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Review

Bad moves: Pros and cons of moving oysters — A case study of global translocations of *Ostrea edulis* Linnaeus, 1758 (Mollusca: Bivalvia)

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A B S T R A C T

The study was aimed at learning lessons from historical translocations of the European native oyster, *Ostrea edulis* and contributing to the debate on best practice for restoration projects. An extensive literature review of over 100 documents spanning 200 years was conducted to look at translocations of *Ostrea edulis* and investigate temperature related reproduction. Differences among geographical locations were assessed by multivariate analysis of reproductive data. Translocations of hundreds to millions of *Ostrea edulis* have taken place over the past 200 years, mainly for commercial purposes. Movements were either single actions or regular events over many years. Whilst 75 separate records of *Ostrea edulis* movements from within European waters were documented, it is likely that many more took place. Introductions have also been made outside Europe for aquaculture; translocations back to European waters, have led to the introduction of pathogens. The timing and duration of reproductive periods and spawning temperature thresholds of *Ostrea edulis* in the middle region of its distribution range were similar. Cluster analysis of documented periods of reproduction indicated that introduced and restocked populations clustered with their putative donor populations. Whilst the Irish production areas clustered together, reproductive cycles in Lough Foyle in the northwest of the island of Ireland showed greater similarity to the now extinct deeper water English Channel beds. Historically, the ability of oysters to breed after translocation was not considered important. Successful reproduction and recruitment is however fundamental to conserving the species. Where translocation of stock is used to restore *Ostrea edulis* in areas where it has been extirpated, this study suggests that restocking should be at high densities and carried out over several years and that harvesting should be restricted to increase the chances of establishing self-sustaining populations.

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1. Introduction

Translocation, the intentional movement of a species from areas where it is common to areas where it has become depleted or locally extinct, has increasingly been used in recent decades as a strategy for the conservation of endangered species (Seddon et al., 2014). Although their effectiveness has been questioned (Wikelski and Cooke, 2006; Peréz et al., 2012), such translocations are usually based on scientific research, generally well-documented and on a relatively small scale. By contrast, there have been few studies on translocations for commercial purposes (Lemer and Planes, 2012), even though several species of commercially exploited oysters have been subject to translocations on an industrial scale for more than one hundred years, mainly in attempts to redress serious regional declines in oyster fisheries around the world (Eyton, 1858; Fullarton, 1891; Browne, 1903; Went, 1962; Carlton and Mann, 1996; Wolff and Reise, 2002).

These movements were typically ad hoc and poorly documented and accelerated the decline of donor populations. For example, supplying large quantities of juvenile oysters to southern England and the Netherlands was in part blamed for the extinction of the highly productive Firth of Forth fishery in Scotland, where output declined by an estimated 99.9% between late 1700s and late 1800 (Fullarton, 1891). Today, few if any oysters remain in the Firth of Forth (Ashton, 2010; Thurstan et al., 2013; Smith et al., 2014). Continued exploitation and outbreaks of unknown diseases in the 19th and 20th centuries further decimated populations already under intense pressure and stocks of *Ostrea edulis* became commercially exhausted or extinct in many areas of the north east Atlantic (Orton, 1933, 1937; Went, 1962; Berghahn and Ruth, 2005).

Restoration of depleted stocks of several species of oyster, including *Ostrea edulis* (Drinkwaard, 1999; Smyth et al., 2009), *Ostrea lurida* (Trimble et al., 2009); *Ostrea chilensis* (Brown, 2011) and *Crassostrea virginica* (Rothschild et al., 1994) has been attempted with varying success throughout the world. Oyster restoration strategies include release of spat from shellfish hatcheries (Spencer, 2002), habitat restoration (Beck et al., 2011) and widespread transfers of adult oysters (broodstock). Early attempts to maintain oyster production in Europe involved large-scale translocations of the Portuguese oyster, *Crassostrea angulata* within European waters and importation of *C. virginica* from the USA (Carlton and Mann, 1996; Wolff and Reise, 2002). During the 20th Century, the Japanese oyster, *Crassostrea gigas*, has been translocated for aquaculture on a global scale (Muehlbauer et al., 2014). *Ostrea edulis* has been introduced to a number of non-European locations, either for aquaculture or to establish fisheries where native species had declined (for examples see Loosanoff, 1955; Glude, 1984; Burke et al., 2008; Haupt et al., 2010).

The natural geographic range of *Ostrea edulis*, the focus of this study, extends from 65°N in Norway, along the coasts of western Europe and the British Isles to North Africa and into the western Mediterranean and the Black Sea (Yonge, 1960), (Fig. 1a). Historically, *Ostrea edulis* formed dense beds supporting high biodiversity in estuaries, sea loughs and deeper water throughout its natural range (Yonge, 1960).

Today, as well as being of commercial interest, owing to the decline of populations and the increasing awareness of the ecological importance of oyster habitat, *Ostrea edulis* is now a focus of conservation interest in Europe under, for example, the Habitats

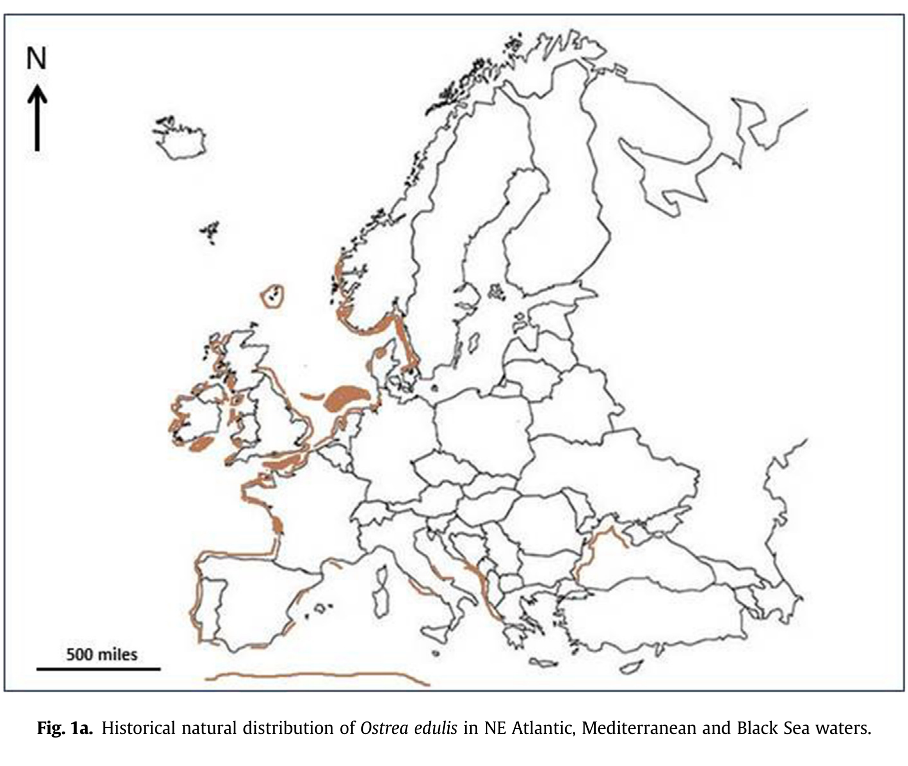

Fig. 1a. Historical natural distribution of *Ostrea edulis* in NE Atlantic, Mediterranean and Black Sea waters.

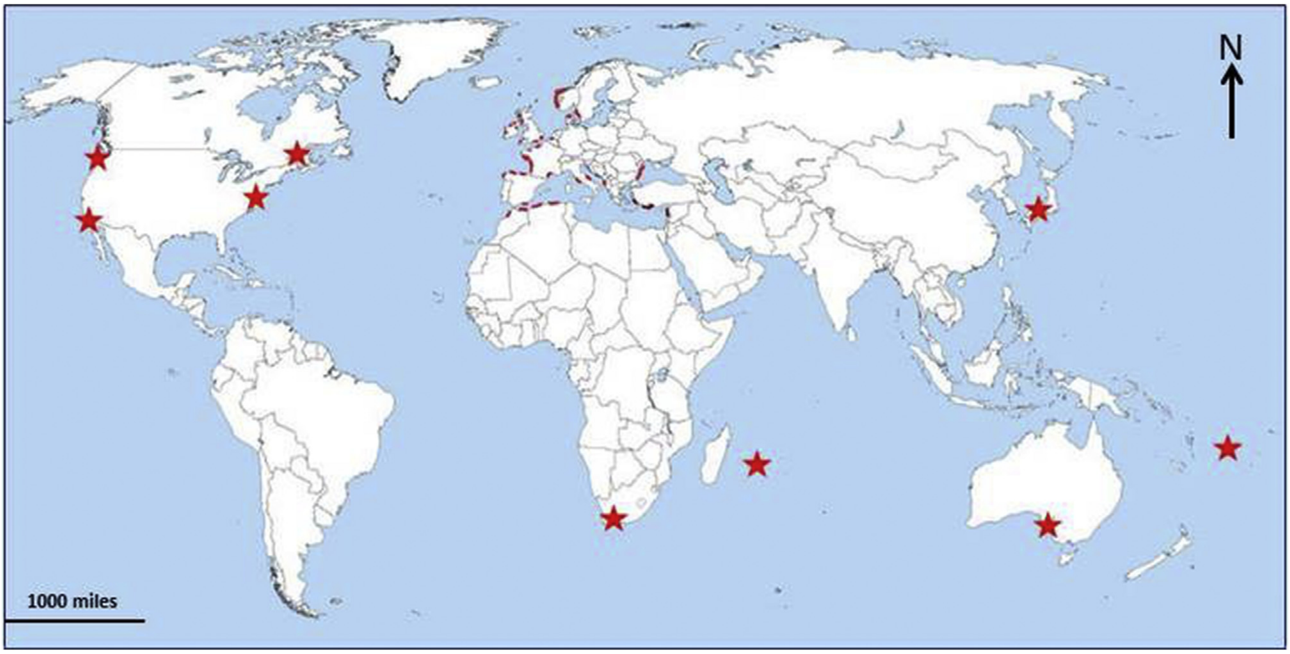

Fig. 1b. Modern distribution of *Ostrea edulis*, showing fragmentations of populations throughout its natural range and locations where European flat oysters have been introduced for aquaculture trials outside Europe..

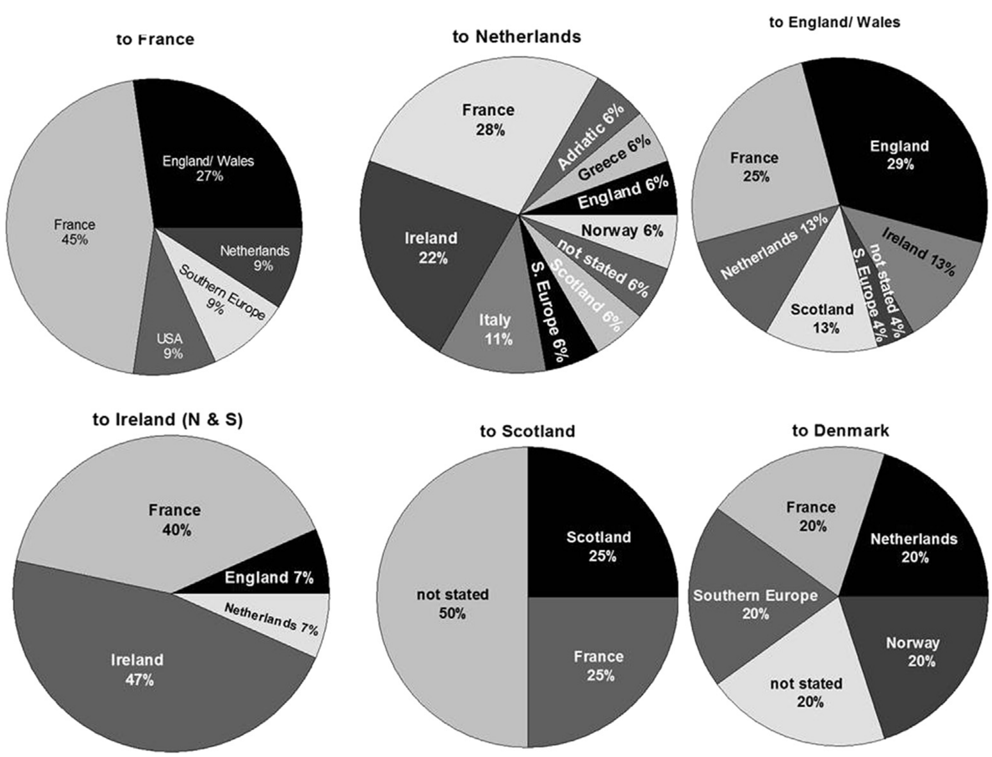

Fig. 1c. Documented records of translocations of *Ostrea edulis* within Europe 1814 to 1970s. The countries depicted in the pie charts have been ranked 1 to 6 in terms of their contribution to *Ostrea edulis* production during the time period covered by the graphs and the slices relate to the proportion (%) of movements of oysters from each of the donor locations.

Directive (92/43/EEC) (OSPAR, 2011). Within the United Kingdom, the species is the subject of a Native Oyster Species Action Plan (NOSAP) under the UK Biodiversity Action Plan, requiring populations to be sustained and enhanced. Although translocation has been put forward as a contributory factor to the slow recovery or failure of some past attempts at *Ostrea edulis* regeneration and the loss of "true natives" (Korringa, 1957; Loosanoff, 1962; Drinkwaard, 1999), it remains a major strategy for enhancement of populations. Risks associated with shellfish translocation, including introduction of non-native species, disease, pests, bacteria and viruses, and impacts on genetic integrity and diversity of native stocks are well established (Brenner et al., 2014). Movements of non-native oyster species such as those of *C. virginica* to Europe in the late 19th and early 20th Centuries brought invasive species, including slipper limpets (*Crepidula fornicata*) and oyster drills (*Urosalpinx cinerea*), to European waters, further accelerating the decline of native oysters (Hancock, 1969; Spencer, 2002; Gosling, 2003). More recently, a shipment of *Ostrea edulis* from the USA to France in 1979 was blamed for introducing the disease bonamiosis, which spread and caused up to 99% mortalities in already threatened European native oyster stocks (Balouet et al., 1983; Robert et al., 1991; Friedman and Perkins, 1994; Boudry et al., 1997).

One potential consequence of translocation is the loss of locally adapted populations or "races", which may impact on reproduction and recruitment (Andrews, 1980; McGinnity et al., 2009). It has been suggested that both *C. virginica* and *Ostrea edulis* may have "spawning races" with distinct tolerances and adaptations to their local environment (Nelson, 1928; Loosanoff and Nomejko, 1951; Korringa, 1957). Rödström and Jonsson (2000) called for comparisons of geographic differences in tolerances of *Ostrea edulis* to be studied to inform strategies for oyster restoration involving translocation. This present study examines historical data on translocations of *Ostrea edulis* and variations in reproduction throughout its geographical range which we hypothesise might limit the potential for translocated oysters to establish a self-sustaining population at the receiving site. *Ostrea edulis* was selected as the focus of this study because although it has been translocated regionally and globally on an enormous scale for over a century translocations have generally failed to re-establish declining stocks.

2. Methods

An extensive literature search was conducted to gain information regarding translocations of *Ostrea edulis* within European waters and to areas outside its natural range to which it has been introduced for aquaculture. Information covering the past 200 years was collated from scientific papers using the keywords native oysters, *Ostrea edulis*, oysters, movement/s, translocations, in bibliographic search engines (Web of Science etc) from 2012 to 2014. Grey reports, fishery reports and newspaper articles available to the authors and oyster fishers' were also consulted over this time period. Sufficiently detailed records of translocations were tabulated, taking care to avoid where possible information duplicated within different reports.

To investigate the timing of temperature-related reproductive events, historical and contemporary data for *Ostrea edulis* populations from the northern hemisphere were collated, mainly from peer-reviewed papers. Reproductive data were not available for the introductions of *Ostrea edulis* to the southern hemisphere.

Data for all stages of reproductive activity from gametogenesis to spawning and brooding to larval release and settlement of juveniles were pooled as the methods of reporting data differed in the literature and in some cases it was unclear whether spawning referred to the release of male gametes into the water column or release of larvae into the plankton following brooding. The metadata were then binary coded prior to analysis (1 = presence, 0 = absence) for each month of the year to represent reproductive cycles in each location. The resultant binary coded matrix was compiled in an MS Excel 2010 spreadsheet (Table 1), then introduced to the Multivariate Statistical Package (MVSP) v. 3.1 (Kovach, 2014).

The Bray Curtis coefficient was selected and applied to transposed data. Cluster analysis was then carried out and also ordination via Principal Components Analysis (PCA), applying Kaiser's rule (Legendre and Legendre, 1983). PCA can provide statistical validation of graphical clusters (Pillar, 1999) and the clustergram and PCA scatterplot were assessed for congruence. A scree plot was produced to find the point at which the decrease in eigenvalues of each axis levels off, indicating that the variation to the left of that point was statistically significant (Cattell, 1966). The data were also analysed in Primer v 6 (Primer Ltd., Plymouth). A distance matrix was produced using the Bray Curtis coefficient (Bray and Curtis, 1957; Clarke, 1993). Non-Metric Multidimensional scaling (nMDS) was selected to ordinate the data. Kruskal's stress values (Kruskal, 1964) act as a measure of the goodness of fit, with <0.10 indicating a true approximation of the data, < 0.20 being "useful", and >20 indicating random results (Clarke, 1993). Ordination was carried out with 100 random restarts. Analysis of variance was carried out using the PERMANOVA test (a non-parametric anova) with 9999 permutations with a random factor of temperature to provide a measure of the statistical significance of differences in reproductive activity amongst geographical locations.

3. Results

3.1. Oyster translocations

Reviewing the literature revealed that translocations of *Ostrea edulis* have taken place on local, regional, national and international scales throughout the 200 year period covered by the literature review. Whilst the natural distribution of *O. edulis* is confined to the NE Atlantic Ocean and the Mediterranean and Black Seas (Fig. 1a), anthropogenic activities in the 19th and 20th Centuries have expanded this range around the world, with introductions for aquaculture trials to potentially replace extirpated natives in Australia, Japan, Mauritius, New Zealand, North America (Canada and the USA), Pacific islands (e.g. Fiji) and South Africa (Fig. 1b).

From over 100 documents spanning ca. 200 years, we documented 75 separate records of translocations within Europe; 11 from Europe to non-European locations; and 6 from stocks established outside the natural distribution range of *O. edulis* to other parts of the world (Appendices 1, 2, 3a and 3b). Many of the translocations between European production areas were maintained over a number of years, whereas others involved a single, unrepeated translocation, mostly to non-European locations (Appendices 1, 2, 3a and 3b).

Most translocations of *Ostrea edulis* in the 19th Century were aimed at restocking oysters for on-growing or fattening for market (Appendix 1). Although numbers and sizes of oysters are poorly documented, they ranged from 500 individuals up to 12 million juvenile oysters; the latter being transferred from the Firth of Forth to Essex for relaying in 1773 (Fulton, 1896) (Appendix 1). Similarly, in the 20th Century, the majority of translocations were to restock beds that had been overexploited or depleted by disease or severe winters (Appendix 2). The scale of translocation ranged from 9000 oysters for an experimental study in Croatian waters to 18 million adults transferred from the Netherlands to the Limfjord, Denmark (Appendix 2). The scale of transfers of *Ostrea edulis* from Europe to non-European waters and from those areas to other parts of the

Table 1
Example of metadata showing presence of reproductive activity with a geographical locations.

Month	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec
Location												
Lough Foyle	0	0	0	0	1	1	1	1	1	0	0	0

Table 2
Temperatures of onset of spawning at locations from the native and introduced geographical range of *Ostrea edulis* from northern to southern latitudes.

Country	Location	Temperature (°C)
Norway	Bergen	25
Denmark	Limfjord	20
Ireland	Lough Foyle	13
Canada	Lockhart Lake	18
Netherlands	Oosterschelde	15
England	Crouch, Essex	15
England	Fal, Cornwall	15
France	Morbihan	15
France	Arcachon	15
Spain	Vigo	12
Spain	Mar Menor[a]	14
Italy[b]	Lago Fusaro	15
Italy[b]	Mare Grande Tarante	15
Italy[b]	Adriatic	13

[a] Alcaraz and Dominguez (1985), Cano et al. (1997).
[b] Carlucci et al. (2010).

world was not clearly documented in the accessible literature other than with a few exceptions such as the transfer of 9000 individuals from the Oosterschelde, Netherlands to Maine, USA for experimental aquaculture (Loosanoff, 1955).

Numbers of oyster movements in Europe between 1814 and 1970 were ranked in descending order from 1 to 6 (1: France; 2: Netherlands; 3: England and Wales; 4: Ireland and Northern Ireland; 5: Scotland and 6: Denmark) (Fig. 1c). France was the main provider of oysters to other areas throughout European waters. For France and the island of Ireland, the majority of recorded oyster movements were from within their own waters. The Netherlands imported oysters from the largest number of different donor populations (9 stated and 1 unstated source, including Mediterranean stocks). Half of Scotland's recorded translocations were from unstated sources. Although the literature revealed that Belgium was a major recipient of oysters from production areas throughout European waters, these movements were mainly for immediate sale to market and small-scale production confined to *claires* (ponds) around Oostend (Dean, 1893).

3.2. Temperature related timing of reproductive events

Temperatures reported for the onset of spawning of *Ostrea edulis* were similar (≥15 °C) throughout its range. Reproductive periods in locations from the middle of the species' natural distribution range (France, SE England and Netherlands) had similar timings, durations and temperature thresholds (Table 2).

The northernmost populations of *Ostrea edulis*, cultivated in the Norwegian pollens spawned at the highest temperature (ca. 25 °C) but for a relatively short period (one to two months). A similar scenario occurred in the introduced populations in eastern North Atlantic waters (Lockhart Lake, Canada) where at least 18 °C was required for onset of spawning (Burke et al., 2008). Populations in the Mediterranean and the introduced population in Californian waters were reproductively active throughout the year. However, those in the Atlantic off the north and north east of Spain and in the Adriatic reportedly spawned at relatively low temperatures (12–13 °C) and brooding individuals have also been recorded in Lough Foyle (55.11°N 7.08°W) at temperatures between 11.2 and 15 °C (Bromley, 2015).

Cluster analysis identified one large nested cluster, consisting of two clusters of smaller, strongly associated groups. Oosterschelde, Crouch (E. England), Morbihan (Brittany) and Loch Ryan formed a very strong cluster, with Arcachon as a slight outlier (Fig. 2a). Linked with this cluster were the north eastern Atlantic locations (Milford and Boothbay Harbours, USA and Lockhart Lake, Canada). Three smaller clusters were made up of: 1) locations in the Mediterranean; 2) Blackwater (E. England) and Norway and 3) Spain, Turkey and California. The Irish populations formed a strong cluster, but Lough Foyle had a stronger association with the now extinct deep water English Channel beds. The Irish locations were also loosely associated with a cluster formed by the Ría de Pontevedra (NW Spain), the Fal (SW England) and Croatian waters. The PCA demonstrated congruence with the cluster analysis (Fig. 2b). PCA extracted 94% of the variance from 23 variables and 25 cases across 4 axes, with the scree plot indicating that Axes 1 and 2 and therefore the associations between the geographical locations were significant and accounted for 75% of the variance in the data. A PERMANOVA test indicated that these differences between reproductive cycles throughout *Ostrea edulis* natural and introduced geographical range were significant ($p < 0.01$). An MDS plot produced a Kruskal's stress value of 0.02, indicating a good fit for the original data and produced the same outliers of California, Adriatic and Norway as the cluster and PCA analyses.

4. Discussion

4.1. Oyster translocations

A considerable amount of information was consulted to extract data regarding translocations and reproductive cycles of *Ostrea edulis*, but it is recognised that this material is incomplete and cannot account for unrecorded movements of oysters, which are likely to have been significant. The reasons for translocations of *O. edulis* have mainly been economic and have changed little over time; oysters are translocated mainly for fattening and growing on to market size (Brown and Ashton, 2013), restocking areas affected by mortalities caused by disease outbreaks, increased sedimentation from land clearance for agriculture, anthropogenic pollution from industrialisation (Harding, 1996) severe winters (Crisp, 1964), or for experimental culture in other areas (Eyton, 1858; Crisp, 1964; Davidson, 1976; Drinkwaard, 1999; Burke et al., 2008; Acarli and Lok, 2009).

Although details of the extent of removal of *O. edulis* and other species of oyster for harvest and translocation are limited there is an extensive literature on its consequences (for review see Beck et al., 2011). The main consequences include loss of habitat and associated biodiversity, reduced larval output from sites where oysters have been removed, transfer of alien species and the loss of the ecosystem services oysters provide as a result of their great capacity for habitat formation and water filtration. For example, overharvesting of *C. virginica* in Chesapeake Bay is reflected in the increased eutrophication as evidenced by historical changes in the ratio of benthic and planktonic diatoms and loss of its associated communities (Jackson et al., 2001 and references therein).

The historical lack of transparency in the recording of movements may in part have been due to growers attempting to preserve high value "brand names" for "true natives" such as the English Whitstable or Colchester, Irish Carlingford, French Gravette (Arcachon) and Italian *Ostrea reale* (Lucrine Lake) in the face of dwindling stocks and increasing imports of juveniles from abroad (Dean, 1893; Browne, 1903). Certainly, the volume of imports to England was so great by the 1800s that Fullarton (1891) stated that "most of the English natives are born in France or Holland, and are fattened at Whitstable or other beds in the South of England".

However, this is only part of the story, French and Dutch oysters translocated to England were likely to have been the descendants of oysters exported from England, Ireland and other parts of Europe to restock ailing French and Dutch beds earlier in the 1800s (Holt, 1903). The larger number of documented translocations to the Netherlands may be more the result of better record keeping than a

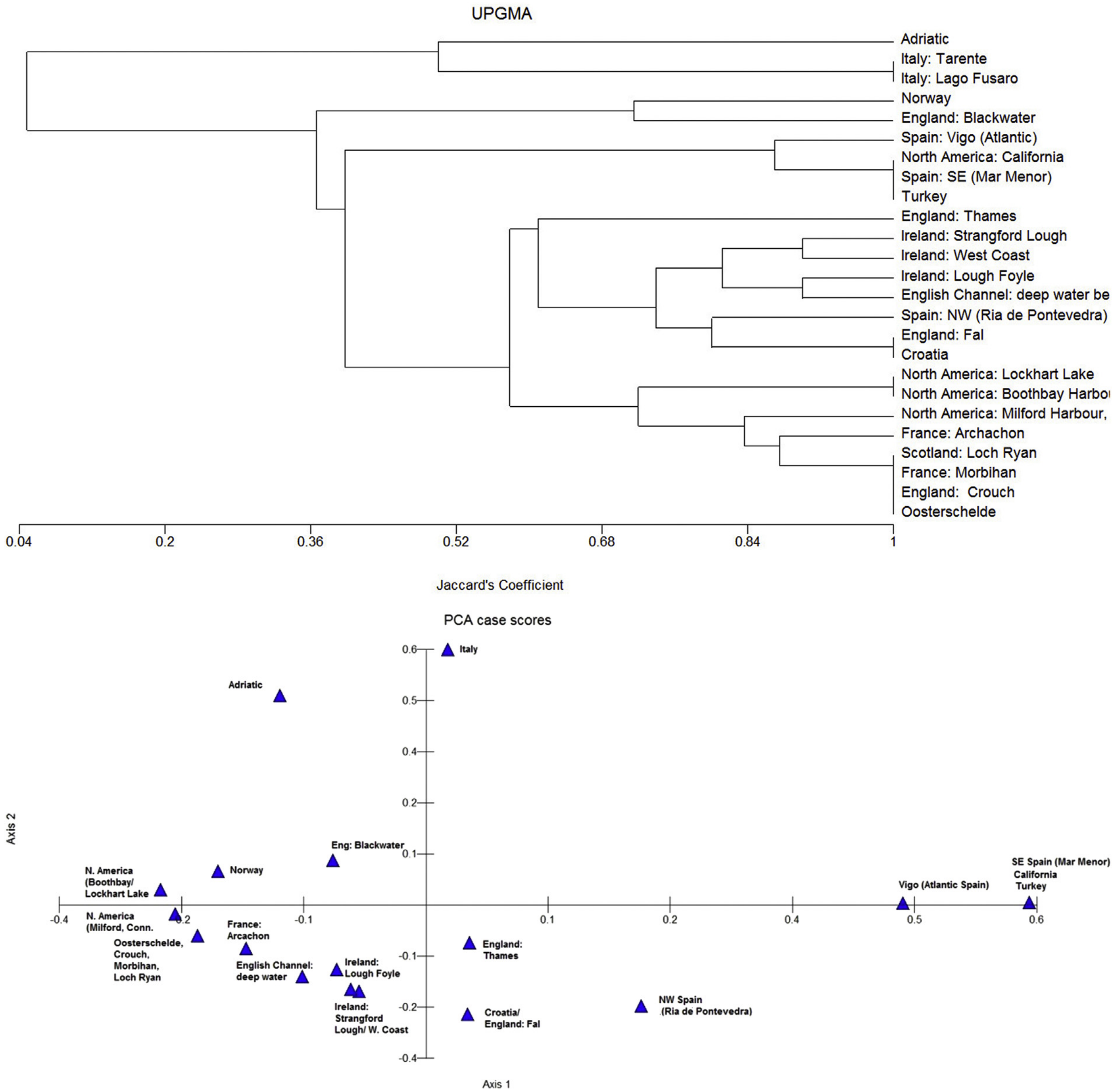

Fig. 2. Clustergram (a) and PCA (b) of reproductive data in *Ostrea edulis* populations throughout its range in the Northern Hemisphere.

true reflection of the scale and origins of oysters in other production areas. Despite all these restocking efforts, stocks of *O. edulis* continued to decline during 19th and 20th centuries so that there are few commercially viable wild stocks now and only remnant populations exist in its natural range. It is possible that restocking generally failed because phenotypic variations in morphology and reproductive cycles meant that translocated individuals were poorly adapted to receiving sites. The lesson learnt is that when restocking use local broodstock or individuals from similar environmental conditions.

4.2. Phenotypic variations in morphology

Phenotypic variation in European ostreids is reflected in their early systematics which recognised several distinct regional species largely based on differences shell shape: *Ostrea edulis* (the British Isles and France); *Ostrea hippopus* (Boulogne), *Ostrea adriatica* (Adriatic), *Ostrea cristata* and *Ostrea lamellosa* (Mediterranean) and *Ostrea gallina* (Atlantic), are all now reassigned as *Ostrea edulis* (Gofas, 2011). High phenotypic variation, particularly in shell shape, is well documented in bivalves (see for example Caill-Milly et al., 2012). Both *C. virginica* and *Ostrea edulis* are thought to have distinct spawning races and “local ectomorphs” adapted to their local environment (Nelson, 1928; Loosanoff and Nomejko, 1951; Korringa, 1957). The complex and reciprocal movements over prolonged periods of time certainly would explain the genetic homogeneity reported in *Ostrea edulis* populations (Launey et al., 2002; Lallias et al., 2010). Similarly, translocations of stocks of the black-lipped pearl oyster, *Pinctada margaritifera*, for pearl production has reduced genetic divergence between geographically distinct populations (Lemer and Planes, 2012). Owing to the known risks associated with shellfish translocations, movements are now subject to international and national legislation (Muehlbauer et al., 2014; Brenner et al., 2014). There remains, however, a lack of enforcement and there is a need for further co-operation and co-ordination between countries (Muehlbauer et al., 2014) and also within countries by local environment and police departments.

4.3. Variations in temperature-related timing of reproductive cycles

The reproductive cycles of marine invertebrates reflect the complex interactions between their life-history strategies and environmental factors. Major components of the reproductive cycle of *Ostrea edulis* include gametogenesis, spawning, brooding, larval release, planktonic larval development and settlement; each of which may show intra- and inter-annual variation related to food availability and temperature. Few studies of *Ostrea edulis* have examined all these elements at a single location and there are semantic issues regarding the term "spawning", which is used by different authors to refer to gamete release (female *Ostrea edulis* retain ova in the mantle cavity) or when larvae are later released by the female into the plankton (see for example Orton, 1937; Korringa, 1957).

In *Ostrea edulis* the 15 °C spawning and brooding threshold appears to hold only for the middle part of its range and links the cluster of production areas in French, English and Dutch waters. Dean (1893) and Korringa (1957) remarked on the striking similarities between reproductive periods in these locations, attributing this to similar hydrography and the amount of reciprocal translocations between these areas producing the potential for interbreeding between stocks. Loch Ryan, Scotland, in contrast to Lough Foyle despite both areas lying near latitude 55°N, was grouped with this middle latitude cluster (Fig. 2a). In the 1950s, oysters were introduced to the loch from waters in Brittany, France where water temperatures are on average 3 °C higher (Millar, 1962, 1968). Millar (1962) showed that the natives reproduced earlier than the introduced oysters and concluded that temperature was "the most important external influence on the breeding cycle" in the loch but that only gonad development was retarded. He also suggested that the longer introduced oysters remained in a system, the more likely they were to align to the local reproductive cycle. However, local conditions are likely to have a bearing on the ability of oysters to adapt; adaptation may be slow or not occur at all. The oysters introduced to Boothbay Harbour, Maine, USA from the Oosterschelde in 1949 had still not formed a viable population by 1957 and were largely being supported by hatchery production (Loosanoff, 1962).

The paradox highlighted by Korringa (1957) and Yonge (1960) that the difference between spawning races does not follow latitude indicated that the most northerly populations of *Ostrea edulis* required the highest temperatures to reproduce successfully, whilst the lowest temperatures leading to the onset of spawning occurred in the more southerly populations. In Norway, the culture system of ponds enabling temperatures in the enclosed areas to rise far higher than ambient seawater (Dean, 1893; Spotswood-Green, 1903; Yonge, 1960) can be used to explain this. However, a non-cultivated, more recently established population of *O. edulis* in Lockhart Lake, Canada only reproduces at temperatures above 18 °C (Burke et al., 2008).

Reproduction also takes place in areas where temperatures rarely reach the optimal thresholds, such as in the now extinct Firth of Forth and deep water North Sea beds, which historically supported highly productive fisheries (Roberts, 2007). Similarly, Andrew (2002) suggested that Lough Foyle oysters might be cold adapted. Our own work in Lough Foyle also indicates that brooding occurs in a few individuals at temperatures below 13 °C and a small proportion of the population may reproduce each year at temperatures below 15 °C (Bromley, 2015). Timing of spawning, brooding and larval release are especially important as gametogenesis would appear a less reliable measure of potential reproductive success; an oyster can begin to develop gonad material but this may be arrested or development cease altogether in adverse conditions (Orton, 1937; Korringa, 1940; UMBSM, 2007). Many studies concentrate on only one aspect of the oyster's reproductive cycle, e.g. gametogenesis or spat settlement. Further clarification of the term spawning and research into the effects of temperature on reproduction is required to avoid drawing incorrect conclusions regarding published and observed timings and temperature thresholds.

Reproductive success in broadcast spawning organisms is dependent upon synchrony, nearest neighbour compatability and nearest neighbour distance (UMBSM, 2007). Oyster stock management should therefore ensure that adults are retained in sufficiently dense populations to overcome dilution effects and reproduce successfully (Roughgarden et al., 1985) especially in locations subject to sporadic, unpredictable recruitment. Planktonic larvae and recently settled spat are the most vulnerable stages of the lifecycle, and losses can be incurred not only via predation but also sudden changes in temperature, salinity and hydrographic regime (Orton, 1937; Mackenzie, 1970; Stjepčević, 1974), influencing recruitment and sustainability (Korringa, 1940; Dekshenieks et al., 2000). Increased temperatures predicted under climate change may result in positive or negative effects on reproductive recruitment (Byrne, 2011).

5. Conclusions

Although translocation has important potential in the management and restoration of *Ostrea edulis* stocks this has rarely been realised. In Europe, millions of *Ostrea edulis* were regularly moved within and between countries and from inshore, deeper water, unregulated public beds to privately owned or chartered beds during the 19th Century for growing on to market size in what were effectively "put and take" fisheries. These translocations failed historically and contributed to the collapse of European oyster fisheries. However, there are also examples of translocations of *O. edulis* stimulating the enhancement of existing stocks, for example the introduction of oysters from Brittany to Loch Ryan in the 1950s (Millar, 1968) and Lough Foyle in the 1970s (Parsons, 1972) may explain why there are still commercial oyster fisheries in both these locations. By contrast, the translocation of oysters from Lough Foyle to Strangford Lough in the 1990s, where they were held in high densities, led to the spread and initial establishment of sub-populations away from the original introduction site due to larval dispersal (Kennedy and Roberts, 1999, 2006). However, stocks subsequently declined as a result of unregulated harvesting (Smyth et al., 2009).

Ostrea edulis is a fairly eurytopic species and natural populations can occur in vast numbers in habitats ranging from estuaries to the open sea on a range of substrata (Cole, 1956; Matthiessen, 2001). Thus, translocations of *O. edulis* are likely to be successful where local conditions fall within the relatively narrow spawning temperatures that have been documented (Table 2). Where it occurs in very high densities self-sustaining populations maintain themselves by large irregular settlements which do not occur every year. For example, in areas such as the deeper North Sea, Firth of Forth, Arklow, Limfjord and Lough Foyle, temperatures rarely reached the optimum needed for regular successful reproduction, and recruitment was sporadic and unpredictable (see Fullarton, 1891; Dean, 1893; McKelvey et al., 1996; Andrew, 2002; Andrews et al., 2011; McGonigle and Cavanagh, 2011; Bromley, 2015). This resilience is lost in severely overfished populations.

Several lessons can be learnt for *O. edulis* regeneration and restoration from the numerous historical movements, the documented effects on both donor and recipient stocks and the variation in success of earlier translocations. We recommend that attempts to restore self-sustaining populations of *O. edulis* involving translocation should ensure that:

1) oysters are from local genetic broodstock or similar environmental conditions to increase the likelihood of successful reproduction
2) oysters are re-laid in high densities, to overcome Allee effects (Kennedy and Roberts, 1999, 2006)
3) translocations are repeated over several years to maintain high densities of broodstock
4) translocated oysters are located at sites which ensures larval dispersal to other suitable settlement sites depending on local hydrographic conditions (Kim et al., 2013)
5) harvesting is restricted and enforced in the recipient location to prevent overfishing of recovering stocks (Cole, 1941; Caddy and Defeo, 2003).

In this way translocation in future can lead to socio-economic and conservation benefits of self-sustaining stocks of *Ostrea edulis*, and other species of oyster, where it has failed in the past.

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Appendices

Appendix 1. Translocations of Ostrea edulis within Europe in the 19th Century and early 20th Century

From	To	Date	No. of oysters	Purpose/other information	Source
England: Chichester, Sussex	England: Colchester, Essex	1814	3 gallons of spat	fisher prosecuted for removal of seed oysters	Eyton, 1858
England	France	pre 1839	not stated	fished by French boats	Eyton, 1858
England: south east	Netherlands	pre 1858	not stated	fished by Dutch vessels	Eyton, 1858
England: Land's End, Cornwall	England: Sandwich, Kent	pre 1858	not stated	growing on/restocking	Eyton, 1858
France	England: Sandwich, Kent	pre-1858	not stated	growing on/restocking	Eyton, 1858
France	England: Whitstable and other southern English beds	late 1800s	not stated	growing on/restocking	Fullarton, 1891
France: Brittany	Ireland: Cork Harbour	1890s	11,000	relaying on licensed bed	Browne, 1903
France/North Sea	Ireland: Galway Bay	1894/95	200,000	relaying	Browne, 1903
France: Arcachon/ Auray	Ireland: Achill Sound	1899/ 1900	50,000 & 100,000	relaying on private beds	Browne, 1903
France: Arcachon	Ireland: Cork Harbour	pre 1903	not stated	relaying on licensed bed For 2–3 years	Browne, 1903
France: Arcachon/ Auray	Ireland: County Kerry	pre 1903	ca. 250,000 plus unstated quantities	relaying on private and licensed beds	Browne, 1903
France: Arcachon/ Auray	Ireland: Muckinish & Galway Bays	1902	70,000	relaying on private beds	Browne, 1903
France: Arcachon/ Auray	Sligo Bay	1900	100,000	relaying on private beds	Browne, 1903
		Pre 1902	not stated	broodstock	
Ireland	England	1840s-1860s	not stated	replenishing beds	Spotswood Green, 1903
Ireland	North Wales: Beaumaris	pre-1858	"great numbers"	fattening for Liverpool market	Eyton, 1858
Ireland	Jersey	1862	not stated	fished by Jersey boats	Spotswood Green, 1903
Ireland	Netherlands	1860s	not stated	restocking	Spotswood Green, 1903
Ireland: Arklow	Ireland: Carlingford	1863	not stated	relaying as "Carlingford" oysters	Spotswood Green, 1903
Ireland: Arklow	Ireland: Dublin Wales: Beaumaris France	1863	64.7 million	immediate sale/relaying	Holt, 1903
Ireland: Arklow	England: Kent, London France Jersey	1864	54.7 million	restocking	Holt, 1903
Ireland: Arklow	Ireland: Dublin, Clontarf England: London, Kent, Fal	1865	29.1 million +10 million	NB: fishery active in unlisted years no numbers for take but values/	Holt, 1903
Ireland: Arklow	France			prices given Higher prices led to continued Fishing as catches decreased (situation reported for other Irish fisheries including Lough Foyle)	Holt, 1903
Ireland: Arklow	not stated	1866	22.1 million	sale/restocking	Holt, 1903
Ireland: Arklow	not stated	1867	38.6 million	sale/restocking	Holt, 1903
Ireland: Arklow	Ireland: Dublin, Sutton, Clontarf, Carlingford Wales: Beaumaris England: London, Kent Netherlands	1868	8.6 million	sale/restocking	Holt, 1903

(*continued*)

From	To	Date	No. of oysters	Purpose/other information	Source
Ireland: Arklow	Ireland: Dublin, Sutton, Clontarf, Carlingford England: London, Kent Netherlands France	1868	8.6 million	sale/restocking	Holt, 1903
Ireland: Arklow	not stated	1869	10.1 million	sale/restocking	Holt, 1903
	not stated	1872	8.6 million		
	not stated	1873	4.8 million 6.1 million		Holt, 1903
	not stated	1874	481,950		
	not stated	1875	331,380		
Ireland: Arklow	not stated	1883	655,200		Holt, 1903
	not stated	1887	1.6 million	Arklow hundred = 126 oysters	
	not stated	1888	113,148	Barrel = 5 to 6 hundreds	
Ireland: Tralee	Ireland: Cork Harbour	late 1800s	not stated	relaying on chartered/licensed beds	Browne, 1903
Netherlands	England: Whitstable and other southern English beds	late 1800s	not stated	growing on/restocking depleted beds	Korringa, 1957
Netherlands	Ireland: Sligo Bay	ca. 1894	250,000	relaying on licensed beds	Browne, 1903
Not stated	Scotland: West Loch Tarbert	1885 –1890	ca. 1 million	growing on/restocking	
Not stated	Shetland Isles: Sullom Voe	1890s	not stated	stocking	Shelmerdine and Leslie, 2009
Scotland: Firth of Forth	England: Thames, Medway Netherlands	pre 1786	millions?	growing on/restocking depleted beds	Fullarton, 1891
Scotland: Firth of Forth	England: Essex	late 1800s	12 million juveniles	growing on	Fulton, 1896
Scotland	England: Sandwich, Kent	pre 1858	not stated	growing on/restocking	Eyton, 1858
Scotland: West Loch Tarbert	not stated	pre 1891	not stated	sold on spat	Fullarton, 18

Appendix 2. Translocations of Ostrea edulis within Europe in the 20th Century

From	To	Date	No. of oysters	Purpose/other information	Source
Adriatic	Netherlands	spring 1967	not stated	restocking after severe 1962/63 winter	Drinkwaard, 1999
Croatia: Mali Ston	Croatia: Lyuta River	2010	9000 juveniles	restocking study	Joksimovič et al., 2011
England, Whitstable and other southern English beds	France: Brittany: Morbihan	1900s	not stated	fattening/growing on/restocking depleted beds	Korringa, 1957
England: Whitstable and Other southern English beds	Netherlands: Oosterschelde	1900s up to 1977	not stated	fattening/growing on/restocking depleted beds	Korringa, 1957
England: Cornwall	England: Colne, Essex	1960s	not stated	restocking after severe 1962/63	Davidson, 1976
England: Solent	England: Colne, Essex	1970s	not stated	restocking	Davidson, 1976
England: Solent	England: East and South coasts	1970s	hundreds of tonnes	restocking	Davidson, 1976
England: Solent	France	1970s	hundreds of tonnes	unclear if market only or market and relaying	Davidson, 1976
England: Solent	England: Fal, Cornwall	1970s	“some”	growing on	Davidson, 1976
England: Solent and Fal	England: Penryn/Percuel, Cornwall	1960s 1970s	not stated	stocking private beds	Davidson, 1976
England: South Coast	England: Crouch/Roach, Essex	1960s & 1970s	“limited restocking”	restocking	Davidson, 1976
England	Netherlands	1977	not stated	restocking	Davidson, 1976
England & Wales	Continental European waters	1950s	large quantities juveniles	restocking (from hatchery)	Davidson, 1976
England & Wales	Northern Ireland	1950s	large quantities juveniles from hatcheries	establishing entirely new fishery location not stated	Davidson, 1976
France: Morbihan, Brittany	France: Arcachon	1931 –1932	“large quantities”	restocking after mass mortality (disease)	Korringa, 1957
France: Morbihan, Brittany	France: Arcachon	1980	not stated	blamed for introduction of *Bonamia* to Arcachon	Robert et al., 1991
France: Morbihan, Brittany	France: Arcachon	1989	small number	experimental culture	Robert et al., 1991
France: Morbihan, Brittany	Netherlands	1950s	not stated	restocking after mass mortality	Korringa, 1957
France	England	1937	40 million (1100 tonnes)	growing on/restocking	Utting and Spencer, 1991

(*continued on next page*)

(*continued*)

From	To	Date	No. of oysters	Purpose/other information	Source
France: Brittany	England: Colne, Essex	1960s	not stated	restocking post 1962/63 winter	Davidson, 1976
France: Brittany	England: Beaulieu River	not stated	not stated	stocking	Davidson, 1976
France: Brittany	England: Penryn/Percuel	1960s & 1970s	not stated	stocking private beds	Davidson, 1976
France: Brittany	Scotland: Loch Ryan	1958 to 1960	4 to 6 million	restocking	Millar, 1968
France: Brittany	Netherlands	early 1960s Spring 1967	6 million 15 million	restocking after 1962/63 winter	Drinkwaard, 1999
France: Normandy	France: Marennes-Oleron	regularly	not stated	growing on	Buestel et al., 2009
France: Atlantic coast & hatcheries	France: Mediterranean	regularly	not stated	growing on	Buestel et al., 2009
France	Limfjord, Denmark	post 1931	not stated	juveniles. took over from Dutch owing to disease on Dutch beds	Andrews et al., 2011
France	Netherlands	up to 1977 1980	not stated not stated	restocking blamed for introduction of *Bonamia* to Netherlands	Troost, 2009
France	Netherlands: Wadden Zee	pre 1962	large quantities	growing on/restocking	Drinkwaard, 1999
France: Brittany UK (hatcheries)	Ireland: Lough Foyle	1972	ca. 250,000	experimental laying	Parsons, 1972
Greece	Netherlands	up to 1977	not stated	restocking	Drinkwaard, 1999
Ireland: Tralee	Ireland: Cork Harbour	Early 1900s 1902	not stated 5000	relaying on chartered/licensed beds	Browne, 1903
Ireland: Tralee	Ireland: Kenmare	1900 1901	16,000 12,000	relaying on licensed bed	Browne, 1903
Ireland: Tralee	Ireland: Derryquin	1901–1903	46,000	relaying	Browne, 1903
Ireland: Tralee	Ireland: Bantry Bay	1901	10,000	relaying	Browne, 1903
Ireland: Tralee	Ireland: Shannon Estuary	1902	125,000 + 250,000	relaying	Browne, 1903
Ireland: Galway Bay		1902	37,000	relaying	Browne, 1903
Ireland: Carlingford	Ireland: Galway Bay	1902	20,000	relaying on licensed bed	Browne, 1903
Ireland: Kilkieran Bay	Ireland: Biterbury & Cashel Bays	pre 1903	300,000 to 500,000 pa	relaying on licensed/chartered beds	Browne, 1903
Ireland: Lough Foyle	Ireland: Strangford Lough	1997	ca. 125,000	commercial re-sale	Kennedy and Roberts, 1999
Ireland	Netherlands	spring 1967 up to 1977	"some" not stated	restocking after 1962/63 winter restocking	Drinkwaard, 1999I
Italy	Netherlands	up to 1977	not stated	restocking	Drinkwaard, 1999
Netherlands	Denmark: Limfjord	1922 1923–1925 1931	200,000 (2 year olds) 2 million per annum 18 million	restocking. Switched to French stocks after 1931 owing to disease in Dutch oysters	Andrews et al., 2011
Netherlands: Oosterschelde	France: Morbihan, Brittany	1922 to 1930s	many millions over several years	restocking after 1921/22 mass mortality owing to disease	Korringa, 1957
Netherlands France	Wales	early 1960s	not stated	blamed for introduction of gill disease and Dutch shell disease	Davidson, 1976
Norway	Netherlands	up to 1977 e.g. 1963/64	not stated >20 million juveniles	restocking	Drinkwaard, 1999
Norway	England: Colne, Essex	1960s	not stated	restocking post 1962/63 winter	Davidson, 1976
Norway	Denmark: Limfjord	1940s	3 to 5 juveniles pa	restocking (switched from French and Dutch stock)	Andrews et al., 2011
Not stated	England: West Mersea/Blackwater, Essex	1960s & 1970s	not stated	restocking	Davidson, 1976
Not stated	Netherlands	1970s	"considerable quantities"	restocking	Drinkwaard, 1999
Not stated	Denmark: Limfjord	to 1980s	not stated	restocking declining beds	Brock, 1993
Portugal	not stated	1920s & 1970s	not stated	restocking post mass mortality	Andrews, 1980
Southern European waters	France Britain Netherlands Denmark	not stated	not stated	restocking	Andrews, 1980
Spain	not stated	1920s & 1970s	not stated	restocking post mass mortality	Andrews, 1980

Appendix 3a. Translocations of Ostrea edulis from Europe to areas outside Europe in the 20th Century

From	To	Date	No. of oysters	Purpose/other information	Source
Not stated	Fiji	1977	not stated	growth trials in private venture	Glude, 1984
Not stated	Mauritius	1972	not stated	growth trials – stock all lost within 4 months	Glude, 1984
Wales: Conwy Lab	Eastern Canada	1957–1959	not stated	did not survive winters	Andrews, 1980
Not stated	Canada: New Brunswick	2000s	not stated	established natural population	Burke et al., 2008
Netherlands	Canada: Prince Edward Island	not stated	not stated	hardy after ca. 30 years' selection	Andrews, 1980
Netherlands: Oosterschelde	USA: Maine	1947–1949	ca. 9000	feasibility study. Sent by Korringa led to hatchery and natural population	Loosanoff, 1955 Davis and Calabrese, 1969
Not stated	Australia: Oyster Harbour, Albany, Western Australia	mid 1800s to 1940s	not stated	trial introductions. Appear to have become naturalised	Morton et al., 2003
Not stated	Japan	not stated	not stated	failed feasibility trial	Andrews, 1980
Not stated	South Africa: Southern Cape	ca. 1894/95	not stated	failed attempts for culture	Haupt et al., 2010
Not stated	Israel	1976	not stated	aquaculture trials	ISSG, 2012
	Japan	1952			
	Namibia	1990			
	New Zealand	1985			
	Tonga	1975			

Appendix 3b. Translocations of Ostrea edulis from areas outside Europe to other areas in the 20th Century

From	To	Date	No. of oysters	Purpose/other information	Source
USA: Maine	USA: Milford Harbour, Connecticut	11/10/1949	not stated	feasibility study	Loosanoff, 1955 Davis and Calabrese, 1969
USA: Maine	USA: North Bay, Washington	1951	"many"	feasibility study	Loosanoff, 1955
USA: Connecticut	USA: California	1965	not stated	growing on/experiments	Wilson and Simons, 1985
USA: Connecticut	USA: California, Washington State, Alaska	1950s & 1960s	not stated	feasibility studies	Davis and Calabrese, 1969
USA: California	France: Brittany	1979	not stated	blamed for introduction of *Bonamia* to Europe	Friedman and Perkins, 1994
USA	New Zealand	not stated	not stated	blamed for introduction of *Bonamia* to *Tiostrea chilensis* in New Zealand	Boudry et al., 1997

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