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Canadian Science Advisory Secretariat (CSAS)

Research Document 2013/001

Pacific Region

Assessing potential benthic habitat impacts of small-scale, intertidal aquaculture of the geoduck clam (*Panopea generosa*)

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May 2013

Canada

Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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Published by:

Fisheries and Oceans Canada
Canadian Science Advisory Secretariat
200 Kent Street
Ottawa ON K1A 0E6

http://www.dfo-mpo.gc.ca/csas-sccs/
csas-sccs@dfo-mpo.gc.ca

ISSN 1919-5044

Correct citation for this publication:

Sauchyn, L., Pearce, C.M., Blackburn, J., Keddy, L., and Williams, S. 2013. Assessing potential benthic habitat impacts of small-scale, intertidal aquaculture of the geoduck clam (*Panopea generosa*). DFO Can. Sci. Advis. Sec. Res. Doc. 2013/001. vi + 34 p.

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ABSTRACT

The geoduck clam (*Panopea generosa*) is the largest burrowing clam in the world, adults living up to a metre below the sediment surface. In order to extract them, harvesters use high-volume water hoses to liquefy the surrounding sediment. High-density culture of clams and/or harvesting to a depth of a metre or slightly more could have profound effects on the local benthic environment, but little research has examined the possibility. We seeded a small-scale (3 x 20 m) intertidal plot at 0.5 m above chart datum with juvenile clams at a commercial density and harvested them a year later using industry-standard techniques. We took sediment samples within the harvest zone (0 m) and at varying distances (5, 10, 25, 50 m) along three transects (onshore, parallel to shore, and offshore) from the area of impact at various times (ranging from a month prior to seed out-planting through to 12 months post-harvest). We examined various sediment qualities (*i.e.* grain size, percent organics, total carbon, total nitrogen, sulphide concentration, and redox) as well as infaunal diversity and quantity. Results showed that many of the measured variables were not significantly negatively affected by either the culture or harvesting processes. Those that were affected include the following. The silt and clay fraction of the sediment increased significantly immediately after (1 day) harvesting, but only within the culture plot (0 m) and the impact was short-lived, returning to baseline values within 123 days after harvesting. The sulphide concentration decreased significantly after out-planting at distances up to 25 m from the culture plot, but the values remained within the normal to oxic zones (described in Wildish et al. 1999), indicating little to no ecological impact. There was a significant increase in total carbon and redox potential 123 days after harvesting. These changes, however, were not seen 1 day after harvest and they occurred at all distances along all transects, suggesting that they were likely due to an external event, not the harvest *per se*. In addition, the variations in total carbon and redox were not great enough to have significant ecological implications. There was a lack of seasonal increase in infaunal abundance and richness after harvesting, but only in the harvest zone (0 m) and not at 10 m. The study, unfortunately, cannot assess the rate of recovery of the infaunal community after harvesting due to the subsequent seasonal decline in abundance and richness and lack of long-term sampling. Although there were few ecologically significant, long-term impacts of small-scale, short-term intertidal geoduck culture/harvest in the present study, changes in habitat, size of the culture plot, frequency of culture, and seasonal timing of out-planting and harvest may alter the degree of impact on, and rate of recovery of, the marine environment. The interpretation of the results of the study should be used with caution until further research (currently underway) validates findings for larger-scale operations and over a broader range of potential ecological indicators.

Évaluation des effets potentiels sur l'habitat benthique de l'aquaculture à petite échelle en zone intertidale de la panope du Pacifique (*Panopea generosa*)

RÉSUMÉ

La panope du Pacifique (*Panopea generosa*), est la plus grosse palourde fouisseuse du monde. Les spécimens adultes sont enfouis jusqu'à un mètre sous la surface des sédiments. Pour les extraire, les pêcheurs utilisent des tuyaux d’eau à grand débit permettant de liquéfier les sédiments environnants. La culture à forte densité de la panope du Pacifique et la récolte à un mètre de profondeur ou un peu plus pourraient avoir des répercussions importantes sur le milieu benthique local, mais cette possibilité n'a été étudié que par très peu de recherche. Nous avons ensemencé, à une densité commerciale, une parcelle relativement petite (3 x 20 m) en zone intertidale à 0,5 m au-dessus du zéro des cartes avec des panopes du Pacifique juvéniles, puis nous les avons récoltées une année plus tard en utilisant les techniques standards du secteur. Nous avons prélevé des échantillons de sédiments dans la zone de récolte (0 m) et à diverses distances (5 m, 10 m, 25 m et 50 m) le long de trois transects (côtier, parallèle à la côte et extracôtier) de la zone d’impact à différentes périodes (variant d'un mois avant l'ensemencement jusqu'à doux mois après la récolte). Nous avons examiné différentes caractéristiques de la qualité des sédiments (p. i.e.. la taille des grains, le pourcentage de matière organique, la teneur totale de carbone et d'azote, la concentration des sulfures et le potentiel redox) ainsi que la diversité et la quantité de l'endofaune. Les résultats ont démontré que bon nombre de variables mesurées n'ont pas beaucoup été affectées de façon négative et significative par la culture ou le processus de récolte. Les variables qui ont été affectées comprennent les suivantes : la fraction de limon et d'argile du sédiment, qui a augmenté de façon significative immédiatement après la récolte (un jour), mais seulement à l'intérieur de la parcelle de culture (0 m). Les effets ont été de courte durée, puisque le milieu a repris ses valeurs de référence dans les 123 jours après la récolte. La concentration des sulfures a diminué de façon significative après l'ensemencement à des distances jusqu'à 25 m de la parcelle de culture, mais les valeurs sont demeurées dans la normale des zones oxiques (décrites dans Wildish et al. 1999), ce qui indique qu'il y a eu peu ou pas de répercussions écologiques. Il y a eu une augmentation significative de la teneur totale en carbone et du potentiel redox 123 jours après la récolte. Cependant, ces changements n'ont pas été observés un jour après la récolte, et sont intervenus à toutes les distances le long de tous les transects, ce qui pourrait signifier qu'ils étaient probablement attribuables à un événement externe, et non à la récolte en soi. De plus, les variations de la teneur totale en carbone et du potentiel redox n'étaient pas assez importantes pour avoir des répercussions écologiques considérables. Il y avait un manque l'abondance et la richesse saisonnières de l'endofaune n’ont pas augmenté après la récolte, mais seulement dans la zone de récolte (0 m) et non à 10 m. Malheureusement, l'étude n'a pas permis d'évaluer le taux de rétablissement de la communauté endofaunique après la récolte en raison de la diminution saisonnière de l'abondance et la richesse, et du manque de prélèvement d'échantillons à long terme. Même si la culture et la récolte intertidales de panopes du Pacifique à court terme et à petite échelle a eu peu d'effets importants à long terme sur le plan écologique dans le cadre de cette étude, les changements d'habitat, de taille de la parcelle de culture, de fréquence de la culture et de chronologie saisonnière de l'ensemencement et de la récolte peuvent modifier les répercussions sur le milieu marin et sur son taux de rétablissement. L'interprétation des résultats de l'étude doit être utilisée avec prudence jusqu'à ce que des recherches plus poussées (qui sont en cours) valident les constatations portant sur des activités à plus grande échelle et sur un plus vaste éventail d'indicateurs écologiques potentiels.

INTRODUCTION

The Pacific geoduck clam (*Panopea generosa*) is the most valuable dive fishery in British Columbia (BC), Canada and Washington (WA), USA. In BC, from 2004 to 2008, the fishery's average total landing was approximately 1.6 million kg year^{-1} and average total export value was CA$39 million year^{-1} (DFO 2011). Over the same period in WA, the wild fishery averaged about 2.1 million kg year^{-1} worth US$22.5 million year^{-1} (Washington Department of Fish and Wildlife, unpublished data). Since the early 1990s, there has been considerable interest in geoduck enhancement and culture as a potentially highly successful new industry in BC (Heath 2005). In response to the widespread interest, geoduck broodstock has been collected and juvenile seed successfully produced. In 2005, five subtidal geoduck culture sites were selected and are currently under tenure with the BC Provincial Government (BC Ministry of Agriculture). There are currently no intertidal geoduck tenures in the province. In 2010 in BC, 51,700 kg of cultured geoduck were harvested, worth approximately CA$1.1 million (BC Ministry of Agriculture statistics). In WA, subtidal geoduck enhancement has been active since 1991 and commercial subtidal culture since 1996 (Beattie 1992). Unlike BC, WA has begun to culture geoduck clams in the intertidal (with the first harvest in 2001) and produced 613,000 kg of clams worth US$18.5 million in 2010 (Washington Department of Fish and Wildlife, unpublished data). Despite widespread interest in geoduck culture in BC there is little known on the ecology or biology of this species and especially little is known on the potential impacts of subtidal or intertidal culture and harvest on the marine environment. To date, other than a review by Dumbauld et al. (2009), no peer-reviewed studies have been published on the potential impacts of geoduck culture and harvest.

Intertidal geoduck clam culture involves out-planting hatchery-produced seed, growing out the geoducks for a minimum of 5–8 years, and harvesting them using a high-volume water jet (or 'stinger', in industry parlance). Initially, several hatchery-produced seed (shell length: 12–20 mm) are placed in PVC tubes (diameter: 10–15 cm, length: 30 cm) that have been imbedded in the sediment. The tubes prevent the seed from drying at low tide and help to reduce predation (Beattie 1992), increasing geoduck survival from less than 1% to 30–40% (Beattie and Blake 1999). After 1 to 2 years, the tubes are removed and market-size geoducks (shell length: 15 cm or greater) are harvested 5 to 6 years after out-planting (sometimes longer, depending on the environment). The geoducks are harvested using a high-volume water jet that liquefies the sediment around the clam, allowing it to be removed by the harvester. Adult geoducks may be buried to a depth of 1 m and sediment liquefaction may occur down to such depths. They may be harvested by a point-source technique where individual clams are harvested one by one in isolation of each other (technique used in the wild fishery where clam densities are lower) or a swath technique where the entire geoduck plot is disturbed (technique typically used in aquaculture due to higher clam densities).

Potential impacts of geoduck culture on the marine environment may be caused by three main activities: 1) change in material processes (*i.e.* filter feeding, biodeposition), 2) addition of physical structure (tubes or netting), and 3) sediment disturbance caused during out-planting and harvesting (Dumbauld et al. 2009). Filter feeding by geoducks may cause local phytoplankton depletion (less food for other infauna), a decrease in turbidity due to the removal of suspended particulate material, and the removal of larvae from the water column (as suggested by Spencer et al. 1997 and Straus et al. 2008). Geoducks may also alter nitrogen and phosphorus pools via the uptake of dissolved nutrients (Straus et al. 2008). Biodeposition may lead to an increase in the organic carbon and nitrogen content of the sediment and subsequent change in community structure, increased microbial activity, increased benthic oxygen demand, and potential anoxia (Haven and Morales-Alamo 1966, Kautsky and Evans 1987). Sedimentation of biodeposits could also alter sediment grain size. The addition of tubes may affect local hydrodynamics, increasing sedimentation rates (Spencer et al. 1997, Straus et al. 2008) and enhancing larval settlement and recruitment (Eckman 1983).

Among the several stages of culture, harvesting is likely to have the greatest impact on the marine environment. During harvesting, sediment is disturbed to a depth of approximately 1 m and re-suspended, with the potential loss of fine sediment and organic matter and subsequent deposition at some distance from the harvest area (Short and Walton 1992, Palazzi et al. 2001). Disturbance of the sediment during harvesting may also cause the release of nutrients and dissolved organic matter to the overlying water column (Straus et al. 2008), exposure of anoxic sediment, and oxygenation of sediment pore water (Palazzi et al. 2001, Straus et al. 2008). Finally, the depression left behind after harvesting may promote deposition of organic and inorganic matter, larvae, and adult and juvenile fauna (Nowell and Jumars 1984, Savidge and Taghon 1988). The infaunal community may also be impacted during harvesting by damage (especially to soft-bodied organisms and polychaete tubes); burial, removal, suspension, and loss to currents; and exposure to predation (Goodwin 1978, Breen and Shields 1983, Straus et al. 2008). The sediment plumes generated during harvesting may also impact egg and larval development (Davis 1960, Davis and Hidu 1969).

The objective of the present study was to assess the potential benthic impacts of intertidal geoduck culture from out-planting of seed, over 1 year of grow out and up to 6 months after harvesting. The study was conducted on a relatively small-scale (*i.e.* 3 x 20 m plot), but used industry-standard techniques (see Methods below) for seeding and harvesting. Benthic samples were taken within the area of culture/harvest and at various distances (maximum: 50 m) from the plot in order to determine the spatial extent of impact. We examined changes in sediment grain size, organic matter, organic carbon content, nitrogen content, sulphide levels, and redox potential to assess potential impacts of geoduck culture and harvest on sediment physics and chemistry. We also examined patterns in the abundance, richness, evenness, and diversity of infauna to assess potential impacts on the infaunal community. While previous internal reports in BC (Breen and Shields 1983) and WA (Goodwin 1978, Short and Walton 1992, Cain and Bradbury 1996, Bradbury 1999, Palazzi et al. 2001) have addressed the impact of subtidal geoduck harvesting in the commercial fishery, there has been no study of the impacts of any stage of intertidal geoduck culture on the marine environment, despite current intertidal culture in WA and widespread interest in BC.

METHODS

EXPERIMENTAL DESIGN

To investigate the impact of intertidal geoduck clam culture on the marine environment, we conducted a 2-year farming study at Nanoose Bay (49°16.0’N, 124°11.2’W), BC. This bay (width: 1.4 km, length: 3.4 km) is situated on the east coast of Vancouver Island and opens to the Strait of Georgia to the east. The dominant northwest and southeast winds run the length of the bay. Cross winds are rare. The average depth of the bay is 18 m, with a maximum depth near the mouth of 48 m. This study was conducted on the extensive, gradually-sloping sandflat at the western end of the bay (Fig. 1).

On 22 July 2005, hatchery-produced geoduck seed were hand planted in 240 PVC tubes in a 3 x 20 m plot, located at 0.5 m above chart datum. These tubes were pushed into the beach sediment by hand and remained in place until harvest one year later. These tubes were covered individually with plastic mesh (for predator protection) with 0.5 m spacing between them and 2 seed per tube. Average shell length and wet weight of the juvenile clams at out-plant were 29.6 ± 0.2 mm (n=480) and 9.8 ± 0.2 g (n=480), respectively. One year later, on 11 July 2006, the geoducks were hand dug and the entire plot (60 m^2) was 'harvested' (via swath-harvest technique) to a depth of ~1 m using a high-volume (maximum pressure: 40–45 PSI) water jet produced by a Honda WH29 pump. At this time the clams were 46.5 ± 0.4 mm (n=215) shell length and 36.6 ± 1.1 g (n=223) wet weight (average survival over the 1 year: 47.7 ± 2.5%). Although the geoducks were obviously not market size (typically about 1 kg) after a single year of growth, the plot was harvested as if they were adults. Harvesting was done while the plot was exposed during a low tide. Benthic sediment samples were collected 32 days prior to out-planting; 25, 118, 191, 311, and 353 days after out-planting; and 1, 123, and 191 days after harvesting (Table 1). On each date, samples were collected at 0, 5, 10, 25, and 50 m along transects running onshore (shallow), parallel to shore in a north-east direction (parallel), and offshore (deep) from the plot (Fig. 2). The 0-m sampling station was common to all transects and located 1.5 m within the north-eastern side of the plot. All other distances were measured from this 0-m station (Fig. 2). The 25- and 50-m sampling stations along the shallow transect were located in an eelgrass bed, as was the 50-m sampling station on the parallel transect.

SEDIMENT ANALYSIS

To determine the organic matter content and size distribution of the surface-layer sediment, 3 replicate 2-cm deep surface scrapes were collected. The sediment was taken to the laboratory and immediately frozen at -20°C. Prior to analysis, the samples were defrosted in an incubator (8–10°C) and homogenized. Approximately 50 g wet weight of sediment from each replicate sample was transferred to pre-weighed, pre-combusted, acid-washed crucibles and dried at 60–70°C for 48–72 hours (to constant weight) to determine the sediment dry weight. The sediment was then combusted in a muffle furnace at 550°C for 6 hours to determine the ash weight. The organic matter content (% dry weight) was calculated as:

$$\%\ \text{organic matter} = 100 - [\text{ash weight (g)} / \text{dry weight (g)} \times 100]$$

The ashed sediment from each sample was sorted in a sediment shaker for 10 minutes using nested 20-cm diameter sieves and classified according to the Wentworth (1922) scale: gravel (>2000 µm), very coarse sand (2000–1000 µm), coarse sand (1000–500 µm), medium sand (500–250 µm), fine sand (250–125 µm), very fine sand (125–63 µm), silt and clay (<63 µm). The median grain size was calculated following Krumbein and Sloss (1963) and the silt and clay content as a percent of the total ash weight.

Three replicate sediment cores (diameter: 6.6 cm, depth: 10 cm) – sub-sampled at 2- and 4-cm depth using 10-ml plastic syringes (cut off at the ends) – were collected to determine the total carbon and nitrogen content at 2-cm depth and the redox potential and sulphide content at 2- and 4-cm depths. The syringes were capped air tight in the field and taken to the laboratory on ice, where 5 ml of sediment from the 2-cm samples were immediately frozen at -20°C and later analyzed for total carbon and total nitrogen content by flash combustion in a Carlo Erba NA-1500 CHN analyzer. The total carbon and nitrogen contents were expressed as a percent of the sample dry weight. The remaining sediment from the 2- and 4-cm deep samples were stored air-tight in the dark on ice and analyzed within 24 hours of collection for redox potential and sulphide content. Prior to analysis, the samples were removed from the ice and left in the dark at room temperature (20°C) for 1 hour. To determine the redox potential (E_0, mV), 5 ml of sediment were transferred to a glass vial and a redox electrode (attached to a millivolt meter) was inserted. The redox potential was adjusted as relative to the normal hydrogen electrode (E_{NHE}, mV) using the formula:

$$E_{NHE} = E_0 + C$$

where C is the potential (mV) of the reference electrode normal to the hydrogen ion, which is equal to 204 at 20^{o}C (Wildish et al. 1999). To determine the sulphide content (µM), an additional 5 ml of sediment were transferred to another glass vial and mixed with 5 ml of sulphide anti-oxidant buffer (SAOB). The potential (mV) of the solution was determined using a platinum electrode and converted to the sulphide content using sodium sulphide (Na_2S) as a standard. Results of sulphide and redox measurements are discussed in terms of the environmental levels established by Wildish et al. (1999): “oxic a” (sulphide = <300 µM, redox = >+100 mV); “oxic b” (sulphide = 300–1300 µM, redox = 0–100 mV); “hypoxic” (sulphide = 1300–6000 µM, redox = -100–0 mV); “anoxic” (sulphide = >6000 µM, redox = <-100 mV).

INFAUNAL ANALYSIS

To characterize the infaunal community before, during, and after geoduck culture, 3 replicate sediment cores (diameter: 6.6 cm, depth: 10 cm) were collected at 0 and 10 m along the parallel transect 32 days before out-planting, 25 and 191 days after out-planting, and 1 and 191 days after harvesting (Table 1). The reason that these two particular distances were chosen for sampling was that the cost of infaunal identification limited the number of samples that could be processed and the impact was likely to be greatest closest to the culture plot (so if any effect was going to be evident, it would be seen at 0 and/or 10 m). The fauna were collected on a 0.5-mm (mesh size) brass sieve and fixed in 10% phosphate-buffered formalin. After a minimum of 7 days, the formalin was decanted and the samples rinsed and preserved in 70% ethanol. The preserved samples were then re-screened to 850 µm. Adult and juvenile nermertians, annelids, nematodes, phoronids, molluscs, arthropods, and echinoderms were counted and identified to the lowest possible taxon by the same person (an infaunal taxonomist) throughout the study. For each sampling date and distance, the infaunal abundance (number of individuals per core), species richness (number of species per core), Shannon-Weiner diversity index (H’, $\log_e$), Margalef’s species richness (d), Pielou’s evenness (J), and the abundance of the dominant phyla (number of individuals in phylum per core) were calculated.

STATISTICAL ANALYSIS

To test for an effect of geoduck culture on the benthic sediment characteristics at Nanoose Bay, we used separate analyses of variance (ANOVA) for median grain size, silt and clay, organic matter, total carbon, total nitrogen, sulphide content, and redox potential. Initially we included 3 (fixed) factors in each analysis: 1) time (sampling date, see Table 1), 2) transect (shallow, parallel, deep), and 3) distance (0, 5, 10, 25, 50 m). However, in each analysis the time and transect interaction term was significant suggesting that the benthic environment along each transect behaved in a different way. We therefore analyzed the sediment characteristics along each transect separately with 2-way ANOVAs (time and distance) for median grain size, silt and clay content, organic matter content, total carbon content, and total nitrogen content, and 3-way ANOVAs for sulphide level and redox potential (where depth was also included as a fixed factor). A significant ANOVA result was followed by a Tukey’s HSD test to determine which sampling dates or distances differed based on the dependent variable examined. The assumptions of normality and homogeneity of variance were tested using the

Shapiro-Wilk and Levene's tests, respectively. The median grain size was $\log_{10}$ transformed and the silt and clay, organic matter, total carbon, and total nitrogen contents were arcsine transformed to meet the above assumptions.

To test for an effect of geoduck farming on the infaunal community we used 2-way ANOVAs for infaunal abundance, species richness, Shannon-Weiner diversity, Margalef's species richness, Pielou's evenness, and abundance of dominant phyla with time and distance (0 and 10 m) as factors. Infaunal abundance was $\log_{10}$ transformed and the abundances of the dominant phyla were square-root transformed to meet the assumptions of homogeneity of variance and normality. A significant result was followed by a Tukey's HSD test to determine which sampling dates or distances differed, based on the dependent variable examined. Only significant ($P<0.05$) differences among dates and distances or between depths are discussed. Power analysis of the data collected in this study suggested that there was a high level of sensitivity to detect impacts of geoduck culture should they occur.

RESULTS

SEDIMENT ANALYSIS

Median Grain Size

At Nanoose Bay, 81% of the sediment was classified as coarse to fine sand. The average median grain sizes along the shallow, parallel, and deep transects were 332 ± 17 (SE) µm, 298 ± 10 µm, and 304 ± 12 µm, respectively. There was no change over time in median grain size along the shallow and parallel transects (Fig. 3a, b and Table 2). Along the deep transect, grain size peaked 191 days after out-planting due to an increase in grain size 50 m from the experimental plot (Fig. 3c, Table 2). Median grain size was also similar across all distances, except at 50 m along the parallel and deep transects.

Silt and Clay

The silt and clay content of the sediment varied over time and across distance along each transect (Fig. 4, Table 2). With all distances considered together, the change in the silt and clay content over time did not correspond to geoduck out-planting or harvesting. However, the significant time and distance interaction terms suggest different patterns of change over time at each distance. To determine if the silt and clay content varied with culture activity at any distance from the experimental plot, the significant time and distance interaction terms for each transect were assessed by Bonferroni-corrected 1-way ANOVAs ($\alpha = 0.01$) for each distance, with time as the single factor. Again at 5, 10, 25, and 50 m, the variation in the silt and clay fraction did not correspond with culture activity. In contrast, at 0 m, the silt and clay content peaked immediately (1 day) after harvesting, with a return to seasonal levels by the next sampling period (123 days) (Fig. 4). There was also a peak at 0 m after out-planting; however, it did not differ significantly from the silt and clay content before out-planting.

Organic Matter

The organic matter content varied over time and across distance along each transect (Fig. 5, Table 2). Along the shallow and parallel transects, the organic matter content was highest at 50 m, likely due to the presence of eelgrass at that distance. The difference among distances was less 353 days after out-planting and after harvesting, leading to a significant interaction term for the shallow and parallel transects. Along the deep transect, the organic matter content was highest at 10 and 25 m, particularly from 311 days after out-planting onwards. This difference was greatest 353 days after out-planting and 1 day post-harvest, again leading to a significant time and distance interaction term. Across all three transects, the organic matter content dropped significantly immediately after harvesting within the culture plot (Fig. 5).

Total Carbon

Along each transect, the total carbon content was significantly higher 123 and 191 days post-harvest compared to all other sampling dates (Fig. 6, Table 2). This increase was not seen 1 day after harvest though and was evident at all sampling distances, both observations suggesting that increased carbon content after harvesting was not directly linked to the harvest process *per se*. Across all sampling dates, total carbon content was highest at 50 m along the shallow and parallel transects, again likely due to the presence of eelgrass beds.

Total Nitrogen

Like the organic matter content of the sediment, the total nitrogen content varied over time, but not in relation to culture activity (Fig. 7, Table 2). Rather, along the shallow and parallel transects, the total nitrogen content appeared to vary with season. Total nitrogen was lowest in the winter (118 and 191 days after out-planting, and 123 and 191 days post-harvest) and highest in the summer (25 and 353 days after out-planting, and 1 day post-harvest). Like organic matter and total carbon content, total nitrogen content was highest at 50 m along the shallow and parallel transects. The difference among distances was less 123 and 191 days post-harvest leading to a significant time and distance interaction term for both shallow and parallel transects. Along the deep transect, the total nitrogen content was highest at 25 m; however, not at every sampling date, again leading to a significant time and distance interaction.

Sulphide Content

The sulphide content of the sediment was highest before out-planting along all 3 transects (Fig. 8, 9 and Table 2). Along the shallow transect, the sulphide content was also significantly higher 25 days after out-planting compared to 191 days after out-planting and 123 and 191 days post-harvest. To determine if the sulphide content decreased over time at each distance from the experimental plot, the significant time and distance interaction terms for the shallow and deep transects were assessed by Bonferroni-corrected ANOVAs (α = 0.01) for each distance, with time as the single factor. Along the shallow transect, the sulphide content was significantly higher before out-planting compared to all subsequent dates at 0, 5, 10, and 25 m. At 50 m, the sulphide content was higher before out-planting compared to 191 days post-harvest and higher 25 days after out-planting compared to 123 and 191 days post-harvest. Along the deep transect, the sulphide content was significantly higher before out-planting compared to all other dates at 0, 5, and 10 m. In contrast, at 25 and 50 m, there was no significant decrease in sulphide content over time. Overall, sulphide content was highest at 50 m along the shallow transect and at 0, 5, and 10 m along the deep transect.

Of the 2 depths sampled, the relative sulphide content was higher at 4 cm compared to 2 cm along all three transects; significantly higher along the shallow and deep transects and marginally non-significant (P = 0.052) along the parallel transect (Table 2). To determine if the sulphide content decreased at both depths over time, the significant time and depth interaction terms for the shallow and deep transects were followed by Bonferroni-corrected ANOVAs (α =

0.025) for each depth, again with time as a factor. At 4 cm along the shallow transect, the sulphide content was highest before out-planting and higher 25 days after out-planting compared to 123 and 191 days post-harvest (Fig. 9). The sulphide content was higher before out-planting compared to 191 days after out-planting and all subsequent dates at 2-cm depth along the shallow transect (Fig. 8). Along the deep transect, the sulphide content was higher before out-planting compared to all other dates at both 2- and 4-cm depths (Fig. 8, 9).

Redox Potential

The redox potential of the sediment at 2- and 4-cm depths was highest 123 and 191 days post-harvest along all 3 transects (Fig. 10, 11 and Table 2). There was no time and distance interaction for any transect (Table 2), suggesting that changes in the redox potential occurred at all distances up to 50 m from the plot. Overall, the redox potential was lowest at 50 m along the shallow transect and highest at 0 m along the parallel and deep transects. Along all transects the redox potential was consistently higher at 2-cm depth compared to the 4-cm one.

INFAUNAL ANALYSIS

Infaunal abundance and both measures of species richness were highest immediately after out-planting and harvesting. Although these measures appeared to vary with geoduck culture activity, they also varied with season (higher in the summer, which is when seeding and harvesting occurred). All three measures were highest in August 2005 (25 days after out-planting), lowest in January 2006 and 2007 (191 days after out-planting and 191 days post-harvest), and intermediate in June 2005 and July 2006 (before out-planting and 1 day post-harvest) (Fig. 12a-c). There was also a significant time and distance interaction term for abundance (Table 3). Bonferroni-corrected ANOVAs ($\alpha = 0.025$) for both distances revealed that the significant interaction term was due to the lack of increase in abundance at 0 m immediately after harvesting. Pielou's evenness was significantly higher 191 days after out-planting compared to 1 day after harvesting at 10 m only, leading to a significant interaction term (Fig. 12d, Table 3). The Shannon-Weiner diversity index did not vary over time (Fig. 12e, Table 3). There was no significant difference between 0- and 10-m distances for any of the above measures (Table 3).

Similar to total infaunal abundance, the abundance of arthropods and echinoderms was highest in the summer, after out-planting and harvesting, and lower in the winter (Fig. 13a,b). For both arthropods and echinoderms there were also significant time and distance interaction terms (Table 3). Again, Bonferroni-corrected ANOVAs ($\alpha = 0.025$) for each distance revealed that the significant interaction terms were due to the absence of an increase in abundance at 0 m immediately after harvesting. Overall, arthropod abundance was higher at 10 m from the plot than at 0 m (Table 3). Annelid abundance was highest 25 days after out-planting and significantly higher at 10 compared to 0 m (Fig. 13c). The abundance of nemerteans was highest and the abundance of molluscs lowest 191 days after harvesting (Fig. 13d,e). Densities of larger infauna (> 6.6 cm diameter core), such as large clams and crabs, were not measured.

DISCUSSION

There was no change in the median sediment grain size during geoduck cultivation/harvest; however, there was an increase in the silt and clay fraction immediately after harvesting, but only within the culture plot (0 m). This is likely due to the fact that sediment liquefaction will result in larger, heavier particles sinking within the harvest hole leaving a larger percentage of smaller, lighter particles at the surface. By day 123 post-harvest, the silt and clay fraction had returned to values similar to those observed during the previous fall and winter within the 0-m plot. Studies on the impact of subtidal geoduck harvest also found no change in the median grain size of the sediment due to harvesting (Goodwin 1978, Breen and Shields 1983). However, when comparing the sediment structure directly within holes generated during harvesting to un-harvested areas, Goodwin (1978) found that the silt and clay content was lower within the holes. Subtidal geoduck harvesting generates a sediment plume, largely composed of fine material, which is carried downstream resulting in a loss of silt and clay from the harvest holes (Short and Walton 1992, Palazzi et al. 2001). Under subtidal conditions the majority of the suspended sediment settles within 1 m of the holes (Short and Walton 1992). In the intertidal, when harvesting is done with the tide out and little or no overlying water, the fine sediment likely settles even closer, resulting in an increase in the silt and clay content of the surrounding surface sediment where the 0-m samples were collected. The present study was not able to address the local spatial extent of the change in silt and clay content, as the 0-m samples were the only samples collected within the culture plot. It is possible that changes occurred to the sediment structure elsewhere within the culture plot and to a distance up to the 5-m sample locations. The change in silt and clay content was limited to within 3.5 m of the edge of the culture plot, was no longer apparent 123 days after harvesting, and was not great enough to significantly impact the median grain size (from 0.325 ± 0.006 (SE) % silt and clay before harvest to 0.764 ± 0.121 % silt and clay immediately after). In Puget Sound (WA), the re-suspension of fine sediment during subtidal harvesting is no greater than that caused by typical tidal currents and during periods of high wave action (Short and Walton 1992). This is also likely true of the high-energy intertidal sandflat in Nanoose Bay (Pearce, personal observation).

Neither the organic matter nor the total nitrogen content of the sediment varied due to geoduck out-planting or harvesting. The presence of eelgrass at 50 m along the shallow and parallel transects and natural seasonal variation caused a greater change in the organic matter and nitrogen contents than any potential change due to geoduck culture. Similarly, in Puget Sound, the presence of eelgrass had a greater impact on organic content of the sediment than out-planting geoduck (Dumbauld et al. 2009). In contrast to the organic matter and nitrogen contents, there was a significant increase in the total carbon content of the sediment after harvesting. As there was no concurrent change in the total organic content, this increase is most likely due to the addition of inorganic carbon to the upper sediment. The increase in carbon could be caused by the presence of shell fragments generated during harvest due to the damage of infauna or the mixing of inorganic carbon from deeper within the sediment (Straus et al. 2008). However, the increase in carbon content occurred at all distances up to 50 m from the plot and was not particularly evident immediately (1 day) after harvest, suggesting that an external input of inorganic carbon, such as from river-borne sediments (Burd et al. 2008a), may better account for the increase. Even with the increase, the average total carbon content remained less than 2% over the entire course of cultivation, suggesting that the total organic carbon content must have been, at most, less than 2%. This concentration of organic carbon is too low to cause anoxic conditions and negatively impact the infaunal community in sandy habitats on the east coast of Vancouver Island (Hyland et al. 2005, Burd et al. 2008a).

The sulphide content of the sediment significantly decreased after geoduck out-planting at both 2- and 4-cm depths. The decrease in sulphide was greater at distances closer to the culture plot and depths closer to the sediment surface and was likely due to the disturbance and exposure of anoxic sediment during the process of out-planting (Straus et al. 2008). However, the change in sulphide level is unlikely to have had a significant ecological impact (Hargrave et al. 2008). Even prior to out-planting the sulphide content of the sediment was very low, with an average level across all distances and transects of 162 ± 17 (SE) µM and 332 ± 44 µM at 2-

and 4-cm depths, respectively. These levels are below/near the “oxic a” zone (<300 µM) defined by Wildish et al. (1999). In addition, the variation in sediment sulphide content between non-eelgrass (0, 5, and 10 m) and eelgrass sites (25 and 50 m) along the shallow transect was as great as the decrease due to out-planting.

The redox potential of the sediment increased after harvesting (at day 123), possibly due to an increase in pore-water oxygen concentration from water forced into the sediment from the ‘stinger’ during harvesting (Fenchel and Riedl 1970, Palazzi et al. 2001). However, the increase in redox potential occurred at all distances up to 50 m from the culture plot and was not evident 1 day after harvest suggesting that, as with total carbon, the increase may have been due to a factor external to the harvesting activity. Similar to sulphide content, the change in the redox potential is unlikely to have negatively impacted the infaunal community (Pearson and Stanley 1979). Throughout the cultivation process, the average redox potential was greater than 150 mV, again above the threshold for “oxic a” conditions (100 mV) established by Wildish et al. (1999). The low sulphide content and high redox potential are characteristics of the dynamic sandy environment on the east coast of Vancouver Island (Fenchel and Riedl 1970, Burd et al. 2008b).

Like the high natural background variability in abiotic conditions, the high seasonal variability in total infaunal abundance, species richness, Margalef’s species richness, and the abundance of arthropods, echinoderms, and annelids masked potential impacts due to out-planting or harvesting. The high variability in abundance and rapid re-population of the harvested area also masked any potential impacts of subtidal geoduck harvesting on the faunal community (Goodwin 1978, Breen and Shields 1983, Cain and Bradbury 1996, Bradbury 1999). However, within the culture plot (0 m) in the present study and in Goodwin’s research, the seasonal increase appeared to be reduced by harvesting. The low infaunal abundance and species richness within the plot (compared to the 10-m distance) immediately after harvesting may be due to damage, removal and loss of infauna, or exposure of infauna to predators (Goodwin 1978, Breen and Shields 1983, Straus et al. 2008). The lack of increase in abundance of arthropods and echinoderms within the harvest plot immediately after harvesting may also suggest active avoidance by more mobile infauna during harvesting. The natural seasonal decline in abundance and species richness in the winter (191 days after harvest) and the lack of subsequent sampling during the following summer after the harvest makes it difficult to assess the degree of recovery of the infaunal community at 0 m after harvesting. In addition, we were unable to assess the impact of infauna larger than, or whose orientation within the sediment prevented them from being collected within, the sample corer (diameter: 6.6 cm, depth: 10 cm).

In the present study – with a very small-scale out-plant plot (3 x 20 m), short growout period (1-year), and a single harvest – there did not appear to be significant, long-term impacts on the benthic environment and infauna, especially in relation to the scale of natural variation. Larger-scale commercial-sized productions carried out with repetitive growout periods would have to be explored to determine the potential benthic impacts of larger-scale operations. In addition, annual variability pre-production would need to be determined to have a suitable baseline estimate. Even given the small-scale nature of the study, our results are in agreement with studies of the impact of subtidal geoduck harvesting where changes to the benthos (sediment re-suspension and loss of fines) were limited in spatial extent to the area around the harvest plot (Goodwin 1978, Short and Walton 1992) and any potential impact on macrobenthic fauna was masked by high natural variability and rapid recovery (Goodwin 1978, Breen and Shields 1983, Cain and Bradbury 1996, Bradbury 1999). In general, the impact and rate of recovery from benthic shellfish culture and harvest depend on the: 1) type of gear used (Hall and Harding 1997, Spencer et al. 1997, Collie et al. 2000, Kaiser et al. 2006); 2) habitat (Collie et al.

2000, Ferns et al. 2000, Dernie et al. 2003a, Kaiser et al. 2006, Constantino et al. 2009); 3) spatial and temporal intensity (Simenstad and Fresh 1995, Collie et al. 2000, Dernie et al. 2003b, Zajac and Whitlatch 2003, Morello et al. 2006); and 4) seasonal timing (Goodwin 1978, Kaiser et al. 1998, Spencer et al. 1998).

Benthic shellfish harvest gear that remove sediment (*e.g.* hydraulic and tractor dredges) tend to have a greater impact on the marine environment than harvest equipment that for the most part leaves sediment in place (*e.g.* hand rake, geoduck 'stinger') (Spencer et al. 1997, Kaiser et al. 2006). Dredging for cockles may cause a decrease in infaunal abundance, species richness, and density (Hall and Harding 1997, Ferns et al. 2000); an increase in median grain size; and a decrease in silt and clay (Piersma et al. 2001). Scallop dredging may lead to a decrease in infaunal abundance, density, and change in community structure (Thrush et al. 1995, Currie and Parry 1996). Finally, dredging for clams may result in a decrease in infaunal abundance, species richness, diversity, and biomass (Hall et al. 1990, Kaiser et al. 1996, Spencer et al. 1998, Tuck et al. 2000, Constantino et al. 2009); an increase in median grain size (Hall et al. 1990, Constantino et al. 2009); and a decrease in silt and clay (Tuck et al. 2000). In contrast, there is little impact (Brown and Wilson 1997, Kaiser et al. 2001, Badino et al. 2004) to no impact (Peterson et al. 1987, Boese 2002) of hand raking for cockles and Manila clams, and a limited spatial and temporal effect of intertidal and subtidal geoduck harvesting (Goodwin 1978, Breen and Shields 1983, Short and Walton 1992, Cain and Bradbury 1996, Bradbury 1999, this study).

Recovery of the benthic environment following shellfish harvesting can vary from years (Currie and Parry 1996, Spencer et al. 1998, Piersma et al. 2001), to months (Hall et al. 1990, Thrush et al. 1995, Currie and Parry 1996, Kaiser et al. 1996, Hall and Harding 1997, Ferns et al. 2000, Tuck et al. 2000), to days (Ferns et al. 2000, Tuck et al. 2000, Constantino et al. 2009). Much of the variation in the degree of initial impact and rate of recovery is related to habitat, including depth, local hydrodynamics, and sediment-size structure. Sandy, intertidal habitats, such as the sandflat in Nanoose Bay, are dynamic, high-energy environments where the resident fauna are adapted to frequent disturbance and high levels of natural variability, such that the impacts of harvesting tend to be limited and recovery rapid, especially compared to muddy or biogenic habitats (Hall and Harding 1997, Ferns et al. 2000, Dernie et al. 2003a). In South Wales, cockle dredging in mud caused a greater decrease in infaunal abundance and diversity than in sand and recovery was much longer, greater than 174 days compared to 14 days in sand (Ferns et al. 2000). Dernie et al. (2003a) also found that pits (1 x 4 m) refilled twice as fast in sand (105 days) than in mud or muddy sand (213 days). Infauna in sandy environments tend to be small, motile, and often have more than one recruitment event per year, favouring both active immigration of juveniles and adults and larval settlement in disturbed areas (Savidge and Taghon 1988, Hall and Harding 1997, Shull 1997). Local hydrodynamic conditions in sandy environments also favour passive immigration of juvenile and adult fauna into disturbed areas through bed-load transport, by currents in the overlying water column, and with eroding sediment (Grant 1981, Savidge and Taghon 1988). High levels of active and passive immigration, such as in sandy habitats, lead to more rapid recovery in disturbed patches (Grant 1981, Savidge and Taghon 1988, Shull 1997). The degree and nature of impact and recovery following geoduck culture may, therefore, be more severe in more stable mud or biogenic habitats.

Eelgrass (*Zostera marina* and *Z. japonica*) occurs with geoducks in both shallow subtidal and intertidal sand habitats and could be affected by geoduck culture/harvest. While eelgrass beds did occur near our research plot (within 25 m on the shallow transect and 50 m on the parallel transect) we did not examine potential impacts on the vegetation other than mapping the edge of the beds and observing no obvious change in this attribute over the course of the research. Geoduck culture may negatively impact nearby seagrass beds through shading by addition of physical structure and increased turbidity, altered patterns of re-suspension and sedimentation due to biodeposition and harvesting, and direct physical disturbance during out-planting or harvesting (Everett et al. 1995). In Puget Sound, out-planting geoduck in eelgrass beds reduced eelgrass density by 30% and harvesting reduced shoot density by 70% (Dumbauld et al. 2009). Hand raking for Manila clams in an eelgrass bed in South Carolina reduced eelgrass biomass by 25%; however, the eelgrass recovered within the following year (Peterson et al. 1987). Alternatively, geoducks could actually strengthen seagrass production by: 1) increasing light availability via filtering of suspended particles in the water column (Newell and Koch 2004); 2) enriching the water column or sediment with nutrients contained in faeces or pseudofaeces, thereby releasing the plants from nutrient limitation (Reusch et al. 1994, Peterson and Heck 2001b, Newell et al. 2002); or 3) decreasing epiphyte levels on seagrass blades via direct filtering of epiphyte propagules or providing suitable refuge for epiphyte grazers (Peterson and Heck 2001a, Duffy et al. 2001). In subsequent larger-scale intertidal (15 x 30 m plot) and subtidal (60 x 100 m plot) studies, we have found no significant negative impacts of 'stinger' harvesting on nearby (within 5 m) eelgrass beds in terms of bed boundaries, biomass, shoot density, or shoot length (Pearce, personal observation).

Spatial and temporal intensity and the seasonal timing of culture activities also may influence the degree of impact and rate of recovery. Large-scale disturbances tend to increase recovery time by limiting the extent of active and passive immigration into disturbed areas (Savidge and Taghon 1988, Zajac and Whitlatch 2003). On the same intertidal sandflat, the infaunal community recovered in 20 days following a 100-cm^2 disturbance while the community required 4 months to recover following a 1000-cm^2 disturbance (Shull 1997, Zajac and Whitlatch 2003). The area of disturbance during commercial geoduck cultivation will likely be larger than the research plot (3 x 20 m) used in the present study, so scale effects need to be considered. However, ongoing research at a larger scale (intertidal: 15 x 30 m, subtidal: 60 x 100 m) is confirming what we have shown in the present study: effects of geoduck harvesting on the benthic environment (including sediment characteristics, infauna, nearby eelgrass beds) are minor to non-existent (Pearce, personal observation).

More frequent disturbance will also cause greater impact on the environment by limiting the time for recovery. For example, increasing the frequency of clam dredging in the Adriatic Sea led to a greater decrease in infaunal abundance, biomass, diversity, and species evenness (Morello et al. 2006). Repeated geoduck culture at the same site may cause a greater impact on the marine environment than found in the present study. Finally, timing of culture activities is also important in determining impact and recovery, especially in relation to larval recruitment, growth, and natural disturbance regimes (Goodwin 1978, Kaiser et al. 1998, Spencer et al. 1998). In our study, both geoduck out-planting and harvesting occurred during the summer months when infaunal abundance and richness were high, which may have dampened the impact of culture on the infaunal community (Goodwin 1978). However, harvesting did appear to limit the seasonal increase in abundance within the culture plot which may influence the structure of the infaunal community in subsequent years. Further research is required to examine the potential impacts of culture/harvest scale, timing, and frequency on the benthic environment.

SUMMARY AND CONCLUSIONS

During small-scale (3 x 20 m) and short-term (1-year) intertidal geoduck culture/harvest there was an accumulation of silt and clay and a reduction in infaunal abundance and richness within the culture plot immediately after harvesting. There was also a decrease in the sulphide content after out-planting and an increase in total carbon content and redox potential after harvesting. Changes in the silt and clay content and infaunal community were limited to the area directly around the harvest zone and recovery of the sediment size structure was rapid (within 123 days). Due to the seasonal decline in infaunal abundance and richness post-harvest and lack of long-term sampling it is difficult to assess the rate of recovery of the infaunal community after harvesting. Increases in total carbon content and redox were not evident immediately after harvesting (not seen until 123 days post-harvest) and occurred at all sample distances (up to 50 m), suggesting that the variation was not harvest related. In addition, the magnitude of change in sulphide content, total carbon content, and redox potential was not great enough (and/or in the right direction) to have significant ecological implications.

Although there were few ecologically significant, long-term impacts of intertidal geoduck culture in this study, changes in habitat, size of the culture plot, frequency of culture, and seasonal timing of out-planting and harvest may alter the degree of impact on, and rate of recovery of, the marine environment. Larger-scale research is required to examine potential effects due to commercial-scale, more frequent culture/harvest events occurring at various times of the year. Additional work would include a higher-power experimental design to evaluate the potential effects of anti-predator tubes and nets (which provide structure and could lead to changes in abundance and diversity of some organisms) and harvesting. Potential impacts of culture/harvest on local sensitive aquatic vegetation (*e.g.* eelgrass), water column properties, and larger infaunal organisms should be examined.

ADVICE

The following question was posed by Fishery and Aquaculture Management in the official Request for Science Information and/or Advice: “*Does harvesting geoduck in the intertidal or subtidal marine environment have a significant environmental impact?”* The current small-scale (3 x 20 m) and short-term (1-year) intertidal study revealed few ecologically-significant effects of intertidal geoduck culture/harvest. There were two notable exceptions. The silt and clay fraction of the sediment increased significantly immediately after (1 day) harvesting, but only within the culture plot (0 m) and the impact was short-lived, sediment structure returning to baseline values within 123 days after harvesting. There was also a lack of seasonal increase in infaunal abundance and richness after harvesting in the harvest zone (0 m), an increase evident at 10 m outside the disturbed plot. The study, unfortunately, cannot assess the rate of recovery of the infaunal community after harvesting due to the subsequent seasonal decline in abundance and richness and lack of long-term sampling. These two impacts were restricted to the area of harvest and the change in sediment composition was relatively short-lived (123 days). It must be noted, however, that changes in habitat, size of the culture/harvest plot, frequency of culture, and seasonal timing of out-planting and harvest may alter the degree of impact on, and rate of recovery of, the marine environment. Further research is required to examine potential culture/harvest effects due to commercial-scale, more frequent culture/harvest events occurring at various times of the year in varying environments.

ACKNOWLEDGEMENTS

Funding for this project was provided by the British Columbia Ministry of Agriculture, the British Columbia Ministry of Forests/British Columbia Timber Sales, the Aquaculture Collaborative Research and Development Program of Fisheries and Oceans Canada, and Manatee Holdings Ltd. Total carbon and total nitrogen analyses were performed by Dr. Maureen Soon (University of British Columbia, Department of Earth and Ocean Sciences) and infaunal identification and enumeration was done by Sandy Lipovsky (Columbia Science). The following people (in alphabetical order) provided technical assistance in the field and/or laboratory: YuXin An, Damien Barnes, Anya Dunham, Caroline Fox, Cristina Gruending, March Klaver, Rob Marshall, Chanelle Mathieu, Debbie Paltzat, Ryan Sherman, and Laura Skinner.

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APPENDIX 1: TABLES AND FIGURES

Table 1. Stage of geoduck farming and days from out-plant or harvest for each sampling date at Nanoose Bay, British Columbia.

Sampling date	Stage of farming	Days from out-plant or harvest
20 June 2005*	before out-planting	-32
16 August 2005*	after out-planting	25
17 November 2005	after out-planting	118
29 January 2006*	after out-planting	191
29 May 2006	after out-planting	311
10 July 2006	after out-planting	353
12 July 2006*	after harvesting	1
5 November 2006	after harvesting	123
18 January 2007*	after harvesting	191

* Sampling dates at which infaunal samples were collected.

Table 2. Results of analyses of variance of the effects of different stages of intertidal geoduck culture (time) on the benthic environment at five distances from the culture plot (0, 5, 10, 25, 50 m) along three transects (shallow, parallel, deep) at Nanoose Bay, British Columbia. Significant results are indicated in bold.

Variable	Transect	Source	df	MS	*F*	*P*
Median grain size	Shallow	Time	8	0.413	0.727	0.667
		Distance	4	1.086	1.911	0.115
		Time x Distance	32	0.284	0.500	0.986
		Error	90	0.568		
	Parallel	Time	8	0.027	1.709	0.107
		Distance	4	0.122	7.657	**<0.001**
		Time x Distance	32	0.027	1.699	**0.027**
		Error	90	0.016		
	Deep	Time	8	0.019	4.085	**<0.001**
		Distance	4	0.102	1.761	**<0.001**
		Time x Distance	32	0.013	2.790	**<0.001**
		Error	90	0.005		
Silt and clay	Shallow	Time	8	0.003	34.659	**<0.001**
		Distance	4	0.041	471.741	**<0.001**
		Time x Distance	32	0.001	7.313	**<0.001**
		Error	90	<0.001		
	Parallel	Time	8	0.002	35.328	**<0.001**
		Distance	4	0.010	140.483	**<0.001**
		Time x Distance	32	<0.001	5.273	**<0.001**
		Error	90	<0.001		
	Deep	Time	8	0.002	35.715	**<0.001**
		Distance	4	0.002	32.715	**<0.001**
		Time x Distance	32	<0.001	7.042	**<0.001**
		Error	90	<0.001		
Organic matter	Shallow	Time	8	<0.001	8.447	**<0.001**
		Distance	4	0.003	59.893	**<0.001**
		Time x Distance	32	<0.001	5.489	**<0.001**
		Error	90	<0.001		
	Parallel	Time	8	<0.001	5.067	**<0.001**
		Distance	4	0.002	45.332	**<0.001**
		Time x Distance	32	<0.001	3.740	**<0.001**
		Error	90	<0.001		
	Deep	Time	8	0.001	43.279	**<0.001**
		Distance	4	0.001	37.485	**<0.001**
		Time x Distance	32	<0.001	7.256	**<0.001**
		Error	90	<0.001		
Total carbon	Shallow	Time	8	0.007	39.963	**<0.001**
		Distance	4	0.001	8.880	**<0.001**
		Time x Distance	32	<0.001	1.255	0.201
		Error	90	<0.001		
	Parallel	Time	8	0.008	38.198	**<0.001**
		Distance	4	0.002	8.290	**<0.001**
		Time x Distance	32	<0.001	1.100	0.354
		Error	90	<0.001		
	Deep	Time	8	0.012	37.886	**<0.001**
		Distance	4	<0.001	0.982	0.422
		Time x Distance	32	<0.001	0.552	0.970
		Error	90	<0.001		

Variable	Transect	Source	df	MS	*F*	*P*
Total nitrogen	Shallow	Time	8	<0.001	14.716	**<0.001**
		Distance	4	<0.001	27.417	**<0.001**
		Time x Distance	32	<0.001	2.876	**<0.001**
		Error	90	<0.001		
	Parallel	Time	8	<0.001	10.941	**<0.001**
		Distance	4	<0.001	31.201	**<0.001**
		Time x Distance	32	<0.001	2.354	**0.001**
		Error	90	<0.001		
	Deep	Time	8	<0.001	15.665	**<0.001**
		Distance	4	<0.001	49.230	**<0.001**
		Time x Distance	32	<0.001	3.009	**<0.001**
		Error	90	<0.001		
Sulphide content	Shallow	Time	8	0.234	21.432	**<0.001**
		Distance	4	0.168	15.396	**<0.001**
		Depth	1	0.172	15.738	**<0.001**
		Time x Distance	32	0.019	1.723	**0.013**
		Time x Depth	8	0.044	4.047	**<0.001**
		Distance x Depth	4	0.005	0.497	0.738
		Error	200	0.011		
	Parallel	Time	8	0.196	20.935	**<0.001**
		Distance	4	0.019	2.000	0.096
		Depth	1	0.036	3.813	0.052
		Time x Distance	32	0.010	1.053	0.399
		Time x Depth	8	0.019	2.004	0.051
		Distance x Depth	4	0.010	1.066	0.374
		Error	201	0.009		
	Deep	Time	8	0.082	26.019	**<0.001**
		Distance	4	0.038	11.995	**<0.001**
		Depth	1	0.021	6.583	**0.011**
		Time x Distance	32	0.019	5.917	**<0.001**
		Time x Depth	8	0.010	3.307	**0.001**
		Distance x Depth	4	0.005	1.587	0.179
		Error	201	0.003		
Redox potential	Shallow	Time	8	165697.420	52.312	**<0.001**
		Distance	4	18794.318	5.933	**<0.001**
		Depth	1	53639.227	16.934	**<0.001**
		Time x Distance	32	714.848	0.226	1.000
		Time x Depth	8	3605.542	1.138	0.339
		Distance x Depth	4	147.501	0.047	0.996
		Error	212	3167.494		
	Parallel	Time	8	127856.995	42.555	**<0.001**
		Distance	4	14034.348	4.671	**0.001**
		Depth	1	6941.337	2.310	0.130
		Time x Distance	32	2934.909	0.977	0.508
		Time x Depth	8	1558.212	0.519	0.842
		Distance x Depth	4	1529.356	0.509	0.729
		Error	212	3004.492		
	Deep	Time	8	82185.650	35.911	**<0.001**
		Distance	4	9505.181	4.153	**0.003**
		Depth	1	10478.237	4.579	**0.034**
		Time x Distance	32	2661.246	1.163	0.262
		Time x Depth	8	1138.554	0.497	0.857
		Distance x Depth	4	1285.830	0.563	0.691
		Error	212	2288.574		

Table 3. Results of analyses of variance of the effects of different stages of intertidal geoduck culture (time) on the infaunal community at 0 and 10 m from the culture plot along the parallel transect at Nanoose Bay, British Columbia. Significant results are indicated in bold.

Variable	Source	df	MS	*F*	*P*
Abundance	Time	4	1.060	46.094	**<0.001**
	Distance	1	0.094	4.099	0.056
	Time x Distance	4	0.183	7.980	**0.001**
	Error	20	0.023		
Species richness	Time	4	63.200	13.167	**<0.001**
	Distance	1	10.800	2.250	0.149
	Time x Distance	4	8.800	1.833	0.162
	Error	20	4.800		
Margalef's species richness	Time	4	1.019	3.039	**0.041**
	Distance	1	0.708	2.110	0.162
	Time x Distance	4	0.336	1.003	0.429
	Error	20	0.335		
Pielou's evenness	Time	4	0.058	4.344	**0.011**
	Distance	1	0.003	0.259	0.616
	Time x Distance	4	0.054	3.996	**0.015**
	Error	20	0.013		
Shannon-Weiner diversity	Time	4	0.280	2.553	0.071
	Distance	1	0.201	1.836	0.191
	Time x Distance	4	0.107	0.974	0.444
	Error	20	0.110		
Arthropod abundance	Time	4	39.777	56.952	**<0.001**
	Distance	1	10.540	15.091	**0.001**
	Time x Distance	4	11.420	16.351	**<0.001**
	Error	20	0.698		
Echinoderm abundance	Time	4	0.501	4.486	**0.009**
	Distance	1	0.010	0.087	0.772
	Time x Distance	4	0.804	7.208	**0.001**
	Error	20	0.112		
Annelid abundance	Time	4	17.027	51.201	**<0.001**
	Distance	1	2.143	6.442	**0.020**
	Time x Distance	4	0.594	1.786	0.171
	Error	20	0.333		
Nemertean abundance	Time	4	2.709	5.155	**0.005**
	Distance	1	1.388	2.641	0.120
	Time x Distance	4	0.496	0.944	0.459
	Error	20	0.526		
Molluscan abundance	Time	4	1.176	3.162	**0.036**
	Distance	1	0.073	0.196	0.663
	Time x Distance	4	0.306	0.822	0.526
	Error	20	0.372		

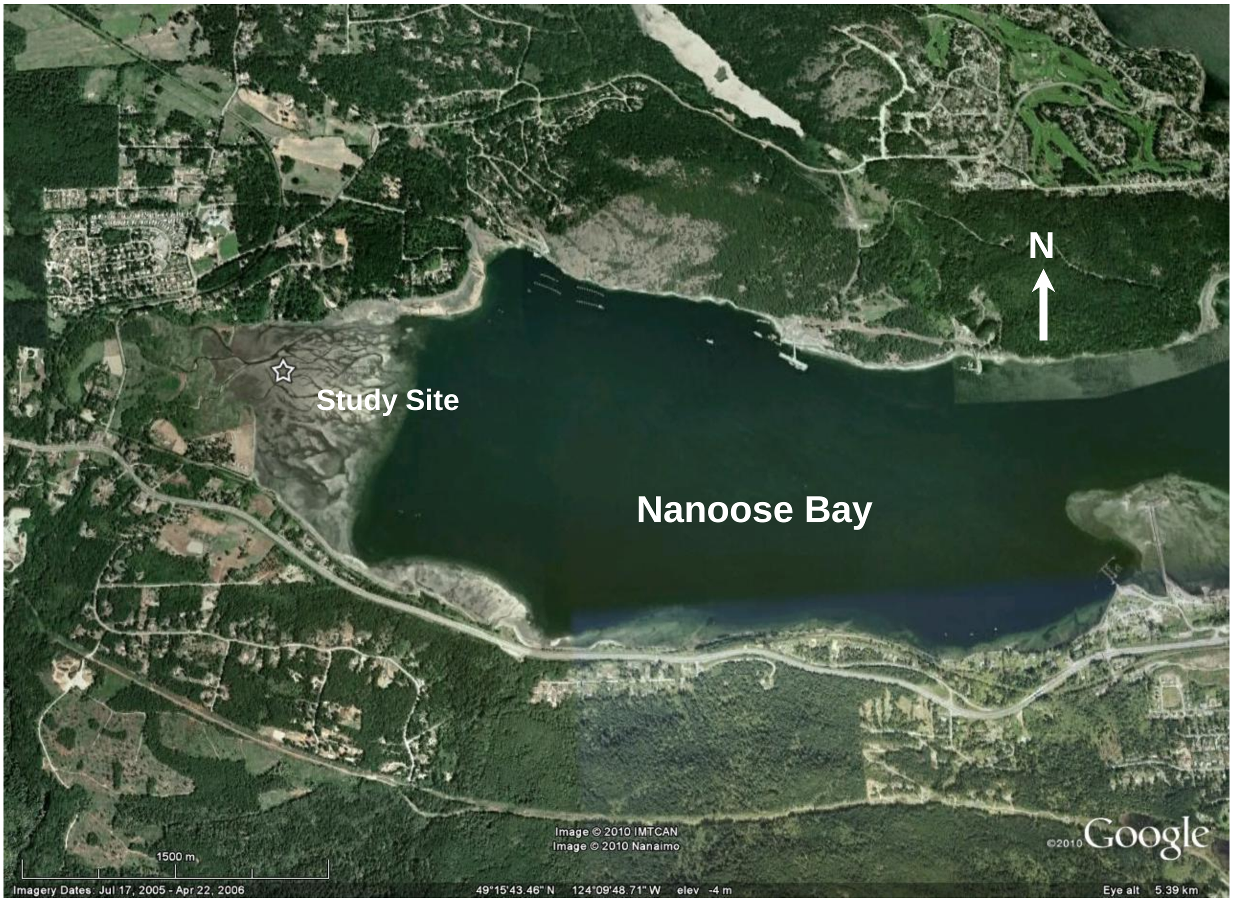

Figure 1. Aerial photograph of Nanoose Bay, British Columbia, showing position of study site.

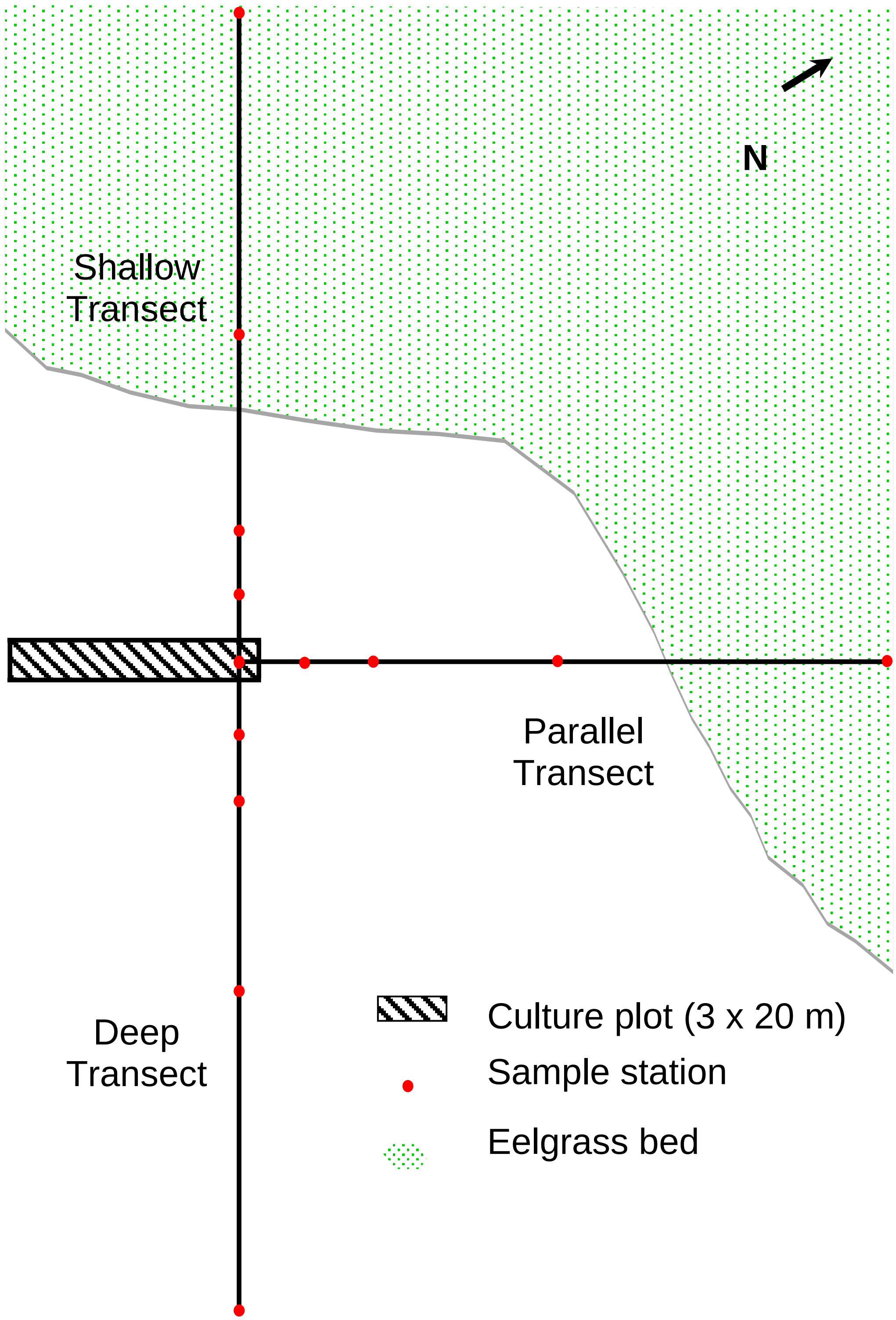

Figure 2. Diagrammatic representation of the study site at Nanoose Bay, British Columbia showing the 0, 5, 10, 25, and 50 m sample stations along the three transects (shallow, parallel, and deep) relative to the geoduck culture plot (3 x 20 m). The area of the eelgrass bed is also shown.

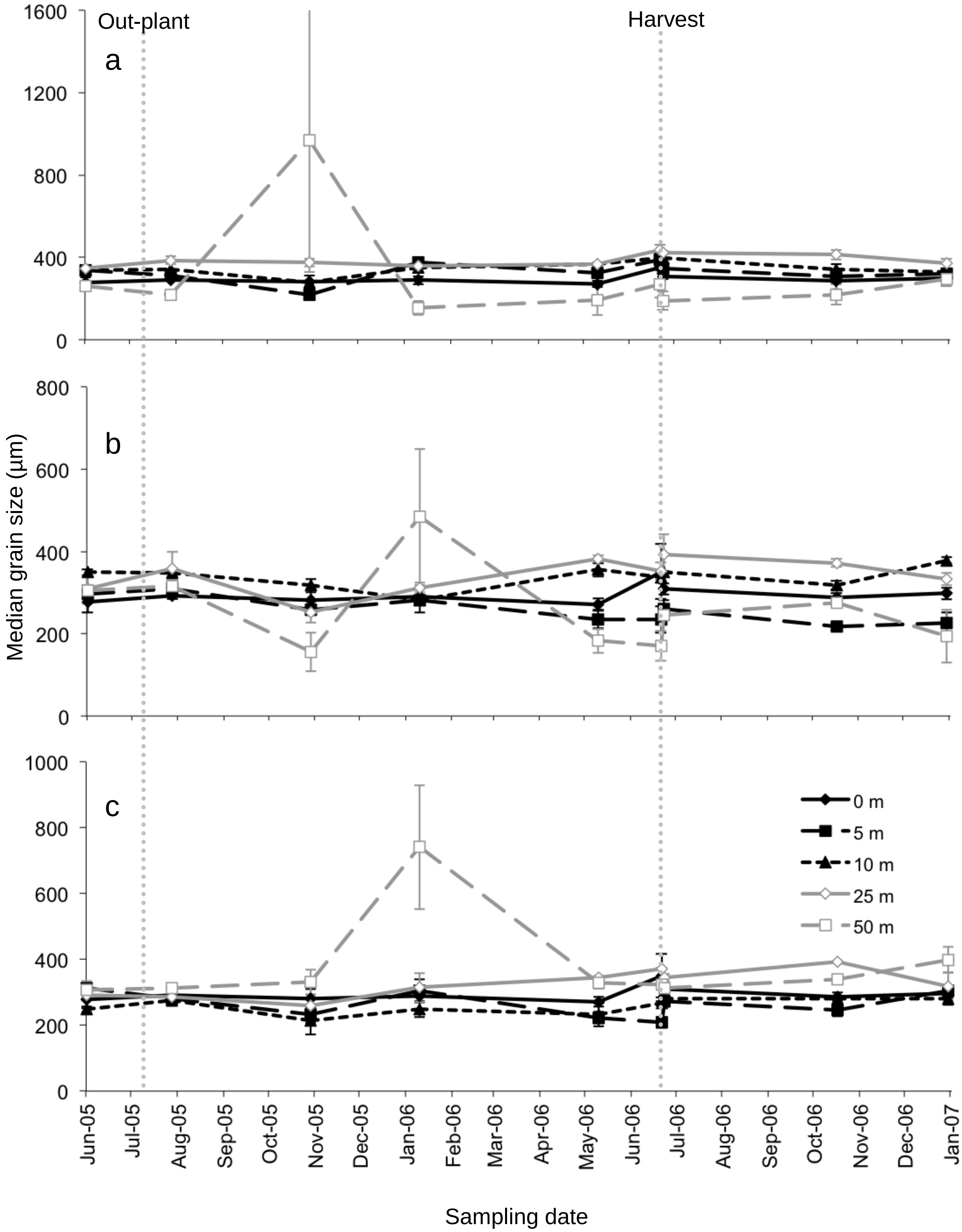

Figure 3. Median grain size of the sediment along the a) shallow, b) parallel, and c) deep transects during intertidal geoduck culture at Nanoose Bay. Data are mean ± 1 SE (n=3).

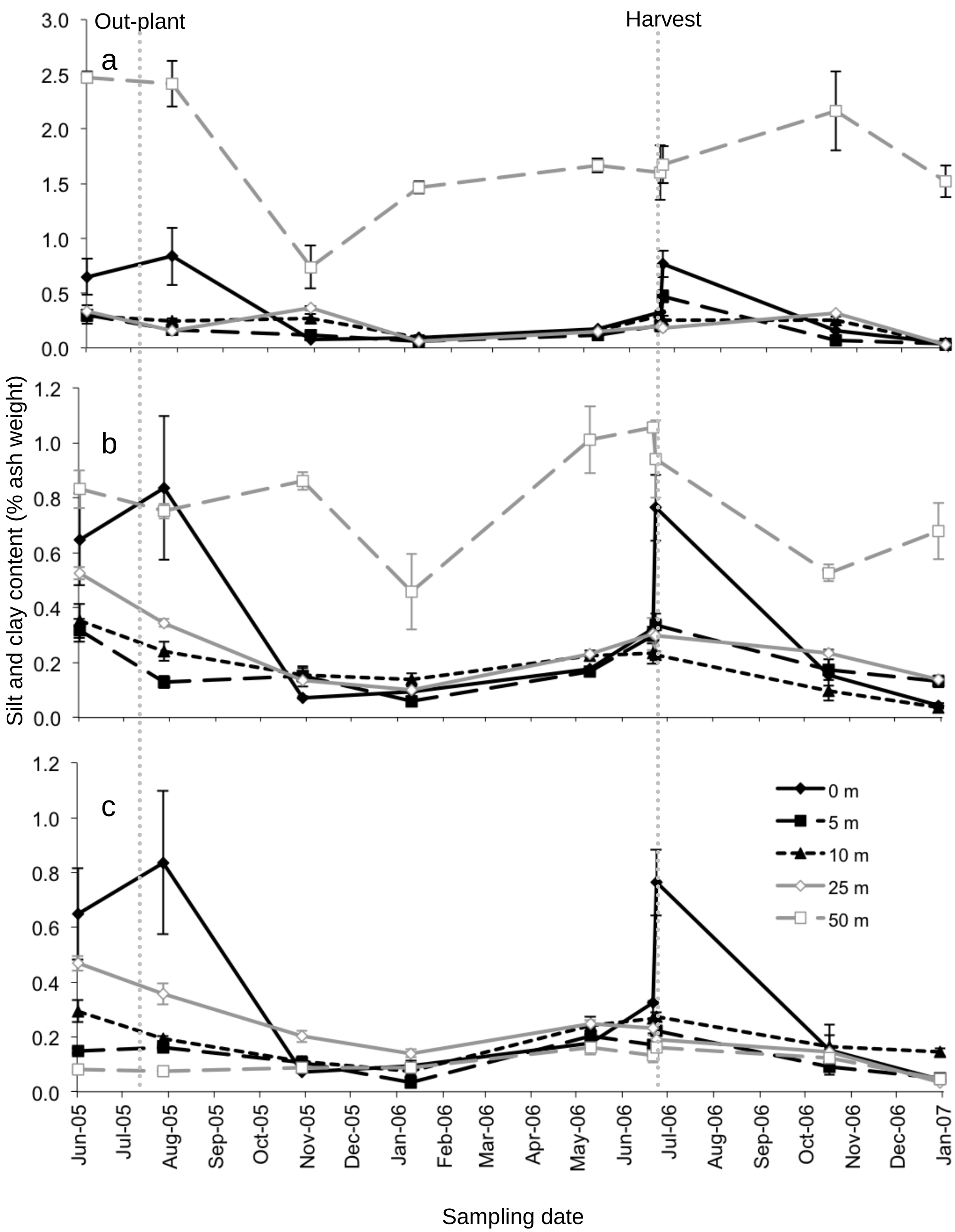

Figure 4. Silt and clay content of the sediment along the a) shallow, b) parallel, and c) deep transects during intertidal geoduck culture at Nanoose Bay. Data are mean ± 1 SE (n=3).

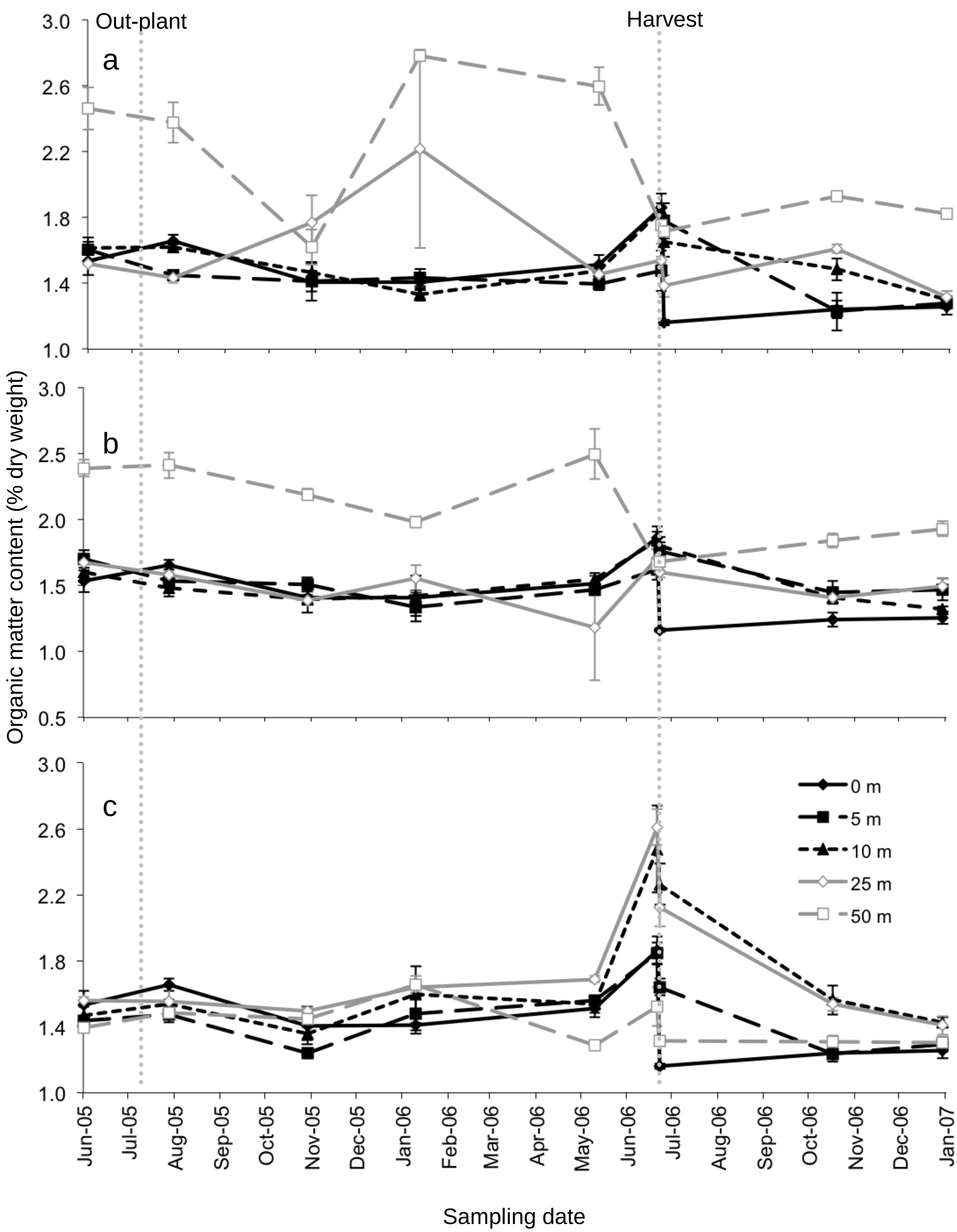

Figure 5. Organic matter content of the sediment along the a) shallow, b) parallel, and c) deep transects during intertidal geoduck culture at Nanoose Bay. Data are mean ± 1 SE (n=3).

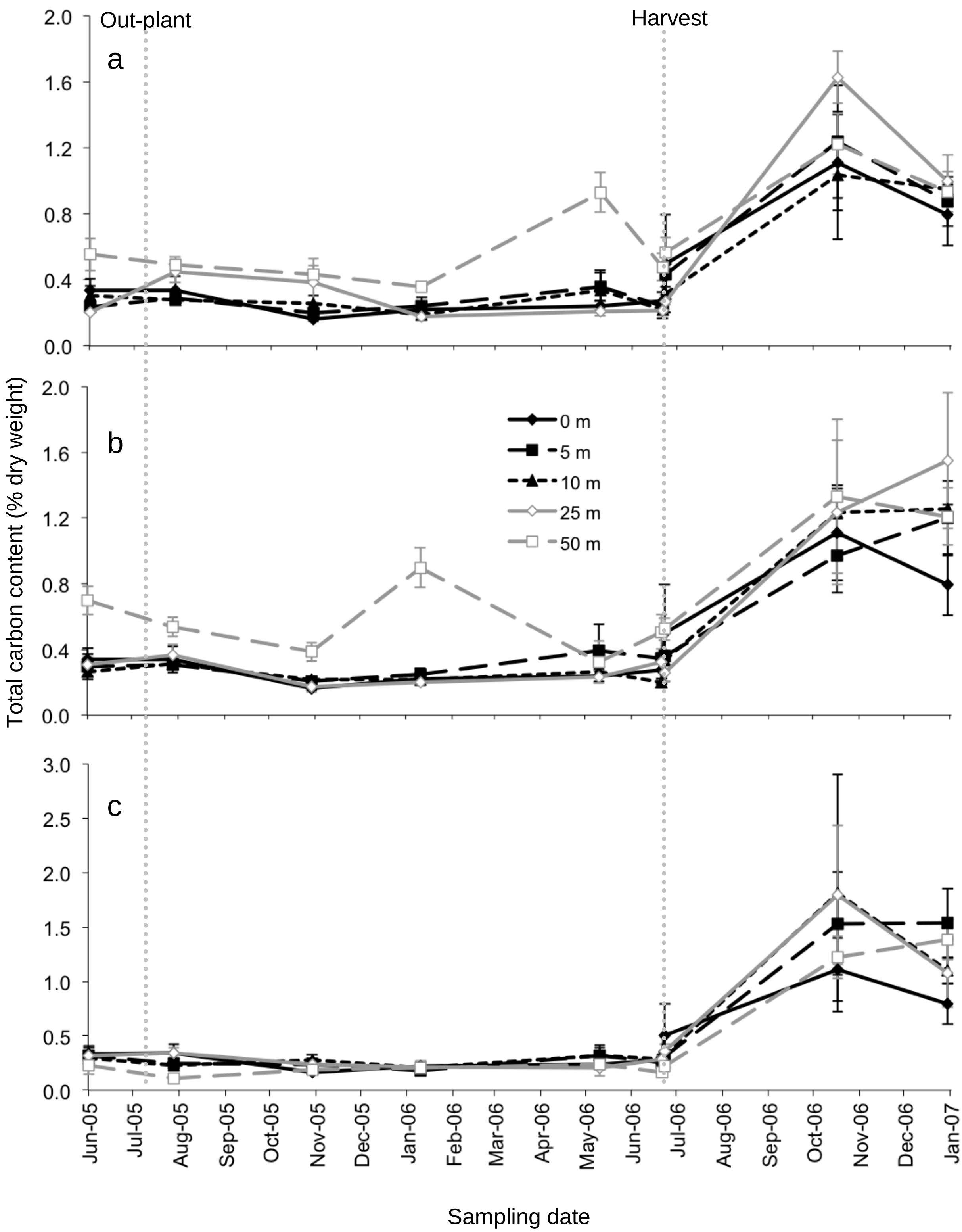

Figure 6. Total carbon content of the sediment along the a) shallow, b) parallel, and c) deep transects during intertidal geoduck culture at Nanoose Bay. Data are mean ± 1 SE (n=3).

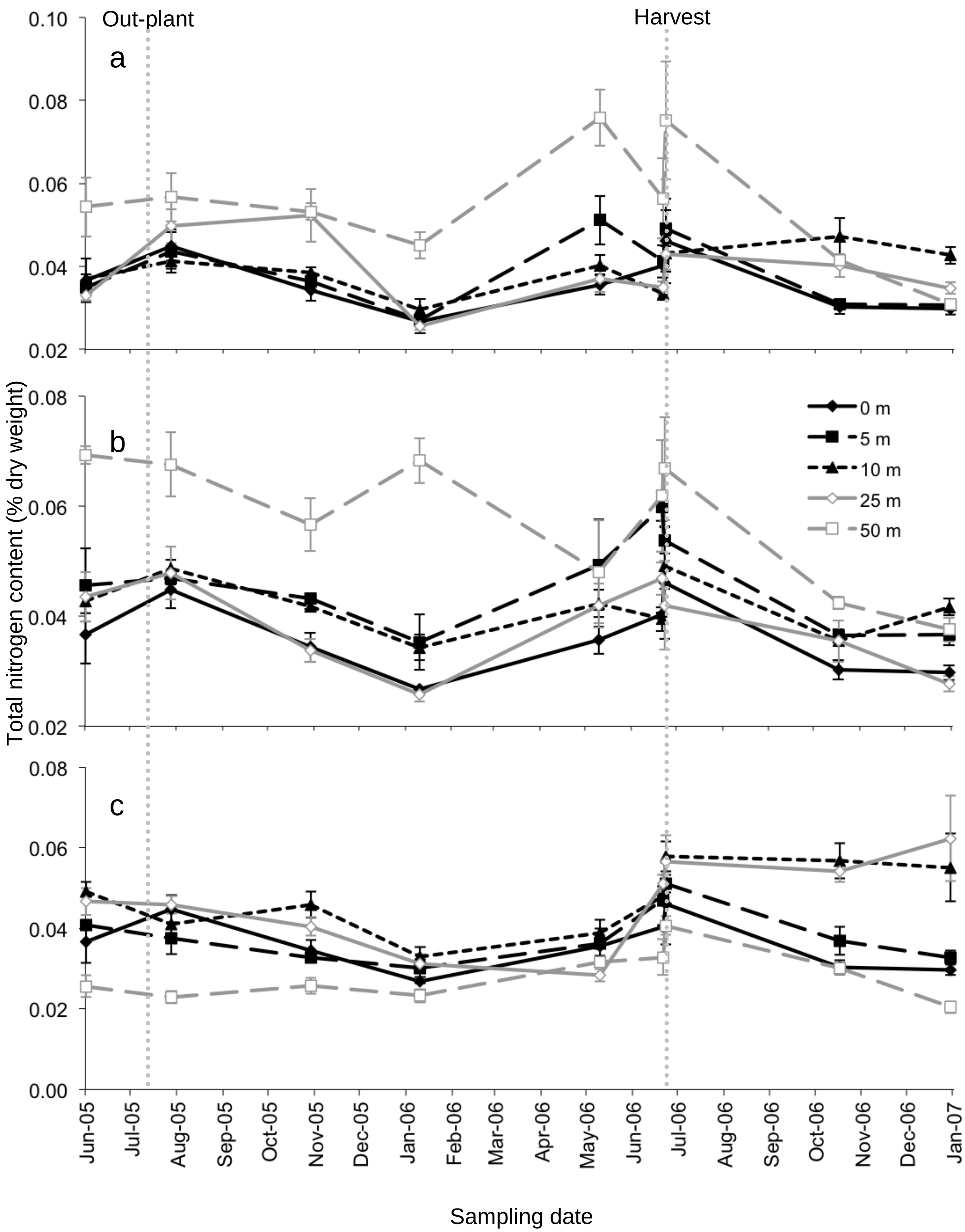

Figure 7. Total nitrogen content of the sediment along the a) shallow, b) parallel, and c) deep transects during intertidal geoduck culture at Nanoose Bay. Data are mean ± 1 SE (n=3).

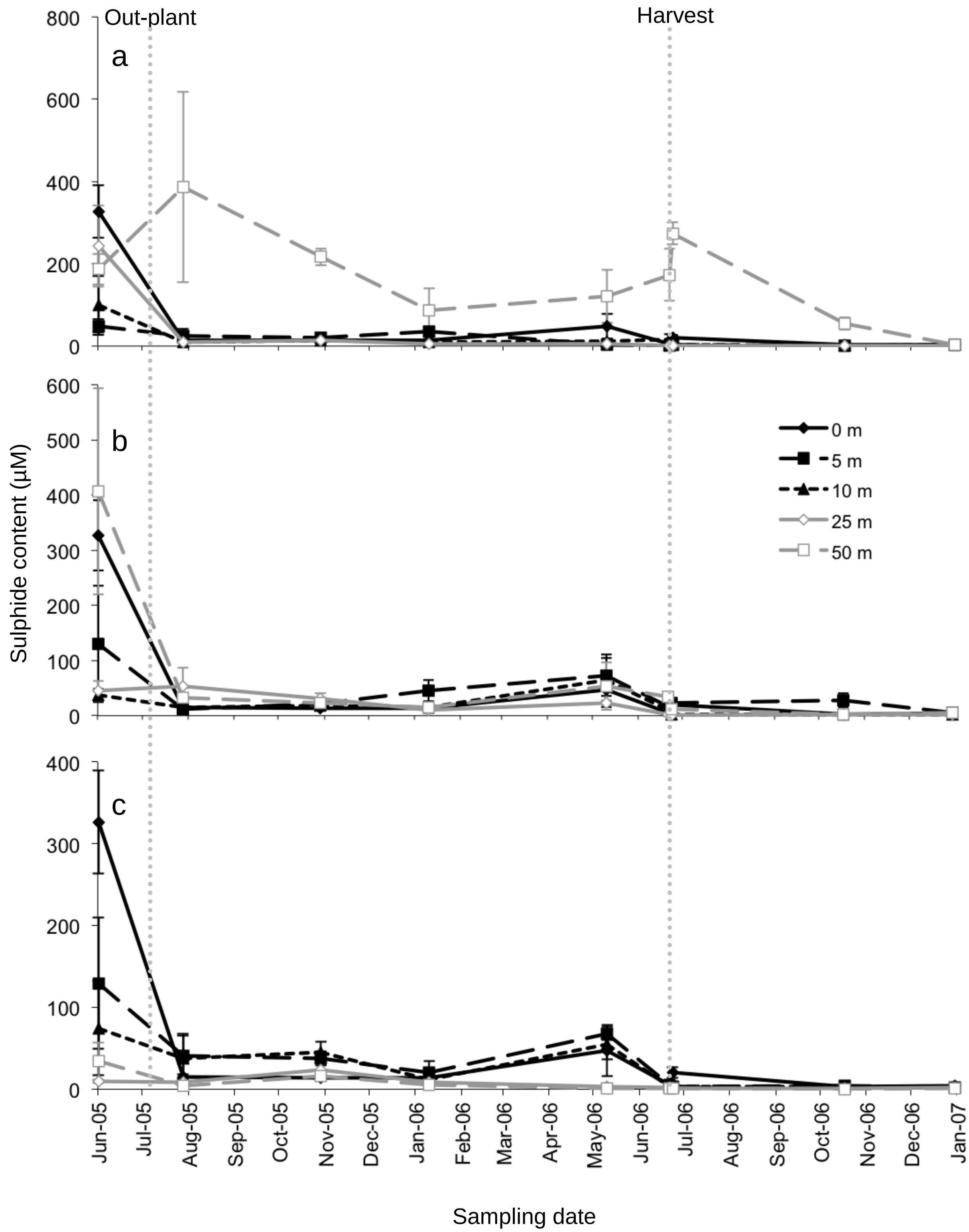

Figure 8. Sulphide content of the sediment at 2-cm depth along the a) shallow, b) parallel, and c) deep transects during intertidal geoduck culture at Nanoose Bay. Data are mean ± 1 SE (n=3).

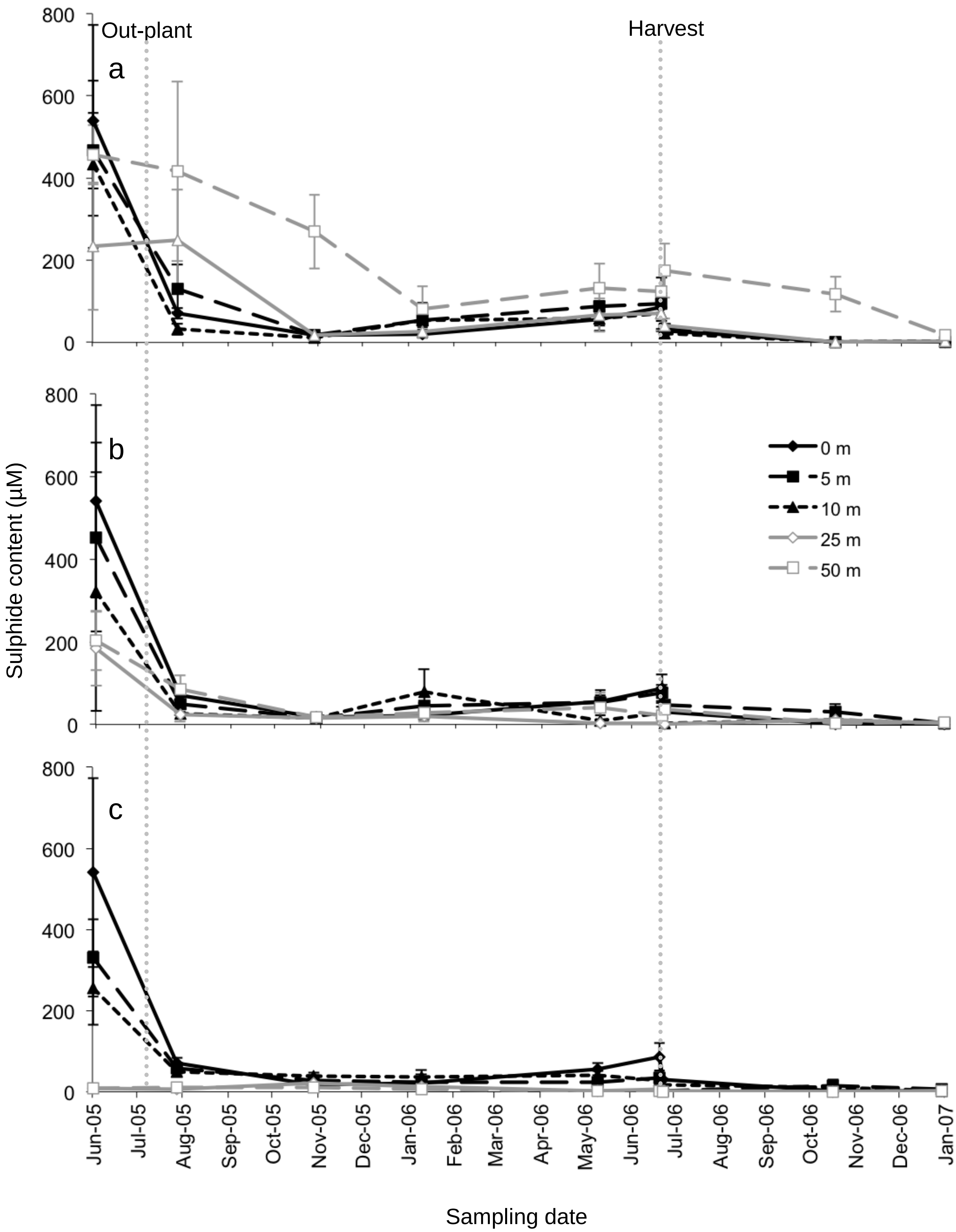

Figure 9. Sulphide content of the sediment at 4-cm depth along the a) shallow, b) parallel, and c) deep transects during intertidal geoduck culture at Nanoose Bay. Data are mean ± 1 SE (n=3).

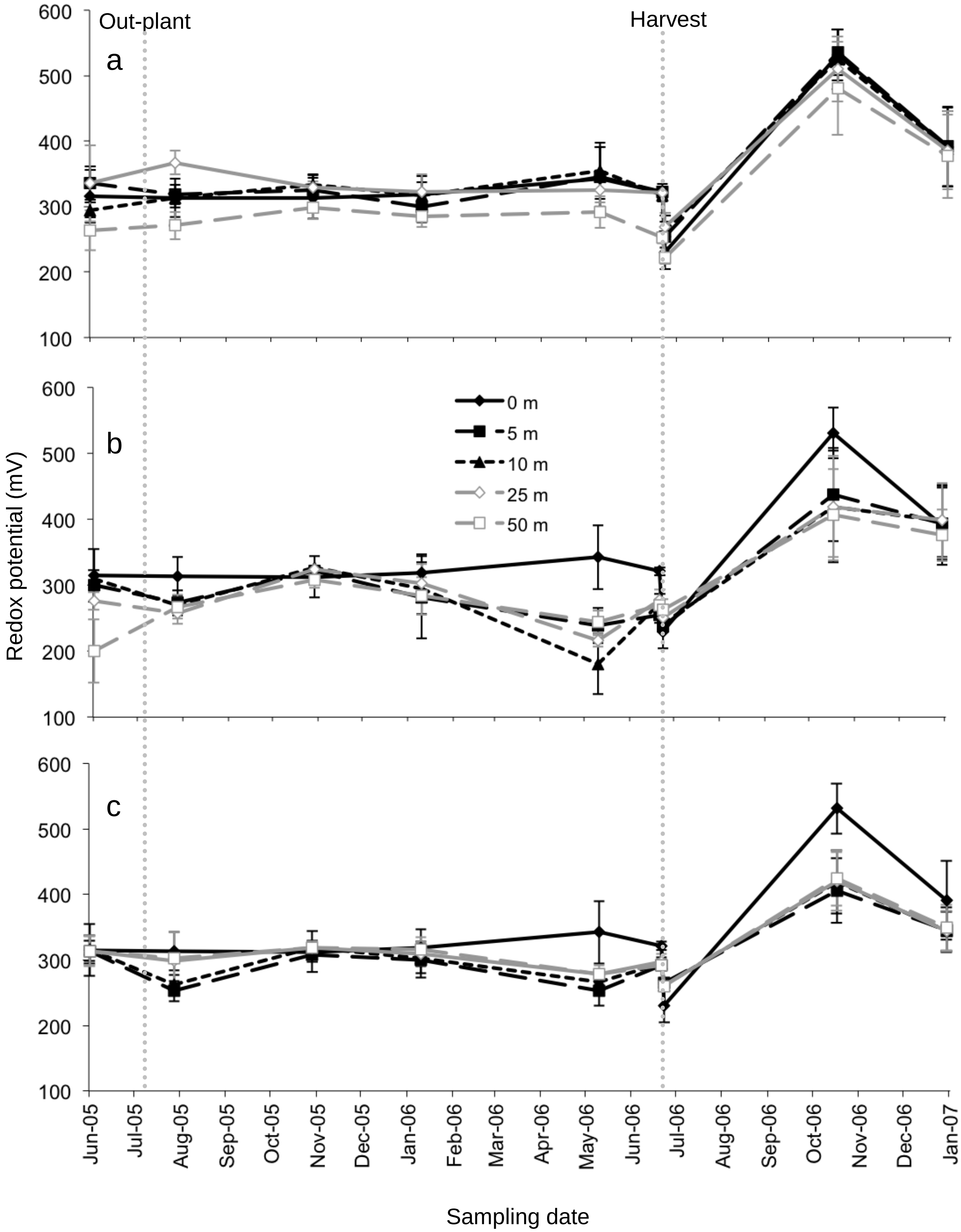

Figure 10. Redox potential of the sediment at 2-cm depth along the a) shallow, b) parallel, and c) deep transects during intertidal geoduck culture at Nanoose Bay. Data are mean ± 1 SE (n=3).

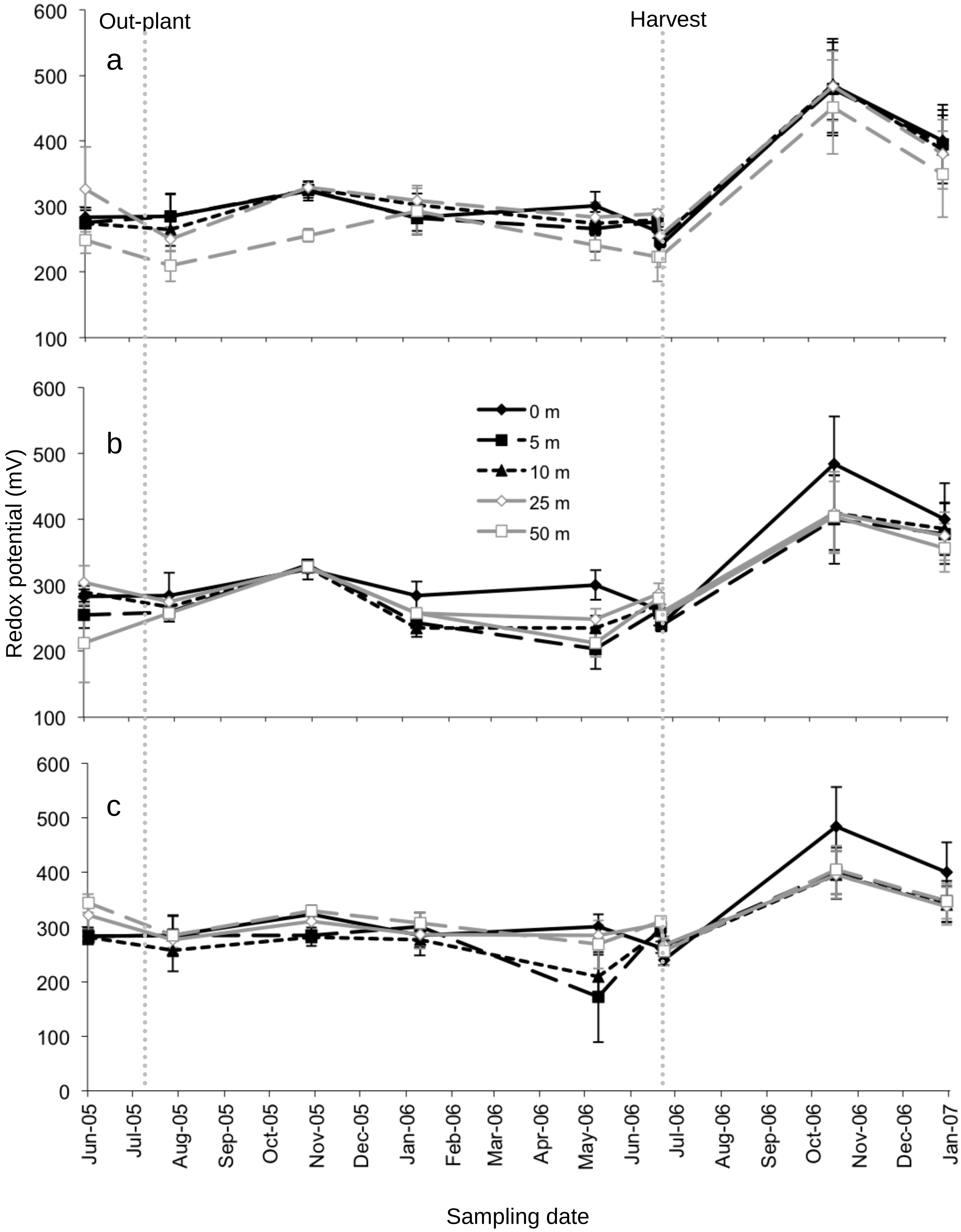

Figure 11. Redox potential of the sediment at 4-cm depth along the a) shallow, b) parallel, and c) deep transects during intertidal geoduck culture at Nanoose Bay. Data are mean ± 1 SE (n=3).

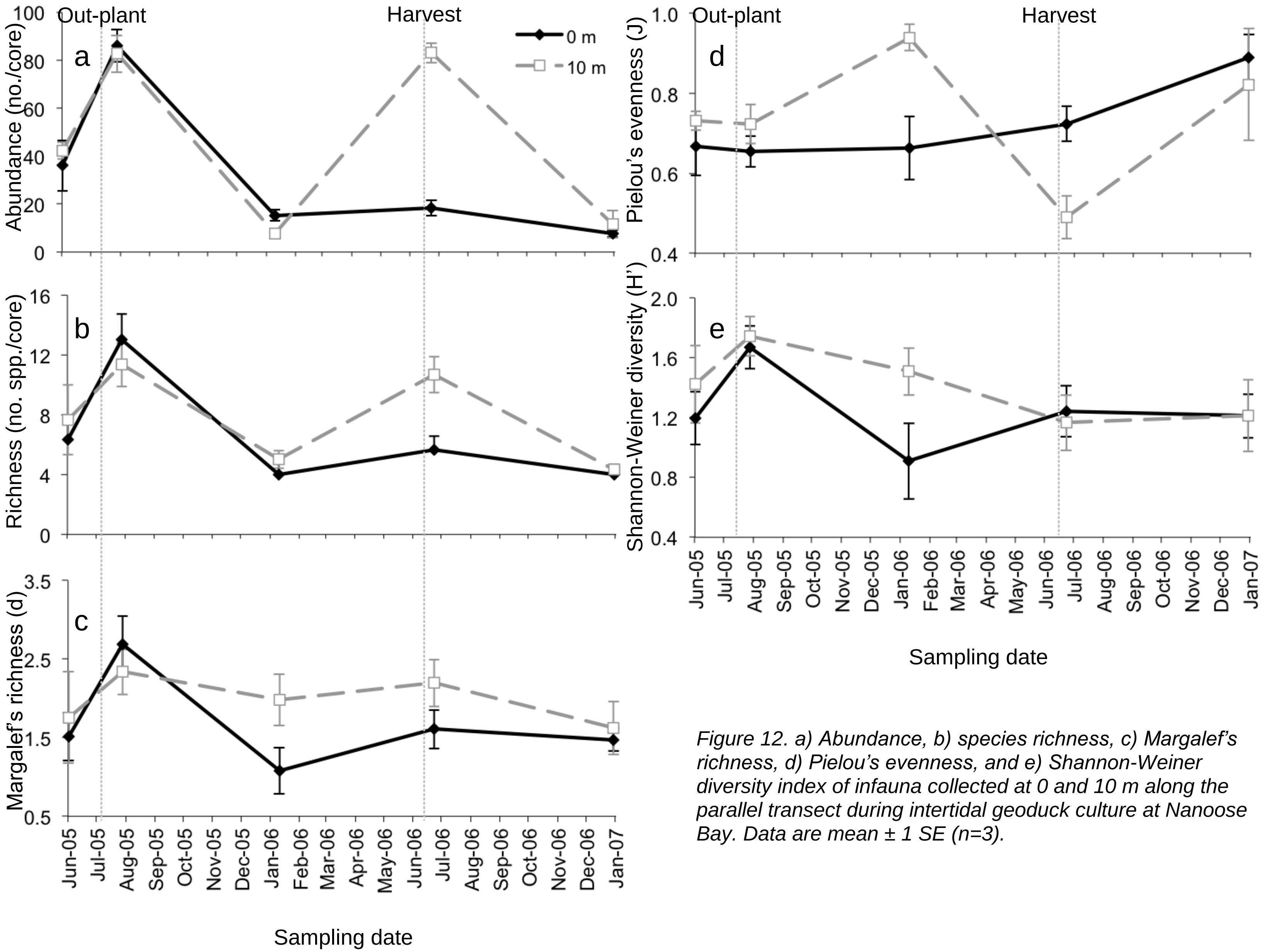

Figure 12. a) Abundance, b) species richness, c) Margalef's richness, d) Pielou's evenness, and e) Shannon-Weiner diversity index of infauna collected at 0 and 10 m along the parallel transect during intertidal geoduck culture at Nanoose Bay. Data are mean ± 1 SE (n=3).

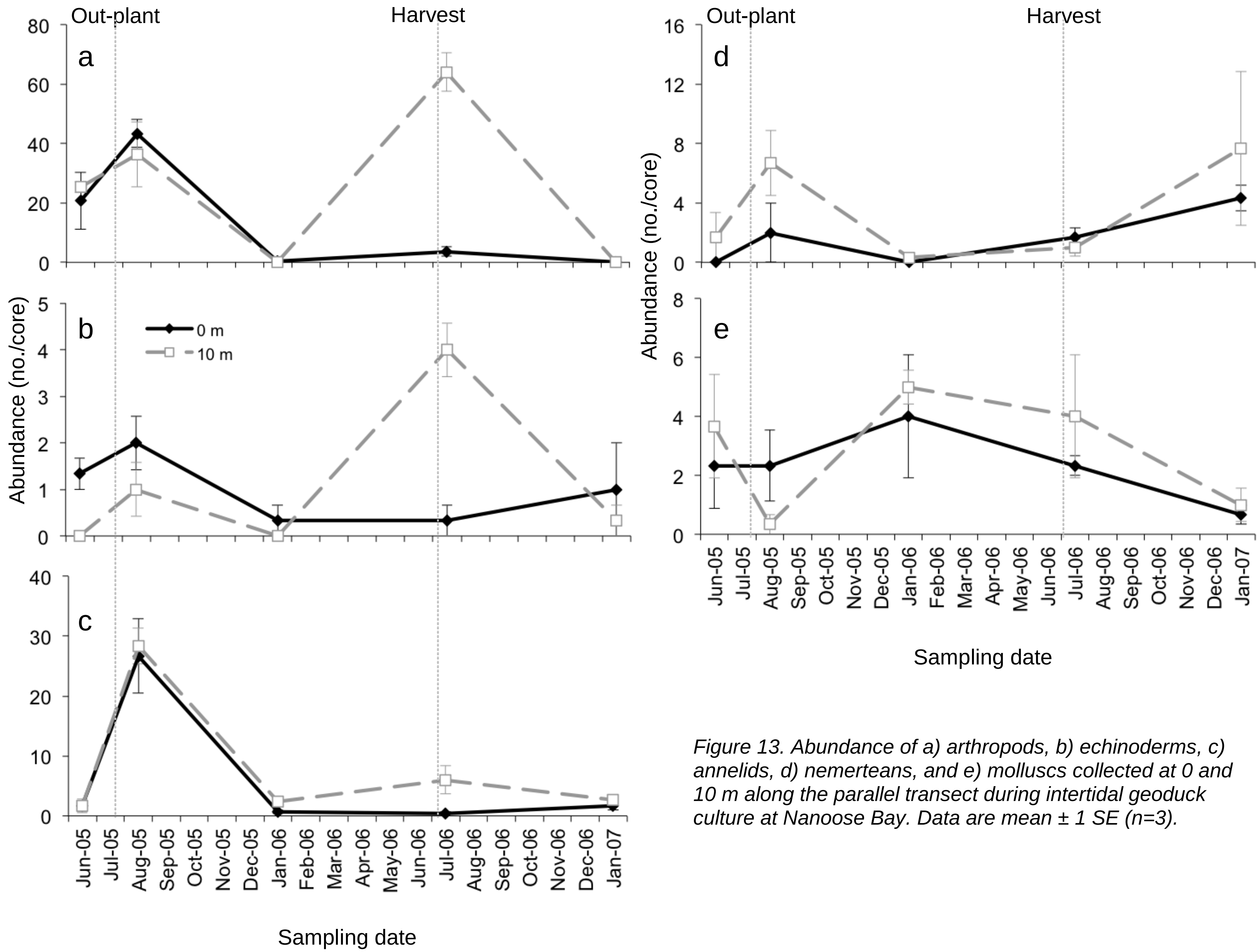

Figure 13. Abundance of a) arthropods, b) echinoderms, c) annelids, d) nemerteans, and e) molluscs collected at 0 and 10 m along the parallel transect during intertidal geoduck culture at Nanoose Bay. Data are mean ± 1 SE (n=3).