

Shellfish aquaculture and conservation of two Puget Sound molluscs: the Pinto abalone
(*Haliotis kamtschatkana kamtschatkana*) and the Pacific geoduck (*Panopea generosa*)

Kristina M. Straus

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PREVIEW

University of Washington

Abstract

Shellfish aquaculture and conservation of two Puget Sound molluscs: the Pinto abalone (*Haliotis kamtschatkana kamtschatkana*) and the Pacific geoduck (*Panopea generosa*)

Kristina M. Straus

Chair of the Supervisory Committee:
Associate Professor Carolyn S. Friedman
School of Aquatic and Fishery Sciences

I examined aquaculture and conservation of two taxa native to Washington, USA (WA): Pinto abalone (*Haliotis kamtschatkana kamtschatkana*) and Pacific geoduck (*Panopea generosa*). Because pinto abalone populations continue to decline in WA despite fisheries closures, conservation aquaculture may be necessary. To determine appropriate culture methods, juveniles were reared in habitat-enriched or conventional tanks. No differences in survivorship or growth were observed but abalone behavior differed between rearing treatments. Abalone from habitat-enriched tanks changed habitats more often and spent different proportions of time in available habitats. Results demonstrate that rearing conditions affect abalone behavior and should be considered for abalone restoration.

Abalone are commonly misidentified, increasing the challenge of abalone management and conservation. I developed sequence-based genetic markers for species identification of Eastern Pacific abalone. I applied these tools and determined that flat abalone (*H. walallensis*) are a cryptic species in WA. Several individuals collected for the pinto abalone conservation aquaculture program were identified as flat abalone. Use of these individuals as broodstock may have led to interspecific hybridization and been detrimental to pinto abalone restoration. Results highlight the importance of molecular tools in abalone management, especially if conservation aquaculture is used.

To examine the potential genetic implications of geoduck aquaculture, I used five microsatellite loci to conduct two studies comparing genetic diversity in wild and cultured geoducks. In both studies, cultured geoduck showed reduced genetic diversity and effective number of breeders (N_b). In one study, I examined geoduck seed produced in two hatcheries. Parentage assignment revealed that in one hatchery, many parents contributed to each seed cohort, with the largest full-sib family comprising 11-31% of the offspring. In contrast, 94% of the seed from the second hatchery were from a single full-sib family. In a complementary study, I examined five year classes of cultured geoducks. Sibship assignment revealed that year classes were comprised of nine to 25 full-sib families and many individuals unrelated to others at the full-sib level. Results from both studies demonstrate that hatchery practices affect genetic diversity; these results may aid in developing geoduck culture practices that minimize genetic risk to wild populations.

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Chapter I

Literature Review

BACKGROUND

Human beings have likely always made changes to their immediate surroundings, but due to human population growth and increasing resource use, the rate at which humans perturb natural ecosystems has increased dramatically since the industrial revolution. Although it took many thousands of years for the human population to reach one billion, the population increased from one billion in 1804 to six billion in 1999 (United Nations Population Division 2000), and has since grown to 6.8 billion (U.S. Census Bureau, 2010). Concurrent with the increasing population, per capita consumption has increased 3% per year starting in the 1970s (Hawken et al. 1999). The escalation of human population and consumption has led to increasing pressures on organisms and ecosystems from factors including habitat loss, over exploitation, exotic species, pollution, and climate change (Groom et al. 2006). There are few, if any, environments left on earth that are undisturbed by humankind (Sanderson et al. 2002) and many species are in decline (International Union for the Conservation of Nature 2010). Given this situation, the need to understand the “principles and tools” necessary to conserve biodiversity in a landscape of human perturbation grows greater with each passing year (Soule 1985).

The need to conserve a species becomes obvious, and urgent, when that species has declined to the point that extinction is likely without conservation efforts. The United States (U.S.) Endangered Species Act and the Convention on International Trade in Endangered Species are powerful examples of national and international legislation,

respectively, that aim to conserve species that have declined to this degree. However, it is also important to consider conservation while species remain relatively healthy. Scientists must aim to understand the likely effects of human activity and work to provide solutions that could mitigate adverse environmental effects, before damage is realized (Redford and Sanjayan 2003). The conservation spectrum can thus include “rescuing” endangered species from extinction (e.g. by captive rearing and release of offspring; Meretsky et al. 2000) as well as preserving the long-term viability of a species in the context of changing human use of an environment. My dissertation research examined conservation of two species residing in Puget Sound that are at opposite ends of this conservation continuum.

Puget Sound is an estuarine fjord comprising the inland waters of Washington State. Over four million people reside in the Puget Sound region, and the human population of this area has grown by an average of 40,000 people per year since the 1940s (Culliton 1998, Fraser et al. 2006). This increase in human population has been accompanied by changes to the Puget Sound ecosystem including habitat alteration, increased contaminant levels, and increased harvest. The Puget Sound shoreline has been extensively altered by activities including diking, filling, and removing vegetation (Rice 2006). Harvest within Puget Sound has also altered the ecosystem; many taxa have experienced substantial declines due in part to over exploitation. The reduced abundance and population density of these taxa may have changed the ecosystem in ways that scientists and managers do not fully understand.

Inhabitants of Puget Sound face multiple threats and many taxa are at risk. Currently, three molluscs, 25 fish, and five marine mammal species that spend at least a portion of their lives in the Puget Sound are protected as endangered, threatened, or of concern (WDFW 2009b). Many taxa including some rockfishes (*Sebastes* spp; Parker et al. 2000), salmonids (*Oncorhynchus* spp.; WDFW 2009a), and the pinto abalone (*Haliotis kamtschatkana kamtschatkana*; Rothaus et al. 2008) continue to decline despite fisheries management efforts. Conservation aquaculture is a tool that may be used to conserve or restore aquatic species in such cases (McCormick and Brogan 2003, Preston et al. 2007, Steffens 2008). In fact, the U.S. Fish and Wildlife Service have used conservation aquaculture for 30% of the freshwater fish species listed under the Endangered Species Act (Johnson and Jensen 1991). However, aquaculture also has potentially deleterious effects on marine environments; aquaculture has been implicated in disease introductions (Burreson et al. 2000), habitat changes (Krost et al. 1994, Nizzoli et al. 2006), and decline of marine populations (Ford and Myers 2008). Aquaculture may also expose wild populations to genetic risk such as homogenization of populations or loss of genetic diversity (Gilk et al. 2004, Utter 1998, Utter and Epifanio 2002). I examined aquaculture and conservation of two taxa native to the Puget Sound: restoration aquaculture for pinto abalone (*Haliotis kamtschatkana kamtschatkana* Jonas, 1845) and the potential genetic effects of commercial geoduck (*Panopea generosa* Gould 1850) aquaculture on wild conspecifics.

PINTO ABALONE RESTORATION AQUACULTURE

Abalone are herbivorous gastropod molluscs in the genus *Haliotis*, which includes 56 recognized species (Geiger 2000) that inhabit tropical and temperate oceans worldwide. Abalone are patchily distributed, tending to be found in nearshore subtidal rocky habitats with abundant kelp. Eight abalone taxa are found in the Eastern Pacific (*H. rufescens*, *H. kamtschatkana kamtschatkana*, *H. k. assimilis*, *H. walallensis*, *H. fulgens*, *H. corrugata*, *H. cracherodii*, *H. sorenseni*). These abalone were once abundant along the west coast of North America but have suffered catastrophic declines due to over-harvest (Hobday et al. 2001, Rothaus et al. 2008), climate changes (Rogers-Bennett 2007, Tegner et al. 2001, Vilchis et al. 2005), and disease (Altstatt et al. 1996, Haaker et al. 1992b, Miner et al. 2006, VanBlaricom et al. 1993). Two abalone species (*H. cracherodii* and *H. sorenseni*) are federally protected by the U.S. Endangered Species Act as endangered and three additional species are listed as species of concern (*H. fulgens*, *H. corrugata*, and *H. k. kamtschatkana*; (National Oceanic and Atmospheric Administration 2009).

The pinto abalone (*H. k. kamtschatkana*) ranges from Point Conception, California to Yakutat, Alaska and is the northernmost abalone species worldwide (Geiger 2000). The pinto abalone is the predominant abalone in Washington State and the only known abalone in British Columbia, Canada (B.C.) and Alaska. Pinto abalone populations throughout the range experienced substantial declines during the second half of the twentieth century, and most fisheries were closed in the 1990s. Commercial harvest of pinto abalone in B.C. peaked at over 400 metric tons in 1979 and declined until the fishery was closed in 1990 (Jamieson 2001). Population densities continued to decline

despite a complete harvest moratorium, falling by 43% between 1993 and 1997 (Campbell 2000). The pinto abalone was designated as threatened under the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in 2000 and was uplisted to endangered in 2009 (COSEWIC 2009). In the United States, commercial fisheries for Pinto abalone existed in California and Alaska but were closed in the 1990s due to declines in abalone abundance. Pinto abalone were never commercially fished in Washington State, but a recreational fishery existed for many years. This fishery was closed due to sustainability concerns in 1994. In California and in Washington State, pinto abalone abundance has continued to decline despite complete harvest closures (Rogers-Bennett 2007, Rothaus et al. 2008). The Pinto abalone was federally listed as a species of concern in 2004 (National Oceanic and Atmospheric Administration 2009) and is currently recognized as both a State Candidate species and a Species of Concern within Washington State (WDFW 2009b).

At ten index stations monitored by the Washington Department of Fish and Wildlife (WDFW) in the San Juan Island Archipelago, abalone abundance declined by 77% between 1992 and 2006 (Rothaus et al. 2008). Such reduced numbers make pinto abalone vulnerable to the Allee effect: a situation in which decreased population size leads to decreased reproduction and survival (Allee et al. 1949). In abalone, fertilization success may be limited when spawning animals are separated by more than one to two meters (Babcock and Keesing 1999, Riffell et al. 2004). Recruitment declines suggestive of the Allee effect have been documented when abalone population densities decrease below a threshold level (0.15-0.3 abalone per m²), which varies by taxa and location (Richards

and Davis 1993, Shepherd and Brown 1993). In 1994, half of the WDFW index stations contained abalone at densities suitable for successful fertilization; by 2006, densities at all ten index stations were below this threshold (Rothaus et al. 2008). Additional data from both length frequency analyses and juvenile abundance surveys indicate very low recruitment over several years (Bouma 2007, Rothaus et al. 2008). Taken together, these data suggest low population density induced recruitment failure. The Allee effect has been implicated in the failure of multiple sedentary marine species to recover from overfishing (Bell 2008, Stoner and Ray-Culp 2000). Population densities of pinto abalone may be too depressed for natural recovery; restoration efforts such as aggregating reproductive adults so that they are in close proximity to one another when they spawn (Tegner 1992) and supplementing wild populations with hatchery-reared juveniles may be necessary to successfully restore pinto abalone populations in Washington State.

Restoration efforts involving the release of hatchery-reared larvae or juveniles into the wild to conserve or restore wild populations (hereafter conservation aquaculture) have been conducted with several species of fishes (Araki et al. 2007, Cummings et al. 1997a, DeHaan et al. 2008) and invertebrates (McCormick and Brogan 2003, Preston et al. 2007). Release of aquacultured larvae or juveniles has also been used to enhance fished populations limited by recruitment (hereafter enhancement or stock enhancement) in a wide variety of taxa (Arnold 2008, Bell et al. 2008, Bell et al. 2005, Dixon et al. 2006, McEachron et al. 1998). Despite years of efforts in many taxa, success rates in stock enhancement projects are often low (reviewed by Bell et al. 2006 and Leber et al. 2005). For example, hatchery production of pink salmon (*Oncorhynchus gorbuscha*) is thought

to have replaced rather than augmented wild fish production in Prince William Sound, Alaska (Hilborn and Eggers 2001) and yellow croaker (*Larimichthys crocea*) stock enhancement efforts in China failed to reverse population declines and restore the fishery (Liu and de Mitcheson 2008).

Abalone have been outplanted for conservation or enhancement purposes in many countries including Japan (Ino 1966, Kojima 1995), New Zealand, the U.S. (Tegner and Butler 1985b) and others (reviewed by McCormick et al. 1994 and Tegner and Butler 1989). Survival of outplanted juveniles after one year has varied from less than 1% (Goodsell et al. 2006, Rogers-Bennett and Pearse 1998, Tegner and Butler 1985a) to over 30% (Davis 1995, Dixon et al. 2006, Schiel 1992). Variable success may be due to many factors, including the health, size, and shell color of juvenile abalone, habitat where abalone are planted, and predation (McCormick et al. 1994).

Behavioral differences between cultured and wild abalone may also contribute to juvenile mortality. Behavioral differences between hatchery-reared and wild fishes are thought to contribute to predation in outplanted fishes - much of which occurs shortly after release (reviewed by Olla et al. 1998 and Salvanes and Braithwaite 2005a). Although this phenomenon is less well known in invertebrates, hatchery-reared blue crabs (*Callinectes sapidus*) bury in sediment less often than do wild conspecifics and hatchery crabs experience increased predation in the wild (Davis et al. 2004). In laboratory experiments, hatchery-reared abalone differed in movement patterns and habitat-selection and were more easily preyed upon than were wild conspecifics (Schiel and Welden 1987, Tegner

and Butler 1989). Rearing conditions within the hatchery have been shown to affect behavior in a variety of aquatic species (Berejikian et al. 2000, Brown et al. 2003, Lee and Berejikian 2009, Salvanes and Braithwaite 2005b). For example, Berejikian et al. (2000) illustrated that steelhead (*Oncorhynchus mykiss*) reared in habitat-enriched tanks (supplemented with structures, overhead cover and underwater feeders) socially dominated conspecifics reared in conventional tanks.

Given the increasing numbers of threatened and endangered aquatic species worldwide and the desire to supplement declining populations with captive-reared animals, it is imperative to optimize culture methods for successful restoration. Rearing conditions for conservation aquaculture must be designed to minimize behavioral differences between cultured and wild abalone, while simultaneously maximizing growth and survivorship in the hatchery. The balance between growth and survivorship in the hatchery and subsequent survival in the wild must be considered in order to develop a cost-effective and successful enhancement program. As a first step towards determining whether rearing conditions can affect this balance, I examined the growth, survivorship and behavior of pinto abalone reared in habitat-enriched (supplemented with coralline algae encrusted rocks, sea urchins, and native macroalgae) and conventional tanks. A better understanding of the culture conditions necessary to produce juveniles that demonstrate high survival in the wild is critical to effectively restore abalone populations in Washington State.

If conservation aquaculture is to be used to help restore pinto abalone, genetic concerns must also be incorporated into the development of captive rearing strategies. Aquaculture poses genetic threats to wild populations including loss of genetic variability and homogenization of populations (Utter 1998, Waples 1991); first and foremost, a restoration program must do no harm. As pinto abalone conservation aquaculture commences, we must understand how genetic diversity is structured in this species and incorporate this knowledge into hatchery management. Otherwise, outplanting hatchery-reared juveniles may result in declines in the genetic diversity of wild populations and homogenization of populations. Population structure varies widely among abalone species, and the detection of this structure varies depending on the markers used. In the red abalone (*H. rufescens*), one allozyme locus (Kirby et al. 1998) and 41 of 163 amplified fragment length polymorphism (AFLP) markers (Gruenthal et al. 2007) showed significant genetic divergence among populations. However, this genetic divergence was not detected using additional allozyme loci, microsatellites, and mitochondrial DNA (mtDNA) sequences (Burton and Tegner 2000, Gruenthal et al. 2007, Kirby et al. 1998). In contrast, black abalone (*H. cracherodii*), a sympatric species, shows significant population structure at all markers examined (allozyme, AFLP, microsatellite, and mtDNA loci (Chambers et al. 2006, Gruenthal and Burton 2008, Hamm and Burton 2000), with the pattern in AFLP and microsatellite markers suggesting isolation by distance (Gruenthal and Burton 2008). In Australia, weak genetic differentiation at allozyme loci was found among populations of both *H. laevigata* and *H. rubra* (Brown 1991b, Brown and Murray 1992). A later study using three molecular markers (randomly amplified polymorphic DNA, minisatellites, and microsatellites)

found significant population structure in Australian *H. rubra* with a strong signature of isolation by distance (Huang et al. 2000). The Taiwanese abalone (*H. diversicolor* Reeve, 1846) shows extremely high population structure, with fixed mtDNA differences between populations separated by only 35 km (Jiang et al. 1995).

Previous research detected little population structure in the pinto abalone (Withler et al. 2003). Withler et al. (2003) used eight microsatellite loci to analyze genetic diversity in pinto abalone from 31 sites in B.C. and one site in Southeast Alaska. Little evidence of differentiation was found among coastal B.C. locations but these sites differed from sites in the Queen Charlotte Islands and Alaska. Results indicated that 99.6% of variation was found within abalone samples with only 0.4% partitioned among samples. In initial studies examining mtDNA genetic diversity within Washington State abalone, we uncovered evidence of several genetically distinct abalone. At the mtDNA genes encoding cytochrome oxidase *c* subunit I (COI) and cytochrome oxidase B (CytB), these animals diverged strongly from other pinto abalone. At COI, these divergent individuals grouped not with pinto abalone but with flat abalone (*H. walallensis*). Although the historical distribution of flat abalone may have extended to southern Washington State, these animals are not known to be here presently and have not been in Washington's inland marine waters (Geiger 2000).

It should be noted that these divergent abalone cannot be distinguished from pinto abalone using gross morphology; they are morphologically similar to but genetically distinct from pinto abalone. There are several ways to explain this observation: 1) the

genetically divergent individuals may form a reproductively isolated sympatric population of pinto abalone, 2) they may be flat abalone, 3) they may belong to another species of abalone or 4) they may be hybrids between pinto abalone and a second species.

Abalone color and morphology vary substantially depending upon habitat and diet (Leighton 2000) and abalone are commonly misidentified due to phenotypic plasticity. In one case, twenty white abalone (*H. sorenseni*) were collected for use as broodstock in the white abalone recovery program (McCormick and Brogan 2003). These individuals were morphologically identified as white abalone, but genetic analyses revealed that one abalone was *H. kamtschatkana* (either pinto or threaded abalone (*H. k. assimilis*), the southern sub-species; Gruenthal and Burton 2005). In another case, researchers examining phylogenetic relationships among Indo-Pacific abalone using the mtDNA gene cytochrome oxidase II (Degnan et al. 2006) found that two abalone identified as *H. varia* were actually members of a previously unknown taxon, a morphologically cryptic species basal to the entire Indo-Pacific clade.

Before we ascertain which abalone taxa are present in Washington State, managers cannot accurately assess abalone populations nor plan appropriate conservation actions. My work to examine genetic diversity and species identification in Washington State abalone is particularly timely because pilot scale pinto abalone restoration programs which require identification (e.g. conservation aquaculture and adult aggregation) are currently being conducted by WDFW in collaboration with the University of Washington and the Puget Sound Restoration Fund. Several genetically divergent individuals are now held in the conservation aquaculture facility, but their use as broodstock has been

discontinued until their taxonomic status is determined. If these individuals are not pinto abalone, their inclusion as broodstock could have serious consequences for pinto abalone recovery. At the least, using these animals in culture could lead to wasted effort, as interspecific abalone hybrids often show reduced survivorship and fertility (Coleman and Vacquier 2002). No long term increase in abalone numbers would be expected if non-viable offspring were outplanted. Outplanting viable hybrid offspring could also negatively affect pinto abalone; hybridization has led to the extirpation or extinction of many species (Rhymer and Simberloff 1996).

POTENTIAL GENETIC EFFECTS OF GEODUCK AQUACULTURE

The Pacific geoduck (*Panopea generosa* (until recently = *P. abrupta*, (Vadopalas et al. 2010); hereafter geoduck) is an extremely large hiatellid clam; the largest individuals have shells over 200 mm long and weigh more than 3.25 kg (Goodwin 1976, Goodwin and Pease 1991a). Geoducks are found in the Eastern Pacific from Baja California, Mexico to Alaska, USA (Anderson 1971, Coan et al. 2000, Morris et al. 1980). Geoducks are filter-feeders that generally burrow 50-60 cm into soft sediments (Goodwin 1976) from the low intertidal to subtidal habitats more than sixty meters deep (Goodwin 1976), with pilot video-surveys suggesting that geoducks may be found to 110 meters (Jamison et al. 1984). Geoducks are very long-lived; many individuals have been aged at over 100 years (Campbell and Ming 2003, Goodwin 1976, Shaul and Goodwin 1982, Sloan and Robinson 1984). Geoducks likely influence the ecosystem through filter feeding and biodeposition, as has been documented in other bivalves (Newell 2004).

Geoducks are thought to be dioecious (Goodwin 1976) but some evidence suggests that they may be protandrous hermaphrodites. A highly skewed sex ratio is observed in young clams; two studies identified more than 90% of small (SL < 100 mm, (Anderson 1971) or young (<11 years, (Sloan and Robinson 1984) clams as male. At three locales within Puget Sound, 77% of two year old geoduck and 67% of three to five year old geoduck were identified as male (B. Vadopalas, unpublished data). In histological examinations of 253 geoducks, one individual was observed with both oocytes and spermatozoa (Campbell and Ming 2003); researchers at the University of Washington have observed a similar rate of occurrence (B. Vadopalas, unpublished data). Geoduck clams broadcast spawn. Their fertilized eggs develop into planktotrophic larvae (Sloan and Robinson 1984) that remain planktonic for 47 days at 14°C (Goodwin et al. 1979). Geoducks are fished commercially in Washington State, Alaska, and B.C. (Hoffmann et al. 2000). Commercial geoduck fisheries began in Washington State in 1970 (Washington Department of Natural Resources 2000) and in B.C. in 1976 (Muse 1998). Market demand for geoduck was limited when the fishery commenced but both Asian and domestic markets have grown over time (Washington Department of Natural Resources 2000). Between 1992 and 1999, an average of 1.6 million pounds of geoducks were harvested per year, which generated between five and seven million dollars annually in Washington State (Washington Department of Natural Resources 2000). Between 1999 and 2008, an average of 4.3 million pounds of geoduck clams were harvested annually (Mel Stanley, WDFW, personal communication to Brent Vadopalas on Oct. 15, 2009). The geoduck fishery is now the most lucrative clam fishery along the Pacific coast of North America (Washington Department of Natural Resources 2000).