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SCIENCE ADVICE FOR GENETIC EFFECTS FROM SHELLFISH AQUACULTURE IN SOUTHERN CALIFORNIA AND THE GULF OF AMERICA

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Science Advice for Genetic Effects from Shellfish Aquaculture in Southern California and the Gulf of America

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Executive Summary

The purpose of this report is the present a synthesis of knowledge about aquaculture of shellfish in the context of potential cultured-wild interactions and subsequent genetic effects on wild populations. The scope of effects from aquaculture in this report is focused on genetic effects related to cultured-wild interactions and loss of genetic diversity due to escaped/dispersed culture-origin individuals surviving in the wild. This report does not specifically address potential ecological effects such as competition of invasive species with native species, disease, or other factors, although information provided in this report may inform evaluations of ecological risk.

Candidate species for marine aquaculture were selected by NOAA based on known industry interest, potential for significant industry development, environmental suitability in each respective region, and environmental and technical feasibility for farming offshore in federal waters. Species included here do not represent an exhaustive list of potential species that could be cultivated in federal waters, nor an explicit endorsement by NOAA of these species for cultivation.

Based on a synthesis of each of the candidate species (presented in Chapters 2 and 3), an assessment of the influence of species and population dynamics on the genetic risk level was determined for each species as a qualitative assessment of potential for genetic effects to wild populations from commercial culture of shellfish. A summary of findings related to genetic risk for each of the species in the Southern California and Gulf of America regions are shown in the tables below. More detailed factors contributing to these findings are tabulated in Chapter 4.

The genetic risk level is based on specific risk factors that would influence genetic effects to wild populations from aquaculture, based on species and population characteristics. The risk factors are: potential for maturity in culture (e.g. harvest after maturity would present greater genetic risk), dispersal duration and settlement requirements (longer lengths of time larvae may disperse presents a greater risk; wide range of suitable settlement environments and/or high fouling abilities presents a greater risk), current thinking on wild population abundance (low/patchy/declining abundance of the local population would mean greater demographic contribution from cultured gametes, with potential for greater genetic risk), biological characteristics in cultured strains that may differ from wild populations (e.g. triploidy), and knowledge of genetic population structure species on a regional level.

The evaluation of uncertainty in the risk level is based on available data to support findings on wild population status and genetic structure and diversity. The Low/Moderate/High assessment for the genetic risk level and uncertainty presented in the tables is based on a broad review of the available research and scientific literature regarding wild population dynamics and characteristics for each species. The risk levels do not account for culture production levels, escape rates or other operational factors. As such the genetic risk levels in the table can be considered for factors that influence risk but should not be construed as a full assessment of genetic risk from aquaculture.

Southern California Candidate Shellfish Species for Aquaculture: Summary of Risk Factors, Uncertainty in assessment, and Priorities to Minimize Genetic Effects from Aquaculture of Shellfish

Species name	Common name	Probable Genetic Risk Level	Uncertainty in Risk Level	Management Priorities to Minimize Genetic Effects
Ostrea lurida	Olympia oyster	High: reaches sexual maturity prior to harvest, wild populations display local adaptation at small scales and show extensive genetic diversity.	High: little known about dispersal and survival.	Broodstock genetic management plan focused on locally adapted populations; genetic diversity monitoring.
Magallana gigas	Pacific oyster	Low: non-native species, sterilization is relatively effective, if diploid then reaches sexual maturity prior to harvest, but one metapopulation along the U.S. Coast.	Low.	Broodstock genetic management plan; genetic diversity monitoring.
Crassadoma gigantea	Purple-hinged rock scallop	Moderate: reaches sexual maturity prior to harvest, though population structure suggests one population in Southern California.	High: genetic structure is likely among regions due to biology of species and patchy distribution.	Broodstock management; genetic diversity monitoring.
Venerupis philippinarum	Manila clam	Moderate: naturalized species, reaches sexual maturity prior to harvest – for 2+ years; unknown genetic structure, but there is a high potential for genetic bottlenecking of naturalized populations due to aquaculture origins.	High: no information about population or genetic structure of this species in Southern California.	Broodstock genetic management plan; genetic diversity monitoring.
Tivela stultorum	Pismo clam	High: reaches sexual maturity prior to harvest, information is lacking on the fishery.	High: limited information about the wild population in Southern California.	Broodstock genetic management plan; genetic diversity monitoring.
Mytilus californianus	California mussel	Low to Moderate: abundant wild population, potential high survival of cultured larvae.	Low: stable population along the California coast.	Broodstock genetic management plan; genetic diversity monitoring.

Species name	Common name	Probable Genetic Risk Level	Uncertainty in Risk Level	Management Priorities to Minimize Genetic Effects
Mytilus galloprovincialis	Mediterranean mussel	Low: naturalized species, lower probability of maturation before harvest, sterilization potential. Ecological effects of invasion may contribute to loss of genetic diversity.	Low.	Genetic diversity monitoring; harvest before maturity.
Haliotis spp.	Abalone	Low to High: If genetic diversity is sufficient in commercial operations, escaped larvae may effectively supplement populations; where genetic diversity is low or lines are highly domesticated, larval escape will likely harm natural populations.	Low: extensive data on population structure in Southern California.	Maintain supplementation level diversity in commercial hatcheries.

Gulf of America Candidate Shellfish Species for Aquaculture: Summary of Risk Factors, Uncertainty in assessment, and Priorities to Minimize Genetic Effects from Aquaculture of Shellfish

Species name	Common name	Probable genetic risk level	Uncertainty in risk assessment	Management priorities to minimize genetic effects
Argopecten irradians	Bay scallop	Moderate to high: potential of harvest before maturity, existence of supplementation programs and effectiveness of sterilization techniques.	Moderate: limited information about the wild population.	Genetic diversity; seeding time; siting; harvest before maturity; sterilization.
Crassostrea virginica	Eastern oyster	Moderate to high for culture of diploid oysters: reaches sexual maturity prior to harvest and potential for introgression; low for culture of triploid oysters.	Low: state-managed fisheries; extensive data on population structure.	Genetic diversity monitoring.
Venerupis philippinarum	Manila clam	Low to none: non-native species, population status unknown but assumed to be nonexistent in the Gulf; potential for ecological effects of species introduction should be evaluated.	Low.	Broodstock management; genetic diversity monitoring.

Species name	Common name	Probable genetic risk level	Uncertainty in risk assessment	Management priorities to minimize genetic effects
Lytechinus variegatus	Variegated sea urchin	Moderate: high wild abundance and potential of harvest before maturity is unknown.	High: limited information about the wild population.	Genetic diversity, siting; harvest before maturity.
Mercenaria mercenaria	Quahog	High: ease of growth in wild populations, reaches sexual maturity prior to harvest, ability to hybridize and displace native species.	Low: known ability to hybridize and introgress with native species.	Harvest before maturity; carefully consider native species prior to development in new areas.

1.0 How Cultured Organisms Escape and Consequences of Escape

The purpose of this report is to present a synthesis of knowledge about aquaculture of shellfish in the context of potential cultured-wild interactions and subsequent genetic effects on wild populations. The scope of effects from aquaculture in this report is focused on genetic effects related to cultured-wild interactions and loss of genetic diversity due to escaped/dispersed culture-origin individuals surviving in the wild.

Candidate species for marine aquaculture were selected by NOAA based on known industry interest, potential for significant industry development, environmental suitability in each respective region, and environmental and technical feasibility for farming offshore in federal waters. Species included here do not represent an exhaustive list of potential species that could be cultivated in federal waters, nor an explicit endorsement by NOAA of these species for cultivation.

In considering risk, Kaplan and Garrick (1981) suggest defining and addressing three questions: (1) what can go wrong; (2) what is the likelihood of that happening; and (3) what are the consequences? With that guidance in mind, the following sections describe how and the likelihood that cultured organisms may escape (Section 1.1, Escape Background and Categories) and the consequences of escaped cultured organisms (Section 1.2, Consequences of Escape).

1.1 Escape Background and Categories

Shellfish raised in aquaculture pose a genetic risk to their wild conspecifics primarily through the release of gametes or larvae into the water column. Juvenile and larval shellfish originating from aquaculture sites are considered shellfish escapes, with the potential to introduce genetic effects to wild populations of the same species or through hybridization with closely related species. Gametes can be released from farm sites by species that mature before reaching market size during the grow-out period. Additionally, gametes may originate from individuals lost due to accidental damage to grow-out containers (e.g., bags, baskets, or cages) that are placed on the seabed, suspended in the water column, or floated near the surface. Cultured shellfish can also be released if grow-out infrastructure (e.g., longlines) is damaged or lost. Over time, shellfish may also adhere to other aquaculture infrastructure and vessels (e.g., buoys, anchors, fixed lines, maintenance boats) due to previous spawning at the grow-out site, potentially releasing gametes once mature.

Genetic risks associated with shellfish culture can be managed through strategic siting, engineering design, and nursery practices. However, any shellfish culture program must account for the potential risk of unintentional releases due to factors such as storm events, wave action, vessel collisions, handling mistakes, predator attraction, and gear malfunctions. The primary risk factors concerning genetic effects from shellfish aquaculture include:

- Maturity in culture before attaining market size, leading to gamete release into surrounding waters.
- Vulnerability, abundance, and genetic diversity of wild populations.
- The culture of non-native or naturalized species and the implications for genetic diversity.

Gamete Escape

Shellfish species generally reproduce by releasing gametes into the water column, with the exception of some species like the Olympia Oyster (*Ostrea lurida*), which fertilize and develop larvae internally before releasing them. When egg and sperm gametes successfully combine, they form zygotes that develop into free-swimming larvae. During the larval stage, these juveniles drift within the water column for several weeks before settling on the seafloor and undergoing metamorphosis into their benthic form. Oysters and mussels prefer hard substrates for settlement, while clams burrow into the seafloor.

The release of gametes is the primary consideration regarding genetic risks to wild populations from shellfish culture. The risk of gamete-based escape is minimal if shellfish are harvested before reaching sexual maturity. However, many cultured shellfish species, such as diploid Eastern oysters (*Crassostrea virginica*) and Manila clams (*Venerupis philippinarum*), mature sexually before harvest at grow-out sites when they have attained market size. For these species, there remains a risk of gamete release and subsequent reproduction of cultured individuals in the wild.

Depending on the proximity of the grow-out site to wild conspecifics, there is potential for gametes to mix with those spawned from wild-origin shellfish. This may be more successful in species where environmental or biological cues trigger synchronous gamete release from both wild and cultured shellfish. Hermaphroditism, seen in some species, may further improve the chances of successful cultured-wild fertilization. However, if cultured individuals are not physically close to wild populations, the gamete concentration may not be sufficient for successful fertilization between cultured and wild individuals (Jackson 2021). In these cases, fertilization among cultured gametes would be more likely. Larvae developed from the culture-origin gametes would then have a greater potential to drift during the pelagic larval development stages (lasting weeks in most species) into or near naturally occurring populations.

If recruitment of the drifting cultured larvae is successful into the natural environment and if the culture-origin progeny are in proximity to wild conspecifics, there is a much greater risk of cultured-wild hybridization and introgression as these individuals mature and potentially repeatedly spawn with the same cues as naturally occurring individuals. Cultured-origin individuals may also recruit into natural populations over time in a stepping-stone manner from more distant culture sites, with successful dispersal and recruitment getting closer to wild individuals, reefs, or beds with each subsequent generation, if suitable intermediate habitat exists. There is some concern that aquaculture gear or vessels may provide these intermediate habitat stepping stones.

Outcomes from gamete dispersal will depend on the magnitude of both gamete and larval dispersal and the successful settlement of dispersed individuals. Some natural populations may be swamped by cultured recruits, while others receive little to no cultured larvae or gametes. This is largely dependent on water current patterns between grow-out sites and suitable coastal habitats. The potential consequences of gene flow from culture-origin genotypes into natural populations will be discussed in greater detail below.

Episodic Escape

Farm loss can result from gear failure events such as grow-out container failure or loss, cage malfunction, bag tearing, or damage to mooring lines. These incidents are considered episodic losses in shellfish culture operations and may occur due to factors such as marine mammal entanglements, vessel collisions, predator attraction, or the impact of waves and currents at the farm site. Such losses contribute to marine debris in the wild, emphasizing the importance of recovery efforts to minimize debris and potential genetic effects. If shellfish lost from grow-out sites due to these incidents mature enough to release gametes, or if mobile species like scallops move toward suitable habitat, there is a potential for culture-wild interactions resulting from episodic losses.

To minimize episodic events, the best available containment technology should be used, including clear marking of farm site boundaries and predator deterrents. However, despite these measures, episodic events may still occur at sites.

Large-scale Escape and Catastrophic Events

A large-scale loss of a shellfish farm refers to the loss of a substantial portion of a farm system or even the entire farm. This can occur due to similar reasons as episodic escapes but under more severe conditions, such as major storm events, leading to greater damage and loss of grow-out infrastructure. Consequently, a larger number of shellfish may be lost from the grow-out site. As with episodic escapes, culture-wild interactions can occur if the lost shellfish survive to a point where they can release gametes, or if they survive long-term and/or disperse to suitable habitats (e.g., for mobile species of scallops).

Summary

Gamete escape from shellfish culture programs is the primary driver of potential culture-wild interactions. Effective operation planning, along with careful design and siting of farm systems, can significantly minimize the risk of gear loss or damage to farm infrastructure. Regular reporting on inventory and operational conditions, including incidents of gear loss and container system failures, is essential. This reporting provides valuable information for refining operational techniques and optimizing industry practices, thereby reducing the potential for negative interactions between cultured and wild shellfish populations.

1.2 Escape Risk Factors

In the following section, we address risk in the context of factors that contribute to the likelihood of escaped/dispersed organisms interacting with wild populations.

Survival of larvae

In many shellfish species desirable for cultivation, individuals reach maturity before attaining market size. This is common in various oysters, clams, and scallops. However, there are exceptions. For example, California mussels (*Mytilus californianus)* and Mediterranean mussels (*Mytilus galloprovincialis*) reach market size around the same time they reach maturity, allowing them to be harvested before full maturity. For species that mature during grow-out, there is a potential for gamete release and subsequent metamorphosis into free-swimming larvae of culture origin in the water column.

Gametes are short-lived, typically lasting only a few hours, as observed in the Eastern oyster (*C. virginica*) (Shumway 1996) and the giant scallop (*Placopecten magellanicus*) (Bayer et al. 2016). Consequently, the window for cultured-wild fertilization is brief, making it more likely that fertilization will occur among cultured gametes rather than between cultured and wild gametes.

Regardless of whether larvae originate from cultured, cultured-wild, or wild gametes, the factors governing larval survival are generally similar. All species in this report have a pelagic larval duration, ranging from a week in species like the Olympia oyster (*O. lurida*) (Bulseco 1982, Pritchard et al. 2015) and bay scallops (*Argopecten irradians*) (Castagna 1975), to up to four weeks in species like the purple-hinged rock scallop (*Crassadoma gigantea*) and Manila clams (*V. philippinarum*) (Toba 1992, Gillespie et al. 2012), although durations vary due to a multitude of factors. While certain mechanisms may help retain larvae near spawning locations (e.g., swimming behaviors or high weight-to-volume ratios) (Shaw and Hassler 1989, Kennedy 1996), larvae can still be dispersed over long distances during the pelagic stage. Despite retention mechanisms, larval distribution is predominantly controlled by water currents during the pelagic stage (Kennedy 1996), which greatly influences larval survival by transporting them towards or away from suitable habitats. Wild larvae or cultured-wild larvae may experience different water current patterns than those originating from offshore aquaculture grow-out sites, leading to variations in larval survival based on location.

Larval survival is also influenced by abiotic factors in the pelagic environment, such as temperature and salinity. Larvae have much narrower physiological tolerances to these parameters compared to mature individuals, which can lead to mortality during the larval phase (Eierman and Hare 2013). Biotic factors, such as food availability and predation risk, also vary in the natural environment and can result in very low, but also variable, survival rates for larvae (Kennedy 1996, Eierman and Hare 2013).

Due to these influences, mortality is very high during the pelagic larval stages (Eierman and Hare 2013), with daily mortality rates commonly ranging from 13% to 28% in larval shellfish studies (Kennedy 1996, and references therein). It has been estimated that out of tens of millions or even trillions of eggs spawned, the number of individuals surviving through metamorphosis may only be in the hundreds to tens of thousands, or there may be no successful settlement at all (Fitch 1950, Kennedy 1996, Heres et al. 2022).

Encounter

The likelihood of encounter between culture-origin shellfish and wild conspecifics depends on several factors. These include the proximity of the grow-out site to wild populations, patterns of water currents between grow-out sites and suitable habitats, the availability of suitable settlement substrates, and the abundance of wild conspecific populations. Regarding gamete mixing, it is more probable that culture-origin gametes will interact with each other rather than with wild-origin gametes from offshore operations, primarily due to the distance between these sources.

For culture-origin larvae produced at a grow-out site, the proximity of the site to wild populations significantly influences the likelihood of encounter. Many shellfish species have been observed to disperse potentially considerable distances, ranging from 13 km to over 100 km from their parental sources (Shaw and Hassler 1989, Carson et al. 2010, López-Duarte et al. 2012, Rogers-Bennett et al. 2016, Robins et al. 2017). For most of these species, this dispersal range exceeds the distance anticipated from offshore operations to conspecific populations. However, water current patterns between grow-out locations and conspecific habitat can either facilitate or hinder dispersal between these sites. These patterns may also vary seasonally and with weather events (Powers et al. 2023). Importantly, the likelihood of encountering specific wild populations may be disproportionate, influenced by prevailing currents that determine the trajectory of drifting larvae.

Another critical aspect in assessing the likelihood of encounter is the ease or difficulty with which drifting larvae can locate suitable settlement substrates and access conspecific habitat. The specificity of settlement materials varies among species. For example, Mediterranean mussels (*M. galloprovincialis*) and Pacific oysters (*Magallana gigas*) can settle on diverse substrates such as rocks, wood, and vegetation in addition to shell (Robinson et al. 2007, Robins et al. 2017). In contrast, species like the Olympia oyster (*O. lurida*) preferentially settle on old shells (Bulseco 1982, Pritchard et al.2015).

Accessibility to conspecific habitat also varies. Species inhabiting coastal intertidal and subtidal zones, such as the California mussel (*M. californianus*) (Suchanek 1981), or those found along beaches with coarse sand or gravel, like the Manila clam (*V. philippinarum*) (Quayle 1949, Goulletquer 1997), may be more readily encountered by drifting cultured larvae. In contrast, species inhabiting bays, estuaries, and sounds, such as the Olympia oyster (*O. lurida*) (Couch and Hassler 1989) and bay scallops (*A. irradians*) (Bert et al. 2011), may present more challenges for larvae to access. The ability of drifting larvae to encounter populations in these

locations can vary with daily tides, seasonal changes, or other factors influencing currents into or out of these areas (e.g., drift cells, wind patterns, water runoff).

Recruitment

The recruitment of culture-origin or culture-wild origin larvae into a conspecific population, a process that includes settlement and subsequent survival to sexual maturity, is a crucial factor in assessing the potential genetic impact of cultured individuals on natural populations. Recruitment is a multifaceted process in shellfish species, characterized by variations not only in substrate preferences (as discussed previously) but also potentially in response to other cues such as settlement cultch quality and the presence of mature individuals, predators, and competitors (Kennedy 1996).

While larvae may be competent to settle, the recruitment process can be influenced by factors akin to a "Goldilocks" scenario, where conditions must be just right for successful settlement and metamorphosis. For instance, in species like the Mediterranean oyster (*M. galloprovincialis*), settlement and metamorphosis may be delayed, possibly up to 7 weeks, reflecting the species-specific complexities involved in larval recruitment (Heres et al. 2022).

Post-settlement survival presents a significant challenge for shellfish, with young spat often facing high mortality rates (Eierman and Hare 2013). As reviewed in Kennedy (1996, and references therein), studies have shown severe mortality rates among young Eastern oyster (*C. virginica*) spat, ranging from 86% to 100% in some sites, and up to 100% in other cases, primarily due to intense predation. Similarly, Von der Meden et al. (2012) conducted simulations on early mortality estimates for brown mussel (*Perna perna*) spat, estimating mortality rates between 31% and 94% within the first two days post-settlement, with average rates around 66% to 67%. While these estimates are model-based, they highlight the rapid and significant mortality pressures that affect newly settled shellfish spat.

Importantly, Von der Meden et al. (2012) noted the scarcity of empirical data on survival during this critical settlement phase for marine shellfish and other benthic invertebrates, underscoring the gaps in our understanding of early post-settlement dynamics in these organisms.

Beyond the initial settlement period, shellfish continue to face mortality risks as they grow towards maturity, although these risks may decrease with increasing size. However, mortality rates can rise again as shellfish reach sizes targeted by recreational or commercial fisheries, where applicable (e.g., for species like the Pismo clam (*Tivela stultorum*); Fitch 1950).

Survival rates to maturity are generally exceedingly low for both wild and culture-origin larvae. While many factors influencing the recruitment success of newly settled spat are likely similar between larvae of wild and cultured origin, there are specific factors that may further reduce the success of settlement and recruitment in cultured larvae. These factors include extended durations in the pelagic phase, which can impact body condition and energy reserves necessary for successful metamorphosis, and competition for limited space and food in intertidal zones.

Moreover, genetic fitness issues in selected lines could exacerbate survival disparities between cultured and wild larvae and spat, as discussed below.

Summary

The likelihood of culture-wild interactions hinges significantly on the spawning capability of cultured shellfish and the subsequent survival, dispersal, and recruitment of their larvae into wild populations. These processes vary considerably among species, yet they share similarities with the challenges faced by wild populations, including high mortality rates across these developmental stages.

1.3 Consequences of Escaped Organisms

The presence of culture-origin escapes in the wild pose significant risks to wild populations by diminishing their fitness, reducing genetic diversity, and altering differentiation among populations (Waples et al. 2012, Lowell 2021). The potential consequences of these escapes are detailed below.

Fitness Effects

Due to differences between wild and cultured environments, aquaculture species, even if spawned directly from wild-caught broodstock, will develop trait differences adapted to culture conditions (Glover et al. 2004, Liu et al. 2015, Bolstad et al. 2017). These differences may result from genetic changes in the captive population or phenotypic plasticity, where a single genotype is expressed differently under varying environments (Wringe et al. 2015, and references therein). These culture-adapted differences, whether intentionally targeted through selective breeding or unintentionally gained, can occur quickly, sometimes within one or a few generations for certain aquaculture species (Islam et al. 2020, Milla et al. 2021, and references therein).

As phenotypes become optimized for culture settings, cultured organisms would experience lower fitness in the natural environment compared to their wild counterparts due to morphological, behavioral, or physiological changes (Reisenbichler and Rubin 1999, Wringe et al. 2015). While most of the available information regarding lower fitness in cultured lines comes from studies on fish, there is some experimental work to suggest this may similarly occur in shellfish based on two of the better-studied shellfish species, the Pacific oyster (*M. gigas*) and the Eastern oyster (*C. virginica*) (Taris et al. 2007, McFarland et al. 2020, McDonald et al. 2023).

When cultured organisms survive to encounter and reproduce with wild populations, there is a potential risk that the introgression will lead to intermediate culture-wild optimized traits and/or lower fitness of those individuals in the natural population (McGinnity et al. 2003, Naylor et al. 2005, Yang et al. 2019). Over successive generations, as there is a continued influx of cultured individuals into natural populations and subsequent introgression between cultured and wild animals, the fitness of the natural population could be reduced through the introduction of

maladapted traits and the fixation of deleterious alleles (Baskett et al. 2013, Bolstad et al. 2017, Glover et al. 2017, Yang et al. 2019, Bradbury et al. 2020).

Most evidence for reduced fitness, lowered population viability, and changes to wild population demography resulting from cultured-wild introgression comes from fish, specifically salmonids (McGinnity et al. 2003, Bolstad et al. 2017, Skaala et al. 2019, Sylvester et al. 2019, Solberg et al. 2020). Although introgression of cultured shellfish into natural populations has been documented (e.g., Jaris et al. 2019, Puritz et al. 2022, Zhao et al. 2024), there is very little information available on the impacts of this introgression on the fitness of the mixed populations. However, it is reasonable to expect similar impacts resulting from the interbreeding between cultured shellfish and wild conspecifics.

Fitness consequences in natural populations will vary based on the number of cultured individuals breeding with their wild counterparts, the degree of domestication of the cultured organisms, and the size and resilience/health of the wild population (Glover et al. 2017). Larger wild populations, or populations that receive some gene flow from other locations, may better withstand potential fitness impacts compared to species with low abundance or depleted populations (Taris et al. 2007, Lorenzen et al. 2012, Baskett et al. 2013, Diserud et al. 2022). The population genetic structure of the wild population is another consideration for evaluating fitness impacts (Lorenzen et al. 2012). For species exhibiting significant population genetic structure, cultured organisms may homogenize genetically distinct, locally adapted populations, potentially leading to the loss of fitness. By definition, locally adapted populations have higher fitness within their native region compared to an introduced population in the same environment (Savolainen et al. 2013). Genomic swamping from cultured organisms could eradicate localized genomic adaptation in distinct populations, leading to lowered fitness across the formerly adapted populations.

Genetic Diversity

Genetic diversity, the variation in genes among individuals in a population or species, is crucial for evolutionary processes that shape physical and behavioral traits over time (Frankham 1996, Palstra and Ruzzante 2008, Sonsthagen et al. 2017). This diversity is influenced by species biology (e.g., distribution, population size, dispersal behavior, mating system, and generation time) and human activities such as harvest, species introductions, propagation, and habitat loss (Amos and Hardwood 1998). Evolutionary forces increase genetic diversity through mutations and decrease it via genetic drift or selective sweeps (Amos and Hardwood 1998, Waples et al. 2012). Immigration from other populations can also enhance genetic diversity.

Genetic diversity provides long-term resilience, allowing populations to withstand or quickly adapt to new stressors (Barrett and Schluter 2008, Schindler et al. 2010, Waples et al. 2012). Loss of genetic diversity can hinder a population's ability to respond to new selective pressures, such as environmental changes and pathogens (Tringali and Bert 1998, Araki and Schmid 2010, Lorenzen et al. 2012, Waples et al. 2012). While the reduction of genetic diversity in cultured populations is documented, its impact on species viability is not fully understood (Araki and

Schmid 2010, Gruenthal and Drawbridge 2012, Hornick and Plough 2019). A population's ability to withstand or recover from a loss of genetic diversity depends on factors that influence demographic and evolutionary processes in the species (Milinkovitch et al. 2013, Sonsthagen et al. 2017).

Effective Population Size

The effective population size (Ne) estimates an idealized population size that assumes random mating and no selection, immigration, or mutation. It reflects the same rate of genetic change as the actual census population (N) (Ryman and Laikre 1991, Tringali and Bert 1998, Husemann et al. 2016). Ne measures the fraction of the gene pool passed to the next generation (Franklin 1980). According to Waples et al. (2018), the census size influences demographic and ecological processes, while Ne affects inbreeding, genetic drift, genetic diversity, and adaptive potential. The ratio between Ne and N predicts the rate of change in population processes under different scenarios (Waples et al. 2018).

Large effective populations maintain higher genetic diversity and preserve it more easily. Natural selection is more effective in these populations. Conversely, small effective populations have less genetic diversity, lose it faster, and are more susceptible to genetic drift, which can fix alleles that reduce overall fitness. They also face a higher risk of inbreeding depression (Roman and Darling 2007, Ponzoni et al. 2010, Waples et al. 2012, Yáñez et al. 2014, Sonsthagen et al. 2017).

Discrepancies between Ne and N often arise from biological characteristics like unequal sex ratios, spawning or mating strategies, or unequal reproductive success (Waples et al. 2012, Sonsthagen et al. 2017). In marine fish and invertebrates, Ne can be smaller by two to six orders of magnitude compared to N, largely due to variances in reproductive success (Hedgecock and Pudovkin 2011). This results in Ne/N ratios often much smaller than 0.01, as seen in many marine species, including shellfish like the Pacific oyster (*M. gigas*), Eastern oyster (*C. virginica*), European flat oyster (*O. edulis*), and great scallop (*Pecten maximus*) (Hedgecock 1994, Frankham 1995, Gaffney 2006, Lallias et al. 2010, Sun and Hedgecock 2017, Morvezen et al. 2016).

Recent research indicates that these low Ne/N ratios may be biased downward due to inadequate sample sizes and violations of Ne calculation assumptions (Waples et al. 2016). Even accounting for factors like longevity, fecundity, and reproductive success variance, extreme conditions or variances are needed to reduce Ne/N below 0.01 (Waples 2016). Studies with larger sample sizes have revealed higher Ne/N ratios (> 0.1) in some marine fish, suggesting earlier estimates might have been biased (Waples et al. 2018, Jones et al. 2019, Tringali and Lowerre-Barbieri 2023). While this does not necessarily discount the possibility of smaller Ne/N ratios for other organisms, investigating this bias is challenging, as precise estimates of Ne require sampling about 1% of the population over time, which is often impractical for marine species (Marandel et al. 2019).

Effective Population Size and Genetic Diversity of Cultured Animals

Aquaculture breeding programs differ significantly from other animal breeding programs due to the high fecundity, early-life mortality rates, and large number of animals produced (Fisch et al. 2015). These programs typically start with a small number of wild individuals, leading to reduced genetic diversity in cultured populations compared to their wild counterparts (Lorenzen et al. 2012). High reproductive variance within these programs results in disproportionate offspring production, with fewer mate-pairings represented among the offspring than the potential maximum number of breeders, as observed in the Eastern oyster (*C. virginica*) (Hornick and Plough 2019) and the purple-hinged rock scallop (*C. gigantea*) (Jackson 2021). Additionally, intentional or unintentional selection and differential survival in early life stages further skew the broodstock representation in the offspring (Frost et al. 2006, Fisch et al. 2015, O'Leary et al. 2022). These factors often lead to much smaller effective population sizes and reduced genetic variation in cultured programs, as seen in shellfish species like the silver-lipped pearl oyster (*Pinctada maxima*) (Lind et al. 2009), Pacific geoduck (*Panopea generosa*) (Straus et al. 2015), blue mussel (*Mytilus edulis*) (Gurney-Smith et al. 2017), Eastern oyster (*C. virginica*) (Hornick and Plough 2019), and Kumamoto oyster (*Crassostrea sikamea*) (Ma et al. 2023).

Genetic diversity in cultured populations tends to decrease over time (Aho et al. 2006), raising concerns about long-term sustainability and inbreeding prevention in breeding programs (Danancher and Garcia-Vazquez 2011, Prado et al. 2018). This loss of diversity can destabilize breeding programs and reduce the genetic variance needed for selective breeding (Ponzoni et al. 2010). It also increases genetic drift, leading to genetic differentiation between cultured and wild populations, as reported in several shellfish species (Lallias et al. 2010, Morvezen et al. 2016, Hornick and Plough 2019, Bramwell et al. 2024). Maintaining high genetic diversity in cultured populations is vital but challenging due to the costs and resources required for larger breeding programs.

Risk of Escaped Cultured Animals on Genetic Diversity

The risk to wild populations arises when escaped cultured organisms survive, reproduce with wild conspecifics, and significantly contribute to the next generation (Laikre et al. 2010, Lorenzen et al. 2012). This can reduce the total effective population size (NeT; combined escapee-wild population) and genetic diversity in wild populations, a phenomenon known as the Ryman-Laikre effect (Waples et al. 2016). While this risk is higher for small or fragmented populations, it can also impact large populations by significantly reducing Ne (Waples et al. 2016).

The impact of the Ryman-Laikre effect varies based on species biology, demographics, and genetic structure. Tringali and Bert (1998) found that while some species show minimal impact, others, especially those that have experienced population crashes, can suffer significant Ne reductions (Tringali 2023). Despite genetic diversity losses in cultured populations, some aquaculture species have shown no genetic variation loss in wild populations where release of cultured individuals has occurred (e.g., Tringali and Bert 1998, Kitada et al. 2009, Laikre et al. 2010, Gow et al. 2011, Nakajima et al. 2014, Katalinas et al. 2018, Hornick and Plough 2019). However, introgression of cultured individuals has reduced genetic diversity in others (e.g., Eldridge and Naish 2007, Eldridge et al. 2009, Kitada et al. 2009, Christie et al. 2012). Most of this information comes from studies on fish species, with limited research available on the impact of cultured shellfish on wild conspecifics (Lowell 2021).

While NeT might theoretically be sufficient to maintain population diversity in the mixed culture-wild population, significant reductions can still result in the loss of genetic diversity and adaptive potential (Kardos et al. 2021). Large effective populations are most at risk due to the potential for substantial Ne reduction. However, if cultured individuals have low survival and reproduction rates in the wild, the Ryman-Laikre effect may be negligible (Waples et al. 2012, Glover et al. 2017).

Potential for Mitigation

To minimize genetic consequences to wild conspecific populations, a culture program can implement several strategies. Harvesting shellfish before they reach sexual maturity is a clear way to reduce genetic impacts, though this is only feasible if the premature size has market potential.

Culture program siting should consider the spatial scale of locally-adapted populations, marine biogeography, and dispersal factors from the farm site, ensuring alignment with local population connectivity patterns. Broodstock should be sourced from nearby populations, with collections from multiple locations to represent the population's spatial and temporal variation (Waples et al. 2012).

Best breeding practices in a culture setting should aim to increase the effective population size in cultured offspring by maximizing mating combinations and ensuring multiple spawning events

are represented in the offspring. Techniques such as equalizing gametes before fertilization, isolating male and female gametes, and conducting partial or full factorial spawning crosses can help maximize the effective broodstock size (Straus et al. 2015, Jackson 2021). Strip-spawning may facilitate large numbers of pair-wise fertilization crosses, though success varies by species (Hornick and Plough 2019). While this process might be more manageable for shellfish than for fish due to their smaller size, it still requires significant labor and hatchery infrastructure. There is also the potential for continued Ne reductions due to unequal egg quality and variance in early life stages (Hornick and Plough 2019).

Long-term breeding program goals should include the use of genetic markers to maintain genetic diversity and avoid inbreeding. Pedigree tracking, with or without genetic markers, can assist in these efforts (Ryman and Laikre 1991, Ponzoni et al. 2010, Yáñez et al. 2014, Fisch et al. 2015, Hargrove et al. 2015).

The impacts of genetic diversity loss and the Ryman-Laikre effect on wild populations are complex and difficult to predict, but certain life-history traits can help mitigate these effects. Traits such as long lifespans, overlapping generations, and large census sizes provide some protection (Tringali and Bert 1998, Katalinas et al. 2019). Migration from neighboring populations can quickly restore genetic diversity in mixed populations, although it can also result in a loss of diversity as genes migrate away from impacted populations (Ingvarsson 2001, Waples et al. 2012). To minimize the Ryman-Laikre effects, the genetic contribution of cultured individuals to the next generation in the wild should be kept below 10%, with 5% being a more conservative threshold (Waples et al. 2012, 2016). If cultured individuals have low survival or reproduction rates in the wild, their genetic impact will be lower than census data suggest (Waples et al. 2016). Rigorous monitoring of the proportion and genetic contribution of escaped animals, along with regular genotyping, is crucial (Waples et al. 2016).

Rotating large numbers of wild broodstock into a program annually and retiring older broodstock after 3 to 4 years may help increase genetic diversity and prevent differentiation between wild and cultured populations (Hornick and Plough 2019). In a stock supplementation program, maintaining between 50 and 200 breeders can preserve genetic variability and represent up to 99% of the population diversity (Tringali and Bert 1998). Similarly, Gruenthal and Drawbridge (2012) found that 74 effective breeders in a White Seabass program represented 99% of wild genetic diversity; accounting for spawning behaviors, this required maintaining between 140 and 200 broodstock fish to achieve that effective population size in commercial operations. Although low-frequency gene variants might still be lost, using reasonable broodstock sizes may retain most existing genetic diversity (Tringali and Bert 1998, Gruenthal and Drawbridge 2012).

For some species, sterilization techniques are available to halt the reproductive behaviors of shellfish, significantly reducing the risk of culture-wild interactions and genetic diversity loss. Sterility in shellfish can be achieved through triploid induction (Straus et al. 2015), resulting in individuals that either fail to develop sexually mature gonads or produce minimal gametes compared to diploid individuals (Yang 2022). Triploid lines are used commercially for Pacific oysters and Eastern oysters, and experimentally in other shellfish species (e.g., Barber and Mann

1991, Straus et al. 2015, Herbert et al. 2016, Yang et al. 2018, Culver et al. 2022; see Piferrer et al. 2009 for an extensive list of triploid shellfish). While sterilization prevents captive individuals from reproducing, the trade-offs of this approach should be carefully evaluated.

Other measures to reduce larval contribution to wild populations include manipulating environmental or hatchery conditions to favor highly skewed sex ratios in cultured shellfish, which has been observed in the development progression in several hermaphroditic species (Jackson 2021). Although this approach does not eliminate gamete release, it can reduce the number of culture-origin larvae produced at a grow-out site.

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2.0 Southern California Candidate Species for Marine Aquaculture

2.1 Geographic range

The north, central north, south, and central south portions of the Southern California bight were considered in these evaluations.

2.2 Shellfish Candidate Species for Marine Aquaculture

2.2.1 Olympia oyster (Ostrea lurida)

2.2.1.1 Range/Description

Olympia oysters (*Ostrea lurida*) are found along the west coast of North America, from southern Alaska to Baja California, residing in estuaries, sounds, tidal ranges, and bays (Couch and Hassler 1989). In the mid-1800's, this species supported a large fishery, and experienced intense harvest pressure. In the late 1800's, the introduced *Crassostrea virginica* gained favor over the smaller and stronger tasting *O. lurida* (White et al. 2009a). As a result of overharvest, pollution, loss of habitat, and competition with introduced species, most of the *O. lurida* populations have been drastically reduced from their historical abundances with an estimated 90% to 99% reduction in population size (Bulseco 1982, Ridlon et al. 2021), or are now considered functionally extinct with greater than 99% of former population sizes, except for the relatively healthy population in British Columbia (Beck et al. 2011). Stock assessment or abundance data is lacking, but a harvesting ban is in place due to the low population numbers (Pritchard et al. 2015). However, even with the reduction in harvesting pressure, populations have not rebounded due, in part, to very limited natural recruitment (Ridlon et al. 2021).

Olympia oysters were first farmed in the U.S. around 1890 in Puget Sound's tidelands until massive population decline in the early to mid-1900s (Couch and Hassler 1989). Commercial production is focused in southern Puget Sound, Washington, with some limited farming occurring in northern California. While there is a growing interest in the commercial aquaculture of Olympia oysters, the current focus remains on supplementation efforts. The first supplementation aquaculture program began in Washington in 2013 (Ridlon et al. 2021). Since then, various small-scale supplementation programs have been implemented to restore Olympia oysters. As noted by Blake and Bradbury (2012), it may be possible to use commercial culture to aid restoration efforts through the supply of hatchery seed if wild individuals are used as the source, or broodstock practices can ensure regionally-relevant and genetically diverse spat.

2.2.1.2 Biological Characteristics

Sexual maturity in this species is typically attained about a year after settlement (Coe 1931b). Olympia oysters display sequential hermaphroditism, initially developing male gonads followed by female gonads, and then continue to alternate between male and female gonadal development throughout their lifespan (White et al. 2009b). Spawning can be triggered by water temperatures of 16-18°C, occurring once or twice yearly between spring and fall (Couch and Hassler, 1989). Males release clumps of sperms, which induces other males in the area to release gametes (White et al. 2009b). Unique to this species, sperm are brought into the mantle cavity in females to internally fertilize eggs, and develop into larvae that remain for approximately 10 to 12 days in a brood chamber (Coe 1931a, Bulseco 1982, Pritchard et al. 2015). After being discharged the larvae remain planktonic on average for 11 to 16 days, although this duration may range between 7 days and 8 weeks, prior to settling on old shells (preferred), and metamorphosing into juveniles (Bulseco 1982, Pritchard et al. 2015). A spawning event can yield 250,000 to 300,000 larvae. Though active spawning may not be occurring, all stages of sexual reproduction are present within a single population throughout the year (Coe 1931a, Oates 2013). Olympia oysters can grow to 6-8 cm in length and 2.5-3.5 cm in depth, with their shell shape varying based on the surface they grow on (Couch and Hassler, 1989). The maximum age for this species remains unknown.


Image from the Washington Dept. of Fish and Wildlife

2.2.1.3 Population Structure

Silliman 2019 conducted a study on Olympia oysters from Northwest British Columbia to Southern California, identifying six distinct populations. Genetic breaks were observed at well-known biogeographical barriers. The Southern California population spans from San Diego Bay to Monterey Bay, with the bay itself acting as a biogeographical barrier. The Northern California population extends from San Francisco Bay to Humboldt Bay, showcasing genetic diversity even within sites in San Francisco Bay. There is a distinct population in Oregon, including Netarts Bay and Yaquina Bay. An additional population found in Willapa Bay, Washington, which also genetically grouped with Coos Bay, Oregon, this is most likely due to anthropogenic introduction from Willapa Bay to Coos Bay. The Oregon and Willapa/Coos Bay populations share phylogeographic history and both display lower genetic diversity compared to the California populations. Puget Sound and parts of British Columbia constitute a significantly different population compared to the Klasho Inlet and Barkley Sound in British Columbia. Despite a shared evolutionary history between these regions, genetic exchange between them is

significantly reduced. Overall genetic diversity was highest in Southern California due likely to three nonexclusive mechanisms. The first is the California current facilitates asymmetric gene flow southward, accumulating genotypes in the south. The second mechanism is that northern populations have experienced heavy extirpation and population bottlenecks from glacial cycles. Lastly, there is possible admixture from a sister species of *O. conchaphila* to the south which increases genetic diversity in the southern populations (Silliman 2019).

2.2.1.4 Aquaculture

As most culture programs are geared towards restoration, juveniles are produced from locally sourced broodstock (Blake and Bradbury 2012), making sure to collect broodstock of varying sizes to collect both sizes based on their hermaphroditic patterns of gonadal development (Bulseco 1982). and are then conditioned in a hatchery for approximately a month while increasing temperature to simulate seasonal conditions associated with the start of spawning (Wasson et al. 2020). After spawning, and the internal fertilization and brooding period (again 10 – 12 days on average), the larvae are released and are able to be collected from the water column and separated from the brood individuals (Wasson et al. 2020). During this period, the larvae are fed live phytoplankton cultures, and examined for development stages, once larval eye spots and feet are observed, shells or other substrate may be moved into the tanks to induce settlement (Marks 2020, Ridlon et al. 2021, Wasson et al. 2020). The duration of the post-settlement phase in a hatchery likely varies by location and objective, but one month was used by Wasson et al. (2021) prior to outplanting at the grow-out site. Grow-out may occur by scattering the settled substrate in a tidal habitat (if done for restoration), or may occur by hanging culture lines of shells that the juveniles have settled on, or in mesh bags, or cages (Bulseco 1982, Wasson et al. 2021).

Olympia oysters reach market size of 3.5-4 cm in 3-4 years (Couch and Hassler 1989, Beahrs 2012). Typically, sexual maturity is reached about a year after settlement (Coe, 1931b), therefore they would be sexually mature during grow out and have the potential to release gametes during cultivation.

2.2.1.5 Considerations on genetic risk to wild conspecifics

Comprehensive abundance data for Olympia oysters is limited, but studies indicate significant population declines along the West Coast of North America. Recent genetic research by Silliman (2019) revealed regional population structure in this species, and that the genetic diversity of Olympia oysters in Southern California surpasses that of any other area within its native range, which may amplify the impact of escaped aquaculture oysters on local populations. These oysters exhibit distinct local adaptations, such as timing of reproduction and resilience to salinity fluctuations (Seale and Zacherl 2009, Barber et al. 2016, Bible and Sandford 2016, Maynard et al. 2018, Silliman 2019). Fine-scale genetic diversity and local adaptation may exist in Southern California, which is crucial for strategic broodstock selection. Ridon et al. (2021) identified the greatest genetic risk associated with hatchery-reared Olympia oysters as the loss of genetic diversity and local adaptation, echoing the concerns outlined in the Washington plan to restore

this species (Blake and Bradbury, 2012). Notably, Ridon et al. (2021) highlighted estuaries in California with the highest conservation priorities based on factors such as population isolation and local extinction risk; these included Elkhorn Slough, Morro Bay, Carpinteria Marsh, and Mugu Lagoon. Therefore, extra precautions should be taken to prevent genetic introgression from offshore culture of *O. lurida* impacting these locations, or a careful broodstock plan should be implemented to preserve regional genetic diversity.

The extent that larvae of this species disperse after release remains uncertain, yet given their limited population connectivity, extensive dispersal may not occur frequently. There is also a lack of information regarding survival and settlement rates of dispersed cultured Olympia oysters in the wild, and little information available for wild populations, so high uncertainty exists regarding the ability of cultured *O. lurida* to encounter and successfully introgress into wild populations.

Given that cultured stock will reach sexual maturity prior to harvest, and the presence of locally-adapted populations exhibiting genetic structure at small scales, and the high level of genetic diversity within Southern California populations, the potential genetic risk to wild populations from the culture of *O. lurida* is high. Mitigating these risks involves using local broodstock and carefully considering hatchery conditions, given the strong carryover effect (i.e., inherited acclimatization in offspring based on conditions experienced by parents) of Olympia oysters on reproduction based on parental environmental conditions (Camara and Vadopalas 2009, Spencer et al. 2020). Procuring new broodstock regularly can also help minimize inbreeding and maximize genetic diversity within cultured populations, further reducing genetic risks to wild populations of escaped/dispersed Olympia oysters (Camara and Vadopalas 2009). In addition, using oceanographic-based water particle modeling to determine which populations may be most impacted from larvae dispersed from aquaculture operations may help to focus monitoring efforts to detect potential impacts, and guide broodstock selection.

2.2.1.6 References

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2.2.2 Pacific oyster (Magallana gigas)

2.2.2.1 Range/Description

The Pacific oyster, *M. gigas, s*ynonymous with *Crassostrea gigas*, is native to Japan and Korea, but has been introduced globally for aquaculture purposes, including in the U.S., Canada, the U.K., France, China, New Zealand, Australia, South Africa, and South America (Mann et al. 1991, Orensanz et al. 2002, Miossec et al. 2009). As reviewed in White et al. (2009), the Pacific oyster may have been introduced in Washington as early at 1899, but concerted efforts to introduce and culture this species did not occur until 1919 when it helped to revitalize the oyster industry in Washington which had recently experienced a decline in the over-harvested Olympia oyster, and suffered population crashes in the newly introduced Eastern oyster (*Crassostrea virginica*).

Image from NOAA Fisheries

The Pacific oyster has since become one of the primary oyster species cultivated worldwide due in part to its broad tolerance to environmental conditions, fast growth and large sizes, and relative ease in culturing (White et al. 2009), however, these attributes have also led to its global success in becoming established in the wild in many of the regions where it has been introduced for commercial culture (Ruesink et al. 2005). Along the west coast of North America, the Pacific oyster is both cultured and is found in naturalized populations from California to southeast Alaska, and there is limited abundance data for these naturalized populations. However, they often coexist with the native Olympia oyster along that distribution (Nosho 1989, Shaw 1997, Kornbluth et al. 2022) providing essential habitat.

2.2.2.2 Biological Characteristics

Pacific oysters are considered to be some of the larger and faster growing oysters in culture; their typical shell length ranges between 8 and 20 cm, although they can reach lengths up to 40 cm (Nehring 2006). These oysters are oviparous hermaphrodites, initially spawning as males in year one and subsequently transitioning to females (Héral and Deslous-Paoli 1991). However, they have been observed to repeatedly transition between sexes depending on environmental conditions (Yasuoka and Yusa 2016). Although they can live up to 30 years, they reach sexual maturity in approximately a year, and exhibit very high fecundity where they are capable of producing 50-100 million eggs within 3-4 weeks over multiple spawning periods (Nehring 2006). The timing of spawning is influenced by temperature and varies by location (Dean 1979,

Héral and Deslous-Paoli 1991, Kobayashi et al. 1997), but generally occurs during warmer water temperatures periods (Chávez-Villalba et al. 2007, Beck et al. 2024).

Fertilization of eggs occurs in the water column, and larval Pacific oysters remain free-swimming and planktonic for 2-3 weeks before settling on substrates like rocks, mud, sand, or other oysters (Orensanz et al. 2002), in water less than 40 m deep, and more commonly less than 15 m deep (Robins et al. 2017). Robins et al. (2017) used particle tracking modeling to evaluate potential distances over which Pacific oyster larvae may disperse from sites in the UK near the Irish Sea. After modeling three types of dispersal strategies for the swimming larval stage, they found that the average radial dispersal distances away from the release site ranged from 13 to 39 km. Although this modeling was based on a different location, it suggests that dispersal potential for this species is likely far greater than the distances from offshore grow-out sites to coastal habitats where dispersal cultured oysters may interact with naturalized populations or other shellfish species, or establish new naturalized populations. However, the prevailing currents between the farm and coastline would still largely determine how frequently dispersal would occur between these sites.

2.2.2.3 Population Structure

Although Pacific oysters are not native to the West Coast of North America, naturalized populations now exist away from aquaculture sites along this coast, and in many of the locations around this world where this species was introduced for aquaculture, making the Pacific oyster one of the most successful invasive marine invertebrate species (Ruesink et al. 2005, Faust et al. 2017). Interestingly, as water temperatures warm, naturalized populations may further spread into areas once too cold for successful recruitment in natural settings (Beck et al. 2024).

In British Columbia, Sutherland et al. (2020) sampled five naturalized Pacific oyster populations and found very low genetic differentiation, attributing this to significant human-mediated dispersal around Vancouver Island. They also compared genetic data from populations in France, Japan, and China, which revealed only weak genetic divergence between these distant populations. The introduction of Japanese broodstock in the last century, along with anthropogenic dispersal, facilitated one-way gene flow to various parts of the world. Additionally, data from Sutherland et al. (2020) suggested that the effective population size (N_e) ranges from hundreds to a few thousand, supporting sweepstakes reproductive success. Hedgecock and Pan (2021) examined 11 naturalized Pacific oyster populations in Washington and four populations being cultured nearby from the Molluscan Broodstock Program (MBP) program to investigate if MBP cohorts had seeded the surrounding areas. They discovered that genetic divergence was seven times greater between cultured and naturalized populations, than among the sampled naturalized populations, suggesting farmed cultures in this location were not currently seeding the naturalized populations. Like Sutherland et al. (2020), they found evidence to suggest low effective population size, large genetic drift, and high gene flow among the 11 wild naturalized populations, supporting the notion of one large North American Pacific oyster metapopulation. These findings also align with previous research by Sun and Hedgecock (2017), who also observed high gene flow in British Columbia, Washington, and even Japan. While the

naturalized populations in the northern region of the west coast have been examined, there is a lack of genetic connectivity information within the state of California.

2.2.2.4 Aquaculture

Pacific oysters are extensively studied in aquaculture settings, as this species is known for their rapid adaptability to selective pressures, facilitating the quick selection of desirable traits (de Melo et al. 2016). In commercial settings, broodstock oysters are conditioned for approximately a month prior to volitional spawning using thermal shock, or to strip spawning of gametes. The larvae are then raised in land-based tanks until they are settled onto artificial (e.g., PVC pipes) or natural (e.g., whole shell or microcultch (finely ground oyster shells)) materials.

Alternatively, an approach known as remote settling has been developed and widely adopted on the Pacific U.S. coast, becoming a standard practice for many oyster and clam growers, including Pacific oysters. In this approach, pediveliger larvae are purchased from a hatchery at a considerably lower cost compared to larger spat. During the pediveliger stage, when shellfish are on the verge of settling and undergoing metamorphosis, they are processed and shipped to growers. This method shifts the settling and nursery responsibilities to the growers rather than hatchery operators (Hudson et al. 2019).

The spat set on microcultch for the half shell market are grown in a hatchery or sea-based nursery with an upwelling system until they reach 10 to 13 mm, after which they are transitioned to a grow-out system that may utilize bottom, off-bottom or suspended culture approaches (FAO 2024). Spat grown on whole shell in mesh begs are transferred to nursery or grow out beds where they will be grown as clumps or clusters for the jarred market.

Large-scale efforts have been made in both sea-based aquaculture and hatchery production of Pacific oysters with grow out in nearshore bays and inlets (Guo et al. 1999, Langdon et al. 2003, NRC 2004). While offshore farming for Pacific oysters has been explored in several European countries, it is currently in the experimental phase (Ferreira et al. 2009, Buck and Langan 2017, Palmer et al. 2020). In the United States, offshore production is complicated due to product landing issues related to compliance with the National Shellfish Sanitation Program (T. King, personal communication). Preliminary results indicate that offshore farming demonstrates superior growth rates, survival rates, and quality indices (e.g., the ratio of meat to total animal weight) compared to coastal farms (Gentry et al. 2017, Heasman et al. 2020, Palmer et al. 2021).

Pacific oysters typically achieve a market size of 70 to 100 grams live weight within 18-30 months, this timeline is influenced by temperature and salinity conditions (NMFS 2022). They also attain sexual maturity and exhibit high fecundity within just one year, enabling them to release gametes during the grow-out process. Reproductive sterility has been achieved in Pacific oysters by crossbreeding diploid and tetraploid oysters to produce triploid oysters, which have much smaller reproductive potential compared to diploids (Herbert 2016).

2.2.2.5 Considerations on genetic risk to wild conspecifics

First, since the Pacific oyster was introduced to North America, no native populations exist in this region that could be adversely affected by aquaculture practices. This species reaches reproductive maturity before the end of the grow-out period, and as demonstrated in the Robins et al. (2017) particle modeling study, larval dispersal can exceed distances from offshore culture sites to coastal habitats, although the frequency of this dispersal will depend on the prevailing currents at the farm site and along the coast. High levels of population connectivity have been observed among northern populations, which correspond to the long larval dispersal capabilities modeled in this species, however, effective population sizes have been reported to be surprisingly low (Hedgecock and Pan, 2021). At the present, there are no genetic connectivity studies available for populations in California.

Based on the Pacific oyster not being a native species, and the high population connectivity/lack of genetic spatial structure observed in other portions of the U.S. west coast, the genetic risk to naturalized populations from the culture of the Pacific oyster is low. Although this species may reach sexual maturity prior to harvest, the use of triploid lines leads to sterility in most individuals, and greatly reduces impacts on naturalized populations from culture operations. While there is some concern about non-native Pacific oysters outcompeting native species, this has not been an issue in the U.S. (NOAA Fisheries 2023).

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2.2.3 Purple-hinged rock scallop (Crassadoma gigantea)

2.2.3.1 Range/Description

Purple-hinged rock scallops (*Crassodoma gigantea*) are native to the West Coast of North America, spanning from British Columbia to Baja California, Mexico (MacDonald et al. 1991). Thriving in a range of oceanic conditions, they inhabit depths from the subtidal zone to 80 meters (Culver et al. 2022). Distinguishing them from other scallop species, *C. gigantea* permanently attaches to hard substrates using byssal threads after a free-swimming larval phase (Culver et al. 2006). In their natural habitat, they are typically found in crevices, beneath boulders, and affixed to hard surfaces (CDFG, 2001). Due to their patchy distribution, populations of *C. gigantea* are particularly vulnerable to overharvesting and local depletion (Culver et al. 2022). Consequently, commercial harvesting of rock scallops is prohibited in California, as the California Department of Fish and Game (CDFG) determined that their distribution and abundance were insufficient to sustain a commercial market (CDFG 2001). Despite this, the species remains sought after by sport divers and shore collectors. Estimating their landings is challenging; however, records from the CDFG indicate that, between 1978 and 1987, an average of 930 scallops were harvested annually by divers on commercial sport diving boats in the Channel Islands (CDFG 2001).

Purple hinged rock scallops are of particular interest from an aquaculture perspective due to their substantial size, ranging from 4 to 8 inches (Culver et al. 2022), and possessing highly valuable large adductor muscles that makes them well-suited for live and half-shell markets (Culver et al. 2006). As highlighted by Culver et al. (2006), there has been ongoing interest in commercially culturing this species since the 1970s. However, certain challenges, such as ensuring a consistent seed supply and developing effective grow-out approaches to maintain the marketability of the shell, given the scallop's unique byssal attachment, have hindered the development of the industry for *C. gigantea*.

2.2.3.2 Biological Characteristics

Purple-hinged rock scallops are known for their longevity, with a lifespan of at least 20 years (Culver et al. 2022). These scallops typically attain sexual maturity at 55 mm, or approximately 2 years of age (Jackson 2021). Moreover, they are believed to exhibit protandry, a phenomenon where newly mature individuals are predominantly male and later transition to females as they grow larger and older (Jackson 2021).

As broadcast spawners, *C. gigantea* releases gametes into the water multiple times throughout the year (Shumway and Parsons 2016, Lowell 2021). While specific fecundity estimates for this species are lacking, it is presumed to have high fecundity, akin to other scallop species that can produce hundreds of thousands to millions of eggs in a single spawning event, with larger individuals typically producing more gametes (Laurén 1982, MacDonald et al. 1991, Cochard and Devauchelle 1993, Jackson 2021).

The spawning seasons of *C. gigantea* vary across its range, with observations in Southern California occurring from October to January and earlier in northern regions, ranging from June to August in the Puget Sound and June to October in British Columbia (Lowell 2021).

Gametes are believed to have a relatively short lifespan in the natural environment, as evidenced by Bayer et al. (2016), who found that fertilization success dropped to zero percent in 24-hour-old eggs of the giant scallop (*Placopecten magellanicus*). Despite this, the pelagic larval duration for purple-hinged rock scallops is considerably longer, estimated at around 4 weeks (Shumway and Parsons 2016). Additionally, they undergo a prolonged metamorphosis from the pediveliger to juvenile stage compared to other bivalve species (Culver et al. 2022).

While young juveniles of purple-hinged rock scallops may engage in short bursts of swimming, they permanently attach to substrates between 6 and 12 months of age, typically when reaching a shell height of approximately 25 to 30 mm. However, if dislodged, they possess the ability to reattach to the substrate (Culver et al. 2006, Lowell 2021). Consequently, due to this unique characteristic, they exhibit much lower adult dispersal compared to other scallop species.

2.2.3.3 Population Structure

Population structure spanning from Alaska to Southern California was assessed through thousands of single nucleotide polymorphisms (SNPs) (Lowell 2021). Although the signal was low, significant population structure was observed between the Salish Sea regions and all coastal populations, which formed a continuous metapopulation. Lowell (2021) proposed that the Victorian Sill potentially restricts dispersal between coastal waters and the Salish Sea. Interestingly, no genetic differentiation was observed between the two California regions sampled in this study, Monterrey Bay and Catalina Island, nor did they display genetic structure with other northern coastal regions. These findings were surprising given the extensive geographic range of the sampling, the limited adult dispersal, and the statistical power of genomic approaches (Lowell 2021). Consequently, Lowell (2021) suggested that although these

populations may experience sufficient connectivity to prevent genetic structure among locations, they may still function as demographically independent populations. Therefore, local depletions or loss of genetic diversity due to aquaculture activities may be slow to replenish through migrants for this long-lived species.

No effective population (N_e) or census population size estimates are available for this species. However, in other bivalve species with similar reproductive characteristics, N_e may be much lower than the wild census size due to high fecundity and high early mortality (Li and Hedgecock 1998, Hedgecock et al. 2007). In *C. gigantea*, patchily distributed populations may be more susceptible to the loss of genetic diversity through genetic drift.

2.2.3.4 Aquaculture

Rock scallops are currently being considered for aquaculture in the United States, with research on farming protocols ongoing since the 1970s (Culver et al. 2006, Jackson 2021, Culver et al. 2022). However, challenges have been encountered in culturing this species, primarily due to the availability of seed for commercial farms and the preference of rock scallops to grow attached to substrates (Shumway and Parsons 2016, Culver et al. 2022). Generally, wild-collected broodstock have shown better spawning performance in cultured settings compared to hatchery-maintained broodstock (Culver et al. 2022).

According to Jackson (2021), wild mature *C. gigantea* can be collected and conditioned in a hatchery by providing ample live algal feeds and gradually raising the water temperature to induce volitional mass spawning. Gonadal maturity can be checked by gently gaping the scallops and visualizing the color of the gonads, with bright red to orange indicating females and pale white indicating males. However, developing effective broodstock conditioning protocols for hatchery-maintained populations has been challenging, with the most successful method involving laborious chemical induction via injection of serotonin into the gonad or adductor muscle (Culver et al. 2022).

Given the patchy and small populations of this species, the development of effective broodstock conditioning protocols will be crucial for the commercial development of aquaculture, especially considering the potential restriction of access to wild populations due to their limited abundance (Culver et al. 2022).

The hatchery and grow-out techniques outlined by Jackson (2021) for *C. gigantea* appear to closely align with anticipated commercial culturing approaches for this species. Larvae were fed the same live algal mix as the broodstock, and at 38 days post-fertilization, metamorphosis and settlement were induced by filling the tanks with artificial seaweed. Subsequently, at 5 months post-fertilization (at a shell height of 5 mm), the scallops were transferred to pearl nets with 3 mm mesh and suspended in grow-out locations. As the scallops grew, they were transferred to larger nets, with lantern nets (4 mm mesh size) used when the mean shell height reached 10 mm (approximately 13 months post-fertilization), and then to 10 mm mesh cages when the mean shell height reached 40 mm (approximately 18 months post-fertilization). To minimize

biofouling, the cages were suspended between 3 and 5 meters below the surface and hung off of longlines or mussel floats, depending on the location (Jackson 2021).

Although unattached *C. gigantea* scallops may develop a shell shape with higher market value and are easier to harvest, attached individuals were observed to grow significantly faster in both shell deposition and tissue growth (Culver et al. 2006). Despite being labor-intensive, Culver et al. (2006) demonstrated that artificial attachment of scallops to a substrate at an early stage, before the capacity for byssal attachment, resulted in higher growth rates, regular shell form, and offered the opportunity to incorporate trademarks or other markings into the shell for farm-of-origin distinction. This attachment process was required only once, eliminating the need for an intermediate grow-out step (Culver et al. 2006).

At 12 months, Culver et al. (2022) observed the sex of their scallops histologically, reporting that 50.1% were male, 3.5% were female, 0.93% were hermaphrodites, and 44.9% did not yet have germ cells. However, they identified the first ripe scallop at 20 months, with the majority reaching maturity by 26 months. In contrast, Jackson (2021) documented the size and age of first maturation as 55 mm shell height and 25 months, respectively. Although there is a slight variation between these findings, commercial harvest is not expected until scallops reach 100 to 110 mm shell height, or 3 to 4 years of age (Jackson 2021), indicating that this species will become reproductively mature and initiate spawning during the grow-out period.

Jackson (2021) discovered that current hatchery practices, employing mass spawning techniques, could significantly diminish genetic diversity in the offspring produced. Despite 75% of the broodstock spawning in her experiment, only 17 to 35% of the total broodstock were represented as effective breeders based on genotyped offspring. This reduction was attributed to family-specific survival of early life-stages, skewed sex ratios, and high variance in reproductive output and success. To enhance the number of effective breeders, Jackson suggested measures such as equalizing gametes prior to fertilization and implementing partial or full factorial spawning designs, although their practical implementation may pose challenges. Nonetheless, maintaining genetic diversity in the hatchery is crucial during the period between maturation and harvest in grow-out to avoid impacting genetic diversity in wild stocks. Additionally, it may be vital for future sourcing of potential broodstock depending on the duration required to develop successful hatchery conditioning protocols. Triploidy is being explored in this species, with preliminary data indicating the potential of developing tetraploid rock scallops as the mechanism to achieve triploid offspring. If successful, this approach could prove effective in mitigating or eliminating genetic risks to wild populations (Culver et al. 2022).

2.2.3.5 Considerations on genetic risk to wild conspecifics

Information on the wild abundance of rock scallops is currently lacking due to their patchy and often cryptic nature. According to a recent genomic study by Lowell (2021), *C. gigantea* exhibits genetic uniformity across sampled locations on the west coast from Alaska to California, except for some low but notable structure observed in the Salish Sea. However, as discussed by Lowell (2021), if only low levels of migration maintain connectivity among these populations, there

could be greater potential for localized depletions or impacts on genetic diversity in these patchily distributed populations that may be slow to replenish.

As outlined in Shumway and Parsons (2016), modeling of scallop larval dispersal indicates that while patterns vary by species regarding vertical movements in the water column, dispersal is primarily controlled by tidal patterns or wind-driven currents depending on habitat. With a larval duration of approximately 4 weeks, it is likely that *C. gigantea* larvae from an offshore site can reach the coastline and settle in habitats near existing populations or act as stepping stones to those populations. The skewed sex ratio in young *C. gigantea* due to their protandrous development may initially reduce larval dispersal from culture sites, as fewer females would mean fewer fertilized eggs and larvae. Although gametes (primarily sperm) may still be released, effective dispersal (i.e., successful fertilization) of gametes is believed to occur over shorter distances and time intervals. While female proportions may increase in cultured individuals prior to harvest, the smaller size of these individuals may result in lower fecundity compared to wild individuals (Jackson 2021).

Currently, most *C. gigantea* broodstock is sourced from wild populations, which reduces the genetic risks associated with the potential dispersal of cultured individuals into the wild. However, certain spawning practices and behaviors of these scallops may lead to significantly reduced genetic diversity in cultured offspring, which could in turn diminish genetic diversity in wild populations if introgression occurs. This scenario could be particularly impactful for the smaller populations described for this species.

Based on these considerations, the culture of *C. gigantea* likely represents a moderate risk to natural populations of this species. Implementing hatchery techniques such as factorial breeding designs, equalizing gametes prior to fertilization, and genotyping of offspring may be crucial for increasing genetic diversity in offspring (Jackson 2021), which could help mitigate impacts from culture operations. Additionally, conducting oceanographic or particle modeling to understand prevailing currents from grow-out sites could help identify populations at higher risk and prioritize monitoring efforts to detect any early impacts from culturing activities.

If the ongoing progress in developing triploid *C. gigantea* using tetraploids proves successful, it could significantly mitigate, if not entirely eradicate, the genetic risks posed by escaped gametes to wild populations (Culver et al. 2022).

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2.2.4 Manila clam (Venerupis philippinarum)

2.2.4.1 Range/Description

Manila clams (*Venerupis philippinarum*, synonymous with *Ruditapes philippinarum*, *Tapes semidecussata*, *T. philippinarium*, and *T. japonicas*) originate from the entire East Coast of Asia, spanning from northern Russia through Indonesia to the East Coast of India (Goulletquer 1997 and references therein). Flourishing in shallow, subtropical to temperate waters with coarse sand and/or gravel, these clams were intentionally introduced to Hawai'i from Japan in 1920 (Yap 1977), and later unintentionally spread to the West Coast of the United States alongside Pacific Oyster imports (Quayle 1949, Goulletquer 1997). Their range has since expanded along the West Coast, reaching from British Columbia to San Diego in California (CDFG 2001, Talley et al., 2015). Additionally, the species has been introduced to Europe and the UK, where naturalized populations now thrive in various regions, including Italy, France, and Ireland (FAO 2024).

The commercial value of Manila clams as an aquaculture species has significantly contributed to their spread. In 2020, Manila clams ranked second in global mollusc production, accounting for 24 percent of production, following cupped oysters (*Crassostrea* spp.; 30.7 percent) (FAO 2022). Their rapid growth rate, extended shelf life (7 to 10 days), and remarkable tolerance to eutrophication, salinity, and temperature fluctuations have bolstered their popularity in aquaculture (Toba 1992, Martini et al. 2023). Along the West Coast, naturalized Manila clam populations support recreational fisheries across California, Oregon, and Washington.

2.2.4.2 Biological Characteristics

Manila clams are separate-sex broadcast spawners, with instances of reported hermaphroditism being very rare (Ponurovsky and Yakolev 1992). They typically reach sexual maturity at sizes ranging from 15 to 20 mm, which may be achieved within their first year in warmer climates like southern Japan and Hawai`i. However, in colder regions such as the Puget Sound, the maturation

process may extend to 2 to 3 years, with sizes ranging between 22-35mm (Yap 1977, Ponurovsky and Yakolev 1992). Spawning times and frequency exhibit considerable variation by location, occurring year-round in more tropical regions like Hawai`i, whereas in colder areas like northern Japan, spawning may occur only once a year (Gillespie et al. 2012). Fecundity is size-dependent, with larger females measuring approximately 40mm long capable of producing between 1.5 to 2.4 million eggs, while newly matured females may only produce 200,000 to 400,000 eggs (Yap 1977, Ponurovsky and Yakolev 1992, Gillespie et al. 2012).

The period from fertilization to metamorphosis and settlement typically ranges from 2 to 4 weeks in Manila clams, contingent upon factors such as temperature and food supply. Upon settlement, which occurs when the larvae reach sizes between 165 and 235 µm, they attach themselves to hard surfaces or other bivalve shells using byssal threads (Toba 1992, Gillespie et al. 2012). Dispersal primarily occurs during the pelagic larval stages, with limited movement observed among adults once they are within their burrowing substrates (Gillespie et al. 2012). Growth rates vary by location, with the fastest growth typically observed in the first 4 to 5 years of life, and the maximum reported age recorded as 14 years in British Columbia (Gillespie et al. 2012).

2.2.4.3 Population Structure

Currently, there are no population genetics studies on Manila clams in California. However, Cordero et al. (2017) undertook sampling in seven regions across Asia and Europe, along with two regions in the state of Washington: one in the Puget Sound and another in Willapa Bay. Surprisingly, these two Washington regions did not display significant differences in either mitochondrial COI DNA or microsatellite markers. Comparisons of these Washington regions with European samples revealed varying levels of differentiation, ranging from no genetic structure to low but significant structure. Notably, the European populations had been transplanted from the Washington populations in the 1950s. Considering that populations in California were also transplanted from the Washington population, and ongoing aquaculture operations continue to import larvae from Oregon and Washington (Wilson and Batanides 2016), it is plausible that they might yield similar results and could be considered one metapopulation along the West Coast. Nevertheless, it is important to conduct genetic assessments of California populations to support this theory.

2.2.4.4 Aquaculture

Like other shellfish species, hatcheries condition broodstock Manila clams, whether collected from the wild or cultivated, by manipulating water temperatures, providing excess feed, and occasionally subjecting the broodstock to air exposure or hormonal treatments to induce synchronous spawning year-round; strip spawning may also be employed as necessary (Toba 1992). Within 24 hours of fertilization, larvae hatch and become free-swimming until they are ready to settle, which typically occurs between 170 and 240 µm within approximately 2 weeks in culture (FAO 2024). The larvae can settle in tanks with or without substrate, although sand or ground oyster shell is commonly utilized to increase surface area for the larvae; survival rates through metamorphosis in hatcheries range between 25 and 50 percent (Toba 1992). Nursery

grow-out involves two stages: in the primary stage, newly settled clams are reared in land-based downwelling tanks until they reach approximately 1 mm in shell length; in the secondary stage, the clams are grown out to 6 to 8 mm shell length in upwelling systems (e.g., FLUPSYS, or intertidal trays/rafts) until they are ready for deployment in grow-out sites (Toba 1992, Dumbauld et al. 2009).

In the culture of this species, it is a common practice to transport either clam larvae (prior to setting) or clam seed (prior to grow-out) among aquaculture operations specializing in the culture of different life-cycle stages or focusing on commercial grow-out (Toba 1992, Wilson and Batanides 2016, FAO 2024). In particular, a method known as remote settling has been developed and widely adopted on the Pacific U.S. coast, becoming a standard practice for many oyster and clam growers. In this approach, pediveliger larvae are purchased at a considerably lower cost compared to larger spat. During the pediveliger stage, when shellfish are on the verge of settling and undergoing metamorphosis, they are processed and shipped to growers. This method shifts the settling and nursery responsibilities to the growers rather than hatchery operators (Jones et al. 1993).

The grow-out process to reach harvest size is primarily conducted through bottom culture in intertidal sites or oyster ponds. Here, clams are planted onto substrates such as gravel, sand, or shell, and then shielded with plastic or nylon mesh netting to deter predation while the clams dig into the substrate. Harvesting is typically carried out by manually or mechanized raking of the implanted area (Dumbauld et al. 2009, FAO 2024). Additionally, suspension-based culture methods are being explored for Manila clams, with indications suggesting that clams cultured in this manner may yield a higher-priced product (Sakurai et al. 2021). In suspension culture, Manila clams are placed in net cages containing suitable substrates and then suspended from floating rafts or longlines. Regardless of the approach chosen, the FAO (2024) notes that Manila clams generally reach market size at 30 mm or larger in China, with harvest occurring after 10 to 16 months. In North America, the desired harvest size is slightly larger, ranging between 30- and 40-mm shell length, with harvest typically taking place after 16 to 30 months.

Along the West Coast of the United States, numerous aquaculture facilities farm Manila clams. In California, this species is the only clam commercially cultivated. At present, approximately half of the registered shellfish operations in California are engaged in the cultivation of Manila clams, with the highest production recorded in Tomales and Humboldt Bays (CDFW 2020). Notably, California lacks hatchery facilities for this species and instead relies on the importation of clam larvae from Oregon, Washington, and Hawai`i (Wilson and Batanides, 2016). According to Wilson and Batanides, California shellfish operations typically focus on supplying clam seed to other farmers rather than growing clams to marketable size.

2.2.4.5 Considerations on genetic risk to conspecifics

Evaluating genetic risk from Manila clam aquaculture raises interesting considerations. First, since this species was introduced to North America, no native populations exist in this region that could be adversely affected by aquaculture practices. Nonetheless, given the presence of

naturalized Manila clam populations along the West Coast, that support recreational fisheries in California, Oregon, and Washington, some consideration of the genetic risks may be warranted.

The population genetic study by Cordero et al. (2017) indicated no genetic structure in the two sampled locations in Washington. However, California lacks similar genetic structure studies. Considering that California primarily imports clam larvae from the Pacific Northwest and Hawai`i, ongoing gene flow through this mechanism might inhibit substantial genetic differentiation between these West Coast regions, despite their distinct environmental conditions. Additionally, the genetic diversity in naturalized Manila clam populations may be limited because they originated solely from aquaculture activities, which are susceptible to genetic bottlenecking. Nevertheless, without empirical studies addressing these questions, these theories remain speculative.

For Manila clams cultivated for commercial aquaculture harvest (typically at a minimum of 30 mm shell height), it's evident that these clams will likely reach reproductive maturity and spawn during the grow-out process, considering that sexual maturity can occur as early as 15 to 20 mm shell height. However, if the culture of Manila clams in California predominantly focuses on supplying seed for other aquaculture operations, with most facilities receiving larvae from out-of-state hatcheries and growing the clams to 8 mm shell height before shipment elsewhere, then the genetic risk associated with this activity would mainly involve the potential escape from the upwelling/FLUPSY systems situated in coastal environments. This level of escape is likely to be much lower compared to the potential dispersal of millions of larvae from grow-out sites, although the larger size of seed individuals would likely enhance their survival potential in a natural setting compared to individual larvae.

However, some sites in California do participate in the grow-out and harvesting of Manila clams. In such cases, oceanographic and water particle tracking models can help determine the prevailing direction of potential spread of Manila clams away from farm sites. Even if cultured offshore, the 2 to 4 weeks of larval duration is sufficient to transport larvae from offshore sites to coastal habitats, and as observed globally, this species has demonstrated the ability to establish new populations under suitable conditions.

For grow-out sites, while there is evidence supporting a metapopulation on the Pacific coast, the genetic risk of cultured Manila clams on naturalized populations is likely moderate considering the length of time that this species will release gametes in culture (two years or longer), and that naturalized populations may already have lower genetic diversity in their populations due to their aquaculture origins (although both genetic structure and diversity remain areas of uncertainty in California). For sites supplying Manila clam seed, there is also a moderate risk to naturalized populations, largely due to uncertainty in the potential for escape from the upwelling/FLUPSY systems, and the higher likelihood of survival at seed versus larval stages. Studies that help to evaluate how likely escape may be from these upwelling systems, and studies to examine the genetic structure and diversity of this species would be important to help reduce uncertainty about the risk of culture.

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2.2.5 Pismo clam (Tivela stultorum)

2.2.5.1 Range/Description

The Pismo clam can be found in temperate waters ranging from Stinson Beach, California, through Bahía Magdalena, Baja California Sur, Mexico; this range also includes the northern Channel Islands (Fitch 1950, CDFW 2022). The primary populations of Pismo clams are concentrated in San Diego, Ventura, Santa Barbara, San Luis Obispo, and Monterey counties while smaller populations exist in the northern Channel Islands and along the beaches stretching from Ventura to San Diego (CDFW 2022). Typically, Pismo clams inhabit sandy beaches that face strong waves, with depths ranging up to 80 feet (24 meters), although they are seldom discovered beyond 40 feet (Fitch 1950, CDFW 2022). Compared to other clam species, the Pismo clam tends to inhabit relatively shallow depths in the sediment (under 12 inches of depth) (Weymouth 1922). Following a significant decline in abundance, the commercial fishery for Pismo clams was closed in 1947, and the sale of these clams in California has been prohibited since then (Shaw and Hassler 1989, CDFW 2022). Presently, the species supports a recreational fishery managed by the state, with regulations specifying size limits for legal harvest and seasonal closures in certain areas of California. Despite efforts to manage the fishery, the Pismo clam population continued to decline through the 1990s, attributed in part to overharvesting, predation by sea otters, and coastal erosion and shifting (Shaw and Hassler 1989, CDFW 2022, Marquardt et al. 2022, 2023). However, there has been a recent notable increase in the population of Pismo clams in Central California due to successful recruitment (CDFW 2022). Nonetheless, legal-sized individuals remain scarce throughout their range in California, with recent data indicating that clam populations consist predominantly of individuals smaller than the legal size limit of 4.5 inches (southern portion of the range) / 5 inches (northern portion of the range), with only 2% of individuals exceeding half the size of the legal limit (Marquardt et al. 2023). As of now, no formal stock assessments have been conducted for Pismo clams, leaving the population status unknown across its range (CDFW 2022, Marquardt et al. 2023).

2.2.5.2 Biological Characteristics

The Pismo clam exhibits remarkable longevity, with the oldest documented specimen estimated to be 53 years old (CDFW 2022). Known for its substantial size, this species has been highly prized in both commercial and recreational contexts. The largest recorded individual measured 7.4 inches in length and weighed 3.5 lbs. (CDFW 2022). However, despite its impressive size potential, the Pismo clam exhibits slower growth compared to many other bivalve species (Coe

and Fitch 1950). According to Coe and Fitch (1950), annual length increases are modest in the first two years, ranging from 21 to 25 mm, with growth rates diminishing thereafter.

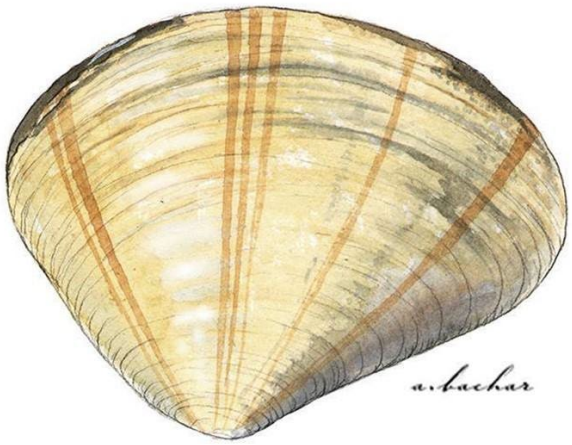

Image from California Dept. of Fish and Wildlife

Coe and Fitch (1950) estimated that it may take up to 7 years for Pismo clams to reach the legal length of 5 inches. However, more recent studies suggest that in the southern portion of California, these clams may require 9 to 12 years to attain the legal size of 4.5 inches (Marquardt et al. 2022). Interestingly, geographical variations in growth rates have been observed, possibly linked to differences in water temperature (Coe and Fitch 1950). Consequently, Marquardt et al. (2022) found that clams in Southern California reach legal size approximately 2 years earlier than their estimates for clams in central California.

The timing of sexual maturity in Pismo clams exhibits variation across different regions. In Southern California, these clams typically reach sexual maturity during their first full summer, while at the northern extent of their range, maturity is typically achieved during the second summer of life (Coe and Fitch 1950). According to Marquardt et al. (2022), Pismo clams are capable of reproduction at a size of less than 20 mm, which corresponds to their first year of life, providing them with multiple opportunities to spawn before reaching the legal recreational harvest size.

Pismo clams employ synchronous broadcast spawning, a reproductive strategy where both males and females release their eggs and sperm into the water simultaneously. Although hermaphroditism in Pismo clams is rare, instances have been documented (Weymouth 1922). Similar to other broadcast spawning species, Pismo clams exhibit high fecundity, with large females measuring over 3 inches capable of producing between 10 and 20 million eggs (Coe and Fitch 1950). The spawning season typically begins in late July or early August, peaks in late summer, and concludes in November, as reported by Fitch (1950) and later confirmed by Marquardt et al. (2022).

Information on the larval period of Pismo clams remains limited, as noted by Coe (1947), but it is estimated to last approximately 3 weeks. During this dispersal period, larvae may be transported alongshore for distances ranging from 40 to 100 miles. However, due to their high weight-to-volume ratio, Pismo clam larvae may remain near the bottom during that time potentially resulting in shorter dispersal distances than would be otherwise expected (Shaw and Hassler 1989). Once settled, the clams anchor themselves using byssal threads until they reach a

larger size, at which point they can burrow more effectively with their foot. Subsequently, they may only sporadically reposition themselves within the sediment, exhibiting limited horizontal movement (CDFW 2022).

Similar to many broadcast spawning species, early survival rates of Pismo clam larvae are remarkably low. Fitch (1950) approximated that only 33,000 adult clams survived from an estimated 120 trillion eggs spawned in a less than 10-mile stretch of beach. Once mature, the mortality for these clams remains high, with estimates ranging from 67 to 75 percent mortality once they reach legal size, depending on the location (Fitch 1950, CDFW 2022).

2.2.5.3 Population Structure

Currently, there is no data available regarding the genetic population structure of Pismo clams. Nonetheless, Coe and Fitch (1950) did report variations in their life history between the Southern California region and the northern edge of their range, indicating the potential presence of some local adaptation to environmental parameters, however, it is unknown whether that variation has a genetic basis based on the available information.

2.2.5.4 Aquaculture

At present, there are no commercial or supplementation aquaculture programs for Pismo clams. Some research has been conducted on conditioning techniques for this species, revealing that serotonin injections can induce spawning and oocyte maturation (Alvarado-Alvarez et al. 1996). Recently, funding has been allocated for research projects aimed at closing the life cycle of Pismo clams led by Sean Bignami at Concordia University, and developing aquaculture protocols for this species led by Ben Ruttenberg at California Polytechnic State University, San Luis Obispo. These research projects are currently underway and if successful, these studies have the potential to establish hatchery protocols and create protocols that could support a cost-effective commercial aquaculture pipeline for the Pismo clam (Ferreira 2021).

2.2.5.5 Considerations on genetic risk to wild conspecifics

Assessing genetic risks associated with commercial aquaculture for the Pismo clam is challenging due to significant uncertainties. Limited abundance data exists for wild populations across their range, and no stock assessment has been conducted for this species. Key aspects of their life history, particularly early life stages, remain poorly understood (Shaw and Hassler 1989), and conflicting estimates on growth rates and size at maturity add to the uncertainty (e.g., Coe and Fitch 1950 and Marquardt et al. 2022), possibly influenced by ecosystem changes over time (Doney et al. 2012). Moreover, there are no published population genetic studies or assessments of population connectivity for the Pismo clam. Additionally, hatchery and production methods have yet to be developed for this species, although ongoing research may yield this information in the near future (Ferreira 2021).

Given the slower growth rate of Pismo clams compared to other shellfish species, commercial aquaculture operations may involve extended grow-out periods spanning several years. As Pismo

clams can attain sexual maturity at sizes as small as under 20 mm within their first or second years (Coe and Fitch 1950, Marquardt et al. 2022), it is likely that spawning would occur during the grow-out phase of commercial production. With an estimated larval duration of 3 weeks (Coe 1947), larvae would likely disperse over distances greater than those between an offshore production site and potential coastal habitats. The impact of this larval dispersal on wild populations would depend on prevailing currents in the region. Notably, Pismo clam larvae may exhibit a more benthic behavior compared to other species, potentially limiting their dispersal distance on average (Shaw and Hassler 1989). However, further research is needed to fully understand this aspect of the Pismo clam's life history and its implications for larval dispersal.

The Pismo clam populations across California have faced notable declines, with few large, legally sized individuals remaining within this range (CDFW 2022). Despite observed recruitment at various sites (Marquardt et al. 2023), these diminished populations may be particularly vulnerable to adverse effects from dispersed cultured larvae, including genetic drift and reduced genetic diversity resulting from the introduction of cultured larvae.

With consideration to their population declines, and the high degree of uncertainty in key biological characteristics and genetic structure of this species, the genetic risk to wild populations from the culture of the Pismo clam is likely high. Therefore, hatchery strategies, such as utilizing locally sourced broodstock and maintaining a sizable and genetically diverse broodstock, are likely to be important considerations for the culture of the Pismo clam.

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2.2.6 California mussel (Mytilus californianus)

2.2.6.1 Range/Description

The California mussel, *Mytilus californianus*, is indigenous to the western coast of North America, spanning from the Aleutian Islands in the north to Isla Socorro, Mexico in the south (Suchanek 1981 and references therein). Within the contiguous U.S., it predominantly inhabits rocky intertidal zones in wave-exposed intertidal and subtidal environments, occasionally reaching depths of up to 30 meters (Suchanek 1981). *M. californianus* typically forms dense mussel beds, displaying a competitive edge over various species, including other mussel varieties, for space in the wave-exposed sections of the intertidal zone (excluding bays) (Paine 1974, Blanchette et al. 2007).

Although there is no formal population assessment, the California Department of Fish and Wildlife (CDFW 2020) notes that the California mussel is one of the most prevalent invertebrates along the California coast, with long-term monitoring suggesting a stable population trend over the past three decades. However, abundance varies within California, with higher concentrations typically found from Monterey Bay northwards. Conversely, Central and Southern California, including the Channel Islands, tend to exhibit lower abundances, though localized pockets of more abundant *M. californianus* populations may exist within these regions (Smith et al. 2009).

From a commercial perspective, the California mussel attains a relatively large size compared to other mussel species found along the West Coast (Suchanek 1981) and is reputedly highly palatable (Trevelyan and Chang 1983). Historically, both bay (*Mytilus trossulus*) and sea mussels (*M. californianus*) were commercially harvested in California until the 1920s, when the fishery declined due to an increase in paralytic shellfish poisoning cases (CDFW 2001). Presently, a recreational fishery exists in California, which is subject to seasonal quarantines due to biotoxin accumulation, as well as a small, intermittent commercial fishery in Southern California. Both the commercial and recreational fisheries are regulated by The California Department of Fish and Wildlife (CDFW 2020).

2.2.6.2 Biological Characteristics

California mussels employ broadcast spawning as their reproductive strategy, with sexually ripe individuals capable of spawning year-round, although peak spawning periods vary depending on location (Suchanek 1981, Shaw et al. 1988, Curiel and Caceres-Martinez 2004). Like many marine invertebrates, fecundity increases with size, although reported estimates of egg production by larger females vary widely, ranging from 5 to 40 million eggs as reviewed in Schmidt (1999). Following fertilization, larvae develop and become mobile within a 48-hour timeframe (Shaw et al. 1988). Laboratory experiments conducted by Shaw et al. (1988) suggest larvae are ready to settle between 17- and 24-days post-fertilization, although Suchanek (1981) estimated a slightly longer pelagic duration of 2 to 4 weeks. Upon the development of eye spots, *M. californianus* larvae exhibit a preference for settling on filamentous materials such as byssal

threads of mussels, mussel shells, barnacles, certain types of algae, and ropes (Paine 1974, Shaw et al. 1988).

Following settlement, the growth of California mussels hinges on factors like food availability, water temperature, and the duration of tidal exposure (Coe and Fox 1944). Coe and Fox (1942) discovered that sexual maturity primarily correlates with size, typically occurring at around 70 mm in length, corresponding to approximately 1 year of age. However, Shaw et al. (1988) identified sexually mature individuals as small as 25 mm, at approximately 4 months old. While growth rates may vary by location (Phillips 2007), California mussels can achieve lengths of 80 to 86 mm within a year of settling, 120 mm within 2 years, and between 140 and 150 mm within 3 years (Shaw et al. 1988). The maximum size for the California mussel falls between 200 and 250 mm, nearly double the reported maximum size of *M. edulis* (Shaw et al. 1988). Suchanek (1981) further notes that *M. californianus* exhibits greater longevity than *M. edulis*, with lifespans ranging from 7 to 20 years in the intertidal zone and potentially extending from 50 to 100 years in deeper subtidal regions with less frequent disturbance.

Image from California Dept. of Fish and Wildlife

2.2.6.3 Population Structure

Addison et al. (2008) conducted a comprehensive study examining the population structure of *M. californianus* across a vast 4000 km range, spanning from Elfin Cove, Alaska, through British Columbia, Canada, Washington, Oregon, northern and southern California, to Punta Baja, Mexico. Using a combination of allozymes, single-copy nuclear DNA, and maternal and paternal mitochondrial DNA sequences, the study surveyed between 391 and 889 individuals, depending on the marker type. Despite this extensive sampling effort, no significant genetic differentiation was detected among the populations.

The authors speculated that this lack of differentiation could be attributed to the observed long dispersal distances typically observed among larvae of *Mytilus* species, potentially spanning between 20 and 50 km. This extensive potential for dispersal, coupled with the California mussel's year-round spawning and long lifespan, results in larvae being transported across a wide array of oceanographic conditions. These conditions may include seasonal variations and oceanic

oscillation events like El Niño, effectively diluting any localized genetic signals among populations.

In a study examining gene expression patterns among populations of *M. californianus* collected from British Columbia, Oregon, California, and Baja California, Place et al. (2008) discovered variations in physiological responses among these mussels, likely attributed to the differing physical parameters present at each site. While this doesn't necessarily imply underlying genetic differences, it does suggest the presence of local selective pressures acting across smaller spatial scales for this species.

Recently, a high-quality reference genome for the California mussel was published (Paggeot et al. 2022). This resource may provide opportunities for future higher-resolution genomic population analyses, or investigations into local adaptation within *M. californianus.*

2.2.6.4 Aquaculture

Despite its large size, palatability, and favorable growth compared to the widely cultivated blue mussel (*M. edulis*), aquaculture endeavors for the California mussel have remained limited (Trevelyan and Chang 1983). While there was interest and research conducted on aquaculture for this species in the 1980s, efforts failed to yield significant production of California mussels (Yamada and Dunham 1989).

Because of the limited production efforts for the California mussel, information on culturing protocols remains limited. However, there have been successful achievements in hatchery-based spawning, larval culture, and settlement (Trevelyan and Chang 1983). Recent work by Churches et al. (2022) further supports the feasibility of hatchery-based aquaculture for this species. Their efforts focused on developing protocols for hatchery and nursery operations applicable in commercial settings. They successfully induced spawns, conditioned and ripened gametes, settled larvae onto "fuzzy" ropes, and retained juveniles during re-socking. Additionally, growth metrics collected by the authors indicate that the California mussel performs equally or even better than other commercially relevant Mytilid species in market metrics. This research suggests promising avenues for the advancement of aquaculture practices for *M. californianus*.

For commercial culture of California mussels, hatchery, nursery, and grow-out procedures are likely to resemble those used for blue mussels. Spawning can be achieved through methods such as shell scraping and hydrogen peroxide solution immersion (Trevelyan and Chang 1983), or temperature shock and/or gamete stripping, similar to techniques employed for blue mussels (FAO 2024). Larvae are typically fed generously until they reach settlement stage. Following settlement, and once they reach approximately 1 mm in size, they are transferred to a nursery where they remain until they reach sizes of 6 to 10 mm. Subsequently, they are moved to a grow-out system in the natural environment (FAO 2024).

In offshore environments, longline and/or raft systems are commonly employed for mussel culture, as discussed in Hoagland et al. (2003) and McKindsey et al. (2006). These systems

utilize buoyed long lines or rafts to support numerous suspended vertical lines of mussels attached to ropes or contained in mesh socks. During the grow-out phase, mussels may be periodically thinned or de-clumped to promote optimal growth. Removed mussels can be reattached to ropes or placed in the mesh socks for continued growth.

Given the absence of specific information regarding the target markets for California mussel commercial culture, estimating the expected grow-out duration for this species is challenging. However, comparisons can be drawn with other mussel species to provide a rough estimate. For example, blue mussels are typically harvested at approximately 40 mm in size, which takes 12 to 15 months to attain, although in some cases, such as raft culture in Maine, *M. edulis* may be harvested a little later at 18 months (FAO 2024). In contrast, Mediterranean mussels (*M. galloprovincialis*) are ready for the market at around 60 mm, which may be achieved in approximately a year (Theodorou et al. 2011). Considering that California mussels reach 70 mm after a year (Coe and Fox 1942), harvest may similarly occur around the 12-month mark for this species, or possibly earlier due to their fast growth, depending on the targeted market preferences and size requirements.

2.2.6.5 Considerations on genetic risk to wild conspecifics

The information available suggests that cultured California mussels may reach sexual maturity prior to harvest, as individuals can mature at relatively small sizes. Coe and Fox (1942) found maturity occurring at around 70 mm shell length (approximately 1 year of age), while Shaw et al. (1988) identified sexually mature individuals as small as 25 mm (or 4 months of age). Given the species' capability for year-round spawning (Suchanek 1981), it is reasonable to assume that spawning may occur prior to harvest at culture sites.

Larvae from offshore operations could disperse over long distances during the 2-to-4-week pelagic duration, and certainly disperse at distances greater than between offshore sites and coastal rocky intertidal habitats. Moreover, the tendency for mussels to settle on ropes suggests that aquaculture equipment in the marine environment could serve as stepping-stone populations or non-harvested populations that remain in the natural environment, potentially interacting with wild populations.

While larvae have some swimming capabilities, their dispersal is primarily controlled by local currents. This could result in certain wild populations being impacted more frequently than others, or alternatively, larvae being transported away from suitable settling habitats (Shaw et al. 1988). These factors highlight the importance of water current modeling and the monitoring of prioritized sites to understand potential impacts on wild populations from California mussel aquaculture.

The findings from the population genetic study by Addison et al. (2008) suggest that there is no significant spatial genetic structure over the 4000 km sampled range of California mussels. This implies that if broodstock were sourced locally or regionally for aquaculture purposes, cultured individuals introgressing into the wild populations would not disrupt local population structure.

However, while population structure may remain intact, dispersed individuals from aquaculture operations may still pose a risk of reducing the genetic diversity of wild populations. Nonetheless, given the species' abundance throughout its range and the indication of stable populations (CDFW 2020), wild populations may have the capacity to absorb some impact from the introgression of cultured larvae with reduced genetic diversity.

The competitive advantage of the California mussel, as documented by Paine (1974) and Blanchette et al. (2007), suggests that if larvae from aquaculture operations are transported to new suitable habitats currently unoccupied by *M. californianus*, they may have a higher likelihood of successfully establishing themselves compared to other species with a lesser competitive edge. Once established in these new habitats, the cultured mussels could serve as a conduit for the continued input of cultured genes into wild populations. Given the species' longevity and the potential for continuous gene flow from aquaculture sources, this could have long-term implications for the genetic composition and adaptation of wild populations of California mussels.

Although the absence of detected population structure and the presence of large wild population sizes imply a reduced risk from dispersed cultured individuals, the long lifespan, extensive pelagic dispersal, and competitive edge of *M. californianus* suggest additional risks to wild populations from its aquaculture. Consequently, the genetic risk to wild populations from this species is deemed moderate to low. Employing breeding designs or broodstock rotations to capture greater genetic diversity can potentially mitigate these impacts. Assessing current patterns in proximity to grow-out sites throughout the year can aid in prioritizing locations for monitoring cultured-wild interactions. Moreover, utilizing higher resolution genetic or genomic techniques to identify signals of local adaptation, if present, can enhance understanding of dispersal risks associated with commercial cultivation of this species.

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2.2.7 Mediterranean mussel (Mytilus galloprovincialis)

2.2.7.1 Range/Description

Mytilus galloprovincialis, the Mediterranean mussel, is part of the blue mussel species complex, which also encompasses *M. edulis* and *M. trossulus*, and potentially other blue mussel species like *M. chilensis*, *M. desolationis*, *M. planulatus*, and *M. platensis*. The taxonomic classification and distinctiveness of these species are subjects of debate (Westfall and Gardner 2010, Oyarzun et al. 2016, Zbawicka et al. 2022). Among these, *M. galloprovincialis* is the most widely distributed mussel species; although it was originally believed to be endemic to the Mediterranean, it is now found in various regions worldwide, including the northeast Atlantic, Japan, South Africa, Australia, New Zealand, Tasmania, Chile, and the west coast of North America (Wonham 2004, and references therein). Along the northeast Pacific, *M. galloprovincialis* ranges from Baja California, Mexico to central California, with patchier occurrences extending up into Washington (Suchanek et al. 1997). Blue mussels, in general, tend to inhabit lower-energy environments compared to *M. californianus* and are commonly found in bays and estuaries (Geller 1999, Braby and Somero 2006).

The Mediterranean mussel is believed to have undergone multiple introductions into California and other regions along the western coast of North America, both intentionally for aquaculture purposes and inadvertently through transportation on/in ship hulls, ballast water, or other marine equipment (Suchanek et al. 1997, Wonham 2004, Grosholz et al. 2015). In Southern California, it is speculated that the initial introduction and establishment occurred in the early-to-middle 1940s, coinciding with a period of significant and rapid growth in mussel populations (Geller 1999). Despite being introduced, *M. galloprovincialis* is now so well-established in California that it is no longer managed as an invasive species (López-Duarte et al. 2012).

Along the U.S. west coast, *M. galloprovincialis* has emerged as the most prevalent mussel species from Tomales Bay to San Diego, California, while the native blue mussel, *M. trossulus*, dominates north of Tomales Bay in California and extends into Oregon and Washington (Geller 1999, Suchanek et al. 1997). Temperature is considered a crucial factor influencing this

distribution pattern between the two species (Suchanek et al. 1997). Interestingly, in regions where *M. galloprovincialis* and *M. trossulus* coexist, hybridization zones form, with the largest spanning from Cape Mendocino through Monterrey and encompassing San Francisco Bay (Suchanek et al. 1997, Rawson et al. 1999, Braby and Somero 2006). Populations within the hybrid zone are dynamic, with the proportion of hybrid individuals fluctuating annually (Braby and Somero 2006). In one study, hybrid genotypes ranged from 13 to 44% (Rawson et al. 1999). Additional hybridization zones have been identified along the west coast, including Whidbey Island, Washington, and San Diego Bay; however, these areas are believed to be influenced by ongoing introductions of either *M. galloprovincialis* or *M. trossulus* (Suchanek et al. 1997).

While size is recognized as highly variable in blue mussels, Braby and Somero (2006) discovered that *M. galloprovincialis* consistently reached larger sizes (up to 100 mm in length) compared to *M. trossulus* (up to 50 mm) within their California range. Given their larger size, ease of cultivation, and palatability, *M. galloprovincialis* holds significant interest for aquaculture purposes (Wonham 2004). The aquaculture of this species in California is overseen by the California State Lands Commission and the California Department of Fish and Wildlife (CDFW).

2.2.7.2 Biological Characteristics

The Mediterranean mussel has several general life-history characteristics that include rapid shell growth, a short lifespan, resistance to desiccation, and early reproductive maturity (Carson et al. 2010, Okaniwa et al. 2010, and references therein). Similar to other blue mussel species, *M. galloprovincialis* is a broadcast spawning species with high fecundity, potentially producing millions to tens of millions of eggs depending on body size (Kautsky 1982). Spawning seasons vary by location: in Tokyo Bay, Japan, spawning occurs from November to March (Okaniwa et al. 2010); along the Pacific coast of Baja California, Mexico, spawning takes place from autumn to early spring, peaking in early winter (Curiel-Ramirez and Caceres-Martinez 2004); and in San Diego, California, spawning is reported to peak in the spring (López-Duarte et al. 2012).

Fertilized eggs of the Mediterranean mussel develop into larvae with a pelagic duration typically ranging from 2 to 4 weeks, although Carson et al. (2010) noted a mean dispersal period of 21 days for this species. According to their study, larval recruits in San Diego County, California, exhibited a mean dispersal distance of 37 km, with some indication that *M. galloprovincialis* may disperse more widely than *M. californianus* in this area, potentially spanning over 100 km in a single recruitment event (López-Duarte et al. 2012). However, due to their presence in bays and estuaries, Mediterranean mussels also demonstrate higher levels of local retention of larval recruits compared to *M. californianus* (Carson et al. 2010). The larvae eventually settle and adhere to diverse substrates, including rocks, wood, vegetation, and amidst other mussels, leading to the formation of expansive mussel beds (Robinson et al. 2007).

Size and growth rates vary significantly for *M. galloprovincialis* depending on their location (e.g., Ceccherelli and Rossi 1984, Braby and Somero 2006, Okaniwa et al. 2010). In Japan, individuals can reach sizes of 35 to 40 mm within a year of settling (Okaniwa et al. 2010), while

in the Mediterranean, harvest sizes of up to 50 mm have been achieved within 14.5 months (Ceccherelli and Rossi 1984). Maximum shell sizes of around 70 mm were estimated for *M. galloprovincialis* in Japan (Okaniwa et al. 2010), whereas Braby and Somero (2006) reported maximum sizes exceeding 100 mm for this species in California. Mussels in Japan were projected to attain the maximum size in only 3 to 4 years, although specimens as old as 12 years were also identified (Okaniwa et al. 2010). However, most populations were dominated by younger mussels in the 2-to-3-year age range (Ceccherelli and Rossi 1984, Sukhotin and Flyachinskaya 2009, Okaniwa et al. 2010). Across locations, *M. galloprovincialis* is capable of reaching sexual maturity within their first year, typically corresponding to a shell length of around 20 mm (Ceccherelli and Rossi 1984, Okaniwa et al. 2010).

2.2.7.3 Population Structure

species complex has been dedicated to redefining their taxonomic statuses, particularly in identifying cryptic species (e.g., Sarver and Loudenslager 1991). For *M. galloprovincialis* specifically, Daguin and Borsa (2000) identified three distinct groups on a global scale: a northeastern Atlantic group (including introduced populations from South Africa), a Mediterranean group (encompassing introduced populations from the eastern and western coasts of the North Pacific, as well as Chile), and an Australasian group (comprising Australia, Tasmania, and New Zealand). However, ongoing debate persists regarding the origins of introduced populations. For instance, California populations may have originated from an Atlantic North European population, as suggested by Ouagajjou et al. (2023), which contrasts with the findings of McDonald and Koehn (1988) and Daguin and Borsa (2000), who placed the origins of California populations in the Mediterranean.

Overall, populations of this species typically exhibit low levels of genetic structure among locations, with significant genetic differentiation observed only in samples spanning broad geographic ranges. For instance, Wenne et al. (2022) utilized 53 single nucleotide polymorphism (SNP) loci to analyze genetic differentiation in over 1000 individuals collected from 36 locations across the range of *M. galloprovincialis* in the Mediterranean Sea, Black Sea, and the Sea of Azov, along with 11 reference sites. Their study revealed differentiation among four groupings: the Atlantic Ocean, the western Mediterranean, the Aegean Sea, and the Black and Marmara Seas. However, even in this extensive study, less genetic differentiation was observed than anticipated, especially across regions recognized as biogeographic boundaries. The authors proposed that anthropogenic activities such as hull fouling, ballast water, drilling rigs, and aquaculture might have contributed to the current levels of genetic homogeneity (Wenne et al. 2022). Similarly, Diz and Presa (2009) found only minimal genetic structure across northwest Iberian estuaries near Galicia, Spain, with the highest degree of local differentiation detected across an oceanographic boundary in this area. They suggested that the transport of aquaculture seed between regions likely diminished natural genetic divergence that had previously existed (Diz and Presa 2009).

No population genetic studies of *M. galloprovincialis* have been identified for the eastern North Pacific coastline. However, considering the global patterns observed elsewhere, the relatively

brief duration of the Mediterranean mussel's presence as an introduced species on the western coast of North America, and the hypothesized multiple introductions to and within this coastline (e.g., seed movement from California to Washington), it is anticipated that there would be minimal to no genetic structure across this range (Wonham 2004). Nonetheless, genomic resources, including a reference genome, are now available for *M. galloprovincialis*, for any research groups interested in investigating population connectivity along the western North American coast (Mugarella et al. 2016).

Despite the absence of population genetic studies for the region, several investigations have explored hybridization and introgression between the native *M. trossulus* and introduced *M. galloprovincialis* along the U.S. west coast, particularly in California. Although hybrids were identified in regions of sympatry, multiple genetic studies have not found substantial evidence for extensive introgression between these two species beyond first-generation backcrosses (Rawson and Hilbish 1995, Rawson et al. 1999, Saarman and Pogson 2015). Occasional instances of low-level introgression were observed in both directions, with slightly more frequent introgression from *M. trossulus* into *M. galloprovincialis* (Saarman and Pogson 2015). The authors of these studies suggest that strong genetic barriers to interbreeding have likely limited more extensive introgression (Rawson and Hilbish 1995, Rawson et al. 1999, Saarman and Pogson 2015).

Even in the absence of genetic introgression between these species, the introduced *M. galloprovincialis* may still exert ecological impacts on the native *M. trossulus* (Saarman and Pogson 2015). Lockwood and Somero (2011) discovered that *M. galloprovincialis* is more adapted to warmer conditions compared to *M. trossulus*, which thrives in colder environments. As *M. galloprovincialis* has expanded its populations northward, it has displaced *M. trossulus* from its native range in southern and central California (Geller 1999, Rawson et al. 1999, Braby and Somero 2006, Lockwood and Somero 2011, Saarman and Pogson 2015). Although not substantiated with genetic evidence presently, the displacement by *M. galloprovincialis* could potentially have genetic repercussions on *M. trossulus* as a species by causing the loss of locally adapted genetic variation present in those southerly populations, which may have enabled the species to endure in the warmer segments of its range.

2.2.7.4 Aquaculture

M. galloprovincialis is a popular and widespread aquaculture species due to its ease of culture, high growth rate, resistance to desiccation and parasites, and its palatability (Wonham 2004, Carson et al. 2010, and references therein).

Cultivation of the Mediterranean mussel follows a process similar to other mussel species. Seed collection methods vary: larvae may settle naturally onto rope collectors, which are then wrapped around larger ropes and suspended from longlines (Cáceres-Martínez 1997, Peharda et al. 2007). Alternatively, seed, approximately 3 months old, can be directly collected from wild mussel beds and spread onto ropes; the seed is temporarily held in place by dissolving mesh or cotton (Kamermans 2008, FAO 2009). Another approach involves conditioning broodstock for

spawning. This method uses approaches, such as thermal shock, to trigger spawning in tanks (Kamermans 2008). After larvae are cultured and settled onto ropes, they are transferred to a nursery until reaching a suitable size for grow-out in natural environments (Kamermans 2008). Commercial seed producers offer options to streamline these initial stages for growers (Wonham 2004).

The grow-out phase can be conducted through bottom culture or suspended culture using ropes or mesh socks attached to long-lines or rafts (Cáceres-Martínez 1997, Peharda et al. 2007, FAO 2009). During this period, declumping and thinning of mussel lines are crucial for optimal growth of mussels (FAO 2009). Grow-out durations vary based on region and the desired market size. In Baja California, Mexico, mussels are typically harvested between 60 and 70 mm after 7 to 8 months (Cáceres-Martínez 1997), while in northern Spain, it takes 9 months to reach a minimum marketable size of 50 to 60 mm (Azpeitia et al. 2016). However, in regions like the Adriatic Sea, the production cycle may extend significantly, taking 14.5 months to 18 to 24 months to reach market size, approximately 50 mm (Ceccherelli and Rossi 1984, Peharda et al. 2007).

Given that reproductive maturity typically occurs in under a year, when mussels reach around 20 mm in size, it is anticipated that cultured mussels could spawn before harvest. However, spawning can affect the quality of mussel flesh, which has prompted research into methods for producing sterile mussels. Approaches currently under investigation involve generating functionally sterile triploid and tetraploid *M. galloprovincialis*, with tetraploid individuals being utilized to consistently produce triploid mussels (Yamamoto and Sugawara 1988, Komaru et al. 1995, Kiyomoto et al. 1996, Kamermans 2008).

2.2.7.5 Considerations on genetic risk to wild conspecifics

The Mediterranean mussel has earned a place among the top 100 most invasive species globally (Lowe et al. 2000). Its life-history traits have facilitated its establishment in numerous regions following introductions, including California, as well as patchier populations in Oregon and Washington (Grosholz et al. 2015). It is likely that new introductions or translocations will occur due to the species' ability to foul on hulls of ships and raft on natural and artificial floating objects, such as litter, debris, and mariculture-related gear (Suchanek et al. 1997, Wenne et al. 2022), or to be transported through ballast water on ships (Lins et al. 2021).

The duration of grow-out for *M. galloprovincialis* will vary depending on the specific conditions of the grow-out location. However, it is likely that some, if not most, mussels may reach reproductive maturity before harvest. With a pelagic larval duration estimated to range between 2 and 4 weeks, this species possesses the capacity to disperse over long distances (Suchanek et al. 1997), surpassing the distances from potential offshore culture sites to suitable habitats along the coast. As reported by López-Duarte et al. (2012), cultured Mediterranean mussels grown in one area of the Southern California Bight would be expected to spread to other suitable habitats throughout the region.

Water current modeling can be highly valuable in assessing the potential impact of recruits arriving from aquaculture operations on different regions. For instance, the dispersal patterns of *M. galloprovincialis* larvae in San Diego Bay were found to vary seasonally, with southward dispersal occurring in spring and early summer, and northward dispersal in late summer or fall in most years (López-Duarte et al. 2012). Such information can help predict the spatial distribution of larvae originating from aquaculture sites and assist in understanding the potential implications of their dispersal patterns.

While there is a lack of genetic population structure information available for California, studies have shown genetic homogeneity across relatively newly colonized areas. This trend has been observed in various regions, suggesting that it could hold true for California as well (Diz and Presa 2009, Le Corre et al. 2015, Ouagajjou et al. 2015, McQuaid et al. 2015).

Given that *M. galloprovincialis* is an introduced species and the high likelihood of continued introductions through various means, coupled with the probable lack of genetic structure among established populations, aquaculture of this species in Southern California is expected to pose little-to-no genetic risk to the established Mediterranean mussel populations in this region.

Despite the expected low genetic risk posed by aquaculture of *M. galloprovincialis* in Southern California, it is important to consider its ecological impacts from culture of this species further north. This species has already displaced the native *M. trossulus* in the southern portions of its range (Geller 1999) and has eradicated indigenous mussel species in other areas where it has been introduced (e.g., South Africa) (Carson et al. 2010). Continual recruitment from culture operations may pose a risk to *M. trossulus* populations further north of the central California hybrid zone, which could result in a genetic impact to that species in terms of reduced genetic diversity. For now, *M. trossulus* may have a competitive advantage over *M. galloprovincialis* in cooler water. However, monitoring of native mussel populations may become more important as water temperatures rise, potentially providing *M. galloprovincialis* with another opportunity to further displace the indigenous *M. trossulus*.

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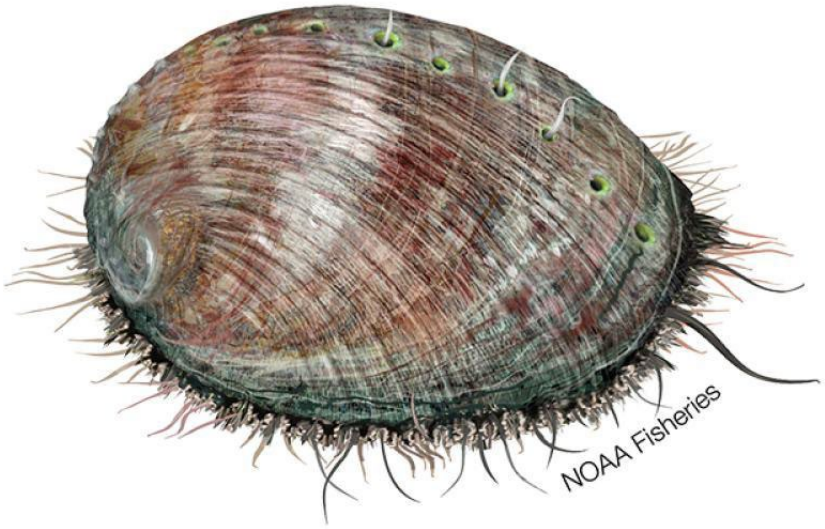
2.2.8 Abalone (Haliotis spp.)

2.2.8.1 Range/Description

The commercial abalone aquaculture industry has grown into a global enterprise with an annual value of nearly $2.6 billion USD (Hernández-Casas et al. 2023). In recent years, the production of cultured abalone has experienced substantial growth, rising from 2,800 tons in 2000 to 184,660 tons in 2018 (González et al. 2012, Vervalle et al. 2013, Hernández-Casas et al. 2023). This expansion is attributed to an increased demand and a decline in natural stocks due to overexploitation and disease (An et al. 2011, Brokordt et al. 2014), positioning abalone as one of the few marine species where farm production dominates the global market (Gordon and Cook 2013). Cultivated abalone now constitutes over 95% of the market (Hernández-Casas et al. 2023), with approximately 15 to 20 out of the roughly 56 abalone species actively produced in commercial aquaculture worldwide (Elliott 2000, Amparyup et al. 2010).

California is home to seven native abalone species, but the majority of domestic abalone farms focus on three species: red (*Haliotis rufescens*), green (*H. fulgens*), and to a lesser extent, pink abalone (*H. corrugata*) (CDFW 2013). Among these, red abalone is the dominant culture species, characterized by rapid growth and attaining large sizes in aquaculture. Widely favored in the U.S. market, red abalone is also globally renowned as one of the most valuable mollusk species (Hubbard et al. 2011, Aguilar-Espinoza et al. 2013, Brokordt et al. 2014). The high market value and established popularity of abalone as a delicacy make them an appealing choice for aquaculture endeavors (Lafarga de la Cruz and Gallardo-Escárate 2011, Moodley et al. 2014).



Among the three abalone species, *H. rufescens*, with a range extending from Oregon to Baja California, Mexico, is the most temperate species (Hubbard et al. 2011). The green and pink abalone, with their more southerly distributions, are particularly suitable for aquaculture in Southern California due to their tolerance for higher water temperatures (McBride and Conte 1996). Their ranges extend from Point Conception, CA, to the southern portion of Baja California, Mexico (NMFS 2009). Besides being of interest for abalone culture in Southern California, these species are also integral to valuable commercial production in Mexico.

Infectious diseases and parasites have been substantial contributors to declines in wild abalone populations, as well as obstacles to aquaculture production, resulting in significant losses in both cost and time (Franchini et al. 2011, Moodley et al. 2014). (Franchini et al. 2011, Moodley et al. 2014). Withering Syndrome (WS), caused by the bacterium *Candidatus xenohaliotis californiensis*, a Rickettsiales-like organism (Friedman et al. 2000), poses a serious and chronic threat to both wild and farmed abalone globally (González et al. 2012). Originating off the California coast in the 1980s, WS initially devastated black abalone (*H. cracherodii*) populations, necessitating their listing as an endangered species. Subsequently, the disease has continued to impact pink, green, red, and the already endangered white abalone (*H. sorenseni*) populations along the west coast (González et al. 2012, Burge et al. 2014). Abalone are also susceptible to infections with *Vibrio* species, abalone herpes virus, abalone viral ganglioneuritis, and parasitic worm infestations (Corbeil et al. 2016, Friedman et al. 2014). Due to the combined impacts of disease and population decline resulting from overharvesting over several decades, commercial harvest for all wild abalone species is currently closed in California.

There is significant variability in disease expression among abalone species at different temperatures, with warmer-acclimated species, like pink and green abalone (with thermal preferences of 25.0 and 25.4 °C, respectively), exhibiting lower susceptibility compared to colder-acclimated species such as red abalone (with a thermal preference of 18.8 °C) (Diaz et al. 2006, Friedman et al. 2014). Thermal stress is considered a contributing factor to the restoration challenges for red abalone in the southern part of its distribution, leading to increased disease-related mortality and difficulties in producing mature gametes (Rogers-Bennett et al. 2010). The impact of thermal stress in these species may be further compounded by additional stressors like ocean acidification and anoxic events, which are already affecting other molluscan shellfish production facilities (De Wit and Palumbi 2013). For commercially established red abalone, there is growing interest in identifying and harnessing genetic variation that could improve thermal tolerance in this species. Additionally, broadening commercial interest to focus more on abalone species acclimated to warmer temperatures in the U.S. might become appealing for the abalone industry if there is a desire to expand cultivation into warmer regions, such as Southern California.

2.2.8.2 Biological Characteristics

Abalone, herbivorous marine gastropod mollusks, exhibit varying depth preferences among species, with the red, green, and pink abalone typically found in the intertidal zone to a depth of approximately 20 meters (Leighton and Robinson 2008). Red abalone holds the distinction of being the largest abalone species globally, reaching sizes of up to 30 cm and weighing nearly 2 kg (Leighton and Robinson 2008). Abalone are dioecious, meaning they possess either male or female reproductive organs. For red abalone, sexual maturation estimates based on histological examinations indicate that 50% of females become reproductive at shell lengths between 105-130 mm, while for males, the range is 75-95 mm; individuals under 50 mm could not be sexually differentiated (Rogers-Bennett et al. 2004). In pink abalone, maturation is thought to occur between 59 and 119 mm, and around 100 mm in green abalone (Tutschulte 1976). These species exhibit high fecundity, with the number of eggs increasing with female size, though older

individuals may produce lower-quality eggs (Rogers-Bennett et al. 2004). Younger abalone may produce hundreds of thousands of eggs, while larger individuals can produce up to 12 million eggs (Giorgi and DeMartini 1977, Ault 1985).

These abalone species are broadcast spawners, releasing gametes of both sexes into the water column (Leighton and Robinson 2008). Ault (1985) observed that natural spawning typically occurs from April through July, peaking in May, a finding supported by more recent work estimating spawning dates in June and July (Rogers-Bennett et al. 2016). Individuals can spawn more than once in a year, usually with a 2 to 3-month interval (Ault 1985). The eggs of these species are relatively large and contain a yolk sac (Leighton and Robinson 2008). Following fertilization, the eggs become demersal until the hatching of the trochophore larva, which possesses cilia aiding in minimal motility (Miyake et al. 2017). The trochophore then transforms into a veliger, featuring a heavily ciliated swimming band, and subsequently develops cilia on the sole of the foot in preparation for settlement (Leighton and Robinson 2008).

Abalone are benthic during their juvenile and adult stages, relying on snail-like (or in this case, actual snail) movement for shorter distance dispersal. The potential for longer dispersal distances arises during the planktonic larval stages. Pelagic larval duration in abalone, as discussed in Miyake et al. (2017), ranges from 1 to 3 weeks, influenced by species and local conditions. Despite their limited swimming abilities, larval movement in the water column, particularly upward movement, can lead to varying degrees of dispersal depending on water currents at different depths (Miyake et al. 2017). Modeling and observational data in Rogers-Bennett et al. (2016) suggest that a single spawning event may have seeded larvae at two sites 18 km apart, with modeling indicating dispersal distances ranging from 20 to over 100 km, though most simulations were under 70 km. Taking regional currents into account, the modeling in that study strongly suggested unidirectional dispersal towards the south based on prevailing currents during that period in the Southern California Bight (Rogers-Bennett et al. 2016). Studies reviewed in Miyake et al. (2017) reveal similar projected dispersal distances for green, pink, and red abalone, with estimated distances varying widely from tens of meters to over a hundred kilometers. Miyake et al. (2017) propose that both short- and long-distance dispersal patterns occur in a given spawning season for *Haliotis* species.

2.2.8.3 Population Structure

Multiple population genetic studies have been conducted for red, pink, and green abalone along the eastern Pacific coastline, covering various portions of their ranges. Notable studies include those by Gruenthal et al. (2007), De Wit and Palumbi (2013), and Smith (2022) for red abalone; Diaz-Viloria et al. (2009), Coates et al. (2014), and Mares-Mayagoitia et al. (2021) for pink abalone; and Gutierrez-Gonzalez et al. (2007), Gruenthal et al. (2014), and Mejia-Ruiz et al. (2020) for green abalone. These studies consistently show that dispersal in these species maintains population connectivity among populations separated by tens to hundreds of kilometers. Despite shifts from assessments using a few genetic markers to genome-wide coverage, the observed patterns persist.

Some genetic structure has been identified between distant offshore locations compared to mainland populations. For instance, green abalone sampled in Isla Guadalupe, located 250 km off the west coast of Baja, exhibited differences compared to populations sampled along the Baja California peninsula (Gutiérrez-Gonzalez et al. 2007). F_{ST} outlier analyses of transcriptomic data in red abalone have suggested that, despite broad-scale population connectivity over hundreds of kilometers, there may still be locally adaptive variation at a smaller scale (De Wit and Palumbi 2013). These findings align with the dual mode of abalone dispersal proposed by Miyake et al. (2017), involving both long- and short-distance dispersal.

Genetic resources have been extensively developed for various *Haliotis* species worldwide, providing valuable tools for broodstock management in aquaculture and facilitating the implementation of genetic/genomic selection. For example, markers have been generated to characterize variation in wild and farmed populations, characterize variation in traits of interest, and identify quantitative trait loci (QTLs) for important traits (e.g., Kang et al. 2011, Rhode et al. 2012, Aguilar-Espinoza et al. 2013, De Wit and Palumbi 2013, Gruenthal et al. 2014). Genetic linkage maps have also been constructed for several abalone species using various genetic methods (e.g., amplified fragment length polymorphisms (AFLPs), microsatellites, and single nucleotide polymorphisms (SNPs) (Liu et al. 2006, Sekino and Hara 2007, Vervalle et al. 2013), and reference genomes have been developed for various species including those along of commercial and conservation interest in California (e.g., Masonbrink et al. 2019, Griffiths et al. 2022, and Orland et al. 2022). These genetic resources contribute to enhancing breeding programs, understanding population dynamics, and supporting conservation efforts.

Hybridization emerges as a promising approach to enhance production traits in aquaculture settings, leveraging heterosis for accelerated growth, heightened survival rates, environmental adaptability, and desired market qualities (Elliott 2000). Globally, more than 50 different hybrid crosses have been explored, with over 95% and 50% of farmed abalone being hybrids in China and Australia, respectively (Guo 2009). Hybrid crosses have demonstrated significant improvements in survival (by 100%) and growth (by 30%) following severe disease-related losses in culture (Lafarga de la Cruz and Gallardo-Escárate 2011). Notably, hybrids exhibit increased thermal stress tolerance, as seen in hybrids of the temperate-adapted red abalone (*H. rufescens*) and the warm-adapted green abalone (*H. fulgens*), displaying superior warm-temperature tolerance and improved growth rates compared to either species individually (Lafarga de la Cruz and Gallardo-Escárate 2011). This makes hybridization a noteworthy strategy for advancing the U.S. abalone industry.

2.2.8.4 Aquaculture

In commercial hatcheries, the conditioning of broodstock abalone for spawning primarily involves temperature manipulation, ample provision of kelp as food, and, to a lesser extent, manipulation of photoperiods (Leighton and Robinson 2008). Various methods, including gamete stripping, desiccation, thermal shock, ultraviolet light exposure over seawater, and submersion in diluted hydrogen peroxide baths, have been employed to induce spawning in abalone species (Leighton and Robinson 2008). Nursery conditioning significantly enhances

both growth and fecundity in cultured stocks compared to wild populations, with fecundity in nursery-conditioned animals being 260% greater than that of abalone conditioned under natural conditions (Ault 1985).

Spawning results in the extrusion of negatively buoyant eggs and milt from the abalone, and fertilization takes place either in tanks or by collecting gametes and mixing them in smaller volumes of water to achieve specific crosses. Larval cultures are maintained for 4 to 5 days, after which the larvae are ready to settle (Leighton and Robinson 2008). Settlement can be induced using compounds such as GABA, and once settled, the abalone are cultivated on diets of diatoms and later macroalgae until they reach a size suitable for stocking in offshore cages, typically between 30 and 40 mm or larger. The duration of this growth period may range from months to over a year, depending on the species (Viera et al. 2016). Abalone are housed in offshore grow-out structures such as cages, barrels, tubes, and baskets, which are either kept on long-lines or suspended as part of Integrated Multi-Trophic Aquaculture (IMTA) systems near or within macroalgal lines or fish cages (Preece and Mladenov 1999, Troell et al. 2009, Qi et al. 2013, Viera et al. 2016).

Abalone typically take between 2 and 5 years to reach market size (Brokordt et al. 2014). The targeted market size for red abalone at one commercial farm, for example, is approximately 70 to 90 mm, corresponding to a 3- to 4-year-old animal (https://culturedabalone.com). Traits such as growth, which exhibit significant heritable variation among individual animals (Elliott 2000), have prompted interest in utilizing genetic selection to enhance this, and other economically valuable characteristics in these species (Van der Merwe et al. 2011, Brokordt et al. 2014).

2.2.8.5 Considerations on genetic risk to wild conspecifics

The commercial culture of red, green, and pink abalone is interesting from an aspect of assessing genetic risk from escapes on natural populations. Due to the extended duration abalone spend in culture before reaching maturity (3 to 4 years) and the size at which they can become reproductive (refer to the Behavior section), it is plausible that a portion of cultured abalone may reach reproductive age and spawn in offshore grow-out structures. Population structure studies, modeling, and observational data indicate larval dispersion over extensive distances, with populations showing genetic connectivity at scales exceeding hundreds of kilometers. However, some evidence also suggests local adaptation may occur (e.g., De Wit and Palumbi 2013). As described by Miyake et al. (2017), this duality may indicate that oceanographic processes both confine larvae to smaller scales and facilitate sufficient long-distance dispersal to prevent genetic differentiation. At these dispersal scales, it is likely that larvae from cultured operations could interact with wild abalone populations.

The wild populations of red, green, and pink abalone have faced significant reductions due to disease and over-harvesting, resulting in fishery closures. These populations may be more vulnerable to genetic impacts such as gene swamping, loss of diversity, or an increased load of harmful alleles from escaped cultured larvae (refer to the discussion by Gruenthal et al. 2014). Considering these factors, offshore cultivation of abalone species appears to carry a high risk of

genetic impact on wild populations. However, as noted by Ault (1985), mariculture of these species could serve a dual purpose by providing marketable products and contributing to the replenishment of wild stocks. If hatcheries employ strategies to maximize genetic diversity in cultured populations, offshore aquaculture might mitigate negative effects of dispersed larvae and potentially benefit wild populations. For example, Gruenthal et al. (2014) found that a minimum of 100 broodstock individuals, replaced each generation, would be needed for green abalone restoration based on the calculated effective population size in the southern part of the Southern California Bight. The required broodstock size depends on various factors, including culture procedures, replacement frequency, and, importantly, the genetic diversity and effective population size of the species and populations in the operation's range. However, this approach may limit opportunities for the selection of cultivated lines.

Genetic impacts from past attempts at stock replenishment through outplanting have yielded conflicting results. Gaffney et al. (1996) observed dominant genetic signals of red abalone outplanted in 1979 in mature abalone sampled on San Miguel Island in 1992, which were distinct from non-supplemented populations. They also reported a loss of genetic diversity in hatchery lines. However, in a subsequent study, Burton and Tegner (2000) did not detect genetic signatures of the outplanted individuals at San Miguel Island when sampled in 1999. They found that allelic frequencies and genetic diversity levels in that location were similar to other populations and to pre-outplant levels. It is evident that careful attention to hatchery practices will be critical to balance the needs of a commercial operation with responsible supplementation of wild populations through escaped cultured larvae spawned from abalone during the grow-out phase.

Additionally, utilizing detailed information on oceanographic processes in the region of the grow-out site is crucial to predict locations most likely to receive larvae from farm sites. As mentioned above, dispersal away from a site may be asymmetric based on seasonal currents or longer-term current oscillations. This information can guide broodstock selection and monitor genetic signals of introgression of cultured individuals into natural populations. Due to the different potential outcomes from offshore abalone culture, the genetic risk to wild populations varies, ranging from low to high based on the approaches used.

Exploring sterilization approaches will be a valuable avenue for operations seeking to employ selection of cultivated lines. Hybridization, despite its potential benefits, yields low fertilization rates (10 to 36%) and extremely low post-larval and juvenile survival rates (0.1 to 1% and 0.1 to 5%, respectively) (Lafarga de la Cruz and Gallardo-Escárate 2011). Investigating the mechanisms behind this diminished fertility and survival can perhaps accelerate development of sterilization techniques applicable to both hybrid and pure species abalone culture.

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3.0 Gulf of America Candidate Species for Marine Aquaculture

3.1 Geographic Range

Regions considered in this analysis were in the west, central, east, and southeast of the Gulf of America (hereafter, 'Gulf').

3.2 Shellfish Candidate Species for Marine Aquaculture

3.2.1 Bay scallop (Argopecten irradians)

3.2.1.1 Range/Description

Bay scallops, scientifically known as *Argopecten irradians*, are indigenous to the Northwest Atlantic, with a range extending from southern Massachusetts to the Gulf (Gosner 1999). There are three subspecies of *Argopecten irradians*. Firstly, *A. i. irradians* is predominantly found along the Atlantic coast, spanning from New Hampshire to New Jersey. South of this region, *A. i. concentricus* is distributed from New Jersey to North Carolina and extends into the Gulf along the Florida coastline and eastern coastal Gulf. Lastly, *A. i. amplicostatus* inhabits the area from Louisiana to Galveston, Texas, and into northern Mexico (Hemond and Wilbur 2011, and references therein). Bay scallops primarily inhabit shallow waters of bays and estuaries, spending most of their life cycle in seagrass beds (Bert et al. 2011).

In 1994, both commercial and recreational fisheries targeting Florida Gulf Bay scallops were closed due to population declines, prompting abundance surveys conducted by the Florida Fish and Wildlife Conservation Commission (FWC). Their findings revealed population fluctuations occurring in broad 5- to 7-year cycles, marked by shifts from low to high abundance and vice versa over just one or two seasons (FWC 2023). These population dynamics are closely tied to various factors, including natural conditions such as the abundance of seagrass meadows, salinity levels, occurrences of red tides, hurricanes, and other environmental variables (Bert et al. 2014, and references therein). Additionally, anthropogenic influences, such as the impact of fishing efforts, greatly affect these scallop populations. The bay scallop's short lifespan and variable abundance pose challenges for stock assessments compared to longer-lived species.

In the northwest Gulf, there is a lack of data on the abundance and distribution of bay scallops in Alabama, Mississippi, and Louisiana. This scarcity is likely due to the low abundance of seagrass beds in these regions, suggesting the absence of bay scallops in these areas. In Texas, *A. i. amplicostatus* exhibits low densities and undergoes "boom and bust" cycles approximately every 10 to 15 years (Withers and Hubner 2009). Notably, Laguna Madre in Texas stands out as

the only location with notably high relative abundance, attributed to extensive seagrass coverage and favorable salinity levels.

Bay scallops are managed at the state level, such as in Texas and Florida, with county-specific regulations in Florida establishing season and bag limitations for recreational harvest.

3.2.1.2 Biological Characteristics

Bay scallops are hermaphroditic broadcast spawners, with each individual releasing eggs and sperm in separate pulses, typically releasing sperm first and then eggs to facilitate cross-fertilization (Castagna 1975), although self-fertilization is known to occur (Arnold et al. 2005). Gametes remain viable for only a short period, usually minutes to hours; following fertilization eggs develop into veligers within a few hours (Castagna 1975). The pelagic larval duration is typically estimated to last from 5 to 8 days (Castagna 1975), although longer durations ranging from 10 to 14 days have also been observed for this species (Geiger et al. 2010). This pelagic duration suggests that larvae are capable of dispersing long distances from the source populations (Geiger et al. 2010), although the success rate of most larvae transported over long distances may be low (Arnold et al. 1998). It is more common for larvae to be retained locally for self-seeding and population replenishment, but occasional successful long-distance dispersal events may occur (Arnold et al. 1998). Ultimately, water currents largely determine the patterns of transport or retention, and depending on the location, some populations may continuously be replenished by larvae arriving from more distant populations (Liu et al. 2015).

As the larvae develop, they settle onto eelgrass blades or other support structures and attach using byssal threads, where they metamorphose into spat. They remain attached to the blades until they reach a size of 20 to 30 mm, after which they release themselves and live benthically. This attachment period is crucial for their survival, as settling in the benthic habitat prior to reaching this size results in high mortality (Castagna 1975, Geiger et al. 2010). Even after detaching and dropping into the benthic substrate, eelgrass beds continue to serve as important habitat for this species (Geiger et al. 2010). Although juveniles and adults are capable of short-distance movements, they typically remain within the seagrass beds throughout their life cycle (Bert et al. 2014).

In Florida, bay scallops typically have a lifespan of 12 to 18 months (Geiger et al. 2010), although in rare cases, a small number of individuals may survive for as long as 24 months (Castagna 1975, Lu and Blake 1997). Consequently, this species is believed to spawn only once, typically around the age of 12 months (Geiger et al. 2006, Geiger et al. 2010). Spawning times for the Florida Gulf bay scallops (*A. i. concentricus*) vary by location, with northern populations on the west coast of Florida spawning as early as August, while southern populations spawn closer to October (Blake et al. 2000, Geiger et al. 2010). While spawning is usually triggered by a rapid drop in water temperature, other environmental shocks may also induce spawning (Blake et al. 2000, Geiger et al. 2006, Geiger et al. 2010).

Prior to spawning, wild bay scallops typically reach a size between 40 and 50 mm by July, and may attain a maximum size of 60 mm by December at 15 months of age. However, mortality is high soon after spawning, and only a few individuals survive to reach this larger size (Blake et al. 2000). There is ongoing debate regarding whether this mortality is linked to the energetic demands of spawning or some other aspect related to senescence (e.g., Geiger et al. 2006, Bricelj et al. 1987).

Due to its short life-cycle, this species experiences significant fluctuations in abundance due to variations in annual recruitment success (Castagna 1975, Arnold et al. 1998, Liu et al. 2015). Poor recruitment years can occur for various reasons. For instance, larval survival may be significantly reduced by high levels of rainfall, which decrease salinity and increase turbidity, conditions to which the larval stages are particularly sensitive (Bert et al. 2014). Consequently, populations of this species may not possess the same ability to buffer stressors as longer-lived species.

3.2.1.3 Population Structure

Although *A. i.concentricus* can be found both in the Gulf and along the Atlantic U.S. coastlines, Hemond and Wilbur (2011) found highly significant genetic differentiation between these regions. Therefore, this section will focus solely on patterns detected within the Gulf. *A. i. concentricus* is present along the Florida Gulf coastline and extends into the northwestern Gulf from the Florida panhandle to the Chandeleur Islands, Louisiana, albeit at very low abundances in these areas (Withers and Hubner 2009). In the western Gulf, the subspecies *A. i. amplicostatus* ranges from Galveston Bay, Texas to northern Mexico (Withers and Hubner 2009). Currently, no genetic studies have been published on population structure in the northwestern Gulf. However, ongoing research by Bassem Allam and his team at Stony Brook University is examining

population structure in bay scallops along the northeast U.S. coast down to Texas. Preliminary findings indicate genetic differentiation between Florida and Texas populations. Recently, the team published a chromosomal-level genome assembly for *A. irradians* (Grouzdev et al. 2024), offering a valuable tool for further analyses of population structure and for assessing introgression patterns from cultured to wild populations.

Genetic differentiation has been observed among Florida Gulf populations (e.g., Bert et al. 2011); however, the population structure patterns may not be straightforward based on geography (Arnold et al. 1998, Bert et al. 2014). Bert et al. (2014) utilized allozyme-locus and mitochondrial DNA markers to investigate population structure and connectivity for four consecutive generations of bay scallops along the entire Florida Gulf coastline. They discovered that bay scallops (*A. i. concentricus*) exhibit a complex metapopulation genetic structure characterized by both source and sink populations in terms of recruitment. Gene flow originates from larger and more stable core populations to sink populations, combined with classic metapopulation dynamics, where all populations have the potential to contribute recruits to one another (Bert et al. 2014); this pattern resembled those identified by Arnold et al. (1998). Within this framework, populations at Steinhatchee and Homosassa emerge as the primary source populations along the Gulf coastline, although smaller, peripheral subpopulations such as St. Joseph (panhandle) and the southerly Pine Island locations may also be important sources of recruits, although they are considered to be less stable or not as reliably connected to the other populations. Importantly, Bert et al. (2014) discovered that this metapopulation was sensitive to total collapse, with the peripheral subpopulations at high risk of extinction. However, at the time of the study, the source populations were considered large, with sufficient available habitat. Nonetheless, the authors found that the short-lived bay scallops lacked the population-level buffering capacity of longer-lived species. They concluded that maintaining core abundances and carefully managing this species in those sites is a priority for the long-term perpetuation of subpopulations and, more generally, for the species across the Florida Gulf range.

Due to declining population abundance across its range, stock enhancement programs have been developed for bay scallops. A genetic monitoring program was initiated to detect signals of contribution from these activities (Wilbur et al. 2005). Between 10,200 and 30,600 hatchery-produced scallops were placed in cages at multiple sites over three years and allowed to spawn naturally with wild populations (Wilbur et al. 2005). However, the authors did not observe any genetic contribution from these stock enhancement efforts resulting in significantly different allele frequencies in sampled scallops at the local or regional levels. They suggested that either the larval contributions from the hatchery stock were overwhelmed by recruitment from wild populations, and/or the study lacked the statistical power to detect these contributions, especially for culture-origin individuals at lower frequencies in the natural environment. Bert et al. (2011) recommended that broodstock for these efforts be collected from the same population to minimize potential genetic harm to wild scallops. They also suggested implementing comprehensive genetic monitoring programs moving forward to assess any impacts. It is logical that the same guidelines apply to commercial operations utilizing grow-out sites in the natural environment.

Hybridization between subspecies *A. i. irradians* and *A. i. concentricus* has been documented, at least experimentally, with maintained fertility in the produced offspring (Wang et al. 2024). Fertilization rates, hatching rates, and metamorphosis rates were also comparable between purebred and crossbred cohorts. Although this experimental approach was conducted in highly domesticated commercial broodstocks in China to mitigate high levels of inbreeding (Wang et al. 2024), it remains uncertain how readily this may occur in the natural environment. Nonetheless, it emphasizes the importance of utilizing locally collected broodstock in hatchery programs, especially in regions of the Gulf where more than one subspecies coexists when it is likely that larvae may be dispersed away from grow-out sites.

It may be feasible to employ methods such as induced triploidy to significantly reduce recruitment from commercial grow-out sites. Tabarini (1984) demonstrated the induction of triploidy in *A. irradians* through chemical treatment of fertilized eggs, although a 6% failure rate was noted even with higher chemical concentrations. Apart from exhibiting greater muscle weight compared to diploid scallops, the majority of triploid individuals did not develop ripe gonads during the summer months, unlike diploid scallops which did ripen and spawn. Further research is necessary to ensure that individuals do not revert to diploid states as they mature, a phenomenon observed in other shellfish species (Beaumont 2000).

3.2.1.4 Aquaculture

Bay scallops, encompassing all subspecies, are highly valued in aquaculture due to their rapid growth, ease of conditioning and cultivation, as well as their strong market demand and value (Castagna 1975, Adams et al. 2001). While some efforts have been made to develop cultivation techniques along the Gulf coast of Florida (e.g., Lu and Blake 1997, Blake et al. 2000, Adams et al. 2001), as well as in the northeast (Castagna 1975, Knickerbocker et al. 2009), China currently leads as the largest global producer of bay scallops (Blake et al. 2000, Knickerbocker et al. 2009). Recognizing the declining and irregular abundance of bay scallop populations across most of their range, aquaculture programs to support stock enhancement efforts for this species were also initiated in 1998 (Arnold et al. 2005, Wilber et al. 2005).

According to Castagna's (1975) research on culturing bay scallops, conditioning typically involves providing abundant live algal cultures, followed by a decrease in water temperatures to induce gonad maturation. Spawning is triggered by rapid and brief thermal shocks, using either hot or cold water. After spawning and fertilization, trochophore larvae develop within 8 to 12 hours, progressing to straight-hinged larvae within 16 to 24 hours. Larval settlement occurs within 5 to 7 days, influenced by factors like temperature and food availability. However, Lu and Blake (1997) observed settlement 11 days post-fertilization, while Blake et al. (2000) reported settlement between 10 to 14 days. Larvae attach using byssus threads to vertical surfaces like wood, mylar, fiberglass (Castagna 1975), strips of black plastic Astroturf® (Lu and Blake 1997), or black plastic ribbons (Blake et al. 2000).

Following metamorphosis, the spat were transferred to nylon mesh bags along with the settlement substrate, and then placed into cages to prevent predation and suspended in the natural environment for growth (Lu and Blake 1997). Alternatively, some methods involve brushing the spat off the substrate after 30 days, followed by placement into nursery bags, typically made of

200-micron nylon mesh, for initial grow-out (Blake et al. 2000). According to Adams et al. (2001), spat were stocked into nursery bags at 4 to 5 mm and remained there for approximately 4 months. When the scallops reach a suitable size, typically 7 to 10 mm (Lu and Blake 1997), the scallops are transferred from the bags to mesh cages, lantern nets, or Japanese pearl nets for further grow-out to market size (Castagna 1975, Knickerbocker et al. 2009). In Florida, this final grow-out phase takes around 5 months, from June to October (Adams et al. 2001). These cages may be positioned in frames attached to the bottom in shallower areas, or suspended off floats or longlines in deeper waters (Lu and Blake 1997, Blake et al. 2000, Adams et al. 2001). Fouling on cages and scallop shells necessitates cleaning every 2 to 4 weeks, which is considered a labor-intensive aspect of culturing this species (Lu and Blake 1997). Although scallops placed in higher productivity environments, such as estuaries and bays, tend to grow faster, those placed offshore in deeper waters, away from fouling environments, also exhibit good growth and produce high-quality scallops, but require far less cage maintenance (Knickerbocker et al. 2009).

The production season for bay scallops typically spans less than a calendar year (Adams et al. 2001, Milke et al. 2006), and they can reach market size (40 to 50 mm) in as little as 5 to 7 months (Castagna 1975, Knickerbocker et al. 2009), although this timeline may vary depending on the location. For instance, in Tampa Bay, scallops grew from 9.5 mm to 50 mm in about 7 months, while in Georgia, they increased from 9.8 to 49 mm in 8 months, and in North Carolina, from 9 mm to 50 mm in 8 months (Lu and Blake 1997, and references therein).

While Zheng et al. (2006) note that bay scallops are harvested before reaching maturity in China, it remains uncertain whether this practice would be feasible in the Gulf. Harvesting typically occurs from September through October, coinciding with gonad maturation (Lu and Blake 1997). While some populations along the Florida Gulf coastline spawn as late as October, others begin spawning as early as mid-July (Lu and Blake 1997). Consequently, it is likely that at least some scallops may be spawning prior to harvest. This issue might be mitigated by methods such as induced triploidy, as discussed earlier.

3.2.1.5 Considerations on genetic risk to wild conspecifics

As highlighted by Lu and Blake (1997), bay scallops are particularly susceptible to both human-induced and natural environmental changes. This vulnerability stems largely from the species' reliance on successful recruitment in any given year to sustain populations, given their short lifespan limited to a single spawning season. This characteristic has led to significant fluctuations in population abundance and persistence of bay scallops, making smaller populations particularly vulnerable to collapse. While population genetic studies do not offer a straightforward understanding of connectivity, larger populations, such as those along the Florida Gulf coastline (e.g., Steinhatchee and Homosassa), may serve as a crucial source of recruits for populations across the region (Bert et al. 2014).

Given their short life cycle and the timing of harvest in the fall, it is probable that cultured scallops will spawn during grow-out in late summer and early fall. With their pelagic larval duration, there is a potential for larvae to disperse from offshore sites to suitable coastal habitat. Water current modeling, and possibly the use of spat collector bags (as used by Arnold et al. 1998), could aid in determining which populations are more likely to receive larval recruits. This information could be valuable for prioritizing monitoring and mitigation efforts.

Bert et al. (2014) strongly advocated for careful hatchery practices in aquaculture to preserve genetic diversity and stressed the importance of genetic monitoring programs to evaluate genetic impacts in the wild populations. While their study focused on restoration-based culture, the principles also apply to commercial aquaculture practices. To protect bay scallops in the Gulf, it might be prudent to strategically select sites to minimize the dispersal of larvae from grow-out sites to "core" populations like Steinhatchee and Homosassa, or to populations with similar functions elsewhere in the Gulf (e.g., the potential "core" population in Laguna Madre, Texas). Preserving genetic diversity and preventing genetic impacts on these larger populations should be a priority if they serve to replenish other subpopulations.

From a management standpoint, Bert et al. (2014) recommended a similar approach, prioritizing these core populations to ensure their abundances and habitats are maintained. This strategy could help sustain bay scallop populations and their genetic diversity in the Gulf region. The populations of bay scallops along the Texas coast, *A. i. amplicostatus*, remain relatively understudied, although it is likely that most life-history traits are shared among these subspecies. However, there may be differences in certain characteristics among various regions (e.g., Barber and Blake 1983). Currently, there is no available information regarding the genetic structure among these populations.

Nevertheless, it's essential that broodstock be sourced close to the grow-out sites, taking into account which populations may receive the majority of cultured larvae from these sites. Strategies such as harvesting the bay scallops prior to spawning or utilizing triploidy to reduce the overall number of larvae dispersing from culture sites could significantly mitigate any potential genetic impacts. These approaches could help safeguard the genetic integrity of bay scallop populations along the Texas coast and beyond.

Considering the life-history characteristics of bay scallops, along with the volatility in population abundances and the potential genetic risks outlined in Bert et al. (2014), aquaculture of this species may pose a moderate-to-high genetic risk to wild populations. However, implementing approaches to ensure that core populations are largely unaffected by aquaculture practices could lower this risk to a moderate level. Furthermore, if hatchery practices prioritize maintaining a high level of genetic diversity in offspring, and if scallops are harvested prior to sexual maturation or approaches are used to delay or prevent gonadal maturation, then the genetic risk to wild bay scallops could be further reduced. These measures are crucial for safeguarding the genetic integrity of wild populations while supporting aquaculture efforts.

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3.2.2 Eastern Oyster (Crassostrea virginica)

3.2.2.1 Range/Description

Eastern oysters, scientifically known as *Crassostrea virginica*, are bivalve mollusks native to the East Coast of the Americas. Their range extends from the Gulf of St. Lawrence in Canada down to Venezuela and includes the Gulf and the Caribbean Islands (Dugas et al. 1997, Wallace 2001, NOAA 2007 and references therein). These oysters typically inhabit shallow estuaries and subtidal regions, and in the southern part of their range, can also be found in intertidal zones (Shumway 1996, Dugas et al. 1997, NOAA 2023). The cup-shaped morphology of the shells gives rise to one of their common names, the American cupped oyster.

Throughout their range in the U.S., Eastern oysters (*C. virginica*) are heavily exploited by fisheries and, more recently, aquaculture to supply a large commercial market. Beyond their commercial value, these oysters are also highly valued for their ecological roles. They contribute to improving water quality and clarity and act as ecosystem engineers by creating habitats through the generation of oyster reefs (Coen et al. 2007, La Peyre et al. 2019).

Historically, the northeastern U.S. Atlantic coast experienced extreme overharvest of *C. virginica*. This overharvest, combined with other factors such as habitat loss and pollution, led to significantly diminished populations in the northeast mid-Atlantic regions. The Eastern oyster fishery in the Gulf has shown variability largely due to fluctuating environmental conditions. Oyster landings increased from the 1960s and peaked in the early 1980s, then declined, but rose again after the early 1990s. More recently, the fishery has faced considerable losses in oyster reefs due to a combination of factors, including habitat loss, channelization, oil and gas facilities, and natural events such as hurricanes (NOAA 2007, La Peyre et al. 2014, and references therein). States in the Gulf have continued to see declines in wild oyster harvests, and traditional clutching approaches (used to settle wild spat) have resulted in inconsistent, poor, or nonexistent wild harvests depending on the state (GSMFC 2023).

Oyster fisheries in the Gulf are managed at the state level, where each state employs its own approach to Eastern oyster management. These approaches typically involve a combination of strategies, including opening or closing fishing sites or the fishery itself, establishing daily harvest quotas, and regulating daily effort units (NOAA 2007). Among the Gulf states, Louisiana accounts for the largest annual landings of *C. virginica*, representing an average of 36% of the nationwide oyster landings based on market value across all species from 2000 to 2019 (Louisiana Wildlife and Fisheries 2020). Texas and Florida are

also significant producers of Eastern oysters in the Gulf; however, these states have seen significant declines in abundance. In Florida, the largest oyster habitat was in Apalachicola Bay on the west coast, however, a massive crash between 2010 and 2022 reduced the abundance from 10,000 acres of oysters to only 500 acres in 2022, and in 2020 that region was closed to harvest (GSMFC 2023). In Texas, Galveston Bay once supported most of the state's annual commercial oyster harvest (~71%) (NOAA 2007, GSMFC 2023), however, now Galveston and San Antonio Bays are areas of low abundance, while Aransas Bay appears to be increasing in abundance (GSMFC 2023). Alabama and Mississippi also have oyster fisheries, though they are smaller than those in Louisiana, Florida, and Texas (NOAA 2007).

3.2.2.2 Biological Characteristics

Eastern oysters are protandric hermaphrodites, initially maturing as males and later developing into females (Thompson et al. 1996, Park et al. 2012). While size is believed to partially influence when this shift occurs, other factors such as environmental and physiological stressors, as well as the proximity and sex of nearby oysters, also play a role (NOAA 2007 and references therein). However, as reviewed by Shumway (1996), oysters in warmer waters, such as those in the Gulf, often make this switch earlier and may function as females during their first year.

Gonad maturation in Eastern oysters is correlated with water temperature, with a minimum temperature required to initiate gametogenesis. These temperatures vary across their range, such as 17°C in Long Island Sound and 20 to 26°C in different parts of the Gulf (Hayes and Menzel 1981, Shumway 1996). It is believed that temperature fluctuations between 5 to 10°C, in either direction, induce spawning (Hayes and Menzel 1981). Oysters can spawn multiple times throughout the season, and populations in warmer waters have a longer spawning season (Hayes and Menzel 1981, Shumway 1996). Due to this protracted spawning season and faster growth in warmer temperatures, *C. virginica* south of North Carolina may reach sexual maturity in their first year and reportedly can spawn only 12 weeks after attachment, allowing them to spawn in their first season during the fall months (Hayes and Menzel 1981, Shumway 1996). Fecundity estimates for this species range widely, from 2 to 115 million eggs per female, largely depending on the size of the female (NOAA 2007).

Gametes of Eastern oysters are generally short-lived, surviving only a few hours. At warmer temperatures, such as 30°C, the first larval stage can develop as quickly as three hours after fertilization (Shumway 1996). The initial larval form, known as the trochophore, lasts for 1 to 2 days and does not feed, while subsequent larval stages are planktotrophic (NOAA 2007). The duration of the pelagic larval stage varies based on biological and physical parameters, such as food availability and temperature (Goodwin et al. 2019), but is generally believed to last between 2 and 3 weeks, including in the Gulf (Kennedy 1996, Goodwin et al. 2019).

When dispersal was modeled for this species, it was found that in low to moderate energy regimes, over 95% of larvae would settle within 50 km of their release point. In higher energy periods, over 95% of larvae would settle within 100 km of release. However, the majority of modeled particles dispersed between 10 and 20 km from point of release (Powers et al. 2023).

Once the larvae develop into the pediveliger stage, metamorphosis and settlement may be initiated by environmental cues such as salinity or chemicals released by mature oysters (NOAA 2007). Larvae typically settle on shells or other hard substrates (NOAA 2007). Recruitment of larvae in the Gulf varies by region, but has been recorded from spring (March/April) through fall (October/November) (Kennedy 1996, and references therein). Once attached, the oysters remain sessile for the rest of their life cycle.

Growth at all stages is faster in warmer water temperatures (e.g., in Texas), allowing *C. virginica* to reach harvest size (76 to 90 mm) within 12 to 24 months (C. Hollenbeck, personal communication). In colder regions, such as Long Island Sound, it may take 4 to 5 years for Eastern oysters to reach 90 mm (Shumway 1996, NOAA 2007). While egg and larval stages are more sensitive, adult Eastern oysters can tolerate a broad range of temperatures (-2°C to 36°C) and salinities (5 to 40 ppt). In the Gulf, temperatures as high as 49.5°C during emersion may be tolerated for short periods (Shumway 1996). Generally, Eastern oysters exposed to extremes at either end of the range for long durations suffer negative consequences (Shumway 1996). In the Gulf, *C. virginica* can live for 25 to 30 years and reach up to 30 cm in length (Carriker 1996, NOAA 2007).

3.2.2.3 Population Structure

Numerous population genetic structure studies have been conducted on *C. virginica* throughout their U.S. distribution, including the Gulf. Early studies identified distinct populations in the Atlantic and Gulf (Reeb and Avise 1990, Hoover and Gaffney 2005), with a transition zone on the eastern coast of Florida (Karl and Avise 1992, Hare and Avise 1996). Recent analyses using whole genome re-sequencing confirmed a significant phylogeographic break between *C. virginica* in the eastern United States and the Gulf, with a mean pairwise F_{ST} of 0.105 (Puritz et al. 2022). Sequencing of individuals from select domesticated lines revealed admixed ancestry between the two coastlines, with heterozygosity maintained despite several generations having passed since those occurrences (Puritz et al. 2022).

Studies have also identified genetic structure within the Gulf. The strongest differentiation is observed between Eastern oyster populations along the Texas coastline (e.g., Laguna Madre, Port Aransas) and other Gulf locations (King et al. 1994, Hoover and Gaffney 2005, Varney et al. 2009). This was supported by Thongda et al. (2018), who used single nucleotide polymorphism (SNP) markers to detect significant genetic structure between samples from the Texas Gulf coast (Corpus Christi, Upper Laguna Madre, and Lower Laguna Madre) and those from the northern Gulf (Florida, Alabama, Louisiana, and Sabine Lake, Texas).

In other regions of the Gulf, low but significant population structure was detected across four sampled sites in the northern Gulf using a RADSeq approach. However, the resolved pattern did not follow a geographically-based isolation-by-distance model (Johnson and Kelly 2020). The authors were surprised that genetic differentiation (F_{ST} of 0.02) was not higher across the freshwater boundary of the Mississippi River. They hypothesized that this might reflect management efforts for the Eastern oyster, which could have involved moving individuals across

this boundary through practices like transplanting seed from one location to another or outplanting hatchery-produced seed (Johnson and Kelly 2020). The increased utilization of genomic approaches may reveal finer-scale resolution of genetic differentiation among Eastern oysters in the Gulf. Such approaches have recently detected low but significant spatial structure among populations in different portions of the Atlantic coast (e.g., Bernatchez et al. 2019, Puritz et al. 2022).

Significant genomic resources have been developed for the Eastern oyster, including genome assemblies (e.g., Gómez-Chiarri et al. 2015, Puritz et al. 2024), a high-density genotyping array (e.g., Xuereb et al. 2023, Guo et al. 2023), and transcriptomic sequencing (e.g., Eierman and Hare 2014). Additionally, coordinated efforts have been made to develop genetic resources and research projects aimed at advancing the aquaculture of this species (e.g., Allen et al. 2020). These resources have already enhanced the understanding of the genomic impacts of culture and domestication on this species (e.g., Hornick and Plough 2022, Zhao et al. 2024) and will likely be crucial for future evaluations of genetic population structure throughout the Eastern oyster's range.

3.2.2.4 Aquaculture

Both enhancement and commercial aquaculture of Eastern oysters have been ongoing for decades along the East Coast and in the Gulf. A less intensive aquaculture approach involves creating suitable settlement sites to encourage wild oyster seed to settle, or transplanting oyster seed from one location (e.g., public grounds, high-density areas, or disturbed areas) to another suitable location for grow-out to market size or for restoration purposes. This method is relatively low-cost and requires minimal technology or infrastructure (NOAA 2007, FAO 2009).


Image from NOAA Fisheries

The most intensive type of oyster culturing involves spawning oysters in a hatchery, which requires tank infrastructure not only for the broodstock and larvae but also for culturing the algae used as food (Wallace 2001). In hatcheries, broodstock oysters are fed cultured algae and kept at controlled temperatures until they become sexually mature. Alternatively, ripe oysters are collected from the wild and brought into the hatchery for spawning. Spawning is typically initiated using heat shock with warm water. Oysters are then separated by sex, and after 20 to 30 minutes of spawning, the gametes are washed through fine mesh to remove debris. The gametes are mixed for fertilization, and the fertilized eggs are placed in aerated tanks for larval development (FAO 2009).

During larval development, larvae may be sorted by size grades using sieves as a form of early phenotypic selection (FAO 2009). When larvae are ready to settle, after approximately 14 to 16 days, they are placed in different tanks containing microcultch (finely ground oyster shells) if the goal is to grow oysters singly for the half-shell market. If the goal is to grow oysters in aggregates, they are placed on oyster shell cultch in mesh bags (Wallace 2001, FAO 2009). Alternatively, pediveligers may be shipped at this stage to producers without their own hatchery (FAO 2009). Due to the high costs of culturing algae as feed, oyster seed is placed into the natural environment for grow-out as quickly as possible (Wallace 2001, FAO 2009).

In on-bottom grow-out, oysters may be cultured in mesh bags attached to longlines. Cultchless seed is placed in these bags and held intertidally on a hard bottom, where they are emersed during low tides (FAO 2009). In off-bottom grow-out, cultchless seed may be grown in trays, which can be switched to bags once the shells have hardened. Alternatively, they may be grown in bags, lantern nets, or mesh culture tubes attached to longlines, rafts, or floats from which they are suspended in the water column (FAO 2009).

As oysters grow, they are sorted into bags with progressively larger mesh sizes and lower densities of oysters (Wallace 2001). Spat grow rapidly and have been found to reach sexual maturity in culture within 4 months in parts of the Gulf (Wallace 2001). As mentioned earlier, marketable size is 75 to 90 mm, which can be reached within 12 to 36 months, depending on environmental parameters and food availability (Wallace 2001).

Commercial aquaculture production of Eastern oysters, achieved through the selection and breeding of fully captive specimens, is rapidly increasing, particularly along the mid-Atlantic coast (Allen et al. 2021). These efforts, both with and without the use of genetic tools, have largely focused on improving commercially relevant traits such as growth, yield, and disease resistance in Eastern oysters (e.g., Ford and Haskin 1987, Rawson and Feindel 2012, Frank-Lawale et al. 2014, Proestou et al. 2016), including in the Gulf (e.g., Casas et al. 2017). More recently, genomic approaches and toolsets have been applied to these efforts (e.g., Guo et al. 2023, McCarty et al. 2023, Xuereb et al. 2023).

To further improve growth, with the added benefit of preventing sexual maturation and/or greatly reducing fecundity in large individuals, methods to induce triploidy in Eastern oysters have been developed (Barber and Mann 1991, Yang et al. 2018). One method induces triploidy through chemical induction (Allen and Bushek 1992). Another approach to generating triploids is through mating of tetraploid and diploid individuals. While it is challenging to produce tetraploid lines (e.g., Yang 2022), there are successful tetraploid lines currently available in the Gulf. As a result, the majority of cultured Eastern oysters in the Gulf are triploids derived from this tetraploid/diploid mating approach (e.g., Wadsworth et al. 2019).

While triploidy may not completely eliminate the production of gametes, many studies have found significant reductions in the number and quality of gametes produced, and lower fertilization success in triploid Eastern oysters (Allen and Downing 1986, Wadsworth et al. 2019, Matt and Allen 2020, Yang 2022); for example, in Yang (2022), an average of 1.66% of female

triploid oysters developed mature gonads. While triploidy appears to be a good option to reduce genetic risk to natural populations from domesticated lines, triploid oysters may be more sensitive to certain types of environmental stress (e.g., thermal stress), which can lead to high mortality under some conditions (Wadsworth et al. 2019, Bodenstein et al. 2023).

3.2.2.5 Considerations on genetic risk to wild conspecifics

As reviewed by NOAA (2007), key biological characteristics of Eastern oysters in warmer regions like the Gulf include high fecundity, early maturity, extended spawning seasons, and rapid colonization potential. These attributes also increase the potential genetic risk from aquaculture on wild conspecific populations. With an estimated pelagic larval duration of 2 to 3 weeks (Kennedy 1996), larvae can disperse up to 100 km from the point of release in high-energy regimes (Powers et al. 2023), potentially transporting larvae from offshore grow-out sites to natural populations. However, shorter dispersal distances are more common (Powers et al. 2023). Understanding regional dispersal, transport, and connectivity patterns is crucial for protecting existing shellfish beds (Goodwin et al. 2019) and identifying which populations may be most impacted by recruits from commercial Eastern oyster production.

Highly differentiated populations of Eastern oysters have been identified along the Texas Gulf coast, specifically in areas such as Corpus Christi and Upper and Lower Laguna Madre (King et al. 1994, Hoover and Gaffney 2005, Varney et al. 2009, Thongda et al. 2018). Additionally, smaller but still significant genetic structure has been found in the northern Gulf (Johnson and Kelly 2020). To minimize genetic risks to wild populations, it is recommended that broodstock or spat be collected from nearby estuaries for spawning or grow-out, with particular care taken to preserve the unique genetic populations along the Texas coast.

In the Eastern oyster biological review (NOAA 2007), the risk of mature cultured oysters spawning during the grow-out period was acknowledged, along with the potential for genetic introgression of cultured genotypes into wild oyster populations. At that time, genetic analyses along the Atlantic coast indicated that such introgression had not yet widely occurred (NOAA 2007). However, more recent studies have identified genetic introgression from cultured oysters into natural populations in various regions along the Atlantic coast (Kutsumi 2017, Jaris et al. 2019, Puritz et al. 2022, Zhao et al. 2024). Higher-resolution genomic approaches could potentially reveal that introgression is more common between cultured and wild Eastern oysters than previously thought, given sufficient time and resources for a comprehensive investigation.

The increased use of selected lines in oyster aquaculture underscores the importance of understanding the potential for introgression and its impact on wild populations. Evidence suggests that domesticated lines may exhibit reduced fitness in natural or simulated natural settings. For example, McDonald et al. (2023) found that selected oyster lines had inadvertently lost some adaptability, such as tolerance to varying salinity levels, when compared to wild counterparts. If this reduced fitness were to be transferred to wild populations, it could negatively impact natural Eastern oyster populations. However, Carlsson et al. (2008) observed low rates of introgression from selected *C. virginica* lines into natural populations during supplementation

efforts. They attributed this to selection against domesticated traits, the relative scale of cultured to wild individuals, and predation, which limited the integration of cultured oysters into the wild population. These findings suggest that the large size of wild eastern oyster populations and natural selection against domesticated traits may mitigate impacts from aquaculture escapes.

The use of triploid oysters has become increasingly common in Eastern oyster culture. These triploid individuals either lack mature gonads or have significantly reduced fecundity in the small percentage of individuals that do develop gonads. As a result, the use of triploids greatly reduces the potential for genetic impacts on wild Eastern oyster populations (NOAA 2007, Yang 2022). While some larvae may recruit from aquaculture sites utilizing triploids, the genetic signal would likely be overwhelmed by the exponentially larger contributions from fertile wild individuals.

The genetic risk to conspecific Eastern oyster populations varies depending on whether diploid or triploid oysters are utilized during grow-out. If triploids are used, the genetic risk to natural oyster beds is likely low, as the small amount of potential genetic contribution would be overwhelmed by the naturally spawning oysters. Similarly, if spat cultivation (without a hatchery program) is used to augment natural production, the risk is also low, provided practices include only moving individuals over short distances to account for population structure. However, if diploid animals are used in a hatchery program, the risk will likely depend largely on the degree of domestication and breeding strategies employed by the hatchery. For diploid, selected lines that have diverged from natural populations, as commonly found in genetic studies, the genetic risk to natural populations is likely moderate to high.

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3.2.3 Manila Clam (Venerupis philippinarum)

The Manila clam is a candidate species for shellfish culture for both the Gulf and Southern California. See the species profile of Manila clam in the Southern California candidate species discussion (Section 2.2.4, *Manila Clam*).

Manila Clam is not native to the Gulf, and there is no known existence of wild Manila Clam in the region.

3.2.3.1 Range/Description

Manila clams (*Venerupis philippinarum*, synonymous with *Ruditapes philippinarum*, *Tapes semidecussata*, *T. philippinarium*, and *T. japonicas*) originate from the entire East Coast of Asia, spanning from northern Russia through Indonesia to the East Coast of India (Goulletquer 1997 and references therein). Flourishing in shallow, subtropical to temperate waters with coarse sand and/or gravel, these clams were intentionally introduced to Hawai'i from Japan in 1920 (Yap 1977), and later unintentionally spread to the West Coast of the United States alongside Pacific oyster imports (Quayle 1949, Goulletquer 1997). Their range has since expanded along the West Coast, reaching from British Columbia to San Diego in California (CDFG 2001, Talley et al., 2015). Additionally, the species has been introduced to Europe and the UK, where naturalized populations now thrive in various regions, including Italy, France, and Ireland (FAO 2024). However, no reports exist of the spread of this species into the Gulf.

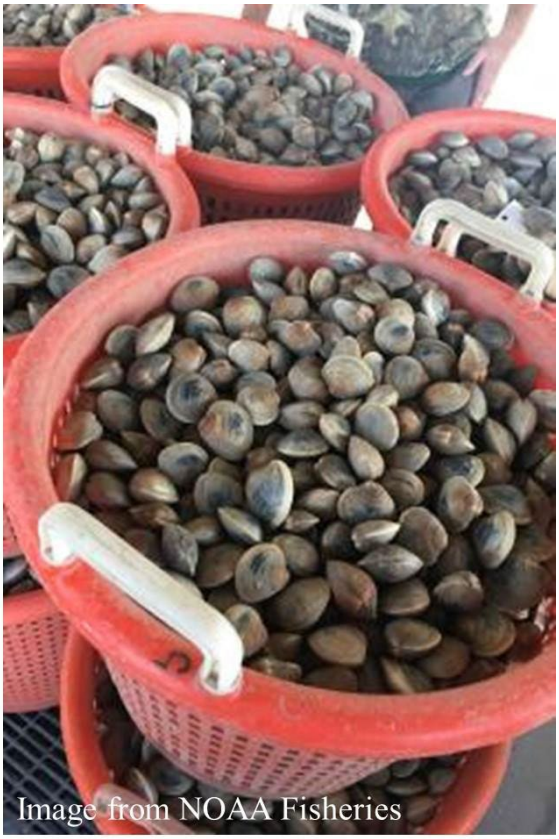
Image from NOAA Fisheries

The commercial value of Manila clams as an aquaculture species has significantly contributed to their spread. In 2020, Manila clams ranked second in global mollusc production, accounting for 24 percent, following cupped oysters (*Crassostrea* spp.; 30.7 percent) (FAO 2022). Their rapid growth rate, extended shelf life (7 to 10 days), and remarkable tolerance to eutrophication, salinity, and temperature fluctuations have bolstered their popularity in aquaculture (Toba 1992, Martini et al. 2023). Although no populations have been reported in the Gulf, this species' tolerance to these varied environmental parameters may enable them to be cultured in the Gulf, and potentially spread away from culture sites.

3.2.3.2 Biological Characteristics

Manila clams are separate-sex broadcast spawners, with instances of reported hermaphroditism being very rare (Ponurovsky and Yakolev 1992). They typically reach sexual maturity at sizes ranging from 15 to 20 mm, which may be achieved within their first year in warmer climates like southern Japan and Hawai`i. However, in colder regions such as the Puget Sound, the maturation process may extend to 2 to 3 years, with sizes ranging between 22-35mm (Yap 1977, Ponurovsky and Yakolev 1992). Spawning times and frequency exhibit considerable variation by location, occurring year-round in more tropical regions like Hawai`i, whereas in colder areas like northern Japan, spawning may occur only once a year (Gillespie et al. 2012). Fecundity is size-dependent, with larger females measuring approximately 40 mm long capable of producing between 1.5 to 2.4 million eggs, while newly matured females may only produce 200,000 to 400,000 eggs (Yap 1977, Ponurovsky and Yakolev 1992, Gillespie et al. 2012).

The period from fertilization to metamorphosis and settlement typically ranges from 2 to 4 weeks in Manila clams, contingent upon factors such as temperature and food supply. Upon settlement, which occurs when the larvae reach sizes between 165 and 235 µm, they attach themselves to hard surfaces or other bivalve shells using byssal threads (Toba 1992, Gillespie et al. 2012). Dispersal primarily occurs during the pelagic larval stages, with limited movement observed among adults once they are within their burrowing substrates (Gillespie et al. 2012). Growth rates vary by location, with the fastest growth typically observed in the first 4 to 5 years of life, and the maximum reported age recorded as 14 years in British Columbia (Gillespie et al. 2012).

3.2.3.3 Population Structure

Currently, there are no population genetics studies on Manila clams in the Gulf, as no populations have yet been reported.

3.2.3.4 Aquaculture

Like other shellfish species, hatcheries condition broodstock Manila clams, whether collected from the wild or cultivated, by manipulating water temperatures, providing excess feed, and occasionally subjecting the broodstock to air exposure or hormonal treatments to induce synchronous spawning year-round; strip spawning may also be employed as necessary (Toba 1992). Within 24 hours of fertilization, larvae hatch and become free-swimming until they are ready to settle, which typically occurs between 170 and 240 µm within approximately 2 weeks in culture (FAO 2024). The larvae can settle in tanks with or without substrate, although ground oyster shell is commonly utilized to increase surface area for the larvae; survival rates through metamorphosis in hatcheries range between 25 and 50 percent (Toba 1992). Nursery grow-out involves two stages: in the primary stage, newly settled clams are reared in land-based downwelling tanks until they reach approximately 1 mm in shell length; in the secondary stage, the clams are grown out to 6 to 8 mm shell length in upwelling systems (e.g., FLUPSYS, or intertidal trays/rafts) until they are ready for deployment in grow-out sites (Toba 1992, Dumbauld et al. 2009).

In the culture of this species, it is a common practice to transport either clam larvae (prior to setting) or clam seed (prior to grow-out) among aquaculture operations specializing in the culture of different life-cycle stages or focusing on commercial grow-out (Toba 1992, Wilson and Batanides 2016, FAO 2024). In particular, an approach known as remote settling has been developed and widely adopted on the Pacific U.S. coast, becoming a standard practice for many oyster and clam growers, and may be utilized for Manila clams in the Gulf. In this approach, pediveliger larvae are purchased from a hatchery at a considerably lower cost compared to larger spat. During the pediveliger stage, when shellfish are on the verge of settling and undergoing metamorphosis, they are processed and shipped to growers. This method shifts the settling and nursery responsibilities to the growers rather than hatchery operators (Jones et al. 1993).

The grow-out process to reach harvest size is primarily conducted through bottom culture in intertidal sites or oyster ponds. Where clams are implanted onto substrates such as gravel, sand, mud, or shell, and then shielded, if necessary, from predators, with plastic or nylon mesh netting to deter predation. Harvesting is typically carried out by manually or mechanized raking of the implanted area (Dumbauld et al. 2009, FAO 2024). Additionally, suspension-based culture methods are being explored for Manila clams, with indications suggesting that clams cultured in this manner may yield a higher-priced product (Sakurai et al. 2021). In suspension culture, Manila clams are placed in net cages containing suitable substrates and then suspended from floating rafts or longlines. Regardless of the approach chosen, the FAO (2024) notes that Manila clams generally reach market size at 30 mm or larger in China, with harvest occurring after 10 to 16 months. In North America, the desired harvest size is slightly larger, ranging between 30- and 40-mm shell length, with harvest typically taking place after 16 to 30 months.

No aquaculture activities for this species in the Gulf were identified in this review. It is anticipated that the warm temperatures may accelerate growth in this species, however, the region may also exceed the warmer thermal limits of this species.

3.2.3.5 Considerations on genetic risk to wild conspecifics

With the absence of information available on potential culturing activities in the Gulf, and without the presence of Manila clams in this region, it is challenging to evaluate genetic risk from the aquaculture of this species. As there are currently no native, or naturalized populations known at this time in the Gulf, the culture of this species would pose no risk to conspecific populations, as they do not exist. However, as with any introduced species, there is greater potential to impact indigenous species through various ecological interactions, and those interactions may result in genetic impacts on those native species. Evaluation of which species may be impacted should be evaluated; it is likely that potential risks to indigenous species changes depending on the location within the Gulf.

For Manila clams cultivated for commercial aquaculture harvest (typically at a minimum of 30 mm shell height), it is evident that these clams will likely reach reproductive maturity and spawn during the grow-out process, considering that sexual maturity can occur as early as 15 to 20 mm shell height. This may lead to the potential dispersal of millions of larvae from grow-out sites. In

such cases, oceanographic and water particle tracking models can help determine the prevailing direction of potential spread of Manila clams away from farm sites. Even if cultured offshore, the 2 to 4 weeks of larval duration is sufficient to transport larvae from offshore sites to coastal habitats, and as observed globally, this species has demonstrated the ability to establish new populations under suitable conditions.

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3.2.4 Variegated Sea Urchin (Lytechinus variegatus)

3.2.4.1 Range/Description

Variegated sea urchins (*Lytechinus variegatus*) are a temperate to tropical species native to the southeast and Gulf coasts of the United States. They can be found from North Carolina through Florida, into the Gulf, and as far south as the Caribbean and Brazil (Moore et al. 1963, Watts et al. 2007). Temperature is considered the primary factor influencing the latitudinal and regional distribution of this species (Watts et al. 2007). These urchins are commonly found in calm, clear waters such as seagrass beds, on rocks, or in sandy areas (Hill and Lawrence 2003), and are rarely found below depths of 7 to 10 meters (Moore et al. 1963). They have a low tolerance for turbid water with suspended sediment (Moore et al. 1963).

Sea urchins support a highly specialized fishery where their gonads are a valuable seafood product in Asian and European markets (Gibbs 2011). The popularity of sea urchin roe, which refers to both male and female gonads, has long been established in Japan and has recently spread to other countries (Sun and Chiang 2015). This has led to overfishing of sea urchins globally, with declines observed in Japan, the Pacific U.S., the Atlantic U.S., and more recently in Chile (Sun and Chiang 2015).


Image from NOAA Teacher at Sea Blog

To meet market demand and potentially reseed wild populations, sea urchin aquaculture is gaining more attention (Harris and Eddy, Sun and Chiang 2015). In certain markets, such as the live sea urchin market, cultured roe commands higher prices than wild roe due to improved consistency (Unuma et al. 2015). Despite its high value, developing high-density aquaculture for sea urchins has been challenging, primarily due to the reliance on fresh/live macroalgae for feed. Sea urchins raised on frozen macroalgae or formulated feeds often produce roe lacking the desirable color, consistency, or taste (Gibbs 2011, Sun and Chiang 2015, Unuma et al. 2015). This challenge has led to alternative aquaculture approaches, such as sea ranching (culturing and releasing sea urchins for later harvest) and gonad enhancement (capturing wild urchins and fattening them with seaweed to improve market value) being employed in various regions around the world (e.g., Eddy and Harris 2015, James et al. 2015, Sun and Chiang).

Within the Gulf, commercial harvest of sea urchins ranged from 10 to 16 metric tons between 2010 and 2022, according to NOAA Fisheries data (NOAA Fisheries 2023). Sea urchin management in the Gulf is handled at the state level. In Florida, for instance, the harvest is regulated by the Florida Fish and Wildlife Conservation Commission. Although *L. variegatus* is one of 17 commercially valuable species out of 850 identified sea urchin species (Harris and Eddy 2015), it has not yet been explored for the sushi industry (Gibbs 2011). However, *L. variegatus* is frequently captured and used as a model organism to support research in developmental, genetic, and ecotoxicological studies (Qiao et al. 2003, Gibbs 2011, Cunningham et al. 2023). Consequently, the market potential of *L. variegatus* as an aquaculture species remains unknown.

3.2.4.2 Biological Characteristics

L. variegatus are common throughout the Gulf and can be found in high densities of about 40 individuals per square meter (Moore et al. 1963). However, they may also aggregate at very high densities of 250 to 600 per square meter, forming what are called urchin fronts. These fronts move through seagrass beds, denuding large areas. While sea urchins primarily feed on seagrass, they are generally classified as omnivores and will ingest nearly anything they encounter, including phytoplankton, other animals, and even plastic and Styrofoam (Hill and Lawrence 2003, Watts et al. 2007, Hammer et al. 2013, Barnard 2016).

Compared to other sea urchin species, *L. variegatus* grows rapidly, reaches reproductive maturity early, and has a short lifespan (Watts et al. 2007). The maximum size of this species varies across its distribution. In the central portion of its range, the largest recorded size is 90 mm in test diameter, while in Saint Joseph Bay, Florida, the largest size is 60 mm in test diameter (Beddingfield and McClintock 2000). In this Florida location, most *L. variegatus* reach 35 mm within one year and generally 45 mm by two years of age (Beddingfield and McClintock 2000). Gonads in this species develop when the test diameter reaches approximately 40 mm, which could correspond to an age between one and two years (Moore et al. 1963, Beddingfield and McClintock 2000). *L. variegatus* is thought to have a maximal lifespan of four years (Beddingfield and McClintock 2000, Amir et al. 2020).

Sea urchins exhibit separate sexes and are broadcast spawners (Harris and Eddy 2015). For *L. variegatus*, spawning times and duration depend on location but may occur from spring to late summer or early fall (Beddingfield and McClintock 2000, McCarthy and Young 2002, Hill and Lawrence 2003, Cunningham et al. 2023). Spawning events have been reported to follow a lunar rhythm (Moore et al. 1963). Sea urchins are capable of reproducing throughout their lifetime after reaching sexual maturity (Tennent 1910, Moore et al. 1963, McCarthy and Young 2002).

Generally, larvae of *L. variegatus* develop rapidly following a spawning event, although temperature and food availability can influence their pelagic duration (McEdward and Herrera 1999). According to McEdward and Herrera (1999), swimming blastulae may form within 4 to 5 hours post-fertilization, and metamorphosis with settlement may be completed within 9 to 11 days under suitable conditions. However, another study with less favorable experimental

conditions reported metamorphosis occurring 33 to 37 days post-fertilization (McEdward and Herrera 1999, and references therein). The average pelagic duration under natural conditions remains unknown, but a broad range is likely.

3.2.4.3 Population Genetics

Sea urchins, particularly *L. variegatus*, are popular subjects for genomic studies aiming to examine the evolution and development of echinoderms (Davidson et al. 2020). However, little is known about the population structure of this species across its range, including in the Gulf. As described by Zigler and Lessios (2004), it has been suggested that *L. variegatus* comprises three subspecies: *L. variegatus atlanticus* in Bermuda, *L. variegatus carolinus* distributed from North Carolina around Florida and into the Gulf to the Yucatan Peninsula, and *L. variegatus variegatus* from southern Florida throughout the Caribbean and south to Brazil. However, patterns of distribution among these subspecies varied by genetic marker, and there was also evidence of introgression among the proposed subspecies (Zigler and Lessios 2004).

Wise (2011) conducted phylogenetic analyses on specimens collected from Beaufort, North Carolina, the northern Gulf, and the Florida Keys. Two distinct clades were identified, with strong genetic differentiation (F_{ST} = 0.89) separating Clade 1, consisting entirely of *L. variegatus* specimens from the Florida Keys, from Clade 2, which contained samples from all three regions. Interestingly, no significant differentiation was detected among samples within Clade 2, despite their wide geographic range. The author suggested that Clade 1 might represent the *L. v. variegatus* subspecies, while Clade 2 represented the *L. v. carolinus* subspecies. Additionally, it was proposed that these clades may actually represent cryptic species rather than subspecies (Wise 2011).

This species stands to benefit greatly from genomic approaches to investigate spatial structure at a finer scale, for example, within the Gulf, as well as more broadly throughout its range. Such approaches could provide a more definitive evaluation of subspecies and cryptic species. The recently developed draft genome for *L. variegatus* (Davidson et al. 2020) will be a valuable resource for further evaluation of population genetic structure and species identification/confirmation.

3.2.4.4 Aquaculture

Due to their rapid growth rate, high fecundity, and disease resistance, sea urchins are considered to have high potential for aquaculture (Hammer et al. 2013). Sea urchin enhancement culture has been practiced in Japan for several decades, but cultivation outside of Japan has only begun fairly recently (Hammer et al. 2013). An example of these recent efforts is the closed cycle culture of *L. variegatus* which has been successfully conducted on a small scale at the University of Alabama at Birmingham (Alabama Gulf Seafood 2016). More recently, there has been interest on the U.S. east coast, and in the Gulf, on exploring the polyculture of Eastern oysters (*C. virginica*) and the Atlantic purple sea urchin (*Arbacia punctulata*) (east coast; Mizuta et al. 2023) and the green sea urchin (*L. variegatus*) (Gulf) (https://shellfish.ifas.ufl.edu/wp-

content/uploads/Sturmer-Urchins-May-Workshops-Final.pdf). Initial results in the Gulf, indicate some benefit to the Eastern oysters by culturing them with green urchins, but additional studies are planned to further evaluate this benefit and to explore the growth and gonad indices in the sea urchins.

Although specific culturing methods for *L. variegatus* have not been identified, general approaches to sea urchin culture, which are likely similar, were described by Unuma et al. (2015) for species cultured in Japan. These methods are summarized here. Broodstock conditioning involves manipulating water temperature and feeding the broodstock liberally. Spawning is induced by potassium chloride (KCl) injections (or acetylcholine for *L. variegatus*; Hammer et al. 2013) or through partial dissection of the animal. Induced *L. variegatus* females may produce over 6 million eggs (Hammer et al. 2013). Eggs and sperm are collected separately and combined in specific ratios for fertilization, followed by multiple washes of the eggs to reduce the likelihood of polyspermy.

Larvae are reared in tanks with gentle aeration as they pass through multiple larval stages. They become competent to settle once the rudiment extends past the stomach length. At this stage, larvae are placed in settlement tanks with vertical plates used for settlement and postlarval rearing. These plates are coated with diatoms or algae (e.g., *Ulvella lens*) as a food source. When juvenile sea urchins reach 5 to 10 mm in test diameter, they are detached from the plates using a mild KCl solution and moved into intermediate cages in the sea, where they are fed approximately weekly with macroalgae, preferably brown macroalgae. They may be released at this stage or at 30 mm in size if being used for reseeding.

The sea urchins may be grown out to market size in cages or crate structures suspended from longlines or placed benthically. One or both of these approaches are used in Japan, China, and Norway (Liu and Chang 2015, James et al. 2015, Unuma et al. 2015). In Japan, the duration from fertilized egg to the 5 to 10 mm size is 7 months, and it takes 10 months to reach the 30 mm size. Grow-out to market harvest typically takes 2 to 3 years in Japan, though this varies by location (Unuma et al. 2015). However, for the fast-growing *L. variegatus*, market size is reached within a year (Hammer et al. 2013).

To produce commercially desirable gonads, culture conditions such as temperature, salinity, oxygen levels, lighting, and diet formulations must be carefully controlled (Hammer et al. 2013). Feed during the culturing stage significantly impacts the marketability of the roe, and due to the difficulty in obtaining live/fresh macroalgae, extensive research has been conducted to develop formulated feeds (Unuma et al. 2015). One approach to address this issue is to switch from formulated feeds to a finishing diet of macroalgae for 2 months to enhance roe quality (Unuma et al. 2015).

While there are currently no commercially developed feeds for tropical sea urchins like *L. variegatus*, preliminary work by the University of Alabama and Texas A&M University has shown promising results with both good growth and roe development (Hammer et al. 2013). Based on the experimental culturing approaches and successful feed development described for

L. variegatus, this species appears to have great potential to become a robust aquaculture species throughout its range in the U.S.

3.2.4.5 Considerations on genetic risk to wild conspecifics

An aspect of sea urchin culture that sets it apart from other shellfish species assessed in this report is the focus on the sexually mature gonad as the targeted product. This increases the likelihood of gametes and/or fertilized eggs being dispersed from a grow-out site before harvest. While the pelagic larval duration remains unknown in natural settings for this species, experimental culture has shown it ranging from 1.5 to 5 weeks. This suggests that even at the lower end of this duration, dispersed larvae from offshore sites could reach coastal habitats and wild *L. variegatus* populations. Water current and particle modeling may help assess which wild populations are more likely to receive dispersed cultured recruits from a grow-out site.

Currently, there is limited information available on the genetic population structure of this species. While no differentiation was observed among the proposed *L. v. carolinus* samples from North Carolina, the Florida Keys, and the northern Gulf, the genetic approaches utilized were suitable for phylogenetic analyses but may have lacked the resolution to detect subtle levels of differentiation. This information is crucial for predicting genetic impacts from offshore aquaculture of this species on natural populations. Additionally, with potential subspecies in shared portions of the range, which have demonstrated at least some ability to cross-breed experimentally (Wise 2011), it will be important to genetically identify the broodstock and determine which subspecies/species exists in a given location.

Given the current available information and the high level of uncertainty resulting from the lack of additional data, there appears to be at least a moderate genetic risk to wild populations from the aquaculture of *L. variegatus*. However, this risk may be mitigated as more information becomes available for the species.

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3.2.5 *Quahog (Mercenaria mercenaria)*

3.2.5.1 Range/Description

The northern quahog, *Mercenaria mercenaria*, inhabits the western Atlantic coast from the Gulf of St. Lawrence, Canada, to the Florida Keys and is not the indigenous quahog species in the Gulf (Abbott 1974, Arnold et al. 2009). Conversely, the southern quahog, *M. campechiensis*, is native to the Gulf and ranges from the mid-Atlantic in Chesapeake Bay to Florida, the Gulf, the Yucatán Peninsula, and Cuba (Abbott 1974). In the Gulf, it is present in bays and sounds across all Gulf states, including Florida, Alabama, Mississippi, Louisiana, and Texas (MacKenzie et al. 2002b). *M. mercenaria* predominantly inhabits inshore areas and shallower, muddier regions of the intertidal and subtidal coastal waters. In contrast, *M. campechiensis* is found further offshore (in parts of its range), dwelling in sand, silt-sand bottoms, and along the edges of seagrass meadows in deeper and more saline waters than *M. mercenaria* (Eversole 1987, Foighil et al. 1996, MacKenzie et al. 2002a). *M. campechiensis* attains a slightly larger maximum size (150 mm) than *M. mercenaria* (120 mm) (Roegner and Mann 1990, MacKenzie et al. 2002a).

Image from NOAA Fisheries

The northern quahog has significant economic importance, supporting a thriving commercial industry that initially relied on harvesting from wild populations but has gradually shifted towards aquaculture as the primary source for this market following a decline in commercial harvest (Jackson 2008, Song et al. 2022). The aquaculture of this species experienced a remarkable 14-fold growth between 1991 and 1999, evolving into a $56 million USD industry in the United States, with Florida emerging as one of the two leading states in production (Jackson 2008, Arnold et al. 2009, Sturmer et al. 2009, Song et al. 2022).

To bolster the growth of the aquaculture industry, experimental outplanting of *M. mercenaria* and hybrid *M. mercenaria* x *M. campechiensis* has been conducted along the Gulf Florida coastline since the late 1960s (Arnold et al. 2009). Since 1993, quahog aquaculture efforts off the western Florida coast have consistently favored *M. mercenaria* due to its more desirable aquaculture traits compared to *M. campechiensis*. The primary market for these clams is fresh consumption on the half-shell, requiring the clams to be alive and healthy when prepared at restaurants. Unfortunately, *M. campechiensis* can only survive post-harvest for several days, whereas *M. mercenaria* and hybrids between these two species can endure for up to two weeks (Arnold et al. 2000). Consequently, numerous locations along the western Florida coast exhibit established populations of both species and hybrids (Foighil et al. 1996, Arnold et al. 2009).

The aquaculture industry has actively pursued artificial hybridization, focusing on F1 hybrids of *M. mercenaria* and *M. campechiensis*, as well as the offspring of backcrosses with *M. campechiensis*, which have demonstrated a significantly faster growth rate, leading to up to 40% less time required to reach market size (Menzel 1977). Given the challenges posed by elevated water temperatures in *M. mercenaria* aquaculture (Song et al. 2022), hybridization has been investigated as a strategy to enhance resilience to environmental stressors, with some reported success in specific crosses, such as using female *M. mercenaria* and male *M. campechiensis* (Song et al. 2022).

3.2.5.2 Biological Characteristics

Quahogs are highly fecund broadcast spawning shellfish, that are also protandrous sequential hermaphrodites with distinct sexes, meaning they transition from males to females as they grow (Eversole 1987, Roegner and Mann 1990). The spawning activity of these clams spans from spring through fall, occurring in water temperatures above 20°C, although the specific timing varies by location (Eversole 1987, Roegner and Mann 1990). It is worth noting that excessively warm water temperatures can result in mortality during egg development (MacKenzie et al. 2002a). In optimal conditions, males initiate spawning, subsequently prompting nearby females to release their eggs for fertilization in the water column (Eversole 1987). Smaller females, falling below legal collection size, may spawn around 2.4 million eggs, while larger females have the capacity to release up to 16.8 million eggs (Mackenzie et al. 2002a, Bricelj and Malouf 1980).

As discussed in MacKenzie et al. (2002a), the eggs of quahogs undergo direct development into pelagic larvae, progressing through the straight hinge stage, followed by the veliger stage. The final planktonic stage is the pediveliger, characterized by the presence of a foot, enabling both crawling and swimming at this stage (MacKenzie et al. 2002a). Once the individuals shed their velum (small hairs aiding in motility), they settle on the seafloor and eventually burrow into the sediment using their feet. The pelagic larval duration varies, with faster settlement observed in warmer water, and ranges from 18 to 24 days at 18°C to 7 to 14 days at 30°C (MacKenzie et al. 2002a). This pelagic period prior to metamorphosis plays a crucial role in determining the distance over which individuals are dispersed (Cowen and Sponaugle 2009). Following settlement, juveniles and adults exhibit limited dispersal ability, classifying them as benthic sedentary species (Ropp et al. 2023).


Image from NOAA Fisheries

In the Gulf, wild quahogs take approximately 2 years from the settlement stage to reach market size, but this varies considerably by location with both shorter and longer periods observed

(MacKenzie et al. 2002a). Growth is most rapid in smaller stages and gradually slows as the animals increase in size. In the southeastern U.S., *M. mercenaria* exhibits the fastest growth from December through March, with a slowdown in growth observed from June to November. These quahogs typically attain sexual maturity at a length ranging between 22 to 33 mm, which corresponds to around 2 years of age (Jackson 2008). In their natural habitats, these clams can have a lifespan of up to 46 years (MacKenzie et al. 2002a).

3.2.5.3 Population Structure

There has been ongoing debate regarding whether the native distribution of *M. mercenaria* includes any locations in the Gulf. However, genetic studies have provided support for the theory that *M. campechiensis* is the only indigenous species of hard clam on the west coast of Florida, and *M. mercenaria* did not naturally occur in the Gulf until introduced by human activities (Foighil et al. 1996, Arnold et al. 2004, Baker et al. 2008). Baker et al. (2008) proposed that the southern tip of the Florida peninsula likely served as a natural barrier to the dispersal of *M. mercenaria* into the Gulf, citing warm water temperatures as a physiological limitation on its distribution. There were also questions about whether *Mercenaria* sampled from Texas represented a subspecies of *M. mercenaria* (*M. mercenaria texana*). However, Dillon and Manzi (1989) found that these samples were instead a subspecies of *M. campechiensis* (*M. campechiensis texana*).

No population genetic studies have specifically investigated the higher resolution genetic structure of either *M. mercenaria* or *M. campechensis* within the Gulf. A recent population genomic study utilized a DArTseq™ genotyping by sequencing approach to characterize 15 populations of *M. mercenaria* along the east coast of North America, spanning from Prince Edward Island, Canada, to South Carolina (Ropp et al. 2023). The study identified six genetically distinct populations, generally reflecting an isolation-by-distance pattern. The results, as reviewed by the authors, confirm previously identified patterns of low but significant structure and reveal additional structure not detected in previous studies (Ropp et al. 2023). According to Ropp et al. (2023), despite the species' long dispersal duration, particularly at those latitudes, the observed patterns suggest that realized dispersal likely occurs over a shorter distance than expected. This maintenance of recruitment appears to be influenced by coastal currents, indicating a more regional geographic range for dispersal within the Gulf (Ropp et al. 2023).

Genetic studies have been instrumental in assessing the impact of introductions of *M. mercenaria* on the native *M. campechiensis*. Introductions of *M. mercenaria* into the Gulf have been documented since the late 1950s, persisting with the ongoing large-scale aquaculture of hard clams in Florida (Arnold et al. 2009). The study by Arnold et al. (2009) revealed genomic changes in all wild Florida populations of *M. campechiensis* where documented introductions of *M. mercenaria* took place. Notably, regardless of the magnitude of the introduction, wild specimens expressed *M. mercenaria* or hybrid genotypes (Arnold et al. 2009), even in habitats where *M. campechiensis* had a selective advantage. The authors of the study predict that if the few species-specific refuges in the eastern Gulf break down, all hard clams in the eastern Gulf are likely to become hybrids eventually. This transformation is expected to decrease fitness in

these species due to increased susceptibility to gonadal neoplasia in *M. mercenaria*, coupled with reduced fecundity in hybrid individuals (Arnold et al. 2009).

In a study conducted by Hargrove et al. (2015), the genetic characterization of wild and cultured populations of *M. mercenaria* along the eastern and western coasts of Florida was the primary focus. The findings revealed slightly higher levels of allelic richness and observed heterozygosity in wild stocks compared to cultured populations, although these differences did not reach statistical significance. Genetic differentiation was observed among hatchery stocks, with less differentiation between hatchery and wild stocks. However, no differentiation was detected among wild stocks sampled from five sites on the Atlantic and Gulf coasts of Florida. The results suggest the presence of some genetic drift in the hatchery stocks, potentially attributable to selection or culturing practices. The authors recommend the consideration of long-term genetic goals, including measures to avoid inbreeding, in hatchery practices (Hargrove et al. 2015).

3.2.5.4 Aquaculture

In commercial hatcheries, the spawning of broodstock clams is induced through temperature cycling (Sturmer et al. 2003). Typically, sexually matured individuals from the survivors of 1- to 2-year-old cohorts are selected to become broodstock (Song et al. 2022). The free-swimming larval stages undergo growth and metamorphosis over a period of 8 to 14 days, settling at a size of 200 to 300 microns. These settled larvae are then cultured in the nursery within raceways until they reach a size of 1 to 5 mm (Arnold et al. 2000, Sturmer et al. 2003).

Establishing and maintaining hatcheries demand substantial investments, leading to a scenario where most growers opt not to operate their own hatcheries but instead purchase seed from commercial hatcheries, although some larger growers may develop their hatcheries, occasionally selling surplus seed to other nurseries and growers (Sturmer et al. 2003). Seed is available for purchase at various stages, including hatchery size (1 mm seed), field nursery size (5 mm), or larger seed (12 to 15 mm shell length), with prices increasing significantly across these size categories (Sturmer et al. 2003).

An alternative method known as remote settling has been developed and widely adopted on the Pacific U.S. coast, becoming a standard practice for many oyster and clam growers. In this approach, pediveliger larvae are purchased at a considerably lower cost compared to 1-5 mm spat. During the pediveliger stage, when shellfish are on the verge of settling and undergoing metamorphosis, they are processed and shipped to growers. This method shifts the settling and nursery responsibilities to the growers rather than hatchery operators (Sturmer et al. 2003). Using the remote settling approach, production to a 1-mm seed size typically takes between 5 to 8 weeks (Sturmer et al. 2003).

The most straightforward form of clam culture involves stocking the natural bottom with seed clams and then covering the area with mesh to shield the seed from predation. Other methods include trays filled with sediment and covered with protective mesh, as well as large cages that

are partially buried in the sediment (Jackson 2008). The belt-bag system utilizes a series of mesh bags connected to a bridle of heavy rope anchored to the bottom in intertidal and shallow subtidal habitats (Arnold et al. 2000, Jackson 2008). This approach, or one involving an enclosed cage attached to a "belt" line, is likely to be employed in offshore culture.

Clams are harvested at various sizes, with the smallest, known as "littlenecks," commanding the highest prices. The targeted size for quahogs is 25 mm in shell thickness (Jackson 2008). The clams are typically allowed to grow to approximately 50 mm in shell length, a process that takes on average between 1 to 1.5 years (Arnold et al. 2000). In Cedar Key, Florida, quahogs are usually harvested after a 10 to 14-month grow-out period, starting with 4 to 6 mm seed (Jackson 2008). Grow-out periods in Alabama and Mississippi are estimated to take 18 months to reach the same size due to the more northern latitude (Jackson 2008). Some domestication practices, such as genetically marking individuals for traceability back to the hatchery, are employed in hatcheries (Song et al. 2022).

3.2.5.5 Considerations on genetic risk to wild conspecifics

The introduction of *M. mercenaria* into the Gulf has had detrimental effects on the native species, *M. campechiensis*. Natural populations in areas where aquaculture has been conducted now comprise both species and hybrids. Pure *M. campechiensis* genotypes have become scarce along the Florida coastline, and the genomic introgression of *M. mercenaria* into *M. campechiensis* populations may pose a threat to the fitness of the native species, leading to increased susceptibility to gonadal neoplasia and reduced fertility (Arnold et al. 2009). However, in other parts of the Gulf, *M. campechiensis* populations still exist without hybridization. According to a study by Foighil et al. (1996), the western Gulf may harbor a distinct population or subspecies of the indigenous *M. campechiensis*. Consideration of aquaculture development in areas where pure *M. campechiensis* still occurs, and where aquaculture operations have not previously existed, should be weighed with the likely consequences on the native species. As demonstrated, the potential genetic risk to natural populations of the native species (*M. campechiensis*) from culturing *M. mercenaria* is high. However, based on current information, continued aquaculture in established aquaculture areas would not likely represent a significant additional genetic risk to introduced populations of *M. mercenaria* or the native *M. campechiensis.*

In this situation, the genetic consequences of propagation approaches for *M. mercenaria* can impact both this species and *M. campechiensis* in the wild. Hargrove et al. (2015) observed that current propagation techniques for *Mercenaria mercenaria* effectively capture levels of genetic diversity similar to those observed in wild stocks, with some indication of genetic drift associated with broodstock selection and breeding practices. Although the authors emphasized the importance of considering the long-term genetic health of populations, current practices seem to involve genetically varied broodstock periodically supplemented with new individuals.

Dispersal away from culture sites is a critical consideration regarding the spread of *M. mercenaria* genotypes into wild *M. campechiensis* populations. While it may take up to 2 years

for these species to reach sexual maturity in the wild, which is largely based on size, some individuals may reach maturity more quickly, and thus spawning is possible from cultured quahogs during grow-out. Species with extended planktonic stages, (e.g., 7-24 days in *Mercenaria*) are expected to have long-distance dispersal, however, environmental dynamics and biological mechanisms may limit this potential (MacKenzie et al. 2002a, Baker et al. 2008). Movements by even minimally motile larvae may result in greater retention in a given area (Cowen and Sponaugle 2009). High-resolution genomic studies of *M. mercenaria* along the Atlantic coast suggest that effective dispersal may be shorter than expected (Ropp et al. 2023), and with faster-developing larvae in warmer waters, dispersal in the Gulf may be further limited. This limitation could help restrict the spread of *M. mercenaria* away from regions where aquaculture is conducted. Water current modeling in the regions of grow-out sites can help to determine patterns of likely dispersal away from grow-out sites and identify populations of wild quahogs likely to receive the cultured recruits.

High priorities for research related to the growth of *M. mercenaria* aquaculture in the Gulf should include extensive sampling along the Gulf States using higher resolution genomic/genetic approaches. This would help identify patterns of population connectivity among *M. campechiensis* populations, determine locations of potential biogeographic breaks, and detect the spread of *M. mercenaria* genotypes. Such research is crucial for identifying populations of pure *M. campechiensis* to focus conservation efforts on, guarding against the spread of cultured genotypes. Additionally, it can pinpoint potential populations where approaches such as cryopreservation should be considered.

This research may also guide decisions on how and if to grow the industry with introduced *M. mercenaria*, and the best approaches to mitigate genetic impacts on and protect the remaining unimpacted populations of *M. campechiensis*. Understanding population dynamics and genetic connectivity is essential for sustainable aquaculture practices and the conservation of native clam species in the Gulf.

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4.0 Genetic Risk Factors and Management Measures

Shellfish culture candidate species for Southern California and Gulf discussed in Chapters 2 and 3 are summarized in the below tables, with an emphasis on risk factors that could potentially contribute to genetic effects to wild populations. Risk factors are specifically related to reproduction and the potential for cultured-wild interactions, and subsequent reduced population fitness and decline in genetic diversity.

The assessment of genetic risk levels considers specific species and population dynamics that may influence genetic impacts on wild populations due to aquaculture activities. These risk levels are determined by evaluating key factors related to species and population characteristics that could affect genetic interactions with wild counterparts. The risk factors are: potential for maturity in culture (e.g. harvest after maturity would present greater genetic risk), dispersal duration and settlement requirements (longer lengths of time larvae may disperse presents a greater risk; wide range of suitable settlement environments and/or high fouling abilities presents a greater risk), current thinking on wild population abundance (low/patchy/declining abundance of the local population would mean greater demographic contribution from cultured gametes, with potential for greater genetic risk), biological characteristics in cultured strains that may differ from wild populations (e.g. triploidy), and knowledge of genetic population structure species on a regional level.

The evaluation of uncertainty in the risk level is based on available data to support findings on wild population status and genetic diversity. The Low/Moderate/High assessment for the genetic risk level and uncertainty presented in the tables is based on a broad review of the available research and scientific literature regarding wild population dynamics and characteristics for each species. The risk levels do not account for culture production levels, escape rates or other operational factors. As such the genetic risk levels in the table can be considered for factors that influence risk but should not be construed as a full assessment of genetic risk from aquaculture.

4.1 Southern California Aquaculture Candidate Species – Summary of Genetic Risk Factors

Table 4.1. Shellfish Genetic Risk Factors – Southern California

Part A: Population Dynamics and Reproduction

Species Name	Common Name	Native to Region	Population health	Spawning Type	Pelagic Larval Phase Duration	Spawning Season
Ostrea lurida	Olympia oyster	Yes.	Poor.	Hermaphrodite, viviparous and larviparous.	Up to 8 weeks; Average of 11 to 16 days.	Spring and Fall, highly temperature dependent.
Magallana gigas	Pacific oyster	No.	Healthy.	Synchronistic, broadcast, oviparous hermaphrodites.	2 to 3 weeks.	Summer, highly temperature dependent.
Crassadoma gigantea	Purple-hinged rock scallop	Yes.	Low abundance; vulnerable to overharvesting.	Synchronistic, broadcast, protandrous hermaphrodites.	4 weeks.	October to January.
Venerupis philippinarum	Manila clam	No.	Healthy.	Separate-sex, broadcast.	2 to 4 weeks.	Late spring to early fall.
Tivela stultorum	Pismo clam	Yes.	Vulnerable, recovering.	Synchronistic, broadcast, occasional hermaphroditism.	3 weeks.	July to November, peaking in late summer.
Mytilus californianus	California mussel	Yes.	Healthy.	Separate-sex, broadcast.	2 to 4 weeks.	Year-round.
Mytilus galloprovincialis	Mediterranean mussel	No.	Unknown.	Separate-sex, broadcast.	2 to 4 weeks.	Autumn to early spring, peaking in early winter.
Haliotis spp.	Abalone	Yes (red, pink, and green abalone considered).	Vulnerable; closed fisheries.	Separate-sex, broadcast.	1 to 3 weeks.	Spring and summer.

Part B: Culture Information

Species Name	Common Name	Maturity Size	Maturity Age	Market Size	Age at Attainment of Market Size	Current Aquaculture Status
Ostrea lurida	Olympia oyster	Unknown.	1 year after settlement.	3.5 to 4.0 cm.	3 to 4 years.	Commercial domesticated and Supplementation in the U.S.
Magallana gigas	Pacific oyster	< 2 cm.	Within 1 year.	70 to 100 grams (about 4 cm).	18 to 30 months.	Commercial on the U.S. Pacific Coast.
Crassadoma gigantea	Purple-hinged rock scallop	5.5 cm.	20 to 26 months.	10 to 11 cm.	3 to 4 years.	No commercial or supplementation programs.
Venerupis philippinarum	Manila clam	1.5 to 2.0 cm.	Within 1 year.	3 to 4 cm.	16 to 30 months.	Commercial on the U.S. Pacific Coast.
Tivela stultorum	Pismo clam	< 2 cm.	Within 1 year	Unknown—legal size limit for wild collection of 4.5 inches in California (11.5 cm).	Variable by region, possibly 9 to 12 years.	No commercial or supplementation programs.
Mytilus californianus	California mussel	2.5 to 7.0 cm.	Within 1 year.	No information available, but likely about 7 cm compared to other cultured species of mussel.	Likely 12 months.	No commercial or supplementation programs.
Mytilus galloprovincialis	Mediterranean mussel	2 cm.	Within 1 year.	6 to 7 cm.	Variable by region—about 7 to 8 months from start of grow-out in Baja California culture.	Commercial on the U.S. Pacific Coast.
Haliotis spp.	Abalone	Red Abalone: 10.5 cm to 13.0 cm; Pink Abalone: 5.9 to 11.9 cm; Green Abalone: 10.0 cm.	3 to 4 years.	7 to 9 cm.	3 to 4 years.	Commercial on U.S. Pacific Coast.

Part C: Assessment of Risk and Uncertainty

Species Name	Common Name	Potential for Gamete Release in Culture	Priorities for Research	Probable Genetic Risk Level	Uncertainty in Risk Level	Management Priorities to Minimize Genetic Effects
Ostrea lurida	Olympia oyster	Very High: reaches maturity two years before harvest size.	Genetic diversity monitoring, natural reproduction in culture; sterilization techniques.	High: reaches sexual maturity prior to harvest, wild populations display local adaptation at small scales and show extensive genetic diversity.	High: little known about dispersal and survival.	Broodstock genetic management plan focused on locally adapted populations; genetic diversity monitoring.
Magallana gigas	Pacific oyster	High: reaches maturity before harvest size.	Genetic diversity monitoring; population genetics; sterilization techniques.	Low: non-native species, sterilization is relatively effective, if diploid then reaches sexual maturity prior to harvest, but one metapopulation along the U.S. Coast.	Low.	Broodstock genetic management plan; genetic diversity monitoring.
Crassadoma gigantea	Purple-hinged rock scallop	High: reaches maturity before harvest size.	Estimates of wild abundance; genetic diversity monitoring; sterilization techniques.	Moderate: reaches sexual maturity prior to harvest, though population structure suggests one population in Southern California.	High: genetic structure is likely among regions due to biology of species and patchy distribution.	Broodstock management; genetic diversity monitoring.
Venerupis philippinarum	Manila clam	Very High: reaches maturity two years before harvest size.	Genetic diversity monitoring; population genetics; monitoring of containment/ escape from upwelling/FLU PSY systems.	Moderate: naturalized species, reaches sexual maturity prior to harvest – for 2+ years; unknown genetic structure, but there is a high potential for genetic bottlenecking of naturalized populations due to aquaculture origins.	High: no information about population or genetic structure of this species in Southern California.	Broodstock genetic management plan; genetic diversity monitoring.

Species Name	Common Name	Potential for Gamete Release in Culture	Priorities for Research	Probable Genetic Risk Level	Uncertainty in Risk Level	Management Priorities to Minimize Genetic Effects
Tivela stultorum	Pismo clam	Very High: reaches maturity within first year.	Genetic diversity monitoring; stock assessment; population genetics; information on wild fishery.	High: reaches sexual maturity prior to harvest, information is lacking on the fishery.	High: limited information about the wild population in Southern California.	Broodstock genetic management plan; genetic diversity monitoring.
Mytilus californianus	California mussel	Moderate: harvest size coincides with age of maturity, but may occur earlier.	Estimates of wild abundance; maturity timing; genetic diversity monitoring.	Low to Moderate: abundant wild population, potential high survival of cultured larvae.	Low: stable population along the California coast.	Broodstock genetic management plan; genetic diversity monitoring.
Mytilus galloprovincialis	Mediterranean mussel	Moderate to high: maturity occurs before reaching harvest size, but harvest can be done within first year.	Genetic diversity monitoring; population genetics; estimates of wild abundance; sterilization techniques.	Low: naturalized species, lower probability of maturation before harvest, sterilization potential. Ecological effects of invasion may contribute to loss of genetic diversity.	Low.	Genetic diversity monitoring; harvest before maturity.
Haliotis spp.	Abalone	High: reaches maturity before harvest.	Sterilization techniques; genetic diversity monitoring.	Low to High: If genetic diversity is sufficient in commercial operations, escaped larvae may effectively supplement populations; where genetic diversity is low or lines are highly domesticated, larval escape will likely harm natural populations.	Low: extensive data on population structure in Southern California.	Maintain supplementation level diversity in commercial hatcheries.

4.2 Gulf of America Aquaculture Candidate Species – Summary of Genetic Risk Factors

Table 4.2. Shellfish Genetic Risk Factors – Gulf of America

Part A: Population Dynamics and Reproduction

Species Name	Common Name	Native?	Population health	Spawning Type	Pelagic Larval Phase Duration	Spawning Season
Argopecten irradians	Bay scallop	Yes	Variable across the Gulf region.	Synchronistic, broadcast, hermaphrodite.	5 to 14 days.	Year-round, primarily September to January.
Crassostrea virginica	Eastern oyster	Yes	Significantly declined from historic levels.	Hermaphrodite.	2 to 3 weeks.	Year round except winter months.
Venerupis philippinarum	Manila clam	No	Unknown.	Separate-sex, broadcast.	2 to 4 weeks.	Summer time/ when water is warm.
Lytechinus variegatus	Variegated sea urchin	Yes.	Healthy.	Separate-sex, broadcast.	1.5 to 5.0 weeks.	May to late summer.
Mercenaria mercenaria	Quahog	No.	Introduced *M. mercenaria* is unknown; native *M. campechiensis*shows indications of introgression from *M. mercenaria* in near aquaculture operations with spread of hybrids away from those areas.	Separate-sex, broadcast.	7 to 24 days.	Spring to fall.

Part B: Culture Information

Species Name	Common Name	Maturity Size	Maturity Age	Market Size (Shell Length)	Age at attainment of Market Size	Current Aquaculture Status
Argopecten irradians	Bay scallop	4 to 5 cm.	12 months.	4 to 5 cm.	5 to 8 months from start of grow-out.	Commercial in China, Supplementation in the U.S.
Crassostrea virginica	Eastern oyster	Unknown.	3 months after attachment.	7.5 to 9.0 cm.	12 to 24 months.	Commercially domesticated and Supplementation in the U.S.
Venerupis philippinarum	Manila clam	1.5 to 2.0 cm.	Within 1 year.	3 to 4 cm.	16 to 30 months.	Commercial on the U.S. Pacific Coast; Not cultured in the Gulf currently.
Lytechinus variegatus	Variegated sea urchin	4 cm.	1 to 2 years.	3 to 10 cm.	1 to 2 years.	Experimental in the U.S.
Mercenaria mercenaria	Quahog	2.2 to 3.3 cm.	2 years.	5 cm.	1 to 1.5 years.	Commercial on U.S. east and Gulf coasts.

Part C: Assessment of Risk and Uncertainty

Species Name	Common Name	Potential for Gamete Release in Culture	Priorities for Research	Probable Genetic Risk Level	Uncertainty in Risk Level	Management Priorities to Minimize Genetic Effects
Argopecten irradians	Bay scallop	Moderate: reaches harvest size around the age of maturity.	Estimates of wild abundance; population genetics; reduced fertility through triploid use.	Moderate to high: potential of harvest before maturity, existence of supplementation programs and effectiveness of sterilization techniques.	Moderate: limited information about the wild population.	Genetic diversity; seeding time; siting; harvest before maturity; sterilization.
Crassostrea virginica	Eastern oyster	High for diploids as they reach maturity before harvest size; low for triploids.	Genetic diversity monitoring; investigating frequency of introgression and impacts from introgression.	Moderate to high for culture of diploid oysters: reaches sexual maturity prior to harvest and potential for introgression; low for culture of triploid oysters.	Low: state-managed fisheries; extensive data on population structure.	Genetic diversity monitoring.
Venerupis philippinarum	Manila clam	High: reaches maturity before harvest size.	Genetic diversity monitoring.	Low to none: non-native species, population status unknown but assumed to be nonexistent in the Gulf; potential for ecological effects of species introduction should be evaluated.	Low.	Broodstock management; genetic diversity monitoring.
Lytechinus variegatus	Variegated sea urchin	Moderate: reaches harvest size around the age of maturity.	Genetic diversity monitoring.	Moderate: high wild abundance and potential of harvest before maturity is unknown.	High: limited information about the wild population.	Genetic diversity, siting; harvest before maturity.
Mercenaria mercenaria	Quahog	Moderate: reaches harvest size around the age of maturity.	Fine-scale population genetics.	High: ease of growth in wild populations, reaches sexual maturity prior to harvest, ability to hybridize and displace native species.	Low: known ability to introgress into native species and hybridize.	Harvest before maturity; carefully consider native species prior to development in new areas.

4.3 Escape Prevention Measures and Best Management Practices

Operational procedures to minimize escape risk and action measures are procedures taken to minimize or avoid escapes leading to potential cultured-wild genetic interactions from program gene flow into wild populations. While the implementation of one or a combination of these measures would not provide an absolute guarantee against unintended gene flow from an aquaculture program, these measures are designed to effectively minimize the risk of this kind of escape.

The following operational procedures, and action-level measures are listed for situations where a reactive response to a medium-level or large-scale escape event is required.

4.3.1 Operational Procedures to Minimize Escape Risk

Operational procedures to minimize escape risk are available to improve program containment and reduce the risk of culture/wild genetic interactions from culture program escapes. Implementation of these procedures is primarily the aquaculture operator's responsibility.

These measures may be implemented when feasible and reasonable, and not all measures may be practical in every situation. The feasibility and appropriateness of implementation for each of these measures would be determined in coordination with the Regional Aquaculture Coordinators.

Measure Shellfish-1 Onshore Procedures

Locate the aquaculture operation to minimize loading from wave action, wind and marine currents.

Broodstock used for reproduction in the hatchery should be harvested from the local population, which can be defined as the region surrounding the site that contains locally-adapted wild stock. If the shellfish breeding program (hereafter referred to as the program) were to employ domestication or strain selection, additional steps would be needed to understand the risk that implementation of intentional selection would have on natural populations, and further steps may be needed to minimize the risk of maladapted traits passing from cultured lines to wild shellfish populations. However, mitigation steps may include developing selected strains with reduced or delayed reproductive maturity, and/or developing sterile lines.

Sterilization (if applicable)

Sterilization techniques such as triploid induction are used for several species of shellfish, and this has been shown to produce favorable results for commercial aquaculture, in that cultured stock are typically reproductively sterile, but also exhibit desirable qualities for culture such as higher growth rates. Theoretically, if sterilization can be successfully implemented this could potentially eliminate risks associated with culture-wild interbreeding. However, it should be noted that approaches such as triploidy are not 100% effective in inducing sterility. Other approaches may be explored, such as gene editing broodstock lines to create sterile offspring

with a higher success rate, if sterility is the primary goal. On a species basis, the tradeoffs for sterilization and optimization of sterilization techniques should be tested and evaluated.

Measure Shellfish-2 Program siting

Locate the grow-out system to minimize loading from wave action, wind and marine currents.

Shellfish culture programs should be sited in such a way that forces from wave action, wind and marine currents can be minimized, to the extent feasible. Siting decisions should take advantage of land features to reduce marine forces acting on the aquaculture system where possible. Minimizing damage potential to shellfish stock through strategic siting of the program will reduce the potential for losses during severe weather events.

In locations where severe storms are common, such as in the Gulf, submersible features of the grow-out container system (e.g., cages, bags, or suspended lines) to an adequate depth should be engineered into the system to minimize potential for damage to the system or inventory, if possible, with permitting restrictions and user conflicts.

Measure Shellfish-3 Grow-out System Design

Engineer grow-out facility to minimize risk of failure.

The mooring system for grow-out containers should have a strength rating to withstand tensioning and marine forces, including forces acting on attached shellfish. Lines should be tensioned to minimize risk of marine mammal entanglements, which could be another force acting on the container system. As such, an adequate factor of safety is needed to prevent line failure when in operation (e.g., worst-case wave heights and/or storm conditions over a specified time horizon, such as engineering to withstand a once in a 50/100/etc. year storm). The lines should be designed to resist fouling to maintain adequate strength in a marine environment. Materials and engineering of the system should conform to ISO standards.

Causes of potential aquaculture losses include:

- Failure of moorings or grow-out containers due to forces in the marine environment
- Biofouling of materials, leading to failure
- Damage by large predators
- Vessel or propeller strike
- Operational errors during inspection or harvest

Measure Shellfish-4 Grow-out System Management

Surveillance of Grow-out System Condition

The culture site should be monitored on a periodic basis at a sufficient frequency to ensure security of the program. Training of staff should be implemented to respond to various issues, including:

- Line or cage damage.
- Presence of predators.

Best practices for inventorying

- Maintain detailed inventory of lines, including estimated time to harvest size.
- Provide a continuous record of grow-out container condition through the applicable regulatory agencies.

Prevent release of sexually reproductive material from the grow-out system

- Minimize the potential for culture release of egg/sperm by harvesting before maturity.

Measure Shellfish-5 Implement large-scale event prevention measures

Limit access surrounding the facility using buoys, lights or other methods

The boundary of the aquaculture system should be clearly marked with signage identifying restrictions, purpose of the site and lease information. Markers should be designed to be clearly visible to vessel operators. Lighting may be incorporated into site marking where appropriate and where lighting would not cause a visual disturbance.

Use warning measures to restrict vessels from the area

If possible, reactive measures such as audible sources and lights could be installed to warn vessels operating near the aquaculture boundary. However, potential detriment to other species from such measures, including to endangered species, would need to be evaluated before implementing these approaches.

Use deterrent measures to keep predators from entering the grow-out system area

If possible, reactive measures such as audible sources and lights may be used to repel or deter predators from damaging seed lines or opportunistically feeding at the aquaculture site. Air bubble generators or exclusion nets can also be effective predator deterrents, if feasible. However, potential detriment to other species from such measures, including to endangered species, would need to be evaluated before implementing these approaches.

Implement submersible systems or other protection measures for severe weather events

For offshore installations, aquaculture systems could implement submersible designs so they can be lowered below sea level in the event of severe weather, if allowed by permitting regulations and user conflicts. These systems should be designed to be raised and lowered as necessary to suspend maintenance during submerged periods and resume normal operation during moderate conditions, if feasible.

Plan for removal of ancillary equipment during severe weather events

A rapid response plan should be implemented to allow for removal or protection of surface level infrastructure to minimize potential for container system damage and loss of maintenance capabilities.

Implement alarm systems including auto-dialing to ensure rapid response to large-scale events

A recovery plan should be developed to respond to damage and equipment losses within the aquaculture system. Possible components of the plan include an alarm system, staffing and required equipment for gear recovery, repair and reinstallation methods and restoration of inventory losses.

Measure Shellfish-6 Offshore Harvest and Transfer procedures

Minimize opportunities for harvest losses from grow-out to harvest vessel

Safe handling procedures should be used, and containment measures should be implemented to reduce the risk of product loss during handling and transfer of grow-out containers and harvested shellfish stock.

Minimize opportunities for harvest losses from harvest vessel to processor

Safe handling methods should be used when transferring market size shellfish from the harvest vessel to minimize any potential for losses.

Measure Shellfish-7 Advance Science of Aquaculture Genetic and Ecological Interactions

Ongoing monitoring and research of wild shellfish populations and the environment will inform sustainable carrying capacities of shellfish culture in a given region, as well as risk thresholds for additional action.

Address data gaps of wild populations

Areas of further research for individual species are described in Chapter 3 and Chapter 4. Some items for research include genetic structure, population structure, life history, reproductive behavior, population demographics, and effective population size.

Environmental monitoring

Monitor the genetic status of wild populations through genetic sampling of individuals from surrounding wild populations. Genetic markers should be utilized to identify genotypes that can be traced to aquaculture origin.

4.3.2 Action Level Measures

Action level mitigation measures are implemented in the event of an escape event deemed to pose a significant genetic or ecological risk.

Action Shellfish-1 Reducing program inventory

Program inventory could be reduced in cases where a program is following operating requirements but operating above a sustainable level from a gene flow perspective. Modifications to operations can be evaluated along with reducing inventory to a level that reduces program risks to a sustainable level.

Action Shellfish-2 Temporary or permanent cessation of operations

Cessation of operations may be required for programs not in compliance with operating requirements, or for situations where the program is linked to substantial ecological degradation from culture gene flow to the local population.

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