

Contrasting the community structure and select geochemical characteristics of three intertidal regions in relation to shellfish farming

L.I. BENDELL-YOUNG*

Department of Biological Sciences, Simon Fraser University, 8888 University Avenue, Burnaby, British Columbia, Canada V5A 1S6

Date submitted: 12 January 2005 Date accepted: 3 March 2006

SUMMARY

Little is known about the impacts of intensive shellfish farming on intertidal ecosystems. To assess such impacts, several indices of ecosystem structure and select geochemical characteristics were contrasted among three intertidal regions, which represented a gradient of shellfish farming activities, namely (1) no active aquaculture, (2) actively farmed for three years and (3) actively farmed for five years. All three intertidal regions were located in Baynes Sound (British Columbia, Canada) and were geographically similar. Among the three beaches, species richness, community composition, bivalve abundance, biomass, distribution, and composition and surficial sediment per cent organic matter (carbon) and silt were compared. The intertidal regions that had been used for farming for three and five years had lower species richness, different bivalve composition, abundance and distributions, and a foreshore community dominated by bivalves, as compared to the intertidal region where no active farming occurred. Beaches that were actively farmed also had greater accumulations of organic matter and silt. Simplification of the intertidal benthic community, coupled with accumulations of organic matter and increased siltation, may have altered the ecology of the foreshore region used for intense shellfish harvesting. To access the foreshore for shellfish farming in a sustainable manner, studies are needed to determine the scale to which intensive use of the foreshore for shellfish purposes alone is feasible without undue harm to the environment.

Keywords: aquaculture, biodiversity, ecological impacts, shellfish

INTRODUCTION

The interface between ocean and land, the intertidal or foreshore region, faces a number of cumulative threats. These include accelerated rates of coastline erosion and increases in the incidence of severe weather events as a consequence of global warming (see Jickells & Rae 1997) and the

ever-increasing pressures from human population growth. Intertidal ecosystems are also habitat for wildlife, serve as nurseries and have an important role in the cycling of essential nutrients such as nitrogen (Emmerson *et al.* 2001). Ensuring the integrity of these systems is not only important from an ecological point of view, but also from an anthropocentric perspective, as intertidal systems play key roles in supporting various fisheries of economic importance.

This study focuses on some of the environmental concerns associated with shellfish aquaculture as currently applied for the economically desired species *Venerupis philippinarum* (the Manila clam) on the foreshore of the west coast of British Columbia (Canada). Declines in the global stocks of fish (Hutchings 2000) have led to intense pressures to develop aquaculture as an alternate protein source (Naylor *et al.* 2000). In many countries, including Canada, this enterprise, notably shellfish aquaculture, is in its fledgling stage facing increasing concerns as to the environmental sustainability of existing practices (Simenstad & Fresh 1995; Kaiser *et al.* 1998; Sorokin *et al.* 1999; Bartoli *et al.* 2001).

Farming of the foreshore for Manila clams involves a number of invasive farming practices. The region to be used for shellfish farming is first cleared of all surface species and competing bivalves. The area is then seeded with hatchery-reared seed. To protect the crop from predators (such as other invertebrates and avian predators), the seeded region is covered with fine plastic mesh anti-predator netting. Currently, there are no regulations as to amounts of the intertidal region that can be covered by netting; as a result, substantial regions of the intertidal can be subject to cover (Jamieson *et al.* 2001). Other practices include the use of vexar netting and substrate modification for beach stabilization, use of vehicles on the intertidal region for accessing farm sites, as well as dense coverage of the intertidal with the Pacific oyster (*Crassostrea gigas*), another desired shellfish crop, for a hardening-off period prior to entry into markets.

Little is known of the cumulative effects of such practices on the ecology of the intertidal region, for example its species richness, distributions and abundances. Of the various practices described above, possibly the use of anti-predator netting is the most invasive. In addition to habitat loss, nets become covered in a dense layer of algae (*Ulva* spp.), but how this changes the ecology of the intertidal region is unknown.

The objective of this study was to provide some assessment of the effects of anti-predator netting on the intertidal community of the foreshore. To meet this objective, we compared

*Correspondence: Dr Leah Bendell-Young Tel: +1 604 291 5621 Fax: +1 604 291 3496 e-mail: bendell@sfu.ca

three beaches experiencing different intensities of shellfish farming harvest on Denman Island, Baynes Sound and Lambert Channel located off the east side of Vancouver Island, British Columbia, Canada. The Island and associated Sound are part of the Gulf Island Archipelago and, as such, form a unique ecological region of Canada. The Baynes Sound region has been ranked as the most important wetland complex on Vancouver Island and is internationally recognized as important for migratory waterbirds (Dawe *et al.* 1998), as well as providing habitat for at least six salmonid species (Jamieson *et al.* 2001). Despite its ecological importance, and as a consequence of its high biological productivity, Baynes Sound and regions adjacent to the Sound are home to British Columbia's largest shellfish aquaculture industry with 45% of the total cultured production of clams and oysters originating from this region (Jamieson *et al.* 2001).

Components of intertidal biodiversity were contrasted among the three beaches, which included a beach with no anti-predator net used only for recreational and wild shellfish harvesting within a provincial park (i.e. 'low intensity'), a commercially-leased beach actively farmed for three years (i.e. 'intermediate intensity') and a commercially-leased beach actively farmed for five years ('high intensity'). Ecosystem structure was examined through measurement of species richness, abundance and distribution, basic community composition, and surface sediment organic matter content and silt accumulation.

METHODS

Two beaches within Baynes Sound and one within Lambert Channel were selected for study based on similarity of beach type (slope, tide exposure, substrate) and the degree of the intensity of shellfish farming. Beach A (49° 32' N, 124° 30' W), an area of 9000 m², represented the least impacted beach influenced by recreational and wild-harvesting pressures. Farmed Beach B (49° 35' N, 124° 50' W) an area of 12 000 m², was a medium impact beach. At time of sampling it had been in operation for approximately three years, and was seeded with approximately 10% of the area under nets. Beach C (49° 30' N, 124° 46' W) was the most impacted beach, and was seeded and had anti-predator nets covering approximately 80% of the beach. At time of sampling, Beach C's lease had been in operation for approximately five years. The sampling area of Beach C, being steeper than the other two, was 200 m². Nets (mesh size approximately 1 cm²) were in direct contact with the surface of the beach at low tide and were lifted only slightly when covered by the tide.

Sampling occurred during summer months (late May, June and July), based on the field methods of Gillespie and Kronlund (1999). At each beach, a reference line was established roughly parallel to the water's edge 3.2 m above chart datum. Transects were aligned perpendicular to this line and their positions along the reference line chosen using

a random number table. Transects were 0.5 m wide and ran along parallel compass bearings to 1.4 m above chart datum. Six 0.5 × 0.5 m quadrats were dug to a depth of 30 cm along the length of each transect. To account for community changes due to tidal elevation, quadrats were evenly spaced along each transect with the position of the first quadrat in the first 1/6 interval randomly determined. Each beach was sampled at six tide elevations with one quadrat per transect falling in each of the six elevations. Each tide elevation over the course of the three months was sampled at least in triplicate with a minimum of 54 samples per beach (i.e. 3 transects × 6 tide elevations × 3 quadrats = 54). Within each quadrat all surface plant and animal species were identified and recorded. Each quadrat was dug and the substrate screened using a 5-mm mesh to include subsurface fauna with all retained fauna counted and identified to species. The length of all bivalves to the nearest 0.1 mm were also recorded. All organisms and sediments removed from the quadrat were replaced to minimize sampling impact. To determine organic matter content and grain size (% silt), sediment core (cylinder sampler 5.2 cm diameter) samples to a depth of 10 cm were collected from each beach; however tide elevations 1 and 2, 3 and 4, and 5 and 6 were combined, resulting in three tide elevations rather than six as for species analysis. On each beach, 3–6 core samples of 212 cm³ volume were collected per tide elevation over two sampling periods. Particle size was determined using a modified hydrometer method, the settling of different particle sizes in a stationary liquid to determine per cent silt (Brady 1998) and organic matter was determined through loss on ignition (ashing of sample at 600 °C for 4 h).

Data analysis

To determine differences in community and geochemical characteristics among the three study beaches, a sampling design similar to that of Bendell-Young *et al.* (1989), Bendell-Young and Pick (1997) and Bendell-Young (1999) for freshwater lakes and wetlands was applied. Sampled beaches were similar with respect to slope, tide exposure and the type of substrate, save for the intensity of shellfish farming practices. Observed differences among the three beaches were then related to difference in farming practices.

All statistical analysis with the exception of the jackknife estimates of species richness was implemented by Statistical Analysis Systems 8.0 (SAS 8.0). Jackknife estimates were determined after Krebs (1998) using Excel[®] (Bendell-Young & Wilson 2001). Jackknife estimates have been shown to be robust estimators of species richness, especially when the number of sampled quadrats is low (i.e. in estimating the true number of species, thereby reducing bias), and also allow for estimates of variance (Krebs 1998).

Jackknife estimates of species richness (Krebs 1998) were calculated for each tidal elevation on each beach then compared in pairs (for example A versus B) using Student's t test ($\alpha = 0.008$ for each pairwise, overall $\alpha = 0.05$ for each

tide elevation). Each tidal elevation was examined separately to keep vertical community changes from influencing richness values within each intertidal zone. Values were means of 12 quadrats at each tide elevation for beach A and 14 for beaches B and C. To determine the effect of intensive clam culture on community composition, species were categorized as surface dwelling, sub-surface dwelling or bivalves. Surface-dwelling flora and fauna species included barnacles, mussels, crabs and algae. Sub-surface species were primarily polychaetes, but included others such as the ghost shrimp. To compare community structure, frequency plots of the numbers of species and frequencies of occurrence were constructed for each beach; however, species were grouped into surface, sub-surface and bivalve categories.

All bivalves recovered in each quadrat were counted and length to the nearest 0.1 mm measured. A sub-sample of the four most frequently occurring bivalves was taken for allometric analysis. At least 20 each of *V. philippinarum*, *Protothaca staminea* (native littleneck clam), *Nuttallia obscurata* (varnish clam) and *Macoma* spp. were weighed to the nearest 0.1 g (wet weight shell plus meat) to obtain length-weight relationships that in turn allowed for bivalve biomass estimates for each beach. Average lengths of the four dominant bivalve species displayed the known size difference among the four most common bivalves, where *N. obscurata* \approx *P. staminea* > *V. philippinarum* > *Macoma* spp. Length-weight relationships used to convert average length of each of the four species into an average biomass were determined as:

$$\begin{aligned} V. philippinarum: \log(y) &= 3.17\log(x) - 3.98 \quad (r^2 = 0.99) \\ P. staminea: \log(y) &= 3.11\log(x) - 3.71 \quad (r^2 = 0.99) \\ Macoma \text{ spp.}: \log(y) &= 3.11\log(x) - 4.11 \quad (r^2 = 0.98) \\ N. obscurata: \log(y) &= 3.37\log(x) - 4.36 \quad (r^2 = 0.97) \end{aligned}$$

To assess differences in abundance and distribution of bivalves among the three beaches, average total number of bivalves, % composition of all bivalves based on total number of individuals, average biomass and % composition of the four most common bivalves based on the biomass per 0.25 m² were determined and plotted for each of the six tide elevations. The biomass of each of the four species in the 0.25 m² quadrat was summed to obtain the total biomass for each tidal elevation. Overall average biomass for beach B and C was calculated as the average of the six tide elevations; for beach A, overall biomasses were calculated for four tide elevations, the two lowest being omitted as no bivalves were recovered.

Average numbers of individuals per 0.25 m² at each tide elevation and among the three beaches, and average bivalve biomass among the three beaches were determined through one-way ANOVA ($\alpha = 0.05$).

Silt and organic matter content at the three tidal elevations at each of the beaches were compared by one-way ANOVA (3–6 replicates/location at two sampling periods) with $\alpha = 0.05$.

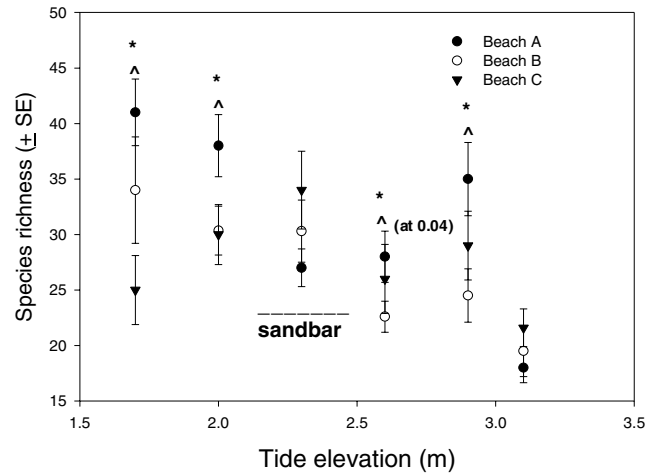


Figure 1 Jackknife estimates of mean species richness for each tide elevation on each beach. Student's t test results ($\alpha = 0.008$ for each pairwise comparison, $\alpha = 0.05$ for each elevation): * = A differs from B, ^ = A differs from C. Beach A, $n = 12$; beaches B and C, $n = 14$.

RESULTS

Total number of species recovered from the beach A, B and C were 50, 32 and 35. Jackknife estimates indicated that beach A had significantly greater species richness than beaches B and C ($p = 0.008$) with the exception of the highest tide level and at elevation 4 where a sandbar occurred (Fig. 1). Beach A contained a greater number of epifaunal and floral species as compared to the farmed beaches B and C, in which bivalves and sub-surface species had greater relative abundance (Fig. 2). Beach A contained greater numbers of species generally and of rare species than beaches B or C (Fig. 2).

Bivalve abundance for beach A was significantly higher and lower at the high and low tide elevations, respectively, than farmed beaches B and C (Fig. 3a; ANOVA $p < 0.05$). Based on the number of individuals present at each tide elevation, bivalve composition also differed among the three beaches; for beach A, the non-native Manila and the native littleneck were the dominant species, with abundances reaching up to 300 individuals per 0.25 m² quadrat, but only at high tidal elevations (Fig. 3b). In contrast, for beaches B and C, total number of bivalves was more evenly distributed along the intertidal (Fig. 3a), with the Manila dominating at beach B and Manila and *Macoma* spp. dominating in beach C (Fig. 3b).

Biomass estimates at each tide elevation for the three beaches follow a similar pattern as the number of individuals at each tide elevation for each beach, although overall biomass was not statistically different among beaches (Fig. 4a; ANOVA $p > 0.05$). On a biomass basis the dominant bivalves for all three beaches were the manila and littleneck, with the varnish clam being of importance at the highest tide elevation in beach C (Fig. 4b). This was in contrast to numerical

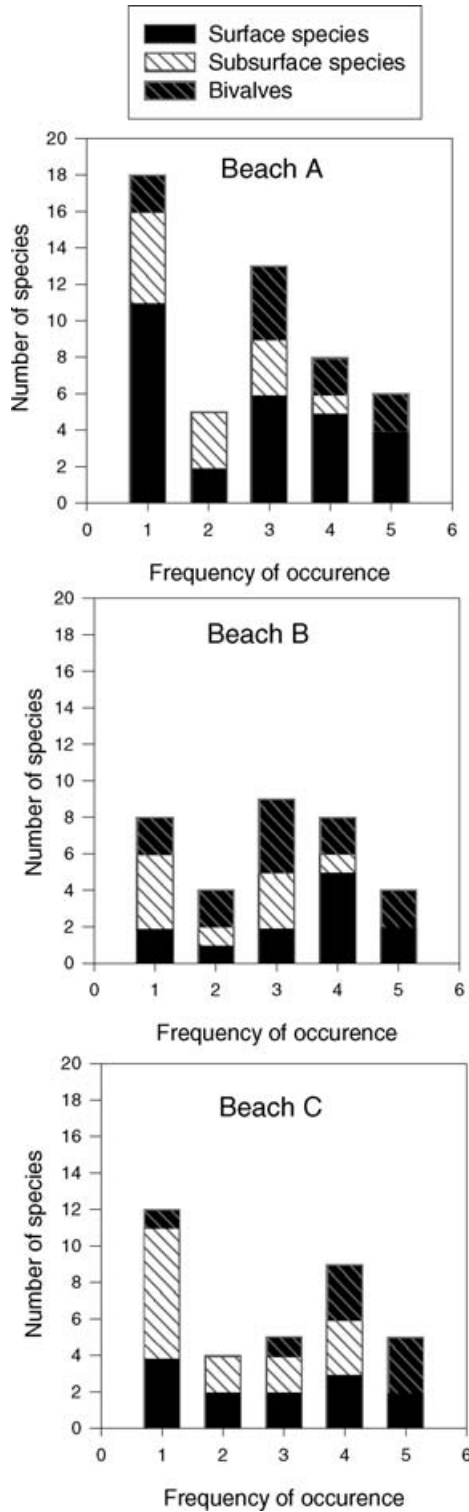


Figure 2 Species frequency plots for the three beaches. Frequency of occurrence grouped as: 1 = 1–5, 2 = 6–10, 3 = 11–100, 4 = 101–1000 and 5 = 1000+.

abundance data (Fig. 4*b*). Beach A had lower organic matter and silt content than the two other beaches (Fig. 5*a, b*; ANOVA $p < 0.05$).

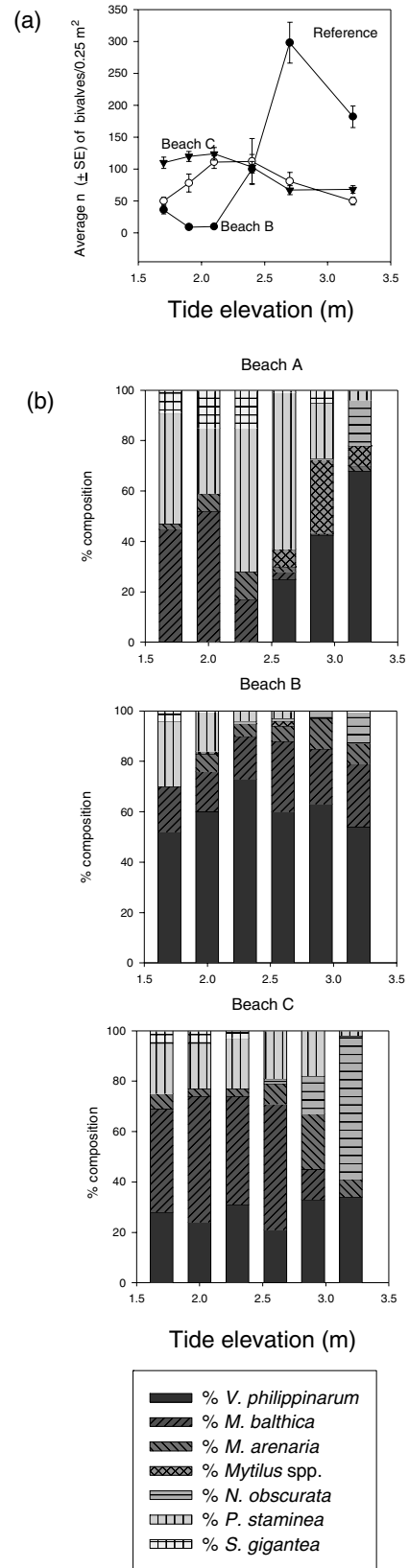


Figure 3 (a) Average number of bivalves (number of individuals per 0.25 m²) versus tide elevation for the three beaches and (b) per cent composition (based on number of individuals per 0.25 m²) versus tide elevation for the three beaches.

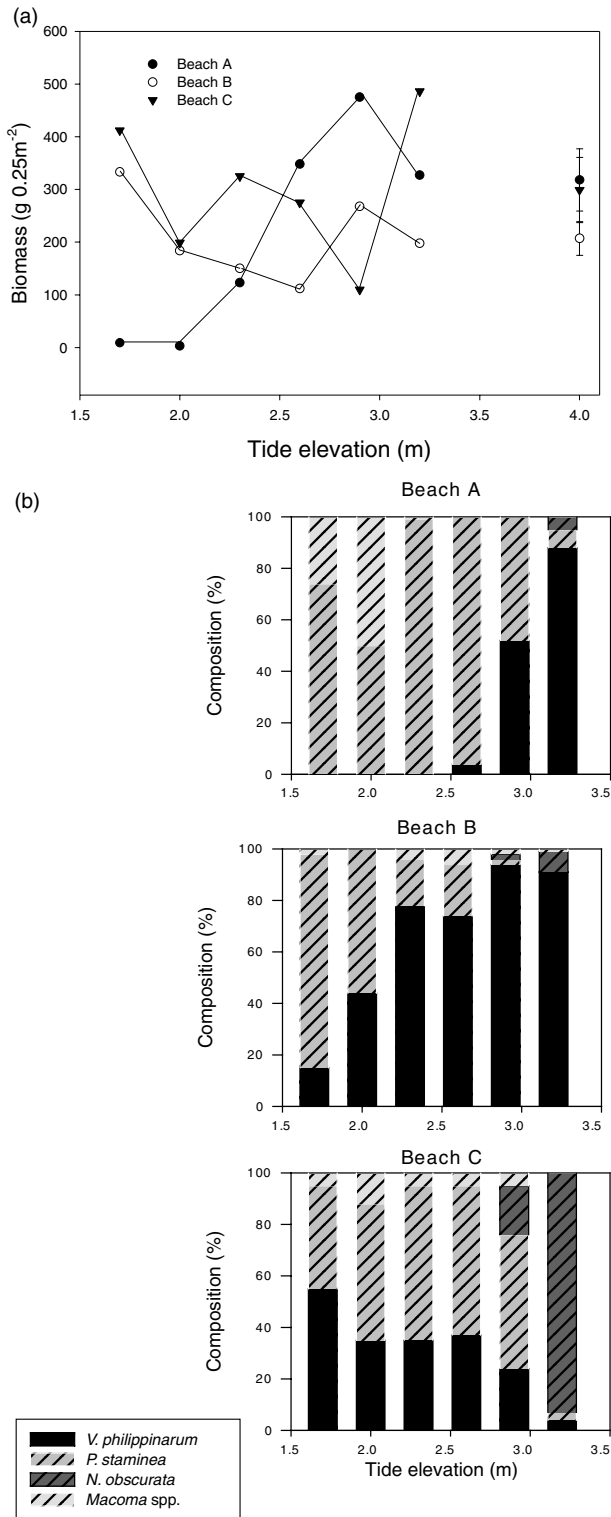


Figure 4 (a) Biomass estimates for the four most commonly occurring bivalves (weight of bivalves in g per 0.25 m²) determined at each tide elevation for the three beaches. Values at 4.0 m tide elevation are means of the six tide elevations for beach B and C and the four tide elevations for beach A. (b) Per cent composition based on the contribution of the four most commonly occurring bivalves to the total biomass of bivalves per 0.25 m² for each tide elevation for the three beaches.

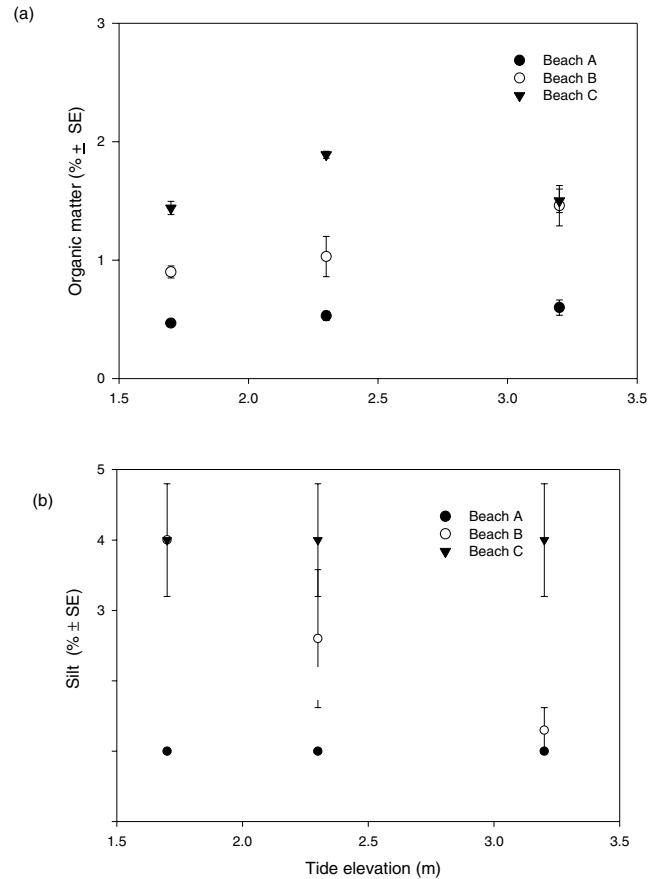


Figure 5 Comparison of (a) % organic matter (carbon) and (b) % silt in surface sediments of the three beaches at low, mid and high tide.

DISCUSSION

Baynes Sound is one of the most ecologically sensitive regions along the west coast of British Columbia, yet 90% of its intertidal beaches are under shellfish tenure (Jamieson *et al.* 2001), with further expansions currently in progress. This use of the intertidal solely for shellfish farming purposes has been made in the absence of sound scientific study of how much of the intertidal region can be used for shellfish farming purposes without compromising its ecology. This study is first to raise such a question for this region and it has attempted to address some of the ecological concerns, such as whether shellfish farming which uses predator netting affects the diversity of the intertidal. The findings should also be applicable to geographically similar areas also facing the same threats to their coastal regions.

Since ecological characteristics of the intertidal zone can vary spatially for natural reasons, the intertidal areas studied here were chosen based on similarities in beach type (i.e. slope, tide exposure and substrate) and the intensity of shellfish harvest, such that any observed differences could be more readily attributed to shellfish farming practices.

Major findings were that the greatest intensity of farming was associated with a decrease in species richness, altered species abundance and distribution, change in community intertidal structure composed of surface species, sub-surface species and bivalves, to one composed primarily of bivalves, and greater accumulations of surface sediment silt and organic matter.

Other studies have reported intensive shellfish farming leading to loss of benthic diversity, increased sedimentation and anoxia (Sorokin *et al.* 1999; Bartoli *et al.* 2001; Beadman *et al.* 2004) and change in species composition towards domination of netted regions of foreshore by deposit feeding worms (Spencer *et al.* 1997). Loss of species richness could have important consequences for the ecological functioning of the intertidal zone (McCann 2000; Tilman 2000).

Emmerson *et al.* (2001) investigated the role of diversity in the flux of nutrients, specifically ammonia nitrogen ($\text{NH}_4\text{-N}$), in mesocosms containing a gradient of intertidal invertebrate species richness. As richness was reduced from three species to one, variance in the flux of nitrogen increased, as did variability in the coefficients of determination (R^2), that is, the response of the ecosystem became less predictable. Taking these lines of evidence together, current shellfishery practices, which reduce species richness, could decrease intertidal ecosystem stability that in turn could affect the overall productivity of these systems.

The physical presence of the anti-predator nets is associated with accumulation of fine silt and organic matter directly under the net (Simenstad *et al.* 1993; Spencer *et al.* 1997). The build-up of organic material in parts of the Sacca di Goro (Italy) subject to intense clam farming practices has led to dystrophic events causing anoxia and massive mollusc mortality in cultivated areas (Bartoli *et al.* 2001). Bartoli *et al.* (2001) recommended that shellfish farmers should carefully consider sustainable densities of clams (*Tapes philippinarum*) to prevent the risk of sedimentation and water anoxia, a recommendation relevant to farming practices currently practised on the west coast of Canada.

A significant finding was the link between shellfish farming and the abundances and distribution of bivalves. For beach A, the non-native Manila and the native littleneck were the dominant species, with maximum abundance and biomass occurring only at high tidal elevations. In contrast, for beaches B and C, total numbers of bivalves were more evenly distributed along the intertidal. That beach B and C showed a fairly even bivalve distribution from low to high tidal elevation dominated primarily by the manila clam, is not unexpected given the practice of seeding with only manila and the removal of other indigenous species. The location of the bivalves on beach A can possibly be ascribed to the presence of the intertidal predator, the moon snail (*Euspira lewisii*, previously *Polinices lewisii*). Unlike the farmed beaches where the shellfish farmers remove this predator, there is no such practice on beach A. Large moon snail densities occur there. The moon snail is sub-tidal, although it will travel at the surface to higher tidal elevations in search of prey (Snively 1978). Generally, however, it remains below mid-tide, and in

the case of beach A, and as suggested by the location of the bivalves, below 2.5 m in elevation above the low tide mark. In the presence of anti-predator netting and shellfish farmers, no such predation pressure occurs.

Potential consequences of intensive shellfish farming on foreshore ecology and future research needs

Given the importance of Baynes Sound as an internationally recognized bird area, and staging and wintering area for many migratory species (Dawe *et al.* 1998), Vermeer and Butler (1989) have recommended that Baynes Sound and surrounding areas of critical bird habitat be protected so that existing bird populations can be maintained. Despite this, the expansion of the shellfish aquaculture continues in this ecologically sensitive region of the west coast of British Columbia.

Anti-predator nets could restrict access of shore birds and sea ducks to the intertidal region, possibly during key periods of their life history, such as before and after breeding and during migration. This could prove detrimental to existing populations, which are already in decline (Goudie *et al.* 1994). However, in the absence of information on the amount of bivalves required to sustain the existing populations dependent on Baynes Sound for some part of their life history, it is difficult to assess just what impacts loss of intertidal habitat could have.

Research directed at understanding the role of the intertidal region in ecosystem function is still in its early stages (Emmerson *et al.* 2001). For example, the shift in community composition from one in which both surface and subsurface species are present to one in which only sub-surface species are present could have important consequences for the cycling of key nutrients such as carbon and nitrogen. Surface species that are absent from the farmed beaches include filter-feeders such as the blue mussel (*Mytilus* spp.) and barnacles (*Balanus* spp.) that engineer benthic-pelagic coupling. In the absence of these surface species, the two-way movement from the overlying water column to the surface sediments could be much reduced, possibly limiting the flux of much needed nutrients to the benthic community.

Very little is known about the ecological importance of the intertidal zone. It is important for example as nurseries and feeding grounds, however, comprehensive understanding of which species use the intertidal for what purposes and when is still limited. The importance of the intertidal zone in the nutrient flux of coastal systems as a whole and what changes in community structure, such as those caused by shellfish farming, will do to that nutrient flux are poorly understood. Use of the intertidal for sustainable shellfish farming needs firm understanding of its ecology.

ACKNOWLEDGEMENTS

I thank the students and their field assistants who contributed to various components of this project and two anonymous

reviewers for comments which improved the manuscript. Portions of this study were used towards a cooperative education term for K. Lipsett (sediment geochemical attributes) and an independent study semester for D. Munro (community composition). G. Gillespie and B. Adkins of Fisheries and Oceans provided financial support. I am most grateful to the leaseholders for allowing the students access to their leases.

References

- Bartoli, M., Nissoli, D., Viaroli, P., Turolla, E., Castaldelli, G., Fano, A. & Rossi, R. (2001) Impact of *Tapes philippinarum* farming on nutrient dynamics and benthic respiration in the Sacca di Goro. *Hydrobiologia* **455**: 203–212.
- Beadman, H.A., Kaiser, M.J., Galanidi, M., Shucksmith, R. & Willows, R.I. (2004) Changes in species richness with stocking density of marine bivalves. *Journal of Applied Ecology* **41**: 464–475.
- Bendell-Young, L.I., Harvey, H.H., Dillon, P.J. & Scholer, P.J. (1989) Contrasting behaviour of Mn in the surficial sediments of 13 south-central Ontario lakes. *Science of the Total Environment* **78/79**: 129–139.
- Bendell-Young, L.I. & Pick, F. (1997) Contrasting the geochemistry of aluminum among wetlands. *Water, Air and Soil Pollution* **81**: 219–240.
- Bendell-Young, L.I. (1999) Contrasting the geochemistry of Fe, Mn and Zn along a fen to bog gradient. *Applied Geochemistry* **14**: 719–734.
- Bendell-Young, L.I. & Wilson, D. (2001) A laboratory and field exercise in biodiversity. Laboratory manual BISC 329, Experimental Techniques, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada: 14 pp.
- Brady, N.C. (1998) *The Nature and Properties of Soils*, 12th edition. New York, NY, USA: MacMillan.
- Dawe, N.K., Buechert, R. & Tretheway, D.E.C. (1998) Bird use of Baynes Sound-Comox Harbour, Vancouver Island, British Columbia. 1980–1981. Technical Report Series No. 286, Canadian Wildlife Service, Pacific and Yukon Region, British Columbia, Canada.
- Emmerson, M.C., Solan, M., Emes, C., Paterson, D.M. & Raffaelli, D. (2001) Consistent patterns and the idiosyncratic effects of biodiversity in marine ecosystems. *Nature* **411**: 73–77.
- Gillespie, G.E. & Kronlund, A.R. (1999) A manual for intertidal clam surveys. Canadian Technical Report Fisheries and Aquatic Science 2270, Canada: 144 pp.
- Goudie, R.I., Brault, S., Conant, B., Kondratyev, A.V., Peterson, M.R. & Vermeer, K. (1994) The status of sea ducks in the North Pacific rim: toward their conservation and management. *Transactions of the North American Wildlife and Natural Resources Conference* **59**: 27–49.
- Hutchings, J. (2000) Collapse and recovery of marine fishes. *Nature* **406**: 882–885.
- Jamieson, G.S., Chew, L., Gillespie, G., Robinson, A., Bendell-Young, L., Heath, W., Bravender, B., Tompkins, A., Nishimura, D. & Doucette, P. (2001) Phase 0 review of the environmental impacts of intertidal shellfish aquaculture in Baynes Sound. Canadian Science Advisory Secretariat Research Document 2001/125, ISSN 1480-4883, Canada [www document]. URL <http://www.dfo-mpo.gc.ca/csas/>
- Jickells, T.D. & Rae, J.E. (1997) *Biogeochemistry of Intertidal Sediments*. Cambridge, UK: Cambridge Environmental Chemistry Series, Cambridge University Press: 139 pp.
- Kaiser, M.J., Laing, I., Utting, S.D. & Burnell, G.M. (1998) Environmental impacts of bivalve mariculture. *Journal of Shellfish Research* **17**: 59–66.
- Krebs, C.J. (1998) *Ecological Methodology*. New York, NY, USA: Harper Collins Publishers, Inc.: 645 pp.
- McCann, K.S. (2000) The diversity-stability debate. *Nature* **405**: 228–233.
- Naylor, R., Goldberg, R., Primavera, J.H., Kautsky, N., Beveridge, M., Clay, J., Folke, C., Lubchenco, J., Mooney, H. & Trueil, M. (2000) Effect of aquaculture on world fish supplies. *Nature* **405**: 1018–1024.
- Simenstad, C.A. & Fresh, K.L. (1995) Influence of intertidal aquaculture on benthic communities in Pacific-Northwest estuaries. Scales of disturbance. *Estuaries* **18**: 43–70.
- Simenstad, C.A., Weitkamp, L.A. & Cordell, J.R. (1993) Effects of substrate modification on littoral flat epibenthos: assemblage structure changes associated with predator exclusion nets. FRI-UW-9310, Fisheries Research Institute, University of Washington, Seattle, WA, USA.
- Snively, G. (1978) *Exploring the Seashore in British Columbia, Washington and Oregon*. Vancouver, Canada/London, UK: Gordon Soules Book Publishers Ltd/Pacific Search Press: 240 pp.
- Sorokin, I., Giovanardi, O., Pranovi, F. & Sorokin, P. (1999) Need for restricting bivalve culture in the southern basin of the Lagoon of Venice. *Hydrobiologia* **400**: 141–149.
- Spencer, B.E., Kaiser, M.J. & Edwards, D.B. (1997) Ecological effects of intertidal Manila clam cultivation: observations at the end of the cultivation phase. *Journal of Applied Ecology* **34**: 444–452.
- Tilman, D. (2000) Causes, consequences and ethics of biodiversity. *Nature* **405**: 208–211.
- Vermeer, K. & Butler, R. (1989) The ecology and status of marine and shoreline birds on the Strait of Georgia BC Proceedings of a Symposium, Canadian Wildlife Service. Technical Report, Canadian Wildlife Service, Pacific and Yukon Region, British Columbia, Canada.