Population Attributes of the Invasive Varnish Clam (*Nuttallia obscurata*) in Whaling Station Bay, Hornby Island, British Columbia

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POPULATION ATTRIBUTES OF THE INVASIVE VARNISH CLAM (*Nuttallia obscurata*) IN WHALING STATION BAY, HORNBY ISLAND, BRITISH COLUMBIA

by

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Gordon, C.M., Martin, R.B., Lee, B.A., and Sutherland, T.F. 2018. Population attributes of the invasive varnish clam (*Nuttallia obscurata*) in Whaling Station Bay, Hornby Island, British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 3144: vii + 25 p.

Population attributes of the varnish clam, *Nuttallia obscurata*, were examined at 3 different tidal elevations along a cross-shore transect at Whaling Station Bay, Hornby Island, British Columbia. Sediment and clam samples were collected at each sampling station to determine sediment substrate texture, clam population composition (clam density, biomass, age) as well as condition index. Varnish clam density increased with increasing tidal height, while shell length and individual clam tissue biomass decreased. The mid-tidal station hosted the largest clam population when considering a combination of density and biomass attributes. Clams are likely influenced by the interaction of cross-shore gradients of physical variables (temperature, salinity, sediment structure, submergence period) and biological factors (food availability, selective predation, and recruitment). In general, the well-sorted, fine sands of the Whaling Station Bay transect supported smaller range in clam attributes (tissue weight-at-length; shell breadth-at-length) relative to those inhabiting mixed sediment substrates in other intertidal areas of the Strait of Georgia.

RÉSUMÉ

Gordon, C.M., Martin, R.B., Lee, B.A., et Sutherland, T.F. 2018 Paramètres des populations envahissantes de palourde lustrée (*Nuttallia obscurata*) à Whaling Station Bay dans l'île Hornby (Colombie-Britannique). Rapp. tech. can. sci. halieut. aquat. 3144: vii + 25 p.

Les paramètres des populations de palourde lustrée, *Nuttallia obscurata*, ont été examinés à trois hauteurs de marée le long d'un transect perpendiculaire au trait de côte à Whaling Station Bay sur l'île Hornby (Colombie-Britannique). Des échantillons de sédiments et de palourde ont été prélevés à chaque station d'échantillonnage pour déterminer la structure du substrat des sédiments, la composition de la population de palourdes (densité des palourdes, biomasse, âge) ainsi que l'indice de condition. La densité des palourdes lustrées augmente proportionnellement à l'accroissement de la hauteur de la marée alors que la longueur de coquille et la biomasse des tissus des individus diminuent. La station à hauteur de marée moyenne hébergeait la plus grande population de palourdes si l'on tient compte de la combinaison des paramètres de densité et de biomasse. Les palourdes sont probablement influencées par l'interaction de gradients de variables physiques de la section perpendiculaire au trait de côte (température, salinité, structure sédimentaire, période de submersion) avec des facteurs biologiques (aliments disponibles, prédation sélective et recrutement). En général, les sables fins bien classés du transect de Whaling Station Bay abritaient des palourdes plus petites (poids des tissus selon la longueur, largeur de la coquille selon la longueur) que celles vivant dans les substrats de sédiments mixtes des zones intertidales du détroit de Georgie.

INTRODUCTION

The varnish clam, *Nuttallia obscurata*, arrived in British Columbia (B.C.) in the early 1990's by means of larval transport in ballast water via trans-oceanic shipping (Merilees and Gillespie, 1995; Mills, 1999; Coan et al. 2000; Larson et al. 2003). Native to Korea and the Japanese Islands of Kyushu, Honshu and Shikoku, the varnish clam has been found in major estuaries in Oregon and Washington, U.S., as well as in southern British Columbia (Strait of Georgia and west coast of Vancouver Island) and continues to expand its distribution northward (Forsyth, 1993; Gillespie et al. 1999; Gillespie and Bourne, 2000, 2005; Dinnel and Yates 2000). The varnish clam has a wide coastal range with the southern limit reported as far south as Alsea Bay, Oregon, U.S. (Coan et al. 2000).

Research to date has shown that varnish clams are primarily found on beaches with mixed sand, gravel and mud substrates and typically inhabit sediment depths of 8-10 cm, with a maximum burial depth of 20 cm in the upper intertidal zone (Gillespie et al. 1999; Byers, 2002; Dudas et al. 2005; Dudas and Dower 2006). Varnish clams were found predominantly in the upper third of the intertidal zone on Savary Island, B.C., with decreasing abundance in the middle and lower intertidal zones (Gillespie et al. 1999). The long siphons of varnish clams allow them to bury deeper into sediment compared to other clam species of comparable size and shell type, thereby increasing their viability in the harsh environment of the upper inter-tidal zone. Varnish clams are capable of filter-feeding, pedal-sweep feeding of the sediment surface and siphon deposit feeding to collect deposited organic material (DFO, 2001). Dudas et al. (2005) reported that varnish clams spawn from late-spring to early-summer.

Invasive species are defined as "non-native" species to the ecosystem whose introduction is likely to cause economic or environmental harm, or harm to human health (Executive Order 13112, Federal Register 1999). Being a successful invader, varnish clams have the potential to outcompete or displace native clam species and influence biodiversity. For example, the varnish clam population density on Savary Island increased four-fold between 1997 and 1999, while other bivalves, such as the Manila clam (*Venerupis philippinarum*) increased by two-fold (Gillespie et al. 1999).

However, the overall spatial magnitude and extent of potential impacts resulting from varnish clam invasion are currently unknown.

This study examines clam population at different tidal elevations in Whaling Station Bay (WSB), Hornby Island, British Columbia (Figures 1 and 2). Whaling Station Bay is located approximately 50 km southeast of Savary Island within the northern Strait of Georgia. The tidal flat of WSB is approximately 0.4 km wide and 0.3 km in length in a direction perpendicular to shore. Three stations corresponding to different tidal elevations (mid, low and high) were sampled for varnish clam population attributes as well as sediment grain size (Figure 2). Understanding varnish clam preferences with respect to tidal elevation and substrate texture may provide insight in to the invasive potential of varnish clams as well as their impact on native species. Collecting and assessing varnish clams at three locations along the intertidal zone also allowed examination of clam size, age and health as a function of intertidal elevation.

MATERIALS AND METHODS

FIELD SURVEY AND COLLECTION OF CLAMS AND SEDIMENT

Varnish clams were collected from three different tidal elevations in the intertidal zone at WSB located on Hornby Island, British Columbia (Figure 1). The high and low intertidal stations were sampled on August 22, 2013, while the mid intertidal station was sampled on August 26, 2013. The high (WSB-A), mid (WSB-B), and low (WSB-C) stations were located within the upper half of the tidal flat that was accessible during the study (Table 1). The geographical location of the high intertidal station was determined using triangulation of prominent waterfront buildings and shoreline rock structures, with latitude and longitude coordinates pinpointed using Google Earth software (Table 1). The distance between the relatively higher, mid, and lower intertidal stations was approximately 35 m at a bearing perpendicular to the shoreline. Clams were collected from a single station quadrat at each tidal height with an approximate area of 0.20 m^2 and a depth of 0.20 m. A shovel was used to carefully remove sediment and clams from a quadrat and then placed on the beach surface. The sediment-clam mixture was handsifted and clams that were visible to the human eye were placed in labeled Ziploc bags and stored in a cooler prior to being transported to a freezer.

A sediment sample was collected at each sampling station and placed in a freezer bag for determination of sediment grain size. Each sediment sample was treated with sodium hypochlorite (NaOCl) to remove organic matter prior to grain size analysis. The pipette method was used to quantify silt and clay content, while wet sieving was used to quantify the sand fractions (McKeague, 1978). All results were reported as percent on a dry weight basis for the following categories: >2000 μm, <2000 μm, <1000 μm, <500 μm, <250 μm, <100 μm, <63 μm, <4 μm, <2 μm. Textural classes were determined by calculating the sand, silt, and clay proportions, where the silt–clay boundary was set at 2 μm following the Canadian soil classification system.

The tidal elevation of each sampling station was determined using tide tables published by the Canadian Hydrographic Service (http://www.charts.gc.ca/index-eng.asp) and the time that the incoming tidal water passed over each station (WSB-A, WSB-B, and WSB-C).

LABORATORY ANALYSES OF CLAMS

Varnish clams were identified by the presence of both a shiny brown periostracum and a purplish-white shell near the umbo and on the interior surface of the shell (Gillespie et al. 1999). The number of varnish clams observed at each station was recorded. The maximum dimension of the anterior-posterior axis was recorded as shell length, while the maximum lateral axis was recorded as shell width. The maximum dimension from the umbo to the ventral edge was recorded as shell breadth. The length, width and breath of each varnish clam shell were determined using a Fisher Scientific electronic digital calliper (06-664-16). Clam tissues were removed from the each shell using a scalpel and placed into individual pre-weighed aluminum drying dishes. Wet, dry and ashed weights of clam tissues were measured using a Sartorius BP211D/BL610 analytical balance to 10^{-5} degree of precision. Tissue samples were dried using a Fisher Scientific Gravity Oven at 55°C for 24 hours or until a constant sample weight was achieved. Tissue samples were desiccated for 2 hours prior to dry weight determinations to avoid potential condensation during the cooling process. Dried samples were then ashed at 550°C for 2 hours in a Thermolyne 1400 furnace. Ash-free dry weight (AFDW) was calculated as the differential weight between oven dried and ashed clam tissues. The organic content of clam tissue was calculated as the differential weight between dry and ashed values, expressed as percent. The age of each varnish clam was determined by counting annuli (Quayle and Bourne 1972). Distances between the growth rings were measured using a Fisher Scientific electronic digital calliper (06-664-16) to 0.5 mm precision.

Mean clam shell length, width, breadth, age, wet weight, dry weight, AFDW and condition index were calculated at each tidal elevation. The condition index of each varnish clam was determined by dividing the AFDW by shell length to characterize the overall physiological status of each clam (Lucas and Beninger 1985). AFDW was used over wet weight and dry weight to eliminate the bias due to water content fluctuations in the clam tissue and contamination from sediments. Population densities were determined for each station by dividing the number of varnish clams collected at each tidal elevation by the sampling area. Total biomass at each tidal elevation was calculated by dividing the total varnish clam AFDW at each tidal elevation by the sampling area. The average growth rate was quantified by dividing the mean clam age by the mean shell length.

Statistical analysis was performed using SYSTAT 13^{TM} software (Systat Software Inc, Illinois, USA) between the high intertidal zone (station WSB-A) and the mid intertidal zone (station WSB-B) for mean varnish clam AFDW, mean varnish clam condition index and mean varnish clam age. As the low intertidal zone station (WSB-C) had a small total varnish clam sample size (n=6), it was not included in the statistical comparison. Statistical significance was set at the 0.05 probability level.

A general linear regression model was used for the following analyses: 1) varnish clam length vs. tissue (AFDW) across WSB sampling stations (current study site); 2) varnish clam length vs. tissue (AFDW) across WSB, Robbers Passage, and Bamberton intertidal sites; and 3) varnish clam shell length vs. breadth across WSB and a combined data set from Robbers Passage and Bamberton sites (Dudas, 2005). All three study sites are located on Vancouver Island, British Columbia: 1) WSB: northeast coast (Hornby Island); 2) Robbers Passage: southwest coast (Barclay Sound); and 3)

Bamberton: southern coast (Saanich Inlet). Study site was included as a categorical factor to estimate potential differences between study sites and an interaction term was added to evaluate heterogeneity in regression slopes among substrate types. Data were log transformed.

RESULTS

The sediment texture across all stations was well sorted with the majority (>95%) of sediment falling within 2 size categories: 1) 105-250 micron (fine sand); and 2) 250-500 micron (medium sand) (Figure 3). Fine sand comprised 70.2% (WSB-A), 84.5% (WSB-B), and 92.3% (WSB-C) of total sediment, while medium sand accounted for 28.6% (WSB-A), 14.1% (WSB-B), and 6.1% (WSB-C) of the total. The increase in fine sand content across the stations coincided with decreasing intertidal height in the upper tidal flat (Table 1).

A monospecific population of Varnish clams was observed at both the high (730 clams$*$m^{-2}) and mid (648 clams$*$m^{-2}) intertidal stations where no other clam taxa were present (Table 2). The low intertidal station (WSB-C) was characterized by a lower clam density (23 clams$*$m^{-2}) and showed a Varnish to Butter clam ration of 3:1. Although total Varnish clam density and tissue biomass at WSB-C was lower relative to those at WSB-A and WSB-B, individual clam tissue weight did not reflect a similar difference across stations (Figure 4; Table 2). Inter-station differences in clam siphon-hole densities surrounding each sampling quadrat reflected the relative differences in measured clam densities between stations. T-test results show a significance difference in mean individual clam tissue biomass (p=0.001) between WSB-A and WSB-B stations. However, a significant difference was not found between mean clam age between WSB-A and WSB-B stations (p=0.935). In general, the mid-station clams had higher individual biomass, shell length mode (Figure 5) and condition index (function of tissue AFDW vs shell length), despite similar mean ages.

Clam size frequency histograms reveal an offset in peak clam shell lengths between WSB-A and WSB-B stations, with the mid-intertidal station showing a higher number of larger clams (Figure 5). A flat frequency histogram characterized with low abundance and missing clam length categories is observed for WSB-C, suggesting low recruitment and an aging population. With respect to clam age vs shell length relationship, an overlap in data variation is observed across sampling quadrats (Figure 6).

A condition index based on the relationship between clam tissue weight (AFDW) and shell length was examined to determine clam health status (Marin et al. 2003; Mohite et al. 2009). A strong correlation was observed between clam tissue weight (AFDW) and shell length for varnish clams across all 3 stations (Model: r^2 = 0.814; $p<0.001$) (Figure 7). Although the relationship was not affected by sampling station location ($p=0.055$), heterogeneity was observed between station-specific regression slopes ($p=0.036$). It appears that clam health is consistent across WSB sampling sites given the statistical outcomes and the fact that the majority of data fell within the 95% confidence limits associated with the regression.

The clam shell length and tissue relationship across WSB (current study), Robbers Passage, and Bamberton (Dudas, 2005) (Figure 8) was highly correlated (Model: r^2 = 0.956; $p<0.001$) with no effect across sampling sites ($p=0.179$) and homogeneity observed amongst regression slopes ($p=0.260$). In terms of the relationship between shell length and shell breadth across WSB and the combined Bamberton and Robbers Passage data set (Model: $r^2=0.958$; $p<0.001$;), study site ($p=0.020$) and data heterogeneity influenced the regression slope ($P<0.001$) (Figure 9). The ternary plot of gravel-sand-silt percentages revealed different sediment textures between the 3 sampling sites that aligned along a fairly constant mud content (near zero) and across inverse proportions of sand and gravel (Figure 10). The gravel content was zero at WSB and highest at Robbers Passage. Well sorted sediment was observed at WSB, with poorly to very poorly sorted sediment at Bamberton, and very poorly sorted sediment at Robbers Passage (Dudas 2005).

DISCUSSION

The distribution of Varnish clam diversity and biomass along the intertidal transect may reflect a trade-off between environmental variables (e.g. temperature), food supply (submergence period), wave action, sediment texture and selective predation across the tidal flat elevation gradient (Gillespie et al. 1999, Byers 2002, Lum 2011). In general, the clam community structure along the WSB transect was of composed of both varnish clams (99.16%) and butter clams (0.84%), with the high (WSB-A; 3.5 m above chart datum) and mid (WSB-B; 2.8 m above chart datum) tidal elevations represented solely by varnish clams. Other studies have also found mono-specific varnish clam populations above an intertidal height of 2.5 m (Gillespie et al. 1999, Byers 2002, Lum 2011). The facultative feeding structure of the varnish clam, that involves both deposit (pedal) and suspension feeding, likely favours survival at higher tidal elevations where suspension feeding may be limited by shorter immersion times. In addition, long siphons, characteristic of varnish clams, may promote deep burial depths (up to 20 cm) and help: 1) prevent desiccation and exposure to extreme temperatures for this thin-shelled species; and 2) afford protection from bird/crab predation. For example, Byers (2002) noted that a greater burial depth and lower crab predation rate occurred in sandier sediment relative to that of a mud substrate. Overall, it appears that the presence of a well-sorted sandy substrate along with deep burial depths of the clams observed in the current study contribute to the presence of a mono-specific community of high-density varnish clams in the high intertidal zone.

Intertidal clam communities are typically exposed to a variety of strong environmental gradients, including temperature, salinity, wave stress, substrate type, inter-species competition, and predation which contribute to population variability (Bricelj and Malouf 1984; Hart et al. 1998; Mann 1979; Lorio and Malone 1995). The extent of wave action (redistribution and/or loss of recruits) and predation pressure may be outweighed by the benefits of longer submersed feeding periods as reflected by a relatively high individual clam biomass. For example, varnish clam densities at higher (WSB-A = 730 No.m^{-2}) and mid (WSB-B = 648 No.m^{-2}) tidal elevations were greater than those observed at the lower tidal elevation approximately 1.7 m above chart datum (WSB-C = 23.1 No.m^{-2}). Varnish clam recruitment may be favoured at protected high-intertidal heights characterized by the deposition of finer sediments and extreme environmental variables (e.g. temperature, salinity). For example, the size of the varnish clam settlement stage (180 – 200 microns; Dudas and Dower, 2006) overlaps with the dominant sediment size (150 – 500 microns) deposited in the upper tidal flats. In addition, varnish clam larvae have a relatively higher tolerance of high temperature and salinity values during the pre-settlement phase relative to that of other clam larvae (Dudas and Dower, 2006).

The clam population at the lowest tidal height shows a very low density and total biomass with recruitment and juvenile size classes missing from its frequency distribution. These findings are consistent with other investigations where the lower densities of varnish clams have been observed in the lower reaches of tidal flats (Gillespie et al. 2001, 2005; Lum, 2011). Varnish clams in lower tidal elevations may be exposed to a different type of predation pressure associated with flatfish that nip on exposed siphon tips. Indeed, Sasaki et al. (2002) observed predation of the siphon tips of a congener clam species, *Nuttallia olivacea*, by a local flatfish population.

It appears that optimal growing conditions may exist at the mid-intertidal station based on quadrat biomass (Table 2), mean biomass per individual (Figure 4C), shell-length mode (Figure 5), shell length-at-age (Figure 6), and condition index estimates (Table 3; Figure 7). Given the sparse clam population in the low intertidal zone, statistical comparisons were made between clam attributes observed in the higher tidal heights (Table 3). Varnish clam growth rates can vary between intertidal heights as well as between various bays located along the British Columbia coastline. The mean age of varnish clams between the intertidal zones was 4.6 years while the mean shell length was 32.56 mm (Table 2). The average varnish clam shell length at 4 years of age was 29.58 mm, yielding an average growth rate of 7.19 mm per year (Figure 6). This value is lower than growth rates reported for varnish clams on the west coast of Vancouver Island, which reached 38 mm total length in 4 years (growth rate of 9.5 mm per year) (Gillespie et al. 2005).

Varnish clam condition index and shell attributes were compared between WSB, Robbers Passage, and Bamberton. The very poorly-sorted and sandy-gravel substrate of Robbers Passage supported the largest clam tissue weights and shell lengths relative to that of the well-sorted fine sediments along the single transect at WSB (Table 4; Figures 8, 9). Sediment texture at Bamberton fell intermediate to that of Robbers and WSB, being characterized by poorly-sorted substrates and lower clam tissue weights per equivalent shell lengths. It is possible that poorly-sorted, mixed substrates that are inherently patchy provide a larger habitat diversity that support a larger range of clam tissue-shell biomass relative to that of the well-sorted sands found at WSB, where over 95% of sediment fell between 105-500 microns (fine-medium sand). Further, mixed substrates consisting of gravel may produce stronger and wider shells through abrasion under hydrodynamic influences, thereby enhancing survival of older-age and larger-size classes (Table 5; Figure 10). In keeping with these observations, broader clams with thicker shells were observed on an energetic coarse-sediment beach on the opposite side of Hornby Island, where high water velocities are generated along the beaches of Shingle Spit (St.John and Pond 1992; St.John et al. 1992). In summary, it appears that the varnish clam is very flexible in its survival strategies as it adapts to different substrate conditions, with high-intertidal elevations being more conducive to its potential as a successful invasive species. Additional information is required to determine a hierarchy of variables (e.g. food supply, substrate type, tidal elevation) that influence varnish clam recruitment, growth, and reproduction.

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Table 1: Locations of intertidal sampling stations in Whaling Station Bay (WSB), Hornby Island, British Columbia (see Figures 1 and 2).

Station	*Tidal elevation (above chart datum)*	*Latitude*	*Longitude*
WSB-A	High (3.5 m)	49°31'32"N	124°36'22"W
WSB-B	Mid (2.8 m)	49°31'33"N	124°36'23"W
WSB-C	Low (1.7 m)	49°31'34"N	124°36'24"W

Table 2: Clam attributes at 3 tidal elevations in Whaling Station Bay, Hornby Island, British Columbia. WSB = Whaling Station Bay; VC = Varnish clam; No. = Number; g = Grams; AFDW = Ash-free dry weight; SL = Shell length; SD = Standard deviation.

Variable	Attribute	WSB	WSB-A	WSB-B	WSB-C
Tidal elevation		*All elevations combined*	*High intertidal*	*Mid intertidal*	*Low intertidal*
Varnish clam *(Nuttallia obscurata)*	Percentage	99.16%	100.00%	100.00%	75.00%
	No. of clams	236	99	131	6
Butter clam *(Saxidomus gigantea)*	Percentage	0.84%	0.00%	0.00%	25.00%
	No. of clams	2	0	0	2
VC Density (No. m^{-2})	Mean (SD)	467 (386)	730	648	23.1
VC Biomass per quadrat (g AFDW m^{-2})	Mean (SD)	47.2 (38.7)	66.4	72.5	2.62
VC Biomass per clam (g AFDW $clam^{-1}$)	Mean (SD)	0.10542 (0.01260)	0.09090 (0.03890)	0.11190 (0.05224)	0.11346 (0.02491)
VC Age (years)	Mean (SD)	4.6 (0.17)	4.5 (0.82)	4.5 (0.77)	4.8 (0.98)
VC Shell length (mm)	Mean (SD)	32.56 (5.80)	31.19 (5.46)	33.42 (5.83)	36.31 (6.16)
VC Condition index (g AFDW SL^{-1})	Mean (SD)	0.0030 (0.00021)	0.0028 (0.00084)	0.0032 (0.0011)	0.0031 (0.00038)

Table 3: Statistical comparisons of biomass, age and condition index of varnish clams collected at different intertidal heights in Whaling Station Bay. WSB = Whaling Station Bay; VC= Varnish clam; g = Grams; AFDW = Ash-free dry weight; SL = Shell length; (SD) = Standard deviation; * = Statistical significance.

Variable		***WSB-A High intertidal***	***WSB-B Mid intertidal***	***P-value***
VC Biomass per clam (g AFDW $clam^{-1}$)	Mean (SD)	0.09090 (0.03890)	0.11190 (0.05224)	0.001*
VC age (years)	Mean (SD)	4.5 (0.82)	4.5 (0.77)	0.935
VC Condition index (g AFDW SL^{-1})	Mean (SD)	0.0028 (0.00084)	0.0032 (0.0011)	0.003*

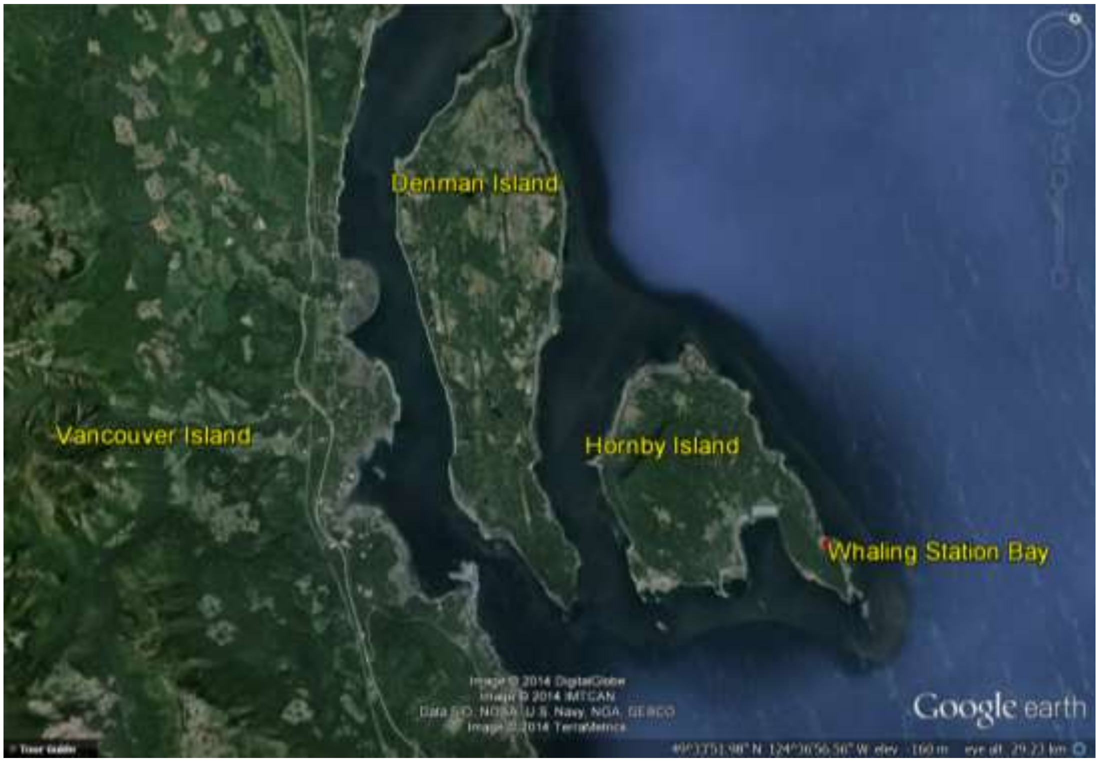

Figure 1: Location of Whaling Station Bay on Hornby Island, British Columbia (Google Earth[1]).

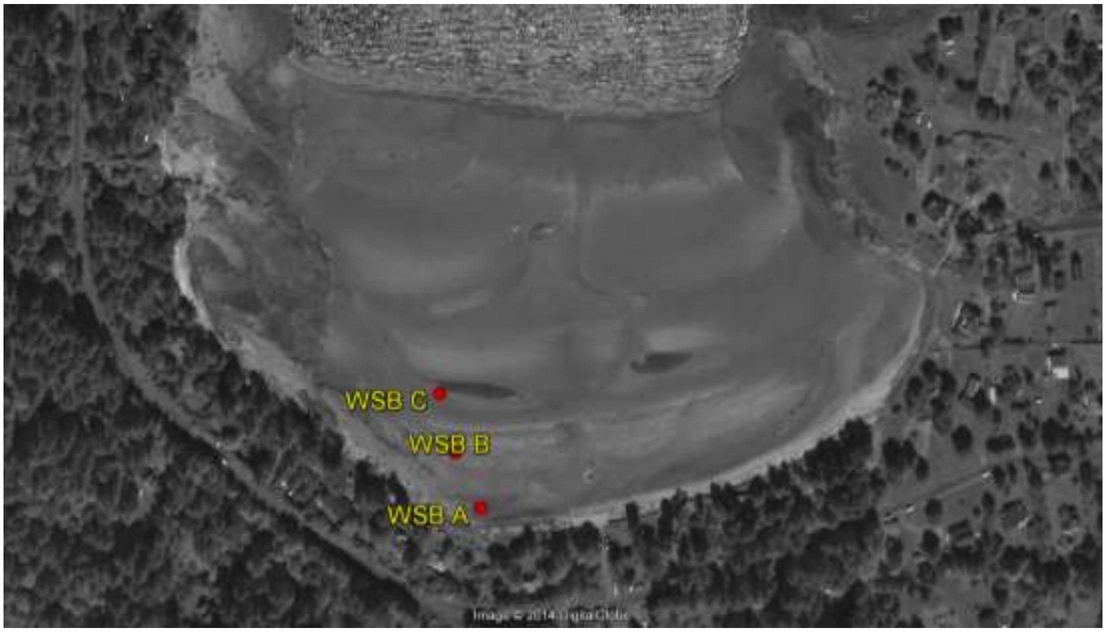

Figure 2: Locations of intertidal sampling stations at Whaling Station Bay (WSB), Hornby Island, British Columbia (Google Earth[2]).

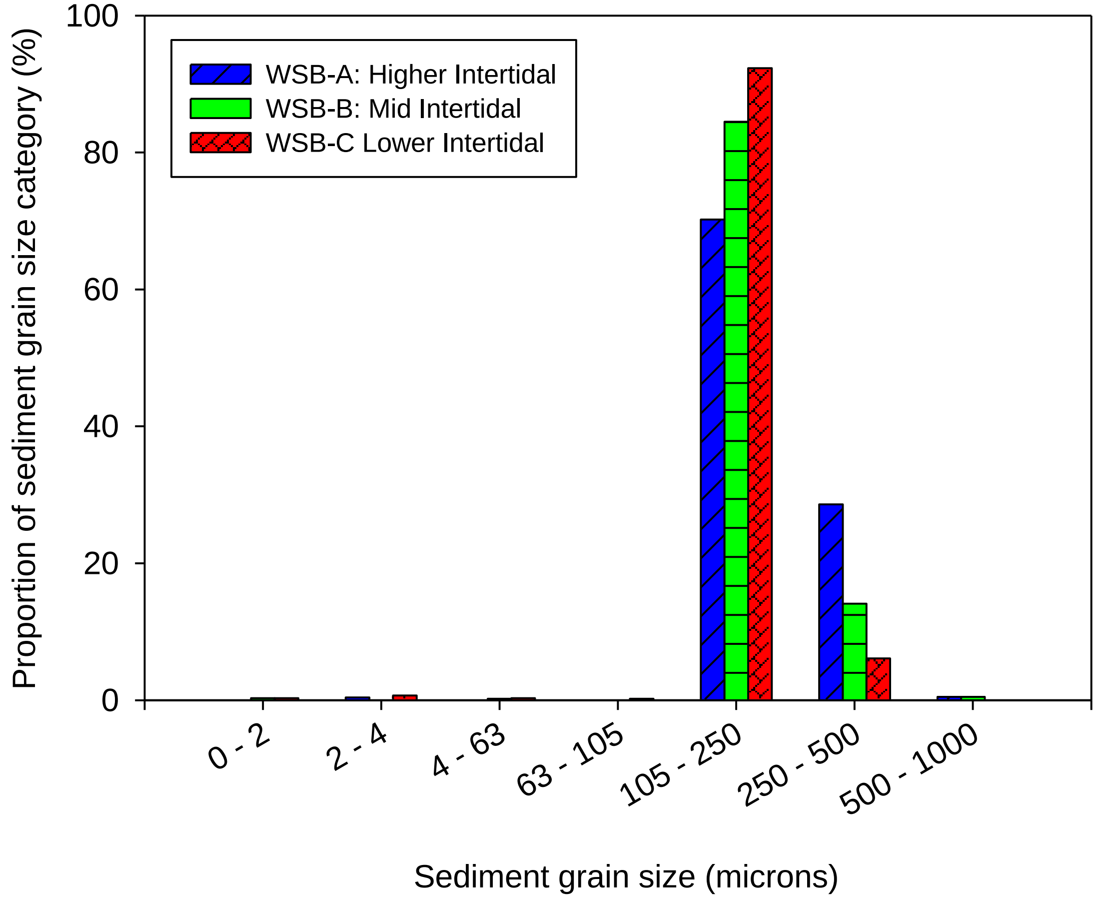

Figure 3: Sediment grain size distribution at three different tidal elevations at Whaling Station Bay (WSB), Hornby Island.

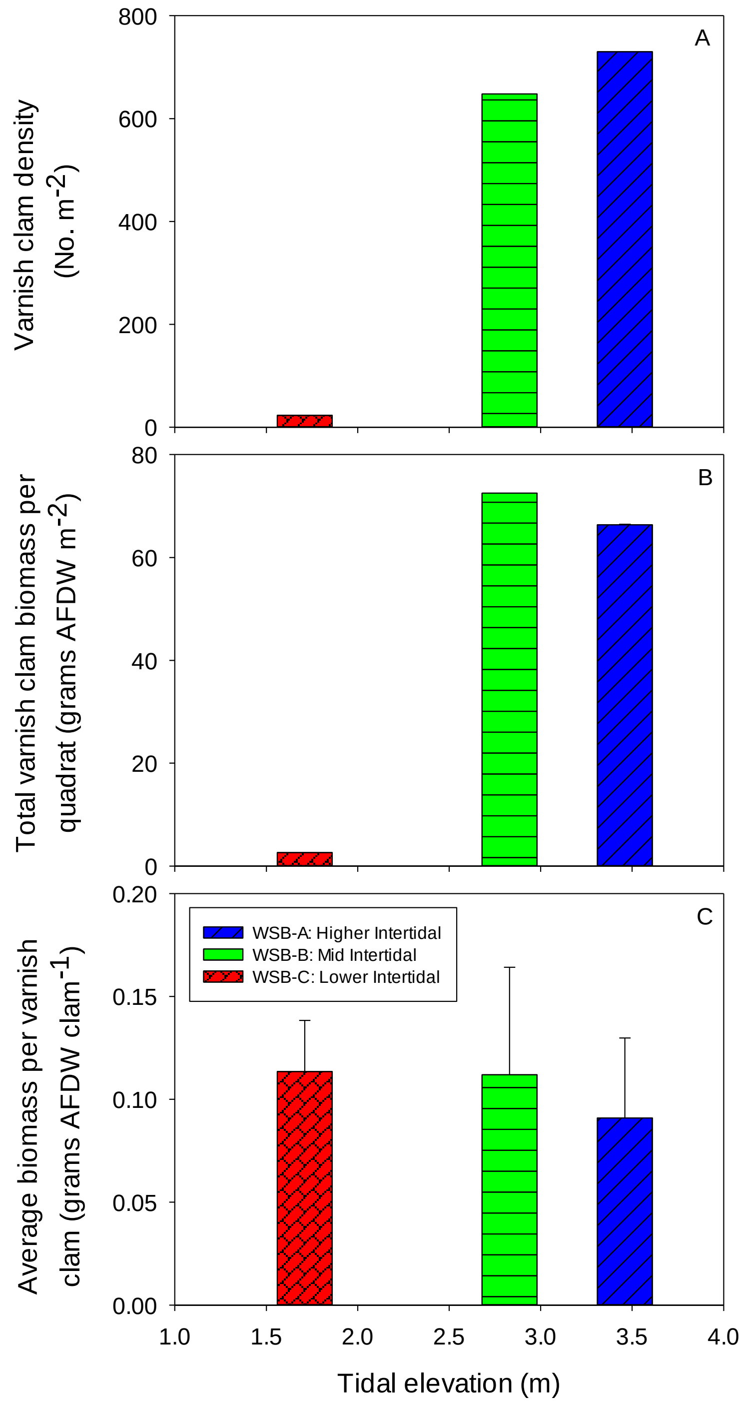

Figure 4: Varnish clam density (A), total varnish clam biomass per quadrat (B), and mean biomass per varnish clam (C) at three tidal elevations at Whaling Station Bay, Hornby Island.

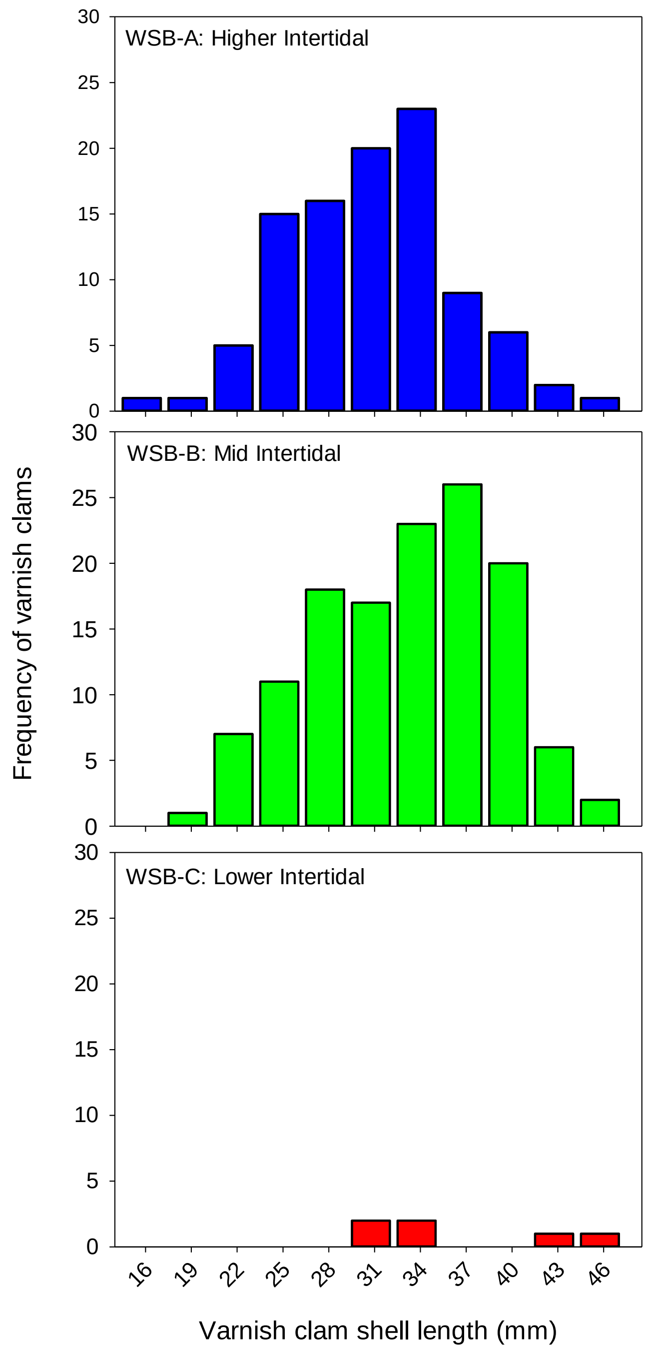

Figure 5: Length-frequency distributions of varnish clams collected at higher (WSB-A), mid (WSB-B) and lower (WSB-C) intertidal elevations at Whaling Station Bay (WSB), Hornby Island.

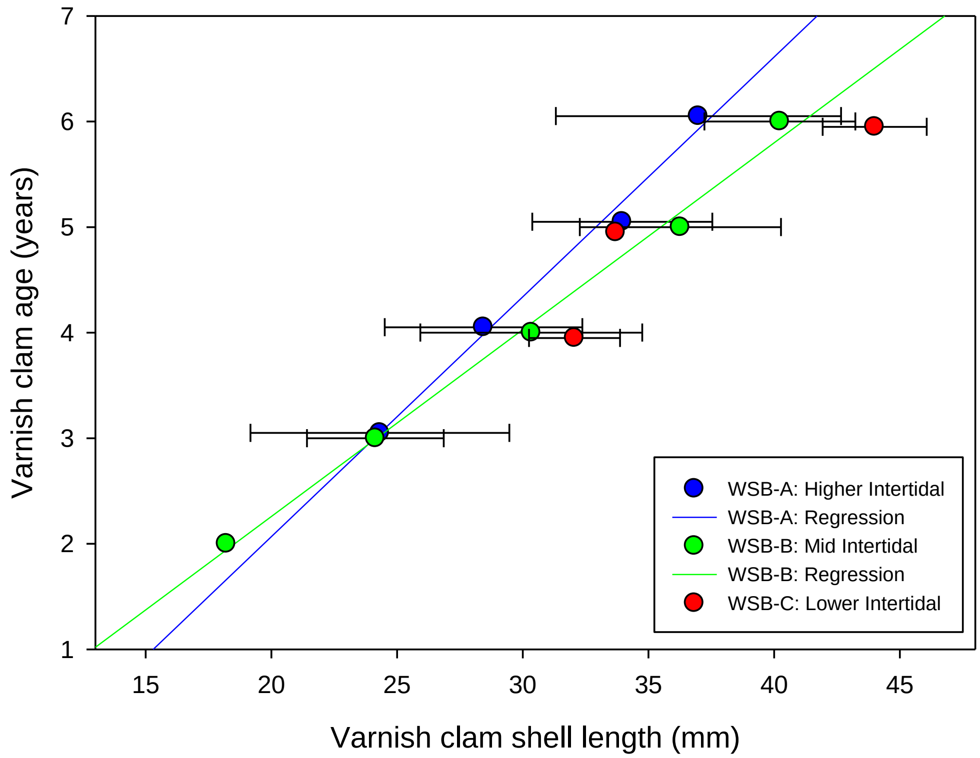

Figure 6: Relationship between mean clam shell length (mm) and age for varnish clams collected from Whaling Station Bay, Hornby Island.

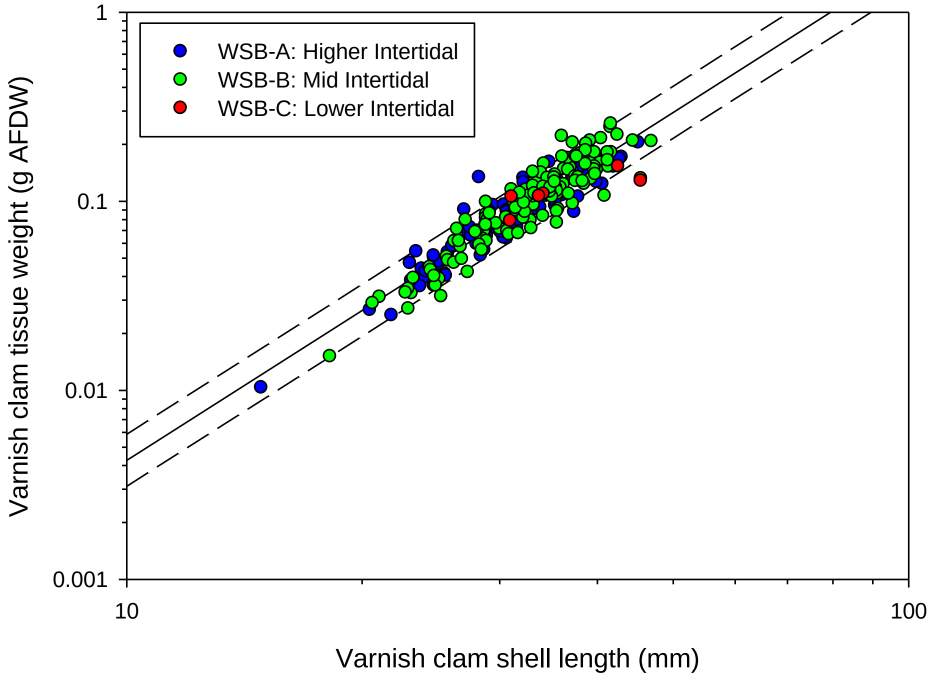

Figure 7: Relationship between varnish clam tissue weight and shell length at 3 tidal elevations at Whaling Station Bay, Hornby Island. Solid line represents a linear regression, while dotted lines represent 95% confidence limits. AFDW = Ash-free dry weight.

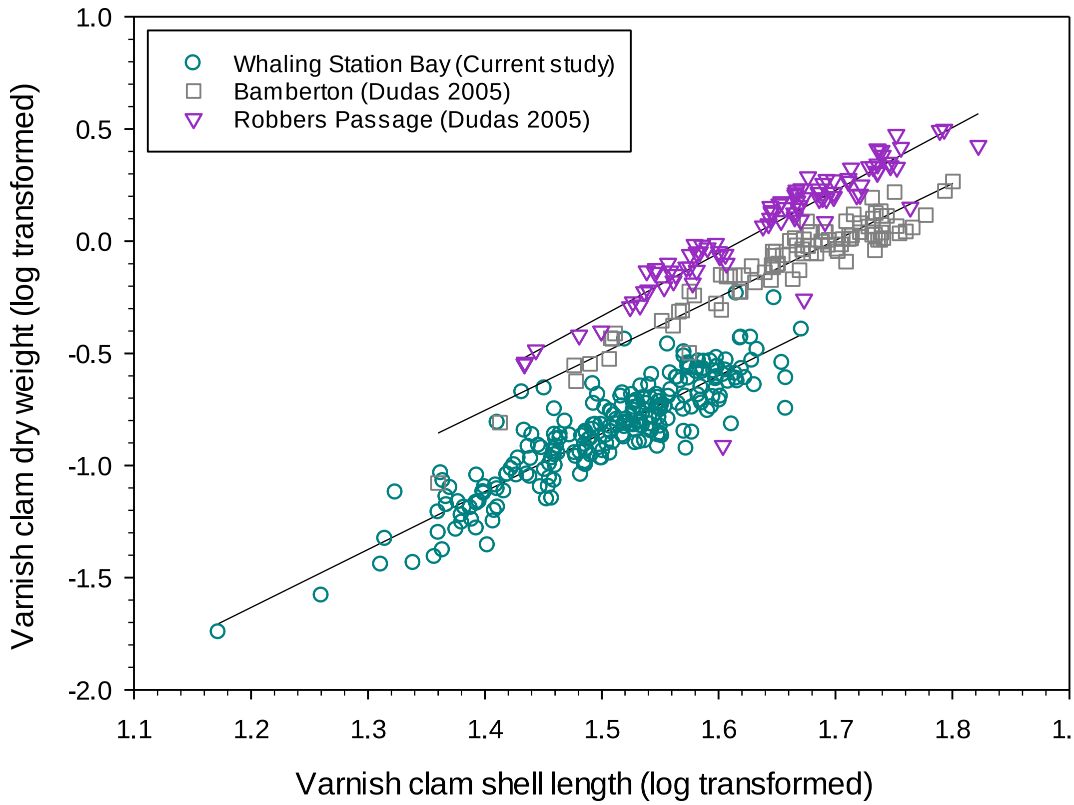

Figure 8: Relationship between shell length and tissue dry weight for varnish clams collected at Whaling Station Bay (Hornby Island, this study), Robbers Passage (Barclay Sound, Dudas 2005) and Bamberton (Saanich Inlet, Dudas 2005).

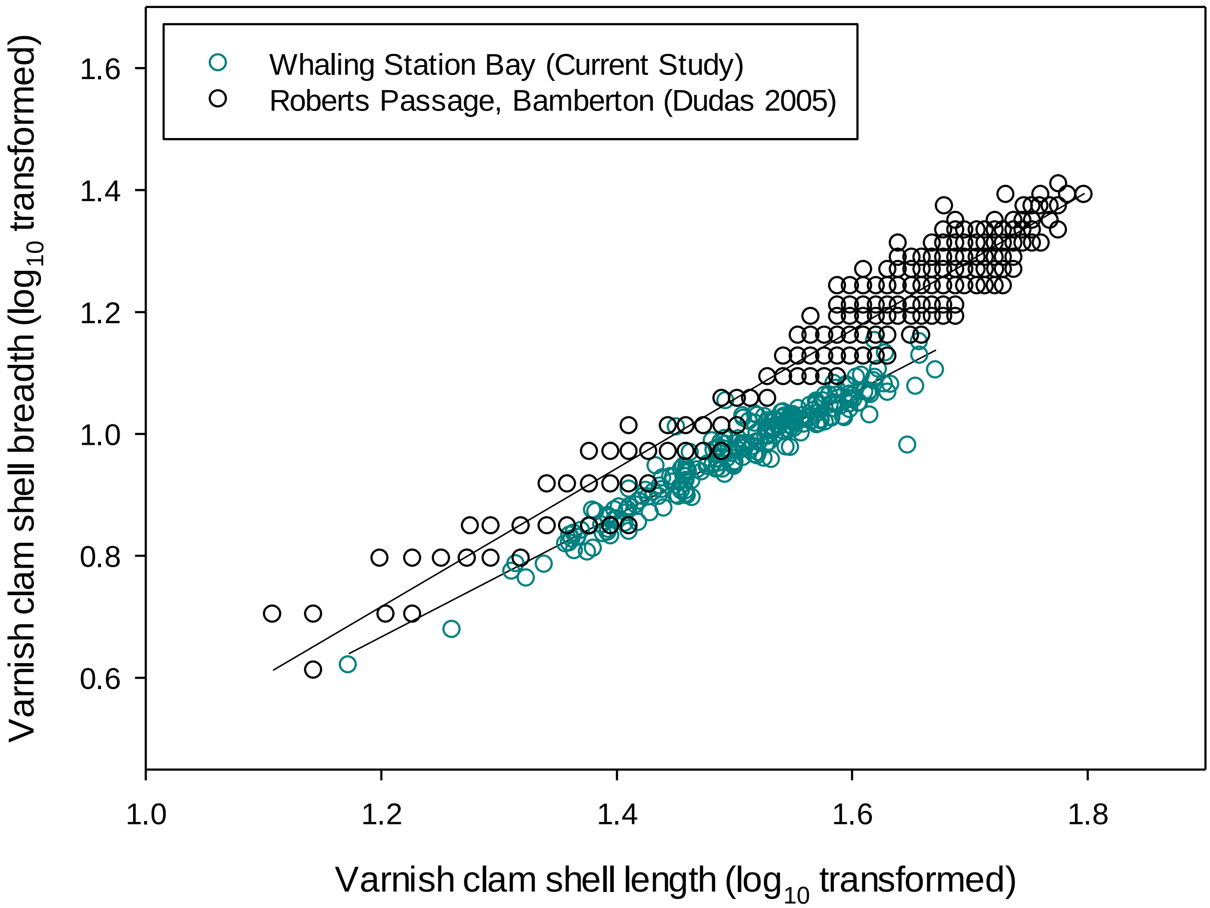

Figure 9: Relationship between shell length and breadth for varnish clams collected at Whaling Station Bay (Hornby Island, this study), Robbers Passage (Barclay Sound, Dudas 2005), and Bamberton (Saanich Inlet, Dudas 2005).

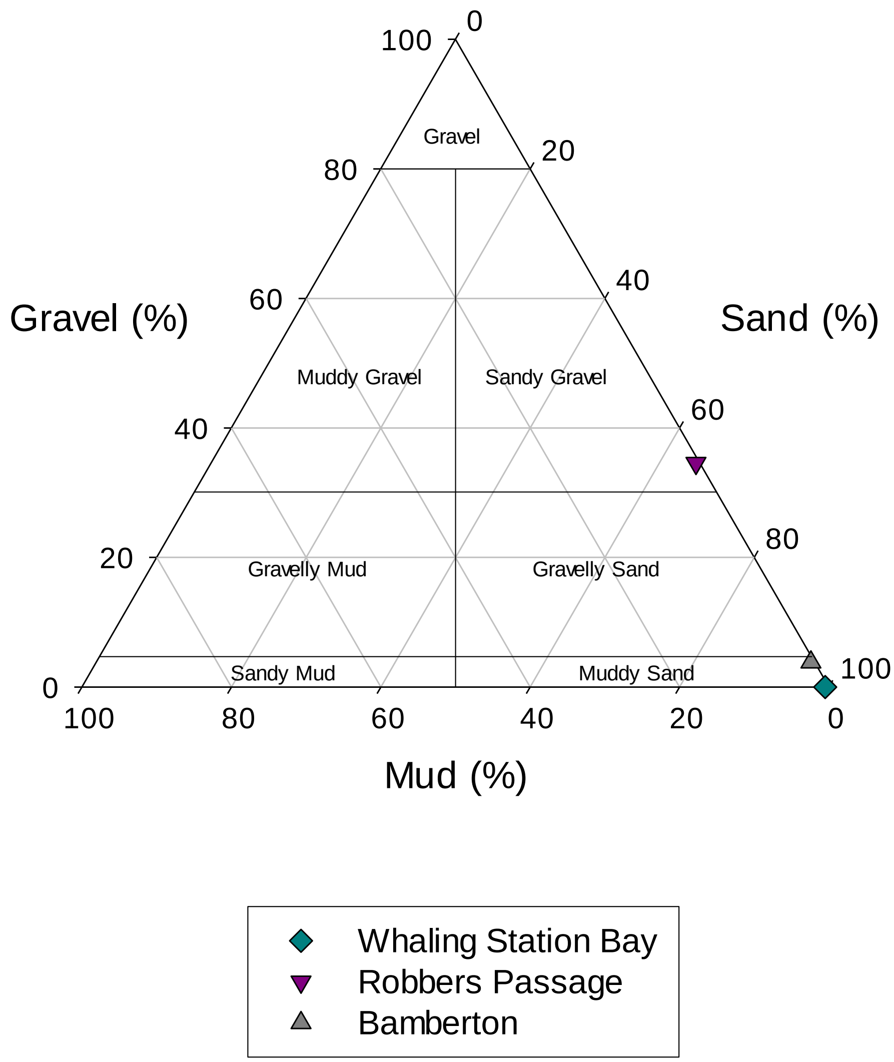

Figure 10: Ternary plot showing substrate composition observed at Whaling Station Bay (Hornby Island, this study), Robbers Passage (Barclay Sound, Dudas 2005) and Bamberton (Saanich Inlet; Dudas 2005).