Effects of Geoduck Aquaculture on the Environment

A Synthesis of Current Knowledge

Washington Sea Grant

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by

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This literature review summarizes the state of knowledge about geoduck clams and the potential environmental effects of geoduck aquaculture on the Puget Sound environment.

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Biological and Environmental Status

Chapter 1

General Life History

1.1 Introduction

The Pacific geoduck, *Panopea generosa* (Gould, 1850), incorrectly referred to as the fossil species *Panopea abrupta* (Conrad, 1849) in much of the literature from 1984-2010 (Vadopalas et al. 2010), is a large hiatellid clam found in soft and subtidal substrates in the Northeast Pacific from California to Alaska. It may also occur west to Japan (Anderson 1971, Coan et al. 2000). Pacific geoduck are found in soft substrate from the low intertidal to more than 60 m (Goodwin 1976). Pacific geoduck are extremely long-lived, with many examples of animals more than 100 years old (Goodwin 1976, Shaul and Goodwin 1982, Sloan and Robinson 1984, Campbell and Ming 2003). Geoduck are broadcast spawners that commonly spawn in the spring and summer (Sloan and Robinson 1984, Campbell and Ming 2003). They produce larvae that remain planktonic for 47 days at 14 °C (Goodwin et al. 1979). Postlarvae settle onto the substrate and develop into juveniles that burrow into the sediment. Lucrative commercial Pacific geoduck fisheries exist in Washington and Alaska, British Columbia (Hoffmann et al. 2000), and Baja California (Aragon-Noriega et al. 2012). Other *Panopea* clam species occur worldwide, from Japan (*P. japonica*) to Argentina (*P. abbreviata*), New Zealand (*P. zelandica*), Mexico (*P. globosa*), and other regions; *P. glycimeris* was recently documented off the coast of Sicily (Scotti et al. 2011). The geography of these species is discussed in Section 1.7. This document will refer to Pacific geoduck as simply "geoduck" and make specific references to other species as appropriate.

There is a dearth of peer-reviewed information on *P. generosa* and its congeners. This is particularly true for intertidal *P. generosa* in Puget Sound, as no Washington State regulatory authority currently surveys intertidal geoduck. Thus, although published reports on geoduck population parameters are available, these publications consider only subtidal geoduck clams. Our common understanding of geoduck clams incorporates a significant amount of information about *P. generosa* that was originally published in Washington and Canadian technical reports and not subjected to peer review. Two particularly notable cases in point: It is not clear from the peer-reviewed literature whether geoduck are found in high abundance below 25 m. However, nearly every paper cites the same initial video work which indicates they are found to 110 m (Jamison et al. 1984). Additionally, it is not clear whether *P. generosa* is found only from Baja California to Alaska, or whether it also occurs west to Japan (Coan et al. 2000).

1.2 Taxonomy

Phylum: **Mollusca**
Class:**Bivalvia**
Subclass: **Heterodonta**
Order: **Myoida**
Superfamily: **Hiatelloidea**
Family: **Hiatellidae**
Genus: ***Panopea***
Species: ***generosa***

1.3 Shell structure and age estimation

P. generosa is a massive clam; individuals have been documented at more than 200 mm shell length (SL) and 3.25 kg (Goodwin 1976, Goodwin and Pease 1991). Each of its valves has a broad, continuous pallial line with a short pallial sinus, smooth inner margins, a single cardinal tooth, and a porcelaneous interior. The two adductor scars on each valve are roughly equal in shape, and each has a hinge plate, or chondrophore. A valve is composed of three layers: The outer layer is the proteinaceous periostracum, and upon microscopic examination the two inner layers reveal seasonal growth patterns in their microstructure. Shaul and Goodwin (1982) developed an acetate peel technique that uses these growth patterns, or annuli, to estimate geoduck age. This technique has been used to determine age at maturity of geoduck in British Columbia (Campbell and Ming 2003), and to produce age-frequency distributions for Washington, British Columbian, and Mexican geoduck collections for fishery management (e.g., Breen and Shields 1983, Goodwin and Shaul 1984, Sloan and Robinson 1984, Calderon-Aguilera et al. 2010a).

With any age estimation technique, it is important to verify that the growth patterns tallied are in fact annual. Shaul and Goodwin (1982) conducted two verification experiments. The first examined growth-band counts from two groups of geoduck, sampled within and adjacent to a channel that had been dredged 26 years previously. The authors suggested that since clams could not have survived the dredging, none of those within this area were more than 26 years old. Annuli counts supported this hypothesis. However, patchiness in the settlement of year classes coupled with spatially and temporally variable recruitment has been observed (Vadopalas 2003, Valero et al. 2004). Thus, highly variable numbers of successful progeny per year class could yield the observed results.

The second verification experiment used a mark-and-recapture design. The authors marked the shells of 91 hatchery-reared geoduck and then outplanted them. After seven years in the substrate, eight growth lines were discerned in each of the three recovered geoduck, a confirmation of an annual growth pattern. Concordance between mean sea surface temperatures and growth band width also provides strong evidence for annual growth-line deposition in *P. generosa* (Noakes and Campbell 1992, Strom et al. 2004), although bias must be recognized when *P. generosa* shells are used for climate reconstruction (Hallmann et al. 2008). More recently, annual growth-line deposition was validated directly using evidence from radioactive carbon produced during the bomb testing period (1957-1967), that was incorporated in depositional layers in geoduck shells (Kastelle et al. 2011, Vadopalas et al. 2011).

Using these age estimation techniques, the oldest geoduck recorded was 146 years old and the oldest reproductive geoduck recorded was 107 years old (Sloan and Robinson 1984). A technical report documents a geoduck from the Queen Charlotte Islands estimated to be 168 years old (Bureau et al. 2002) but this report may not have been subject to peer-review. Accurate age estimates can affect fishery management (but see Lochead et al. 2012a).

1.4 Anatomy

A detailed study of the external and internal anatomy of *P. generosa* was conducted by Yonge (1971). The interior anatomy of *P. generosa* is similar to other bivalves (Fig 1). However, geoduck have extremely large, fused siphons and mantles that cannot be fully retracted into their shells, distinguishing them from other clams in the region. The mantle region has posterior siphon apertures and the pedal aperture, a small slit located dorsally on the anterior end. Enormous mucous glands are on the internal surface of the pedal aperture. The geoduck orients itself with the posterior siphon towards the surface, where seawater containing dissolved oxygen and suspended microalgae is circulated through the inhalant siphon.

The featherlike ctenidia, often referred to as gills, are not actually analogous, as they actively perform a feeding role in addition to gas exchange. Through highly organized ciliary movements, the ctenidia trap, sort, and transport food particles to the labial palps, which convey food into the esophagus and reject non-food particles (Yonge and Thompson 1976). Rejected particles are bound with mucus and periodically ejected as pseudofeces via the inhalant siphon. Accepted food particles are also mucus-bound, but upon entering the esophagus they are transported via cilia to the stomach and the crystalline style, a gelatinous rod that contains digestive enzymes. The style rotates freely in the ciliated style sac against the gastric shield in the stomach. The food moves from the stomach to the digestive gland, where most of the intracellular digestion takes place. After digestion, material enters the intestine and is discharged from the anus. Feces are expelled via the exhalant siphon. The gonad follicles are interspersed in the visceral mass, and depending on season and condition can vary from a few millimeters to more than one centimeter thick.

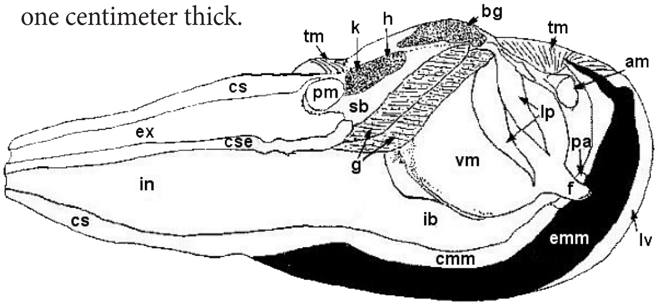

Figure 1. *Sketch of the internal organization of the major organs of the geoduck clam,* Panopea generosa. *The right valve and right side of the muscular mantle and siphon have been cut away to reveal the fused siphons and the arrangement of the internal organs. The thin mantle (tm) that lines the inner surface of the right valve to the pallial line has been turned over the dorsal edge of the left valve (lv). Other labels on the sketch are am - anterior adductor muscle, bg - brown gland, cmm - cut surface of muscular mantle, cs - cut surface of siphon, cse - cut surface of septum, emm - external surface of muscular mantle, ex - excurrent channel, f - foot, g – gills (ctendia), h - heart, ib - infrabranchial chamber, in - incurrent channel, k - kidney, lp - labial palps, lv - left valve, pa - pedal aperture, pm - posterior adductor muscle, sb - suprabranchial chamber, tm - thin mantle, vm - visceral mass. Figure and legend from Bower and Blackburn 2003.*

1.5 Reproduction

Adult geoduck are highly fecund broadcast spawners, but the age when they reach reproductive maturity is unclear. Sloan and Robinson (1984) examined 404 geoduck from British Columbia and placed the youngest mature male at seven years and the youngest mature female at eight years. However, Campbell and Ming (2003) examined 182 geoduck from two sites in British Columbia and found that 50% reached maturity at three years on Gabriola Island and at two years on Yellow Bank. Reproductive senescence has not been observed in geoduck (Sloan and Robinson 1984). All “old” (> 50 yr) geoduck examined appeared reproductively active, with morphologically active sperm or ova. Ripe males as old as 107 years and ripe females as old as 89 years were documented, with no apparent reduction in fecundity (Sloan and Robinson 1984).

Gametogenesis in Pacific geoduck follows an annual cycle. In Puget Sound and British Columbia, spawning commences in the spring and peaks in June and July (Anderson 1971, Goodwin 1976, Sloan and Robinson 1984, Campbell and Ming 2003). Goodwin (1976) examined histological sections of gonad from 124 geoduck from six locations in Puget Sound and characterized them according to five phases of gametogenesis. He found that 50% were in the early active phase in September and 92% were ripe in November. The clams were 100% ripe in May, and by August 50% were spent. Ripe males were found in every month they were collected, from 14% in August to 100% in April. Females had a more contracted spawning season with no ripe females collected from August to October. Sloan and Robinson (1984) reported similar seasonal changes in gametogenic condition for 365 geoduck from British Columbia.

P. globosa, the Cortez geoduck, spawns during low temperatures in the Gulf of California (Aragon-Noriega et al. 2007) as gametogenesis is initiated by a sharp temperature decrease (Calderon-Aguilera et al. 2010b). In general accord with these studies, *P. generosa* held at lower temperatures during gametogenesis exhibited greater reproductive development and spawning activity (Marshall et al. 2012). Arambula-Pujol et al. (2008) conducted an analysis of the reproductive cycle of *P. globosa* and found that distinct annual cycles driven by temperature were more protracted in *P. generosa* and *P. zelandica* than in *P. globosa*. In contrast to *P. generosa*, *P. globosa*, and *P. zelandica*, the congener *P. abbreviata* spawns throughout the year, with limited seasonal variation (Zaidman et al. 2012).

In the smaller size classes, Pacific geoduck show an uneven sex ratio with higher proportions of males than females (Sloan and Robinson 1984, Campbell and Ming 2003). Sloan and Robinson (1984) observed a steady decrease in the proportion of males, from 90% of all individuals ≤ 10 yr to 47% of those ≥ 51 yr. Campbell and Ming (2003) observed that 41% of geoduck < 90 mm shell length were immature and 54% were males. Of the mature geoduck < 90 mm shell length, 92.5% were male and only 7.5% female. In geoduck ≥ 90 mm shell length, the sex ratio was essentially equal (52% males: 48% females). There are at least two explanations for these disparate sex ratios. Goodwin (1976) suggested that geoduck are dioecious, with sex determined by development and males maturing sooner or at smaller sizes than females. It is also possible that a portion of these young male geoduck are protandrous hermaphrodites that will reverse sexes at some point as they age. Of 253 geoduck sampled histologically by Campbell and Ming (2003), one individual was a hermaphrodite, with a gonad containing both oocytes and spermatozoa. Although many bivalves are dioecious (Coe 1943), hermaphroditism has been documented. The Northern quahog, *Mercenaria mercenaria* is generally considered protandrous, and bisexual gonads have been observed in it (Eversole et al. 1980). Protandrous hermaphrodism has also been observed in both the Pacific oyster, *Crassostrea gigas* (Guo et al. 1998) and pearl oyster, *Pinctada margarifera* (Dolgov 1991). Additionally, evidence suggests that the New Zealand geoduck *P. zelandica* is protandric (Gribben and Creese 2003).

1.6 Life cycle

Reproductive development has been well documented in some bivalve species (reviewed in Sastry 1979). Longo (1987) describes the general meiotic process in clams, using *Spisula solidissima* as an example. Geoduck are thought to be dioecious (but see Section 1.5) facultative repeat broadcast spawners. Synchronization of spawning is not well understood, but the detection of sperm from one male in seawater may cue mass spawning in the aggregation (Sastry 1979). Fertilization occurs externally and meiosis progresses through the expulsion of both polar bodies The duration of the meiotic cycle is affected by temperature; at a salinity of 30 practical salinity units (PSU), meiosis took 106 min. at 11 °C, 78 min. at 15 °C, and 56 min. at 19 °C (Vadopalas 1999). Salinity also affects meiotic duration. At 15 °C, completion of meiosis took 106 min. at 24 PSU, 81 min. at 27 PSU, and 78 min. at 30 PSU (Vadopalas 1999).

The male and female pronuclei break down subsequent to the completion of meiosis in the ova and prior to the first mitotic division (Longo 1987). Goodwin (1973) described the combined effects of salinity and temperature on the timing of geoduck clam embryonic development. The optimal temperature and salinity ranges reported for embryonic development were 6-16 ºC and 27.5-32.5 PSU, respectively (Goodwin 1973). Outside these ranges, a significant reduction in normal development from the embryonic to the larval stage was observed. However, temperature and salinity tolerance can vary significantly between developmental stages in clams (Sastry 1979).

Goodwin et al. (1979) found that after approximately 48 hours of embryonic growth, the trochophore developed into an actively swimming and feeding veliger larva (straight-hinge or D-stage) (Goodwin et al. 1979). The veliger stage lasted 47 days at 14 ºC (Goodwin et al. 1979), during which the larva fed on microalgae and grows from 111 to 381 µm in shell height (Goodwin et al. 1979). Using a novel trapping and identification approach, Becker et al. (2012) observed two discrete pulses of Pacific geoduck larval abundance in Quartermaster Harbor, a discrete embayment in the main basin of Puget Sound. The first pulse was evident in early March and the second in early June. Changes in size frequency distributions may indicate some larval retention, but more research is necessary to determine the generality of this finding.

During early metamorphosis, larval geoduck settle to the bottom, lose their vela, develop primary ctenidia and spines on their shells, and begin active crawling (Goodwin et al. 1979). Over the next several weeks, the ctenidia finish forming, the siphon grows, and the mantle is fused. During this stage geoduck use their feet both to crawl and to transfer detrital food to their mouths (a process called pedal-palp feeding) (King 1986). After two to four weeks as postlarvae, they will have reached 1.5 to 2 mm shell length, burrowed into the substrate, and begun filter feeding (King 1986).

Goodwin (1976) examined the growth of subtidal geoduck in Puget Sound using a mark-and-recapture methodology. Growth was fastest in the first three years of life, with valve length increasing by 20 to 30 mm/year. After ten years, growth slowed considerably (Goodwin 1976). Valves continued to increase in thickness throughout life, enabling age estimation based on shell layers visible in thin sections of the chondrophore (detailed in Section 1.3). Strom et al. (2004) confirmed that geoduck growth is rapid for the first ten to fifteen years but then slows, and shell length essentially stops expanding after age 25. Growth rate also varies significantly along environmental gradients such as temperature, substrate and depth, and among geographic sites (Goodwin and Pease 1991, Hoffmann et al. 2000, Campbell et al. 2004).

Goodwin (1976) collected 2,037 geoduck from unexploited stocks in multiple Puget Sound locales and found an average shell length of 158 mm with an average range from 124 mm to 171 mm, depending on location. Only four individuals over 200 mm were collected (Goodwin 1976). A later study of 11,154 geoduck found the average shell length and weight to be 135 mm and 872 g respectively, with a range from 49 to 212 mm and 28 to 3250g (Goodwin and Pease 1991). Cruz-Vasquez et al. (2012) determined that for *P. globosa*, the logistic growth model is superior to three other models including the Von Bertalanffy model currently used for *P. generosa* in both Mexico (Calderon-Aguilera et al. 2010b) and Washington state (Bradbury and Tagart, 2000; Hoffmann et al. 2000).

Although many sources (e.g., Goodwin and Pease, 1991, Campbell et al. 2004, Zhang and Hand, 2006) indicate that adult geoduck reach a burial depth of about one meter, this may be closer to a maximum: average adult burial depths observed by Anderson (1971) and Goodwin (1976) were 52 and 50-60 cm, respectively.

1.7 Distribution

In addition to *P. generosa*, naturally occurring populations of various species of *Panopea* clams occur world-wide, including Japan (*P. japonica*), Argentina (*P. abbreviata*), New Zealand (*P. zelandica*), and Mexico (*P. globosa*). A small (N = ~300) population of *P. glycimeris* was recently documented off the coast of Sicily (Scotti et al. 2011). *P. generosa*, the most massive species in the genus, has been reported in coastal waters of the Western Pacific from Baja California to Alaska (Morris et al. 1980) and in estuarine environments along the West Coast of North America and in Japan (Coan et al. 2000). However, *P. generosa* may not actually occur in Japan, and the congener *P. japonica,* known to occur, there, may have been mistakenly identified as *P. generosa*.

P. globosa, although occasionally identified as *P. generosa*, is clearly a distinct species (Leyva-Valencia et al. 2012; Rocha-Olivares et al. 2010; Suárez-Moo et al. 2012). *P. globosa* was considered endemic to the Gulf of California but has been recently documented in Magdalena Bay, on the Pacific coast of the Baja Peninsula (Leyva-Valencia et al. 2012; Suárez-Moo et al. 2012). *P. generosa* has been documented as far south as Punta Eugenia on the Pacific coast of the Baja California Peninsula (Coan and Valentich-Scott 2012).

Using traditional approaches, Rocha-Olivares et al. (2010) identified distinct morphological differences between the Cortez geoduck, *P. globosa*, and the Pacific geoduck, *P. generosa*. Higher-resolution morphological differentiation, using geometric morphometrics, corroborated the interspecific differences, discerned morphometric differentiation at the intraspecific level in *P. globosa* (Leyva-Valencia et al. 2012), and documented a population of *P. globosa* in Magdalena Bay. Genetic analyses subsequently corroborated this finding (Suárez-Moo et al. 2012). Thus the endemism of *P. globosa* to the Gulf of California has been falsified, and it is now established that both *P. generosa* and *P. globosa* both occur on the Pacific coast of Baja California.

Although introduction to the NW Atlantic was suggested as early as 1881 (Hemphill 1881), to our knowledge, there have been no intentional introductions of *P. generosa* to other regions. *P. generosa* is abundant in Puget Sound, where a commercial fishery for subtidal geoduck commenced in 1970.

1.8 Habitat

Adult geoduck are found in sand, mud, mud-sand, mud-gravel, sand-gravel, and mixed loose substrates (Goodwin and Pease 1991). They can tolerate temperatures down to 8 °C (Goodwin et al. 1979), but long-term temperature and salinity tolerances have not been established. Known geoduck aggregations occur in the Strait of Juan de Fuca, where salinities are typically less than 32 practical salinity units (Herlinveaux and Tully 1961), and in South Puget Sound, where temperatures can exceed 22 °C.

In Puget Sound, geoduck are contagiously distributed in small patches and beds of high abundance with an average bed density of 1.7 geoduck $\cdot$ m^{-2} (Goodwin and Pease 1991). In this study, geoduck density ranged from 0 to 22.5 geoduck $\cdot$ m^{-2} and individuals tended to aggregate within the beds in groups containing an average of 109 animals

(Goodwin and Pease 1991). Conspecific aggregation is common for many bivalve species and is important for spawning synchronization and fertilization success (Sastry 1979). It appears that bed density increases with depth up to ~25 m; (Campbell et al. 1998), but mean length and weight decrease with depth (Goodwin and Pease 1991).

Geoduck are found in low intertidal to subtidal waters. Existing evidence of deepwater stocks is limited. Two pilot studies of a single area in Case Inlet, South Puget Sound, although not subjected to peer review, revealed what appear to be significant aggregations of geoduck clams below the 18 m mean lower low water (MLLW) fishing limit to a depth of 110 m (Jamison et al. 1984). Two confirmed Pacific geoduck were retrieved using a ROV from 35 m MLLW in Hood Canal (Vadopalas et al. 2012). There are additional anecdotal accounts of geoduck observed at even greater depths, but it must be noted that no thorough examinations resulting in peer-reviewed publications have looked for geoduck at depths greater than 25 m. From these few data, subtidal geoduck abundance in Puget Sound was estimated to be 25,800,000 individuals, based on very limited video reconnaissance (Jamison et al. 1984).Washington's geoduck resource management plan postulates that these deepwater stocks contribute to recruitment and recovery of fished areas, but data are lacking to support this important assumption.

Chapter 2

Spatial and Genetic Structure of Wild Geoduck

2.1 Introduction

Many marine bivalves, including geoduck, tend to aggregate (Fegley 2001) and exhibit temporal changes in abundance. On broad spatial scales, subtidal geoduck are found in all the subbasins and straits of Washington's inland marine waters; on smaller scales, the distribution of geoduck is highly variable (Goodwin and Pease 1991). Although some spatial and genetic information is available on subtidal geoduck, we have none on intertidal geoduck clams. Neither the Washington Department of Natural Resources (WDNR), the Washington Department of Fish and Wildlife (WDFW) nor the treaty tribes regularly survey intertidal geoduck, so data on intertidal population size, density and aggregation is lacking. Geoduck are occasionally reported in creel surveys of recreational harvesters, which provide some anecdotal information on where geoduck are found but no information on population parameters.

2.2 Population size

The WDFW and several Washington treaty tribes regularly survey subtidal geoduck to determine biomass and population size (Hoffmann et al. 2000). For these purposes, Puget Sound is divided into six geoduck management regions that are based on legal tribal fishing boundaries (Hoffmann et al. 2000) and have little to do with local oceanography or geoduck biology (Fig. 2). Transects are conducted perpendicular to shore between 5.5 and 21.5 m below MLLW. Counts are based on visual identification of either a geoduck siphon or a siphon depression along a 0.91 m wide band delineated by the transect line. Visual counts are corrected by a seasonal "show" factor, specific to each tract, to account for the portion of geoduck undetected by virtue of their retracted siphons (Goodwin 1977). WDFW uses these dive survey data to make management decisions for the commercial geoduck fishery, so that 2.7% of the estimated available biomass in each region can be legally harvested each year.

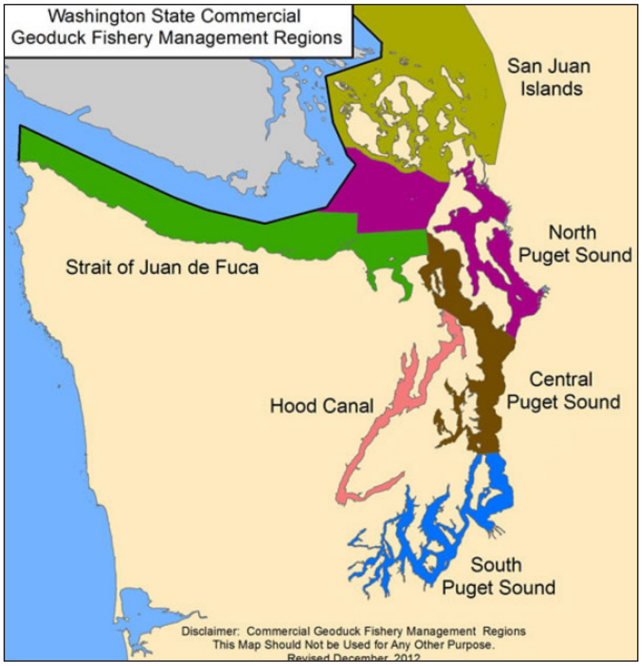

Figure 2. *Geoduck management regions in the state of Washington (Washington Department of Fish and Wildlife 2012).*

2.3 Population density

Goodwin and Pease (1991) analyzed subtidal geoduck density relative to geographic area, latitude, water depth, and sediment type in Puget Sound. Based on 8,589 transects, average geoduck density was 1.7 geoduck · m^{-2}, with a range of 0 to 22.5 geoduck · m^{-2}. Densities varied significantly according to geographic area, latitude, water depth, and sediment type. The highest regional densities were observed in South Sound (2.0 geoduck · m^{-2}) and the lowest in North Sound (0.2 geoduck · m^{-2}). Within Washington, an inverse relationship between geoduck density and latitude was observed, but this relationship did not extend to British Columbia, where geoduck density was higher (Goodwin and Pease 1991). On the west side of Vancouver Island, geoduck densities ranged from 0 to 13 geoduck · m^{-2}, with an average of 4.9 geoduck · m^{-2} (Fyfe 1984). To the extent studied, geoduck density was found to increase with depth in both Washington (to 18 m; Goodwin and Pease 1991) and British Columbia (to 25 m; Campbell et al. 1998), but mean length and weight decreased with depth (Goodwin and Pease 1991). Geoduck densities also varied in different sediment types, across all regions. The lowest densities were observed in mud (1.2 geoduck · m^{-2}) and the highest in mud-sand and sand habitats (2 to 2.1 geoduck · m^{-2}).

2.4 Aggregation

In Puget Sound, subtidal geoduck are contagiously distributed in small patches and beds of high abundance (Goodwin and Pease 1991). Within these beds, aggregations contained an average of 109 animals (Goodwin and Pease 1991). Goodwin and Pease (1991) hypothesized that aggregations of geoduck may result from larval attraction to adult conspecifics, patchy distribution of substrate type, or biotic attractants or deterrents, but these correlations have not been investigated. The aggregation pattern within a geoduck bed has been characterized as a Type III concentration (Hilborn and Walters 1992), with most locations within the bed exhibiting intermediate density, and fewer locations with either low or high abundance (Campbell et al. 1998).

Wild geoduck are particularly vulnerable to overexploitation because of their gregariousness and longevity, and must be carefully managed for sustainability. Management strategies are often structured by aggregations (*P. globosa*, Aragon-Noriega et al. 2012, Leyva-Valencia et al. 2012; *P. abbreviata*, Morsan et al. 2010; *P. generosa*, Bradbury and Tagart, 2000, Campbell et al. 1998, Hoffmann et al. 2000).

Contagious distribution has also been observed in the Northern quahog (*Mercenaria mercenaria*) (Saila et al. 1967). In this study, 22% of quadrats sampled contained high *Mercenaria* densities while 29% contained very few or no Northern quahog. Conspecific aggregation is common in many bivalve species and is important for spawning synchronization and fertilization success in broadcast spawners (Sastry 1979). For example, synchronous spawning was observed in an estimated 54,000 mussels (*Mytilus californianus*) and fertilization success was estimated to be 80% (Gosselin 2004); fertilization success was also shown to increase dramatically with proximity to the red sea urchin (*Strongylocentrotus franciscanus*) (Levitan et al. 1992).

2.5 Recruitment and temporal changes

Groups of geoduck aggregations are structured as individual beds connected through the dispersal of planktonic larvae (Orensanz et al. 2004, Zhang and Hand 2006). Therefore, recruitment to a particular bed is not related to the reproductive capacity of the clams within that bed (Orensanz et al. 2004). Instead, recruitment may depend on the reproductive and environmental conditions local to other beds as well as largerscale environmental variables that may affect spawning, survival, and larval flow. There is currently no accurate way to model geoduck recruitment as recruitment in one area is likely linked with reproductive capacity in unknown areas, and may be related to unknown geographic and oceanographic parameters that vary temporally and spatially.

Two studies in British Columbia examined geoduck density and recruitment in the same plots over nine years, with controlled fishing pressure (Campbell et al. 2004, Zhang and Campbell, 2004). Campbell et al. (2004) defined recruitment as the density of six-to-seven-year-old geoduck · m^{-2} while Zhang and Campbell (2004) defined recruitment as the number of one-year-old geoduck · m^{-2}. Campbell et al. 2004 found that heavy fishing pressure reduced geoduck population densities and average geoduck age, but that densities slowly increased through recruitment once fishing was halted. Zhang and Campbell (2004) found that severe harvesting (> 90% removal) negatively impacted recruitment at one site in the short term (≤ 3 years) but did not affect long-term recruitment. At the second site, the most heavily harvested plot had the highest short- and long-term recruitment levels. However, the highest recruitment before the experiment began was also observed at this site, suggesting that recruitment is highly variable on a small spatial scale regardless of fishing pressure. Neither study documented long-term negative effects of geoduck fishing on subsequent recruitment and both studies observed that recruitment varied on large and small spatial scales.

One important advantage of broadcast spawning and a pelagic larval stage, in addition to higher dispersal potential, may be the periodic high success in recruitment (Ripley 1998). Long-lived species like geoduck can weather lengthy periods when environmental characteristics are not conducive to high recruitment because they may experience very large recruitment events when environmental conditions are ideal (Ripley 1998). Studies that have back-calculated historic recruitment patterns from age-frequency data (Orensanz et al. 2004, Valero et al. 2004, Zhang and Hand 2006) suggest that while geoduck recruitment is characterized by substantial interannual variation, a decades-long recruitment trend occurs across a huge geographic scale. Recruitment in both British Columbia and Washington declined from 1920 to 1975, bottomed out around 1975, and then rebounded, reaching pre-decline levels in the early 1990s (Orensanz et al. 2004, Valero et al. 2004, Zhang and Hand 2006).

This decline is not thought to have been anthropogenic as it began long before the commencement of geoduck fisheries and is evident in both pristine and disturbed locales. Instead, recruitment patterns appear to be correlated with environmental parameters including sea surface temperature (low temperature = low recruitment) and discharge from large rivers (high discharge = low recruitment) (Valero et al. 2004). Multiple parameters shifted in the mid-1970s in the Pacific Ocean (Ebbesmeyer et al. 1991); collectively these changes are referred to as a “regime shift” (Francis et al. 1998), and studies have documented their impact at both the ecosystem and organismal levels (Hare and Mantua 2000, Clark and Hare 2002, Tolimieri and Levin 2004). Previous studies have shown that environmental variables correlate with recruitment, for example, sea surface temperature is positively correlated with year-class strength in native littleneck clams (*Leukoma staminea*) (Orensanz 1989).

2.6 Population genetics, adaptation, and larval dispersal

In marine species, larval dispersal affects genetic stock structure and population dynamics; an understanding of larval dispersal is vital for proper management. The extent to which populations are connected spatially and temporally depends on larval dispersal, as larvae are the primary migrating propagules in broadcast-spawning marine invertebrates. Much of the research on dispersal and recruitment of broadcast-spawning marine invertebrates has relied on the untested assumption that larvae behave as passively drifting particles distributed randomly throughout the water column. There is mounting evidence that larval dispersal of marine fish and invertebrates may be tied to complex interactions between the environment and larval behavior. In fact, Shanks and Brink (2005) falsified the hypothesis that bivalve larvae disperse passively via ocean currents. Studies by Taylor and Hellberg (2003), Zacherl (2005), and Carson et al. (2013) have further challenged this notion using genetic and microchemical analyses.

Many clams can use their feet to achieve some degree of active movement in response to wave action, tidal movement, substrate displacement by storms, strong currents, or disturbance (Yonge and Thompson, 1976, Prezant et al. 1990). By contrast, geoduck adults have only small vestigial feet and little capacity for movement. Adult movement is restricted to siphon extension and retraction; once exposed, adults cannot right themselves or dig back into the substrate. Geoduck aggregations connect mainly via planktonic larval dispersal, with potential small-scale dispersal of juveniles.

Larval dispersal therefore plays the primary role in facilitating gene flow and determining population structure. Gene flow is correlated with dispersal in numerous organisms (Bohonak 1999), including many marine fish and shellfish species (reviewed in Shaklee and Bentzen 1998). For example, marine species with planktonic larvae tend to have higher gene flow and less population differentiation than direct-developing species (Waples 1987, Ward 1990, Ayre and Hughes 2000, De Wolf et al. 2000, Collin 2001). Panmixia (random mating) has been observed on broad geographic scales in broadcast-spawning invertebrates, especially those with long larval stages (e.g., *Mytilus galloprovincialis,* Skalamera et al. 1999; *Littorina striata,* De Wolf et al. 2000; *Strongylocentrotus franciscanus,* Miller et al. 2006). However, genetic structure at a variety of spatial scales has also been observed in such broadcast-spawning marine invertebrates as the Eastern oyster, *Crassostrea virginica* (Karl and Avise 1992), the sea urchins *Strongylocentrotus purpuratus* (Edmands et al. 1996) and *S. franciscanus* (Moberg and Burton 2000), the lagoon cockle, *Cerastoderma glaucum* (Mariani et al. 2002), the limpet *Siphonaria jeanae* (Johnson and Black 1984), and the black abalone *Haliotis cracherodii* (Chambers et al. 2006, Hamm and Burton 2000).

The complex hydrology and bathymetry of Puget Sound suggests a potential for restricted dispersal and population subdivision of marine invertebrates. However, Puget Sound's freshwater inputs and surface outflow may increase the propensity of passive surface particles to disperse in a seaward direction. Molluscan populations colonized by pelagic larvae drifting seaward from populations in inner inlets could thus exhibit either genetic homogeneity or directional gene flow. A study examining population structure in the native littleneck clam (*Leukoma staminea*) and the macoma clam (*Macoma balthica*) within Puget Sound found that although the two species have similar reproductive and dispersal strategies, their population structure was quite different (Parker et al. 2003). *L. staminea* showed substantial population structure at all loci examined while *M. balthica* populations were not highly differentiated. The amount of population structure within Puget Sound is clearly species-dependent and should not be generalized, even among species that share reproductive characteristics.

In the last decade, several studies have examined population structure in geoduck (Van Koeveringe 1998, Vadopalas et al. 2004, Miller et al. 2006). Using the cytochrome oxidase III subunit (COIII) of the mitochondrial genome, Van Koeveringe (1998) investigated the population structure of geoduck in British Columbia and was unable to falsify the null hypothesis of panmixia. However, statistical power to detect population subdivision was low in this study because only a single locus was used and sample sizes were small.

Vadopalas et al. (2004) examined population differentiation in geoduck from sites in the Strait of Juan de Fuca/Georgia Strait/Puget Sound complex and one site in Southeast Alaska using 11 allozyme and seven microsatellite loci. Similar patterns of genetic differentiation were detected with both marker classes. In general, little differentiation was detected among geoduck aggregations regionwide, although the Freshwater Bay collection in the Strait of Juan de Fuca was differentiated from other collections. The authors speculate about causes of this seemingly random genetic differentiation and suggest three possibilities. The observed pattern may represent genetic isolation, as Freshwater Bay is characterized by oceanographic conditions that may inhibit immigration. The observed pattern may also represent selection because, for the allozymes tested, the differentiation of Freshwater Bay was driven by a locus (*GPI*) that is thought to be under temperature selection in *Mytilus edulis* (Hall 1985). Finally, the observed pattern may simply represent stochastic variation. Genetic homogeneity on a broad spatial scale and heterogeneity on a fine scale have been observed in other marine invertebrates, including a barnacle (*Balanus glandula*, Sotka et al. 2004), a limpet (*Siphonaria jeanae*, Johnson and Black 1984), and a sea urchin (*Strongylocentrotus purpuratus*, Edmands et al. 1996). This geographical variation suggests that focusing on a species' average gene flow can mask important intraspecies variation that may reflect selection or local oceanographic conditions.

Miller et al. (2006) used eight microsatellite loci to analyze population differentiation in geoduck from Washington to northern British Columbia and observed more genetic structure at broad spatial scales than Vadopalas et al. (2004) detected. Overall, they report an isolation by distance structure. While both Miller et al. (2006) and Vadopalas et al. (2004), observed panmixia at small (50-300 km) scales, Miller et al. (2006) detected stepping-stone gene flow at larger (500-1000 km) scales. The east and west coasts of Vancouver Island and the Queen Charlotte Islands were found to be significantly differentiated, possibly because oceanographic conditions limit gene flow between these regions but also because environmental parameters (e.g., high waves and disturbance on one side of Vancouver Island, sheltered conditions on the other) may impose adaptive constraints.

Vadopalas et al. (2012) examined temporal and microspatial variation in geoduck using both microsatellites and allozymes on two extensively sampled Puget Sound aggregations for which individual ages were estimated using techniques outlined in Strom et al. (2004). Spatial shifts in allele frequencies and year-class strength were observed, suggesting that patchy settlement may be due to an interaction between hydrology and larval behavior during dispersal (Vadopalas et al. 2012). Distinct genetic differences between *P. generosa* and *P. globosa* were observed at ribosomal DNA loci (primarily ITS-1) by Rocha et al. (2010); the two species also exhibited high divergence at the mitochondrial CO1 locus (Suárez-Moo et al. 2012).

While we have a fairly good understanding of neutral genetic differentiation (i.e. gene flow) via microsatellite and allozyme analyses of wild Pacific geoduck aggregations (Vadopalas et al. 2004, 2012, Miller et al. 2006), differences arising from selection (i.e. local adaptation) are more important for determining the consequences of gene flow from cultured stocks (Crandall et al. 2000, Pearman 2001). Panmixia indicated by neutral molecular markers can mask adaptive variation among populations (Utter 1998); Reed and Frankham (2001) found only weak correlation between quantitative variation in life history traits and neutral molecular markers. Adaptive differentiation (i.e., genetic differences produced by natural selection) can be measured via quantitative genetic approaches (Storfer 1996, Reed and Frankham 2001) or by characterizing molecular differences via high-throughput sequencing technologies and identifying specific alleles associated with variation in survival, fecundity, or growth (e.g., Hemmer-Hansen et al. 2007, Limborg et al. 2012, Pespeni et al. 2012). But such information is currently lacking for geoduck.

Chapter 3

Geoduck Community and Habitat of Puget Sound

3.1 Introduction

A comprehensive review of the community characteristics and structure of Puget Sound's sandy intertidal is beyond the scope of this review. Instead we briefly discuss topics that may contribute to our understanding of geoduck and geoduck aquaculture in Puget Sound, including natural biota, water quality, sediment quality, and recovery after natural disturbances. A common theme running through this discussion is that oceanographic and ecological conditions in Puget Sound vary dramatically on a variety of spatial and temporal scales.

3.2 Natural biota

A broad range of physical factors (e.g. current, substrate type, temperature, salinity) and biological factors (e.g. predation, competition) are known to affect the distribution and abundance of benthic flora and fauna. In estuarine systems, the primary physical processes are wave energy, salinity, and sediment structure (Dethier and Schoch 2005). Salinity in particular plays a key role: Low and variable salinity are associated with reduced species diversity (Carriker 1967, Constable 1999, Smith and Witman 1999). One challenge to understanding patterns in estuarine systems is that oceanographic variables are often linked; for example, wave action may dictate sediment type and salinity may vary with temperature (Clarke and Green 1988). A second challenge is that environmental factors and the distribution and abundance of organisms all tend to be extremely variable in estuaries, and this variation (or patchiness) occurs on many spatial and temporal scales. Variation within sites is often highly significant, which makes detecting patterns at larger spatial scales difficult (Morrisey et al. 1992).

One study overcame this problem of scale by using a nested sampling design to assess the distribution and abundance of benthic organisms in Puget Sound (Dethier and Schoch 2005). Because sediment type is known to influence benthic community composition (Gray 1974, Kennish et al. 2004,Coleman et al. 2007), only the most common beach type in Puget Sound (primarily sand with cobble and pebbles) was sampled. More than 165 taxa were identified in this study, with 85% belonging to four phyla: annelida, mollusca, arthropoda, and rhodophyta. Of these, 134 were identified at the species level and 23 at the genus level, and ten were grouped into complexes. Twenty-six primary producers, 139 invertebrates, and 1 fish (a gunnel) were found. Unfortunately, geoduck were not identified to species but were grouped into "clam siphons (unident)." No discernible distribution pattern for clam siphons (unident) was observed. The complete list of all species found in this study is in Appendix A of Dethier and Schoch (2005).

High variability in the abundance of particular species was observed at many spatial scales, as well as some broader ecological patterns were observed. Species richness increased steadily with latitude in Puget Sound, as temperature, salinity, wave action, and substrate became more marine. This trend has been previously observed and linked to oceanographic variables (Constable 1999, Ysebaert and Herman 2002). In North Puget Sound, salinity was about 3 practical salinity units higher than in the South Sound, sea surface temperature was about 3 °C lower, and wave energy and sediment size were somewhat higher. Despite this positive general correlation between species richness and latitude, there were exceptions. Barnacles and grapsid crabs were abundant throughout the Sound, and their twenty taxa were patchily distributed with no obvious geographic trend. Additionally, some other taxa were more abundant in South Puget Sound. These taxa tended to be either cultured directly (e.g., *Crassostrea gigas*) or associated with taxa cultured in the region (e.g., *Crepidula fornicata).*

Like many benthic invertebrates in Puget Sound, geoduck are patchily distributed (Goodwin and Pease 1991) (see Section 2.4). This patchiness may reflect the distribution of preferred abiotic characteristics and/or ecological associations. In a study conducted in British Columbia, juvenile geoduck were found clustered around full-sized adult clams (Fyfe 1984). It is possible that adult conspecifics provide settlement cues for larvae, or that more juvenile geoduck survive in microhabitats replete with adults. Goodwin and Pease (1991) used a subtidal transect methodology (based on non-parametric tests, not adjusted for multiple comparisons) to determine that geoduck density correlated positively with a number of other taxa. These included chaetopterid polychaete worms (*Spiochaetopterus costarum* and *Phyllochaetopterus prolifica*), sea pens (*Ptilosarcus gurneyi*), horse clams (*Tresus* sp.), red rock crabs (*Cancer productus*), moon snails (*Polinices lewisii*), and laminarian kelp (*Laminaria* spp.). A positive correlation between chaetopterid polychaete density and the density of various other invertebrate taxa has been observed, suggesting that these tube-building worms may facilitate the presence of other species (Morrisey et al. 1992). The association of red rock crabs and moon snails with geoduck is likely because these predators are attracted to areas of high geoduck density. Other positive correlations may be coincidental. Goodwin and Pease (1991) found only one negative correlation: Geoduck densities were significantly lower in quadrats containing red algae (phylum Rhodophyta), one of the four most common phyla found by Dethier and Schoch (2005) in their survey of Puget Sound.

3.3 Oceanography, water quality and sediments of Puget Sound

Puget Sound is an estuarine fjord composed of a series of basins separated by sills. Water enters and leaves the Sound primarily through Admiralty Inlet, which connects to the Strait of Juan de Fuca. Within Admiralty Inlet, Puget Sound consists of three major branches: the Main Basin/South Sound to the south, Hood Canal to the southwest, and Whidbey Basin to the northeast. A sill (at Tacoma Narrows) separates the deep Main Basin from the shallower South Sound, which has many branching inlets. Northern Whidbey Basin has an additional outlet to the Strait of Juan de Fuca called Deception Pass, which is shallow and extremely narrow. The water in Puget Sound is about 90% oceanic and 10% fresh (Ebbesmeyer and Barnes 1980), with most of the fresh water provided by the Skagit, Stillaguamish, and Snohomish rivers (Babson et al. 2006). Its circulation is driven by tidal currents, riverine input, and density differences between river and marine water. Puget Sound is generally well oxygenated outside southern Hood Canal, where hypoxia has been associated with fish kills (Babson et al. 2006).

Babson et al. (2006) used a modeling approach to examine seasonal and interannual variations in circulation and residence time in Puget Sound. At the seasonal scale, salinity in the Strait of Juan de Fuca had a larger effect on circulation than seasonal changes in river flow. However, at an interannual scale, changes in river flow had a larger effect than salinity. According to the model, the rate of circulation had high interannual variance, with residence times between 1992 and 2001 varying from 33 to 44 days in Whidbey Basin and 64 to 121 days in southern Hood Canal (Babson et al. 2006). Cox et al. (1984) predicted residence times of > 9 months in Hood Canal based on current records. Khangaonkar et al. (2012) used an unstructured grid model to examine annual biogeochemical cycles of phytoplankton, dissolved oxygen, and nutrients in Puget Sound. Their results suggest that seasonal variation in temperature, sunlight, and water exchange with the Pacific strongly influence phytoplankton species abundance, dissolved oxygen, and nutrient dynamics in Puget Sound. Although dissolved oxygen concentrations at the whole Puget Sound scale were dominated by water coming in from the Strait of Juan de Fuca, dissolved oxygen levels in sub-basins could be affected by anthropogenic discharges (Khangaonkar et al. 2012).

Human activity has heavily affected Puget Sound's shoreline, water quality, and sediments. At least one-third of the shoreline has been extensively altered by such activities as bulkhead construction, diking, filling, and devegetation (Rice 2006). A study examining shoreline alteration found that light intensity, air temperature, and substrate temperature were significantly higher on altered beaches without shoreline vegetation than on vegetated beaches (Rice 2006). Biological differences were also observed between the beaches, with smelt eggs containing live embryos reduced by half on the altered beaches.

High levels of chemical contaminants, including polychlorinated biphenyls (PCBs), have been documented in Puget Sound (Stein et al. 1993). PCBs have biological implications. Benthic flatfish in Puget Sound display effects of contaminant exposure such as reproductive dysfunction, reduced immune function, and toxicopathic diseases (Johnson et al. 1998). There is some evidence that fish in urbanized areas of Puget Sound have higher contaminant exposure and lower survival than fish in less urban areas (Johnson et al. 1998). An extensive survey of sediment quality conducted at 300 locations in Puget Sound (2363 km^2) also indicated that urban areas had higher contaminant levels (Long et al. 2005). Sediments were classified as degraded, intermediate, or high-quality based on toxicity levels, exogenous chemical concentrations, and levels of human perturbation. The authors found that 1% in Puget Sound were degraded, 31% were intermediate, and 68% were high-quality. Degraded conditions were associated with urbanization and industrial harbors, especially near the urban centers of Seattle, Tacoma, and Bremerton. But the authors concluded that compared to other U.S. estuaries and marine bays, Puget Sound sediments showed minimal evidence of toxicant-induced degradation.

Biological toxins such as paralytic shellfish poisoning (PSP) toxin and domoic acid (DA) are also present in Washington waters. DA is a toxic amino acid produced by diatoms in the genus *Pseudonitzchia* (Bates et al. 1989), while PSP is produced by dinoflagellates in the genus *Alexandrium* (Curtis et al. 2000). Dungeness crab (*Cancer magister*) and razor clam (*Siliqua patula*) fisheries on Washington's outer coast have been periodically closed because of DA since 1991 (Horner et al. 1993). Domoic acid is a particular challenge for razor-clam gatherers, as these clams can retain DA for up to a year (Trainer and Bill 2004). Low levels of DA and some *Pseudonitzchia* species have been observed in Puget Sound (Trainer et al. 2007) since 1991, and no DA concentrations above the regulatory limit of 20 ppm have been detected in Puget Sound geoduck (Bill et al. 2006). No information is available on the retention time or depuration of domoic acid by geoduck.

Curtis et al. (2000) examined PSP in Puget Sound geoduck and found that toxin concentrations varied significantly among individual clams but that generally, geoduck in shallow water (7 m mean lower low water, or MLLW) contained higher concentrations of PSP toxin than deepwater (17 m MLLW) geoduck. The toxin was concentrated in the gonadovisceral mass; toxin levels were below critical levels in mantle and siphon tissues, which were safe to consume even when the viscera were highly toxic.

3.4 Recovery after natural disturbances

Levels of natural disturbance vary widely in Puget Sound, from calm, static areas to areas characterized by repeated disturbance. Here we briefly discuss the literature on recovery after natural disturbance, with a focus on sandy intertidal habitats. Disturbance events vary widely on spatial, temporal, and intensity scales. Recolonization by benthic infauna also varies over space and time according to life-history characteristics, environmental conditions, and biotic interactions (Zajac and Whitlatch 2003). In deep subtidal habitats, larval settlement by opportunistic species is the primary method of recolonization, and succession proceeds in a somewhat predictable manner (McCall 1977, Rhoads et al. 1978). Following major disturbance such as a storm, juveniles and adults are often important recolonizers (Dobbs and Vozarik 1983). In shallower habitats, the infaunal community is often dominated by opportunistic species. Here, larvae are the primary recolonizers after disturbance, but succession is unpredictable and endpoints vary widely (Zajac and Whitlatch 1982a, b).

In shallow and intertidal environments, recovery after disturbance is greatly influenced by hydrodynamic factors (Eckman 1983). Many studies of sandy intertidal habitats have focused on how hydrodynamic factors influence recolonization (Turner et al. 1995, Palmer 1988, Norkko et al. 2001). Recolonization generally moves quickly in the sandy intertidal because in addition to larval settlement, adults and juveniles may actively burrow or be moved by bedload transport. For example, adult crustaceans colonized disturbed patches via passive dispersal within 24 days, with ambient densities attained approximately one month after disturbance (Grant 1981). In another experiment, researchers observed that colonization mechanisms differed widely among infaunal polychaete species but that densities in disturbed areas returned to ambient levels within twenty days (Shull 1997). However, these experiments were relatively small-scale and short term. Zajac and Whitlatch (2003) conducted an experiment to determine whether the trend of quick recovery after disturbance in sand flats held true at larger spatial scales (1 m^2) over longer periods (4.5 months versus days) The researchers examined population and community structure as well as sediment grain size as a measure of physical disturbance. Sediment grain-size distribution differed significantly in defaunated patches but returned to ambient levels after about two months. Populations of most species reached ambient levels two to three months after the sediment was defaunated, and the community structure returned to ambient conditions after four months. Published studies of recovery after disturbances (e.g., geoduck harvest) in Puget Sound are lacking. In British Columbia, Lochead et al. (2012b) collected shells from dead geoduck. The authors estimated that 89% of the geoduck deaths in 1991-1992 were likely due to wave disturbance of sediments during intense storms. During those years, however, strong recruitment pulses were also evident (Lochead et al. 2012b), suggesting recolonization can occur after significant disturbance.

Chapter 4

Predator-Prey Interactions

4.1 Introduction

Predation and competition play critical roles in regulating the distribution and abundance of benthic invertebrates (Virnstein 1977, Peterson 1982, Wilson 1990). The relative importance of pre- and post-settlement factors in structuring benthic communities is debated (Olafsson et al. 1994, Caley et al. 1996), but predation is considered more important than competition in regulating invertebrate populations (Micheli 1997). Because very few peer-reviewed studies examining geoduck predator–prey interactions are available, we include literature on predator–prey interactions involving other infaunal bivalve species.

4.2 Predation risk and geoduck life-history stages

Panopea generosa has a life cycle typical of many marine invertebrates, characterized by a planktonic larval stage and benthic juvenile and adult stages (Goodwin et al. 1979). Few studies have quantified predation on bivalve larvae, and we are not aware of any peer-reviewed literature that examines predation on geoduck larvae specifically. But species with type III life-history strategies, such as geoduck, generally suffer their highest mortality during the larval stage. Ingestion of bivalve larvae has been documented in a wide range of taxa, including polychaetes (Johnson and Brink 1998), fish (Bullard et al. 1999, Young and Davis 1992), ctenophores (Purcell et al. 1991), and heterotrophic dinoflagellates (Johnson and Shanks 2003). A large body of literature also documents the ingestion of bivalve larvae by bivalve adults (Andre et al. 1993; Tamburri and Zimmer-Faust 1996; Lehane and Davenport 2004, 2006; Pechenik et al. 2004; Zeldis et al. 2004). Filter-feeding taxa including many annelids and mollusks are abundant in benthic habitats of Puget Sound (Dethier and Schoch 2005). Given that geoduck at 14° C spend approximately 47 days as veligers (Goodwin et al. 1979), some proportion of geoduck larvae are probably ingested by filter feeders before settlement.

The population-level effects of filter feeders on bivalve larvae are difficult to quantify and are likely to be site- and species-specific. Some research has indicated that predation from filter-feeding bivalves has negative effects on bivalve recruitment (Andre and Rosenberg 1991, Andre et al. 1993). For example, researchers observed that 75% of common cockle (*Cerastoderma edule*) larvae were consumed when passing over high concentrations of adult conspecifics in laboratory experiments. Larvae in these experiments had a mean survival time of 64 seconds and settlement was reduced by one-third (Andre et al. 1993). However, other research indicates that predation by filter feeding has little or no ecological effect (Black and Peterson 1988, Ertman and Jumars 1988). In an apparent paradox, some species of bivalve larvae appear to preferentially settle near conspecific or other bivalve filter feeders (Ahn et al. 1993, Snelgrove et al. 1999, Tamburri et al. 2007). Using laboratory flume experiments, Tamburri et al. (2007) found that although *Crassostrea gigas* larvae were attracted to a soluble cue from adult conspecifics, more than 95% settled without predation. Larvae that passed very close to the valve were ingested by adult oysters and suffered mortality but due to weak ciliary currents, as little as 1 mm distance afforded protection. In field surveys of oyster reefs in Washington State, the estimated gape surface area was 5.2% of the plane surface area of the reef, suggesting that larvae passing over oyster reefs have a low probability of being ingested (Tamburri et al. 2007).

After settlement, geoduck spend several weeks as postlarvae. At this stage, geoduck are active crawlers and have spines on their shells (Goodwin et al. 1979, Velasquez, 1992) which may deter some predation. After two to four weeks as postlarvae, geoduck will have reached 1.5 to 2 mm in shell length and burrowed into the substrate (King 1986). Clam burial depth is directly related to shell and siphon length (Zwarts and Wanink 1989), as juvenile clams must remain shallowly buried to maintain contact with the water column. It has been shown that predation risk decreases with burial depth (Virnstein 1977, Holland et al. 1980, Haddon et al. 1987, Zwarts and Wanink 1989, Zaklan and Ydenberg 1997), thus, clams are most vulnerable to predation while they are small and shallowly buried. Two examples illustrate this point: Haddon et al. (1987) observed that predation on intertidal green surf clams (*Paphies ventricosa*) by the paddle crab (*Ovalipes catharus*) declined linearly with increasing burial depth. Likewise, blue crabs (*Callinectes sapidus*) consumed significantly more soft-shelled clams (*Mya arenaria*) buried at 5 and 10 cm than clams buried at 15 and 20 cm.

New Zealand pie crust crabs (*Cancer novaezelandiae*) and juvenile Dungeness crabs (*Cancer magister*) selectively forage on smaller soft-shelled clams (Creswell and McLay 1990, Palacios 1994), which may be due to burial depth but may also be directly related to size. Creswell and McLay (1990) documented that the New Zealand pie crust crab can crush smaller clams but must chip away at the shells of larger clams, increasing handling times and energetic costs. Given the lack of significant protection from their valves and extensive exposure of mantle and siphon tissues, juvenile and adult geoduck are likely to be extremely vulnerable to predation until they attain a depth refuge. However, as geoduck gain 20 to 30 mm on shell length per year and burrow deeper in the substrate during their first two to three years (Goodwin 1976), they may relatively quickly attain at least partial predation refuge.

Adult geoduck are generally found at 50- 60 cm burial depth (Goodwin 1976) although maximum depth is believed to be closer to one meter (e.g., Zhang and Hand 2006). Predation on adult geoduckis generally considered rare (Anderson 1971), but sea star predation has been observed (Mauzey et al.1968, Sloan and Robinson 1983). Natural mortality rate estimates of adult geoduck range from 0.0226 · y^{-1} to 0.039 · y^{-1} (Bradbury and Tagart 2000, Zhang and Campbell 2004). In addition, geoduck of all size classes may be vulnerable to siphon cropping, which has been shown to affect bivalve feeding and growth (Peterson and Quammen 1982, Kamermans and Huitema 1994, Nakaoka 2000).

4.3 Geoduck predators

Most studies on predation in marine soft-bottomed communities have focused on epibenthic predators, although predatory infauna also appear to play an important role (Ambrose, Jr. 1984). Research has documented predation on both adult and juvenile soft-shelled clams (*Mya arenaria)* and macoma clams (*Macoma balthica*) by infaunal organisms, including the nemertean worm *Cerebratulus lacteus* (Kalin 1984, Rowell and Woo 1990, Bourque et al. 2001) and the polychaetes *Nereis virens* and *Arenicola marina* (Ambrose 1984, Hiddink et al. 2002). At least one species of carnivorous nemertean and many carnivorous polychaetes, including a congener to *Nereis virens,* are found in Puget Sound (Dethier and Schoch 2005). Juvenile geoduck likely experience predation from predatory infauna, but this has not been investigated.

Common epibenthic bivalve predators include crabs, sea stars, gastropods, fish, birds, and mammals (Dame 1996). Research indicates that crabs influence clam distribution and abundance in soft-bottom habitats (Virnstein 1977). Common crabs in Puget Sound that prey on bivalves and are presumably capable of feeding on geoduck juveniles include the red rock crab (*Cancer productus*), graceful crab (*Metacarcinus gracilis*), and Dungeness crab (*C. magister*) (Jensen 1995). Dungeness crab prey on juvenile *M. arenaria,* and field studies suggest that this clam may be limited to areas of low Dungeness crab density (Palacios 1994). Stomach content analyses indicates that Dungeness crabs under one year ($\leq$ 60 mm) consume large quantities of bivalves (*Cryptomya californica*, *Macoma* sp. and *Tellina* sp.) in Grays Harbor, Washington (Stevens et al. 1982). Few studies have been done on the feeding habits of the red rock crab or graceful crab, and no studies have been completed that specifically examine crab predation on geoduck.

Many sea star species consume infaunal clams (Mauzey et al. 1968); sea stars at high densities have been shown to influence community structure and reduce bivalve population densities (Ross et al. 2002, Ross et al. 2004). The sea stars *Pisaster brevispinus* and *Pycnopodia helianthoides* have been observed consuming both juvenile and adult geoduck in the Pacific Northwest (Mauzey et al. 1968, Sloan and Robinson 1983). *P. brevispinus* is a large sea star commonly found on soft bottom sub-tidal habitats in Puget Sound (Mauzey et al. 1968) that preys efficiently on large, deeply buried bivalves by digging feeding pits (Van Veldhuizen and Phillips 1978). Sloan and Robinson (1983) reported that *P. brevispinus* in British Columbia fed preferentially on deeply buried clams, with geoduck making up one-third of its diet. Mauzey et al. (1968) also observed *P. brevispinus* consuming geoduck at Alki Point in Seattle, but noted that this occurred only occasionally there. The feeding pits created by *P. brevispinus* averaged 11.6 cm deep, with the deepest reaching 18 cm (Sloan and Robinson 1983). The circumoral tube feet extended on average an additional 16.6 cm, with the longest measured 23 cm (Sloan and Robinson 1983). These data suggest that *P. brevispinus* can prey on geoduck buried up to 40 cm. Adult geoduck at full burial depth are likely to be safe from *P. brevispinus* predation, but adult clams that are unable to burrow through an inpenetrable layer may be vulnerable. *Pycnopodia helianthoides* is another large Puget Sound sea star that can feed on infaunal clams by digging feeding pits (Mauzey et al. 1968). Large geoduck shells (95.8 mm average shell length) have been found at *P. helianthoides* feeding-pits, suggesting that this species can excavate deeply buried clams (Sloan and Robinson 1983). Geoduck may account for up to one-third of the diet of *P. helianthoides* (Sloan and Robinson 1983).

Although gastropod predation on infaunal bivalves is well documented (Peitso et al. 1994, Weissberger 1999, Kingsley-Smith et al. 2003, Savini and Occhipinti-Ambrogi 2006), there have been no published accounts of gastropod predation on geoduck. The moon snail (*Polinices lewisii*), a predatory gastropod common in Puget Sound, has been observed feeding on bivalves including littleneck clams (*Leukoma staminea*) and surf clams (*Spisula solidisima*) (Peitso et al. 1994). A congener, *P. pulchellus,* has also been observed feeding on the common cockle, *Cerastoderma edule* (Kingsley-Smith et al. 2003). Although not found in Puget Sound, *Rapana venosa* is another predatory gastropod that preys on mussels, oysters, and infaunal clams including northern quahog (*Mercenaria mercenaria*) and soft-shelled clams (*M. arenaria*) (Savini and Occhipinti-Ambrogi 2006). Although adult geoduck are likely to reach a depth refuge from gastropod predation, the impact of gastropod predation on juveniles should be investigated.

Juvenile clams are also preyed upon by many fish species. Whole juvenile bivalves have been found in the stomachs of such fish as English sole (*Parophrys vetulus*) and staghorn sculpin (*Leptocottus armatus*) in Grays Harbor, Washington (Armstrong 1991, Williams 1994). The European flounder (*Platichthys flesus*) forages on juvenile soft shell clams (*M. arenaria*) up to 12 mm in shell length (Moller and Rosenberg 1983). Fishes and crustaceans can also exert nonlethal predation pressure on bivalve populations by siphon-cropping (Armstrong 1991, Kamermans and Huitema 1994, Peterson and Quammen 1982, Sandberg et al.1996, Tomiyama and

Omori 2007). In order to feed, infaunal bivalves extend their siphons above the sediment, which exposes this soft tissue to predators. Meyer and Byers (2005) conservatively estimated that 10% of the clams *Leukoma staminea* and *Venerupis philippinarum* on San Juan Island exhibit cropped siphons at any given time (Meyer and Byers 2005). Geoduck siphons have been found in the stomachs of such fish as cabezon (*Scorpaenichthys marmoratus*) and spiny dogfish (*Squalus acanthia*) (Anderson 1971).

Siphon-cropping may negatively affect bivalve growth (Peterson and Quammen 1982, Kamermans and Huitema 1994, Irlandi and Mehlich 1996, Nakaoka 2000). Irlandi and Mehlich (1996) examined the effects of browsing fish on northern quahog (*M. mercenaria*) and the Atlantic bay scallop (*Argopecten irradians*). They observed that while both shellfish species showed lower weights and decreased shell growth, only scallop growth was significantly influenced by the presence of the nipping fish. Peterson and Quammen (1982) observed that littleneck clams (*L. staminea*) grew significantly less when caged with siphon-cropping fishes. The authors noted that clam feeding activity was unaffected by siphon-cropping fishes and concluded that the reduced growth resulted from energy being redirected to siphon regeneration (Peterson and Quammen 1982). However, other studies have demonstrated that siphon-cropping by fishes or arthropods affects bivalve feeding behavior (Irlandi and Peterson 1991, Kamermans and Huitema 1994, Irlandi and Mehlich 1996, Nakaoka 2000). For example, scallops spent more time with their valves closed in the presence of siphon-cropping fish (Irlandi and Mehlich 1996). It has been shown that clams such as *Nuttallia olivacea* regenerate their siphons relatively quickly (Tomiyama and Ito 2006) and that even intensive cropping (>25 times per individual per season) did not have serious impacts on *N. olivacea* (Sasaki et al. 2002, Tomiyama and Omori 2007).

While siphon-cropping does not generally cause death, it leads to decreased burial depth in *M. balthica* (De Goeij et al. 2001), *L. staminea*, and *V. philippinarum* (Meyer and Byers 2005). This decrease may facilitate secondary predation (Zwarts and Wanink 1989). De Goeij et al. (2001) observed that *M. balthica* buried less deeply after siphon-cropping and became increasingly vulnerable to avian predators including oystercatchers and red knots. However, Meyer and Byers (2005) found that this result was species-specific. The authors removed the top 40% of the siphon to simulate cropping in both *L. staminea* and *V. philippinarum*, and noted that cropped individuals burrowed 33 to 50% less deeply than intact conspecifics. These clams were then used in a field experiment on San Juan Island, Washington, where clams *Cancer* crabs are the primary agents of lethal clam predation. In *V. philippinarum*, cropped individuals experienced nearly double the mortality rate of intact individuals. In contrast, no significant increase in *L. staminea* mortality was observed (Meyer and Byers 2005). The authors attribute this difference to the fact that *L. staminea* has a longer siphon than *V. philippinarum* and can remain buried at relatively safe depths even after cropping. Although siphon-cropping has been noted on geoduck (Anderson 1971), no information is available indicating the extent, severity, affected size classes, tissue regeneration rates, or effects on burial depth.

Predation by birds can play a large role in structuring the intertidal marine invertebrate community (Clegg 1972, Cummings et al. 1997). Much research documents bird predation in rocky intertidal communities, and studies have also identified the importance of avian predators in marine soft-bottom communities (Richardson and Verbeek 1987, Szekely and Bamberger 1992, Thrush et al.1994, Zharikov and Skilleter 2003, Lewis et al. 2007). Two species of scoter, surf (*Melanitta perspicillata*) and white-winged (*M. fusca*), are thought to play a large role in shaping community structure by consuming huge quantities of clams while they overwinter in British Columbia (Lewis et al. 2007). *Venerupis philippinarum* and varnish clams (*Nuttallia obscurata*) were the primary prey of both scoters, making up 72 to 76% of their diets (Lewis et al. 2007). Other birds are also capable of consuming clams; northwestern crows (*Corvus caurinus*) have been observed digging and consuming *V. philippinarum* in British Columbia (Richardson and Verbeek 1987), and canvasbacks (*Aythya valisineria*) feed on multiple clam species, including *M. balthica, Macoma mitchelli, Mya arenaria*, and *Rangia cuneata* (Perry and Uhler 1988). The predatory bird species listed above spend at least some part of the year in Puget Sound, and could potentially be important predators on juvenile geoduck.

The sea otter (*Enhydra lutris*) has been well documented as a keystone predator in both rocky and soft-bottom habitats throughout its range in the northeastern Pacific (Garshelis et al. 1986, Kvitek et al. 1998). Sea otters were hunted to extinction off the coast of Washington early in the 20th century (Gerber et al. 2004). However, over the last decade, Washington's otter population has expanded dramatically, from 59 individuals translocated from Alaska (Jameson et al. 1982) to at least 550 (Kvitek et al. 1998, Gerber et al. 2004). Sea otters exert a strong influence on infaunal prey communities in soft-sediment habitats (Kvitek et al. 1992). Direct observations of feeding otters at 11 sites in Southeast Alaska showed infaunal clams to be their primary prey. The abundance, biomass, and size of prey bivalves were inversely related to duration of sea otter occupancy (Kvitek et al. 1992). However, otter-cracked shells of the deep-burrowing clams *Tresus capax* and *P. generosa* were only rarely found, even at otter foraging sites where these clams accounted for the majority of available prey biomass, suggesting that these species have a partial depth refuge from otter predation (Kvitek and Oliver 1992, Kvitek et al. 1993). It is important to note that otters have been observed excavating clams up to 0.5m deep (Hines and Loughlin 1980) and could certainly prey on juvenile and possibly on adult geoduck. No research has been done on this topic specific to Puget Sound.

B

Ecological Effects of Geoduck Aquaculture

Chapter 5

Abiotic and Biotic Effects

5.1 Introduction

Although Pacific geoduck have been cultured in Washington State to enhance wild stocks since 1991 (Beattie 1992) and on a commercial scale since the mid1990s (Brown and Thuesen 2011), little work had been done on the ecological impacts of these practices until the initiation of the Washington Sea Grant Geoduck Aquaculture Research program in 2008. Most of the research conducted under the auspices of this program has not yet been subjected to formal peer review. For this reason, we draw heavily on literature describing effects of cultivating other filter-feeding bivalves to provide a framework for thinking about the potential effects of geoduck aquaculture. Although there is a large body of literature on the environmental impacts of bivalve aquaculture, most of it has examined oyster and mussel culture (Crawford et al. 2003; Lehane and Davenport 2004, 2006; Zeldis et al. 2004; Grant et al. 2007a), while fewer have focused on clam culture (Spencer et al. 1997, Jie et al. 2001, Nizzoli et al. 2006, Munroe and McKinley 2007, Whiteley and Bendell-Young 2007). We have focused on clam culture whenever possible, although we present examples from oyster and mussel culture when necessary. In this Section, we will discuss the potential biotic and abiotic effects of geoduck aquaculture on water quality, substrate, community structure, and carrying capacity. The potential for genetic perturbation and disease transmission from cultured to wild stocks will be reviewed in later chapters.

5.2 Water quality

Many bivalves feed by filtering suspended particulate matter from the water column. Filtration rates have not been published for *Panopea generosa*, but rates can be estimated because bivalve filtration appears to be correlated with size (Winter 1978, Powell et al. 1992). If geoduck filtration is similar to that in other lamellibranchs of similar size, filtration rates could range from 7 to 20 $L \cdot hr^{-1}$ per individual (Powell et al. 1992) as estimated from shell length in oysters. The veracity of this estimate is uncertain, however, since a geoduck of a given shell length is far more massive than an oyster of the same length. The range reported is due to the fact that even within a species and size class, the filtration rate varies depending on many environmental parameters plus the condition, health status, and satiation level of the individual.

Although geoduck filtration rates are not known, it is clear that high densities of suspension feeding bivalves can dramatically impact water quality in myriad ways (Newell 2004). Numerous studies have shown that filter-feeding bivalves can locally decrease phytoplankton abundance in both natural (Asmus and Asmus 1991, Cressman et al. 2003, Grizzle et al. 2006) and cultured settings (Strohmeier et al. 2005, Grizzle et al. 2006). In tidal creeks in North Carolina, water upstream of oyster reefs contained an average of 25% more chlorophyll *a* than water downstream (Cressman et al. 2003). Phytoplankton depletion has also been documented in both natural and farmed beds of mussels (*Mytilus edulis*). Phytoplankton biomass was reduced by 37% after passing over an intertidal mussel bed (Asmus and Asmus 1991), and the concentration of chlorophyll *a* decreased with passage through a mussel farm in Norway, with more than 50% of the phytoplankton entering depleted at the middle of the farm (30 m) (Strohmeier et al. 2005). Evidence indicates that the Northern quahog is also an efficient filter feeder: Chlorophyll *a* was 62.3% lower downstream from a Virginia quahog farm than upstream (Grizzle et al. 2006). Additionally, it has been suggested that bivalve filter feeding controls plankton concentrations on a larger scale (Cloern 1982, Grant et al. 2007a). Cloern (1982) suggests that bivalve filter feeding is the principal mechanism controlling phytoplankton biomass in South San Francisco Bay. Evidence gathered using airborne remote sensing indicates that high densities of bivalves in an aquaculture setting deplete phytoplankton on an ecosystem scale (Grant et al. 2007a). Grant et al. (2007a) found reduced chlorophyll throughout a blue mussel (*M. edulis*) farm in eastern Canada with successive depletion of chlorophyll in the direction of flow through the farm. In addition to reducing the concentration of phytoplankton, filter-feeding bivalves may also change the composition of phytoplankton species by selective filtration (Shumway et al. 1985).

In addition to removing phytoplankton, bivalve filter feeding removes inorganic particles from the water column, reducing turbidity (Newell 2004). The reduced turbidity results in deeper light penetration, which can improve the condition for submerged aquatic vegetation (SAV), including sea grasses (Newell and Koch 2004). Wall et al. (2008)

found that high-density bivalve treatments (i.e., mussels, oysters, or clams) reduced chlorophyll *a*, increased light penetration, and increased productivity of eelgrass (*Zostera marina*) in laboratory mesocosms. Eelgrass growth increased on average 48 ± 9.3% when bivalves were present relative to controls without bivalves. There are several cases of dramatic ecosystem changes attributed to the robust filtering ability of bivalves. The loss of historical oyster reefs in Chesapeake Bay, for example, has been associated with phytoplankton blooms, increased turbidity and the loss of SAV (Moore et al. 1996, Moore and Wetzel 2000, Jackson et al. 2001). Wall et al. (2011) produced a conceptual model based on mesocosm experiments to explain the relationship between nutrient loading and bivalve filtration. Increased nutrient loading promotes phytoplankton growth, while higher densities of adult bivalves act to reduce phytoplankton abundance; thus feeding by adult bivalves reduces growth of small bivalves and planktivorous fish by reducing food availability but increases seagrass growth because of improved light penetration (Wall et al. 2011).

Introduced clams have had a striking impact on several U.S. ecosystems. The introduction of the Asiatic clam (*Corbicula fluminea*) in the Potomac River estuary decreased turbidity and was linked to the reappearance of eelgrass in areas from which it had been absent for fifty years (Phelps 1994). On the other hand, invasive clams (*Potamocorbula amurensis*) introduced in San Francisco Bay have altered food-web dynamics via phytoplankton depletion to the detriment of native copepods (Kimmerer et al. 1994). It has also been shown that some mussel species ingest zooplankton (e.g., Davenport et al. 2000, Zeldis et al. 2004, Lehane and Davenport 2006).

Filter feeding also removes nitrogen and phosphorus from the water column, nutrients that may ultimately be removed from the ecosystem via the harvest of cultured bivalves. *Crassostrea virginica* meat and shell (dry weight) contain nitrogen (7% and 0.3%, respectively) and phosphorus (0.8% and 0.1%, respectively) (Galtsoff 1964). Thanks to this nutrient-removal capacity, bivalve aquaculture can improve water quality. Several authors have suggested aquaculture approaches to mitigate eutrophication pressure in coastal systems (Newell 2004, Lindahl et al. 2005, Zhou et al. 2006) if the ecological carrying capacity (Section 5.7) is not exceeded (but see comments by Nizzoli et al. 2011). Carmichael et al. (2012) explicitly demonstrated that oysters (*C. virginica*) remove nitrogen produced from anthropogenic sources. However, efforts to use bivalves for bioremediation will be most effective when nitrogen loads are moderate, suitable bivalve habitat is available, and oysters can be used; the authors point out that these conditions are not typically met where action is most needed (Carmichael et al. 2012).

5.3 Substrate

Many marine bivalves, like geoduck, filter particles from the water column and deposit them onto the substrate, both with and without digestion (feces and pseudofeces respectively; together called biodeposits). Although geoduck biodeposition has not been explicitly examined, biodeposition in other species is well studied. Bivalve biodeposits are high in carbon and nitrogen (Kautsky and Evans 1987, Giles and Pilditch 2004), show high microbial activity, and may increase denitrification (Kaspar et al. 1985). Biodeposition increases the flow of particulate nutrients to the sediment, increases sediment oxygen demand, and may increase dissolved nutrients in the water column (Giles and Pilditch 2006). It thus plays a key role in benthic-pelagic coupling (Kautsky and Evans 1987) and can have substantial ecological effects. For example, the presence of the mussel *Modiolus americanus* significantly increased the productivity of turtle grass (*Thalassia testudinum*) in Florida (Peterson and Heck 2001). Increased growth was due to mussel biodeposition: Mussels increased the nutrient content of the sediment and when plants took up these nutrients they exhibited enhanced growth (Peterson and Heck 2001). A similar study examined interactions between eelgrass (*Z. marina*) and an introduced mussel (*Musculita senhousia*) in California (Reusch and Williams 1998). This experiment demonstrated that mussel presence generally increased eelgrass productivity, although at high densities mussels inhibited eelgrass rhizome extension. Ruesink and Rowell (2012) observed increased size and branching of individual shoots within intact eelgrass meadows that had been planted with geoduck; the authors hypothesized that nutrient release by geoduck facilitated increased size and growth. However, the presence of geoduck also reduced shoot density, which suggests that the response may have been associated with reduced intraspecific competition (Ruesink and Rowell 2012).

Multiple field and laboratory studies have examined the effects of increased biodeposition resulting from high concentrations of bivalves in a culture setting. The biodeposition rates of the scallop *Chlamys farreri* were 34 to 133 mg dry material · $ind.^{-1}$ · day^{-1}, with mean rates of carbon, nitrogen, and phosphorus biodeposition of 4.00, 0.51, 0.11 mg · $ind.^{-1}$ · day^{-1} respectively for a year-old scallop (Zhou et al. 2006). It is well documented that benthic respiration and sediment ammonia concentrations are higher under longline mussel farms than at reference sites (Kaspar et al. 1985, Hatcher et al. 1994, Christensen et al. 2003, Giles et al. 2006). Changes in sediment and water have also been documented in Manila clam (*V. philippinarum*) culture. In a study of a lagoon system in Northern Italy, water at reference sites had five to nine times more nitrogen and phosphorus than aquaculture sites, while the latter showed significantly more dissolved P and increased ammonia concentrations in the sediment than the former (Nizzoli et al. 2006). Nizzoli et al. (2011) found evidence of seasonal "hotspots" of nutrient flux in the same lagoon, with net nitrogen and phosphorus release associated with clams substantially higher than reference sites. Because of these results, the authors cautioned against assuming the clams might help mitigate cultural eutrophication, particularly during the summer when nutrient inputs from other sources are low (Nizzoli et al. 2011).

As biodeposition increases organic carbon levels and thus sediment oxygen demand (Giles and Pilditch 2006), high rates of biodeposition may lead to anoxic conditions. The mechanism for anoxia was demonstrated at an oyster farm in France (Castel et al. 1989). Oyster biodeposition raised sediment carbon levels, which increased oxygen demand. These changes led to anoxia, which caused localized changes in benthic diversity (Castel et al. 1989). Contrary to these trends however, a study examining longline subtidal oyster and mussel farms in Tasmania found no differences between farm and control sites in sediment deposition, sediment sulphide concentrations, organic carbon content, or water turbidity. This may be due to the low stocking densities used in Tasmanian shellfish farms (Crawford et al. 2003). Similarly, a study by Harbin-Ireland (2004) in Drakes Estero, California, found no difference in organic matter in areas surrounding subtidal oyster racks; thus site-specific factors, including gear placement and flow, are likely critical determinants of effects. For example, in experimental plots in Coos Bay, Oregon, Everett et al. (1995) found increased biodeposition in oyster stake plots, while nearby rack plots experienced reduction in carbon content.

Many studies have shown that shellfish aquaculture can lead to increased sedimentation (Giles et al. 2006, Mallet et al. 2006, Zhou et al. 2006). As biodeposits accumulate on the benthos at shellfish aquaculture operations, sediment grain size is frequently reduced and organic content increases (Hargrave et al. 2008, Dumbauld et al. 2009). For example, sedimentation was found to be nearly 2.5 times greater under scallop (*C. farreri*) cultures than at reference sites in China (Zhou et al. 2006). However, these studies generally examine suspended or off-bottom aquaculture. Dumbauld et al. (2009) describe limited experimental evidence suggesting on-bottom oyster culture promotes smaller grain size and higher organic content relative to reference sites in Willapa Bay, but caution that general patterns likely hinge on the underlying attributes of local sediment and flow patterns.

Clam species including geoduck are vulnerable to predation in the early stages of culture and are grown under protective netting during the early stages when they are vulnerable to predation (Spencer et al. 1992). This practice has been shown to increase the survival of juvenile Manila clams (*V. philippinarum*) in the United Kingdom and Spain (Spencer et al. 1992, Cigarria and Fernandez 2000) as well as juvenile soft-shell clams (*Mya arenaria*) in eastern Maine (Beal and Kraus 2002). Netting has also been implicated in increased sedimentation (Spencer et al. 1996, 1997; Goulletquer et al. 1999). Spencer et al. (1996) found sedimentation four times higher on netted Manila clam plots than on non-netted plots. Goulletquer et al. (1999) also observed increased sedimentation on netted Manila clam plots. Spencer et al. (1997) compared netted Manila clam plots, netted plots without clams, and control plots without nets or clams and found that it was the nets rather than the clams that caused increased sedimentation. In contrast, a study in British Columbia compared paired netted and non-netted Manila clam plots and found no significant differences in sedimentation or gravel accumulation (Munroe and McKinley 2007). It appears that the influence of predator exclusion netting on sedimentation is site-specific; these effects should be investigated in geoduck aquaculture in Puget Sound.

5.4 Effects of tubes

There is only one peer-reviewed study available on the ecological impacts of the mesh-covered polyvinylchloride (PVC) tubes currently used to protect seed in geoduck aquaculture. Brown and Thuesen (2011) used trapping surveys at a single location in Eld Inlet, Washington, to examine the species, composition, relative abundance, and diversity of mobile benthic macrofauna at a geoduck aquaculture site and a reference site. Although Coleman rarefaction analysis found that species richness was significantly higher at the aquaculture site, the total number of taxa was low; the result can be attributed to the larger number of graceful crab (*Metacarcinus gracilis,* formerly *Cancer gracilis*) captured at the reference site. Overall, more organisms were captured in traps set on the reference site than within the geoduck aquaculture site. The limited spatial and temporal scope of the study makes interpretation and generalization of the results difficult. The use of PVC tubes is unique to geoduck culture, and culture techniques are evolving rapidly; thus, in Section 5.5 we consider the role of other bivalves and related gear on community structure of infauna, epifauna and mobile macrofauna.

5.5 Community structure

The effects of shellfish aquaculture on benthic faunal communities are strongly debated, as many contrasting effects have been reported. For instance, mussel culture led to increased species diversity in a small Nova Scotian cove (Grant et al. 1995), benthic macrofauna density was lower at French oyster aquaculture sites relative to reference sites (Castel et al. 1989), and no significant differences in benthic infauna were observed between farms (mussel and oyster) and reference sites in Australia (Crawford et al. 2003). The impacts of clam harvest on the surrounding benthic community are covered in Section 5.6 below.

In general, effects on benthic infauna are most pronounced in soft sediment habitats directly below, or immediately adjacent to, shellfish aquaculture operations as a function of organic enrichment via biodeposits (Dumbauld et al. 2009). In off-bottom aquaculture (e.g., suspended culture), the balance of biodeposition and water flow, which removes deposits, tends to be the strongest determinant of community structure (Dahlback and Gunnarsson 1981, Mattsson and Linden 1983, Grant et al. 1995, Crawford et al. 2003). Crawford et al. (2003) compared the benthic environment under longline mussel and oyster farms in Tasmania, Australia, and found that benthic community structure was not significantly different between farm and reference sites. Greater differences in benthic infauna were found among farms than between farm and reference sites, suggesting that local conditions may dictate how the benthic environment is affected by shellfish aquaculture. Grant et al. (1995) found relatively minor changes in benthic macrofauna between mussel culture and reference sites in Nova Scotia. Reference sites showed higher abundance of benthic macrofauna but lower biomass, and species diversity was higher at the farm sites. Conversely, the benthic community under a New Zealand longline mussel farm experienced dramatic declines in species diversity, from a healthy and diverse complex of species to a community consisting entirely of infaunal polychaetes (Kaspar et al. 1985).

Benthic communities associated with on-bottom culture operations are also affected by changes in structural complexity and space competition, and these effects can be difficult to parse from changes in biodeposition (Dumbauld et al. 2009). Castel et al. (1989) compared rack and bag and on-bottom oyster aquaculture sites in Arcachon Bay, France, to reference sites and observed dramatic changes to the benthic community; meiofauna levels were three to four times higher at the oyster farms, while macraofauna levels were approximately 50% lower at the oyster farm (Castel et al.1989). In studies comparing benthic habitats in Willapa Bay, Washington, abundance was higher in on-bottom oyster aquaculture and eelgrass beds than in unstructured mudflat habitat (Hosack et al. 2006), and and diversity was similar (Ferraro and Cole 2007). Quintino et al. (2012) used a nested experimental design to specifically investigate the relative contributions of biodeposition and oyster trestles in the Ria de Aveiro lagoon, Portugal. They found that the diversity and biomass of the benthic community were reduced only when oysters were present on the structures, indicating that the structures alone had no effect and biodeposition influenced changes in the benthic community (Quintino et al. 2012).

Hard structures placed on or above low-relief mud or sand habitats represent a novel substrate in the form of solid surfaces fixed in space (e.g., Wolfson et al. 1979). Yet the architecture and relief of suspended mussel rafts or rack-and-bag and on-bottom oyster culture operations described above differ dramatically from conditions in clam aquaculture. Simenstad and Fresh (1995) examined infauna and epifauna communities at Manila clam aquaculture sites covered with protective netting and adjacent reference areas. Those authors concluded that responses were site-specific and likely driven by inherent levels of natural disturbance. Whitely and Bendell-Young (2007) likewise observed few impacts of Manila clam aquaculture on bivalve community structure; aside from increased Manila clam abundance at farm sites, no differences in bivalve species composition were found between farm and reference sites. In contrast, Spencer et al. (1997) found that the netting used to reduce Manila clam predation led to changes in benthic community composition consistent with organic enrichment. Particularly, they observed an increase in surfacedeposit-feeding worms with the opportunistic *Pygospio elegans* dominating the fauna in the first six months of clam culture and other surface deposit-feeding worms dominating after one year. In the non-netted plots a sub-surface deposit-feeding worm, *Scoloplos armiger,* dominated the community. The authors suggest that competition from surface deposit-feeding worms on the netted plots may have excluded *S. armiger*. Structures associated with clam culture can become fouled with algae, which may provide additional emergent habitat. Powers et al. (2007) observed higher densities of mobile invertebrates and small fish around clam culture bags than in adjacent reference areas. Community structure around the fouled aquaculture gear was similar to that in nearby seagrass areas (Powers et al. 2007).

Mobile consumers such as fish and macroinvertebrates are often drawn to structures on low-relief soft-sediment habitats (e.g., Davis et al. 1982), a pattern attributed to enhanced resource supplies for detritivores (e.g., sea cucumbers), herbivores (e.g., urchins and some crab species) and predators (e.g., sea stars and other crab species) (Inglis and Gust 2003, Dubois et al. 2007). Moreover, these structures may serve as refugia that reduce predation risk (e.g., Dealteris et al. 2004), especially for juvenile life-history stages (e.g., Powers et al. 2007). For instance, a striking increase in predators under longline mussel culture was also observed in New Zealand, with mean densities of the sea star *Coscinasterias muricata* up to 39 times greater at farm sites than at reference sites (Inglis and Gust 2003). A decrease in suspension feeders and an increase in predators has also been noted beneath oyster farms (Dubois et al. 2007).

The habitat value of aquaculture gear may be comparable to that of naturally occuring structures. Dealteris et al. (2004) observed higher densities of several fish and invertebrates and greater species richness around rack-and-bag oyster culture than in seagrass beds and unstructured reference areas in Point Judith Pond, Rhode Island. Elsewhere in Narragansett Bay, Tallman and Forrester (2007) found that scup (*Stenotomus chrysops*) and tautogs (*Tautoga onitis*), two species commonly associated with hard-bottom habitats, were more abundant at oyster grow-out sites consisting of tiered bags than on natural or artificial reefs. Although the scup grew more quickly on natural rocky reefs, they showed higher fidelity to oyster bags (Tallman and Forrester 2007).

Intertidal geoduck culture operations are sited in locations that may overlap with bird foraging habitat. Sea and shorebirds, particularly waders (e.g., plovers and oystercatchers) and divers (e.g., scaup and scoters), may benefit from an increased concentration of cultured bivalves or high abundance of other prey associated with shellfish or aquaculture gear (Dumbauld et al. 2009, Forrest et al. 2009, and references therein). Some bird species may be drawn to aquaculture sites by the provision of new perching and roosting areas (e.g., buoys and platforms) that can be used for hunting or resting (Roycroft et al. 2004). Conversely, potential negative effects associated with shellfish aquaculture may result from direct disturbance by personnel working at farm sites or indirectly through changes in prey abundance and displacement from foraging areas (Kaiser et al. 1998, Bendell-Young 2006). Moreover, some species may be at risk of entanglement in aquaculture gear (Forrest et al. 2009). Responses depend largely on species-specific food and habitat requirements, likely producing additional effects on other trophic levels (e.g., Connolly and Colwell 2005).

Overall, these interactions are not well studied in clam aquaculture. One paper examines the effects of shellfish aquaculture on winter scoter populations in Baynes Sound, British Columbia (Zydelis et al. 2006). Baynes Sound is an area of extensive shellfish culture that produces approximately 50% of British Columbia's cultured shellfish (Ministry of Sustainable Resource Management 2002, as cited by Zydelis et al. 2006). Over 20% of the intertidal in Baynes Sound is used for shellfish cultivation, and clam netting covers 2.9% (Carswell et al. 2006). However, the authors found no correlation between shellfish aquaculture variables and bird density and concluded that winter scoter populations and the current aquaculture practices were mutually sustainable. Similar conclusions were reached in a study looking at the impact of on-bottom mussel culture on bird assemblages (Caldow et al. 2003). Although bird assemblages changed after the mussels were placed, two key species increased in abundance, and none decreased.

5.6 Effects of harvest

Geoduck are commercially harvested using pressurized water to quickly liquefy and dig out sediment. This may alter abiotic conditions in the sediment (e.g., grain size, oxygen, nutrient levels) as well as the community of benthic organisms. This method is unique to geoduck culture. Ruesink and Rowell (2012) examined the effects of this harvest on eelgrass, but no comprehensive study examines its effects on sediment and fauna. We instead review the available data on other forms of clam harvest, including dredging, hydraulic harvest, and hand raking. The breadth and depth of disturbances from these forms of harvest, while not directly comparable, may help illuminate the effects of geoduck harvest.

The environmental effects of intertidal clam harvest have been examined in both Europe and North America for species including the Manila clam (*V. philippinarum*), common cockle (*Cerastoderma edule*), and Northern quahog (*M. mercenaria*) (Peterson et al. 1987, Kaiser et al. 1996, Hall and Harding, 1997, Spencer et al. 1998, Badino et al. 2004). In general, suction or mechanical harvest is a physical disturbance associated with sedimentary andinfaunal changes. In most cases, mechanical harvest reduced both the number of species present and their abundance. For example, both the sediment and the benthic community were highly disturbed by mechanical harvest of Manila clams in Italy (Badino et al. 2004). A significant decrease in benthic organisms was observed after harvest. Dredging also resuspended the top layer of sediment and brought deeper anoxic sediments up, which could potentially reduce the rate of recolonization. Harvesting clams by hand raking has also been documented to mix sediment layers (Badino et al. 2004) and reduce infaunal species abundance and richness in the short term (Brown and Wilson 1997). However, Boese (2002) found that hand raking for cockles (*Clinocardium nuttalli*) and digging for gaper (*Tresus capax*) and butter clams (*Saxidomus giganteus*) in Yaquina Bay at Newport, Oregon, did not impact infaunal species number or abundance. Likewise, raking or dredging for Northern quahog, (*M. mercenaria*) did not appear to affect the species composition or density of small benthic macroinvertebrates in North Carolina (Peterson et al. 1987).

Rates of recolonization by benthic fauna can range dramatically depending on oceanographic conditions (sediment type and stablility, wave action, currents), season, location, scale of disturbance, and whether recolonization occurs primarily through adult movement or larval settlement (Hall and Harding 1997, Kaiser et al. 1998). Hall and Harding (1997) found that immediately following suction-dredge cockle harvesting, sites had an average of 30% fewer species and 50% fewer individuals. However, after 56 days the faunal assemblages at these disturbed sites were not significantly different from those at control sites. A similar study found that suction-dredge harvesting of Manila clams at an aquaculture site suspended the sandy layer, leaving the underlying clay substrate intact, and significantly reduced both infaunal diversity and the mean number of individuals per sample (Kaiser et al. 1996). However, after seven months neither sediment composition nor benthic fauna were significantly different from those at control sites. The authors concluded that clam cultivation did not have long-term effects on the substrate or benthic community.

The spatial scale of disturbance is likely to impact recovery, and most studies have taken place on small scales. However, Hall and Harding (1997) found that the benthic fauna at harvested sites came to resemble to those at control sites within three months of harvest, regardless of the scale of disturbance, which ranged from 225 to 2,025 m^2. Although aquaculture harvest is likely to take place at a larger scale than those examined in the study, the authors emphasized that those areas might be patchily distributed and unlikely to further extend the trajectory of recovery. It is clear, however, that these results are likely specific to both site and harvest technology, and need to be tested against geoduck culture in Puget Sound.

Clam harvest has also been shown to affect seagrass. Raking and light dredging to harvest Northern quahog reduced seagrass biomass by 25%, but recovery was complete within one year (Peterson et al. 1987). On the other hand, heavy dredging in the same area caused a 65% decline in seagrass biomass, and full recovery had not been documented after four years (Peterson et al. 1987). A separate study showed that raking did not affect eelgrass (*Zostera marina L.*) cover or biomass, but digging clams individually reduced them no significant differences were observed after ten months (Boese 2002). Individually digging clams was also shown to reduces shoot density and biomass of the seagrass *Zostera noltii* (Cabaco et al. 2005), although it is unclear how long these changes persisted because this study did not include temporal change data. Ruesink and Rowell (2012) conducted the only study of geoduck harvest effects on eelgrass. At the end of a two-year experiment, geoducks were harvested using a sediment-liquefaction method similar to commercial techniques, which resulted in a 70% reduction in eelgrass density in experimental plots. Although the plots were tracked over the following year, a dramatic loss of eelgrass in both the treatment and reference plots precluded any assessment of recovery (Ruesink and Rowell 2012).

5.7 Carrying capacity

Before discussing carrying capacity in bivalve aquaculture, we must define the term. Two distinct definitions of carrying capacity are frequently used in aquaculture. Production carrying capacity (PCC) is the level of culture at which production is maximized without negatively affecting the growth of the cultured species (Carver and Mallet 1990). It would be relatively simple to determine PCC for geoduck in the field simply by expanding the density of cultured clams while monitoring growth rates. PCC is reached when growth rates begin to fall. However, there are likely to be significant ecological changes in the surrounding community before PCC is reached. Byron et al. (2011a) contend that bivalve aquaculture should be addressed as an issue in ecosystem-based management (EBM), as such an approach considers the ecosystem and the diverse socioeconomic interests of stakeholder groups. Under ecosystem-based management, ecological carrying capacity (ECC) is a more important metric. ECC is the highest level of culture that can be undertaken without precipitating significant changes in ecological processes, individual species, or communities in the surrounding habitat (Gibbs 2007); ECC is by definition lower than PCC. For example, Jiang and Gibbs (2005) predicted the carrying capacity of the greenshell mussel (*Perna canaliculus*) in the Tasman/Golden Bay system in New Zealand using a steady, linear food web model. Production carrying capacity was estimated to be a mussel yield of 310 $t \cdot km^{-2} \cdot year^{-1}$. By contrast, environmental carrying capacity was pegged at a yield of 65 $t \cdot km^{-2} \cdot year^{-1}$, approximately 20% of PCC. The model indicated that introducing mussel culture at production carrying capacity would lead to decreased mean ecosystem trophic levels as bivalves replaced zooplankton as primary phytoplankton consumers (Jiang and Gibbs 2005).

Determining ECC for geoduck in Puget Sound would be a challenging exercise, although, by determining ECC in multiple isolated embayments that vary substantially from one another, we could potentially estimate ECC for the whole Sound. However, ECC can vary dramatically within and across regions. For example, the environmental carrying capacity of Narragansett Bay, Rhode Island, was estimated to be 297 $t \cdot km^{-2}$, more than 625 times current levels of production (Byron et al. 2011b). (The potential for increase is largely driven by high primary productivity and energy throughput to detritus in the system.) This, however, was less than half the ECC of adjacent lagoons (722 $t \cdot km^{-2}$; Byron et al. 2011c), indicating the importance of basin-specific patterns. In this case, the unique zooplankton assemblage of Narragansett Bay contributed to the discrepancy in ECC values (Byron et al. 2011b).

Studies of the environmental impacts of aquaculture often focus on effects upon the benthos under farms. This may be more appropriate for finfish culture, where ecological carrying capacity is most often dictated by benthic ability to absorb waste products. Carrying capacity in bivalve aquaculture is more often dictated by the amount and availability of food in the water column. Because cultured bivalves compete with other filter feeders, bivalve aquaculture has the potential to displace other animals in the food web. For example, at the theoretical production carrying capacity, the food web collapses into a nutrient-phytoplankton-bivalve web because the bivalve culture has out-competed zooplankton and other benthic filter feeders (Gibbs 2004). Similarly, increased production in oyster aquaculture beyond ecological carrying capacity in an Ecopath model of Narragansett Bay resulted in overgrazing of microzooplankton (Byron et al. 2011b).

Estimating bivalve carrying capacity is not an easy task, because increased bivalves in culture may alter nutrient cycling (Section 5.3); quantifying bivalve carrying capacity is an active area of research. Many NPZ (nutrient-phytoplankton-zooplankton) models have been developed that predict the carrying capacity of bivalves in coastal regions (Bacher et al. 1997, Smaal et al. 1997, Duarte et al. 2003, Grant et al. 2007b). An alternative approach is to use performance indicators such as clearance efficiency or phytoplankton depletion footprints to assess the impact of the culture in real time (Gibbs 2007). It should be noted that both approaches (models and performance indicators) rely heavily on filtration rate data, which are currently lacking for geoduck.

There are no available peer-reviewed studies on geoduck carrying capacity or bivalve carrying capacity in Puget Sound. We have chosen not to review carrying capacity for other bivalves in other bodies of water because this would not add to our knowledge about geoduck culture in Puget Sound. However, we will give one example to illustrate that location and model selection dramatically influence predictions. Sara and Mazzola (2004) used two models to assess the production carrying capacity of the mussel *Mytilus galloprovincialis* in two Italian locations. Numerous parameters including current, filtration rate, and chlorophyll *a* were measured and included in the models. The two locations differed widely in currents and phytoplankton availability, and thus, in regards to estimated carrying capacity. Using the original Incze model (Incze et al. 1981), the predicted PCC for the two regions was 2,034 tons in the better locale and 403 tons in the poorer. Using the Incze modification (Martincic 1998, as cited by Sara and Mazzola 2004), the predicted carrying capacity was 200 tons in the better locale and 160 tons in the poorer (Sara and Mazzola 2004). Clearly, model selection is an important factor, and location may be highly influential in estimating carrying capacity and determining appropriate siting for a farm.

Chapter 6

Disease

6.1 Introduction

An understanding of the relationship between host, pathogen, and the environment, as well as the ecological impacts of disease in aquatic systems, is critical for proper management and prevention of infectious disease outbreaks in both aquaculture and natural settings. There are many studies dedicated to this topic but few peer-reviewed articles on diseases specific to Pacific geoduck. However, Bower and Blackbourn (2003) conducted numerous surveys and experiments regarding wild Pacific geoduck health. We believe the information they present, while not peer-reviewed, is valuable. and so we discuss their work below. In Section 6.4, we refer extensively to the web publication of Bower and Blackbourn (2003). We will also discuss literature related to transmission, prevalence, and distribution of diseases in other marine bivalve species in Washington and highlight work specific to clams in the *Panopea* genus.

6.2 Aquaculture impacts on disease prevalence and distribution in the Pacific Northwest

Many pathogens that cause disease in shellfish are facultative forms ubiquitous in aquatic systems. In nature, a high percentage of apparently normal and healthy animals harbor potential pathogens without clinical signs or overt evidence of disease. The development of disease in aquaculture systems often occurs via disruption of the environment in which the animals are reared. Unfavorable conditions such as crowding, temperature fluctuations, inadequate dissolved oxygen, excessive handling, inadequate diets, and toxic substances may stress the animals; if the level of stress exceeds the ability to adjust, clinical disease may occur (Meyer 1991). Contact between individuals greatly affects the dynamics of infectious disease. High host density increases contact rates between infected and uninfected individuals (May et al. 1981).Dense populations therefore tend to have more parasites, which means some epizootics could be due to increasing host density as well as outside stressors (Arneberg 2001). Factors that determine the taxonomic range of hosts that can be infected by a specific pathogen are also veryimportant. Host specificity relates both to the co-evolution of host susceptibility and pathogen virulence, as well as to factors underlying the emergence of new pathogens. How pathogens evolve and adapt to new hosts is crucial to understanding the fundamental basis for the origin of infectious diseases as well as the emergence of new pathogens.

Several factors underlie the increase in reported shellfish disease outbreaks. Transportation of stocks as well as climate change have been implicated in the expansion of dermo and possibly MSX (multinucleated sphere unknown) diseases of Eastern oysters (*Crassostrea virginica*) in the United States (Andrews 1996, Cook et al. 1998, Hofmann et al. 2001). Parasites have been introduced into new areas through increased shipment of host shellfish for aquaculture (Elston et al. 1986, Bustnes et al. 2000). These newly introduced animals may be susceptible to local pathogens (Ford et al. 2002). There are many examples of species that have acted as vectors for the spread of hitchhiking species that function as predators, competitors, and pathogens to natives (Ruiz et al. 2000). In addition, non-native species may serve as reservoirs for enzootic pathogens formerly at low abundance, facilitating their proliferation to levels that threaten native species (Bishop et al. 2006).

In addition to disease, shellfish fall prey to introduced predators. Two major predators have been introduced with Pacific oyster seed over the years: the Japanese oyster drill (*Ocenebra japonica*) and the turbellarian flatworm *Pseudostylochus ostreophagus*. These species are now prevalent in various oyster-growing bays in the state of Washington and in Humboldt Bay in California (Chew 1991). Culture conditions in shellfish hatcheries may also be a source of disease outbreaks as the high densities under which animals are grown and the high temperatures maintained favor the proliferation and transmission of opportunistic pathogens (Elston and Wilkinson 1985, LeDeuff et al. 1996)

Numerous shellfish disease outbreaks have occurred in the Pacific Northwest in association with the introduction of non-native species and the transfer of culture animals. These outbreaks may have been exacerbated by intensive shellfish aquaculture. Bacterial diseases with low host specificity, such as *Vibrio* spp., and host-specific parasites such as *Bonamia ostreae* and *Mikrocytos mackini* have had major impacts on shellfish aquaculture. While a number of these diseases have become established in Puget Sound, it is important to note that of the etiological agents discussed in this section, only *Vibrio tubiashii* has been observed in geoduck (Elston et al. 2008).

Summer mortality of the non-native Pacific oyster (*Crassostrea gigas*), the most commonly cultured species in the Pacific Northwest, stems from a combination of stress at or near spawning time and high summer temperatures (Cheney et al. 2000). Summer mortality has also been associated with numerous bacteria, mostly species of *Vibrio* and *Nocardia*, but it remains unclear whether these bacteria act as primary pathogens or opportunists (Paillard et al.

2004). High but sporadic *C. gigas* spat mortality rates has been observed during the summer in both naturalized and cultured oysters. Summer mortality seems to have a complex etiology, with several factors implicated. These include environmental conditions, physiological and genetic host parameters, and infectious agents (Soletchnik et al. 1999). Two *Vibrio* strains that have been associated with summer mortality outbreaks and which experimental challenge shows to be potentially pathogenic for *C. gigas* spat have been phenotypically and genotypically identified: *Vibrio splendidus* biovar I (Lacoste et al. 2001) and biovar II (Le Roux et al. 2002). Nocardiosis is a bacterial disease that is also an important component of summer mortality associated with Pacific oysters (*C. gigas*) (Friedman et al. 1991). The disease causes yellow lesions on the body. and although *C. gigas* is the principal species affected, a few specimens of the European flat oyster (*Ostrea edulis*), cultivated near areas of infected *C. gigas* have been found with a similar disease (Elston 1990). Nocardiosis originated in Japan and has since been reported in California, Washington, and British Columbia (Elston 1990, Friedman et al. 1991, Friedman and Hedrick 1991).

Denman Island disease is characterized by focal lesions of hemocyte infiltration (pustules) on the surface of the body and/or within the mantle, labial palps, and adductor muscle of *C. gigas* (Hervio et al. 1996, Hine et al. 2001, Bower et al. 2005). The etiological agent, *Mikrocytos mackini*, is a small intracellular parasite (Farley et al. 1988). The development of clinical disease upon infection with *M. mackini* requires three to four months at temperatures less that 10°C (Hervio et al. 1996). In addition to *C. gigas*, *M. mackini* produces disease and mortality in other species of economically important oysters, such as *C. virginica*, *O. edulis*, and *O. lurida* during laboratory challenges (Bower et al. 1997). Preliminary evidence suggests that these alternate species may be more susceptible to infection and the resulting disease than the typical host *C. gigas*. To date, *M. mackini* has been detected on the West Coast of North America from southern British Columbia to Washington (Bower et al. 2005). In laboratory bath-exposure experiments, infection prevalence approached 100% and mortalities were observed in small *C. gigas* (about 18mm in shell length). Geoduck of a similar age (about 8mm in shell length) were shown to be resistant to infection by *M. mackini* in the same experiment (Bower et al. 2005).

Bonamiasis of the European flat oyster (*O. edulis*) was first described in oysters from France in 1979 (Comps et al. 1980). It has since spread to other European countries associated with the transfer of oysters. Bonamiasis was transplanted to Washington from a California hatchery, and remains an important disease in the Pacific Northwest (Elston 1990). It is caused by an intracellular haplosporidian parasite, *Bonamia ostreae*, that infects the blood cells of oysters causing cumulative mortality rates of up to 80% within six months of introduction (Balouet et al. 1983). In laboratory experiments, *B. ostreae* was transmitted to uninfected oysters via the water column. However, close proximity to infected oysters is believed to be necessary for effective transmission (Elston et al. 1986).

The export and juvenile transplant of live bivalves for aquaculture raises concerns about the vulnerability of the wild populations to disease and the ability of bivalves to harbor and transfer pathogens to new areas and species. To determine the risks of the inadvertent introduction of pathogens from transfers of juvenile geoduck for grow-out and the marketing of live geoduck from areas within the current distribution of known etiological agents, the susceptibility of *P. generosa* to endemic and naturalized diseases must be assessed.

6.3 Parasites and diseases associated with geoduck aquaculture

There is one peer-reviewed report of a protozoan parasite associated with disease and mortaly in cultured Pacific geoduck larvae at an experimental hatchery in Washington state. Kent et al. (1987) identified the etiological agent as an *Isonema*-like flagellate that penetrates the mantle and proliferates within the coelom, ultimately resulting in the death of heavily infected geoduck larvae. This flagellate is not known to infect juvenile or adult geoduck, nor oyster larvae grown in the same hatchery facility as infected geoduck larvae (Elston 1990). No other reports of invasive, pathogenic *Isonema* sp. affecting cultured geoduck larvae have been published, and attempts to obtain infected larvae to perform transmission experiments were unsuccessful (Kent et al. 1987). This suggests that crowded conditions within the culture system may have predisposed larvae to infection and resulting mortality. Another peer–reviewed study of a bacterial disease documented the pathogenicity of *Vibrio tubiashii* on cultured geoduck larvae; both toxigenic effects and invasive vibriosis were evident(Elston et al. 2008).

In a preliminary study, cultured juvenile geoduck (*P. generosa*) planted at four locations in the Strait of Georgia along British Columbia were surveyed for infectious diseases (Bower and Blackbourn 2003). Upon histological examination, none of the 795 cultured geoduck showed signs of infectious diseases or pathogenic organisms. However, further research is required to characterize the distribution and effect of any pathogens or diseases impacting cultured and wild geoduck clams.

6.4 Parasites and diseases associated with wild geoduck

Bower and Blackbourn (2003) conducted a disease survey of 146 wild adult geoduck (*P. generosa*) that appeared abnormal when harvested by the commercial fishery along the coast of British Columbia. Abnormalities included dark periostracum, warts, inclusion bodies, and protozoan infections. The authors observed wild geoduck with dark, thickened integument (periostracum) on the siphon and/or mantle that appeared brown, black, or rust-colored. Histological examination determined that the underlying epithelium and musculature were healthy, and the surface discoloration and thickening were variously attributed to fungal infections, protozoan colonization, multiple layers of periostracum being secreted, and an unknown waxy acellular material. Preliminary transmission experiments were conducted to determine if the observed fungus was infectious. Healthy cultured juvenile geoduck were used as potential fungal recipients. Attempts to transmit the fungus by prolonged contact and cohabitation were unsuccessful after 82 days; attempts to isolate the fungus on aseptic culture media also failed. More sensitive methods of detecting and identifying the fungus (or fungi) are needed to fully assess involvement in geoduck integument abnormalities.

Bower and Blackbourn (2003) also noticed warts, or regions of smooth, raised, gray-pink or cream-colored lesions, on both the siphons and mantles of wild geoduck. The warts consisted of swellings of the periostracum filled with necrotic cells. Upon histological examination, Bower and Blackbourn (2003) observed no obvious etiological agent in conjunction with the warts; in order to determine whether the lesions were caused by an infectious organism, they inoculated, via syringe injection, healthy cultured juvenile geoduck with warts collected from wild adult geoduck. Both control (injections without wart material) and experimental animals developed pustules reminiscent of warts found on the wild adults. The development of warts on control animals indicated the lesions may be a consequence of the response of the clam to foreign material or a non-specific stimulus. The histopathology of the induced warts was similar to that observed in naturally infected wild geoduck; an etiological agent was not detected. Whether the warts result from a response to an invading infectious pathogen or to mechanical damage remains unresolved. Other geoduck gross abnormalities noted include blisters, scars, discoloration of internal tissues, and nodules associated with the inner valve surface, none of which appeared to be caused by an etiological agent.

Bower and Blackbourn (2003) observed a high prevalence of intracellular prokaryote microcolonies (inclusion bodies) in the epithelial cells of the gill filaments and palps of geoduck.. However, the infection intensity was very low, hindering the specific identification of what appeared to be rickettsia or chlamydia-like parasites. These bacteria occur in healthy animals without apparent detriment (Elston 1990), are commonly observed in wild bivalve mollusks including Northern quahogs (*Mercenaria mercenatia*), soft-shelled clams (*Mya arenaria*), Eastern oysters (*C. virginica*), Atlantic bay scallops (*Argopectin irradians*), Pacific razor clams (*Siliqua patula*), Manila clams (*Venerupis philippinarum*), and Japanese scallops (*Patinopecten yessoensis*). (Harshbarger et al. 1977, Meyers 1979, Morrison and Shum 1982, Elston 1986). However, extensive mortality in cultured giant clams (*Hippopus hippopus*) in the Philippines and Micronesia has been associated with heavy gill infections of rickettsia-like organisms (Norton et al. 1993). It has been suggested that overcrowding and low exchange rates of water in land-based culture tanks predisposed *H. hippopus* to increased intensity of infection, clinical disease, and mortality.

A similar rickettsia-like organism, *"Candidatus Xenohaliotis californiensis,"* is the etiological agent of withering syndrome, a chronic wasting disease responsible for mass mortality in wild black abalone (*Haliotis cracherodii*) and for significant losses of cultured red abalone (*H. rufescens*) (Haaker et al. 1992, Friedman et al. 2000, Moore et al. 2001). Experiments show that this pathogen can be transmitted via the water column, and that above normal temperatures have a synergistic effect on the disease (Moore et al. 2001, Friedman et al. 2002).

Two unidentified parasites have been observed in geoduck. Bower and Blackbourn (2003) observed clam protozoan unknown (CLPX) in the wall of the gonad, in the musculature of the siphon, mantle and foot, and under the epithelial lining of the water channels and mantle cavity. However, prevalence and infection intensity were low. CLPX resembles an unidentified protozoan observed in the Pacific littleneck clam (*Leukoma staminea*), which may be an early developmental stage of a vermiform apicomplexan parasite (Desser and Bower 1997). Between 70 and 100% of the clams in some Pacific littleneck populations were infected with the vermiform stage of this parasite ((Desser and Bower 1997), but it has not been found in geoduck and Bower and Blackbourn (2003) found no evidence of associated pathology.

Bower and Blackbourn (2003) also observed a second parasite, apicomplexan protozoan unknown (APX), in the palps, mantle, and gills of geoduck, again with infections occurring at very low prevalence and intensity. As of 2003, there was no evidence of associated pathology (Bower and Blackbourn 2003). Parasitism by apicomplexans has been documented in Pacific littleneck (*L. staminea*) and Manila clams (*V. philippinarum*) with no evidence of associated disease (Desser and Bower 1997, Marshall et al. 2003).

Wild geoduck have been observed in commensal relationships with turbellarians (free-living flatworms) and small pea crabs (family *Pinnotheridae*); no evidence of pathology was found in the *Panopea generosa* (Bower and Blackbourn 2003). A new species of turbellarian worm, *Paravortex pan-*

opea n. sp., was recently identified in the congener *Panopea abbreviata*; this likely commensal does not appear to cause disease in the host (Brusa et al. 2011). The nemertean worm *Malacobdella arrokeana* also appears to be commensal, not parasitic, with *Panopea abbreviata* (Vazquez et al. 2009). On the other hand, the green alga *Coccomyxa parasitica* occurs at relatively high prevalence (~80%) in the siphon tips of *P. abbreviata* and is associated with low condition indices, suggesting parasitism (Vazquez et al. 2010). The commensal pea crab *Pinnaxodes gigas* (Pinnotheridae) was first reported in *P. globosa* in 2011 (Emparanza et al. 2011). Because commensal organisms are often not host-specific, precautions should be taken to prevent their being introduced into non-indigenous areas and transferred to other bivalves. With no known methods of control, transfers of commensal organisms could have negative environmental repercussions.

Meyers et al. (2009) described viruses associated with wild *P. generosa* (in addition to the species *L. staminea*, *Crassodoma gigantea*, and *C. gigas*) in Alaskan waters. The investigators found an aquareovirus in *P. generosa* in six pooled samples of five individuals, indicating a presumed prevalence of 20 to 100%, but did not observe any signs of pathogenicity (Meyers et al. 2009).

To stop the spread of infectious organisms to uninfected individuals, stocks, and populations, we need (a) accurate identification of the pathogens responsible for disease outbreaks, (b) sensitive detection of pathogens in subclinical carriers and abnormal hosts, and (c) accurate differentiation between benign and significant infectious organisms. Although Bower and Blackbourn's preliminary work was initiated to address the health status of Pacific geoduck, to understand the potential ecosystem effects of geoduck disease will require further exploration of the risks, distribution, prevention, and management of geoduck pathogens.

Chapter 7

Genetic Effects on Wild Conspecifics

7.1 Introduction

Before beginning or expanding an aquaculture program, it is important to consider the genetic risks to wild populations associated with culture activities. Genetic risk is broadly defined as exposing a natural population to genetic change by human action (Currens and Busack 1995). With culture of a native species, such as geoduck in Puget Sound, these risks center on the potential loss of natural genetic variation, which serves to buffer the population against natural selective forces (Hoftyzer et al. 2008, Camara and Vadopalas 2009). In this section, we will discuss potential adverse genetic effects of geoduck aquaculture on wild stocks, the level of risk, and methods of risk reduction.

In many marine bivalves, observations at neutral molecular markers of weak genetic structure or even panmixia indicate significant gene flow and may suggest a lack of adaptive differentiation, as predicted by the biological characteristics of high fecundity, broadcast spawning, and pelagic larval propagules. Natural selection can, however, increase the survival of locally adapted populations, as measured by markers associated with adaptive genes (Marshall et al. 2010). On the other hand, the large populations and substantial within-population genetic variation provide ample opportunity for natural selection to occur in different ecological niches.

Studies of species hypothesized to have high gene flow over large spatial scales have demonstrated the occurrence of local adaptation (e.g., Atlantic herring, Gaggiotti et al. 2009; Atlantic cod, Bradbury et al. 2010). The assumption of low adaptive differentiation in marine invertebrates has likewise been challenged (e.g., Palumbi 2004 and references therein; Levin 2006 and references therein). For example, in the purple sea urchin (*Strongylocentrotus purpuratus*), Pespeni et al. (2012) observed significant differentiation of functional genes between populations in distinct locales. Riginos and Cunningham (2005) provide strong evidence for local adaptation in the *Mytilus* spp. complex, which has been observed even on small spatial scales. Yanick et al. (2003), and Sanford and Worth (2010) used reciprocal transplants to demonstrate local adaptation in the snail *Nucella canaliculata*. If wild populations are genetically adapted to local environmental conditions, interbreeding with shellfish from other locales might disrupt patterns of local adaptation. Local adaptation can arise from a complex of environmental parameters, such as disease, temperature, and salinity, at a particular locale.

Even in species with high gene flow such as geoduck, adaptive genetic differentiation can occur if post-settlement selection is strong. Such genetic differentiation, referred to as balanced polymorphism (Grosberg and Cunningham 2001), can be distinguished using molecular tools from the true local adaption that arises via restricted gene flow (Sanford and Kelly 2011). The distinction between true local adaptation and balanced polymorphism is important because with the latter, high gene flow provides more genotypes for selection to act upon, yielding more overall population resiliency than when differentiation arises due to low gene flow.

However, characterizing local adaptation, is not trivial (Savolainen et al. 2007). Phenotypic fitness traits must be directly compared in individuals from potentially divergent populations in both their home sites and in sites with different environmental conditions. If wild populations are not locally adapted, in many cases they can be treated as a single population even when restricted gene flow is evident (Crandall et al. 2000), as ecological exchangeability may obviate conservation of populations.

7.2 Genetic comparison of wild and cultured geoduck populations

Hatchery-reared shellfish may differ genetically from their wild counterparts for multiple reasons. Broodstock may be collected from distant geographic points and thus be adapted to a different set of environmental conditions. Additionally, selection processes in a shellfish hatchery are by design vastly different from selection processes in the natural environment. Geoduck, like most broadcast spawning invertebrates, have type III survivorship, characterized by very high larval mortality. In contrast, the hatchery environment is designed to minimize larval mortality (i.e. to relax many selective forces). Active artificial selection may also be effected in geoduck hatcheries through breeding, culling of larval stocks, or changes in environmental parameters such as temperature and salinity. Finally, the extremely high fecundity of geoduck, typical of many marine invertebrates, can reduce the genetic effective population size (N_e) in the hatchery, because relatively few broodstock pairs may produce entire hatchery cohorts (e.g., Hedgecock and Sly 1990). The literature on cultured oysters contains ample evidence that N_e can be much lower in hatchery than in wild populations (Hedgecock and Sly 1990, Gaffney et al. 1992, Hedgecock et al. 1992, Saavedra 1997). A reduced genetic effective population size can lead to a drastic reduction of genetic variability in the progeny. Once outplanted, purifying selection will not necessarily purge the effects of domestication in the same or subsequent generations, because the genes under selection in the hatchery will not necessarily be subjected to selection during adulthood or in subsequent generations. More detailed descriptions of potential genetic effects of hatchery culture are beyond the scope of this review; for more details see Camara and Vadopalas (2009) and Hedgecock and Coykendall (2007).

In some cases, hatchery shellfish have been found to be genetically distinct from their wild counterparts, often due to reduced genetic variability (Hedgecock et al. 1992, Apte et al. 2003, Evans et al. 2004, Yu and Chu 2006, Li et al. 2007). The Japanese scallop (*Patinopecten yessoensis*) has been cultured in China for two decades. Using six microsatellite loci, Li et al. (2007) documented that three hatchery populations of *P. yessoensis* in China were significantly less variable than wild Japanese populations, with fewer alleles per locus and lower heterozygosities. Similarly, Apte et al. (2003) used three classes of genetic markers (allozymes, mitochondrial DNA, and random amplified polymorphic DNA) to show that cultured greenshell mussels (*Perna canaliculus*) were genetically differentiated from wild populations. It has also been documented that cultured abalone (*Haliotis rubra* and *H. midae*) are genetically differentiated from wild abalone; the cultured abalone had fewer alleles per locus, and approximately 40% of the relatively infrequent microsatellite alleles present in wild collections were lost in cultured samples (Evans et al. 2004). In addition, alleles that were relatively rare in the wild collections were often the most frequent in the cultured groups, and relatedness levels were high in two cultured groups. In the pearl oyster (*Pinctada fucata*) from southern China, both wild and cultured populations showed a high proportion of polymorphic loci, but cultured populations had more fixed loci than the corresponding wild populations (Yu and Chu 2006). Arnaud-Haond et al. (2004) postulated that high reproductive success among farmed *Pinctada margaritifera* reduced naturally occurring patterns of wild genetic differentiation; Lemer and Planes (2012) detected genetic drift in this species attributable to effects of low-diversity hatchery releases ten years earlier. Kong and Li (2007) detected significant genetic differentiation between cultured and wild populations of the clam *Coelomactra antiquate* using amplified fragment length polymorphism (AFLP). These studies suggest the possibility of genetic differentiation between hatchery and wild geoduck.

7.3 Genetic implications concerning wild and cultured geoduck

In order to protect the genetic integrity of wild geoduck, we must understand their population structure and determine whether hatchery populations are genetically differentiated from wild populations We have a fairly good understanding of the neutral genetic differentiation of wild geoduck aggregations (Vadopalas et al. 2004, 2012; Miller et al. 2006); Straus (2010) estimated the effective number of breeders in a hatchery and examined genetic differentiation among wild and hatchery geoduck. If hatchery and wild geoduck are genetically differentiated, genetic risks to wild geoduck populations will increase. The reasons why hatchery geoduck may differ from wild geoduck populations are discussed above; we will now discuss the potential implications of those differences. For example, broodstock may be collected from distant geographic points and thus be adapted to a different set of environmental conditions. If these animals breed with wild conspecifics, it may lead to outbreeding depression, a reduction in wild fitness that follows mating between members of distant populations (Lynch 1991, Allendorf and Ryman 1987, Allendorf et al. 2001). Outbreeding depression has been observed in myriad species, including nematodes (Dolgin et al. 2007), partridges (Barilani et al. 2007), and copepods (Brown 1991), and has been observed in crosses between wild and domesticated salmonids (e.g., Tymchuk et al. 2006, 2007).

Even if broodstock is collected locally, hatchery populations may differ from wild populations due to random genetic drift or adaptation to hatchery conditions through planned or inadvertent selection. These differences may reduce the fitness of cultured geoduck and cultured-wild hybrids in the natural environment (Lynch and O'Hely 2001, Ford 2002). As the differentiation between wild and cultured populations increases, so does the potential for negative genetic interactions between wild and cultured populations. For example, faster growth in the intertidal environment may be selected for in the hatchery, but intraspecific introgression of the same traits may be maladaptive for wild geoduck. Lynch and O'Hely (2001) modeled these dynamics and showed that if the captive population does not receive gene flow from the wild population, even low levels of gene flow from the captive to the wild population will likely shift the average phenotype of the wild population toward the average culture phenotype. This shift may still occur if gene flow also runs from the wild to the cultured population, but it will be less pronounced (Lynch and O'Hely 2001). Therefore, if differences exist between wild and cultured geoduck populations, minimizing gene flow from the cultured to the wild is vital to maintaining the genetic integrity of the wild population.

In previous studies, little evidence of wild stock structure was found among Puget Sound geoduck collections via analyses of variation at both allozyme and microsatellite loci (Vadopalas et al. 2004, 2012; Miller et al. 2006). Thus disruption of neutral genetic stock structure is not a primary concern. However, genetic variability at presumed neutral microsatellite loci is high in wild populations; of the 15 published microsatellite loci for geoduck clams (Vadopalas and Bentzen 2000, Kaukinen et al. 2004, Vadopalas et al. 2004), all expected heterozygosities exceed 0.90. This hypervariability is a strong indication that wild geoduck populations have high levels of genetic variability that could be perturbed by an influx of cultured genotypes. Straus (2010) used five microsatellite loci to directly compare genetic diversity in groups of wild and cultured geoduck. Straus (2010) observed reduced genetic diversity in cultured geoduck populations. The results of this work demonstrate the effect of hatchery practices on genetic diversity in farmed populations, and can help guide efforts to minimize these effects. Again, minimizing gene flow between farmed and wild populations is the key to maintaining natural genetic variability in wild geoduck.

One way to minimize gene flow between wild and cultured geoduck populations may be to harvest the clams prior to maturation. Cultured geoduck are outplanted for four to six years before harvest (Ruesink and Rowell 2012), but, as discussed in Section 1.5, the age of reproductive maturity is currently unclear. If the estimate by Sloan and Robinson (1984) is correct, geoduck do not mature during the culture cycle and there is no need for concern about genetic interactions between cultured and wild geoduck. However, if the estimate by Campbell and Ming (2003) is correct, geoduck mature before harvest and could potentially spawn multiple times. Age at reproductive maturity varies by location (Campbell and Ming 2003) and should be examined for intertidal geoducks at potential culture sites. Additionally, as discussed in Section 1.5, young geoduck show a highly skewed sex ratio with over 90% of small (shell length < 100 mm) and young (< 11 years) individuals identified as male (Anderson 1971, Sloan and Robinson 1984, respectively). If such skewed ratios continue in commercially grown geoduck until harvest, the likelihood of reproductive success would be significantly reduced. As gamete age and density affect fertilization success (Williams and Bentley 2002, Kupriyanova 2006, Hodgson et al. 2007), skewed sex ratios will also reduce reproductive success between cultured and wild geoduck where the watercourse distance between aggregations is sufficient to dilute gamete broadcasts and hinder fertilization (Levitan et al. 1992).

Cultured geoduck are typically planted in much higher densities than occur in the natural environment; densities in wild aggregations in Puget Sound average 1.7 clams · m^{-2} (Goodwin and Pease 1991), while intertidal culture densities average about 13.5 clams · m^{-2} (J.P. Davis, pers. comm.). Proximity and spawning synchrony are the strongest predictors of individual reproductive success, with the likelihood of gamete union increasing exponentially with proximity. Thus, if male and female cultured geoducks spawn in synchrony, reproductive success is likely to be much higher in cultured than in wild populations. Under this scenario, most of the cultured-wild genetic interactions will occur between naturalized progeny and wild geoducks, rather than direct interaction between outplants and their wild counterparts.

7.4 Risk Reduction

There are many ways to reduce the potential for genetic interactions between cultured and wild shellfish. A number of strategies outlined in Camara and Vadopalas (2009) for native oysters also apply to geoduck. Broodstock can be collected each year from the wild population with which their cultured progeny will potentially interact. Collecting local, wild broodstock annually maintains population structure, preserves any local adaptations in the wild populations, helps maintain high levels of genetic variation in the progeny, reduces long-term domestication selection, and increases the hatchery N_e over generations. Using large numbers of wild broodstock and ensuring roughly equal reproductive success also increases the hatchery N_e and can help retain high levels of genetic variation in the offspring. The hatchery setting can also be designed to mimic the natural environment so their selection regimes will be similar (Maynard et al. 1995). The most risk-averse strategy would use land-based aquaculture to completely isolate the cultured geoduck from wild populations. While this is possible with some other species, it is currently not feasible for geoduck, as culture methods are constrained to intertidal or subtidal outplants.

Sex control of cultured populations is an additional method of risk reduction that has been advocated to prevent genetic change to wild populations (Piferrer et al. 1993). The production of monosex populations for release is most useful when used with exotic species (Thorgaard and Allen 1988, Quillet et al. 1991). Sterility, however, prevents genetic interactions between cultured and wild populations, and may be very useful in the culture of geoduck. Sterility is conferred on shellfish primarily through triploid induction. Triploid bivalves are produced either by crossing tetraploids and diploids (Guo et al. 1996) or by suppressing the extrusion of the first or second polar body in developing zygotes (reviewed in Beaumont and Fairbrother 1991). Triploids have been used in aquaculture settings because they exhibit reduced or absent gonadogenesis or gametogenesis and retain product quality during the spawning season, and because they may exhibit increased growth (Brake et al. 2004, Nell and Perkins 2005, Mallia et al. 2006). Triploidy techniques have been developed for geoduck (Vadopalas and Davis 2004) but the efficacy of triploidy in conferring sterility on the species and the permanence of the triploid state must be verified prior to using it to mitigate potential genetic risks.

In commercial aquaculture, harvest management may have some utility for risk reduction. Harvesting geoduck before they reach the age of sexual maturity reduces the chances of lifetime reproductive success in cultured geoduck. However, any avoidance of genetic risk via harvest management may be counteracted by the increased probability of individual reproductive success due to high culture densities. Using sterile outplants (Piferrer et al. 2009) and/or managing harvest to preempt reproduction could mitigate risks by reducing genetic interactions between farmed and wild geoduck populations.

C
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