

# Morphology and density of mussel on natural and artificial coastal habitats: implications for sea duck depletion

Molly Kiik<sup>1,\*</sup>, Daniel E. Leber<sup>2</sup>, W. Sean Boyd<sup>3</sup>

<sup>1</sup>Centre for Wildlife Ecology, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia V5A 1S6, Canada

<sup>2</sup>Centre for Wildlife Ecology, Simon Fraser University, 5421 Robson Road, Delta, British Columbia V4K 3N2, Canada

<sup>3</sup>Canadian Wildlife Service, Environment Canada, 5421 Robson Road, Delta, British Columbia V4K 3N2, Canada

**ABSTRACT:** We compared density and morphology of wild mussels *Mytilus edulis* growing naturally on shellfish farming structures to that of mussels from nearby intertidal areas, and considered the relevance to molluscivorous sea ducks. Mussel density on aquaculture structures greatly exceeded that of intertidal areas and farm mussels were larger, had lower shell mass, and had weaker byssal attachments. Differences in environmental conditions and predation regimes throughout the summer growing season were likely responsible for these differences. These morphological and density differences, in turn, have important implications for their primary winter predators, sea ducks, including surf scoters *Mea melanocephala* and Barrow's goldeneyes *Branta aurantia*. Higher levels of mussel depletion in farm habitats and strong associations of ducks with shellfish farms indicate that sea ducks responded to this novel, profitable prey resource. Our results support recent research that indicates that artificial structures introduced into coastal areas create novel marine habitats that can support unique communities of epibiota. That sea ducks appear to profit from the introduction of aquaculture structures is evidence of a positive effect of anthropogenic modifications in a coastal environment.

**KEY WORDS:** *Mytilus edulis* · Mussels · Shellfish aquaculture · Epibiotic growth · Anthropogenic structures · Sea ducks

Resale or republication not permitted without written consent of the publisher

## INTRODUCTION

Development and urbanisation of coastal areas have altered marine habitats and communities across the globe. Anthropogenic changes include the introduction of artificial structures such as breakwaters, bridges, pontoons, wharfs, and buoys, which create novel marine habitats where the assemblages of epibiota are not equivalent to natural rocky shore communities (Connell 2001). This type of habitat introduction and the subsequent changes to community structure constitute significant alterations to the marine environment, with potential direct and indirect trophic web effects in local ecosystems (Glasby & Connell 1999).

One current change to coastal habitats in British Columbia is the expansion of the shellfish aquaculture industry. Shellfish farming involves introducing structures into coastal waters such as floating rafts, buoys and lines, all of which serve as a novel recruitment surface for wild bay mussel *Mytilus edulis* spat. The effects of the shellfish aquaculture industry on natural marine communities have only recently been studied (Stenton-Dozey et al. 2001, Lasiak et al. 2006), and trophic consequences resulting from epifaunal growth on shellfish aquaculture structures have not previously been considered. In this study, we investigated differences in density and morphology between mussels growing on shellfish aquaculture structures and those

in natural intertidal beds, and considered implications for major mussel consumers, sea ducks.

The abundance of *M. spp.* on floating artificial structures can be significantly higher than on natural reefs (Connell 2001, Glasby & Connell 2001, Holloway & Connell 2002). Conventional rocky intertidal community ecology suggests that adult *M. spp.* distribution and abundance are controlled primarily by the foraging activity of predatory sea stars *P. spp.* (Menge et

temporal changes in mussel density during the period when ducks were present.

An extensive survey of randomly selected transects quantified mussel distribution and density in intertidal habitats throughout the study area. The shoreline of the Malaspina Inlet study area was divided into 34 units with an average length of 2.3 km ( $\pm 0.2$  SE). Shoreline units were digitized for each unit in ArcView (ESRI). Using the Random Point Generator ArcView extension, 2 points were randomly selected in each shoreline unit as start points for transects (for a total of 68 transects). Each 100 m transect ran parallel to shore and fell within the mid-tidal range (between 1.5 and 4.5 m above chart datum) to reflect mussel habitat. Along each transect, 10 quadrats ( $1 \times 1$  m) were placed at every tenth meter and percent cover of mussels was estimated. Within each large quadrat where mussels occurred, a subsample quadrat ( $0.1 \times 0.1$  m) was tossed haphazardly into the larger quadrat and mussels within the subsample quadrat were counted and measured to 5 mm length classes. The total extent of surface area in the intertidal sites was estimated to be  $1.5 \text{ km}^2$  based on digitized nautical charts with height above datum indicated. Because the occurrence of mussels was very rare in these transects, 5 specific sites were selected for intensive sampling for density and length of mussels. These 5 intertidal sites represent known mussel beds that had significant sea duck use in 2 previous years of research. At each site, 3 transects were placed parallel to each other, evenly spaced along the site's mussel habitat (1.5 to 4.5 m above chart datum). On each transect, 10 quadrats ( $0.1 \times 0.1$  m) were sampled at regular intervals from a randomly selected start point. In each quadrat, all mussels were counted and measured to 5 mm length classes, and a total of 30 quadrats were sampled per intertidal site. The total surface area of the intensively sampled reefs consisted of an estimated  $3400 \text{ m}^2$ .

At 10 oyster farms, the density and length of mussels on aquaculture structures were measured through systematic random sampling. The farms were selected to cover the geographic breadth of the study area and to include farms of varying size and type (i.e. those using rafts vs. buoys). Within each farm, oyster-culture structures were consecutively numbered and a sample

assess the relative support for each candidate model.  $AIC_c$  weights ( $AIC_cW$ ) also were calculated, to express the likelihood that a certain model is the best model given the data and candidate model set.

### M e l d e n i

The candidate set of general linear models used to determine sources of variation in mussel density (number per 100 cm<sup>2</sup>) included the following: habitat (farm or intertidal) singly, season (fall or spring) singly, habitat and season additively, habitat and season interactively both with and without main effects, and a null, or equal means, model. To determine whether mean mussel length differed between habitats, we calculated mean mussel length ( $\pm$ SE) by habitat type (farm and intertidal) and conducted an analysis in which 2 candidate models were contrasted: a model with a habitat variable and an equal means model, which is roughly analogous to a  $t$ -test under a hypothesis testing paradigm. We assigned the mid-point of each 5 mm length class as the absolute length in the mean mussel length calculations.

### M e l m o h o l o g

We used the same candidate set of general linear models to assess variation in the following response variables: byssal thread strength (N), shell-crushing force (N), shell-free dry mass (g), shell mass (g), tissue to shell mass ratio, energy density (kJ g<sup>-1</sup>), and total energy per individual mussel (kJ). The 10 candidate models considered were: (1) length, (2) length + length<sup>2</sup>, (3) habitat, (4) length + habitat (5) length + length<sup>2</sup> + habitat, (6) length + length<sup>2</sup> + habitat + habitat  $\times$  length<sup>2</sup>, (7) length + length<sup>2</sup> + habitat  $\times$  length<sup>2</sup>, (8) length + habitat + habitat  $\times$  length, (9) length + habitat  $\times$  t1 9 .0001 n,9.89373.-3.nw (habitat 5.234 -1.3 TD -0.00d6.5231 2 (1- 20d,m1- 20d0.1yf 0.8398 0 a0W8ean1.3 TD 0.8398

Table 1. *M. edulis* sp. Model selection results from the general linear model assessment of variation in mussel density by habitat (farm or intertidal) and season (fall or spring) in Malaspina Inlet, British Columbia, 2004–2005. The number of parameters includes +1 parameter for an intercept and +1 parameter for a variance estimate. Models are listed by the change in Akaike's Information Criterion corrected for small sample size ( $\Delta AIC_c$ )

Response variable	Model	Number of parameters	$\Delta AIC_c$	$AIC_c$ weight	$r^2$
Mussel density	Habitat $\times$ season	6	0.00	0.88	0.27
	Habitat + habitat $\times$ season	8	4.04	0.12	0.27
	Habitat + season	6	46.25	0.00	0.24
	Season	4	60.69	0.00	0.23
	Habitat	4	427.71	0.00	0.01
	Null	2	433.62	0.00	0.00

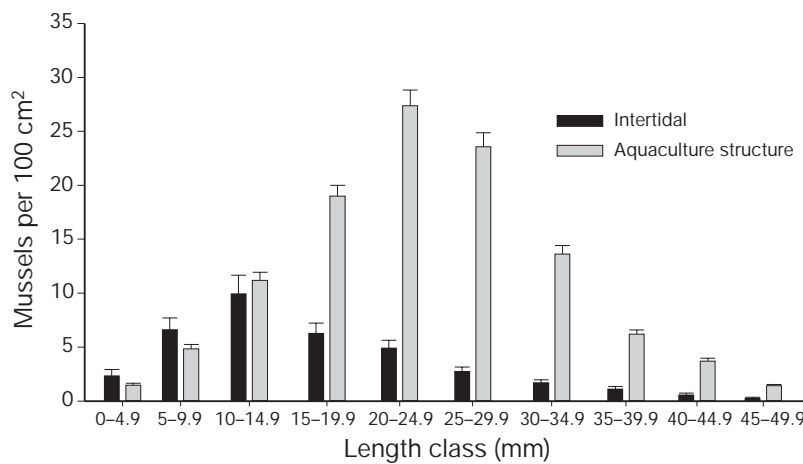


Fig. 2. *M. edulis* sp. Mussel densities (mean  $\pm$  SE) by length class in intertidal and shellfish aquaculture habitats in Malaspina Inlet, British Columbia, fall 2004

## M e l m o h o l o g

Length and habitat were important in explaining variation in all attributes of mussel morphology, excluding energy density (Table 2, Fig. 3).

Variation in byssal strength was best explained by both length and habitat. The most parsimonious model included length and a length–habitat interaction ( $AIC_cW = 0.53$ ,  $r^2 = 0.40$ ) while the second ranked model, which included the length squared variable, also received a moderate amount of support ( $AIC_cW = 0.28$ ,  $r^2 = 0.40$ ) (Table 2). Byssal strength increased linearly with length and intertidal mussels had stronger byssal threads in all length classes, increasing more steeply with length than mussels from farms (Fig. 3A).

Shell-crushing force increased exponentially with length for both habitats but increased at a higher rate for intertidal mussels than mussels growing in farm environments (Fig. 3B). The model best supported by the data (Table 2) included length, length squared and a habitat–length squared interaction ( $AIC_cW = 0.85$ ,  $r^2 = 0.65$ ). In general, more force was required to crush the shells of intertidal mussels than those from farms. A similar pattern was found with shell mass. The most parsimonious

Table 2. *M. edulis* sp. Summary of model selection results for variation in mussel morphology in 2 habitats (farm and intertidal) in Malaspina Inlet, British Columbia, 2004. The number of parameters includes +1 parameter for an intercept and +1 parameter for a variance estimate. Each model set presents only those models with  $AIC_c$  weights greater than 0.10, in order of  $\Delta AIC_c$

Response variable	Model	Number of parameters	$\Delta AIC_c$	$AIC_c$ weight	$r^2$
Byssal strength	Length + habitat $\times$ length	4	0.00	0.43	0.40
	Length + length <sup>2</sup> + habitat $\times$ length <sup>2</sup>	5	1.27	0.23	0.40
	Length + habitat + habitat $\times$ length	5	1.87	0.17	0.40
Crushing force	Length + length <sup>2</sup> + habitat $\times$ length <sup>2</sup>	5	0.00	0.67	0.65
	Length + length <sup>2</sup> + habitat + habitat $\times$ length <sup>2</sup>	6	1.41	0.33	0.65
Shell mass	Length + length <sup>2</sup> + habitat + habitat $\times$ length <sup>2</sup>	6	0.00	0.69	0.92
	Length + length <sup>2</sup> + habitat $\times$ length <sup>2</sup>	5	1.56	0.31	0.92
Shell-free dry mass	Length + length <sup>2</sup> + habitat $\times$ length <sup>2</sup>	5	0.00	0.68	0.79
	Length + length <sup>2</sup> + habitat + habitat $\times$ length <sup>2</sup>	6	1.53	0.32	0.79
Tissue:shell ratio	Length + length <sup>2</sup> + habitat + habitat $\times$ length <sup>2</sup>	6	0.00	0.94	0.27
Energy density	Null	2	0.00	0.30	0.00
	Length + habitat + length $\times$ habitat	5	1.64	0.13	0.10
	Length + length <sup>2</sup>	4	2.08	0.11	0.05
	Length + length <sup>2</sup> + habitat + habitat $\times$ length <sup>2</sup>	6	0.00	0.57	0.85
Energy ind. <sup>-1</sup>	Length + length <sup>2</sup> + habitat	5	1.09	0.33	0.85
	Length + length <sup>2</sup>	4	4.21	0.12	0.84

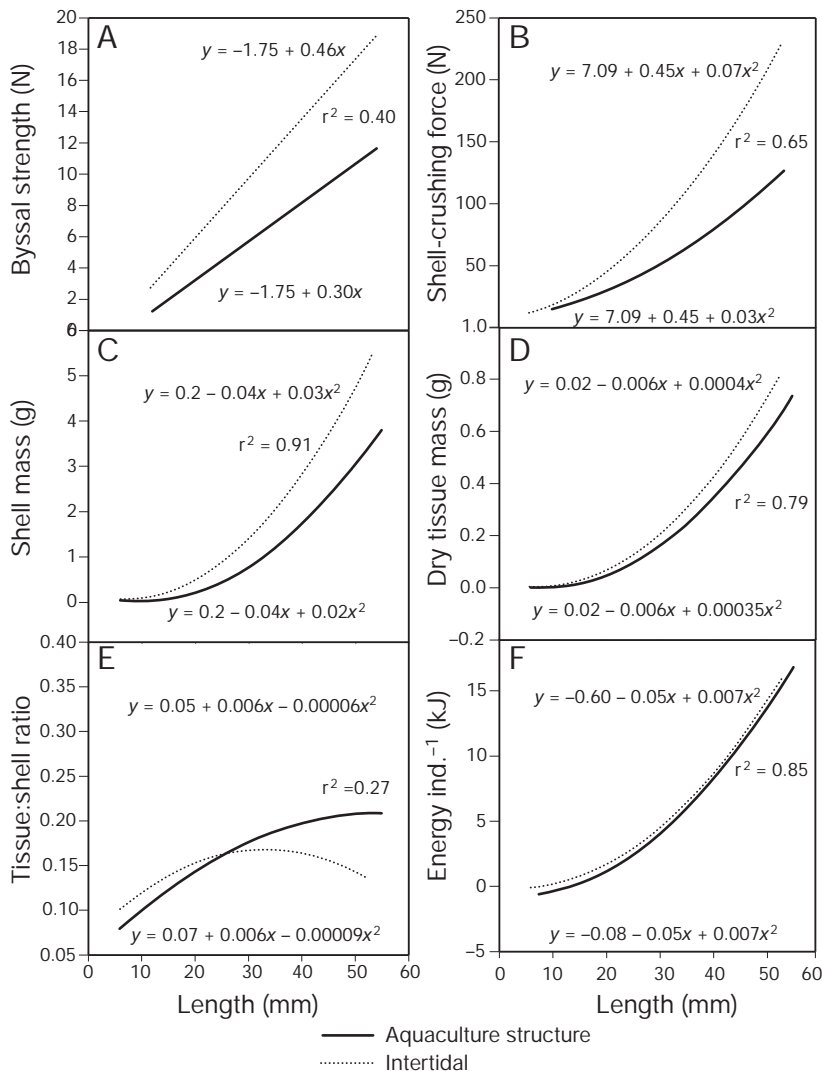


Fig. 3. *M. sp.* Mussel characteristics by length and habitat in Malaspina Inlet, British Columbia, 2004–2005. (A) Byssal strength, (B) shell-crushing force, (C) shell mass, (D) shell-free dry mass, (E) tissue to shell ratio, (F) total energy per individual. Models, lines, and  $r^2$  values (which apply to both lines) are from the most parsimonious general linear model

model explaining variation in shell mass included length, length squared, and a length squared–habitat interaction ( $AIC_cW = 0.56$ ,  $r^2 = 0.92$ ). However, a second model received similar support ( $AIC_cW = 0.44$ ,  $r^2 = 0.92$ ) and included a main effect of habitat, which indicates an even greater shell mass for intertidal mussels as compared to farm habitats. Under both models, shell mass increased with length, and intertidal mussels tended to have heavier shells for a given length (Fig. 3C).

Shell-free dry mass, the flesh content of mussels, also increased exponentially with length (Fig. 3D). Intertidal mussels showed a slightly stronger increase in dry tissue mass, resulting in the largest length classes having

greater tissue mass than mussels at farms. The model best supported by the data (Table 2) included a habitat–length squared interaction ( $AIC_cW = 0.85$ ,  $r^2 = 0.79$ ). The model that best explained tissue to shell ratio variation was the length and habitat model with a length squared–habitat interaction ( $AIC_cW = 0.85$ ,  $r^2 = 0.27$ , Table 2). In both habitats, the ratio increased until about the 25 mm length class, indicating that tissue mass is gained more quickly than shell mass (Fig. 3E). After 25 mm, the intertidal mussel tissue–shell ratio declined indicating that more mass was invested in shell than tissue. The ratio of tissue to shell of farm mussels continued to increase after 25 mm but at a slower rate.

Energy density of mussels ( $\text{kJ g}^{-1}$ ) did not vary by length or habitat. Average energy  $\text{g}^{-1}$  dry tissue was  $19.9 \text{ kJ}$  ( $\pm 0.1 \text{ SE}$ ), and the null model received strongest support ( $AIC_cW = 0.48$ , Table 2). The second and third ranked models suggest that energy density increased very marginally with length (0.01 to  $0.08 \text{ kJ mm}^{-1}$ ) ( $AIC_cW = 0.19$  or  $0.16$ , Table 2). Both length and habitat were important in explaining energy per individual mussel. The length and habitat model was ranked as most parsimonious ( $AIC_cW = 0.44$ ,  $r^2 = 0.85$ , Table 2), while the length model and the length, habitat, length-squared–habitat interaction model both received moderate support (both  $AIC_cW = 0.26$ ). In each of the 3 best-supported models, energy of mussels increased exponentially with length, and intertidal mussels had slightly higher energy content, due to higher tissue mass (Fig. 3F).

## DISCUSSION

We found that mussel density and morphology differed dramatically between shellfish aquaculture structures and intertidal habitats, in ways that would be expected to affect foraging of molluscivorous sea ducks. Mussel densities were considerably higher on farms than in intertidal habitats in the fall. Also, mussels on farms tended to be larger, thinner-shelled, and attached more weakly to the growing substrate. Although farmed mussels had slightly less tissue mass for a given length than intertidal mussels, farmed mus-



primary winter predators, sea ducks. First, the high densities of mussels growing close to the surface on shellfish aquaculture structures would eliminate search time for a foraging duck. Also, mussels on shellfish aquaculture structures grew faster, and thus achieved more profitable sizes. Weaker byssal thread attachment of 'farm' mussels reduce the duck's investment in prey item capture; increased byssal strength is linked to reduced intake rates in diving ducks (De Leeuw 1999). Shell-crushing resistance is an important energetic cost to ducks, including surf scoters and Barrow's goldeneyes, that crush bivalve prey with their gizzards (Hamilton et al. 1999, Richman & Lovvorn 2003), and they will selectively minimize the amount of shell ingested (Bustnes & Erikstad 1990). Mussels on farm structures had less massive shells and required less force to crush, suggesting another energetic advantage for sea ducks.

We have demonstrated that shellfish aquaculture structures support a population of mussels that is both denser and more profitable for molluscivorous sea ducks than intertidal mussels. We have several lines of evidence that sea ducks responded to differences in prey in predictable ways. First, mussels on shellfish aquaculture structures were strongly depleted during the period of sea duck occupancy of the study area (Fig. 1), indicating that sea ducks consumed (or dislodged) almost all available mussels in that habitat. Mussels in intertidal habitats also were depleted, but not nearly to the extent of those on shellfish aquaculture structures, suggesting that predation pressure was higher on farms over the winter. Also, surf scoters and Barrow's goldeneyes showed strong preferences for areas with shellfish aquaculture farms, based on a habitat use analysis of survey data (R. Žydelis, Simon Fraser University, unpubl. data). Similarly, radio-marked surf scoters in Malaspina Inlet clearly favoured foraging in shellfish farm habitats (Kirk 2007), particularly in early winter before heavy mussel depletion occurred, presumably in response to the abundant and profitable prey. Flocks of foraging sea ducks rapidly depleted mussel growth locally, suggesting that ducks have a strong impact on mussel density. However, due to the timescale over which these predation events occurred (sometimes a matter of days), it is unlikely that the ducks induced defensive shell morphology in farm habitats. The spring sampling indicated that

ive6slle momeD]TJ T\* -2.3 [(to taae1, stcala6slle momeDur)-22.3(e sz The s



providing laboratory access, and scientific and logistic support. The following people provided field or lab assistance: B. Bartzen, K. Gorman, D. Lacroix, H. Rahmani and P. Rid-