



An Overview of the Life Cycle, Reproduction and Factors Influencing Recruitment Success of Tropical Oysters

Joanna W. Doinsing¹ and Julian Ransangan^{2*}

1. Politeknik Sandakan Sabah, Education Hub, Batu 10, Jalan Sungai Batang, 90000 Sandakan, Malaysia.

2. Borneo Marine Research Institute, Universiti Malaysia Sabah, 88400 Jalan UMS, Kota Kinabalu, Sabah, Malaysia.

*Corresponding Author: liandra@ums.edu.my

ARTICLE INFO

Article History:

Received: June 13, 2021

Accepted: Feb. 19, 2022

Online: May 2, 2022

Keywords:

Early embryonic development,
Larval development,
Sex determination,
Gametogenesis,
Settlement,
Climate change

ABSTRACT

The aquaculture of tropical oysters is a valuable prospective seafood industry. The extremely rapid growth rates of tropical oysters make them attractive to aquaculture candidates. Hence, fundamental knowledge of the biology, life cycle, reproduction and factors affecting recruitment is essential for the successful aquaculture development of these species. This paper attempted to provide an overview of the current knowledge of early embryonic and larval development, and the factors affecting the sex determination, gametogenesis, settlement, and the recruitment success of tropical oysters, as well as the effects of climate change on the recruitment success. Closed culture, stock restocking, stock enhancement, and sea ranching are among the efforts that can be implemented to boost the recruitment success of these valuable species.

INTRODUCTION

Oysters have long been recognized as species of recreational and commercial importance (Pollack *et al.*, 2013). They are one of the most valuable edible molluscs belonging to the family Ostreidae, order Ostreoida, class Bivalvia, in the phylum of Mollusca (Turgeon *et al.*, 1988; Fakhrina *et al.*, 2018). In tropical countries, tropical oyster is one of the attractive species for aquaculture candidate (Chen *et al.*, 2013; Mazón-Suástegui *et al.*, 2017; FAO, 2018). Its alluring feature is due to its exceptionally rapid growth rates, in which many obtain market size (7 to 11 cm) in less than a year (Joseph, 1998; Nowland *et al.*, 2020).

In Malaysia, oyster is one of the favorite shellfishes that has become a constant part of Malaysians' annual food cycle (Nor Idayu *et al.*, 2015), with the highest production in

the year 2009 (2128.20 tonnes) (DOF, 2018). Ng (1979) reported that in Malaysia, there are four genera of oysters and their respective species, namely: *Crassostrea* (*C. belcheri* and *C. iredalei*) currently accepted as *Magallana* (*M. belcheri* and *M. bilineata*); *Saccostrea* (*S. echinate* and *Saccostrea* spp); *Ostrea* (*O. folium*) currently accepted as *Dendostrea* (*D. folium*); and *Hyotissa* (*H. hyotis*). Of all the species in Malaysia, *M. bilineata* and *M. belcheri* have demonstrated aquaculture potential and are highly demanded in markets compared to other local oyster species, viz. *S. cucullata* and *D. folium* (Ng *et al.*, 1982; Zulfigar & Tan, 2000).

The successful cultivation of oysters depends mainly on the good source of natural spats (NAOO, 2018), hence the recruitment event by natural local spatfall. Oyster production in Malaysia has remained stagnant since 2009 (2128.20 ton), with only a one-year sharp rise in 2017 (1402.24 tons) (DOF, 2018). The oyster production was then reduced to 455.22 ton in 2018 (DOF, 2018). The inadequate supply of seeds is one of the reasons the oyster industry in Malaysia is unable to take off completely (Tan *et al.*, 2014). The understanding of the reproduction and overall factors affecting sex determination, gametogenesis, settlement, and recruitment success of oysters is valuable to improve the success rate of reproduction and the production of oysters. Hence, this paper attempted to review the current knowledge of life cycle, reproduction and factors influencing the recruitment success of tropical oysters.

LIFE CYCLE AND REPRODUCTION

1. Embryonic Development

Oysters can attain sexual maturity when they reach 50 to 80mm in shell size, and internally, the gonadal tissue of sexually matured oysters exhibits creamy-white in color (Rosell, 1990; Fakhрина *et al.*, 2018). A germinal epithelium produces gametes within a web of follicles enveloped by connective tissue (Bayne, 2017). The mature eggs and sperm pass through the gonoducts to the genital canal before being discharged into the mantle cavity (Bayne, 2017). *Ostrea* and *Crassostrea*, the two genera of oysters, exhibit distinct spawning patterns (Naik & Gowda, 2015). In *Ostrea*, the discharged eggs from the ovary are retained in the mantle cavity while the sperms are released into the water column (Naik & Gowda, 2015). Whereas in *Crassostrea*, both eggs and sperms are subjected to a sequence of rhythmic adductor muscle contractions, resulting in the gametes being discharged into the surrounding water via the mantle's exhalant opening (Naik & Gowda, 2015; Bayne, 2017).

The fertilization of oysters begins with the chance encounters of eggs and sperms (Naik & Gowda, 2015). In *Ostrea*, the eggs are fertilized by sperms from outside the shell, and the larval life takes place partially inside the shell before being released into the surrounding waters, but in *Crassostrea*, fertilization occurs in the water column (Naik & Gowda, 2015; Maathuis *et al.*, 2020). The size, timing and morphology of various

embryonic developmental stages are summarized in Table (1). Once inseminated by sperm, the fertilized egg becomes spherical, bursting out the germinal vesicle covering the egg yolk to form a zygote (Nor Idayu *et al.*, 2015).

Upon successful fertilization, the first polar body developed at the beginning of 3 to 10 minutes for *C. iredalei* and 10 to 25 minutes for *C. cucullata* (Nor Idayu *et al.*, 2015; Syafriadiman, 2017). *C. iredalei* germinated the second polar body with a 1 μ m-thick vitelline coat in approximately 5 to 10 minutes, followed by cell divisions from 2-cell to 4-cell, 16-cell, 32-cell to 64-cell in approximately 10 to 20 minutes (Nor Idayu *et al.*, 2015). In contrast, cell divisions in *C. cucullata* occurred in 30 to 80 minutes following fertilisation (Syafriadiman, 2017). Within 3 hours of fertilisation, most *C. iredalei* embryos reached the morula stage and began to rotate before further developing to free-swimming ciliated blastula covered with microvilli (Nor Idayu *et al.*, 2015). In 16 to 18 hours of fertilisation, *C. iredalei* embryo differentiated into an active oval trochophore measuring about 45.42 to 48.30 μ m (Nor Idayu *et al.*, 2015). On the other hand, *C. cucullata* embryos develop into the gastrula stage within 2 to 3 hours of fertilization, followed by the trochophore stage with larvae size measuring about 53 \pm 4 μ m within 6 to 10 hours (Syafriadiman, 2017). In the trochophore stage, larvae begin to swim with the aid of cilia crowned at the apical organ (anterior sections) and long flagellum (Fakhrina *et al.*, 2018).

2. Larval Development

Table (2) presents the size, timing, and morphology of various larval developmental stages. In 24 hours, both *Crassostrea iredalei* and *C. cucullata* larvae fully developed a shell called prodissoconch I, which was secreted as a unit by the shell gland (Fig. 1) (Bussarawit & Cedhagen, 2012; Syafriadiman, 2017). These veliger larvae are known as D-shaped larvae because of the distinctive "D" shape of the shell valves (Laing & Bopp, 2018). The outside surface of the valves was smooth, with the dorsal margin of the hinge forming a straight line and a rounded ventral margin (Bussarawit & Cedhagen, 2012). The anterior end was slightly rounded off compared to the posterior (Bussarawit & Cedhagen, 2012). These translucent, densely granulated larvae have a well-developed velum covered with small cilia that serve as swimming and feeding organs (Gosling, 2015; Nor Idayu *et al.*, 2015; Hamli *et al.*, 2019).

The fully shelled D-larva grows fast in the subsequent stage and develops into circular and knobby umbonate veliger, or veliconco, as its mantle secretes additional shell material to form a second larval shell called prodissoconch II. This process occurred between days 5 and 13 for *C. iredalei* and between days 6 and 21 for *C. cucullata* (Fig. 1) (Bussarawit & Cedhagen, 2012; Gosling, 2015; Nor Idayu *et al.*, 2015; Syafriadiman, 2017). The prodissoconch II exhibits a sharp bordered from prodissoconch I and has concentric growth lines (Bussarawit & Cedhagen, 2012; Gosling, 2015). At this point,

the larvae move vertically by the velum facing down and the umbo area at the top (Nor Idayu *et al.*, 2015).

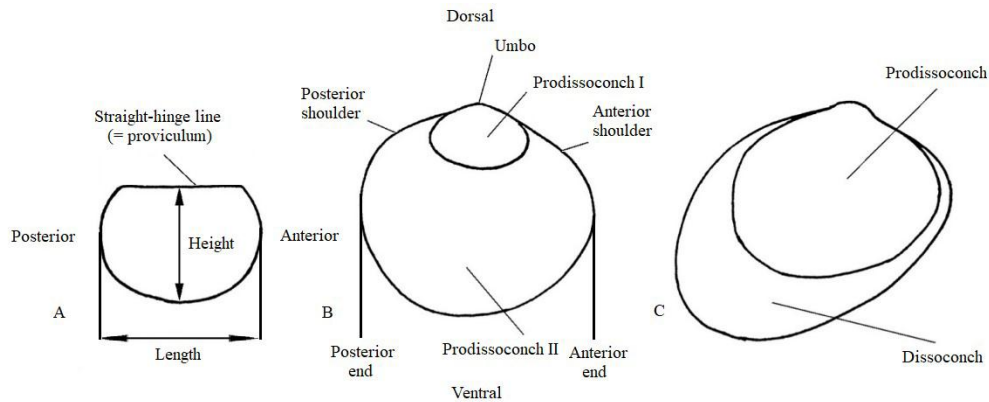


Fig. 1. The different stages of an oyster. **A.** Veliger larva, also known as a D-shaped larva or a straight-hinge larva. **B.** Veliconcha made up of prodissoconch I and prodissoconch II. **C.** Prodissoconch (P) and dissoconch (D) in the early bottom-living stage. Adapted and modified from Rees (1950) and Bussarawit and Cedhagen (2012).

For *C. iredalei*, the stage of eye larvae begins on day 12 to day 16 with the formation of a small dark circular dot at the base of the gill rudiment (Nor Idayu *et al.*, 2015; Fakhrina *et al.*, 2018). However, for *C. cucullata*, there was no record of the time this stage occurred (Syafriadiman, 2017). At this point, the development of the internal organ, the stomach, the digestive tract, and the adductor muscle is evident through the transparent shell, and the larvae move vertically upward, beating the velum quickly and downwards, slowing down the ciliary motion (Nor Idayu *et al.*, 2015). Foot (pseudopod), anterior muscle adductor, and gill rudiment are developed in the shell though not yet fully functional (Nor Idayu *et al.*, 2015). This stage marks the start of competent larvae ready for settlement (Laxmilatha *et al.*, 2011; Nor Idayu *et al.*, 2015; Rodriguez-perez *et al.*, 2019).

At the pediveliger level, larvae developed the functional pseudopod and gills with brown colouration formed along shell edges (Nor Idayu *et al.*, 2015; Fakhrina *et al.*, 2018). The pediveliger larvae are capable of swimming with the velum and crawling with foot-like appendages besides its external cilia (Nor Idayu *et al.*, 2015; Perrino & Ruez Jr., 2019). As the velum became smaller, the foot became more developed (Syafriadiman, 2017). Pediveliger larvae are now transformed from free-swimming pelagic larvae to crawling plantigrades, searching for a suitable hard substrate for settlement (Gosling, 2003; Nor Idayu *et al.*, 2015; Ramadhaniaty *et al.*, 2018). The time for the occurrence of plantigrade for *C. iredalei* was not recorded, whilst the time for the occurrence of plantigrade for *C. cucullata* was recorded from day 24 to day 26 (Nor

Idayu et al., 2015; Syafriadiman, 2017). The postlarval shell of the bottom-living stage after metamorphosis is called dissoconch (Fig. 1) (**Bussarawit & Cedhagen, 2012**). Dissoconch has a distinct texture with concentric growth lines and is usually sharp bordered by the metamorphic line from prodissoconch (Fig. 2) (**Bussarawit & Cedhagen, 2012**). In this stage, fasciole can be seen running from the posterior end of prodissoconch I through prodissoconch II in the left valve and into a small emargination at the posterior margin of the larval shell, and a complementary sulcus also appears on the posterior aspects of the right valve (Fig. 2) (**Bussarawit & Cedhagen, 2012**).

During settlement, plantigrade secreted a small drop of cement from the byssal gland in the pseudopod on the found suitable substrate (**Nor Idayu et al., 2015; Fakhrina et al., 2018**). Once settled, larvae metamorphosed into a spat on day 16 onwards and continued until day 21 for *C. iredalei* and day 25 to day 30 for *C. cucullata* by disintegrating pseudopod and velum (**Nor Idayu et al., 2015; Syafriadiman, 2017; Fakhrina et al., 2018**). In the spat stage, labial palps appeared, and gills were fully developed (**Nor Idayu et al., 2015**).

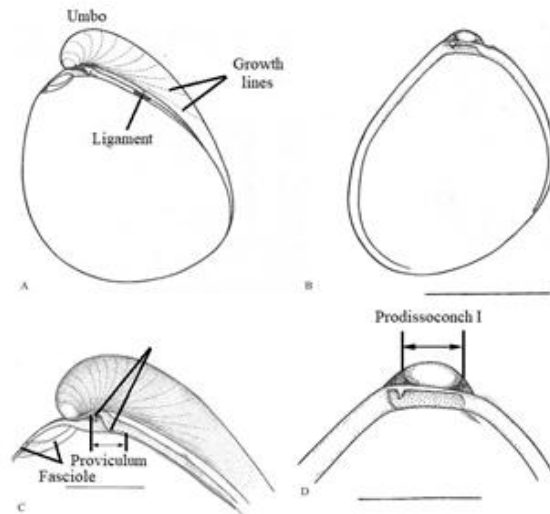


Fig. 2. Terminology used to describe oyster larvae. Adapted and modified from **Bussarawit and Cedhagen (2012)**.

FACTORS AFFECTING RECRUITMENT SUCCESS

1. Sex Determination

Sex ratio, gametogenesis in adults (fecundity) are essential for long term population success (Fig. 3). Sex determination describes the development of individual sex characteristics and is thus inextricably linked to the population's sex ratio (**Coralie et al., 2020**). Sex determination, its following sex ratios and reproductive capacity will have

flow-on effects on larval supply and population size of oysters (**Parker *et al.*, 2018**). For example, a decrease in the number of females would indirectly reduce the supply of offspring, which may affect recruitment into the population (**Chávez-Villalba *et al.*, 2011**; **Thomas *et al.*, 2014**; **Parker *et al.*, 2018**). On the contrary, a decrease in the number of males may limit the number of mates, and a reduction in either sex may limit the population's genetic diversity resulting in population bottlenecks and inability to adapt to change (**Chávez-Villalba *et al.*, 2011**; **Parker *et al.*, 2018**).

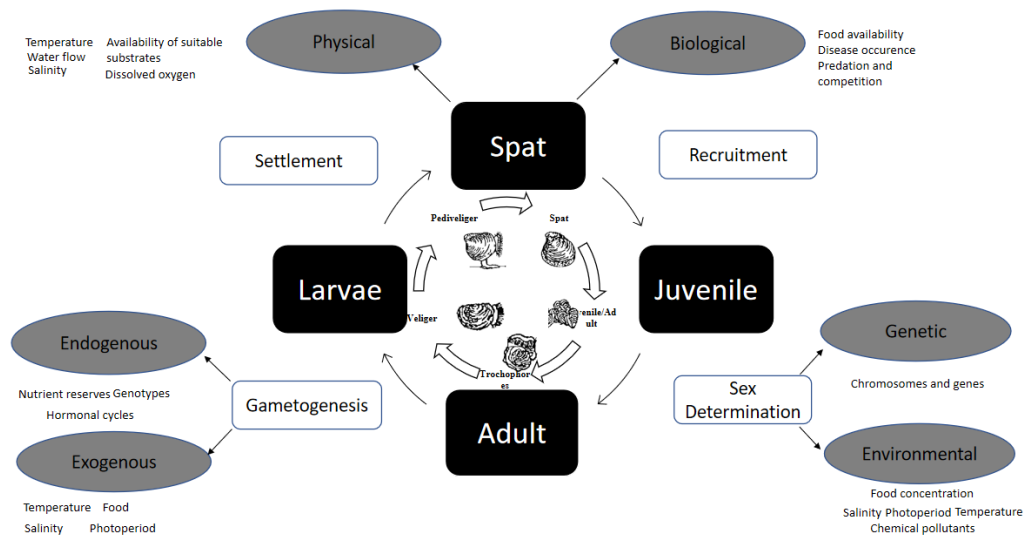


Fig. 3. Summary of the factors affecting sex determination, gametogenesis, settlement, and recruitment of oysters (Photos adopted from **Wallace *et al.* (2008)**).

In many marine organisms, sex is determined at or before conception and remains either male or female throughout their lives (**Charnov & Bull, 1977**; **Parker *et al.*, 2018**). Nevertheless, in oysters, sex determination in these species is influenced by either genetic and environmental variables or by the interaction of both (**Hedrick & Hedgecock, 2010**; **Santerre *et al.*, 2013**). The sex determining mechanisms are remarkably diverse for many species of bivalves, ranging from strict dioecy or gonochorism (individual exists as either male or female), simultaneous hermaphroditism (individual functions male and females at the same time) or sequential hermaphroditism (individuals exist as one sex and then switch to the other sex) (**Breton *et al.*, 2018**; **Parker *et al.*, 2018**). The sexuality of oysters is typically referred to as protandric hermaphroditism that matures in early life as males and transitions to females in later years (**Guo *et al.*, 1998**; **Parker *et al.*, 2018**).

Studies have shown that sex is primarily governed by a single locus model with a dominant male allele (M) and a protandric recessive female allele (F), which resulted in FM oysters as permanent males that do not change sex and FF genotypes oysters as

protandric females, that are capable of changing sex (Guo *et al.*, 1998; Dove & O'Connor, 2012). A combination of secondary genes and environmental factors such as temperature, salinity, food concentration, photoperiod, as well as chemical pollutants are believed to influence the rate of sex change of these protandric females (Saout *et al.*, 1999; Andrew *et al.*, 2010; Chávez-Villalba *et al.*, 2011; González-Araya *et al.*, 2013; Santerre *et al.*, 2013; Gomes *et al.*, 2014; Teaniniuraitemoana *et al.*, 2016). Some evidences suggest that males predominate when the environment is less favourable, and females would be preferentially found in a rich environment (Steele & Mulcahy, 1999, Chávez-Villalba *et al.*, 2011).

2. Factors Influencing Gametogenesis

The reproductive cycle of bivalves is influenced by the complex interaction of exogenous factors such as water temperature, food, photoperiod, salinity and endogenous factors such as hormonal cycles and genotypes (Gosling, 2015; Maneiro *et al.*, 2017). Water temperature and food availability are the two most important factors affecting gametogenesis (Bernard *et al.*, 2011; Ezgeta Balić *et al.*, 2020), with water temperature influencing gonad maturation and food boosting fertility, gamete quality and larval survival (Utting & Millican, 1997; Li *et al.*, 2011; Vaschenko *et al.*, 2013; Teaniniuraitemoana *et al.*, 2016). There is evidence to show that gametogenesis is positively correlated with temperature, as observed in a field experiments on *Crassostrea gasar* by Gomes *et al.* (2014), Castilho-Westphal *et al.* (2015) and Legat *et al.* (2021), as well as laboratory experiment by Ramos *et al.* (2014).

For populations with a similar temperature regime, like tropical species, the food supply, nutrient reserves in bivalves directly support gonadal development and reproductive cycle (Giese, 1969; Gabbott, 1975; Li *et al.*, 2011). Bivalves are usually classified as either conservative or opportunist, based on the relationship between nutrient reserves and gonad development cycles (Bayne, 1976). Conservative bivalves rely on their stored nutrient reserves, whereas opportunistic bivalves use energy from available food for gonadal development (Asaduzzaman *et al.*, 2020).

In contrast to the relatively stable water temperature regimes, tropical oysters are frequently exposed to large and rapid variations in salinity throughout the monsoonal wet season (Nowland *et al.*, 2019). This period of extensive freshwater run-off is commonly coupled with an increase in phytoplankton and is thought to be responsible for reproduction in tropical oysters (Angell, 1986; Nowland *et al.*, 2019). It has been demonstrated by Paixão *et al.* (2013) that during periods of high rainfall and low salinity, the number of mature individuals increased, while during the months of low rainfall and high salinity, they discovered oysters in the spawning stage. Additionally, Gomes *et al.* (2014) reported that *Crassostrea gasar* conditioned in salinity 24 developed much more gonadal tissue than oysters conditioned in salinity 34.

Photoperiod is another crucial factor, though to a lesser extent, that affect the reproductive cycle of bivalves (Saout *et al.*, 1999). Previous study showed that the gametogenic cycle of bivalves could be influenced by coupled modifications of temperature and photoperiod (Saout *et al.*, 1999; Fabioux *et al.*, 2005). There is further evidence to support these hypotheses. Habekorn *et al.* (2010) reported that the increase of temperature and daylight hours allowed oysters to develop from early gametogenesis to a large portion of mature gonads within one month.

Evidence from other studies found that fluctuations of sex steroids such as testosterone, estrogen and progesterone are related to sexual maturation cycles in some bivalves' species, indicating the importance of sex steroids on reproduction (Croll & Wang 2007; Gosling, 2015). It has been experimentally demonstrated that the injection of the estrogenic compound in the oyster *Crassostrea gigas* stimulated vitellogenesis (Li *et al.*, 1998; Gosling, 2015). This fact is supported by the findings that exposure to an estrogenic compound in *Saccostrea glomerata* can aid in the transition of protandric males from male-intersex-female gametal state, in addition to increasing vitellogenesis (Andrew *et al.*, 2010).

3. Factors Affecting Settlement and Recruitment Success

The recruitment success of oysters depends on abiotic and biotic variables. The abiotic variables include water temperature, salinity, dissolved oxygen, water flow conditions, availability of suitable settlement substrate, and the biotic variables include food availability, disease occurrence, predation and competition with other organisms for space and resources (Kennedy, 1986; Camp *et al.*, 2015; Gosling, 2015). Amid these, water temperature and salinity signify two vital ecological variables affecting the embryonic and larval development of the tropical oyster (Nowland *et al.*, 2019).

Tropical oyster larvae live in relatively temperature stable habitats, in contrast to temperate oyster species, which undergo large water temperature changes (Nowland *et al.*, 2019). Peck *et al.* (2014) demonstrated that tropical invertebrates were less resistant to temperature increase than temperate species. When compared to temperate species, tropical oysters may have narrower ranges of water temperature tolerance as a result (Nowland *et al.*, 2019). In contrast, the large and rapid salinity fluctuations during the monsoonal wet season make the prediction of optimum salinity for many tropical oyster species difficult (Nowland *et al.*, 2019). Several prior studies on the independent effects of water temperature and salinity on the larvae of tropical oyster species have been published (Tan & Wong, 1996, Xu *et al.*, 2011; Huo *et al.*, 2014). However, research on the interactive effects of water and temperature on the larvae of tropical oyster species is limited. According to an earlier study of Coeroli *et al.* (1984), an optimum temperature of 29°C and a salinity of 20-30 psu were observed for *Saccostrea echinate* larval growth. Additionally, Lemos *et al.* (1994) recommended an optimum temperature of 30°C and a salinity of 25-35 psu for better larval development of *Crassostrea rhizophorae*.

With the intensity and frequency of hypoxic occurrences in the coastal marine systems, it is critical to understand the role of hypoxia in structuring coastal ecosystems (**Diaz & Rosenberg, 1995; Lenihan & Peterson, 1998**). For bivalves, the hypoxic occurrences can be operationally classified as moderate hypoxia ($4 \text{ mg L}^{-1} \geq \text{O}_2 \geq 2 \text{ mg L}^{-1}$), severe hypoxia ($2 \text{ mg L}^{-1} \geq \text{O}_2 \geq 0.5 \text{ mg L}^{-1}$), and anoxia ($< 0.5 \text{ mg L}^{-1}$) (**Renaud, 1986; Diaz & Rosenberg, 1995; Turner *et al.*, 2005**). It has been shown in **Baker and Mann (1992)** that hypoxia could inhibit recruitment. **Johnson *et al.* (2009)** verified this by demonstrating that the longer an oyster larva is exposed to moderate hypoxia, the less likely it is to be successfully recruited to the habitat. This could be a strategy used by oyster pediveliger larvae to reduce energy-intensive activities, decreasing oxygen use in oxygen-limiting environments (**Widdows *et al.*, 1989; Baker & Mann, 1992**).

Settlement success is dependent on larvae's ability to land, attach and metamorphose rapidly to avoid being washed away by fluid stresses or being moved to areas where they can be buried by sediment (**Turner *et al.*, 1994; Jonsson *et al.*, 2004, Fuchs *et al.*, 2007**). **Abelson and Denny (1997)** suggested that water flow could influence settlement through one or more of these three ways: the flow may affect the encounter between larvae and the substratum, or their post-encounter behaviours or both by exerting hydrodynamic forces on settling larvae; the flow may provide a settlement cue that triggers the active behaviour of motile larvae; the flow may mediate numerous settlement cues, such as sediment load, attractants' concentration and light intensity. Previous evidence showed that oysters preferred decreased wave action areas (**Ortega, 1981; Abbe, 1986**) and low-flow conditions (**Bushek, 1988**). This theory is backed up by the evidence in **Whitman and Reidenbach (2012)**, who reported that larger larval aggregations were observed near the down current sides of roughness components with low-flow zones.

The settlement of oyster larvae is primarily determined by the availability of suitable settlement substrates (**Marshall & Dunham, 2013; Smyth *et al.*, 2018; Preston *et al.*, 2020**). Oyster larvae are known to exhibit active substrate selection (**Turner *et al.*, 1994, Zimme-Faust & Tamburri, 1994**). Oyster larvae select appropriate settlement locations based on local hydrodynamics (**Fredriksson *et al.*, 2010; Koehl & Hadfield, 2020**). If their first landing site is unsuitable, they can release themselves back into the flow and test the next substrate they encounter (**Soniat *et al.*, 2004; Fuchs *et al.*, 2007**). Conflicting results have been reported in the literature concerning factors determining the settlement. **Smyth *et al.* (2018)** have suggested that the availability of hard substrate rather than its type determined the settlement, whereas others have argued instead that the properties of the hard substrates are crucial determinants for oyster settlement (**Preston *et al.*, 2020; Smyth *et al.*, 2020**). A report published in **Powell *et al.* (2018)** suggested that the presence of live or box dead oysters, with articulated shells is key for recruitment in several oyster species.

The availability of suitable food is suggested to be important for oyster larvae growth and settling (**Devakie & Ali, 2000; Robert *et al.*, 2017**). A positive correlation between larval development and food availability has been experimentally proven; however, above $1500 \mu\text{m}^3 \mu\text{L}^{-1}$, larva growth stagnates (**Robert *et al.*, 2017**). Another study by **Devakie and Ali (2000)** reported that larval settlement increased with increased food density up to $100 \times 10^3 \text{mL}^{-1}$ cells, but the settlement was reduced at the higher food density.

In addition, post-settlement mortality caused by the "enemies" can also affect recruitment success (**Baggett *et al.*, 2014**). The oyster's "enemies" can be categorized into four groups: the parasites, the competitors, the predators and the harmful alga bloom (HABs) (**Fujiya, 1970**). The types of "enemies" that could cause harm to oysters vary widely with culture techniques and surrounding waters (**Arakawa, 1990**). The most evident harm to intensive farming methods involving submersions in the water, such as raft hanging and long line culture, is from competitors with similar feeding habits such as mussels (*Mytilus* spp. and *Brachiodontes* sp.), tunicates, sponges and barnacles (**Arakawa, 1990; Leblanc *et al.*, 2003**). At the same time, bottom-dwelling predators such as oyster drills (murices, naticids) and starfish are the most visible harm to farms, involving natural reproduction and sowing techniques or the rack hanging practices in shallow water regions or on sea floors (**Fujiya, 1970; Arakawa, 1990**). Parasites such as protozoan (*Perkinsus beihaiensis*) and metazoan (*Polydra* sp.) are commonly seen to infest oysters cultured by both techniques (**Arakawa, 1990; Suja *et al.*, 2020**). In addition to mass mortalities, HABs are known to cause acute to chronic physiological and pathological alterations that lead to impediments to aquaculture farms through reduction of the bivalve fitness or following the closure of production due to long term contamination with toxins detrimental to human health (**Basti *et al.*, 2019**).

4. Effects of Climate Change on Recruitment Success

The effects of climate change on the global ocean have been reported worldwide (**Doney *et al.*, 2012**). Climate change has already begun to influence the environment. More is on the way: temperature rises, sea level rises, ocean acidification, changes in rainfall and hence salinity, and nutrients concentration and quality (**Philippart *et al.*, 2011**).

The effects of climate change, particularly rising water temperatures and ocean acidity, have had and will also continue to impact oyster populations. Rising water temperature is reported to affect marine organism's survival, growth, reproduction, health, and phenology (**Doney *et al.*, 2012**). Warming could cause changes in the primary production, food web structure and function and, as a result, alters in life cycle processes such as shellfish spat fall and physiological stressors that contribute to lower growth and production (**Allison *et al.*, 2011**). A study by **Compton *et al.* (2007)** found that warming water temperatures will significantly influence the survival, distribution, and productivity

of tropical rather than the temperate shellfish species, resulting in a future shift to culture species in aquaculture farms.

Carbon dioxide (CO₂) emissions from human activity have resulted in an unprecedented increase in the level of atmospheric CO₂ (**Chan *et al.*, 2012**). The ocean absorbs one-third of this CO₂, a process known as "ocean acidification" (**Zeebe *et al.*, 2008**). This excess CO₂, which lowers the pH, is detrimental to oyster fertilisation and embryonic development and results in heterogeneous-sized D-larvae with varying degrees of impairment (**Kurihara *et al.*, 2007**; **Dineshram *et al.*, 2012**; **Thiyagarajan & Ko, 2012**; **Barros *et al.*, 2013**). The decrease in the pH of surface waters will also concurrently lower CO₃²⁻ and the degree of CaCO₃ saturation in the surface waters, causing difficulties for marine calcifying organisms such as oysters in forming calcareous (CaCO₃) structures (skeletons and shells) (**Chan *et al.*, 2012**). Delayed larval growth (e.g., calcification) exposes them to predators for an extended period, making them more vulnerable to physiological disorders such as metabolic energy deficiency, weakened metabolism and protein synthesis (**Talmage & Gobler, 2009**; **Thiyagarajan & Ko, 2012**).

Additionally, changes in temperature, irradiance, the chemical composition of seawater, nutrients, water stratification, grazing pressures, phytoplankton species, and strain interactions caused by climate change are likely to alter the prevalence and toxicity of HAB (**Wells *et al.*, 2015**). The prevalence and toxicity of HAB, in turn, affect shellfish's behaviour and physiology and its aquaculture activities (**Basti *et al.*, 2019**).

EFFORTS TO ENHANCE THE RECRUITMENT SUCCESS

"Recruitment limitation" is common among tropical marine animals (**Battaglione & Bell, 2004**). Even when there are plenty of reproducing adults, the natural supply of juveniles falls short of the habitat's carrying capacity (**Battaglione & Bell, 2004**). For example, in shellfish, pelagic larvae may die in large numbers due to insufficient food or they are washed away by currents from coral reefs, preventing successful settlement and resulting in post-settlement predation (**Battaglione & Bell, 2004**).

Closed culture, stock restocking, stock enhancement and sea ranching attempt to rectify this situation by supplying as many juveniles as the habitat can carry (**Munro & Bell, 1997**; **Doherty, 1999**). In closed culture, broodstock progeny are grown to maturity in a closed system before being used as broodstock for the next generations (**Grant *et al.*, 2017**). In captive propagation for conservation, it is a common practice to make every attempt in preventing domestication so that wild individuals retain their genetic identity (**Grant *et al.*, 2017**). Individuals in commercial culture, on the other hand, are often selectively bred for traits that increase hatchery yield (**Grant *et al.*, 2017**), which often

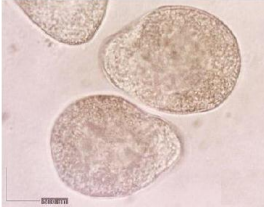
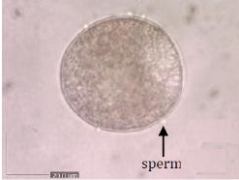
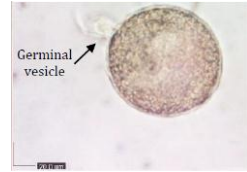
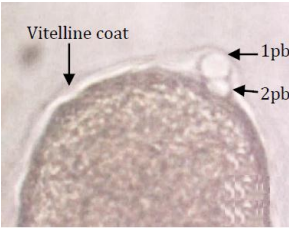
results in the effect of escaped cultured individuals on the wild populations (**Waples *et al.*, 2012; Karlsson *et al.*, 2016**).

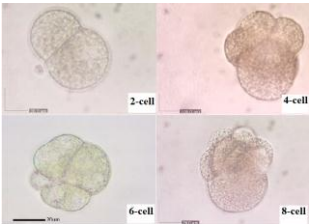



Restocking involves releasing cultured juveniles into a natural habitat to replenish significantly the reduced spawning biomass above pre supplementation levels (**Bartley & Bell, 2008**). On the other hand, stock enhancement is intended to optimise harvests by supplementing the natural supply of juveniles to overcome recruitment limitations (**Doherty, 1999; Bell *et al.*, 2005; Lorenzen, 2005; Munro & Bell, 2008**). Sea ranching involves releasing juveniles reared in hatcheries into open coastal environments for subsequent harvest at the adult stage in "put, grow and take" operations with no intention of allowing released juveniles to supplement spawning biomass, as in restocking, or to improve year classes, as in stock enhancement (**Bartley & Bell, 2008**).

CONCLUSION

Recruitment of oysters with a complex life cycle, in which externally fertilised eggs produce the pelagic larval stage that progresses to a sessile benthic life, includes larval availability, survivorship through early life, settlement to the benthos, as well as the the growth and survival of newly settled individuals. The successful recruitment of tropical oysters is generally influenced by abiotic factors such as temperature, salinity and substrate availability and biotic factors such as food availability, predation, diseases, parasites, and competition. However, the detailed effects of these parameters on tropical oysters' recruitment success are still poorly understood. Further research is needed to gain more information on how these parameters affect the reproduction of tropical oysters. Closed culture, restocking, stock enhancement and sea ranching may be used to improve oyster recruitment with the consideration of the high cost of implementation and the significant ecological and genetic threats to its wild counterpart.


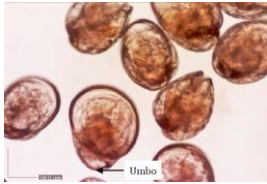
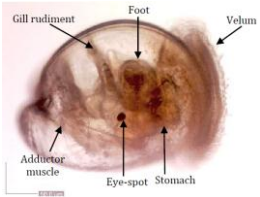
Table 1. Egg Development of tropical oyster. Adapted and modified from **Nor Idayu *et al.* (2015)** and **Syafriadiman (2017)**.




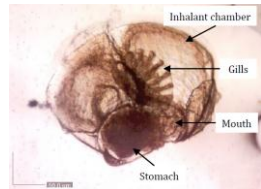
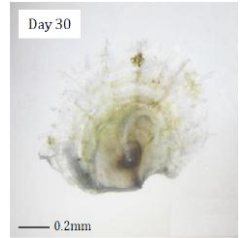
Stage	<i>C. iredalei</i> (<i>M. bilineata</i> *) (Nor Idayu <i>et al.</i> , 2015).		<i>C. cucullata</i> (<i>Saccostrea cucullata</i> *) (Syafriadiman, 2017).		Morphology
	Size (µm)	Time after fertilisation	Size (µm)	Time after fertilisation	
Unfertilised egg	-	-	45±4	-	 <p>Unfertilized egg in tear-drop shaped.</p>
Fertilised egg	-	-	-	-	 <p>Egg surrounded by sperm.</p>  <p>Burst of germinal vesicle after insemination.</p>
1 st pb	45-50	3-10m	45±4	10-25m	 <p>1st and 2nd polar body covered with vitelline coat.</p>
2 nd pb		5-10m	-	-	

2 to 32-cell	10-20m	1 st cleavage: 46±5	30-50m	 <p>2-cell, 4-cell, 6-cell and 8-cell.</p>
		2 nd cleavage: 47±2	48-60m	
		3 rd cleavage: 49±2	65-75m	
		4 th cleavage: 50±8	76-80m	
Morula	2-3hr	-	-	 <p>Rotating morula consisting of 16 or more cell with a mulberry appearance.</p>
Blastula	3-5hr	-	-	 <p>Free-swimming ciliated blastula</p>
Gastrula		51±3	2-3hr	
Trochophore	16-18hr	53±4	6-10hr	 <p>Oval-shaped trochophore with several bands of cilia.</p>

*Currently accepted name.

Table 2. Larval Development of tropical oyster. Adapted and modified from **Nor Idayu *et al.* (2015)** and **Syafriadiman (2017)**.

Stage	<i>C. iredalei</i> (<i>M. bilineata</i> *) (Nor Idayu <i>et al.</i> , 2015).		<i>C. cucullata</i> (<i>Saccostrea cucullata</i> *) (Syafriadiman, 2017).		Morphology
	Size (µm)	Time after fertilisation	Size (µm)	Time after fertilisation	
Veliger larvae in D-shaped	63-77	D1-5	57±7	D1	 <p>Translucent and densely granulated D-shaped larvae with well-developed velum.</p>
Umbo	74-251	D5-12	62-188	D6-21	 <p>Vertically moved circular and knobby umbone.</p>
Eye-spot	144-267	D12-16			 <p>Appearance of small dark circular dot at the base of gill rudiment.</p>

Pediveliger	195-350	D12-16	222±28	D20-23	 	<p>Pediveliger with gill rudiment.</p> <p>Pediveliger with foot.</p>
Plantigrade			265±29	D24-26		<p>Transformation from free-swimming pelagic larvae to crawling benthic stage.</p>
Spat	490>	D16>	359±62	D25-30	 	<p>Metamorphosed spat functional gills (velum and foot disintegrated).</p> <p>Spat at 30 days old.</p>

*Currently accepted name.

ACKNOWLEDGEMENTS

This research work was financially supported by the Postgraduate Research Grant (GUG0439-1/2020) from the Universiti Malaysia Sabah.

REFERENCES

- Abbe, G.R.** (1986). A review of some factors that limit oyster recruitment in Chesapeake Bay. *Am. Malacol. Bull.*, 3: 59–70.
- Abelson, A. and Denny, M.** (1997). Settlement of marine organisms in flow. *Annu. Rev. Ecol. Syst.*, 28: 317–339.
- Allison E.H.; Badjek M.C. and Meinhold K.** (2011). The implications of global climate change for molluscan aquaculture. In Shumway, S. E. (Ed.), *Shellfish Aquaculture and the Environment*. John Wiley & Sons Ltd, Chichester, pp. 461-490.
- Andrew, M.N.; O'Connor, W.A.; Dunstan, R.H. and MacFarlane, G.R.** (2010). Exposure to 17 α -ethynylestradiol causes dose and temporally dependent changes in intersex, females and vitellogenin production in the Sydney rock oyster. *Ecotoxicology*, 19: 1440–1451. <https://doi.org/10.1007/s10646-010-0529-5>.
- Angell, C.L.** (1986) *The Biology and Culture of Tropical Oysters*. ICLARM Stud. Rev., Vol. 13. International Centre for Living Aquatic Resources Management, Manila, Philippines.
- Arakawa, K.Y.** (1990). Competitors and fouling organisms in the hanging culture of the pacific oyster, *Crassostrea gigas* (Thunberg). *Mar. Behav. Phys.*, 17(2): 67–94. <https://doi.org/10.1080/10236249009378759>.
- Asaduzzaman, M.; Akter, S.; Hoque, N.F.; Shakil, A.; Noor, A.R.; Akter, M.N. and Rahman, M.M.** (2020). Multifaceted linkages among eco-physiological factors, seasonal plankton dynamics and selective feeding behavior of the green mussel (*Perna viridis*) in the south-east coast of the Bay of Bengal. *J. Sea Res.*, 164: 101933. <https://doi.org/10.1016/j.seares.2020.101933>.
- Baggett, L.P.; Powers, S.P., Brumbaugh, R.; Coen, L.D.; DeAngelis, B.; Greene, J.; Hancock, B. and Morlock, S.** (2014). *Oyster Habitat Restoration Monitoring and Assessment Handbook*. Nature Conservancy, Arlington VA, USA, 96pp.
- Baker, S.M. and Mann, R.L.** (1992). Effects of hypoxia and anoxia on larval settlement, juvenile growth, and juvenile survival of the oyster *Crassostrea virginica*. *Biol. Bull.*, 182(2): 265–269. <https://doi.org/10.2307/1542120>.

- Barros, P.; Sobral, P.; Range, P.; Chícharo, L. and Matias, D.** (2013). Effects of sea-water acidification on fertilisation and larval development of the oyster *Crassostrea gigas*. *J. Exp. Mar. Biol. and Ecol.*, 440: 200-206. <https://doi.org/10.1016/j.jembe.2012.12.014>.
- Bartley, D.M. and Bell, J.D.** (2008). Restocking, stock enhancement, and sea ranching: Arenas of progress. *Rev. Fish. Sci.*, 16(1–3): 357–365. <https://doi.org/10.1080/10641260701678058>.
- Basti, L.; Nagai, K.; Segawa, S.; Tanaka, Y.; Suzuki, T. and Nagai, S.** (2019). Harmful algal blooms and shellfish aquaculture in changing environment. *Bull. Jpn. Fish. Res. Educ. Agency*, 49: 73–79.
- Battaglione, S.C. and Bell, J.D.** (2004). The restocking of sea cucumbers in the Pacific Islands. In: Bartley, D.M. and Leber, K.M. (Eds.), *Marine Ranching*. FAO Fish. Tech. Pap., pp. 109-132.
- Bayne, B.L.** (1976). Aspects of reproduction in bivalve molluscs. In: Wiley, M. (Ed.), *Estuarine Processes 1*. Academic Press, pp. 432–448. <https://doi.org/10.1016/B978-0-12-751801-5.50043-5>.
- Bayne, B.L.** (2017). Reproduction, In: *Biology of Oysters*. Academic Press, Vol. 41, pp. 565–701. <https://doi.org/10.1016/B978-0-12-803472-9.00009-1>.
- Bell, J.D.; Rothlisberg, P.C.; Munro, J.L.; Loneragan, N.R.; Nash, W.J.; Ward, R. D. and Andrew, N.L.** (2005). Restocking and stock enhancement of marine invertebrate fisheries. *Adv. Mar. Biol.*, 49: 1–370.
- Bernard, I.; De Kermoisan, G. and Pouvreau, S.** (2011). Effect of phytoplankton and temperature on the reproduction of the Pacific oyster *Crassostrea gigas*: Investigation through DEB theory. *J. Sea Res.*, 66(4): 349-360. <https://doi.org/10.1016/j.seares.2011.07.009>.
- Breton, S.; Capt, C.; Guerra, D. and Stewart, D.** (2018). Sex-determining mechanisms in bivalves. In: Leonard, J. (ed.), *Transitions Between Sexual Systems*. Springer, Cham, pp. 165-192. https://doi.org/10.1007/978-3-319-94139-4_6.
- Bushek, D.** (1988). Settlement as a major determinant of intertidal oyster and barnacle distributions along a horizontal gradient. *J. Exp. Mar. Biol. and Ecol.*, 122: 1–18. [https://doi.org/10.1016/0022-0981\(88\)90208-0](https://doi.org/10.1016/0022-0981(88)90208-0).
- Bussarawit, S. and Cedhagen, T.** (2012). Larvae of commercial and other oyster species in Thailand (Andaman Sea and Gulf of Thailand). *Steenstrupia*, 32(2): 95–162.

- Camp, E.V.; Pine III, W.E.; Havens, K.; Kane, A.S.; Walters, C.J.; Irani, T.; Lindsey, A.B. and Morris Jr, J.G.** (2015). Collapse of a historic oyster fishery: diagnosing causes and identifying paths toward increased resilience. *Ecol. Soc.*, 20(3): 45. <http://dx.doi.org/10.5751/ES-07821-200345>.
- Castilho- Westphal, G.G.; Magnani, F.P. and Ostrensky, A.** (2015). Gonad morphology and reproductive cycle of the mangrove oyster *Crassostrea brasiliiana* (Lamarck, 1819) in the baía de Guaratuba, Paraná, Brazil. *Acta Zool.*, 96(1): 99-107. <https://doi.org/10.1111/azo.12055>.
- Chan, V.B.S.; Li, C.; Lane, A.C.; Wang, Y.; Lu, X.; Shih, K.; Zhang, T. and Thiagarajan, V.** (2012). CO₂-driven ocean acidification alters and weakens integrity of the calcareous tubes produced by the serpulid Tubeworm, *Hydroides elegans*. *PLoS ONE*, 7(8): e42718. <https://doi.org/10.1371/journal.pone.0042718>.
- Charnov, E.L. and Bull, J.** (1977). When is sex environmentally determined? *Nature*, 266(5605): 828–830.
- Chávez-Villalba, J.; Soye, C.; Huvet, A.; Gueguen, Y.; Lo, C. and Le Moullac, G.** (2011). Determination of gender in the pearl oyster *Pinctada margaritifera*. *J. Shellfish Res.*, 30(2): 231–240. <https://doi.org/10.2983/035.030.0206>.
- Chen, T.P.; Chang, T.; Chiau, W. and Shih, Y.** (2013). Social economic assessment of coastal area industrial development: An application of input-output model to oyster farming in Taiwan. *Ocean Coast. Manage.*, 73: 153–159. <https://doi.org/10.1016/j.ocecoaman.2012.12.007>.
- Coeroli, M.; De Gaillande, D. and Landret, J.P.** (1984). Recent innovations in cultivation of molluscs in French Polynesia. *Aquaculture*, 39(1-4): 45-67. [https://doi.org/10.1016/0044-8486\(84\)90258-8](https://doi.org/10.1016/0044-8486(84)90258-8).
- Compton, T.J.; Rijkenberg, M.J.; Drent, J. and Piersma, T.** (2007). Thermal tolerance ranges and climate variability: a comparison between bivalves from differing climates. *J. Exp. Mar. Biol. Ecol.*, 352(1): 200-211. <https://doi.org/10.1016/j.jembe.2007.07.010>.
- Coralie, B.; Anne-sophie, M.; Elise, M.; Jean-baptiste, L. and Lionel, D.** (2020). Sex determination in the oyster *Crassostrea gigas*: A large longitudinal study of population sex ratios and individual sex changes. *Aquaculture*, 515: 734555.
- Croll, R.P. and Wang, C.** (2007). Possible roles of sex steroids in the control of reproduction in bivalve molluscs. *Aquaculture*, 272(1-4): 76-86. <https://doi.org/10.1016/j.aquaculture.2007.06.031>.

- Devakie, M.N. and Ali, A.B.** (2000). Salinity-temperature and nutritional effects on the setting rate of larvae of the tropical oyster, *Crassostrea iredalei* (Faustino). *Aquaculture*, 184: 105–114. [https://doi.org/10.1016/S0044-8486\(99\)00312-9](https://doi.org/10.1016/S0044-8486(99)00312-9).
- Diaz, R.J. and Rosenberg, R.** (1995). Marine benthic hypoxia: A review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanogr. Mar. Biol., Annu. Rev.*, 33: 245-303.
- Dineshram, R.; Wong, K.K.; Xiao, S.; Yu, Z.; Qian, P. Y. and Thiyagarajan, V.** (2012). Analysis of Pacific oyster larval proteome and its response to high-CO₂. *Mar. Pollut. Bull.*, 64(10): 2160-2167. <https://doi.org/10.1016/j.marpolbul.2012.07.043>.
- DOF (Department of Fisheries Malaysia)** (2018). Annual fisheries statistic 2009-2018. Available at: [https://www.dof.gov.my/dof2/resources/user_29/Documents/Perangkaan Perikanan/2018 Jilid 1/Table_akua_2018_-new.pdf](https://www.dof.gov.my/dof2/resources/user_29/Documents/Perangkaan%20Perikanan/2018%20Jilid%201/Table_akua_2018_-new.pdf), accessed [14-01-2021].
- Doherty, P.J.** (1999). Recruitment limitations as the theoretical basis for stock enhancement in marine populations. In Howell, B.R.; Moksness, E. and Svasand, T. (Eds.), *Stock Enhancement and Sea Ranching*. Fishing News Books a Blackwell Publishing Company, Oxford, pp. 9–21.
- Doney, S.C.; Ruckelshaus, M.; Duffy, J.E.; Barry, J.P.; Chan, F.; English, C.A.; Galindo, H.M.; Grebmeier, J.M.; Hollowed, A.B.; Knowlton, N.; Polovina, J.; Rabalais, N.N.; Sydeman, W.J. and Talley, L.D.** (2012). Climate change impacts on marine ecosystems. *Annu. Rev. Mar. Sci.*, 4: 11–37. <https://doi.org/10.1146/annurev-marine-041911-111611>.
- Dove, M.C. and O'Connor, W.A.** (2012). Reproductive cycle of Sydney rock oysters, *Saccostrea glomerata* (Gould 1850) selectively bred for faster growth. *Aquaculture*, 324–325: 218–225. <https://doi.org/10.1016/j.aquaculture.2011.10.022>.
- Ezgeta Balić, D.; Radonić, I.; Bojanić Varezić, D.; Zorica, B.; Arapov, J.; Stagličić, N.; Jozić, S.; Peharda, M.; Briski, E.; Lin, Y. and Šegvić-Bubić, T.** (2020). Reproductive cycle of a non-native oyster, *Crassostrea gigas*, in the Adriatic Sea. *Mediterr. Mar. Sci.*, 21(1): 146-156. <https://doi.org/10.12681/mms.21304>.
- Fabioux, C.; Huvet, A.; Le Souchu, P.; Le Pennec, M. and Pouvreau, S.** (2005). Temperature and photoperiod drive *Crassostrea gigas* reproductive internal clock. *Aquaculture*, 250: 458–470. <https://doi.org/10.1016/j.aquaculture.2005.02.038>.

- Fakhrina, M.N.; Christianus, A. and Ehteshamei, F.** (2018). Production of tropical oyster seed in hatchery. *J. Surv. Fish. Sci.*, 5(1): 7–19. <https://doi.org/10.18331/SFS2018.5.1.2>.
- FAO.** (2018). The state of world fisheries and aquaculture 2018: Meeting the sustainable development goals. FAO Fisheries and Aquaculture Department, Rome, Italy.
- Feely, R.A.; Orr, J.; Fabry, V.J.; Kleypas, J.A.; Sabine, C.L. and Langdon, C.** (2009). Present and future changes in seawater chemistry due to ocean acidification. *Geophys. Monogr. Ser.*, 183: 175-188. <https://doi.org/10.1029/2005GM000337>.
- Fredriksson, D.W.; Steppe, C.N.; Wallendorf, L.; Sweeney, S. and Kriebel, D.** (2010). Biological and hydrodynamic design considerations for vertically oriented oyster grow out structures. *Aquac. Eng.*, 42(2): 57-69. <https://doi.org/10.1016/j.aquaeng.2009.11.002>.
- Fuchs, H.L.; Neubert, M.G. and Mullineaux, L.S.** (2007). Effects of turbulence-mediated larval behavior on larval supply and settlement in tidal currents. *Limnol. Oceanogr.*, 52(3): 1156-1165. <https://doi.org/10.4319/lo.2007.52.3.1156>.
- Fujiya, M.** (1970). Oyster farming in Japan. *Helgoländer Wiss. Meeresunters.*, 20: 464–479.
- Gabbott, P.A.** (1975). Storage cycles in marine bivalve molluscs: A hypothesis concerning the relationship between glycogen metabolism and gametogenesis. In Barnes, H. (Ed.), *Proceedings of Ninth European Marine Biology Symposium*. Aberdeen University Press, Aberdeen, pp. 191-211.
- Giese, A.C.** (1969). A new approach to the biochemical composition of the mollusk body. *Oceanogr. Mar. Biol.*, 7: 175–229.
- Gomes, C.H.A.M.; Silva, F.C.; Lopes, G.R. and Melo, C.M.R.** (2014). The reproductive cycle of the oyster *Crassostrea gasar*. *Braz. J. Biol.*, 74(4): 967–976. <https://doi.org/10.1590/1519-6984.04912>.
- González-Araya, R.; Quillien, V. and Robert, R.** (2013). The effects of eight single microalgal diets on sex-ratio and gonad development throughout European flat oyster (*Ostrea edulis* L.) conditioning. *Aquaculture*, 400: 1-5. <https://doi.org/10.1016/j.aquaculture.2013.02.036>.
- Gosling E.** (2003). *Bivalve Molluscs*. Fishing News Books, Blackwell Publishing, p. 443.

- Gosling, E.** (2015). Reproduction, settlement and recruitment. Marine Bivalve Molluscs, Second Edition. John Wiley and Son, Ltd., pp. 157-202.
- Grant, W.S.; Jasper, J.; Bekkevold, D. and Adkison, M.** (2017). Responsible genetic approach to stock restoration, sea ranching and stock enhancement of marine fishes and invertebrates. *Rev. Fish Biol. Fish.*, 27: 615–649. <https://doi.org/10.1007/s11160-017-9489-7>.
- Guo, X.; Hedgecock, D.; Hershberger, W. K.; Cooper, K.; Allen, S.K.; Guo, X.; Hedgecock, D.; Hershberger, W.K.; Cooper, K. and Jr., S.K.A.** (1998). Genetic determinants of protandric sex in the Pacific oyster, *Crassostrea gigas* Thunberg. *Evolution*, 52(2): 394–402.
- Haberkorn, H.; Lambert, C.; Le Goïc, N.; Guéguen, M.; Moal, J.; Palacios, E.; Lassus, P. and Soudant, P.** (2010). Effects of *Alexandrium minutum* exposure upon physiological and hematological variables of diploid and triploid oysters, *Crassostrea gigas*. *Aquat. Toxicol.*, 97(2): 96-108. <https://doi.org/ff10.1016/j.aquatox.2009.12.006>.
- Hamli, H.; Idris, M.H.; Hena, M.K.A. and Rajae, A.H.** (2019). Fisheries assessment, gametogenesis and culture practice of local bivalve: A review. *Pertanika J. Trop. Agric. Sci.*, 42(1): 103-124.
- Hedrick, P.W. and Hedgecock, D.** (2010). Sex determination: genetic models for oysters. *J. Hered.*, 101(5): 602-611. <https://doi.org/10.1093/jhered/esq065>.
- Huo, Z.; Wang, Z.; Liang, J.; Zhang, Y.; Shen, J.; Yao, T.; Su, J. and Yu, R.** (2014). Effects of salinity on embryonic development, survival, and growth of *Crassostrea hongkongensis*. *J. Ocean Univ. China*, 13(4): 666-670. <https://doi.org/10.1007/s11802-014-2206-4>.
- Johnson, M.W.; Powers, S.P.; Senne, J. and Park, K.** (2009). Assessing in situ tolerances of eastern oysters (*Crassostrea virginica*) under moderate hypoxic regimes: implications for restoration. *J. Shellfish Res.*, 28(2): 185-192. <http://dx.doi.org/10.2983/035.028.0202>.
- Jonsson, P.R.; Berntsson, K.M. and Larsson, A.I.** (2004). Linking larval supply to recruitment: flow-mediated control of initial adhesion of barnacle larvae. *Ecology*, 85(10): 2850-2859. <https://doi.org/10.1890/03-0565>.
- Joseph, M.M.** (1998). Mussel and oyster culture in the tropics. In: De Silva, S.S. (Ed.), *Tropical Mariculture*. Academic Press, pp. 309-360.

- Karlsson, S.; Diserud, O.H.; Fiske, P. and Hindar, K.** (2016). Widespread genetic introgression of escaped farmed Atlantic salmon in wild salmon populations. *ICES J. Mar. Sci.*, 73(10): 2488–2498. <https://doi.org/10.1093/icesjms/fsw121>.
- Kennedy, V.S.** (1986). Expected seasonal presence of *Crassostrea virginica* (Gmelin) larval populations, emphasising Chesapeake Bay. *Am. Malacol. Bull., Spec. Ed.*, 3: 25–29.
- Koehl, M.A.R. and Hadfield, M.G.** (2010). Hydrodynamics of larval settlement from a larva's point of view. *Integr. Comp. Biol.*, 50(4): 539-551. <https://doi.org/10.1093/icb/icq101>.
- Kurihara, H.; Kato, S. and Ishimatsu, A.** (2007). Effects of increased seawater pCO₂ on early development of the oyster *Crassostrea gigas*. *Aquat. Biol.*, 1(1): 91-98.
- Laing, I. and Bopp, J.J.** (2009). Oysters: Shellfish farming. *Encyclopedia of Ocean Sciences*, 3rd Edition. Academic Press, Oxford, pp. 274-286.
- Laxmilatha, P.; Rao, G.S.; Patnaik, P.; Rao, T.N.; Rao, M.P. and Dash, B.** (2011). Potential for the hatchery production of spat of the green mussel *Perna viridis* Linnaeus (1758). *Aquaculture*, 312(1-4): 88-94. <https://doi.org/10.1016/j.aquaculture.2010.12.031>.
- Leblanc, A.R.; Landry, T. and Miron, G.** (2003). Fouling organisms of the blue mussel *Mytilus edulis*: Their effect on nutrient uptake and release. *J. Shellfish Res.*, 3(3): 633–638. <https://doi.org/10.2983/035.029.0302>.
- Legat, J.F.A.; Puchnick- Legat, A.; Sühnel, S.; Pereira, A.L.M.; Magalhães, A.R.M. and de Melo, C.M.R.** (2021). Reproductive cycle of the mangrove oyster, *Crassostrea gasar* (Adanson, 1757), in tropical and temperate climates. *Aquac. Res.*, 52(3): 991-1000. <https://doi.org/10.1111/are.14954>.
- Lemos, M.B.N.; Nascimento, I.A.; De Araujo, M.M.S.; Pereira, S.A.; Bahia, I. and Smith, D.H.** (1994). The combined effects of salinity, temperature, antibiotic and aeration on larval growth and survival of the mangrove oyster, *Crassostrea rhizophorae*. *J. Shellfish Res.*, 13(1): 187-192.
- Lenihan, H.S. and Peterson, C.H.** (1998). How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyster reefs. *Ecol. Appl.*, 8(1): 128-140.
- Li Q.; Osada, M.; Suzuki, R.; Mori, K.** (1998). Changes in vitellin during oogenesis and effect of estradiol 17-β on vitellogenesis in the Pacific oyster *Crassostrea gigas*. *Invertebr. Reprod. Dev.*, 33: 87–93.

- Li, Q.; Yang, L.; Ke, Q. and Kong, L.** (2011). Gametogenic cycle and biochemical composition of the clam *Macra chinensis* (Mollusca: Bivalvia): Implications for aquaculture and wild stock management. *Mar. Biol. Res.*, 7: 407–415. <https://doi.org/10.1080/17451000.2010.515686>.
- Lorenzen, K.** (2005). Population dynamics and potential of fisheries stock enhancement: practical theory for assessment and policy analysis. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.*, 360: 171–189. <https://doi.org/10.1098/rstb.2004.1570>.
- Maathuis, M.A.M.; Coolen, J.W.P.; Van Der Have, T. and Kamermans, P.** (2020). Factors determining the timing of swarming of European flat oyster (*Ostrea edulis* L.) larvae in the Dutch Delta area: Implications for flat oyster restoration. *J. Sea Res.*, 156: 101828. <https://doi.org/10.1016/j.seares.2019.101828>.
- Maneiro, V.; Silva, A.; Pazos, A.J.; Sánchez, J.L. and Pérez- Parallé, M.L.** (2017). Effects of temperature and photoperiod on the conditioning of the flat oyster (*Ostrea edulis* L.) in autumn. *Aquac. Res.*, 48(8): 4554-4562. <https://doi.org/10.1111/are.13280>
- Marshall, R.D. and Dunham, A.** (2013). Effects of culture media and stocking density on biofouling, shell shape, growth, and survival of the Pacific oyster (*Crassostrea gigas*) and the Manila clam (*Venerupis philippinarum*) in suspended culture. *Aquaculture*, 406–407: 68–78. <https://doi.org/10.1016/j.aquaculture.2013.05.003>.
- Mazón-Suástegui, J.M.; Rivero-Suárez, S.E.; Betanzos-Vega, A.; Saucedo, P.E.; Rodríguez-Jaramillo, C. and Acosta-Salmón, H.** (2017). Potential of sites in northern Cuba for developing an industry of the native mangrove oyster (*Crassostrea rhizophorae*). *Lat. Am. J. Aquat. Res.*, 45(1): 218–222.
- Munro, J.L. and Bell, J.D.** (1997). Enhancement of marine fisheries resources. *Rev. Fish. Sci.*, 5(2): 185-222. <https://doi.org/10.1080/10641269709388597>.
- Munro, J.L. and Bell, J.D.** (2008). Enhancement of Marine Fisheries Resources. *Rev. Fish. Sci.*, 5(2): 185–222. <https://doi.org/10.1080/10641269709388597>.
- Naik, G. and Gowda, G.** (2015). Biological aspects of edible oysters: A review. *Int. J. Innov. Res. Sci. Eng. Technol.*, 4(6): 4245-4252.
- NAOO (National Oceanic and Atmospheric Administration)** (2018). What is spat? <https://oceanservice.noaa.gov/facts/spat.html>, accessed [03-12-2021].
- Ng, F.O.** (1979). Experimental culture of a flat oyster (*Ostrea folium* L.) in Malaysian waters. *Malays. Agric. J.*, 52(2): 103–113. <http://agris.fao.org/agris-search/search.do?recordID=US201301307455>.

- Ng, F.O.; Pang, J. and Tang, T.P.** (1982). Bivalve culture in Asia and the Pacific. In Davy, F.B. and Graham, M. (Eds.), Proceedings of a Workshop Held in Singapore - 16-19 February 1982, International Development Research Centre, Ottawa, p. 90.
- Nor Idayu, A.W.; Mohd Saleh, M.T.; Zainodin, J.; Natrah Fatin, M.I.; Annie, C.; Cob, C.Z. and Aziz, A.** (2015). Early development of tropical oyster *Crassostrea iredalei* (Faustino 1932). Adv. Environ. Biol., 9(21): 1–8.
- Nowland, S.J.; O'Connor, W.A.; Penny, S.S., Osborne, M.W.J. and Southgate, P.C.** (2019). Water temperature and salinity synergistically affect embryonic and larval development of the tropical black-lip rock oyster *Saccostrea echinata*. Aquac. Int., 27(5): 1239-1250.
- Nowland, S.J.; O'Connor, W.A.; Osborne, M.W.J. and Southgate, P.C.** (2020) Current Status and Potential of Tropical Rock Oyster Aquaculture, Rev. Fish. Sci. Aquac., 28(1): 57-70. <https://doi.org/10.1080/23308249.2019.1670134>.
- Ortega, S.** (1981). Environmental stress, competition and dominance of *Crassostrea virginica* near Beaufort, North Carolina, USA. Mar. Biol., 62: 47–56. <https://doi.org/10.1007/BF00396950>.
- Paixão, L.; Ferreira, M.A.; Nunes, Z.; Fonseca-Sizo, F. and Rocha, R.** (2013). Effects of salinity and rainfall on the reproductive biology of the mangrove oyster (*Crassostrea gasar*): Implications for the collection of broodstock oysters. Aquaculture, 380: 6-12. <http://dx.doi.org/10.1016/j.aquaculture.2012.11.019>.
- Parker, L.M.; O'Connor, W.A.; Byrne, M.; Dove, M.; Coleman, R.A.; Pörtner, H.; Scanes, E.; Virtue, P.; Gibbs, M. and Ross, P.M.** (2018). Ocean acidification but not warming alters sex determination in the Sydney rock oyster, *Saccostrea glomerata*. Proc. Royal Soc. B, 285(1872): 20172869.
- Peck, L.S.; Morley, S.A.; Richard, J. and Clark, M.S.** (2014). Acclimation and thermal tolerance in Antarctic marine ectotherms. J. Exp. Biol., 217(1): 16-22. <https://doi.org/10.1242/jeb.089946>
- Perrino, J.E. and Ruez Jr., D.R.** (2019). Eastern oyster (*Crassostrea virginica*) filtration efficiency of chlorophyll-*a* under dynamic conditions in the Hudson-Raritan Estuary at Pier 40, New York City. Open J. Ecol., 9: 238–271. <https://doi.org/10.4236/oje.2019.97019>.

- Philippart, C.J.; Anadón, R.; Danovaro, R.; Dippner, J.W.; Drinkwater, K.F.; Hawkins, S.J.; Oguz, T.; O'Sullivan, G. and Reid, P.C.** (2011). Impacts of climate change on European marine ecosystems: observations, expectations and indicators. *J. Exp. Mar. Biol. Ecol.*, 400(1-2): 52-60. <https://doi.org/10.1016/j.jembe.2011.02.023>.
- Pollack, J.B.; Yoskowitz, D.; Kim, H.-C. and Montagna, P.A.** (2013). Role and value of nitrogen regulation provided by oysters (*Crassostrea virginica*) in the Mission-Aransas Estuary, Texas, USA. *PLoS ONE*, 8(6): 1–8. <https://doi.org/10.1371/journal.pone.0065314>.
- Powell, E.N.; Hofmann, E.E. and Klinck, J.M.** (2018). Oysters, sustainability, management models, and the world of reference points. *J. Shellfish Res.*, 37(4): 833-849. <https://doi.org/10.2983/035.037.0413>.
- Preston, J.; Fabra, M.; Helmer, L.; Johnson, E.; Harris- Scott, E. and Hendy, I.W.** (2020). Interactions of larval dynamics and substrate preference have ecological significance for benthic biodiversity and *Ostrea edulis* Linnaeus, 1758 in the presence of *Crepidula fornicata*. *Aquat. Conserv.: Mar. Freshw. Ecosyst.*, 30(11): 2133-2149.
- Ramadhaniaty, M.; Setyobudiandi, I. and Madduppa, H.H.** (2018). Morphogenetic and population structure of two species marine bivalve (Ostreidae: *Saccostrea cucullata* and *Crassostrea iredalei*) in Aceh, Indonesia. *Biodiversitas Biodiversitas*, 19(3): 978-988. <https://doi.org/10.13057/biodiv/d190329>.
- Ramos, C.D.O.; Gomes, C.H.A.D.M.; Magalhães, A.R.M.; Dos Santos, A.I. and De Melo, C.M.R.** (2014). Maturation of the mangrove oyster *Crassostrea gasar* at different temperatures in the laboratory. *J. Shellfish Res.*, 33(1): 187-194. <http://dx.doi.org/10.2983/035.033.0118>.
- Renaud, M.** (1986). Hypoxia in Louisiana coastal waters during 1983: Implications for fisheries. *Fish. Bull.*, 84: 19–26.
- Robert, R.; Vignier, J. and Petton, B.** (2017). Influence of feeding regime and temperature on development and settlement of oyster *Ostrea edulis* (Linnaeus, 1758) larvae. *Aquac. Res.*: 1–18. <https://doi.org/10.1111/are.13297>.
- Rodriguez-Perez, A.; James, M.; Donnan, D.W.; Henry, T.B.; Møller, L.F. and Sanderson, W.G.** (2019). Conservation and restoration of a keystone species: Understanding the settlement preferences of the European oyster (*Ostrea edulis*). *Mar. Pollut. Bull.*, 138: 312-321. <https://doi.org/10.1016/j.marpolbul.2018.11.032>.

-
- Rosell, N.C.** (1990). Slipper-shaped oyster (*Crassostrea iredalei*) in the Philippines. In Menzel, W. (Ed.), *Estuarine and Marine Bivalve Mollusk Culture*, CRC. Press. Inc., Boston, pp. 308–313.
- Santerre, C.; Sourdain, P.; Marc, N.; Mingant, C.; Robert, R. and Martinez, A.S.** (2013). Oyster sex determination is influenced by temperature — First clues in spat during first gonadic differentiation and gametogenesis. *Comp. Biochem. Physiol. Part A Mol. Integr. Physiol.*, 165(1): 61–69. <https://doi.org/10.1016/j.cbpa.2013.02.007>.
- Saout, C.; Quéré, C.; Donval, A.; Paulet, Y.M. and Samain, J.F.** (1999). An experimental study of the combined effects of temperature and photoperiod on reproductive physiology of *Pecten maximus* from the Bay of Brest (France). *Aquaculture*, 172: 301–314. [https://doi.org/10.1016/S0044-8486\(98\)00406-2](https://doi.org/10.1016/S0044-8486(98)00406-2).
- Smyth, D.; Mahon, A.M.; Roberts, D. and Kregting, L.** (2018). Settlement of *Ostrea edulis* is determined by the availability of hard substrata rather than by its nature: Implications for stock recovery and restoration of the European oyster. *Aquat. Conserv.: Mar. Freshw. Ecosyst.*: 1–10. <https://doi.org/10.1002/aqc.2876>.
- Smyth, D.M.; Horne, N.S.; Ronayne, E.; Millar, R.V.; Joyce, P.W.; Hayden-Hughes, M. and Kregting, L.** (2020). Wild gregarious settlements of *Ostrea edulis* in a semi- enclosed sea lough: a case study for unassisted restoration. *Restor. Ecol.*, 28(3): 645-654. <https://doi.org/10.1111/rec.13124>.
- Soniat, T.M. and Burton, G.M.** (2005). A comparison of the effectiveness of sandstone and limestone as cultch for oysters, *Crassostrea virginica*. *J. of Shellfish Res.*, 24(2): 483-485.
- Steele, S. and Mulcahy, M.F.** (1999). Gametogenesis of the oyster *Crassostrea gigas* in southern Ireland. *J. Mar. Biol. Assoc. U.K.*, 79: 673–686. <https://doi.org/10.1017/S0025315498000836>.
- Suja, G.; Lijo, J.; Kripa, V.; Mohamed, K.S.; Vijayan, K.K. and Sanil, N.K.** (2020). A comparison of parasites, pathological conditions and condition index of wild and farmed populations of *Magallana bilineata* (Roding, 1798) from Vembanad Lake, west coast of India. *Aquaculture*, 515: 1–8. <https://doi.org/10.1016/j.aquaculture.2019.734548>.
- Syafriadiman.** (2017). Larval development of tropical oyster *Crassostrea cucullata* in laboratory condition. *Imp. J. of Interdiscip. Res.*, 3(8): 670-673.

- Talmage, S.C. and Gobler, C.J.** (2009). The effects of elevated carbon dioxide concentrations on the metamorphosis, size, and survival of larval hard clams (*Mercenaria mercenaria*), bay scallops (*Argopecten irradians*), and Eastern oysters (*Crassostrea virginica*). *Limnol. Oceanogr.*, 54(6): 2072-2080.
- Tan, S.H. and Wong, T.M.** (1996). Effect of salinity on hatching, larval growth, survival and settling in the tropical oyster *Crassostrea belcheri* (Sowerby). *Aquaculture*, 145(1-4): 129-139. [https://doi.org/10.1016/S0044-8486\(96\)01338-5](https://doi.org/10.1016/S0044-8486(96)01338-5).
- Tan, S.H.A.; Chang, G.O.; Poi, K.Y. and Teh, C.P.** (2014). Oyster culture in Malaysia: Opportunities and challenges. *J. Sci. Technol. Trop.*, 10(2): 99–108.
- Teaniniuraitemoana, V.; Leprêtre, M.; Levy, P.; Vanaa, V.; Parrad, S.; Gaertner-Mazouni, N.; Yannick, G.; Arnaud, H. and Le Moullac, G.** (2016). Effect of temperature, food availability, and estradiol injection on gametogenesis and gender in the pearl oyster *Pinctada margaritifera*. *J. Exp. Zool. A. Ecol. Genet. Physiol.*, 325(1): 13-24. <https://doi.org/10.1002/jez.1992>.
- Thiyagarajan, V. and Ko, G.W.K.** (2012). Larval growth response of the Portuguese oyster (*Crassostrea angulata*) to multiple climate change stressors. *Aquaculture*, 370: 90-95. <https://doi.org/10.1016/j.aquaculture.2012.09.025>.
- Thomas, Y.; Dumas, F. and Andréfouët, S.** (2014). Larval dispersal modeling of pearl oyster *Pinctada margaritifera* following realistic environmental and biological forcing in Ahe atoll lagoon. *PLoS ONE*, 9(4): e95050. <https://doi.org/10.1371/journal.pone.0095050>.
- Turgeon, D.D.; Bogan, A.E.; Coan, E.V.; Emerson, W.K.; Lyons, W.G.; Pratt, W.L.; Roper, C.F.E.; Scheltema, A.; Thompson, F.G. and Williams, J.D.** (1988). Common and scientific name of aquatic invertebrates from the United States and Canada: Mollusks. *Am. Fish. Soc. Spec. Publ.*, 16: 1–277.
- Turner, E.J.; Zimmer-Faust, R.K.; Palmer, M.A.; Luckenbach, M. and Pentchef, N.D.** (1994). Settlement of oyster (*Crassostrea virginica*) larvae: Effects of water flow and a water-soluble chemical cue. *Limnol. and Oceanogr.*, 39(7): 1579-1593. <https://doi.org/10.4319/lo.1994.39.7.1579>.
- Turner, R.E.; Rabalais, N.N.; Swenson, E.M.; Kasprzak, M. and Romaine, T.** (2005). Summer hypoxia in the northern Gulf of Mexico and its prediction from 1978 to 1995. *Mar. Environ. Res.*, 59(1): 65-77.

- Utting, S.D. and Millican, P.F.** (1997). Techniques for the hatchery conditioning of bivalve broodstocks and the subsequent effect on egg quality and larval viability. *Aquaculture*, 155: 45–54. [https://doi.org/10.1016/S0044-8486\(97\)00108-7](https://doi.org/10.1016/S0044-8486(97)00108-7).
- Vaschenko, M.A.; Hsieh, H.L. and Radashevsky, V.I.** (2013). Gonadal state of the oyster *Crassostrea angulata* cultivated in Taiwan. *J. Shellfish Res.*, 32(2): 471-482. <https://doi.org/10.2983/035.032.0227>.
- Waples, R.S.; Hindar, K. and Hard, J.J.** (2012). Genetic risks associated with marine aquaculture. NOAA Technical Memorandum NMFS-NWFSC-119. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service.
- Wells, M.L.; Trainer, V.L.; Smayda, T.J.; Karlson, B.S.O.; Trick, C.G.; Kudela, R.M.; Ishikawa, A.; Bernard, S.; Wulff, A.; Anderson, D.M. and Cochlan, W.P.** (2015). Harmful algal blooms and climate change: Learning from the past and present to forecast the future. *Harmful Algae*, 49: 68-93. <https://doi.org/10.1016/j.hal.2015.07.009>.
- Whitman, E.R. and Reidenbach, M.A.** (2012). Benthic flow environments affect recruitment of *Crassostrea virginica* larvae to an intertidal oyster reef. *Mar. Ecol. Prog. Ser.*, 463: 177-191.
- Widdows, J.; Newell, R. and Mann, R.L.** (1989). Effects of hypoxia and anoxia on larval survival, energy metabolism and feeding of oyster larvae (*Crassostrea virginica*, Gmelin). *Biol. Bull.*, 177: 154–166. <https://doi.org/10.2307/1542120>.
- Xu, F.; Guo, X.; Li, L. and Zhang, G.** (2011). Effects of salinity on larvae of the oysters *Crassostrea ariakensis*, *C. sikamea* and the hybrid cross. *Mar. Biol. Res.*, 7(8): 796-803. <https://doi.org/10.1080/17451000.2011.569555>.
- Zeebe, R.E.** (2008). Carbon emissions and acidification. *Science*, 321: 51-52. <https://doi.org/10.1126/science.1159124>.
- Zimme- Faust, R.K. and Tamburri, M.N.** (1994). Chemical identity and ecological implications of a waterborne, larval settlement cue. *Limnol. and Oceanogr.*, 39(5): 1075-1087. <https://doi.org/10.4319/LO.1994.39.5.1075>.
- Zulfigar, Y. and Tan, S.H.A.** (2000). A review of oyster culture in Malaysia. Thailand Research Fund, Bangkok, pp. 75–79.