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Sustainable large-scale production of European flat oyster (Ostrea edulis) seed for ecological restoration and aquaculture: a review

Bérenger Colsoul[1,2], Pierre Boudry[3], María Luz Pérez-Parallé[4], Ana Bratoš Cetinić[5], Tristan Hugh-Jones[6], Isabelle Arzul[7], Nicolas Mérou[7], Karl Mathias Wegner[8], Corina Peter[1], Verena Merk[1] and Bernadette Pogoda[1,8]

1 Biological Institute Helgoland, Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Helgoland, Germany
2 Faculty of Mathematics and Natural Sciences, Christian-Albrechts-Universität zu Kiel, Kiel, Germany
3 LEMAR, Ifremer, CNRS, IRD, Univ. Brest, Plouzané, France
4 Instituto de Acuicultura, Universidade de Santiago de Compostela, Santiago de Compostela, Spain
5 Department of Aquaculture, University of Dubrovnik, Dubrovnik, Croatia
6 Atlantic Shellfish Ltd, Cork, Ireland
7 LGPMM, Ifremer, La Tremblade, France
8 Wadden Sea Station, Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, List/Sylt, Germany

Correspondence
Bérenger Colsoul, Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Am Handelshafen 12, 27570 Bremerhaven, Germany.
Email: berenger.colsoul@awi.de

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Abstract

The conservation and active restoration of European flat oyster (*Ostrea edulis*) populations are a major focus of ecological restoration efforts to take advantage of the wide-ranging ecosystem functions and services this species provides. Accordingly, additional and new demands for seed oysters have arisen. In commercial aquaculture (mariculture), the production of *O. edulis* is still largely based on natural seed collection. Considering the specific requirements, related to ecological restoration, such as the absence of pathogens and the preservation of high genetic diversity, the current supply is insufficient. Despite the development of breeding and controlled reproduction techniques for this species since the late 1930s, seed production today is mainly based on empirical concepts. Several of the issues that producers still face are already subjects of research; many others are still unanswered or even unaddressed. This review provides a summary of all available knowledge and technologies of *O. edulis* seed production. Furthermore, it provides a detailed reflection on implications for restoration, future challenges, open questions and it identifies relevant research topics for sustainable seed supply. The study covers the following aspects on (i) biology of the species, (ii) stressors – including pathogens and pollutants, (iii) genetics, (iv) history of production technologies, (v) seed production in polls, (vi) seed production in ponds and (vii) seed production in hatcheries. Future research needs on sex determinism, gametogenesis, cryopreservation, nutrition, selective breeding, pathogens and disease, and the development of reliable protocols for production are highlighted.

Key words: breeding, hatchery, reproduction biology, shellfish, spat, technology.

Introduction

In Europe, the conservation of the European flat oyster *Ostrea edulis* (Linnaeus 1758) populations is in the focus of ecological restoration efforts to profit from the ecosystem services of this biogenic reef-engineer species. Praised for its culinary, medicinal and ecological virtues, this oyster species is today at the core of many scientific projects or actions by governmental and non-governmental organizations for its aquaculture, restocking, restoration or reintroduction in its former range all over European coasts (Pogoda *et al.* 2019). *Ostrea edulis* and its beds (referred to

here as 'reefs') provide many ecosystem services and functions such as substrate formation and biodiversity enhancement (Haelters & Kerckhof 2009; Todorova *et al.* 2009). It therefore contributes to objectives defined by: the OSPAR Convention for the Protection of the Marine Environment of the North-East Atlantic, the EU Habitats Directive (Directive 92/43/EEC) and the EU Marine Strategy Framework Directive (Directive 2008/56/EC) (Pogoda 2019).

Over the 20th century, European stocks of *O. edulis* have been severely depleted by overfishing, leading to numerous reseeding and restocking projects, mostly based on translocations (Bromley *et al.* 2016a; Pogoda 2019). Those included 19th and 20th century translocations from adult, seed and juveniles of *O. edulis* within Europe and from non-European areas to Europe (Bromley *et al.* 2016a). These shellfish movements, as a consequence, are most likely responsible for the introduction and further dispersal of parasites and pests such as the introduction of bonamiosis into Europe from the USA in 1979, the introduction of gill disease into Wales from the Netherlands in the 1960s and the introduction of Asian rapa whelk into the Black Sea from the Far East in 1949 (Zolotarev & Terentyev 2012; Brenner *et al.* 2014; Bromley *et al.* 2016a). Some of these diseases and pests have drastically reduced or depleted the stocks and beds of *O. edulis* throughout European waters (Zolotarev & Terentyev 2012; Pogoda 2019). As the aquaculture of European flat oyster has also been affected extensively by some diseases, a large part of the oyster industry has turned away from cultivating this species (see Section Bonamiosis). This has had obvious consequences for the development of production technologies when compared to other shellfish species of commercial interest, such as the Pacific oyster (*Crassostrea gigas*).

Today, as Lallias *et al.* (2010) have listed, oyster population restoration can be conducted in three distinct ways: (i) The strategy of releasing larvae into the wild; (ii) The strategy of producing older seeds (spat) and releasing them into the wild; (iii) The strategy of translocating adult oysters. Considering the risks of transferring pathogens and invasives by adults translocations and the potential negative impact on remaining wild beds, the third strategy should not be applied (Bromley *et al.* 2016a; Pogoda *et al.* 2019). Given the fertility rate of *O. edulis*, the low survival rate of larvae in the wild, the availability or the lack of suitable substrates for settlement (Smyth *et al.* 2018; Colsoul *et al.* 2020), as well as the lack of control within a restoration area, the first strategy is certainly not viable unless applying it under specific, risk limiting conditions. Consequently, the second strategy, seeding with juveniles (i.e. seed or 'spat'), seems to be the best option for *O. edulis* restoration projects.

Currently, both aquaculture and ecological restoration are limited by access to seed as the current production techniques does not allow for a regular, substantial and sustainable seed production meeting the specific expectations and objectives of the two sectors (i.e. aquaculture and restoration; Pogoda *et al.* 2019). In addition to the previously mentioned shortage of seeds, there are also different objectives in regard to the need in seed quality. The needs of *O. edulis* aquaculture are generally focused on: survival, growth, weight gain, gastronomic aspect (visual and content), tolerance to exoneration or resistance to diseases, whereas for ecological restoration, the needs are mainly high genetic variability and survival and/or disease tolerance (Sas *et al.* 2020).

The higher the genetic diversity within a population, the less vulnerable it is for any disturbance as for example being infected and depleted by a pathogen (Hughes *et al.* 2008). According to this, it seems obvious that any ecological restoration project will aim for the highest possible genetic diversity in order to increase population resillience (e.g. fitness, response to diseases), avoid inbreeding and ensure its long-term adaptability (e.g. changing environment).

Today, a plethora of ways of producing or collecting *O. edulis* seed exists, ranging from traditional methods based on sea-based collection of seed to very modern production in controlled environments, that is land-based hatcheries. Protocols for the production and collection of *O. edulis* seed depend on site conditions, technology and the physiological condition of the spawning broodstock. The knowledge about ecophysiological and environmental drivers is still limited for this species and this limits the development of successful breeding methods. It is essential to define and compare technical achievements, research gaps, advantages and disadvantages of different seed-supply technologies to identify optimal seed quality for the specific goals and settings of ecological restoration.

For this reason, this review focuses on the description of production systems (Chapter 7) and biological knowledge of *O. edulis* (Chapter 3–4).

In addition, in Chapter 6, the history of seed production is reviewed to understand present production systems and future development. Depending on the historical period, technological progress and geographical location, the supply of seed had different goals. The technological progress was always directly related to the goals, which were mainly shaped by the demands of their historical period. From the beginnings of aquaculture to today's ecological restoration, a short synthesis of the historical development of the supply of seed from *O. edulis* is presented here.

In order to overcome current barriers and limitations of oyster restoration, the Native Oyster Restoration Alliance (NORA), a network of scientists/institutions, nature conservation bodies/organizations and aquaculture producers was founded and seed production was identified as a key limiting factor for restoration and defined as a critical

knowledge gap (Pogoda *et al.* 2019). Against this background, the aim of this review was to collect and integrate all available knowledge to identify useful approaches for successful *O. edulis* seed production, to meet current and future demands of ecological restoration efforts with the European flat oyster.

Methods

The search for bibliographic data was conducted in four steps. The first was the collection of peer-reviewed literature in the three major bibliographic search engines: Google Scholar, ISI Web of Science and Scopus Document Search (Appendix S1). Keywords used for the literature search were *O. edulis*, European flat oyster and European oyster. These main keywords were then combined in pairs with relevant keywords concerning the prevailing subjects in this review (for a detailed description of the search process see Supporting Information). In addition to the fundamental search of existing literature, an alert for new publications (all keywords) was set up on Google Scholar during the writing phase of the review in order to add the most recent data possible. As the Latin name of *O. edulis* Linnaeus 1758, changed over time, new searches (name alone and paired with second keyword) were carried out with the list of 20 Latin names (Table 1). The resulting literature (Table 1) was then consulted individually to determine its potential value to this review.

Since many peer-reviewed publications were published in other languages, the second step of the bibliographic research included the collection of data in languages other than English. The keywords already used in the first step were translated to Norwegian, German, Dutch, French and Spanish and again searched for in Google Scholar.

In the third step, the data were supplemented by searching for relevant information in the grey literature, as the documentation of European oysters production began very early (4th century BCE) and techniques were often developed without publication in peer-reviewed articles.

The fourth and last step was performed after analysing the relevance of the documents collected in the previous steps. Once the literature was sorted, the references of each of the documents were screened for additional scientific titles and journals. Those were added to the final bibliography on which this review is based on (Appendix S2).

Four limitations to this bibliographic search were identified: (i) Some of the articles, books, chapters, reports and other documents of interest are old, not digitized, printed in a small number of copies or even stored in foreign libraries and therefore difficult or not possible to access; (ii) Patents were excluded and numerous reports, PhD theses and academic studies were not considered until the fourth step cited above; (iii) Language was a major limitation in the database search and the understanding of the documents: English, French, German, Norwegian and Spanish were translated; (iv) The totality of bibliographic research was limited to the Latin alphabet.

Table 1 Synonym Latin names of *Ostrea edulis* (according to Gofas (2004)): List of the number of results by names in the database Google Scholar, ISI Web of Science and Scopus Document Search

Species	Descriptor	Google Scholar	ISI Web of Science	Scopus Document Search
Monoeciostrea europa	Orton, 1928	1	0	0
Ostrea adriatica	Lamarck, 1819	4	1	0
Ostrea corbuloides	Danilo and Sandri, 1855	1	0	0
Ostrea cristata	Born, 1778, (Poli, 1795)	84	1	5
Ostrea cumana	Gregorio, 1883	1	0	0
Ostrea cyrnusii	Payraudeau, 1826	2	0	0
Ostrea depressa	Philippi, 1836	9	1	0
Ostrea exalbida	Gmelin, 1791	1	0	0
Ostrea hippopus	Lamarck, 1819	39	1	2
Ostrea lamellosa	Brocchi, 1814	363	4	4
Ostrea leonica	Fréminville in Taslé, 1870	1	0	0
Ostrea parasita	Turton, 1819	0	0	0
Ostrea parasitica	Turton, 1819	40	3	0
Ostrea rostrata	Gmelin, 1791	9	5	0
Ostrea saxatilis	Turton, 1807	2	0	0
Ostrea scaeva	Monterosato, 1915	2	0	0
Ostrea striatum	da Costa, 1778	1	2	0
Ostrea sublamellosa	Milachewitch, 1916	76	0	0
Ostrea taurica	Krynicki, 1837	58	1	0
Ostrea vulgare	da Costa, 1778	1	1	0

After analysing the data collected, it was decided that this review will not cover, or will only cover very partially, the following phases and/or elements of production: site selection, water treatment, substrate/collector production, nursery, food production (i.e. microalgae), technical materials and education.

Biological background

Relevant biological aspects of *O. edulis* are presented here to understand seed production procedures, and to discuss difficulties in production and needs of technological advances. This chapter does not intend to provide a detailed overview of the biology of *O. edulis* but provides a

review of important elements that affect reproduction, spatfall and other operational phases within the oyster production cycle.

Genus *Ostrea*

Taxonomy

According to the World Register of Marine Species (Gofas 2004), 408 species are currently listed within the genus *Ostrea* which was first described by Linnaeus in 1758. After removing uncertain taxonomy, synonyms, misidentifications and extinct species, the genus *Ostrea* today considers 16 living species (Table 2). All these species breed their embryos between the demibranchs in the pallial cavity until swarming, for example the release of larvae (Chaparro *et al.* 2018).

From 1758 onwards, *O. edulis* is described as a species in the genus *Ostrea*. However, the species was described over time and places also by authors other than Linnaeus, using different Latin names; all of them now summarized and reclassified as *O. edulis* (Table 1). A large number of vernacular names in different alphabets and other forms of writing exist, all of which are describing the species *O. edulis* (Anonymous 2008).

Species identification within the genus Ostrea

The morphology of the species within the *Ostrea* genus is in some cases relatively similar, for example *Ostrea stentina*, a sympatric species of *O. edulis* found in the waters of Tunisia, Spain and Portugal (González-Wangüemert *et al.* 2004). Although it is very difficult to morphologically distinguish the two species in the juvenile stages, *O. stentina* remains smaller as adults.

The Australian flat oyster (*Ostrea angasi*) is also very similar to *O. edulis* (Crawford 2016). On the morphological level, the species appears very close already when observing the larval sizes and other reproductive characteristics (Table. 2). In addition, Hurwood *et al.* (2005) even suggests that *O. angasi* is a recent colonizer of Australia or that these two taxa are, in fact, the same species. Morton *et al.* (2003), on the other hand, distinguishes these two species using mitochondrial DNA markers.

Although other species of the genus *Ostrea* were introduced into Europe (e.g. *O. chilensis*, *O. angasi*, *O. puelchana* reported by Grizel *et al.* (1983), Bougrier *et al.* (1986) and Pascual *et al.* (1991) none of these species seems to have proliferated and thus cause identification difficulties within the current European range of *O. edulis*.

Geographical range

European range

Ostrea edulis is distributed from 65° North in Norway to 30° North at Cape Ghir in Morocco. The species naturally occurs in the Norwegian Sea, North Sea, English Channel, Celtic Sea, Bay of Biscay and Mediterranean including Adriatic Sea, Black Sea and Azov Sea (Ivanov 1964; Bromley *et al.* 2016a).

The characteristic habitat type of all species within the genus *Ostrea* are waters of relatively high salinity, clear or with low turbidity (Marteil 1976). Found in coastal areas, estuarine and marine habitats, the species thrives in subtidal and sublittoral areas with no or short emergence time (Martin *et al.* 1997).

In 2018, the European countries producing *O. edulis* in aquaculture in the order of volume (≥1 ton in live weight per year) produced were: France, Spain, Ireland, Croatia, UK, Norway, Montenegro, Portugal and the Channel Islands (Fig. 1). Together, these countries produced to a total of ca. 1407 tons of oysters (FAO 2020). Despite this, production exists in Sweden, Denmark and the Netherlands.

The total production per catch of the fishery in 2018 (in Europe) was ca. 684 tons. The producing countries in order of volume (≥1 ton in live weight per year) were Denmark, Croatia, Spain, Tunisia, France, Portugal, UK, Sweden and Greece.

The considerable decrease in production (aquaculture and fishery catches) observed over the last 5 years highlights the difficulties in obtaining seeds for both the aquaculture and the restoration sector.

Extended range

Ostrea edulis was translocated outside Europe mainly for cultivation purposes (Bromley *et al.* 2016a). It was imported particularly to Australia in the mid-1800s and 1940s, to South Africa in 1894, to the USA in 1947, to Japan in 1952, to Canada in 1957 and in the 2000s, to Mauritius in 1972, to Tonga in 1975, to Israel in 1976, to Fiji in 1977, to Mexico in 1984, to New Zealand in 1985 and to Namibia in 1990 (Funes & Jiménez 1989; Bromley *et al.* 2016a).

The success of these transfers has not been studied here. However, to our knowledge, with the exception of Canada, the USA and Namibia (see below), no recent data have been found in the literature.

Aquaculture records exceeding 1000 tons exist in the USA (from 1984 to 2013), in South Africa (only in 1992) and in Namibia (from 2003 to 2015; FAO 2020). In addition, a natural population of *O. edulis* (as non-native species) has been established in Canada, in the province of Nova Scotia (Vercaemer *et al.* 2006) and in the province of New Brunswick (Burke *et al.* 2008a; Burke *et al.* 2008b).

Sex change and sex ratio

Ostrea edulis is an asynchronous hermaphrodite with a rhythmic consecutive sexuality: several sexual inversions

Table 2 Life cycle characteristics of the genus *Ostrea* (modified after Castanos *et al*. (2005) and Gofas (2004))

Species	Descriptor	Maximal no. of brooders (%)	Days of incubation	Days of planktonic life	Size of egg (μm)	Size of swarmed larvae (μm)	Larval setting size (μm)	Fertility (larvae $\times 10^6$)	References
Ostrea algoensis‡	Sowerby II, 1871	NA	NA	NA	NA	NA	NA	NA	Jozefowicz and Foighil (1998)‡
Ostrea angasi‡	Sowerby II, 1871	16	NA	12–20	NA	186–203	300–320	0.03–1.52	Suquet *et al*. (2018)†, Jozefowicz and Ó Foighil (1998)‡
Ostrea chilensis‡	Philippi, 1844	2.6–48	21–56	5 min–48 h	220–323	390–556	426§–556	0.05–0.06	Suquet *et al*. (2018)†, Jozefowicz and Ó Foighil (1998)‡, Buroker (1985)§
Ostrea circumpicta‡	Pilsbry, 1904	NA	NA	NA	NA	NA	NA	NA	Kang *et al*. (2004) ‡
Ostrea conchaphila‡	Carpenter, 1857	NA	NA	NA	NA	NA	NA	NA	Jozefowicz and Ó Foighil (1998)‡
Ostrea denselamellosa‡	Lischke, 1869	NA	NA	NA	NA	NA	NA	NA	Jozefowicz and Ó Foighil (1998)‡
Ostrea edulis‡	Linnaeus, 1758	13–20.6	5.5–18§	6–14§	114–150§	160–200§	270–320§	0.09–1.8§	Suquet *et al*. (2018)†, Jozefowicz and Ó Foighil (1998)‡, Spärck (1925)§, Erdmann (1935), Loosanoff and Davis (1963), Walne (1974), Carbonnier *et al*. (1990), Martin *et al*. (1997)
Ostrea lurida§	Carpenter, 1864	55	10	7–23	100–110	165–189	250–325	0.215–0.3	Suquet *et al*. (2018)†, Castanos *et al*. (2005)‡
Ostrea permollis‡	Sowerby II, 1871	NA	7–9	30–33	60–80§	107–127	290	0.221	Jozefowicz and Ó Foighil (1998)‡, Buroker (1985)§
Ostrea puelchana§	d'Orbigny, 1842	20	5–7	17–20	60–90	110–130	284	1.9	Suquet *et al*. (2018)†, Jozefowicz amd Ó Foighil (1998)‡
Ostrea stentina‡	Payraudeau, 1826	3.1–13.3	NA	10–30	NA	123–140	270–320	NA	Jozefowicz and Ó Foighil (1998)‡

No life cycle data were found for the following species: *Ostrea angelica* Rochebrune, 1895, *Ostrea atherstonei* Newton, 1913, *Ostrea futamiensis* Seki, 1929, *Ostrea libella* Weisbord, 1964, *Ostrea megodon* Hanley, 1846. NA are data not available.
†Existing data on spermcasting.
‡Existing data on brooding.
§Updated data.

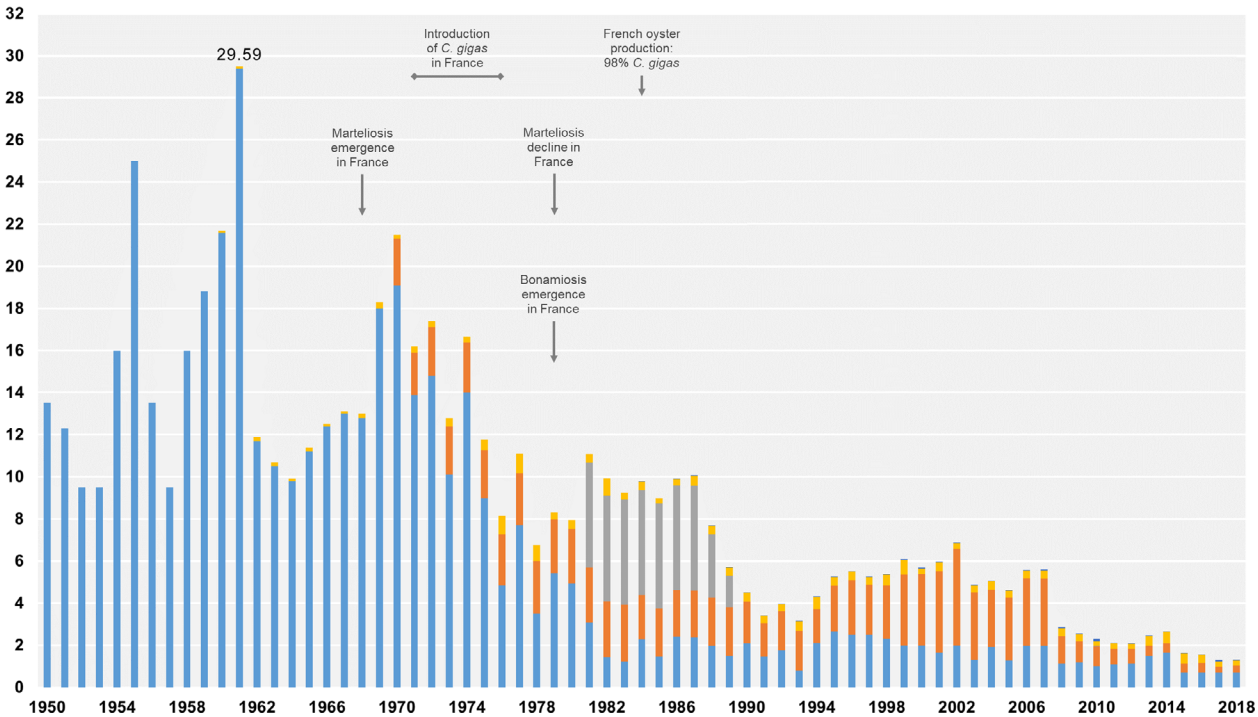

Figure 1 Histogram of *Ostrea edulis* aquaculture production in Europe from 1950 to 2018 (FAO 2020) with some key French events (Héral 1990; Grizel & Héral 1991). The data include only the values corresponding to the European flat oysters; the volumes are in live weight and cumulated by country, independently of the main FAO production areas. (■) Other European countries: Bosnia-Herzegovina, Channel Islands, Croatia, Greece, Montenegro, Morocco, Norway, Portugal, SFR of Yougoslavia, Sweden, The Netherlands, Tunisia, UK; (■) Ireland; (■) Italy (1981–1989; 2010–2011); (■) Spain and (■) France.

can occur during the same breeding season (Marteil 1976). The tendency to protandria (i.e. the initial adult phase is male) is common and the formation of male gametes occurs in the post-settlement autumn (Davaine 1853; Cole 1942). This phase is not functional, and gametes are often lysed (Martin *et al.* 1997). The oyster then enters the female phase for the beginning of the following season. The occurrence of embryos has been observed already in one-year-old oysters (see Section Fertility). Information on the viability and survival of these embryos is scarce; however, Merk *et al.* (2020) reports a development of veliger larvae in these young oysters.

The sex change is much faster in the female-male direction, performed within days under optimal conditions (Yonge 1960). This rapid change, and gonads not emptying completely when male gametes are released, may result in the presence of both types of gametes within one oyster (Martin *et al.* 1997). Male and female gametes are present in the oyster follicles at the same time but with different stages of maturation (Maneiro *et al.* 2017b).

The occurrence of sexual inversion depends on several factors such as latitude, temperature and nutrition (Marteil 1976; Martin *et al.* 1997; Eagling *et al.* 2018): optimal nutrition may increase the number of female spawners (Orton 1927).

The number of sex changes can vary between locations: once per season in Scandinavia (Yonge 1960), two to three times in the UK (Walne 1974) and more than three times in France (Martin *et al.* 1997). The determinism of sex change may also be influenced by internal factors such as the action of nerve nodes (Martin *et al.* 1997), but so far, no studies on neuroendocrine reproductive control are available for *O. edulis*.

A balanced sex ratio of the spawning population is relevant for successful reproduction in the field (Kamphausen *et al.* 2011; Zapata-Restrepo *et al.* 2019). Monitoring, and, if possible, management of the sex ratio is essential for the optimization of larval production in the hatchery. *Ostrea edulis* anaesthesia and *in vivo* magnetic resonance imaging, monitoring the sex ratio and gametogenesis, developed by Culloty and Mulcahy (1992), Davenel *et al.* (2010) and Suquet *et al.* (2010) provide non-invasive alternatives.

Gametogenesis

It is hypothesized that *O. edulis* enters a winter sexual rest period which length can vary with latitudes (e.g. Norway,

the Netherlands, France, Croatia). Temperature and food availability play a predominant role for the initiation and progress of gametogenesis (Martin *et al.* 1997). Cole (1942) in Wales and Marteil (1976) in France define the onset of gametogenesis at around 10°C, while Wilson and Simons (1985) in Ireland observed the beginning of gamete redevelopment at a mean temperature above 7°C, but none of the identified studies report a geographical comparison.

Other parameters such as food, oyster age, size, salinity and the length of the photoperiod also seem to affect gametogenesis (Mann 1979; Cano *et al.* 1997; Joyce *et al.* 2013).

Nutrition and food availability is equally important during the winter phase as it is during the entire gametogenesis process. In winter, energy reserves might be stored and mobilized in springtime for gamete production (Gérard *et al.* 1997). On the other hand, Ruiz *et al.* 1992 report that *O. edulis* is in San Cibran (Spain) an opportunistic organism that concentrates its breeding efforts on a short period of favourable conditions which depends directly on the availability of nutrients in the environment.

As previously mentioned in 3.3, the physiological state of the oysters (age and size) can vary according to different factors such as latitude and therefore influence the gametogenesis, which has an impact on the fertility rate.

The influence of salinity, however, is still under debate. Problems in resuming gametogenesis for salinities close to 20 have been observed in an estuarine area (Gérard *et al.* 1997) and beyond 20 and up to 36 (under the species' usual living conditions), no influence is assumed (Martin *et al.* 1997).

As daylight has also been shown to have a profound influence on other mollusc species, the positive effect of a prolonged photoperiod on the gonadal development (also called sexual glands, gonadal glands or gonads) of *O. edulis* during autumn and winter conditioning (light intensity reflecting the spring conditions in the environment) was shown in experimental hatchery conditions (Maneiro *et al.* 2016; Maneiro *et al.* 2017b).

An assessment of the maturity of gonadal development can be carried out following macroscopic criteria. A practical scale for the evaluation of the stages within the sexual cycle of *O. edulis* was established by Marteil (1959), see Table 3. As mentioned above in chapter 3.3, other methods (anaesthesia, *in vivo* magnetic resonance imaging, histology) and protocols exist for determining maturation. As an example, Maneiro *et al.* 2016 describe a method for the determination of gonadal development using histology and stereology techniques.

Spawning and fertility

Spawning

The minimum gamete emission (i.e. release of eggs into the pallial cavity of females and release of spermatozeugmata from the male oyster) temperature has been extensively studied and varies according to regions and geographical conditions (Table 4). Depending on latitude, the minimum critical temperature is between 14 and 16°C (Marteil 1976). However, spawning events of the northern population are observed at 25°C in breed polls, while populations in Spain and the Adriatic Sea start spawning (or can spawn) at 12–13°C (Bromley *et al.* 2016a).

Different stimuli induce spawning in mature oysters: presence of gametes (Gendreau 1988; Chapter 7.4.4), sudden changes in temperature and salinity (Marteil 1976) or a change in temperature combined with wave and current actions (Lubet 1991). Lunar cycles have been argued/demonstrated to affect gamete release by Orton (1927), Korringa (1940), Walne (1974) and Martin *et al.* (1997), but may also be an effect of other factors correlated to such cycles, for example tidal ranges/coefficients (Lubet 1991).

The reproductive strategy of *O. edulis* females is internal brooding (Figure 2). By keeping the offspring inside the female's mantle cavity, embryos are protected from external conditions (Mardones-Toledo *et al.* 2015). In the male phase, *O. edulis* performs sperm casting, where functional males release spermatozeugmata, clusters composed of a central nucleus: spermatozoa are fixed by the head and the flagella radiates freely (Hassan *et al.* 2017; Suquet *et al.*

Table 3 Practical scale for evaluating the stages of the sexual cycle in *Ostrea edulis* modified and translated into English (modified after Marteil (1959) and Martin *et al.* (1997))

Stage	Description	Term
5-0	Empty gonad – corresponds to sexual rest or the end of the expulsion of gametes or larvae	Very thin or thin oysters
1	Beginning of gametogenesis: multiplication of germ cells	Low greasy oysters
2	Gonads well developed but gamete dissociation remains difficult	Greasy oysters
3	Maximum response: gone hypertrophied, a thick white-cream layer envelops the visceral mass, abundant gametes are obtained by very light pressure	Very greasy oysters
4	Gamete emission – incubation in females	Spawning/brooding
4a	The eggs have just been emitted and form a milky white mass in the pallial cavity	Milky (white-sick oysters)
4b	End of incubation: the larval shells give the mass of the embryos a greyish-slate colour	Slate colour (grey/black-sick) oysters (colour evolution: from gray to faint blue, and then black)
5	Completely empty gonad: clearly visible digestive mass, greyish colour of the flesh	Confused with stage 0/spent gonad

Table 4 Onset spawning temperature of *Ostrea edulis* (modified after Bromley *et al*. (2016a))

Temperature (°C)	Country	Location	Reference
25	Norway	Bergen	Bromley *et al*. (2016a)
20.5	England	NA	Bayne (2017)
18–22	Israel	Eilat	Shpigel (1989)
20	Denmark	Limfjord	Bromley *et al*. (2016a)
18	Canada	Lockhart Lake	Bromley *et al*. (2016a)
16	Wales	Conwy, Conwy	Walne (1974)
15	The Netherlands	Oosterschelde	Bromley *et al*. (2016a)
15	England	Crouch, Essex	Bromley *et al*. (2016a)
15	England	Fal, Cornwall	Bromley *et al*. (2016a)
15	France	Morbihan	Bromley *et al*. (2016a)
15	France	Arcachon	Bromley *et al*. (2016a)
15	Italy	Lago Fusaro	Carlucci *et al*. (2010)
15	Italy	Mare Grande Tarante	Carlucci *et al*. (2010)
14	Croatia	Mali Ston Bay	Bratoš *et al*. (2002)
14	Spain	Mar Menor	Cano *et al*. (1997)
13	South Africa	NA	Bayne (2017)
13	Ireland	Lough Foyle	Bromley *et al*. (2016a)
13	Italy	Adriatic	Carlucci *et al*. (2010)
12	Spain	Vigo	Bromley *et al*. (2016a)

2018). Spermatozeugmata have a mean diameter of 64 ± 3 μm, and spermatozoa are released in 21 ± 3 min. The mean curvilinear velocity of spermatozoa movement is 68.5 ± 8.7 μm s^{-1} (Suquet *et al*. 2018).

Male oysters are generally more sensitive to stimulation and emit their gametes first (usually in one event, but possibly incomplete, successive or extended in time). These first spawnings then lead to the spawning of adjacent males and, subsequently, to the spawning of females (His *et al*. 1999). Nelson and Allison (1940) extracted a substance called 'diantline' from oyster sperm which causes, among other things, the relaxation of smooth muscles in female oysters, thus promoting the release of eggs (Martin *et al*. 1997) through the gills into the pallial cavity (Yonge 1960), where they are fertilized by spermatozoa from spermatozeugmata inhaled by the female (His *et al*. 1999).

The number of spawning events per year, the intensity of spawning and the spawning period vary with geographical regions and climatic conditions (Korringa 1940): In Scandinavia, the breeding period is short with only one spawning per year (Yonge 1960). If conditions interfere with the development of gametogenesis and spawning, reproduction will be impaired or natural recruitment will be negligible (Martin *et al*. 1997).

Fertility

The term fecundity and fertility are often confused in the literature for *O. edulis*. According to the definition of Allee *et al*. (1949) which Walne (1964) follows, the term fecundity refers to the production of male and female gametes, while the term fertility refers to the production of embryos and larvae.

The fertility rate of *O. edulis* varies between oyster age, studies and authors (Table 5). The different numbers may be explained by different abiotic factors, such as temperature during gametogenesis (Martin *et al*. 1997). As *O. edulis* can live up to 14 years (Richardson *et al*. 1993), data on both fecundity and fertility rate of the 7- to 14-year-old specimens would be of great importance for predicting population dynamics, but so far do not exist in the reviewed literature.

Incubation and swarming

Incubation phase

Literature on embryo development and early larval stages is scarce. The bibliographic search revealed only Davaine (1853), Horst, (1884), Fernando and MacBride (1931) and Gendreau (1988). The different stages are schematised in Figure 2. Dantan and Perrier (1913) report that during the developmental phase between embryo and larva, there appears to be little or no mortality. For the purpose of artificial breeding trials, Gendreau (1988) describes the ex vivo development of embryos and larvae, summarized in Box 1 and Figure 2. This information may serve as a basis for the development of artificial reproduction techniques for *O. edulis*.

Box 1. Kinetics of *ex vivo* development of embryos and early larval stages at 20°C (Gendreau 1988)

15–20 min after fertilization the oocytes increase in volume. The first polar globules appear around 30 min and the second around 85 min after fertilization. The subsequent development asynchronism is reported to be observable at each stage. The polar lobes appear around 210 min after fertilization and remain observable for 2 h and 30 min. The two-cell stage is observed for 2 h and 40 min, starting from 270 min after fertilization. After 6 h, the four-cell stage is observable for 4 h. Beyond that, the superposition of the increasing number of cells makes it difficult to distinguish the different developmental kinetics. The embryos pass through the stages of morula, blastula and gastrula to become young trochophore larvae within the first 24 h. The trochophore larvae carry a prototroch that allows them to be mobile, however without being able to swim freely. During the next 24 h, the ciliature extends into a crown. On days three and four, the larvae carrying a velum begin to swim.

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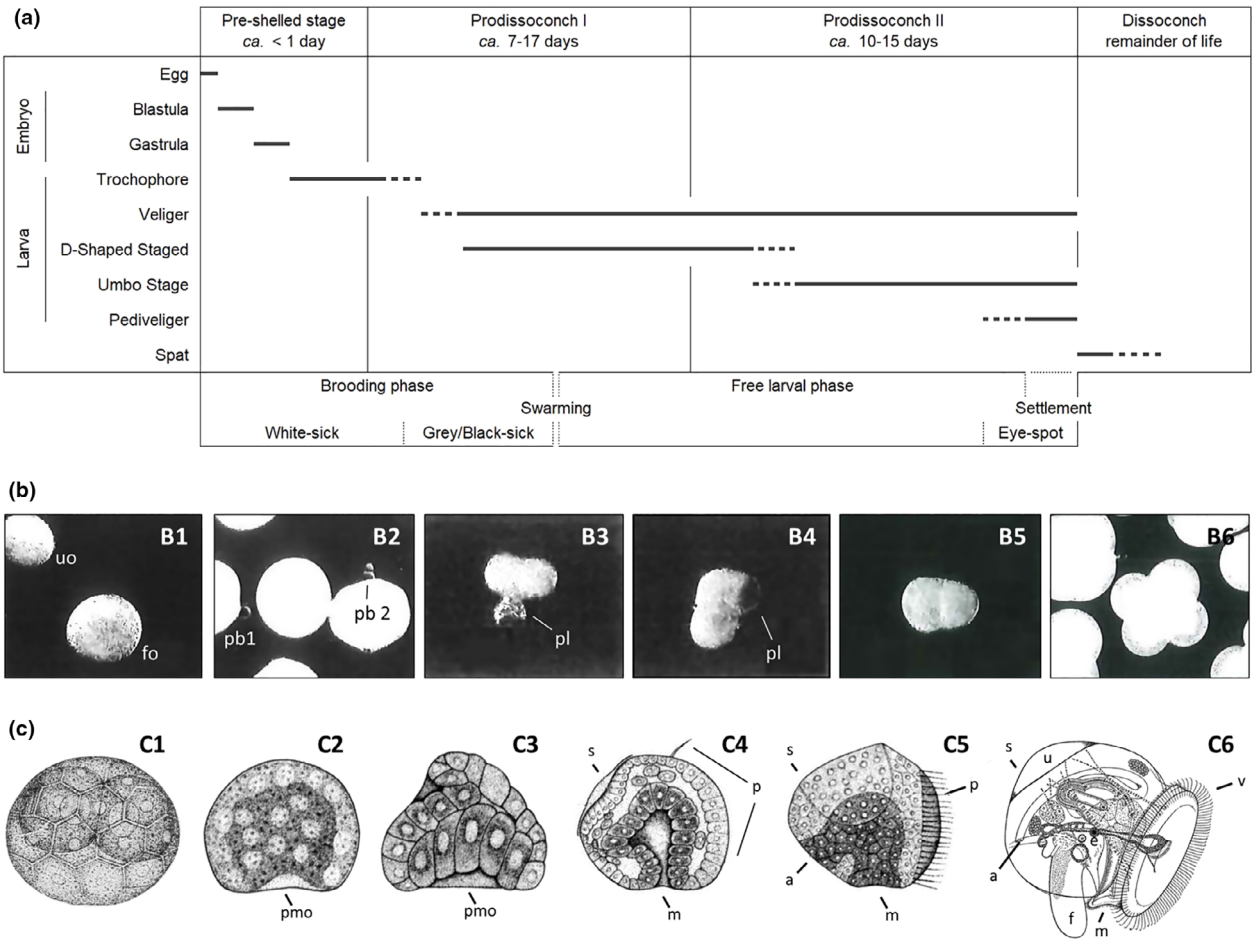

Figure 2 (a) Development of the prodissoconch in relation to other common terms describing larval shell, body and development stages of *Ostrea edulis*. Dashed lines indicate uncertainty or transition. The duration of stages may be highly variable. Modified after Waller (1981). (b) Embryonic development of *O. edulis*: (b1) Fertilized oocytes (fo), Unfertilized oocytes (uo); (b2) Polar body I (pb1), Polar body II (pb2); (b3) Polar lobe (pl) appearance; (b4) Polar lobe (pl) resorption; (b5) Two-cells stage; (b6) Four-cells stage. Photographs and descriptions modified after Gendreau (1988). (c) Early development schemes of *O. edulis*: (c1) Morula/Blastula stage; (c2) Gastrula stage; (c3) Early trochophore; (c4) Middle trochophore; (c5) Late trochophore; (c6) Fully developed larva. (pmo) Presumptive mouth opening; (m) Mouth; (s) shell; (p) Prototroch; (a) Anus; (v) Velum; (u) Umbo; (e) Eye spot; (f) Foot. (c1–c5) Modified after Horst (1884) and Waller (1981), (c6) Modified after Erdmann (1935) and Yonge (1960). As an additional information, the development stages (b1–c4) correspond to the white-sick stage; the grey-sick stage is only represented here in (c5); the black-sick stage is not represented here.

It is suggested that dead larvae are detected by brooding oysters (*O. chilensis*) and ejected from the pallial cavity with pseudofaeces (Chaparro *et al*. 2018). Females may reject some of their own viable veliger along with dead larvae. This was observed in *O. edulis* (Gray *et al*. 2019) although according to Walne (1974), there is very little or no loss of larvae during the incubation period. The brooding period lasts 7–10 days (Orton 1936). At 15–16°C, the white-sick stage is therefore reached after about 3.25 days of incubation, the grey-sick stage is reached 1.75 days later and the black-sick stage within four more days. Spärck (1925) states a different timeline for the larval development: the black-sick stage is reached after 3.5 days and, depending on the temperature, it takes 5.5 additional days at 15°C or 2.0 days at 19°C until swarming. At 13.5, 17.5 and 23°C, the length of the incubation period varies among 18, 14 and 7 days, respectively, Erdmann (1935). At low temperatures, Erdmann (1935) observed a delay in swarming and larger dimensions of swarming larvae as well as advanced larval developmental stages.

Swarming

After the development of the larvae during internal brooding, swarming (i.e. release of the larvae from the female

Table 5 The fertility of *Ostrea edulis* related to the age and the size of the brooding oyster: summary of the data found in the literature

Fertility per oyster (embryos-larvae $\times 10^6$)	Mean diameter of oysters (mm)	Approximative age of oysters (years)	Reference
0.0916	38	1	Cole (1941)
0.1000	34	1	Dantan and Perrier (1913)
0.1000	40	1	Walne (1974)
0.1000	NA	1	Gaarder and Bjerkan (1934)
0.2180	NA	2	Cole (1941)
0.2400	NA	1	Orton (1937)
0.2470	NA	2	Dantan and Perrier (1913)
0.2500	NA	2	Gaarder and Bjerkan (1934)
0.4626	60	3	Cole (1941)
0.5250	NA	3–4	Orton (1937)
0.5400	57	2	Walne (1974)
0.7304	NA	3	Dantan and Perrier (1913)
0.8000	NA	3	Gaarder and Bjerkan (1934)
0.2765 – 0.8296	NA	NA	Philpots (1890)
0.8400	70	3	Walne (1974)
0.9029	70	4	Cole (1941)
1.0000	NA	>3	Gaarder and Bjerkan (1934)
1.0129	Very large oysters	NA	Möbius (1883)
0.8000–1.1000	75	NA	Utting *et al.* (1991)
1.1000	79	4	Walne (1974)
1.2600	84	5	Walne (1974)
1.3600	87	6	Walne (1974)
1.5000	90	7	Walne (1974)
1.8000	Very large oysters	NA	Eyton (1858)

oyster in the wild) is induced by strong contractions of the adductor muscle and the opening of the shell resulting in the ejection of the veliger larvae in clouds (Erdmann 1935). This action is repeated several times with short and long intervals, the whole swarming can be completed within a few hours (Korringa 1940).

Regarding the swarming periodicity of *O. edulis*, Korringa (1940) summarized that: (i) temperature is not the only factor in the process of larval release; (ii) slight differences in salinity seem to be irrelevant; (iii) swarming takes place on both clear and rainy days, which indicates that there is no influence of wind; (iv) swarming depends directly on the frequency of spawning and the duration of incubation (as mentioned above).

Post-swarming larval stages

Larval development and survival

Larval size during swarming depends on the incubation conditions and therefore indirectly on the latitude and the related environmental parameters, ranging from 160 to 200 μm when released into the water (Table 2).

Erdmann (1935), Yonge (1960) and Waller (1981) offer exhaustive descriptions of larval development of *O. edulis*. A short synthesis of larval sizes and developmental stages is available in Acarli and Lok (2009).

The influence of salinity and temperature on larval survival was examined in the laboratory (Davis & Ansell 1962), Davis & Calabrese 1969): At a salinity of 10, larvae die within days, at 12, larvae do not grow and 10 days post-swarming, mortality rate is > 90%. Larvae reared at salinities between 15 and 17.5 grow, but die before metamorphosis, at 20, growth is moderate without mortality. *Ostrea edulis* larvae show high growth and settlement rates at salinities > 22.5 and are able to settle at salinities as low as 15. Temperature should range between 17.5 and 30°C (growth) or between 12.5 and 27.5°C (survival). Below 10 and above 30°C, survival rates are low.

Another relevant parameter is hydrogen sulphide and its impact on *O. edulis* larvae. However, this does not seem to be described in the literature, despite recurrent problems in the natural environment and in breed polls (Korringa 1940; Yonge 1960). Data are available from Theede *et al.* (1969) on adult *O. edulis* in the Black Sea and states a survival of 5 days at hydrogen sulphide concentrations between 0 and 5.6 $cm^3\ L^{-1}$ seawater; however, the tolerance to abiotic conditions between adult and larve cannot be compared.

The larval survival rate in the natural environment is related to multiple parameters (Fig. 3) such as food abundance, predation and sediment movements and is not described in full detail here. Diseases, pathogens, contaminants and predators will be discussed in chapters 5.1–5.3.

Pelagic larval period

The planktotrophic pelagic larval life of *O. edulis* in the natural environment appears to be directly related to temperature. According to Korringa (1940), this phase lasts 6–7 days at a temperature of 22°C, or 12 days at 18°C. Further, for Marteil (1976) and Buroker (1985), it can extend from 6 to 14 days for temperatures ranging from 18 to 20°C.

Larval behaviour

Information on the behaviour of *O. edulis* larvae is available for veliger larvae (Erdmann 1935), for settlement behaviour (Cole & Knight-Jones 1949; Rodriguez-Perez *et al.* 2019), for swimming behaviour and pressure responses (Cragg & Gruffydd 1975), and for free swimming searching

behaviour, crawling behaviour and cementing, including an estimation of the maximum larval swimming speed of 500 mm h^{-1} and other locomotion characteristics (Cranfield 1973).

The settlement of *O. edulis* is influenced by many factors such as larval quality, hydrodynamic conditions or the physico-chemical quality of the seawater. The parameters light, temperature, biofilm and collector type or substrate are briefly described here:

According to Cole and Knight-Jones (1949), Bracke and Polk (1969) and Walne (1974), the influence of light changes during the larval cycle. Larvae show negative phototropism at settlement stage (Bracke & Polk 1969) and preferences for dark collectors (Cole & Knight-Jones 1949). Walne (1974) highlights the nycthemeral preference of larvae to settle during daytimes: intense illumination at the end of the larval breeding period could promote both the speed and the intensity of the settlement. Thus, negative phototropism seems to characterize larvae at the beginning of metamorphosis and light could therefore act as a catalyst for settlement (Carbonnier *et al.* 1990).

Marteil (1976) summarizes that warmer temperatures reduce pelagic life span and potentially increase larval survival rate. In addition, an increase in temperature at the time of metamorphosis could favour the fixation of larvae (Carbonnier *et al.* 1990). Furthermore, Nielsen and Petersen (2019) report that the success of spawning and spat fall of flat oysters in the Limfjorden in Denmark is directly related to the summer temperature.

The biological film, which is built up on substrates or collectors, also plays an important role in the settlement of *O. edulis* larvae (Walne 1958). It is indicated that in aquaculture, a 2–3 week soaking of the collectors can increase the settlement rate. The bacterial film produced by *Shewanella colwelliana* induced settlement of *O. edulis* in hatchery (Tritar *et al.* 1992). Further studies highlight the role of biofilm for inducing settlement (Rodriguez-Perez *et al.* 2019), but so far, this subject has been rarely studied.

Within the natural tolerance range of the species, salinity has practically no impact on larval development (Marteil 1976). Variations in salinity nevertheless can induce settlement if they are confined and a gradual return to the initial salinity is ensured (Carbonnier *et al.* 1990).

Other parameters and mechanisms influencing settlement are developed in various studies: pH (Cole & Knight Jones 1949; Carbonnier *et al.* 1990), substrate type and composition (Cole & Knight Jones 1949; Korringa 1976; Guesdon *et al.* 1989), orientation angles and shape of the substrate (Cole & Knight Jones 1949; Korringa 1976; Colsoul *et al.* 2020), colour and transparency of the substrate (Herman 1937; Cole & Knight Jones 1949; Walne 1974), presence of conspecifics or other species (Cole & Knight Jones 1949; Rodriguez-Perez *et al.*2019).

Oyster nutrition

Oysters show two strategies of food uptake: either directly absorbing dissolved substances from the seawater or ingesting suspended particles (Héral 1990).

Rice *et al.* (1980) demonstrated the direct absorption of dissolved organic matter by the net uptake of amino acids from seawater by *O. edulis* larvae. Laboratory experiments indicate that lipids in solution can be absorbed rapidly by juveniles and pediveligers of Pacific oysters (*C. gigas*; Fankboner & De Burgh 1978). In addition, Bamford and Gingles (1974) highlighted the absorption of glucose in the gills of adult oysters (*C. gigas*). Furthermore, mussel embryos (*Mytilus edulis*) and larvae are capable of absorbing dissolved organic substances; however, there is no evidence that larvae are able to grow and develop only by feeding on dissolved organic matter (Widdows 1991).

The ingestion of suspended particles by adult *O. edulis* includes both mineral and organic particles which are filtered and retained on the surface of the gills and surrounded by mucus (Héral 1990). The food is then sorted, ingested and partly digested. The remaining material passes through the intestine and is evacuated through the anus as faeces. If particulate matter is too abundant or too large it is directly ejected by the gills and labial palps or bound together by mucus, dropped into the mantle and ejected as pseudofaeces. Particle size ingested by *O. edulis* ranges from micro- and nanoplankton down to picoplankton (ca. 200–0.2 μm; Cole 1937; Cano *et al.* 1997; Marshall *et al.* 2010). Groups of bacteria, fungi and tripton (non-living particulate matter) are also consumed (Martin *et al.* 1997).

According to the bibliographical search, the feeding of adult *O. edulis* and larvae on bacteria has never been tested extensively.

Stressors

Oyster diseases and pathogens

Pathogens, such as bacteria, copepods, fungi, microalgae, polychaetes, protozoa, sponges and viruses, can induce diseases, mortalities or significant malformations in *O. edulis*, (Table 6; Chapter 4.1.1–4.1.4). High mortalities occur in the past, and their causes were not always discovered. Orton (1937) reports three examples of high mortality from unknown causes: in 1877 in France (Arcachon), in 1895 in the Netherlands and in 1098 in Norway.

A massive mortality event of (adult) *O. edulis* following establishment of commercial culture in Europe (England, Wales, the Netherlands, France and Italy) appeared in 1920 (Orton 1937; Grizel 1985; Héral 1990). The exact cause of these deaths was unclear, but disease, possibly an infection by a protozoan and unusual temperatures are assumed (Marteil 1976; Grizel 1985).

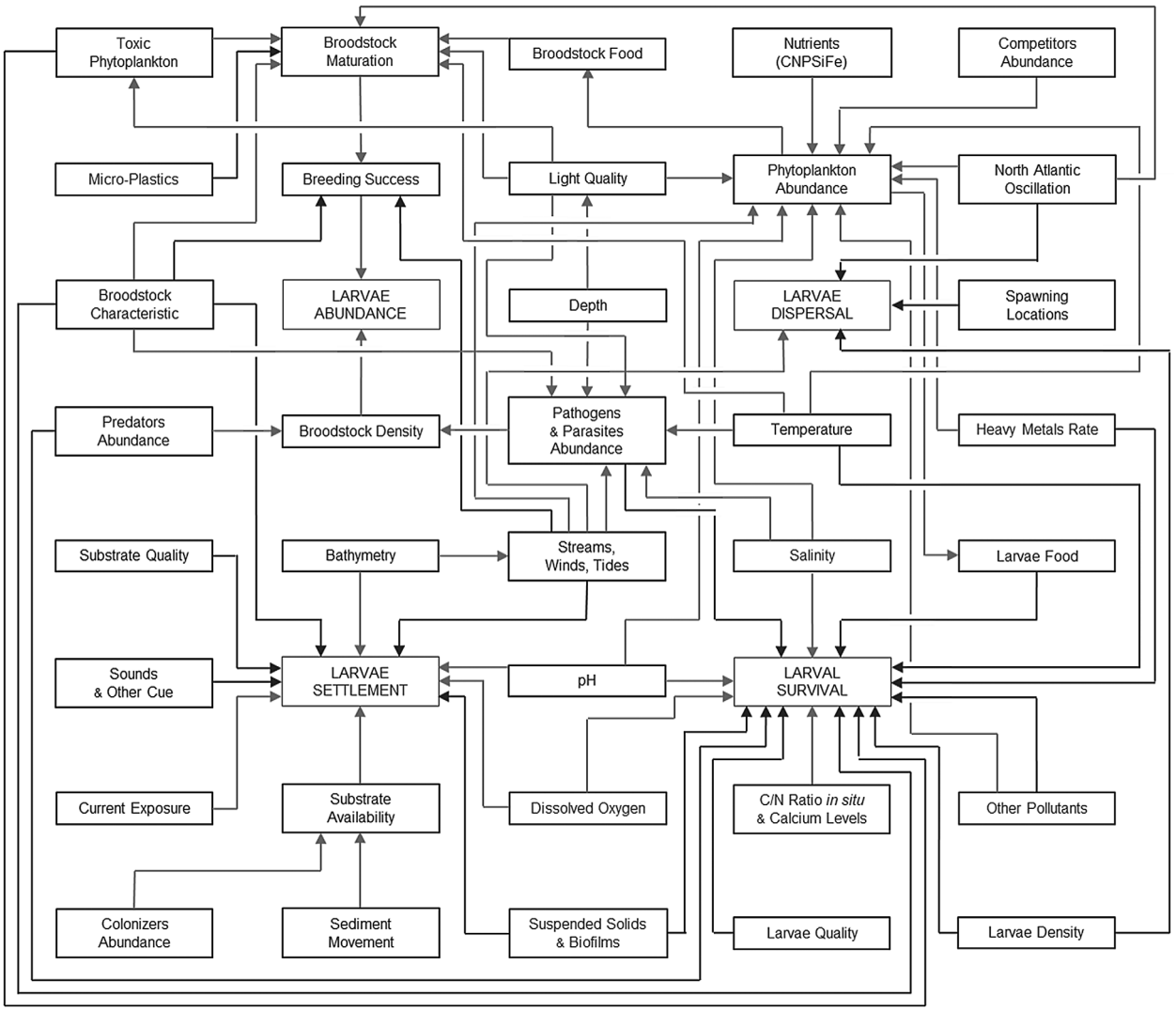

Figure 3 Drivers of spat recruitment intensity: conceptual diagram of the four main parameters and their associated potential factors (biological, chemical, physical).

The two major known diseases of adult *O. edulis* are Marteliosis and Bonamiosis, and these are described below.

Marteiliosis

Another massive mortality event in Europe was reported on *O. edulis* as 'Abers disease' in the literature and was caused by the protozoan *Marteilia refringens*. From 1968 onwards, this protist spread to the majority of Breton farms (France) and was responsible of the marteiliosis disease (Héral 1990). From 1974 onwards, it then further induced massive mortalities at production centres all over France. The spread of the disease across Europe is not documented, but *M. refringens* can be found (either in *O. edulis* or in other bivalves) in Albania, Croatia, France, Greece, Italy, Morocco, Portugal, Slovenia, Spain, Sweden, Tunisia and the UK among others (Carrasco *et al*. 2015). *Marteilia refringens* was detected in Dutch flat oyster stocks in the period 1974–1977 (van Banning 1979b), but not recorded any more in yearly surveys since 1978 (Haenen & Engelsma 2020). Mortality mostly affects two-year-old oysters and can reach up to 90% mortality among oysters (Carrasco *et al*. 2015; Anonymous 2018). For all characteristics of *O. edulis* diseases, see Table 6.

Bonamiosis

Immediately after the decline of marteiliosis in France in 1979, bonamiosis appeared. This infection by the haplosporidian *Bonamia ostreae* induced what is commonly referred to as the third wave of large-scale *O. edulis* mortality in Europe. This led to a partial abandonment of the

cultivation of *O. edulis* in favour of other species of commercial interest such as *C. gigas*. The parasite was reportedly introduced into Europe (France and Spain) following movements of oysters from the USA (Friedman & Perkins 1994; Bromley *et al.* 2016a). First detected in France in 1979, bonamiosis rapidly spread all over Europe: the Netherlands, Spain and Denmark in 1980, England in 1982, Ireland in 1987 and since then continued to spread to other European countries including Italy, Wales, Northern Ireland, the Netherlands, but also outside Europe to Canada and Morocco (van Banning 1987; Culloty & Mulcahy 2007). More recently, *B. ostreae* has been detected in New Zeeland in *O. chilensis* (Lane *et al.* 2016). This parasite particularly affects the older oysters and causes a mortality of 50–80% of the stock while infection rate is lower in young oysters (Grizel 1985; Héral 1990).

Ostrea edulis can be infected by *B. ostreae* from the larval stage onwards (Arzul *et al.* 2011). Prevalence and pathogenic impact on *O. edulis* is eventually affected by water depth (Lama & Montes 1993). Oyster larvae are potentially acquiring the pathogen from the water column during filter feeding or from the pseudofaeces of a brooding adult (Flannery *et al.* 2016). Some populations show increased resistance indicating that genetic advantages against the infection exist and populations can potentially adapt and evolve resistance (Naciri-Graven *et al.* 1998; Lynch *et al.* 2005; Vera *et al.* 2019).

The fast spread and high virulence of these pathogens highlight the need of taking precautions when translocating oysters to cultivation, breeding or ecological restoration sites (Sas *et al.* 2020).

Shell drillers

Concerning shell-boring parasites, it is worth mentioning polychaetes and sponges. Within the group of shell-boring polychaetes having *O. edulis* as host, different species of the genus *Polydora* and the genus *Boccardia* exist (Lauckner 1983; Robert *et al.* 1991). For shell-boring sponges with *O. edulis* as host, species of the genus *Cliona* are prevalent, with in particular *Cliona celata* (Hoeksema 1983) and *Cliona viridis* (Rosell *et al.* 1999) in Europe. In the literature selected in this review, no data were found on the impact of the above-mentioned parasites on growth, weight gain or mortality of *O. edulis*.

Specific larval diseases

As Orton (1937) quotes, and important to underline, by far the greatest mortality for *O. edulis* occurs in the larval stage, whether in the natural environment, or in production.

The diseases occurring in hatcheries are mostly caused by bacteria and not by protozoans (Helm *et al.* 2004). Bacteria can originate from the non-treated broodstock, the algal and the larval cultures. Bacteria that cause large-scale mortalities mostly belong to the genus *Vibrio* sp. and can trigger severe epizootics in hatcheries.

Vibrio spp. are ubiquitous in the marine environment and their genetic as well as their ecological variability led to the emergence of several diseases in oyster aquaculture (Mardones-Toledo *et al.* 2015; Travers *et al.* 2015). Accordingly, many strains can have pathogenic potential (Wendling *et al.* 2014). Virulence however can vary between host populations and environments (Wendling & Wegner 2015; Wendling *et al.* 2017), making specific predictions and effects on wild populations difficult.

A list of bacteria of the genus *Vibrio* affecting *O. edulis* larvae is presented in Table 6.

Pollutants

The term pollutant is applied here in the sense of contaminants. The first pollution problems for bivalve populations appeared in the beginning of the 20th century (His *et al.* 1999). Prytherch (1924) seems to be the first to state that pollution is one of the main factors in the decline of oyster beds. The toxicity of these contaminants can have physiological and morphological impacts on adult oysters but can also affect eggs, embryos and larvae. Heavy metals can affect embryogenesis, larval growth, larval survival, settlement, respiration and in some cases chromosomes (His *et al.* 1999).

Zinc and Chlorine are two components that could be found in a hatchery: the first in the water (inlet), the second in the discharge water (outlet). Zinc concentrations of 100–500 $\mu g\ L^{-1}$ cause reduced growth, increased incidence of abnormal development and increased mortality of *O. edulis* larvae (Calabrese *et al.* 1977). Chlorine concentrations up to a level of 10 000 $\mu g\ L^{-1}$ do not affect *O. edulis* larvae. At a concentration of 20 000 $\mu g\ L^{-1}$, a significant proportion of larvae is still able to survive and grow. However, for chlorine concentrations between 50 000 and 200 000 $\mu g\ L^{-1}$, larval survival and growth are low (Waugh 1964).

Literature data on the impact of several heavy metals and detergents on growth, mortality and settlement rate of *O. edulis* larvae are provided in Table 7. A relatively new pollutant in the environment is microplastics which adsorbs different pollutants from the environment allowing them to enter the mantle cavity of the filter feeding oysters. However, the effects of microplastics on the respiration rate, the filtration rate and the growth rate of adult *O. edulis* are minimal (Green 2016), whereas no data on the general health status and potential long-term effects exist so far. Further research on nanoplastics is to be expected, as we know for *C. gigas*, nanoplastics can affect

Table 6 List of internal pathogens and parasites of *Ostrea edulis* having a potential impact on its host and offspring (modified after Anonymous (2018))

Group	Species	Descriptor	Size (μm)	Host impact	Geographical distribution	Infection period	Diagnostic	Transmission	References§
Algae	*Gyrodinium aureolum*‡	Hulburt 1957	13–36	Necrosis of the central area of the digestive gland	(Laboratory test)	No specific period	Gross observation‡	NA	Partensky and Vaulot (1989), Smolowitz and Shumway (1997)
Bacteria	*Nocardia crassostreae*‡	Friedman *et al*. 1998	NA	Adult oyster Mortality (can be present in every tissue)	Canada, Europe (The Netherlands)	Late summer and fall	Tissue imprint Histology PCR ISH	Direct	Engelsma *et al*. (2008)
Bacteria	*Vibrio alginolyticus*	Miyamoto *et al*. 1961	NA	High larval mortality (challenged with pathogen: up to 100%)	(Laboratory test)	No specific period	PCR	Direct	Tubiash *et al*. (1965)
Bacteria	*Vibrio anguillarum*‡	Bergeman 1909	NA	Larval mortalities	Europe (Spain‡)	No specific period	PCR	Direct	Lodeiros *et al*. (1987)
Bacteria	*Vibrio coralliilyticus*	Ben-Haim *et al*. 2003	NA	Larval Mortalities	USA, New Zealand, Europe (France)	No specific period	PCR	Direct	Dubert *et al*. (2017)
Bacteria	*Vibrio neptunius*	Thompson *et al*. 2003	NA	High larval mortalities (>98%)	Europe (Spain)	No specific period	PCR	Direct	Prado *et al*. (2005), Dubert *et al*. (2017)
Bacteria	*Vibrio ostreicida*	Prado *et al*. 2014	NA	High larval mortalities (86.4–98.5%)	Europe (Spain)	No specific period	PCR	Direct	Dubert *et al*. (2017)
Bacteria	*Vibrio tubiashi*‡	Hada *et al*. 1984	NA	Larval mortalities (lethal exotoxins (to larvae), bacillary necrosis)	USA, Europe (Spain‡)	Infect the larvae during the brooding period	PCR	Direct	Lodeiros *et al*. (1987)
Copepod	*Herrmannella duggani*‡	Holmes *et al*.1991	490–1560	Reduce gills size (present in the shell cavity)	Europe (Ireland)	Uncertain	Gross observation‡ Histology‡	Direct	Holmes and Minchin (1991)
Copepod	*Mytilicola intestinalis*	Steuer 1902	>1000	Minimal impact on host (present in the gut lumen)	USA, Japan, Europe	Uncertain	Gross observation Histology	Direct	Hepper (1956)

Table 6 (continued)

Group	Species	Descriptor	Size (μm)	Host impact	Geographical distribution	Infection period	Diagnostic	Transmission	References§
Fungus	*Ostracoblabe implexa*	Born *et al.*	1.5–2.5	Shell abnormalities	India, Canada (Nova Scotia), Europe (UK, France, the Netherlands)	Summer (temperature > 22°C)	Gross observation Histology	NA	Dollfus 1921, Orton, 1937, Li *et al.* (1983), Anonymous (2018)
Protozoan	*Bonamia exitiosa*†	Hine *et al.* 2001	3.0 ± 0.3	Oyster mortality in *O. chilensis* but not in *O. edulis* (present in haemocytes; all tissues can be invaded)	Australia, New Zealand, Tasmania, Europe (Croatia, France, Italy, Portugal, Spain, Tunisia, UK)	Throughout the year (with a peak during Australian autumn)	Tissue imprint Histology PCR ISH Electron microscopy	NA	Abollo *et al.* (2008), Anonymous (2018), Helmer *et al.* (2020)
Protozoan	*Bonamia ostreae*†	Pichot *et al.* 1980	2–5; 2.4 ± 0.5 (mean diameter)	Oyster mortality (present in haemocytes; all tissues can be invaded; larvae can be infected)	USA, Europe (Belgium, Denmark, England, France, Italy, Morrocco, Netherland, Northern Ireland, Spain, Wales), New Zealand	Throughout the year (with a peak in late winter-early spring). Incubation period: 3–4 month in infected area	Tissue imprint Histology PCR ISH Electron microscopy	Direct	Abollo *et al.* (2008), Arzul *et al.* (2009), Lane *et al.* (2016)
Protozoan	*Haplosporidium armoricanum*	Van Banning 1977	Sporont (length: 9.8 ± 2.5; width: 7.9 ± 1.9), Spore (length: 4.1 ± 0.4; width: 2.9 ± 0.3)	Occasional oyster mortality (present in the connective tissue)	Europe (France, Netherland, Spain)	Uncertain	Tissue imprint Histology	NA	van Banning (1977), Azevedo *et al.* (1999), Hine *et al.* (2007)
Protozoan	*Hexamita inflata*	Dujardin 1841	8–18	Shell disease and mortality (present in the blood stream)	USA, Canada, Europe	Uncertain	Gross observation‡	NA	Mackin *et al.* (1951), Khouw (1965), van Banning (1979a)

Table 6 (continued)

Group	Species	Descriptor	Size (μm)	Host impact	Geographical distribution	Infection period	Diagnostic	Transmission	References§
Protozoan	*Marteilia refringens*†	Grizel *et al.* 1974	7–35 (primary cell)	Oyster mortality (extracellular parasite of the digestive gland)	Europe (Albania, Croatia, France, Greece, Italy, Morocco, Portugal, Spain, Sweden, Tunisia, UK)	Spring-summer (temperature >17°C)	Tissue imprint Histology PCR ISH Electron microscopy	Intermediate host: copepod (*Paracartia grani*)	Berthe *et al.* (2004), Virvilis and Angelidis (2006), López-Sanmartín *et al.* (2015)
Protozoan	*Mikrocystos mackini*†	Farley *et al.* 1988	*ca.* 2	Oyster mortality (intracellular parasite in the connective tissue cells)	USA, Canadian (west coast)	From winter to late spring. Incubation period: 3–4 month in infected area (temperature < 10°C)	Tissue imprint Histology PCR ISH Electron microscopy	Direct	Bower *et al.* (1997), Gagné *et al.* (2008)
Protozoan	*Perkinsus mediterraneus*	Casas *et al.* 2004	97.4–167	NA	Spain (Balearic Islands)	Late summer and autumn‡	Histology Electron microscopy	NA	Alderman and Gras (1969), Casas *et al.* (2004), Casas *et al.* (2008)
Protozoan	*Pseudoklossia* (*Genus of*)	NA	*ca.* 10	Parasite present in the kidney‡	France	NA	Histology Electron microscopy	NA	Tige *et al.* (1977)
Unknown	Unknown (haemocytic neoplasia)‡	NA	NA	NA	France (Brittany)	NA	Histocytology Histology	NA	Balouet *et al.* (1986)

Table 6 (continued)

Group	Species	Descriptor	Size (μm)	Host impact	Geographical distribution	Infection period	Diagnostic	Transmission	References§
Virus	*Herpesviridae* (family of)	NA	Larvae: 0.118 ± 0.008 (herpes-like virus particles; enveloped virions)	Occasional larvae and juvenile mortality (present in the connective tissues)	USA, Australia, New Zealand, Europe	Summer (temperature > 19°C)	Histology PCR ISH Electron microscopy	Direct	Comps and Cochennec (1993), Renault *et al*. (2000), Renault and Arzul (2001), da Silva *et al*. (2008)
Virus	*Papovaviridae* (family of)	NA	NA	(Present in connective tissues; gametocytes)	USA, Australia, Korea, Japan, Europe (France)	NA	Histology Electron microscopy	Direct	Anonymous (2018)

ISH, *in situ* hybridization; NA, data not available; PCR, polymerase chain reaction.

†Exotic and non-exotic diseases to be immediately notified to the national competent authority in Europe by the annex IV, part II of the Council Directive 2006/88/EC of 24 October 2006 (Anonymous 2006a).

‡Assumption to be confirmed.

§Main references found in the literature search.

Table 7 List of known pollutants and their effects on the mortality, growth and metamorphosis of larvae of *Ostrea edulis* (modified after His *et al*. (1999))

Pollutants	Initial age of exposed larvae	Exposure temperature (°C)	End-point	EC_{50}/LC_{50} (μg L^{-1})	Reference
Heavy metals					
Copper	48 h	NA	Mortality	1–3	Alzieu *et al*. (1980)
Mercury	1–3 days	4.2	Mortality	3.3 (μg metal ion L^{-1})	Connor (1972)
Zinc	96 h	NA	Growth (length)	100–500	Walne (1970)
Detergents					
Actusol	NA	NA	NA	20 000–40 000	His *et al*. (1999)
BP 1002	NA	NA	Growth (2 days)	2500–7500	His *et al*. (1999)
Corexit	NA	NA	NA	40 000–80 000	His *et al*. (1999)
Farrells	NA	NA	NA	6000–8000	His *et al*. (1999)
FO-300-B	NA	NA	NA	4000–8000	His *et al*. (1999)
Gamlen	1 week	23	Growth (2 days)	*ca*. 1000	His *et al*. (1999)
Houghtosol	1 week	23	Growth (2 days)	*ca*. 1000	His *et al*. (1999)
Kudos	1 week	23	Growth (2 days)	*ca*. 5000	His *et al*. (1999)
Linear alkylate sulphonate	1 day	NA	Mortality (6 h)	1000†	Renzoni (1973)
Dodecylbenzene LAS 12C	NA	NA	Growth (1 week)	50‡	
	8–10 days	NA	Settlement (6 h expo.)	1000§	
Polyclens	1 week	23	Growth (2 days)	1000–5000	His *et al*. (1999)
Slickaway	NA	NA	NA	10 000–20 000	His *et al*. (1999)
Slik	1 week	23	Growth (2 days)	*ca*. 1000	His *et al*. (1999)
Sorbent-C	NA	NA	NA	*ca*. 100 000	His *et al*. (1999)
Teepol	1 week	23	Growth (2 days)	5000–10 000	His *et al*. (1999)
Tetrapropylene benzene	1 day	NA	Mortality (6 h)	2000†	Renzoni (1973)
Sulphonate	NA	NA	Growth (1 week)	50‡	
	8–10 days	NANA	Settlement (6 h expo.)	1000§	
Tri-butyltin TBT	48 h	NA	Mortality	3.4	Thain and Waldock (1986)

EC50, toxicant concentration causing 50% reduction in the end-point; LC50, toxicant concentration causing 50% mortality; NA, data not available. Several detergents were assayed as mixtures: in these cases, only the active components are mentioned and their percentages in the assayed mixture provided. Concentrations are expressed as μg L^{-1} of active components.

†Referred to as 'lethal concentration'.

‡Mentioned as 'seriously affecting' growth.

§Mentioned as 'significantly reducing' settling and metamorphosis.

their early life stages, that is from the gametogenesis to larvae (Tallec *et al*. 2018).

As the list of pollutants in this review is not exhaustive, the emerging pollutants, notably PAHs, are not mentioned here.

Oyster predators

Predation on adult and juvenile *O. edulis* can be multitrophic and induce high mortalities. The main predators are invertebrates such as crustaceans, echinoderms and gastropods. In the class of gastropods, potential predators are for example the Atlantic dogwinkle *Nucella lapillus*, European sting winkle *Ocenebra erinaceus*, the Japanese oyster drill *Ocinebrellus inornatus*, the Asian rapa whelk *Rapana venosa* and the Atlantic oyster drill *Urosalpinx cinerea* (Philpots 1890; Hancock 1954; Garcia-Meunier *et al*. 2002; Zolotarev & Terentyev 2012). Examples for *O. edulis* preying echinoderms are the common starfish *Asterias rubens* (Whilde 1985). For crustaceans, the brown crab *Cancer pagurus* and the shore crab *Carcinus maenas* (Mascaró & Seed 2001a; Mascaró & Seed 2001b) can be named. On a higher trophic level, there are also fish and birds preying on flat oysters. Predation on adult *O. edulis* by fish is noted in France and in the Adriatic Sea (Spencer 2008; Glamuzina *et al*. 2014). The fish species named there are the sea-bream *Sparus aurata*, the common stingray *Dasyatis pastinaca* and the common eagle ray *Myliobatis aquila*. The main diving avian predators of marine bivalves in Europe are the common eider *Somateria mollissima* and the common scoter *Melanitta nigra* (Fox *et al*. 2003; Spencer 2008); however, no data on the impact of these on *O. edulis* were found in the literature considered in this review.

The larvae of *O. edulis* are also subject to predation; known predators on these early stages are provided in Table 8.

Table 8 List of known and presumed predators of *Ostrea edulis* larvae in the literature. NA is data not available

Name	Descriptor	Reference
Aurelia aurita	Linnaeus, 1758	Aase *et al*. (1986)
Chaetognatha† (larval stage zoea of the phylum)	NA	Auby and Maurer (2004)
Cladocera† (Superorder)	Latreille, 1829	Auby and Maurer (2004)
Crepidula fornicata	Linnaeus, 1758	Korringa (1951a)
Decapoda† (larval stage zoea of the order)	Latreille, 1802	Auby and Maurer (2004)
Noctiluca scintillans	(Macartney) Kofoid and Swezy, 1921	Dodgson (1922)

†Assumption to be confirmed.

Genetics

Population genetics

Lapègue *et al*. (2007) provides a valuable summary of research efforts conducted on nuclear genetic diversity and the geographical structure of *O. edulis* populations in Europe. Studies using enzymatic markers (Saavedra *et al*. 1995), microsatellites (Launey *et al*. 2002; Sobolewska & Beaumont 2005) and mitochondrial DNA (Diaz-Almela *et al*. 2004) have shown moderate differentiation between Atlantic and Mediterranean *O. edulis* populations. A significant correlation between geographical and genetic distances was found (Launey *et al*. 2002), supporting the distance-by-isolation model; excluding the case of populations at the limit of geographical distribution, such as the populations sampled in Norway and the Black Sea in the study of Diaz-Almela *et al*. (2004).

Ostrea edulis stocks have been subject to numerous transfers – as mentioned earlier in the introduction – for various reasons, although mainly for commercial interests (Bromley *et al*. 2016a). These movements of animals from different stocks have potentially diluted the structure and genetic diversity of naturally occurring populations. A minority of ancestors succeeds in replacing an entire population while the majority fails to procreate. Partial inbreeding may occur temporarily (Hedgecock *et al*. 2007) but gene flow resulting from larval dispersal ensures the connectivity between populations.

Selective breeding

The selection of certain genetic characteristics in oyster aquaculture appears to have gained momentum since the late 1960s (Newkirk 1980). Genetic improvement through selective breeding since then focused on growth, weight gain, survival rate, disease resistance/tolerance, shell shape, shell colour or, more recently, intertidal tolerance of flat oysters. In some cases, growth may induce a better survival rate because oysters grow to their commercial size before diseases hit.

Selection to improve growth

The earliest reported selection for growth in *O. edulis* was carried out in Nova Scotia, Canada (Newkirk & Haley 1982). Encouraging results on individual (mass) selection of growth rate and weight gain were obtained between 1977 and 1990. However, a profound influence of the environmental parameters rather than an influence of the selection on the results is discussed (Newkirk & Haley 1982). Nevertheless, Toro and Newkirk (1990) show differences between two groups of oysters where the selection has a significant influence on growth rate, but no influence on survival rates.

Selection to improve resistance to bonamiosis

Genetic selection as a tool against mass mortality, for example caused by bonamiosis (see 5.1.1), was first discussed in France in 1985 (Baud *et al*. 1997), in Ireland in 1988 (Lynch *et al*. 2014) and in Spain in 2001 (da Silva *et al*. 2005) resulting in experimental breeding programmes for improving resistance. A significant increase in survival and a lower prevalence of the parasite in some oyster stocks was achieved. Mass selection can increase the resistance to a disease (Naciri-Graven *et al*. 1998) but also resulted in significant losses of genetic diversity and subsequent inbreeding, leading to the development of family-based selection. Despite these encouraging results, the low proportion of *O. edulis* produced in hatcheries, the biological specificities of the species and the technical difficulties of breeding have slowed down or even stopped the progress of breeding programmes.

So far, no large-scale breeding programme has been launched for *O. edulis* (Lapègue *et al*. 2007). Apart from the approach at Rossmore Breeding Ponds, where the seventh generation survivors of oysters that are surviving bonamiosis are breeding. In most years since the bonamiosis reached the site of Rossmore in 1987, between 10 000 and 20 000 oysters has been used every year, to breed another generation (Lynch *et al*. 2014).

The search for quantitative trait locus (QTL) for bonamiosis resistance in *O. edulis* is a promising approach (Lallias *et al*. 2009), and the recent development of a SNP

array (Gutierrez *et al.* 2017; Vera *et al.* 2019) opens up new perspectives such as genomic selection.

Crossbreeding and hybridization

The production of crossbred animals resulting from a crossing between different oyster stocks/origins in order to obtain a better performance is a method to improve production developed in agriculture and aquaculture. This increase in performance can be explained by the process of heterosis (Newkirk 1980).

Interspecific hybridization and crossbreeding have been tested for *O. edulis* without notable success. Cross-breeding experiments by Newkirk (1986) showed little evidence of a better vigour of hybrids from two different broodstock origins. An interspecific hybridization of *O. edulis* and *C. gigas* did not produce conclusive results: a low rate of oocyte evolution and replications without cell divisions after fertilization are reported (Gendreau 1988).

Polyploidy

Research on the modification of chromosome numbers in bivalve aquaculture appeared in the 1980s to prevent the spawning phase but also as a potential pathway for obtaining resistant animals (Gendreau 1988; Nell 2002). So far, two types of polyploid oysters, triploids and tetraploids, were developed. Tetraploids oysters are produced for further crossing diploid oysters, resulting in the production of triploids oysters (Yang *et al.* 2018).

Triploid oysters may increase (in some cases and species) the growth rate (Guo *et al.* 1996), may allow the protection of the hatchery product and may decrease the genetic impact of hatched oysters and natural populations (Hedgecock 2011). However, differences in survival rates between diploids and triploids are not clear due to interactions with diseases or other stressors and the difference of ploidy level for each situation and oyster species (Nell 2002).

The first induction of polyploidy applied to oysters, in this case triploidy, was described for *C. virginica* (Stanley *et al.* 1981). In 1988, a method for artificial fertilization of *O. edulis* and extra-pallial larval breeding (triploids, tetraploids, allotriploids) was described and allowed experiments with different methods of polyploidy induction (Gendreau 1988; Gendreau & Grizel 1990). Later triploidy was induced by meiosis I blockage (instead of meiosis II blockage) and resulted in increased growth rates (Hawkins *et al.* 1994).

Gendreau (1988) tested two methods of inducing triploidy: induction by chemical treatment and induction by hyperbaric treatment. The first method consists of treating fertilized eggs during their preliminary phase with the expulsion of one of the two polar globules of cytochalasin B. A standard protocol was adapted to *O. edulis* based on the standard method of Downing and Allen (1987) with a treatment temperature of 20°C and an increased duration of the treatments up to 20 min. The second method, the hyperbaric treatment, consists of applying a pressure shock at the time of expulsion of the polar globules and the first mitotic cleavage. 10 and 120 min after fertilization, a pressure of 48.2633 MPa is applied every 10 min for a period of 5 min. This hyperbaric treatment is a viable method but the time of application has a significant influence on the frequency of induced polyploidy: ranging between 48% and 73% of triploids (Gendreau 1988).

Results obtained with the chemical induction of triploidy by cytochalasin B (treatment of 1 mg L^{-1}) are ca. 69% of triploid oysters larvae (Gendreau 1988; Gendreau & Grizel 1990). The triploidization method used by Hawkins *et al.* (1994) is almost identical.

The production of tetraploids of *O. edulis* was described and tested by Gendreau (1988) and Gendreau and Grizel (1990) applying the same methods: cytochalasin B (chemical) and hyperbaric treatment. Results for hyperbaric treatment are identical to triploidy induction, but only a 16% tetraploidy level was obtained (Gendreau 1988). Induction by chemical treatment induced a rate in the range of 40–53% tetraploidy (Gendreau & Grizel 1990).

As mentioned above, triploid oyster production is uniquely dedicated to aquaculture and has no direct application in ecological restoration.

Spawning induction and artificial fertilization will be discussed in chapter 7.4.

Seed exploitation

Growing demands and the development of oyster aquaculture

Early days: the ancient world

For thousands of years, oysters have been fished and harvested as a relevant food source, but also for other usages. The use of oysters for healing wounds for example was already mentioned by Hippocrates of Kos in his time (Voultsiadou *et al.* 2010). Only little is known about the cultivation of oysters in the Mediterranean antique (Yonge 1960). However, some Roman production methods and the first Greek trials are documented. These methods still persist today, although they were not developed based on scientific knowledge.

During the 4th century BCE, Aristotle initiated the scientific approach of oyster reproduction in his 'Treatise on animal generation' in Greece and documented the history of seed breeding and production testing (Barthélemy-Saint Hilaire 1887). According to his writings, oysters were found by sailors landing in Rhodes, growing on broken clay pots

and other shards thrown into the water. These are the first references of oyster seed collection. Furthermore, Aristotle describes first attempts of breeding trials: adult oysters were transplanted from the island of Lesbos into a nearby sea. There, they grew rapidly but did not seem to reproduce.

This precious documentation was undoubtedly the inspiration for a Roman named Caius Sergius Orata. Gaius Plinius Secundus reports that this Sergius Orata successfully established oyster beds in the area of Baiae or Puteoli for the first time in the 1st century BCE. The methods of cultivation he used and how the supply of juveniles was organized is unknown. It is likely that at that time young oysters were collected at sea and placed in the salt waters of Lucrin or Fusaro lakes for refining and reproduction (Coste 1861; Locard 1900). Since then, Italy was the European leader in inventing and using advanced marine mollusc farming methods until the 19th century (Corlay 2001).

New momentum: seed collection and production in the modern age

In the 17th century, oyster culture in France began in salt marsh pools of the Atlantic coast, followed by culturing stocks in constructed ponds (Héral 1990). Seed oysters were collected or dredged and placed in these ponds until they grew to a size where they could be sold (Héral 1990; Buestel *et al.* 2009). From the 18th century on, natural beds of *O. edulis* were overexploited on the French Atlantic coast due to high demands. Accordingly, decrees were issued which forbid the harvesting of *O. edulis* during the breeding season (Héral 1990).

The decline in natural oyster stocks all around Europe raised the concerns of public authorities at that time. Research and experimentation programmes were set up in France as well as in other European countries. All this scientific and administrative expense had one objective: the regeneration of natural oyster beds, mainly driven by commercial demands (Roché 1898).

Modern oyster culture, defined as the culture of oysters from captured seed, began in the 1850s (Héral 1990). Simultaneously, several different techniques for seed capture were developed around Europe.

In 1852, de Bon and Coste were commissioned by Napoleon III to restore the French oyster stocks. They initiated a repletion and reseeding programme mainly based on using wooden seed collectors similar to those used in Italy at that time. This project marked the beginning of French oyster culture with the control of seed supply (Goulletquer & Héral 1997).

In 1878, the Norwegian Government also investigated the possibilities of restoring the depleted Norwegian oyster beds (Strand & Vølstad 1997) and discovered the remains of natural beds in so-called polls: shallow, well-sheltered salt-water pools where the water temperature did rise sufficiently high in summer to allow larval development (Korringa 1976). These polls (breed polls) were used for oyster farming, and a system hanging collectors for collecting seed was developed. These cultures were intended to restore the depleted oyster beds for a re-establishment of the commercial fishery (Strand & Vølstad 1997).

From 1868 on, the oyster species *C. angulata* was accidentally introduced from Portugal, leading to the colonization of the French Atlantic coasts (Buestel *et al.* 2009). It was produced in parallel with *O. edulis* and replaced the flat oyster at the main culture sites after the mortality events in the 1920's (Buestel *et al.* 2009, see also chapter 5.1). Thereafter, the development of production technologies for the European flat oyster was less relevant and stagnated.

An overview of seed production systems in different European countries (restricted to Belgium, England, Germany, Italy, the Netherlands, Portugal and Spain) is presented in Dean (1891). It identified three categories: (i) Countries with no seed production (Belgium); (ii) Countries allowing stocks to develop and then exploit the biomass surplus of these oyster beds (Germany, Portugal and Spain, Denmark and Ireland; Kristensen 1997; Culloty & Mulcahy 2007); (iii) Countries using seed collectors for the settlement of oyster larvae at sea or in breeding ponds (Italy, France, England and the Netherlands).

The European flat oyster was and still is of interest also in the eastern Mediterranean. In Croatia, oyster farming was regulated by the law already in 16th century, and the wild seed has been collecting on tree branches or later on clay roofing tiles set on the seabed by the 1980-ties, but bunches of plastic nets and series of plastic discs hanged on suspended longlines are widely used today (Korringa 1976; Skaramuca *et al.* 1997; Benovic 1997; Tomšić & Lovrić 2004; Bratoš *et al.* 2004). Turkey and Bulgaria established seed production or collection only since the end of the 20th century (Alpbaz & Temelli 1997). For all other countries along the Black and Mediterranean Seas, no information on *O. edulis* production methods was available in the reviewed literature.

Further progress with controlled breeding: controlled fertilization and hatcheries

So far, the extensive culture of *O. edulis* was not always economically viable. In the 20th century, processes to stabilize this industry were developed, which were directly related to the development of production techniques for hollow oyster seed, the flagship product of the shellfish industry.

In 1849, controlled fertilization of oysters and reseeding of depleted oyster grounds with these larvae was suggested for the first time in France (Roché 1898). However, it was not until 1879 that the first artificial reproduction tests

were carried out on American oysters (*C. virginica*) in the laboratory (Brooks 1879). In order to meet the rising demands, artificial reproduction techniques were further promoted. In the United Kingdom, artificial breeding of *O. edulis* was developed mainly by the work of Cole (1937), who successfully reared a high number of larvae to metamorphosis in large outdoor tanks (Alagarswami 1982). Bruce *et al.* (1940) were probably the first to develop laboratory methods for rearing larvae of *O. edulis*. In the following decades, a considerable effort was made to identify and cultivate phytoplankton species for feeding flat oysters (Loosanoff & Davis 1963; Walne 1965; Mann 1984).

Since then, the production of oyster seed on land has developed and evolved considerably: from experimental laboratory production to large-scale hatcheries. Between the 1960s and 1980s, significant advances were achieved in broodstock conditioning, larval culture and survival, larval energetics, composition of algal feeding and cultchless seed production (Mann 1984). The first true and complete manual for hatchery bivalve culture was provided by Dupuy *et al.* (1977) for *C. virginica*.

By comparing the first manual from Dupuy *et al.* (1977) to the current general manual (not specialized on a given species) on marine bivalve hatchery of Helm *et al.* (2004), many evolvements in hatchery design, breeding operations and production success have been achieved (Mann 1984; Helm *et al.* 2004; Goulden *et al.* 2013). Nevertheless, although knowledge of seed production in *O. edulis* hatcheries is substantial, seed exploitation is still mainly based on the collection of seed from natural stocks.

New demands: oyster reef restoration in the context of ecological restoration

The restoration of oyster habitats in the context of ecological restoration is a new development. It can be clearly distinguished from reseeding and restocking attempts that aim at the stabilization of commercial exploitation and at the satisfaction of market demands via aquaculture or fishery.

The beginning of ecological restoration as a discipline dates back to the 1860s. It was founded in southern Europe for forest environments and reforestation (Vallauri *et al.* 2002) and constantly increased in relevance over a number of different environments and scales, such as terrestrial, freshwater and marine ecosystems (Clewell & Aronson 2013). Today, it is defined as the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed and is recognized as a critical tool for mitigation and active conservation (Gann *et al.* 2019).

Oyster habitat restoration desires the restoration of ecological functions of oyster reefs, which are manifold and diverse. They include biodiversity enhancement, increase in water quality (by clearance of the water column), nutrient removal, sediment fixation, bentho-pelagic coupling and coastal stabilization (Coen & Luckenbach 2000; Pogoda 2019).

In Europe, the restoration of *O. edulis* has gained momentum and presents a new stakeholder in seed oyster exploitation with specific demands regarding quality and quantity. The topic is of interest for governmental or non-governmental nature conservation organizations, for researchers and resource managers, focusing on habitat restoration and biodiversity enhancement, as well as for commercial producers (Laing *et al.* 2006; Kerckhof *et al.* 2018; Pogoda 2019).

Seed production

Different production approaches and techniques exist for the production of seed oysters. An overview, including detailed descriptions and application ranges is presented here.

Seed collection

In Europe, today, the majority of *O. edulis* seeds for aquaculture production come from wild collection, also called sea-based collection (Anonymous 2006b).

The two main collection techniques that exist today are as follows: (i) the placement of cultch/collectors such as bivalves shells on the seabed as in the case of in the Netherlands (Lake Grevelingen), in England (Blackwater estuary and the Fal river), in Scotland (Loch Ryan) and in Ireland (Lough Foyle, Galway Bay and Tralee Bay), (Fig. 4) (Engelsma *et al.* 2010; Bromley *et al.* 2016b; Eu-Commission 2018; McGonigle *et al.* 2020; Anonymous 2020a; Anonymous 2020b; Anonymous 2020c; Anonymous 2020d); (ii) the suspension of collectors or even the placement of collector on bottom bound structures such as tube nets (Fig. 5b) filled with bivalve shells (mainly *M. edulis* shells) over oyster beds or limed conical discs made of plastic (Fig. 5d) in cages as in Quiberon Bay and Brest Bay in France (Arzul *et al.* 2006). The second technique is also used in Mali Ston Bay and the West Coast of Istria in Croatia (Zrnčić *et al.* 2007), and in Kotor Bay in Montenegro (Peraš *et al.* 2018) using plastic discs or empty plastic nets suspended between two metal rods (Bratoš Cetinić & Bolotin 2016).

In both techniques, collectors are placed in the time window of the swarming (see Section Swarming) of *O. edulis* larvae. Long after the collection period, when the spat size reaches 5–6 mm, the collectors can be transferred to grow-out areas or the spat removed (Anonymous 2006b).

Seed collection has several advantages: the low investment and operating costs (preparation, deployment and

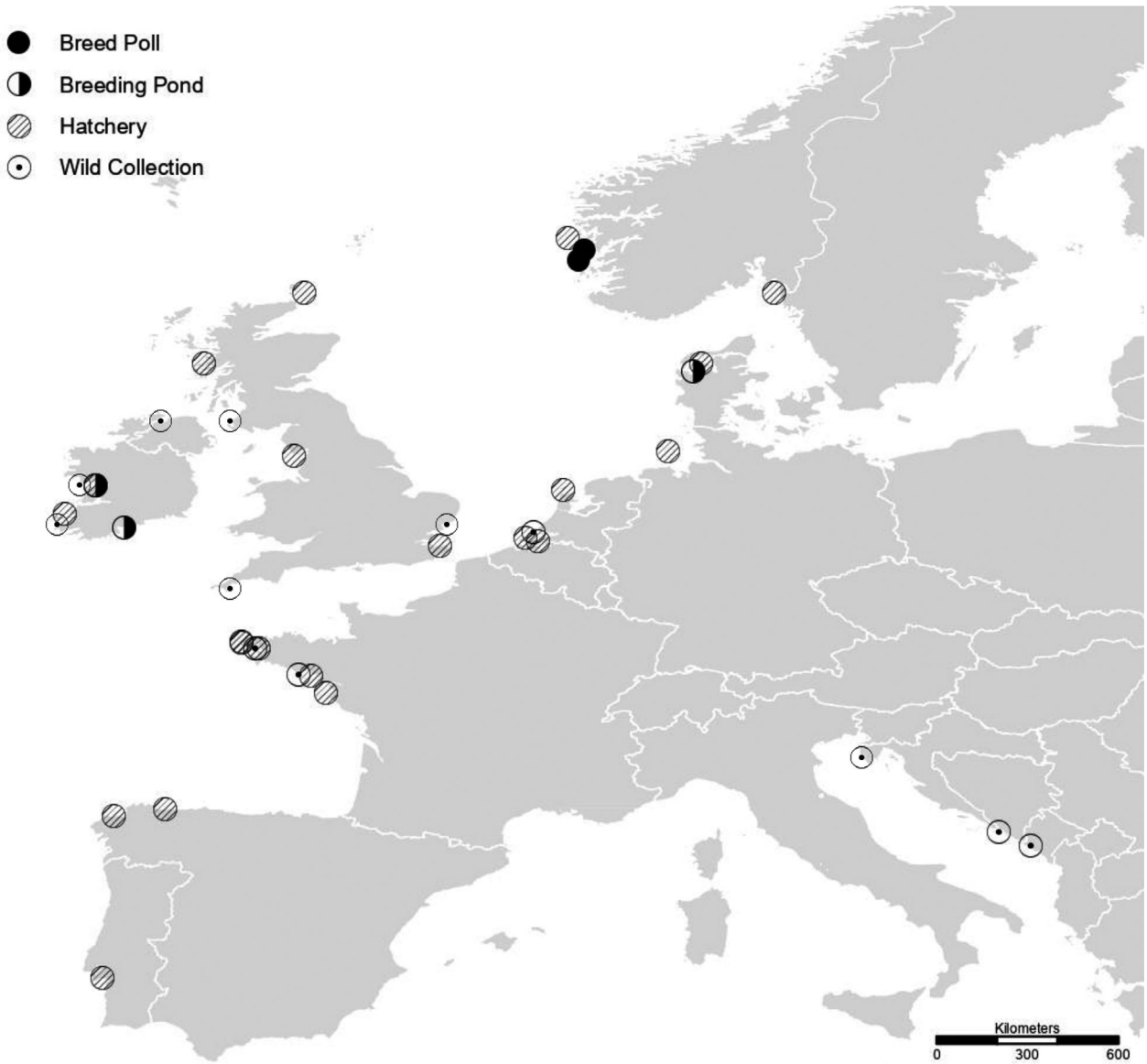

Figure 4 Map of distribution of seed suppliers of *Ostrea edulis* in Europe: production (see Table 9) and collection sites (see chapter 7). (●) breed poll; (◑) breeding pond; (▨) hatchery and (⊙) wild collection.

harvesting), compared with a hatchery for example; the number of broodstock can potentially (under optimal biological and hydrological conditions) induce a high genetic variability (Diaz-Almela *et al*. 2004; Lallias *et al*. 2010); the number of collectors and oysters breeding (under optimal biological and hydrological conditions) can allow a very high productivity (see chapter 6.1 and Fig. 1).

Seed collection has however major disadvantages: this technique is not possible everywhere in Europe, the production is seasonal, does not allow genetic selection, is not recommended for translocation scenarios in ecological restoration (zu Ermgassen *et al*. 2020b) and the settlement rate is dependent on environmental conditions. Regarding this last aspect, as mentioned in chapter 3.7.1, the settlement of *O. edulis* may be affected by numerous factors (see chapter 3, 4 and Fig. 3), and therefore, the production is dependent on the environment. Major fluctuations can be observed from year to year (Tardiveau 2020), which affect the production and its stability considerably in some years.

The collection of *O. edulis* larvae in the wild is an appropriate and sustainable approach in areas where reproductive flat oyster populations remain. Accordingly, a renewed interest from science and production perspectives to improve and increase and/or stabilize the production to

meet new demands from restoration measures can be expected.

Nevertheless, the variety, efficiency and long-term effects of wild seed collection techniques are not included here as the literature on the subject is very large and existing results of the performance are stated non-comparably. Furthermore, this complex aspect involves a wide number of factors to be considered and would qualify for a full review itself.

An example of seed collection (non-sea-based) techniques from the past: the Fusaro lake in Italy (Box 2).

Box 2. Lake Fusaro

Seed collection of oyster from the past inevitably includes the example of the salt lake of Fusaro in Italy. Located between Lake Lucrin and Cape Misene, it was considered and described by Coste (1861) and Dean (1891). This example, which includes a temporary closure of the salt lake, is at the boundary between collection and production techniques. Coste (1861) reported in his report on oyster farms in Italy that at Lake Fusaro he observed from distance to distance the most ordinarily circular spaces occupied by stones that would have been transported there. These stones are piled up in a pyramidal manner simulating rocks. These stones are then covered by oysters that were imported for example from Taranto. These dummy rocks or artificial beds of oysters with a diameter of between two and three metres are surrounded by piles planted at regular intervals close enough to each other to circumvent (Figure 5a). These circumferential piles protrude slightly above the surface of the water so that they can be grasped and removed when necessary. Next to these artificial benches, other piles, linked together by a rope from which bundles of wood are hung for seed collection, are aligned in a straight line (Figure 5c).

The characteristics of Lake Fusaro are more broadly described by Dean (1891). At that time, the lake was crescent-shaped with a circumference of 4.8 km. At each end, canals would have allowed communication with the sea. The depth of the lake would have been 1.5 m on average, with deeper areas of up to two meters. This shallow depth allowed its temperature to grow quite easily and temperature regulation was possible by admitting new seawater.

At the end of the 1960s, the Lake Fusaro industry was destroyed by volcanic causes and poor management and maintenance of the breeding sites (Dean 1891). However, oyster farming was re-established in the 1880s, abandoning the pyramid-shaped collectors described by Coste (1861). It seems that the management of Lake Fusaro as a closed lake was largely a failure. These failures to have been due to a strong rise in temperature, forcing the producers to frequently renew the seawater and consequently let the larvae escape from the lake, but it is also reported that the settlement was very irregular from year to year in Fusaro.

We found no trace in the literature of the fate of seed production methods in Fusaro since then (Dean 1891).

Breed polls

Definitions

The traditional Norwegian breeding system of *O. edulis* is the Østerspoll (here suggested as 'breed poll'), for which many synonyms exist: Norwegian oyster pond, salt-water pond, salt lake, poll, landlocked heliothermic marine basin, Norwegian oyster bassin, Norwegian oyster-poll, small oyster lagoon, landlocked fjord, heliothermic poll or even solar pond. It should not be confused with what is called 'spat-poll', basseng or Norwegian spatting pond, which are larger, shallower basins not closed and exposed to tidal exchanges within the fjords. 'Spat-polls' are generally used for the *O. edulis* spat grow-out whereas the 'breed polls' is solely reserved for breeding. Other types and names of basins are described in the literature as 'Bukt' and 'Kil' (Gaarder & Bjerkan 1934; Bøhle 1984) but do not seem to meet the requirements necessary for reproduction.

The poll is a natural biotope, distinct from a fjord and is suggested as a specific geographical feature (Matthews & Heimdal 1980): Polls are enclosed systems, a few kilometres long and 5–12 (metres) deep (Friele 1899). The sill depth is less than the depth of the pycnocline (few metre depths, e.g. 4–8 m). For the cultivation of *O. edulis*, polls can be closed temporarily.

Kirkland *et al.* (1980) describes heliothermic processes for these polls: Solar radiation is absorbed and converted into heat by the dark, muddy bottom of the poll. Conditions required for the development of heliothermal energy are density differences between the upper layer (mixolimnion), intermediate layer (chemocline) and lower layer (monimolimnion). The upper layer of water can be relatively fresh (e.g. salinity of 5.5 at Espevick, Norway) and floats on a brine. Salinity passively affects the density by evaporation, eventually out balanced by soluted salt. A salinity difference of one per cent between upper and lower layer will obtain a temperature of up to 25–30°C within the chemocline for a short period in summer (Gaarder & Bjerkan 1934; Korringa 1940).

The fresh top layer prevents vertical heat exchange because the warm salt water remains heavier than the

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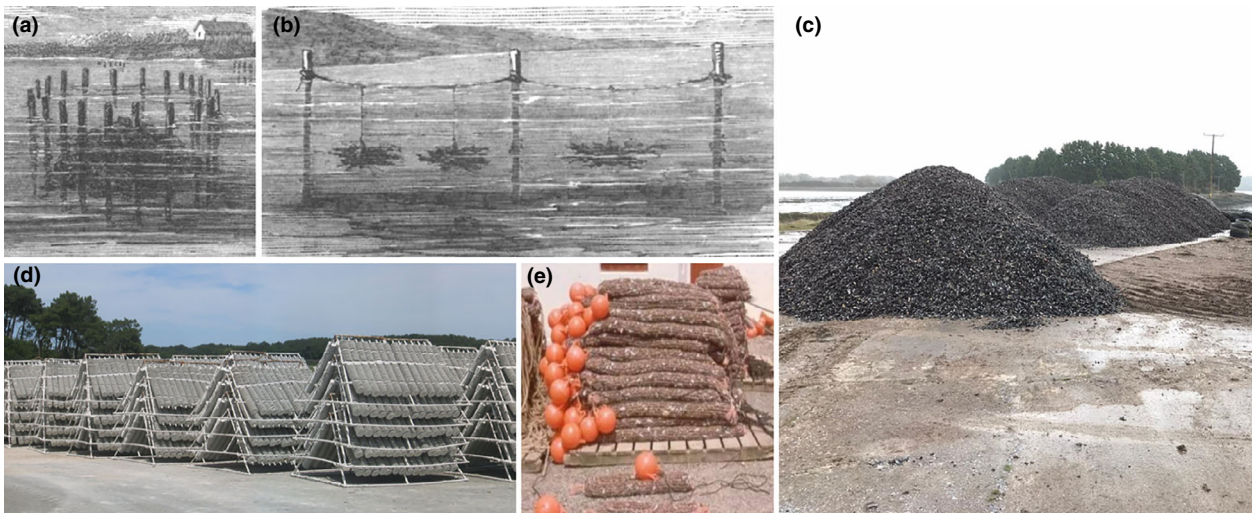

Figure 5 Seed collection: examples of oyster spat collectors from the past and present. (a) Artificial oyster beds surrounded by wooden piles used in the salt lake of Fusaro in Italy; (b) wood piles placed in a straight line and joined by a rope that suspends bundles of branches piles used in the Fusaro lake in Italy and today in Croatia; (c) pile of cultch (*Mytilus edulis* shells) in deposit before placement on the seabed of the Loch Ryan, UK; (d) Another example of a collector used nowadays in Brittany, France: the plastic limed disc, here on a cage for future immersion in a lime bath and then in the sea; (e) tubular nets filled with mussel shells, here attached on floating buoy for longlines. Modified after Coste (1861) (a,b) and photographs from Tristan Hugh-Jones (c), Hélène Cochet (d), Anonymous (2006b) (e).

cooler top layer. During the day, the upper layer transmits most of the solar rays, at night it serves as a cover (Gaarder & Bjerkan 1934; Korringa 1940). Due to these very specific hydrographic conditions, water temperatures stay constantly high enough for the oysters to reproduce successfully – even in these high latitudes.

Breed polls sustain and contribute to *O. edulis* production in Norway (Fig. 6). Information on breed polls used for *O. edulis* aquaculture is available in Strand and Vølstad (1997).

Breeding protocol

Breeding operations begin with the supply of broodstock within the breed poll (Korringa 1976). Although adult oysters are present inside the breed polls, a significant production of larvae will require the addition of several thousand 3- to 4-year-old oysters. Broodstock is suspended in the warm water layer that provides a sufficient oxygen level as the muddy soil eventually lacks oxygen during mid-summer and leads to the formation of hydrogen sulphide (Korringa 1940; Yonge 1960). A

Figure 6 Breed polls schematics and illustrations of a breed poll: (a) view from above of a breed poll and connectivity to the Fjord, (d) drain that can be closed, (f) inlet of freshwater; (b) profile view of a breed poll and connectivity to the fjord, (d) drain that can be closed; (c) schematic of the method for hanging seed collectors, (sc) suspended seed collectors; (d) view of the dam of the Innerøy Poll in Norway; (e) aerial view of the Innerøy Poll. Modified after Gaarder and Bjerkan (1934) and photographs from KVB and Anonymous (2017).

prominent suspension method is longlines with broodstock baskets.

The second step of a breeding operation is the preparation and installation of the collectors. In Friele (1899) and Korringa (1976), two types of collectors are described: (i) collectors made of dried branches of birch (*Betula* spp.) or common juniper (*Juniperus communis*) without their thorns and (ii) collectors consisting of square mesh pieces made of galvanized wire. The first collector type is suspended from a longline with a ground weight. As for the second type of collector, two square pieces are superposed and often intertwined with twigs of juniper, hazelnut (*Corylus* spp.) or birch (never with Alder *Alnus* spp). Eventually, these collectors are coated with cement. Details of current practices were not found in the literature.

Shortly before the larvae are ready for settlement, regular water sampling determines optimal timing for collector installation. At a density of about four to five larvae per litre and a good larval development, the exposure period can be estimated. Since larval concentration is not equal throughout the whole depth of the breed poll, empirical observations, which may take a few years, are necessary. Accordingly, the installation depth of the collectors can be estimated (Korringa 1976). As collectors are affected by biofouling, they are removed from the water, landed for a drying period and then returned back for collection (Korringa 1976).

Finally, the last operation is harvesting the seed. After the settlement of larvae is completed, the breed poll will be reopened for water exchange with the fjord. The seed overwinters on the collectors within the breed poll. During spring, the producers harvest the juveniles by boat and special detaching tools.

Food supply

Natural food supply in the breed polls is highly efficient: oysters grow quickly and are marketable with 3 years (Yonge 1960). However, in less sunny summers, phytoplankton is less abundant, which leads to lower growth rates and significant harvest losses (Korringa 1976). Klaveness (1990) has shown how, among other factors such as temperature and salinity, fluctuations in *O. edulis* production can be explained by a total or partial lack of food and subsequent malnutrition of larvae. Various experiments and measurements were carried out to understand and optimize algal production and thus optimize the production of *O. edulis* in breed polls (Klaveness & Johansen 1990; Klaveness 1990; Klaveness 1992; Ulvestad & Strand 1997).

Risks and diseases

The first systematic monitoring of the health status of *O. edulis* in Norwegian breed polls was carried out in 1989 (Mortensen 1992). Until 2016, none of the parasites *B. ostreae*, *B. exitiosa* and *M. refringens* were detected. The protist *B. ostreae* was initially detected in Western Norway in 2009 (Engelsma *et al.* 2014) where also *M. refringens* occured for the first time in 2016 (Mortensen *et al.* 2018). However, they did not occur in breed polls so far.

A known risk is the potential mixture of water layers within a breed poll: (i) mixed bottom and middle waters may cause hydrogen sulphide mortality in broodstock and seed (Yonge 1960); (ii) mixed layer of freshwater with the seawater underneath may result in the inability of the heliothermal process (cited above) to warm seawater (Korringa 1976). In addition, Korringa (1976) reports that oysters reproducing at high temperatures in the breed polls appear to be sensitive to low winter temperatures that, combined with low salinities due to high rainfall, result in elevated mortalities. In general, mortality as well as predation pressure is low in the suspended culture systems (Korringa 1976).

Performance and further development

During the bibliographic search and analysis of this production technique, very little data were found on the output numbers of annual seed harvested. According to Strand and Vølstad (1997), between 1903 and 1988 an estimated average of 3.2 million *O. edulis* seed were produced per year in breed polls. Production peaked in 1989 with 12 million spat, but fell back to only one million in 1990. No comparable data regarding collector type, production in breed poll or seed size were available.

In the 1880s, a number of production companies were created with high investments in breed polls. However, it seems that this effort was only temporary. Only two companies were identified a century later (Strand & Vølstad 1997): Ostravigpoll and Espevikpoll. There is no recent reference to the production and the current state of this technique. But obviously, breed polls are also used as nurseries for hatchery seed (Anonymous 2011).

The unpredictability and limited capacity of the traditional production of *O. edulis* in breed polls have resulted in newly developed production technologies (Strand & Vølstad 1997).

Breed polls maintain a high genetic diversity (Lallias *et al.* 2010), which supports ecological restoration of *O. edulisa*; although this system is specific to Norway. A renewed interest from science and production perspectives to improve and increase breed poll production to meet new demands from restoration measures could be expected.

Floating breeding bags in breed poll

Inspired by the large-scale production of juvenile flatfish in underwater plastic bags, these techniques were successfully adapted for the production of *O. edulis* larvae (Naas *et al.* 1986; Naas 1991).

In the initial experiments, this technique consisted of semi-transparent plastic bags with conical bottoms that are filled with seawater filtered at 200 μm at a salinity of 30. These polyethylene semi-floating bags had a depth of 2.7 m and a volume of five cubic metres. Between three and six broodstock oysters were placed inside them. During the pelagic phase of the larvae, no water renewal was carried out and for the settlement phase, PVC sheets were inserted into the bags to settle onto.

This system is estimated to produce 130 000 *O. edulis* spat per plastic bag, containing three broodstock oysters and achieving an average settlement rate of 7.9%. Although this seems to be a low-cost method that requires very little expertise on seed production, this method does not seem to be used or is at least no longer cited in the literature today.

Breeding ponds

Definitions

The 'breeding ponds' (suggested name here) production technique, also known as 'spatting ponds', is carried out in entirely man-made ponds. Many projects, trial reports, production protocols, book chapters or even scientific articles refer to them as 'oyster ponds'. This vague term can be confusing. Thus, it is necessary here to clearly distinguish oyster storage ponds (before marketing or merely in winter), refining and greening ponds typical of the Marennes-Oleron region (France), reparking or grow-out ponds or even purification ponds, which do not contribute to seed production itself.

The development of this technique for the production of oysters in Europe dates back to the 1860s (Spencer 2008). Examples regularly cited in the literature are as follows: the Beaulieu river breeding ponds (Hampshire, UK), the Hayling island breeding ponds (Hampshire, UK), the Breneguy breeding ponds (Locmariaquer, France), the Conway breeding ponds (Conwy, UK), the River Yealm breeding ponds (England, UK), the Port Erin breeding ponds (Isle of Man, UK), the Tholen breeding ponds (Tholen, the Netherlands) and the Rossmore breeding ponds (Cork, Ireland) (Beaulieu 1890; Dean 1890; Orton 1937; Hughes 1940; Korringa 1951b; Walne 1974; Hugh Jones 1999; Spencer 2008).

Examples

As reported, the Hayling Island Breeding Ponds were enormously successful in 1868, when 80 million spat were produced from 32 ha (Spencer 2008). Seed was collected from bundles of twigs, wooden hedges, shells, slates or even stones.

Following this resounding success, productions in breeding ponds were also developed elsewhere but only with temporary success as in the case of most of the French attempts. But despite these irregularities, the Breneguy Breeding Ponds operations in France were fruitful and promising and followed a general routine (Dean 1890): (i) During winter, the pond dries out for at least 2 months, which allows the basin to purify itself deeply by crumbling and mixing muddy dried areas with gravel and clay, but also by removing plants and animals (e.g. potential predators, competitors); (ii) Shortly after early spring, water is gradually admitted into the breeding ponds; (iii) After a period of about a week, spawning oysters are introduced and dispersed (across about 40 m^2) to deeper waters; (iv) The exchange of water by tide occurs at least once a day until the first observation of larvae when the breeding ponds subsequently are closed – this is also the signal for the placement of the collectors; (v) The breeding ponds stay closed until autumn, resulting in larval retention and optimized settlement. Water renewal is only necessary a case of massive evaporation; (vi) Collectors with oyster seed can be collected.

Furthermore, it is important to have a large surface area of the pond in order to secure good air absorption and good water circulation through the wind, to have a minimal but continuous supply of new seawater to compensate for evaporation and to ensure a sufficient water depth to protect against sudden changes in temperature or salinity.

However, in 1979, new breeding ponds were built in Cork, Ireland (Fig. 7). The problem of production variability over consecutive years was addressed and successfully solved by building many ponds: 22 in total. These shore based man-made ponds are 20 × 20 m by 2 m deep and contain 1000 m^3 of seawater during production. A single pump conveys the water, and no filter or sterilization of seawater is carried out. Underground drains, allowing the transfer of water and ensuring better management control, connect the breeding ponds. The drains are lined with butyl rubber but can be made of hard rubber as well. The breeding protocol, although similar to that of Breneguy, provides more specific information: (i) Breeding ponds are filled with seawater only once a year in summer; (ii) No food is added. Food is provided by the pond ecosystem including microalgae blooms (Rogan & Cross 1996); (iii) Temperature, pH, pond colour, weather conditions and reproduction stage of oysters (Table 3) are constantly monitored. The collectors used here are mainly mussel shells (*M. edulis*) scattered one by one at the bottom of the tanks for manual harvesting. In other breeding ponds such as in Ireland and Denmark (Fig. 4 and Table 9), other collector types are used such as flat plastic collectors or plastic 'coupelles' with or without slaked lime.

Although there are a multitude of possible designs for the creation and operation of breeding ponds, three practical handbook/manuals exist today in the literature: the

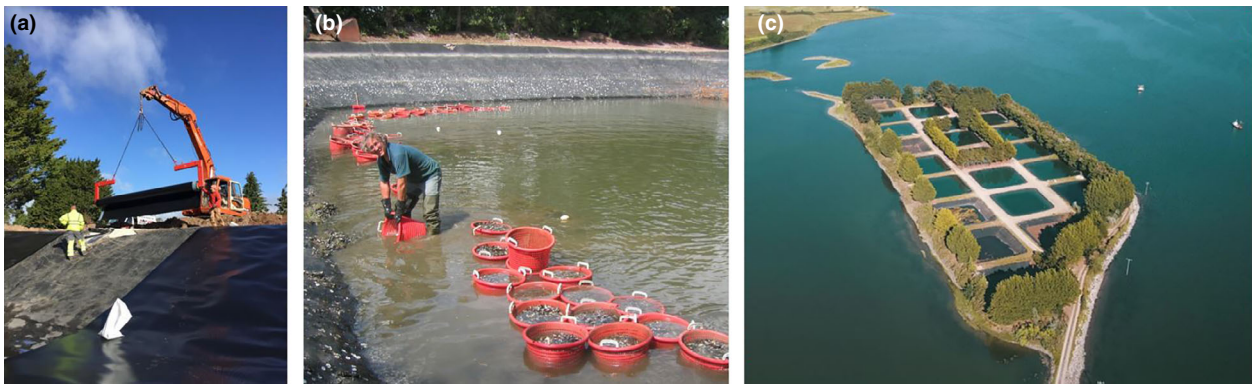

Figure 7 Rossmore Breeding Ponds (Cork, Ireland): (a) repair/construction of breeding ponds in 2019: installation of the liner; (b) harvesting of seed on shell and placement in baskets for transport to the grow-out site; (c) aerial view of the 21 breeding ponds. Photographs from Tristan Hugh-Jones.

manual of Connellan (1995), the report of Syvret *et al.* (2017) and the manual of Strand *et al.* (2018).

Performance

The bibliographical search identified only scarce information on the production of oysters in breeding ponds and even less on their performance. However, at Rossmore Breeding Ponds, when 75% of the breeding ponds are productive, the expected yield is in the range of 2 million five-millimetre size seed per pond (Spencer 2008). The actual production from the breeding ponds of Rossmore for the years 1993–2003, in years after the developement of bonamiosis (since 1987 in Cork) are shown in Appendix S3.

In general, breeding ponds maintain a high genetic diversity (Lallias *et al.* 2010), which supports ecological restoration of *O. edulis*. Accordingly, a renewed interest from science and production perspectives to improve and increase breeding pond production to meet new demands from restoration measures can be expected.

Hatcheries

Hatchery production of *O. edulis* was investigated by applied scientific approaches as irregular and insufficient supply of wild seed had increased the importance of hatcheries in the production of oyster seed. The EU-funded projects SETTLE (FRP/2007–2013 Grant 222043), OYSTERECOVER (FP7-SME-2008-2 Grant 243583) and LARVDEVOPTI (FP7-PEOPLE Grant 273851), focused on several critical aspects of flat oyster production both in hatcheries and in the field. However, the state of the art in hatchery production of *O. edulis* is still incomplete and does not provide a reliable protocol for flat oyster conditioning and larval production in hatcheries throughout the year.

Several critical and challenging steps in hatchery production have to be addressed to generate a constant supply of healthy oyster seed: (i) Broodstock has to be conditioned to accelerate gonad development to increase the number of produced larvae. Successful broodstock conditioning will also allow maturing and spawning outside the natural season; (ii) High, synchronized and reliable settlement success and metamorphosis have to be established to secure successful post-settlement growth and survival.

The further development and application of specific techniques, such as artificial fertilization, cryopreservation, remote setting, polyploid production support the respective steps in hatchery production or have the potential to do so in the future.

Biosecurity

Biosecurity in bivalve hatcheries can be summarized in three levels (Spark *et al.* 2018): (i) Identification and control of biological and non-organic inputs (e.g. water, air, feed, animals, pathogens and employees); (ii) Internal biological and non-organic control; (iii) Control of production products and effluents (e.g. water, live animals, faeces and dead animals). This broad field will not be covered here in its entirety, but references on some points will be given below.

The water treatment of *O. edulis* hatchery is carried out today by different methods: chlorination, ultraviolet radiation, pasteurization or ozonation (Prado *et al.* 2010). The storage of untreated water may increase the risks (Jones 2006).

The treatment of broodstock and their fouling before entering the hatchery is a crucial phase (Coatanea *et al.* 1996). The elimination of fouling and epibionte for *O. edulis* can be carried out in different ways, which can be summarized as follows (van den Brink & Magnesen 2018): manual scrapping, brine bath, chlorine bath or in a cement mixer.

Table 9 List of seed suppliers of *Ostrea edulis*

Country	Name	Addresses	Production technology	Status and aim	*Bonamia* sp. free spat
Canada	Dalhousie University Aquaculture Center	Truro, Nova Scotia, B2N 5E3 1-902-893-6600 – www.dal.ca	Hatchery	Active? Research	NA
Denmark	Dansk Skaldyrcenter	Øroddevej 80 7900 Nykøbing Mors – www.skaldyrcenter.dk	Hatchery	Active Research	NA
Denmark	Venø Fish Farm AS – Aquamind AS	Sønderskovvej 9 Venø 7600 Struer – www.venoe.dk	Breeding Ponds	Active? Commercial	NA
England, UK	Colchester Oyster Fishery Ltd	Pyefleet Quay, East Road, East Mersea, Colchester, Essex, CO5 8UN – www.colchesteroysterfishery.com	Breeding Ponds†	Active? Commercial	NA
England, UK	Seasalter (Walney) Ltd	Old Gravel Works, South Walney Island, LA14 3YQ Cumbria, England – www.morecambebayoysters.co.uk	Hatchery	Active Commercial	Yes
England, UK	Seasalter Shellfish (Whitstable) Ltd	Old Roman Oyster Beds, Reculver, Herne Bay, CT6 6SX Kent – www.oysterhatchery.co.uk	Hatchery and Breeding Ponds	Active? Commercial	NA
France	CRC Bretagne Nord Shellfish Technical Centre of Porscav	Rue de l'Aber 29810 Lampaul-Plouarzel – www.cnc-france.com	Hatchery	Active Restocking	NA
France	Ferme Marine de l'île d'Arun EARL	Chemin de la pointe du Glugeau 29460 Hanvec	Hatchery	Active Commercial	NA
France	IFREMER Experimental site of Argenton	Presqu'île du Vivier 29840 Argenton – wwz.ifremer.fr/argenton	Hatchery	Active Research	NA
France	Novostrea Bretagne SAS	Banastère 56370 Sarzeau – www.novostrea.net	Hatchery	Active Commercial	NA
France	Ostrea Marinove SCEA	Le Terrain Neuf 85740 L'Epine – www.marinove.fr	Hatchery	Active Commercial	Yes
Germany	AWI Biological Institute Helgoland	Ostkaje 1118 27498 Helgoland – www.awi.de	Hatchery	Active Research	NA
Ireland	Atlantic Shellfish Ltd	Rossmore, Carrigtwohill, Co. Cork – www.oysters.co.uk	Breeding Ponds	Active Commercial	NA
Ireland	Cartron Point Shellfish Ltd	New Quay, Burrin, Co. Clare	Hatchery and breeding ponds	Active Commercial	NA
Ireland	Tralee Bay Hatchery Co Ltd	The Ponds, Kilshannig Castlegregory, Tralee, Co Kerry – www.traleebayhatchery.com	Hatchery	Active Commercial	NA
The Netherlands	NIOZ Experimental Hatchery	Zuiderhaaks 18 1797 SH 't Horntje, Texel – www.nioz.nl	Hatchery	Active Research	Yes
The Netherlands	Roem van Yerseke BV	Postbus 25 4400AA Yerseke – www.roemhatchery.nl	Hatchery	Active? Commercial	NA
The Netherlands	Stichting Zeeschelp	Jacobahaven 1 4493ML Kamperland – www.zeeschelp.nl	Hatchery	Inactive Commercial	NA
Norway	Bømlo Skjell AS	Agapollen Fv22, 5420 Rubbestadneset	Breed Poll	Active Commercial	Yes
Norway	Scalpro AS	Svartevikvegen 5 Oygarden 5337 Rong	Hatchery	Active? Commercial	Yes
Norway	Storestraumen Østers AS	Innerpollen 5200 Os	Breed Poll	Active Commercial	Yes
Norway	Sunnhordland Havbruk	Mølstrevåg 5550 Sveio	Breed Poll	Active Commercial	Yes
Portugal	Marvellous Wave SA – Aquanostra®	Estrada Nacional N10, Pavilhão D22. 2910-130 Setúbal – www.aquanostra.pt	Hatchery	Active Commercial	NA

Table 9 (continued)

Country	Name	Addresses	Production technology	Status and aim	*Bonamia* sp. free spat
Scotland, UK	FAI Farms Ardtoe Marine Research Facility	Ardtoe, Acharacle PH364LD Argyll – www.faifarms.com	Hatchery	Active? Commercial	NA
Scotland, UK	Orkney Shellfish Hatchery Ltd	Lobster Ponds, Lambholm, Orkney KW17 2RR – www.orkneyshellfishhatchery.co.uk	Hatchery	Active Commercial	NA
Spain	A Ostreira SL	Lugar del Porto de Barizo 15113 Malpica de Bergantiños La Coruña	Hatchery	Active Commercial	Yes
Spain	Centro de Cultivos Marinos de Ribadeo	Peirao de Porcillán, s/n 27700 Ribadeo Lugo	Hatchery	Active?	NA
Sweden	Ostrea Aquaculture	Hamnevägen 38 45205 Sydkoster – www.aquaculture.se	Hatchery	Active Commercial	Yes

The wild seed collection areas are not listed here. The status and production objectives are for information purposes only (last update: 11.2018). The last update of the URL links is 02.2020. NA are data not available.
†Assumption to be confirmed.

For the identification of internal parasites and pathogens, it is possible to perform a screening by sampling and destroying a few individuals for analysis (e.g. histological, PCR) or by non-destructive screening (Kamermans P, Blanco A, van Dalen P, Peene F, Engelsma M. unpublished data).

Bacterial control in *O. edulis* rearing facilities is achieved both by treatment of the water upstream using, the systems mentioned above, by prophylactic management of employees, and with antibiotics or probiotics.

The most common antimicrobial agents registered in the literature of this review for water treatment of *O. edulis* were the following: Chloramphenicol (Tubiash *et al.* 1965; Jeffries 1982), Penicillin (Jeffries 1982) and Streptomycin (Tubiash *et al.* 1965). Although curative use of such agents is not prohibited, their regular preventive use is highly detrimental in hatcheries for two main reasons: the first being the risk of long-term resistance of the bacteria to the treatments, and the second being the risk of dissemination of these agents or resistant bacteria in the natural environment (Dubert *et al.* 2017).

The large-scale use of probiotics in bivalve hatcheries is recent (Prado *et al.* 2010; Goulden *et al.* 2013; Dubert *et al.* 2017). As an example, Kesarcodi-Watson *et al.* (2012) demonstrates that three strains of probiotics (*Alteromonas macleodii* 0444, *Neptunomonas* sp. 0536, *Phaeobacter gallaeciensis*) have provided significant protection against different pathogens of the genus *Vibrio*.

Food production

Food production in bivalve hatcheries is still mainly dependent on microalgae culture (Helm *et al.* 2004). Robert and Gérard (1999) summarizes that the quantity and quality of food varies according to the animal stages and production must meet nutritional requirements. They indicate as follows: for larval rearing, the quantity of microalgae required is less than for other stages of production (ca. 15–20 L of microalgae at a concentration of 6×10^6 cell mL^{-1} per day per 10^6 larvae according to Muller-Feuga 1997); however, the nutritional and biological quality must be high. For broodstock conditioning, the quantity of microalgae is high (ca. 0.5–2 L of microalgae at a concentration of 6×10^6 cell mL^{-1} per day per oyster according to Muller-Feuga 1997) and the quality can highly influence gametogenesis.

Alternatives to microalgae are being investigated through various studies. Alternatives such as bacteria and thraustochytrids, yeasts, preserved microalgae (concentrated, refrigerated, frozen), dried or powdered microalgae, microalgal pastes, microcapsule, lipid microspheres and lipid emulsions are described in Robert and Trintignac (1997), Knauer and Southgate (1999), Brown and McCausland (2000), and Rikard and Walton (2012). These alternatives, complements or partial replacements of diet are still in an experimental stage and require optimization before large-scale use.

Broodstock conditioning

Broodstock conditioning of *O. edulis* is especially difficult outside the natural season, with the gonadal development being in a resting period. Thus, the time needed to obtain mature gametes is linked to the initial gonadal maturation state of the oysters. However, broodstock conditioning can be improved by regulating external factors such as temperature, photoperiod, diet quality and ration. Only a few studies have addressed the effects of these factors on flat oyster gametogenesis and conditioning. Early studies report that the duration of gametogenesis depends on water temperature (Korringa 1940; Mann 1979; Wilson & Simons 1985).

Millican and Helm (1994) showed that microalgae supplements accelerate spawning in *O. edulis* and increase the number of released larvae. More recently, the positive effect of increased photoperiod and increased temperature on gonadal development, cultch and larval production of the flat oyster during autumn and winter conditioning was reported (Maneiro *et al.* 2016; Maneiro *et al.* 2017b). Using a gradient of daylight (8–16 h) and 4 weeks of conditioning in winter at a temperature gradient of 14–18°C, a successful conditioning of *O. edulis* oysters was achieved in autumn after 10 weeks (Maneiro *et al.* 2017b) and in winter after 4 weeks (Maneiro *et al.* 2016). Total larval production was two to three times higher, while oysters under other conditioning regimes displayed a delay in the spawning process (Maneiro *et al.* 2016; Maneiro *et al.* 2017b). In contrast, Joyce *et al.* 2013 did not find any effect of photoperiod, uncoupled from temperature, on the rate or timing of gametogenesis in *O. edulis*. However, the light intensity used in these experiments was ca. 20 times lower.

Food availability but also nutritional value, size and digestibility of microalgae affect broodstock conditioning and the reproductive performance of flat oysters (Millican & Helm 1994; Maneiro *et al.* 2017a; Maneiro *et al.* 2020). A food ration equal to 6% (dry weight algae/dry weight oyster per day and per oyster) of a mixed diet of microalgae (10% *Isochrysis nuda*, 10% *Tisochrysis lutea*, 10% *Tetraselmis suecica*, 10% *Diacronema lutheri*, 25% *Skeletonema* spp., 10% *Phaeodactylum tricornutum* and 25% *Chaetoceros* spp.) was confirmed to be effective for *O. edulis* conditioning in both autumn and winter. In addition, mortality of the broodstock remained low (Maneiro *et al.* 2017b). The value and positive effects of a mixed diet for flat oyster conditioning are reported by several authors (González-Araya *et al.* 2011; González-Araya *et al.* 2012b; Nielsen *et al.* 2016), also after analysing the physiological and biochemical performance of the larvae. A mixed diet of *Chaetoceros neogracile* and *Rhodomonas salina* also promoted a better and faster gonadal development and improved larval development (González-Araya *et al.* 2012a; González-Araya *et al.* 2013).

Spawning induction

In 1988, different techniques for spawning stimulation were compared for the first time, with the aim to allow the induction of triploidy: induction by chemical, thermal and biological stimuli (Gendreau 1988). Gendreau reports that induction by chemical (serotonin) stimuli caused an emission of a few dozen non-viable oocytes, induction by thermal stimuli only triggered the emission of male gametes and the induction by biological stimuli induced the laying of mature female oysters. The resulting protocol therefore is divided into two parts in order to obtain all gametes, male and female, necessary for fertilization. Thermal stimuli are implemented by successive variations in seawater temperature between 16 and 25°C in which oysters are immersed during a 1-h period. Biological stimuli consist of the addition of male/female gametes of marine bivalves (e.g. *O. edulis*, *C. gigas*), which were previously destroyed by ultrasound, into the water of the broodstock tank. Also, for polyploidy induction purposes, a similar thermal shock was performed for the induction of spawning (Hawkins *et al.* 1994).

First attempts of artificial fertilization

The bibliographic search identified two descriptions of artificial fertilization methods in the work of Gendreau (1988) and Hawkins *et al.* (1994).

After the induction of the female spawning, the emissions of some oocytes from the valves are carefully observed and as soon as they are detected the designated oyster is sacrificed, opened and the oocytes are collected immediately with the use of a pipette (Gendreau 1988). The oocytes are then pooled and sieved in order to remove faeces and other miscellaneous debris. Afterwards, they are counted and fertilized with spermatozeugmata present in the dissociation phase. A ratio of spermatozoa to oocytes between 5 and 10 should be applied to avoid the phenomenon of polyspermy. The survival rate of the larvae between fertilization and the day before metamorphosis was 10%.

Hawkins *et al.* (1994) sacrifices all broodstock immediately after spawning induction in order to remove male and female gametes. The ratio of spermatozoa to oocytes applied here is 50:1 at a fertilization temperature of 20°C. The survival rate is not reported in this study.

Cryopreservation

Cryopreservation of oyster gametes, embryos and larvae is of high relevance and of future interest for aquaculture and for restoration as it provides several advantages: saving time and space for broodstock conditioning operations including food production, possibly influencing genetic diversity via cryopreserved gametes during controlled breeding, developing genetic selection programmes or protecting endangered species strains.

The bibliographic search identified two studies in this relatively new field, conducting cryopreservation research on sperm and larvae of *O. edulis* (Vitiello *et al.* 2011; Horváth *et al.* 2012). The chronological cryopreservation operations are described in Appendix S4.

Horváth *et al.* (2012) stated that although the motility results are poor, sperm survival rates were relatively high and suggested further fertilization tests to confirm the effectiveness and performance of male gamete cryopreservation.

Additionally, Horváth *et al.* (2012) investigated the cryopreservation of trochophore and veliger larvae. After concentrating the larvae to a density of 800 larvae mL^{-1} in

filtered water and adding 5–20% dimethyl sulfoxide, freezing and thawing were carried out with a similar method. Two conclusions seem evident: More advanced stages of larvae appear more resistant to the cryoprotective toxicity and cryopreservation survival than earlier stages. As larval survival 24 h after thawing was zero, further research is required to establish this technique.

Larvae collection and larval rearing

Although the above-mentioned trials are at the experimental stage, today, hatchery production of *O. edulis* is carried out by natural swarming and collection of larvae by overflowing the rearing water into a second tank equipped with a sieve (ca. 90–150 μm) that retains the larvae (Fig. 8; Helm *et al.* 2004).

Hatchery larval density varies in the literature of this review between one and nine larvae per mililitre in the water of rearing tanks (flow-through systems and static water systems; Walne 1974; Helm *et al.* 2004; González-Araya *et al.* 2012b). However, in the same flow-through structures as González-Araya *et al.* 2012b, rearing of *C. gigas* larvae at a concentration of 150 larvae per mililitre was successfully tested (Asmani *et al.* 2017), suggesting that increasing larval densities may be possible.

Within Anonymous (2014), monitoring of *Vibrionaceae* bacterial load is conducted during the broodstock conditioning period, the spawning and brooding period, as well as during the larval phase. The maximum thresholds recommended in the water of the rearing tanks during these three phases are, respectively: 500 bacteria per mililitre, 500 bacteria per mililitre and 3 bacteria per *O. edulis* larvae.

The influence of aeration rate in rearing tanks on *O. edulis* embryos and larvae was investigated in Helm and Spencer (1972).

The influence of the ration, regime and diet of *O. edulis* larvae was investigated by Lane (1989), Millican and Helm (1994), Marshall *et al.* (2010), Acarli (2011), González-Araya (2012), Robert *et al.* (2017) and González-Araya and Robert (2018).

Metamorphosis

Settlement and metamorphosis are essential steps in hatchery production, which are regulated by external chemical factors and physical cues (Hadfield *et al.* 2001).

Larval mortalities occurring during settlement can be related to contamination, for example by bacteria (González-Araya *et al.* 2012b). *O. edulis* is susceptible to *B. ostreae* infection prior to metamorphosis. Larval survival of these early stages increases with reduced exposure of oyster larvae to external, contaminated environments and with usage of uninfected broodstock (Flannery *et al.* 2014; Flannery *et al.* 2016). As an alternative to the use of antibiotics in hatchery, new approaches to control bacterial infections were developed using probiotics (Prado *et al.* 2009). A low pH was also found to reduce bacterial growth and therefore increase the survival of veliger and pediveliger larvae (Prado *et al.* 2016).

The regulation of external factors allows high levels of competence and settlement. Robert *et al.* (2017) recommended a temperature of 25°C and a bispecific microalgal diet (*C. neogracile* and *T. lutea*) for survival rates of up to 99% and high settlement rates (68%).

Competent larvae can be induced to settle and metamorphose by functional analogues of the natural inducers. Several studies have been carried out testing these chemical analogues on flat oysters. GABA (Gamma aminobutyric acid) and epinephrine have been reported to improve larval settlement and metamorphosis under laboratory and hatchery conditions without affecting the survival of the

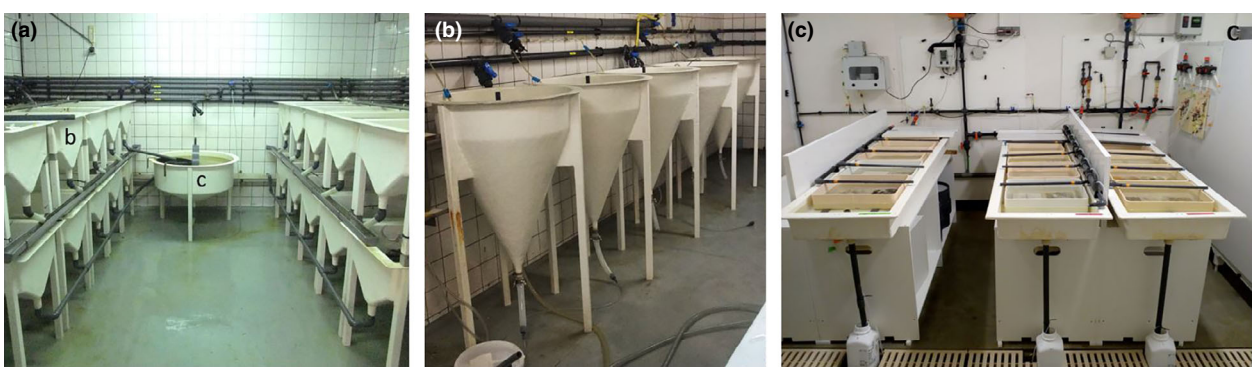

Figure 8 Yerseke Hatchery (a,b) and Argenton Hatchery (c): pictures of three phases of hatchery production. (a) Broodstock conditioning room with (b) the broodstock tanks and (c) the larval collection tank by overflow of water from the tanks (b). (b) Larval culture rooms with cylindrical-conical basins. (c) Larval settlement room with flat-bottomed sieves in three rearing tanks. Photographs from Bérenger Colsoul.

larvae (García-Lavandeira *et al.* 2005; Mesías-Gansbiller *et al.* 2013).

In aquaculture, for marketing reasons such as the appearance and shape of the shell (Mizuta & Wikfors 2018), mechanization, reduction of transport and operating costs; the production of cultchless spat was developed. Aside from the settlement of *O. edulis* larvae on micro-cultch, Hidu *et al.* (1975) have also investigated the use of polished marble in hatchery. Although Hidu reports that the substrate is very attractive for the larvae, a persistent problem of this technique is the survival of spat after their removal from the substrate and the damage the removal technique inflicts.

Remote setting

The marketing of eyed oyster larvae for subsequent settlement, also called remote setting, is a technique developed in the late 1970s on cupped oysters by American commercial hatcheries and introduced to Europe (France) in 1987. In 1989, 90% of oyster production on the west coast of the USA and in Canada came from seed produced by this technique (Guesdon *et al.* 1989). In Europe, remote setting was relevant for *C. gigas* production in the past; today, this technique is almost abandoned.

In France, Guesdon *et al.* (1989

), Carbonnier *et al.* (1990) and Coatanea *et al.* (1992) tested remote setting on flat oysters. Remote setting is a seed collection technique, controlled and carried out by producers in their facilities using eye larvae ready to settle that are provisioned by hatcheries. The principle of the method is therefore to split the work of hatcheries and producers, leaving hatcheries with the sole task of producing larvae.

The major potential interest in aquaculture is to obtain seed at a lower cost than from a hatchery by pre-growing the seed in a land-based structure. For restoration, the main interest here is the non-dependence on owning and operating a hatchery and the potential of growing larvae as early as possible in the water body of the respective restoration operation.

There are advantages and disadvantages of hatchery seed over wild seed. Here are some arguments in favour of hatchery seed: control of collection density per collector, control of breeding cycles (shift or shorten: season independence), control of homogeneity in size and distribution of seed on collectors, choice of collector or settlement substrate, selection of broodstock (e.g. allowing genetic selection or diversity) and potential control of pathogens and predators. The limitation of detaching operations for aquaculture purposes should also be considered: detaching can be mechanized on certain collector types and the use of cultch eliminates detaching.

The three studies indicate that remote setting is feasible but requires numerous optimizations, notably in larval transport and survival before obtaining a transferable protocol for seed producers. To this end, it is important to note that the influence of starvation on *O. edulis* larvae was investigated in the four following studies: Millar and Scott (1967), Holland and Spencer (1973), Robert *et al.* (1988) and Labarta *et al.* (1999). In addition, Millar and Scott (1967) reported that no mortality was observed in recently swarmed larvae for a period of several days.

A summary of these remote setting operations for *O. edulis* found in the above cited trials is provided in Appendix S5.

Conclusions

Ecological restoration of the European flat oyster has great potential in the frame of large-scale marine nature conservation initiatives. Restoration projects and programmes are being established in a number of European countries. Currently, the production of seed oysters (details on the terminology used are provided in Appendix S6) in both, high quality and quantity, presents a limiting factor (Pogoda *et al.* 2019). The existing knowledge on the biological background and current production technologies, relevant for successful production and tailored to the specific needs of restoration, are integrated here to provide implications for restoration, further challenges and open questions.

Implications for restoration and further challenges

As commercial production of *O. edulis* was driven by aquaculture demands so far, and has clearly shifted to *C. gigas* production in general, revived traditional techniques and modern approaches of sustainable production need to be synchronized, tested and developed to meet the demands of ecological restoration.

One notable example is the consideration of *O. edulis* seed production in breed polls in order to better understand the performance and potential future developments of this technique, both for ecological restoration and aquaculture. This particular technique, used only in Norway so far, should also be assessed in other regions. Next to breed polls, custom-built breeding ponds have many advantages and are gaining interest due to the new demands by restoration initiatives. The mechanization of livestock operations in accordance with the production-cost ratio as well as the monitoring and automated management of zootechnical parameters such as temperature will optimize and promote the application of breeding ponds. However, although their size is usually limited, the development of breed polls and breeding ponds may encounter limitations from environmental restrictions, limited appropriate sites

and constrained access to coastal areas. The variable success in seed production as well as the current intense work routine going along with these facilities also limits the interest in these systems by new producers. Breeding pond technique, although being successful and the focus of scientific research for 40 years, for example at the Conwy Fisheries Laboratory, was neglected in favour of hatchery production (Walne 1974; Spencer 2008). A comeback of this approach seems ecologically reasonable and should be encouraged.

Current hatchery production techniques still encounter knowledge gaps and challenges in broodstock management and the setting of optimum conditioning parameters. Further challenges include the choice of adult broodstock oysters. The implementation of selection programmes focusing on strains tolerant to specific diseases and adapted to site-specific environments on the one hand, and preserving a high genetic diversity of restored *O. edulis* populations on the other hand is of major importance (Pogoda *et al.* 2020; zu Ermgassen *et al.* 2020a).

In the past, declining oyster stocks were substituted by translocation or introduction of new stocks for fishery and aquaculture (Roché 1898; Korringa 1946; Bromley *et al.* 2016a). Ecological restoration of *O. edulis* is relatively recent and aims at ecosystem function and recovery. Major challenges related to genetic aspects are to avoid transfers of pathogens and diseases, to achieve sustainable survival rates and to retain a high genetic diversity (Hughes *et al.* 2008; Lallias *et al.* 2010).

Maintaining genetic diversity within the natural population, genetic improvement of a population facing low genetic diversity and the creation of a genetically diverse pool in the event of a reintroduction of the species are important aspects that have to be considered for seed oyster production (Gaffney 2006; Pogoda *et al.* 2019), for example via the joint development and implementation of best practice, involving research, conservation policy and industry. Seed production methods make a difference for the genetic diversity as described by Lallias *et al.* (2010) and resumed here: (i) Large-scale production techniques in breed polls and breeding ponds achieve an increased genetic diversity compared with hatcheries; (ii) In *Bonamia*-free areas, large-scale productions in breed polls and breeding ponds are therefore relevant technologies; (iii) In areas where bonamiosis is present, the use of resistant or tolerant strains is an important alternative.

In summary, the adaptation and improvement of hatchery and breeding pond techniques could increase genetic diversity in produced seed oysters (Saavedra 1997).

Open questions and proposed research topics

A number of open research questions remain to be addressed, both on the fundamental aspects of ecophysiology, as well as on the basic biology of oysters, focusing on the development of new applications for seed production:

(**1**) The sex determinism and the understanding of factors leading to sex change are still poorly understood. No research projects investigated the regulation or control of this reproduction phase. However, managing the sex ratio of broodstock is a relevant tool to increase *O. edulis* seed production.

(**2**) A deeper understanding of the mechanisms of gametogenesis would allow controlling or synchronizing the onset of gametogenesis. This would facilitate production planning in hatcheries, as well as the management of spawning and swarming periods in semi-controlled environments such as breeding ponds. In addition, a reliable protocol for induction of settlement, synchronization and successful metamorphosis should be provided.

(**3**) Cryopreservation of gametes and embryos is a promising technique for the development of oyster aquaculture and conservation of genetic resources in the near future, but the method needs to be investigated and established thoroughly. The use of cryopreserved gametes would require to develop artificial fertilization larval rearing methods.

(**4**) Further research on the role of alternative nutrition will clarify and define the impact of nanoplankton and picoplankton such as bacteria, detritus or dissolved organic matter, which seems to influence oyster growth, but has not been investigated in *O. edulis* so far.

(**5**) No commercial-scale selective breeding programme currently exists despite the possibility to select certain strains resistant to known pathogens, such as *B. ostreae*. Investigating the impact of different production systems of selected strains on the genetic variability of natural populations will be needed for the long-term success of oyster restoration in the future.

(**6**) Pathogens and diseases affecting *O. edulis* are numerous, and their ranges may shift in the future. Although many governmental and international regulations exist, transfers of marine invertebrates across Europe and the world as well as the transfer of substrate and seawater (ballast) still exist. Different climatic conditions will affect the spread and intensity of diseases. Respective consequences for *O. edulis* production need to be investigated.

(**7**) As sea-based seed collection is an important seed production technique, the effects of climate change on reproductive patterns and potential of wild populations should be evaluated further.

(8) Many aspect related to breeding pond production must be (re)investigated, for example why production in some ponds fail when adjacent ponds are successful.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Detailed methods for data search.

Appendix S2. List of the 602 publications selected and analysed (update 12.2019).

Appendix S3. Table of the breeding programme and production records from 1987 at Rossmore Breeding Ponds.

Appendix S4. Synthesis of chronological cryopreservation operations of *Ostrea edulis* sperm (spermatozeugmata) from Vitiello *et al.* (2011) and Horváth *et al.* (2012).

Appendix S5. Summary of remote setting operations for *Ostrea edulis* according (and translated in English) to Guesdon *et al.* (1989), Carbonnier *et al.* (1990) and Coatanea *et al.* (1992).

Appendix S6. Glossary of some terms used in this review.