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Positive Feedback Loop between Introductions of Non-Native Marine Species and Cultivation of Oysters in Europe

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Abstract: *With globalization, agriculture and aquaculture activities are increasingly affected by diseases that are spread through movement of crops and stock. Such movements are also associated with the introduction of non-native species via hitchhiking individual organisms. The oyster industry, one of the most important forms of marine aquaculture, embodies these issues. In Europe disease outbreaks affecting cultivated populations of the naturalized oyster* Crassostrea gigas *caused a major disruption of production in the late 1960s and early 1970s. Mitigation procedures involved massive imports of stock from the species' native range in the northwestern Pacific from 1971 to 1977. We assessed the role stock imports played in the introduction of non-native marine species (including pathogens) from the northwestern Pacific to Europe through a methodological and critical appraisal of record data. The discovery rate of non-native species (a proxy for the introduction rate) from 1966 to 2012 suggests a continuous vector activity over the entire period. Disease outbreaks that have been affecting oyster production since 2008 may be a result of imports from the northwestern Pacific, and such imports are again being considered as an answer to the crisis. Although successful as a remedy in the short and medium terms, such translocations may bring new diseases that may trigger yet more imports (self-reinforcing or positive feedback loop) and lead to the introduction of more hitchhikers. Although there is a legal framework to prevent or reduce these introductions, existing procedures should be improved.*

Keywords: biological invasions, hitchhikers, mollusc diseases, non-indigenous species, OsHV-1, oyster farming, pathways, vectors

Ciclo de Retroalimentación Positiva entre la Introducción de Especies Marinas No-Nativas y el Cultivo de Ostras en Europa

Resumen: *Con la globalización, las actividades de agricultura y acuacultura son afectadas cada vez más por enfermedades que se extienden por medio del movimiento de cultivos y ganado. Dichos movimientos también están asociados con la introducción de especies no-nativas por medio de organismos individuales que viajan como pasajeros en otros organismos o mercancía. La industria de las ostras, una de las formas más importantes de acuacultura marina, encarna estos problemas. En Europa, los brotes de enfermedades que afectaron a las poblaciones cultivadas de la ostra naturalizada* Crassostrea gigas *causaron grandes perturbaciones al final de la década de 1960 y al inicio de la década de 1970 y los procedimientos de mitigación involucraron una importación masiva de un stock de la extensión nativa de la especie en el Pacífico noroeste de 1971 a 1977. Evaluamos el papel que tuvieron las importaciones de stocks en la introducción de una especie marina no-nativa (incluyendo patógenos) desde el Pacífico noroeste hacia Europa por medio de una*

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valoración crítica y metodológica de datos registrados. La tasa de descubrimiento de especies no-nativas (un representante de la tasa de introducción) de 1966 a 2012 sugiere una actividad continua de vectores a lo largo de todo el periodo. Los brotes de enfermedades que han afectado a la producción de ostras desde 2008 pueden ser un resultado de importaciones del Pacífico noroeste, y dichas importaciones se están considerando una vez más como una respuesta a la crisis. Aunque es un remedio exitoso en términos de corto y mediano plazo, dichas reubicaciones pueden traer consigo nuevas enfermedades que pueden activar aun más importaciones (auto-reforzantes o ciclo de retroalimentación positiva) y llevar a la introducción de más especies que viajan como pasajeros. Aunque hay un marco de trabajo legal para prevenir o reducir estas introducciones, se deben mejorar los procedimientos existentes.

Palabras Clave: cultivo de ostras, enfermedades de moluscos, especies no-nativas, invasiones biológicas, OsHV-1, pasajeros, senderos, vectores

Introduction

Movement of crop and livestock species often triggers the spread of diseases and can affect both agriculture (Ferguson et al. 2001; Kilpatrick et al. 2006) and aquaculture (Green et al. 2011; Oidtmann et al. 2011). It can also lead to the introduction of hitchhiking alien species that are detrimental to those activities or to the surrounding ecosystems (Hulme 2005; Guillemaud et al. 2011). Pinpointing pathways (i.e., routes) (sensu Lockwood et al. 2007) and vectors of transport for introduction events is an investigative process that often necessarily relies on a posteriori hypotheses. The combination of pathways and vectors can result in complex and multiple dispersal patterns (Wilson et al. 2008), especially in the light of globalization and changes in connectivity in ecosystems influenced by human activities. In the case of long-distance human-mediated dispersal, aquaculture practices involving the transport of live shellfish, especially oysters, have been identified, along with maritime traffic (ballast water and fouling), as the main vectors for alien introductions in marine systems (Elton 1958; Molnar et al. 2008).

In Europe the majority of oyster production is in France, where the shellfish industry supports around 20,000 jobs (CNC 2012) along the Atlantic and Mediterranean coasts. *Crassostrea gigas* (syn. *Crassostrea angulata*), which originates from the northwestern (NW) Pacific, is the most intensively cultivated oyster species in Europe and worldwide (FAO 2014). This species was originally introduced from East Asia into Portugal, where it naturalized probably around the 16th century (O'Foighil et al. 1998). Portuguese *C. gigas* successfully established on French Atlantic coasts by the late 19th century and became the main cultivated species in the 1920s, after the decline of the native flat oyster *Ostrea edulis* due to overfishing and mortality (Goulletquer & Héral 1997). The switch of species allowed French oyster production to double in the following decades (Héral & Deslous-Paoli 1991). In the 1960s, aquaculture trials of imported Japanese *Crassostrea gigas* spat were undertaken in France (1963) and in the Netherlands (1964) (Drinkwaard 1999; Goulevant 2004). These were mostly unofficial trials intended to boost production at a time of declining performance of Portuguese *C. gigas* (Grizel & Héral 1991). In 1966 and 1970, French oyster stock and production were hit by 2 successive disease outbreaks, gill disease and haemocyte disease, associated with irido-like viruses (Comps & Duthoit 1976; Renault 2008). The start of these episodes of mortality was coincident, in both time and space, with aquaculture trials of Japanese *C. gigas* (Goulevant 2004), suggested as the source of the irido-like virus (Maclachlan & Dubovi 2011). To save their industry, oyster farmers, later aided by French authorities, imported oysters from the North Pacific (Goulevant 2004). Several hundred tons of adult *C. gigas* were imported from British Columbia, Canada, from 1971 to 1973 to restore spawning stocks, and 10,015 t of spat (on spat collectors) were imported from Japan to sustain short-term production from 1971 to 1977 (Grizel & Héral 1991). These operations were an economic success, but it led to the introduction of multiple non-native hitchhiker species to European waters, such as the Japanese invasive seaweeds *Undaria pinnatifida* and *Sargassum muticum* that were observed in Europe since the early 1970s (Pérez et al. 1981; Critchley et al. 1983). These ecosystem engineers are now widespread and are major components of many European coastal systems (Schaffelke & Hewitt 2007). From 2008 onwards, massive mortalities of *C. gigas* spat have been reported, mainly attributed to a herpesvirus (AHAW 2010; Segarra et al. 2010). This disease outbreak poses a new threat to the oyster industry, and a rescue might involve further massive importation of oyster stock.

With the prospect of such importations and their known risks in terms of biosecurity, we systematically evaluated the role of oyster shipments in current and past introductions of non-native marine species. Asia is the area of origin for *C. gigas* oysters and their hitchhikers known to have been introduced to Europe (e.g., Gruet et al. 1976), so we focused on the NW Pacific to Europe pathway (i.e., species introduced by the routes joining these 2 regions). We compiled data on marine non-native species (including parasites and viruses of oysters) that have been introduced by this pathway and assessed the likelihood that oyster shipments, relative to maritime traffic (ballast water and fouling), were the vector. Marine introductions have other potential vectors (e.g., aquarium trade, fishing nets, canals) (Minchin et al. 2009), so we also scrutinized the literature to determine the relevance of these vectors to the NW Pacific to Europe pathway

Because no information on post-1977 oyster imports was available, we determined the frequency and timing of primary introductions (i.e., first records of non-native species in the primary location of introduction) as an indicator of pathway and vector activity.

Methods

Species Selection and Scoring

Data relevant to introduced (as defined by Blackburn et al. 2011) marine species in Europe (i.e., northeastern Atlantic and Mediterranean and Black Seas) were gathered. They were obtained from comprehensive lists of non-native species: DAISIE (2013), the Global Invasive Species Database (ISSG 2013), and other literature sources. These data were filtered to retain introductions related to the pathway NW Pacific to Europe (without removing possible indirect, stepping-stone, movements via a third area) by keeping only species native to the NW Pacific (i.e., Japanese archipelago and surroundings).

For all retained species, we carried out a comprehensive bibliographic review (Supporting Information), in which we focused on their initial introduction into Europe (i.e., circumstances of first observations). Species were grouped into 3 categories: those specifically associated with oysters (viruses, bacteria, parasitic unicellular eukaryotes, and parasitic crustaceans); non-parasitic animal (invertebrate) species; and algae (macroalgae and microalgae) introduced into coastal communities. Organisms in the first category are all (at least occasionally) pathogenic, whereas those in the second and third categories are hitchhikers because their association with oysters (as epibionts or propagules inside the valves) is facultative or transient. Hitchhikers usually are non-pathogenic species, although they can have a negative impact on aquaculture activities and ecosystems (Schaffelke and Hewitt 2007; Molnar et al. 2008).

For the NW Pacific species selected, we assessed the likelihood of primary introduction events being linked to the movement of *C. gigas* from the NW Pacific to Europe by scoring them (see bibliographic review in Supporting Information). All primary introduction events prior to known imports of *C. gigas* from Asia for aquaculture purposes were rejected and assigned a negative score (−) because it is unlikely these events are related to the NW Pacific to Europe oyster trade. Although the oyster trade could potentially be involved in almost any other marine introduction, we used the most parsimonious (plausible) explanation and considered a pathway to be very likely linked to this vector (++) only if the primary introduction event occurred at a locality with oyster farming activities within 2 km of the observation and the species involved, or some of its closest relatives, can be epibionts or endobionts of oysters. Primary introduction events outside the 2 km radius of oyster farming activities and within 15 km of known international maritime traffic lanes or hubs were scored only as likely (+) because other vectors could not be excluded.

Temporal Trends

Primary introduction events scored as very likely (++) were chronologically plotted alongside data for European and French production of *Crassostrea gigas* for 1950–2012. Production data were retrieved from the Food and Agriculture Organisation database (FAO 2014). A linear regression was performed on the cumulative number of introductions over time. Because oyster production is influenced by numerous parameters, including biological (e.g., recruitment, natural mortality, and diseases), environmental (e.g., temperature, abundance of food resources), and socioeconomic factors (e.g., market values), it was used only as a descriptive timeline. Graphic output was created in SigmaPlot 10.0 (Systat Software).

Results

From exhaustive lists of non-native marine species in Europe, 68 species native to the NW Pacific (Table 1) were retained. Detailed examination of initial European records confirmed that maritime traffic and aquaculture were the most plausible candidate vectors (see Supporting Information for details).

Ten species received negative scores (−) because we considered them unlikely to have been introduced through oyster imports. The most recent introduction, *Perinereis linea*, probably occurred through the bait trade (Arias et al. 2013). The remaining species with negative scores were introduced prior to 1963, the year of the first known imports of *C. gigas* from the NW Pacific for aquaculture purposes (Goulevant 2004).

Some post-1963 introductions, such as the macroalga *Hypnea flexicaulis* and the invertebrates *Botrylloides violaceus, Caprella mutica, Didemnum vexillum, Hemigrapsus takanoi, Hemigrapsus sanguineus*, and *Tricellaria inopinata*, were first found in areas where *C. gigas* was cultured but where the involvement of other overseas maritime vectors could not be excluded. These species were not retained for the final estimate. Introduction of the parasite *Bonamia ostreae* was unambiguously linked to the oyster trade but via a different pathway (i.e., imports of *O. edulis*, and not *C. gigas* oysters, from California) (Cigarria & Elston 1997).

Forty-eight species were retained as very likely to have been introduced through the NW Pacific to Europe pathway with the oyster trade as vector (Table 1). Although not recorded for the first time in direct

Table 1. First records, used as a proxy for primary introduction events[a], of northwestern Pacific marine species introductions into Europe and likelihood that these introduction are associated with transfer of oysters (*Crassostrea gigas*).

Year	*Scientific name*	*Category[b]*	*Region of first observation in Europe (ISO code for country)*	*Likelihood of first introduction by* C. gigas *trade from the NW Pacific to Europe pathway[c]*
1600s	*Crassostrea gigas* (= *Crassostrea angulata*)	2	Atlantic (PT)	–
1832	*Neosiphonia harveyi*	3	Atlantic (F)	–
1845	*Codium fragile* subsp. *fragile*	3	Atlantic (IE)	–
1893	*Bonnemaisonia hamifera*	3	Atlantic (UK)	–
1876	*Gonionemus vertens*	2	Mediterranean (F)	–
1896	*Diadumene lineata*	2	Atlantic (UK)	–
1905	*Colpomenia peregrina*	3	Atlantic (F, UK)	–
1941	*Rapana venosa*	2	Black Sea (RU)	–
1953	*Styela clava*	2	Atlantic (UK)	–
1966	Ostreid irido-like virus	1	Atlantic (F)	++
1968	*Grateloupia subpectinata*	3	Atlantic (UK)	++
1969	*Grateloupia turuturu*	3	Atlantic (UK)	++
	Marteilia refringens	1	Atlantic (F)	++
1970	*Myicola ostreae*	1	Atlantic (F)	++
1971	*Undaria pinnatifida*	3	Mediterranean (F)	++
1972	*Sargassum muticum*	3	Atlantic (F)	++
	Venerupis philippinarum	2	Atlantic (F)	+
1975	*Aiptasia pulchella*	2	Atlantic (F)	++
	Anomia chinensis	2	Atlantic (F)	++
	Balanus cf. *amphitrite*	2	Atlantic (F)	++
	Fistulobalanus cf. *albicostatus*	2	Atlantic (F)	++
	Hydroides ezoensis	2	Atlantic (F)	++
1976	*Saccharina japonica*	3	Mediterranean (F)	++
1977	*Mytilicola orientalis*	1	Atlantic (F)	++
1978	*Chrysymenia wrightii*	3	Mediterranean (F)	++
1979	*Bonamia ostreae*	1	Atlantic (F)	+
	Lomentaria hakodatensis	3	Mediterranean (F)	++
1981	*Sphaerotrichia firma*	3	Mediterranean (F)	++
1982	*Arcuatula senhousia*	2	Mediterranean (F)	++
	Perophora japonica	2	Atlantic (F)	++
	Tricellaria inopinata	2	Mediterranean (IT)	+
1983	*Watersipora subtorquata*	2	Atlantic (F)	++
1984	*Dasya sessilis*	3	Mediterranean (F)	++
	Derbesia rhizophora	3	Mediterranean (F)	++
	Laurencia okamurae	3	Mediterranean (F)	++
	Ulva pertusa	3	Mediterranean (F)	++
1985	*Grateloupia asiatica*	3	Mediterranean (F)	++
	Grateloupia lanceolata	3	Mediterranean (F)	++
1986	*Caulacanthus okamurae*	3	Atlantic (F)	++
1988	*Antithamnion nipponicum*	3	Mediterranean (F)	++
1988	*Nitophyllum stellato-corticatum*	3	Mediterranean (F)	++
1989	*Laurencia brongniartii*	3	Atlantic (F)	+
1991	Ostreid herpesvirus (OsHV-1)	1	Atlantic (F)	++
1991	*Didemnum vexillum*	2	Atlantic (NL)	+
1992	*Haminoea japonica*	2	Atlantic (F)	++
1993	*Caprella mutica*	2	Atlantic (NL)	+
	Polysiphonia morrowii	3	Atlantic (F)	++
1994	*Ahnfeltiopsis flabelliformis*	3	Mediterranean (F)	++
	Chondrus giganteus f. flabellatus	3	Mediterranean (F)	++
	Grateloupia patens	3	Mediterranean (F)	++
	Hemigrapsus takanoi	2	Atlantic (F)	+
	Dasysiphonia japonica	3	Atlantic (F)	++
	Lithophyllum yessoense	3	Mediterranean (F)	++

Continued

Table 1. Continued.

Year	Scientific name	Category[b]	Region of first observation in Europe (ISO code for country)	Likelihood of first introduction by C. gigas trade from the NW Pacific to Europe pathway[c]
1995	*Ocenebra inornata*	2	Atlantic (F)	++
1995	*Alexandrium catenella*	3	Mediterranean (F)	++
1996	*Celtodoryx ciocalyptoides*	2	Atlantic (F)	++
1997	*Gracilaria vermiculophylla*	3	Atlantic (F)	++
	Herposiphonia parca	3	Mediterranean (F)	++
1998	*Pterosiphonia tanakae*	3	Mediterranean (F)	++
1999	*Botrylloides violaceus*	2	Atlantic (NL)	+
	Hemigrapsus sanguineus	2	Atlantic (F, NL)	+
2002	*Rugulopteryx okamurae*	3	Mediterranean (F)	++
2005	*Nemalion vermiculare*	3	Mediterranean (F)	++
2008	*Polyopes lancifolius*	3	Atlantic (F)	++
2009	*Hypnea flexicaulis*	3	Mediterranean (IT)	+
2010	*Gelidium vagum*	3	Atlantic (NL)	++
	Gracilariopsis chorda	3	Atlantic (F)	++
	Pyropia suborbiculata	3	Atlantic (ES)	+
2012	*Perinereis linea*	2	Mediterranean (ES)	-

[a] *A primary introduction event is the first arrival of a given non-native species in a new biogeographical area (e.g., Europe), whereas secondary introductions refer to the spreading, natural or human mediated, of that species in the new area.*

[b] *Key: 1, parasites and diseases; 2, invertebrates (excluding parasites); 3, algae.*

[c] *Key: –, not likely or no sufficient information; +, likely, but other vectors could not be excluded; ++, very likely. Details on taxonomy, comments, and relevant bibliography are in Supporting Information.*

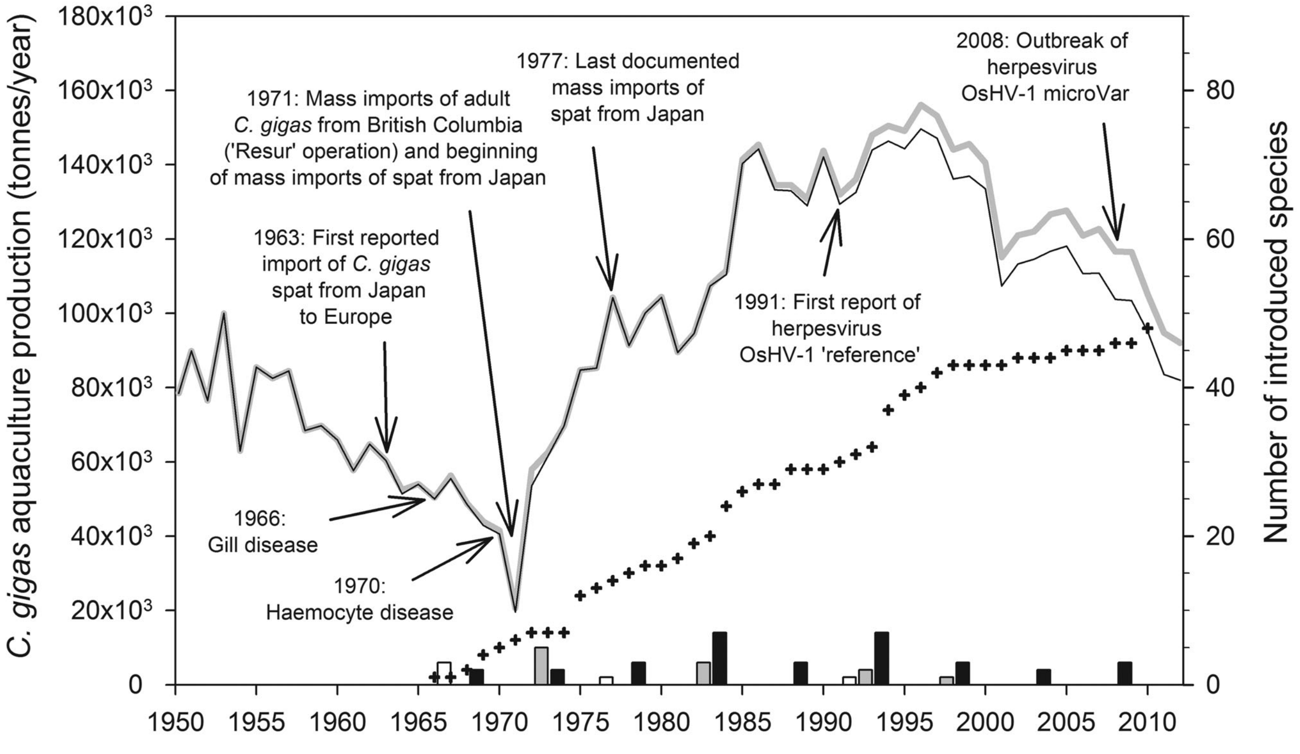

Figure 1. European (grey line) and French (black line) production of Crassostrea gigas *oysters (1950–2012) (FAO 2014) and cumulative (+) and 5-year totals (bars) for numbers of primary introductions of marine North Pacific species into Europe attributed to imports of* C. gigas *(white bars, parasites and diseases; grey bars, invertebrates; black bars, algae).*

proximity (within 2 km) of oyster farming facilities, we included the seaweeds *Grateloupia subpectinata*, *G. turuturu*, and *Sargassum muticum*, based on general consensus in the literature. Forty-five of these 48 species were first observed in France, 22 on Atlantic shores and 23 in the coastal Mediterranean lagoon of Thau. The other localities were the south of England (2 species) and the Oosterschelde Estuary in the Netherlands (1 species). For *Caulacanthus okamurae*, *Gelidium vagum, Haminoaea japonica, Ocenebra inornata*, and *Sargassum muticum*, a secondary introduction from Japan to Europe via British Columbia with *C. gigas* transfers (stepping stone pathway) appeared plausible (Supporting Information). The rate of discovery of introductions into Europe was steady from 1966 to 2010 (linear regression, $R^2 = 0.98$; $p < 0.000001$): constant rate of 1.16 introduced species/year (Fig. 1).

Discussion

Through our systematic method, we selected species introduced from the NW Pacific into Europe and were able to scrutinize the circumstances of initial introductions. Assignment to the vector oyster import, rather than to other vectors such as maritime traffic, was mostly based on geographical considerations (i.e., first observation in the vicinity of oyster farms). Other considerations also tended to support this assignment for the majority of the species. For instance, species living in symbiosis with oysters (parasites and viruses) are most likely, by their nature, to have arrived with oysters. In terms of macroalgae, these organisms accounted for 66% of the species retained in the final list. Whereas modern maritime vectors can carry high loads of hitchhiker propagules (e.g., Verling et al. 2005), species-level macroalgal surveys showed that boats carry only few very tolerant cosmopolitan groups, either as propagules in ballast water (Flagella et al. 2007) or growing on hulls (Mineur et al. 2007*a*). No evidence has been found to show the presence on maritime vectors of the species (or even distantly related taxa) selected in the present study. On the other hand, oyster shipments include a wide array of species (including some presently selected), even after cleaning processes (Mineur et al. 2007*b*). General conditions of transport of oysters—a few days in optimal, moist, stable conditions via air transport—are more suitable for survival of hitchhiking organisms than several weeks of ocean navigation (on hulls or in ballast tanks of ships) involving numerous environmental changes (mainly salinity and temperature). Although vectors linked to maritime vectors were not excluded in a number of cases, no clear evidence was found for their involvement in the NW Pacific to Europe pathway. Therefore, the number of species assumed to be very likely introduced through oyster imports is a conservative estimate.

Although European inventories of marine biodiversity cover all coastal regions (Costello et al. 2013), records of primary introductions during the last 50 years indicate that the main oyster farming regions (e.g., Thau Lagoon, Oosterschelde Estuary, Gulf of Morbihan) are common places of introductions of NW Pacific origin. Commercial transfers of shellfish across oceans have been reported since the 19th century. For instance, imports and trials of *Crassostrea virginica* from the East Coast of the United States were undertaken in France during the 1860s (Fischer 1865), followed by England and Denmark (Carlton & Mann 1996). Occasional imports of *C. gigas* from the NW Pacific to Europe during that period, with potential release of hitchhikers (e.g., *Bonnemaisonia hamifera*, *Colpomenia peregrina*, *Diadumene lineata*), cannot be completely ruled out. To a certain degree, historical production, movement, and trade of oysters in Europe are documented (e.g., Philpots 1890; Schodduyn 1931; Edwards 1976; Héral & Deslous-Paoli 1991; Drinkwaard 1999). So far, no historical mention of such imports taking place before 1963 has emerged. Nonetheless, Edwards (1976) considered that such imports could have occurred as early as the 17th century. As an alternative to the hull-fouling hypothesis, this could explain the origin of the *C. gigas* (= *C. angulata*) population in the Tagus Estuary (Portugal).

We found a constant rate of discovery of alien species from 1966 onwards. Although we used the arrival of new exotic species as a proxy for (reported or unreported) imports of oysters, caution must be exercised in correlating the 2 parameters (Haydar & Wolff 2011). In their earliest stages, most biological invasions are likely to be undetectable and to fall below some detection threshold, depending on population density and survey effort (Carey 1996; Lockwood et al. 2007). This could lead to an unknown lag between a primary introduction event and first observation. Reported imports of North Pacific *C. gigas* oysters ceased after 1977 (Grizel & Héral 1991), so the rate of primary introductions associated with this pathway would be expected to have declined. Nonetheless, there was a constant rate of discovery from 1966 to 2010. Considering the lag between introductions and first observations, a potential explanation of this rate of discovery is the slow discovery, spanning several decades, of an original pool of species introduced in the 1970s. However, some of the most recent introductions seem to have been detected soon after they occurred, before they began to spread (Mineur et al. 2010, 2012). We therefore suggest that the constant discovery rate of non-native marine species is more likely the result of regular arrivals of new introduced species and could be considered as forensic evidence that unreported imports and relaying of oysters from the North Pacific into Europe occurred after 1977.

Another piece of evidence supporting our inference of unreported post-1977 oyster imports from East Asia concerns recent outbreaks of ostreid herpesviruses, which affects *C. gigas* stock (AHAW 2010; Segarra et al. 2010; Renault et al. 2012). Ostreid herpesviruses DNA sequences available from different parts of the world show East Asia to be an area where most of the genetic diversity occurs. The area contains some ostreid herpesviruses identical (or very close) to the European genotypes (OsHV-1 'reference' and μVar) and many endemic genotypes in both cultured and wild symptom-free populations of different native *Crassostrea* species (Moss et al. 2007; Shimahara et al. 2012; Hwang et al. 2013). Asia also appears to be the main center of diversity for *Crassostrea* (with Atlantic *C. virginica* being the result of a much older speciation event) (Reece et al. 2008), which may indicate host-pathogen coevolution processes. Therefore, an Asian origin for ostreid herpesviruses that have emerged in Europe could be hypothesized (F.M. et al., unpublished data). Alongside ostreid herpesviruses, the presence of pathogenic bacteria, such as *Nocardia crassostreae* and *Vibrio aestuarianus*, on European shores, possibly introduced with oyster transfers from the North Pacific (Supporting Information), is associated with important summer mortalities of both juvenile and adult oysters (Garnier et al. 2007). Due to their severity, those diseases are presently threatening the future of the European oyster industry.

Importing new oyster brood stocks from the native area was a successful policy during the 1970s crisis. It not only saved the oyster industry, but also helped increase production to its highest level (Buestel et al. 2009). Similar initiatives on a smaller scale were probably sporadically undertaken after 1977 until the 2000s, as our data tend to show. Large scale importations have been again considered by the French Ministry of Agriculture as an answer to the high mortality of oysters since 2008 (Le Maire 2010). Although maintaining or increasing brood stock diversity may effectively induce resistance against locally emerging diseases, such practices are well known for bringing new non-native species, including pathogenic species (Renault 1996). Emergence of new pathogens coupled with intensification of cultivation methods (e.g., increasing stock densities, spat production in hatcheries, use of triploids) may therefore be responsible for the high mortality that triggers more imports in a positive feedback loop (Fig. 2).

Such sequences of events, starting with trials of exogenous strains or cultivars carrying pathogens that prompt more imports of these strains or cultivars as a remedy, have parallels with the wine blight that affected French vineyards in the 19th century. The destruction of French vineyards was caused by accidental introduction of the phylloxera *Daktulosphaira vitifoliae* with American vines, which lead to more imports of resistant vine rootstocks from North America (Campbell 2005).

Mortalities caused by new pathogens can induce short-term declines of production, whereas selection pressure is exercised on the stock. Over the long term, adding new strains may be a viable option for monospecific aquaculture or agriculture activities because it can maintain genetic diversity of broodstock and resistance to a wide range of pathogens (e.g., Kellerhals et al. 2012).

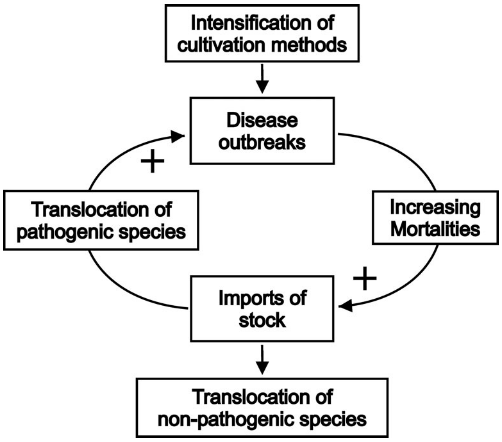

Figure 2. Schematic diagram of the positive (self-reinforcing) feedback loop between outbreak of diseases and imports of Crassostrea gigas *stock to Europe that leads to the appearance of translocated non-native (pathogenic and non-pathogenic) species.*

Since their early beginnings, the European and especially French oyster industries have regularly faced such fluctuations in the now long established populations of *Crassostrea gigas*, first with the Portuguese and then with the Japanese strain (Buestel et al. 2009). The European oyster industry, mostly based on *C. gigas*, is important for sustaining a steady economic activity in coastal areas that otherwise rely on seasonal incomes from tourism. However, there are strong divergences in the long-term vision for the future of this industry. For instance, oyster farmers express great concern about the potential impact that the massive release of triploid *C. gigas* produced in hatcheries can have on naturalized diploid stock (Brest 2013). Private initiatives to maintain or increase genetic variability trough the import of new stock, would therefore not be surprising, especially during episodes of production decline.

Following a first European Directive in 1991, trade in and transfers of shellfish have been regulated by European legislation, which authorizes all movements inside Europe, and restrictions can be temporarily implemented during disease outbreaks (EC 1991, 1995, 2003, 2006). Although imports from outside Europe are severely restricted, present legislation still leaves windows of opportunities for imports of live shellfish from the Pacific region for aquaculture purposes (e.g., west coast of North America) (EC 2004*a*, 2008, 2009) or for food retail (e.g., from Japan and South Korea) (EC 2004*b*; SANCO 2013).

Apart from having consequences for the oyster industry itself, oyster imports can bring diseases that may affect native mollusk species due to host-switching (Peeler et al. 2011). Also, one major side effect, as our results show, is the release and establishment of associated alien species in the coastal environment. Biological invasions are now becoming a key priority for European authorities, which are presently developing regulations (EC 2013*a*), and they recognize the failure of the present "fragmented and incoherent policy set up at EU and national levels" (EC 2013*b*). This, coupled with the difficulties faced by the oyster industry, provides an opportunity for a thorough assessment and rethinking of the different practices of shellfish transfers and an opportunity to involve all the different partners and stakeholders in the discussion. Stronger education strategies and transparency are likely to be more efficient than restrictive policy. For instance, informing oyster farmers about the risks introduced hitchhikers can pose (e.g., shellfish predators, biofouling, smothering organisms) may be an easier way to implement preventative methods against external (Mineur et al. 2007*b*) or internal (Dijkema 1992) hitchhikers. The quest for new broodstock of *C. gigas* could also emphasize trials of invasive populations that have established in Europe and exhibit high genetic diversity (Rohfritsch et al. 2013). Some of these populations may not be affected by current disease outbreaks and could be a potential alternative to imports from the native area.

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Supporting Information

A bibliographic review of northwestern Pacific marine species introduced into Europe (Appendix S1) is available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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