Pacific cupped oyster - *Crassostrea gigas*

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Biology, ecology and genetics

Distribution

Originating from the north eastern Asia, *Crassostrea gigas* is endemic to Japan, but has been introduced and translocated, mainly for aquaculture purpose, into several countries, almost worldwide (1). In North America, the species can be found from Southeast Alaska to Baja California, while in European waters the species is cultured from Norway to Portugal as well as in Mediterranean Sea (Fig.1) (2). Biological characteristics make it suitable for a wide range of environmental conditions, although it is usually found in coastal and estuarine areas within its natural range. Although highly variable, the invasiveness pattern of *C. gigas* has been demonstrated in several countries and therefore considered as a pest or a noxious species in those areas (3).

Fig. 1. *Distribution of the Pacific cupped oyster in Europe (2)*

Biology

C. gigas is bivalve mollusc. It is a plankton feeder, filtering phytoplanktonic species for food (filter-feeder) and also ingesting detritic particulate organic matter. *C. gigas* is an oviparous oyster with a high level of fecundity. It changes sex during life, usually spawning first as a male, and subsequently as a female. Spawning is temperature dependent and occurs in summer (15-20°C) synchroneously. Reproductive effort is high, a female producing 20-100 million eggs per spawning (diameter 50-60µm). Fertilisation is external and takes place in the seawater column. At first larvae are free-swimming and planktonic; developing for 2 to 3 weeks before metamorphosis and finding a suitable clean hard substrate to settle on. Highly sensitive to environmental conditions, a very small percentage of larvae survives to become spat. Natural habitat is intertidal and the species can be found down to 15m deep on either hard or soft substrate. The species can resist temporarily to very low salinity (5ppt). The swimming stage and capacity to survive in various environmental conditions facilitate the species dispersion along coastal areas (1).

Population genetics

In Europe, the Pacific oyster was massively introduced after the viral disease that crashed down the Portuguese oyster production by the end of the 1960s. Therefore numerous studies focused on their relationship. *C. gigas* and *C. angulata* had been first classified as two different species based on their apparently separated geographical distribution. However, following morphological comparison, experimental hybridization (4) and allozyme data (5), some authors concluded that there was only a single species grouping Portuguese and Pacific oysters. Yet, significant phenotypic differences between the two taxa were observed. *C. gigas* shows a superior production yield in the wild in France (6). Differences were also shown in terms of their ecophysiological characteristics (7). Furthermore, genetic differences have been observed at several levels: karyotype analyses (8), mitochondrial (9) and microsatellites (10) studies. In this latter study, a low but significant genetic difference was observed between the French *C. gigas* populations sampled.

Based on these worldwide genetic resources analyses, there might be two putative contact zones, one between France and the south of Portugal where "naturalized" *C. gigas* and *C. angulata* populations have been described, and a second one between Japan and Taiwan. In parallel to the observation of the absence of reproductive barriers under controlled conditions (11), evidence was given for hybridization between *C. angulata* and *C. gigas* in a wild Portuguese population where the two taxa are in contact due to recent transportation of *C. gigas* stocks for aquacultural production (12).

Little is know about genetic adaptation following its introduction into new environments. Results from a common garden experiment comparing progenies of French and Japanese broodstock suggested that the observed differences might be imputable to local adaptation of the French stock since their introduction (6). Polymorphism of presumed selected genes has also been proposed as an alternative method to investigate local adaptation under specific selective pressures such as pollutants (13). Recently, the European Research Training Network on Fisheries-induced Adaptive Changes in Exploited Stocks (FishACE) was set up to investigate the prevalence and consequences of fisheries-induced adaptive changes in French *C. gigas* populations (14).

Breeding and culture practices

Production

Oyster fisheries (*i.e.* exploitation of natural populations as common resource) have, in many cases, shown poor sustainability. Restoration of over-exploited stocks has often been of limited success due to continued exploitation, habitat degradation or diseases. Pacific cupped oyster capture fisheries was never very relevant, with a production of only a few tonnes /year.

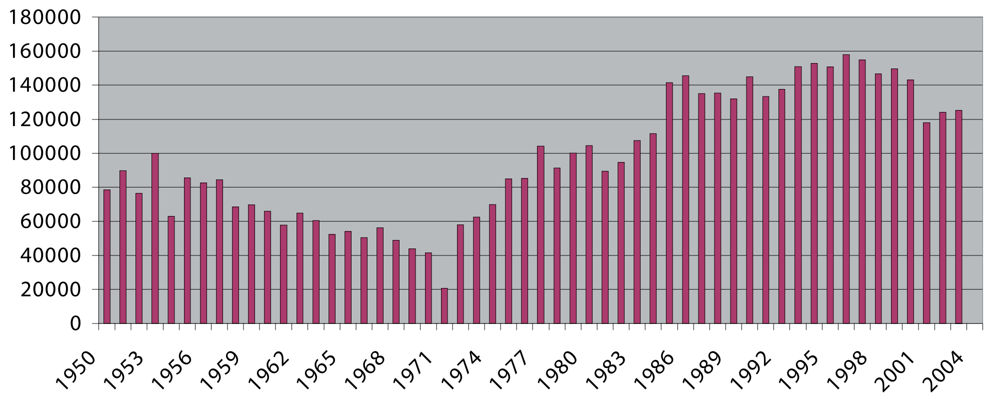

Fig. 2. *Pacific cupped oyster aquaculture production in Europe (15)*

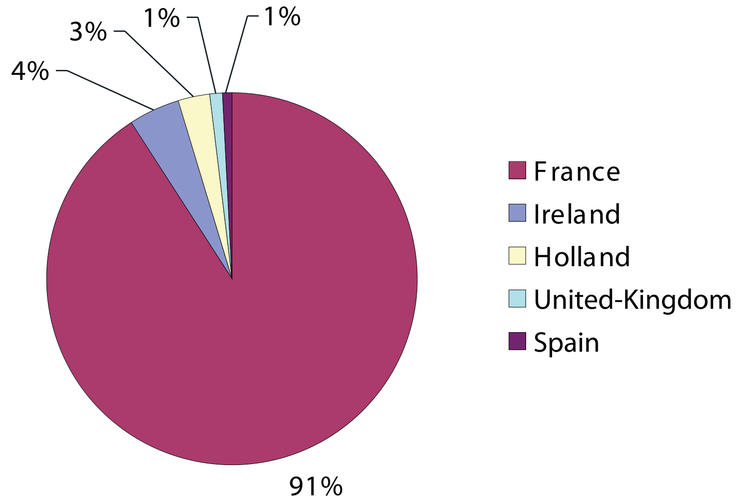

Fig. 3. *Pacific cupped oyster aquaculture production in 2004 in Europe, by main producing countries (15)*

Aquaculture, on the other hand, currently provides most of the marketed oysters and seems to provide a longer term productivity of nearshore marine and estuarine habitats. Farmers grow seed collected from the wild. To date, hatcheries secure availability of seed and allow the production of genetically improved oysters, through polyploidy and selective breeding (see section below). China is the world's leader with 3.75 out of a total production of 4.6 million tonnes in 2004 (i.e. 81% of the world production). European production now ranges around 120,000 tonnes/year (Fig.2), with France, Ireland, Spain, Ireland and U.K as major producers (Fig.3).

Hatchery practices

In most countries, the production is still mainly based on wild captured spat. From the first reported in vitro oyster fertilisation in 1879 to the appearance of modern production hatcheries, hatchery practices have seen more than one hundred years of development (16). During the 1960s and 1970s, knowledge about oyster reproduction and rearing techniques improved greatly. The most recent developments concern the use of high density flow-trough larval systems (as an alternative to batch culture), gamete cryo-preservation and artificial diets.

Today, hatcheries successfully achieve controlled development of spat (immature settled oysters), from fertilisation to post-larvae for many oyster species. Oysters are alternate hermaphrodites. Synchronous hermaphrodites are rare and selfing is likely to be extremely low. In cupped oysters males and female gametes are directly released in the water. Strip-spawning is a common practice in cupped oysters and a fully mature female may yield more than 100 millions eggs. Under good growing conditions, oysters can produce gametes after a few months so that a one-year generation time is feasible. However, generation time is usually 2-3 years.

The proportion of spat produced in hatcheries has increased considerably the last decades, notably in countries were summer water temperature is too low to allow reproduction (e.g. *C. gigas* on the west cost of North America). Additionally, the production of triploid cupped oysters and the establishment of selective breeding programmes enhanced the development of hatchery-produced spat. In Europe, the main commercial hatcheries are established in France, Channel Islands, U.K. and Ireland. In France, most hatchery spat is triploid.

Grow-out

Due to their large worldwide use, oysters are cultured under various rearing strategies and growout equipment from fully extensive to semi-intensive techniques (17). Intensive culture is restricted to early stages (i.e. hatchery and nursery) because large scale production of algal food is not yet cost-effective at later stages. After several months of rearing in open waters, wild oyster spat is either removed from the spat collectors to be deployed onto culture grounds (on bottom) on sticks, or into oyster bags on trestles, baskets, suspensions or stay for pregrowing on the collectors, therefore requiring a thinning out or density decrease. This is done in coastal bays as well as inland using semi closed oyster ponds where seawater fills in by gravity and tide effect. Usually, oyster density-stocking biomass is adapted to local carrying capacity and by adapting mesh size to oyster size to maximize current pattern and food availability, ultimately to reduce the rearing cycle time span. Usually, oysters are sorted, graded and stored in clean water before marketing, to remove mud and grit and operate a slight depuration.

Selective breeding

The most significant genetic improvement for the production of cupped oysters to date (18) has been obtained through the breeding of triploids, especially since the development of tetraploids in the mid 1990s (19). Triploid oysters have a much reduced gametogenesis (but are not fully sterile) and re-allocate part of their resources to growth and survival. To date, about 50% of hatchery-produced *C. gigas* are triploid obtained by crossing diploid females with tetraploid males (i.e. “natural triploid”). Chemically induced triploids have been shown to have lower performance compared with natural triploids (20).

Quantitative genetics studies suggest that significant gains, for disease resistance or for other traits of aquacultural interest, could be obtained using selective breeding programmes. However, the limited extent of hatchery-propagation (*versus* natural recruitment) and/or various technical difficulties and biological characteristics of some species have slowed the development of selective breeding programmes. Mass (i.e. individual) selection have been efficiently used to improve growth (21). To date, family-based selective breeding programmes have been established in U.S.A. (22), Australia (Thoroughbred oysters by Australian Seafood industries) and New Zealand (23), mainly to improve growth, yield and shell shape in *C. gigas*. Interestingly, the use of non additive variance and heterosis in breeding programmes is also being investigated in that species (24). In Europe, where both natural and hatchery-propagated spat are farmed, no large scale selective breeding programmes have yet been started for *C. gigas*.

Marker assisted selection, using microsatellites for mixed families approach or QTLs, is currently being investigated. In *C. gigas*, special attention has been paid in Europe to “summer mortalities”, for which the causal factors are still unclear. Results have shown that family-based selective breeding can improve spat survival, with no negative impact on growth. As a high heritability was estimated for spat survival against summer mortality (25) current QTL mapping efforts (26) are likely to be successful. In addition, a micro-array approach is in progress to identify differentially expressed genes between resistant and sensitive lines.

Interaction studies

Compared with fish species, very little is known about interaction between farmed and wild oyster populations. This is mostly because most farmed oysters are not yet domesticated nor selected.

Conclusions/Implications

For the wild European populations of *Crassostrea gigas*, the three main points that need to be considered when dealing with the genetic impact of aquaculture on wild populations are:

– Oyster farming is mainly based on these "wild" populations, with commercial hatcheries producing now about 20% of the spat (mainly triploids). Although this species has been introduced recently, we can consider the populations as "naturalized".
– The two closely related species C. gigas and C. angulata hybridize. Hence a genetic impact has already been observed on one reluctant population of *C. angulata* in Southern Europe where *C. gigas* aquaculture is present. Even if *C. angulata*, the "Portuguese" oyster, has proved to be originated from Asia since at least 400 hundred years, it is now considered as a European species in Southern Europe.
– *C. gigas* is reproducing and settling now in more northern areas and can be considered as invasive.

Therefore, in order to better analyse the genetic impact of aquaculture on oyster populations, research are needed to (a) characterize the invasiveness of *C. gigas* in Europe [as it is becoming to be done in some countries (27)], (b) investigate the introgression from *C. gigas* to *C. angulata* in the aquaculture areas of southern Europe, (c) investigate at the European level the genetic differences between populations and possible local adaptation.

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. Putative negative impact of farming triploid oysters (in Europe: *C. gigas*; in USA: *C. ariakensis*, *C. virginica* and *C. gigas*; in Australia: *S. commersialis*) is related to their partial sterility. Triploidy is not considered as a safe genetic confinement tool as triploids can effectively breed. The impact of this partial sterility on wild populations is poorly known and needs to be investigated. Another risk may come from tetraploid broodstock that are fully fertile. The fate of tetraploid in the wild (*i.e.* their fitness relative to diploids and the impact of their breeding with diploids) is of concern in Europe but needs to be investigated.

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