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Spread of the slipper limpet *Crepidula fornicata* (L. 1758) in Europe. Current state and consequences*

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SUMMARY: The present distribution of the slipper limpet *Crepidula fornicata* in Europe is described in detail for each country, and an overview provided thanks to new information. Main observations of introduction and spread, obtained from the literature, are discussed. For most of them, we observe that both aspects are due to oyster harvesting and farming. In the most heavily infested areas (France, England, the Netherlands), activities of dredging, harvesting and oyster farming have been disrupted. In France, these activities are so much hampered that treatment methods are now developed.

Key words: Slipper limpet, *Crepidula fornicata*, invasions, Europe.

RESUMEN: EXPANSIÓN DE LA SEBA *CREPIDULA FORNICATA* (L., 1758) EN EUROPA. SITUACIÓN ACTUAL Y CONSECUENCIAS. – Se presenta la distribución actual de la seba *(Crepidula fornicata)* en Europa, para cada país, a través de las informaciones más recientes. Se discuten las principales observaciones sobre la introducción y proliferación de esta especie, obtenidas de la bibliografía. En la mayoría, la ostreicultura es responsable de ambas fases. En las áreas más afectadas (Francia, Inglaterra, Holanda), el dragado y la ostreicultura se han visto perturbadas. El impacto de esta especie introducida sobre las activida-des marisqueras es muy importante, por lo que se deberían desarollar medios de erradicación.

Palabras clave: Seba, *Crepidula fornicata*, invasiones, Europa.

BIOLOGY

Crepidula fornicata (Linné 1758) is a marine gastropod belonging to the family Calyptraeidae (Blainville 1824). Hoagland (1977), in her systematic study of the family, suggested retaining this commonly-used term rather than the family name Crepidulidae (Fleming 1822) which refers only to the genus *Crepidula* (Lamarck 1799).

This benthic gastropod, which is commonly called slipper limpet, bears a calcareous and slightly spiralled shell about 6 cm long. It is a suspension-feeder, filtering phytoplankton and particulate organic matter. This feeding mode allows it to find sufficient food to develop large populations, unlike other grazing patellids (Hoagland, 1977).

Along European coasts, this species is an oyster pest. It is generally found on the coastal infralittoral grounds, but stranded populations can be observed on the lower part of certain exposed shores. We have found this species from MLWS down to depths of 60 meters in the western Channel. Populations are particularly developed in wave-protected areas such as bays or estuaries or on the inland side of exposed islands. Being ubiquist, eurythermal and euryhaline, this species can be observed in all kinds of environments, i.e., rocky, gravel or sandy bottoms, as well as in muddy areas, where it reaches its highest densities (Hamon and Blanchard, 1995).

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Numerous studies have dealt with slipper limpets, because of two specific characteristics. The first relates to its behaviour. Individuals settle on top of each other, forming clusters. In high-density areas, this creates amazing numbers of stacks giving the aspect of puddings. The second characteristic relates to its sexuality. Similar to several other gastropods, it is protandric, with direct external fertilization. The youngest specimens are male and can inseminate several females lying below. Sexual determinism is rather poorly understood (Collin, 1995). The eggs are protected in bags, and only viable larvae are released. The survival rate is high.

These two physiological particularities, and its considerable adaptability, mainly explain its success. The natural predation rate seems to be low in Europe, where the species was introduced accidentally from America a century ago and has expanded since then, and it appears that the observed European spread will not slow down in the immediate future.

ORIGIN

The genus *Crepidula* has numerous species, most of them confined to the American coasts (Hoagland, 1977). In Europe, only *Crepidula unguiformis* (Lamarck, 1822) and *C. gibbosa* (Defrance, 1818) are native, found in the Mediterranean and Adriatic seas (Hoagland, 1977).

All other species found on our seashores have been introduced. Minchin *et al.* (1995) mention the observation in 1865, in Ireland, of a single specimen of *Crepidula plana* (Say, 1822), but the species never became established in Europe. *C. calyptraeiformis* (Deshayes, 1830) has now been introduced into Alacant harbour (Spain) from South America (Zibrowius, 1991). *C. fornicata* has shown the most spectacular success.

Crepidula fornicata is a native of the North-American Atlantic coast, where it is consistent with three congeneric species: *C. plana, C. convexa* (Say, 1822) and *C. aculeata* (Gmelin, 1791). Walne (1956) described its native geographical area as ranging from Escuminac point (47°N) on the Canadian coastline to the Caribbean islands. This species can be observed in bays and estuaries, and on grounds inshore.

At the end of the 19th century, this species became established in Great Britain, where it thrived. Why only this species settled, and not other *Crepidula*, remains a question. It was imported along with American oysters (*Crassostrea virginica*

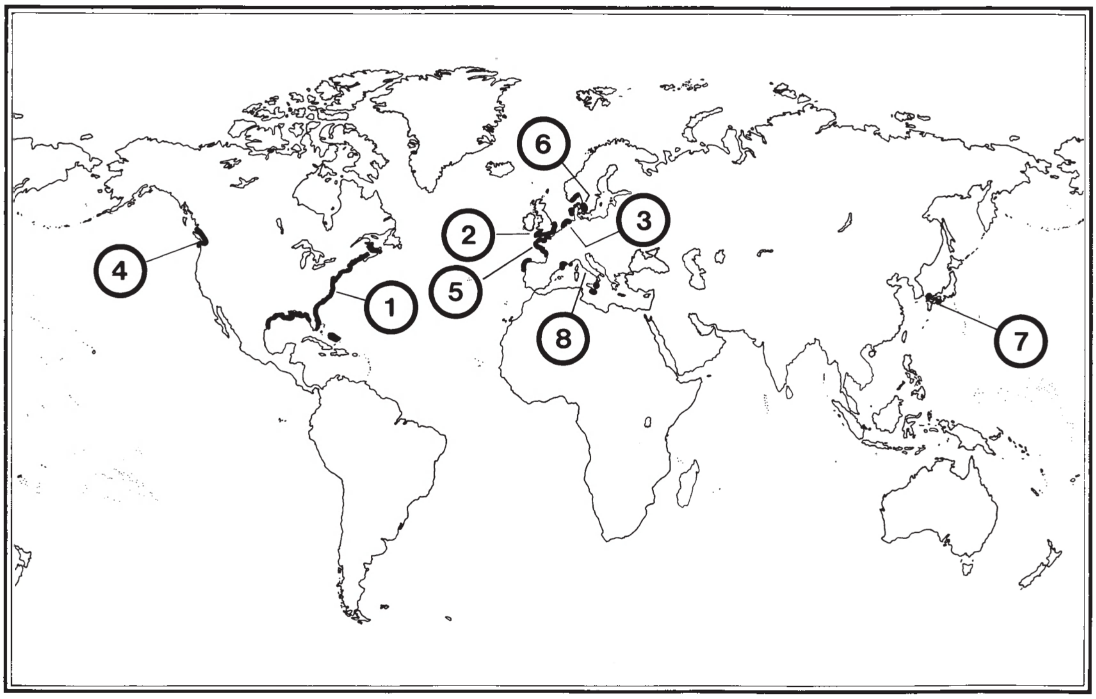

FIG. 1. – World-wide distribution of the slipper limpet (*Crepidula fornicata*) and steps of spread: 1, From Canadian border down to Gulf of Mexico. 2 (1880's), Eastern coast of England. 3 (1910's), Belgium, Germany and the Netherlands. 4 (1930's), Northwestern USA. 5 (1940's), South England and France. 6 (1950's), Denmark, Sweden and Norway. 7 (1970's), Japan. 8 (1970's), Spain and Mediterranean spots.

Gmelin, 1791) which were dredged on beds of Atlantic estuaries. Large quantities of oysters were imported at the end of the last century (Utting and Spencer, 1992; Minchin *et al.*, 1995). Among oysters, many adult limpets were shipped and released in Irish and English ponds. Here they found a favourable environment to settle and develop. Specimens were accidentally carried from place to place, and progressively created new populations. Over recent decades they have spread worldwide, through international shipping. Today the geographical range spans throughout the northern hemisphere (Fig.1).

DISTRIBUTION

Outside Europe

In its native country, *Crepidula fornicata* is now common from Canada to Mexico and is the "most densely packed of the three *Crepidula* species" in New England (Hoagland, 1974, 1977, 1979). In the western USA, it was imported along with oysters in Puget Sound during the 1930's and is now common along the Washington State coastline (Hoagland, 1974, 1977). Some specimens were found on the Uruguayan coast (Walne, 1956), but no others have been mentioned.

In 1968, introduced populations were observed in the bays of Tokyo and Sagami in Japan (Habe and Maze, 1970). This species is now distributed along the coasts of Honshu and Shikoku Islands (Kosuge, Malac. Inst. Tokyo, pers. com.). No specimens have been observed along the African coasts; those described by Dautzenberg in Dakar do not belong to this species (Gofas, Museum Paris, pers. com.). No populations have been mentioned in Indian seas as indicated by Deshayes (1830).

Europe

Unknown in European malacological lists a hundred years ago, the species appeared in Europe via England. Several papers were published, giving detailed first observations, in Great Britain and mainland Europe. No one has provided a general overview of distribution since Adam and Leloup (1934), for Great Britain, the Netherlands, France, and Belgium. The geographical distribution of the species now stretches over 24 degrees of latitude, affecting all European shores (Fig.2).

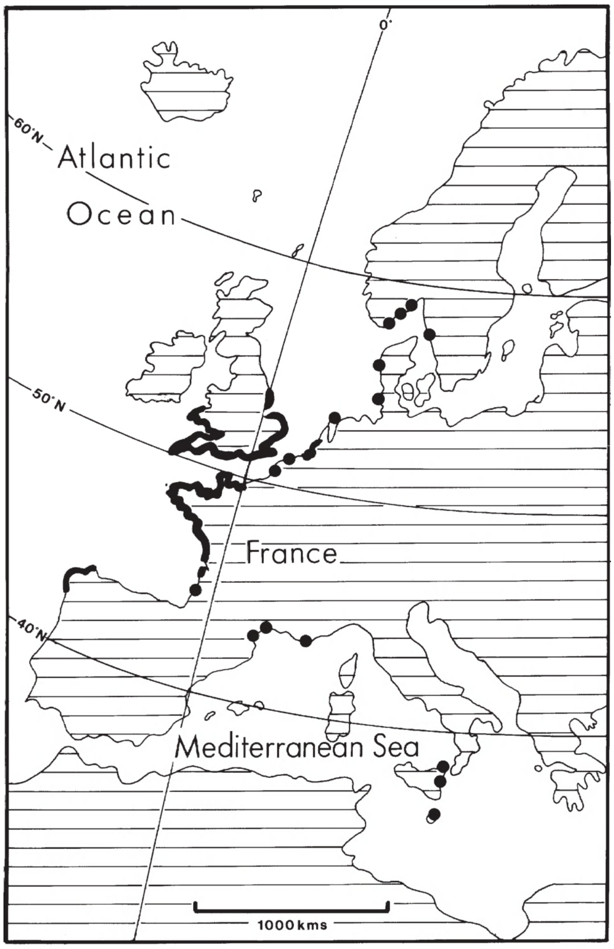

FIG. 2. – European distribution of *Crepidula fornicata*.

a) Great Britain: Utting and Spencer (1992) explain how the slipper limpet landed with American oysters, from the late 1870's to the 1920's, when the latter were imported to boost the English oyster trade after overfishing of *Ostrea edulis* (Linné, 1758) in traditional beds. *Crepidula fornicata* was first observed on oyster beds in Liverpool Bay in 1872 (Mac Milan, 1938), then on the eastern side of England in different localities: Cleethorpes (53°, 34 N), Brightlingsea and Thames estuary where a rapid spread over oyster beds was observed (Crouch, 1893). A progressive extension northwards, but especially on the southern coast, was described in numerous papers (Crouch, 1893; Cole, 1915, 1952; Walne, 1956).

On the Channel coast, the first observation was made in 1913 in the oyster ponds of Bosham, in Portsmouth Bay (Cole, 1952), and around 1930 in the Solent (Barnes *et al.*, 1973). A progressive spread was observed westwards during World War II just reaching Start Point around 1960. Specimens arrived directly in Cornwall in 1944 at Falmouth Bay due to boat hull fouling (Cole, 1952). Spencer (1974) described the distribution area, from the Suffolk seaside on the eastern coast, to mid-Wales on the western side. Currently, distribution seems to be the same as that shown by previous mapping (Spencer, pers. com.), but densities are higher. Oyster beds of the Thames estuary are heavily infested.

From England, the species spread through the North Sea, either through natural transport of larvae, or through oysters transported towards the Netherlands.

b) Belgium: The first continental country to be invaded was Belgium. As early as 1911, a living specimen, of unknown origin, was discovered on oysters in Ostende, then a second on a *Buccinum undatum* (Linné, 1758) in 1923 (Adam and Leloup, 1934). In 1934, the slipper limpet had become common in Ostende and Blankenberghe, on oysters and mussels imported from the Netherlands, since they were not locally farmed (Adam and Leloup, 1934). Today, because of strong currents along the shore, no slipper limpets are observed on the sandy coast, but they are numerous in the Ostende harbour and its pond where oyster farming is developed (Polk, 1976; Christiaens, pers. com.).

c) France: The history of the spread of the species in France has been detailed in a recent paper (Blanchard, 1995). Its rapidity (50 years), and the present biomass of several million tons illustrate the scale of the phenomenon quite well. Hull fouling and oyster farming are the two main reasons behind this. Before World War II, only a few specimens were present in the oyster beds of South Brittany and Charentes, because the open water storage of foreign shellfish was strictly forbidden by law. Some larvae may have travelled through the Channel (Cole, 1952).

In 1949, some specimens were collected on mussel beds in Normandy, some others in Brest, on *Pecten maximus* (L.). These animals came from populations imported during Allied shipping operations, from Great-Britain or directly from the USA (Blanchard, 1995). Only fouling can explain such a rapid introduction at the same time, never observed elsewhere (Cole, 1952). From Brest, the spread increased along the Atlantic coast due to oyster transfers (Marteil, 1963).

During the 70's, direct and massive importations of *Crassostrea gigas* (Thunberg, 1793) were made. At all the sites, they were followed by the appearance of large limpet populations. These Japanese oysters were imported urgently from Japan and the USA and, most of the time, directly laid at sea without any sanitary precautions. Many foreign species were imported in this way and the introduction of the Japanese oyster is considered as an ecological disaster by many authors (Zibrowius, 1991).

Today, millions of metric tons of *Crepidula fornicata* are present on the French coast, from the Seine estuary to the Mediterranean lagoons. Two major areas are heavily colonized: the Norman gulf in the western Channel, and the mid-Atlantic coast such as the Bay of Marennes-Oléron. Both have oyster culture grounds. In both, correlated problems, ecological and economical, are increasing.

d) The Netherlands: Since the direct introduction of American oysters was forbidden, the slipper limpet was introduced from England, either with the water stream carrying larvae from the Channel to the North Sea, or with imported *Ostrea edulis* oysters (Adam and Leloup, 1934). Two shells were found in Bergen-aan-Zee in 1922, and the first live animals were observed in Zandvort on beached wood in 1926, on oyster beds in the Scheldt estuary in 1929, and in Zeeland in 1931, where their rapid spread was noted (Korringa, 1949). From 1935 to 1950, slipper limpets were harvested and the expansion was stabilized in the Scheldt estuary.

Today, the gastropod is still spreading on mussel and oyster plots in Oosterschelde and Lake Grevelingen (Dijkema, 1995). Since the closing of Grevelingen Lake in 1971, the slipper limpet biomass grew so quickly that in 1988 it made up half of the macrozoobenthos (Nienhuis, 1992). In the Wadden Sea *Crepidula fornicata* is absent from Dutch intertidal mussel beds, and rare in subtidal ones. Some years ago, spreading populations of slipper limpet were observed in the Western-Scheldt estuary where they had never existed before. The present situation is serious and the large-scale shellfish industry is thinking of protecting itself against this competitor, by requiring its collection for industrial treatment and use, as previously was done between 1935 and 1950 (Dijkema, 1995).

e) Germany: Werner (1948) found some slipper limpets in mussel beds, in the Wadden Sea, in northern Frisen (Hessland, 1951). They are still present nowadays, but with low densities in the sublittoral and are found "very seldom" in littoral areas (Meixner, pers. com.). Some years ago, Dankers (pers. com.) observed them along Sylt island, near Denmark where they arrived in 1934 (Forsman, 1951). Along the shore, populations are absent because of rough hydrographical conditions. They are not mentioned in the German oyster centre.

f) Denmark: The slipper limpet appeared in 1932 in the Limfjord, with imported Dutch oyster seed (Sparck, 1949; Hessland, 1951). It settled there, becoming rapidly common, then spreading in 1948-1949 to the north-western Kattegat, where its density remained low (Spark, 1949; Hessland, 1951). Today it is still associated with oyster farming on the western coast of Jutland and in the Limfjord, where densities do not seem to be high. This oyster centre was doubtless at the origin of the spread in the Scandinavian waters in the 1950's.

g) Norway: In Norway, *Crepidula fornicata* is mentioned on Hoisaeter's current malacological list (1986), but seems to be rare. It appeared in 1963, in Grimstad, then some specimens were found along the south-eastern coast in Skagerrak (Bergan, 1969; Dommasnes and Schram, 1973; Bergstad, 1974). Six observations have been given, from west to east: Landøya near Mandal, Ny Hellesund, Scottevik near Lillesand, Skåtøy, Kragerø, and Tjøme, but it is possible that the slipper limpet exists in many other places (Bergstad, 1974). The reason for its presence on this coast is more likely due to larval natural transport or boat fouling, than to the presence or trade of oysters, since oysters are hardly farmed here. Only one oyster was found in the area of Skottevik by Bergstad (1974), who noted the possibility of transport by ice. The northern limit of the limpet's geographical distribution is here; Tjøme, in the Oslo fjord, is situated on the latitude of 59°10 N.

h) Sweden: Live slipper limpets were observed in 1950 for the first time on the Bohuslan coast of Sweden (Forsman, 1951; Hessland, 1951). These were young animals (20-30mm length) attached to *Buccinum undatum* or *Cyprina* sp.. The larvae arrived easily from Denmark transported by the flow during 1.5 days, in 1948 or 1949 (Hessland, 1951). Hoisaeter (1986) does not mention it, but some specimens are sometimes found in grabs (Waren, Stockholm Museum, pers. com.). The limpet probably did not spread south of the Oresund path, between Denmark and Sweden, and has not been described in the Baltic fauna.

i) Ireland: A recent paper (Minchin *et al.*, 1995) explains how this species was first found in Ireland in 1902, on English oysters imported from the Essex river, for growth trials in Ballinakill Bay. It has since been recorded in several localities, either on imported oysters or not (Arnold, 1960) but have then always disappeared. Today, Ireland has no true established *Crepidula* population, but the recent easing of oyster transport restrictions by the European Community makes the introduction of limpets possible (Minchin *et al.*, 1995).

j) Spain: In Spain, the slipper limpet was first discovered in the ria of Aldán (Galicia) in the second part of the 70's, arriving with oysters (*Crassostrea gigas*) from France and Ireland (Rolán, 1983; Rolán *et al.*,1985). It is now common in the estuaries of Vigo, Arousa and Ensenada de Aldán (Otero-Schmitt, pers. com.), where it is observed on the bottom, but also on oysters hanging on floating rafts. It seems that the limpet's distribution is limited to these areas of Galician estuaries, where the animal can find a calm environment on the rough Atlantic coast.

k) Portugal: There is no observation of *Crepidula fornicata* in Portugal, and no indication that it is spreading, neither on the western Atlantic side, nor on the southern seaside. It does not seem able to settle on such shores because of strong currents, but also because oyster farming is limited (Albuquerque de Matos, pers.com.).

Along the Mediterranean coasts, *Crepidula fornicata* has not really spread. It appeared in 1982 in Thau lagoon after the transport of Atlantic oysters from the French Charentes grounds (Zibrowius, 1991). We can find some specimens today in several oyster growing zones, in France (Thau, Leucate), in Sicily and Malta. No observation has been made on the Catalonian shores (Pena, pers. com.), or on the southern Spanish ones, nor in Morocco or Algeria (Ferez, pers. com.).

l) Italy: Four dead slipper limpets were observed in 1973 by Di Natale in Riposto on the eastern side of Sicily, but many live ones were collected between 1974 and 1979 on Lake Faro beach, on the north-eastern seaside, along the Messina Strait. They were attached to *Mytilus edulis*, introduced with large stocks of mussels from Holland or Portugal (Di Natale, 1982). We have noted previously (above) that this species seems absent in Portugal. No recent observations have been made and none have ever been made on the mainland seaside.

m) Malta: Cachia (1981) found limpets in Malta, on the shores of Marsaxlokk Bay, in 1973, and in the Marsamxett harbour with oysters in 1975. In 1966 (pers. com.), he had already found three juveniles on the northern coast of the island. The introduction there was probably caused by hull fouling. Marsaxlokk Bay (35°50 N) is the southern limit of the present distribution of the species in Europe. No mention of it has been made in the eastern part of the Mediterranean Sea.

DISTRIBUTION PARAMETERS

Chronology

Three main stages can be observed in the chronology of the slipper limpet spread into and across Europe. First, Great-Britain developed its own populations. Because of oyster farming development, in France and in the Netherlands, spats and adults were exchanged between the Thames estuary, the Atlantic seaside and the Scheldt beds. Before World War II the limpets spread in the North Sea, reaching the Limfjord in Denmark.

During the later phase of the war, a hitherto unseen large-scale shipping operation took place between North-America and Northern-Europe, serving all main harbours and bays. This is when slipper limpets were first observed in Sweden and Germany. After the war, oyster farming started again with many exchanges, leading to the sudden appearance and development of large limpet populations in the Netherlands, France (Marteil,1965) and England (Cole, 1952).

In 1970, the Portuguese oyster (*Ostrea angulata* Lamarck, 1819) became diseased, and its trade dropped worldwide. The Japanese oyster (*Crassostrea gigas*) was quickly imported into all European beds. Many simultaneous slipper limpet observations occured at this time: Mediterranean lagoons, Sicily, Spain, France (Arcachon, Marennes, Norman gulf), etc. Other marine species were also brought into Europe with this importation (Zibrowius, 1991).

Today, we observe a new stage in the spread, in France and in the Netherlands, perhaps due to a change in environmental conditions, which are more favourable to phytoplankton development and thus to some filter feeders. Oyster exchange is perhaps no longer the main reason of the spread.

Spreading causes

a) Natural transport

The ciliated larva of the slipper limpet can move by itself, but is most often carried by water movement during its three-week long pelagic life. It can travel several kilometers a day. This could explain its presence on the Swedish or Norwegian coasts, coming from Denmark within 36 hours (Hessland, 1951), or in Holland, coming from England (Adam and Leloup, 1934) and travelling about 150 kms in a favourable, regular and strong current. Dispersal along northern European shores could be mainly influenced by the direction of currents (Hessland, 1951).

Numerous migratory crustaceans (crabs, spider crabs, or lobsters) have been seen bearing slipper limpets which will scatter them when moulting. Exogean molluscs such as *Pecten maximus*, or *Buccinum undatum* often carry limpets and can cover long distances. Frazier *et al.* (1985) noted that *Crepidula fornicata* is observed on Atlantic turtles *Caretta caretta*.

The slipper limpet can also attach itself to floating material: Korringa (1949) observed it on drift wood in the North Sea. Fouling on ship hulls is one of this species main means of transport. Limpet populations in Malta (Cachia, 1981), and on the Channel French coast (Cole, 1952; Blanchard, 1995), can be explained in this way.

Water ballasts of vessels can transport limpet larvae for several days, releasing them into harbours or bays where they settle. This observation has been made in Hamburg (Gollasch, Zool. Museum Hamburg, pers. com.).

The importance of spreading could be facilitated by a lack of specific predators in Europe. Some of the commonly observed predators (crabs, flatfishes, asterids, drilling gastropods) are harvested with limpet populations. Hoagland (1974) observed that *C. fornicata* is subject, in the USA, to a greater number of predators that the other two species of *Crepidula*, thus explain-

TABLE 1. – Relation between oyster farming and slipper limpet in Europe, from published references.

	INTRODUCTION		SETTLEMENT	
COUNTRIES	VIA OYSTER FARMING	OTHER MEANS	IN OYSTER BEDS	IN OTHER AREAS
ENGLAND	With *Crassostrea virginica* (Mac Milan, 1938), then transferred	Fouling in Cornwall (Cole, 1952)	In Essex and Kent (Crouch, 1893), in Cornwall (Cole, 1952)...	In the Solent (Barnes *et al.*, 1973)
IRELAND	Several introductions with English or American oysters (Minchin *et al.*, 1995)		No	No
BELGIUM	With English (?) oysters (1911) and from Holland in 1934 (Adam and Leloup, 1934)		Ostende and Blankenberghe (Adam and Leloup, 1934; Polk, 1976)	
GERMANY	?	Larval transport from Holland (?), hull fouling in 1945-50`s	In mussel beds (Hessland, 1951)	
THE NETHERLANDS	From England (Adam and Leloup, 1934)	Floating wood (Korringa 1949) and larval transport from England (Adam and Leloup, 1934)	Scheldt estuaries and Grevelingen lake (Dijkema, 1995)	+
DENMARK	Probably with Dutch spat in 1932 (Sparck, 1949)		Oyster culture in western Jutland in Limfjord (Hessland, 1951)	+
SWEDEN	Not proven (Hessland, 1951)	Larval transport from Denmark (Hessland, 1951)	In natural oyster beds (Hessland, 1951)	+
NORWAY	No	Larval transport in Skagerrak or in icebergs (Forsman, 1951)		Dead shells, calcareous sand (Forsman, 1951)
FRANCE	With *O. edulis* before WWII and Japanese oyster in the 1970`s (Blanchard, 1995)	Fouling of Allied ships in 1944-50`s, possible crossing of larvae (Cole, 1952)	Most of French oyster beds (Blanchard, 1995)	Bays and estuaries of the Channel and Atlantic seaside
PORTUGAL		No introduction observed		No settlement observed
SPAIN	From France or Ireland with Japanese oysters (Rolán, 1985)		Galician estuaries, under floating rafts (Rolán, 1983; Rolán *et al.*, 1985)	+
ITALY		From Holland or Portugal with mussels (Di Natale, 1982)	Mussel beds in Sicily (Di Natale, 1982)	On lagoon beaches
MALTA		Hull fouling in 1975 (Cachia, 1981)	"With oysters" in Marsamxett (Cachia, 1981)	On beaches

ing the relatively weak spread along the US coasts. European lists of potential predators and their quantitative evaluation must be compared for various areas and countries, for a better analysis.

b) Human activity

Human activity at sea is the main reason for the present European spread, through oyster farming and shellfish harvesting. Once some specimens have settled in an oyster bed, or in an area inhabited by shellfish, the population is than scattered by dredging. Unsuitable species or empty shells with limpets are thrown overboard. In the northern countries, Hessland (1951) noted that apart from natural larval transport, "this species is also disseminated by the agency of man, especially in England and Denmark". The following observations made in France are also valid everywhere.

b.1) Oyster farming

Introduction and settlement of *Crepidula fornicata* in Europe are closely related to oyster *(Ostrea edulis)* farming. There are large similarities between these two species (Hoagland, 1977): both are suspension-feeders, have a variable morphology and the ability to change sex, are fixed to an underwater support, generally hard to avoid muddy sediment and biodeposits. Some oysters and members of the Calyptraeidae can breed larvae before hatching. This family can be compared to the Anomiidae, whose behaviour is similar to that of oysters (Hoagland, 1977).

Sticking: This phenomenon is common to all oyster species. All farmed oysters in Europe are infested. We can also observe that adults or juveniles are equally infested.

Ecology: Environmental parameters conducive to the spreading of limpets are very similar to those of natural oyster beds: water movement, depth, salinity, suspension matter, type of bottom, etc. Several publications have underlined the parallels (Hoagland, 1977; Korringa, 1949).

Obstacle supply: For oyster farming, beds are modified. Oyster spats are glued onto collectors which are often made using empty shells. Wooden, metallic or plastic frames are also used. All these materials are laid out on the seashore, where they slow down current speed, allowing limpet larvae to drop and fix onto them. Oyster mortality also means many empty shells where limpets can adhere.

Bottom modifications: For vehicles, trails are constructed on the shore between oyster beds. When the oysters are themselves grown directly on the bottom, they need it hard and not muddy. Thus many areas are hardened with gravel, sand, or crushed shells. Unfortunately, this sediment is what slipper limpets prefer, too. Oyster ponds or beds produce a large biomass of organic matter (biodeposits), not found elsewhere. Its effect on limpet larvae is unknown, but could be positive. Calcium phosphate ($CaPO_3$) is often laid as a fertilizer for shell development in the beds. Here again, its effect on slipper limpets is unknown.

Oyster exchange: Dijkema (1995), in describing Dutch oyster fishery and farming, showed the importance of oyster *(Ostrea edulis)* transport between England, France, the Netherlands and Denmark, in the 19th and early 20th centuries. In the beginning, the imported oysters were sold directly. Progressively, small ones where sown on sheltered beds for ongrowing. This technique was practiced everywhere (Utting and Spencer, 1992; Minchin *et al.*, 1995), thus the associated fauna were directly introduced. Everywhere, the direct import of *Crassostrea gigas* from USA or Japan in the 1970's without systematic checks, was the begining of numerous slipper limpets colonies.

Cleaning ponds: Traditional pond cleaning operations consist of throwing away the undesirable species, thus embankments are sometimes seen around oyster ponds. Grouping the slipper limpets together is a good way to help fertilize them.

b.2) Harvesting

In coastal shellfish beds, where the bottom is normally sandy or mixed with gravel and where carbonate is high, bivalves and gastropods are present in great density, as also are slipper limpets. In these areas, harvesting is facing the limpet problem.

Scattering: Harvest selection is followed by disposal of various unused species, such that the slipper limpet is regularly scattered in the same bays over many years. Adults or eggs are taken from the harvested point to other areas, sometimes quite distant. Our observations in the Norman gulf, in the western Channel, show that during a day's dredging for scallop, tons of limpets are scattered in that way.

Bottom modification: Heavy dredges, or trawl boards, plough long furrows where limpets and dead shells accumulate. These environments, if not disturbed, are very comfortable for slipper limpets (low velocity, biodeposition, supports). They rapidly develop new stacks there and spread (Hamon and Blanchard, 1994). Passing regularly and mixing the bottom with fishing gears pulls out fine particles and hardens the bottom area, thus providing a better sediment for limpets.

Breakage: Harvesting shellfish leads to many broken shells which become supports for slipper limpets. Broken stacks can also create new multiple supports.

IMPACT OF THE SPREAD

Several consequences due to the spread of the slipper limpet along the European coast have been observed. These can be combined into two categories: ecological and economic.

Ecological impacts

Spatial competition. Slipper limpet stacks, when numerous, prevent other larvae and juveniles from settling. Few other large bivalves can move or settle among dense limpet populations. This disturbs the fishing activity using trawls and dredges. In the Norman gulf (France), many traditional fishing areas have been abandoned and activities shifted.

Bottom raising. High densities of limpets raise the bottom in two ways. By disturbing the normal water flow, the limpet population stops and traps the finer particles of the suspended matters. Secondly, the large biodeposits of such populations accumulate. The bottom gains several centimeters of mud each year as in the Bay of Brest. Elsewhere, in onshore oyster-beds, high densities of limpets create obstacles to running water during ebb tide and water stays there disturbing the oyster metabolism.

Trophic competition. Slipper limpets compete for food with other species feeding on phytoplankton and suspended matter, such as mussels, oysters, etc. When limpets reach large densities, available food decreases, and all species become weaker. We can also imagine that their reproductive and growth rates become lower (Dijkema, 1995). Several studies on limpets food are necessary to confirm this competition.

Economic consequences

Dense limpet populations disturb fishery or oyster farming activities to such an extent that, in some bays (Scheldt estuaries in Zeland, Thames estuary in Great Britain, the Norman gulf or Marennes bay in France), cleaning operations are necessary. Expensive treatment methods are developed in France, and public spending is constantly increasing. Yet applying regulations at the earliest observations would suffice to halt this spread. We observe now in dense areas the consequences of insufficient surveillance and precautions during the importation period. Present activities hampered by slipper limpets are those which, for a hundred years, contributed to their spread, accidentally or not. The backlash comes late. It was foreseeable and avoidable.

CONCLUSIONS

The slipper limpet spread in Europe has become a serious problem. For a hundred years, this species found environmental conditions so favourable that we observe not only a wide geographic distribution, from Scandinavian coasts to the mid Mediterranean, but also particularly local and massive spreads. Some plots of heavy spread exist today in the Thames or Solent estuaries in England, in the Norman gulf in France, or in the Scheldt estuaries in the Netherlands. Others are appearing elsewhere.

Every year, several species are accidentally or purposely imported; some of them die, while others survive and can develop large populations without creating any damage. Reasons for such a spread in Europe have not been explained completely. On the U.S. coasts, no observations have been made of such densities. Anthropogenic activities are, as we have seen, the main reasons for the spread, but some environmental parameters are also necessary for the population to develop. It would be interesting to compare environmental conditions between American plots and several European ones to explain the reasons for success or failure. We can also wonder, amongst all the *Crepidula* species living on the eastern American coast, why only *C. fornicata* thrives in Europe. Research of industrial uses must also be carried out, since, for dealing with this spread, the only effective treatment known is their regular harvest to reach a minimum density.

The European oyster industry is facing a serious problem for the quality of its environment in several places, in France, England and the Netherlands. If a real effort is made by all parties concerned (professional organisations, scientists and regulating authorities), this industry will be able to face the problem, and allow the preservation of shellfish aquaculture.

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