is a busy shipping area of cargo, fishing and leisure boats. Along the Norwegian coast *H. japonica* has been observed to spread very rapidly (Husa et al. 2004). The high rate and pattern of spreading within Norway suggest that the local spread is most likely due to boat traffic along the coast (Husa et al. 2004). Bjærke (2004) analysed samples of *H. japonica* from several places along its area of distribution in Norway by the AFLP fingerprint method. She found different groupings and high similarity between the northernmost and the southernmost samples, suggesting both multiple secondary introductions into Norway and spreading from site to site along the coast.

H. japonica may spread short distances by ship's traffic in a number of ways, e.g. attached to the hull of ships or growing on ropes, or other types of equipment transported by ships, as well as on buoys, as fragmented thalli in ballast water or other water bodies transported by ships e.g. for transportation of fish, or entangled in different types of fishing gear or equipment used in aquaculture. Under stressed conditions *H. japonica* is easily fragmented, and the fragments have a high rate of survival and regeneration after exposure to high environmental stress (Husa and Sjøtun 2006). However, since *H. japonica* has a relatively fragile thallus and is e.g. not found in wave-exposed areas, it is not very likely to have spread over long distances attached to the hull of ships. On the other hand, in a study of benthic algae growing on hulls of ships arriving in Mediterranean harbours a number of small and delicate species in the order Ceramiales were observed (Mineur et al. 2007a).

H. japonica may also have spread by ballast water within Europe. The first recording of *H. japonica* in North Europe was from a site close to Bergen (Lein 1999), which is one of the main ports in Norway. A study of origin of ballast water from ships arriving at the oil terminals around Bergen showed that the main part of the ballast water came from ports between North France and Germany (Dragsund et al. 2007). However, not far from the locality where *H. japonica* was first observed in Norway, an oyster producer was keeping imported oysters from south Europe in tanks during the 1990s, with water running from the tanks directly to the sea (S. Mortensen, pers. comm.). If *H. japonica* were growing on the oysters, fragments or spores of *H. japonica* would easily escape to the surrounding areas. Thus, we cannot rule out that oyster import was the vector for the first introduction to Scandinavia. This demonstrates how difficult it is to determine vectors for introductions, and also how difficult it is to limit secondary introductions.

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Annex 1. Recordings of *Heterosiphonia japonica* in Europe. The year of first observation in various countries is given. Information is based on personal communication, unpublished data (V. Peña and I. Bárbara) and publications. Available information about reproductive status of *Heterosiphonia japonica* in samples is included. * shows year of first recording in a country, ** indicates an oyster cultivation farm nearby.

Location	Geographic coordinates		Date	Site description and Additional information	Source
	Latitude	Longitude			
Denmark					
Fredrikshavn, Kattegat	57°27' N	10°33' E	2004*		R Nielsen (pers. comm.)
Hirsholmene, Kattegat	57°29' N	10°36' E	2005		R Nielsen (pers. comm.)
Dråby Vig, Limfjorden, Denmark	56°52' N	08°51' E	2005		Thomsen et al. (2007), verified by R Nielsen
Gjeller Odde, Limfjorden	56°35' N	08°18' E	2005		Thomsen et al. (2007), verified by R Nielsen
Thisted Bredning, Limfjorden	56°57' N	08°47' E	2005		Thomsen et al. (2007), verified by R Nielsen
France					
Roscoff, Brittany	48°43' N	03°59' W	1984*	** Female gametophytes	M Verlaque and J Cabioch (pers. comm.)
Thau lagoon, Mediterranean	43°25' N	03°39' E	May 1998	Subtidal in shellfish farm** Tetrasporophytic plants	Verlaque (2001), M Verlaque (pers. comm.)
Rozegat, Brittany	48°19' N	04°23' W	September 2003	Subtidal on maërl bed	V Peña and J Grall, unpublished data; SANT-Algae
Camaret, Brittany	48º17' N	04º34' W	November 2004	Subtidal on maërl bed	V Peña and J Grall, unpublished data; SANT-Algae
Golf, Brittany	47º31' N	02º53' W	November 2004	Subtidal on maërl bed	V Peña and J Grall, unpublished data
Mount St. Michel	48º37' N	01º30' W	August 2001	**	I Bárbara, unpublished data; SANT-Algae
Thau lagoon, Mediterranean	43°25´ N	03°38´ E	April 2002	Subtidal in shellfish farm**	Verlaque et al. (2005), M Verlaque (pers. comm.)
Thau lagoon, Mediterranean	43°26´ N	03°38´ E	2002	Subtidal in shellfish farm** Not recorded outside the Thau lagoon	Verlaque et al. (2005), M Verlaque (pers. comm.)
Thau lagoon, Mediterranean	43°23´ N	03°34´ E	2002	Subtidal in shellfish farm** Not recorded outside the Thau lagoon	Verlaque et al. (2005), M Verlaque (pers. comm.)
Thau lagoon, Mediterranean	43°22´ N	03°33´ E	2002	Subtidal in shellfish farm** Not recorded outside the Thau lagoon	Verlaque et al. (2005), M Verlaque (pers. comm.)
Thau lagoon, Mediterranean	43°25' N	43º25' N	2002	Subtidal in shellfish farm** Not recorded outside the Thau lagoon	Verlaque et al. (2005), M Verlaque (pers. comm.)
Logonna, Brittany	48°19' N	04°19' W	April 2005	Subtidal on maërl bed	V Peña and J Grall, unpublished data; SANT
Rade de Brest, Brittany	48°20' N	04°29' W	April 2005	Subtidal on maërl bed	V Peña and J Grall, unpublished data; SANT
Belle Île, Brittany	47°19' N	03º07' W	April 2005	Subtidal on maërl bed	V Peña and J Grall, unpublished data; SANT
Morlaix, Brittany	48°42' N	03°56' W			V Peña and J Grall, unpublished data; SANT
Arcachon Basin, Gironde	44°39' N	01°14 W			M Verlaque (pers. comm.)

Annex 1 (continued).

Location	Geographic coordinates		Date	Site description and Additional information	Source
	Latitude	Longitude			
Ireland					
Newquay, Co. Clare	53°09' N	09°04' W	2002*	Intertidal and below ** Not recorded outside the area	S Kraan, F Rindi and MD Guiry, verified by V Husa
Italy					
Sea coastline of Lido island, Venice lagoon			1999*	** Not recorded outside the Venice lagoon	Sfriso and Curiel (2007), A Sfriso (pers. comm.)
The Netherlands					
Yerseke, Oosterschelde	51°29' N	04°04' E	1994*	** Abandoned oyster farm	Stegenga (1997)
Strijenham, Oosterschelde	51°31' N	04 09' E	1994		Stegenga (1997)
Oosterschelde	51°31' N	04 08' E	1995		H Stegenga (pers. comm.)
Oosterschelde	51°28' N	04°07' E	1995		H Stegenga (pers. comm.)
Oosterschelde	51°31' N	03°59' E	1995		H Stegenga (pers. comm.)
Oosterschelde	51°33' N	03°54' E	1995		H Stegenga (pers. comm.)
Oosterschelde	51°37' N	03°53' E	1995		H Stegenga (pers. comm.)
Oosterschelde	51°36' N	03°41' E	1995		H Stegenga (pers. comm.)
Grevelingen	51°45' N	03°50' E	1995		H Stegenga (pers. comm.)
Gorishoek, Oosterschelde	51°31' N	04°04' E	May 2004	Female and male gametophytes	H Stegenga (pers. comm.)
Grevelingen	51°46' N	03°52' E	2005		H Stegenga (pers. comm.)
Grevelingen	51°47' N	03°53' E	2005		H Stegenga (pers. comm.)
Grevelingen	51°43' N	03°59' E	2005		H Stegenga (pers. comm.)
Grevelingen	51°42' N	04°05' E	2005		H Stegenga (pers. comm.)
Grevelingen	51°40' N	04°05' E	2005		H Stegenga (pers. comm.)
Sint Phillipsland	51°36' N	04°10' E	2005		H Stegenga (pers. comm.)
Oosterschelde	51°35' N	03°59' E	2005		H Stegenga (pers. comm.)
Oosterschelde	51°36' N	03°58' E	2005		H Stegenga (pers. comm.)
Oosterschelde	51°37' N	03°56' E	2005		H Stegenga (pers. comm.)
Oosterschelde	51°38' N	03°52' E	2005		H Stegenga (pers. comm.)
Oosterschelde	51°40' N	03°44' E	2005		H Stegenga (pers. comm.)
Oosterschelde	51°38' N	03°42' E	2005		H Stegenga (pers. comm.)
Oosterschelde	51°38' N	03°43' E	2005		H Stegenga (pers. comm.)
Oosterschelde	51°37' N	03°40' E	2005		H Stegenga (pers. comm.)
Oosterschelde	51°36' N	03°43' E	2005		H Stegenga (pers. comm.)
Oosterschelde	51°36' N	03°51' E	2005		H Stegenga (pers. comm.)
Oosterschelde	51°32' N	03°54' E	2005		H Stegenga (pers. comm.)
Oosterschelde	51°29' N	04°12' E	2005		H Stegenga (pers. comm.)
Oosterschelde	51°30' N	04°10' E	2005		H Stegenga (pers. comm.)
Canal through Zuid-Beveland	51°28' N	04°00' E	2005		H Stegenga (pers. comm.)

Annex 1 (continued).

Location	Geographic coordinates		Date	Site description and Additional information	Source
	Latitude	Longitude			
The Netherlands					
Veerse Meer	51°30' N	03°51' E	2005		H Stegenga (pers. comm.)
Westerschelde estuary, near Vlissingen	51°26' N	03°36' E	2005		H Stegenga (pers. comm.)
Norway					
Skårsundet, Austevoll	60º08' N	05º09' E	1996*	Subtidal **	Lein (1999)
Skogsøy	58°00' N	07°34' E	November 2000	Subtidal, sand	Husa et al. (2004)
Hoersholmen	58°27' N	05°53' E	November 2000	Subtidal, sand	Husa et al. (2004)
Laksholmen	58°55' N	05°34' E	November 2000	Subtidal, sand	Husa et al. (2004)
Sauholmen	59°04' N	05°25' E	November 2000	Subtidal, sand	Husa et al. (2004)
Selen	59°15' N	05°21' E	November 2000	Subtidal, sand	Husa et al. (2004)
Hansavågen	59°25' N	05°14' E	November 2000	Subtidal, hard rock	Husa et al. (2004)
Hestholmen A	62°12' N	05°28' E	February 2001	Subtidal, hard rock	Husa et al. (2004)
Haakonsholmen	62°20' N	05°47' E	February 2001	Subtidal, hard rock	Husa et al. (2004)
Grisholmen	62°20' N	05°46' E	February 2001	Subtidal, sand	Husa et al. (2004)
Terøyholmen	62°31' N	06°13' E	February 2001	Subtidal, sand	Husa et al. (2004)
Lyngholmen	62°31' N	06°12' E	February 2001	Subtidal, sand	Husa et al. (2004)
Pampusholmane	62°31' N	06°11' E	February 2001	Subtidal, sand	Husa et al. (2004)
Fugløya	63°05' N	07°46' E	February 2001	Subtidal, sand	Husa et al. (2004)
Hansøya	63°06' N	07°48' E	February 2001	Subtidal, sand	Husa et al. (2004)
Ramsøya	63°11' N	07°56' E	February 2001	Subtidal, hard rock	Husa et al. (2004)
Store Havreøya	63°19' N	08°10' E	February 2001	Subtidal, sand	Husa et al. (2004)
Henningsholmen	63°18' N	08°10' E	February 2001	Subtidal, sand	Husa et al. (2004)
Grønskaget	63°18' N	08°07' E	February 2001	Subtidal, sand	Husa et al. (2004)
Klubbeneset	61°52' N	05°11' E	March 2001	Subtidal, sand	Husa et al. (2004)
Notaholmen	62°41' N	06°41' E	March 2001	Subtidal, hard rock	Husa et al. (2004)
Saugøy	56º34' N	05º08' E	April 2001	Subtidal, sand	Husa et al. (2004)
Romsholmen	59º35' N	05º08' E	April 2001	Subtidal, sand	Husa et al. (2004)
Nautøy	59º35' N	05º08' E	April 2001	Subtidal, sand	Husa et al. (2004)
Teløysund	59º56' N	05º15' E	April 2001	Subtidal, sand	Husa et al. (2004)
Smedasundet	59º55' N	05º16' E	April 2001	Subtidal, sand	Husa et al. (2004)
Blaenesøy	59º59' N	05º15' E	April 2001	Subtidal, sand	Husa et al. (2004)
Herdlesund	60º33' N	04º57' E	April 2001	Subtidal, hard rock	Husa et al. (2004)
Lykløy	60º33' N	04º57' E	April 2001	Subtidal, sand	Husa et al. (2004)
Ytstøy	60º33' N	04º57' E	April 2001	Subtidal, hard rock	Husa et al. (2004)
Steinholmen	60º40' N	04º54' E	April 2001	Subtidal, hard rock	Husa et al. (2004)

Annex 1 (continued).

Location	Geographic coordinates		Date	Site description and Additional information	Source
	Latitude	Longitude			
Norway					
Toska	60º39' N	04º57' E	April 2001	Subtidal, sand	Husa et al. (2004)
Feitholmen	60º43' N	04º53' E	April 2001	Subtidal, sand	Husa et al. (2004)
Guleskjeret A	60º56' N	04º57' E	April 2001	Subtidal, hard rock	Husa et al. (2004)
Bjorøy	60º56' N	04º58' E	April 2001	Subtidal, hard rock	Husa et al. (2004)
Lyngholmen	60º56' N	04º58' E	April 2001	Subtidal, hard rock	Husa et al. (2004)
Røyrvika	61º03' N	04º49' E	April 2001	Subtidal, sand	Husa et al. (2004)
Samsonholmen	61º03' N	04º49' E	April 2001	Subtidal, sand	Husa et al. (2004)
Tårnholmen	61º04' N	04º49' E	April 2001	Subtidal, sand	Husa et al. (2004)
Hasløy	61º13' N	04º58' E	April 2001	Subtidal, hard rock	Husa et al. (2004)
Sauesundøy	61º19' N	05º02' E	April 2001	Subtidal, hard rock	Husa et al. (2004)
Grovholmen	61º19' N	05º01' E	April 2001	Subtidal, hard rock	Husa et al. (2004)
Flatøy 3	61º19' N	05º02' E	April 2001	Subtidal, hard rock	Husa et al. (2004)
Svanøya	61º29' N	05º02' E	April 2001	Subtidal, hard rock	Husa et al. (2004)
Nekkøysundet	61º34' N	04º56' E	April 2001	Subtidal, sand	Husa et al. (2004)
Hestøy	61º34' N	04º51' E	April 2001	Subtidal, hard rock	Husa et al. (2004)
Hollendervågen	61º36' N	04º52' E	April 2001	Subtidal, sand	Husa et al. (2004)
Langøya	61º36' N	04º50' E	April 2001	Subtidal, hard rock	Husa et al. (2004)
Smørhamn	61º46' N	04º56' E	April 2001	Subtidal, sand	Husa et al. (2004)
Benken	61º46' N	04º57' E	April 2001	Subtidal, sand	Husa et al. (2004)
Bukkasundet	60°14' N	05°12' E	August 2001	Subtidal, sand	Husa et al. (2004)
Eggholmen	60°15' N	05°12' E	August 2001	Subtidal, sand	Husa et al. (2004)
Flatevossen	60°16' N	05°12' E	August 2001	Subtidal, hard rock	Husa et al. (2004)
Tyssøy	60°18' N	05°09' E	August 2001	Subtidal, sand	Husa et al. (2004)
Håkjærholmen	60°19' N	05°09' E	August 2001	Subtidal, sand	Husa et al. (2004)
Kvitura	60°18' N	05°12' E	August 2001	Subtidal, sand	Husa et al. (2004)
Sletta	60°16' N	05°12' E	August 2001	Subtidal, hard rock	Husa et al. (2004)
Rossevik	60°17' N	05°08' E	August 2001	Subtidal, hard rock	Husa et al. (2004)
Grønavik	60°14' N	05°08' E	August 2001	Subtidal, sand	Husa et al. (2004)
Kuøy	60°04' N	05°04' E	August 2001	Subtidal, hard rock	Husa et al. (2004)
Kjøholmen	60°05' N	05°12' E	September 2001	Subtidal, sand	Husa et al. (2004)
Parakholmen	60°07' N	05°13' E	September 2001	Subtidal, sand	Husa et al. (2004)
Lambøy	60°06' N	05°15' E	September 2001	Subtidal, sand	Husa et al. (2004)
Hausneset	60°15' N	05°17' E	September 2001	Subtidal, hard rock	Husa et al. (2004)
Herøy	60°14' N	05°16' E	September 2001	Subtidal, hard rock	Husa et al. (2004)
Moldvikane	60°13' N	05°15' E	September 2001	Subtidal, hard rock	Husa et al. (2004)
Bjelkarøy	60°14' N	05°13' E	September 2001	Subtidal, hard rock	Husa et al. (2004)

Annex 1 (continued).

Location	Geographic coordinates		Date	Site description and Additional information	Source
	Latitude	Longitude			
Norway					
Kvalvik	60°12' N	05°10' E	September 2001	Subtidal, hard rock	Husa et al. (2004)
Grimseidpollen	60°15' N	05°16' E	September 2001	Poll, subtidal	Husa et al. (2004)
Eidespollen	60°14' N	05°03' E	September 2001	Poll, subtidal	Husa et al. (2004)
Spildepollen	60°14' N	05°03' E	September 2001	Poll, subtidal	Husa et al. (2004)
Førdespollen	60°12' N	05°09' E	September 2001	Poll, subtidal	Husa et al. (2004)
Skogsvågen	60°15' N	05°05' E	September 2001	Poll, subtidal	Husa et al. (2004)
Busepollen	60°03' N	05°12' E	September 2001	Subtidal, sand	Husa et al. (2004)
Fjæreidpollen	60°23' N	05°02' E	September 2001	Subtidal, sand	Husa et al. (2004)
Terneholmen, Arendal	58°27' N	08°45' E	August 2002		F Moy (pers. comm.)
Buøy, Arendal	58°30' N	08°54' E	October 2002		F Moy (pers. comm.)
Svanøya	61°29' N	05°02' E	August 2003	Subtidal, hard rock, sand	Husa et al. (2008)
Nekkøya	61°34' N	04°56' E	August 2003	Subtidal, hard rock	Husa et al. (2008)
Fanøyvågen	61°37' N	04°48' E	August 2003	Subtidal, sand	Husa et al. (2008)
Skorpa	61°37' N	04°50' E	August 2003	Subtidal, sand	Husa et al. (2008)
Batalden	61°38' N	04°49' E	August 2003	Subtidal, sand	Husa et al. (2008)
Smørhavn	61°46' N	04°56' E	August 2003	Subtidal, hard rock, sand	Husa et al. (2008)
Husevågsøy	61°53' N	05°07' E	August 2003	Subtidal, sand	Husa et al. (2008)
Gangsøy	61°53' N	05°07' E	August 2003	Subtidal, sand	Husa et al. (2008)
Høvåg, Lillesand	58°10' N	08°14' E	2004		J Rueness (pers. comm.)
Langøy	61°03' N	04°43' E	August 2004	Subtidal, hard rock, sand	Husa et al. (2008)
Utvær west	61°02' N	04°30' E	August 2004	Subtidal, hard rock, sand	Husa et al. (2008)
Utvær, south	61°02' N	04°31' E	August 2004	Subtidal, hard rock	Husa et al. (2008)
Steinsundholmen	61°04' N	04°49' E	August 2004	Subtidal, hard rock	Husa et al. (2008)
Tårnholmen	61°04' N	04°50' E	August 2004	Subtidal, hard rock	Husa et al. (2008)
Steinsund bru	61°03' N	04°49' E	August 2004	Subtidal, hard rock, sand	Husa et al. (2008)
Steinsundøy	61°03' N	04°50' E	August 2004	Subtidal, hard rock, sand	Husa et al. (2008)
Flatøy	61°03' N	04°43' E	August 2004	Subtidal, hard rock	Husa et al. (2008)
Skogaholmen	61°02' N	04°43' E	August 2004	Subtidal, hard rock, sand	Husa et al. (2008)
Arøy, Kragerø	58°53' N	09°34' E	August 2004		F Moy (pers. comm.)
Drøbak	59°39' N	10°37' E	January 2005		J Rueness (pers. comm.)
Stølsvika, Arendal	58°25' N	08°45' E	June 2005		F Moy (pers. comm.)
Bastua, Arendal	58°24' N	08°44' E	June 2005		F Moy (pers. comm.)
Tvillingholmen, Grimstad	58°18' N	08°34' E	June 2005		F Moy (pers. comm.)
Lamholmen, Lillesand	58°14' N	08°23' E	June 2005		F Moy (pers. comm.)
Kvåsefjorden, Kristiansand	58°07' N	08°11' E	June 2005		F Moy (pers. comm.)

Annex 1 (continued).

Location	Geographic coordinates		Date	Site description and Additional information	Source
	Latitude	Longitude			
Norway					
Grønsfjorden, Lindesnes	57°58' N	07°03' E	June 2005		F Moy (pers. comm.)
Ålo, Søgne	58°02' N	07°41' E	September 2005		PA Åsen (pers. comm.)
Grønsfjorden, Lindesnes	58°02' N	07°02' E	September 2005		PA Åsen (pers. comm.)
Sandefjorden	59°04' N	10°14' E	November 2005		H Steen (pers. comm.)
Risør	58°42' N	09°14' E	November 2005		H Steen (pers. comm.)
Lauvvika	58°53' N	05°02' E	July 2006		F Moy (pers. comm.)
Langøya	62°50' N	07°07' E	August 2006		F Moy (pers. comm.)
Flåøy, Tingvollfjorden	62°45 N	08°27' E	August 2006		F Moy (pers. comm.)
Tvekremholmen, Tingvollfjorden	62°59' N	08°01' E	August 2006		F Moy (pers. comm.)
Øyaholmen, Dalsøya	61°21' N	05°21' E	August 2006		F Moy (pers. comm.)
Spain					
Ría de Muros-Noia, Galicia	42º45' N	09 04' W	August 1988*	Intertidal and subtidal Tetrasporophytic plants	Peña and Bárbara (2006a); SANT-Algae
Ría de Ferrol, Galicia	43º27' N	08º18' W	September 1988	Intertidal and subtidal Tetrasporophytic plants	Peña and Bárbara (2006a); SANT-Algae
Ría de Vigo, Galicia	42º13' N	08º44' W	March 1994	Intertidal	Peña and Bárbara (2006a); SANT-Algae
Ría de A Coruña, Galicia	43º21' N	08º23' W	July 1994	Intertidal and subtidal Tetrasporophytic plants	Peña and Bárbara (2006a); SANT-Algae
Port of Bilbao	43º21' N	03º01' W	1995	On jetties in the port at 1-6 meters depth	A Secilla, verified by I Bárbara
Ría de Arousa, Galicia	42º32' N	08º56' W	July 1995	Intertidal and subtidal Tetrasporophytic plants	Bárbara et al. (2003); Peña and Bárbara (2006a); SANT-Algae
Ría de Arousa, Galicia	42º32' N	08º52' W	January 1997	Intertidal and subtidal	Peña and Bárbara (2006a); SANT-Algae
Ría de Arousa, Galicia	42º31' N	08º49' W	January 1997	Intertidal	Peña and Bárbara (2006a); SANT-Algae
Ría de Arousa, Galicia	42º34' N	08º56' W	April 1997	Intertidal and subtidal	Peña and Bárbara (2006a); SANT-Algae
Ría de Arousa, Galicia	42º29' N	08º50' W	January 1998	Intertidal	Peña and Bárbara (2006a); SANT-Algae
Barrañán, Galicia	43º18' N	08º32' W	August 1998	Intertidal and subtidal	Peña and Bárbara (2006a); SANT-Algae
Ría de Viveiro, Galicia	43º44' N	07º37' W	September 2002	Subtidal	Peña and Bárbara (2006a); SANT-Algae
Ría de Arousa, Galicia	42º34' N	08º57' W	January 2004	Intertidal and subtidal Tetrasporophytic plants	Peña and Bárbara (2006a); SANT-Algae
Ría de Vigo, Galicia	42º15' N	08º44' W	March 2004	Subtidal on maërl bed Tetrasporophytic plants	Peña and Bárbara (2006a); SANT-Algae
Ría de Vigo, Galicia	42º14' N	08º47' W	March 2004	Subtidal on maërl bed	V Peña and I Bárbara , unpublished data
Ría de Arousa, Galicia	42º35' N	08º54' W	April 2004	Subtidal on maërl bed Female and tetrasporophytic plants	SANT-Algae 19533 (V Peña, unpublished data)
Ría de Arousa, Galicia	42º33' N	08º58' W	April 2004	Subtidal on maërl bed Tetrasporophytic plants	V Peña and I Bárbara, unpublished data
Ría de Arousa, Galicia	42º29' N	08º53' W	June 2004	Subtidal on maërl bed Tetrasporophytic plants	V Peña and I Bárbara, unpublished data

Annex 1 (continued).

Location	Geographic coordinates		Date	Site description and Additional information	Source
	Latitude	Longitude			
Spain					
Ría de Pontevedra, Galicia	42°24' N	08°42' W	June 2004	Subtidal on maërl bed Tetrasporophytic plants	V Peña and I Bárbara, unpublished data
Ría de Pontevedra, Galicia	42°24' N	08°44' W	June 2004	Subtidal on gravel	V Peña and I Bárbara, unpublished data
Ría de Pontevedra, Galicia	42°23' N	08°43' W	June 2004	Subtidal on gravel Tetrasporophytic plants	V Peña and I Bárbara, unpublished data
Ría de Arousa, Galicia	42°36' N	08°52' W	July 2004	Subtidal on maërl bed Female and tetrasporophytic plants	SANT-Algae 19534 (V Peña, unpublished data)
San Ciprián, Galicia	43°42' N	07°28' W	September 2004	Intertidal and subtidal	Peña and Bárbara (2006a); SANT-Algae
Ría de Vigo, Galicia	42°14' N	08°49' W	September 2004	Subtidal on maërl bed Tetrasporophytic plants	Peña and Bárbara (2006a); SANT-Algae
Ría de Vigo, Galicia	42°15' N	08°46' W	September 2004	Subtidal on maërl bed Tetrasporophytic plants	Peña and Bárbara (2006a); SANT-Algae
Ría de Vigo, Galicia	42°14' N	08°51' W	September 2004	Subtidal on gravel	V Peña and I Bárbara, unpublished data
Ría de Vigo, Galicia	42°15' N	08°50' W	September 2004	Subtidal on maërl bed	V Peña and I Bárbara, unpublished data
Ría de Vigo, Galicia	42°15' N	08°48' W	September 2004	Subtidal on maërl bed	V Peña and I Bárbara, unpublished data
Ría de Vigo, Galicia	42°16' N	08°42' W	September 2004	Subtidal on gravel, sand	V Peña and I Bárbara, unpublished data
Ría de Vigo, Galicia	42°15' N	08°42' W	September 2004	Subtidal on gravel, sand	V Peña and I Bárbara, unpublished data
Bay of Plentzia, outside the Port of Bilbao	43°25' N	02°57' W	2005	Subtidal Tetrasporophytic plants	A Secilla, verified by I Bárbara
Ría de Pontevedra, Galicia	42°20' N	08°48' W	February 2005	Subtidal on maërl bed	Peña and Bárbara (2006a); SANT-Algae
Ría de Aldán, Galicia	42°17' N	08°49' W	February 2005	Subtidal on gravel	V Peña and I Bárbara, unpublished data
Ría de Aldán, Galicia	42°17' N	08°50' W	February 2005	Subtidal on maërl bed	V Peña and I Bárbara, unpublished data
Ría de Vigo, Galicia	42°13' N	08°45' W	May 2005	Subtidal on maërl bed Tetrasporophytic plants	V Peña and I Bárbara, unpublished data
Ría de Vigo, Galicia	42°13' N	08°46' W	May 2005	Subtidal on maërl bed	V Peña and I Bárbara, unpublished data
Ría de Pontevedra, Galicia	42°22' N	08°44' W	June 2005	Subtidal on maërl bed Tetrasporophytic plants	Peña and Bárbara (2006a); SANT-Algae
Ría de Arousa, Galicia	42°34' N	08°53' W	June 2005	Subtidal on maërl bed	Peña and Bárbara (2006a); SANT-Algae
Ría de Arousa, Galicia	42°34' N	08°55' W	June 2005	Subtidal on maërl bed Tetrasporophytic plants	V Peña and I Bárbara, unpublished data
Ría de Arousa, Galicia	42° 33'N	08°59' W	June 2005	Subtidal on maërl bed Tetrasporophytic plants	V Peña and I Bárbara, unpublished data
Ría de Arousa, Galicia	42°32' N	08°58' W	June 2005	Subtidal on maërl bed Tetrasporophytic plants	V Peña and I Bárbara, unpublished data
Ría de Arousa, Galicia	42°31' N	08°58' W	June 2005	Subtidal on maërl bed	V Peña and I Bárbara, unpublished data
Ría de Arousa, Galicia	42°31' N	09°00' W	June 2005	Subtidal on maërl bed	V Peña and I Bárbara, unpublished data
Ría de Arousa, Galicia	42°29' N	08°59' W	June 2005	Subtidal on maërl bed	Peña and Bárbara (2006b); SANT-Algae

Annex 1 (continued).

Location	Geographic coordinates		Date	Site description and Additional information	Source
	Latitude	Longitude			
Spain					
Ría de Arousa, Galicia	42º29' N	09º00' W	June 2005	Subtidal on maërl bed	Peña and Bárbara (2006b); SANT-Algae
Ría de Arousa, Galicia	42º28' N	09º00' W	June 2005	Subtidal on maërl bed Female and tetrasporophytic plants	Peña and Bárbara (2006b); SANT-Algae
Ría de Pontevedra, Galicia	42º19' N	08º46' W	June 2005	Subtidal on maërl bed	V Peña and I Bárbara, unpublished data
San Ciprián, Galicia	43º42' N	07º27' W	July 2005	Subtidal	Peña and Bárbara (2006a); SANT-Algae
Ría de Arousa, Galicia	42º30' N	08º53' W	August 2005	Subtidal on maërl bed	V Peña and I Bárbara, unpublished data
Ría de Arousa, Galicia	42º30' N	08º55' W	August 2005	Subtidal on maërl bed	V Peña and I Bárbara, unpublished data
Ría de Arousa, Galicia	42º33' N	08º53' W	November 2005	Subtidal on maërl bed	V Peña and I Bárbara, unpublished data
Ría de Arousa, Galicia	42º30' N	08º52' W	November 2005	Subtidal on maërl bed	V Peña and I Bárbara, unpublished data
Ría de Vigo, Galicia	42º11' N	08º53' W	December 2005	Subtidal on maërl bed	Peña and Bárbara (2006b); SANT-Algae
Ría de Muros-Noia, Galicia	42º47' N	09º01' W	June 2006	Subtidal on maërl bed Tetrasporophytic plants	V Peña and I Bárbara, unpublished data
Ría de Pontevedra, Galicia	42º23' N	08º55' W	June 2006	Subtidal on maërl bed	Peña and Bárbara (2006b); SANT-Algae
Ría de Vigo, Galicia	42º12' N	08º53' W	June 2006	Subtidal on maërl bed	Peña and Bárbara (2006b); SANT-Algae
Ría de Arousa, Galicia	42º31' N	08º53' W	August 2006	Subtidal on maërl bed Tetrasporophytic plants	V Peña and I Bárbara, unpublished data
Ría de Arousa, Galicia	42º32' N	08º55' W	May 2008	Subtidal on maërl bed Male plant	V Peña and I Bárbara, unpublished data
Sweden					
Sydkoster	58°51' N	10°02' E	2002*		Axelius and Karlsson (2004)
Eleven	58°53' N	10°59' E	October 2003	Subtidal protected	Axelius and Karlsson (2004)
Medskär	58°52' N	11°04' E	October 2003	Subtidal protected	Axelius and Karlsson (2004)
Persgrunden	58°41' N	10°50' E	2004	Wave exposed	J Karlsson (pers. comm.)
Vinga	57°37' N	11°36' E	2006	Subtidal	Wallentinus (2006)
UK					
Milford Haven, Wales	51°42' N	05°02' W	1999*		CA Maggs (pers. comm.)
Alturlie Point, Moray Firth, Scotland	57°31' N	04°09' W	2004	Stony shore. ** 5 yrs earlier	FC Küpper and CN Campbell (pers. comm.)
Bembridge, Isle of Wight	50°41' N	01°04' W	April 2005		R Lord, verified by CA Maggs
Poole Bay, Dorset	50°39' N	01°52' W	May 2005	Subtidal on maërl bed Tetrasporophytic plants **	V Peña and K Collins, unpublished data