Effects of Geoduck Aquaculture on the Environment:

A Synthesis of Current Knowledge

Washington Sea Grant

Technical Report WSG-TR 08-01

by

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This literature review summarizes the state of knowledge of geoduck clams and the potential environmental effects of geoduck aquaculture on the Puget Sound environment. It was prepared for Washington Sea Grant to satisfy requirements established by the 2007 Washington State Legislature in SSHB 2220.

ERRATA

October 27, 2009

Title Page:

Amended to include Technical Report WSG-TR-08-01.

Page 2.

Added an omitted reference that provides valuable detail on the external and internal anatomy of *Panopea generosa* (Yonge, 1971), and added an important detail regarding the mucous glands near the pedal gape.

Page 2.

Added a space between "anterior" and "pedal".

Page 3.

Corrected the fact that pseudofeces are expelled via the inhalant, not the exhalant siphon.

Page 34.

Corrected italics of the scientific name "*Candidatus* Xenohaliotis californiensis".

Throughout.

Corrected the species name to *Panopea generosa* Gould, 1850. We added the citation for this correction (Vadopalas et al., *in press*) to the reference list.

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A. 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 the majority of the recent literature (Vadopalas et al., in press)) is a large hiatellid clam, found in soft intertidal and subtidal substrates in the Northeast Pacific from California to Alaska, and it may be found west to Japan (Anderson 1971, Coan et al. 2000). Geoducks are found in the low intertidal to depths of more than 60 m (Goodwin 1976). Geoducks are extremely long-lived, with many examples of animals aged at over 100 yr (Goodwin 1976, Shaul and Goodwin 1982, Sloan and Robinson 1984, Campbell and Ming 2003). Geoducks are broadcast spawners that commonly spawn in the spring and summer (Sloan and Robinson 1984, Campbell and Ming 2003) and produce larvae that remain planktonic for 47 d at 14°C (Goodwin et al. 1979). Postlarvae settle onto the substrate and develop into juveniles that burrow into the sediment. Lucrative commercial geoduck fisheries exist in the states of Washington and Alaska, and in British Columbia (Hoffmann et al. 2000).

There is a paucity of peer-reviewed information on *Panopea generosa* or its congeners. This is particularly true for intertidal *P. generosa,* as no tribe or regulatory agency currently surveys intertidal geoduck clams. Thus, although published reports on geoduck population parameters are available, these publications focus on subtidal geoduck clams. Part of our common understanding about geoduck clams is derived from the substantial amount of information and data on *P. generosa* originally published in Washington State and Canadian technical reports, which were not subjected to peer-review. There are two particularly noteworthy cases in point: whether geoducks are found in high abundance below 25 m is unclear from the peer-review literature; however, nearly every paper cites the same pilot video survey work that indicates geoducks are found to 110 m (Jamison et al. 1984). Additionally, whether *P. generosa* is found only from California to Alaska, or is also found south to Baja California (Morris et al. 1980) and/or west to Japan (Coan et al. 2000), is unclear.

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

No detailed diagrammatic views of geoduck shell morphology have been published. For definitions of technical terms and detailed anatomical diagrams on bivalve shell morphology, we refer the reader to Coan et al. (2000). *Panopea generosa* is a massive clam, with the largest individuals documented at more than 200 mm shell length (SL) and 3.25 kg (Goodwin 1976, Goodwin and Pease 1991). The valves of this species have a broad, continuous pallial line with a short pallial sinus, smooth inner margins, a single cardinal tooth, an external ligament, and a porcelaneous interior. The two adductor scars are roughly equal in shape, and each valve has a hinge plate, or chondrophore. The valve comprises three layers, the outer two of which reveal seasonal growth patterns in the microstructure upon microscopic examination. 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 size and age at maturity of geoduck clams in British Columbia (Campbell and Ming 2003) as well as to produce age–frequency distributions for Washington State and British Columbia geoduck collections (e.g., Breen and Shields 1983, Goodwin and Shaul 1984, Sloan and Robinson 1984). Important to any age-estimation technique is verification 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 geoducks, sampled within and adjacent to a channel that had been dredged 26 yr previously. The authors projected that since clams could not have survived the dredging, only those that were sampled from the adjacent areas could exceed 26 yr of age. Annuli counts supported this hypothesis. However, patchiness in settlement of year classes coupled with spatially and temporally variable recruitment have been observed (e.g., 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 (Shaul and Goodwin 1982) used a mark-and-recapture design. The authors marked shells of 91 hatchery-reared geoducks and then outplanted the clams. After 7 yr in the substrate, eight growth lines were discerned in each of the three recovered geoducks—a confirmation of an annual growth pattern. More recently, concordance between mean sea-surface temperatures and growth-band width provides strong evidence for annual growth-band deposition in *P. generosa* (Noakes and Campbell 1992, Strom et al. 2004).

Using these age estimation techniques, Sloan and Robinson (1984) determined the oldest geoduck recorded was age 146 and the oldest reproductive geoduck recorded was age 107. A technical report documents a geoduck from the Queen Charlotte Islands that was estimated to be 168 yr old (Bureau et al. 2002) but this report may not have been subject to peer-review.

1.4 Anatomy

A detailed study of the external and internal anatomy of *Panopea generosa* was conducted by C. Yonge (1971). The interior anatomy of *P. generosa* is similar to other bivalves. However, geoducks have an extremely large, fused siphon and mantle that cannot be fully retracted into their shell, which distinguishes them from other clams in the region (Fig. 1). The mantle region has posterior siphon apertures and an anterior pedal aperture bordered by enormous mucous glands. The geoduck orients itself with the

posterior siphon towards the surface, where seawater containing dissolved oxygen and suspended microalgae is circulated via ciliated ctenidia down through the inhalant siphon. The ctenidia perform both gas exchange and feeding functions. The ctenidia trap, sort, and transport food particles to the labial palps, which then sort food particles into the esophagus (Yonge and Thompson 1976). Rejected food particles are bound with mucus and periodically ejected as pseudofeces via the inhalant siphon. After entering the esophagus, the mucus-bound particles are transported via cilia to the stomach and crystalline style. The crystalline style is a freely rotating gelatinous rod that contains enzymes involved in digestion. 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 > 1 cm thick.
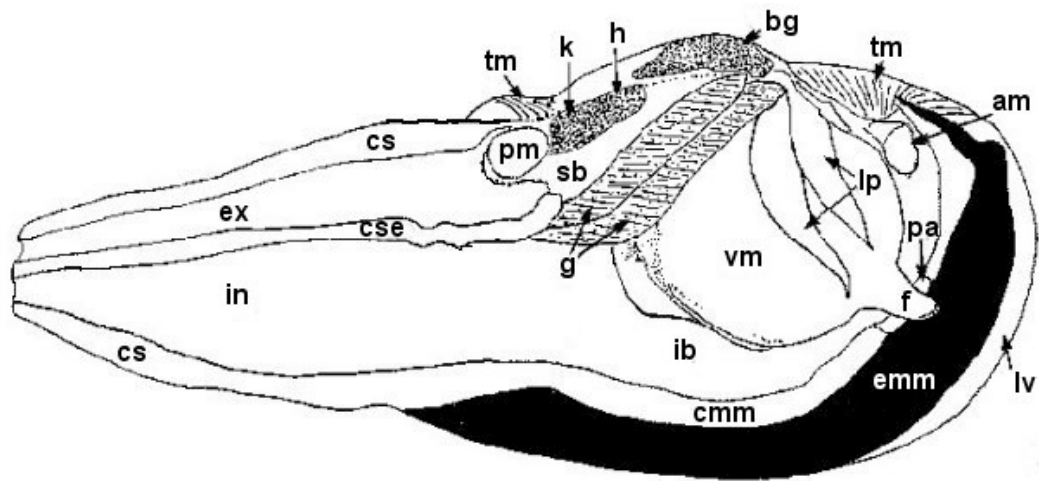
Figure 1. Sketch of the internal organization of the major organs of the geoduck clam, *Panopea generosa*. The right valve and right side of the muscular mantle and siphon have been dissected away to reveal the fused siphons and the arrangement of the internal organs. The thin mantle (**tm**) that lines 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, **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 et al. 2003).

1.5 Reproduction

Adult geoducks are highly fecund broadcast spawners but age of reproductive maturity is unclear. Sloan and Robinson (1984) examined 404 geoduck clams from British Columbia and aged the youngest mature male at 7 yr and the youngest mature female at 8 yr. However, Campbell and Ming (2003) examined 182 geoducks from two sites in British

Columbia and found that age at 50% maturity was 3 yr for geoducks from Gabriola Island and 2 yr for geoducks from Yellow Bank. Reproductive senescence has not been observed in geoducks (Sloan and Robinson 1984). All "old" (> 50 yr) geoducks examined appeared reproductively active, with morphologically active sperm or ova. Ripe males as old as 107 yr and ripe females as old as 89 yr have been documented, with no apparent reduction in fecundity with age (Sloan and Robinson 1984).

Gametogenesis in geoducks follows an annual cycle. In Puget Sound (the 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 gonads from 124 geoducks from six locations in Puget Sound and characterized them into five phases of gametogenesis. He found that 50% were in the early active phase in September and 92% were ripe in November. Clams were 100% ripe in May and by August 50% were spent. Ripe males were found every month 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 geoducks from British Columbia.

Geoducks show an uneven sex ratio with higher proportions of males than females observed in the smaller size classes (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 all geoducks ≥ 51 yr. Campbell and Ming (2003) observed that 41% of geoducks < 90 mm SL were immature. Of the mature geoducks < 90 mm SL, 92.5% were male with only 7.5% female. In geoducks ≥ 90 mm SL, the sex ratio was essentially equal (52% males:48% females). There are at least two possible explanations for these disparate sex ratios. Goodwin (1976) suggested that geoducks are dioecious, with sex determined by development and males maturing younger and smaller than females. Also, a portion of these young male geoducks may be protandrous hermaphrodites, which will reverse sexes at some point as they age. Of 253 geoducks sampled histologically by Campbell and Ming (2003), one individual was a hermaphrodite, with a gonad containing both oocytes and spermatozoa. Although most bivalves are dioecious (Coe 1943), hermaphroditism has been documented. The northern quahog, *Mercenaria mercenaria*, is generally considered protandrous, and bisexual gonads have been observed (Eversole et al. 1980). Protandrous hermaphrodism has also been observed in the Pacific oyster, *Crassostrea gigas* (Guo et al. 1998), and the pearl oyster, *Pinctada margarifera* (Dolgov 1991). Additionally, evidence suggests that a congener, the New Zealand geoduck, *Panopea zelandica*, experiences protandry (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. Geoducks are thought to be dioecious (but see section 1.5), facultative, repeat-broadcast spawners. Synchronization of spawning in many marine invertebrates is not well understood, but the detection of sperm in seawater from one male may cue mass spawning in the aggregation (Sastry 1979). Fertilization occurs

externally and meiosis progresses through expulsion of both polar bodies. The duration of the meiotic cycle is affected by temperature: at 30 PSU salinity, meiosis took 106 min at 11°C, 78 min at 15°C, and 56 min at 19°C (Vadopalas 1999). Salinity was also shown to affect 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).

Subsequent to the completion of meiosis in the ova, the male and female pronuclei break down 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 6–16ºC and 27.5–32.5 PSU, respectively (Goodwin 1973). Outside these ranges, a considerable reduction in normal development from the embryonic to the larval stage was observed. However, temperature and salinity tolerance can vary considerably between developmental stages in clams (Sastry 1979).

After approximately 48 h of embryonic development, the geoduck trochophore develops into an actively swimming and feeding veliger larva (straight-hinge or D-stage) (Goodwin et al. 1979). The veliger stage lasts 47 d at 14ºC (Goodwin et al. 1979), during which the larva feeds on microalgae and grows from 111 to 381 μm in shell height (Goodwin et al. 1979). Studies on the behavior of geoduck veliger larvae are depauperate.

During early metamorphosis, geoduck veliger larvae settle to the bottom, lose their velum, develop primary ctenidia and spines on the shell, and begin active crawling (Goodwin et al. 1979). Over the next several weeks, ctenidia formation is completed, the siphon grows, and the mantle is fused. During this stage geoducks use their foot to crawl and to transfer detrital food to the mouth (pedal-palp feeding) (King 1986). After 2 to 4 wk as post-larvae, geoducks will have reached 1.5 to 2 mm SL and will have burrowed into the substrate and begun filter feeding (King 1986). Juveniles resemble adults, and valve length increases approximately 30 mm per yr for the first 3 yr (Goodwin 1976).

Goodwin (1976) examined the growth of subtidal geoducks in Puget Sound using a mark and recapture methodology. Growth was fastest in the first 3 yr of life, with valve length increases ranging from 20 to 30 mm per yr. After 10 yr, growth rate slowed considerably (Goodwin 1976). Valves continue to increase in thickness throughout life, enabling age estimation based on shell layer visible in thin sections of the chondrophore (detailed in section 1.3). A recent study confirmed that geoduck growth is rapid for the first 10–15 yr, but then growth rates decline, with shell length expansion essentially halted after 25 yr (Strom et al. 2004). Growth rate also varies considerably 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 geoducks 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 > 200 mm were collected (Goodwin 1976). A later study of 11,154 geoducks found the average shell length and weight to be 135 mm and 872 g, respectively, with a range of 49–212 mm and 28–3,250 g (Goodwin and Pease 1991). Although many sources (e.g., Goodwin and Pease 1991, Campbell et al. 2004, Zhang and Hand 2006) indicate that adult geoducks of

this average shell length reach a burial depth of about 1 m, average adult burial depths observed by Anderson (1971) and Goodwin (1976) were 52 and 50-60 cm, respectively.

1.7 Distribution

Populations of various species of *Panopea* clams occur naturally world-wide, including Japan, Argentina, and New Zealand. *P. generosa*, one of the more massive species in the genus, is reported to occur in coastal waters of the northeast 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, the congeners *P. japonica* and *P. globosa*—known to occur in Japan and the Gulf of California, respectively—may have been mistakenly identified as *P. generosa*. Although introduction to the northwest Atlantic was suggested as early as 1881 (Hemphill, 1881), to our knowledge, there have been no intentional introductions of *P. generosa* to the northwest Atlantic or other regions.

1.8 Habitat

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

In Puget Sound, geoducks are contagiously distributed in small patches and beds of high abundance with an average bed density of 1.7 geoducks per m^2 (Goodwin and Pease 1991). Goodwin and Pease (1991) observed that geoduck density ranged from 0 to 22.5 per m^2 and individuals tended to aggregate within the beds, in groups containing an average of 109 animals. Conspecific aggregation is common for many bivalve species and is important for spawning synchronization and fertilization success (Sastry 1979). It appears that geoduck density increases with depth to 25 m but mean length and weight decrease with depth between 3 and 20 m (Goodwin and Pease 1991).

Geoducks are found in the low intertidal to subtidal waters. Existing evidence of deep-water stocks in Puget Sound is limited to two pilot studies of a single area in Case Inlet (South Puget Sound). Although not subjected to peer-review, the video surveys conducted in these studies revealed what appear to be substantial aggregations of geoduck clams starting below the 18-m mean lower low water (MLLW) fishing limit to a depth of 110 m (Jamison et al. 1984, Goodwin unpubl. data). There are additional anecdotal accounts of geoducks observed at even greater depths, but no thorough examinations resulting in peer-reviewed publications have looked for geoducks at depths > 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). A postulation in the Washington State geoduck resource management plan is that these deep-water stocks contribute to recruitment and recovery of fished areas, yet data are lacking to support this important assumption.

Chapter 2: Spatial and Genetic Structure of Wild Geoduck

2.1 Introduction

Many marine bivalves including geoducks tend to aggregate (Fegley 2001) and exhibit temporal changes in abundance. On broad spatial scales in the inland marine waters of Washington, subtidal geoducks are found in all subbasins and straits; on smaller spatial scales, geoduck distribution varies considerably (Goodwin and Pease 1991). Although some information is available on subtidal 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 geoducks, so information about intertidal population size, density, and aggregation is lacking. Geoducks are occasionally reported in creel surveys of recreational harvesters, which provide some anecdotal information on where geoducks are found but no information on population parameters.

2.2 Population Size

Subtidal geoducks are regularly surveyed to determine geoduck biomass and population size by the WDFW and several of the Washington Treaty tribes (Hoffmann et al. 2000). For these purposes, Puget Sound is divided into six geoduck management regions based on legal tribal fishing boundaries (Hoffmann et al. 2000); the regions have little to do with local oceanography or geoduck biology. Transects are conducted perpendicular to shore between 5.5 m and 21.5 m below MLLW. Counts are based on visual identification of either a geoduck siphon or a siphon depression sighted 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, such that 2.7% of the estimated available, harvestable biomass in each region is legal to harvest each year.

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. On the basis of 8,589 transects, average geoduck density was 1.7 geoducks per m^2, with a range of 0–22.5 geoducks per m^2. Densities varied significantly among geographic area, latitude, water depth, and sediment type. The highest regional densities were observed in South Puget Sound (2.0 geoducks m^{-2}) and the lowest were recorded in North Puget Sound (0.2 geoducks m^{-2}). Within Washington State, an inverse relationship between geoduck density and latitude is observed, but this relationship does not extend to British Columbia where geoduck density is higher (Goodwin and Pease 1991). On the west side of Vancouver Island, geoduck densities ranged from 0 to 13 geoducks per m^2, with an average of 4.9 geoducks per m^2 (Fyfe 1984). Geoduck density was found to increase with depth to the extent studied in both Washington State (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 geoducks m^{-2})

and the highest densities were observed in mud–sand and sand habitats (2–2.1 geoducks m^{-2}).

2.4 Aggregation

In Puget Sound, subtidal geoducks are contagiously distributed in aggregated patches (Goodwin and Pease 1991). An average of 0.64 aggregations per 41.8 m^2 quadarat was found, with each aggregation containing an average of 109 animals (Goodwin and Pease 1991). Goodwin and Pease (1991) hypothesized that geoduck aggregations 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).

Contagious distribution has also been observed in the northern quahog (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 for 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 in the red sea urchin (*Strongylocentrotus franciscanus*) was also shown to increase dramatically with proximity to conspecifics (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). Thus, the recruitment to a particular bed is not related to the reproductive capacity of geoducks within that bed (Orensanz et al. 2004). Instead, recruitment may depend on the reproductive and environmental conditions local to other beds as well as larger-scale environmental variables that may effect spawning, survival, and larval flow. There is currently no accurate way to model geoduck recruitment, as recruitment in one area is linked with reproductive capacity in unknown areas, and may be related to unknown geographic and oceanographic parameters that vary temporally and spatially.

Two recent studies examined geoduck density and recruitment in British Columbia over 9 yr in the same plots with controlled fishing pressure (Campbell et al. 2004, Zhang and Campbell 2004). Campbell et al. (2004) defined recruitment as the density of 6- to 7-yr geoducks per m^2 while Zhang and Campbell (2004) defined recruitment as the number of 1-yr-old geoducks per m^2. Campbell et al. 2004 found that heavy fishing pressure reduced geoduck population densities and average geoduck age, but that densities slowly increased due to 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 yr) but did not affect long-term recruitment patterns. At the second site, the most heavily harvested plot had the highest short- and long-term recruitment levels. However, the highest recruitment was also observed at this site before the experiment

began, 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; both studies observed that recruitment varied at large and small spatial scales.

Ripley (1998) suggested that, in addition to dispersal potential, an important advantage of broadcast spawning and pelagic larvae 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). Recent studies that have back-calculated historical 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 multi-decadal recruitment trend can be observed across a huge geographic scale. Recruitment in British Columbia and Washington State declined during 1920–1975, reached a minimum 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). The decline is not thought to be anthropogenic as it began long before the commencement of geoduck fisheries and is evident in pristine and disturbed locales. Instead, recruitment patterns appear to be correlated with environmental parameters including sea surface temperature (low temperatures = low recruitment) and discharge from large rivers (high discharge = low recruitment) (Valero et al. 2004). Multiple environmental 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 the organismal level (Clark and Hare 2002, Hare and Mantua 2000, Tolimieri and Levin 2004). Previous studies have shown that environmental variables are correlated with bivalve recruitment; for example, sea surface temperature is positively correlated with year-class strength in native littleneck clams (*Protothaca 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 therefore vital for effective management. The extent to which populations are connected spatially and temporally is dependent 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 untested assumptions that larvae behave as passively drifting particles distributed randomly throughout the water column. There is mounting evidence, however, 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) recently falsified the hypothesis that bivalve larvae disperse passively via ocean currents. Studies by Taylor and Hellberg (2003) and Zacherl (2005), entailing genetic and microchemical analyses, respectively, have further challenged the idea that marine invertebrate larvae disperse passively.

Many clams can use their foot for 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). In contrast, geoduck adults have only a small vestigial foot and are not capable of much movement. Adult movement is restricted to siphon extension and retraction and, once exposed, adults cannot right themselves or dig back into the substrate. Thus, primary connectivity among geoduck aggregations is established via planktonic larval dispersal, with potential small-scale dispersal of juveniles.

In geoducks, larval dispersal plays the primary role in facilitating gene flow and determining population structure. Gene flow is correlated with dispersal in many 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, Collin 2001, De Wolf et al. 2000). Panmixia (random mating within a population) has been observed at broad geographic scales in broadcast-spawning invertebrates, especially those with a long larval stage (e.g., *Littorina striata,* De Wolf et al. 2000; *Strongylocentrotus franciscanus*, Miller et al. 2006; *Mytilus galloprovincialis*, Skalamera et al. 1999). However, genetic structure at a variety of spatial scales has also been observed in broadcast-spawning marine invertebrates including 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* (Hamm and Burton 2000, Chambers et al. 2006).

The complex hydrology and bathymetry of Puget Sound suggests the potential for restricted dispersal and population subdivision of marine invertebrates in the region. 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 (*Protothaca 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). *P. staminea* showed substantial population structure at all loci examined while *M. balthica* populations were not highly differentiated. The level of population structure within Puget Sound is clearly species-dependent and should not be generalized, even for species that share reproductive characteristics.

In the last decade, several studies have examined population structure in geoduck clams (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 clams 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 geoducks from sites in the Strait of Juan de Fuca–Georgia Strait–Puget Sound complex and one site from Southeast Alaska using 11 allozyme and 7 microsatellite loci. Similar patterns of genetic differentiation were detected with both marker classes. In general, little differentiation was detected among geoduck aggregations throughout the region 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 make emigration challenging. The observed pattern may also represent selection; 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 has 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 the average gene flow for a species can mask important within-species variation that may reflect selection or local oceanographic conditions.

Miller et al. (2006) used eight microsatellite loci to analyze population differentiation in geoducks from Washington to northern British Columbia and observed more genetic structure at broad spatial scales than was detected by Vadopalas et al. (2004). Overall, they report an isolation-by-distance structure. While Miller et al. (2006) and Vadopalas et al. (2004) observed panmixia at small (50–300 km) scales, Miller detected stepping-stone gene flow at larger (500–1,000 km) scales. The east and west coasts of Vancouver Island and the Queen Charlotte Islands were found to be considerably differentiated, possibly because oceanographic conditions limit gene flow between the regions but also because environmental parameters (e.g., high waves and disturbance on one side of Vancouver Island, the other sheltered) may impose adaptive constraints.

While we have a fairly good understanding of neutral genetic differentiation (i.e., gene flow) via microsatellite and allozyme analyses of wild geoduck aggregations (Vadopalas et al. 2004, 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) is best measured with quantitative genetic approaches (Storfer 1996, Reed and Frankham 2001), but such information is currently lacking for geoduck clams.

Chapter 3: Physical and Biological Characteristics of the Puget Sound Sandy Intertidal Zone

3.1 Introduction

A comprehensive review of the community characteristics and structure of the sandy intertidal of Puget Sound is beyond the scope of this review. Here, we briefly discuss topics which may contribute to our understanding of geoducks 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 (e.g., current, substrate type, temperature, salinity) and biological (e.g., predation, competition) factors are known to affect the distribution and abundance of benthic marine organisms. In estuarine systems, the primary physical processes driving the distribution of benthic flora and fauna include wave energy, salinity, and sediment structure (Dethier and Schoch 2005). Salinity in particular plays a key role: low and variable salinity are correlated 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 estuaries tend to be extremely variable in environmental factors and the distribution and abundance of organisms, and that this variation or patchiness occurs on many spatial and temporal scales. Within-site variation is often considerable, which makes detecting patterns at larger spatial scales difficult (Morrisey et al. 1992).

A recent 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 the benthic community (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% of the taxa belonging to four phyla: annelida, mollusca, arthropoda, or rhodophyta. Of these, 134 were identified to species, 23 to genus, and 10 were grouped into complexes. Twenty-six primary producers, 139 invertebrates, and 1 fish (a gunnel) were found. Unfortunately, geoducks were not identified to species but were grouped into "clam siphons (unident)." No discernable distribution pattern for clam siphons (unident) was observed by the authors. The complete list of all species found in this study is in Appendix A of Dethier and Schoch (2005).

Although high variability in abundance of particular species was observed at many spatial scales, some broader ecological patterns were observed. Species richness increased steadily with latitude as temperature, salinity, wave action, and substrate became more marine. This trend has been previously observed and appears linked to oceanographic

variables (Constable 1999, Ysebaert and Herman 2002). In North Puget Sound, salinity was about 3 PSU higher, sea surface temperature was about 3ºC lower, and wave energy and sediment size were somewhat higher than in the south Sound. Despite the positive correlation of species richness with latitude within Puget Sound, there were exceptions. For example, barnacles and grapsid crabs were abundant throughout the Sound and 20 taxa were patchily distributed with no obvious geographic trend. Additionally, some 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 this region (e.g., *Crepidula fornicata)*.

Like many benthic invertebrates in Puget Sound, geoducks are patchily distributed (Goodwin and Pease 1991; see also section 2.4). Patchiness may be influenced by distribution of preferred abiotic characteristics, or ecological associations, or both. In a study conducted in British Columbia, juvenile geoduck clams were found clustered around full-sized adult geoducks (Fyfe 1984). It is possible that adult conspecifics provide settlement cues for larval geoducks or that survival of juvenile geoducks is higher in microhabitats replete with adult geoducks. Goodwin and Pease (1991) used a subtidal transect methodology and determined that geoduck density was positively correlated with a number of taxa (based on non-parametric tests, not adjusted for multiple comparisons). The commonly co-occurring taxa include chaetopterid polychaetes (*Spiochaetopterus costarum* and *Phyllochaetopterus prolifica*), sea pen (*Ptilosarcus gurneyi)*, horse clams (*Tresus* spp.), red rock crabs (*Cancer productus*), moon snails (*Polinices lewisii*), and laminarian kelp (*Laminaria* spp.). A positive correlation between chaetopterid polychaete density and density of various invertebrate taxa has been observed and suggests that these tube-building worms may facilitate the presence of other species (Morrisey et al. 1992). The correlation between red rock crabs/moon snails and geoducks is likely because these geoduck 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 considerably 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 is connected to the Strait of Juan de Fuca. After Admiralty Inlet, Puget Sound consists of three major branches: the Main Basin/South Sound, Hood Canal in the southwest, and Whidbey Basin to the northeast. A sill (Tacoma Narrows) separates the deep Main Basin from the shallower South Sound, which is characterized by many branching inlets. Whidbey Basin has an additional outlet to the Strait of Juan de Fuca (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 freshwater provided by the Skagit, Stillaguamish, and Snohomish rivers (Babson et al. 2006). Circulation in Puget Sound is driven by tidal currents, riverine input, and density differences between river and marine water. Puget Sound is generally well oxygenated, with the exception of 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 affect 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 d in Whidbey Basin and 64 to 121 d in southern Hood Canal (Babson et al. 2006); Cox et al. (1984) predicted residence times of > 9 mo in Hood Canal based on current records.

Human activity has heavily affected Puget Sound shorelines, water quality, and sediments. At least one-third of the Puget Sound shoreline has been extensively altered by activities including diking, filling, and devegetating (Rice 2006). A recent study examining shoreline alteration found that light intensity, air temperature, and substrate temperature were considerably higher on altered beaches (without shoreline vegetation) than on vegetated beaches (Rice 2006). Rice (2006) also observed biological differences between the beaches; for example, smelt eggs containing live embryos were 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. For example, benthic flatfish in Puget Sound experience effects of contaminant exposure such as reproductive dysfunction, reduced immune function, and development of toxicopathic diseases (Johnson et al. 1998). Some evidence indicates that fish from urban areas of Puget Sound have increased levels of contaminant exposure and reduced survival compared with fish in less urban areas (Johnson et al. 1998). An extensive survey of sediment quality conducted at 300 locations in the greater Puget Sound (2,363 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 level of human perturbation. The authors found 1% degraded, 31% intermediate, and 68% high-quality sediments in the greater Puget Sound. Degraded conditions were associated with urbanization and industrial harbors, especially near the urban centers of Seattle, Tacoma, and Bremerton. Long et al. (2005) indicate that compared with other U.S. estuaries and marine bays, Puget Sound sediments showed minimal evidence of toxicant-induced degradation.

Biological toxins including paralytic shellfish poisoning toxin (PSP) and domoic acid (DA) are also present in Washington State. DA is a toxic amino acid produced by diatoms in the genus *Pseudonitzchia* (Bates et al. 1989) while PSP is produced by dinoflagellates from 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 due to domoic acid (DA) since 1991 (Horner et al. 1993). DA is a particular challenge for razor clam fisherman, as razor 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 DA concentrations below the regulatory limit of 20 ppm have been detected in Puget Sound geoducks (Bill et al. 2006). No information is available on the retention time or depuration of DA by geoducks. Curtis et al. (2000) examined PSP in Puget Sound geoducks and found that toxin concentrations varied considerably among individual clams but that generally, geoducks in shallow water (7 m MLLW) contained higher concentrations of PSP toxin

than deeper water (17 m MLLW). 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 repetitive natural disturbance. To the authors' knowledge, no work has been published that examines disturbance patterns and recovery within Puget Sound. 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 of benthic infauna also varies over space and time in ways dependant upon 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 a 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 (Palmer 1988, Turner et al. 1995, 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 through bedload transport. For example, adult crustaceans colonized disturbed patches (897 cm^2) via passive dispersal within 24 d, with ambient densities attained approximately 1 mo after disturbance (Grant 1981). In another experiment, researchers observed that colonization mechanisms differed widely among infaunal polychaete species but that densities in disturbed areas (100 cm^2) returned to ambient levels within 20 d (Shull 1997). These experiments, however, were relatively small-scale and short-term. A recent experiment was conducted 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 of time (4.5 mo versus days) (Zajac and Whitlatch 2003). The researchers examined population and community structure as well as sediment grain size as a measure of physical disturbance. Defaunated patches differed considerably in sediment grain size distribution, but this distribution returned to ambient levels after about 2 mo. Population abundances of most species reached ambient levels 2–3 mo after the sediment was defaunated, and the community structure returned to ambient conditions after 4 mo. Published studies of recovery after disturbances in Puget Sound (e.g., geoduck harvest) are lacking.

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). Although the relative importance of pre- and post-settlement factors in structuring benthic communities is debated (Olafsson et al. 1994, Caley et al. 1996), 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 Stage

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, but theory dictates that species with type III life-history strategies, like geoducks, incur highest mortalities during the larval stage. We are not aware of any peer-reviewed literature that examines predation on geoduck larvae specifically, but ingestion of bivalve larvae has been documented in a wide range of taxa, including polychaetes (Johnson and Brink 1998), fish (Young and Davis 1992, Bullard et al. 1999), ctenophores (Purcell et al. 1991), and heterotrophic dinoflagellates (Johnson and Shanks 2003). A large body of literature also documents ingestion of bivalve larvae by bivalve adults (Andre et al. 1993; Tamburri and ZimmerFaust 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 geoducks at 14ºC spend 47 d as veligers (Goodwin et al. 1979), some proportion of geoduck larvae likely are 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 s and settlement was reduced by one-third in these areas of high adult concentrations (Andre et al. 1993). Other research, however, 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% of larvae settled without predation. Larvae that passed very close to the valve gape of an adult were ingested and suffered mortality but, owing to weak ciliary currents, as little as 1 mm distance afforded protection. In field surveys of oyster reefs in Washington State, the

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, geoducks spend several weeks as postlarvae. At this stage, geoducks are active crawlers and have spines on their shells (Goodwin et al. 1979, Velasquez 1992) which may deter some predation. After 2-4 wk as postlarvae, geoducks are 1.5 to 2 mm SL and have 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 in order 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. We include two examples to 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. Similarly, blue crabs (*Callinectes sapidus*) consumed considerably more soft-shelled clams (*Mya arenaria*) buried at 5 and 10 cm than those buried at 15 and 20 cm.

New Zealand pie crust crab (*Cancer novaezelandiae*) and juvenile Dungeness crabs selectively forage on smaller sizes of 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, thus increasing handling times. Given the lack of significant protection from their valves and extensive exposure of mantle and siphon tissues, juvenile and adult geoducks are likely to be extremely vulnerable to predation until they attain a depth refuge. However, as geoducks grow 20-30 mm SL per yr and bury deeper in the substrate during their first 2-3 yr (Goodwin 1976), they may relatively quickly attain at least partial predation refuge. Adult geoducks are generally found at 50–60 cm burial depth (Goodwin 1976) although maximum depth is believed to be closer to 1 m (e.g., Zhang and Hand 2006). Predation on adult geoducks is generally considered rare (Anderson 1971) but sea star predation on adult geoducks has been observed (Mauzey et al. 1968, Sloan and Robinson 1983). Natural mortality rate estimates of adult geoducks range from 0.0226–0.039 per yr (Bradbury and Tagart 2000, Zhang and Campbell 2004). Additionally, geoducks 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 adult and juvenile soft-shelled clams (*Mya arenaria)* and the macoma clam (*Macoma baltica*) by infaunal organisms including the nemertean worm *Cerebratulus lacteus* (Kalin 1984, Bourque et al. 2001, Rowell and Woo 1990) and the polychaetes *Nereis virens* and *Arenicola marina* (Ambrose, Jr. 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 geoducks likely experience predation from predatory infauna, but this has not been documented.

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). Crab predation on clams in general is discussed in section 4.2. 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*), the graceful crab (*C. gracilis*), and the Dungeness crab (Jensen 1995). Dungeness crab prey on juvenile *Mya arenaria* and field studies suggest that the distribution of this species may be limited to areas of low Dungeness crab density (Palacios 1994). Stomach content analyses indicate that Dungeness crabs under 1 yr (≤ 60 mm) consumed 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 feeding habits of the red rock crab or the graceful crab and no studies have been completed that examine crab predation on geoducks.

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 juvenile and adult geoduck clams in the Pacific Northwest (Mauzey et al. 1968, Sloan and Robinson 1983). *Pisaster 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 geoducks, but noted that this occurred only occasionally at Alki Point, Washington. The feeding pits created by *P. brevispinus* averaged 11.6 cm deep, with the deepest pit reaching 18 cm (Sloan and Robinson 1983). The circumoral tube feet extended on average an additional 16.6 cm, with the longest measured being 23 cm (Sloan and Robinson 1983). These data suggest that *P. brevispinus* can prey on geoducks buried up to 40 cm. Adult geoducks at full burial depth are likely to be safe from *P. brevispinus* predation, but adult clams that are unable to burrow through an impenetrable 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 SL) have been found at *P. helianthoides* feeding-pits, suggesting that this species can excavate deeply buried clams (Sloan and Robinson 1983). It has been suggested that geoducks 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), no published accounts of gastropod predation on geoducks exist. The moon snail (*Polinices lewisii*) is a predatory gastropod that is common in Puget Sound and has been observed feeding on bivalves including littleneck clams (*Protothaca stamina*) and surf clams (*Spisula solidisima*) (Peitso et al. 1994). A congener, *Polinices 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 (*Mya arenaria*) (Savini and Occhipinti-Ambrogi 2006). Although adult clams are likely to reach a depth refuge from gastropod predation, the impact of gastropod predation on juvenile geoducks should be examined.

Juvenile clams are also preyed upon by many fish species. Whole juvenile bivalves have been found in fish stomachs, such as the English sole (*Parophrys vetulus*) and the staghorn sculpin (*Leptocottus armatus*) in Grays Harbor, Washington (Armstrong 1991, Williams 1994). The European flounder (*Platichthys flesus*) forages on juvenile soft shell clams (*Mya arenaria*) up to 12 mm SL (Moller and Rosenberg 1983). Fishes and crustaceans can also exert non-lethal predation pressure on bivalve populations by siphon-cropping (Peterson and Quammen 1982, Armstrong 1991, Kamermans and Huitema 1994, 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 *Protothaca staminea* and *Venerupis philippinarum* exhibit cropped siphons on San Juan Island at any given time. Geoduck siphons have been found in the stomachs of fish including cabezon (*Scorpaenichthys marmoratus*) and spiny dogfish (*Squalus acanthias*) (Anderson 1971).

While siphon-cropping does not generally cause death, it may negatively affect bivalve growth (Peterson and Quammen 1982, Kamermans and Huitema 1994, Irlandi and Mehlich 1996, Nakaoka 2000,) or result in decreased burial depth in *Macoma balthica* (de Goeij et al. 2001), *Protothaca staminea*, and *Venerupis philippinarum* (Meyer and Byers 2005). This decrease in burial depth 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 *P. staminea* and *V. philippinarum*, and noted that cropped individuals burrowed 33–50% shallower than intact conspecifics. These clams were then used in a field experiment on San Juan Island, Washington, where clams experienced mortality primarily from *Cancer* crabs. In *V. philippinarum*, cropped individuals experienced nearly double the mortality rate of intact individuals. In contrast, no significant increase in *P. staminea* mortality was observed (Meyer and Byers 2005). The authors attribute this difference to the fact that *P. staminea* has a longer siphon than *V. philippinarum*, and was able to remain buried at relatively safe depths even after cropping. Although siphon-cropping of geoducks has been noted (Anderson 1971), no published information is available indicating the extent, severity, affected size classes, tissue regeneration rates, and 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). Although much of this research documents bird predation in rocky intertidal communities, recent studies have 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 2007). Two species of scoters—surf (*Melanitta perspicillata*) and white-winged (*M. fusca*)—are thought to play a large role in shaping community structure by consuming large quantities of clams while they overwinter in British Columbia (Lewis 2007). Manila clams (*Venerupis philippinarum*) and varnish clams (*Nuttallia obscurata*) were the primary prey items of both scoters, constituting 72–76% of their diet (Lewis 2007). Other birds are also capable of consuming clams; for example, northwestern crows (*Corvus caurinus*) have been observed digging and consuming Manila clams in British Columbia (Richardson and Verbeek 1987) and canvasbacks (*Aythya valisineria*) feed on multiple clam species including *Macoma balthica, Macoma mitchelli, Mya arenaria*, and *Rangia cuneata* (Perry and Uhler 1988). All of these bird species spend at least some part of the year in Puget Sound, and could potentially be geoduck predators.

The sea otter, *Enhydra lutris,* has been well documented as a keystone predator in both rocky and soft bottom habitats throughout their range in the northeastern Pacific (Garshelis et al. 1986, Kvitek et al. 1998). Sea otters were hunted to extinction off the coast of Washington State early in the 20th century (Gerber et al. 2004). However, over the last decade, the Washington State sea otter population has expanded, from the initial translocation of 59 individuals from Alaska (Jameson et al. 1982) to at least 550 animals (Kvitek et al. 1998, Gerber et al. 2004). The prevailing view is that sea otter populations were never established east of the San Juan Islands or in Puget Sound and are not established there now (G. VanBlaricom, Univ. Washington, pers. comm.). Yet recent sightings of individual sea otters have been made at San Juan and Whidbey Islands, near Federal Way, off the Nisqually Delta, and in southern Puget Sound (unpublished observations verified by the Univ. Washington School of Aquatic and Fishery Sciences, the WDFW, and the Cascadia Research Collective; G. VanBlaricom, Univ. Washington, Seattle, pers. comm.). Sea otters exert a strong influence on infaunal prey communities in soft-sediment habitats (Kvitek et al. 1992). Direct observations of feeding sea otters at 11 sites in Southeast Alaska showed infaunal clams to be the primary prey utilized by otters throughout the region. Bivalve prey abundance, biomass, and size 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 *Panopea generosa* were 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 et al. 1993, Kvitek and Oliver 1992). It is important to note that otters have been observed excavating clams up to 0.5 m deep (Hines and Loughlin 1980) and could certainly prey on juvenile or possibly adult geoducks. No research has been conducted on this topic specific to Puget Sound.

B. Ecological Effects of Geoduck Aquaculture

Chapter 5: Abiotic and Biotic Effects

5.1 Introduction

Although geoducks have been cultured in Washington State for enhancement of wild stocks since 1991 (Beattie 1992) and on a commercial scale since 1996 (J.P. Davis, Taylor Resources, Inc., Quilcene, Washington, pers. comm.), little work has been done on the ecological impacts of these practices. Research that has been conducted comprises primarily pilot-scale studies that have not been subjected to formal peer-review. For this reason, we refer to the literature on aquaculture effects of other filter-feeding bivalves to provide a framework for considering the potential effects of geoduck aquaculture. Although there is a large body of literature on the environmental impacts of bivalve aquaculture, the majority of these studies have 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 have taken examples from oyster and mussel culture when necessary. It is important to note that many of these examples are from suspended or rack culture, which have a greater potential to effect the environment because more animals may be cultured in a given area. There are many ways that aquaculture can disturb the environment, and these disturbance events vary on spatial, temporal, and intensity scales (Simenstad and Fresh 1995). In this section, we discuss the potential biotic and abiotic effects of geoduck aquaculture on water quality, substrate, community structure, and carrying capacity. The potential for disease transmission and genetic perturbation from cultured to wild stocks will be reviewed in later sections.

5.2 Water Quality

Many bivalve molluscs feed by filtering suspended particulate matter from the water column. Filtration rates have not been published for *Panopea generosa*; however, rates can be estimated because bivalve filtration may 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 per h per individual (Powell et al. 1992) as estimated from shell length in oysters. The veracity of this estimate is uncertain, however, since a geoduck at 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, high densities of suspension-feeding bivalves clearly can impact water quality in a myriad of ways (Newell 2004). It has been suggested that high densities of bivalves in suspended culture could rapidly recycle ingested organic matter back to the water as inorganic nutrients and could thus stimulate phytoplankton growth (Sorokin et al. 1999, Nizzoli et al. 2006). However, 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 culture 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 natural and farmed beds of blue 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 increasing distance into a mussel farm in Norway, with more than 50% of the phytoplankton entering the farm 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 of a Virginia *Mercenaria* farm than it was upstream (Grizzle et al. 2006). Additionally, bivalve filter feeding may control plankton concentrations on a larger, ecosystem 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. Using airborn remote sensing, Grant et al. (2007a) found reduced chlorophyll throughout an *M. edulis* farm in eastern Canada, with successive depletion of chlorophyll in the direction of flow through the farm. As well as 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). 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). Introduced clams have also 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 50 yr (Phelps 1994). Alternatively, invasive clams (*Potamocorbula amurensis*) introduced to the 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 zooplankters (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, and these nutrients may ultimately be removed from the ecosystem via 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). Because of this nutrient removal ability, bivalve aquaculture can improve water quality and 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.

5.3 Substrate

Many marine bivalves, like geoducks, filter particles from the water column and deposit them into the substrate, both with and without digestion (feces and pseudofeces respectively; together called biodeposits). Although geoduck biodeposition has not been examined, biodeposition in other species is well studied. Northern quahog (*Mercenaria mercenaria*) have a lower biodeposition rate than mussels or oysters (Tenore and Dunstan 1973), which may be due to differences in filtering behavior under conditions of excess phytoplankton. Oysters and mussels maintain high clearance rates and increase their biodeposition under high phytoplankton concentrations while clams including *Venerupis pullastra, M. mercenaria* and *Cerastoderma edule* reduce their clearance rates (Beiras 1993, Hawkins et al. 1998, Grizzle et al. 2001). 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). Biodeposition thus plays a key role in benthic–pelagic coupling (Kautsky and Evans 1987) and can have substantial ecological effects. For example, natural densities of the mussel (*Modiolus americanus*) notably increased 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 these nutrients were taken up by the plants, the plants exhibited enhanced growth (Peterson and Heck 2001). A similar study examined interactions between eelgrass (*Zostera 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.

Multiple field and laboratory studies have examined the effects of increased biodeposition resulting from high concentrations of bivalves in a culture setting. Biodeposition rates of a 1-yr-old scallop, *Chlamys farreri,* were 34-133 mg dry material per individual per d with mean rates of C, N, and P biodeposition of 4.00, 0.51, and 0.11 mg per individual per d, respectively (Zhou et al. 2006). Benthic respiration and sediment ammonia concentrations are well documented to be higher under longline mussel farms than at reference sites (Hatcher et al. 1994, Kaspar et al. 1985, Christensen et al. 2003, Giles et al. 2006). Prokaryotes in the sediment may also differ between cultured and control areas, with sulfate reducing and sulfur oxidizing bacteria more abundant in sediments under shellfish farms (Asami et al. 2005).

Changes in the sediment and water from *Venerupis philippinarum* culture have also been documented. Water at the control sites had five to nine times more particulate nitrogen and phosphorus while the culture sites, with 300 to 800 individuals per m^2, showed considerably more dissolved phosphorus and increased ammonia concentrations in the sediment (Nizzoli et al. 2006). Because biodeposition increases organic carbon levels and thus sediment oxygen demand (Giles and Pilditch 2006), high biodeposition rates may lead to anoxic conditions. The mechanism for anoxia was demonstrated at an oyster farm in France (Castel et al. 1989). Oyster biodeposition elevated sediment carbon levels, which increased oxygen demand. These changes led to anoxia, which caused localized changes in benthic diversity: levels of meiofauna increased to 3-4 times their former

abundance and macrofauna levels declined to approximately 50% of their former abundance (Castel et al. 1989). Contrary to these trends, however, a study examining longline subtidal oyster and mussel farms in Tasmania, Australia, found no differences in sediment deposition, sediment sulphide concentrations, organic carbon content, or water turbidity between farm and control sites. This may be due to low stocking densities used in Tasmanian shellfish farms (Crawford et al. 2003).

Many studies have shown that shellfish aquaculture can lead to increased sedimentation (Giles et al. 2006, Mallet et al. 2006, Zhou et al. 2006). For example, sedimentation was found to be nearly 2.5 times greater under scallop (*Chlamys farreri*) cultures than at reference sites in China (Zhou et al. 2006). However, these studies generally examine suspended or off-bottom aquaculture and may not be relevant to culture of infaunal organisms like geoducks.

Many clam species including geoducks are vulnerable to predation in the early stages of culture and are grown under protective netting (Spencer et al. 1992). This practice has been shown to increase survival of juvenile Manila clams (*Venerupis philippinarum*) in the U.K. and in 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, Spencer et al. 1997, Goulletquer et al. 1999, Bendell-Young 2006). Spencer et al. (1996) found sedimentation four times higher on netted Manila clam plots than on non-netted Manila clam plots. Spencer et al. (1997) compared netted clam plots, netted plots without clams, and control plots without nets or clams, and found that it was the nets themselves rather than the Manila clams that caused increased sedimentation. In contrast, a recent 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 likely that the influence of predator exclusion netting on sedimentation is site-specific; these effects should be examined for geoduck aquaculture in Puget Sound.

5.4 Effects of Tubes

There is no peer-reviewed information available on the ecological impacts of the mesh-covered polyvinylchloride (PVC) tubes currently used in geoduck aquaculture to protect seed from predation and dessication. As this system both appears unique to geoduck culture and is rapidly evolving, no data are available to review.

5.5 Community Structure

The effects of shellfish aquaculture on the benthic faunal community are strongly debated as many contrasting effects have been reported: for example, Grant et al. (1995) reported increased species diversity due to mussel culture, Beadman et al. (2004) reported decreased species richness due to oyster culture, and Crawford et al. (2003) observed no significant differences in benthic infauna between mussel and oyster farms and reference sites. As there are no data available for geoducks, we briefly review the literature from mussel and oyster aquaculture and discuss the available papers for clam culture. The impacts of clam harvest on the surrounding benthic community are covered in following text.

Crawford et al. (2003) compared the benthic environment under longline mussel and oyster farms in Australia and found that benthic community structure was not significantly different between farm and control sites. Greater differences in benthic infauna were found among farms than between farm and control 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. Reference sites showed higher abundance of benthic macrofauna but lower biomass, and species diversity was higher at the farm sites.

In contrast, Beadman et al. (2004) examined the infaunal benthic community under mussels cultured at four densities: 2, 3, 5, and 7.5 kg mussles per m^2 and found that infaunal communities comprised fewer individuals and species at the three highest mussel densities. Castel et al. (1989) compared an oyster farm in France to reference sites and observed dramatic changes to the benthic community: meiofauna levels were 3-4 times higher at the oyster farm while macrofauna levels were approximately 50% lower at the oyster farm (Castel et al. 1989). 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). 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 reference sites (Inglis and Gust 2003). A decrease of suspension feeders and an increase of predators have also been noted beneath oyster farms (Dubois et al. 2007).

Whitely and Bendell-Young (2007) examined the impact of Manila clam aquaculture on bivalve community structure. Aside from an increased abundance of Manila clams at farm sites, bivalve species composition did not differ significantly between farm and reference sites. However, farm sites showed higher similarity to one another than to reference sites, indicicating a decline in regional distinctness. 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, independent of the presence of clams. Particularly, they observed an increase in surface deposit feeding worms with the opportunistic *Pygospio elegans* dominating the fauna in the first 6 mo of clam culture and other surface deposit-feeding worms dominating after 1 yr. In the non-netted plots, the community dominant was a sub-surface deposit feeding worm, *Scoloplos armiger*. Spencer et al. (1997) suggest that competition from surface deposit-feeding worms on the netted plots may have excluded *S. armiger*. Powers et al. (2007) found that macroalgal and epifaunal growth on clam netting could also alter the community composition by enhancing nursery habitat for juvenile fishes and mobile invertebrates. They compared biomass and community structure at two clam lease sites—an eelgrass bed and an unstructured sand flat. Macrofaunal and epifaunal biomass at the aquaculture sites were significantly greater than on the sand flat but did not differ significantly from the eelgrass bed. Similarly, significantly more mobile invertebrates and fishes were found at the culture sites than the unstructured sand flat, and community structure on the culture sites was more similar to that of the seagrass bed than to the unstructured sand flat.

Intertidal geoduck culture operations are sited in locations where birds forage at low tide. Although people have speculated about the effects of shellfish aquaculture on birds

(Kaiser et al. 1998, Bendell-Young 2006), this interaction is not well studied. Zydelis et al. (2006) examined the effects of shellfish aquaculture on winter scoter populations on the western side of Baynes Sound, British Columbia. 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). More than 20% of the intertidal in Baynes Sound is used for shellfish cultivation; clam netting covers 2.9% of the total intertidal area and 0.3-19.3% of optimal clam habitat (Carswell et al. 2006). However, the authors found no correlation between shellfish aquaculture variables and scoter density, concluding 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 and none decreased in abundance. At this site, the authors conclude that mussel aquaculture may have beneficial effects for birds owing to increased habitat complexity and changes to the benthic fauna. The effects of shellfish aquaculture on birds are likely to vary depending on location, bird species, and aquaculture methods. These effects should be examined for geoduck aquaculture in Puget Sound.

5.6 Effects of Harvest

Geoducks are harvested using pressurized water to quickly dig/liquefy the sediment. This may alter the abiotic condition of the sediment (grain size, oxygen, nutrient levels, etc.) as well as alter the community of organisms in the benthos. This method is unique to geoduck harvest and no peer-reviewed papers have been published which examine these questions. Here we 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 elucidate effects of geoduck harvest.

The environmental effects of intertidal clam harvest have been examined in Europe and North America for species including the Manila clam, the common cockle (*Cerastoderma edule*), and the northern quahog (Peterson et al. 1987, Hall and Harding 1997, Kaiser et al. 1996, Spencer et al. 1998, Badino et al. 2004). In general, suction or mechanical harvest is a physical disturbance associated with sediment and benthic faunal changes. In most cases, mechanical harvest reduced the number of species present and their abundance. For example, the sediment and the benthic community were highly disturbed by mechanical harvest of Manila clams in Italy (Badino et al. 2004). A considerable decrease of 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 the sediment layers (Badino et al. 2004) and reduce infaunal species abundance and richness immediately following harvest (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, Oregon, did not impact infaunal species number and abundance. Similarly, raking or dredging for northern quahogs did not appear to affect the species composition or density of small benthic macroinvertebrates in North Carolina (Peterson et al. 1987).

Recolonization rates of benthic fauna can range dramatically depending on physical conditions (sediment type and stablility, wave action, current), 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 intertidal cockle harvest, in Scotland, suction-dredged sites had an average of 30% fewer species and 50% fewer individuals. However, after 56 d, the faunal assemblages at these disturbed sites were not significantly different from control sites. A similar study in southeast England examined the sediment structure and benthic community immediately following and 7 mo after suction-dredge harvesting for Manila clams at an aquaculture site (Kaiser et al. 1996). Harvest suspended the sandy layer but left the underlying clay substrate and subtantively reduced both infaunal diversity and the mean number of individuals per sample. However, after 7 mo, neither the sediment composition nor the benthic fauna were significantly different from control sites. The authors conclude that clam cultivation does not have long-term effects on the substrate or the benthic community at this location. 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 were similar to control sites within 3 mo of harvest, regardless of the scale of disturbance, which ranged from 225 m^2 to 2025 m^2. Although aquaculture harvest is likely to take place at a larger scale than that examined in the study, the authors emphasize that those areas might be patchily distributed and unlikely to further extend the trajectory of recovery. However, these results are very likely specific to site and harvest technology, and they need to be examined with geoduck culture in Puget Sound.

Clam harvest has also been shown to affect seagrass. Raking and light dredging to harvest northern quahogs caused a 25% decrease in seagrass biomass, but recovery was complete within 1 yr (Peterson et al. 1987). Alternatively, heavy dredging caused a 65% decline in seagrass biomass and full recovery was not documented after 4 yr (Peterson et al. 1987). A separate study showed that clam raking did not affect eelgrass (*Zostera marina* L.) cover or biomass, but digging clams individually reduced eelgrass cover and biomass, although no significant differences were observed after 10 mo (Boese 2002). Individually digging clams was also shown to reduce shoot density and biomass of the seagrass *Zostera noltii* (Cabaco et al. 2005), although how long these changes persisted is unclear because temporal change data were not included in this study.

5.7 Carrying Capacity

Before beginning a discussion on carrying capacity in bivalve aquaculture, this term needs to be defined. In an aquaculture context, three distinct definitions of carrying capacity are used. Production carrying capacity (PCC) is the level of culture at which production is maximized without negatively affecting growth of the cultured species (Carver and Mallet 1990). Determining PCC for geoducks would be relatively simple in the field by simply expanding the density of cultured geoduck while monitoring growth rates. PCC is reached when growth rates begin to fall. However, significant ecological changes in the surrounding community are likely before PCC is reached, and this level of development may be unacceptable to many stakeholders.

Ecological carrying capacity (ECC) is the highest level of culture that can be undertaken without leading to 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. The PCC was estimated at a mussel yield of 310 t per km^2 per yr. In contrast, the ECC was estimated at a mussel yield of 65 t per km^2 per yr, approximately 20% of PCC. The model indicated that introducing a mussel culture at production carrying capacity would lead to decreased mean trophic levels for the ecosystem as bivalves replaced zooplankton as the primary phytoplankton consumers (Jiang and Gibbs 2005).

A third definition of carrying capacity has recently been introduced in the aquaculture literature. Social carrying capacity (SCC) incorporates both PCC and ECC while taking into account demands of both the population (socioeconomic and cultural factors including employment, fisheries, and recreation) and the environment (McKindsey et al. 2006). No models have yet been developed that estimate SCC in an aquacultural setting. Determining ECC for geoducks 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. Any discussion of carrying capacity for geoducks in Puget Sound should acknowledge that the commercial fishery has extracted large quantities of geoducks annually since 1970. This represents a net loss of geoduck even with the addition of geoduck culture at the present level.

Studies on the environmental impacts of aquaculture often focus on the effects to the benthos under farms. This may be more appropriate for finfish culture where ecological carrying capacity is most often dictated by the 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. As 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 PCC, the food web collapses into a nutrient–phytoplankton–bivalve culture because the bivalve culture has out-competed zooplankton and benthic filter feeders (Gibbs 2004).

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 nutrient–phytoplankton–zooplankton models have been developed that predict the carrying capacity of bivalves in coastal regions (Bacher et al. 1997, Duarte et al. 2003, Grant et al. 2007b, Smaal et al. 1997). These models however have been developed independently of one another and rarely incorporate relationsips parameterized in earlier models. It has been suggested that new "open source" ECC models be developed that allow free access to the mathematical code such that independent researchers could parameterize the models with their data and add sub-models of their specialties (Newell, 2007). Alternative to modeling, performance indicators such as clearance efficiency or phytoplankton depletion footprints can be used 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, currently lacking for geoducks.

No peer-reviewed studies are available for geoduck carrying capacity or bivalve carrying capacity in Puget Sound. We have chosen not to review carrying capacity for different bivalves in different bodies of water because this would not add to our knowledge about geoduck culture in Puget Sound. However, we 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 Mediterranean locations. Numerous parameters, including current, filtration rate, and chlorophyll *a*, were measured and included in the model. The two regions differed widely with regard to current and phytoplankton availability and, thus, with regard to estimated carrying capacity. Using the original Incze model (Incze et al. 1981), the predicted PCC for the two regions was 2,034 t in the better locale, and 403 t in the poor locale. Using the Incze modification (Martincic 1998 as cited in Sara and Mazzola 2004), the predicted carrying capacity was 200 t in the better locale and 160 t in the poor locale (Sara and Mazzola, 2004). Clearly, model selection is an important step, and location may be highly influential in estimating carrying capacity and determining appropriate siting for a farm.

Chapter 6: Disease

6.1 Introduction

Disease is an inherent part of all aquatic ecosystems; thus, it is important to explore the factors affecting its presence and severity. A complete 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. While many studies are dedicated to this topic, peer-reviewed research on diseases specific to geoduck clams is lacking for cultured animals and completely absent for wild stocks. However, Bower and Blackbourn (2003) conducted numerous surveys and experiments regarding wild geoduck health. Although not peer-reviewed, we feel the information presented in their studies is valuable and we discuss their work below. We also discuss literature related to transmission, prevalence, and distribution of diseases in other marine bivalve species in Washington State and highlight preliminary work specific to geoducks.

6.2 Aquaculture Impacts on Disease Prevalence and Distribution in the Pacific Northwest

Many pathogens that cause disease in shellfish are facultative forms and are ubiquitous in aquatic systems. In nature, a high percentage of apparently normal and healthy animals harbor potential pathogens without clinical signs or evidence of overt disease. The development of disease in aquaculture systems often occurs via disruption in the environment in which the animals are being reared. Unfavorable conditions, such as crowding, temperature fluctuations, inadequate dissolved oxygen, excessive handling, inadequate diets, or toxic substances may stress the animals; if the level of stress exceeds the ability to adjust, susceptibility to 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). For this reason, dense populations tend to have more parasites, meaning that 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 of great importance. Host specificity relates to the co-evolution of host susceptibility and pathogen virulence, as well as to the 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 recent increase in reported shellfish disease outbreaks. Transportation of stocks as well as climate change have been implicated in the expansion of disease. For example, prevalence of Dermo, caused by *Perkinsus marinus*, and Delaware Bay Disease, also known as MSX (multinucleated sphere unknown) caused by *Haplosporidium nelsoni*, has increased among eastern oysters, *Crassostrea virginica*, because of higher water temperatures and the relocation of infected stocks along the eastern and southern U.S. coasts (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). Many examples exist of species that have acted as vectors for the spread of hitch-hiking species that serve as predators, competitors, and pathogens to natives (Ruiz et al. 2000). Also, 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 were introduced with Pacific oyster seed over the years: the Japanese oyster drill (*Ocenebra japonica*) and the turbellarian flatworm (*Pseudostylochus ostreophagus*). These two species have become well established in various oyster-growing bays in the state of Washington as well as in Humboldt Bay in California (Chew 1991). Shellfish aquaculture, which has increased markedly over the past few decades, can also be a source of disease outbreaks caused by culture conditions themselves. The high densities under which animals are grown and the high temperatures sustained in hatcheries favor the proliferation and transmission of opportunistic pathogens (e.g., Elston 1990). For example, LeDeuff et al. (1996) found that cultured Pacific oyster larvae reared at 25–26°C were more susceptible to herpes-like viral infections than those reared at 22–23°C. Elston and Wilkinson (1985) found that infection by an irido-like virus of larval Pacific oysters in high-density hatcheries resulted in oyster velar virus disease (OVVD). The etiological agent of withering syndrome, *Candidatus Xenohaliotis californiensis*, may have also extended its geographic range in California via the outplanting of hatchery-reared abalone, suggesting a link between aquaculture and the present distribution of this pathogen (Friedman and Finley 2003).

Shellfish disease outbreaks have occurred in the Pacific Northwest in association with the introduction of non-native species and transfer of culture animals (Elston 1990). These outbreaks may have been exacerbated by intensive shellfish aquaculture. Bacterial diseases with low host specificity, such as *Vibrio* spp., as well as host-specific parasites, including *Bonamia ostreae* and *Mikrocytos mackini*, have impacted shellfish aquaculture. While a number of these diseases have become established in Puget Sound, it is important to note that none of the etiological agents discussed throughout this section have been observed in wild or cultured geoducks.

Summer mortality of the non-native Pacific oyster (*Crassostrea gigas*), which is the most commonly cultured species in the Pacific Northwest, stems from a combination of stress at or near spawning time and high summer temperatures. Summer mortality has also been associated with numerous bacteria, mostly species of the *Vibrio* and *Nocardia*, but it remains unclear whether these bacteria act as primary pathogens or as opportunists (Paillard et al. 2004). High but sporadic *C. gigas* spat mortality rates have been observed during the summer in naturalized and cultured oysters. Summer mortality seems to have a complex etiology with several factors implicated, including environmental conditions, physiological and genetic host parameters, and infectious agents (Soletchnik et al. 1999). The two *Vibrio* strains that have been associated with summer mortality outbreaks, and which are potentially pathogenic for *C. gigas* spat as shown by experimental challenge, have been phenotypically and genotypically identified as *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 *C. gigas* (Friedman et al. 1991). The disease causes yellow lesions on the body and, although *C.*

gigas is the principal oyster affected, a few specimens of the European flat oyster (*Ostrea edulis*), cultivated near areas of infected Pacific oysters, have been reported to have 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 3-4 mo of temperatures < 10°C (Hervio et al. 1996). In addition to *C. gigas*, *M. mackini* produces disease and mortalities in other species of economically important oysters such as *C. virginica*, *O. edulis*, and *O. conchaphila* 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 usual host *C. gigas*. To date, *M. mackini* has been detected on the west coast of North America from southern British Columbia to Washington State (Bower et al. 2005). In laboratory bath exposure experiments, a prevalence of infection approaching 100% and mortalities were observed in the small *C. gigas* (~18 mm in shell length). However, in the same laboratory exposure experiment, similar-aged geoduck clams (*Panopea generosa*, ~8 mm in shell length) were resistant to infection (Bower et al. 2005).

Bonamiasis of the European flat oyster (*Ostrea edulis*) was first described in oysters from France in 1979 (Comps et al. 1980) and 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*, which infects the blood cells of oysters, causing cumulative mortality rates ≤ 80% within 6 mo 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. Determining the risks of the inadvertent introduction of pathogens with the transfers of juvenile bivalves for grow-out and the marketing of live *Panopea generosa* from areas within the current distribution of known etiological agents requires that the susceptibility of *P. generosa* to endemic and naturalized diseases 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 mortalities among cultured 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 clams, or oyster larvae grown in the same hatchery facility as infected larval

geoduck clams (Elston 1990). No other reports of the 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 may suggest that crowded conditions within the culture system may have predisposed larvae to infection and the resulting mortalities.

In a preliminary study, cultured juvenile geoduck clams planted at four locations in the Strait of Georgia, British Columbia, were surveyed for infectious diseases (Bower and Blackbourn 2003). Upon histological examination, none of the 795 cultured geoducks 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 Disease Associated with Wild Geoducks

Bower and Blackbourn (2003) conducted a disease survey of 146 wild adult geoducks clams 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 individuals with a dark, thickened periostracum on the siphon, and/or mantle that appeared brown, black, or rust colored. Histological examination determined that the underlying epithelium and musculature was intact and healthy, while surface discoloration and thickening were sometimes 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 clams were used as potential fungal recipients. Attempts to transmit the fungus by prolonged contact and cohabitation were not successful after at least 82 d; 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 creamy-colored lesions on the siphon and mantle of wild geoducks. 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 clams with warts collected from wild adult geoducks. 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 non-specific stimulus. The histopathology of the induced warts was similar to that observed in naturally infected wild geoducks; 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.

A high prevalence of intracellular prokaryote microcolonies (inclusion bodies) in the epithelial cells of the gill filaments and palps of geoduck clams were observed by Bower and Blackbourn (2003). However, the infection intensity was very low, hindering the specific identification of these parasites believed to be *Rickettsia* or *Chlamydia*-like organisms. These bacteria are commonly observed in the tissues of a variety of wild bivalve mollusks throughout the world—including northern quahogs, soft clams, Eastern oysters, bay scallops (*Argopectin irradians*), Pacific razor clams, Manila clams, and Japanese scallops (*Patinopecten yessoensis*) (Harshbarger et al. 1977, Meyers 1979, Morrison and Shum 1982, Elston 1986)—and they occur in healthy animals without apparent detriment (Elston 1990). However, extensive mortalities in cultured giant clams (*Hippopus hippopus*) have been associated with heavy gill infections of *Rickettsia*-like organisms in the Philippines and Micronesia (Norton et al. 1993). It was 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 mortalities. 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 responsible for extensive losses of cultured red abalone (*H. rufescens*) (Haaker et al. 1992, Friedman et al. 2000, Moore et al. 2001). Experiments illustrate 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 are associated with geoduck clams. 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 of geoduck clams. However, prevalence and intensity of infection was low. CLPX resembles an unidentified protozoan observed in the Pacific littleneck clam, which has been speculated to be the early developmental stage of a vermiform apicomplexan parasite (Desser and Bower 1997). The vermiform stage of the parasite commonly found in Pacific littleneck clams (70–100% of the clams were infected in some populations; Desser and Bower 1997) has not been found in geoduck clams and Bower and Blackbourn (2003) found no evidence of associated pathology. Bower and Blackbourn (2003) also observed another parasite, apicomplexan protozoan unknown (APX), in the palps, mantle, and gills of geoduck clams, 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 well documented in clams throughout the world including Pacific littleneck clams and Manila clams with no evidence of associated disease (Desser and Bower 1997, Marshall et al. 2003).

Wild geoducks have also been observed in commensal relationships with turbellarians (free living, flatworms) and small pea crabs (family Pinnotheridae); no evidence of pathology was found (Bower and Blackbourn 2003). Because commensal organisms are often not host-specific, precautions should be taken to prevent them from being introduced to non-indigenous areas to avoid transfer to other bivalves. With no known methods of control, transfers of commensal organisms could have negative environmental repercussions.

To stop the spread of infectious organisms among infected and uninfected individuals, stocks, or populations, the following is required: (a) accurate identification of the pathogens responsible for disease outbreaks, (b) sensitive detection of pathogens in sub-clinical carriers or abnormal hosts, and (c) accurate differentiation between benign and significant infectious organisms (Harvell et al. 2004). Although Bower and Blackbourn's preliminary work was initiated to address the health status of geoduck clams, the risks, distribution, prevention, and management of geoduck-related diseases need further exploration to develop an understanding of potential effects of geoduck disease on the ecosystem.

Chapter 7: Genetic Effects on Wild Conspecifics

7.1 Introduction

Before beginning or expanding an aquaculture culture program, it is important to consider the genetic risks to the wild populations associated with these 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. In this section, we discuss potential adverse genetic effects of geoduck aquaculture on wild stocks and the level of risk as well as methods of risk reduction.

7.2 Genetic Comparison of Wild and Cultured Bivalve 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, the selection processes in a shellfish hatchery are, by design, vastly different from the selection processes in the natural environment. Geoducks, like most broadcast spawning invertebrates, have type III survivorship, characterized by very high larval mortalities. In contrast, the hatchery environment is designed to minimize larval mortalities and thus relaxes many selective forces. Active artificial selection may also take place in geoduck hatcheries through breeding programs, culling of larval stocks, or changing environmental parameters such as temperature and salinity. Finally, the extremely high fecundity of geoducks, 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 (Hedgecock and Sly 1990). Ample evidence exists in the literature on cultured oysters 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 result in a drastic reduction of genetic variability in the progeny. Once outplanted, purifying selection will not necessarily purge 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

Hatchery shellfish have been found to be genetically distinct from their wild counterparts, which is often due to reduced genetic variability and genetic drift (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 2 decades. Using six microsatellite loci, Li et al. (2007) documented that three hatchery populations of *P. yessoensis* in China were notably less variable than wild Japanese populations, with fewer alleles per locus and lower heterozygosities. Similarly, Apte (2003) used three classes of genetic markers (allozymes, mtDNA, and RAPDs) to document that cultured Greenshell mussels (*Perna canaliculus*) were genetically differentiated from wild populations. Also, cultured abalone (*Haliotis rubra* and *H. midae*) were shown to be genetically differentiated from wild abalone; the cultured abalone had fewer alleles per locus with approximately 40% of relatively infrequent microsatellite alleles present in

wild collections lost in cultured samples (Evans et al. 2004). In addition, alleles 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 pearl oysters (*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). Although these studies suggest the possibility of genetic differentiation between hatchery and wild geoducks, this has not been investigated.

7.3 Genetic Implications Concerning Wild and Cultured Geoducks

In order to protect the genetic integrity of wild geoducks, we must understand the population structure of wild geoducks and determine whether hatchery populations are genetically differentiated from wild populations. In previous studies, little evidence of wild stock structure was found among Puget Sound geoduck collections via analyses of variation at allozyme and microsatellite loci (Vadopalas et al. 2004, 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. Minimizing gene flow between cultured and wild populations is the key to maintaining natural genetic variability in wild geoduck clams.

While we have a fairly good understanding of neutral genetic differentiation of wild geoduck aggregations (Vadopalas et al. 2004, Miller et al. 2006), work needs to be done to determine the effective population size of hatcheries and examine genetic differentiation among wild and hatchery geoducks. If hatchery and wild geoducks are genetically differentiated, genetic risks to wild geoduck populations may increase. Reasons why hatchery geoducks may differ from wild geoduck populations were discussed previously, while here we discuss 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 (Allendorf and Ryman 1987, Allendorf et al. 2001, Lynch 1991). Outbreeding depression has been observed in a myriad of 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 (Tymchuk et al. 2006, Tymchuk et al. 2007).

Even if broodstock are collected locally, hatchery populations may differ from wild populations owing to random genetic drift or different selective pressures in the hatchery. These differences may reduce the fitness of cultured geoducks and cultured–wild hybrids in the natural environment (Lynch and O'Hely 2001, Ford 2002). As the differentiation between wild and cultured populations increases, the potential for negative genetic interactions between wild and cultured populations increases. 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 geoducks. 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 towards the average culture phenotype. If gene flow does occur from the wild population to the cultured population, this shift is less pronounced but may still occur (Lynch and O'Hely 2001). Thus, if differences exist between wild and cultured geoduck populations, minimizing gene flow from cultured to wild populations is vital to maintaining genetic integrity of wild populations.

One way to minimize gene flow between wild and cultured populations of geoduck clams is to harvest the geoducks before they mature. Cultured geoducks are outplanted for 4 to 8 yr before harvest (J.P. Davis, Taylor Resources, Inc., Quilcene, Washington, pers. comm.), but as was discussed in section 1.5, age of reproductive maturity is currently unclear. If the Sloan and Robinson (1984) estimate is correct, geoducks do not mature during the 4- to 8-yr culture cycle and there is no need for concern about genetic interactions between cultured and wild geoducks. However, if the Campbell and Ming (2003) estimate is correct, geoducks mature and may spawn multiple times before harvest. Age at reproductive maturity also varies by location (Campbell and Ming 2003) and should be examined for intertidal geoducks at potential culture sites. Additionally, as was discussed in section 1.5, young geoduck show a highly skewed sex ratio with more than 90% of small (SL < 100 mm, Anderson 1971) or young individuals (< 11 yr, Sloan and Robinson 1984) identified as male. If such strongly skewed sex ratios remain among commercially grown geoducks until harvest, the likelihood of reproductive success among cultured geoducks would be considerably reduced. As gamete age and density affect fertilization success (Williams and Bentley 2002, Kupriyanova 2006, Hodgson et al. 2007), skewed sex ratios will reduce reproductive success especially if the watercourse distance between cultured and wild geoduck aggregations is great enough to prevent downstream fertilization. However, deviations from a 1:1 sex ratio would also decrease effective population size of the cultured populations.

Cultured geoducks are typically planted in higher densities than the average density in the natural environment: densities in wild aggregations in Puget Sound average 1.7 geoducks per m^2 with a range of 0–22 geoducks per m^2 (Goodwin and Pease 1991), while intertidal culture densities average about 13.5 geoducks per m^2 (J.P. Davis, Taylor Resources, Inc., Quilcene, Washington, 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 high-density aggregations of male and female cultured geoducks spawn in synchrony, fertilization success is likely to be much higher in cultured than in most 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 wild congeners.

7.4 Risk Reduction

There are many ways to reduce the potential for genetic interactions between cultured and wild geoducks. The current practice is to collect broodstock each year from the wild population with which their 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 fertilization success also increases the hatchery N_e and can help retain high levels of genetic variation in the offspring. The hatchery environment can also be designed to mimic the natural environment, so that the selection regimes are similar (Maynard et al. 1995). The most risk-averse strategy would use land-based aquaculture to completely isolate the cultured geoducks from wild populations. While this is possible in some species, it is currently not feasible for geoducks 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 has the most utility if used in exotics (Thorgaard and Allen 1988, Quillet et al. 1991). Sterility, however, prevents genetic interactions between the cultured population and wild populations, and may be very useful in the culture of geoduck clams. Sterility can be conferred on shellfish primarily via triploid induction. Triploid bivalves are produced either by crossing tetraploids and diploids (Guo et al. 1996) or by administering some form of shock to developing zygotes to suppress the first or second polar body extrusion (reviewed in Beaumont and Fairbrother 1991). Triploids have been used in aquaculture settings because they exhibit reduced or absent gonadogenesis or gametogenesis, retain product quality during the spawning season, and often show increased growth (Brake et al. 2004, Nell and Perkins 2005, Mallia et al. 2006). Triploidy techniques have been developed for *Panopea generosa* (Vadopalas and Davis 2004), but the efficacy of triploidy in conferring sterility in geoducks and the permanence of the triploid state must be verified prior to using this technique.

For commercial aquaculture, harvest management of geoducks may have some utility for risk reduction. While geoducks are outplanted for 4–6 yr (J.P. Davis, Taylor Resources, Inc., Quilcene, Washington, pers. comm.), they are not sexually mature during this whole culture cycle and they are harvested while still young. This truncation of the reproductive period reduces the chances of lifetime reproductive success in cultured geoducks. However, any avoidance of genetic risk via harvest management may be counteracted by the increased probability of individual fertilization success among cultured geoducks due to high culture densities. Using sterile outplants or managing harvest to preempt reproduction, or both, could mitigate risks by reducing cultured–wild interactions.

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