European flat oyster - *Ostrea edulis*

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Biology, ecology and genetics

Distribution

The European flat oyster, *Ostrea edulis,* a native of Europe, occurs naturally from Norway to Morocco in the North-Eastern Atlantic and in the whole Mediterranean Basin (Fig.1) (1). It has been a harvested species for at least 6000 years. Natural populations are also observed in eastern North America, from Maine to Rhode Island, following intentional introductions in the 1940s and 1950s. The species was also introduced in Canada for aquaculture purpose 30 years ago and some populations naturalised in Nova Scotia, New Brunswick and British Columbia. These stocks were imported from naturalised populations in Maine whose ancestors originated in the Netherlands (2).

Fig. 1. *Distribution of O. edulis (1)*

Biology

Ostrea edulis, whose lower (left) valve is convex and upper (right) valve is flat, lives on firm ground in shallow coastal waters down to a depth of 20 m. The oyster, which is a prominent mollusc in the intertidal zone, like other bivalves, can reach other sea areas in its larval stage. The length of the adult oyster is around 10-12 cm. *O. edulis* can be found in estuaries, and tolerates salinities of up to 23 ‰. It often occurs in large beds on muddy-sand, muddy-gravel and rocks. Oysters filter phytoplankton and other particulate material from the seawater.

O. edulis is a protandric hermaphrodite, changing sex generally twice during a single reproductive season. Oysters function as males early in the spawning season and later change to females before changing to males again. *O. edulis* exists as a series of physiologically different strains, and genetic differentiation has been demonstrated along the European coastline. *O. edulis* produces up to 1 million eggs per spawning that are liberated into the pallial cavity where they are fertilised by externally released sperm. Following an incubation period of 8-10 days, depending on temperature, larvae (160 µm in size) are released into the environment and spend 8 to 10 days as a pelagic dispersal stage before settlement. Appropriate larval growth and survival rates are obtained in 20‰ salinity, although they can survive at salinities as low as 15‰.

Population genetics

The nuclear genetic diversity and geographical structure of *O. edulis* populations has been investigated, mostly by using enzymatic markers (1, 3), but more recently with microsatellite and mitochondrial markers (4, 5, 6). These studies have revealed moderate differentiation between Atlantic and Mediterranean populations (*Fst* = 0.058 between the two seas). Based on a lower genetic diversity of Atlantic populations, it was considered that these Atlantic stocks originated from Mediterranean populations, after the last quaternary glaciation (1), some clinal and V-shaped patterns of allelic frequencies were interpreted as the result of interglacial secondary contact of Atlantic and Mediterranean stocks (3). The question of the genetic discontinuity between the two basins was thus left open, and has recently been reassessed. A survey based on 5 microsatellite loci (5) has revealed a good correlation between genetic and geographic distances supporting isolation-by-distance as a model and rejecting non-equilibrium scenarios (colonisation or secondary contact). A more recent study (6) compared mitochondrial and nuclear data and showed that the geographically extreme populations sampled in Norway and in the Black Sea appeared particularly differentiated. Furthermore, a clear reduction of female gene flow has been observed and has been interpreted as being a consequence of a biased sex ratio, a higher variance in reproductive success of females and the presence of epizooites. Moreover, the individuals that settled on a collector during two weeks in spring 1994 in a Mediterranean population showed a significantly lower variability in reproductive success than the local adult population (7).

The conditions exist for local adaptation to occur and local patterns of genetic diversity to be observed and analysed. In order to further document this hypothesis, two experiments were conducted at population level. First, brooding females were sampled in the wild and the number of males fertilizing a given female estimated. Then, parentage was analysed for the individuals reared under experimental conditions. Fertilized eggs resulting from successive mass spawnings were collected from a population of potential parents kept in hatchery and with known genotypes. Resulting relative contribution of each progenitor showed a high variance in the reproductive success of males. Furthermore, different patterns of spawning were distinguished: unique, successive or extended in time, providing insight into the reproduction dynamics of this species.

As with other bivalves, heterozygozity deviations from the Hardy-Weinberg equilibrium have been reported in *O. edulis* for allozymes (8, 9) and microsatellites (5). In addition a positive correlation between multi-locus heterozygosity (MLH – both allozymes and microsatellites) and life history traits such as growth or survival has been demonstrated in *O. edulis* (9, 10, 11).

Breeding and culture practices

Production

Ostrea edulis has been part of the human diet for many centuries. The Romans built ponds to stock and sort oysters. In the 17th century, oyster spat were collected on rocks, separated from each other and deployed into ponds in salt marshes on the Atlantic coast of France. A decline in activity in salt marshes facilitated oyster culture development by expanding grow-out acreage availability. During the 18th and 19th centuries, fishing effort led to over-exploitation, failing recruitment, and destruction of European natural beds, which were also affected by extremely cold winters. Shortage in seed supply prompted the managers to develop cultural practices aimed to sustain a repletion and reseeding programme. Within the past forty years production of *Ostrea edulis* showed a drastic decline from a peak output of nearly

30,000 tonnes in 1961, due to the impact of two parasitic epizooites (*Bonamia ostreae* and *Marteilia refringens*) in the 1960s (12) and a consequential shift to the rearing of the Portuguese cupped oyster (*Crassostrea angulata*), then the Pacific cupped oyster (*Crassostrea gigas*).

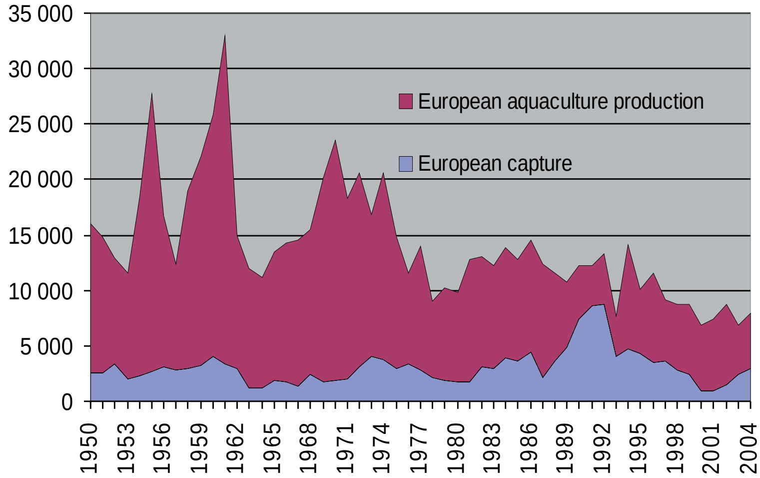

Fig. 2. *Capture fisheries and aquaculture production of O.edulis in Europe (in tonnes) (13)*

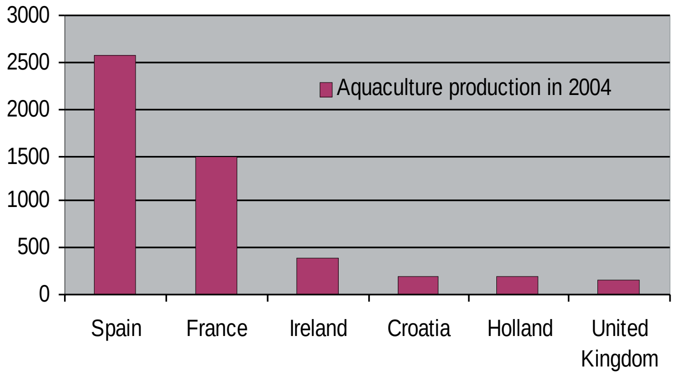

Fig. 3. *Aquaculture production of O. edulis in Europe by country (in tonnes) (13)*

The recruitment of natural spat from this species has been strongly reduced and for instance, the French production of flat oyster by a factor of 20 since the 1960s, but is still 1,500 tonnes/year at present. In 2004, 51% of the production was in Spain (2,575 tonnes) and 30% in France (1,500 tonnes). Ireland and Croatia were the other countries that produced more than 200 tonnes in 2004 (Fig. 2, 3). Catches of wild *O. edulis* represents 10 to 30% of the total tonnage of oysters marketed in the recent years. The production of the European flat oyster represented less than 0.11% of the total global production of all farmed oyster species in 2004. The bulk of the world production (96.2%) was the cultured Pacific cupped oyster, *Crassostrea gigas*.

European flat oysters are traditionally consumed fresh and eaten on the half shell. As the available supply has decreased, average prices have dramatically increased: the wholesale average price for *O. edulis* is commonly 3 to 5 times greater than the cheaper Pacific cupped oyster (*C. gigas*). Therefore, the product now occupies a niche market, and is considered as a luxury seafood item - an expensive delicacy for specialised consumers. However, the value of farmed *O. edulis* production in 2004 was US$ 20.3 million. Hence, its culture remains an important industry in the limited areas where it is reared.

Hatchery practices

In most countries, the production of *O. edulis* is still mainly based on wild spat. During the 1960s and 1970s, knowledge about oyster reproduction and rearing techniques improved greatly. However, larval rearing techniques and equipment still rely more on empirical concepts and practice rather than on detailed knowledge of the species biology.

Oysters are alternate hermaphrodites. Synchronous hermaphrodites are rare and selfing is likely to be extremely low. Because flat oysters brood their larvae, strip-spawning is not possible. A single female can release 1-2 million larvae. Under good growing conditions, oysters can produce gametes after a few months such that one-year generation interval is feasible. However, generation interval is usually 2-3 year. In Europe, the main commercial hatcheries are established in France (mostly producing *C. gigas*), the Channel Islands (*C. gigas* and *O. edulis*), U.K. and Ireland.

Selective breeding

The most significant genetic improvement for the production of oysters to date has been obtained through the breeding of triploids. However, in flat oysters, the brooding phase makes the production of polyploids much more difficult and triploid flat oysters are not currently farmed. Quantitative genetics studies suggest that significant gains for disease resistance could be obtained using selective breeding programs. In Europe, where both natural and hatchery-propagated spat are farmed, no large scale selective breeding programmes have yet been started for *O. edulis*. However, several experiments to improve resistance against *B. ostreae*, one of the major parasites and cause of heavy mortality of this species, have been carried out, notably in Ireland (14) and France (15). Results have shown a significant gain in survival and lower prevalence of the parasite in selected stocks. The French experimental breeding programme demonstrated that mass (i.e. individual) selection can improve disease resistance (15). However, the limited extent of hatchery-propagation (*versus* natural recruitment) and/or various technical difficulties and biological characteristics of this species have slowed the development of selective breeding programs. Loss of genetic variability has been documented in mass selected populations (16) indicating that a higher number of breeders should be selected and that the number of progeny tested should be restricted and standardized (17). Also, family-based approaches may be an alternative. Current research includes the development of a genetic map and the search for QTLs of survival to bonamiosis in *O. edulis* (18).

Interaction studies

Compared with fish species, very little is known about interaction between farmed and wild oyster populations because most farmed oysters are neither selected nor domesticated. One of the concerns regarding the genetic impact of farmed oysters on natural populations is about effective population size of hatchery propagated stocks relative to wild populations. This is especially the case for the *O. edulis* in its native area (*i.e.* Europe). Recent studies have suggested that the effective population size of populations might be severely reduced due to much fewer breeding females than males (6). Wild populations may be strongly affected by extensive cultivation of hatchery-propagated spat that is likely to have a low genetic variation. However, such negative impact remains to be demonstrated. The same kinds of questions are asked for the American oyster, *Crassostrea virginica*, when restoring oyster reefs by hatchery-propagated stocks.

Conclusions/Implications

Data are available on the structuring of the oyster populations in Europe. Although man has been interfering for a long time with flat oyster wild stocks, a low level of genetic structure can still be detected at the European scale. However, the Eastern Mediterranean and Black seas need to be further studied. Here, sampling and efforts are made through the MARBEF Network of Excellence (19). Knowledge of the structuring and the genetic diversity is particularly important in these Eastern Mediterranean countries (Russia, Turkey, Croatia) because some of these are producing or want to develop a production of flat oysters. Research on local adaptation of the populations need to be carried out in order to characterise them as a genetic resource and to estimate the potential impact of domesticated and selected strains.

The effective population size and genetic variation of hatchery propagated stocks relative to wild populations needs to be estimated and recommended broodstock management protocols followed in order to avoid genetic impacts on wild populations.

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