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DISTRIBUTION, ABUNDANCE, AND HABITAT ASSOCIATIONS OF A LARGE BIVALVE (*PANOPEA GENEROSA*) IN A EUTROPHIC FJORD ESTUARY

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ABSTRACT Marine bivalves are important ecosystem constituents and frequently support valuable fisheries. In many nearshore areas, human disturbance—including declining habitat and water quality—can affect the distribution and abundance of bivalve populations, and complicate ecosystem and fishery management assessments. Infaunal bivalves, in particular, are frequently cryptic and difficult to detect; thus, assessing potential impacts on their populations requires suitable, scalable methods for estimating abundance and distribution. In this study, population size of a common benthic bivalve (the geoduck *Panopea generosa*) is estimated with a Bayesian habitat-based model fit to scuba and tethered camera data in Hood Canal, a fjord basin in Washington state. Densities declined more than two orders of magnitude along a north–south gradient, concomitant with patterns of deepwater dissolved oxygen, and intensity and duration of seasonal hypoxia. Across the basin, geoducks were most abundant in loose, unconsolidated, sand substrate. The current study demonstrates the utility of using scuba, tethered video, and habitat models to estimate the abundance and distribution of a large infaunal bivalve at a regional (385-km²) scale.

KEY WORDS: assessment, Bayesian model, bivalve, cryptic, geoduck, habitat, Hood Canal, hypoxia, *Panopea generosa*, Puget Sound, scuba, videography

INTRODUCTION

Wild and cultured marine bivalves can act as important ecosystem engineers in marine and estuarine ecosystems (e.g., Jones et al. 1994), where they provide habitat, regulate primary productivity, and couple energy and nutrients in pelagic and benthic environments (Prins et al. 1998, Newell et al. 2002, Burkholder & Shumway 2011, Carmichael et al. 2012, Dame 2012). Wild bivalve populations also support important fisheries worldwide, with capture production exceeding 1.6 million t in 2012 (FAO 2014). These fisheries are economically important because unit price values for bivalves tend to exceed those for finfish and other invertebrates (Gosling 2003). In many nearshore areas, human disturbance can affect the distribution and abundance of wild bivalve populations, which may complicate ecosystem or fishery management approaches (Dame et al. 2002, Dame 2012). Moreover, chronic perturbations associated with continued human population growth and development in urban and suburban watersheds are expected to accelerate declines in shellfishery yields through the effects of nutrient loading and other disturbances (Kennish 2002).

The inland marine waters of Washington state (i.e., Puget Sound and the Strait of Juan de Fuca) support valuable wild subtidal bivalve harvests and a growing human population. Puget Sound in particular experiences significant stressors, including habitat alteration, contamination, as well as eutrophication resulting in low dissolved oxygen (LDO). Seasonal LDO and periods of hypoxia (defined as dissolved oxygen

concentrations less than 2 mg/L [Diaz 2001]) are most intense in Hood Canal, a narrow and deep fjord basin that comprises the westernmost portion of Puget Sound. Oxygen levels typically decline in deeper waters of the southern reaches of Hood Canal throughout the course of the boreal summer, and hypoxic conditions may expand to depths less than 20 m for short periods (Newton et al. 1995). Localized wind events can cause upwelling of this hypoxic layer to the surface, leading to precipitous decreases in dissolved oxygen throughout the water column on the scale of hours to days (Palsson et al. 2008, Kawase & Bang 2013). Although historical reconstructions suggest LDO and periodic hypoxia are regular features of the basin (Brandenberger et al. 2011), “fish kill” events and evidence of stress and mortality among invertebrates in 2002 to 2004 and 2006 have focused attention on the impact of seasonal conditions on ecosystem health (Fagergren et al. 2004, Newton et al. 2007, Palsson et al. 2008). Subsequent studies have characterized a north–south gradient of declining dissolved oxygen levels with a strong seasonal component (see Kawase and Bang [2013] and references therein) that is associated with changes in the distribution and behavior of fish and macroinvertebrates (Parker-Stetter & Horne 2008, Essington & Paulsen 2010, Froehlich et al. 2014). Notably, these previous studies have not specifically evaluated LDO effects on regional bivalve populations.

One of the most commercially and culturally valuable bivalve species in these waters is the geoduck *Panopea generosa* (Gould 1850), which has historically been harvested for subsistence, and in more recent decades by recreational clam diggers and commercial operations. Geoducks are large (>2 kg), long-lived (>100 y),

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deeply burrowing (~1 m) bivalves that inhabit soft, unconsolidated sediments in intertidal and subtidal areas. The species often dominates the benthic biomass of Puget Sound, the Strait of Juan de Fuca, and the Strait of Georgia, British Columbia, in suitable subtidal habitats (Goodwin & Pease 1989). Recent concern for geoduck populations in Hood Canal—particularly those in areas affected periodically by LDO—has prompted resource management agencies to call for concerted monitoring and assessment efforts within the basin (Sizemore & Blewett 2006).

Determining the abundance and distribution of infaunal clams is complicated by their cryptic habit. In subtidal areas, assessments for several species are done using dredges or grabs, but efficiency varies with sediment type and other environmental factors, as well as the apparatus used (Kennish & Lutz 1995, Ragnarsson & Thórarinsdóttir 2002, Gosling 2003). Moreover, these methods are typically very labor intensive and require a large number of samples, particularly for patchily distributed species that occur at low densities. Dredges also fail to capture small-scale patterns in sediment type, topography, and ecological interactions, which provide important context for understanding patterns (Ragnarsson & Thórarinsdóttir 2002). In Washington, British Columbia, and Alaska, geoduck assessments are conducted by divers in conjunction with harvest, which yields high-resolution data (Campbell et al. 1998, Muse 1998, Bradbury et al. 2000, Siddon 2007). However, these visual surveys are restricted to *a priori* designated tracts at relatively shallow depths (<21 m [Goodwin & Pease 1989]) compared with the maximum reported for the species (at least 110 m, as reported by Goodwin and Pease [1991]). Although remote photographic and videographic methods have been used elsewhere to assess populations of infaunal bivalves in deeper waters (Ragnarsson & Thórarinsdóttir 2002), this approach has not yet been used for geoducks.

The scale and extent of environmental stressors affecting Hood Canal underscores the importance of developing a suitable, scalable approach for evaluating broad-scale changes in geoduck distribution across depths and regions of the basin. Moreover, concerns about resilience of geoduck populations in general (Orensanz et al. 2004, Valero et al. 2004) and sustainability of geoduck fisheries (Khan 2006) provide the impetus for assessing abundance. Herein the distribution and substrate affinities of geoducks are documented in Hood Canal with scuba and tethered camera surveys. Abundance of present-day geoduck populations is estimated using a Bayesian habitat-based model, and this information is used to evaluate patterns among habitats across the entire basin.

MATERIALS AND METHODS

Study Area

Hood Canal is a long (~90 km), narrow (~2.4 km) fjord that constitutes the westernmost subbasin of Puget Sound (Burns 1985) (Fig. 1). The volume of Hood Canal (~ 2.1×10^{10} m³; based on MHW datum) is nearly 13% of all Puget Sound marine waters. To account for the heterogeneous hydrographic conditions in the overall study area, survey stations were selected in four distinct geographic regions; North, Middle, South, and Lynch. The North region is bordered by South Point (47°50'3.18" N, 122°41'15.25" W), and Lowfall (47°48'53.78" N, 122°39'18.36" W) in the north, and approximates the location of

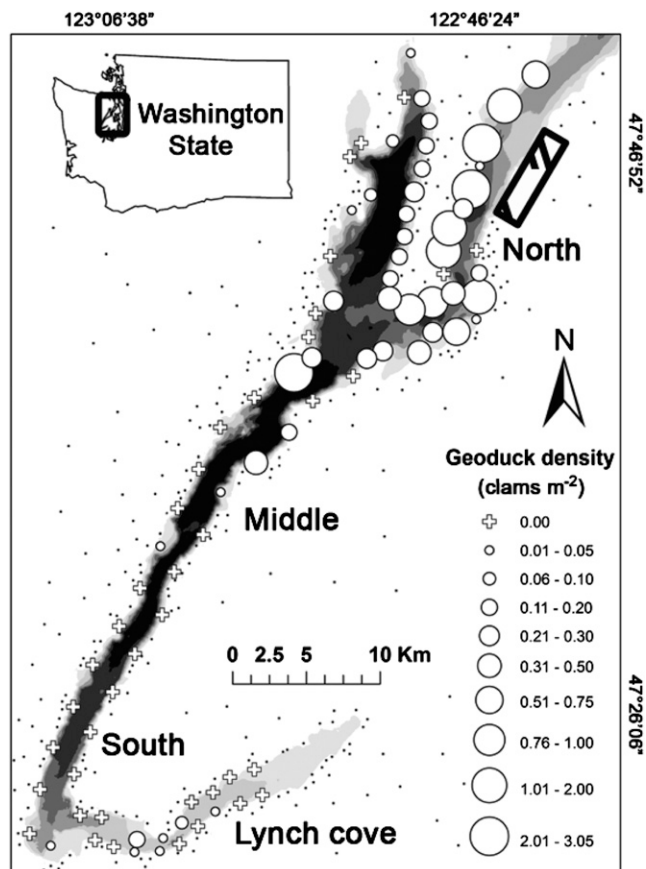


Figure 1. Geoduck density estimates in scuba surveys by transect position. Estimated densities are proportional to the area of each circle. Crosses indicate transect locations where no geoducks were observed. The four regions used in the analysis are shown: North, Middle, South, and Lynch Cove. Relative water depth is indicated by shading; land area is stippled. No surveys were conducted within the secure area of the Naval Base Kitsap installation at Bangor, Washington (box).

a prominent sill at the only opening to the subbasin. The Middle region is demarcated to the north by Quatsop Point (47°38'47.35" N, 122°54'15.83" W), where it abuts the North region, and Chinom Point (47°31'42.33" N, 123°1'2.56" W) to the south, where it abuts the South region. Data describing the physical oceanography of Hood Canal are available from the Hood Canal Dissolved Oxygen Program (<http://www.hoodcanal.washington.edu>). Since 2000, data have been collected as part of a citizen's monitoring program (Hood Canal Dissolved Oxygen Program 2007a) and the Oceanic Remote Chemical Analyzer system (Hood Canal Dissolved Oxygen Program 2007b). The North region is typically normoxic whereas the Middle region rarely experiences LDO or hypoxia in bottom waters. The South region encompasses the Great Bend and is divided from the Lynch region at Sister's Point (47°21'41.04" N, 123°02'08.82" W). The South region experiences seasonally protracted LDO in deeper waters, with hypoxic conditions extending periodically into shallow water (<20 m), whereas bottom waters in the Lynch region experience chronic hypoxia.

Scuba Surveys

A total of 87 sites were surveyed using scuba to assess the distribution and densities of geoducks in nearshore waters of

Hood Canal (Fig. 1). A stratified design was used, with sampling sites placed at 1.6-km increments around the entire shoreline, starting in Lynch Cove. A total of 63 and 23 sites were sampled from June through September in 2007 and 2008, respectively. In 2009, one site was surveyed near Tahuya in the South region, which was not surveyed during the first 2 y because of logistical constraints. Some areas falling within the Bangor Naval Base restricted access area were not sampled (Fig. 1). Diving protocol and survey methods were modified from Miller et al. (1994) and Bradbury et al. (2000). At each site, two divers descended to an initial starting depth of 21 m MLLW and swam a strip transect on a compass heading toward shore and perpendicular to depth contours; each diver surveyed a 1-m swath. The divers stopped every 5 m along the strip transect (10 m²; henceforth, “segment”) to record clam counts, habitat features, depth, and predominant (>90% coverage) substrate. Substrate type was classified using the following categories: bedrock/boulder (diameter, >256 mm), cobble (diameter, <256 to ≥4 mm), sand (diameter, <4 to ≥0.06 mm), and fines (diameter, <0.06 mm). Where cobble and sand substrates were well mixed and neither comprised more than 90% coverage, the substrate was called cobble/sand. The number of segments surveyed per site varied as a result of differences in bottom slope.

Because geoduck survey counts are based on observations of siphons, which are visible when clams are actively filtering water (i.e., the “show”), only a proportion of the total population of geoducks in a given area can be counted at any time. Therefore, a “show-factor” multiplier (i.e., the proportion of geoducks with visible siphons) must be estimated at the time and location of the survey, and applied to the uncorrected diver counts post hoc. The Washington Department of Fish and Wildlife/Washington Department of Natural Resources maintain three geoduck show plots within Hood Canal that are used to estimate the local show factor at the time of surveys. Within a show plot, the geoduck density is known, so by comparing survey counts with the known densities in these areas, the show factor can be estimated (Bradbury et al. 2000). The nearest available show plot was surveyed once per week during all survey weeks in all 3 y to generate weekly show-factor estimates for survey data. This sampling frequency was deemed appropriate after analysis of 2007 show-plot data (when show plots were surveyed more frequently) indicated strong temporal autocorrelation in show factor on a scale of 7–10 days.

Tethered Camera Surveys

To determine the distribution of geoducks beyond safe diving depths, tethered camera surveys were conducted offshore on a random stratified sample of 40 of the 87 sites sampled using scuba (20 sites each in 2008 and 2009). Sites were selected randomly within the four geographic regions to ensure broad spatial coverage throughout Hood Canal. The tethered camera (Deep Blue Pro Color Underwater Video System; Ocean Systems Inc., Everett, WA) was equipped with two lasers (beam width, 5.5 cm) and two underwater lights, and was tethered to a digital video recorder (Canon HV20 Camcorder; Canon USA, Lake Success, NY) on the support vessel. At each site, a survey consisted of four deployments targeting depth strata of 20 m, 30 m, 40 m, or 50 m for 5-min “drifts” in each stratum. The position of the boat and the water depth at 1-min intervals were recorded while allowing the boat to drift above the target

coordinates using an integrated GPS/depth sounder on the support vessel; these intervals were used for binning video analyses in the laboratory. All showing geoducks were counted, and habitat features, depth, and predominant substrate were recorded. Estimates of the area surveyed were calculated as the product of the distance drifted during all 1-min intervals of each deployment and the mean width (in meters) of the camera’s field of view, as determined from the ratio of mean distance between lasers on the viewing monitor and the entire viewing area (actual distance between lasers, 10 cm).

Statistical Analyses

To determine the set of predictor variables that best explained the field data, and to estimate the effects of those parameters on geoduck density, generalized linear mixed models (GLMM) (Breslow & Clayton 1993) with a Poisson error distribution and a log-link function were used. The response variable in these models was the count of geoducks per transect segment, and the predictor variables were region, depth, and substrate; sampling site was a categorical variable with random effects. From these effects, a set of candidate models was developed consisting of all combinations of terms, as well as an intercept-only “null” model. For all models, fixed terms were included on the linear set of predictors to account for area sampled (10 m² for all scuba transect segments, variable for tethered camera; *AREA*) and for the show factor (*showFactor*) for each survey date. Thus, the statistical model was

$$Y = \exp[\eta + \ln(\text{AREA}) + \ln(\text{showFactor})]$$

$$\eta = X\beta + Z\alpha,$$

where Y is the number of geoducks observed in a transect segment, X is the matrix of fixed-effects independent variables, β is a vector of fitted coefficients for fixed effects, Z is the design matrix indicating the site for each datum, and α is a random effect parameter assumed to be drawn from a normal distribution, with a mean of zero and a variance estimated from the data.

Multiple models with unique combinations of covariates were fit to the data by minimizing the negative log-likelihood using the lme4 package for the R statistical system (R Development Core Team 2008). Akaike’s information criterion corrected for overdispersion (QAIC) was used to select the subset of models that best fit the data (Burnham & Anderson 2002). Overdispersion implies a greater frequency of extreme events (i.e., greater geoduck densities) than expected from the probability density function, and introduces a bias toward selecting more complicated models. In addition to correcting for overparameterization, QAIC penalizes more complicated models based on the degree of overdispersion that is estimated from each model. The analysis was performed separately for the scuba data and the tethered camera data.

Bayesian Estimation and Prediction

The best-fitting model from the likelihood-based GLMM was used to estimate Bayesian posterior probability density functions for each model parameter, which were then combined with the GIS output to estimate probability density functions

for total geoduck abundance in each region of Hood Canal. Five Markov-Chain Monte Carlo (MCMC) simulations, each for 400,000 iterations, were run using openBUGS software, and every 10th iteration was saved. Starting values for each chain were randomized around the maximum likelihood estimate. Convergence of chains was evaluated using the Gelman–Rubin test on each parameter and by confirming low autocorrelation in the MCMC. A uniform prior was used for the fixed-effects coefficients and the hyperdistribution mean (−10 to 10), as well as the hyperdistribution standard deviation (0.01–10).

The Bayesian posterior probability distributions were used to predict geoduck densities in each region in Hood Canal based on the areas containing each depth and substrate classification. For each iteration of the MCMC simulation, a predicted geoduck density was generated for any area in Hood Canal based on its depth, substrate type, and region in which the area occurs. By summing these predictions over all areas within a region, total abundance of geoducks in each region was estimated. This was repeated for each simulated draw from the posterior distribution, thereby generating probability distributions of total geoduck abundance by region. Posterior inferences were drawn by fitting nonparametric kernel density smoothers to the posterior draws.

This analysis requires geographic information on the amount of area in each region within specified depth bins and with characteristic substrate types. Geographic information system data layers were generated for the three ecogeographic variables that were included in the GLMM: region, depth, and substrate. All calculations were performed on geospatial data sets using the built-in functionality of ArcGIS 9.0 and Spatial Analyst tools (ESRI, Redlands, CA). The starting point for the geospatial modeling was a digital elevation model of combined bathymetry and topography for the Puget Lowland available through the University of Washington, School of Oceanography (Finlayson 2005). All data, regardless of native projection, were reprojected as UTM Zone 10N, WGS 1984.

The depth layer was generated by reclassifying the digital elevation into 1-m- and 20-m-depth bins for depths of 0–60 m and more than 60 m, respectively, with the analysis extent set to the Region layer. Sediment data were obtained for the North region from the Naval Oceanographic Office (Stennis Space Center, Bay St. Louis, MS) and reduced from the original 28 sediment categories to five broad sediment types: bedrock/boulder, cobble, cobble/sand, sand, and fines. Mapped substrate data are not available from the other regions. Instead, data collected in scuba surveys were used to generate estimated proportions of the total area in each region consisting of each substrate category; this approach provides a reasonable approximation in the absence of detailed bottom mapping and substrate classification data. To use these data, each region and depth-specific polygon had to be subdivided into subareas based on the proportion of area that consisted of each substrate type.

RESULTS

Geoduck Distribution and Abundance

Geoduck densities varied markedly across regions and depths. The scuba data indicated strong regional contrasts in geoduck densities (Fig. 1). Geoduck densities were substantially

greater in the North region compared with the other three regions. For instance, geoduck densities at intermediate depths ranged from 0–9 geoducks/m² in the North, 0–2 geoducks/m² in the Middle region, and 0–0.6 geoducks/m² in the South and Lynch Cove regions. In all regions, geoduck densities were generally low at shallow depths (<3–4 m), peaked at intermediate depths, and showed some indication of declining thereafter (Fig. 2). Within the North region, the trend with depth was difficult to discern because of the high variability in geoduck counts among segments. A strong declining trend with depth was evident in the Middle region, whereas a possible increasing trend with depth was apparent in the Lynch Cove region. However, variation in depth trends across regions cannot be determined conclusively because of substantial patchiness in geoduck densities, which can give rise to spurious differences resulting from chance events.

The tethered camera surveys confirmed that geoduck densities declined with depth beyond 20 m (Fig. 2). The North region had the most informative data because densities were generally greatest there. Within the depth range surveyed by both scuba

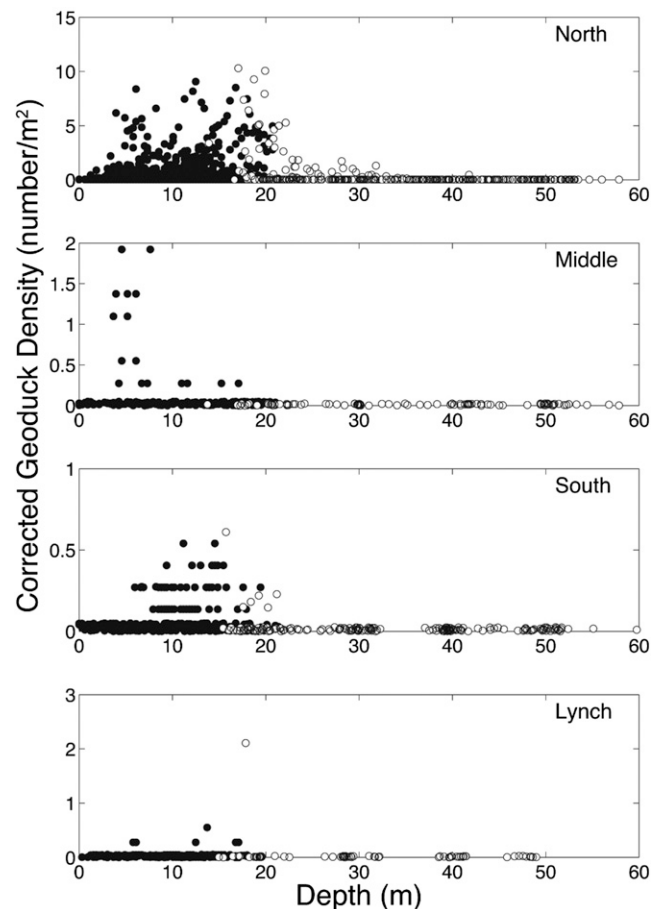


Figure 2. Mean geoduck density (corrected for show factor) versus depth based from scuba (black circles) and tethered camera (open circles) surveys. Show factor ranged from 22.7%–84.1% (mean, 58.0%) and 46.0%–74.0% (mean, 58.0%) of known geoducks in show plots for scuba and tethered camera surveys, respectively (see text for details). Each black circle represents a single 10-m² transect segment in scuba surveys; each open circle represents a density estimate from a single 1-minute drift in tethered camera surveys. A small amount of jitter was added to densities so that the number of observations can be seen.

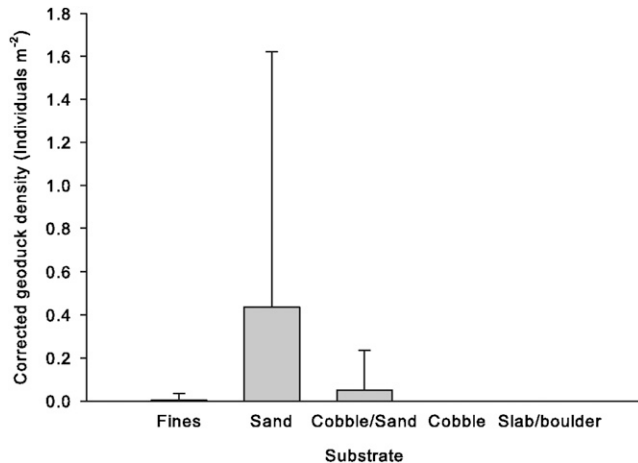


Figure 3. Mean geoduck density (\pm SE) by substrate type, estimated from scuba data.

and tethered camera, geoduck densities were similar between the two sampling methods (Figs. 2). The tethered camera data show a sharp decline in geoduck densities at depths greater than 20 m, generally declining to near zero around 30 m. Only a single geoduck was observed at depths greater than 40 m (Fig. 2).

Geoduck densities also varied substantially by substrate type (Fig. 3). Densities were greatest in scuba transect segments classified as sand, and cobble/sand mixture sites had notable but still reduced geoduck densities. Sites categorized as fines had virtually no geoducks present, and no geoducks were observed in sites categorized as cobble or bedrock/boulder.

The initial GLMM fits indicated an unexpected fitted relationship with depth; density was predicted by the models to increase with depth. These fitted values were inconsistent with the general observation that geoduck densities declined with depth, and resulted from the apparent nonlinearity in the effect of depth, particularly the decline in geoduck densities at shallow depths. To account for this, a new predictor variable was added that described how densities declined with depth at shallow but not deep depths. Specifically, depth was standardized so that the data had a mean of zero and a standard deviation of one. A predictor variable was then added equal to standardized depth squared (depth^2) if the standardized depth was less than zero (i.e., the actual depth was below the mean of all sampled depths), and was zero otherwise. This allowed for a “dome-shaped” effect of depth expressed as a collection of linear coefficients on predictor variables.

Model selection indicated that the additional nonlinear depth predictor variable greatly improved the model fits, so this term was added to all models that also had depth as a predictor (Table 1). The full model provided the best fit and contained all fixed effects, including the modified depth^2 predictor, indicated as $\text{depth}^2(-)$ to denote that it only applies to those sites with a negative standardized depth. The next best fitting model (depth, $\text{depth}^2[-]$, and substrate) had a ΔQAIC value of 11, providing further support that the collection of depth and substrate predictor variables was informative.

The model coefficients provide further information about the magnitude and direction of fixed effects (Fig. 4). When fitting the GLMM to categorical data, the algorithm uses the first level for each categorical predictor as the reference state to which all others are relative. In this case, all parameter estimates denote the predicted geoduck density relative to sand substrate in the North region. All other parameter estimates are negative, indicating that densities are greatest in the North and in sand substrates (Fig. 4). Because these effects are on a log scale, the model predicts stark differences between the North and all other regions, after accounting for differences in substrate types and depths. For instance, geoduck densities in the Middle, South, and Lynch regions are estimated to be 3.9%, 0.7%, and 3%, respectively, of those in comparable depths and substrates in the North region. Even stronger effects are evident for substrate. Mixed cobble/sand is predicted to have 10% of the densities of sites categorized as sand, whereas sites categorized as fines have densities that are 7% of those in sand (Fig. 4). The model estimates near-zero density in bedrock/boulder and cobble substrates (SE could not be calculated for these estimates using numerical approximations).

The same model selection procedures were used on the tethered camera data, for which each datum was a single 1-min segment of a tethered camera deployment, and site was a random effect. However, because there were multiple data segments per deployment, a second random effect (called deployment) was included and nested within each site random effect. Because the data did not span the shallow depths where geoduck densities appeared to decline (based on scuba data), the $\text{depth}^2(-)$ term was not used in model selection; only a log-linear depth effect was used. The best-fitting model included depth only as a predictor variable (Table 2). There was weak evidence for a region effect ($\Delta\text{QAIC} = 0.8$), although by convention more complicated models are not favored over simpler models that have lower QAIC scores. The best-fitting

TABLE 1.

Model selection results for 8 GLMM to predict geoduck densities in scuba data (selected model in bold type).

Model	No. of fixed effects	ΔQAIC^*	QAIC* weight	Cumulative weight
Depth + $\text{depth}^2(-)$ + substrate + region	10	0	1.00	1.00
Depth + $\text{depth}^2(-)$ + substrate	7	11.1	0.00	1.00
Substrate + region	7	108	0.00	1.00
Substrate	5	120	0.00	1.00
Depth + $\text{depth}^2(-)$ + region	6	269.8	0.00	1.00
Depth + $\text{depth}^2(-)$	3	279.1	0.00	1.00
Region	4	362.2	0.00	1.00
Depth	2	377.8	0.00	1.00

* Akaike's information criterion corrected for overdispersion.

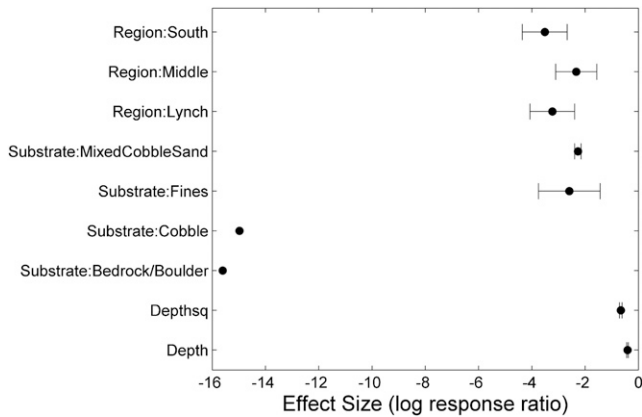


Figure 4. Estimated coefficients (\pm SE) from the generalized linear model depicting the effect of depth, depth squared (Depthsq), region, and substrate on geoduck densities. Coefficients are log-response ratios, and within categorical variables are expressed as a log-ratio relative to a reference level within that category. Reference levels were sand and North for substrate and region, respectively.

model had depth coefficient (\pm SE) equal to -0.18 ± 0.02 , which equates to a 16% decline in geoduck densities with each 1 m of depth over the full range of depths (13–61 m). The lack of significant substrate and region effects in this analysis is a result of the fact that this analysis spanned the maximum depth extent of geoducks, so that differences among substrates and regions at these depths were relatively few compared with the more important influence of depth. The data and model therefore predict that geoduck densities are reduced to 99.5% of their maximum value at depths greater than 30 m.

For each vector of model parameters produced by the MCMC output, the predicted geoduck abundance in each polygon was calculated based on its depth, substrate, and region. It was necessary to specify a maximum depth range at which geoduck densities were of an appreciable level to warrant consideration and to extrapolate the estimated depth effect via scuba data (depth range, 0–22 m) out to alternative maximum depth extents of geoduck ranges. Thus, four alternative models were considered about the maximum depth extent: 25 m, 30 m, 35 m, and 40 m. Of these, the 30-m and 35-m maximum depth range are most consistent with the tethered camera data.

The application of the GLMM to predict region-specific densities indicated large differences in total geoduck abundances between regions (Table 3). Because of the aforementioned region effects, the high proportion of area that had favorable substrate, and the larger total area, the estimated geoduck abundances in the North region were roughly two orders of magnitude greater than the South and Lynch regions, and roughly 50-fold greater than in the Middle region. In fact, the modal geoduck abundance in the North region was roughly 30-fold greater than the summed abundance over all other areas (Table 3). The 95% Bayesian credibility intervals were fairly large, spanning a roughly fourfold range of abundance in the North region and between 30-fold (South, Middle) and 40-fold (Lynch Cove) in the other regions. However, the credibility intervals were narrow compared with the large difference among regions. The lower bound for the North region (between 1.5 and 1.7 million; Table 3) was substantially greater than the upper bound for any other region (range, 0.07–0.4 million). The estimated abundances were not highly sensitive to the estimated maximum depth extent, especially compared with the precision of the estimates. For instance, in the North region, the 95% prediction interval for the scenario that assumes a 25-m maximum depth extent was 1.5–5.0 million geoducks, which shifted to 1.7–5.5 million geoducks for the 35-m maximum depth scenario.

DISCUSSION

The current study represents one of the first attempts to estimate the distribution and total abundance of a large infaunal bivalve (geoduck) at the scale of an entire fjord estuary (385 km²). Geoduck density exhibited regional variability and was greatest near the mouth of the fjord (i.e., North region) at depths between 10 m and 15 m (Figs. 1 and 2). Across the basin, geoduck distribution was spatially patchy and highest in loose, unconsolidated sediments, which is similar to patterns reported by Goodwin and Pease (1991). Unlike that study, geoduck densities in the current study associated strongly with sand substrate (Fig. 3) rather than other unconsolidated sediments (e.g., mud, gravel). Goodwin and Pease (1991) also suggest that geoducks may be abundant at depths up to 61 m in Puget Sound based on their own work and analysis of other studies; however, in the current study, densities declined dramatically beyond 20 m, and no geoducks were observed at depths of more than 31 m in Hood Canal (Fig. 2).

TABLE 2.

Model selection results to predict geoduck densities in tethered camera data (selected model in bold type).

Model	No. of fixed effects	Δ QAIC*	QAIC* weight	Cumulative weight
Depth	2	0	0.47	0.47
Depth + region	5	0.8	0.31	0.78
Depth + substrate	6	2.5	0.13	0.91
Depth + substrate + region	9	3.5	0.08	0.99
Depth + substrate + region + depth \times region	12	8.3	0.01	1.00
Null	1	87.6	0.00	1.00
Substrate	5	90.6	0.00	1.00
Region	4	91.5	0.00	1.00
Substrate + region	8	94.7	0.00	1.00

* Akaike's information criterion corrected for overdispersion.

TABLE 3.
Bayesian prediction intervals of geoduck abundance ($\times 1,000$) by region and model (maximum depth range).

	Posterior mode	Posterior median	50% Interval	80% Interval	95% Interval
North					
25	2,622	2,813	2,294–3,420	1,901–4,084	1,528–4,997
30	2,796	3,002	2,448–3,651	2,029–4,360	1,631–5,333
35	2,875	3,122	2,546–3,798	2,110–4,537	1,696–5,549
40	2,949	3,199	2,609–3,893	2,162–4,652	1,737–5,689
Middle					
25	47.49	80.31	45.8–136.0	25.82–213.4	12.1–353.3
30	50.57	85.58	49.8–144.9	27.51–227.4	12.8–376.1
35	52.88	89.47	51.0–151.5	28.75–237.7	13.4–392.9
40	54.15	91.61	52.2–155.1	29.42–243.3	13.7–402.1
South					
25	6.95	13.1	7.26–22.7	4.1–36.07	1.86–60.57
30	7.37	13.88	7.69–24.05	4.34–38.23	1.97–64.2
35	7.78	14.64	8.11–25.39	4.58–40.35	2.08–67.78
40	8.21	15.47	8.57–26.83	4.84–42.66	2.19–71.67
Lynch Cove					
25	25.44	39.44	21.73–68.5	11.61–111.42	5.17–188.3
30	26.86	41.89	23.08–72.74	12.35–118.32	5.51–200.09
35	27.85	43.66	24.07–75.8	12.89–123.31	5.75–208.7
40	28.13	44.16	24.35–76.67	13.04–124.72	5.82–211.15

Average densities estimated in the North region of Hood Canal were roughly one third those observed by Goodwin and Pease (1991) in central and south Puget Sound. Nevertheless, densities are far greater in the North region near the mouth of the fjord (north of Quatsop Point) than in any other portion of Hood Canal, and southern regions, which experience more frequent and intense periods of LDO and hypoxia, had the lowest geoduck densities. Differences in the availability of optimal substrate magnify disparities in total abundance between northern and southern regions, because sand is proportionally more available in the North region, where geoducks are more abundant, than all other regions combined. Peak mean densities were approximately 0.3 geoduck/m², although local densities are highly variable, reaching 2 geoducks/m² in some locales. That said, the analyses distinguished between the effects of substrate and region on local geoduck densities to account for the availability of preferred substrate. Notably, densities were greatly reduced in southern regions of Hood Canal, even in areas that otherwise had optimal (sand) substrate.

Although commercial harvest of geoducks has occurred in Hood Canal since 1970, fishing pressure does not explain the pattern of distribution and abundance described here. In fact, fishing intensity has historically been—and continues to be—greatest in the North region, and geoducks have never been harvested commercially in the South and Lynch regions (Washington Department of Fish and Wildlife, unpubl. data). Moreover, shell aging of extant populations suggests that geoducks in southern regions are, on average, smaller and younger than their counterparts in northern regions, and patches of relict shell indicative of a mass mortality event have been observed in some locations of southern Hood Canal (Valero 2011). Mass mortality of bivalves has been attributed to bottom-water hypoxia in several coastal embayments (e.g., Buzzelli et al. 2002, Seitz et al. 2009). Given the data and other

evidence presented here, the most parsimonious explanation for the pattern of distribution and abundance observed in this study is that current geoduck populations are responding to environmental gradients in Hood Canal, most notably dissolved oxygen. Geoducks, like other bivalves, have limited behavioral responses available to reduce exposure to potentially lethal hypoxia events (e.g., Long et al. 2008), and previous work has already demonstrated significant impacts of LDO on other sessile organisms in Hood Canal (Essington & Paulsen 2010).

Although patches of relict shell suggest that southern Hood Canal once harbored greater geoduck densities, this study and recent work (e.g., Valero 2011) suggest that current conditions may prohibit recovery of geoduck populations presumably affected by past mass mortality events. Local bathymetry and patterns of geoduck larval advection and diffusion do not favor large recruitment pulses of exogenous larvae to the region. Simulation models indicate substantial transport potential for larval propagules released in the North region, but dispersal distance within southern Hood Canal, including Lynch Cove, is very limited (Valero 2011). In general, the pattern reflects the slow exchange between regions and the particularly long residence time of water in southern Hood Canal (about 85.5 days [Babson et al. 2006]).

Bayesian habitat models are useful for estimating abundance of patchy species with strong habitat affinities. The analysis described here considered uncertainty and precision of region-specific density estimates explicitly. Because of patchiness in geoduck densities observed in surveys, modeled distributions were broad, which contributed to the range of population estimates. Estimating abundance from field studies required several assumptions that can influence absolute abundance estimates, yet relative patterns in geoduck distribution were robust to those assumptions. In general, geoduck densities were assumed to follow a nonmonotonic pattern with depth,

first increasing and then decreasing at depths greater than approximately 10 m. Error distributions on estimated quantities (e.g., mean densities) were also assumed to follow a Poisson probability density function typical of count or density data, reflecting the high probability of observing few individuals and the long tail of decreasing probabilities of high densities of geoducks.

Results of the current study suggest that future work should examine the likely impact of environmental stressors, including deteriorating water quality, on the abundance and distribution of geoducks and other sessile organisms in Hood Canal. Monitoring for and assessing impacts require suitable, scalable methods for estimating abundance of these cryptic and frequently patchy organisms. An additional ethical consideration for routine monitoring in ecosystems under stress is the degree to which sampling methods create further disturbance; common sampling gear can disrupt substrate and damage or kill associated fauna (Gosling 2003). Although visual methods provide an alternative to dredges and grabs, such monitoring is a particular challenge for organisms inhabiting depths beyond routine safe limits for the use of scuba. Concordance

between scuba and tethered camera results in the current study (Fig. 2) suggest these methods are complementary. Overall this work demonstrates the utility of using a combination of scuba, tethered video, and Bayesian habitat models to develop estimates of regional population abundance that consider uncertainty and precision of the survey methods.

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