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Contributors

Brian Beal, University of Maine at Machias, Machias, Maine, USA & Downeast Institute, Beals, Maine, USA

Stephan Bullard, University of Hartford, West Hartford, Connecticut, USA

Juan Carlos Castilla, Departamento de Ecología y Estación Costera de Investigaciones Marinas (ECIM), Las Cruces, Chile & Pontificia Universidad Católica de Chile, Santiago, Chile

Daniel P. Cheney, Pacific Shellfish Institute, Olympia, Washington, USA

Peter Cook, University of Western Australia, Albany, Western Australia, Australia

R. LeRoy Creswell, Florida Sea Grant Extension Program, Fort Pierce, Florida, USA

Michael Dadswell, Acadia University, Wolfville, Nova Scotia, Canada

Leslie-Anne Davidson, Fisheries and Oceans Canada, Moncton, New Brunswick, Canada

Christopher V. Davis, Pemaquid Oyster Company, Inc., Waldoboro, Maine, USA

Jonathan P. Davis, Baywater Shellfish Farms, Bainbridge Island, Washington, USA

Megan Davis, Florida Atlantic University, Harbor Branch Oceanographic Institution, Ft. Pierce, Florida, USA

Carole R. Engle, Engle-Stone Aquatic$ LLC, Strasburg, VA, USA

Jorge Diogène Fadini, Institute for Food and Agricultural Research and Technology, Sant Carles de la Ràpita, Tarragona, Spain

Lynne Falconer, University of Stirling, Stirling, United Kingdom

Tessa Getchis, Connecticut Sea Grant, Groton, Connecticut, USA

Ximing Guo, Rutgers University, Haskin Shellfish Research Laboratory, Port Norris, New Jersey, USA

Kevin Heasman, Cawthron Institute, East Nelson, New Zealand

Zenjie Jiang, Yellow Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences, Qingdao, China

Richard C. Karney, Martha's Vineyard Shellfish Group, Inc., Vineyard Haven, Massachusetts, USA

John Kraeuter, University of New England, Biddeford, Maine, USA & Haskin Shellfish Research Laboratory, Port Norris, New Jersey, USA

Gregg W. Langlois, California Department of Public Health, Richmond, California, USA

César Lodeiros, Universidad Técnica de Manabí, Bahía de Caráquez, Ecuador & Instituto Oceanográfico de Venezuela, Cumaná, Venezuela

Patricio H. Manríquez, Centro de Estudios Avanzados en Zonas Áridas (CEAZA) and Laboratorio de Ecología y Conducta de la Ontogenia Temprana (LECOT), Coquimbo, Chile

José Manuel Mazón-Suástegui, Centro de Investigaciones Biológicas del Noroeste, La Paz, B.C.S., Mexico
Thane A. Militz, University of the Sunshine Coast, Maroochydore, Queensland, Australia
Steve L. Morton, NOAA/NOS, Charleston, South Carolina, USA
Carter Newell, Pemaquid Mussel Farms, Bucksport, Maine, USA
Guilherme Sabino Rupp, Centro de Desenvolvimento em Aquicultura e Pesca, Florianópolis, Santa Catarina, Brazil
Samia Sarkis, Living Reefs Foundation, Bermuda
Sandra E. Shumway, University of Connecticut, Groton, Connecticut, USA
Aad Smaal, Wageningen Marine Research, Zierikzee, the Netherlands
Roxanna Smolowitz, Roger Williams University, Bristol, Rhode Island, USA
Paul C. Southgate, University of the Sunshine Coast, Maroochydore, Queensland, Australia
Trevor C. Telfer, University of Stirling, Stirling, United Kingdom
Alex Walsh, smartPAINT, Inc., East Falmouth, Massachusetts, USA
William Walton, Auburn University Shellfish Lab, Dauphin Island, Alabama, USA

Preface

Culture of bivalve molluscs has been carried out for centuries, but only in the past few decades have technological advances allowed the efforts to prosper based upon land-based hatchery systems coupled with coastal grow-out.

Until R.R.L. Guillard (1957) isolated and cultured phytoplankton as a food source for bivalve larvae, it was not possible to consider growing shellfish in captivity. His success opened the door for future efforts and the establishment of hatcheries (see Shumway et al., 2017). Technology has progressed considerably since that time, hatchery production of bivalve larvae is now routine, genetic and molecular techniques are used routinely to improve broodstock and battle diseases, and sophisticated models are used to assist growers in site selection and carrying capacity. Governmental regulations have taken hold, global marketing has flourished, and environmental issues have given way to the quest for best management practices and sustainability. Shellfish aquaculture is a successful and sustainable global venture.

Pioneers in the field of shellfish aquaculture faced enormous challenges, including practical, biological and social problems, yet they persevered. Among them, in no particular order, Peter Walne, Peter Korringa, Neil Bourne, Ken Chew, Paul Galtsoff, Victor Loosanoff, Carl Medcof, Fushi Zhang, James Mason, Michael Castagna, Paul Chanley, Ravena Ukeles, Robert Guillard, Herb Hidu, Hal Haskin, Cary Matthiessen, and all those who followed laid the groundwork for what is today a global industry worth billions of dollars.

Walne (1954) published a book based on his Buckland lectures entitled *Culture of Bivalve Molluscs*, which focused primarily on the European flat oyster (*Ostrea edulis*). It was one of the first efforts to summarize knowledge in the field of shellfish aquaculture and it is ironic that he chose to focus on one of the species still most challenging to culture today. Spencer (2002) presented a more general text entitled *Molluscan Shellfish Farming*, also based partially on Buckland lectures, which acknowledged advances in the field, and expanded to include chapters covering issues of importance to the newly developed industry – bivalve predators and their control, criteria for site selection for bivalve aquaculture, and processing for human consumption. During these past several decades there have been numerous publications based on specific species and geographic regions, but no comprehensive effort covering the key species and concerns of the shellfish aquaculture industry.

This book is not meant to be a treatise on all aspects of the biology, ecology, and aquaculture efforts for all species of bivalves, there have been numerous books published that cover all of these aspects and the reader is directed to those volumes for more in-depth and specific information (see the Further Reading list). Rather, it is meant to be a useable text for those interested in an up-to-date introduction to the field and to guide those who decide to join the shellfish aquaculture industry.

This book would not have been possible without the contributions of many experts and they are all thanked for their generous sharing of time and knowledge. Nigel Balmforth, 5m Books, made the work a reality. A great debt of gratitude and thanks goes to Noreen Blaschik Favreau who battled through various drafts and got them all ready for publication. Her efforts are intangible and truly appreciated. Thanks to Eric Heupel who designed the cover, and finally, thanks to Gus for his unwavering support through it all.

In Walne's epilogue, he noted that 'once hatcheries can be shown to be commercially profitable, it is clear that, with continual advance in knowledge, their potential for producing very large quantities of seed stock is considerable', and that 'It is the writer's hope that this book will help to spread information on one way in which this might come about.' His vision was fulfilled and it is hoped that the current volume will provide a useful manual and provide newcomers with the information necessary to spark their imagination and continue the effort to grow and utilize shellfish to their fullest potential.

Sandra E. Shumway
2021

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CHAPTER 1

Farming oysters for food and profit

Jonathan P. Davis, Christopher V. Davis, and William Walton

Introduction

Edible oysters have been near the center of human folklore and gastronomic enjoyment for millennia. As the preeminent marine and evolutionary biologist, C.M. Yonge (1960) wrote, “There is much to say about oysters,” and indeed, the voluminous literature on oysters attests to the many kinds of resources available to assist the aspiring shellfish farmer. Oysters grow quickly, are full of protein and nutrients, are flavorful, and easily acquired. While a rich fossil record exists for oysters beginning in the Jurassic period about 200 million years B.C., oysters were clearly an important part of native people’s diets as evidenced by the presence of shell middens in many parts of the world dominated by oyster shells. Globally and historically, oyster fisheries have been notoriously difficult to manage. This may be due, in part, to the requirement, at least in the wild, for oyster larvae to attach to hard surfaces (such as adult oyster shell). Harvesting large oysters in the wild often results in the loss of the attached juveniles (called ‘spat’) as well as the loss of available substrate for future recruitment. These simple characteristics of the oyster life history, combined with its amenability to culture probably encouraged humans to initiate their cultivation, once local and easily accessible wild stocks were depleted. The Roman knight, Sergius Orata, is credited by many sources to have farmed what is known today as the European flat oyster (*Ostrea edulis*) in coastal lagoons, or *ostrearia* in the Bay of Naples as early as the 1st century B.C., apparently quite successfully according to the account of Carazzi (1893). Similarly, oyster culture in China can be traced back to over 2400 years ago according to the writer Fan Li and his book *Pisciculture* as briefly described by Wijsman et al. (2019). Quite simply, oysters were, and remain, an easily acquired food that has been greatly desired by humans for centuries. Their ecological role as both reef builders and ecosystem engineers in temperate estuaries has also been broadly recognized. For volumes focused exclusively on this commercially and ecologically important bivalve see Kennedy et al. (1996) and Bayne (2017).

Oysters are by their nature easily exploited and the demise of oyster reefs has been well-documented on a worldwide basis (Beck et al., 2011). Serial depletion of cultured oysters is similar to an observed pattern for many species grown for aquaculture (You and Hedgecock, 2019). Often a shellfish disease first induces widespread mortality and the population collapses. Once that

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species is depleted, another is often introduced. W.K. Brooks (1891) wrote an important volume on the demise of wild oysters (*Crassostrea virginica*) in the Maryland portion of the Chesapeake Bay in the late 1800s, while a recent volume describes the vast ecological changes associated with the loss of eastern oysters from the Chesapeake Bay estuary, including the proposed, but ultimately rejected proposal to introduce the Asian oyster (*C. ariakensis*) to the Chesapeake Bay estuary (Kennedy, 2018). Similarly, the European flat oyster (*O. edulis*) was depleted in France in the 1920s and replaced first with the what was referred to then as the Portuguese oyster (*C. angulata*), and then by *C. gigas*, the Pacific or Japanese oyster (Buestel et al., 2009). Not to be outdone, the commercial fishery for the native oyster on the North American west coast (*O. lurida*) was commercially extinct by the late 1800s in much of its range though extensive efforts, particularly in southern Puget Sound, to rear this species in intertidal claires similar to those used for the culture of *O. edulis* in France, ultimately failed (Goulletquer, 2004; White et al., 2009). Since 1920, commercial sea farming of oysters on the US west coast has focused on the Pacific oyster, once this oyster was successfully transplanted from Japan to Washington State between 1905–1919 (Steele, 1964). The long history of the relationship of oysters to mankind clearly suggests that the demand for oysters has historically outstripped the wild supply and that oyster farmers continually adapted methods and species to meet the demand. In short, methods for cultivating oysters have changed and they will continue to evolve. Successful oyster farmers tend to be resilient and innovative. To be successful, growers must embrace innovation and have the capacity to adapt continuously to a climate in rapid flux, shortages of seed, and other fundamentals and changing business conditions. In short, a can-do attitude is perhaps the fundamental determinant for success.

Because oysters are grown throughout the world, methods of cultivation vary by place and species from simple farming approaches, which rely on natural recruitment, to sophisticated approaches, which include large-scale hatchery production and precision farming from seed to market. The focus of this chapter is to provide practical information to the aspiring oyster farmer to assist in the development of sustainable production of oysters for artisanal use or profit. Much goes into the development of a shellfish farm and, while oysters are cultured in abundance around the world, the ultimate success of an operation will require careful attention to site considerations (see Chapter 10), the species cultivated, and the many details associated with developing farm-based production. While pearl-producing oysters are commonly farmed in subtropical and tropical parts of the world (see Chapter 9), the general focus of this chapter is to provide information on culture techniques for edible oysters.

Biology and ecology of oysters

A thorough understanding of the general biology and ecology of oysters is essential for the aspiring oyster farmer because the success of any operation ultimately depends upon both recognizing and responding to problems in the culture system (hatchery, nursery, or grow-out) before they become uncontrolled calamities resulting in mortality and loss of the crop.

As bivalves, oysters belong to a large and diverse group of molluscs that inhabit both hard substrates and firm sediments as surface dwelling (epibenthic) animals in mainly intertidal estuarine and marine waters on all continental coastlines except Antarctica. Historically, oysters were exceedingly common, occurring in large intertidal and subtidal assemblages, or beds occupying many hectares of intertidal or bottom lands. Oysters are generally classified as belonging to taxonomic families that are characterized by a cupped left (lower) valve and flatter right (upper) valve (for example, *Crassostrea* spp., *Saccostrea* spp.), or two, relatively flatter valves (for example, *Ostrea* spp., *Tiostrea* spp.). In all oysters, the two valves are joined by an elastic ligament at the anterior end. A single adductor muscle, attached to the interior surface of both valves, when contracted serves to hold the valves together, especially when oysters are exposed to air during low tide. When under water the adductor muscle is generally not contracted, and the flexible hinge serves to prop the valves a few millimeters to enable essential bivalve function. Utilizing a highly efficient, cilia-driven feeding and respiratory current over specially modified tissues referred to as ctenidia (gills), microscopic phytoplankton and detrital material are retained and may be ingested. The inhalant current brings suspended materials to the ctenidial surface where highly evolved particle selection and sorting of particles may occur. These behaviors have been extensively studied in bivalves generally including oysters and demonstrate highly evolved mechanisms for particle capture, handling, and nutrient extraction (Ward and Shumway, 2004; for a recent review see Rosa et al., 2018). Oysters generally process large quantities of seawater, but feed discontinuously depending on the availability and quality of seston among other factors (Cranford et al., 2009). Feeding behavior in oysters was also comprehensively reviewed by Bayne (2017). A feature of bivalves associated with feeding on microscopic materials in the water column and certainly shared by oysters is the production of biodeposits. These may be produced as either pseudofeces or feces (fecal pellets). Pseudofeces consist of organic and inorganic materials collected on the ctenidia and labial palps prior to ingestion and rejected by the oyster as unconsolidated materials in mucus. True feces are produced following ingestion and absorption by the animal and are recognized as fecal pellets similar in features to other suspension feeding bivalves.

The sex life and life history of oysters is similar to other bivalves. Oysters may be predominantly male or female, sequentially male and female on an annual basis, or protandric – tending to be male as younger oysters and then changing sex as they get older and larger to become female. Suffice to say that sex and sexuality in oysters is complicated and has been a subject of significant interest for many investigators since the late 1800s. Generally, oysters undergo a cycle of reproduction characterized by the seasonal allocation of resources to germinal tissue development, generally in response to increasing temperature and food availability followed by the spawning of gametes stimulated by a number of environmental cues. Cupped and rock oysters shed gametes directly into the water column where fertilization and development to the larval stages occurs. Flat oysters diverge significantly from this life history pattern as females deposit their eggs directly into their mantle cavity where the eggs are fertilized by sperm (contained in sperm balls) inhaled by the female from surrounding waters. Eggs are fertilized within the mantle cavity and embryos are brooded for a period of time prior to their release into the water column as well-developed veliger larvae. For all oysters, spawning is generally followed by a period of nutrient rebuilding/reallocation of nutritional resources to growth.

Oyster larvae are microscopic and begin life as a fertilized egg only ~50 µm in diameter for *Crassostrea* species. Following fertilization, oyster larvae pass through several developmental stages, all the while feeding on microscopic materials once they become veligers. This stage is characterized by a unique, ciliated organ supremely adapted to enable the oyster larvae to swim and simultaneously feed on microscopic materials in the water column. Depending on

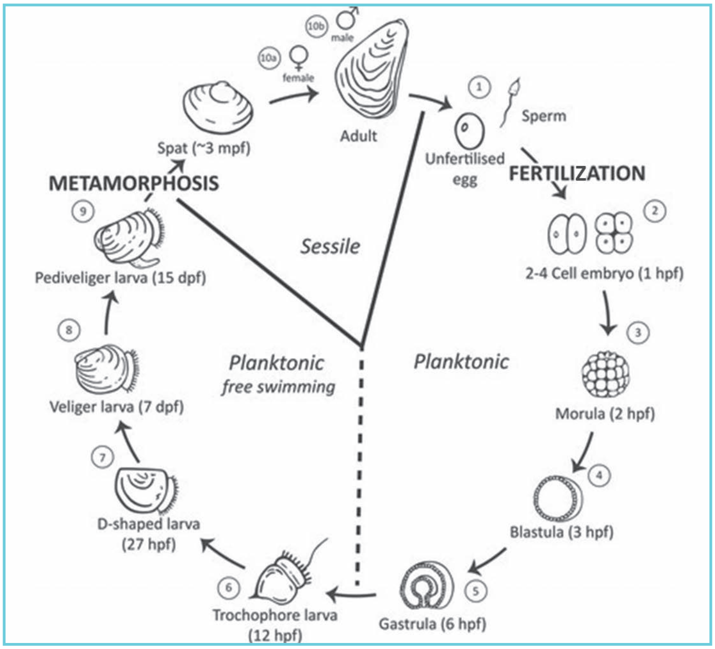

Figure 1.1 Diagram of the oyster life history (hpf = hours post fertilization, mpf = months post fertilization, dpf = days post fertilization). Oyster farmers utilize the cementation stage at the end of the larval period to facilitate subsequent juvenile production. Source: https://commons.wikimedia.org/wiki/File:Oyster_life_cycle.png.

the species and environmental conditions, oyster larvae live in the plankton for days to weeks prior to settling to the bottom as pediveligers. At this stage the typical *Crassostrea* oyster larvae is ~275–300 µm in diameter (Fig. 1.1). Oyster larvae, as is the case for monomyarian bivalves, generally settle and cement themselves via the left valve onto a hard substrate and quickly initiate metamorphosis to the juvenile stage, often in the company of other oysters. There they remain and grow to maturity and remain sedentary for the rest of their lives.

The role of feeding and feeding behavior in oysters is highly relevant to the siting of farms specific to the availability of adequate nutrition and overall carrying capacity to support multiple farms on the same bay or estuary. Oysters respond to temperature, seston quality, and quantity, and can exquisitely modulate their feeding behavior relative to food availability and other physiographic parameters (see extensive review by Bayne, 2017). Oysters are also known for their prodigious filtration capacity that en masse, often in reefs of many millions of individuals, can process huge volumes of seawater on a daily basis. Overstocking of farms and induced trophic risk can be an important source of mortality of oysters. Water filtration behaviors for oysters have been assessed for many species and, as is similar for other bivalves, filtration rates for individual oysters are highly variable and dependent on body size, seawater temperature, physiological state, and the availability of suspended food. Because oyster reefs provide significant habitat for other aquatic organisms for all or part of their lives, oysters are often referred to as ecosystem engineers. Oysters living in either natural reefs or intensive aquaculture have the capacity to impact water filtration dynamics, nutrient cycling, provision of habitat, and influence food web dynamics. Oysters are increasingly recognized for the ecosystem goods and services they can provide to the marine environment (Smaal et al., 2019).

The role of feeding, biodeposition, and growth in bivalves, including their ecological role in estuarine nutrient cycling, has been extensively modeled (Hawkins et al., 2002; Grant et al., 2005). More recently, modeling efforts have been employed to help site shellfish farms for optimized production (Ferreira et al., 2007; Silva et al., 2011; Hawkins et al., 2013; Newell et al., 2019, and see Chapter 10), including modeling ecosystem benefits specific to molluscan aquaculture (Saurel et al., 2012; Grant and Pastres, 2019; Rose et al., 2019). The stocking density of shellfish, ambient physiographic information, and flux of suspended seston all influence feeding in shellfish and therefore require detailed resolution of the variability in feeding for site specific application of modeling. These data currently are generally lacking for most shellfish sea farm locations and model validation for sites worldwide is urgently needed. Environmental data and especially the application of farm models is important to optimize shellfish production, especially for larger farms where social and ecological carrying capacities are important considerations.

The impacts on farming due to a changing climate are also important to considerations. Growers of Pacific oysters in the Pacific northwest of North America have been significantly impacted by changing ocean and estuarine water chemistry related to continental upwelling, resulting in increased dissolved carbon dioxide and reduced aragonite saturation state, leading to decreased availability of carbonate in the seawater to supply oyster embryos, especially during the first 24 hours of development (Barton et al., 2015). A reduced energetic capacity to biomineralize shell efficiently under low aragonite saturation conditions was proposed as a primary cause for reduced hatchery production of oysters (Waldbusser et al., 2013; Waldbusser and Salisbury, 2014), though other investigations on Pacific oysters found that the supply of endogenous reserves was not a limiting factor during early shell formation in larvae. Rather, constraints on the kinetics regulating rate processes associated with calcification in larvae under low aragonite saturation conditions were proposed to explain commonly observed hatchery failures associated with corrosive seawater conditions (Frieder et al., 2017). The oyster industry in the US Pacific northwest adapted quickly to increasingly corrosive seawater conditions by buffering incoming hatchery seawater with sodium carbonate to simply increase aragonite saturation and enabled a resumption in oyster production for most hatcheries. Looking ahead, impacts to oysters due to a changing climate may not be so simply resolved, as significant challenges will emerge that require continued applied research and implementation of adaptation strategies to help ensure a viable oyster industry into the future.

Oyster aquaculture

On a worldwide basis, oyster aquaculture is generally practiced in near-shore waters between the mid-intertidal to subtidal depths of generally less than 5 m. By a wide margin, cupped oysters (*Crassostrea* spp. and *Saccostrea* spp.) are the focus of interest. China, Japan, and Korea lead the world in production of farmed oysters by a considerable amount, though oysters of a variety of species are reared on all continents except Antarctica. China is the major producer far and away of cupped oysters accounting in 2017 for almost 4.9 million metric tons (MT) produced (FAO, 2017). There are about 15 species of oysters grown or harvested commercially around the world. While most oysters are produced in China, there were an additional 978,918 MT of oysters produced by a further 22 countries (Table 1.1). See Box 1.1 for a brief description of the major oyster species cultivated worldwide. There are other cultured edible oysters, including tropical mangrove oysters (*C. rhizophorae*, *C. corteziensis*, *C. gasar*, and *C. tulipa*);

Table 1.1 Production (metric tons) of the major species of oysters harvested or cultivated worldwide. Adapted from Food and Agriculture Organization of the United Nations, Fisheries and Aquaculture Department, statistical collections: global aquaculture production (2017).

Common name	Scientific name	Country	Metric tons produced, 2017
Chilean oyster	*Crassostrea chiliensis*	Chile	377
Cortez oyster	*Crassostrea corteziensis*	Mexico	7,358
Cupped oyster	*Crassostrea* spp.	Thailand	14,981
		Netherlands	2,900
		Brazil	2,700
		USA	2,639
Eastern oyster	*Crassostrea virginica*	USA	112,408
		Canada	5,788
European oyster	*Ostrea edulis*	France	710
		Netherlands	350
		Spain	287
		Ireland	237
Flat and cupped oysters nei	*Ostrea and Crassostrea* spp.	Australia	8,925
		Portugal	1,455
Gasar cupped oyster	*Crassostrea gasar*	Senegal	194
Hong Kong oyster	*Crassostrea hongkongensis*	China (2018)	*1,800,000*
Indian backwater oyster	*Crassostrea madrasensis*	India	4,000
Mangrove cupped oyster	*Crassostrea rhizophorae*	Cuba	1,089
Pacific oyster	*Crassostrea gigas*	China (2018)	*1,240,000*
		Korea, Republic of	315,255
		Japan	173,800
		France	64,200
		USA	25,845
		Taiwan Province of China	23,179
		Ireland	9,822
		Canada	8,012
		Mexico	7,534
		Australia	3,004
		United Kingdom	2,294
		New Zealand	1,834
		Channel Islands	1,312
		Spain	806
		Portugal	600
		Morocco	411
		Namibia	400
		South Africa	336
		Italy	145
Portugese oyster	*Crassostrea angulata*	China (2018)	*2,100,000*
Slipper cupped oyster	*Crassostrea iredalei*	Philippines	22,944

Cuban production of mangrove oysters, for example, was 1089 MT in 2017 (FAO, 2017). Culture operations for other mangrove species, however, have historically been small in scale with total production of mangrove oysters outside of Cuban production being less than 19 MT (FAO, 2017).

Box 1.1 A brief description of the major species of oysters produced in the world (with Ximing Guo, personal communication, 2020).

Crassostrea gigas – Pacific (Japanese) oyster

Pacific oysters are the most widely produced oyster in the world (introduced to over 60 countries) with major hatchery production in Asia where this species is also native (northern China, Japan and Korea). Pacific oysters have been widely introduced for aquaculture in Australia, New Zealand, France, the UK, Germany, the Netherlands, Spain, North America (west coast), Brazil, Morocco, Algeria, Namibia and South Africa among other locations. Devastating losses due to Ostreid herpesvirus 1-μVar (Pacific Oyster Mortality Syndrome [POMS]) have impacted production, mainly in Asia, Australia, New Zealand and France but breeding for resistance has proved to be an effective strategy for reducing mortalities.

Crassostrea virginica – eastern oyster

Native to eastern North America and long harvested on North American East and Gulf coasts from Chaleur Bay, New Brunswick, Canada to western Texas, eastern oysters are widely farmed and popular in half-shell markets. This oyster is also susceptible to diseases that severely limited wild production over the last 50 years, though breeding for disease resistance and more recently the use of triploids has been effective on the US east coast to boost production. Production in the Gulf of Mexico (western Florida, Louisiana, Mississippi, and Texas) is mainly from wild set though farming of hatchery produced seed is increasing. Changes in freshwater inputs have recently impacted wild production in the eastern Gulf of Mexico. Limited culture of *C. virginica* also occurs in California and Washington State with a small naturalized population in western North America located in southern British Columbia.

Crassostrea angulata – Portuguese or Fujian oyster

This small, thin-shelled and deeply cupped species is found intertidally along the coast of China south of the Yangtze River and is utilized for aquaculture production in southern China (primarily Fujian Province). Seed are primarily obtained via natural recruitment, although hatchery production, especially of triploids, is on the rise. In China, Portuguese oysters are favored for their reported superior flavor compared to *C. gigas*.

Crassostrea hongkongensis

Widely cultured in southern China primarily in Guangdong and Guangxi Provinces, the "white meat" oyster has been important for southern Chinese oyster production for the last 700 years. Much of the production was historically based on on-bottom culture due to the prevalence of typhoons but raft culture has proliferated in recent years.

Crassostrea sikamea – Kumamoto oyster

Native to Ariake Bay in southern Japan, southern Korea and southern China, Kumamoto oysters were originally transplanted to the US West Coast from Japan in the 1940s. *C. sikamea* broodstocks were re-introduced from the Ariake Sea in 2006 to retain the genetic identity of naturalized stocks in North America. Today, Kumamoto oysters remain a premium oyster cultured on the US West Coast for domestic and international half-shell markets.

Crassostrea iredalei – Philippine cupped oyster

Widely cultured at a small scale in the Philippines and Malaysia, the Philippine oyster is important in local diets and has attracted increased attention in recent years for aquaculture production.

Crassostrea madrasensis – Indian backwater oyster

Culture methods are well developed for this widespread, low-salinity tolerant and fast-growing intertidal oyster native to the Bay of Bengal. Culture and harvest of wild populations is widespread in eastern India (particularly in the state of Tamil Nadu) and Bangladesh.

Ostrea edulis – European flat oyster

Native to western Europe from Norway to Morocco, European flat oysters are farmed today, mainly in France but production is limited due to disease. Flat oyster production has been largely supplanted by the Pacific oyster. Only *O. edulis* grown in the Belon estuary in France are legally recognized as Belon oysters. Introduced and naturalized in North America, European flat oysters are harvested in small quantities, primarily in Maine.

Ostrea lurida – Olympia oyster

The flat oyster native to western North America was formerly abundant in estuaries along the west coast, particularly in the coastal estuaries from Northern California to Washington State and Puget Sound. Decimated by over-harvest in the late 1800s, Olympia oysters are being restored into former habitats but the species was largely displaced for aquaculture production by the Pacific oyster, beginning in the 1920s. Olympia oysters today are enjoying a comeback with small scale but active sea farming for this species mainly in Washington State.

Ostrea angasi – Australian mud oyster

Native populations of this flat oyster in southern Australia were severely overharvested with new commercial production currently reported to be augmenting Pacific oyster culture operations impacted by POMS in the last few years.

Saccostrea glomerata – Sydney rock oyster

Native to eastern Australia the Sydney rock oyster is extensively cultured in estuaries on both coasts using intensive off bottom tray-based production. Devastating losses due to QX, the protozoan parasite, *Marteilia sydneyi*, has resulted in contraction of the industry in New South Wales in recent years; however, breeding efforts initiated since 1997 have resulted in increased resistance to mortalities.

Hatchery and nursery techniques

Sourcing oyster seed is one of the earliest decisions a farmer has to make in establishing a successful farming operation. Multiple factors come into play with the farmer essentially having three choices: (1) collecting juvenile oysters, referred to as spat, from the wild; (2) remotely setting larvae acquired from a shellfish hatchery; or (3) acquiring juvenile oysters through the hatchery and nursery process. Collection of wild spat remains an economical and common method for acquiring juveniles for grow-out and was formerly the basis for most production in Asia, including China. In the last few decades, however, a significant portion of the vast Chinese oyster production is now hatchery produced (Guo et al., 1999), as is the case for most world production. Oyster hatcheries come in many different forms, from small, seasonal operations that produce 1 million seed annually for one farm operation, to large industrial hatcheries that produce billions of oyster seed annually, which supply significant segments of the industry. Hatchery production offers the oyster farmer numerous advantages over the collection of wild spat as a source of seed. Reliability of production and timing of seed availability alone will likely offset any additional costs to the farmer, particularly in growing areas that have a short optimal growth season. For example, in northern New England, oyster farmers generally acquire hatchery-reared eastern oyster seed in late May or early June after water temperatures have seasonally warmed to at least 15°C (Fig. 1.2). Attempts to rear small (< 5 mm shell height [SH]) *C. virginica* seed in Maine waters below 15°C typically results in minimal growth and is often accompanied by high rates of mortality

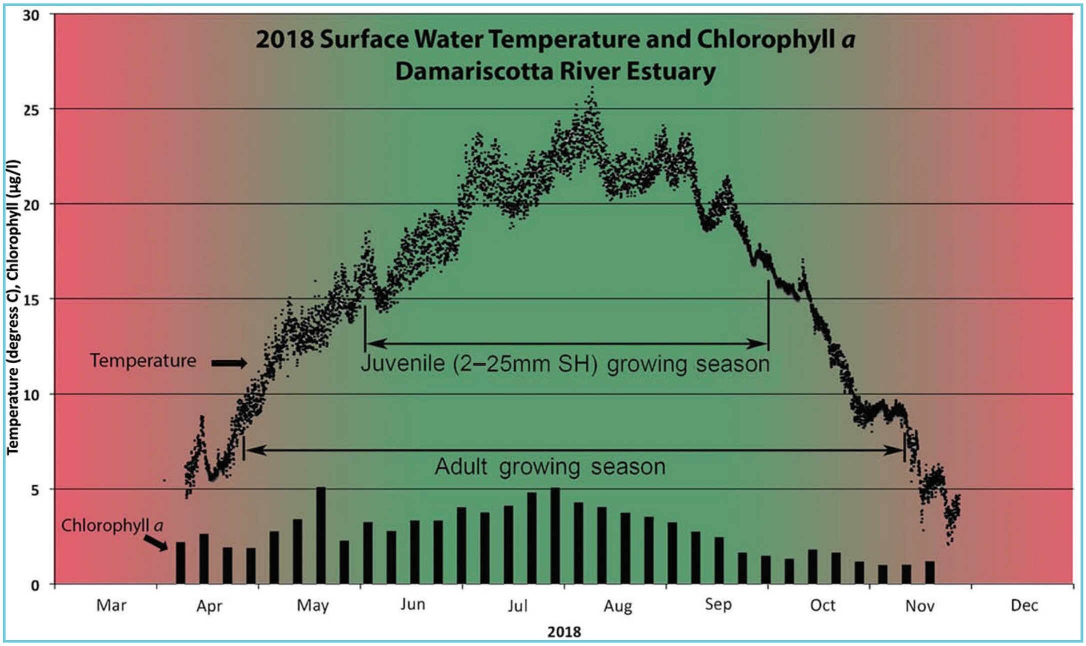

Figure 1.2 Damariscotta River, Maine surface water temperature and seasonal chlorophyll content set the optimal growing season for eastern oysters in this location. Image courtesy of Chris Davis. Data obtained from University of Maine Land/Ocean Biogeochemical Observatory buoy.

should less optimal water temperatures exceed 1 to 2 weeks. Given the relatively short 4 to 5 month growing season for juvenile oysters in northern New England waters, most farmers find it essential that hatchery seed availability coincides with the onset of suitable environmental growing conditions. In contrast, in warmer regions, such as the Chesapeake Bay or Gulf of Mexico, growers may start seed at different times through the year to ensure year-round harvest. Hatchery production of seed also affords the opportunity to take advantage of genetic improvements (for example, disease resistance, higher yield, optimal market characteristics, and polyploidy) that may be extremely important to the grower. In southern New England and the mid-Atlantic US, for example, the availability of hatchery-produced, disease-resistant eastern oyster seed enables the industry to exist in the face of two highly virulent protozoan diseases. Australian, New Zealand, and French oyster industries similarly rely today on disease-resistant strains of Pacific oysters that are only available through hatchery production. While the details of hatchery operations are similar for many bivalves and beyond the scope of this chapter, the fundamentals of hatchery culture specific to oysters are discussed below. These include broodstock management, methods of larval rearing, and methods for setting and rearing juveniles to a size suitable for out-planting to farms.

Broodstock management – applying breeding science to oysters

Sourcing broodstock

Most oyster hatcheries take care to ensure that the broodstock parental lines they select are well-suited to the growing environment in which the offspring will be cultivated. Often, sourcing oysters for broodstock from the same general locale where oysters are intended to be cultivated is a good, fundamental practice. The existence of distinct physiological/genetic races for oysters has been long-established with traits of interest to oyster farmers varying according to locality. Hatchery operators should never introduce oysters for broodstock from outside the general region, unless specific guidance is attained and where warranted disease testing and permitting conditions (for example, holding in quarantine) rigorously applied. There have been numerous examples of oysters harboring pests and diseases and introducing them to an oyster growing region with catastrophic consequences. As an example, a massive die off of eastern oysters in the 1950s due to the MSX pathogen (multinucleated sphere unknown although the causative agent later identified as *Haplosporidium nelsoni*) in Delaware and Chesapeake Bays most likely arose following an illegal transplant of Pacific oysters. In fact, today shellfish producers increasingly use oyster broodstocks bred for some level of disease resistance. The emergence of the MSX pathogen resulted in one of the most important selective breeding programs in the US being established by researchers at Rutgers University. Following four decades of line selection of survivors exposed to waters infected by MSX, the lines from Rutgers University have demonstrated remarkable resistance (although not immunity) to *H. nelsoni* infections, so much so that oysters can be commercially reared to market size prior to succumbing to the disease (Guo et al., 2008). Line breeding programs targeting other oyster pathogens, such as Dermo (*Perkensis marinis*), roseovarius oyster disease (ROD) (*Roseovarius crassostreae*), Denman Island Disease (*Mikrocytos mackini*), and Bonomia (*Bonomia ostreae*), have similarly yielded resistant broodstock lines made available to hatcheries (Proestou et al., 2016). Similar efforts have focused on enhancing growth and yield for various species of oysters including *C. virginica*, *O. edulis* (Newkirk, 1988), *O. chiliensis* (Toro and Newkirk, 1991), and *C. gigas*. A public breeding program focused on Pacific oysters (Molluscan Broodstock Program) housed at Oregon State University on the US west coast was established in 1996 with the intent to increase the average yield in farmed Pacific oysters (de Melo et al., 2016). Long-term breeding in Pacific oysters has been an integral part of the industry in France, Australia, and New Zealand as well. Oysters are also amenable to production improvement through a combined approach that takes advantage of selection in combination with crossbreeding. Higher yields in Pacific oysters are observed following crossing of unrelated, partially inbred oyster lines to induce heterosis or hybrid vigor (Hedgecock and Davis, 2007). Advantages to a combined selection/crossbreeding approach include a reduced risk of inbreeding, a problem inherent to shellfish breeding program, generally. The advantage of using broodstock resistant to diseases of oyster stocks will become increasingly important in the years ahead as increased disease incidence impacts oyster production areas around the world. Recently, the emergence of *Ostreid herpesvirus* 1-µVar (Pacific Oyster Mortality Syndrome [POMS]) has refocused growers around the world on the importance of genetics and breeding in oysters (Dégremont et al., 2015). Emerging diseases combined with the increasing emphasis on marketing oysters having specific traits (for example, survival, meat yield, shell color) coupled with market driven, increased pressure on oyster growing regions to produce more oysters, will likely increase the emphasis on optimizing the management of oysters for their genetic resources.

Conditioning, spawning, and larval culture

The interplay among availability of nutritional resources and endogenous changes due to environmental influences (temperature, food supplies, and light/dark cycles) that serve to initiate reproduction should be controlled by the operator to the extent possible to ensure success. Oysters used for broodstock are more often selected for convenience than for their qualitative value for gamete production. Hatchery operators routinely condition oysters for reproduction outside of the normal window for natural production and much depends upon the nutritional status of the oysters in the field, especially when gamete maturation is attempted outside of the natural cycle of reproduction. The physiological state of broodstock oysters specific to storage metabolism and resources, is therefore important to assess. Control over the nutrition of oysters in the field is difficult to achieve, but having oysters in good condition relative to stored reserves (for example, glycogen content) is nevertheless important. Adequate stored glycogen reserves are used during the conditioning phase to invest eggs, for example, with adequate energy stores (mainly lipids) through the process of vitellogenesis. Both early embryogenesis and healthy larval activity, once feeding stages are reached, are enhanced by having adequate lipid reserves in the egg.

Hatchery operators do not routinely screen oyster broodstocks for glycogen content nor are gametes regularly assessed for lipid content, but the operator should attempt to introduce oysters that have adequate energy stores whenever possible. Using Pacific oysters as an example, the movement of oysters to ‘fattening ground’ or areas that are richer in natural phytoplankton abundance at certain times of the year relative to other locations has been a feature that growers in the Pacific northwest of North America have long used to ensure that oysters subsequently brought into the hatchery environment for broodstock are in the best condition possible. While regulating storage cycles in oysters has been a minor component of hatchery management for oyster production, recent work suggests that better control over these stored energy reserves in oyster broodstocks is important to consider.

Once in the hatchery, it is important to optimize the feeding protocols that supply both daily energy needs and support gamete production. Oysters are typically fed a mix of hatchery cultured algae over a period of 4 to 6 weeks at an elevated seawater temperature (typically 18–24°C) to induce a shift from storage metabolism to gametogenesis. Cultured species used for conditioning oysters typically include the Prymnesiophytes *Tisochrysis lutea* (formally *Isochrysi* aff. *galbana* clone Tahiti T-Iso) and *Pavlova lutheri* (National Marine Fisheries Service Milford Shellfish Laboratory clone 459), the diatoms *Chaetoceros calcitrans* and *C. gracilis*, and the green alga, *Tetraselmis suecica*, among others. A basic guideline for broodstock oyster feeding is to supply an equivalent mix of live algae (based on cell volume) totaling at least 2×10^9 (T-iso equivalent) cells per oyster per day, or about 5% of their tissue mass per day (see Chapters 12 and 13).

A number of research investigations conducted in the early 1980s (Lannan et al., 1980; Muranaka and Lannan, 1984) documented the relationships between temperature, supplemental feeding, and the rate of gametogenesis in Pacific oysters. Managers generally introduce broodstock into the hatchery for conditioning in late fall and early winter, depending on the schedule for first spawns of the season. Protocols described in Muranaka and Lannan (1984), for example, prescribe an approach based on the use of degree days. Oysters are generally placed into broodstock tanks with either running seawater or seawater that is changed out every day or so, at the ambient temperature they were experiencing in the field. The temperature is ramped 1°C per day until the conditioning temperature is reached (usually between 18–24°C). Oysters are maintained at the prescribed temperature for the number of days required to produce ripe (viable) gametes, based on a prescribed feeding regime and degree days. Following these simple protocols will assist hatchery managers in producing broodstock oysters that are ready to spawn well provisioned gametes as needed to produce regular larval cohorts.

Broodstock use, spawning, and rearing larvae to the pediveliger stage

One of the goals of hatchery technicians is to produce large numbers of viable larvae while at the same time maintaining a high degree of genetic variability in the offspring. Given the high fecundity in cupped oysters (*Crassostrea* spp. and *Saccostrea* spp.), conceivably, very low numbers of parents can satisfy the larval needs of the hatchery, but if low parental numbers are used, issues related to low genetic variability in the offspring may come into play, which can result in poor overall fitness and/or viability with the potential of inbreeding depression occurring in subsequent generations should offspring be used as future broodstock. Thus, it is important to bring into reproductive condition as many broodstock as possible for each spawning event in order to optimize genetic diversity. It is similarly important to use as many male and female oysters as possible. Ideally, the hatchery operator will collect gametes from male and females and conduct pairmatings (use sperm from one male to fertilize the eggs from a single female) and then combine multiple pairmatings into one culture for rearing.

Cupped oysters of the genus *Crassostrea* are oviparous, broadcast spawners that release ova or sperm directly into the water column where fertilization occurs. Spawning is typically achieved using thermal ramps (3–8°C) of slowly increasing seawater temperature. Shallow baths containing broodstock oysters may be warmed by heat lamps, immersion heaters, or the addition of warmed seawater. Male oysters generally initiate shedding of gametes first. Spawning males are immediately removed from the water bath and placed into individual containers and allowed to continue to spawn. Similarly, once females commence spawning they are similarly rinsed and separated into individual spawning dishes and allowed to continue to shed gametes. Eggs from each parent are counted and generally pooled with each parent contributing an equal number of gametes. Similarly, sperm from males is pooled prior to use. Ideally, within 30–60 minutes of the initial spawning event, the egg suspension is fertilized by the addition of sperm at a ratio of approximately 4–10 sperm cells per egg, as confirmed by microscopic examination. As mentioned earlier, hatcheries are generally interested in maximizing genetic diversity of the offspring, in which case, having an equal number of males and females will provide the greatest effective population size.

Oysters are among a small group of bivalves that do not require that gametes be shed naturally, as both eggs and sperm are viable once exposed to seawater. Under some mating designs, especially when gamete contamination must be avoided, there are significant advantages to this approach. The process entails a thorough cleaning of the exterior shells and then removal of the left valve. A scalpel is used to lightly penetrate the ripe gonad to release either the eggs or sperm. A squeeze bottle filled with 1-µm filtered sea water is useful to wash excised gametes into a clean container. The gametes are then sexed by microscopy and eggs and sperm set aside until all broodstock have been stripped. Pooling of eggs and sperm will depend on the mating scheme, but ought to be accomplished within a 1 hour timeframe.

Spawning in flat oysters within the genus *Ostrea* may also be initiated using thermal ramps by inducing males to release sperm (as accumulations of sperm in balls). Sperm balls or individual sperm are inhaled by ripe females and individual sperm fertilize eggs retained in the female mantle cavity. Brooding of fertilized embryos occurs for 1 week or more prior to the release of larvae into the water column. European flat oysters, for example typically release larvae of 170–190 µm shell length between 6 and 8 days post spawn.

The culturing of larvae can be accomplished using either batch or flow-through culture systems. In the batch culture system, larvae suspensions are typically held in conical-bottom tanks or flat-bottom tanks when larger culture volumes (> 1000–2000 L) are required. Culture water (filtered to 1–5 µm) is changed every 48–72 hours to ensure that accumulation of metabolites does not create stressful conditions (Creswell et al., 1990). Both continuous or batch feeding of microalgae of the appropriate species and cell concentration depends upon the size, age, and concentration of larvae in the culture tank. In contrast, flow-through culture systems allow for considerably higher larvae concentrations, thus allowing for a significantly smaller footprint in the hatchery (Fig. 1.3). Typically, flow-through systems continually add filtered, algae-rich culture water at rates of up to 18 water replacements per day. Appropriately sized discharge screens (often referred to as 'banjo' screens) ensure that larvae are not flushed out of the system. Supan (2014) described setting up a flow-through larval system for oysters. Table 1.2 provides some useful parameters for the culture of *C. virginica*. The advantages of flow-through systems include a smaller footprint for tanks, elimination of oyster waste products, and oysters maintained on a continuous algal supply. The disadvantages include greater water flow, heat, and algal requirements. The fine points of larvae culture is beyond the scope of this chapter and the reader is encouraged to consult Helm et al. (2004) and Supan (2014) who provide a comprehensive discussion on approaches to the larval culture of oysters (see also Chapter 12).

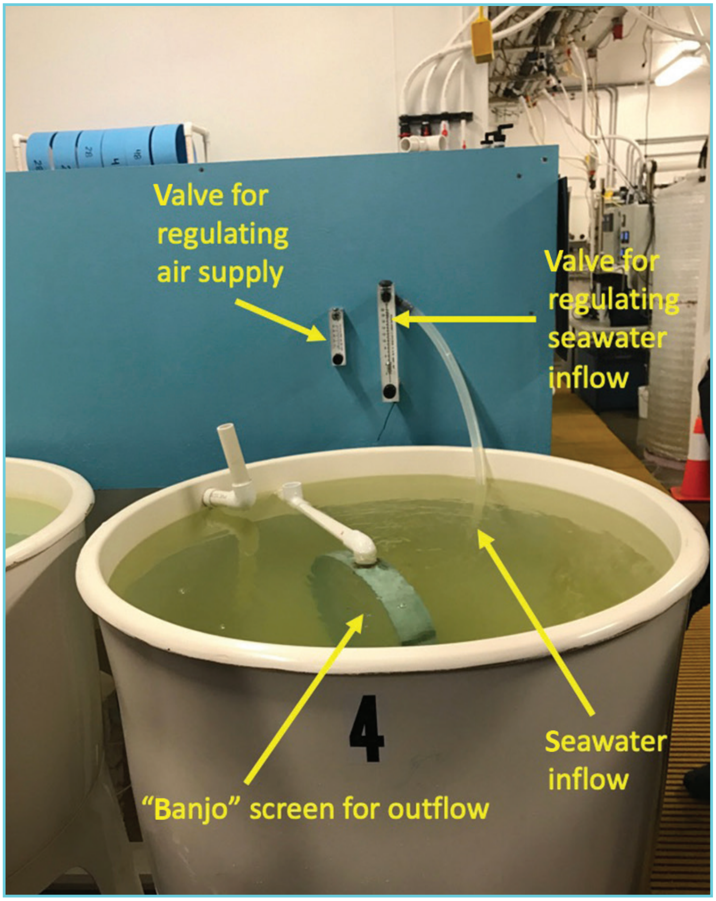

Figure 1.3 Larval continuous flow-through system. A 'banjo' screen combined with circulation via an air diffuser assist in preventing larvae from being impinged on the outflow screen. Courtesy of Pacific Hybreed, Inc.

Table 1.2 *Crassostrea virginica* larval culture parameters. Adapted from Creswell et al. (1990) and Margaret et al. (1993).

Approximate days/ development post spawn	Larvae size SL (µm)	Seive size (µm)	Larval density (static tank) (per mL)	Larval density (flow-through with 12–18 turnovers per 24 h) (per mL)	Phytoplankton density (cells.mL^{-1})
Eggs	45	22	10	0	-
D-hinge	75	45	5	200	20,000–25,000
2–3	120–130	63	5	150	20,000–25,000
4–5 (umbones developed)	135–170	90	5	130	25,000–30,000
6	180–200	125	5	130	30,000-40,000
day 8 (pediveliger)	240–260	150	4	100	50,000
10	260–280	165	4	100	60,000
day 11–12 (eyed larvae)	280–300	180	3	75	70,000–80,000
day 14 (setting)	330	212	1.5	50	100,000–150,000

Settlement and metamorphosis

The pediveliger stage in oysters commences late in the larval cycle, typically between 14 and 21 days from egg stage in modern facilities. For *Crassostrea* oysters, larvae are between 250–275 μm in length. Pediveligers are characterized by the presence of a pigmented 'eyespot,' a ciliated foot and upward spiral swimming behavior that is often associated with copious mucus production and clumping of larvae. Hatchery protocols are adjusted at this time to provide satisfactory conditions for successful settlement and metamorphosis. Accommodating for the cementation stage in the oyster life history requires that favorable substrate be made available to pediveligers with clean oyster shell providing the ideal substrate, facilitating a gregarious setting response (Fig. 1.4). Depending upon the end use of the oysters, whole shell or micro-cultch can be used as a setting surface, generating clusters of spat on shell or single seed, respectively.

To generate spat on shell clusters, pediveliger (Fig. 1.5) larvae are introduced into static setting tanks, stocked with clean, whole oyster shells (or other favorable substrate) with filtered seawater that is generously aerated. Hatchery technicians may monitor the rate of settlement and either remove the shell from the culture tanks when the desired number of oysters have set on individual shells or add additional larvae. Once the oysters have cemented themselves to the shell cultch and have been allowed a period of growth (typically at least 3 days), the shell bags, with the attached spat, can be transferred to the field nursery.

Oyster farmers targeting the 'half shell' market tend to pay particular attention to the shell shape and thus often obtain single oysters from the shellfish hatchery. Micro-cultch, composed of ground oyster shell chip is offered to pediveligers in lieu of whole shell. Resembling a fine powder, shell chip is typically ground from whole shell using a hammer mill followed by sieving on appropriately sized screens to produce micro-cultch in the 250–300 μm diameter size, essentially the same size as the pediveliger. Once cementation and metamorphosis have occurred, the oyster rapidly outgrows the micro-cultch, producing a "single" oyster. Single oyster seed are typically raised in various types of nurseries (for example, land-based upwellers, floating upweller

Figure 1.4 Pacific oyster spat set onto oyster shells contained in mesh cultch bags. Shells in bags are later spread onto beaches for grow-out. Courtesy of Taylor Shellfish Company.

Figure 1.5 An oyster pediveliger, competent to settle and metamorphose, is characterized by an eye spot and extended foot. Courtesy of Chris Davis.

systems, and so on) to a size more easily handled by oyster farmers (for example, sufficiently large to be retained on 2-mm mesh screens).

A variation of setting oysters on cultch or micro-cultch is 'remote setting' whereby eyed larvae are drained from the larval tanks and shipped to field setting nurseries oftentimes a great distance from the hatchery. Eyed larvae may be stored under refrigerated conditions (6–8°C) for at least 4 days before setting. The reduced cost of eyed larvae to the oyster farmer compared to 2–3 mm shell height post set can justify the cost of building a remote setting system.

Triploid oysters

The first development and application of triploidy in animals (organisms containing three sets of chromosomes in each cell nucleus) occurred in cupped oysters within the genus *Crassostrea* in the 1980s when researchers at the University of Maine modified triploid induction techniques developed for salmonids to produce triploid *C. virginica* (Stanley et al., 1984). Sexual reproduction in bivalves, including oysters, is unusual in that meiosis in eggs is not complete until the egg is fertilized and following two sequential meiotic chromosome divisions that release 2N and then 1N sets of chromosomes in the form of two polar bodies expelled from the fertilized egg. In diploids, the release of first and second polar bodies reduces the egg from an initial 4N state to 2N (diploid) and haploid (1N) state, respectively. The sperm adds another chromosome set and results in a diploid (2N) embryo. Induced triploid methods simply prevent the release of either the first or (more commonly) the second polar body. Historically, chemical induction of triploid oysters largely relied upon the application of either the fungal metabolite cytochalasin B or the purine, 6-dimethylaminopurine to inhibit the release/formation of a polar body. Unfortunately, 100% production of triploid larvae is rarely achieved using these methods due to asynchrony in developmental rates within individual embryos. The work initiated in Maine was further developed in the US Pacific northwest for Pacific oysters. Advantages to triploid oysters are due to their increased marketability due to the reduced capacity to produce gametes and tendency to become 'spawny' or 'watery,' as compared to diploids under similar environmental conditions. The Pacific oyster was particularly amenable to triploid development as marketability for triploids was enhanced during the summer months compared to diploids in the productive grow-out areas in Washington State (Allen and Downing, 1986) (Fig. 1.6). Triploid oysters also generally grow faster than diploids under conditions favorable for oyster growth as the energy normally contributed to reproduction is thought to be diverted toward enhanced tissue growth. To reduce the need for chemical treatments and to achieve

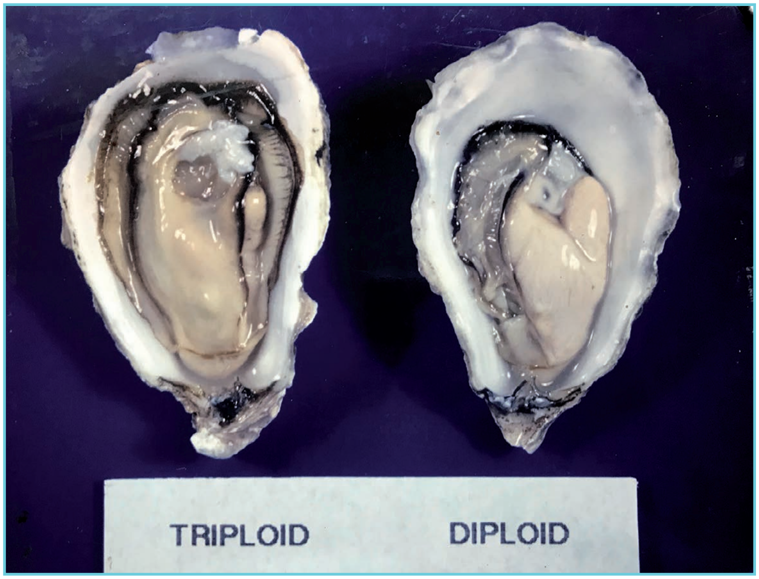

Figure 1.6 Diploid and triploid Pacific oysters. Note extensive development of germinal tissue in the diploid (female) compared to the triploid oyster. Courtesy of Joth Davis.

100% triploid induction, researchers at the University of Washington and Rutgers University undertook a new approach. Initially working with Pacific oysters and later eastern oysters, they were able to produce tetraploid (4N) oysters that when mated with diploid oysters, resulted in 100% "natural" triploid offspring (Guo et al., 1996). Generally, tetraploid males are crossed with diploid females. Today, all triploid production of oysters using tetraploid broodstock in matings with diploid females is commonplace and a mainstay of hatchery production for much of the industry in Europe, North America, and Australia. Triploid oysters are often observed to outperform diploid in many environments, including growing locations impacted by disease (Matthiessen and Davis, 1991; Dégremont et al., 2012). In recent years, however, high loss rates (up to 90%) in triploid oysters have been observed by growers in different parts of the world, related perhaps to increased susceptibility to multi-stress responses associated with excessive heat or cold, dissolved oxygen or disease pressure (Davis, J., unpub. obs.; Guévélou et al., 2019). The oyster farmer may desire to assess carefully their region and farm site for its suitability for triploid production and caution is recommended until triploid oyster mortality patterns are better understood and resolved.

Land- and field-based nursery culture of oysters

There are a number of options available for raising seed oysters from a smaller (more affordable) size to a more easily handled size for grow-out. Many growers, especially as they increase the size of their operation, may seek to add or expand their nursery operations. Typically, farmers may choose to operate a field nursery on the farm, employing fine mesh containers with an active program of grading and splitting seed, or opt to cultivate seed under more controlled conditions in some type of upwelling system.

Upwelling systems

The function of shellfish upwellers is to provide a secure growing environment for high density three-dimensional culture of juvenile (1–25 mm shell length [SL]) seed while providing optimal rates of water flow containing the natural seston that supports feeding, growth, and the removal of waste products. The benefits of three-dimensional upwellers compared to two-dimensional nursery systems, such as floating screens or raceways, include enhanced growth rates, reduced space requirements, exclusion of predators, and the ease and efficiency of handling large quantities of small oysters. These advantages may be offset by greater capital and operating costs as well as access and dependence on a reliable source of energy to run a system dependent on pumping seawater. Given the high densities of seed oysters held in upwellers, it is essential that the systems have alarms should a pump fail and the oysters are left in stagnant flow conditions. Under such conditions, levels of dissolved oxygen can rapidly become depleted resulting in mortality. When possible, upwelling systems should be designed to drain the water should a pump failure occur, thereby reducing the risk of loss given that oyster seed can survive out of water for considerably longer periods of time than under submerged, but stagnant conditions.

Upwellers consist of silos, bins, or 'bottles' constructed with an appropriate mesh size on the bottom to contain the seed while allow for adequate water flow up through a bed of shellfish seed (Fig. 1.7). Round silos are often constructed of thin walled (schedule 20) PVC pipe, plastic barrels and buckets, or custom fabricated fiberglass while rectangular bins usually consist of coated plywood, plastic sheet stock, or molded fiberglass. The silo bottom is covered by mesh fabric designed to contain the seed oysters while allowing for suitable water flow. It is critical that the mesh size (diagonal dimension) be no greater than half the shell height of the smallest seed oysters to assure full containment. The bottom mesh may consist of woven polyester monofilament fabric, extruded polyethylene plastic mesh netting, or stainless steel screening which is glued or mechanically fastened to the silo or bin.

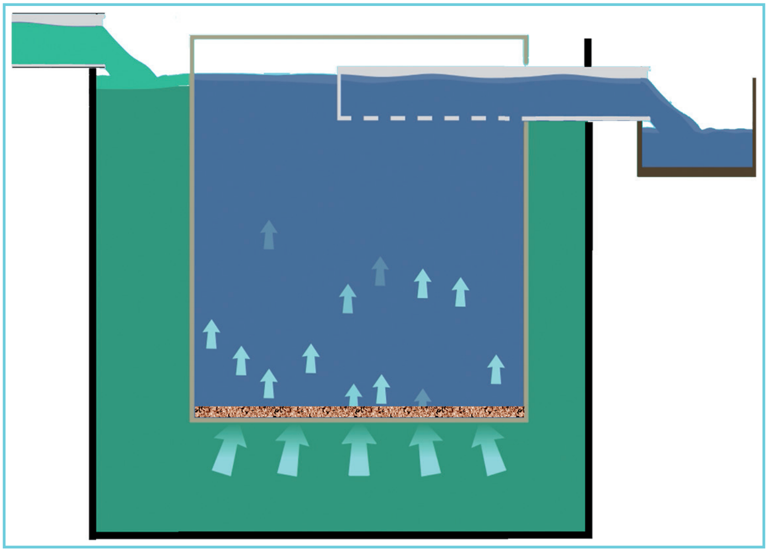

Figure 1.7 Illustration of a forced flow upweller system for oysters. Courtesy of Chris Davis.

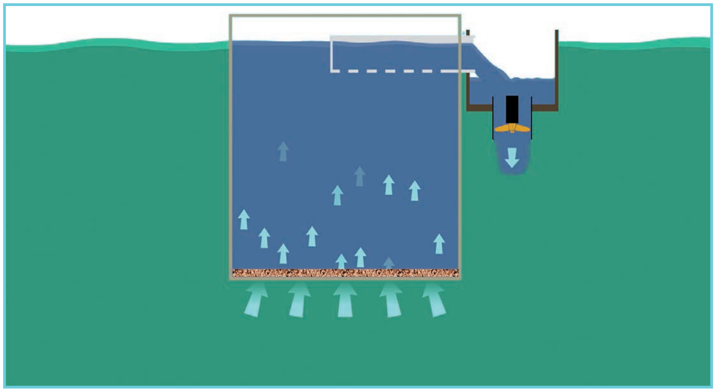

Figure 1.8 Illustration of a passive flow upweller system for oysters. Note the discharge pump lies downstream of the upweller. Courtesy of Chris Davis.

Land-based oyster upweller systems can provide a secure nursery culture environment both indoors and outdoors given suitable access to a seawater source. Most land-based systems employ a forced flow design whereby incoming water floods a tank containing the silos with water being forced through the silos in order to exit through a discharge trough (Fig. 1.7). Pumping requirements tend to be higher given the greater head (lift) needed onshore depending upon the elevation of the upwellers above sea level.

Floating **Up**weller **Sy**stems (FLUPSY) dramatically reduce energy costs given that water pumps require minimal lift to create the needed flow. Both forced and passive designs can accomplish this, although passive systems tend to be more efficient and require less maintenance and cleaning of biofouling organisms as they function by evacuating the water through the exit trough which contains the discharge pump (Fig. 1.8). Several US companies manufacture turnkey systems, although many oyster farmers construct their own to their specific design and needs (Fig. 1.9).

Water flowing through the upweller silos needs to be sufficient to deliver algae-rich water throughout each silo while minimizing downstream depletion effects such that oysters on the surface layer do not receive significantly less food than those closer to the water source.

Figure 1.9 A large multi-bin upwelling system in Washington State. Water flow in large systems are best driven by slow turning paddle wheels. Courtesy of Taylor Shellfish Company.

Figure 1.10 Small-scale tubular upweller system for use with juvenile oyster seed. Courtesy of Chris Davis.

Tubular upweller systems can be used for small oysters (2–10 mm SH) whereby the water flow can be adjusted to suspend and tumble the oysters in the water column (Fig. 1.10). Use of a hand-held fluorometer to monitor inflow and outflow levels can be useful in managing the seed size, density, and water flow conditions. Figure 1.11 illustrates the ease of direct measurement of outflowing water (5 µg/L) from an upweller silo. Note that incoming water was 9 µg/L indicating a 44% decrease in seston levels. Levels of seston depletion can easily exceed 80% if the flow conditions are too low for the size and quantity of oyster seed as illustrated by a 3-day time series of chlorophyll-*a* levels in an overstocked upweller (Fig. 1.12). Long experience with oyster nursery systems suggests that managing the upweller system to achieve seston reductions lower than 40–50% of ambient incoming water results in optimal oyster growth at a high density of seed. Channelizing of water flow through the oyster seed can occur under certain seed size, seed density, and flow rate conditions, depending upon the configuration of the silo or bin and can result in the uneven distribution of feed throughout the silo and thus uneven growth. Since biofouling can present a significant obstacle depending on the site, good farm husbandry requires regular cleaning and grading of seed to ensure uniform and optimal rates of growth. Access to a source of fresh water to regularly rinse the oyster seed will greatly reduce the establishment of fouling organisms such as tunicates. Maintaining the appropriate density of oyster seed in the upwelling system is important to monitor, whether in

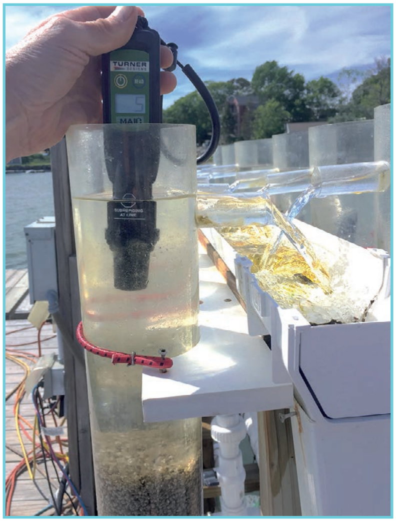

Figure 1.11 Direct measurement (5 µg/L) of in situ chlorophyll-*a* florescence in the discharge of an oyster upweller. Note that the incoming water contained 9 µg/L chlorophyll-*a* based upon florescence. Courtesy of Chris Davis.

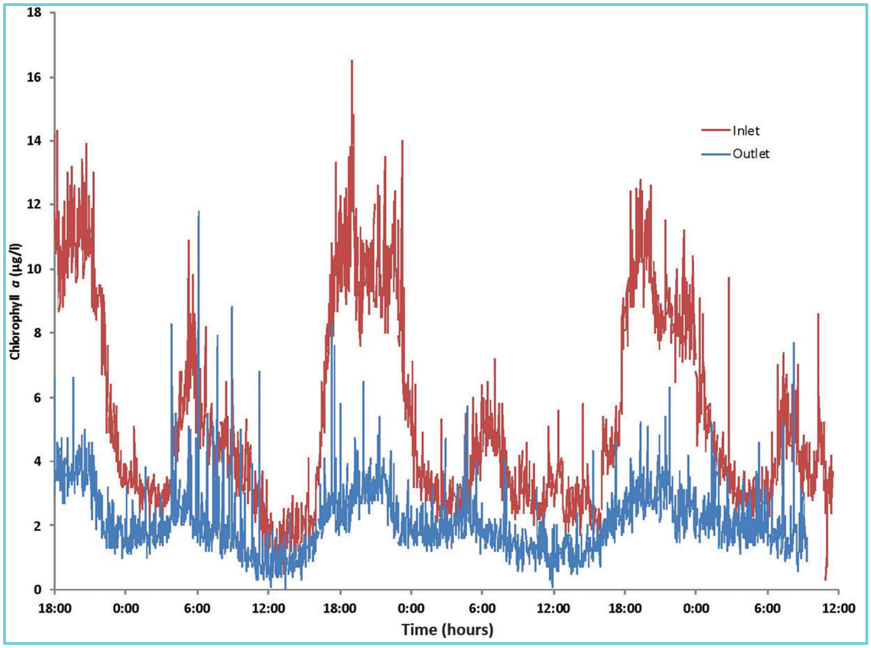

Figure 1.12 Time series (66 hours) of chlorophyll-*a* fluorescence for incoming and discharging water in an oyster upweller. Courtesy of Chris Davis.

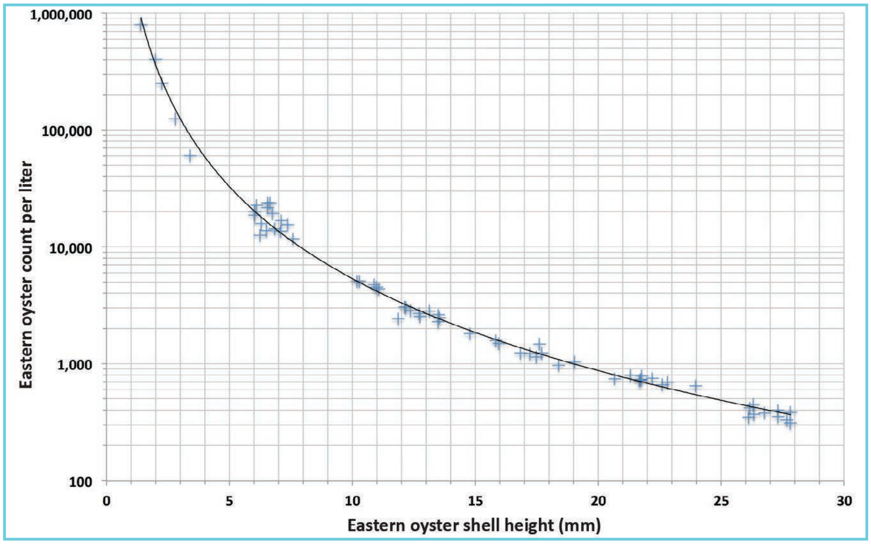

Figure 1.13 Relationship between shell height and count per liter for eastern oysters. Exponentially fitted curve $R^2 = 0.99$. Note that the y-axis is a log-scale. Courtesy of Chris Davis.

large FLUPSY or bottle-based upwellers. In all cases, the growth of seed is critically dependent on flow rate and seston quantity and quality supplying nutrition to oysters. The relationship between oyster size (shell height or biomass) and density (number of oysters per liter) of oysters in the nursery system should be calculated and density maintained within prescribed parameters for optimal system performance (Fig. 1.13).

Oyster grow-out

Site selection

Selecting a site for culturing oysters is the critical first step the new oyster farmer will consider. Siting of commercial grow-out locations depends on a variety of factors, which if not fully assessed will more than likely result in disappointing results. First, a practical note on permitting is necessary. Siting farms in the US and Canada, Australia, and New Zealand, and the European Union require working closely with local, regional, and federal agencies to obtain the permits necessary to establish a farm, cultivate, and sell oysters into commercial markets. Permitting requirements vary by country and region for all the different species being considered for cultivation and important considerations are covered elsewhere in this volume. From a production perspective, first and foremost, areas considered for oyster cultivation must be locations where seawater is reliably clean on a year-round basis with no significant sources of pollution from human habitation, large assemblages of birds and marine mammals, or which have a history of persistent biotoxins.

Oyster cultivation is often conducted in relatively protected bays and estuaries where a level of protection from prevailing winds and stormy weather is afforded. Siting oyster farms in natural assemblages of aquatic vegetation, including seagrasses is often discouraged by permitting agencies though oysters generally thrive in areas having sea grasses in the vicinity. Further, siting of oyster farms should be in areas that are not frequently closed due to biotoxins associated with harmful algal blooms, bacterial pathogens, viruses, or sources of industrial pollution. The volume of commercial and recreational boat traffic must be considered prior to siting an oyster farm, including assessing whether pollution from boating activities has the potential to impact oysters being cultured for human consumption. Proximity to marinas for growing out oysters to market size is often prohibited though nursery operations are often placed in protected anchorages where a power supply is available.

The expected annual range in seawater temperature, salinity, and availability of natural suspended food are very important considerations, and must be assessed in light of the biological requirements for the oyster species planned. As an example, Figure 1.2 illustrates the optimal annual temperature window for growing eastern oysters in productive estuaries along the coast of Maine, USA.

While a full consideration of all the criteria necessary to consider prior to siting an oyster farm is beyond the scope of this chapter, there are several excellent sources of information available (Boxes 1.2 and 1.3). Once the financial resources are in hand, the following considerations are necessary as a minimum when evaluating a site prior to conducting oyster farming. It should be confirmed that the:

- growing waters are safe for shellfish harvest
- substrate conditions are appropriate for the type of aquaculture anticipated
- seawater conditions (tidal currents, annual salinity, temperature, dissolved oxygen, carbonate chemistry conditions) are satisfactory for growing shellfish
- phytoplankton and other sources of shellfish nutrition are sufficient to grow oysters on an annual recurring basis

Box 1.2 Some additional practical resources for oyster farming.

- High density rearing of oyster larvae in flow through systems (Supan, 2014)
- Aquaculture management guide: manual for the identification and management of aquaculture production hazards. NRACAMG-2014 (Getchis, 2014)
- Contained culture cost analysis (Parker et al., 2014)
- Off-bottom culture of oysters in the Gulf of Mexico (Walton et al., 2013)
- Oyster hatchery techniques (Wallace et al., 2008)
- A practical manual for remote setting in virginia (Congrove et al., 2009)
- Small-scale oyster farming for pleasure and profit in Washington (Toba, 2002)
- *Shellfish Aquaculture and the Environment* (Shumway, 2011)
- *Oyster Culture* (Matthiessen, 2001)
- Methods for setting hatchery produced oyster larvae (Jones and Jones, 1983)

Box 1.3 A list of books/articles that address oyster culture.

Hector Bolitho, *The Glorious Oyster.* London, Alfred A. Knopf (1929)
Paul Brocchi, *Traité d'ostréiculture.* Paris, Librairie agricole de la maison rustique (1883)
William K. Brooks, *The Oyster.* Baltimore, MD, Johns Hopkins University Press (1891/1996)
Davide Carazzi, *Ostricultura e mitilicultura.* Milan, Ulrico Hoepli (1893)
Nicolas de La Casinière, *L'Huître.* Genève, Aubanel (2005)
J.J.M.C. Victor Coste, *Instructions pratiques sur la pisciculture.* Paris, Librairie de Victor Masson (1853)
J.J.M.C. Victor Coste, *Voyage d'exploration sur le littoral de la France et de l'Italie.* La Tremblade, le Musée Maritime (1855/1861/1993)
Eleanor Clark, *The Oysters of Locmariaquer.* Chicago, University of Chicago Press (1959)
Pierre Dalido, *L'huître du Morbihan.* Paris, Librairie Marcel Rivière (1948)
Birgit Damer, *Austern – Perlen des Meeres.* Weil der Stadt, Hädecke Verlag (2008)
David Erdal, *Local Heroes.* London, Viking (2008)
Mary J.K. Fisher, *Consider the Oyster.* New York, North Point Press (1941)
Roger Gachet, *Tout savoir sur les huîtres.* Nice, France Europe Éditions (2007)
David Gordon, Nancy Blanton, and Terry Nosho, *Heaven on the Half Shell.* Seattle, WA/Portland, OR, Washington Sea Grant Program/WestWinds Press (2001)
Michel Grelon, *Saintonge – pays des huîtres vertes.* La Rochelle, Éditions Rupella (1978)
Jacques et Ronan Guillet, *L'ostréiculture en Bretagne de 1850 à nos jours.* Spézet/Speied, Coop Breizh (2008)
Bertrand Hallier and Franck Vilboux, *Les huîtres, un océan de saveurs.* Strasbourg, Gyss & Clément (2006)
Robert Hedeen, *The Oyster.* Centreville, Tidewater Publishers (1986)
Rowan Jacobsen, *A Geography of Oysters.* New York, Bloomsbury (2007)
Christine Keiner, *The Oyster Question.* Athens, GA, University of Georgia Press (2010)

- proximity to pollution sources are not a factor for safe harvest of shellfish
- prevalence and occurrence of shellfish pathogens, fouling organisms, predators, disease and the presence of biotoxins are all within acceptable levels of risk
- site is protected from major storm damage and is reasonably secure and accessible.

Grow-out methods – extensive versus intensive?

There are a wide variety of grow-out methods used throughout the world to cultivate oysters and they are generally characterized according to the level of cultivation intensity, where intensity in this case refers to the costs associated with producing an oyster crop. *Extensive* oyster culture is a common approach to oyster farming worldwide and is characterized by a reliance on natural spat settlement, often supplemented by hatchery seed, little control over oyster density on the seafloor with little attention paid to predators and overall oyster density. Advantages to extensive approaches include low overhead and production costs, low labor costs, and overall reduced inputs. *Intensive* methods for rearing oysters are based on the containment of oysters in specialized gear that may be placed either on the seafloor, suspended in the water column, or floating at the water surface, collectively termed 'off-bottom'. A large variety of gear types are available to the oyster grower that serve to contain the oysters and enable the grower to largely control product quality such as growth rate, shell and meat qualities while providing protection from predators. Intensive methods are expensive, and often rely on specialized labor and the availability of hatchery-reared seed. Advantages to intensive oyster culture include increased productivity, better control over predators, use of genetically improved seed, and enhanced product quality. There are advantages and disadvantages to all grow-out methods that are dictated by considerations of relative cost, availability of space, access to markets and upland infrastructure (for example, sucking and processing facilities). These considerations are discussed in the next two subsections.

Extensive culture of oysters

The simplest and most seemingly cost-efficient extensive approach to oyster cultivation is to site farms in the vicinity of habitats that support reliable natural recruitment of oysters for both on-bottom, off-bottom, and longline and raft-based culture. These are farms of sufficient area that the economies of scale enable wild oysters that are recruited annually as pediveligers onto collectors and grown inexpensively to a harvestable size to provide mainly processed (for example, shucked and dried, frozen, or jarred) products. Oyster growing regions in eastern North America, China, South Korea, and Japan fit these criteria. Many operations blend the line between sea farming and wild harvest if spat initially wild caught on collectors is combined with hatchery-produced seed. Increasingly, hatchery seed is utilized on farms and in many cases this is due to the value of potential disease resistance as a result of breeding efforts. Farming methods depend on location, availability of local materials, the annual abundance of oyster larvae and cultural experience. In Asia, rafts constructed of bamboo stringers are used extensively to support strings of oyster, mussel, and scallop shells suspended in the water column. Intertidal sites in China utilize posts inserted into muddy ground that serve to attract oyster spat. In Korea, both rafts, and extensive longlines are used extensively. Spat collection techniques in open waters generally involve placing the cultch material on ropes into the water very close to the time that larval oysters are approaching the settlement phase of their life history. Once oysters settle and metamorphose to the juvenile stage they generally grow quickly and develop more robust valves. At this stage settlement substrates containing the oyster spat may be moved to more favorable locations for further grow-out. Grow-out to a harvestable size may be rapid and significantly less than a year in warm, productive environments, but 2 to 3 years are required to reach a harvestable size in cooler, temperate waters.

Raft and longline based culture using hanging cultch dominates production in Asian countries while intertidal production of oysters for the shucked markets mainly are common in North America. In the Pacific northwest of North America, natural settlement of oysters is accomplished by placing shell bags as bundles, each bag containing 250–300 Pacific oyster shells, on the intertidal beach at the mean low tide level just prior to forecasted settlement of oyster larvae (*C. gigas*) (Fig. 1.4). Once settlement occurs, the spat on shell are maintained in the cultch bag for a period of weeks to months in order that the juvenile oysters grow and "harden" (increase general hardiness and shell thickness) prior to planting. As the success of spat fall on natural collectors varies from year to year, growers are generally looking for 6–20 juvenile oysters per cultch piece, though this standard varies widely. Shell bags are often moved from the spat fall location to a more favorable site for grow-out prior to breaking the bags open and scattering the seed over suitable habitat for grow-out to harvest size.

Settlement substrates used for catching oyster spat are extremely varied depending on the species and where the oysters are grown. Collectors made of oyster shell, shells of other molluscs, wood, plastic, cement coated wood, PVC pipe, plastic plates, and coconut shells encompass the variety of substrates. Custom and ease of use in the specific farm setting required often dictates the method selected. Once settled, oyster spat is grown to a harvestable size using a wide variety of methods that mainly reflect local custom and the experience of the grower.

In parts of the world where natural spat fall may be locally sparse, sporadic, or unreliable on an annual basis, the use of hatchery-produced seed added to natural production can significantly boost production though adding to production costs. Although hatchery production of oysters is covered elsewhere in this chapter, the use of hatchery-produced *C. gigas* pediveligers was pioneered on the North American west coast and is referred to as 'remote setting' and involves placing cultch bags packed with dry, clean oyster shells in bundles into tanks (for example, 5000 L) supplied with warm seawater and microalgae and adding pediveliger larvae competent to settle and metamorphose to the juvenile stage. The section on hatchery and nursery techniques further details the methods used for producing spat for grow-out using remote setting techniques. A variation on growing cultched oysters to harvest size involves inserting the cultch shell through the strands of three-strand twisted line. These strings are bundled and placed into setting tanks and then suspending the line with cultch attached from either posts above the intertidal substrate or hanging from rafts. This approach is extensively used in settings when the ground for growing oysters is too soft to support oysters and has the added advantage of exposing oysters that set on both sides of the cultch to better growing conditions (Fig. 1.14). Oysters set on cultch material may be grown out on the bottom for later harvest and shucking for meat production. Harvesting involves either dredging for oysters at high tide or manually picking oysters at low tide and transporting in large tubs to shucking facilities for processing (Fig. 1.15).

Figure 1.14 Off-bottom intertidal longline culture of oysters in Washington State. Courtesy of Taylor Shellfish Company.

Predator control during the grow-out phase of extensive oyster culture often consumes the oyster farmer's time during this phase of production and must be considered by the grower. Predators of oysters include crabs, sea stars, gastropods, fishes, diving ducks, and marine mammals and vary by region as to their impact. The optimal approach to predator control for oysters grown unprotected on or above the seafloor is beyond the scope of this work, but the shellfish farmer has a choice to potentially build in a level of acceptable loss due to predators by planting more oysters than intended and/or handpicking predators as possible for removal with the appreciation that some loss of the crop will occur. This is often the approach used as control methods can be very expensive. On the US east coast where subtidal culture of *C. virginica* has been conducted for many decades, predator control for sea stars was a regular practice, accomplished by towing large fabric 'mops' over subtidal oyster beds and serve to collect sea stars feeding on the oysters. The non-native gastropod snail (*Ocinebrellus inornatus*), introduced from Japan in imported oyster seed, has plagued intertidal oyster growers on the North American west coast for

Figure 1.15 Pacific oyster culture in tray-based suspended culture in Tasmania, Australia. Courtesy of Joth Davis.

decades with control methods generally relying on handpicking and removing oyster drills at low tide to reduce impacts. Oyster farmers on the east coast of the US also contend with carnivorous snails, in this case, *Urosalpinx cinera*.

Methods for predator control vary around the world and growers finely tuned to the natural history and behavior of the suite of predators impacting their operations will contribute to their success. The most effective approaches are most often the most ecologically sustainable and utilize control methods that simply work to avoid predator interactions. The grower needs constantly to adapt their growing methods that simply work to diminish, discourage, and, hopefully, avoid interactions with predators. While increasing the cost of production, this may involve the use of temporary nets and barriers that are used only when predators are present to simply preclude interactions. Careful attention to the natural environment and the annual rhythm of life and what it brings in terms of both potential risk and reward to the oyster crop cannot be underestimated. In the US Gulf of Mexico, for example, oyster growers often cultivate oysters in areas where predation is reduced by periodic influxes of freshwater.

Intensive culture of oysters

Methods for on- and off-bottom and floating oyster cultivation have increasingly involved the use of hatchery-produced seed grown in specialized systems that has enabled large-scale production of oysters having excellent market characteristics (uniform size, shape, flavor, and high meat content). When appropriate intertidal or subtidal ground for premium half shell culture is not available, growers the world over have turned to using systems that enable oysters to be cultivated under largely controlled conditions. There are significant advantages to cage (bag)-based shellfish culture whether practiced on or off the seafloor. Protection from predators, ease of handling, control over the density of animals over the grow-out phase, potential for co-culture with other invertebrates or seaweeds, and control over inventory are all important attributes to consider. Chief disadvantages include significantly increased costs of the gear, often significantly greater requirements for controlling fouling of both the gear and the crop, and most importantly the necessity for increased handling of shellfish required to produce a premium product. The components associated with sea farming single oysters involve developing critical operating procedures over stocking, handling and grading of oysters from seed to market size.

Stocking, handling, and grading oysters for single oyster production

Single oyster seed is procured from a hatchery or nursery facility and culture usually requires the grower to have available a supply of seed oysters that are the appropriate size for stocking the grow-out gear. This requires the grower to either purchase seed oysters of a uniform size or produce them in a nursery operation for direct stocking. Most gear suppliers offer cages with different mesh sizes so the operator can outplant small seed oysters that are later split into grow-out cages with larger meshes. There is a wide variety of gear available for raising single oysters to a marketable size on intertidal beaches, off-bottom rails and racks, or in suspended culture. Most providers of gear offer cages with differing mesh sizes to accommodate oysters as they grow. The major task for the oyster farmer, therefore, is to either build or procure gear that enable he or she to manage size and density of oysters from the seed stage to harvest. The decision on what gear to build or purchase is dictated by cost, critical site considerations, and important extrinsic factors including expected wave action, durability, handleability, visual considerations, and fouling among others.

Single oyster production, unless practiced on the seafloor without protection from predators, requires a significant investment in handling and grading that if ignored will most often result in uniformly poor results. There are only a few 'commandments' associated with intensive oyster aquaculture. All are based on the biology and immobility of the animal and dictate how grow-out from seed to market size oyster should be approached.

> **Guideline 1** – Overstocking, or crowding, during the growth season will allow only a minority of oysters to grow well, with others having reduced growth and a substantial portion not growing at all or even dying. Overstocking will also result in increased variation in shell shape.

Nursery systems must be designed, therefore, to accommodate oyster seed at a size the farmer can direct stock into cage culture with a minimum of handling. Take note of the section above on nursery culture, whether practiced in bottle culture systems, upweller tanks, FLUPSYs, or intermediate cage culture. The latter approach will be addressed. The second rule of oyster culture, related to Guideline 1, addresses sizing and grading oysters.

> **Guideline 2** – Unless oysters are more or less the same size when stocked into cages, the larger oysters will grow significantly larger, intermediate sized oysters will grow a little and small oysters will not grow, all associated with the availability of suspended food to individual oysters in the cage.

The necessity to control density at all stages of production cannot be overstated. Stocking density of oysters in bags and trays is important to regulate. As a guide, trays and bags should be stocked at no more than 25% of the volume of the unit of culture. Commonly, oyster cages have a volume of 20–25 L and are designed to hold between 100–150 market size oysters at a harvestable size of about 75 mm shell height (for North American markets). This equates to a stocking density at harvestable size of no more than five oysters per liter. Specifications of the gear being considered should be assessed for this parameter and should assist in making fundamental decisions based on the number of cages deployed, farm layout and expected yields.

As oysters grow they must be restocked in bags or trays to allow for further growth. Throughout the cultivation process growers are faced with the periodic need to 'split' oysters as they grow, which is the simple process of dividing oysters (by size or weight) from one unit into two or more to reduce stocking density to avoid the effects of overcrowding. During the splitting process, growers may opt to replace damaged or heavily bio-fouled gear and/or stock oysters into units with a larger mesh size. Though splitting can be done manually simply, with regard to reducing stocking density, many growers use a size grader at this point to assist in the process. This allows a grower to stock like-sized oysters together, which assists with inventory management and allows larger oysters to be stocked into larger mesh bags or baskets. While some growers opt for homemade graders, many farmers utilize mechanical graders to efficiently process large numbers of oysters. These include shaker tables, rotating tubes, and computer-assisted 'vision' sorters. In all cases, graders produce multiple size grades of oysters for either harvest or restocking cages for further growth. Examples include rotary tumblers that utilize aluminum or plastic tubes filled with holes of slowly increasing diameter. Oysters are poured into one end of the grader and as the tube slowly rotates, oysters tumble through the tube (set at a downward angle), falling through the perforations based on their size. Other styles of mechanical graders used in the field utilize vibration to gently move oysters over horizontal screens of increasing diameter. Oysters are sorted by size as they fall through the screens into bins for further processing.

There are three main benefits to routinely sorting the oyster crop by size. First, oysters that are generally all the same size grow more uniformly. Second, oysters that are sorted using mechanical graders have reduced biofouling following grading resulting in cleaner oysters for either harvest or restocking for further growth. Third, grading oysters regularly can increase product quality significantly. Grading oysters regularly has the benefit of improving product quality through a process called 'self-trimming'. Rapidly growing oysters add layers of new shell at the valve margins that is often thin and frilly. Harvesting oysters in this condition (unless produced for the shucked market) can result in greatly reduced shelf life due to harvest induced damage to the fragile shells and loss of internal water (for example, shell liquor) upon exposure to air. Grading oysters via a controlled, tumbling action has the advantage of inducing gentle damage to the shells of live oysters, chipping away at the frill and valve margins without significantly impacting the oyster. Once returned to the sea, oysters will quickly repair the damaged shell by adding additional shell material resulting in thicker, stronger and more robust valves with deeper cups. Additionally, grading oysters regularly can produce oysters that increase the meat to shell volume. These induced changes to the oyster, all due to regular grading and tumbling, result in oysters having higher value for half shell markets.

Grow-out systems for single oysters

Over the last 20 to 30 years there has been a significant advance in the design, production and availability of gear specifically designed for raising oysters. Much of the equipment available today may also be adapted for a wide range of applications, including on-bottom, suspended, and floating operations. The oyster farmer has a wide variety of gear options to consider when setting up a new farm. Much of the available gear may be used in on-bottom, off-bottom longline, in suspension, or floating on the sea surface. For example, cages designed for suspended culture of single oysters are also commonly used in floating culture or systems anchored to the intertidal, whether strictly on-bottom or longline based. Site and permitting considerations will usually dictate what equipment will be used and in what application.

Suspended and floating culture of oysters

For growing oysters suspended in the water column or floating on the surface, there are a variety of systems available. For suspended culture, Japanese pearl nets have long been in use all over the

Figure 1.16 Oysters contained in tubs, picked at low tide, are picked up by a crane and barge at high tide and transported to a shucking house in Washington State. Courtesy of Taylor Shellfish Company.

world. These consist of a wire framework supporting multiple layers of mesh-enclosed spaces for holding oysters from seed to market size. Lantern nets typically come in 5 or 10 tier configurations and are typically stocked with about 100 oysters per tier, or 1000 oysters in a 10-tier net. Nets are hung into the water column from rafts, longlines utilizing buoys for flotation or in midwater configurations (subsurface longlines). Other suspended culture systems include trays that are similarly hung, often with attached weights, from buoys (Fig. 1.16).

Similarly, many systems are based on hanging trays of single oysters from buoys or rafts. Here, growers deploy rafts or longlines suspended by buoys to support subsurface gear, depending on local custom and regulations pertaining to floating aquaculture. A large variety of systems have been developed worldwide. All rely on simply holding oysters in dedicated gear for the months to years required for growth from seed to harvestable size or weight. Floating culture similarly includes gear deployed with flotation in order to maintain the systems on the sea surface. Most commonly, this gear is deployed such that the oysters are living just below the water surface (Fig. 1.17). Floating systems include series of floating bags/baskets, large buoyant cages, and cages that are designed to be flipped up on pontoons to allow air-drying to control biofouling (Fig. 1.18). These systems often have the capacity to flood the pontoons and sink the unit to the bottom to avoid unfavorable conditions (for example, winter ice, tropical storms) and then be emptied and refilled with air to re-float at the surface.

Growing oysters in the intertidal zone

Grow-out of oysters in the tidal zone is a common practice where environmental conditions are satisfactory or are required by permit. Environments that include freezing, excessive heat, or freshwater inputs during the low tide are not appropriate for tidal zone grow-out, but in many locations intertidal oyster farms may be very successful. Access to the farm during the time the tide is out enables labor and equipment to be deployed for maintenance of grow-out systems, predator control, grading, splitting and harvesting, and most other husbandry activities. Oysters

Figure 1.17 Longline culture of eastern oysters in floating cages in Maine. Courtesy of Chris Davis.

cultivated in the intertidal may be deployed in cages either directly on the tide flat (on-bottom cage culture), off-bottom on rails or racks or from longline systems (Fig. 1.19). Rail and rack systems consist of wooden, steel, or plastic frames inserted into the substrate that hold oyster cages a few centimeters to 0.5 m off the bottom (Fig. 1.20). Cages may be secured by straps or lines or other means to the frames. A large variety of approaches have been put to use by growers over the years that take into account site specific parameters that serve to simply increase efficiency during the scarce hours that the tide is low enough for workers to tend to systems.

Other approaches to intertidal grow-out include adjustable longlines where the culture gear is set at a specific tidal height by the grower, depending on the season and the conditions. In many longline systems, this height is adjustable, allowing the grower to adjust the immersion time experienced by the crop. This can be used to control biofouling, to regulate growth rates, and

Figure 1.18 An oyster culture (OysterGro) using a system of floating cages designed for regular rotation to expose cages and oysters to the air to control biofouling. Courtesy of Joth Davis.

Figure 1.19 Intertidal culture of Pacific oysters in an on-bottom longline system in Washington State. Courtesy of Joth Davis.

Figure 1.20 Intertidal trays used to culture Sydney rock oysters in eastern Australia. Courtesy of Joth Davis.

even determine the amount of wave action to which the oysters are subjected (either routinely or during storm events) (Fig. 1.21). In the Pacific northwest of North America where intertidal oyster culture is common, oyster cages, attached to intertidal longlines, may also be supplied with flotation. This enables the cage to rotate on the longline in concert with the tide (Fig. 1.22). When the longlines are covered, cages float in the up position and when the tide falls, the cages rotate into the down position. This daily activity, mediated by tidal height fluctuations, enables the oysters to tumble within the cage at regular intervals and results in higher product quality, similar to that attained by regular grading.

Figure 1.21 Intertidal culture of Pacific oysters using SEAPA trays and an adjustable longline system in South Australia. Courtesy of SEAPA.

Figure 1.22 Intertidal culture of Pacific oysters using a rotating-cage system in Washington State. Cages supplied with floats on one end of the cage float the cage up into the water column when the beach is covered. Cages fall back when next exposed, shuffling oysters on every low tide exchange. Courtesy of Joth Davis.

Diseases and pests

There are numerous diseases and pests that affect oysters at various life stages. In addition to predators and pests of oysters is the influence of a changing climate – warmer seas and air temperature will also likely threaten the capacity to grow oysters in the future. These impacts depend on geographic location, the host oyster species and its life stage, and environmental conditions. As mentioned earlier, many diseases have imposed substantial losses to oyster growers over the years. In fact, diseases and pests have contributed to the serial loss of production for specific species being cultivated in the world over the last 100 years. In western Europe, the native flat oyster (*O. edulis*) was depleted by disease and replaced in aquaculture production with the Portuguese oyster. This species was similarly depleted by disease and sea farming efforts switched to the Pacific oyster (*C. gigas*). As of 2019, Pacific oysters in Europe, Asia, Australia, and New Zealand are currently critically threatened by highly virulent microvariants of oyster herpes viruses, collectively referred to as POMS. The eastern oyster (*C. virginica*) has a long history of disease impacts including Dermo disease (the protozoan *Perkinsus marinus*), MSX disease (the protozoan *Haplosporidium nelsoni*) and ROD. Impacts of disease include a range of sub-lethal effects but often can lead to high levels of mortality in the crop. In most growing regions, there are substantial restrictions and checks on movement of oysters (seed or adults) to decrease the risk of spread of a disease to a new area. Methods to reduce disease prevalence once established in a crop have not generally been adopted due to the costs involved. Rather, most growers manage the effects of disease, either by planning harvest prior to expected losses to disease or by cultivating in areas less prone to disease. At least in the case with some off-bottom farms, some growers are raising oysters to market size before they succumb to disease. Despite these strategies, the predominant strategy to reduce losses to disease has been the development of disease-resistant strains through breeding. In North America, Europe, Australia, and New Zealand, selective breeding programs are in place that focus on the development of oyster broodstock lines resistant to diseases. These programs have been largely effective in reducing losses but require dedicated, long-term research and development efforts.

Growers also attempt to reduce the negative effects associated with competition for resources by other organisms. This typically manifests in off-bottom aquaculture as a biofouling community that en masse can reduce flow to the oysters by attaching to and clogging screens and meshes (adding significantly to flotation requirements for floating culture) as well as compete directly with the oyster crop for suspended plankton (see Chapter 16). Typical 'biofoulers' for oyster growers include barnacles, mussels, wild oysters (termed overset), macroalgae, ascidians, and encrusting bryozoans. In addition, there are organisms that invade the shells of oysters, affecting the shell appearance and possibly weakening the shell. These include mud blister worms and boring sponges. To manage these impacts on both the gear and the oysters, growers may utilize some mix of prevention and control techniques. To prevent establishment of these species, many growers use routine air-drying to impose lethal stress on the undesirable species. Growers may vary the frequency, duration, and timing of air-drying in response to the local site conditions. To control established species, growers may opt for a variety of solutions from highly labor-intensive physical removal (for example, by power washing) to large-scale immersion in dips that pose an osmotic challenge to the biofoulers (for example, brine dips, freshwater dips). Some growers have also used vinegar dips or very brief immersion in boiling water. Typically, growers find these solutions time-consuming and expensive.

Predators pose a fundamental challenge to on-bottom culture in many parts of the world and can also induce losses in off-bottom farms. Common predators include crabs, predatory gastropods, sea stars, some species of fish (for example, drums in the Gulf of Mexico, rays in the Chesapeake Bay, and predatory flatworms). For on-bottom culture, losses to predators can be catastrophic. Typically, predation levels tend to increase in higher salinity waters, so some growers opt to raise oysters at lower salinity sites if they have that option to reduce losses to predation (with relay to higher salinity sites as the crop nears market size). Growers have attempted a number of predator control methods for on-bottom farms, including exclusion, chemical applications, biological control methods, and mechanical removal (for example, sea star 'mops', crab traps). These measures are expensive solutions that yield mixed results. Off-bottom farmers often do not see high levels of loss to predation, as the oysters are protected within the bags or baskets. Despite this initial level of protection, many predators will simply recruit as larvae or enter as juveniles into the bags and grow quickly enough to become a threat to the oysters if not removed. Similarly, some predators, such as predatory gastropods, may inflict predation through the basket if not removed, while others such as predatory flatworms could easily enter a basket. In most off-bottom farms, regular tending of the crop allows growers to remove predators before substantial losses are realized.

Harvesting oysters

In terms of public health, oysters (and some clams) are a special case because they are often eaten live on the half shell and potentially harbor pathogenic bacteria and viruses. As a result, harvesting of oysters is managed with a suite of regulations, including proactive temporary harvest closures when public health criteria cannot be assured (for example, harmful algal blooms, heavy rainfall or high river flow, wastewater treatment plant failures). In some jurisdictions, a minimum size may be required for harvest, most typically 76 mm (3 inches) shell height, while many jurisdictions allow cultured oysters to be sold at whatever size the market demands. Universally, however, there are strict time/temperature limits in each jurisdiction, with specifics varying.

As an example, in the US these regulations are mandated by the Food and Drug Administration via the Interstate Shellfish Sanitation Conference and implemented at the state level through the National Shellfish Sanitation Plan (NSSP). Harvesters must properly tag all commercial harvest and transfer these to a licensed wholesaler. In the US wholesalers and shippers have strict requirements for refrigeration and proper storage to maintain product safety, with many regulatory agencies requiring specific forms of training to increase product safety (such as Hazard Analysis Critical Control Point [HACCP]), including time from post-harvest to refrigeration requirements and training. Some facilities use wet storage to hold stock or depuration tanks, but these are beyond the scope of this chapter, and readers are recommended to determine local regulations and guidelines.

Once harvested, oysters may be sold live in the shell, sold for possible raw consumption by humans, or shucked for the meat. All raw oysters pose a potential human health risk due to the presence of naturally occurring *Vibrio* bacteria, such as *Vibrio vulnificus* and *V. parahaemolyticus*, which can cause illness and even death (particularly in immune-compromised individuals). The species *V. vulnificus* causes 95% of all seafood-related deaths in the United States (Oliver, 2005). Infections from *V. vulnificus* can cause primary septicemia and are the result of consuming raw or undercooked seafood, or wound infections (Hlady, 1997; Oliver, 2013). The second species of concern, *V. parahaemolyticus*, is acquired primarily through ingestion of seafood, and causes acute gastroenteritis (Daniels et al., 2000; Iwamoto et al., 2010; Scallan et al., 2011). Since *Vibrio* spp. are endemic to marine waters and are concentrated in oysters during the filter-feeding process, there are no means to prevent the introduction of *Vibrio* spp. into oysters or other seafood products. This is in contrast to other human pathogens associated with seafood, particularly bivalve molluscs, such as norovirus, *Salmonella* spp., or *Campylobacter* spp. Those pathogens are associated with human fecal contamination, generally via sewage treatment plant discharge. The NSSP provides regulations and guidelines to ensure that shellfish in the US are not harvested from areas impacted by human sewage; however, these guidelines do not control for the naturally occurring *Vibrio* spp. pathogens, as they are autochthonous and have no association with human sewage. *Vibrio* bacteria are primarily managed through time/temperature requirements and/or *Vibrio* control plans as noted above. These programs are very effective, though do not eliminate risk. While many people prefer to eat oysters raw on the half shell, there are four US Food and Drug Administration approved post-harvest processing methods that eliminate *Vibrio* bacteria from oysters: high pressure, low temperature pasteurization, freezing, and irradiation. Each process has specific requirements that can be found in the NSSP. Oysters processed in this fashion are no longer alive, however, and are intended for markets other than for oysters harvested for live, raw consumption.

Emerging issues and opportunities

Despite the relatively straightforward process of cultivation, the oyster aquaculture industry is constantly assessing and adopting new types of gear and methods of production. Off-bottom gear manufacturers are constantly attempting to improve their equipment, with variations on proven gear types as well as innovative new gear designs. The industry is also always looking to increase efficiency through mechanization and reduction of labor, including interest in the development of automated technology and improved inventory management. In addition, there has been interest in the idea of using real-time data monitoring to inform decision-making on the farm.

The world over, hatchery operations are often viewed as proprietary components of a business model and as a result there is often very little exchange of information among operators, even though nearly all shellfish hatcheries suffer from production problems from time to time that significantly impact their operations. A movement toward standardization of fundamental protocols, equipment, and genetic practices, and greater exchange of information would be helpful in order to increase the overall efficiencies of production.

A changing climate including changes to the carbon cycle associated with anthropogenic carbon inputs are also impacting the capacity to grow oysters. As discussed earlier, the oyster industry in many parts of the world is grappling with emerging problems associated with changing oceanic and estuarine carbonate chemistry conditions associated with pH, alkalinity, and reduced aragonite saturation state to properly form shells in larval oysters. While impacts to hatchery operations and the production of larval oysters and seed have been mitigated by adopting mechanical systems that buffer incoming seawater, the long-term outlook for larval and especially seed operations that depend on natural supplies of seawater, is less clear. For oyster farming to move forward it is likely that genetic improvement for traits associated with both disease resistance and increased yield will remain important. For oysters to thrive in different environments in the future it may be necessary to direct breeding in response to simultaneous, multi-stressor laboratory and field challenges in genetic lines that include thermal stress, hypoxia and changing carbonate chemistry conditions.

Partly in response to these changing conditions, there has been interest in producing oysters in land-based systems, including recirculating systems. Nursery culture systems (covered earlier in this chapter) are in use in many locations and there has been interest in extending the nursery phase into a vertically integrated, land-based system for all components of grow-out of oysters to marketable size. Land-based systems offer potential and significant benefits pertaining to security, availability of labor and land (including the potential to grow oysters in inland locations), and control over water quality (pollution and biotoxins), predators, biofouling, and disease. While there is the potential to pump seawater (including processed, saline groundwater) into land-based tanks or troughs, economic considerations, mainly associated with the capacity to supply enough oysters for the operation to be profitable with the amount of algal nutrition required for growth to a marketable size, have tamped down enthusiasm for this approach.

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