Concept 1 – Biology and reproduction of oysters

Part of the AquaVitae MOOC reading material

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This course has received funding from the European Union's Horizon 2020 Research and Innovation Programme under Grant Agreement No 818173. This presentation reflects the views only of the authors, and the European Union cannot be held responsible for any use which may be made of the information it contains.

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Introduction

Oysters are two-shelled molluscs belonging to the class Bivalvia. In the Atlantic region the main oyster species of economic importance are the Pacific cupped oyster (*Magallana/Crassostrea gigas*) and the native European flat oyster (*Ostrea edulis*, in Europe), the mangrove oyster (*Crassostrea gasar*, in Brazil), and the Eastern oyster (*Crassostrea virginica*, in the US). The Pacific oyster originates from Japan but has been introduced to all continents except Antarctica for aquaculture purposes (Padilla 2010), and is now one of the most widely introduced marine invertebrates (Ruesink et al. 2005, Sousa et al. 2009).

Oysters are found in a wide range of habitats from sub-tidal areas (down to 40 m - *O. edulis*) to shallow, intertidal areas (e.g. *M. gigas* and *C. gasar*). Oysters can establish populations in a wide variety of habitat types, e.g. hard substrates, sandy or muddy areas, where they attach to small stones, shell fragments or other debris, or on conspecifics, forming reef-like structures at high densities, or on other bivalve species.

Each species has its own optimal environmental range in which its performance is optimized, and can survive only limited periods of time when the environmental conditions approach the species' critical tolerance limits. As an intertidal species, *M. gigas* is very tolerant to varying condition and has a very broad temperature range for survival, from sub-zero degrees to 30 C (Quayle 1969, Walne 1974, Le Gall & Raillard 1988, Bougrier et al. 1995, Diederich et al. 2005, Diederich 2006, Carrasco & Baron 2010, Strand et al. 2011). The optimal temperature for growth, however, ranges between 20-25 C (Pauley et al. 1988, Wiltshire 2007). Similarly, the tolerance level for salinity ranges between 2-42 ppt (Gunter & Geyer 1955, Pauley et al. 1988, Wiltshire 2007), but the optimal for growth is 15-35 (Gunter & Geyer 1955, Brown & Hartwick 1988, Pauley et al. 1988, Wiltshire 2007). Earlier life stages are more sensitive to temperature and salinity levels. Spawning will e.g. take place between 16-23 C and at salinities of 23-41 ppt (Ruiz et al. 1992, Mann 1979, Ruesink et al. 2005, Dutertre et al. 2010), and larvae has a tolerance limit of 15-30 C and 10-41 ppt (Pauley et al. 1988, Wiltshire 2007), with an optimum for growth at 20-28 C and 19-29 ppt (Nell & Holliday 1988, Wiltshire 2007).

Basic biology

The shape of the two shells of oysters are different, the bottom part is cup-shaped (left valve) while the top shell (right valve) is flat. The two shell sections are connected at a joint, the umbo, with ligaments (Galtsoff, 1964). The major anatomic components of oysters are illustrated in figure 1, and includes the mantle (located between the bulk of the animal and the shell), gills, labial palps, digestive gland and adductor muscle for closing the shell. The mantle is important for the growth of the shell as the epithelium at the mantle edge enables deposition of calcium carbonate present in the water column. The gills and labial palps are important for feeding and the digestive gland for processing the ingested food. The gonads are located between the mantle and the bulk of the animal but are only visible when the animal is in its reproductive stages. At maturity, the gonad covers the entire animal but with a greater concentration of gametes in the posterior region (close to the umbo). The reproductive system is relatively simple, and is basically composed of follicles (which contain the gametes), gonoducts (through which the gametes are expelled), epithelial tissue (forming the boundaries of the gonads), and connective tissue (binds the gonad together during early development and degenerates as maturation is enhanced). During spawning, gametes are released through the gonoducts to the mantle cavity (paleal cavity) and the gametes are expelled through the inhalant or exhalant region.

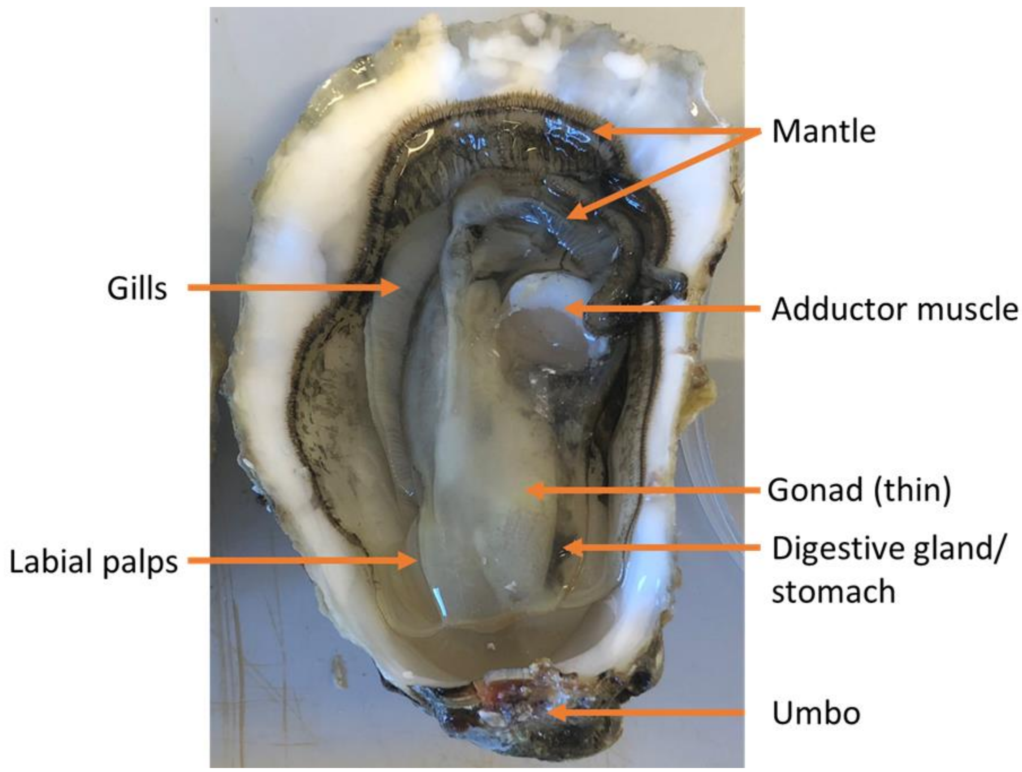


Figure 1. Illustration of histological characters of oysters.

Feeding of oysters

Oysters are filter-feeding organisms that feed on suspended particles in the water column. Their main food is microalgae, but particulate matter in suspension such as organic matter, debris and bacteria, as well as some zooplancton, are also part of their nutrition (Korringa 1952, Newell & Langdon 1996, Laing et al. 2005, Bayne 2017). The preferred size range of food particles for juvenile and adult oysters are 20–30 µm (Beecham 2008), but particles up to 400 µm can be ingested. Oyster larvae can catch food particles in the size range of 0.2 - 30 µm in diameter (Korringa 1952), depending on the larvae stage. An oyster can filter between 5 and 25 L of water per hour depending on size and ambient temperature (Korringa 1952).

The filtration process is a complex feeding mechanism. The beating of cilia on the gill filament creates a flow of water from the inhalant siphon, over the gills, and to the exhalant siphon. Particles transported with the water flow are captured by branchial filaments on the gills and moved to the labial palps where the particles are either accepted and directed to the mouth for ingestion or rejected and subsequently ejected in the form of pseudofeces (particles plus protein mucus). True feces (digested material which has passed through the digestive tract of the animal) are released at the dorsal region through the anus near the adductor muscle. Feces and pseudofeces produced by oysters are called biodeposits.

Life cycle and reproduction

Most oysters are gonochoric (they have separate sexes) and hermaphrodite. Hermaphroditism in bivalves can be subdivided into four types: i) functional hermaphrodite; ii) consecutive hermaphrodite; iii) consecutive rhythmic hermaphrodite; and iv) alternate hermaphrodite. For oysters, consecutive rhythmic hermaphroditism, where individuals have more than one sexual reversal in life, is the most relevant and is displayed both in the genus *Ostrea* (e.g *O. edulis*) and *Crassostrea*. For more information about these types, please refer to Gosling (2015) and Bayne (2017).

Oysters have two phases in their life cycle, one planktonic and one benthic. They reproduce sexually by forming gametes (oocytes and sperm), and have external fertilization. It is not possible to differentiate the sex of an oyster by examining the gonad color (as is possible for some mussel species) as there is no gender dimorphism in oysters. Some authors, however, report a higher incidence of male animals in younger oysters and a higher percentage of females in older oysters for *M. gigas* (Bayne 2017). It is also possible to tell female and male oysters apart during spawning as males release gametes through the exhaling region and females through the inhaling region using countercurrent.

__Stages of the reproductive cycle__

The reproductive cycle in bivalves can be divided into 4 stages: gametogenesis, pre-spawning, spawning and resting (Sühnel et al. 2010, Legat et al. 2021, Figure 2). Gametogenesis is the stage where germ cells start to develop in the follicles wall. Once germ cells are formed, the gamete maturation process proceeds until the gametes are ready to be released (pre-spawning). When gametes are mature and are expelled to the external environment, spawning has occurred. After spawning the animal enters into the resting stage during which absorption of remaining gametes in the gonad happens, followed by glycogen accumulation as an energy source for the next reproductive cycle, which again starts with gametogenesis. During unfavorable conditions, individuals can also regress from pre-spawning to resting without going through the spawning stage.

Macroscopically animals in the gametogenesis stage have low meat quantity and slightly creamy color (Figure 2). Granules can be visible in the gonad. In the pre-spawning stage, the animals are full, heavier than during the gametogenesis stage, with a lot of meat. The gonad can be full of gametes and often has an intense creamy color. During spawning the animals lose weight and the meat is more translucent and watery, especially when the animals spawn almost all gametes. At the start of the resting stage (absorption phase) the animals have a flaccid and translucent appearance, changing to a full animal with a lot of meat at the glycogen accumulation phase. In the resting stage, the glycogen accumulation can make the meat taste sweeter, an appreciated trait by consumers.

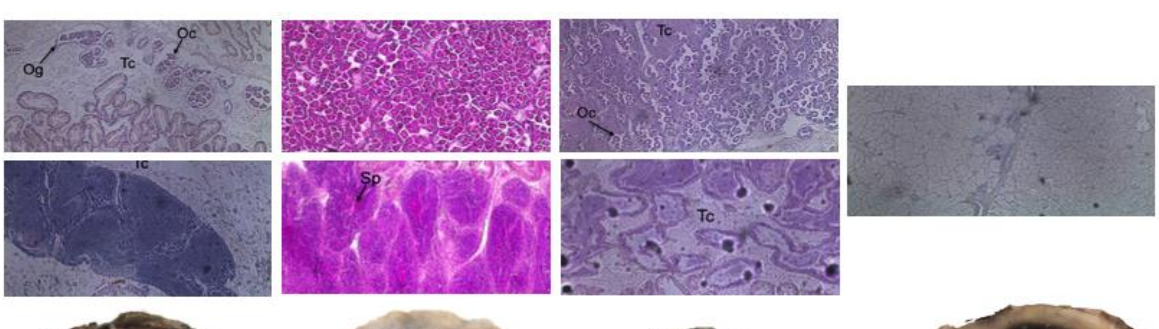


Figure 2. Illustration of the reproductive cycle of oysters by histology (top) and macroscopically (bottom). The first row of the histology illustration represent females and the bottom row with histology illustrations represent males. Histology image from Legat et al. (2021) and adult oyster image from Simone Sühnel personal files.

What affects the reproductive cycle?

The reproductive cycle in bivalves is affected by endogenous and exogenous factor e.g. temperature, photoperiod, salinity and food availability (Fabioux et al. 2005, Dridi et al. 2007, Normand et al. 2008, Gosling, 2015) and consequently vary on both spatial and temporal scales (Enríquez-Díaz et al. 2009, Dutertre et al. 2009). Endogenous factors are e.g. neuroendocrine cycles and genotypes. Recently, steroid hormones such as testosterone, estradiol and progesterone have been identified as being important components involved in the processes of oogenesis, spermatogenesis and spawning (Gosling 2015). Related to exogenous factors, there is evidence that the onset of gametogenesis in temperate environments is largely controlled by temperature (Mann 1979, Fabioux et al. 2005. Gosling, 2015, Bayne, 2017), and temperate oyster populations demonstrate rapid gonadal proliferation when temperatures begin to rise after a cold period inducing a resting stage (Ruiz et al. 1992, Kobayashi et al. 1997, Chavez-Villaba et al. 2002). In tropical conditions, however, where temperatures remain stable through the year, spawning normally occurs year-round (Mackie, 1984), and all stages of the reproductive cycle can be observed simultaneously in one animal (although in different parts of the gonad). Little is known about the controlling factors affecting spawning of species in tropical regions, however salinity has been suggested to act as an exogenous factor affecting the reproductive cycle (Gosling, 2015), especially in tropical regions where salinity shows a large variation while temperature remains stable over the year (Legat et al. 2021). Moreover, the nutritional status of animals, which is directly linked to the availability of food (an exogenous factor), can affect the reproductive cycle of bivalves (Gosling 2015).

Spawning and larval development and settlement

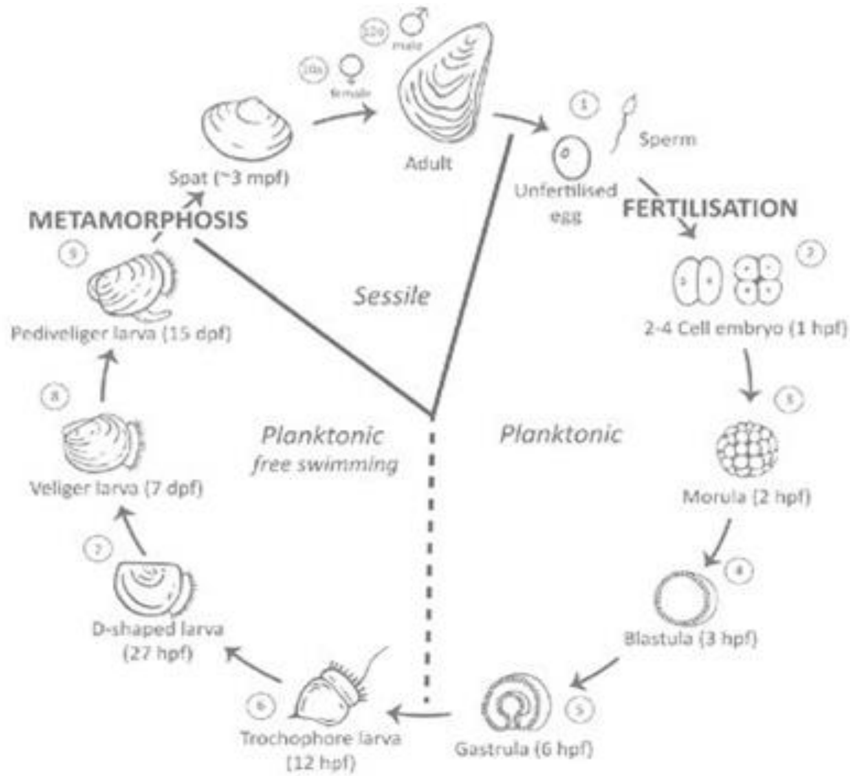
For most species the female and male gametes are released into the water, where fertilization takes place and a planktonic larvae is formed (Figure 3B). Oysters of the genus *Ostrea* represents an exception to this mode of external fertilization, as the females capture sperm (clusters of sperm released by males) after which fertilization occurs in the females paleal cavity and the larvae develop on the females gills until they reach the veliger stage (Figure 3A).

During development the fertilized eggs develop into trochophore larvae, D larvae, veliger larvae and finally pediveliger larvae (Figure 2). The pediveliger larvae has developed a small foot, which is used to explore the surroundings in search for a suitable settlement substrate. Larvae swim freely in the water column for much of the larval phase, but as they approach the end of the larval phase, feeding activity slows and the larvae spend an increasing period of time towards the bottom. This marks the beginning of metamorphosis, a critical stage in development during which extensive mortalities can occur. Successful transformation and survival to the juvenile form is dependent on a number of factors, not least of which is the availability of energy reserves accumulated during the larval phase. Factors affecting larval development and growth will be discussed in concept 2 – hatchery production of oysters.

In the initial stage of metamorphosis, larvae begin to drop out of the water column onto the substrate, crawl around using their foot and search the surface for a suitable place to settle. If the surface is unsuitable they will move off or swim away and seek a more suitable location. This process can be repeated several times and metamorphosis can be delayed for some time if a suitable surface is not found. Once a suitable substrate is found, oyster larvae cement to the substrate and metamorphosis is triggered. It remains unknown what factors trigger the transition but type of substrate along with physical, chemical and biological cues are important. In hatcheries, epinephrine can be used to trigger metamorphosis without substrate (i.e. cultch - crushed oyster shells), to produce individual oyster. In the settlement phase, oysters can also settle on shells, forming an aggregation of oysters on a shell. This is called a cluster. Considerable morphological and physiological changes occur in the animal at this time as it changes from a swimming larva to a settled spat. Once settled, oysters cannot detach and relocate and are consequently stationary.

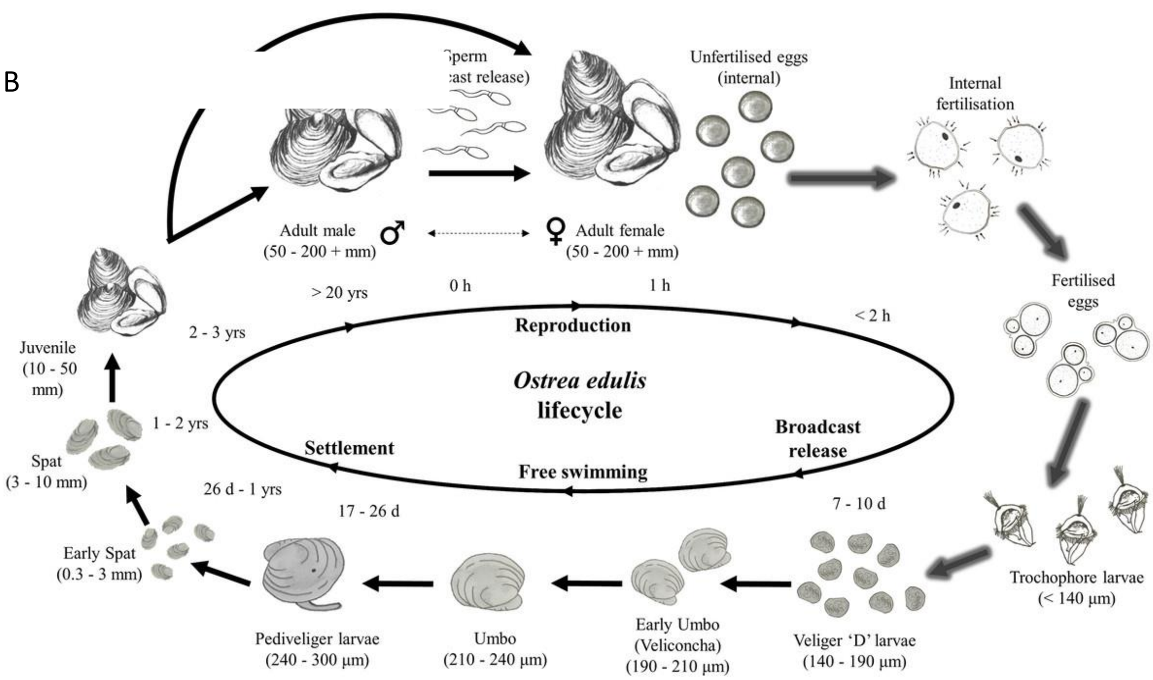
As the seed grows, it becomes first an immature oyster, called spat or seed, that has not yet started the reproductive cycle, and subsequently progres into juvenile and later an adult (mature animal) that starts the reproductive cycle. When the transition from juvenile to adult occurs is affected both by species, but is also affected by the animal's growth, which in turn depends on the temperature, salinity and food availability. This will be discussed further in the concept 4 - Grow-out of oysters.

A



Adult
Sperm
Unfertilised egg
FERTILISATION
2-4 Cell embryo (1 hpf)
Morula (2 hpf)
Blastula (3 hpf)
Gastrula (6 hpf)
Trochophore larva (12 hpf)
D-shaped larva (27 hpf)
Veliger larva (7 dpf)
Pediveliger larva (15 dpf)
METAMORPHOSIS
Spat (~3 mpf)
Sessile
Planktonic free swimming
Planktonic

B



Unfertilised eggs (internal)
Internal fertilisation
Adult male (50 - 200 + mm)
Adult female (50 - 200 + mm)
Fertilised eggs
Trochophore larvae (< 140 µm)
Veliger 'D' larvae (140 - 190 µm)
Early Umbo (Veliconcha) (190 - 210 µm)
Umbo (210 - 240 µm)
Pediveliger larvae (240 - 300 µm)
Early Spat (0.3 - 3 mm)
Spat (3 - 10 mm)
Juvenile (10 - 50 mm)
> 20 yrs
0 h
1 h
< 2 h
2 - 3 yrs
1 - 2 yrs
26 d - 1 yrs
17 - 26 d
7 - 10 d
Reproduction
Ostrea edulis lifecycle
Broadcast release
Free swimming
Settlement

Figure 3. Illustration of the life cycle of Pacific oysters (top figure, A, figure from Vogeler et al. 2016) and oysters in the genus *Ostrea* (bottom figure, B, figure from Helmer et al. 2019).

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