

Ecological Effects of the Harvest Phase Of Geoduck (*Panopea generosa* Gould, 1850) Aquaculture on Infaunal Communities in Southern Puget Sound, Washington

Author(s): Glenn R. Vanblaricom, Jennifer L. Eccles, Julian D. Olden and P. Sean McDonald

Source: Journal of Shellfish Research, 34(1):171-187.

Published By: National Shellfisheries Association

DOI: <http://dx.doi.org/10.2983/035.034.0121>

URL: <http://www.bioone.org/doi/full/10.2983/035.034.0121>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

ECOLOGICAL EFFECTS OF THE HARVEST PHASE OF GEODUCK (*PANOPEA GENEROSA* GOULD, 1850) AQUACULTURE ON INFAUNAL COMMUNITIES IN SOUTHERN PUGET SOUND, WASHINGTON

GLENN R. VANBLARICOM,^{1,2*} JENNIFER L. ECCLES,² JULIAN D. OLDEN² AND P. SEAN MCDONALD^{2,3}

¹U.S. Geological Survey, Washington Cooperative Fish and Wildlife Research Unit, School of Aquatic and Fishery Sciences, College of the Environment, University of Washington, Mailstop 355020, Seattle, WA 98195-5020; ²School of Aquatic and Fishery Sciences, College of the Environment, University of Washington, Mailstop 355020, Seattle, WA 98195-5020; ³Program on the Environment, College of the Environment, University of Washington, Mailstop 355679, Seattle, WA 98195-5679

ABSTRACT Intertidal aquaculture for geoducks (*Panopea generosa* Gould, 1850) is expanding in southern Puget Sound, Washington, where gently sloping sandy beaches are used for field culture. Geoduck aquaculture contributes significantly to the regional economy, but has become controversial because of a range of unresolved questions involving potential biological impacts on marine ecosystems. From 2008 through 2012, the authors used a “before–after–control–impact” experimental design, emphasizing spatial scales comparable with those used by geoduck culturists to evaluate the effects of harvesting market-ready geoducks on associated benthic infaunal communities. Infauna were sampled at three different study locations in southern Puget Sound at monthly intervals before, during, and after harvests of clams, and along extralimital transects extending away from the edges of cultured plots to assess the effects of harvest activities in adjacent uncultured habitat. Using multivariate statistical approaches, strong seasonal and spatial signals in patterns of abundance were found, but there was scant evidence of effects on the community structure associated with geoduck harvest disturbances within cultured plots. Likewise, no indications of significant “spillover” effects of harvest on uncultured habitat adjacent to cultured plots were noted. Complementary univariate approaches revealed little evidence of harvest effects on infaunal biodiversity and indications of modest effects on populations of individual infaunal taxa. Of 10 common taxa analyzed, only three showed evidence of reduced densities, although minor, after harvests whereas the remaining seven taxa indicated either neutral responses to harvest disturbances or increased abundance either during or in the months after harvest events. It is suggested that a relatively active natural disturbance regime, including both small-scale and large-scale events that occur with comparable intensity but more frequently than geoduck harvest events in cultured plots, has facilitated assemblage-level infaunal resistance and resilience to harvest disturbances.

KEY WORDS: aquaculture, benthic, disturbance, extralimital, geoduck, infauna, intertidal, *Panopea generosa*, Puget Sound, spillover

INTRODUCTION

Aquaculture operations are proliferating and diversifying in nearshore marine habitats across the globe (e.g., Naylor et al. 2000, Chopin et al. 2001, Goldberg & Naylor 2005, Buschmann et al. 2009, Lorenzen et al. 2012, Samuel-Fitwi et al. 2012). Although frequently of positive societal benefit, aquaculture enterprises have raised concerns regarding possible negative ecological consequences among resource managers, scientists, conservation advocacy organizations, political leaders and legislators, and the interested lay public (e.g., Simenstad & Fresh 1995, Newell 2004, Sara 2007, Dumbauld et al. 2009, Forrest et al. 2009, Coen et al. 2011, Hedgcock 2011). Since the early 2000s localized but intensive political controversy has emerged in communities near southern Puget Sound, Washington, regarding development of geoduck (*Panopea generosa* Gould, 1850) aquaculture operations on gently sloping intertidal sand habitats. Geoduck aquaculture activity is increasingly contributing to Puget Sound’s total commercial geoduck production that also includes substantial wild harvests. In 2011, cultured geoducks comprised about 25% of the total commercial harvest in Washington and generated revenues of about US\$20 million. As a consequence of expanding geoduck aquaculture operations,

many questions and concerns have emerged regarding ecological effects of harvesting activities.

The focus of the current study was on the evaluation of possible ecological changes to marine ecosystems as a result of habitat disturbances associated with geoduck aquaculture activity in southern Puget Sound. Ecological disturbance is considered here as “any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substratum availability, or the physical environment” (Pickett & White 1985, p. 8). Disturbances in general may be natural or anthropogenic and may occur on a wide range of magnitudes and spatiotemporal scales. Natural disturbances are known to be important determinants of community dynamics in many marine benthic habitats (e.g., Connell 1978, VanBlaricom 1982, Sousa 1984, Dumbauld et al. 2009). However, frequent and intensive anthropogenic disruptions may overwhelm evolved natural resistance or resilience to habitat disturbance in benthic communities (Sousa 1984, Paine et al. 1998).

The geoduck aquaculture cycle includes the following phases, each constituting potential ecological disturbances to resident organisms. Young hatchery clams are outplanted at the initiation of the cycle. At the same time, predator exclusion structures are placed to limit losses of young clams to mobile consumers such as crabs and shorebirds. Structures include arrays of vertically placed PVC tubing extending above the sediment surface. Young

*Corresponding author. E-mail: glennvb@uw.edu
DOI: 10.2983/035.034.0121

clams are placed in sediments within the tubes (typically 3–4 individuals per tube), after which tubes are covered either with large nets that extend over the entire tube field, or individual “cap nets” that cover each tube but leave intervening spaces uncovered. Typical initial stocking density at outplanting is 20–30 clams/m². The tubes and netting are removed 1–2 y after outplanting when clams are sufficiently large and deeply buried that risks of predation are minimal. Tube diameter, tube density, within-tube clam density at outplanting, netting type, and timing of removal of tubes and netting vary by grower preference. Clams are left in place for the grow-out phase until they reach optimal market size.

The culture cycle is terminated by harvest 5–7 y after outplanting. During low tides, individual clam siphons are located visually and marked with small wooden stakes pressed into the sediment. Individual clams so located are subsequently extracted by hand after liquefaction of sediments within a radius of 15–30 cm of the siphon, extending into the sediment the length of the clam siphon. Liquefaction is achieved with a handheld nozzle (“stinger”) supplied with seawater pumped into an attached hose from a small barge offshore. The process is highly efficient in the hands of experienced harvesters, with extraction of each clam requiring 5 sec or less under optimal conditions. Time required for complete harvest of a given cultured plot may range from a few days to many months. Duration of harvest varies with plot size, density of market-size clams, weather and sea conditions, availability of skilled and experienced laborers, and grower preference. Harvests may be done during high tides by divers also using stingers if schedules for extreme low tides are unfavorable in the context of labor availability, market price, or shipping cost conditions.

Disturbance of sediments as a result of cultured geoduck harvests may have ecological consequences that extend beyond cultured plots to adjacent areas of unharvested substrata, causing extralimital changes in benthic communities. There is significant management interest in potential “spillover” effects of geoduck harvest, particularly relating to the regulation of the spatial scope of cultured geoduck plots and the potential requirements for uncultured buffer zones between cultured plot boundaries. Geoduck harvest activities produce disturbances confined to explicit spatial boundaries and create a distinctive interface in physical processes between harvested and unharvested substrata. When harvest occurs, suspended sediments, biogenic detritus, and possibly benthic organisms could be carried onto adjacent sediments either by water pumped across intertidal habitats during harvest or by along-shore currents during flood tides immediately after harvest. The export of benthic organisms, sediment, detritus, and nutrient materials could affect resident infaunal populations at intensities varying with distances from the edges of harvested plots.

Reported here are the results of a field study to determine whether geoduck aquaculture harvest operations alter benthic infaunal invertebrate assemblages of intertidal sandflats in southern Puget Sound. Infaunal assemblages as response variables were chosen for three reasons. First, the opinion of the authors *a priori* was that selected organisms would likely be more sensitive to cultured geoduck harvest effects than other ecosystem components, given that the physical habitats of infauna are directly disturbed in harvest operations by design. Second, benthic infauna and epifauna in the Puget Sound

region are known to be important as prey for mammals, birds, mobile invertebrates, and fish, including juvenile salmonid populations migrating from natal freshwater habitats seaward via Puget Sound. Minimization of detrimental disturbances to significant prey populations is viewed as crucial to restoration of imperiled salmonid populations in the region. Third, the known high densities of infauna in habitats used for geoduck aquaculture ensured that samples collected in the current study would produce high counts of organisms, with zero values rare or absent, facilitating an effective and rigorous community-based investigation in a quantitative context.

Three related hypotheses (identified by number in the subsequent text) were tested using coupled multivariate and univariate statistical methods to evaluate the significance of relevant contrasts:

1. Within plots subject to harvests (“harvest plots”), infaunal assemblages will be similar to those in adjacent plots not designated for harvest (“reference plots”) before harvest occurs.
2. Prior to harvest, infaunal assemblages for a range of distances away from the edge of harvest plots (“transect samples”) will be similar to assemblages in harvest plots and to adjacent reference plots. After harvest, data from transect samples will show a trend of increasing similarity to data from reference plots, and decreasing similarity to data from within harvest plots, with increasing distances away from the edges of harvest plots.
3. Within harvest plots, benthic infaunal assemblages will be altered significantly after completion of harvests as a consequence of harvest-related disturbances.

MATERIALS AND METHODS

Study Areas

The study was conducted at intertidal locations in the southern basin of Puget Sound, Washington. Puget Sound is an estuarine fjord, with the southern basin defined as the interconnected marine waters south and west of Tacoma Narrows (47.27° N, 122.55° W). The surface area of the basin is 449 km² at mean high water, including 67.4 km² of intertidal habitat (Burns 1985). The area contains extensive gently sloping sandy and muddy intertidal habitats, many of which are biologically appropriate for bivalve aquaculture operations. Mean daily tidal fluctuation in the southern basin ranges from 2.7–3.2 m in a mixed semidiurnal pattern (Mofjeld et al. 2002), with a maximum range of 6.5 m for single tidal exchanges at the extreme southern limit of the basin (National Ocean Service, National Oceanic and Atmospheric Administration 2014). Surface water temperatures range annually from ~8 to ~16°C, and salinities range from 27–30, with the exception of periods of dilution from riverine flooding (Collias et al. 1974, Dethier & Schoch 2005).

Three study sites were chosen (Fig. 1) based on three criteria. First, selected sites were involved in production-scale commercial aquaculture at the time of the anticipated field sampling. The study site selections had the purpose of fostering relevance of the current study to the spatial and temporal scales typical of the geoduck aquaculture industry. Second, the culture cycle at selected sites was approaching the terminal harvest phase, which allowed sampling before, during, and after harvest at

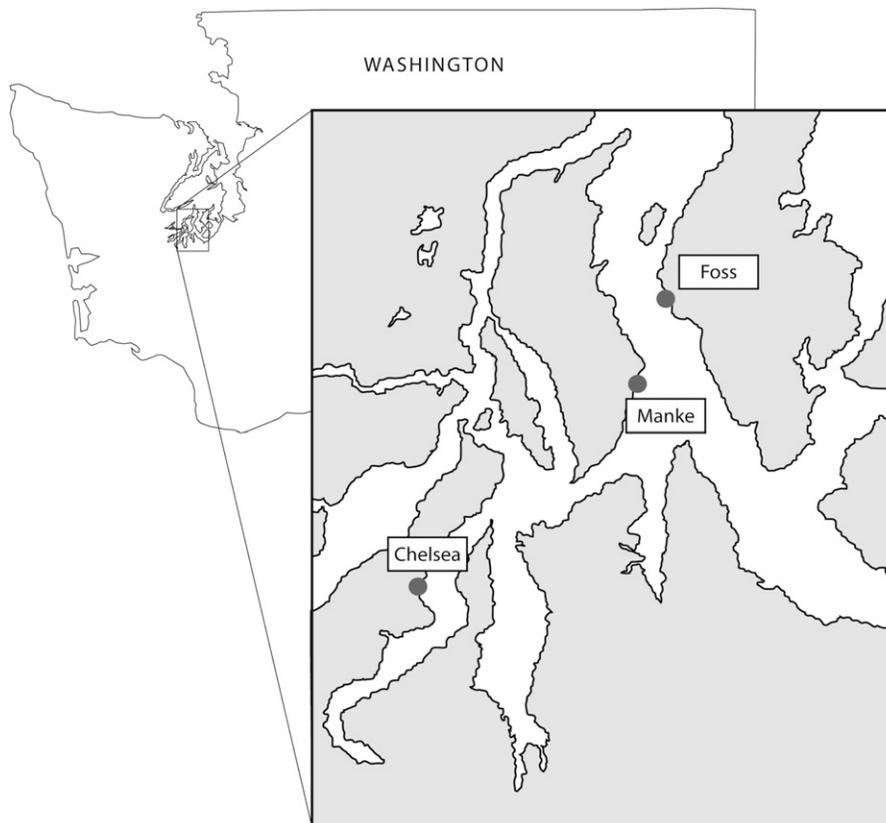


Figure 1. Locations of study sites in southern Puget Sound, Washington. Coordinates (latitude and longitude) for each site are provided in the text. Shaded areas are land; white areas are water.

treatment and adjacent reference plots in time periods ≤ 30 mo. Third, sediments, slope, and exposure to weather and sea were generally similar among the selected sites and were, in all cases, similar to the typical physical attributes of sites customarily used by the geoduck aquaculture industry (gently sloping intertidal sediments that are primarily fine sands with silt/clay fractions $< 20\%$ by mass, and at least moderately protected from exposure to wind and sea by local topography).

The three study sites were as follows. “Foss” (47.22° N, 122.82° W) was located on the eastern shore of Case Inlet near Joemma Beach State Park. “Manke” (47.20° N, 122.84° W) was near Pt. Wilson on the eastern shore of Harstene Island, which forms the western shore of Case Inlet. Cultured plots at Foss and Manke were operated by Taylor Shellfish, Inc. (Shelton, WA) specifically for geoduck aquaculture at the time of the current study. “Chelsea” (47.13° N, 122.96° W) was on the northwestern shore of Eld Inlet. At the time of this study, the cultured plot at Chelsea was owned by Chelsea Farms, LLC (Olympia, WA), with nearby areas used for Manila clam (*Venerupis philippinarum* [Adams and Reeve, 1850]) and Pacific oyster (*Crassostrea gigas* [Thunberg, 1793]) aquaculture as well as for geoducks. Neither Taylor Shellfish, Inc., nor Chelsea Farms, LLC, made any effort whatsoever to influence study design, sampling procedures, generation and analysis of resulting data, or interpretations of results as provided herein or elsewhere.

Sampling Design and Methods

We used a “before–after–control–impact” design (Green 1979), establishing a cultured (i.e., “impact”) plot containing

mature geoducks and an unplanted reference (i.e., “control”) plot, each measuring at least $2,500 \text{ m}^2$, at each of the three sites. Cultured plots at each site were subject to geoduck harvest throughout the course of the study whereas reference plots experienced no harvest activity. None of the study plots had been used for geoduck aquaculture prior to this project. Within each site, the cultured and reference plots were of equal size and shape, with similar sedimentary composition (based on qualitative assessments *a priori*), slope, and elevation within the tidal zone. Cultured and reference plots were separated by a buffer zone of at least 75 m to minimize effects of intrinsic differences resulting from location, and simultaneously provided adequate separation distance to reduce potential extralimital effects of the harvest process on the reference plot (Fig. 2A). Plots were marked with PVC stakes at the two shoreward corners. Cultured and reference plots were divided into 100×100 -unit Cartesian grids, and 10 sampling points were selected randomly within each plot for each sampling date, without replacement across sampling dates. One core sample was collected at each sampling point on each sampling date.

At each site, at least one extralimital transect was established, extending away from each cultured plot and running parallel to the shoreline for a distance of 50–60 m. Each transect extended from an origin at the midpoint of one of the two edges of the cultured plot that ran perpendicular to the shoreline. The entire length of each transect was in an area free of planted geoducks or other types of aquaculture except at Chelsea, where the first 10 m of the transect crossed over a young cohort of

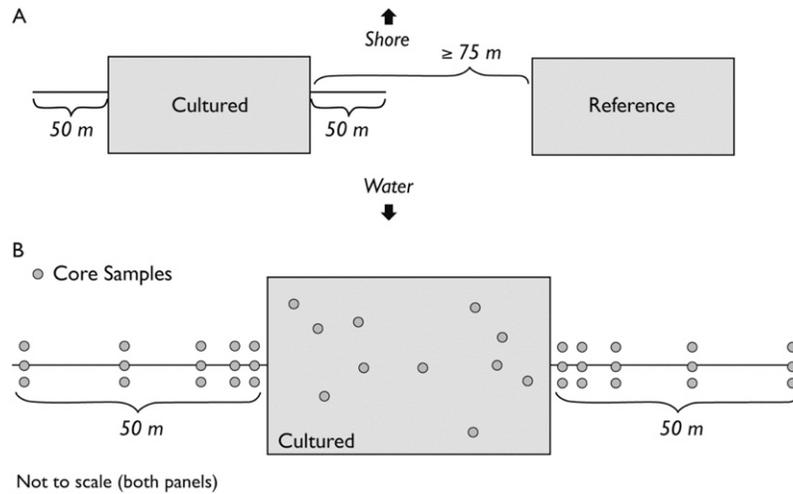


Figure 2. Diagram of physical layout (plan view) used for each of the three study areas. (A) Relative positions of cultured and reference plots at each site and placement of extralimital transects at Foss (only one transect was established at Manke and Chelsea, respectively). (B) Example random placement of core sample sites for cultured plot at each site on each sampling date, and layout of transect core sample placement at Foss. Similar core sample placement protocols were used on the single transects at Manke and Chelsea. Diagrams are not to scale. Additional details are provided in text.

planted geoducks. Areas spanned by transects experienced no harvest activity during the course of the study.

At each site, three benthic core samples were taken on each sampling date at distances of 2, 5, 10, 20, and 50 m from the edge of the cultured plot along the transect (2, 5, 10, 12, 15, 20, 30, and 60 m at Chelsea). At each distance, one sample was taken on the transect line, and one each approximately 30 cm to either side (in shoreward and seaward directions) of the transect line. Core sampling points along the transect lines were shifted slightly (≤ 1 m) to avoid resampling the same point during subsequent sampling events.

Benthic core samples were 5 cm in diameter with a surface area of 19.6 cm², a depth of 10 cm, and a volume of 196 cm³. All contents of each core sample were placed unscreened in 500-mL jars and preserved in 10% buffered formalin solution immediately after collection. According to the laboratory processing methods of Simenstad et al. (1991) and Sobocinski et al. (2010), freshwater was added to each sample followed by mixing until sediments settled to the bottom and elutriated organisms floated to the surface. Fluid was decanted through a 500- μ m screen, and all organisms retained on the collection screen were removed and preserved in 70% isopropanol for eventual identification and enumeration. The process was repeated several times for each sample to ensure that all organisms had been separated from the sediments. Organisms were identified to the level of species or genus when feasible, but in all cases at least to family level. Family-level identification of infaunal organisms has been found to be sufficient for many types of marine environmental studies (e.g., Ferraro & Cole 1990, Somerfield & Clarke 1995, Hernández Arana et al. 2005), including some in Puget Sound (e.g., Dethier 2010). Identified samples were subjected to quality assurance and control checks by specialists to ensure accurate identification. Infaunal biomass densities were not estimated in the current study.

Each site was sampled as often as possible, but no more frequently than monthly, as allowed by low tide patterns and by competing sampling activities at other study sites. The minimum

goal for each site was four monthly sampling events prior to harvest, monthly sampling events during harvest activities for as long as they continued, and four monthly sampling events after completion of the harvest. The study design did not include sampling targeted specifically to times immediately after harvest activity (i.e., within hours to a few days), possibly resulting in underestimation of short-term ecological consequences of harvesting. The actual number of dates sampled was different from site to site as a result of variations in harvest timing and site accessibility. Harvest duration and sampling duration varied by site, and modest differences in sediment composition were detected among sites. As a result, data from each site were analyzed independently and the sites were not considered replicates.

For descriptive summaries, numbers of organisms in each core sample (hereinafter, “sample”) were converted to estimated densities (individual organisms of all species per square meter). For each sampling date, all samples were averaged to single point estimates for each taxon in each plot by date, with certain exceptions as noted later. Standard errors were calculated for each point estimate.

For direct assessment of within-plot harvest effects, analyses were done for the following categories: treatment (samples collected on cultured plots vs. reference plots), date (samples collected on each sampling date), and harvest state (samples collected during different periods of geoduck harvest). Harvest state subcategories were before the geoduck harvest (preharvest), during harvest (midharvest or harvest period), and after harvest (postharvest).

For assessment of extralimital effects of harvesting based on transect sampling, categories were treatment (samples collected in cultured plots and reference plots vs. samples collected at various distances along transects from the cultured plot edges), date (samples collected on each sampling date), and harvest state (samples collected during different periods of geoduck harvest, with subcategories as indicated earlier).

Patterns of abundance in a species of particular interest in a management context—the benthic gammaridean amphipod

TABLE 1.

Dominant infaunal taxa in core sample data selected on the basis of frequencies of occurrence or (for *Americorophium salmonis*) ecological significance.

| Taxon | Category | Frequency | Ecological notes |
|---|---------------------|-----------|------------------|
| <i>Americorophium salmonis</i> (Stimpson, 1857) | Amphipod crustacean | 0.71 | TD, SDSS |
| <i>Cumella vulgaris</i> (Hart, 1930) | Cumacean crustacean | 0.92 | EFDF |
| <i>Rochefortia</i> spp. Vélain, 1877 | Bivalve mollusc | 0.98 | CTD, SF |
| <i>Micrura</i> spp. Ehrenberg, 1871 | Nemertean | 0.94 | M, DF |
| Capitellidae Grube, 1862 | Polychaete annelid | 0.94 | BD, DF |
| Goniadidae Kinberg, 1866 | Polychaete annelid | 0.94 | MCOS |
| Spionidae Grube, 1850 | Polychaete annelid | 0.98 | TD or M, SDSS |
| Hesionidae Grube, 1850 | Polychaete annelid | 0.94 | MCOS |
| Phyllodocidae Örsted, 1843 | Polychaete annelid | 0.81 | MCOS |
| Polynoidae Malmgren, 1867 | Polychaete annelid | 0.81 | MCOS |

Frequency calculations are based on all core samples taken during all sampling events within cultured and reference plots at all three study sites during the study. In the Spionidae, mode of habit (tube dweller or mobile) varies by species. BD, burrow dweller; CTD, commensal dweller in tubes of other invertebrates; DF, deposit feeder; EFDF, epistrate feeder (scrapes attached detrital or living plant or bacterial cells from individual sand grains) when living in sandy habitats, deposit feeder when living in muddy or silty habitats (Weiser 1956); M, mobile; MCOS, mobile carnivore, omnivore, or scavenger (varies by species within the family); SDSS, selective detritivore on sediment surface; SF, suspension feeder; TD, tube dweller.

Americorophium salmonis (Stimpson, 1857)—were evaluated along with organisms occurring frequently in samples. The amphipod *A. salmonis* is known to be an important prey species for juvenile out-migrating salmonid fish populations in Puget Sound, particularly Chinook salmon (*Oncorhynchus tshawytscha* [Walbaum, 1792]).

Multivariate Analyses

Permutation-based analyses of variance (perMANOVAs [Anderson 2001]) were used to test for differences by site, treatment, date, and harvest state according to square root-transformed abundance data and Bray-Curtis indices of community similarity (Bray & Curtis 1957). For extralimital transect data, perMANOVAs were used to evaluate differences by plot type and distance on transects (treatment), date, and harvest state. In addition, the interaction of data subsets representing treatment and harvest state was tested for data collected from treatment and reference plots. A significant

result from a test of the harvest state × treatment interaction term indicated an effect of the harvest state on one of the treatments—specifically, the effect of the midharvest state on the cultured plot or on locations along extralimital transect lines.

Distance-based tests for homogeneity of multivariate dispersion (HMD [Anderson 2006]) were conducted to contrast levels of variability in community structure between treatment and reference plots, and for contrasts among plot data and locations on extralimital transects. Homogeneity of multivariate dispersion uses a Bray-Curtis distance matrix of species data to calculate the average distance in multivariate space between individual samples and the calculated centroid of the sample group. The average distance and the associated variability are compared between groups and tested for significance with permutation tests. An increase in the multivariate dispersion of samples with increased disturbance was predicted by Caswell and Cohen (1991). In addition, a number of environmental impact studies have reported that the variability of species

TABLE 2.

Mean densities (measured in individuals per square meter SE) rounded to nearest integer by site and plot type for all sampling dates during the study as determined from core samples.

| Taxon | Foss | | Manke | | Chelsea | | Culture mean | Reference mean | Overall mean |
|--------------------------------|-------------|---------------|---------------|-------------|---------------|-------------|--------------|----------------|--------------|
| | Culture | Reference | Culture | Reference | Culture | Reference | | | |
| <i>Americorophium salmonis</i> | 3,529 (882) | 11,936 (710) | 1,579 (796) | 2,498 (952) | 15 (8) | 7 (5) | 1,568 (441) | 4,140 (1,080) | 2,854 (597) |
| <i>Cumella vulgaris</i> | 567 (194) | 490 (127) | 435 (80) | 1,531 (307) | 1,611 (540) | 1,630 (637) | 862 (203) | 1,291 (254) | 1,077 (163) |
| <i>Rochefortia</i> spp. | 287 (92) | 367 (113) | 1,462 (419) | 3,395 (743) | 1,181 (190) | 2,584 (497) | 1,061 (194) | 2,332 (388) | 1,696 (227) |
| <i>Micrura</i> spp. | 188 (52) | 520 (94) | 268 (38) | 347 (46) | 192 (35) | 211 (60) | 222 (24) | 347 (40) | 284 (24) |
| Capitellidae | 718 (596) | 310 (185) | 979 (434) | 772 (404) | 4,368 (2,501) | 1,241 (258) | 2,040 (883) | 807 (195) | 1,424 (454) |
| Goniadidae | 1,217 (450) | 1,700 (636) | 900 (234) | 1,436 (452) | 1,369 (366) | 1,125 (268) | 1,139 (182) | 1,401 (261) | 1,270 (162) |
| Spionidae | 766 (154) | 602 (159) | 406 (101) | 833 (150) | 1,567 (446) | 1,499 (367) | 887 (174) | 995 (151) | 941 (115) |
| Hesionidae | 2,728 (449) | 9,495 (3,304) | 4,288 (2,110) | 5,547 (598) | 552 (286) | 848 (280) | 2,634 (920) | 5,014 (1,175) | 3,824 (755) |
| Phyllodocidae | 252 (80) | 126 (47) | 505 (113) | 538 (80) | 124 (47) | 269 (105) | 312 (58) | 341 (55) | 326 (40) |
| Polynoidae | 97 (33) | 146 (58) | 123 (26) | 332 (56) | 187 (51) | 207 (88) | 137 (22) | 242 (41) | 190 (24) |

Listed taxa are those identified and described in Table 1.

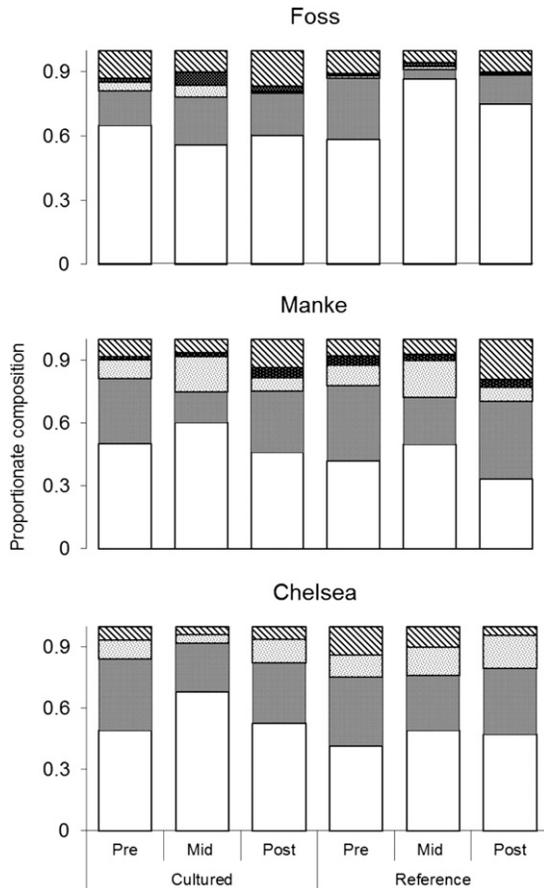


Figure 3. Taxonomic composition of all infauna summed as proportions of numbers of individuals in samples in cultured and reference plots during preharvest, midharvest, and postharvest states at each study site. In each plot, taxonomic categories are from bottom to top, polychaetes, crustaceans, bivalves, echinoderms, and all other taxa combined. The echinoderm category does not appear in the Chelsea plot because numbers in samples were zero or near zero.

abundance in samples collected from disturbed areas was greater than the variability of samples collected from undisturbed areas when evaluated with HMD (Warwick and Clarke 1993). For contrasts of data from treatment and reference plots using HMD analyses, data on infaunal abundance by individual sample were used because averaging samples could mask important intersample variability, given the large number of replicate samples collected. At each site, HMD analyses were used to test differences between the cultured and reference plots within each harvest state, within plots among harvest states, and among samples from plots and varying distances on extralimital transects.

Univariate Analyses

Individual sample diversity was calculated using the Shannon index (Shannon 1948) (also known as Shannon's diversity index), the Shannon-Wiener index, and the Shannon-Weaver index) on log-transformed data (e.g., Warwick et al. 1990). Two-sample *t*-tests were used to assess differences in diversity indices between plots within sites for each sampling date. In addition, one-way univariate analyses of variance (ANOVAs) were used to evaluate the significance of differences in diversity

indices between plot types on each date, between plot types for each harvest state, and within plot types between harvest states.

Some components of our data failed to meet underlying assumptions on which ANOVA methods are based, including normality and homoscedasticity. The subject assumptions are often violated by ecological data, but ANOVA procedures are frequently robust to the discrepancies (e.g., Underwood 1981). Analysis of variance methods have been applied in a number of other studies with data characteristics similar to ours (e.g., Smith & Brumsickle 1989, Warwick et al. 1990, Thrush et al. 1996, Kaiser et al. 1996, Anderson & Underwood 1997, Kaiser et al. 2006).

Generalized linear mixed models (McCullagh & Nelder 1989) were used assuming Poisson-distributed data to examine the factors contributing to abundance of selected individual infaunal taxa from our core samples. These analyses were applied to *Americorophium salmonis* and the nine other individual taxa (species, genera, or families) identified from high frequencies of occurrence in core samples (Table 2). For univariate analyses, data from all sites were considered together. The fixed effects of month, plot type, harvest phase, and their interaction were included, as well as random effects of site. Models were fitted by maximum likelihood assuming a Laplace approximation in the lme4 package (Bates & Maechler 2010) of R software (R Development Core Team 2011). Likelihood ratio tests were used to compare models formally, including the harvest state \times treatment interaction term. Regression coefficients and their 95% confidence intervals were calculated for each model.

RESULTS

Descriptive Patterns

Percentages of sand in benthic habitats were 99.1 at the Foss study site, 98.8 at Manke, and 86.0 at Chelsea (Price 2011). Overall, 50 discernible animal taxa were identified in the samples. The numerically dominant taxa were generally small (maximum length of individuals, <1 cm) and resided on or within a few centimeters below the sediment surface. The sampled benthic communities at all three sites consisted primarily of small polychaete worms (Annelida), crustaceans (Arthropoda), and bivalves (Mollusca) (Tables 1 and 2). Polychaetes were numerical dominants at all sites followed by crustaceans (Fig. 3). Taxonomic compositions of the samples generally resembled those reported previously for southern Puget Sound (Dethier et al. 2003, Dethier 2005, Dethier & Schoch 2005, Dethier 2010, Dethier et al. 2010, Dethier et al. 2012).

Multivariate Contrasts by Site and Plot Type

Infaunal abundance was significantly different among study sites (perMANOVA; Table 3). At Foss and Manke, the infaunal sample data from the cultured plots were significantly different from those of reference plots (perMANOVA; Table 3 and Fig. 4, top and middle panels). At Chelsea the core sample data from the two plots did not differ significantly (perMANOVA; Table 3 and Fig. 4, bottom panel).

The perMANOVA analyses identified a number of significant differences based on site, date, or treatment in contrasts within and between plots (Table 3). However, none of the three assessments of the interaction term harvest state \times treatment were found to be significant (perMANOVA; Table 3). For

TABLE 3.
Summary of permutation-based analyses of variance results
for contrasts at scales of study sites and plots.

| Scale | Contrast | R^2 | df | P value |
|---|-------------------|-------|------|-----------------------|
| Among sites | All sites | 0.37 | 2 | <0.001 |
| | Foss vs. Manke | 0.19 | 1 | <0.001 |
| | Foss vs. Chelsea | 0.44 | 1 | <0.001 |
| | Manke vs. Chelsea | 0.27 | 1 | <0.001 |
| Among sites within plot type, cultured plots | Foss vs. Manke | 0.19 | 1 | <0.001 |
| | Foss vs. Chelsea | 0.41 | 1 | <0.001 |
| | Manke vs. Chelsea | 0.24 | 1 | <0.001 |
| Among sites within plot type, reference plots | Foss vs. Manke | 0.39 | 1 | <0.001 |
| | Foss vs. Chelsea | 0.56 | 1 | <0.001 |
| Within site between plot type, by treatment | Foss | 0.41 | 1 | <0.001 |
| | Manke | 0.45 | 1 | <0.001 |
| | Chelsea | 0.09 | 1 | NS |
| Within site between plot type, by date | Foss | 0.60 | 10 | $0.01 \leq P < 0.05$ |
| | Manke | 0.62 | 16 | <0.001 |
| | Chelsea | 0.75 | 13 | <0.001 |
| Within site between plot type, by harvest state | Foss | 0.18 | 2 | $0.01 \leq P < 0.05$ |
| | Manke | 0.17 | 2 | <0.001 |
| | Chelsea | 0.08 | 2 | NS |
| Within site between plot type, harvest state \times treatment interaction | Foss | 0.02 | 2 | NS |
| | Manke | 0.03 | 2 | NS |
| Within site within plot type, by date, cultured plots | Foss | 1.00 | 10 | <0.001 |
| | Manke | 1.00 | 16 | <0.001 |
| | Chelsea | 1.00 | 13 | <0.001 |
| Within site within plot type, by harvest state, cultured plots | Foss | 0.25 | 2 | NS |
| | Manke | 0.25 | 2 | <0.001 |
| | Chelsea | 0.13 | 2 | NS |
| Within site within plot type, by date, reference plots | Foss | 1.00 | 10 | <0.001 |
| | Manke | 1.00 | 16 | <0.001 |
| | Chelsea | 1.00 | 13 | <0.001 |
| Within site within plot type, by harvest state, reference plots | Foss | 0.32 | 2 | $0.01 \leq P < 0.05$ |
| | Manke | 0.25 | 2 | $0.001 \leq P < 0.01$ |
| | Chelsea | 0.11 | 2 | NS |

NS: $P \geq 0.05$.

within-plot contrasts, there were several cases of significant effects of both date and harvest state on reference plot data, illustrating that harvest state is a proxy for date and emphasizing the premise that the harvest state \times treatment interaction term is the uniquely informative metric for assessment of harvest effects within the current study design. Analytical results were inconsistent with hypotheses 1 and 3 as defined earlier. Because the interaction term was not significant in any case, significant differences between plots at Foss and Manke were likely the result of factors other than harvest-related disturbances.

Results for HMD analyses for cultured and reference plots at the three study sites likewise did not fit expectations consistent with geoduck harvesting as a primary source of disturbance. Eight significant contrasts were identified for comparisons within plot type among harvest states, of which four were in reference plots and four were in cultured plots (Table 4). These

results are inconsistent with the hypothesis of greater compositional variation in cases of frequent disturbance as posited in the literature (e.g., Caswell & Cohen 1991, Warwick & Clarke 1993) if harvesting of cultured geoducks is the primary source of disturbance in cultured habitats. The results are also inconsistent with hypotheses 1 and 3. Occurrence of significant contrasts for HMD values in reference plots is consistent with active sources of variability or disturbance other than geoduck harvesting in the study areas.

Multivariate Contrasts by Distance on Extralimital Transects

There was little indication of trends in summed infaunal densities with increased distance from the cultured plot in three of the four extralimital transects (Fig. 5). On the Foss south transect, a significant trend was observed during the midharvest period. All other variations within transects were consistent with random distributions in space and time.

Significant effects of harvest state \times treatment interaction terms were not detected for any combination of data from plots and transect distances at any of the study sites (perMANOVA; Tables 5, 6, and 7). In comparison, there were many cases of significant terms for contrasts of data from specific transect locations with treatment, date, and harvest state (Tables 6 and 7). Patterns in the results are inconsistent with an ecologically significant effect of harvest extending beyond the limits of the cultured plots. Conversely, the results are consistent with significant variation in transect and plot data based on processes independent of harvest activities. The results are also inconsistent with hypothesis 2.

Within each site, the HMD values for community data from the preharvest state were similar across the cultured and reference plots and the various distances along transects (Tables 8 and 9). At Foss and Manke, the HMD values for cultured plots increased during the midharvest state whereas values in reference plots either remained relatively constant or decreased. For both sites, HMD calculations for cultured plots during the midharvest state were significantly different from values at most transect distances and the reference plot (Table 9). During the postharvest state at Foss, HMD values in the cultured plot remained high whereas values for most transect locations and the reference plot returned to near preharvest levels. At Manke, postharvest HMD values were similar to preharvest values at most transect distances and in cultured and reference plots. Homogeneity of multivariate dispersion values increased for most distances on the Chelsea transect during the midharvest state. However, permutation tests revealed that infaunal data from Chelsea were most similar among locations during midharvest (Table 9). In summary, HMD analyses for transect data were generally inconsistent with hypothesis 2.

Univariate Analyses

Values for the Shannon index for core samples at Foss and Chelsea were similar between the cultured and reference plots over time (Fig. 6, top and bottom panels). At Manke, index values fluctuated more among dates on both plots, but the cultured plot had consistently lower diversity indices (Fig. 6, middle panel). When diversity values were averaged by harvest state, there was a mixture of significant and nonsignificant values in contrasts between plots for each harvest state and within plots among harvest states (Table 10).

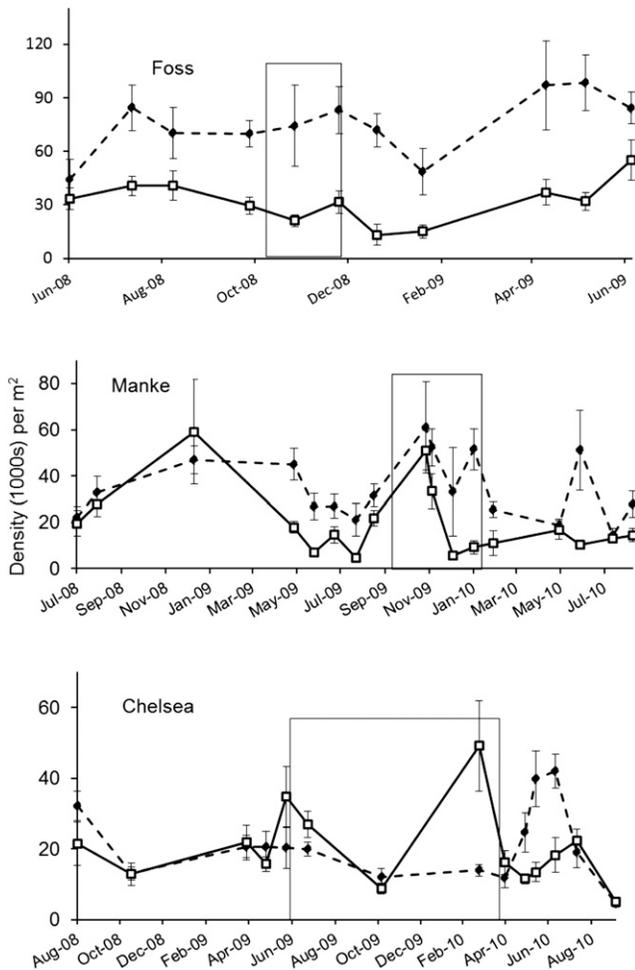


Figure 4. Mean densities of all infauna summed as thousands of individuals per square meter (± 1 SE) from samples in each plot for each sampling date at each study site. Data from cultured plots are shown with white boxes and solid lines, and from reference plots with black diamonds and dashed lines. Vertically oriented rectangles represent midharvest periods on cultured plots. Note that scales on both the horizontal and vertical axes differ among study sites.

Species-specific contrasts, using generalized linear mixed models, provided results in six categories for the 10 taxa analyzed (Table 11). As noted the analyses were based on the protocol that a significant interaction result for harvest state \times treatment was an indication of a significant effect of harvest activities on subject populations, manifested by density data either during or after the harvest events in the study areas. Three taxa, the gammaridean amphipod *Americorophium salmonis*, the cumacean *Cumella vulgaris*, and the polychaete family Capitellidae experienced increased abundance in harvest plots compared with reference plots both during and after harvest activities. Conversely, two other taxa, the bivalve genus *Rochefortia* and the polychaete family Phyllodocidae, experienced reductions in harvest plots compared with reference plots during and after harvests. Two taxa in a third group, the nemertean genus *Micrura* and the polychaete family Spionidae, were not affected positively or negatively by harvests either during or after harvest events. Data for the remaining three taxa indicated more complex population-level response patterns to harvests. The polychaete

family Goniadidae showed increased abundance in harvested plots during harvest compared with reference plots, but the effect did not persist after completion of harvest. The polychaete family Polynoidae was not influenced numerically during harvest, but declined in harvest plots compared with reference plots after harvest was completed. Last, the polychaete family Hesionidae was affected negatively by harvest activities during harvests compared with reference plots, but the negative effect did not persist after harvest was completed.

DISCUSSION

The current study revealed only modest effects on infaunal communities from the harvest phase of geoduck aquaculture operations. Multivariate analyses indicated an absence of significant shifts in community composition (both means and variability) at any of the three study sites as a result of harvesting activities. Similarly, little evidence of a significant “spillover” effect of cultured geoduck harvest operations was found on resident infaunal communities. Univariate ANOVAs provided no evidence of significant impacts of cultured clam harvest on the biodiversity of resident infauna. Of the 10 most frequently sampled infaunal taxa, only three indicated evidence of reduction in abundance persisting as long as 4 mo after conclusion of harvest activities. None of the proportionate changes in the three affected taxa approached local extinction.

Our results led to the rejection of the three hypotheses listed earlier. Some of the data suggested consistency with hypothesis 1, with significant differences between treatment category at the Foss and Manke sites. However, analyses of the harvest state \times treatment interaction term revealed that the subject differences were the result of plot properties independent of harvest-related disturbance effects. Despite scattered temporary exceptions, it is apparent that none of the hypotheses is generally applicable to the study sites.

The results are similar to a recent experimental study of ecosystem-level effects of geoduck aquaculture done in British Columbia, Canada (Department of Fisheries and Oceans 2012). Abundance of resident infauna showed temporary effects of clam harvest disturbance and a strong pattern of seasonal effects. There were observed effects of harvest on sediment chemistry and physical structure within but not beyond the planted area. All observed effects were temporary. Interpretation of results may have been compromised to some degree by the small plot size used in the British Columbia study compared with commercially operated geoduck farms.

The benthic community data collected in the current study revealed variation in community composition among sites. Sediment grain-size distribution at the Chelsea study site was substantially different from the other two sites, which were similar to one another, and likely contributed to community differences (e.g., Gray 1981, Dethier & Schoch 2005). It has been shown that salinity decreases from north to south in Puget Sound (Collias et al. 1974, Dethier & Schoch 2005), and that variation in salinity can affect benthic community structure in a number of locations, including Puget Sound (Tenore 1972, Bulger et al. 1993, Constable 1999, Smith & Witman 1999, Dethier & Schoch 2005). Differences among sites in resident benthic communities were consistent with previous studies that found substantial variation in benthic assemblages among intertidal sand flats in Puget Sound (Dethier et al. 2003, Dethier

TABLE 4.
Summary of homogeneity of multivariate dispersion analytical results for contrasts at scales of study sites and plots.

| Scale | Contrast | df | P value |
|--|------------------------------------|----|-----------------------|
| Among harvest states within plot type, Foss cultured plots | Preharvest vs. midharvest | 1 | $0.001 \leq P < 0.01$ |
| | Preharvest vs. postharvest | 1 | NS |
| | Midharvest vs. postharvest | 1 | $0.001 \leq P < 0.01$ |
| Among harvest states within plot type, Manke cultured plots | Preharvest vs. midharvest | 1 | NS |
| | Preharvest vs. postharvest | 1 | NS |
| | Midharvest vs. postharvest | 1 | NS |
| Among harvest states within plot type, Chelsea cultured plots | Preharvest vs. midharvest | 1 | $0.01 \leq P < 0.05$ |
| | Preharvest vs. postharvest | 1 | $0.01 \leq P < 0.05$ |
| | Midharvest vs. postharvest | 1 | NS |
| Among harvest states within plot type, Foss reference plots | Preharvest vs. midharvest | 1 | NS |
| | Preharvest vs. postharvest | 1 | $0.001 \leq P < 0.01$ |
| | Midharvest vs. postharvest | 1 | NS |
| Among harvest states within plot type, Manke reference plots | Preharvest vs. midharvest | 1 | $0.001 \leq P < 0.01$ |
| | Preharvest vs. postharvest | 1 | NS |
| | Midharvest vs. postharvest | 1 | $0.01 \leq P < 0.05$ |
| Among harvest states within plot type, Chelsea reference plots | Preharvest vs. midharvest | 1 | NS |
| | Preharvest vs. postharvest | 1 | $0.01 \leq P < 0.05$ |
| | Midharvest vs. postharvest | 1 | NS |
| Within sites within plot type, among harvest states | All states, Foss culture plot | 2 | $0.001 \leq P < 0.01$ |
| | All states, Foss reference plot | 2 | $0.001 \leq P < 0.01$ |
| | All states, Manke culture plot | 2 | NS |
| | All states, Manke reference plot | 2 | $0.01 \leq P < 0.05$ |
| | All states, Chelsea culture plot | 2 | NS |
| | All states, Chelsea reference plot | 2 | $0.01 \leq P < 0.05$ |
| Within sites between plot type, within harvest states | Foss, preharvest | 1 | NS |
| | Foss, midharvest | 1 | $0.001 \leq P < 0.01$ |
| | Foss, postharvest | 1 | $0.01 \leq P < 0.05$ |
| | Manke, preharvest | 1 | $0.001 \leq P < 0.01$ |
| | Manke midharvest | 1 | <0.001 |
| | Manke postharvest | 1 | NS |
| | Chelsea preharvest | 1 | NS |
| | Chelsea midharvest | 1 | NS |
| Chelsea postharvest | 1 | NS | |

NS, $P \geq 0.05$.

& Schoch 2005). Intertidal sand flats in Case Inlet, the location of the Foss and Manke study sites, are particularly noteworthy for high beach-to-beach and year-to-year variation in resident benthos (Dethier 2005).

Because of the habitat variations described earlier, it was determined that the three study sites could not be considered replicates. As a result the data were analyzed separately for each site. Such an approach had the unavoidable effect of reducing statistical power for detection of significant differences. Nevertheless, a number of significant differences were found in the data relating to date, a proxy for both season and harvest state, and between study plots within the current study sites. The resulting contention is that the current study had the ability to detect major patterns of variation in the system, and that natural spatial and temporal variability in the subject assemblages were substantially more important than effects of harvest disturbances. When differences were found in abundance patterns between plots within study sites associated with harvest state, it was invariably also found that harvest state was effectively a proxy for seasonal variation in harvested plots. Thus, harvest state unavoidably covaried with date and associated seasonal effects, and was not an informative stand-alone treatment factor for understanding harvest effects. Consistently,

the most informative metric in this study for an unambiguous harvest impact, the harvest state \times treatment interaction term, was not significant in the analyses. Interaction term R^2 values were consistently low, typically explaining less than 5% of variation in the data. When date was used as the explanatory variable, significant values resulted in nearly all cases. Date as a factor had high R^2 values, usually accounting for more than 50% of the variation in the community data set.

With regard to multivariate assemblage contrasts and univariate biodiversity analyses used in the current study, the decision to analyze data from different study sites independently raises questions regarding the propriety of applying ANOVAs to the data (e.g., Hurlbert 1984). The dilemma in design of the current study was the large size and relative scarcity of potential study plots that fit the selection criteria. Hurlbert's (1984) design rubrics to the contrary notwithstanding, Oksanen (2001) has argued that large-scale field studies with attributes such as those used in the current study are fully appropriate for the application of ANOVAs. It is noted that Hurlbert's (1984) dogmatic perspective on design and analysis in field ecology has become increasingly questioned (e.g., Oksanen 2001, Schank & Koehnle 2009). Oksanen (2001) asserts that reflexive application of Hurlbert's dogma to cases

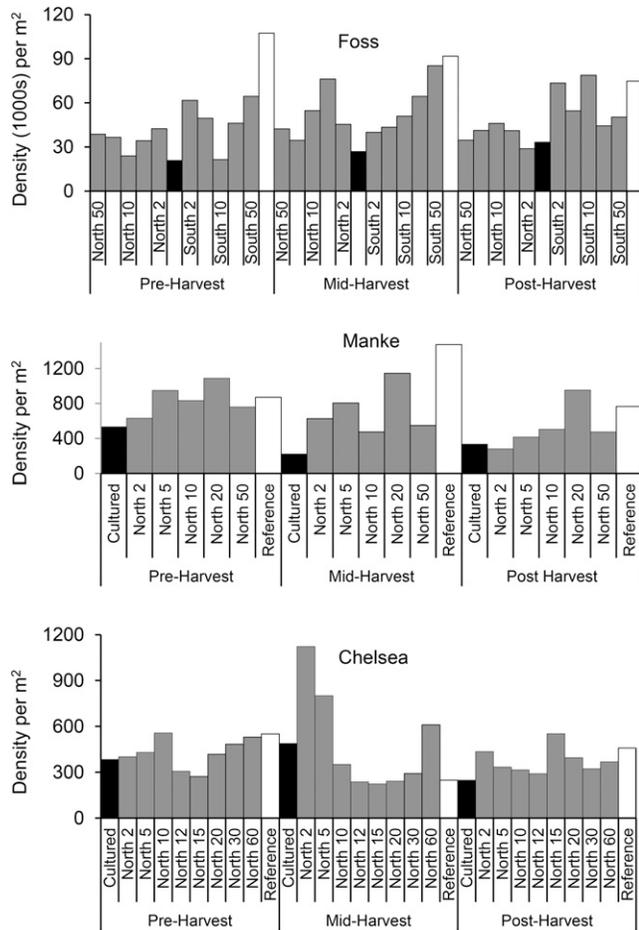


Figure 5. Mean densities of all infaunal organisms summed as individuals per square meter from samples in cultured and reference plots, and on extralimital transects at each distance, within harvest states. Black bars represent densities within cultured plots and white bars represent reference plots. Gray bars indicate densities at specific distances (in meters) from cultured plot edges on transects. Note that scales on both the horizontal and vertical axes differ among study sites.

of design dilemmas such as that in the current study amounts to “entirely unwarranted stigmatization of a reasonable way to test predictions referring to large-scale systems (p. 27).”

In contrast to the results of the current study, other investigations of effects of shellfish harvesting have reported detectable impacts and variable durations of community recovery ranging from a few months to a year (Kaiser et al. 1996, Hall & Harding 1997, Spencer et al. 1998, Mistri et al. 2004, Morello et al. 2006). Results of the current study are also different from many other experimental studies that found significant effects of various types of disturbance on benthic infauna, with recovery times ranging from several weeks up to 9 mo (e.g., VanBlaricom 1982, Smith & Brumsickle 1989, Thrush et al. 1996, Dernie et al. 2003, Zajac & Whitlatch 2003, Kaiser et al. 2006). There are several possible reasons for the strikingly different results in the current study. First, physical habitat modifications associated with geoduck harvest may be unlike other types of harvest-associated disturbances of benthic infauna. Bottom trawling, suction dredge harvesting, and clam raking, as examples, are substantially different methods with

TABLE 5.

Summary of permutation-based analyses of variance results for contrasts within plots and transect locations within study sites by date and by harvest state.

| Transect and contrast | Location on transect (m) | | R^2 | df | P value |
|------------------------------|--------------------------|------|--------|-----------------------|-----------------------|
| | | | | | |
| Foss North, date | 2 | 1.00 | 10 | <0.001 | |
| | 5 | 1.00 | 10 | <0.001 | |
| | 10 | 1.00 | 10 | <0.001 | |
| | 20 | 1.00 | 10 | <0.001 | |
| | 50 | 1.00 | 10 | <0.001 | |
| Foss North, harvest state | 2 | 0.38 | 2 | <0.001 | $0.01 \leq P < 0.05$ |
| | 5 | 0.33 | 2 | NS | |
| | 10 | 0.26 | 2 | NS | |
| | 20 | 0.27 | 2 | NS | |
| | 50 | 0.25 | 2 | NS | |
| Foss South, date | 2 | 1.00 | 10 | <0.001 | |
| | 5 | 1.00 | 10 | <0.001 | |
| | 10 | 1.00 | 10 | <0.001 | |
| | 20 | 1.00 | 10 | <0.001 | |
| | 50 | 1.00 | 10 | <0.001 | |
| Foss South, harvest state | 2 | 0.27 | 2 | NS | $0.01 \leq P < 0.05$ |
| | 5 | 0.29 | 2 | NS | |
| | 10 | 0.27 | 2 | NS | |
| | 20 | 0.27 | 2 | NS | |
| | 50 | 0.37 | 2 | <0.001 | |
| Manke North, date | 2 | 1.00 | 16 | <0.001 | |
| | 5 | 1.00 | 16 | <0.001 | |
| | 10 | 1.00 | 16 | <0.001 | |
| | 20 | 1.00 | 16 | <0.001 | |
| | 50 | 1.00 | 16 | <0.001 | |
| Manke North, harvest state | 2 | 0.23 | 2 | $0.001 \leq P < 0.01$ | $0.001 \leq P < 0.01$ |
| | 5 | 0.16 | 2 | $0.001 \leq P < 0.01$ | |
| | 10 | 0.27 | 2 | <0.001 | |
| | 20 | 0.24 | 2 | <0.001 | |
| | 50 | 0.12 | 2 | $0.001 \leq P < 0.01$ | |
| Chelsea North, date | 2 | 1.00 | 13 | <0.001 | |
| | 5 | 1.00 | 13 | <0.001 | |
| | 10 | 1.00 | 13 | <0.001 | |
| | 12 | 1.00 | 13 | <0.001 | |
| | 15 | 1.00 | 13 | <0.001 | |
| | 20 | 1.00 | 13 | <0.001 | |
| | 30 | 1.00 | 13 | <0.001 | |
| 60 | 1.00 | 13 | <0.001 | | |
| Chelsea North, harvest state | 2 | 0.12 | 2 | NS | NS |
| | 5 | 0.18 | 2 | NS | |
| | 10 | 0.15 | 2 | NS | |
| | 12 | 0.12 | 2 | NS | |
| | 15 | 0.16 | 2 | NS | |
| | 20 | 0.16 | 2 | NS | |
| | 30 | 0.16 | 2 | NS | |
| 60 | 0.26 | 2 | NS | | |

Locations include cultured plot, reference plot, and each sampled distance on transect lines. NS, $P \geq 0.05$.

associated disturbances qualitatively distinctive from one another as well as from geoduck harvest. Second, experimental studies on benthic community disturbance have used methods such as sediment removal, sterilization, and defaunation, setting the point of initiation of observed recovery sequences at 0 abundance by definition. The method by which geoducks are harvested has the potential to displace benthic organisms

TABLE 6.

Summary of permutation-based analyses of variance results for contrasts within plots within study sites and within transect locations by treatment, date, and harvest state (part 1).

| Transect and contrast | Location on transect (m) | R ² | df | P value |
|---|--------------------------|----------------|----|------------------|
| Foss North, cultured plot, treatment | 2 | 0.10 | 1 | 0.01 ≤ P < 0.05 |
| | 5 | 0.17 | 1 | <0.001 |
| Foss North, cultured plot, date | 2 | 0.62 | 10 | 0.001 ≤ P < 0.01 |
| | 5 | 0.59 | 10 | 0.01 ≤ P < 0.05 |
| | 10 | 0.67 | 10 | <0.001 |
| | 20 | 0.68 | 10 | <0.001 |
| Foss North, cultured plot, harvest state | 50 | 0.68 | 10 | <0.001 |
| | 2 | 0.21 | 2 | <0.001 |
| | 5 | 0.18 | 2 | 0.001 ≤ P < 0.01 |
| | 10 | 0.19 | 2 | 0.001 ≤ P < 0.01 |
| Foss North, reference plot, treatment | 20 | 0.18 | 2 | 0.01 ≤ P < 0.05 |
| | 50 | 0.17 | 2 | 0.01 ≤ P < 0.05 |
| | 2 | 0.23 | 1 | <0.001 |
| | 5 | 0.28 | 1 | <0.001 |
| Foss North, reference plot, date | 10 | 0.17 | 1 | 0.001 ≤ P < 0.01 |
| | 20 | 0.17 | 1 | <0.001 |
| | 50 | 0.11 | 1 | 0.01 ≤ P < 0.05 |
| | 10 | 0.64 | 10 | 0.001 ≤ P < 0.01 |
| Foss North, reference plot, harvest state | 20 | 0.59 | 10 | 0.01 ≤ P < 0.05 |
| | 50 | 0.66 | 10 | <0.001 |
| | 2 | 0.18 | 2 | 0.01 ≤ P < 0.05 |
| Foss South, cultured plot, treatment | 10 | 0.16 | 2 | 0.01 ≤ P < 0.05 |
| | 20 | 0.16 | 2 | 0.01 ≤ P < 0.05 |
| | 50 | 0.18 | 2 | 0.01 ≤ P < 0.05 |
| | 2 | 0.15 | 1 | <0.001 |
| Foss South, cultured plot, date | 5 | 0.14 | 1 | <0.001 |
| | 10 | 0.11 | 1 | 0.01 ≤ P < 0.05 |
| | 20 | 0.13 | 1 | <0.001 |
| | 50 | 0.19 | 1 | <0.001 |
| Foss South, cultured plot, harvest state | 2 | 0.58 | 10 | 0.01 ≤ P < 0.05 |
| | 5 | 0.62 | 10 | 0.001 ≤ P < 0.01 |
| | 10 | 0.64 | 10 | <0.001 |
| | 20 | 0.60 | 10 | 0.001 ≤ P < 0.01 |
| Foss South, reference plot, treatment | 2 | 0.16 | 2 | 0.01 ≤ P < 0.05 |
| | 5 | 0.17 | 2 | 0.01 ≤ P < 0.05 |
| | 10 | 0.18 | 2 | 0.01 ≤ P < 0.05 |
| | 20 | 0.16 | 2 | 0.01 ≤ P < 0.05 |
| Foss South, reference plot, date | 2 | 0.19 | 1 | <0.001 |
| | 5 | 0.21 | 1 | <0.001 |
| | 10 | 0.16 | 1 | <0.001 |
| | 50 | 0.18 | 1 | 0.001 ≤ P < 0.01 |
| Foss South, cultured plot, harvest state | 10 | 0.58 | 10 | 0.01 ≤ P < 0.05 |
| | 20 | 0.70 | 10 | <0.001 |
| | 50 | 0.64 | 10 | 0.01 ≤ P < 0.05 |
| | 2 | 0.16 | 2 | 0.01 ≤ P < 0.05 |
| Foss South, reference plot, harvest state | 5 | 0.17 | 2 | 0.01 ≤ P < 0.05 |
| | 10 | 0.17 | 2 | 0.01 ≤ P < 0.05 |
| | 20 | 0.18 | 2 | 0.001 ≤ P < 0.01 |
| | 50 | 0.19 | 2 | 0.01 ≤ P < 0.05 |

Analyses were done for all transect locations (cultured plot and reference plot as well as each transect location), but only statistically significant results are shown.

TABLE 7.

Summary of permutation-based analyses of variance results for contrasts within plots within study sites and within transect locations by treatment, date, and harvest state (part 2).

| Transect and contrast | Location on transect (m) | R ² | df | P value |
|--|--------------------------|----------------|----|------------------|
| Manke North, cultured plot, treatment | 5 | 0.05 | 1 | 0.01 ≤ P < 0.05 |
| | 20 | 0.10 | 1 | <0.001 |
| Manke North, cultured plot, date | 2 | 0.66 | 16 | <0.001 |
| | 5 | 0.62 | 16 | <0.001 |
| | 10 | 0.65 | 16 | <0.001 |
| | 20 | 0.57 | 16 | 0.001 ≤ P < 0.01 |
| Manke North, cultured plot, harvest state | 50 | 0.63 | 16 | <0.001 |
| | 2 | 0.16 | 2 | <0.001 |
| | 5 | 0.16 | 2 | <0.001 |
| | 10 | 0.18 | 2 | <0.001 |
| Manke North, reference plot, treatment | 20 | 0.14 | 2 | <0.001 |
| | 50 | 0.17 | 2 | <0.001 |
| | 2 | 0.09 | 1 | <0.001 |
| | 5 | 0.05 | 1 | 0.01 ≤ P < 0.05 |
| Manke North, reference plot, date | 10 | 0.06 | 1 | 0.001 ≤ P < 0.01 |
| | 20 | 0.06 | 1 | 0.01 ≤ P < 0.05 |
| | 2 | 0.57 | 16 | 0.001 ≤ P < 0.01 |
| | 5 | 0.67 | 16 | <0.001 |
| Manke North, reference plot, harvest state | 10 | 0.64 | 16 | <0.001 |
| | 20 | 0.66 | 16 | <0.001 |
| | 50 | 0.64 | 16 | <0.001 |
| | 2 | 0.16 | 2 | <0.001 |
| Chelsea North, cultured plot, treatment | 5 | 0.19 | 2 | <0.001 |
| | 10 | 0.17 | 2 | <0.001 |
| | 20 | 0.16 | 2 | <0.001 |
| | 50 | 0.14 | 2 | <0.001 |
| Chelsea North, cultured plot, date | 60 | 0.07 | 1 | 0.01 ≤ P < 0.05 |
| | 2 | 0.72 | 13 | <0.001 |
| | 5 | 0.69 | 13 | <0.001 |
| | 10 | 0.75 | 13 | <0.001 |
| | 12 | 0.68 | 13 | <0.001 |
| | 15 | 0.66 | 13 | <0.001 |
| | 20 | 0.67 | 13 | <0.001 |
| Chelsea North, cultured plot, harvest state | 30 | 0.69 | 13 | <0.001 |
| | 60 | 0.66 | 13 | <0.001 |
| | 5 | 0.11 | 2 | 0.01 ≤ P < 0.05 |
| | 20 | 0.11 | 2 | 0.01 ≤ P < 0.05 |
| Chelsea North, reference plot, treatment | 60 | 0.12 | 2 | 0.01 ≤ P < 0.05 |
| | 30 | 0.07 | 1 | 0.01 ≤ P < 0.05 |
| Chelsea North, reference plot, date | 60 | 0.12 | 1 | <0.001 |
| | 2 | 0.69 | 13 | <0.001 |
| | 5 | 0.68 | 13 | <0.001 |
| | 10 | 0.70 | 13 | <0.001 |
| Chelsea North, reference plot, harvest state | 12 | 0.66 | 13 | <0.001 |
| | 15 | 0.64 | 13 | <0.001 |
| | 20 | 0.67 | 13 | <0.001 |
| | 30 | 0.67 | 13 | <0.001 |
| Chelsea North, reference plot, harvest state | 60 | 0.58 | 13 | 0.001 ≤ P < 0.01 |
| | 60 | 0.11 | 2 | 0.01 ≤ P < 0.05 |

Analyses were done and are presented as described in Table 6.

without injury or death, allowing recolonization of disturbed patches immediately after harvest. Third, the scales of disturbances evaluated in other published studies are different from the scale of disturbances occurring at harvest of cultured

geoducks. Most experimental studies reported in the peer-reviewed literature used small patches (surface area, <5 m²) to quantify disturbance effects and implemented a spatially uniform disturbance regime. Geoduck harvest occurs on large

TABLE 8.
Summary of homogeneity of multivariate dispersion analytical results within study sites and plots among transect locations.

| Site | Harvest state | P value |
|---|---------------|-----------------------|
| Within site within harvest state, among transect locations, Foss North | Preharvest | NS |
| | Midharvest | $0.001 \leq P < 0.01$ |
| | Postharvest | $0.001 \leq P < 0.01$ |
| Within site within harvest state, among transect locations, Foss South | Preharvest | $0.01 \leq P < 0.05$ |
| | Midharvest | $0.001 \leq P < 0.01$ |
| | Postharvest | $0.001 \leq P < 0.01$ |
| Within site within harvest state, among transect locations, Manke North | Preharvest | $0.01 \leq P < 0.05$ |
| | Midharvest | <0.001 |
| | Postharvest | $0.01 \leq P < 0.05$ |
| Within site within harvest state, among transect locations, Chelsea North | Preharvest | $0.001 \leq P < 0.01$ |
| | Midharvest | $0.01 \leq P < 0.05$ |
| | Postharvest | NS |

Transect locations include cultured plot and reference plot as well as each sampled location on transects. All indicated contrasts had 6 degrees of freedom. NS, $P \geq 0.05$.

spatial scales (plots that are typically 2,500 m² or larger in surface area) and creates a nonuniform disturbance regime within harvested plots. Survival of outplanted geoducks, typically placed in uniform distributional arrays, is generally less

than 100% over time. Spatial variability of clam mortality is normal within a cultured plot during the multiyear production cycle, often resulting in nonuniform spatial distributions of clams within cultured plots at the time of harvest. It follows that disturbances associated with harvest of a cultured plot will be patchy in space. Another level of patchiness is associated with likely variation among individual cultured clams in detection probability of siphons on the sediment surface at harvest. If the visibility of individual geoducks to a harvester is patchy in space, then clam-by-clam harvest disturbances will also be patchy in space. The scale and patchiness involved in geoduck harvest compared with the uniform disturbance and small scale of other experimental disturbance studies could diffuse any impacts over such a large area so that the effect of harvest is undetectable and possibly trivial from the ecosystem perspective.

The univariate analyses in the current study of selected individual taxa involved inclusion of site as a random effect and are not subject to the criticisms of design as emphasized by Hurlbert (1984). Three taxa were identified with abundance that increased during the harvest phase in cultured plots and remained elevated in the months after completion of harvest. Such patterns suggest the possibility that the presence of adult geoducks at high densities near the termination of the culture cycle had a negative effect on the subject populations, and that

TABLE 9.
Summary of homogeneity of multivariate dispersion analytical results within study sites between cultured plots and transect locations (the latter include the reference plot as well as each sampled location on transects) for each study site.

| Contrast and location (m) | Harvest state | P value, Foss North | P value, Foss South | P value, Manke North | P value, Chelsea North |
|----------------------------------|---------------|-----------------------|-----------------------|-----------------------|------------------------|
| Cultured plot vs. reference plot | Preharvest | NS | NS | <0.001 | NS |
| | Midharvest | <0.001 | <0.001 | <0.001 | NS |
| | Postharvest | $0.01 \leq P < 0.05$ | $0.01 \leq P < 0.05$ | NS | NS |
| Cultured plot vs. 2 m | Preharvest | NS | NS | NS | NS |
| | Midharvest | NS | <0.001 | <0.001 | NS |
| | Postharvest | <0.001 | $0.01 \leq P < 0.05$ | NS | <0.001 |
| Cultured plot vs. 5 m | Preharvest | NS | NS | NS | NS |
| | Midharvest | <0.001 | $0.001 \leq P < 0.01$ | <0.001 | NS |
| | Postharvest | <0.001 | $0.01 \leq P < 0.05$ | $0.001 \leq P < 0.01$ | NS |
| Cultured plot vs. 10 m | Preharvest | NS | $0.01 \leq P < 0.05$ | $0.001 \leq P < 0.01$ | $0.001 \leq P < 0.01$ |
| | Midharvest | $0.01 \leq P < 0.05$ | NS | <0.001 | NS |
| | Postharvest | NS | $0.01 \leq P < 0.05$ | NS | NS |
| Cultured plot vs. 12 m | Preharvest | — | — | — | NS |
| | Midharvest | — | — | — | NS |
| | Postharvest | — | — | — | NS |
| Cultured plot vs. 15 m | Preharvest | — | — | — | NS |
| | Midharvest | — | — | — | NS |
| | Postharvest | — | — | — | NS |
| Cultured plot vs. 20 m | Preharvest | NS | NS | $0.001 \leq P < 0.01$ | NS |
| | Midharvest | $0.001 \leq P < 0.01$ | $0.01 \leq P < 0.05$ | <0.001 | NS |
| | Postharvest | NS | $0.001 \leq P < 0.01$ | $0.01 \leq P < 0.05$ | NS |
| Cultured plot vs. 30 m | Preharvest | — | — | — | <0.001 |
| | Midharvest | — | — | — | NS |
| | Postharvest | — | — | — | $0.01 \leq P < 0.05$ |
| Cultured plot vs. 50 m | Preharvest | NS | NS | NS | — |
| | Midharvest | <0.001 | <0.001 | $0.001 \leq P < 0.01$ | — |
| | Postharvest | $0.01 \leq P < 0.05$ | <0.001 | NS | — |
| Cultured plot vs. 60 m | Preharvest | — | — | — | $0.001 \leq P < 0.01$ |
| | Midharvest | — | — | — | $0.001 \leq P < 0.01$ |
| | Postharvest | — | — | — | NS |

NS, $P \geq 0.05$.

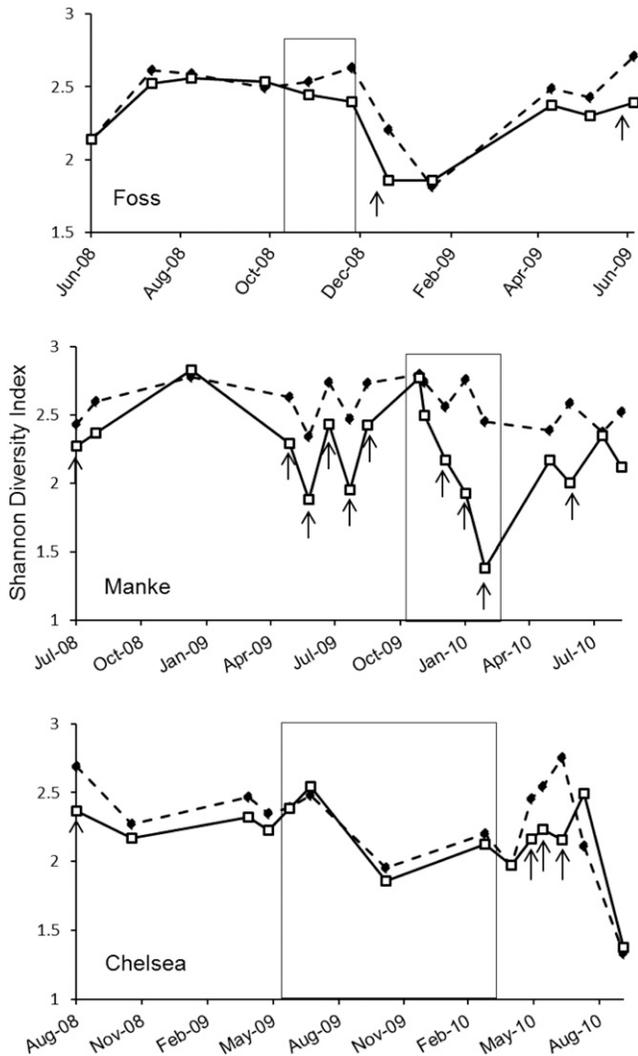


Figure 6. Shannon diversity index values from samples in each plot for each sampling date at each study site. Data from cultured plots are shown with white boxes and solid lines, and from reference plots with black diamonds and dashed lines. Arrows indicate sample dates with significant differences between reference and cultured plots ($P < 0.05$). Vertically oriented rectangles represent midharvest periods on the cultured plots. Note that scales on both the horizontal and vertical axes differ among study sites.

the effect was removed at the time of harvest. The putative mechanisms for such an impact are unclear, but potentially could include modification of chemical or physical attributes of the sediments. Another plausible mechanism is subtle modification of microscale patterns of water movement as a consequence of the high living biomass density of geoducks in cultured plots. Cummings et al. (2001) identified variations in abundance of some species of an infaunal assemblage that were linked inversely to variations in densities in adult populations of a large filter-feeding bivalve. Elucidation of causal linkages between reduced densities of geoducks at harvest and subsequent infaunal abundance patterns was beyond the scope of the current study. The matter would be an informative topic for future study.

It is suggested that a principal reason for the apparent insensitivity of resident infauna to cultured geoduck harvest

disturbances in southern Puget Sound is accommodation of the infaunal assemblage to a significant natural disturbance regime. It has been hypothesized that rates of ecosystem recovery from disturbances correlate with the extent to which species in the subject ecosystem have adapted to past disturbances (e.g., Connell 1978, Connell & Keogh 1985), and that benthic ecosystems in sandy sediments show rapid resilience to disturbances (Collie et al. 2000). The intertidal zone of Puget Sound is affected by an array of disturbance processes that vary by frequency, intensity, physical and chemical attributes, and spatial scale. Disturbances with a high potential for ecological significance in the region include (1) small waves resulting from normal wind shear (e.g., Maunder 1968, Anderson 1972, Clarke et al. 1982, Gabrielson & Lukatelich 1985), (2) wakes from vessel passage (e.g., Crawford 1984, Garrad & Hey 1987, Osborne & Boak 1999, Bishop 2007), (3) thermal stress associated with daytime low tides in summer months (e.g., Dethier 2010, Dethier et al. 2010, Dethier et al. 2012), (4) large waves caused by wind storms (e.g., Lynott & Cramer 1966, Reed 1980, Steenburgh & Mass 1996, Mass & Dotson 2010), (5) flooding events caused by maxima in rainfall or snowmelt in watersheds draining to Puget Sound (e.g., Ferber et al. 1993, Zhu & Newell 1998, Colle & Mass 2000, Frascari et al. 2006, Lohrer et al. 2006, Forrest et al. 2007, Hermand et al. 2008, Warner et al. 2012), and (6) sediment liquefaction and small tsunami generation by seismic activity and associated subaerial and possibly submarine landslides (e.g., Atwater 1987, Hampton et al. 1996, Atwater 1999, Williams & Hutchinson 2000, Sherrod 2001, González 2002, Ichinose et al. 2004, Wiest et al. 2007, Kao et al. 2008, Arcos 2012). Tidally driven along-shore currents may intensify disturbance effects by transporting suspended or epibenthic materials away from disrupted locations (e.g., Adams et al. 2007, Bourrin et al. 2008, Denny et al. 2013). Benthic communities of Puget Sound have likely adapted to the array of natural disturbances and could therefore be resilient to other similar types of physical disturbances, including those of anthropogenic origin. The small-scale and large-scale natural disturbances typical of the area provide a rate of physical intervention to intertidal sedimentary environments substantially greater than rates of significant disturbances caused by geoduck aquaculture operations in a given plot. In addition, it is noted that Puget Sound is quite young in geological and oceanographic contexts, being only 5,000 y of age in current configuration after glacial recession, resultant isostatic rebound, and eustatic sea level rise (Armstrong et al. 1965, Easterbrook 1969, Burns 1985, Thorson 1989, Bucknam et al. 1992, Finlayson 2006). As a consequence, resident marine assemblages may be dominated by relatively opportunistic species arguably accommodated to and relatively unaffected by physical disturbances of various types. Thus, it is argued that the prevailing natural disturbance climate in the region has effectively selected the infaunal assemblage toward tolerance of and resilience to the types of disturbances associated with geoduck aquaculture operations. Naturally evolved characteristics preadaptive to effects of anthropogenic disturbances are known for a number of marine and freshwater benthic species across many habitat types (e.g., Pearson & Rosenberg 1978, Tomassetti & Porrello 2005, Melzner et al. 2009, Gabel et al. 2011).

As also noted in McDonald et al. (2015), it is cautioned that projection of the current study results to larger temporal or spatial scales may be inappropriate in the absence of additional

TABLE 10.
One-way analysis of variance results for Shannon indices of diversity for samples at all sites.

| Study site and scale | Contrast | F value | P value |
|--|----------------------------|---------|-----------------|
| Foss, between treatments | Preharvest | 0.68 | NS |
| | Midharvest | 0.24 | NS |
| | Postharvest | 3.49 | NS |
| Manke, between treatments | Preharvest | 19.24 | <0.001 |
| | Midharvest | 30.12 | <0.001 |
| | Postharvest | 12.92 | <0.001 |
| Chelsea, between treatments | Preharvest | 5.35 | 0.01 ≤ P < 0.05 |
| | Midharvest | 0.001 | NS |
| | Postharvest | 1.60 | NS |
| Foss, within cultured plot, between harvest states | Preharvest vs. midharvest | 0.17 | NS |
| | Preharvest vs. postharvest | 17.74 | <0.001 |
| | Midharvest vs. postharvest | 13.59 | <0.001 |
| Manke, within cultured plot, between harvest states | Preharvest vs. midharvest | 15.36 | <0.001 |
| | Preharvest vs. postharvest | 4.97 | 0.01 ≤ P < 0.05 |
| | Midharvest vs. postharvest | 2.41 | NS |
| Chelsea, within cultured plot, between harvest states | Preharvest vs. midharvest | 0.04 | NS |
| | Preharvest vs. postharvest | 4.79 | 0.01 ≤ P < 0.05 |
| | Midharvest vs. postharvest | 3.04 | NS |
| Foss, within reference plot, between harvest states | Preharvest vs. midharvest | 0.56 | NS |
| | Preharvest vs. postharvest | 3.70 | NS |
| | Midharvest vs. postharvest | 0.67 | NS |
| Manke, within reference plot, between harvest states | Preharvest vs. midharvest | 0.37 | NS |
| | Preharvest vs. postharvest | 4.08 | 0.01 ≤ P < 0.05 |
| | Midharvest vs. postharvest | 4.84 | 0.01 ≤ P < 0.05 |
| Chelsea, within reference plot, between harvest states | Preharvest vs. midharvest | 10.38 | <0.001 |
| | Preharvest vs. postharvest | 3.58 | NS |
| | Midharvest vs. postharvest | 0.14 | NS |

Analyzed contrasts include differences between reference and cultured plots for each state as well as differences between states within each plot. All indicated contrasts had 1 degree of freedom. NS, $P \geq 0.05$.

studies. The sites for the current study were relatively isolated from other geoduck aquaculture plots, and were being used for aquaculture of geoducks for the first time. The data may not provide a sufficient basis for unequivocal extrapolation to cases when a given plot is exposed to a long series of successive

geoduck aquaculture cycles. Likewise, it may not be appropriate to extend the findings of the current study to cases when a number of separate plots are adjacent to one another and encompass significantly larger surface areas than any single plot. Resolution of the questions of larger spatial and

TABLE 11.
Results of univariate assessments of harvest impacts with generalized linear mixed models for abundant or ecologically significant individual infaunal taxa as sampled by coring.

| Taxon | Results of likelihood ratio tests | | Apparent effect of harvest on populations | |
|--------------------------------|-----------------------------------|-----------------|---|---------------|
| | Chi square | P value | During harvest | After harvest |
| <i>Americorophium salmonis</i> | 108.54 | <0.001 | Positive | Positive |
| <i>Cumella vulgaris</i> | 82.13 | <0.001 | Positive | Positive |
| <i>Rochefortia</i> spp. | 38.19 | <0.001 | Negative | Negative |
| <i>Micrura</i> spp. | 0.82 | NS | Neutral | Neutral |
| Capitellidae | 271.51 | <0.001 | Positive | Positive |
| Goniadidae | 15.89 | <0.001 | Positive | Neutral |
| Spionidae | 1.41 | NS | Neutral | Neutral |
| Hesionidae | 362.82 | <0.001 | Negative | Neutral |
| Phyllodoceidae | 24.32 | <0.001 | Negative | Negative |
| Polynoidae | 8.07 | 0.01 ≤ P < 0.05 | Neutral | Negative |

The test statistic is the likelihood ratio test for the interaction term harvest state × treatment. The metric represented is the sign of the coefficient of the interaction term for which harvest phase is before harvest, mid harvest, or postharvest, and treatment is either cultured plot or reference plot. All indicated contrasts had 2 degrees of freedom. Taxa are those described in Tables 1 and 2. NS, $P \geq 0.05$.

temporal scales will be a major challenge for geoduck farmers as they continue production on existing plots and expand into new areas, and will be an important research goal in the interests of informed management policies by natural resource agencies.

ACKNOWLEDGMENTS

Funding for this work was provided by the Washington state legislature, the National Aquaculture Research Program of the National Oceanic and Atmospheric Administration, the Washington State Departments of Ecology and Natural Resources, the Royalty Research Fund of the University of Washington, the Shellfish Management Department of the Point No Point Treaty Council, and the Ecosystems Branch of the U.S. Geological Survey. Access to study sites was facilitated by Taylor Shellfish, Inc.; Chelsea Farms, LLC; and D. Adams, M. Adams, T. Bloomfield, S. Bloomfield, B. Foss, L. Foss, J. Lentz, and

B. Phipps, J. Cordell, M. Dethier, and J. Toft provided guidance and expertise on laboratory procedures and infaunal taxonomy crucial to completion of the current study. K. Armintrout, K. Connelly, B. Cummings, J. Eggers, A. Fuller, A. Galloway, M. Langness, K. McPeck, P. F. Stevick, and many volunteers provided vital laboratory and field support for the project. The staff of the Washington Sea Grant Program, particularly P. Dalton and R. Waters, provided generous and valuable administrative support. C. Schwartz provided expert and patient guidance and artistic skill in improving article graphics. Constructively critical comments were provided on draft versions of the manuscript by D. Cheney, S. Shumway, and two anonymous reviewers. J. Davis and B. Vadopalas provided additional editorial guidance and assistance. The authors offer sincere thanks to all. Any use of trade product or firm name herein is for descriptive purposes only and does not imply endorsement by the U.S. government.

LITERATURE CITED

- Adams, P. N., P. Ruggiero, G. C. Schoch & G. Gelfenbaum. 2007. Intertidal sand body migration along a megatidal coast, Kachemak Bay, Alaska. *J. Geophys. Res.* 112(F02007):1–19.
- Anderson, F. E. 1972. Resuspension of estuarine sediments by small amplitude waves. *J. Sediment. Petrol.* 42:602–607.
- Anderson, M. J. 2001. A new method for non-parametric multivariate analyses of variance. *Austral Ecol.* 26:32–46.
- Anderson, M. J. 2006. Distance-based tests for the homogeneity of multivariate dispersions. *Biometrics* 62:245–253.
- Anderson, M. J. & A. J. Underwood. 1997. Effects of gastropod grazers on recruitment and succession of an estuarine assemblage: a multivariate and univariate approach. *Oecologia* 109:442–453.
- Arcos, M. E. M. 2012. The A.D. 900–930 Seattle-fault-zone earthquake with a wider coseismic rupture patch and postseismic submergence: inferences from new sedimentary evidence. *Bull. Seismol. Soc. Am.* 102:1079–1098.
- Armstrong, J. E., D. R. Crandall, D. F. Easterbrook & J. R. Noble. 1965. Late Pleistocene stratigraphy and chronology in southwestern British Columbia and northwest Washington. *Geol. Soc. Am. Bull.* 76:321–330.
- Atwater, B. F. 1987. Evidence for great Holocene earthquakes along the outer coast of Washington state. *Science* 236:942–944.
- Atwater, B. F. 1999. Radiocarbon dating of a Seattle earthquake to A.D. 900–930. *Seismol. Res. Lett.* 70:232.
- Bates, D. M. & M. Maechler. 2010. lme4. Linear mixed-effects models using S4 classes. Available at: <http://lme4.r-forge.r-project.org/>.
- Bishop, M. J. 2007. Impacts of boat-generated waves on macroinfauna: towards a mechanistic understanding. *J. Exp. Mar. Biol. Ecol.* 343:187–196.
- Bourrin, F., P. L. Friend, C. L. Amos, E. Manca, C. Ulses, A. Palanques, X. Durrieu de Madron & C. E. L. Thompson. 2008. Sediment dispersal from a typical Mediterranean flood: the Têt River, Gulf of Lions. *Cont. Shelf Res.* 28:1895–1910.
- Bray, J. R. & J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* 48:35–49.
- Bucknam, R. C., E. Hemphill-Haley & E. B. Leopold. 1992. Abrupt uplift within the past 1700 years at southern Puget Sound, Washington. *Science* 258:1611–1614.
- Bulger, A. J., B. P. Hayden, M. E. Monaco, D. M. Nelson & G. McCormick-Ray. 1993. Biologically-based salinity zones derived from a multivariate analysis. *Estuaries* 16:311–322.
- Burns, R. E. 1985. The shape and form of Puget Sound. Puget Sound Books, Washington Sea Grant Program, University of Washington. Seattle: University of Washington Press. 100 pp.
- Buschmann, A. H., F. Cabello, K. Young, J. Carvajal, D. A. Varela & L. Henriquez. 2009. Salmon aquaculture and coastal ecosystem health in Chile: analysis of regulations, environmental impacts and bioremediation systems. *Ocean Coast. Manage.* 52:243–249.
- Caswell, H. & J. E. Cohen. 1991. Disturbance, interspecific interaction and diversity in metapopulations. *Biol. J. Linn. Soc. Lond.* 42:193–218.
- Chopin, T., A. H. Buschmann, C. Halling, M. Troell, N. Kautsky, A. Neori, G. P. Kraemer, J. A. Zertuche-Gonzalez, C. Yarish & C. Neefus. 2001. Integrating seaweeds into marine aquaculture systems: a key toward sustainability. *J. Phycol.* 37:975–986.
- Clarke, T. L., B. Lesht, R. A. Young, D. J. P. Swift & G. L. Freeland. 1982. Sediment resuspension by surface-wave action: an examination of possible mechanisms. *Mar. Geol.* 49:43–59.
- Coen, L. D., B. R. Dumbauld & M. J. Judge. 2011. Molluscan shellfish aquaculture and best management practices. In: S. E. Shumway, editor. Shellfish aquaculture and the Environment. Chichester, West Sussex, UK: Wiley. pp. 239–295.
- Colle, B. A. & C. F. Mass. 2000. The 5–9 February 1996 flooding event over the Pacific Northwest: sensitivity studies and evaluation of the MM5 precipitation forecasts. *Mon. Weather Rev.* 128:593–617.
- Collias, E. E., N. McGary & C. A. Barnes. 1974. Atlas of physical and chemical properties of Puget Sound and its approaches. Seattle, WA: University of Washington Press. 235 pages.
- Collie, J. S., S. J. Hall, M. J. Kaiser & I. R. Poiner. 2000. A quantitative analysis of fishing impacts on shelf-sea benthos. *J. Anim. Ecol.* 69:785–798.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310.
- Connell, J. H. & M. J. Keogh. 1985. Disturbance and patch dynamics of subtidal marine animals on hard substrata. In: S. T. A. Pickett & P. S. White, editors. The ecology of natural disturbance and patch dynamics. New York: Academic Press. pp. 125–147.
- Constable, A. J. 1999. Ecology of benthic macro-invertebrates in soft-sediment environments: a review of progress toward quantitative models and predictions. *Aust. J. Ecol.* 24:452–476.
- Crawford, F. S. 1984. Elementary derivation of the wake pattern of a boat. *Am. J. Phys.* 52:782–785.
- Cummings, V. J., S. F. Thrush, J. E. Hewitt & G. A. Funnell. 2001. Variable effect of a large suspension-feeding bivalve on infauna: experimenting in a complex system. *Mar. Ecol. Prog. Ser.* 209:159–175.
- Denny, J. F., W. C. Schwab, W. E. Baldwin, W. A. Barnhardt, P. T. Gayes, R. A. Morton, J. C. Warner, N. W. Driscoll & G. Voulgaris. 2013. Holocene sediment distribution on the inner continental shelf of northeastern South Carolina: implications for the regional

- sediment budget and long-term shoreline response. *Cont. Shelf Res.* 56:56–70.
- Department of Fisheries and Oceans. 2012. Assessing benthic habitat impacts of small-scale, intertidal aquaculture of the geoduck clam (*Panopea generosa*). Canadian Science Advisory Secretariat Scientific Advisory Report 2011/083. Nanaimo, Canada: Center for Science Advice, Pacific Region, Fisheries and Oceans Canada, Pacific Biological Station. 9 pp.
- Dernie, K. M., M. J. Kaiser, E. A. Richardson & R. M. Warwick. 2003. Recovery of soft sediment communities and habitats following physical disturbance. *J. Exp. Mar. Biol. Ecol.* 285:415–434.
- Dethier, M. N. 2005. Spatial patterns and temporal trends in shoreline biota in Puget Sound: analyses of data collected through 2004. Nearshore Habitat Program. Olympia, WA: Washington Department of Natural Resources. 27 pp.
- Dethier, M. N. 2010. Variation in recruitment does not drive the cline in diversity along an estuarine gradient. *Mar. Ecol. Prog. Ser.* 410:43–54.
- Dethier, M. N., J. Ruesink, H. Berry & A. G. Springer. 2012. Decoupling of recruitment from adult clam assemblages along an estuarine shoreline. *J. Exp. Mar. Biol. Ecol.* 422–423:48–54.
- Dethier, M. N., J. Ruesink, H. Berry, A. G. Springer & B. Reeves. 2010. Restricted ranges in physical factors may constitute subtle stressors for estuarine biota. *Mar. Environ. Res.* 69:240–247.
- Dethier, M. N. & G. C. Schoch. 2005. The consequences of scale: assessing the distribution of benthic populations in a complex estuarine fjord. *Estuar. Coast. Shelf Sci.* 62:253–270.
- Dethier, M. N., G. C. Schoch & J. Ruesink. 2003. Spatial and temporal variability of shoreline biota in south and central Puget Sound: 2001 samples and analyses. Nearshore Habitat Program. Olympia, WA: Washington Department of Natural Resources. 46 pp.
- Dumbauld, B. R., J. L. Ruesink & S. S. Rumrill. 2009. The ecological role of bivalve shellfish aquaculture in the estuarine environment: a review with application to oyster and clam culture in west coast (USA) estuaries. *Aquaculture* 290:196–223.
- Easterbrook, D. J. 1969. Pleistocene chronology of the Puget lowland and San Juan islands, Washington. *Geol. Soc. Am. Bull.* 80:2273–2286.
- Ferber, G. K., C. F. Mass, G. M. Lackmann & M. W. Patnoe. 1993. Snowstorms over the Puget Sound lowlands. *Weather Forecast.* 8:481–504.
- Ferraro, S. P. & F. A. Cole. 1990. Taxonomic level and sample size sufficient for assessing pollution impacts on the Southern California Bight macrobenthos. *Mar. Ecol. Prog. Ser.* 67:251–262.
- Finlayson, D. 2006. The geomorphology of Puget Sound beaches. Puget Sound Nearshore Partnership report no. 2006-02. Washington Sea Grant Program. Seattle: University of Washington. 45 pp.
- Forrest, B. M., P. Gillespie, C. D. Cornelisen & K. M. Rogers. 2007. Multiple indicators reveal river plume influence on sediments and benthos in a New Zealand coastal embayment. *N. Z. J. Mar. Freshw. Res.* 41:13–24.
- Forrest, B. M., N. B. Keeley, G. A. Hopkins, S. C. Webb & C. M. Clement. 2009. Bivalve aquaculture in estuaries: review and synthesis of oyster cultivation effects. *Aquaculture* 298:1–15.
- Frascardi, F., F. Spagnoli, M. Marcaccio & P. Giordano. 2006. Anomalous Po River flood event effects on sediments and the water column of the northwestern Adriatic Sea. *Clim. Res.* 31:151–165.
- Gabel, F., M. T. Pusch, P. Breyer, V. Burmester, N. Walz & X.-F. Garcia. 2011. Differential effect of wave stress on the physiology and behaviour of native versus non-native benthic invertebrates. *Biol. Invasions* 13:1843–1853.
- Gabrielson, J. O. & R. J. Lukatelich. 1985. Wind-related resuspension of sediments in the Peel-Harvey estuarine system. *Estuar. Coast. Shelf Sci.* 20:135–145.
- Garrad, P. N. & R. D. Hey. 1987. Boat traffic, sediment resuspension and turbidity in a Broadland River. *J. Hydrol. (Amst.)* 95:289–297.
- Goldburg, R. & R. Naylor. 2005. Future seascapes, fishing, and fish farming. *Front. Ecol. Environ* 3:21–28.
- González, F. I. 2002. Puget Sound Tsunami Sources: 2002 workshop report. Seattle WA: Pacific Marine Environmental Laboratory, National Oceanic and Atmospheric Administration. 36 pp.
- Gray, J. S. 1981. The ecology of marine sediments. Cambridge, UK: Cambridge University Press. 185 pp.
- Green, R. H. 1979. Sampling design and statistical methods for environmental biologists. Chichester, UK: Wiley-Interscience. 257 pp.
- Hall, S. J. & M. J. C. Harding. 1997. Physical disturbance and marine benthic communities: the effects of mechanical harvesting of cockles on non-target benthic infauna. *J. Appl. Ecol.* 34:497–517.
- Hampton, M. A., H. J. Lee & J. Locat. 1996. Submarine landslides. *Rev. Geophys.* 34:33–59.
- Hedgecock, D. 2011. Genetics of shellfish on a human-dominated planet. In: S. E. Shumway, editor. Shellfish aquaculture and the environment. Chichester, West Sussex, UK: Wiley. pp. 339–357.
- Hermand, R., C. Salen-Picard, E. Alliot & C. Degiovanni. 2008. Macrofaunal density, biomass, and composition of estuarine sediments and their relationship to the river plume of the Rhone River (NW Mediterranean). *Estuar. Coast. Shelf Sci.* 79:367–376.
- Hernández Arana, H. A., R. M. Warwick, M. J. Attrill, A. A. Rowden & G. Gold-Bouchot. 2005. Assessing the impact of oil-related activities on benthic macroinfauna assemblages of the Campeche Shelf, southern Gulf of Mexico. *Mar. Ecol. Prog. Ser.* 289:89–107.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* 54:187–211.
- Ichinose, G. A., H. K. Thio & P. G. Somerville. 2004. Rupture process and near-source shaking of the 1965 Seattle-Tacoma and 2001 Nisqually, intraslab earthquakes. *Geophys. Res. Lett.* 31(L10604):1–4.
- Kaiser, M. J., K. R. Clarke, H. Hinz, M. C. V. Austen, P. J. Somerfield & I. Karakassis. 2006. Global analysis of response and recovery of benthic biota to fishing. *Mar. Ecol. Prog. Ser.* 311:1–14.
- Kaiser, M. J., D. B. Edwards & B. E. Spencer. 1996. Infaunal community changes as a result of commercial clam cultivation and harvesting. *Aquat. Living Resour.* 9:57–63.
- Kao, H., K. Wang, R.-Y. Chen, I. Wada, J. He & S. D. Malone. 2008. Identifying the rupture plane of the 2001 Nisqually, Washington, earthquake. *Bull. Seismol. Soc. Am.* 98:1546–1558.
- Lohrer, A. M., S. F. Thrush, C. J. Lundquist, K. Vopel, J. E. Hewitt & P. E. Nicholls. 2006. Deposition of terrigenous sediment on subtidal marine macrobenthos: response of two contrasting community types. *Mar. Ecol. Prog. Ser.* 307:115–125.
- Lorenzen, K., M. C. M. Beveridge & M. Mangel. 2012. Cultured fish: integrative biology and management of domestication and interactions with wild fish. *Biol. Rev. Camb. Philos. Soc.* 87:639–660.
- Lynott, R. E. & O. P. Cramer. 1966. Detailed analysis of 1962 Columbus Day windstorm in Oregon and Washington. *Mon. Weather Rev.* 94:105–117.
- Mass, C. & B. Dotson. 2010. Major extratropical cyclones of the northwest United States: historical review, climatology, and synoptic environment. *Mon. Weather Rev.* 138:2499–2527.
- Maunder, W. J. 1968. Synoptic weather patterns in the Pacific Northwest. *Northwest Sci.* 42:80–88.
- McCullagh, P. & J. A. Nelder. 1989. Generalized linear models, 2nd edition. London: Chapman and Hall. 532 pp.
- McDonald, P. S., A. W. E. Galloway, K. C. McPeck & G. R. VanBlaricom. 2015. Effects of geoduck (*Panopea generosa* Gould, 1850) aquaculture gear on resident and transient macrofauna communities of Puget Sound, Washington. *J. Shellfish Res.* 34:189–202.
- Melzner, F., M. A. Gutowska, M. Langenbuch, S. Dupont, M. Lucassen, M. C. Thorndyke, M. Bleich & H.-O. Pörtner. 2009. Physiological basis for high CO₂ tolerance in marine ectothermic animals: pre-adaptation through lifestyle and ontogeny? *Biogeosciences* 6:2313–2331.
- Mistri, M., E. Cason, C. Munari & R. Rossi. 2004. Disturbance of a soft-sediment meiobenthic community by clam hand raking. *Ital. J. Zool. (Modena)* 71:131–133.

- Mofjeld, H. O., A. J. Venturato, V. V. Titov, F. I. González & J. C. Newman. 2002. Tidal datum distributions in Puget Sound, Washington, based on a tide model. NOAA technical memorandum OAR PMEL-122. Seattle, WA: National Oceanic and Atmospheric Administration, Pacific Marine Environmental Laboratory. 35 pp.
- Morello, E. B., C. Froggia, R. J. A. Atkinson & P. G. Moore. 2006. Medium-term impacts of hydraulic clam dredgers on a macrobenthic community of the Adriatic Sea (Italy). *Mar. Biol.* 149:401–413.
- National Ocean Service, National Oceanic and Atmospheric Administration. 2014. Tide tables 2014: West coast of North and South America including Hawaii: High and low water predictions. Brewer, ME: North Wind Publishing. 422 pp.
- Naylor, R. L., R. J. Goldburg, J. H. Primavera, N. Kautsky, M. C. M. Beveridge, J. Clay, C. Folke, J. Lubchenco, H. Mooney & M. Troell. 2000. Effect of aquaculture on world fish supplies. *Nature* 405:1017–1024.
- Newell, R. I. E. 2004. Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review. *J. Shellfish Res.* 23:51–61.
- Oksanen, L. 2001. Logic of experiments in ecology: is pseudoreplication a pseudoissue? *Oikos* 94:27–38.
- Osborne, P. D. & E. H. Boak. 1999. Sediment suspension and morphological response under vessel-generated wave groups: Torpedo Bay, Auckland, New Zealand. *J. Coast. Res.* 15:388–398.
- Paine, R. T., M. J. Tegner & E. A. Johnson. 1998. Compounded perturbations yield ecological surprises. *Ecosystems (N. Y.)* 1:535–545.
- Pearson, T. H. & R. Rosenberg. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr. Mar. Biol. Ann. Rev.* 16:229–311.
- Pickett, S. T. A. & P. S. White, editors. 1985. The ecology of natural disturbance and patch dynamics. New York: Academic Press. 472 pp.
- Price, J. L. 2011. Quantifying the ecological impacts of geoduck (*Panopea generosa*) aquaculture harvest practices on benthic infauna. Master's thesis, School of Aquatic and Fishery Sciences, College of the Environment, University of Washington. 136 pp.
- R Development Core Team. 2011. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
- Reed, R. J. 1980. Destructive winds caused by an orographically induced mesoscale cyclone. *Bull. Am. Meteorol. Soc.* 61:1346–1355.
- Samuel-Fitwi, B., S. Wuertz, J. P. Schroeder & C. Schultz. 2012. Sustainability assessment tools to support aquaculture development. *J. Clean. Prod.* 32:183–192.
- Sara, G. 2007. Ecological effects of aquaculture on living and non-living suspended fractions of the water column: a meta-analysis. *Water Res.* 41:3187–3200.
- Schank, J. C. & T. J. Koehnle. 2009. Pseudoreplication is a pseudoproblem. *J. Comp. Psychol.* 122:421–433.
- Shannon, C. E. 1948. A mathematical theory of communication. *Bell Syst. Tech. J.* 27:379–423, 623–656.
- Sherrod, B. L. 2001. Evidence for earthquake-induced subsidence about 1100 yr ago in coastal marshes of southern Puget Sound, Washington. *Geol. Soc. Am. Bull.* 113:1299–1311.
- Simenstad, C. A. & K. L. Fresh. 1995. Influence of intertidal aquaculture on benthic communities in Pacific-Northwest estuaries: scales of disturbance. *Estuaries* 18:43–70.
- Simenstad, C. A., C. T. Tanner, R. M. Thom & L. L. Conquest. 1991. Estuarine habitat assessment protocol. Seattle: US Environmental Protection Agency, Region 10. 191 pp.
- Smith, C. R. & S. J. Brumsickle. 1989. The effects of patch size and substrate isolation on colonization modes and rates in an intertidal sediment. *Limnol. Oceanogr.* 34:1263–1277.
- Smith, F. & J. D. Witman. 1999. Species diversity in subtidal landscapes: maintenance by physical processes and larval recruitment. *Ecology* 80:51–69.
- Sobocinski, K. L., J. R. Cordell & C. A. Simenstad. 2010. Effects of shoreline modifications on supratidal macroinvertebrate fauna on Puget Sound, Washington beaches. *Estuaries Coasts* 33:699–711.
- Somerfield, P. J. & K. R. Clarke. 1995. Taxonomic levels, in marine community studies, revisited. *Mar. Ecol. Prog. Ser.* 127:113–119.
- Sousa, W. P. 1984. The role of disturbance in natural communities. *Annu. Rev. Ecol. Syst.* 15:353–391.
- Spencer, B. E., M. J. Kaiser & D. B. Edwards. 1998. Intertidal clam harvesting: benthic community change and recovery. *Aquacult. Res.* 29:429–437.
- Steenburgh, W. J. & C. F. Mass. 1996. Interaction of an intense extratropical cyclone with coastal orography. *Mon. Weather Rev.* 124:1329–1352.
- Tenore, K. R. 1972. Macrobenthos of the Pamlico River estuary, North Carolina. *Ecol. Monogr.* 42:51–69.
- Thorson, R. M. 1989. Glacio-isostatic response of the Puget Sound area, Washington. *Geol. Soc. Am. Bull.* 101:1163–1174.
- Thrush, S. F., R. B. Whitlatch, R. D. Pridmore, J. E. Hewitt, V. J. Cummings & M. R. Wilkinson. 1996. Scale dependent recolonization: the role of sediment stability in a dynamic sandflat habitat. *Ecology* 77:2472–2487.
- Tomassetti, P. & S. Porrello. 2005. Polychaetes as indicators of marine fish farm organic enrichment. *Aquacult. Int.* 13:109–128.
- Underwood, A. J. 1981. Techniques of analysis of variance in experimental marine biology and ecology. *Oceanogr. Mar. Biol. Annu. Rev.* 19:513–605.
- VanBlaricom, G. R. 1982. Experimental analyses of structural regulation in a marine sand community exposed to oceanic swell. *Ecol. Monogr.* 52:283–305.
- Warner, M. D., C. F. Mass & E. P. Salathé, Jr. 2012. Wintertime extreme precipitation events along the Pacific Northwest coast: climatology and synoptic evolution. *Mon. Weather Rev.* 140:2021–2043.
- Warwick, R. M. & K. R. Clarke. 1993. Increased variability as a symptom of stress in marine communities. *J. Exp. Mar. Biol. Ecol.* 172:215–226.
- Warwick, R. M., K. R. Clarke & Suharsono. 1990. A statistical analysis of coral community responses to the 1982–83 El Niño in the Thousand Islands, Indonesia. *Coral Reefs* 8:171–179.
- Weiser, W. 1956. Factors influencing the choice of substratum in *Cumella vulgaris* Hart (Crustacea, Cumacea). *Limnol. Oceanogr.* 1:274–285.
- Wiest, K. R., D. I. Doser, A. A. Velasco & J. Zollweg. 2007. Source investigation and comparison of the 1939, 1946, 1949 and 1965 earthquakes, Cascadia subduction zone, western Washington. *Pure Appl. Geophys.* 164:1905–1919.
- Williams, H. & I. Hutchinson. 2000. Stratigraphic and microfossil evidence for late Holocene tsunamis at Swantown Marsh, Whidbey Island, Washington. *Quat. Res.* 54:218–237.
- Zajac, R. N. & R. B. Whitlatch. 2003. Community and population-level responses to disturbance in a sand flat community. *J. Exp. Mar. Biol. Ecol.* 294:101–125.
- Zhu, Y. & R. E. Newell. 1998. A proposed algorithm for moisture fluxes from atmospheric rivers. *Mon. Weather Rev.* 126:725–735.