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Effects of planting orientation and size on survival of juvenile Pacific geoducks *Panopea generosa*

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ABSTRACT

Objective: Seed mortality in geoduck aquaculture is a major bottleneck for production and is often attributed to predation. In the cultivation of the Pacific geoduck *Panopea generosa*, predator exclusion devices significantly reduce seed mortality, but farmers still report low postplanting survival, and the factors that influence this mortality are largely unknown. We conducted a laboratory study to assess the effect of siphon orientation and clam size (wet weight and shell length) on the postplanting survival of hatchery-reared juvenile Pacific geoducks.

Methods: Juvenile geoducks ($N = 540$) were individually marked, and shell length (mm) and wet weight (g) were measured and used to calculate a condition factor (g/cm). The experimental system consisted of thirty 20-L containers in a flow-through seawater system. Individuals were randomly assigned to a container based on size, and each container was randomly assigned a treatment factor representing the siphon angle with respect to the sediment surface (siphon oriented upright, horizontal, or inverted) at the time of planting. Geoducks were planted at 15 cm depth in each container, and survival was assessed after 14 d.

Results: We found that juvenile geoduck survivorship was dependent on planting orientation and that this relationship was highly size-dependent. Mean survivorship (\pm SD) was highest for geoducks planted upright ($68.5 \pm 7.6\%$), followed by geoducks planted horizontally ($50.7 \pm 8.7\%$) and those that were inverted ($34.1 \pm 11.7\%$). Across all planting orientations, juvenile survivorship was positively correlated with shell length, condition, and wet weight, with the latter two metrics best predicting survival. Orientation did not affect the survivorship of geoducks that had a condition of 1.6 g/cm or a wet weight of at least 2.5 g.

Conclusions: Our results show that planting Pacific geoducks upright increases juvenile survivorship, possibly leading to increased out-planting production. If controlling planting orientation is impossible, we recommend selecting juvenile geoducks of the highest possible condition to maximize survival. To our knowledge, this is the first analysis demonstrating that planting orientation affects mortality in juvenile Pacific geoducks.

KEYWORDS: aquaculture, bivalve mariculture, geoduck culture, *Panopea generosa*, shellfish, shellfish cultivation

LAY SUMMARY

Planting orientation and size influence juvenile Pacific geoduck survival and should be considered by hatcheries to improve survivorship and to maximize yield.

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INTRODUCTION

The Pacific geoduck *Panopea generosa* (hereafter, “geoduck”) is a large, deep-burrowing clam that has been commercially harvested along the Pacific coast of North America since 1970, recently becoming one of the most valuable seafood products in the region. Over 90% of geoducks that are cultivated and harvested in North America are exported to Asia, where high-quality individuals can fetch over Can\$130 per kilogram (GSGislason & Associates, 2012a; Shamshak & King, 2015). This international demand for geoducks has driven market prices from less than \$1 per kilogram in 1970 to \$39.33 per kilogram in 2019 (Fisheries and Oceans Canada, 2023; Shamshak & King, 2015).

The majority of the global market’s wild geoducks are harvested in the Pacific Northwest, specifically Washington State and British Columbia (Shamshak & King, 2015). In 2017, British Columbia landed 1.4 million kg of wild geoduck valued at \$50.2 million (British Columbia Ministry of Agriculture and Food, 2017). This harvest accounted for 34% of the landed value of all wild shellfish in the province but only 12% of the landed weight, making geoduck the second most valuable wild shellfish and third most valuable wild-caught seafood product in the province (British Columbia Ministry of Agriculture and Food, 2017). Similarly, in 2019, Washington State harvested approximately 2 million kg of wild geoduck, with an annual landed value of US\$50 million (Stevick et al., 2021), and geoducks recently contributed 3% of the landed weight but 32% of the value of all wild clam fisheries in the United States annually (National Marine Fisheries Service, 2020). However, despite high demand and high value, total geoduck landings in both Washington State and British Columbia have stagnated or declined over the past 30 years due to conservative fisheries management strategies and licensing restrictions (Fisheries and Oceans Canada, 2023; Shamshak & King, 2015; Stevick et al., 2021). With supply from wild harvest currently capped, any new growth in the geoduck industry is likely to come from aquaculture (Holden et al., 2019).

Geoduck aquaculture operations occur in both intertidal and subtidal zones, requiring porous gravel and soft sediment for optimal production (Davis, 2004; Feldman et al., 2004; Goodwin & Pease, 1991). Prior to planting, geoducks are reared in a hatchery until they reach 3–5 mm shell length. These geoduck “seeds” are often transferred to a nursery to be grown to planting size (5–13 mm; Pearce et al., 2019). To protect the geoducks from predators, intertidal growers plant geoducks by hand into sediment surrounded either (1) by PVC pipes (2–3 individuals/pipe), often covering the pipes with mesh netting for additional protection (Davis, 2004; Feldman et al., 2004); or (2) increasingly with HDPE plastic mesh tubes (Monterey Bay Seafood Watch, 2023). Subtidal growers also plant by hand using scuba divers to sprinkle juvenile geoducks onto the sediment (hereafter, “broadcast planting”). As strong bottom currents preclude the use of PVC pipes in subtidal aquaculture, mesh netting is often used to protect seeded areas from predators (British Columbia Ministry of Lands and Agriculture, 2005; Canadian Aquaculture Systems, 2012). In both intertidal and subtidal operations, removal of predator exclusion devices occurs once the juveniles have reached a sufficient size and refuge depth to minimize predation risk (generally within 2 years

of planting; Davis, 2004; Feldman et al., 2004). Geoducks are then left to grow to market size for 5–7 years. Harvesters use a high-pressure water jet to rapidly liquefy and loosen the sediment around each geoduck, which is then harvested by hand (Feldman et al., 2004; Harbo & Peacock, 1983).

Current geoduck aquaculture research focuses predominantly on methods that enhance postplanting seed survival. Although predator exclusion devices, such as mesh netting and PVC pipes, effectively reduce seed mortality (e.g., Beattie et al., 1995; reviewed by Munroe et al., 2015), considerable variation in juvenile geoduck survivorship remains, warranting additional research into other factors that may influence the survival of cultured geoducks (Feldman et al., 2004). Size at planting, or transfer size, is one factor known to influence survival in several clam species. Recommended minimum transfer size for clams ranges from 8 mm shell length (Marelli & Arnold, 1996) to over 20 mm shell length (Cigarría & Fernández, 2000), with a consensus that larger clams typically have higher survivorship than smaller clams (Beal & Kraus, 2002; Cigarría & Fernández, 2000; Kraeuter & Castagna, 1985). However, considering only shell length to determine transfer size fails to account for weight-specific metabolic costs that could also influence survival (Vladimirova et al., 2003). In other areas of shellfish research, condition factors (also known as “composite metrics” or “condition indices”) that account for both length and weight are used to assess overall health, growth rate, meat yield, and effects of environmental stressors (Lucas & Beninger, 1985; Zeng & Yang, 2021). Although weight-dependent factors likely influence survival, condition factors have not been widely implemented in the context of transfer size, likely because many condition factor calculations are based on ratios of meat or shell weight that require the animal to be sacrificed (Zeng & Yang, 2021). Destructive measurements may be suitable for assessing the health and robustness of shellfish at harvest or during growth experiments, but they are not useful for comparing individual seed health between planting and harvest since they require the individual to be sacrificed. Furthermore, condition indices that require several measurements are unlikely to be used by hatcheries due to the time and cost associated with collecting multiple metrics per animal. Thus, while at least 18 condition indices exist for bivalves (Zeng & Yang, 2021), the vast majority of these are unsuitable for hatchery use, and no standardized index exists for geoducks.

A geoduck’s orientation plausibly influences its survival, as an upright siphon is required to filter feed and respire (Goodwin & Pease, 1989). When geoducks are broadcast planted in subtidal aquaculture, they land haphazardly on the seafloor and are left to burrow into the sediment. Although this allows a geoduck to burrow on its own, ensuring an optimal orientation, juveniles are extremely vulnerable to predation while they are burrowing (Beattie et al., 1995; Goodwin & Pease, 1989). A diver-operated hydraulic seeding machine developed by the Underwater Harvesters Association solves the issue of predation by planting geoducks directly into the sediment (Clapp, 2000). However, this method does not discriminate the orientation in which a geoduck is planted; geoducks that are planted upside down with respect to the sediment surface may be at higher risk of mortality due to suffocation or starvation if they cannot correct their orientation. Although the hydraulic seeding machine is

currently only used by the Underwater Harvesters Association in British Columbia, there is interest in gauging the effect of this planting method on juvenile survival. Laboratory experiments on two other deep-burrowing clams, the soft-shell clam (or softshell) *Mya arenaria* and the stout razor clam (or stout tagelus) *Tagelus plebeius*, showed that juveniles can successfully escape burial under about 10 cm of sediment and recover their normal feeding position (Kranz, 1974). Previous research suggests that juvenile geoducks have some ability to right themselves after burial (Lochead et al., 2012), but the extent to which they can accomplish this is unknown.

In this study, we tested the effects of size and angular orientation on the survival of depth-planted juvenile geoducks. We hypothesized that juvenile geoducks planted with their siphons angled away from the sediment–water interface would show reduced survivorship compared to those planted with their siphons oriented toward the surface of the substrate. We also hypothesized that larger juvenile geoducks would have greater survivorship than smaller individuals. An understanding of how size and planting orientation affect juvenile geoduck survival is broadly applicable to the aquaculture industry with respect to maximizing seed survival, optimizing planting methods, and developing adaptive technologies to improve yield.

METHODS

Setup

We obtained juvenile geoducks ($N = 540$) belonging to a mixed cohort (two or more spawns) and size-sorted sediment (1–3-mm diameter) from Nova Harvest Ltd., a shellfish hatchery located in Bamfield, British Columbia, Canada. Hatchery-raised geoducks were maintained at Nova Harvest in 14–16°C water, which was passed through a 25- μm filter. In the nursery settlement stage, geoducks were raised using locally sourced beach fines (<400 μm). They were then transferred to hatchery rearing conditions, which used pit-run commercially available sand that was prewashed, with a diameter between 1 and 3 mm. Fines were screened out of the sand prior to use, and no organics were added. This sand is the same as was used during our experiment.

Geoducks were transported from the hatchery to the laboratory in a large plastic bin (length \times width \times depth = 50.8 \times 38.1 \times 12.7 cm) containing the same seawater to which they were acclimated. The hatchery from which the geoducks were obtained is located about 300 m from the laboratory where the experiment was conducted. As such, the bin was carried by hand and transportation took only a few minutes.

Experiment

To investigate the effect of planting orientation on juvenile geoduck survival, we experimentally planted geoducks at different orientations and assessed survival after 14 d. We marked each shell with a unique identification number by blotting each side of the shell with a Kimwipe and writing on it with a fine-tipped Sharpie; we then measured shell length (mm) and wet weight (g). Shell length and wet weight were used to calculate a non-destructive condition metric (g/cm), which differs from commonly used metrics of condition in bivalves that require the individual to be sacrificed (Zeng & Yang, 2021). Because size at

planting is primarily determined by shell length (Davis, 2004), we then sorted marked geoducks into five size-classes by shell length (10.0–11.9, 12.0–13.9, 14.0–15.9, and 16.0–18.9 mm). Following previous laboratory studies (e.g., Le et al., 2016), geoducks were acclimated to laboratory conditions for at least 72 h with constant seawater flow prior to the experiment. At the start of the experiment, we randomly assigned individuals from each size-class to thirty 20-L containers (23-cm rim width, 44-cm height); each container was then randomly assigned a treatment factor representing the siphon angle with respect to the sediment surface (siphon oriented upright, horizontal, or inverted) at the time of planting. Consequently, our experiment had 18 geoducks/replicate, with 10 replicates for each of the three treatments. The upright treatment consisted of geoducks that were planted with their siphons pointed straight up, perpendicular to the surface. The horizontal treatment consisted of geoducks that were planted flat on their side, valve down, with their siphon oriented parallel to the sediment surface. The inverted treatment consisted of geoducks that were planted with their siphon pointed straight down into the sediment, perpendicular to the sediment–surface interface. Geoducks were sorted into containers such that there was a similar distribution of shell lengths at each orientation (Figure S1 [see online Supplementary Material]).

We hand-planted geoducks in their respective orientations in 2–3 cm of sediment, with at least 1 cm of space between individuals. After planting, we hand-sprinkled a layer of sediment over individuals to ensure that the siphon angle was secured in sediment, and we then poured 15 cm of sediment on top. This depth was chosen to align with the Underwater Harvesters Association hydraulic seeding machine, which, to the best of our knowledge, plants geoducks at an approximate depth of 10–15 cm. To provide ample space for geoducks at the surface to extend their siphons, each container was filled with seawater to a depth of approximately 5 cm above the sediment. Replicate containers were arranged across six seawater tables (5 containers/table) and interspersed such that no more than two containers of the same treatment were in the same water table. Given that water quality and substrate are known to influence geoduck survival (Goodwin & Pease, 1989, 1991), we visually assessed sediment quality (presence/absence of woody debris, fine silt, or mud) and algal fouling (presence/absence of visible algal growth on most of the sediment surface) as confounding variables throughout the experiment. The containers were checked every 12 h for 14 d to maintain proper water flow. Based on these assessments, two containers were excluded from the analysis due to poor sediment quality (i.e., large amounts of woody material, silt, and other debris were present in the container). The container flow rate was controlled by a valve and was approximately 1.0 ± 0.2 L/min. No food was added during the experiment; however, the seawater inflow was untreated, being sourced from 30-m depth, so food was likely available in the water. Seawater temperature during this experiment ranged from 9.7°C to 11.2°C.

Partway through our study, we discovered holes in 8 of our 30 containers, causing seawater to drain continuously through the bottom of these containers for the duration of the experiment. We categorized each container in the experiment as being either “high-drainage” (water draining observed) or

“low-drainage” (water draining not observed). Because high-drainage conditions could transport water to buried geoducks and influence mortality regardless of orientation, the high-drainage and low-drainage conditions were considered separately for the remainder of the study. The low number of high-drainage containers prevented their inclusion in our statistical analysis; however, we include observations from this treatment in a qualitative capacity.

After 14 d, we extracted all individuals from the sediment by hand and assessed survivorship based on flesh coloration and stiffness of the mantle and siphon. If the siphon was flaccid, did not recoil when touched, and showed black/brown coloration, we considered the individual to be dead. Furthermore, deceased and decaying individuals were significantly reduced in size, making them typically far more difficult to find. Individuals that were not found after sorting were assumed to be dead. After accounting for the excluded containers and the categorization of high- and low-drainage treatments, our low-drainage condition analysis included six containers for the upright planting orientation, seven containers for the horizontal orientation, and seven containers for the inverted orientation. Our high-drainage condition, which was excluded from statistical analysis, included three containers for the upright orientation, two containers for the horizontal orientation, and three containers for the inverted orientation (Table S1 [see online Supplementary Material]).

Statistical analysis

We fitted generalized linear mixed-effects models (GLMMs) with a binomial distribution and a logit link function (also called logistic regression) to examine geoduck survival (lmer package in R; Bates et al., 2015; R Core Team, 2022). We used binary survival (0 = dead after 14 d; 1 = alive after 14 d) as our response variable. Planting orientation (upright, horizontal, or inverted) and one of three continuous size metrics (shell length [mm], wet weight [g], or condition [g/cm]) were treated as fixed effects, and container number was treated as a random effect to account for dependence between containers. A separate model was fitted for each of the three size metrics. Due to differences in experimental conditions and sample size constraints, GLMMs were only fitted to data from the low-drainage containers (results from high-drainage containers are discussed anecdotally). For each model, we used plots of Pearson residuals versus fitted values to visually assess model adequacy (Figure S2). Using the MuMIn package (Bartoń, 2024), we calculated the theoretical marginal and conditional R^2 values (Johnson, 2014; Nakagawa & Schielzeth, 2013; Nakagawa et al., 2017) for each model to measure the variance explained by the fixed effects and the entire model, respectively. Finally, using a 75/25 training/testing approach, we calculated the sensitivity, specificity, and accuracy to assess the predictive power of each model (Table S3).

A Tukey multiple comparison test was used to check for significant differences among planting orientations. This was done via the multcomp package (Hothorn et al., 2008), which accounts for multiple comparisons between levels of fixed effects using the Westfall–Young correction (Westfall, 1997). We calculated the predicted probability of survival for each

planting orientation with condition, and we plotted the average marginal predicted probabilities to visualize the logistic relationship of the model output. The data were visualized using the ggplot2 package (Wickham, 2010). All statistical analyses were conducted in R version 4.2.0 (R Core Team, 2022).

RESULTS

Across all treatments, 289 of 540 geoducks survived to the end of the experiment. Of the geoducks that survived, 113 were buried upright, 94 were buried horizontally, and 82 were buried in an inverted orientation, which translated to overall survival rates of 62.3, 52.2, and 45.6%, respectively. Within low-drainage containers, the mean proportion (\pm SD) of geoduck survival was highest in the upright treatment ($68.5 \pm 7.67\%$; Figure 1A), followed by the horizontal treatment ($50.7 \pm 8.65\%$). The inverted treatment had the lowest mean proportion of surviving juvenile geoducks ($34.1 \pm 11.7\%$; Figure 1A). Interestingly, in the high-drainage containers, we observed high survivorship across all orientations (68.5% for upright and 72.2% for both horizontal and inverted; Figure 1B).

In low-drainage containers, the model containing wet weight and the model containing condition performed similarly in terms of their true positive rate (68.8%) and test accuracy (70%), while the model containing shell length had a true positive rate of 64% and a test accuracy of 65.6%. The wet weight model explained the most variation in survival ($R^2_{\text{marginal}} = 0.485$), followed by condition ($R^2_{\text{marginal}} = 0.459$), whereas shell length had the worst fit to the data ($R^2_{\text{marginal}} = 0.389$).

The GLMMs revealed that the predicted probability of juvenile geoduck survival was positively correlated with size in all planting orientations (Table 1; Figure 2). Survivorship in low-drainage containers approached 100% as the condition increased to a maximum value of 1.6 g/cm and wet weight increased to 2.5 g across all planting orientations (Figure 2). Geoducks that were planted upright reached the maximum probability of survival at a lower condition and lower wet weight than geoducks that were planted in either a horizontal orientation or an inverted orientation. For upright planting, 95, 90, and 75% survival was achieved at conditions of 1.02, 0.87, and 0.68 g/cm, respectively (Table 2), compared to 1.20, 1.06, and 0.86 g/cm for the horizontal orientation and 1.37, 1.24, and 1.06 g/cm for the inverted orientation. For upright planting, 95, 90, and 75% survival was achieved at wet weights of 1.43, 1.23, and 0.89 g, respectively (Table 2), compared to 1.74, 1.54, and 1.20 g for the horizontal orientation and 2.03, 1.80, and 1.49 g for the inverted orientation.

Post hoc tests on the treatment effect indicated statistically significant differences among all treatments for all models (Table 3). The mean probability of survival increased by an average of 22% when geoducks were buried upright compared to inverted ($z = -5.508$, $P < 0.001$; Figure 2; Table 3). There was also an 11.3% increase in the mean probability of survival when geoducks were buried upright compared to horizontal ($z = -3.042$, $P = 0.00235$; Figure 2; Table 3) and an 11.5% increase in the mean probability of survival when geoducks were buried horizontally compared to the inverted orientation ($z = -2.949$, $P = 0.01082$; Figure 2; Table 3).

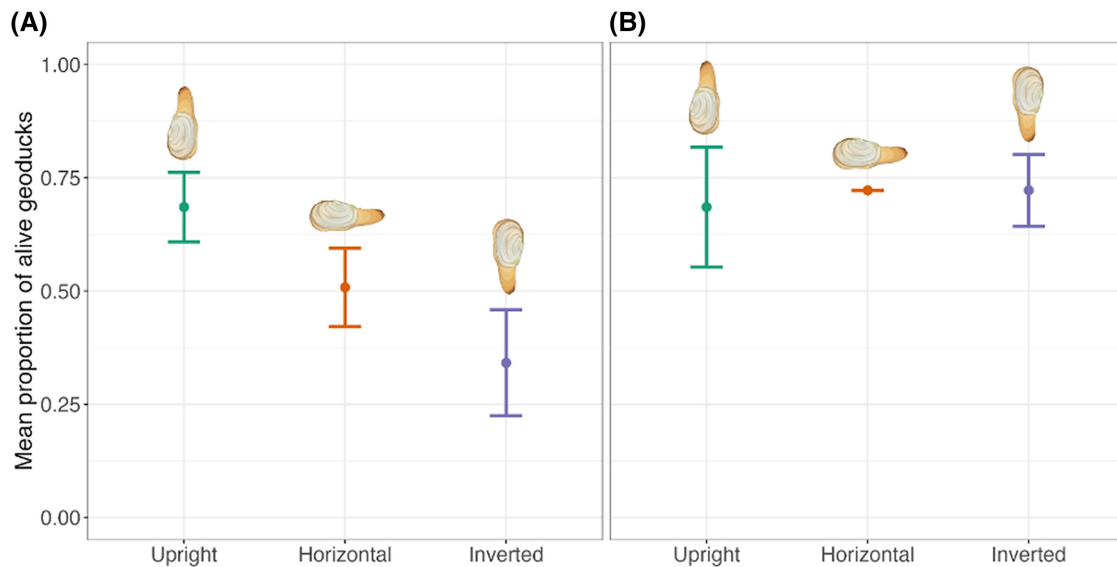


Figure 1. Average proportion of Pacific geoducks that were found alive in each treatment (siphon oriented upright [0°], horizontal [90°], or inverted [180°]) for (A) low-drainage and (B) high-drainage container conditions. Means were obtained by taking the average proportion of geoducks in each container within a treatment. Points are means, and error bars represent \pm SD.

Table 1. Model summary for the probability of survival of juvenile Pacific geoducks in low-drainage containers.

| Size metric | Effect | Term | Estimate | SE | Test statistic | P-value |
|--|--|--------------|-------------|---------|----------------|---------|
| Condition | Fixed | (Intercept) | -2.503 | 0.462 | -5.420 | <0.001 |
| | Fixed | Horizontal | -0.995 | 0.327 | -3.042 | 0.002 |
| | Fixed | Inverted | -1.923 | 0.349 | -5.508 | <0.001 |
| | Fixed | Condition | 5.343 | 0.695 | 7.688 | <0.001 |
| | Random | Bucket ID | 0.157 | | | |
| | Theoretical R^2_{marginal} | | 0.459 | | | |
| | Theoretical $R^2_{\text{conditional}}$ | | 0.463 | | | |
| | Delta R^2_{marginal} | | 0.411 | | | |
| | Delta $R^2_{\text{conditional}}$ | | 0.415 | | | |
| | Shell length | Fixed | (Intercept) | -10.238 | 1.461 | -7.008 |
| Fixed | | Horizontal | -0.943 | 0.310 | -3.044 | 0.002 |
| Fixed | | Inverted | -1.816 | 0.325 | -5.589 | <0.001 |
| Fixed | | Shell length | 0.852 | 0.113 | 7.526 | <0.001 |
| Random | | Bucket ID | 0.000 | | | |
| Theoretical R^2_{marginal} | | | 0.389 | | | |
| Theoretical $R^2_{\text{conditional}}$ | | | 0.389 | | | |
| Delta R^2_{marginal} | | | 0.344 | | | |
| Delta $R^2_{\text{conditional}}$ | | | 0.344 | | | |
| Wet weight | | Fixed | (Intercept) | -1.931 | 0.404 | -4.778 |
| | Fixed | Horizontal | -0.973 | 0.326 | -2.989 | 0.003 |
| | Fixed | Inverted | -1.907 | 0.347 | -5.495 | <0.001 |
| | Fixed | Wet weight | 3.334 | 0.441 | 7.552 | <0.001 |
| | Random | Bucket ID | 0.154 | | | |
| | Theoretical R^2_{marginal} | | 0.485 | | | |
| | Theoretical $R^2_{\text{conditional}}$ | | 0.489 | | | |
| | Delta $R^2_{\text{conditional}}$ | | 0.437 | | | |
| | Delta $R^2_{\text{conditional}}$ | | 0.441 | | | |

DISCUSSION

In this study, we examined the effects of size and planting orientation on the probability that juvenile geoducks would survive a burial event analogous to the outplanting methods used in geoduck aquaculture. Our burial experiment revealed a

consistent positive relationship between size and survival, and wet weight was identified as a better predictor of survival than shell length, which is a common metric used by the industry to optimize the size at planting (Feldman et al., 2004). We also found that in general, geoducks planted upright had the highest

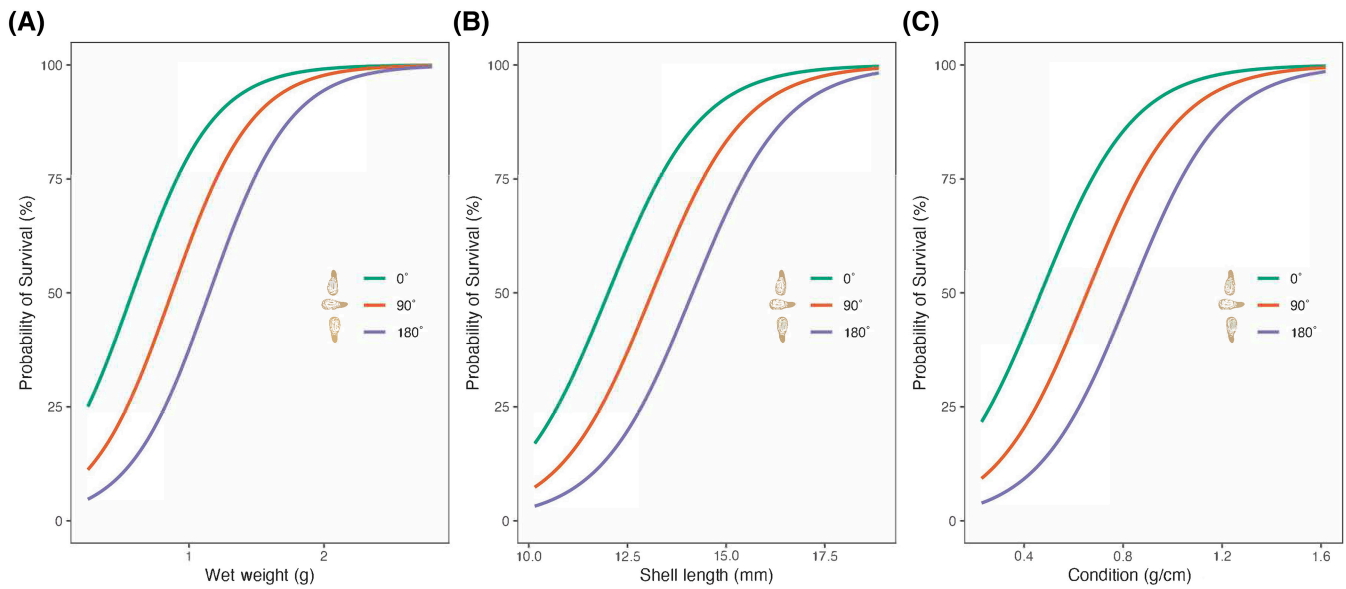


Figure 2. Predicted probability of Pacific geoduck survival (%) from generalized linear mixed-effects models as a function of (A) wet weight (g), (B) shell length (mm), and (C) condition (g/cm) for each planting orientation (siphon oriented upright [0°], horizontal [90°], or inverted [180°]) in low-drainage containers. The green line denotes the upright orientation, the orange line represents the horizontal orientation, and the purple line denotes the inverted orientation.

Table 2. Condition (g/cm), shell length (mm), and wet weight (g) at given probabilities of Pacific geoduck survival for each planting orientation (siphon oriented upright [0°], horizontal [90°], or inverted [180°]).

| Size metric | Probability of survival (%) | 0° | 90° | 180° |
|--------------|-----------------------------|-------|-------|-------|
| Condition | 95 | 1.01 | 1.20 | 1.37 |
| | 90 | 0.87 | 1.06 | 1.24 |
| | 75 | 0.68 | 0.86 | 1.03 |
| Shell length | 95 | 15.43 | 16.49 | 17.55 |
| | 90 | 14.55 | 15.70 | 16.67 |
| | 75 | 13.32 | 14.38 | 15.43 |
| Wet weight | 95 | 1.43 | 1.74 | 2.03 |
| | 90 | 1.23 | 1.54 | 1.80 |
| | 75 | 0.89 | 1.20 | 1.49 |

probability of survival, followed by those planted in horizontal and inverted orientations. However, the effect of planting orientation and the overall probability of survival were mediated by the amount of water drainage present in each container, suggesting that physiological and environmental factors may further influence survival. We discuss these findings in the context of juvenile geoduck burrowing mechanics, and we make recommendations to aquaculturists on the best metric and size based on our results.

Surviving burial events

There is limited targeted research on burial in geoducks despite its perceived importance for influencing mortality. Regular access to oxygenated and nutrient-rich, flowing seawater is important for clam survival (Haider et al., 2018; Le et al., 2016; Long et al., 2008; Saloom & Scot Duncan, 2005; Taylor & Eggleston, 2000). Sudden burial can impede this access and

can account for significant natural mortality in adult geoduck clams, which are almost entirely sedentary (Lochead et al., 2012). In contrast, juvenile geoducks can escape naturally occurring burial events that smother and kill their sedentary adult counterparts (Lochead et al., 2012). Although the mechanism is unclear, it is likely accomplished by a combination of upward vertical movement and siphon elongation.

Several other clam species adjust their burrowing depth in response to hypoxia (Long et al., 2008; Saloom & Scot Duncan, 2005; Taylor & Eggleston, 2000), which is energetically expensive. Further, siphon elongation as a response to smothering or low oxygen concentration has been anecdotally observed in geoducks (Lochead et al., 2012) and has been documented in other soft-shelled clams. Horse clams *Tresus nuttallii* were found to extend their siphons in an attempt to recover from catastrophic burial (MacGinitie & MacGinitie, 1968), while siphon elongation in response to hypoxia was observed in the soft-shell clam (Taylor & Eggleston, 2000) and the Baltic clam (or Baltic macoma) *Macoma balthica* (Seitz et al., 2003). In our study, individuals were able to reach the surface after burial under 15 cm of sediment regardless of planting orientation. Furthermore, most geoducks were recovered approximately 7–8 cm shallower than where they were buried, indicating significant upward vertical movement after burial (T. Rimmer and R. J. Command, personal observation). Our results support anecdotal evidence that reorientation and upward vertical movement are possible in juvenile geoducks but that the ability to survive following this movement is highly size-dependent.

Studies on other clam species have found a similar size-dependent relationship with survival (Beal & Kraus, 2002; Cigarria & Fernández, 2000; Kraeuter et al., 2009), including size-dependent selection of clams by both benthic and intertidal predators (Cigarria & Fernández, 2000; Mascaro & Seed,

Table 3. Multiple comparisons of means using Tukey contrasts from generalized linear mixed-effects model output, comparing differences in the proportion of Pacific geoducks that survived in each planting orientation treatment (siphon oriented upright [0°], horizontal [90°], or inverted [180°]) within low-drainage containers.

| Size metric | Comparison | Estimate | SE | z-value | P-value |
|--------------|----------------------------|----------|--------|---------|---------|
| Condition | 90° vs. 0° | -0.9948 | 0.3270 | -3.042 | 0.002 |
| | 180° vs. 0° | -1.9229 | 0.3491 | -5.508 | <0.001 |
| | 180° vs. 90° | -0.9282 | 0.3211 | -2.890 | 0.004 |
| Shell length | 90° vs. 0° | -0.9434 | 0.3099 | -3.044 | 0.002 |
| | 180° vs. 0° | -1.8163 | 0.3250 | -5.589 | <0.001 |
| | 180° vs. 90° | -0.8730 | 0.2956 | -2.953 | 0.003 |
| Wet weight | 90° vs. 0° | -0.9730 | 0.3255 | -2.989 | 0.003 |
| | 180° vs. 0° | -1.9071 | 0.3471 | -5.495 | <0.001 |
| | 180° vs. 90° | -0.9341 | 0.3206 | -2.914 | 0.004 |

2000; Simmons et al., 2014). With respect to outplanting, survival appears to increase within plots seeded with large versus small individuals for the soft-shell clam (8% increase; Beal & Kraus, 2002) and the Manila clam *Ruditapes philippinarum* (>20% increase; Cigarría & Fernández, 2000). Thus, size is clearly an important factor affecting survival in clams. However, studies investigating the effects of size on other aspects of burrowing have yielded mixed results. Goodwin and Pease (1989) found that geoduck burrowing speed was inversely related to shell length, while Tapia-Morales et al. (2015) found that juvenile geoduck burrowing speed was independent of shell length. A reason for the discrepancy could be that previous studies considered only shell length as a measure of size.

Although condition and wet weight are occasionally used as measures of shellfish health in research (e.g., Sharma et al., 2005; Zeng & Yang, 2021), the current industry standard for planting geoducks in British Columbia is based solely on shell length (Feldman et al., 2004; GSGislason & Associates, 2012b). We found that weight-based metrics of size better predicted juvenile geoduck survival than shell length. Further, we noted that geoducks in our study with a higher condition tended to have larger, more turgid siphons (Rimmer and Command, personal observation). Juvenile geoducks rely on jet propulsion for efficient movement—specifically, the ability of the siphon to forcefully contract and expel water through the pedal orifice (Tapia-Morales et al., 2015). Therefore, while research on the closely related Cortez geoduck *P. globosa* suggests that shell length alone is not correlated with burrowing speed (Tapia-Morales et al., 2015), it is plausible that individuals with a higher condition have the capacity for faster burrowing propulsion via siphons that are more robust relative to their shell length. Body size also appears to be proportional to hypoxia tolerance, with larger individuals of the New Zealand geoduck *P. zelandica* being able to withstand low-oxygen conditions longer than smaller individuals (Le et al., 2016). Together, these factors would increase an individual's odds of postplanting survival relative to less robust geoducks by enabling the individual to move faster through the substrate after depth planting and to more readily access oxygen- and nutrient-rich water. Indeed, our results suggest that condition and wet weight have a greater influence on postplanting survival than shell length alone; thus, we believe that there is a need for similar comparative studies to determine the generality of this relationship in other clam species.

Planting orientation and drainage effects

We found that the probability of survival increased as the angle at which a juvenile geoduck was planted approached 0° (i.e., siphon pointed up and perpendicular to the sediment–surface interface). Survival also increased incrementally among the three treatments, with individuals planted in the inverted (180°) treatment having a 16.6% reduction in mean survival from the horizontal (90°) treatment (34.1% compared to 50.7%, respectively) and a 34.4% reduction in mean survival from the upright (0°) treatment (68.5%; Figure 2). This result was expected, as we predicted that geoducks planted with their siphons pointed away from the surface would need to turn themselves so that the siphon is pointed directly toward the sediment–surface interface to feed and respire, and therefore survival would be inversely correlated with the angle between the siphon and sediment–surface interface at planting. Although we are not aware of another study that has examined planting orientation in juvenile geoducks, our findings are generally supported by Lochead et al. (2012), who found that wild juvenile geoducks can escape burial after natural anastrophic sedimentation events. Taken together with our findings, these results support the ability of juvenile geoducks to overcome disturbed or newly settled sediments to reach the sediment–water interface.

During the experiment, we discovered that several containers had water flowing through the sediment and out the bottom of the container, creating a “high-drainage” effect. Juveniles planted in these high-drainage containers had significantly increased survivorship compared to those planted in low-drainage containers, and planting orientation had no significant effect on survival in high-drainage containers (Table 3). These results may be explained by increased water flow through the full depth of the container, delivering oxygen and nutrients to geoducks regardless of their proximity to the sediment–surface interface and thereby increasing survival relative to low-drainage conditions.

Under rationed or suboptimal food regimes, geoducks appear to have mixed responses that may be influenced by size. In one study on mature geoducks, there were no effects of food rationing on survival or condition over a period of 52 d (Marshall, McKinley, & Pearce, 2014). However, in a study of larval geoducks by the same group of authors, there were significant detrimental effects of food rationing after 17 d (Marshall, Pearce, & McKinley, 2014). In juvenile geoducks, there is evidence that modifying available nutrition to suboptimal conditions can significantly impede growth (Arney et al., 2015) and that

decreasing mesh sizes during outplanting (a proxy for flow) negatively impacts juvenile geoduck growth (Pearce et al., 2019).

Determining the predominant source of mortality in planted juvenile geoducks would involve an in situ comparison of oxygen and nutrient concentrations that is beyond the scope of this study. Regardless of the cause, our findings align with other research showing that clam planting depth can be a source of mortality and that regular access to flowing, oxygenated seawater is an important factor in postplanting survival (Haider et al., 2018; Le et al., 2016; Long et al., 2008; Saloom & Scot Duncan, 2005; Taylor & Eggleston, 2000). This is illustrated by the difference in mean survival between the high- and low-drainage conditions in our study.

Conclusion

To our knowledge, this study is the first analysis of how planting orientation and weight-based size affects mortality in juvenile geoducks. As a whole, the findings of this study suggest that juvenile survival rates may be improved by planting individuals upright and/or planting larger individuals. Our results also demonstrate that juvenile geoducks may be able to reorient themselves and move to the surface even if buried at non upright angles. However, the ability of geoducks to reorient themselves is likely dependent on multiple factors, including body size. In particular, weight metrics of size (e.g., wet weight and condition), which are not currently in widespread use by the industry, appear to be better than shell length when predicting juvenile outplanting survival. We suggest that aquaculturists may maximize survivorship of seeded juvenile geoducks by ensuring that they are planted with their siphons oriented toward the surface and/or are grown as large as possible prior to outplanting.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *North American Journal of Aquaculture* online.

DATA AVAILABILITY

Data that support the findings of this study are available from the corresponding authors upon reasonable request.

ETHICS STATEMENT

There were no ethical guidelines applicable to this study.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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