Aquaculture 262

A Synopsis of the Olympia Oyster (Ostrea lurida)

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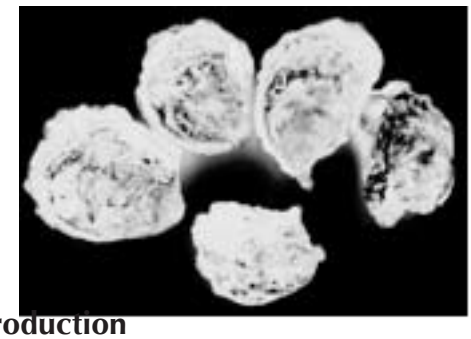


Introduction

The Olympia Oyster, Ostrea lurida (Carpenter 1864), is the only native oyster species that inhabits the west coast of Canada and the United States (McGraw 2009). Although preferably called the Olympia Oyster, other common names include California Oyster, Native Oyster, Shoalwater Oyster, Yaquina Bay Oyster, and Rock Oyster (Couch, Hassler, and Moran 1989). Olympia Oysters have always been historically important, and are commonly collected for use as cocktail oysters. However, anthropogenic effects, including overharvesting and pollution, have caused the species to experience a severe decline. For many reasons, the restoration and expansion of Ostrea lurida in their natural habitat is crucial, and remain one of the main projects of fishery management in the Pacific Northwest.

Ostrea lurida, and a very similar oyster Ostrea conchaphila (Carpenter 1857) were originally considered to be two separate species (Polson et al. 2009). However, in 1985, Harry proposed synonymy between Ostrea lurida and Ostrea conchaphila with the assumption of high phenotypic plasticity. After his proposal based strictly on shell and anatomical characteristics, many scientists questioned the validity of his claim. In a reaction study, Polson et al. (2009) used molecular markers to examine the potential synonymy between the two species, and compared both DNA sequences and post-hoc morphological characteristics. With further research, they found that Carpenter's original classifications (1964) of Ostrea lurida and Ostrea conchaphila as two distinct species were correct (Polson et al., 2009). Ostrea lurida was reinstated as the Olympia Oyster, inhabiting the west coast northward from Baja, California to Sitka, Alaska, and Ostrea conchaphila was stated to inhabit areas from Sinaloa, Mexico southward to Panama (McGraw 2009). In this paper, the scientific name Ostrea lurida will be used interchangeably with its common name, Olympia Oyster. This final determination of species delineation is important for restoration purposes: in order to effectively protect a species, one must understand their characteristics as a species.

Natural History

Males and females cannot be distinguished visually. The process of dissection must be used to determine the sex of the individual. The life cycle of Ostrea lurida is comparable to that of other oysters in the same genus, Ostrea, or the flat oysters (Couch et al. 1989). It is hermaphroditic, meaning the reproductive organs of both male and female sexes are present, and viviparous, meaning fertilization and development occur within the female body (Hopkins, 1935). Coe (1934) described the species as protandric, a form of hermaphrodites in which male organs precede that of the female organs. This anatomical development is most likely due to the fact that spermatogonia proliferate more rapidly than the ovogonia (Coe 1931a). More specifically, the oyster originally spawns as a male, and then alternates between male and female genders per each spawning cycle

(Couch et al. 1989).

After being retained in the female for a period of time, the larvae are released late in development. Metamorphosis occurs, and the larvae transform into juveniles, or spat. The timing of reproduction is heavily dependent on temperature, which is believed to cue spawning and dictate the length of season (Seale and Zacherl 2009). In the southern portion of Ostrea lurida's geographic range, male oysters typically begin to spawn once the water temperature reaches 16°C. Any temperature below this critical point inhibits spawning indefinitely (Coe 1931a, 1931b). Males release ellipsoid clusters or balls of sperm, usually consisting of approximately 250-2000 spermatozoa (Coe 1931b), into the mantle cavity. By means of shell contractions, the sperm balls are released into the seawater, and are then dissolved, enabling the uptake of spermatozoa into the mantle cavity of females, fertilizing the eggs inside her (Coe 1932). The detection of these spermatozoa in the water will proceed to cue synchronous spawning in Olympia Oysters of the same population (Couch et al. 1989). Once the eggs are fertilized, they develop into veliger larvae, a form of planktonic larvae characteristic of many marine mollusks. Approximately 10-12 days later (Hopkins 1936), the veliger larvae, which have already developed into fully shelled individuals (Walne 1974), are discharged, and remain planktonic for 11-16 days (Imai et al., 1954). The larvae eventually attach to a substrate, usually old shells, rocks, wood, or metal. It is most often found that Ostrea lurida settle on the lower or under side of horizontal surfaces. Based on studies by Hopkins (1935), settlement is not due to tropistic reaction to light, but instead to the upper position of the foot on the larvae as it is suspended in the water column.

Clearly, environmental conditions are crucial in the reproduction and development of Ostrea lurida. They are extremely sensitive to both high and low temperatures, usually stable within the ranges of 6°-9°C in winter and 18°-20°C in summer (Hopkins 1935). Most males do not spawn unless water temperatures reach the critical point of 16°C. Furthermore, a low temperature (i.e. a drop below the critical point), halts the cycle of sex alternation until favorable conditions return (Coe 1931a). Alternation will proceed throughout the oyster's life cycle, which can span for 10 plus years if left undisturbed (Aquatic Species at Risk 2006). Ostrea lurida thrive at salinities higher than 25ppt, ranging from estuarine to saline water in the subtidal zone, but can survive short exposures to lower salinity (Korringa 1976). A practical application of environmental manipulation is the eradication of parasitic flatworms, in which growers expose the oysters to a freshwater tide. The Olympia Oysters can survive the short flush of lower salinity, while the flatworms cannot (Couch et al. 1989).

Ostrea lurida are filter feeders, meaning they feed by straining small particles of food from the water. Essentially, they obtain their nutrition from phytoplankton, small photosynthetic organisms that drift within the water column, and particulate organic matter or POM (Lucas and Southgate 2003). Ostrea lurida possess ciliated gills, which create a current to intake water. Food particles are trapped by the cilia lining, and are pushed towards the mouth by way of labial palps. Particles too large for the mouth are bound in mucus, and released as pseudofeces, while undigested food is released as feces. Material that is able to be digested is absorbed as nutrients by the organism (Spencer 2002). To describe the rate of ingestion by the oyster, the following formula may be used:

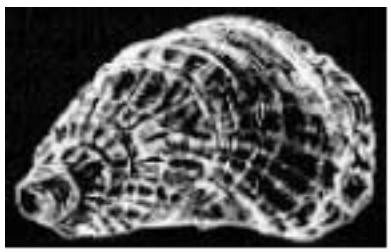
$$IR = [(FR \times PR) \times FC] - Ps$$

where IR represents the ingestion rate of food uptake, FR represents the water's rate of flow through the organism's gills, PR represents the proportion of the food in the water that is withheld in the gills, FC represents food concentration in the water, and Ps represents the rate at which pseudofeces is produced (Lucas and Southgate 2003).

Geographic Range of Ostrea lurida

The historic range of Ostrea lurida, which was once very abundant in the estuaries of the North American west coast, includes Baja, California to Sitka Alaska. According to fossil data from Washington, California, and Oregon, the Olympia Oyster was common (Polson and Zacherl 2009). It existed as early as the late Miocene and early Pliocene in central California, and the late Pleistocene in Northern California (Baker, Richmond, and Terwillinger 1999). Its natural habitat includes rocks in areas near the expanse of the low tide, and mudflats and gravel bars in estuaries and bays (Nosho 1989). However, after a combination of anthropogenic influence from Native Americans, overharvesting, pollution, invasive species, loss of substrate, and urbanization, Olympia Oysters have experienced a severe decline (McGraw 2009). According to Gillespie (2009), populations are not common on the coast of British Columbia, and are typically limited to protected waters. Abundance numbers of the Olympia Oyster are considered stable, but at low levels relative to historic data. Based on other studies, populations in Washington and Oregon are beginning to experience restoration and expansion where numbers were otherwise devastated (McGraw 2009). In addition, Polson & Zacherl (2009) determined that populations in California were also slowly rising based on presence/absence data. Therefore, restoration projects and monitoring efforts are being initiated to restore the current range of Ostrea lurida back to its formerly expansive natural range.

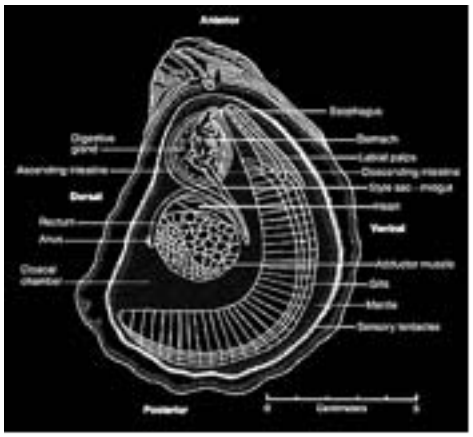
Figure 1: Olympia Oyster (Ostrea lurida). Taxonomically accurate representation (NOAA)



As a side note, one factor to consider is the impact these restoration projects may have on the genetic composition of the oysters. A study by Camara & Vadopalas (2009) discusses the practical options for oyster restoration, and the urgency of planning a well-managed and strategic form of restoration. Restoration should be viewed in the genetic context as well, because the restored population must be "genetically healthy" in order to ensure its future persistence throughout these various genetic regions. This factor is commonly overlooked.

Taxonomy

Figure 2: Diagram showing general anatomy of Olympia Oyster (Ostrea lurida) (NOAA)



The Olympia Oyster belongs to phylum Mollusca, the second largest phylum consisting of approximately 110,000 different species. The basic body plan of all members of this Phylum include a visceral mass, a mantle (the tissue responsible for making the shell), a foot (the muscular portion used for movement), a radula (a scraping tongue), Nephridia and Nephrostomes (used to excrete waste), and gills (associated with the circulatory tract and with feeding) (Karleskint, Turner, and Small 2010). Oysters, along with clams, scallops, and mussels, belong to Class Bivalvia, whose further characteristics include two shells, which are clamped by a ligament and 1-2 adductor muscles. The animal's foot is used to anchor to surfaces, and the oyster is essentially glued to the hard substance it

chooses to settle on. Figure 1 is a drawing of a typical Olympia Oyster, and Figure 2 goes into more detail in regards to basic anatomy.

Olympia Oysters are flat oysters, belonging to the Order Ostreoida and Family Ostreidae (Korringa 1976). Their shell averages 5-8 cm long, and rarely exceeds 9 cm. Typical shape varies, because the oyster will actually conform to the shape of the particular substrate they have settled on (Couch et al 1989), but in general it is elliptical or ovoid. Color range includes a blackish gray shade on the outside, and a shiny gray to pale blue on the inside (Nosho 1989). The outside may be striped a yellow or purplish-brown, and the adductor muscle scar consists of a color very similar to the rest of the oyster (Couch et al. 1989).

Ostrea lurida is a typical flat oyster closely related to the European Flat Oyster, Ostrea edulis (Korringa 1976). Fujio, Yamanaka, and Smith (1983) used gel electrophoresis to survey genetic variation of 25 species of marine mollusks, and determined that the two oysters (Ostrea lurida and Ostrea edulis) had low levels of genetic variation. Both species are characteristic of temperate zones, and differ in the like that Ostrea lurida has a slightly longer pelagic/planktonic phase, and does not require very clean clutch for settling (Korringa 1976). It has also been stated that Ostrea lurida and Ostrea chilensis, the Chilean Oyster, are similar. As with the majority of Ostrea oysters, both have similar brooding behavior in that the female holds her young in the mantle cavity for almost the entirety of their developmental period (Chaparro, Navarrete, and Thompson 2006). Due to the comparative similarities between Ostrea lurida and its closest relatives, Ostrea edulis and Ostrea chilensis, and the fact that extensive culture has not been accomplished with Olympia Oysters at this point in time, technique in broodstock management, spawning, incubation, larval rearing, and processing in the following sections may refer to one or all of these three species.

Ecosystem Services

Oyster reefs, or a dense collection of individuals forming an oyster bed, are crucial to the environment. Serving much like coral reefs, they provide substrate for a variety of organisms (including juvenile fish, worms, crustaceans, and foraging birds), and promote biodiversity by acting as physical habitat structure. Oyster beds also stabilize sediment, resulting in an increased opportunity for aquatic vegetation settlement. Finally, oysters are filter feeders. One indirect consequence of their feeding is the subsequent filtration of surrounding water. A large and robust population of oysters can effectively regulate plankton blooms, therefore decreasing the potential for Red Tide and other harmful algal blooms (Peabody and Griffin 2008). The oysters' presence can also reduce the turbidity of the sea water, and help to balance nutrient input (Peter-Contesse and Peabody 2005). Olympia Oysters are not only a source of food, but also play an important ecological role in our oceans. Their significance is another factor to take into consideration when focusing on restoration efforts of Ostrea lurida.

Culturing Ostrea lurida

Although Olympia Oysters can be cultured for direct human consumption, mainly as cocktail oysters (Korringa 1976), the strong majority are produced to facilitate restoration efforts (McGraw 2009). Both scientists and restoration practitioners have dedicated time and effort to restore Ostrea lurida in areas along the west coast where it previously existed. Over $1 million has been invested so far by NOAA, and at its current rate, this investment will undoubtedly increase (McGraw 2009). Restoration is not only important due to their ecological significance, but also because their severe decline was human-based.

Because the ultimate goal for the Olympia Oyster is typically restoration, technique for its culture may differ slightly from that of other oysters. For example, one of the two strategies used in restoration efforts is

"seeding", or adding new live cultured oysters to a bay or estuary (Peabody and Griffin 2008). Successful cultured reestablishment of Ostrea lurida requires extensive knowledge and careful consideration for various conditions (Peter-Contesse and Peabody 2005). In the following sections, broodstock management, spawning, incubation, larval rearing, and grow-out will assume that the cultured oyster is for restoration purposes. The last two sections on processing and marketing will then discuss the occasion of culture for human consumption.

Broodstock Management

Broodstock is a natural population of sexually mature individuals, which provides gametes for reproduction. Generally, they are kept separate from the rest of the cultured species to prevent the spread of disease. To obtain Ostrea lurida broodstock, adult oysters are harvested from the wild, and transported to the hatchery for spawning (Peabody and Griffin 2008). In selecting appropriate broodstock, one must consider that Ostrea lurida is protandric, meaning that the oyster matures initially as a male. Therefore, it is important that oysters well past sexual maturity are selected, to ensure that both sexes are present in the broodstock (Spencer 2002). Olympia Oysters are very rarely over 9cm in length, so target broodstock should range from 4-8cm (Korringa 1976)

Ostrea lurida are not highly susceptible to overcrowding, so stocking densities can be fairly high. Because they are strictly filter feeders, no feed is used in culturing Olympia Oysters. Instead, a sufficient volume of fine phytoplankton or POM particles (2+μm) must be present in the surrounding water, so that the oysters have access to food (Lucas and Southgate 2003). The higher the density, the more food required. However, the algae concentration cannot reach exceedingly high levels, for a depleted level of oxygen will result. Therefore, the ingestion rate can be calculated via the formula IR = [(FR x PR) x FC] – Ps, and can serve as the basis of the optimum cell concentration of algae. Generally, the optimum cell concentration will increase as the life cycle advances (Lucas and Southgate 2003).

Health management is very important in culturing oysters, and begins as early as the selection of broodstock. One management concern, especially applicable in the restoration of Ostrea lurida, is protecting the genetic identity of the remaining Oyster populations. According to the WDFW (Washington Department of Fish and Wildlife), brood oysters should originate from the same area in which the offspring will be seeded, ensuring that the oysters will be restored according to their natural habitat (Peter-Contesse and Peabody 2005). Related to the research of Camara & Vadopalas, great care should be taken in restoring these oysters. There is potential to cause more harm than good if genetic variation between different populations along the west coast of North America is not taken into consideration (2009). Therefore, collection of broodstock should be completed by non-profit organizations or commercial shellfish farming operations, both in compliance of permit regulations (Peter-Contesse and Peabody 2005).

Another major concern in broodstock health management is the movement or introduction of shellfish diseases. Due to the feeding nature of oysters, they are very susceptible to obtaining diseases from the water (i.e. biotoxins, Red Tide, various bacteria, viruses, and heavy metals). These conditions are not necessarily harmful to the organism, but are rather deleterious to human health if consumed. Therefore, before the production of seed cultivation, brood oysters are tested by shellfish pathologists. Testing guarantees that the collected broodstock is free of shellfish-bourne disease, and will not carry or transfer any pathogens to the remainder of the oysters within the hatchery (Peter-Contesse and Peabody 2005). Health management is crucial in the successful culture of any organism, and will therefore be discussed in the remainder of the sections as well.

Spawning

Spawning of Ostrea lurida is highly dependent on temperature, and usually will not occur unless temperatures reach 16°C or higher (Coe 1931a, 1931b). If occurring in captivity (which is much less common than spat collection), spawning may have to be induced by temperature manipulation or presence of gonads in the water (as mentioned before, the detection of spermatozoa in nature induces all males to spawn) (Lucas and Southgate 2003). Densities can be fairly high, as Ostrea lurida are not susceptible to overcrowding. As long as enough phytoplankton is present to sustain the population, and the rest of the conditions are ideal, spawning will proceed via induction.

Given that broodstock can be separated accurately via sex, the males and females are commonly placed in separate containers for spawning. Since Ostrea lurida are larviparous, fertilization of the egg and early development of the larvae both take place within the gill cavity of the female (Spencer 2002). Therefore, females do not typically "spawn", and larvae are not released until they have developed for approximately 10-12 days (Hopkins 1935).

Another common method, in place of spawning the oysters in captivity, is the technique of spat collection. This process skips the spawning step, and collects larvae directly from the wild on cultch. This technique will be discussed more in the "Larval Rearing" section, but essentially, it is the collection of newly metamorphosed oysters on a hard substrate provided by the oyster farmer. This substrate, typically old oyster shell, rock, or other hard substances, is later transported to the farm, thus providing oysters to be grown in the hatchery.

Incubation

Incubation is when fertilization occurs, and the time period thereafter. Density must be carefully monitored. If there is not enough sperm, fertilization will not occur efficiently, and will therefore result in a lower success rate. On the other hand, if too much sperm is present, there is potential for polyspermy, a condition in which eggs are fertilized by more than one sperm, which results in abnormality (Lucas and Southgate 2003). General abnormalities include those that make the individual infertile, and those that severely decrease their survival rate.

In general, larvae remain within the female for 10-12 days following fertilization (Hopkins 1935). During this time, water movement should be maintained via gentle aeration, and algae should be readily available for once the larvae are ejected from the female.

Larval Rearing

After 10-12 days of development within the female body, veliger larvae are released into the water column (Hopkins 1935). At this point in time, the larvae are approximately 170μm in length, and can remain in this stage for an additional 11-16 days (Imai et al. 1954). Once freely swimming in the broodstock tank, the larvae tend to swim upwards towards the surface of the water. The larvae may then be collected from the broodstock tank by scooping the upper layers of the water with a 90 μm mesh sieve (Spencer 2002), and should be kept separately in preparation for metamorphosis.

Another technique to obtain larvae is via spat collection. Hard substrates, such as old oyster shell, rock, or various kinds of panels, are provided for larvae to settle on. Once the veliger larvae find a suitable surface (usually the underside of a hard substrate), they metamorphose into juveniles, at which point they become sessile (Hopkins 1935).

Unlike the other stages of the oyster life cycle, density during larval rearing must remain relatively low (approximately 1-5 larvae per mL of water). Although densities begin high, they decrease over time due to mortality (Lucas and Southgate 2003). A consistent abundance of algae should be provided for the larvae, due to high energy demands at this point in the life cycle. Accurate levels of algae should be calculated, depending on the density of the culture.

In order to maintain healthy water and healthy larvae, multiple measures should be taken. Firstly, seawater should be filtered with an approximate 1 μm sieve. This step prevents the instance of sediment, organic debris, and zooplankton that may potentially serve as predators or competitors (Lucas and Southgate 2003). Water quality should always be monitored, and kept at a constant temperature and salinity (usually ranging from 16-19°C and 25-30 ppt respectively (Korringa 1976). Finally, culture water should be exchanged consistently to prevent disease (Peabody and Griffin 2008). Through these management techniques, health of the oysters and instance of disease is hopefully reduced. Occasional samples of water should be taken, and bacteriological analysis can be conducted. Health management and caution are both essential in every step of the oyster's life cycle, and ensures that the water present does not exceed the allowable level of toxin (Peter-Contesse and Peabody 2005)

Grow-out

In the case of the Olympia Oyster, grow-out will usually not take place in the hatchery. Instead, since the main goal is restoration, the shells with spat are dispersed on bottom-artificial reefs. The culture then transforms from an intensive culture (where great care and attention is focused onto growing individuals) to an extensive culture (where little care is given). If the juveniles intended for grow-out are singles or have no substrate, then a variety of mesh bags, panels, or cages can be used in this phase (Lucas and Southgate 2003). From this point on, the Ostrea lurida can be left to grow-out into the adult phase. Occasional monitoring is beneficial, as the constant management allows the farmer to keep track of success rate and health of the population. Some typical methods include counting sub-populations, or predetermined plots of the artificial oyster reef (indicating the number alive, the number dead, and the percent survival), and measuring average shellfish length within the sub-population. Another variable to monitor is the water quality of that particular area. This may include temperature, salinity, pH, turbidity, algae levels, and bacteriological analysis (Flimlin 2003).

If the Olympia Oyster is being cultured for human consumption, it takes approximately 3.5 years for each individual to reach its marketable size. The minimum length ranges from 4.5 cm – 5cm (Korringa 1976). Sexual maturity is reached at age one, where individuals initially become male (Aquatic Species at Risk 2006).

It is not necessary to directly feed the oysters during the grow-out phase. As with the rest of the phases during the oyster life cycle, algae should be consistently present to facilitate filter feeding. If algae growth is not naturally occurring within the artificial oyster reef, then additional mass-cultured algae should be provided to maintain a healthy population. The algae should be a small and unicellular species, with examples including Pavlova and Isochrysis (Lucas and Southgate 2003). In addition, the higher the oyster density, the more phytoplankton required for sufficient feeding of the population. During the grow-out phase, densities can be higher. Higher amounts are allowed because the adults are sessile, or are packaged indefinitely into mesh bag or cages. Therefore, a balance must be maintained between food level and population density (Peabody and Griffin 2008).

Health management is extremely important during the grow-out phase, because a disease break-out can impact the entire population if not properly managed. Therefore, regular bacteriological analysis should be conducted on samples from subpopulations of the artificial reef. If any bacteria or viruses are present, it is necessary to use depuration. The process relocates the oysters to a clean water system with flow-through or UV light for 2 weeks, and provides the opportunity for the population to naturally clean themselves through normal filtration behavior. Finally, meticulous water quality measurements

must be taken constantly to ensure the area the oysters are feeding in does not contain biotoxins, bacteria, viruses, or anything else harmful in human consumption (Peabody and Griffin 2008).

Cautionary measures should also be taken to prevent biofouling (which can lower the success rate of the oyster population). Biofouling occurs when organisms, such as barnacles or tunicates, attach themselves to the oysters. This occurrence can have a serious impact by blocking the intake of water, by acting as competition with the oyster, or by adding weight to the system as a whole (Nosho 1989). Fouling can be reduced by scraping and scrubbing oysters and oyster bags, and by planting the oysters in the intertidal zone. This placement exposes the oysters to air, therefore reducing fouling, and inducing the production of a harder shell for defense (Lucas & Southgate, 2003). Finally, steps towards reducing predation should be taken. Planting in the intertidal zone is one option, along with physical removal of the predator if the large enough (such is the case with Pisaster or Cancer magister) (Nosho 1989).

Processing & Marketing

The majority of Olympia Oysters are cultured for restoration purposes; however, in the event that they are grown for human consumption, the processing and marketing of Ostrea lurida include various important aspects. Because oysters are filter feeders, there is great concern and caution taken in the bacteria or viruses they can carry, and the illnesses they can cause. The Department of Health (DOH), Office of Food Safety and Shellfish Programs, or a local environmental health specialist can be contacted to inspect the area's water quality (Nosho 1989). In addition, the Shellfish Sanitation Division of the Health Department should sample a range of oysters from the market, and conduct bacteriological analysis. This form of management will periodically indicate whether or not particular facilities are distributing safe product (Peter-Contesse and Peabody 2008).

In order to ensure the finished product is clean and void of disease, the oyster farmer has numerous options to consider. Firstly, to assure adequate water supply, the method of depuration may be used. Secondly, high pressure methods may be used (though expensive), where the oyster DNA is denatured. Essentially, any bacteria or viruses that may exist within the product will be killed, without needing to cook the oyster itself (Lucas and Southgate 2003).
Overall, marketing is considered to be restricted in the oyster industry, mainly due to the fact that small shellfish growers and farm owners are not skilled in sales promotion. Historically, according to Korringa (1976), primarily restaurants along the west coast purchase cultured Olympia Oysters. They are rarely served on half-shells due to their small size, and are instead stored in jars or tins for the use of cocktail oysters. Although rare, Olympia Oysters are occasionally sold on half-shells, and are advertised as a delicacy. In general, even though Olympia Oysters are available for purchase in certain areas, restoration and reestablishment continue to be the main goal when culturing Ostrea lurida. Through these efforts, hopefully the Olympia Oyster can be restored to its original natural range, and eventually serve as a dependable, sustainable food source in the future.

References

Aquatic Species At Risk - Olympia Oyster. (April 2006). Retrieved April 2010, from <http://www.dfo-mpo.gc.ca/species-especes/species-especes/olympiaoyster-huitreplate-eng.htm>.

Baker, P. N., Richmond, & Terwillinger, N. (1999). Reestablishment of a native oyster, Ostrea conchaphila, following natural local extinction. Paper presented at the Proceedings of 1st National Conference. Marine Bioinvasions, Cambridge, MA.

Camara, M. D., & Vadopalas, B. (2009). Genetic aspects of restoring Olympia Oysters and other native bivalves: Balancing the need for action, good intentions, and the risks of making things worse. Journal of Shellfish Research, 28(1), 121-145.

Carpenter, P. P. (1864). Diagnoses de mollesques nouveaux provenent de Californie et faisant partie du muse de L'institution Smithsonienne. J. Conchyliol XII, 3(5), 129-138.

Chaparro, O. R., Navarrete, L. R., & Thompson, R. J. (2006). The physiology of the larva of the Chilean oyster Ostrea chilensis and the utilisation of biochemical energy reserves during development: An extreme case of the brooding habit. Journal of Sea Research, 55, 292-300.

Coe, W. R. (1934). Alternation of Sexuality in Oysters. The American Naturalist, 68(716), 236-251.

Coe, W. R. (1932). Development of gonads and the sequence of sexual phases in the California Oyster (Ostrea lurida). Bulletin of the Scripps Institution of Oceanography, 3(6), 119-144.

Coe, W. R. (1931). Sexual rhythm in the California Oyster (Ostrea lurida). Science Magazine, 74(1914), 247-249.

Coe, W. R. (1931). Spermatogenesis in the California Oyster (Ostrea lurida). Biological Bulletin, 61(3), 309-315.

Couch, D., Hassler, T. J., & Moran, D. (1989). Olympia Oyster (No. 82 11.124): Fish and Wildlife Service.

Flimlin, G. (2003). Record Keeping for Shellfish Aquaculture.

Fujio, Y., Yamanaka, R., & Smith, P. (1983). Genetic Variation in Marine Molluscs. Bulletin of the Japanese Society of Scientific Fisheries, 49(12), 1809-1817.

Gillespie, G. (2009). Status of the Olympia Oyster, Ostrea lurida Carpenter 1964, in British Columbia. Journal of Shellfish Research, 28(1), 59-68.

Harry, H. (1985). Synopsis of the supraspecific classification of living oysters (Bivalvia: Gryphaeidae and Ostreidae). Veliger, 28, 121-158.

Hopkins, A. E. (1935). Attachment of larvae of the Olympia Oyster, Ostrea lurida, to plane surfaces. Ecology, 16(1), 82-87.

Imai, T., Sukai, S., Okada, H., & Yoshida, T. (1954). Breeding of the Olympia Oyster in tanks and culture experiments in Japanese waters. Tohoku Journal of Agricultural Research, 5(1), 13-25.

Karleskint, Turner, & Small. (2010). Introduction to Marine Biology. Belmont: Brooks/Cole.

Korringa, P. (1976). Farming The Flat Oysters of the Genus Ostrea. New York: Elsevier Scientific Publishing Company.

Lucas, J. S., & Southgate, P. C. (Eds.). (2003). Aquaculture: Farming Aquatic Animals and Plants (1 ed.). State Avenue: Blackwell Publishing.

McGraw, K. A. (2009). The Olympia Oyster, Ostrea lurida Carpenter 1984 along the west coast of North America. Journal of Shellfish Research, 28(1), 5-10.

Nosho, T. (1989). Small-Scale Oyster Farming for Pleasure and Profit: Sea Grant.

Peabody, B., & Griffin, K. (2008). Restoring the Olympia Oyster, Ostrea conchaphila. NOAA: Habitat Connections, 6, 1-6.

Peter-Contesse, T., & Peabody, B. (2005). Reestablishing Olympia Oyster Population in Puget Sound, Washington. Seattle: Washington Sea Grant Program.

Polson, M. P., Hewson, W. E., Eeernisse, D. J., Baker, P. K., & Zacherl, D. (2009). You say Conchapilia, I say lurida: A molecular evidence for restricting the Olympia Oyster (Ostrea lurida Carpenter 1984) to temperate western North America. Journal of Shellfish Research, 28(1), 11-21.

Polson, M. P., & Zacherl, D. (2009). Geographic distribution and intertidal population status for the Olympia Oyster, Ostrea lurida Carpenter 1864, From Alaska to Baja. Journal of Shellfish Research, 28(1), 69-77.

Seale, E. M., & Zacherl, D. C. (2009). Seasonal settlement of Olympia Oyster larvae, Ostrea lurida Carpenter 1984 and its relationship to seawater temperature in two southern California estuaries. Journal of Shellfish Research, 28(1), 113-120.

Spencer, B. E. (2002). Molluscan Shellfish Farming. Malden: Fishing New Books.

Walne, P. R. (1974). Culture of Bivalve Molluscs: 50 Years Experience at Conwy. Farnham: Fishing New Books Ltd.