

ICES Cooperative Research Report
Rapport des Recherches Collectives

No. 299

November 2009

**ALIEN SPECIES ALERT:
CRASSOSTREA GIGAS (PACIFIC OYSTER)**

LAURENCE MIOSSEC
ROSE-MARIE LE DEUFF
PHILIPPE GOULLETQUER



ICES

International Council for
the Exploration of the Sea

CIEM

Conseil International pour
l'Exploration de la Mer

International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer

H. C. Andersens Boulevard 44–46
DK-1553 Copenhagen V
Denmark
Telephone (+45) 33 38 67 00
Telefax (+45) 33 93 42 15
www.ices.dk
info@ices.dk

Recommended format for purposes of citation:

Miossec, L., Le Deuff, R.-M., and Gouilletquer, P. 2009. Alien species alert: *Crassostrea gigas* (Pacific oyster). ICES Cooperative Research Report No. 299. 42 pp.

Series Editor: Emory Anderson

For permission to reproduce material from this publication, please apply to the General Secretary.

This document is a report of an Expert Group under the auspices of the International Council for the Exploration of the Sea and does not necessarily represent the view of the Council.

ISBN 978–87–7482–069–7

ISSN 1017–6195

© 2009 International Council for the Exploration of the Sea

Contents

1	Introduction	1
2	Identification of <i>Crassostrea gigas</i>	2
3	Biology of <i>Crassostrea gigas</i>	4
	3.1 Anatomy	4
	3.2 Behaviour.....	4
	3.3 Tolerances	6
	3.4 Nutrition and feeding	6
	3.5 Disease and predation.....	7
4	Distribution of <i>Crassostrea gigas</i>: origins and worldwide introductions for aquaculture	11
	4.1 Origins.....	11
	4.2 Introductions and translocations.....	11
5	Production and productivity of <i>Crassostrea gigas</i>	17
	5.1 Production	17
	5.2 Productivity	18
6	Environmental factors affecting <i>Crassostrea gigas</i> dispersal	20
	6.1 Temperature and climate change	20
	6.2 Ocean acidification	21
7	Consequences of <i>Crassostrea gigas</i> introductions	23
	7.1 Ecological competition and biodiversity	23
	7.2 Genetic changes in <i>Crassostrea gigas</i>	25
	7.3 Introduction of diseases, parasites, and hitchhiker species	25
	7.4 Control and management procedures	27
	7.5 Economic impacts.....	28
	7.6 Social impacts.....	28
8	Conclusion	30
9	References	31

1 Introduction

Prepared by the Working Group on Introduction and Transfers of Marine Organisms

The Pacific oyster (*Crassostrea gigas*, Thunberg, 1793) is one of 20 species in the genus *Crassostrea*. Although native to the Japan/Korea region, *C. gigas* is a hardy species that has been introduced to a number of countries worldwide, including the US, Canada, the UK, France, Korea, China, New Zealand, Australia, South Africa, and South America, mainly for aquaculture purposes (Mann *et al.*, 1991; Orensanz *et al.*, 2002). As a result, *C. gigas* has become the leading species in world shellfish culture, with an estimated production of 4.6 million t in 2006 (FAO, 2008). Because *C. gigas* does not require additional food to sustain its growth, this species is relatively inexpensive and easy to produce. Its capacity to adapt to various environmental conditions and temperature fluctuations, coupled with its rapid growth and resistance to highly turbid areas, contributes to its success.

2 Identification of *Crassostrea gigas*

The taxonomic status of *Crassostrea gigas* is now well established (Table 2.1).

Table 2.1. The taxonomic status of *Crassostrea gigas* according to the ITIS (Integrated Taxonomic Information System; <http://www.itis.gov/index.html>).

Phylum	Mollusca
Class	Bivalvia
Subclass	Pteriomorpha
Order	Ostreoida
Family	Ostreidae
Genus	<i>Crassostrea</i>
Species	<i>gigas</i>

The identification of oyster species is still based largely on phenotypic characters, and the primary distinguishing feature is shell morphology (Figure 2.1).

Crassostrea gigas has a rough, elongated shell that can reach a length of 20–30 cm and is extremely variable. The two valves are solid but unequal in size and shape (CIESM, 2000). The left (upper) valve is slightly convex, whereas the right (lower) valve is quite deep and cup shaped. One valve is usually cemented to a hard substratum. The valves are sculpted, with large, irregular, rounded radial folds. Radial ribs are present on both valves, starting from the umbo. Usually whitish in colour, they also display purple streaks and spots. The inner surface is partly milky white. The adductor muscle scar is kidney shaped.

Several studies, based on morphology and geographical range, have attempted to isolate characters and traits that can be used for identification and to resolve the relationships between species (Stenzel, 1971; Bernard, 1983; Harry, 1985; Brock, 1990), but this has proven problematic. The high plasticity of morphological characters, which are greatly influenced by habitat, together with the effects of anthropogenic activities on the geographical distribution of this species, has created the need for a more accurate method of identification. In the last decade, molecular biology has contributed some clues that may help to resolve the taxonomic riddle posed by the classification of *Crassostrea* oysters.



Figure 2.1. Shell morphology of the Pacific, or Japanese, oyster (*Crassostrea gigas*, Thunberg, 1793): interior lower valve, showing adductor scar, and exterior lower valve (left); *in situ* photograph (right). Pictures courtesy of Ifremer.

One major outstanding taxonomic question relates to the relative status of the Pacific oyster (*C. gigas*; Figure 2.1) and the Portuguese oyster (*Crassostrea angulata*). These oysters were classified as two separate species: *C. gigas* by Thunberg in 1793 and *C. angulata* by Lamarck in 1819. This classification was influenced primarily by their apparently different geographical distributions, *C. gigas* being found in Asia and *C. angulata* in Europe. However, recent studies using mitochondrial markers have reported the presence of pure populations of *C. angulata* in Taiwan, suggesting an Asian origin of European *C. angulata* populations (Boudry *et al.*, 1998; Huvet *et al.*, 2000). This hypothesis is supported by the observation of mixed populations of *C. angulata* and *C. gigas* in northern China (Yu *et al.*, 2003; Lapègue *et al.*, 2004).

There is no morphological characteristic to differentiate between them because the larval and adult shells of both taxa have similar features (Menzel, 1974; Biocca and Matta, 1982). However, differences in growth performance, ecophysiological criteria, and disease susceptibility have been reported. *C. gigas* grows faster than *C. angulata* and has a lower mortality rate (Bougrier *et al.*, 1986; Soletchnik *et al.*, 2002), which could be explained by differences in clearance rate, oxygen consumption, and feeding activities (Gouletquer *et al.*, 1999; Haure *et al.*, 2003). High mortalities of *C. angulata* were observed between 1967 and 1973 in France, and irido-like viruses were suspected to be the causal agent of these events (Comps, 1988). These viruses were also observed in *C. gigas*, but no associated mortality was observed (Comps and Duthoit, 1976; Comps and Bonami, 1977). This suggests that *C. gigas* and *C. angulata* have different patterns of resistance to virus infection.

The most controversial aspect of comparisons of *C. gigas* and *C. angulata* is their genetic differentiations. Experimental hybridization, followed by studies on the viability and fertility of hybrids, as well as electrophoretic studies of enzyme polymorphism, suggests that *C. gigas* and *C. angulata* are a single species (Mathers *et al.*, 1974; Buroker *et al.*, 1979; Biocca and Matta, 1982; Mattiucci and Villani, 1983; Gaffney and Allen, 1993; Huvet *et al.*, 2001, 2002). Recent studies based on nuclear and mitochondrial DNA have highlighted the close genetic relationship between *C. angulata* and *C. gigas* (Lopez-Flores *et al.*, 2004; Reece *et al.*, 2008). On the other hand, studies on mitochondrial DNA (Boudry *et al.*, 1998; Huvet *et al.*, 2000) and karyotype analyses (Leitao *et al.*, 2004) have demonstrated genetic differences between *C. angulata* and *C. gigas* populations.

Therefore, according to current knowledge, and despite their close similarities, *C. gigas* and *C. angulata* are considered to be two distinct taxa (Figure 2.2).



Figure 2.2. The Portuguese oyster (*Crassostrea angulata*; left), and the Pacific oyster (*Crassostrea gigas*; right). Photos courtesy of Ifremer.

3 Biology of *Crassostrea gigas*

3.1 Anatomy

Oyster flesh is covered by a tegument, known as the mantle, which is involved in the process of shell calcification. Between the two lobes of the mantle is the pallial cavity, a free space divided by the gills into an inhalant and exhalant part where seawater circulation occurs (there are no siphons). In addition to extracting oxygen for respiration, the gills act as a filter that retains particulate matter (Gerdes, 1983; Bougrier *et al.*, 1995, 1998; Gouletquer *et al.*, 1999, 2004). The mouth, which is surrounded by the labial palps, is near the hinge, and the anus is just above the adductor muscle. During the reproductive phase, the gonadal mass is largely diffuse within the body flesh and reaches up to 70% of the total dry meat weigh for adults (Figure 3.1.1).

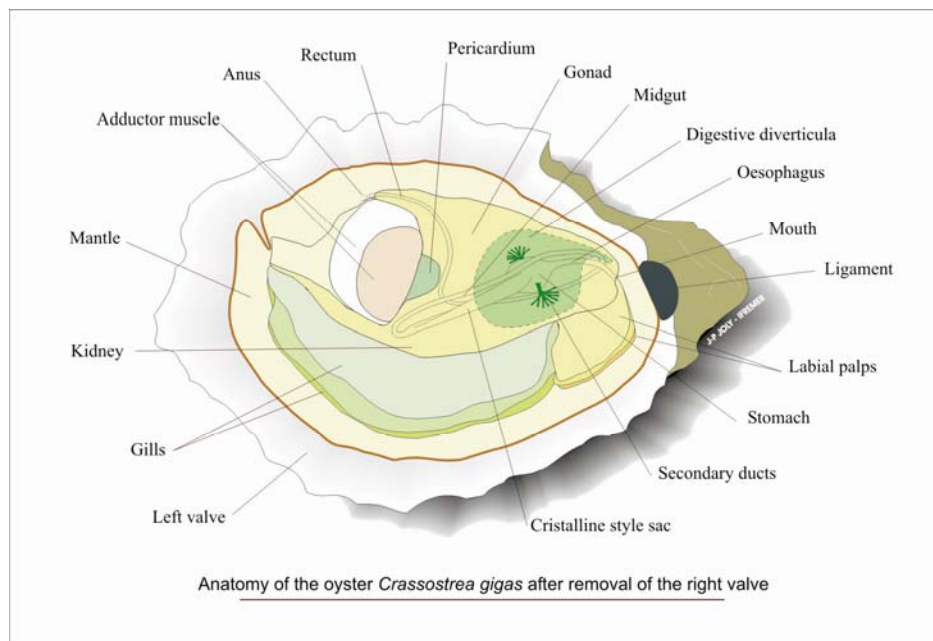


Figure 3.1.1. Anatomy of the Pacific oyster (*Crassostrea gigas*). Courtesy of J-P. Joly, Ifremer.

3.2 Behaviour

3.2.1 Feeding behaviour

Crassostrea gigas is a filter-feeder, extracting phytoplankton particles of organic and inorganic detritus from the seawater (see Section 3.4). It has the ability to select particles by size at the level of the gill and labial palps (Barillé *et al.*, 1997, 2000; Bougrier *et al.*, 1995, 1997). Particles for ingestion are transported towards the mouth by means of mucous secretion and ciliary action, whereas unwanted particles are agglomerated and rejected as pseudofaeces, together with the faeces resulting from the digestive activity. Temperature is the factor that drives all the physiological processes, including filtering activity, metabolism, respiration, and excretion rates (Bougrier *et al.*, 1995, 1998).

3.2.2 Reproductive behaviour

Crassostrea gigas is an oviparous oyster with a high level of fecundity (Deslous-Paoli and Héral, 1988). It changes its sex during life, usually spawning first as a male and subsequently as a female (Héral and Deslous-Paoli, 1990). Once activated (around

12 °C), gametogenesis depends directly on the duration of this temperature (degree days); a temperature of at least 18–20 °C is necessary for spawning, depending on location (Kobayashi *et al.*, 1997; Dean, 1979). For example, on the Atlantic coasts of European countries, spawning occurs in summer at temperatures above 18 °C and optimally at 21–22 °C. Salinity can vary between 25 psu and 35 psu. In the lagoons on the Mediterranean coast, *C. gigas* ceases to reproduce when the summer temperature reaches 24–25 °C and salinity reaches 37–38 psu (Héral and Deslous-Paoli, 1990). Fecundity is high; a female produces 20–100 million eggs per spawning (of diameter 50–60 µm). Fertilization is external, taking place in the seawater column.

The larvae (Figure 3.2.1) are initially free-swimming and planktonic, developing for 2–3 weeks prior to metamorphosis, when they find a suitable clean hard substratum on which to settle. They usually attach to rocks but can settle in muddy or sandy areas (attached to debris, small rocks, shells) or on other oysters, which leads to reef building (Orensanz *et al.*, 2002). The larvae are highly sensitive to environmental conditions and only a very small percentage of them survive to become spat (Figure 3.2.1). The natural habitat is intertidal, and the species can be found to a depth of 15 m on either hard or soft substrata. Larvae can survive for a short period at salinities as low as 5 psu. The swimming stage and the capacity to survive in various environmental conditions facilitate the dispersion of the species along coastal areas and its ability to colonize new areas (CIESM, 2000; NIMPIS, 2009).

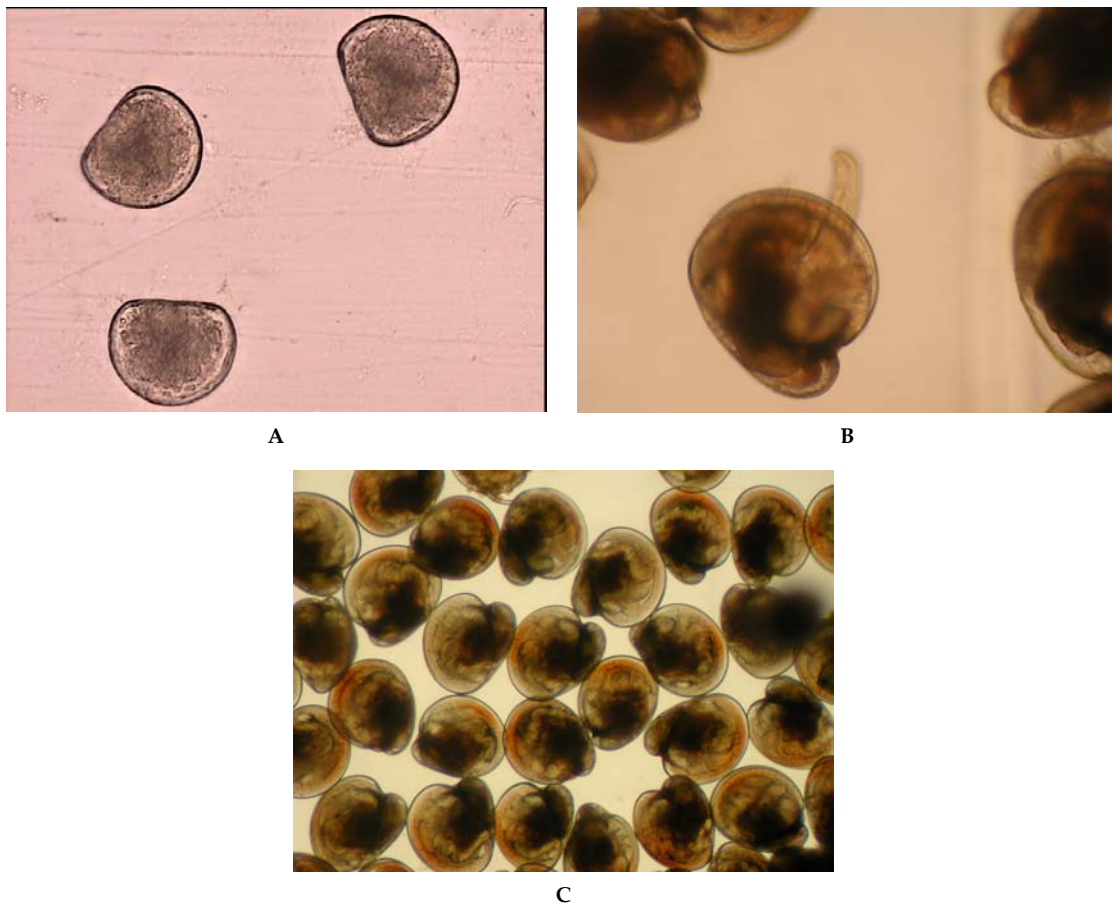


Figure 3.2.1. Larval and young spat stages of the Pacific oyster (*Crassostrea gigas*): (A) straight-hinged stage (75–80 µm); (B) pediveliger larvae (320–350 µm); (C) larvae (300–320 µm). Pictures courtesy of L. Degremont, Ifremer.

3.3 Tolerances

Salinity and temperature tolerances of *C. gigas* vary widely, depending on variety and on geographical location. *C. gigas* is an extremely euryhaline and eurythermic species that can be cultured in oceanic waters or in estuaries with a mean salinity of 15 psu and variations between winter and summer of 2–25%. At this very low level of salinity, juveniles and adults can survive for several weeks by closing their valves. Adults are cultured in saltmarsh ponds in France, where salinity reaches 45–50 psu; mortality is observed above 50 psu (Héral and Deslous-Paoli, 1990). Moreover, a combination of factors, such as temperature–salinity, is more typical of the species' tolerance than single factors (Gouletquer, 1997).

Interactions among factors are also critical. Similarly, physiological status and life stage are critical factors in the tolerance of environmental conditions (Powell *et al.*, 2000, 2002). The oyster's shell affords protection against temporary stresses, including pollutants and abnormal temperature–salinity conditions. Eggs and larvae are obviously more sensitive to environmental changes (His *et al.*, 1999). The optimum salinity range for egg development depends directly on the salinity in the area where the parent stock was grown. Overall growth performance depends largely on local carrying capacity, thus leading to extremely heterogeneous growth.

3.4 Nutrition and feeding

As *C. gigas* is a filter-feeder, its natural diet consists mainly of particles of organic and inorganic matter, including phytoplankton (FAO, 2004a). The composition of this diet, and specifically the ratio of its components, depends largely on environmental conditions and locations (estuarine areas, oceanic waters; Muniz *et al.*, 1986; Deslous-Paoli and Héral, 1988; Milyutin and Frolov, 1997). The adsorption of dissolved organic matter (e.g. amino acids), as well as bacteria, also contributes to the normal diet. Filtered particles are <50 µm and mainly around 10 µm. Nanoplankton can also contribute to the diet. For larval culture, a food concentration of 2 mg l⁻¹ is considered suitable to reach metamorphosis. In contrast, survival rate decreases to zero at a food concentration of ca. 0.5 mg l⁻¹, whereas growth and survival rate are affected when the concentration is <1 mg l⁻¹.

Although *C. gigas* does not require additional food to grow in an open environment, fertilizers can be used to maximize primary productivity and carrying capacity in semi-enclosed ponds and controlled environments (Hussenot *et al.*, 1998; Turpin *et al.*, 2001). Depending on the initial nutrient concentrations in the seawater, and also local irradiance, an NPSi medium can be introduced to balance nutrient ratios and thereby maximize algal blooms. This technique can be used for either individual species or mass production. For example, production of the diatom *Skeletonema costatum* can be maximized by using a medium with an N:P:Si ratio of 10:1:4. A simple three-component medium, supplemented with metals (iron and manganese), and with or without a metal chelator (EDTA), can be used efficiently at low cost (US\$2 for a 10⁶ cells mg l⁻¹ bloom in 100 m³ volume). In this case, a limited inoculum (10⁴ cells mg l⁻¹) can facilitate the bloom. The enrichment of seawater should be carried out so that no environmental impact occurs, and the NPSi medium should be entirely consumed by phytoplankton.

3.5 Disease and predation

3.5.1 Disease

Although *C. gigas* has demonstrated a wide tolerance of disease agents, which explains its worldwide success, several diseases and syndromes have been described (Bower, 2006; OIE, 2009). Owing to its life in open waters and the limitations of its immune system, no curative measures are available for *C. gigas* diseases. Prevention and adoption of best management practices remain the best options for limiting the impacts of disease. In the mid-term, genetic research programmes aimed at domesticating and developing selected disease-resistant (tolerant) strains are in progress.

“Summer mortality” syndrome has been described worldwide and seems to be correlated with high seawater temperatures and reproductive activity (Gouilletquer *et al.*, 1998). Although not fully understood, this syndrome is probably related to combined factors and highly complex interactions between environmental conditions, health status, and opportunistic pathogens. Recent studies have demonstrated the respective roles of environment, physiology, and pathogens, combined with the genetic make-up of oysters, in this syndrome.

The risk of a mortality event increases when particular conditions occur simultaneously, namely: (i) a mild and rainy winter, (ii) a seawater temperature threshold of 18 °C, (iii) a high level of food availability during the preceding spring, (iv) intensive reproductive effort, and (v) genetic susceptibility of the oyster population. An additional stress (chemical, thermal, or associated with cultural practices) is necessary to trigger the mortality event, which in turn will be associated with pathogens such as vibrios or herpes-like viruses (Samain and McCombie, 2008).

Focus on oyster mortality events in France during summer 2008

Abnormal mortality events for *C. gigas* occurred in the major oyster-producing areas of France during summer 2008. These events started during spring, a peak in mortality was recorded towards the end of June, and the epidemic ended approximately two weeks later. This mass mortality essentially affected juveniles <24 months of age, and only those of *C. gigas* species.

Mass mortalities of *C. gigas* have been reported over wide geographical areas and at high intensities wherever the species is cultured, and have occurred in France since the mid-1970s. According to Miossec *et al.* (2009), mortalities in 2008 occurred mostly along the Mediterranean coast of France, followed by the Atlantic coast, Brittany, and Normandy in the English Channel. Losses of *C. gigas* in France fluctuate from year to year. They were particularly high in the 1990s, but in 2008, the summer mortality events began very suddenly, were significantly more severe (up to 100%), and, although starting a little earlier in some areas, affected all the French rearing areas almost simultaneously.

Samples were collected from all of the affected locations and subjected to diagnostic tests. Results indicated that no listed pathogens were involved, but the pathogens Ostreid herpesvirus (OsHV-1) and two vibrio species (*Vibrio splendidus* and *V. aestuarianus*) were detected in most samples, especially in moribund oysters.

Initial investigations on oyster physiology and environmental conditions demonstrated that the model previously developed (Samain and McCombie, 2008) was partly met in this case. An epidemiological study, coordinated by Miossec, is currently underway at Ifremer (La Tremblade) in order to determine the respective

roles of pathogens and oyster transfers with regard to the exceptional intensity of this event in 2008. This study involves a partnership between Ifremer, the shellfish industry, and various French governmental bodies. Further work is required to characterize the virulence of the pathogens identified in association with these mortalities.

Diseases of *C. gigas* and the pathogens involved are described below.

- **Herpesvirus infections** are caused by viruses whose features, cellular locations, and sizes are characteristic of members of the Herpesviridae family (Renault *et al.*, 1994; ICES, 2004). Herpesviruses have been reported in nine different bivalve species worldwide, and their numbers have been shown to increase with the densities of the host (Renault and Novoa, 2004). Ostreid herpesvirus (OsHV-1) can infect several bivalve species and appears to demonstrate both vertical and horizontal transmission patterns. Herpesviruses have been associated with significant larval mortality in hatcheries in France and New Zealand (Hine *et al.*, 1992; Nicolas *et al.*, 1992) and appear to be widespread worldwide (Renault and Novoa, 2004). Irregular high mortalities of juveniles have been associated with herpesviruses since 1991, and OsHV-1 may be associated with the summer mortality syndrome.
- **An oyster velar virus disease (OVVD, Iridoviridae)**, affecting *C. gigas* larvae >150 µm, was reported in hatcheries in Washington State (US) during the 1980s (Elston and Wilkinson, 1985). An iridovirus was also considered to be the epizootic causative agent leading to the disappearance of *C. angulata* in French waters in the 1970s (Comps *et al.*, 1976; Héral and Deslous-Paoli, 1990).
- **Nocardiosis (fatal inflammatory bacteraemia (FIB) or focal necrosis)** is an infection caused by an actinomycete bacterium and is usually associated with mortalities during late summer and autumn. The agent, *Nocardia crassostreae*, is distributed along the west coast of North America from the Strait of Georgia in British Columbia, to California and also Japan (OIE, 2009). Diagnosis is based on the presence of round, yellow-green pustules, up to 1 cm in diameter, on the mantle, gill, adductor muscle, and heart surface. Associated mortalities have reached up to 35% in some localities. DNA probes are available for diagnosis. Although of unknown distribution, the agent appears to be widespread, given the historical movements of *C. gigas*. No control method is available, and the appropriate management option is to limit the transfer of contaminated oysters. Off-bottom culture, as well as rearing oysters outside shallow warm embayments, may reduce the prevalence of the disease.
- **Vibriosis** is the most commonly encountered disease associated with intensive bivalve culture in hatcheries and nurseries. Vibrios are ubiquitous marine bacteria that have been detected in various marine species, including oyster species such as *C. gigas* and *C. virginica*. *Vibrio splendidus* has been analysed in various coastal areas in France (Lacoste *et al.*, 2001; Le Roux *et al.*, 2002; Gay *et al.*, 2004), Spain (Pujalte *et al.*, 1999), Norway (Jensen *et al.*, 2003), the US (Thompson *et al.*, 2004, 2005), and the Pacific Ocean (Urakawa *et al.*, 1999). Moreover, vibrio isolates (*V. splendidus*) have demonstrated a virulence pattern that induces abnormal mortality rates. Recent data investigating the virulence factors in a specific strain of the oyster pathogen *V. splendidus* demonstrate that toxicity is

correlated with the presence of a metalloprotease corresponding to the *vsm* gene. This gene is the major toxicity factor in the extracellular products (Le Roux *et al.*, 2002; Gay *et al.*, 2004; Le Roux *et al.*, 2007; Binesse *et al.*, 2008).

- **“Foot disease”**, resulting from infection with the fungus *Ostracobable implexa*, has been observed in *C. gigas* and the European flat oyster (*Ostrea edulis*) in Canada and European waters. The fungus grows in the shell, causing wart-like protuberances on the inner surface that may weaken the oyster and diminish its marketability. No treatment or prevention measures are available.
- **Mikrocytosis** (Denman Island disease) is related to a small (2–3 µm), intracellular protistan parasite of unknown taxonomic affiliation (OIE, 2009). First reported in 1960, *Mikrocytos mackini* has been observed off the west coast of Canada and is probably ubiquitous throughout the Strait of Georgia and other specific localities around Vancouver Island. Round, green-yellow pustules or abscess-like lesions, up to 5 mm in diameter, occur within the body wall, on the surface of the labial palps or mantle, or in the adductor muscle. Brown scarring on the shell is often observed. Severe infections appear to be restricted to older oysters (>2 years old), although experimental challenges demonstrated that small juvenile oysters were also susceptible to infection. Lesions and mortalities occur in April–May, following a 3–4 month period when seawater temperature is <10 °C. Over a period of 30 years, the prevalence in older oysters has varied between 10% and 40%. Despite the fact that only 10% of the infected oysters usually recover, losses at the production level remain insignificant. Although marketable values, as well as the seed market, are affected by the disease, the economic impact at production level is fairly limited, owing to management practices that circumvent the effect of the disease. These practices include harvesting and moving oysters at locations high in the intertidal area prior to March and not planting oysters at low-tide levels before June. Oysters from infected areas should not be moved to disease-free rearing areas (Bower, 1988).
- **MSX (multinucleated sphere unknown) disease** is caused by the protistan parasite *Haplosporidium nelsoni* (phylum Haplosporidia), which is present in Korea, Japan, the west coast of the US, France, and probably in European waters, as a result of oyster transfers (Friedman, 1996). It is responsible for massive mortalities of the eastern oyster (*C. virginica*; OIE, 2002; NRC, 2004) but, in contrast, appears to be hosted by the Pacific oyster (*C. gigas*) at very low prevalence (<2%) and is not associated with measurable mortality in traditional rearing areas (Renault *et al.*, 2000). Trial introductions of *C. gigas* within the natural geographical distribution range of *C. virginica* have resulted in mortalities of *C. virginica*.
- **“Dermo” or “Perkinsosis”** is caused by the protistan parasite *Perkinsus marinus* and is another OIE notifiable disease occurring in *C. virginica* populations. Like the MSX agent, this parasite can also be present in *C. gigas* without the development of lethal infections (Burreson *et al.*, 1994).
- **“Egg disease”** is caused by *Marteilioides chungmuensis*, a parasitic protistan of the phylum Paramyxia, found in the reproductive system of *C. gigas*. It can infest ripe eggs and cause spawning failures by delaying spawning and destroying ripe oocytes (Park *et al.*, 2001; Ngo *et al.*, 2003).

Other parasites, such as the parasitic copepod *Mytilicola* spp., are thought to affect oyster physiology, resulting in castration and starvation effects.

3.5.2 Predation

C. gigas is predated by a variety of organisms, including seastars, boring gastropods and bivalves, spionid polychaetes, crabs, benthic feeding fish (such as stingrays and sea breams), ducks, and wading birds.

The Japanese oyster drill (*Ocenebrellus inornatus*) is causing major problems in oyster culture in several countries, including Washington State (US) and France (Carlton, 1999; Martel *et al.*, 2004). A turbellarian flatworm (*Pseudostylochus oestrophagus*) is also a major predator of *C. gigas*, attacking primarily young spat. Both species have become well adapted in various oyster-growing bays where they have been introduced. Red rock crab (*Cancer productus*) and green crab (*Carcinus maenas*) are well known predators, as is the veined whelk (*Rapana venosa*).

In addition, parasites such as the copepod *Mytilicola* spp., boring sponges (*Cliona* spp.), and sea worms (*Polydora* spp.) affect oyster physiology and, thereby, can significantly affect oyster culture.

4 Distribution of *Crassostrea gigas*: origins and worldwide introductions for aquaculture

4.1 Origins

Originating in northeast Asia, *C. gigas* is endemic to Japan, where it is also an important and historical aquaculture species. There are various accounts of the origins of oyster culture in Japan, but the earliest written record dates from the 16th century and refers to the now-famous Hiroshima Bay, and is thus the first historical record of *C. gigas* culture worldwide.

Over the past 400 years, the Japanese production of *C. gigas* has increased, reaching a maximum in 1968; for the past ten years, it has attained a stable level. The growth in production was accompanied by both technological innovations and the movement of production areas farther offshore, in response to industrial development in Japan and poorer environmental quality. In 2002, there were 3370 oyster farms in Japan, with *C. gigas* and the Iwagaki oyster (*Crassostrea nippona*) being the major cultured species (<http://web-japan.org/atlas/nature/nat30.html>).

Other Asian countries with well-documented records of oyster aquaculture, including the native *C. gigas*, are Korea (Park *et al.*, 1988) and China (Park *et al.*, 1988). Methods of culture in these two countries combine both traditional and modern, highly specialized techniques. China is reported to be the country with the largest *C. gigas* production worldwide (FAO, 2009).

4.2 Introductions and translocations

Crassostrea gigas has been introduced and translocated from northeast Asia into a number of countries, mainly for aquaculture purposes (CIESM, 2000; CSIRO, 2002; Leppäkoski *et al.*, 2002; Wolff and Reise, 2002; Ruesink *et al.*, 2005; NIMPIS, 2009), but sometimes accidentally, for example, in Denmark (Wang *et al.*, 2007), Norway (Mortensen *et al.*, 2007), Sweden (Wrange, 2008), and New Zealand (Dinamani, 1991).

The major intentional introductions of *C. gigas* worldwide are summarized below, with special focus on introductions targeted at reviving aquaculture. A common factor in the first two examples, the UK and Belgium, is that *C. gigas* was not expected to be able to establish self-sustaining wild populations.

4.2.1 United Kingdom

The first introduction of *C. gigas*, from North America to a quarantine facility at Conwy, Wales, in 1965, was aimed at reviving oyster farming in the UK after the decline of populations of the native flat oyster (*Ostrea edulis*) as a result of overexploitation. At that time, *C. gigas* was not expected to be able to establish wild populations from escaped individuals because seawater temperatures around the UK were cooler than those around Japan.

However, sporadic natural spatfalls of *C. gigas* were reported in 1994 (Spencer *et al.*, 1994), and a survey by Couzens (2006) revealed the presence of small reefs at some sites in Devon. In a further study, Syvret (2008) designated regions around the British coastline as being at high, medium, or low risk from natural recruitment. The regions at highest risk, where recruitment is likely in most years, are south and southeast England. There are already extensive beds of naturally recruited Pacific oysters in some of the estuaries of southeast England. A study by Child *et al.* (1995) of the genetic composition of stocks of naturally recruited oysters in the UK, suggested that

oysters in the River Teign, in Devon, may have been of French origin. A possible explanation of this finding is the natural dispersion of larvae from France by water currents.

4.2.2 Belgium

Another interesting example of the effects of the intentional introduction of *C. gigas* rapidly followed, with its unexpected naturalization in Belgium. The Sluice Dock at Oostende, an artificial pond of 86 ha, diverted from its original purpose, has been used for shellfish mariculture since 1930. Imports of various species of oysters have included *O. edulis* and *C. angulata* from other parts of Europe, *C. virginica* from the east coast of the US, and *C. gigas*. Imported in 1969 and the early 1970s from the Netherlands, *C. gigas* was the only oyster species apparently able to establish self-sustaining populations; specimens survived even after oyster culture, and imports ceased in 1974 (Kerckhof *et al.*, 2007). However, these authors also report that *C. gigas* became established outside areas of culture only in the early 1990s, most probably as a result of an increase in water temperatures. Since then, *C. gigas* has colonized most parts of the Belgian coast, forming massive reefs, and is also found on buoys far offshore. This last observation is significant because it indicates that such man-made floating structures may act as stepping stones in the establishment and dispersal of non-native species, such as *C. gigas* (Kerckhof *et al.*, 2007).

4.2.3 Ireland

Translocations of cupped oysters (the Portuguese oyster, *C. angulata*) from southern Europe to Ireland were first made in the late 1800s (Minchin, 1996). At about the same time, *C. virginica* was imported in deck cargo from Long Island Sound in the US (Minchin and Rosenthal, 2002). This followed the exhaustion of wild flat oyster (*O. edulis*) populations as a result of increased exploitation, facilitated by more rapid distribution by rail. These imported oysters were grown from the half-growing stage and sold after a summer's growth.

Following successful settlements in the early 1900s of the native flat oyster (*O. edulis*) in ponds, some attempts were made to introduce the Portuguese oyster (*C. angulata*) to the west coast of Ireland. These failed because summer temperatures were not sustained at levels high enough to permit settlement (Wilkins, 1989). However, in the 1980s, occasional settlements of the Pacific oyster (*C. gigas*) occurred in lined ponds and in the nearby shallows in Cork Harbour.

However, in many situations where *C. gigas* was introduced to revive existing aquaculture, the species was expected to naturalize and rapidly form self-sustaining populations. Successful illustrations of this objective include the importation of *C. gigas* into Australia, North America, and France.

4.2.4 Australia

The introduction of *C. gigas* into Australia is an example of the successful use of this species as a "replacement species" to compensate for the exhaustion of stocks of native oyster species. Collecting oysters has a long history in Australia (Nell, 1993). Indigenous Australians fished for both the Sydney rock oyster (*Saccostrea glomerata*) and the Australian flat oyster (*Ostrea angasi*). "Middens" (the accumulation of discarded shells after removal of the meat) containing these species occur widely along the Australian coastline and are testimony to this ancient fishing activity (Maguire and Nell, 2007).

The farming of local species of oysters, although a more recent activity (starting approximately 120 years ago), is considered one of the oldest aquaculture activities in Australia. Following European settlement in Australia, the extensive beds of native oysters were exploited commercially for human consumption, but mainly for lime (calcium carbonate) production. As a result, all these beds were overfished and exhausted in the 1800s and early 1900s and have never fully recovered.

The first attempts to revive oyster culture in South Australia with the native flat oyster (*O. angasi*) in 1910–1912 resulted in poor harvests, and new trials conducted in the 1960s also were not successful. Other attempts to revive oyster aquaculture in Australia also involved the introduction of an exotic, hardier species (*C. gigas*), and a first shipment came from Japan to Tasmania in 1947–1948. This was followed by new introductions in 1951–1952, and in 1969, transfers of *C. gigas* from Tasmania to South Australia were made.

The development of *C. gigas* culture in Tasmania and South Australia was initially based on natural, but poor, production (Aquaculture SA, 2003). The real onset of *C. gigas* culture in Tasmania, and thereafter in South Australia, is linked to the development of hatchery-produced spat in the 1980s. In 1985, the culture of *C. gigas* relied mainly on the supply of spat from three Tasmanian hatcheries; later, other hatcheries producing *C. gigas* spat were also established in South Australia.

Although aquaculture of *C. gigas* only developed after spat became available from local hatcheries, this species was rapidly revealed to be highly invasive. The need to protect beds of native oysters from invasion by this exotic species quickly prompted state managers to implement transfer restrictions and eradication programmes in South Australia (Ayres, 1992).

4.2.5 North America

In terms of sustaining aquaculture industry, another successful importation of *C. gigas* was made into North America, where oysters have been part of the human diet for time immemorial. The main native oyster species found in North America are the Olympia oyster (*Ostreola conchaphila*) on the west coast and the eastern oyster (*C. virginica*) on the east coast. With regard to the importation of *C. gigas*, the topic of special focus is the oyster industry on the west coast of North America, where middens of the native Olympia oyster have accumulated wherever Native Americans fished for and ate these oysters.

With the arrival of pioneers, oyster fishing increased. In some bays, such as those in California and Oregon, overfishing, together with the development of coastal industries and associated pollution, resulted in the exhaustion of stocks of *O. conchaphila* as early as the 1850s. Willapa Bay continued to supply *O. conchaphila*, but it too was depleted by the beginning of the 20th century. After the collapse of *O. conchaphila*, attempts to culture the species were made, but a first replacement species (*C. virginica*) was soon used, massive numbers of which were imported from the east coast. *C. virginica* revived the oyster industry on the west coast for a time, but after unexplained mass mortalities of this species were experienced in the 1920s, a second replacement species had to be found.

The first shipment of *C. gigas* spat from Japan arrived in 1922 on the west coast of the US (in Washington State). The species adapted well to this new location and allowed the resurrection of the local oyster industry. Initially relying entirely on imported seed, the culture of *C. gigas* was later aided by a supply of natural spatfall from various western American bays (Willapa Bay and bays in the Hood Canal in

Washington State). The imports of *C. gigas* spat continued until the 1970s, but spat supply for aquaculture now consists mainly of seed produced by local hatcheries. Currently, *C. gigas* is present and cultured on the west coast of North America from California to southeast Alaska (Nosho, 1989; Foster, 1997; Lindsay and Simons, 1997; Shaw, 1997).

On the west coast of Canada, the native oyster is *Ostrea lurida*, the fishery for which stopped in 1940. Oyster aquaculture, which began with the introduction of the eastern oyster (*C. virginica*) at the beginning of the 20th century, had limited success. *C. gigas* was first introduced into British Columbia in about 1912 or 1913. By 1925, natural breeding had occurred. However, significant quantities of spat and adult oysters were imported between 1926 and 1932 from Japan and Washington State, respectively. During this time, natural spawning was observed to have variable success. In 1948, breeding was prolific and widespread. Consequently, the Canadian oyster industry started to develop significantly, using wild spat. Since then, no more oyster importation has been necessary to supply the shellfish industry. *C. gigas* is also produced in hatcheries, where the broodstock are spawned and the larvae raised under controlled growing conditions (Quayle, 1988).

4.2.6 Europe

Similarly, in France, the history of oyster culture consists of a succession of developmental phases, using different species, followed by collapses caused by overfishing and disease. The native flat oyster (*O. edulis*) has been fished for many centuries, and its exploitation in France developed notably during the Roman occupation. The native oyster beds were overexploited in the 18th century, especially along the Atlantic coast (Gouletquer and Héral, 1997), and the culture of *O. edulis* faced several crises in the various French production areas. Some were unexplained (1920, 1950), whereas others were associated with parasites (*Marteilia refringens* in 1968, *Bonamia ostreae* in 1979).

This all favoured the development of the culture of a new species, the Portuguese oyster (*C. angulata*), in France. The first imports of *C. angulata* were made in 1860 and aimed at compensating for the depletion of *O. edulis*. The species then spread along the Atlantic coast, where both *O. edulis* and *C. angulata* were co-cultured. Production of *C. angulata* reached a maximum after 1950, and then started to decrease. Mortalities were observed and explained by overstocking of production units (Héral and Deslous-Paoli, 1990). Production gradually decreased until the outbreak of gill disease in 1966. This disease, caused by an iridovirus, spread rapidly throughout all culture zones, causing massive mortalities between 1970 and 1973, and leading to the total extinction of *C. angulata* in France.

The oyster industry reacted promptly with the “Resur” plan, which consisted of the introduction of a new species, the Pacific oyster (*C. gigas*). Small-scale trials were conducted between 1966 and 1970, followed by the importation of several hundred tonnes of broodstock from Canada (Grizel and Héral, 1991). This very successful operation resulted in abundant spat capture from the first year in the Marennes–Oléron Basin, where the imported broodstock had been placed. At the same time, 10 000 t of *C. gigas* spat were imported from Japan and distributed to all other production areas in France, including the Mediterranean Sea.

Crassostrea gigas exhibited fast growth and good health, and production was able to increase rapidly. Spat capture, very successful in the Marennes–Oléron and the Arcachon basins, was sufficient to supply all the French production sites, and further

imports became unnecessary (Buestel, 2006). The reproductive population of *C. gigas* in France, initially confined to the Atlantic coast, has now become established in more northern latitudes; it is thought that global warming has greatly influenced this move (Cognie *et al.*, 2006), as well as the physiological capacity and adaptability of *C. gigas* to various environments (Cardoso *et al.*, 2007).

As a result of these imports to France, and to various European countries, wild populations of *C. gigas* have now not only colonized all coastal areas in France, but can also be found in more northern European countries. These wild populations can be observed significantly throughout Europe, from Portugal to northern Germany and Denmark (Cardoso *et al.*, 2007; Buck *et al.*, 2006).

A few specimens have also been found along the south coast of Norway. Successful spawning was also reported in early 2000 in a former shellfish farm located south of Bergen. Although the number of naturally settled *C. gigas* found in this part of Norway is low (fewer than 100 individuals), the species has demonstrated its capacity to adapt to this environment and is thought to have spread into the fjord system farther north, where a couple of individuals have also been found (Mortensen *et al.*, 2007). Recent data reveal that the west coast of Sweden has now been colonized by a wild population of *C. gigas*, which was probably introduced by drifting larvae from secondary introductions (Wrangle, 2008; Wrangle *et al.*, 2009).

4.2.7 Africa

The presence of *C. gigas* in African countries is less well documented. However, the species has been cultured for a long time in this continent, notably along the coast of South Africa, where it has been the main cultured oyster species for the past 30 years (Robinson *et al.*, 2005). Although *C. gigas* has been present for a long time along this coast, these authors indicate that naturalized populations of *C. gigas* are only observed in estuaries, not along the open coast.

Cultured for a similar length of time in Tunisia, *C. gigas* has not proved capable of producing sufficient natural spatfall to sustain local aquaculture. The culture of *C. gigas* in Tunisia still relies on imported spat, from Japan since 1972 and now mostly from France (Dridi *et al.*, 2007).

4.2.8 South America

Crassostrea gigas arrived in South America approximately 20 years ago, relatively late compared with most other countries where the species is present as a result of intentional introduction. In the Pacific Ocean, it was introduced into Chile and Peru (Winter *et al.*, 1984) and, in the Atlantic Ocean, into Brazil and Argentina (Pascual and Orensanz, 1996; Orensanz *et al.*, 2002; Escapa *et al.*, 2004). Introductions of *C. gigas* into these last two countries were experimental and for aquaculture purposes. These trials were rapidly abandoned, but the species survived. Orensanz *et al.* (2002) report an explosive increase in the settlement in Argentina between 1998 and 2000. There, reefs of wild *C. gigas* are expanding rapidly and generating dramatic changes in the environment, which these authors predict to be potentially disastrous.

4.2.9 Conclusions/summary

The above reports indicate that *C. gigas* was justifiably considered the hardy species required to sustain aquaculture in many countries worldwide. *C. gigas* has demonstrated its ability to adapt to various latitudes after being introduced by humans (Figure 4.2.1). Subsequent to these intentional introductions, *C. gigas* has

settled and formed wild populations. Initially found in the vicinity of culture areas, the species has demonstrated a capacity to colonize more distant areas.

Indeed, because *C. gigas* is extremely tolerant of a range of seawater temperatures and salinities, it is able to grow in very varied environments, ranging from estuarine areas (brackish waters) to offshore oceanic waters. Natural recruitment areas are usually located in coastal and estuarine waters affected by freshwater input. In fact, the larval survival rate is driven by a temperature–salinity combination that is optimal in slightly desalinated areas.

With regard to suitable rearing areas, the main constraint is carrying capacity. Coastal and estuarine areas are usually highly productive because of freshwater input and the resulting primary productivity, which allows more intensive rearing. The fact that seed is widely available and can be easily transferred allows these areas, as well as other areas where no natural recruitment occurs, to be used for oyster culture. From a geographical point of view, the worldwide distribution of *C. gigas* demonstrates that equatorial and polar regions are the only areas less favourable to culture or colonization.

Although highly variable, the invasive pattern of *C. gigas* has been demonstrated in several countries where, accordingly, it is considered a pest or noxious species (Ayres, 1992; Ashton, 2001; Blake, 2001; Orensanz *et al.*, 2002). Elsewhere, the species poses no problem and is considered in terms of economic interest (McKenzie and Lopez, 1997; Leppäkoski *et al.*, 2002; Escapa *et al.*, 2004). The consequences of the current distribution of *C. gigas* are discussed in Section 5.

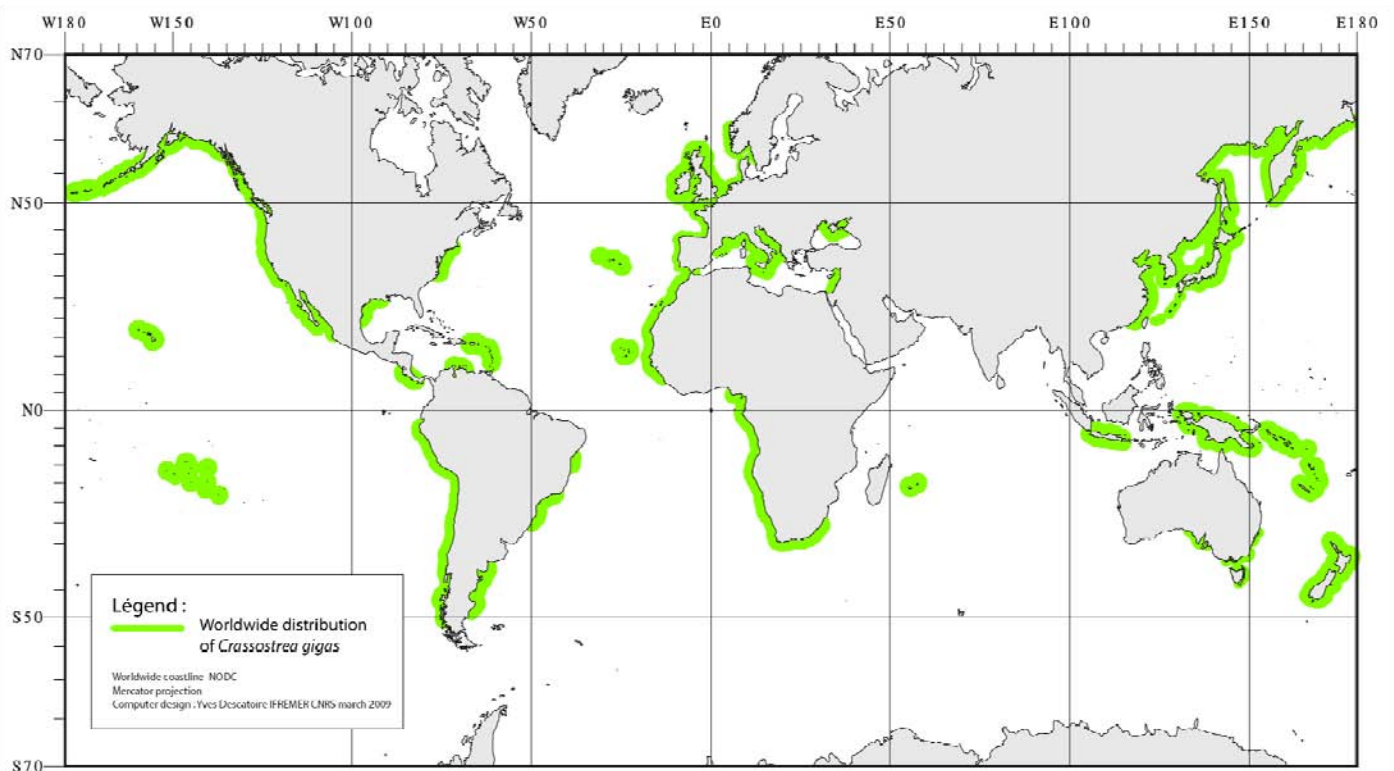


Figure 4.2.1. Worldwide distribution of the Pacific oyster (*Crassostrea gigas*).

5 Production and productivity of *Crassostrea gigas*

5.1 Production

5.1.1 Sea-based production

Traditional, sea-based oyster culture relies mainly on the collection of natural seed in open areas using spat-collecting techniques (Figure 5.1.1). Spat-collectors are deployed at the appropriate location and time (in relation to the spawning season), to facilitate and maximize settlement and recruitment (NRC, 2004). After several months of rearing in open waters, oyster spat from natural falls is either (i) removed from the spat-collectors and deployed onto sticks on (on-bottom) culture grounds or into oyster bags on trestles, baskets, suspensions, or (ii) allowed to stay on the spat-collectors for pre-growth, thus requiring thinning out to decrease their density. This is done in both coastal bays and inland areas, using semi-enclosed oyster ponds that are filled with seawater by gravity and tidal effect. Usually, oyster stocking density is adapted to local carrying capacity by adapting mesh size to oyster size in order to maximize current patterns and food availability, and ultimately to reduce the duration of the rearing cycle.

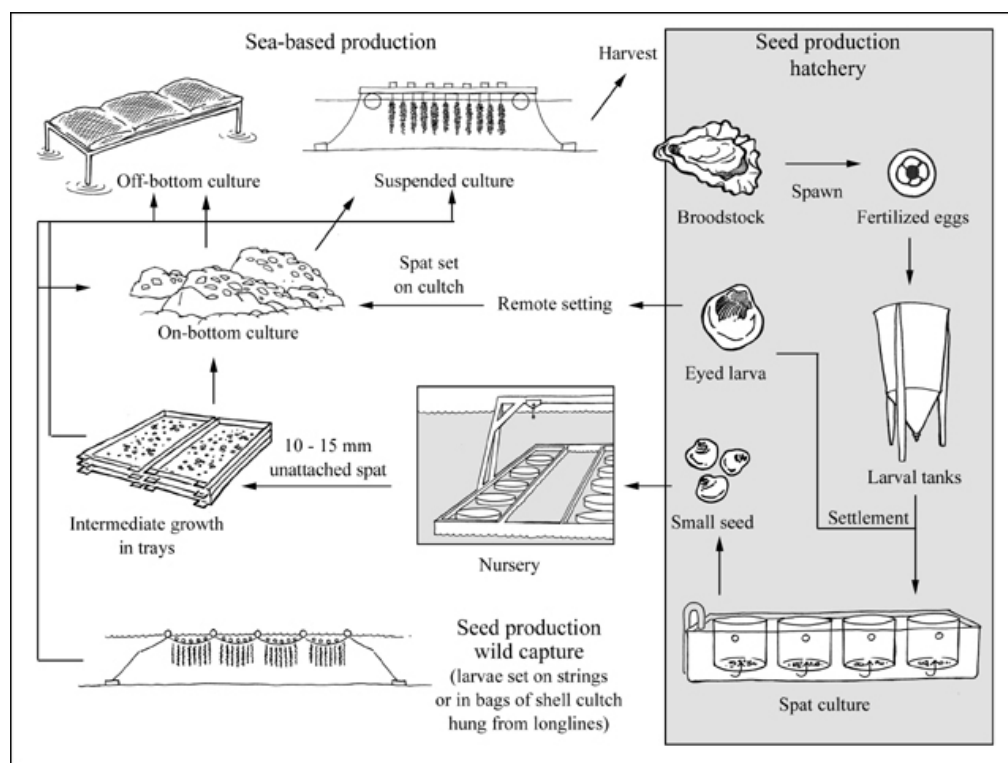


Figure 5.1.1. Traditional and modern rearing techniques (FAO, 2009).

5.1.2 Hatchery production

In areas where no natural recruitment occurs, oyster farmers rely on hatchery production, which is based on mimicking the natural reproductive season, in a controlled environment, by adjusting temperature and algal food for broodstock conditioning (FAO, 1990, 2004a). Once the broodstock are mature, gametes are collected, either by inducing a thermal shock or by stripping the gonads. Fertilization is also carried out in a controlled environment, which includes gamete density, in order to obtain a larval culture.

Larvae are cultured in large tanks (up to 100 m³ in China), and vitamins and antibiotics are provided to maximize survival rate and yield (Guo *et al.*, 1999). Food is provided until metamorphosis (at two weeks), and metamorphosis is facilitated by deploying either spat-collectors, similar to those used in open environments (shell strings, PVC dish, and tubes), or calibrated shell pieces. The latter technique, used in the production of single-cultured oysters, is preferred because it allows oysters to be calibrated and sorted at the micro-nursery and nursery stages of the rearing process. In addition, removing the oyster spat from collectors is unnecessary with this technique, which is less stressful to the oyster and saves time.

Hatchery production has encouraged the development of oyster culture in areas where the natural catch is poor and has permitted the domestication of the species (Degremont, 2003; Ernande *et al.*, 2003; Huvet *et al.*, 2004a). Shellfish farmers have shown great interest in utilizing seed supply from hatcheries, which allows them to work with a constant, year-round supply of seed from selected strains as well as polyploid sterile individuals (triploids; Allen *et al.*, 1989; Gérard *et al.*, 1994; Guo and Allen, 1994).

Several techniques are used for the pregrowth and growth stages, depending on the peculiarities of each rearing area. Oysters are produced using on-bottom and off-bottom techniques, either intertidally or subtidally. Once they reach marketable size, the oysters are harvested and brought ashore to the packing houses, where they are usually sorted, graded, and stored in clean water to remove mud and grit and to undergo slight depuration before being marketed. In polluted areas, depuration is compulsory to avoid public health problems.

5.2 Productivity

The production of *C. gigas* is now based mainly on culture. Indeed, oyster fisheries have demonstrated poor sustainability and reduced product quality. *C. gigas* capture fisheries have never been significant, with a global annual production of no more than 32 000 t (Figure 5.2.1).

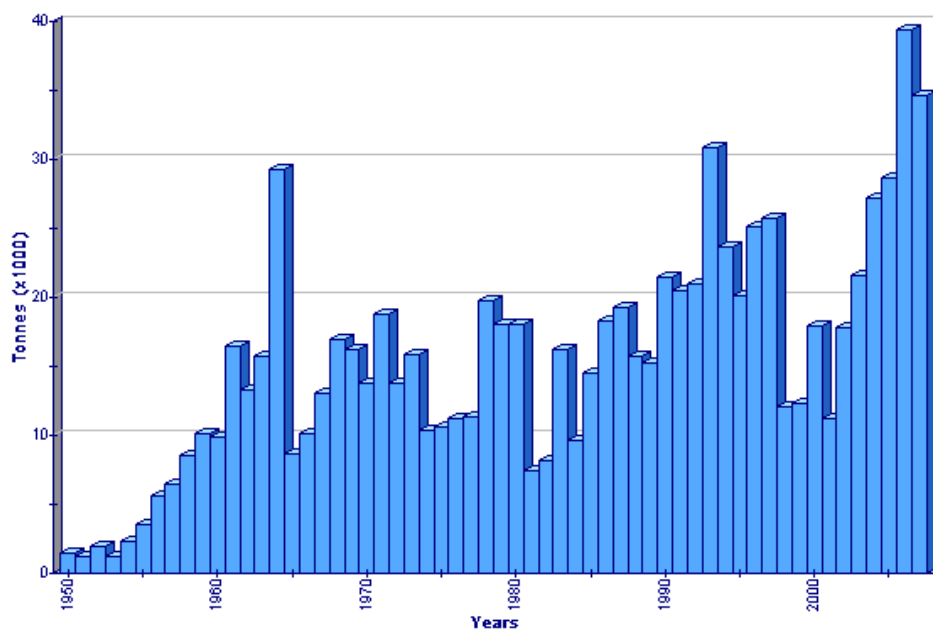


Figure 5.2.1. Global capture production for *Crassostrea gigas* (FAO, 2009).

In 2006, global *C. gigas* aquaculture production (Figure 5.2.2) reached 4.6 million t (FAO, 2008). The main producer, China, had a recorded production of 3.9 million t, followed by Korea (283 000 t), and Japan (208 000 t). European production came next, at around 126 000 t, with France as the major producer (116 000 t), followed by Ireland (6500 t), the UK (1400 t), and Spain (1200 t).

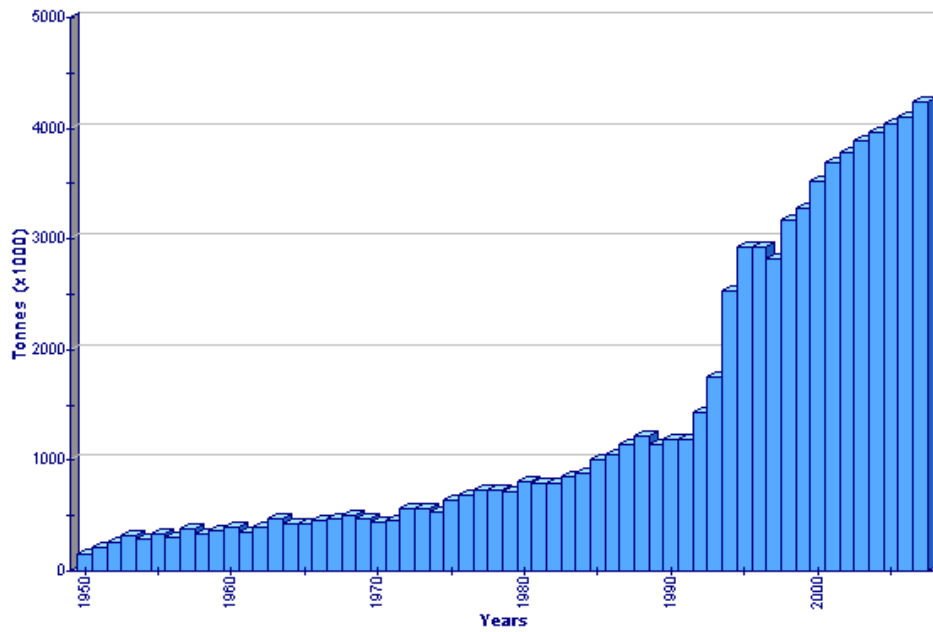


Figure 5.2.2. Global aquaculture production for *Crassostrea gigas* (FAO, 2009).

6 Environmental factors affecting *Crassostrea gigas* dispersal

A native species from Asia, *C. gigas* is now present in a number of countries worldwide (Figure 5). In areas where *C. gigas* has established wild populations, a number of factors appear to have influenced its dispersal.

6.1 Temperature and climate change

During the 1960s and 1970s, a major period of active importations of *C. gigas*, notably to European countries, it was thought that temperature would be the main limiting factor. Indeed, at that time, because the natural distribution of *C. gigas* was in relatively warm waters, the species was not expected to be able to reproduce and establish self-sustaining populations in northern parts of Europe (Drinkwaard, 1999).

The importance of temperature in relation to the reproductive and dispersal patterns of *C. gigas* is mostly supported by biological data on reproductive features (see Section 3.2). The survival of larvae and juveniles is also affected by low winter temperatures. Child and Laing (1998) have reported that the minimum temperature tolerance of juvenile *C. gigas* is approximately 3 weeks at 3 °C.

Although climate change is becoming a major concern worldwide, it also has a proven impact on the geographical distribution of many species. It was noted recently that the invasion and expansion of *C. gigas* in the German Wadden Sea were accelerated by high late-summer water temperatures (Diederich *et al.*, 2005). Similar findings were made on the Belgian coast (Kerckhof *et al.*, 2007) and in France (Cognie *et al.*, 2006). The expansion of *C. gigas* in more northern European countries also seems to be a result of climate change (Wrange *et al.*, 2009). Climate change is frequently considered in terms of global warming, but it will also influence and modify ocean currents. For example, the Gulf Stream is expected to slow down within a few decades (Minobe *et al.*, 2008), which will result in a dramatic decrease in temperatures in the European countries under its influence. Therefore, the long-term effects of climate change may result in changes in the distribution of species and in the current trend of colonization of more northern European latitudes by *C. gigas*.

Current findings, as well as suggesting that water temperature is an important factor in the reproduction of *C. gigas* and the establishment of wild populations, also indicate that other environmental factors should be considered (Cardoso *et al.*, 2007).

In Europe, in an attempt to assess the further expansion of *C. gigas*, Cardoso *et al.* (2007) have carried out a study on the relative physiological performance of wild populations of *C. gigas* along a latitudinal gradient from southwest France (La Rochelle) to the northern part of the Netherlands (Texel, western Dutch Wadden Sea). Their findings indicated large differences in the various length-at-age and mass-at-age data in the locations studied. Overall, they found a general trend of increasing growth and reproduction from La Rochelle to Texel, suggesting that temperature is not the main limiting factor for reproduction and that global physiological conditions, such as optimal food availability and a less stressful environment, are also required. Importantly, they also found that oysters in more northern locations produce a larger number of eggs of smaller size, which prolongs larval development and the pelagic stage, and thus increases larval dispersal capacity and expansion of the population far from the spawning sites.

Syvret (2008) designated regions around the British coastline as being at high, medium, or low risk from natural recruitment, according to temperature profiles. He then applied climate-change predictions to this assessment and concluded that the

medium-risk regions, which included Northern Ireland, Wales, and southwest England, would become high risk for recruitment in most years by 2040.

Occasional wild settlements of Pacific oysters have been found at locations along the Irish coast, including Donegal Bay in northwest Ireland and Strangford Lough on the Irish Sea (Boelens *et al.*, 2005). However, these settlements are not as concentrated as those found in the sheltered bays and inlets on the south coast of England. Sparse settlements are known from the north coast of Wales near Conwy.

Crassostrea gigas was introduced into the lagoons of the northern Adriatic and into Greece for aquaculture purposes in the 1980s and is now a naturalized species (Zenetos *et al.*, 2004; Marino *et al.*, 2006).

Climate-related aspects of the spread of *C. gigas* in Europe

In a meeting report of the Working Group on Introduction and Transfers of Marine Organisms (ICES, 2008), the following climate-related aspects of the spread of *C. gigas* were reported by country.

Ireland. A number of factors promote the spread of *C. gigas*, one of which is climate change. Settlement has occurred on all coasts where there are shallow bays that are sufficiently warmed (Minchin, pers. comm.).

Belgium. Oysters spawn earlier after warm winters, indicating that their spread is probably climate related.

Germany. The observed trend of oyster spread appears to be climate related. As there is no salinity change in the Wadden Sea and no limitation of food, the correlation between change and temperature appears to be climate related.

Norway. There are only one or two locations in southern Norway where *C. gigas* is known in the wild.

Sweden. In summer 2007, specimens of *C. gigas* aged <1 year appeared along almost 300 km of the west coast, which may be considered an indication of a climate-change related spread in oyster distribution from Denmark or Germany, because the previous winter and spring were mild.

United Kingdom. *C. gigas* is spreading.

France. There is a natural spread of *C. gigas* outside farms, with a northward pattern of colonization and spreading. There is great concern about its ecological impacts (e.g. food limitations, the integrity of mudflats), and efforts to remove or reduce escaped populations are underway.

The Netherlands. *C. gigas* is spreading. There are plans to destroy oyster reefs in order to preserve mudflats.

Italy. There have been no recent changes in the distribution of *C. gigas*.

Spain. *C. gigas* is found both in farms and in the wild, but it is not known if temperature affects the populations.

6.2 Ocean acidification

Other reported environmental factors that influence the growth and, potentially, the dispersal of shellfish species are related to ocean acidification. Indeed, anthropogenic emissions of carbon dioxide have already reduced the pH of the surface waters of oceans and will continue to do so. The pH of seawater currently ranges between 7.8 and 8.2 and, on average, is already 0.1 pH unit lower than it was prior to the

industrial revolution (Caldeira and Wickett, 2003). Predictions based on realistic scenarios for future CO₂ emissions suggest that ocean pH will decrease by a further 0.3–0.4 by 2100 (Caldeira and Wickett, 2003).

This process is expected to have dramatic consequences for calcification and the metabolic processes of many marine species. The effects will vary, depending on species. As an example, the ophiuroid brittlestar (*Amphiura filiformis*) will experience an increase in the rate of many of its biological processes; this will be accompanied by other negative effects, notably on its muscle (Wood *et al.*, 2008). In other calcified species, ocean acidification will result in reduced rates of calcification (Gattuso *et al.*, 1999; Feely *et al.*, 2004), as well as in reduced growth (Michaelidis *et al.*, 2005). Gazeau *et al.* (2007) predict that this phenomenon will have a dramatic impact on both cultured and wild populations of mussels (*Mytilus edulis*) and *C. gigas*, whose calcification rates may decrease by 25% and 10%, respectively, by 2100. The effects on larval stages are unknown, but acidification is expected to alter larval survival rates considerably.

Ocean acidification also has an effect on non-calcifying species. Some studies have demonstrated that an increase in the carbon:phosphate ratio can reduce the growth rate of certain phytoplankton and the fecundity of zooplankton (Fernand and Brewer, 2008). However, most of the available data on shellfish are based on controlled experiments. Therefore, more experimental and field data are required in order to fully assess the consequences of this phenomenon, but a dramatic impact on coastal biodiversity and ecosystem functioning can be expected by the end of this century. Field studies, incorporating an ecosystem-based approach, are necessary to test these hypotheses.

7 Consequences of *Crassostrea gigas* introductions

7.1 Ecological competition and biodiversity

In a review related to the impact of bivalve introductions in marine ecosystems, Barber (1997) explains that the intentional introduction of an exotic species may result in direct biological competition with native species, which may be outcompeted for food and space.

Reports indicate that colonization by *C. gigas* has resulted in ecological competition between this exotic species and native species in many places. The increase in *C. gigas* populations constitutes competition not only for food but also for space, with other filter-feeding species, such as cockles (*Cerastoderma edule*) or mussels (*Mytilus edulis*), as reported in Dutch and German waters of the Wadden Sea (Diederich *et al.*, 2005; Van den Berg *et al.*, 2005). However, some authors also emphasize that the decline of *M. edulis* beds observed in the Wadden Sea is a result of the combined effects of invading species, namely *C. gigas* and the slipper limpet (*Crepidula fornicata*), and climate change. Indeed, there is evidence that the decline of *M. edulis* beds is mainly caused by a decline in spatfall, possibly related to mild winters. Successive mild winters and warm summers facilitate spatfalls of *C. gigas* and *Crep. fornicata*, and the presence of these two exotic species in the Wadden Sea only enhances a phenomenon that is primarily provoked by climate change (Nehls *et al.*, 2006) and also favours a higher predation rate of bivalve spat by shrimp and crabs, which are sensitive to cold winters and favoured by warm winters (Nehls and Buttger, 2007).

By outgrowing cockles (*Cerastoderma edule*) in the Wadden Sea, one of Europe's most important wetlands for migratory bird populations, *C. gigas* is also assumed to be responsible for the reduction in food availability for birds feeding on the cockles (Smaal *et al.*, 2005; Van den Berg *et al.*, 2005).

In the western US, it is thought that *C. gigas*, which was primarily introduced to revive the declining shellfish industry (based originally on *Ostreola conchaphila*), contributed to the decline of this last native species, essentially by outcompeting it for food and space (Chew, 1992).

In France, the import of *C. gigas* may have contributed to the depletion of *C. angulata*, the species previously cultured. Indeed, it is thought that *C. gigas* may have been a carrier for the iridovirus responsible for the virtual disappearance of *C. angulata* from French coasts (Grizel and Héral, 1991).

In South Australia, *C. gigas* arrived accidentally in New South Wales as a result of natural breeding and larval transport from other areas, aided by boat carriage and shipments of contaminated native oyster spat. When the settlement of *C. gigas* in several estuaries became obvious in 1973, it was declared a "noxious species", and eradication programmes were instituted to reduce the competition with the native species, *Saccostrea glomerata*, formerly known as *S. commercialis* (Bourne, 1979; Ayres, 1992).

Similarly, *C. gigas* from New South Wales was introduced accidentally to New Zealand via the hulls of ships, as larvae in ballast water, or by larval transport from Tasmania (Bourne, 1979; Dinamani, 1992). *C. gigas* again proved capable of outcompeting the native species, *S. glomerata*, for food and space. In addition, *C. gigas* has greater fecundity and grows to marketable size twice as quickly as *S. glomerata*. Accordingly, it became the dominant species in New Zealand as early as 1977.

In addition to competition for food and space between the introduced *C. gigas* and native species, especially bivalve molluscs, *C. gigas* introductions have also had a significant global impact on local ecosystems in many places. Although such impacts are mainly considered negative, there are also reports of potentially beneficial effects.

In the Wadden Sea (Smaal *et al.*, 2005; Van den Berg *et al.*, 2005; Nehls and Buttger, 2007), along the Belgian coast (Kerckhof *et al.*, 2007), in France (Cognie *et al.*, 2006), and in many other places, *C. gigas* has formed dense reefs and dramatically changed the original habitat. As a result of this change, and competition with native species, significant alteration of the overall biodiversity and biomass can be expected (Kerckhof *et al.*, 2007).

However, several other studies, reviewed by Nehls and Buttger (2007), have demonstrated that the three-dimensional structure of *C. gigas* reefs offers a rich habitat for epibenthic as well as endobenthic species and plays an important role in marine foodwebs, e.g. for birds and other predators. Similarly, Nehring (2003) suggests that *C. gigas* has a beneficial effect on the richness of the environment in the Wadden Sea. Indeed, the decline of native oyster (*O. edulis*) beds resulting from overexploitation in the 18th century has been accompanied by a concomitant decline or disappearance of associated invertebrate populations. The establishment of new *C. gigas* reefs allows the re-establishment of these communities, at least in intertidal zones.

A comparative study conducted by Görlitz (2005) indicates no differences in the species richness of *M. edulis* and *C. gigas* beds, although some species were found in different abundances. Similar densities of barnacles (Cirripedia) were found on oysters and mussels, lower densities of *Semibalanus balanoides* and juvenile crab (*Carcinus maenas*) were found on oysters, and higher densities of *Littorina littorea*, *Ralfsia verrucosa*, and *Polydora ciliata* were recorded on oyster beds, but no loss of species has been documented (Görlitz, 2005). Markert *et al.* (2009) also observed that *Crassostrea* reefs favour species richness, abundance, biomass, and diversity of the macrofaunal communities.

As in the Wadden Sea, the effects of the introduction of *C. gigas* into Willapa Bay (US) have been investigated. Among the alien species reported there, *C. gigas* and cordgrass (*Spartina alterniflora*) may play a particularly important role in structuring previously unstructured tideflats. Thus, *C. gigas* reefs and culture sites provide extensive new hard substrata for fish, invertebrates, and macroalgae (such as *Ulva* spp.). Although oyster expansion has occurred at the expense of burrowing shrimp and other infauna (by changing their natural habitat), it is also thought to be partly responsible for the increased richness and biodiversity recorded locally (Ruesink *et al.*, 2006). However, this apparently beneficial effect of the introduction of *C. gigas* requires further studies in order to better evaluate the long-term consequences on natural ecosystems.

The accuracy of such evaluations obviously depends on the availability of descriptive and quantitative data related to natural ecosystems. This is emphasized in a review by the Argentinean and Uruguayan scientific communities (Orensanz *et al.*, 2002), aimed at evaluating the status of the so-called "Patagonian Shelf Large Marine Ecosystem", a marine protected area classified by UNESCO as part of a World Heritage site. Their findings indicate that most coastal ecosystems between the estuary of the La Plata River and central Patagonia have already been modified following the introduction of species. Although the number of recorded introduced species (31; Orensanz *et al.*, 2002) is relatively small compared with other well-studied

areas, such as San Francisco Bay (150; Cohen and Carlton, 1998) and Chesapeake Bay (180; Ruiz *et al.*, 1999), a significant ecological impact has already occurred in estuarine ecosystems, nearshore, and shallow bays, caused mainly by the effects of five introduced marine species: a barnacle (*Balanus glandula*), a macrofouling bivalve (*Limnoperna fortunei*), a reef-building serpulid worm (*Ficopomatus enigmatus*), kelp (*Undaria pinnatifida*), and the Pacific oyster (*C. gigas*).

The reefs formed by *C. gigas* settlement in shallow bays have expanded explosively since 1998. Dramatic changes are underway as oyster reefs develop and provide a new spatial architecture, representing increased refuge for intertidal communities. In the short term, the new habitats provided by these oyster reefs may benefit the richness of the environment. For example, increased prey abundance will benefit birds that feed on the reefs (Escapa *et al.*, 2004). The long-term effects are unknown, but it is likely that introduced species, including *C. gigas*, will continue to dramatically change local benthic communities (Orensanz *et al.*, 2002). Marine reserves in the San Juan Archipelago (Washington State) were found to contain greater densities of two invaders, *Sargassum minutum* and *C. gigas*, than unprotected areas outside the reserves. The mechanisms involved were still unclear, but these findings underline the potential vulnerability of reserves to biological invasion (Klinger *et al.*, 2006).

7.2 Genetic changes in *Crassostrea gigas*

Hybridization among *Crassostrea* spp. has been well studied and demonstrated in specific cases (NRC, 2004). Crosses between *C. ariakensis* and *C. gigas* are viable, although *C. ariakensis* has been cultured throughout southern China and Japan for more than 300 years (NRC, 2004). Moreover, several *C. gigas* races or morphotypes are found in Japan. Therefore, it is likely that some natural hybridization has already occurred, accompanying the many years of translocation and worldwide introductions. In Washington State (US), hybridization between *C. ariakensis* and *C. gigas* occurred during the period 1960–1990 as a consequence of poor broodstock management. It is thought that a reduction in genetic diversity has occurred in some way.

However, given the high oyster plasticity and the relatively recent availability of genetic markers, it is likely that this process has been underestimated until now. This observation is supported by the identification, in New Zealand Pacific oysters (*C. gigas*), of two rare alleles that had only been previously recorded in *Saccostrea glomerata* (Dinamani, 1992). Such interbreeding between introduced and native species may result in a loss of genetic variability with unknown results (Newkirk, 1979). In addition, natural hybridization between genetically differentiated populations of *C. gigas* and *C. angulata* was demonstrated (Huvet *et al.*, 2004b). Therefore, the remaining populations of the *C. angulata* ecotype in Portugal are threatened by current culture development and extensive transfers of *C. gigas* (Huvet *et al.*, 2000).

7.3 Introduction of diseases, parasites, and hitchhiker species

Historically, concern about intentional introductions was for the production of the introduced species, not for the ecosystem receiving the exotic species. Little care was taken to ensure that only the intended species was introduced (Barber, 1997). As a result, a number of “hitchhiker” species were introduced along with the intended species, and the impact of these additional exotic species on native ecosystems was not generally realized until some time after the original introduction.

Along with imports of *C. gigas*, several hitchhiking marine species were introduced into the west coasts of the US, Europe, and other places. Gouletquer *et al.* (2002) reported that, of the 87 exotic species introduced accidentally into the Atlantic and Channel coasts of France, Spain, and Portugal, 28% were presumed to be associated with oyster shipments, mainly *C. gigas* in the 1970s, and four of these were oyster parasites. These species had various ecological or economic impacts. For example, the establishment of the Manila clam (*Ruditapes philippinarum*) has supported a considerable industry in various places, such as the US (Barber, 1997). Other species, such as the Japanese oyster drill (*Ocenebrellus inornatus*), a flatworm (*Pseudostylochus ostreophagus*), and a parasitic copepod (*Mytilicola orientalis*) have a not insignificant negative effect on oyster or mussel production.

Algae are also represented among the hitchhiker species imported with *C. gigas*. Gouletquer *et al.* (2002) listed 21 introduced seaweeds, of which 13 (62%) were presumably introduced by oysters. For almost the same coastal areas, but also including the Canary Islands and the Azores, Wallentinus, in a ten-year status report for algae and plants (ICES, 2007), listed 30 introduced seaweeds, of which 13 (43%) were presumably introduced with oysters. For the south coasts of France and Spain, together with the Italian coast, she listed 80 introduced seaweeds, of which 42 (53%) were presumably introduced with oysters (ICES, 2007, Table 2.1). In the whole area included in her report (which also included Canada and the US, as well as Baltic Sea coasts), there were 129 introduced seaweeds, of which 50 (39%) were presumably introduced with oysters (ICES, 2007, Table 2.1).

The very high percentage of seaweeds introduced in this way, especially in southern and southwestern Europe, underlines the importance of oysters as a vector, especially of seaweeds, and of the need to mitigate this risk by appropriate treatment of imported adult oysters, using quarantine conditions. As many of these seaweeds have important impacts on the ecosystems through competition and habitat modification, in many cases, they have become a nuisance. Among the most well-known and invasive species that have been introduced in this way are the Japanese brown algae *Sargassum muticum* and *Colpomenia peregrine*, the Japanese kelp *Undaria pinnatifida*, the red algae *Grateloupia turuturu* and *Heterosiphonia japonica*, and perhaps the invasive “*tomentosoides*” subspecies of the green alga *Codium fragile*.

In January 1993, large consignments of half-grown oysters were imported into Ireland from France, despite advice that this would compromise the status of the *C. gigas* stock then in culture. This stock was derived from the quarantined population in Conwy, which was first introduced into Ireland in 1965. In February 1993, the parasitic copepods *Mytilicola orientalis* and *Mytilicola ostrea* were found in imports, and *Myt. Orientalis* subsequently became established in Dungarvan Bay on the south coast of Ireland (Holmes and Minchin, 1995). Following these imports, summer mortality events were recorded for the first time. Recently, small *Crepidula fornicata* males have been found in small numbers associated with imports of half-grown *C. gigas* from France in the 2000s, but were not found to survive in culture in bags on trestles, where they were crushed (Minchin, 2007). It is strongly suspected that *Sargassum muticum* was introduced to Strangford Lough in Ireland with imports of oysters from the Channel Islands (Davison, 1999).

Apart from the parasite *Haplosporidium nelsoni* and the Japanese oyster drill (*Ocenebrellus inornatus*; Garcia-Meunier *et al.*, 2002), few data are available on the introduction of exotic diseases or parasites along with intentional or accidental introductions of *C. gigas*. Transmissions by shipping (*C. gigas* has often been found

attached to the hulls of ships) may result in spawning events upon entry to warm harbours and possibly the release of pathogens. There has been no research into the transmission of pathogens by hull-fouling molluscs (Minchin and Gollasch, 2003).

The worldwide distribution of some pathogens and their recorded impact on many marine species and in many areas suggest that they may have been present in numerous parts of the world since ancient times. It therefore seems unrealistic to try to determine whether, for example, OsHV-1 or *Vibrio* spp. have been present worldwide since ancient times or their current distribution is a result of human activities and/or translocations of species from one part of the world to another.

However, even in the absence of recorded signs of disease, there is a need for more active research and surveys aimed at searching for exotic pathogens. Given the number of translocations of *C. gigas* around the world, it is likely that some exotic pathogens are present at a subclinical level in some areas. Although they may not have a noticeable impact now, the recorded and predicted environmental changes, added to the intensification of culture and changes in cultural practices, could lead to the emergence of new problems. Such comprehensive surveys would help to establish early appropriate sanitary management and prevent future pathological events, notably in culture areas.

7.4 Control and management procedures

There are few published data on eradication or reduction programmes targeted at *C. gigas*, except from Australia (Ayres, 1992), where *C. gigas* is considered a noxious species in areas where it can outcompete native oysters.

A comprehensive methodological approach to best practices for the management of introduced marine species has been developed by the Global Invasive Species Programme (Hilliard, 2005) in Australia. Notably, including lessons from terrestrial bioinvasions and clues to evaluate the side effects of eradication methods, this approach also stresses the importance of risk assessment, surveillance, and the development of adequate information, coordination, and legislative tools. Information tools have been developed by the National Introduced Marine Pest Information System (NIMPIS; <http://www.marine.csiro.au/crimp/nimpis/>; <http://adl.brs.gov.au/marinepests/>), which also aims to provide potential control options. However, none of the methods described have proven to be totally effective for the eradication of *C. gigas* (McEnnulty *et al.*, 2001).

A similar approach has been enforced by northern European countries, where the Nordic-Baltic Network on Invasive Species database (NOBANIS; <http://www.nobanis.org>), based on the Australian information system, was implemented. However, despite these efforts, the Netherlands is the only European country where significant mass reduction trials have been conducted.

With regard to *C. gigas*, there are controversial views that merit emphasis. The species may be considered a pest in the Wadden Sea or in Australia, but at the same time, it supports a large fishery in France. Moreover, in some areas, a distinction must be made between wild and cultured stocks of this species, and their respective ecological and economic impacts, as well as their impacts on other human activities. For example, in France, several studies have been carried out in the Marennes–Oléron Basin (Coïc, 2007), the Gulf of Morbihan (Le Gall, 2006), Bourgneuf Bay (Cognie *et al.*, 2006), and at a national level (Hily *et al.*, 2007). The collection of such data on a national and regional basis is an essential preliminary step towards the determination

of the most appropriate actions, taking into account the particular characteristics of individual sites.

The Marennes–Oléron Basin in France is an example of successful reduction measures. Indeed, the restructuring of leases in the basin, enforced over the last decade, allowed a significant reduction of wild stocks in farmed areas. The thorough removal of wild *C. gigas* and, at the same time, its trophic competitor *Crepidula fornicata* and predator *Ocenebrellus inornatus*, involved the use of powerful machinery, such as caterpillar tractors and snow ploughs, especially equipped for marine activities. A barge was also especially equipped to collect abandoned shellfish gear, to quarry unwanted stones, sand, and mud, and to gather animals for removal from the cleaned areas (Miossec and Gouletquer, 2007).

7.5 Economic impacts

Considering that only ca. 5.25% of its worldwide production originates in its native range, the overall introduction of *C. gigas* has had a highly significant economic impact, with a value amounting to US\$3.305 billion, based on yearly production (FAO, 2004b). In several countries, the introduction of this species has resulted in the establishment of a sustainable shellfish industry, providing direct revenues for thousands of farmers and people involved in associated activities (e.g. equipment provision). Moreover, the highly valuable (and unaccountable) indirect economic impact of the long-term establishment of coastal communities in otherwise unfavourable rural areas plays a significant role in coastal management values. For example, the European oyster crisis in the 1970s, following the rapid disappearance of disease-affected *C. angulata* populations, was resolved by the introduction of *C. gigas*, which saved the collapsing industry (Gouletquer and Héral, 1992; NRC, 2004).

In contrast, the introduction of *C. gigas* has had economic side effects in several countries, such as Australia (New South Wales), where the native Sydney rock oyster was partly outcompeted by the invasiveness of *C. gigas*, leading to several business collapses. In this case, the indirect economic impact is related to the increasing costs of coastal management programmes to limit *C. gigas* reef expansion and of eradication.

7.6 Social impacts

Various aspects of the social impacts of *C. gigas* have been well studied in France. Unpublished observations (C. Hily, pers. comm.) are reported below. Although the relative importance of these aspects may vary, depending on the country or region of concern, they are mostly of global interest.

7.6.1 Farming activities

The socio-economic impact of wild *C. gigas* can be represented by its consequences on other industries in neighbouring areas, particularly shellfish farming and professional fishing activities (C. Hily, pers. comm.; related to work carried out under the Ifremer PROGIG research programme).

Of the potential negative impacts of *C. gigas* on other cultured shellfish species, competition for food is not insignificant, and other nuisances are reported, such as increased difficulties in the upkeep of equipment and its accelerated deterioration after colonization by wild *C. gigas*. In addition, in some areas, wild oyster beds result in an accumulation of mud that creates new difficulties in accessing mussel culture areas. In other areas, the invasion of mudflats by wild *C. gigas* has a physical impact

on the environment and modifies it, affecting commercial fishing activities on mudflats, such as the collection of clams.

On the other hand, some positive effects of wild *C. gigas* are reported. Indeed, wild *C. gigas* can benefit the collection of mussels because of the spat that attach to them. In some places, reefs of wild *C. gigas* are also considered an opportunity to diversify commercial fishing activities and generate income, because they can be exploited and commercialized.

7.6.2 Recreational activities

As with farming activities, the dispersal of *C. gigas* can affect recreational activities in both positive and negative ways. For example, the impact of *C. gigas* on recreational fishing activities can be both positive, where it constitutes a new species to collect, and negative, where it leads to a reduction of other collectable species, particularly those living in mudflats.

However, the presence of *C. gigas* is considered a nuisance with regard to many recreational activities because of its sharp shells. These can cut people while they are swimming or playing in the sea or on beaches during low or mid-low tides. Cuts also occur frequently during nautical activities and recreational fishing.

As a permanent, year-round, coastal user, the *C. gigas* industry is contributing significantly to coastal management. It contributes to the economic sustainability of coastal communities and is a stakeholder in the Integrated Coastal Zone Management process. As the oyster industry requires a high standard of seawater quality for public health reasons, it also contributes to long-term environmental monitoring. Considered a traditional activity in several oyster-producing countries, *C. gigas* culture has been of interest for “green” tourism development.

8 Conclusion

In various places worldwide, overexploitation and poor management, coupled with pollution and pathological events, have led to the exhaustion of stocks of native shellfish species. Consequently, exotic species have been translocated to support the local shellfish industry. The Pacific oyster (*C. gigas*) is probably the best example of a mollusc species that has been introduced to revive existing aquaculture. In several countries, the introduction of this species has resulted in the establishment of a sustainable shellfish industry providing direct revenues for thousands of farmers and others involved in related activities (e.g. equipment providers). This situation could be attributed to the capacity of *C. gigas* to adapt to various environmental conditions.

Translocations of *C. gigas* into new areas were made at a time when management practices were limited. The consequences for the local environments were not estimated and, more generally, not expected. Observations reveal that naturalization of *C. gigas* has occurred in the countries where it was introduced, for example, in neighbouring areas owing to larval dispersion or illegal introductions.

The effects of *C. gigas* introductions on biodiversity are still being debated. Competition with other filter-feeding species for food and space was generally observed, even with species that were overexploited, thus contributing to their decline. However, several studies demonstrated that *C. gigas* reefs could represent new habitat, where a rich community could be observed. Moreover, *C. gigas* could be a source of food for many marine species. For a better evaluation of the positive and negative impacts of the spread of *C. gigas*, an ecosystem-based approach is required.

The expansion of *C. gigas*, especially in northern Europe, is often thought to be related to global warming. Further studies are needed that consider the genetic characteristics of this species and its adaptability to new environments.

It is not always possible to eradicate *C. gigas* once it has been introduced and, in many countries, it is not desirable because *C. gigas* now supports an important aquaculture industry. However, even in these countries, mitigatory programmes are necessary to limit its expansion. However, the negative and positive impacts of these programmes need to be assessed at an experimental scale before they are applied to a wider field scale in the field. Relevant recommendations and comprehensive methodological approaches to best practices for the management of introduced species have been provided in numerous programmes worldwide and are now available for implementation.

Governments and stakeholders are becoming increasingly concerned about the protection of the marine environment and the risk associated with the introduction of exotic species for aquaculture purposes. New regulations concerning the use of alien species in aquaculture have been published, e.g. EC Council Regulation No. 708/2007, concerning use and locally absent species in aquaculture (CEU, 2007). These regulations are often based on the ICES Code of Practice (ICES, 2005). This proposed a framework for good cultural practices when introducing exotic species for aquaculture development, in order to avoid or minimize the possible impact of these and any “hitchhiker” species on the aquatic environment.

Acknowledgements

The authors thank participants of the ICES WGITMO and ICES SGBOSV for valuable and constructive comments on the manuscript.

9 References

- Allen, S. K., Downing, S. L., and Chew, K. K. 1989. Hatchery Manual for Producing Triploid Oysters. Washington Sea Grant Program publication WSG 89-3, University of Washington Press, Seattle, WA. 27 pp.
- Aquaculture SA. 2003. Pacific oyster aquaculture in South Australia. Primary Industries and Resources SA. FS 26/01. 6 pp.
- Ashton, I. 2001. *Crassostrea gigas* invades marine reserves in San Juan Island. In 2nd International Conference on Marine Bioinvasions, 9-11 April 2001, New Orleans, LA, Abstracts. MIT Sea Grant Center for Coastal Resources. Available online at <http://massbay.mit.edu/exoticspecies/conferences/2001/abstracts01>.
- Ayres, P. 1992. Introduced Pacific oyster in Australia. In *The Ecology of Crassostrea gigas in Australia, New Zealand, France and Washington State*, pp. 3-7. Ed. by M. Leffler and J. Greer. University of Maryland Sea Grant publication UM-SG-TS-92.07, Maryland Sea Grant College, College Park, MD. 25 pp.
- Barber, B. 1997. Impacts of bivalve introductions on marine ecosystems: a review. *Bulletin of National Research Institute of Aquaculture (Suppl. 3)*: 141-153.
- Barillé, L., Prou, J., Héral, M., and Razet, D. 1997. Effects of high seston concentration on the feedings, selection and absorption of the oyster *Crassostrea gigas* (Thunberg). *Journal of Experimental Marine Biology and Ecology*, 212: 149-172.
- Barillé, L., Haure, J., Cognie, B., and Leroy, A. 2000. Variations in pallial organs and eulatero-frontal cirri in response to high particulate matter concentrations in the oyster *Crassostrea gigas*. *Canadian Journal of Fisheries and Aquatic Sciences*, 57: 837-843.
- Bernard, F. R. 1983. Catalogue of the Living Bivalvia of the Eastern Pacific Ocean: Bering Strait to Cape Horn. *Canadian Special Publication of Fisheries and Aquatic Sciences*, 61. 102 pp.
- Binesse, J., Delsert, C., Saulnier, D., Champomier-Vergès, M. C., Zagorec, M., Munier-Lehmann, H., Mazel, D., et al. 2008. Metalloprotease *vsm* is the major determinant of toxicity for extracellular products of *Vibrio splendidus*. *Applied and Environmental Microbiology*, 74: 7108-7117.
- Biocca, E., and Matta, F. 1982. *Crassostrea angulata* (Lamarck, 1819), synonym of *Crassostrea gigas* (Thunberg, 1793): morphological and genetic studies. *Parasitologia*, 24: 211-22.
- Blake, J. A. 2001. Shellfish culture as a vector for biological invasions. In 2nd International Conference on Marine Bioinvasions, 9-11 April 2001, New Orleans, LA, Abstracts. MIT Sea Grant Center for Coastal Resources. Available online at <http://massbay.mit.edu/exoticspecies/conferences/2001/abstracts01>.
- Boelens, R., Minchin, D., and O'Sullivan, G. 2005. Climate Change: Implications for Ireland's Marine Environment and Resources. Marine Foresight Series No. 2, Marine Institute, Oranmore, Co. Galway. 40 pp.
- Boudry, P., Heurtebise, S., Collet, B., Cornette, F., and Gérard, A. 1998. Differentiation between populations of the Portuguese oyster *Crassostrea angulata* (Lamarck) and the Pacific oyster *Crassostrea gigas* (Thunberg) revealed by mtDNA RFLP analysis. *Journal of Experimental Marine Biology and Ecology*, 226(2): 279-291.
- Bougrier, S., Ragueneas, G., Bachere, E., Tige, G., and Grizel, H. 1986. Essai de réimplantation de *Crassostrea angulata* en France. Résistance au chambrage et comportement des hybrides *C. angulata*-*C. gigas*. ICES Document CM 1986/F:38. 10 pp.
- Bougrier, S., Geairon, P., Deslous-Paoli, J. M., Bacher, C., and Jonquières, G. 1995. Allometric relationships and effects of temperature on clearance and oxygen consumption rates of *Crassostrea gigas* (Thunberg). *Aquaculture*, 134: 143-154.

- Bougrier, S., Hawkins, A. J., and Héral, M. 1997. Preingestive selection of different microalgae mixtures in *Crassostrea gigas* and, *M. edulis* analysed by flow cytometry. *Aquaculture*, 150: 123–134.
- Bougrier, S., Collet, B., Geairon, P., Geffard, O., Héral, M., and Deslous-Paoli, J. M. 1998. Respiratory time activity of the Japanese oyster *Crassostrea gigas* (Thunberg). *Journal of Experimental Marine Biology and Ecology*, 219: 205–216.
- Bourne, N. 1979. Pacific oysters, *Crassostrea gigas* (Thunberg), in British Columbia and the South Pacific Islands. In *Exotic Species in Mariculture*, pp. 1–51. Ed. by R. Mann. MIT Press, Cambridge, MA. 363 pp.
- Bower, S. M. 1988. Circumvention of mortalities caused by Denman Island oyster disease during mariculture of Pacific oysters. *American Fisheries Society Special Publication*, 18: 246–248.
- Bower, S. M. 2006. Synopsis of infectious diseases and parasites of commercially exploited shellfish: nocardiosis of oysters. Available online at <http://www.pac.dfo-mpo.gc.ca/science/species-especes/shellfish-coquillages/diseases-maladies/pages/nocardoy-eng.htm>.
- Brock, V. 1990. Intergeneric distances between *Ostrea*, *Crassostrea* and *Saccostrea*, studied by means of crossed immunoelectrophoresis. *Marine Ecology Progress Series*, 68: 59–63.
- Buck, B. H., Walter, U., Rosenthal, H., and Neudecker, T. 2006. The development of mollusc farming in Germany: past, present and future. *World Aquaculture*, 37: 6–11 and 66–69.
- Buestel, D. 2006. History, status and future of oyster culture in France. The 1st International Oyster Symposium Proceedings, Tokyo, Japan, July 2005. *Oyster Research Institute News*, 20: 1–11.
- Buroker, N. E., Hershberger, W. S., and Chew, K. K. 1979. Population genetics of the family Ostreidae. I. Intraspecific studies of *Crassostrea gigas* and *Saccostrea commercialis*. *Marine Biology*, 54: 157–169.
- Burreson, E. M., Mann, R., and Allen, S. K. 1994. Field exposure of triploid *Crassostrea gigas* to *Haplosporidium nelsoni* (MSX) and *Perkinsus marinus* (Dermo) in the lower Chesapeake Bay. *Journal of Shellfish Research*, 13: 293.
- Caldeira, K., and Wickett, M. E. 2003. Anthropogenic carbon and ocean pH. *Nature*, 425: 365.
- Cardoso, J. F. M. F., Langlet, D., Loff, J. F., Martins, A. R., Witte, J. I. J., Santos, P. T., and van der Veer, H. W. 2007. Spatial variability in growth and reproduction of the Pacific oyster *Crassostrea gigas* (Thunberg, 1793) along the west European coast. *Journal of Sea Research*, 57: 303–315.
- Carlton, J. T. 1999. Molluscan invasions in marine and estuarine communities. *Malacologia*, 41: 439–454.
- CEU (Council of the European Union). 2007. Council Regulation (EC) No. 708/2007 of 11 June 2007 concerning use of alien and locally absent species in aquaculture. *Official Journal of the European Union*, 28.6.2007. Available online at <http://eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=OJ:L:2007:168:0001:0017:EN:PDF>.
- Chew, K. K. 1992. Ecological and biological considerations for the introduced Pacific oyster to the west coast of the United States. In *The Ecology of Crassostrea gigas in Australia, New Zealand, France and Washington State*, pp. 20–24. Ed. by M. Leffler and J. Greer. University of Maryland Sea Grant publication UM-SG-TS-92.07, Maryland Sea Grant College, College Park, MD. 25 pp.
- Child, A. R., and Laing, I. 1998. Comparative low temperature tolerance of small juvenile European, *Ostrea edulis*, L., and Pacific oysters, *Crassostrea gigas* Thunberg. *Aquaculture Research*, 29: 103–113.

- Child, A. R., Papageorgiou, P., and Beaumont, A. R. 1995. Pacific oysters *Crassostrea gigas* (Thunberg) of possible French origin in natural spat in the British Isles. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 5: 173–177.
- CIESM (Mediterranean Science Commission). 2000. Global invasive species database: *Crassostrea gigas* (mollusc). Available online at <http://www.ciesm.org/atlas/Crassostreagigas.html>.
- Cognie, B., Haure, J., and Barillé, L. 2006. Spatial distribution in a temperate coastal ecosystem of the wild stock of the farmed oyster *Crassostrea gigas* (Thunberg). *Aquaculture*, 259: 249–259.
- Cohen, A. N., and Carlton, J. T. 1998. Accelerating invasion rate in a highly invaded estuary. *Science*, 279: 555–558.
- Coïc, L. 2007. Etude dynamique de l'ostréiculture dans le bassin de Marennes-Oléron depuis l'introduction de l'huître japonaise *Crassostrea gigas*: De la production à la prolifération. Ifremer Master 2, Exploitation des Ressources Vivantes Côtières, IBFA University of Caen, France. 74 pp.
- Comps, M. 1988. Epizootic diseases of oysters associated with viral infections. *American Fisheries Society Special Publication*, 18: 23–37.
- Comps, M., and Bonami, J. R. 1977. Infection virale associée à des mortalités chez l'huître *Crassostrea gigas* Th. *Comptes rendus de l'Académie des Sciences de Paris, D*, 285: 1139.
- Comps, M., and Duthoit, J. L. 1976. Infection virale associée à la "maladie des branchies" de l'huître portugaise *Crassostrea angulata* Lmk. *Comptes rendus de l'Académie des Sciences de Paris, D*, 283: 1595.
- Comps, M., Bonami, J. R., Vago, C., and Campillo, A. 1976. Une virose de l'huître portugaise (*Crassostrea angulata* Lmk). *Comptes rendus de l'Académie des Sciences de Paris, D*, 282: 1991–1993.
- Couzens, G. 2006. The distribution and abundance of the non-native *Pacific oyster*, *Crassostrea gigas*, in Devon—A result of climate change? *Shellfish News*, 22: 5–7.
- CSIRO (Commonwealth Scientific and Research Organization). 2002. Australians select best Pacific collaborative breeding program. *Fish Farming International*, 29: 34–35.
- Davison, D. M. 1999. *Sargassum muticum* in Strangford Lough, 1995–1998: a review of the introduction and colonization of Strangford Lough MNR and cSAC by the invasive brown algae *Sargassum muticum*. Environment and Heritage Service Research and Development Series No. 99/27.
- Dean, D. 1979. Introduced species and the Maine situation. *In Exotic Species in Mariculture*, pp. 149–164. Ed. by R. Mann. MIT Press, Cambridge, MA. 363 pp.
- Degremont, L. 2003. Genetic basis of summer mortality and relationship with growth in juvenile Pacific cupped oyster *C. gigas*. Doctoral thesis, University of Caen, 298 pp.
- Deslous-Paoli, J. M., and Héral, M. 1988. Biochemical composition and energy value of *Crassostrea gigas* cultured in the Bay of Marennes Oléron, France. *Aquatic Living Resources*, 1: 239–249.
- Diederich, S., Nehls, G. J., van Beusekom, E. E., and Reise, K. 2005. Introduced Pacific oysters (*Crassostrea gigas*) in the northern Wadden Sea: invasion accelerated by warm summers? *Helgoland Marine Research*, 59: 97–106.
- Dinamani, P. 1992. Introduced Pacific oysters in New Zealand. *In The Ecology of Crassostrea gigas in Australia, New Zealand, France and Washington State*, pp. 9–12. Ed. by M. Leffler and J. Greer. University of Maryland Sea Grant publication UM-SG-TS-92.07, Maryland Sea Grant College, College Park, MD. 25 pp.

- Dridi, S., Romdhane, M. S., and Elcafsi, M. 2007. Seasonal variation in weight and biochemical composition of the Pacific oyster, *Crassostrea gigas* in relation to the gametogenic cycle and environmental conditions of the Bizert lagoon, Tunisia. *Aquaculture*, 263: 238–248.
- Drinkwaard, A. C. 1999. Introductions and developments of oysters in the North Sea area: a review. *Helgoland Marine Research*, 52: 301–308.
- Elston, R., and Wilkinson, M. T. 1985. Pathology, management and diagnosis of oyster velar virus disease (OVVD). *Aquaculture*, 48: 189–210.
- Ernande, B., Clobert, J., McCombie, H., and Boudry, P. 2003. Genetic polymorphism and trade-offs in the early life-history strategy of the Pacific oyster *C. gigas*: a quantitative genetic study. *Journal of Evolutionary Biology*, 16: 399–414.
- Escapa, M., Isacch, J. P., Daleo, P., Alberti, J., Irribarne, O., Borges, M., Dos Santos, E. P., *et al.* 2004. The distribution and ecological effects of the introduced Pacific oyster *Crassostrea gigas* (Thunberg, 1793) in northern Patagonia. *Journal of Shellfish Research*, 23: 765–772.
- FAO. 1990. Artificial propagation of bivalves: techniques and methods. SF/WP/90/3. UNDP/FAO Regional Seafarming Development and Demonstration Project RAS/90/002, Bangkok, Thailand.
- FAO. 2004a. Hatchery culture of bivalve molluscs. Fisheries Technical Report No. 471. 177 pp.
- FAO. 2004b. Annuaire de statistiques des Pêches 2002. Production de l'Aquaculture. Vol. 94/2. Statistiques No. 181 et Pêches No. 67. FAO, Rome. 206 pp.
- FAO. 2008. Aquaculture production: Quantities 1950–2006. Fishstat Plus. Available online at <http://www.fao.org/fi/statist/fisoft/FISHPLUS>.
- FAO. 2009. Species fact sheet: *Crassostrea gigas*. Available online at http://www.fao.org/fishery/culturedspecies/Crassostrea_gigas/en.
- Feely, R. A., Sabine, C. L., Lee, K., Berelson, W., Kleypas, J., Fabry, V. J., and Millero, F. J. 2004. Impact of anthropogenic CO₂ on the CaCO₃ system in the oceans. *Science*, 305: 362–366.
- Fernand, L., and Brewer, P. (Eds). 2008. Changes in surface CO₂ and ocean pH in ICES shelf sea ecosystems. ICES Cooperative Research Report No. 290. 35 pp.
- Foster, N. R. 1997. The molluscan fisheries of Alaska. *In* The History, Present Condition, and Future of the Molluscan Fisheries of North and Central America and Europe, Vol. 2, Pacific Coast and Supplemental Topics, pp. 131–144. Ed. by C. L. MacKenzie, V. G. Burrell, A. Rosenfield, and W. L. Hobart. NOAA Technical Report NMFS, 128. 217 pp.
- Friedman, C. S. 1996. Haplosporidian infections of the Pacific oyster *Crassostrea gigas* (Thunberg) in California and Japan. *Journal of Shellfish Research*, 15: 597–600.
- Gaffney, P. M., and Allen, K. S. 1993. Hybridization among *Crassostrea* species—a review. *Aquaculture*, 116: 1–13.
- Garcia-Meunier, P., Martel, C., Pigeot, J., Chevalier, G., Blanchard, G., Gouletquer, P., Robert, S., *et al.* 2002. Recent invasion of the Japanese oyster drill along the French Atlantic coast: identification of specific molecular markers that differentiate Japanese, *Ocenebrellus inornatus*, and European, *Ocenebra erinacea*, oyster drills. *Aquatic Living Resources*, 15: 67–71.
- Gattuso, J-P., Frankignoulle, M., and Smith, S. V. 1999. Measurement of community metabolism and significance of coral reefs in the CO₂ source-sink debate. *Proceedings of the National Academy of Science USA*, 96: 13017–13022.
- Gay, M., Berthe, F., and Le Roux, F. 2004. Screening of *Vibrio* isolates to develop an experimental infection model in the Pacific oyster *Crassostrea gigas*. *Diseases of Aquatic Organisms*, 59: 49–56.
- Gazeau, F., Quiblier, C., Jansen, J. M., Gattuso, J. P., Middelburg, J. J., and Heip, C. H. R. 2007. Impact of elevated CO₂ on shellfish calcification. *Geophysical Research Letter*, 34: L07603.

- Gérard, A., Naciri, Y., Peignon, J. M., Ledu, C., and Phelipot, P. 1994. Optimization of triploid induction by the use of 6-DMAP for the oyster *Crassostrea gigas* (Thunberg). *Aquaculture and Fisheries Management*, 25: 709–719.
- Gerdes, D. 1983. The Pacific oyster *C. gigas*. Part 1: Feeding behaviour of larvae and adults. *Aquaculture*, 31: 195–219.
- Görlitz, S. 2005. Neue Riffe im Wattenmeer: Die Pazifische Auster *Crassostrea gigas* und ihre assoziierte Lebensgemeinschaft. Diplomarbeit, University of Kiel.
- Gouletquer, P. 1997. Cycle de reproduction naturelle de l'huître creuse *Crassostrea gigas*. In *La reproduction naturelle et contrôlée des Bivalves cultivés en France*, Nantes (France), 14–15 November 1995, pp. 7–19. Ifremer Rapport Interne DRV/RA/RST/97–11 RA /Brest.
- Gouletquer, P., and Héral, M. 1992. Aquaculture of *Crassostrea gigas* in France. In *The Ecology of Crassostrea gigas in Australia, New Zealand, France and Washington State*, pp. 12–19. University of Maryland Sea Grant publication UM-SG-TS-92.07, Maryland Sea Grant College, College Park, MD. 25 pp.
- Gouletquer, P., and Héral, M. 1997. Marine molluscan production trends in France: from fisheries to aquaculture. In *The History, Present Condition, and Future of the Molluscan Fisheries of North and Central America and Europe*, Vol. 3, Europe, pp. 137–164. Ed. by C. L. MacKenzie, V. G. Burrell, A. Rosenfield, and W. L. Hobart. NOAA Technical Report NMFS, 129. 240 pp.
- Gouletquer, P., Soletchnik, P., Le Moine, O., Razet, D., Geairon, P., Faury, N., and Taillade, S. 1998. Summer mortality of the Pacific cupped oyster *Crassostrea gigas* in the Bay of Marennes Oléron (France). ICES Document CM 1998/CC:14. 21 pp.
- Gouletquer, P., Wolowicz, M., Latala, A., Geairon, P., Huvet, A., and Boudry, P. 1999. Comparative analysis of oxygen consumption rates between cupped oyster spat of *Crassostrea gigas* of French, Japanese, Spanish and Taiwanese origins. *Aquatic Living Resources*, 12: 271–277.
- Gouletquer, P., Bachelet, G., Sauriau, P. G., and Noel, P. 2002. Open Atlantic coast of Europe: a century of introduced species into French waters. In *Invasive Aquatic Species in Europe: Distribution, Impacts and Management*, pp. 276–290. Ed. by E. Leppäkoski, S. Gollasch, and S. Olenin. Kluwer Academic Publishers, Dordrecht. 583 pp.
- Gouletquer, P., Wolowicz, M., Latala, A., Brown, C., and Cragg, S. 2004. Application of a micro respirometric volumetric method to respiratory measurements of larvae of the Pacific oyster *Crassostrea gigas*. *Aquatic Living Resources*, 17: 195–200.
- Grizel, H., and Héral, M. 1991. Introduction into France of the Japanese oyster *Crassostrea gigas*. *Journal du Conseil International pour l'Exploration de la Mer*, 47: 399–403.
- Guo, X., and Allen, S. K. 1994. Reproductive potential and genetics of triploid Pacific oysters, *Crassostrea gigas* (Thunberg). *Biological Bulletin*, 187: 309–318.
- Guo, X., Ford, S. E., and Zhang, F. 1999. Molluscan aquaculture in China. *Journal of Shellfish Research*, 18: 19–31.
- Harry, H. W. 1985. Synopsis of the supraspecific classification of living oysters (Bivalvia: Gryphaeidae and Ostreidae). *Veliger*, 28: 121–158.
- Haure, J. A., Huvet, H., Palvadeau, M., Nourry, C., Pénisson, J. L., Martin, C., and Boudry, P. 2003. Feeding and respiratory time activity in the cupped oysters *Crassostrea gigas*, *Crassostrea angulata* and their hybrids. *Aquaculture*, 218: 539–551.
- Héral, M., and Deslous-Paoli, J. M. 1990. Oyster culture in European countries. In *Estuarine and Marine Bivalve Mollusc Culture*, pp. 153–190. Ed. by W. Menzel. CRC Press, New York. 376 pp.

- Hilliard, R. 2005. Best practice for the management of introduced marine pests: a review; prepared for GISP by URS Australia Pty Ltd. Global Invasive Species Programme, Cape Town, South Africa. 173 pp.
- Hily, C., Lejart, M., and Miossec, L. 2007. The invasion of the Atlantic and Channel coasts of France by the alien oyster, *Crassostrea gigas*: assessment, causes, ecological and socio-economical consequences. The PROGIG research program. Poster presented at the 5th International Conference on Marine Bioinvasions. 21–24 May 2007, Cambridge, MA. MIT Sea Grant College Program, Cambridge, MA.
- Hine, P. M., Wesney, B., and Hay, B. E. 1992. Herpes viruses associated with mortalities among hatchery-reared larval Pacific oysters *Crassostrea gigas*. *Diseases of Aquatic Organisms*, 12: 135–142.
- His, E., Beiras, R., and Seaman, M. N. L. 1999. The assessment of marine pollution–bioassays with bivalve embryos and larvae. *Advances in Marine Biology*, 37: 1–178.
- Holmes, J. M. C., and Minchin, D. 1995. Two exotic copepods imported into Ireland with the Pacific oyster *Crassostrea gigas* (Thunberg). *Irish Naturalists' Journal*, 25: 17–20.
- Hussenot, J., Brossard, N., and Lefebvre, S. 1998. Mise au point d'un enrichissement de l'eau de mer pour produire en masse des microalgues diatomées comme fourrage pour les huîtres affinées ou stockées en claires. *In Marais Maritimes et Aquaculture*, pp. 107–115. Ed. by J. Hussenot and V. Buchet. Actes de Colloque, 19. Editions Ifremer, Plouzané, France. 279 pp.
- Huvet, A., Lapegue, S., Magoulas, A., and Boudry, P. 2000. Mitochondrial and nuclear DNA phylogeography of *Crassostrea angulata*, the Portuguese oyster endangered in Europe. *Conservation Genetics*, 1: 251–262.
- Huvet, A., Balabaud, K., Bierre, N., and Boudry, P. 2001. Microsatellite analysis of 6-hour-old embryos reveals no preferential intra-specific fertilization between cupped oysters *Crassostrea gigas* and *Crassostrea angulata*. *Marine Biotechnology*, 3: 448–453.
- Huvet, A., Gérard, A., Ledu, C., Phélipot, P., Heurtebise, S., and Boudry, P. 2002. Is fertility of hybrids enough to conclude that the oysters *Crassostrea gigas* and *Crassostrea angulata* are the same species? *Aquatic Living Resources*, 15: 45–52.
- Huvet, A., Herpin, A., and Degrémont, L. 2004a. The identification of genes from the oyster *C. gigas* that are differentially expressed in progeny exhibiting opposed susceptibility to summer mortality. *Gene*, 343: 211–220.
- Huvet, A., Fabioux, C., McCombie, H., Lapègue, S., and Boudry, P. 2004b. Natural hybridization between genetically differentiated populations of *C. gigas* and *C. angulata* highlighted by sequence variation in flanking regions of a microsatellite locus. *Marine Ecology Progress Series*, 272: 141–152.
- ICES. 2004. Trends in important diseases affecting the culture of fish and molluscs in the ICES area, 1998–2002. Prepared and edited by the Working Group on Pathology and Diseases of Marine Organisms. ICES Cooperative Research Report No. 265. 26 pp.
- ICES. 2005. Code of Practice on the Introductions and Transfers of Marine Organisms 2005. International Council for the Exploration of the Sea, Copenhagen. 30 pp.
- ICES. 2007. Status of introductions of non-indigenous marine species to the North Atlantic and Adjacent Waters 1992–2002. ICES Cooperative Research Report No. 284. 149 pp.
- ICES. 2008. Report of the Working Group on Introduction and Transfers of Marine Organisms (WGITMO), 12–14 March 2008, Copenhagen, Denmark. ICES Document CM 2008/ACOM:52. 130 pp.
- Jensen, S., Samuelsen, O. B., Andersen, K., Torkildsen, L., Lambert, C., Choquet, G., Paillard C., et al. 2003. Characterization of strains of *Vibrio splendidus* and *V. tapetis* isolated from corkwing wrasse *Symphodus melops* suffering vibriosis. *Disease of Aquatic Organisms*, 53: 25–31.

- Kerckhof, F., Haelters, J., and Gollash, S. 2007. Alien species in the marine and brackish ecosystem: the situation in Belgian waters. *Aquatic Invasions*, 2: 243–257.
- Klinger, T., Padilla, D. K., and Britton-Simmons, K. 2006. Two invaders achieve higher densities in reserves. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 16: 301–311.
- Kobayashi, M., Hofmann, E. E., Powell, E. N., Klinck, J. M., and Kusaka, K. 1997. A population dynamics model for the Japanese oyster, *Crassostrea gigas*. *Aquaculture*, 149: 285–321.
- Lacoste, A., Jalabert, F., Malham, S. K., Cueff, A. E., and Poulet, S. A. 2001. Stress and stress-induced neuroendocrine changes increase the susceptibility of juvenile oysters (*Crassostrea gigas*) to *Vibrio splendidus*. *Applied and Environmental Microbiology*, 67: 2304–2309.
- Lapègue, S., Batista, F. M., Heurtebise, S., Yu, Z., and Boudry, P. 2004. Evidence for the presence of the Portuguese oyster, *Crassostrea angulata*, in Northern China. *Journal of Shellfish Research*, 23: 759–763.
- Le Gall, V. 2006. Effets de l'ostréiculture sur la biodiversité. Etat des connaissances et application au Golfe du Morbihan. Student report, Master 2. Environnement et espaces littoraux, Génie des Anthroposystèmes littoraux, University of La Rochelle, France. 78 pp.
- Le Roux, F., Gay, M., Lambert, C., Waechter, M., Poubalanne, S., Chollet, B., Nicolas, J. L., et al. 2002. Comparative analysis of *Vibrio splendidus* related strains isolated during *Crassostrea gigas* mortality events. *Aquatic Living Resources*, 15: 251–258.
- Le Roux, F., Binesse, J., Saulnier, D., and Mazel, D. 2007. Construction of a *Vibrio splendidus* mutant lacking the metalloprotease gene *vsm* by use of a novel counterselectable suicide vector. *Applied and Environmental Microbiology*, 73: 777–784.
- Leitao, A., Chaves, R., Santos, S., Guedes-Pinto, H., and Boudry, P. 2004. Restriction enzyme digestion chromosome banding confirms *Crassostrea angulata* × *Crassostrea gigas* F1 hybrids. *Journal of Experimental Marine Biology and Ecology*, 343: 253–260.
- Leppäkoski, E., Gollasch, S., and Olenin, S. (Eds). 2002. *Invasive Aquatic Species of Europe: Distribution, Impacts and Management*. Kluwer Academic Publishers, Dordrecht. 583 pp.
- Lindsay, C. E., and Simons, D. 1997. The fisheries for Olympia oysters, *Ostreola conchaphila*; Pacific oysters, *Crassostrea gigas*; and Pacific razor clams, *Siliqua patula*, in the state of Washington. In *The History, Present Condition, and Future of the Molluscan Fisheries of North and Central America and Europe*, Vol. 2, Pacific Coast and Supplemental Topics, pp. 89–113. Ed. by C. L. MacKenzie, V. G. Burrell, A. Rosenfield, and W. L. Hobart. NOAA Technical Report NMFS, 128. 217 pp.
- Lopez-Flores, I., Hérran, R., Garrido-Ramos, M. A., Boudry, P., Ruiz-Rejón, C., and Ruiz-Rejón, M. 2004. The molecular phylogeny of oysters based on a satellite DNA related to transposons. *Genes*, 339: 181–188.
- Maguire, G. B., and Nell, J. A. 2007. History, status and future of oyster culture in Australia. In *The 1st International Oyster Symposium Proceedings*, Tokyo, Japan, 13–14 July 2005. Ed. by K. Mori. Published as *Oyster Research Institute News*, 19: 3–12.
- Mann, R., Burreson, E. M., and Baker, P. K. 1991. The decline of the Virginia oyster fishery in Chesapeake Bay: considerations for introduction of a non endemic species, *Crassostrea gigas* (Thunberg, 1793). *Journal of Shellfish Research*, 10: 379–388.
- Marino, G., Prioli, G., Rampacci, M., D'Ambra, R., Andaloro, F., and Di Marco, P. 2006. Alien marine fish and molluscs introduced into Italy for aquaculture purposes. In *AQUA 2006*, 10–13 May 2006, Florence, Italy, abstract. World Aquaculture Society, Baton Rouge, LA.
- Markert, A., Wehrmann, A., and Kröncke, I. 2009. Recently established *Crassostrea*-reefs versus native *Mytilus*-beds: differences in ecosystem engineering affects the macrofaunal communities (Wadden Sea of Lower Saxony, southern German Bight). *Biological Invasions*, doi 10.1007/s10530-009-9425-4.

- Martel, C., Viard, F., Bourget, D., and Garcia-Meunier, P. 2004. Invasion by the marine gastropod *Ocenebrellus inornatus* in France. I. Scenario for the source of introduction. *Journal of Experimental Marine Biology and Ecology*, 305: 155–170.
- Mathers, N. F., Wilkins, N. P., and Walne, P. R. 1974. Phosphoglucose isomerase and esterase phenotypes in *Crassostrea angulata* and *Crassostrea gigas*. *Biochemical Systematics and Ecology*, 2: 93–96.
- Mattiucci, S., and Villani, F. 1983. Studio elettroforetico dei sistemi gene-enzima in ostriche classificate come *Crassostrea gigas* (Thunberg, 1793) e *Crassostrea angulata* (Lamarck, 1819; Mollusca Ostreidae). *Parasitologia*, 25: 21–27.
- McEnulty, F. R., Jones, T. E., and Bax, N. J. 2001. The Wed-Based Rapid Response Toolbox. Available online at <http://crimp.marine.csiro.au/NIMPIS/controls.htm> (released June 2001, accessed 24 August 2009).
- McKenzie, C. L., and Lopez, A. 1997. Molluscan fisheries of Nicaragua. *In* The History, Present Condition, and Future of the Molluscan Fisheries of North and Central America and Europe, Vol. 2, Pacific Coast and Supplemental Topics, pp. 19–32. Ed. by C. L. MacKenzie, V. G. Burrell, A. Rosenfield, and W. L. Hobart. NOAA Technical Report NMFS, 128. 217 pp.
- Menzel, R. W. 1974. Portuguese and Japanese oysters are the same species. *Journal of the Fisheries Research Board of Canada*, 31: 453–456.
- Michaelidis, B., Ouzounis, C., Paleras, A., and Pörtner, H. O. 2005. Effects of long-term moderate hypercapnia on acid–base balance and growth rate in marine mussels *Mytilus galloprovincialis*. *Marine Ecology Progress Series*, 293: 109–118.
- Milyutin, D. M., and Frolov, A. V. 1997. Effect of environmental conditions on the growth and lipid composition of juvenile Pacific oyster *Crassostrea gigas* in the area of Cape Bolshoj Utrish, Black Sea. *Vestnik Moscow University (Biology)*, 3: 44–48.
- Minchin, D. 1996. Management of the introduction and transfer of marine molluscs. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 6: 229–244.
- Minchin, D. 2007. Rapid coastal survey for targeted alien species associated with floating pontoons in Ireland. *Aquatic Invasions*, 2: 63–70.
- Minchin, D., and Gollasch, S. 2003. Fouling and ships' hulls: how changing circumstances and spawning events may result in the spread of exotic species. *Biofouling*, 19(Suppl.): 111–122.
- Minchin, D., and Rosenthal, H. 2002. Exotics for stocking and aquaculture, making correct decisions. *In* *Invasive Aquatic Species in Europe: Distribution, Impacts and Management*, pp. 206–216. Ed. by E. Leppäkoski, S. Gollasch, and S. Olenin. Kluwer Academic Publishers, Dordrecht. 583 pp.
- Minobe, S., Kuwano-Yoshida, A., Komori, N., Xie, S-P., and Small, R. J. 2008. On the influence of the Gulf Stream on the troposphere. *Nature*, 452: 206–209.
- Miossec, L., and Gouletquer, P. 2007. The Pacific cupped oyster *Crassostrea gigas*: from an introduced species for aquaculture to an invasive species for the ecosystem. *In* 5th International Conference on Marine Bioinvasions, 21–24 May 2007, Cambridge, MA, Abstract Book. MIT Sea Grant College Program, Cambridge, MA.
- Miossec, L., Allain, G., Arzul, I., François, C., Garcia, C., and Cameron, A. R. 2009. First results of an epidemiological study on oyster (*Crassostrea gigas*) mortality events in France during summer 2008. *In* Proceedings of the 12th Symposium of the International Society for Veterinary Epidemiology and Economics, 10–14 August 2009, Durban, South Africa: ISVEE 12, 231. Abstract.
- Mortensen, S., Valero, J., Wrangé, A-L., Harketstad, L. S., Stene, R-O., Christensen, H. T., Dolmer, P., et al. 2007. A northwards expansion of the Pacific oyster *Crassostrea gigas*.

- Poster presented at the 10th International Conference on Shellfish Restoration (ICSR), 12–16 November 2007, Vlissingen, the Netherlands.
- Muniz, E. C., Jacob, S. A., and Helm, M. M. 1986. Condition index, meat yield and biochemical composition of *Crassostrea brasiliana* and *C. gigas* grown in Cabo Frio, Brazil. *Aquaculture*, 59: 235–250.
- Nehls, G., and Buttger, H. 2007. Spread of the Pacific oyster *Crassostrea gigas* in the Wadden Sea. HARBASINS Report, the Common Wadden Sea Secretariat, Wilhelmshaven, April 2007. 54 pp.
- Nehls, G., Diederich, S., Thieltges, D. W., and Strasser, M. 2006. Wadden sea mussel beds invaded by oysters and slipper limpets: competition or climate control? *Helgoland Marine Research*, 60: 135–143.
- Nehring, S. 2003. Pacific oysters in the European Wadden Sea: an irreversible impact in a highly protected ecosystem. *Aliens*, 17: 20–21.
- Nell, J. A. 1993. Farming the Sydney rock oyster (*Saccostrea commercialis*) in Australia. *Reviews in Fisheries Science*, 1: 97–120.
- Newkirk, G. F. 1979. Genetic aspects of the introduction and culture of non indigenous species for aquaculture. *In Exotic Species in Mariculture*, pp. 192–208. Ed. by R. Mann. MIT Press, Cambridge, MA. 363 pp.
- Ngo, T. T. T., Berthe, F., and Choi, K. S. 2003. Prevalence and infection intensity of the ovarian parasite *Marteilioides chungmuensis* during an annual reproductive cycle of the oyster *Crassostrea gigas*. *Diseases of Aquatic Organisms*, 56: 259–267.
- Nicolas, J. L., Comps, M., and Cochennec, N. 1992. Herpes-like virus infecting pacific-oyster larvae, *Crassostrea gigas*. *Bulletin of the European Association of Fish Pathologists*, 12: 11–13.
- NIMPIS (National Introduced Marine Pest Information System). 2009. *Crassostrea gigas* general information. Available online at <http://www.marinepests.gov.au/nimpis> (accessed 24 August 2009).
- Nosho, T. 1989. Small-scale oyster farming for pleasure and profit in Washington. Washington Sea Grant Program publication WSG-S 89–01, University of Washington Press, Seattle, WA. 12 pp.
- NRC (National Research Council). 2004. *Nonnative Oysters in the Chesapeake Bay*. NRC–Ocean Studies Board, National Academies Press, Washington, DC. 325 pp.
- OIE (Office International des Epizooties). 2002. MSX disease (*Haplosporidium nelsoni*) in Canada. Available online at ftp://ftp.oie.int/infos_san_archives/eng/2002/en_021025v15n43.pdf.
- OIE (Office International des Epizooties). 2009. Manual of diagnostic tests for aquatic animals 2003. Available online at http://www.oie.int/eng/normes/fmanual/A_summry.htm.
- Orensanz, J. M., Schwindt, E., Pastorino, G., Bortolus, A., Casas, G., Darrigran, G., Elias, R., et al. 2002. No longer the pristine confines of the world ocean: a survey of exotic marine species in the southwestern Atlantic. *Biological Invasions*, 4: 115–143.
- Park, B. H., Park, M. S., Kim, B. Y., Hur, S. B., and Kim, S. J. 1988. Culture of the Pacific oyster (*Crassostrea gigas*) in the Republic of Korea. Training manual prepared for the training course on oyster farming. UNDP/FAO Regional Seafarming Development and Demonstration Project RAS/86/024, Pusan, Republic of Korea.
- Park, M. S., Choi, D. L., and Jo, Q. T. 2001. Pathogenic effects of ovarian parasites *Marteilioides chungmuensis* on the larval development of Pacific oyster *Crassostrea gigas*. *In Aquaculture 2001*, January 2001, Orlando, FL, Book of Abstracts: 516. World Aquaculture Society, Baton Rouge, LA.

- Pascual, M. S., and Orensanz, J. M. 1996. Introducción y trasplantes de especies marinas en el litoral patagónico. Informes Técnicos del Plan de Manejo Integrado de la Zona Costera Patagónica, Puerto Madryn, Argentina, No. IX: 16.
- Powell, E., Klinck, J., Hofmann, E., and Bochenek, E. 2000. Food quality and feeding strategies in hatchery rearing of Pacific oyster *Crassostrea gigas* larvae: a modelling approach. *Journal of Shellfish Research*, 1: 604.
- Powell, E. N., Bochenek, E. A., Klinck, J. M., and Hofmann, E. E. 2002. Influence of food quality and quantity on the growth and development of *Crassostrea gigas* larvae: a modelling approach. *Aquaculture*, 210: 89–117.
- Pujalte, M. J., Ortigosa, M., Macian, M. C., and Garay, E. 1999. The annual cycle of aerobic and facultative anaerobic marine bacteria associated with Mediterranean oysters and seawater. *International Microbiology*, 2: 259–266.
- Quayle, D. B. 1988. Pacific oyster culture in British Columbia. *Canadian Bulletin of Fisheries and Aquatic Sciences*, 218. 241 pp.
- Reece, K. S., Cordes, J. F., Stubbs, J. B., Hudson, K. L., and Francis, E. A. 2008. Molecular phylogenies help resolve taxonomic confusion with Asian *Crassostrea* oyster species. *Marine Biology*, 153: 709–721.
- Renault, T., and Novoa, B. 2004. Viruses infecting bivalve molluscs. *Aquatic Living Resources*, 17: 397–409.
- Renault, T., Cochenec, N., Le Deuff, R. M., and Chollet, B. 1994. Herpes-like virus infecting Japanese oyster *Crassostrea gigas* spat. *Bulletin of the European Association of Fish Pathologists*, 14: 64–66.
- Renault, T., Stokes, N. A., Chollet, B., Cochenec, N., Berthe, F., Gérard, A., and Burreson, E. M. 2000. Haplosporidiosis in the Pacific oyster *Crassostrea gigas* from the French Atlantic coast. *Diseases of Aquatic Organisms*, 42: 207–214.
- Robinson, T. B., Griffiths, C. L., Tonin, A., Bloomer, P., and Hare, M. P. 2005. Naturalized populations of oysters, *Crassostrea gigas* along the South African coast: distribution, abundance, and population structure. *Journal of Shellfish Research*, 24: 443–450.
- Ruesink, J. L., Lenihan, H. S., Trimble, A. C., Heiman, K. W., Micheli, F., Byers, J. E., and Kay, M. C. 2005. Introduction of non-native oysters: ecosystem effects and restoration implications. *Annual Review of Ecology and Systematics*, 36: 643–689.
- Ruesink, J. L., Feist, B. E., Havey, C. J., Hong, J. S., Trimble, A. C., and Wisheart, L. M. 2006. Changes in productivity associated with four introduced species: ecosystem transformation of a “pristine” estuary. *Marine Ecological Progress Series*, 311: 203–215.
- Ruiz, G. M., Fofonoff, P., Hines, A. H., and Grosholz, E. D. 1999. Non-indigenous species as stressors in estuarine and marine communities: assessing invasion impacts and interactions. *Limnology and Oceanography*, 44: 950–972.
- Samain, J. F., and McCombie, H. (Eds). 2008. Summer mortality of Pacific oyster *Crassostrea gigas*, the Morest project. Editions Ifremer/Quae, Versailles. 379 pp.
- Shaw, W. N. 1997. The shellfish industry of California—past, present, and future. *In The History, Present Condition, and Future of the Molluscan Fisheries of North and Central America and Europe*, Vol. 2, Pacific Coast and Supplemental Topics, pp. 57–65. Ed. by C. L. MacKenzie, V. G. Burrell, A. Rosenfield, and W. L. Hobart. NOAA Technical Report NMFS, 128. 217 pp.
- Smaal, A. C., Stralen, M., and van Craeymeersch, J. A. M. 2005. Does the introduction of the Pacific oyster *Crassostrea gigas* lead to species shifts in the Wadden Sea? *In The Comparative Roles of Suspension-Feeders in Ecosystems*, pp. 277–289. Ed. by R. F. Dame and S. Olenin. NATO Science Series IV, Earth and Environmental Sciences, Vol. 47. Springer, Dordrecht. 359 pp.

- Soletchnik, P., Huvet, A., Le Moine, O., Razet, D., Geairon, P., Faury, N., Gouletquer, P., *et al.* 2002. A comparative field study of growth, survival and reproduction of *Crassostrea gigas*, *C. angulata* and their hybrids. *Aquatic Living Resources*, 15: 243–250.
- Spencer, B. E., Edwards, D. B., Kaiser, M. J., and Richardson, C. A. 1994. Spatfalls of the non-native Pacific oyster, *Crassostrea gigas*, in British waters. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 4: 203–217.
- Stenzel, H. B. 1971. Oysters. *In* Treatise on Invertebrate Palaeontology: Part N–Mollusca 6, Bivalvia Vol. 3 (Oysters), pp. N953–N1224. Ed. by H. B. Stenzel, R. C. Moore, and C. Teichert. The Geological Society of America, Inc. and the University of Kansas Press, Lawrence, KA. 276 pp.
- Syvret, M. L. 2008. Project report–Pacific oyster aquaculture protocol for the UK. *Shellfish News*, 26: 9–11.
- Thompson, J. R., Randa, M. A., Marcelino, L. A., Tomita-Mitchell, A., Lim, E., and Polz, M. F. 2004. Diversity and dynamics of a North Atlantic coastal *Vibrio* community. *Applied and Environmental Microbiology*, 70: 4103–4110.
- Thompson, J., Pacocha, R. S., Pharino, C., Klepac-Ceraj, V., Hunt, D. E., Benoit, J., Sarma-Rupavtarm, R., *et al.* 2005. Genotypic diversity within a natural coastal bacterioplankton population. *Science*, 307: 1311–1313.
- Turpin, V., Robert, J. M., Gouletquer, P., Massé, G., and Rosa, P. 2001. Oyster greening by outdoor mass culture of the diatom *Haslea ostrearia* Simonsen in enriched seawater. *Aquaculture Research*, 32: 801–809.
- Urakawa, H., Kita-Tsukamoto, K., and Ohwada, K. 1999. Restriction fragment length polymorphism analysis of psychrophilic and psychrotrophic *Vibrio* and *Photobacterium* from the north-western Pacific Ocean and Otsuchi Bay, Japan. *Canadian Journal of Microbiology*, 45: 67–76.
- van den Berg, J. B., Kozyreff, G., Lin, H-X., McDarby, J., Peletier, M. A., Planqué, R., and Wilson, P. L. 2005. Japanese oysters in Dutch waters. *Nieuw Archief voor Wiskunde*, 5/6, 131–140.
- Wang, J., Christoffersen, K., Buck, S., and Tao, Y. 2007. The Pacific oyster (*Crassostrea gigas*) in the Isefjord, Denmark. Roskilde University. Department of Environmental, Social and Spatial Change. Environmental Biology Thesis. 49 pp. Available online at <http://rudar.ruc.dk/handle/1800/2735>.
- Wilkins, N. P. 1989. Ponds, Passes and Parcs: Aquaculture in Victorian Ireland. Glendale Press, Dublin. 352 pp.
- Winter, J. E., Toro, J. E., Navarro, J. M., Valenzuela, G. S., and Chaparro, O. R. 1984. Recent developments, status and prospects of the molluscan aquaculture on the Pacific coast of South America. *Aquaculture*, 39: 95–134.
- Wolff, W. J., and Reise, K. 2002. Oyster imports as a vector for the introduction of alien species into Northern and Western European coastal waters. *In* Invasive Aquatic Species in Europe: Distribution, Impacts and Management, pp. 193–205. Ed. by E. Leppäkoski, S. Gollasch, and S. Olenin. Kluwer Academic Publishers, Dordrecht. 583 pp.
- Wood, H. L., Spicer, J. I., and Widdicombe, S. 2008. Ocean acidification may increase calcification rates, but at a cost. *Proceedings of the Royal Society B*, 275: 1767–1773.
- Wrange, A-L. 2008. Japanskt jätteostron invaderar svenska västkusten. *Fauna och Flora*, 103: 8–14.
- Wrange, A-L., Valero, J., Harkestad, L. S., Strand, O., Lidegarh, S., Christensen, H. T., Dolmer, P., *et al.* 2009. Massive settlements of the Pacific oyster, *Crassostrea gigas*, in Scandinavia. *Biological Invasions*, doi 10.1007/s10530-009-9535-z.

- Yu, Z., Kong, X., Zhang, L., Guo, X., and Xiang, J. 2003. Taxonomic status of four *Crassostrea* oysters from China as inferred from mitochondrial DNA sequences. *Journal of Shellfish Research*, 22: 31–38.
- Zenetos, A., Koutsoubas, D., and Vardala-Theodorou, E. 2004. Origin and vectors of introduction of exotic molluscs in Greek waters. *Belgian Journal of Zoology*, 134(Suppl. 1): 161–168.