



The effect of velocity on the suspension feeding and growth of the marine mussels *Mytilus trossulus* and *M. californianus*: implications for niche separation

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Abstract

The role of fluid dynamic factors on the feeding and growth of two sympatric blue mussels was examined in a laboratory flow chamber and in a dockside flow-through chamber. The experiments involved the blue mussels *Mytilus trossulus* and *Mytilus californianus* of two size categories (~ 1 and ~ 2 cm shell length) and water from the Bamfield Inlet. Larger mussels cleared more water of seston than smaller ones, and the clearance rate (CR) of *M. trossulus* increased with velocity ($1-18 \text{ cm s}^{-1}$), whereas *M. californianus* exhibited a somewhat continuous unimodal functional response that peaked at $\sim 12 \text{ cm s}^{-1}$. Although growth decreased with velocity in all experiments over the range of $1-40 \text{ cm s}^{-1}$, the growth rates of *M. californianus* were consistently higher than *M. trossulus*, and this difference extended to the highest velocity. It is evident that *M. californianus* has a fluid dynamically mediated growth advantage over *M. trossulus*, which would explain its dominance in wave-exposed habitats. Given this finding, we conclude that fluid dynamics are important to the evolutionary ecology of blue mussels.

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1. Introduction

Sympatric species of blue mussels in the genus *Mytilus* inhabit temperate coasts where they are ecologically and economically important members of rocky intertidal zones (Bayne, 1976; Seed, 1976;

Suchanek, 1986; Gosling, 1992; Harbo, 1997; Suchanek et al., 1997; Menge, 2000). These benthic suspension-feeding bivalves represent a dominant successional stage both in highly energetic coasts and sheltered embayments with hard substrates (Dayton, 1971; Paine, 1974; Seed and Suchanek, 1992; cf. Berlow, 1999). One of these species, *Mytilus californianus* Conrad, 1837 (California mussel) is a dominant species on wave-exposed coasts. *Mytilus trossulus* A.A. Gould, 1850 (bay mussel) and other members of the blue mussel complex (*Mytilus galloprovincialis* Lamark, 1819, and *Mytilus edulis* Linnaeus, 1758,

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which have been introduced into the region; Heath et al., 1995; Suchanek et al., 1997; Geller, 1999) dominate in wave-sheltered environments and in patches within and above *M. californianus* beds (e.g., Levinton and Suchanek, 1978; Suchanek, 1986; Gosling, 1992; Robles et al., 1995; Martel et al., 1999). This subtle, yet important difference in adult habitat between *M. californianus* and *M. trossulus* is interesting given the potential dispersal of veliger larva in the water column. Recent evidence suggests that limited or lack of recruitment by *M. californianus* in sheltered areas may account for this pattern (Heath et al., 1996; cf., Robles, 1997). Specifically, Heath et al. (1996) found “young” and “old” (i.e., <20 mm and >20 mm shell length, respectively) *M. californianus* only in exposed locations. However, young *M. trossulus* were present in both exposed and sheltered locations, but only older ones were present in sheltered regions. A number of postsettlement factors, including competition, predation, and physiological response to freezing, desiccation, salinity and sediments, have been suggested to explain the differential survival of postlarvae/juveniles in wave-exposed vs. wave-sheltered areas (reviewed in Suchanek, 1986; Seed and Suchanek, 1992). It is possible, however, that fluid dynamic factors, especially the turbulence in wave-exposed vs. wave-sheltered environments, are also responsible for the habitat

segregation seen in adult mussels (Harger, 1970). It would be appropriate, therefore, to determine whether fluid dynamic factors have facilitated the niche separation of *M. californianus* and *M. trossulus*.

The relevance of fluid dynamic factors to aquatic organisms has long been recognised and a dome-shaped or continuous unimodal functional response of both pelagic and benthic organisms to fluid dynamics (namely, turbulence) has emerged, where moderate levels of turbulence promote feeding rates, and high levels inhibit them (MacKenzie et al., 1994; Wildish and Kristmanson, 1997; Ackerman, 1999; Peters and Marrasé, 2000). This is certainly the case in the 10–12 species of marine and freshwater bivalves in which the effect of velocity has been examined experimentally (Table 1; see review in Ackerman, 1999). That review revealed that turbulence led to reduced feeding rates or a unimodal functional response, and that species differ in terms of the range of velocities where maximal suspension feeding or growth rates occur. Moreover, results for a related species to those examined here, *M. edulis*, showed that clearance rates (CR) increased directly with velocity to $\sim 25 \text{ cm s}^{-1}$ beyond which clearance rates declined (Wildish and Miyares, 1990; also see Dame, 1996). The feeding responses of closely related and sympatric *M. californianus* and *M. trossulus* to

Table 1

The response of bivalve suspension feeding and growth to fluid dynamics conditions in experimental chambers (based on Ackerman, 1999)

Species	Feeding/growth response—variable	Chamber conditions
<i>Argopecten irradians</i>	Continuous Unimodal Function—growth rate, growth increment	Laminar–Turbulent
	Inversely related to velocity—growth rate	Laminar–Turbulent
<i>Crassostrea gigas</i>	Directly related to velocity—clearance rate	Laminar
<i>Crassostrea virginica</i>	Continuous Unimodal Function—growth rate	Laminar–Turbulent
<i>Dreissena bugensis</i>	Continuous Unimodal Function—clearance rate	Laminar–Turbulent
<i>Macoma</i> spp.	Inversely related to velocity—feeding rate	Laminar–Turbulent
<i>Mercenaria mercenaria</i>	Directly related to velocity—clearance rate	Laminar
	Directly related to velocity—growth rate	Laminar–Turbulent
<i>Mytilus edulis</i>	Directly related to velocity—clearance rate	Laminar
	Directly related to velocity—pumping rate	Laminar
	Inversely related to velocity—clearance rate	Turbulent
<i>Mytilus</i> sp.	Continuous Unimodal Function—clearance rate, growth rate	Laminar–Turbulent
<i>Ostrea edulis</i>	Directly related to velocity—clearance rate	Laminar
<i>Placopecten magellanicus</i>	Continuous Unimodal Function—growth rate	Laminar–Turbulent
	Inversely related to velocity—growth rate	Turbulent
	Continuous Unimodal Function—clearance rate	Turbulent
<i>Potamocorbula amurensis</i>	Inversely related to velocity—growth rate	Turbulent
<i>Ruditapes decussatus</i>	Continuous Unimodal Function—clearance rate	Laminar–Turbulent

increased water velocity have not been examined, yet differences in the response to turbulence, if they exist, could bear upon the aforementioned ecological and evolutionary mechanisms by which niche separation has occurred in these species. It is the purpose of this study, therefore, to examine the effect of fluid dynamics on the suspension feeding and growth response of *M. californianus* and *M. trossulus* under controlled fluid dynamic conditions. Given the important role these species play in the ecosystems, results from this type of study will also provide essential and important information on the benthic productivity of rocky intertidal zones.

2. Materials and methods

2.1. Collection site

M. californianus and *M. trossulus* were collected during low tides from several sites within ~1 km of Bamfield Marine Sciences Centre (BMSC), Bamfield, British Columbia, Canada. Small individuals (i.e., ~1 cm shell length) of *M. trossulus* were collected on a rock outcrop ~5 m offshore from Aguilar Point (48.5035°N, 125.084°W) in a sheltered region, whereas larger individuals (i.e., ~2 cm shell length) of *M. trossulus* and *M. californianus* were collected on the northwest facing the shore of Wizard Island (48.515°N, 125.0955°W), which is ~1 km northwest of Aguilar Point. These mussels were large enough to be easily identified to species using shell features, such as shape and striations (c.f., Martel et al., 1999), and were collected by hand by carefully cutting their byssal threads just proximal to the attachment plaques. They were then placed in plastic buckets, covered with wet paper towels, and transported to BMSC within 30–60 min.

The mussels were cleaned, sorted by size and species, and placed within glass vessels (9 cm diameter×16 cm long) that were located on seawater tables. Each vessel received a continuous and strong flow of seawater through plastic tubing connected to the BMSC seawater system, which draws unfiltered seawater from a depth of 25 m in Bamfield Inlet. A complete exchange of water was observed every 2–5 min, and the vessels were cleaned every 1–2 days to remove feces and pseudofaeces that had accumulated

on the bottom. Batches of mussels were maintained in this manner for up to 4 weeks, during which time they were observed to feed, move on the side walls, and form new byssal attachments.

2.2. Clearance rate

The response of mussel suspension feeding to velocity was examined in a recirculating flume (180 cm long×17.5 cm wide with 3.5 cm water depth) by examining the change in seston content over time using the approach described in Ackerman (1999). In this case, ~20 l of seawater was pumped directly from ~60 cm depth in Bamfield Inlet using a small submersible pump. Approximately 3 l of this seawater was added to a container that was left undisturbed for ~20 min to allow for dense particles to settle. Three 500 ml samples (1000 ml for the 2 cm mussels) were siphoned from the container and filtered through precombusted and preweighed glass fiber filters (GF/C; Whatman International, Maidstone, England; nominal opening of 1.2 μm) to provide a measure of the initial seston concentration (C_0). This procedure was repeated at the end of an experiment (1 h) using water from the flume to provide a measure of the final seston concentration (C_f). The filters were dried at 60 °C for 12 h before being reweighed.

The flow chamber was filled with 14.5 l of seawater and a batch of mussels of a particular size and species (100 in the case of 1-cm-long mussels, and 20 or 25 in the case of 2-cm-long mussels; Table 2) were placed across the chamber at a downstream distance of 130 cm from the collimators (flow straighteners). Care was taken to ensure that batches were used equally among velocity treatments and that the same batch was not used for at least 1 day following an experiment. Given these precautions, and the observation that the results of a given batch were not biased among treatments (i.e., always low or high), lead us to consider each experiment as an independent sample. The chamber was operated at an average chamber velocity of ~1, 6, 12, and 18 cm s⁻¹, corresponding to laminar and turbulent flow conditions in the first two and last two velocities, respectively [i.e., Reynolds number (Re) based on chamber hydraulic diameter ~4×10², 3.2×10³, 9.1×10³, and 1.9×10⁴; see Ackerman, 1999]. The clearance rate (CR) was determined from the following equation developed by

Table 2

Description of the mussel species and length (mean \pm 1 S.E.) used in the clearance rate experiments

ID	Species	Shell length (cm)	N
<i>Mussels used in 1996 experiments</i>			
A	<i>M. trossulus</i>	1.06 \pm 0.01	100
B	<i>M. trossulus</i>	1.07 \pm 0.01	100
C	<i>M. trossulus</i>	1.06 \pm 0.01	100
D	<i>M. trossulus</i>	1.06 \pm 0.01	100
E	<i>M. trossulus</i>	1.06 \pm 0.01	100
F	<i>M. trossulus</i>	1.05 \pm 0.01	100
G	<i>M. trossulus</i>	1.07 \pm 0.01	100
<i>Mussels used in 1997 experiments</i>			
B	<i>M. trossulus</i>	2.05 \pm 0.01	20
C	<i>M. trossulus</i>	2.01 \pm 0.01	20
D	<i>M. trossulus</i>	1.97 \pm 0.01	20
E	<i>M. trossulus</i>	2.01 \pm 0.01	20
F	<i>M. californianus</i>	1.99 \pm 0.01	20
G	<i>M. trossulus</i>	1.99 \pm 0.01	20
K	<i>M. californianus</i>	2.02 \pm 0.01	20
L	<i>M. californianus</i>	2.02 \pm 0.01	25
<i>Mussels used in 1998 experiments</i>			
A	<i>M. californianus</i>	1.98 \pm 0.03	25
B	<i>M. californianus</i>	2.00 \pm 0.03	25
C	<i>M. californianus</i>	2.01 \pm 0.03	25
D	<i>M. trossulus</i>	1.98 \pm 0.02	25
E	<i>M. trossulus</i>	2.00 \pm 0.02	25

Coughlan (1969; reviewed in Wildish and Kristman-son, 1997),

$$CR = \frac{Vol}{nt} \ln \left(\frac{C_0}{C_t} \right) \quad (1)$$

where Vol is the volume of seawater in the chamber (14.5 l); n is the number of mussels placed in the chamber (100 or 20 [or 25] depending on the size of mussels); t is the time (1 h); and C_0 and C_t are the seston concentration measured at the beginning (when mussels were observed to gape; ~5–10 min after introduction) and end of each experiment, respectively. In addition, the position and behavior (e.g., gape) was monitored at ~15-min intervals.

2.3. Growth rate

A second experiment was undertaken to examine the effect of velocity on the growth of mussels in a continuous flow system assembled from standard National Pipe Thread (NPT) polyvinylchloride (PVC)

plumbing pipe and fittings, which was deployed on BMSC's floating dock in Bamfield Inlet (Fig. 1). The growth chamber drew seawater from a depth of 3 m using a centrifugal pump (Teel 3450 rpm, Dayton Electric, Chicago, IL), which discharged through a manifold of four chambers created from 3 inch PVC pipe (Fig. 1). The flow through each of the chambers was controlled individually by a ball valve 30 cm downstream of the manifold, continued downstream 200 cm to a union coupling where experimental plates were inserted (see below). There was an additional 150 cm of chamber downstream of the union coupling that terminated in a 45° elbow connected to 61 cm of 2 inch PVC pipe that served as a choke valve to maintain constant water level in the chambers. To ensure similar water temperature among all experimental chambers, the chambers were insulated with standard neoprene pipe insulation and wrapped with aluminum foil (note that insulation was added after the first week of operation in 1996).

The mussels for the growth experiments were sorted into five groups of equal initial size (i.e., shell length) for use in each of the growth chambers and for a control group that was suspended on the water intake at a depth of 3 m. Mussels were tethered to a ~8.5 cm piece of fishing monofilament that was glued to the right or left valve of the mussel with instant adhesive (Loctite 420 Superbond; Loctite,

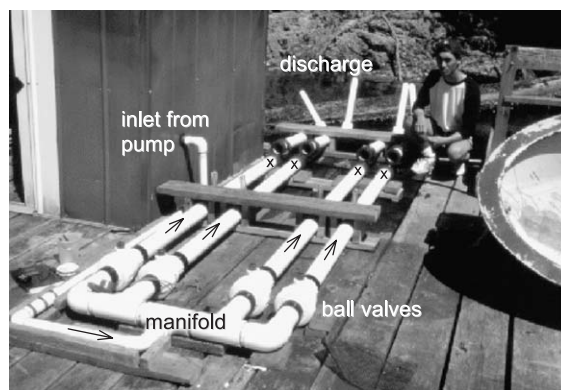


Fig. 1. Photograph of the growth chambers mounted on BMSC's floating dock in Bamfield Inlet. Water flows (indicated by the arrows) from the inlet into the manifold and ball valves (bottom left), down the length of the flow chambers and through the angled choke valves at the discharge. Note the open union couplings near the second wooden platform (next to Mike Nishizaki) where the growth plates were inserted (indicated by x).

Mississauga, ON) and then covered with marine epoxy (Wet and Cold Curing Aqua-Set Epoxy; Crystal-Pac Manufacturing, Burnaby, BC). The tethered mussels were placed in seawater containers and were observed to form new byssal attachments overnight. The tethers were inserted into predrilled holes in a plexiglass plate (plates: 15 cm long×6 cm wide; matrix: 8×3 [i.e., 24 mussels/plate] in 1996, matrix: 10×3 [i.e., 30 mussels/plate] in 1997 and 1998; holes: 3 mm diameter on ~1 cm centers offset 1.5 cm from the edge of the plates). The tethers were held in place by toothpicks that were inserted into the holes and cut to maintain a flush surface, and duct tape was used to cover the tethers on the lower surface of the plates. In the case of the *M. californianus* vs. *M. trossulus* comparison, care was taken to ensure that an equal number of each species were used on each plate in similar positions. The plates were placed in flowing water (~2 cm s⁻¹) and the few mussels that did not form byssal attachments overnight were replaced with new individuals.

The plates were inserted horizontally into the growth chambers on the upstream side of the union coupling between PVC strips that had been glued on the inner surface of the pipe as guides. In this configuration, the mussels were positioned midpipe, oriented upright such that the water flow was parallel to the plate surface. The control plate was suspended vertically on the outside of the intake pipe using a wire guide to expose the mussels to ambient conditions and the same water used in the chambers. The plate was enclosed in polymer mesh bag (nominal opening of 1.5 cm) to prevent predation from fish. The water flow in each chamber was regulated using the ball valve at predetermined velocities (Chamber #1: ~1 cm s⁻¹; Chamber #2: ~10 cm s⁻¹; Chamber #3: ~20 cm s⁻¹; Chamber #4: ~40 cm s⁻¹) that were verified by measuring the time needed to fill known volumes at the discharge. The flows were checked and adjusted once during weekly measurement and once in the intervening interval. The error in the flows was <5%, based on the ratio of the standard deviation to mean flow measured for the 10, 20, and 40 cm s⁻¹ chambers. Inherent difficulties with fine adjustments using a ball valve led to higher errors (e.g., <14%) at 1 cm s⁻¹. The plates were removed during the weekly measurements, and the mussels (identified via their tethers) were measured individu-

ally using dial calipers before being reinserted into the chambers or on the intake pipe for the control plate. The time required to measure the small mussels was ~60 min, but it was more difficult to identify the tethered position of large *M. californianus* and *M. trossulus*. Consequently, only initial and final sizes were measured. Experiments were run as follows: 1996—small *M. trossulus* for 29 days (24 mussels/plate); 1997—small *M. trossulus* for 37 days and *M. californianus* vs. *M. trossulus* for 36 days (30 mussels/plate); and 1998—*M. californianus* vs. *M. trossulus* for 34 days (30 mussels/plate). The mean observation from a given flow chamber was considered as a single observation in the analysis of the data using ANOVA. Although this strategy limited some of the within year comparisons, it was used to avoid the problem of pseudoreplication, as there was only one flow chamber per treatment per experiment.

3. Results

3.1. The effect of velocity on clearance rate

Mussels usually gaped within 5 to 10 min of introduction into the flow chamber and remained open throughout the experiments. Velocity had a strong and positive effect on the ability of small (i.e., 1 cm shell length) *M. trossulus* to clear natural seston from the chamber (Fig. 2A). The clearance rate (CR) increased monotonically from 56±6 ml mussel⁻¹ h⁻¹ [mean±1 standard error (S.E.); number of replicates given above the bar in Fig. 2] at ~1 cm s⁻¹ to 108±12 ml mussel⁻¹ h⁻¹ at ~18 cm s⁻¹. Significant differences among the CR were determined in a single classification ANOVA ($F_{3,17}=6.28$, $P=0.004$) with significant pairwise differences (Tukey HSD test; $P<0.01$) occurring between the results obtained at 18 cm s⁻¹ and those obtained at 1 and 6 cm s⁻¹. It should be noted that a number of the experiments involving these mussels had to be discarded due to mussel spawning (evident from sperm and egg masses in the water and on the bottom of the flume) which introduced seston to the chamber. Spawning was much less evident or rare in the larger mussels of either species.

Larger (i.e., 2 cm shell length) *M. trossulus* had a similar type of response to velocity although their

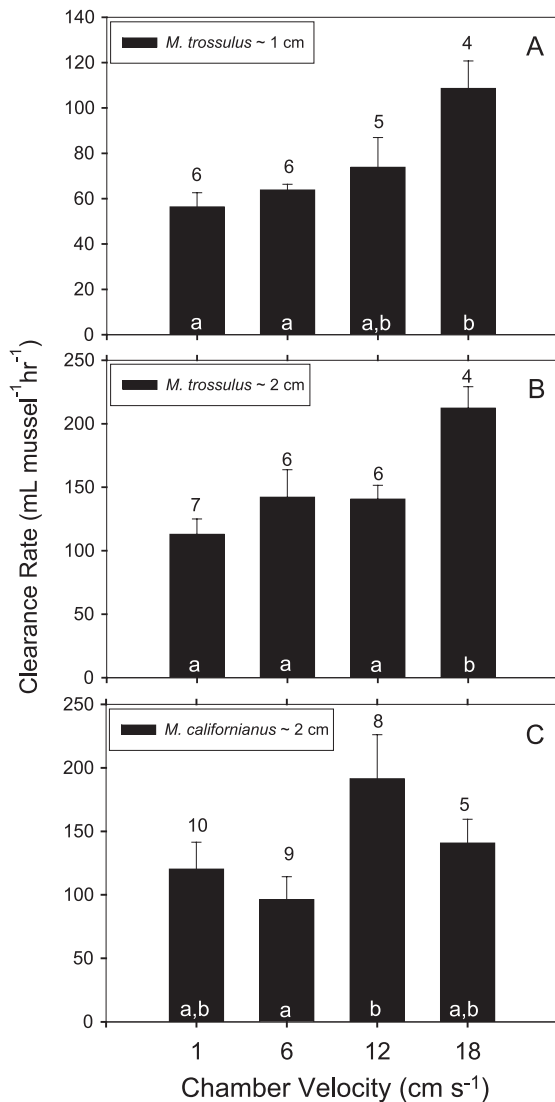


Fig. 2. The effect of velocity on the clearance rate of (A) 1-cm-long *M. trossulus*, (B) 2-cm-long *M. trossulus*, and (C) 2-cm-long *M. californianus*. Bars represent the mean, error bars represent 1 standard error of the mean, and numbers above the bars represent the number of experiments. In each panel, bars with the same letters were not significantly different ($\alpha=0.05$).

clearance rates (CR) were approximately twice those of the smaller mussels (Fig. 2B). The CR increased from 112 ± 12 ml mussel⁻¹ h⁻¹ at 1 cm s⁻¹ to 213 ± 17 ml mussel⁻¹ h⁻¹ at 18 cm s⁻¹. However, the results at 6 and 12 cm s⁻¹ were similar (142 ± 21 and 141 ± 11 ml mussel⁻¹ h⁻¹, respectively). The CR

results obtained at the different velocities were significantly different ($F_{3,19}=5.94$, $P=0.005$) with significant pairwise differences ($P<0.05$) occurring between the results obtained at 18 cm s⁻¹ and those obtained at 1, 6, and 12 cm s⁻¹ (Fig. 2B).

The pattern of results for 2-cm-long *M. californianus* were different from those of either size of *M. trossulus*, although the magnitude of the CR was similar to the 2 cm long *M. trossulus* (Fig. 2C). Velocity had a positive effect on CR although the response was quite complex. *M. californianus* cleared 120 ± 21 ml mussel⁻¹ h⁻¹ at 1 cm s⁻¹, 96 ± 18 ml mussel⁻¹ h⁻¹ at 6 cm s⁻¹, 191 ± 35 ml mussel⁻¹ h⁻¹ at 12 cm s⁻¹, and 141 ± 19 ml mussel⁻¹ h⁻¹ at 18 cm s⁻¹. These results were marginally different ($F_{3,28}=2.79$, $P=0.058$) with significant pairwise differences ($P=0.04$) occurring between the results obtained at 6 and 12 cm s⁻¹ (Fig. 2C).

Differences in CR between and within mussel species are evident in the direct comparison of the *M. trossulus* and *M. californianus* results (Fig. 3). Firstly, there was a clear effect of mussel size on CR, although a comparison for 1-cm-long *M. californianus* was not undertaken. Secondly, the CR for *M. trossulus* and *M. californianus* responded in a positive manner to increased velocity in the flow chamber. Thirdly, whereas *M. californianus* cleared the water at a higher rate than *M. trossulus* at 12 cm s⁻¹, the pattern broke down at higher velocities (18 cm s⁻¹). When the data for the 2-

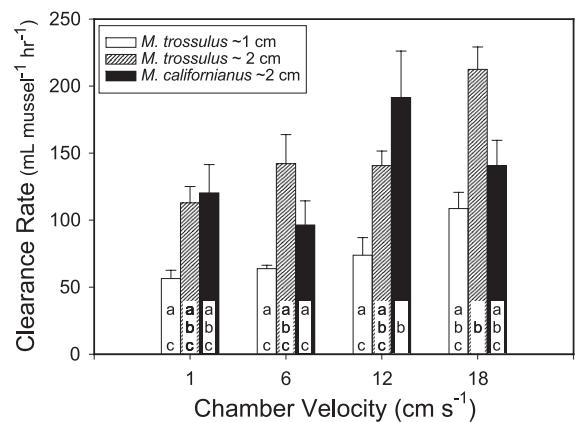


Fig. 3. The effect of velocity on the clearance rate of 1- and 2-cm-long *M. trossulus* and *M. californianus*. Bars represent the mean, error bars represent 1 standard error of the mean, and numbers above the bars represent the number of experiments. In each panel, bars with the same letters were not significantly different ($\alpha=0.05$).

cm-long *M. trossulus* and *M. californianus* were analyzed in a two-way ANOVA, no species effects were found ($F_{1,47}=0.79$, $P=0.379$), but there were significant velocity effects ($F_{3,47}=3.46$, $P=0.024$). There was evidence of an interaction between species and velocity, as indicated by the significant ($P<0.05$) pairwise differences (*M. californianus* at 6 cm s⁻¹ vs. *M. trossulus* at 18 cm s⁻¹ and *M. californianus* at 12 cm s⁻¹), which was supported by a nearly significant interaction term in the two-way ANOVA ($F_{3,47}=2.56$, $P=0.066$).

3.2. The effect of velocity on growth

Velocity had a significant and negative effect on the growth of mussels examined in the dockside growth chambers (Fig. 4). In 1996, the shell length of small *M. trossulus* increased from ~1.1 (1.07 ± 0.01; $n=120$) cm to between ~1.4 and ~1.7 cm over the course of 29 days. Length increased ~25% for the faster flows (~20 and ~40 cm s⁻¹) and ~50% for the slowest flows (~1 and ~10 cm s⁻¹; Fig. 4A). The growth trajectories were somewhat similar for the first 2 weeks and then diverged into two groups (1 and ~10 vs. 20, ~40 cm s⁻¹, and the dock) that became significant at day 22 ($P<0.001$). *M. trossulus* grew to larger sizes in 1997, increasing from ~1.1 (1.06 ± 0.01; $n=150$) cm to between ~1.8 and ~2.2 cm, which represented a 60% and 100% increase at 40 and 1 cm s⁻¹ over the course of 37 days (Fig. 4B). Statistical significant differences in shell length were evident at day 15 ($P<0.05$) when the mussels in the 40 cm s⁻¹ chamber were smaller than in the other treatments. Mussel length was greatest in the 1 cm s⁻¹ chamber, followed by the 10 and 20 cm s⁻¹ chambers and dock, and least on the 40 cm s⁻¹, and mussel lengths in 1996 were smaller than in 1997. These differences were significant in a two-way ANOVA using velocity and year as factors (i.e., $F_{4,4}=6.11$, $P=0.054$, and $F_{1,4}=156.1$, $P<0.001$, respectively). Pairwise comparisons (Tukey HSD) revealed that the average length at 10 cm s⁻¹ was significantly larger than at 40 cm s⁻¹, and that the average length in 1996 was significantly smaller than in 1997.

The differences in growth for the 1-cm-long *M. trossulus* between 1996 and 1997, and the influence of different experimental periods (i.e., 29 vs. 37 days) are evident when the data are presented as growth rate

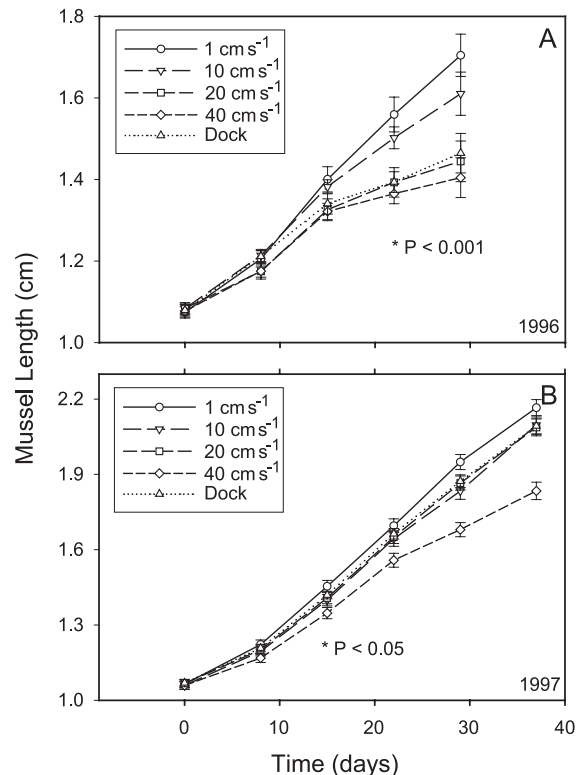


Fig. 4. The effect of velocity on the growth of 1 cm long *M. trossulus* in (A) 1996 and (B) 1997 examined in the growth chambers and under the dock at 3 m depth (see Fig. 1). The points represent the mean of ~24 individuals in 1996 and ~30 in 1997, and error bars represent 1 standard error of the mean. The asterisk (*) indicates the time when statistically significant differences were first detected among the treatments.

(i.e., cm day⁻¹; Fig. 5). The growth rate was much greater in 1997 for all of the treatments (e.g., 0.022 ± 0.002 vs. 0.03 ± 0.001 cm day⁻¹ for the 1 cm s⁻¹ treatment in 1996 and 1997, respectively), and this difference was significant (i.e., $F_{1,4}=69.8$, $P=0.001$). There were also differences among treatments largely related to the lower growth rates at the higher velocities, especially 40 cm s⁻¹ (e.g., 0.011 ± 0.002 vs. 0.021 ± 0.007 cm day⁻¹ for 1996 and 1997, respectively). These were significant (i.e., $F_{4,4}=5.82$, $P=0.058$), but the differences were less evident in 1997 compared to 1996.

In both 1997 and 1998, *M. californianus* achieved longer shell lengths than *M. trossulus* in all treatments over a similar period (Fig. 6). However, it should be noted that the initial lengths were somewhat longer in

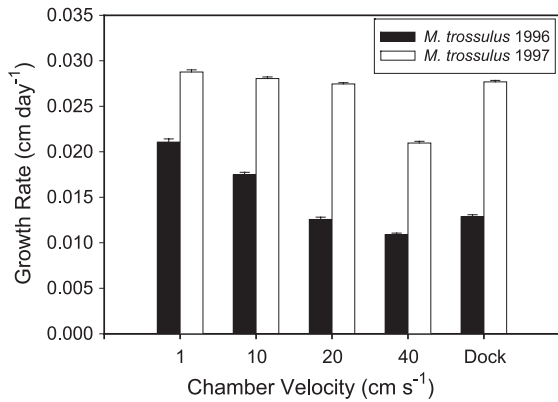


Fig. 5. The effect of velocity on the growth rate of 1-cm-long *M. trossulus* in 1996 (solid bars) and 1997 (open bars) examined in the growth chambers and under the dock at 3 m depth (see Fig. 1). Significant treatments effects were found in a two-way ANOVA using velocity ($F_{4,4}=6.11$, $P=0.054$) and years ($F_{1,4}=156.1$, $P<0.001$). Pairwise comparisons revealed that the average length at 10 cm s⁻¹ was significantly greater than at 40 cm s⁻¹, and that the average length in 1996 was significantly less than 1997. The bars represent the mean of ~24 individuals in 1996 and ~30 in 1997, and error bars represent the standard error of the mean.

1997 (2.28 ± 0.02 and 2.24 ± 0.02 cm in 1997 vs. 2.10 ± 0.01 and 2.10 ± 0.01 cm in 1998, for *M. californianus* and *M. trossulus*, respectively) and the control plate under the dock was lost in 1997. The magnitude of the difference between species was less evident in 1997 (e.g., 2.81 ± 0.09 vs. 2.89 ± 0.06 cm at 1 cm s⁻¹ for *M. trossulus* and *M. californianus*, respectively) than in 1998 (e.g., 2.59 ± 0.08 vs. 2.82 ± 0.05 cm at 1 cm s⁻¹, respectively), perhaps due to the larger overall mussel sizes at the end of the experiment in 1997 (i.e., shell length >2.8 cm in 1997 vs. shell length <2.8 cm in 1998). The effect of velocity on the 2-cm-long mussels was similar as in the case of 1-cm-long *M. trossulus*, where there was less growth at the highest velocities (e.g., 2.76 ± 0.07 vs. 2.84 ± 0.07 cm in 1997 and 2.51 ± 0.07 vs. 2.73 ± 0.02 cm in 1998 for *M. trossulus* and *M. californianus* at 40 cm s⁻¹, respectively). Statistical evaluations in this case were examined using a multi-way ANOVA with velocity, species nested within velocity (~15 individuals of both species were used in each treatment), and year as the factors. Significant differences among velocities were not found ($F_{4,7}=2.83$, $P=0.109$), but both species nested within velocities ($F_{5,7}=8.84$, $P=0.006$) and difference be-

tween years ($F_{1,7}=75.05$, $P<0.001$) were significant. The pairwise difference indicated that *M. californianus* at 1 cm s⁻¹ were significantly larger than *M. trossulus* at 20 cm s⁻¹ and 40 cm s⁻¹, *M. californianus* at 1 cm s⁻¹ were significantly larger than *M. trossulus* at 40 cm s⁻¹, and that mussels in 1997 grew significantly longer than in 1998, as was expected. This would be equivalent to an interaction between

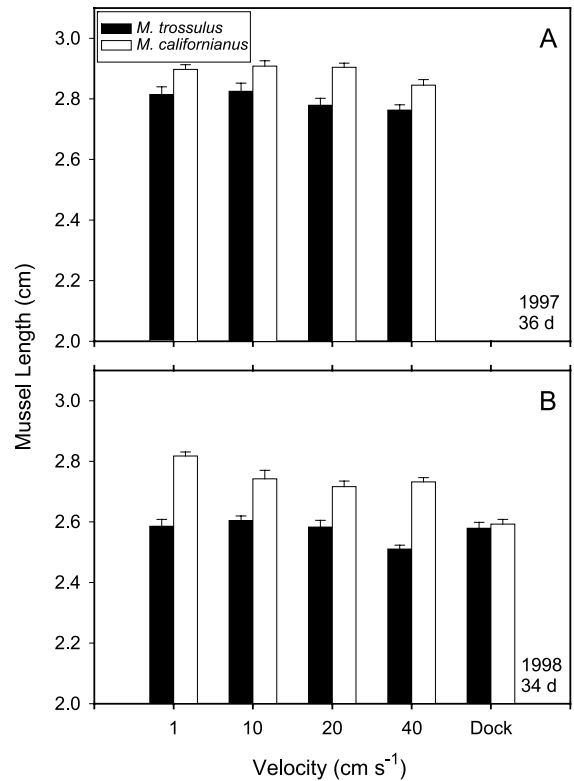


Fig. 6. The effect of velocity on the length of 2-cm-long *M. trossulus* (solid bars) and *M. californianus* (open bars) examined in the growth chambers (see Fig. 1) and under the dock at 3 m depth in (A) 1997 (initial length= 2.24 ± 0.02 and 2.28 ± 0.02 cm, respectively) and (B) 1998 (initial length= 2.10 ± 0.01 and 2.10 ± 0.01 cm, respectively). Significant differences were found in a three-way ANOVA involving species nested within velocities ($F_{5,7}=8.84$, $P=0.006$) and between years ($F_{1,7}=75.05$, $P<0.001$), but velocities were not significant ($F_{4,7}=2.83$, $P=0.109$). The pairwise difference indicated that *M. californianus* at 1 cm s⁻¹ were significantly larger than *M. trossulus* at 20 and 40 cm s⁻¹, *M. californianus* at 1 cm s⁻¹ were significantly larger than *M. trossulus* at 40 cm s⁻¹, and that mussels in 1997 grew significantly longer than in 1998. The bars represent the mean of ~15 individuals, and error bars represent 1 standard error of the mean. Unfortunately, the plate under the dock was lost in 1997.

species within velocities and velocities in other ANOVA designs. Importantly, the pattern described above was evident in the growth rates, and the growth rate of *M. californianus* was consistently greater than *M. trossulus*, especially in 1998 (Fig. 7). An interannual difference was also evident with relatively consistent growth ≥ 0.015 cm day⁻¹ for both species in 1997, but growth was < 0.015 cm day⁻¹ for *M. trossulus* and > 0.015 cm day⁻¹ for *M. californianus* in the growth chambers, despite the difference in the initial sizes in 1997 and 1998.

Placing the growth data into context requires a comparison among years and species (Fig. 8). These data reveal several consistent trends. Firstly, the highest growth rates were seen in the small *M. trossulus* in 1997 and in the lowest velocities in 1996 (open triangular symbols). Secondly, the next highest growth rates were consistently found in *M. californianus*

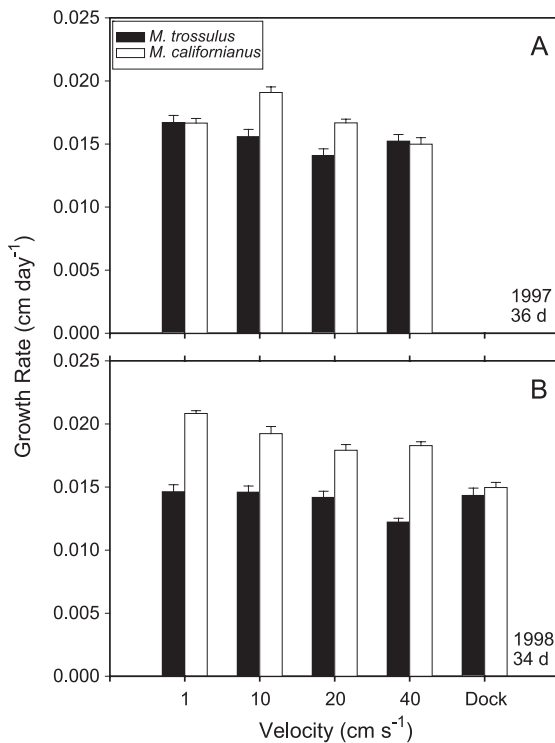


Fig. 7. The effect of velocity on the growth rate of 2-cm-long *M. trossulus* (solid bars) and *M. californianus* (open bars) examined in the growth chambers (see Fig. 1) and under the dock at 3 m depth in (A) 1997 and (B) 1998. The bars represent the mean of ~ 15 individuals, and error bars represent 1 standard error of the mean. Unfortunately, the plate under the dock was lost in 1997 (see Fig. 6).

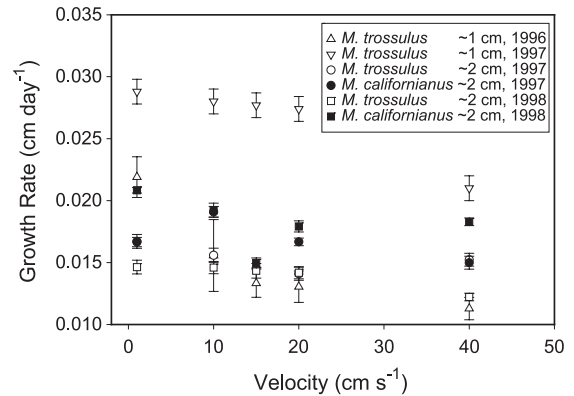


Fig. 8. The effect of velocity on the growth rate of different sized *M. trossulus* (open symbols) and *M. californianus* (solid symbols) examined in the growth chambers and under the dock at 3 m depth (see Fig. 1) between 1996 and 1998. The symbols represent the mean of ~ 24 individuals in 1996, ~ 30 for small mussels (~ 1 cm long) and ~ 15 for large mussels (~ 2 cm long) in other years, and error bars represent 1 standard error of the mean. The control (i.e., under the dock) results were placed at 15 cm s⁻¹ based on observations.

regardless of year or velocity (solid symbols). Thirdly, the growth rates tended to be relatively higher in 1997, especially for large *M. trossulus*. Lastly, the growth rates tended to decrease with increasing velocity as evident across the abscissa, especially for *M. trossulus*. Note that the results for the dock were placed at 15 cm s⁻¹ based on current measurement made before and after low tide (R. Rochette, BMSC, 1998, personal communication).

4. Discussion

It is evident that fluid dynamic factors, namely, velocity in this case, have important effects on the suspension feeding and growth of the blue mussels *M. trossulus* and *M. californianus*, although important species-specific differences were also found. Clearance rates (CR) were enhanced by increasing velocity over the range of 1 – 18 cm s⁻¹, whereas growth rates were reduced by higher velocities over the range of 1 – 40 cm s⁻¹ (Figs. 3 and 8). This would suggest that on the short-term (i.e., h-scale) mussels can access resources provided by the delivery of seston in the flow, but they are also affected by other factors that are evident over longer periods (i.e., month-scale).

There are several possible explanations for this difference, which are not necessarily mutually exclusive. Firstly, the range of velocities examined in the CR experiments only extended over the lower half of the growth experiment, and thus, it is difficult to compare the results directly. Secondly, there may have been ecological interactions in the field related to temporal variation in the plankton and the potential effects of fouling organisms, which included hydroids, that grew on the plates. These organisms were evident on all plates but tended to be denser at the higher velocities, but it is doubtful that they would be responsible for the differences in growth seen between species and sizes of mussels. Thirdly, clearance rate experiments measured the seston (organic and inorganic material) removed from the water in the chamber and may not provide an accurate measure of ingestion rates, as material may also be discarded as pseudofaeces (Wildish and Kristmanson, 1997; Hawkins et al., 1998). This may have been the case in some of our experiments due to the high initial seston concentration, which has been shown to lead to increased pseudofaeces production in mytilids including *M. trossulus* (Jørgensen, 1990; Arifin and Bendall-Young, 1997). However, recent reviews support the use of clearance rate methods as an indication of suspension feeding (Riisgård, 2001). Fourthly, there are likely to be increased costs associated with living at high velocities related to maintaining position under high fluid dynamic forces. These forces would include lift, drag, and shear stress in our experiments given that the velocity was constant (i.e., steady-state conditions). Behavioral responses would include increased tension on the byssal retractor muscle to pull mussels closer to the bottom, and increased byssal thread production to reinforce the attachment (i.e., *behavioral instability*, Ackerman, 1999; see Clarke and McMahon, 1996; Wildish and Kristmanson, 1997). The former response would limit shell gape and thus limit suspension-feeding rates (Jørgensen, 1990), whereas the latter would represent an increased metabolic cost. Lastly, related to this behavioral instability is the imposition of a constant flow that removed the mussels from a tidal cycle that would have included periods of low or no flow. It is unclear how variable tidal flow and/or wave action affect mussel suspension and growth, although growth in *M. galloprovincialis* has a continuous unimodal re-

sponse to wave exposure (Steffani and Branch, 2003). Regardless, models and direct measurements in the field indicate that currents do have important effects on both processes (e.g., Fréchette et al., 1989; see Wildish and Kristmanson, 1997; Ackerman et al., 2001).

In terms of *M. trossulus*, there was a marked increase (i.e., ~doubling) in CR with an increase in mussel size from 1 to 2 cm long, and similar increases in CR across the range of velocities. This result is consistent with other studies that have demonstrated size-dependent results in bivalve species including mytilids (e.g., Jørgensen, 1990; Ackerman, 1999; see Table 1 in Riisgård, 2001). Unfortunately, it was not possible to include small *M. californianus* in the present comparison due to difficulty in identifying them morphologically in the field below 1 cm shell length (Martel et al., 1999). However, it was evident that 2-cm-long mussels of both species had CR that were similar in magnitude. *M. californianus*, however, cleared at the highest rate at 12 cm s⁻¹ and, unlike *M. trossulus*, the CR was relatively lower at the highest velocity (Fig. 2C). Interestingly, physiological differences between the species have also been noted in their ability to eliminate heavy metals such as cadmium, which is presumably related to their water processing ability (e.g., Lares and Orians, 2001). The CR response in *M. californianus* is somewhat reminiscent of the continuous unimodal functional response of suspension feeders to velocity (Table 1; Wildish and Kristmanson, 1997). If this is the case, it would indicate a lower threshold for the onset of the decline in CR relative to *M. edulis* (Wildish and Miyares, 1990) and would suggest that *M. californianus* may be more sensitive to velocity than *M. trossulus*. Although this cannot be established unequivocally due to the limited range of velocities used in the experiment, Ackerman (1999) found that the highest CR in the siphonate bivalve *Dreissena bugensis* occurred at ~9 cm s⁻¹. It is likely that the unfused mantle in *Mytilus* species affords them more flexibility in feeding through the orientation and size of pseudosiphons (e.g., valve gape and siphon area; Newell et al., 2001; Riisgård et al., 2003). The suggestion that *M. californianus* is more sensitive to velocity than *M. trossulus* is opposite to what has been found in other growth studies where velocity effects were more evident in species that were not normally

exposed to energetic flows (Eckman and Duggins, 1993). However, it should be noted that the CR chamber configuration did not permit sufficiently high levels of turbulence to limit suspension-feeding rate as described in the literature (e.g., velocities $>18 \text{ cm s}^{-1}$; Wildish and Kristmanson, 1997; Ackerman, 1999).

Velocity had a significant negative effect on mussel growth that was similar across both species and sizes of mussels (Figs. 4–8). Growth rates were highest at 1 cm s^{-1} , declined through the highest velocity examined— 40 cm s^{-1} , and major differences were observed between species and sizes of mussels and among years. It is likely that the interannual variation in growth rates was related to the 1997/1998 El Niño event when surface waters in the summer of 1997 were warmer than either the summer of 1996 or 1998 (McPhaden, 1999; i.e., $16.5 \pm 0.3 \text{ }^\circ\text{C}$ [$n=21$] in 1996, $17.0 \pm 0.2 \text{ }^\circ\text{C}$ [$n=39$] in 1997, $16.7 \pm 0.2 \text{ }^\circ\text{C}$ [$n=16$] in 1998 based on the water samples in Fig. 9). In addition, there was evidence of higher seston concentrations in Bamfield Inlet in 1997 compared to 1996 as determined from the initial seston concentrations (C_0 ; Fig. 9) used in the suspension feeding experiments. Both of these factors would explain why the growth in 1997 was higher than in the other years. Specifically, there were significantly higher growth rates for the 1-cm-long *M. trossulus* in 1997, and this

was also the case for 2-cm-long individuals, although the increase in growth was not as large. The situation did not, however, apply to *M. californianus*, which had relatively higher growth in 1998 (Figs. 7 and 8) during the 1998/1999 La Niña event. Indeed, the increase in seston concentration in 1997 may have lowered the differences between the two species, perhaps due to a wider ecological tolerance on the part of *M. trossulus* (i.e., a wider range of habitats; Gosling, 1992). It is important to note that the growth rate in *M. californianus* was consistently higher than *M. trossulus* at the 2 cm size, with the possible exception of the 40 cm s^{-1} chamber in 1997 when the difference was small (Figs. 6 and 7). This would indicate that *M. californianus* has a relative advantage in terms of growth over *M. trossulus*, which appears to increase with velocity. Regardless, the magnitude of the growth rates determined here are consistent with those observed for *M. trossulus* in Prince William Sound, AK (e.g., $\sim 0.5 \text{ cm year}^{-1}$ for 2-cm-long individuals; Millstein and O’Clair, 2001) and *M. edulis* in general (see Table 8 in Jørgensen, 1990).

4.1. Ecological implications

A number of ecological implications arise from these results. Specifically, relatively higher seston concentrations and temperatures in the water lead to relatively higher growth rates in the mussels (i.e., bottom-up controls). This result is consistent with studies by Menge (2000) and McQuaid and Lindsay (2000) who found that increased seston due to oceanographic conditions (e.g., coastal upwelling) led to increased mussel growth. We do not have detailed time series of the seston concentration nor do we have an explanation for the relatively higher seston concentrations in 1997/1998 El Niño other than a possible increased detrital fraction from internal sources (i.e., kelp), and terrestrial sources due to runoff (Cayan et al., 1999). Kelp detritus is an important food source to suspension feeders including *M. trossulus* (Duggins et al., 1989).

These results demonstrate that there are significant differences between *M. californianus* and *M. trossulus* in terms of their suspension feeding and growth. In the case of suspension feeding, it may be that *M. californianus* is able to take advantage of periods of relatively low energetic conditions during wave trains to suspen-

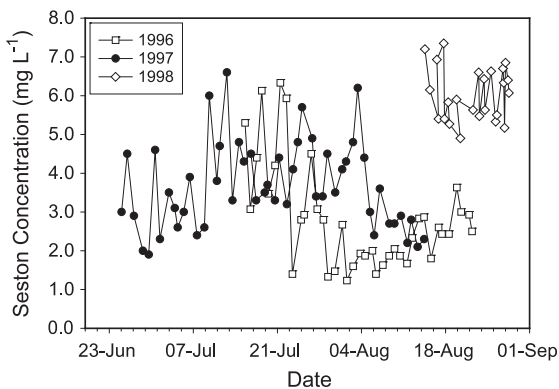


Fig. 9. The seston concentration in Bamfield Inlet in 1996, 1997, and 1998, as determined from the initial seston concentration measured in the clearance rate experiments. The symbols represent the mean of three 1 l samples. The corresponding mean water temperatures at the time of collection were $16.5 \pm 0.3 \text{ }^\circ\text{C}$ [$n=21$] in 1996, $17.0 \pm 0.2 \text{ }^\circ\text{C}$ [$n=39$] in 1997, $16.7 \pm 0.2 \text{ }^\circ\text{C}$ [$n=16$] in 1998. Note that 1997/1998 was an El Niño year and 1998/1999 was a La Niña year.

sion feed, which might explain their higher CR at 12 cm s⁻¹. Similar behavioral responses to waves have been observed in lobster foraging (Robles et al., 2001). Clearly, in situ field research will be needed to address this possibility, although there is evidence of higher growth in wave-exposed habitats vs. sheltered ones for the South African mytilid, *Perna perna* (e.g., 0.011 and 0.007 cm day⁻¹, respectively; McQuaid and Lindsay, 2000). *M. californianus* has a growth advantage over *M. trossulus* that is related to velocity, especially when seston is limited. Such a growth advantage would lead to a fluid dynamically mediated competition for *M. californianus* over *M. trossulus*. In the case of the spatial difference in juvenile and adult habitats of *M. trossulus* (Heath et al., 1996), the absence of adult *M. trossulus* in wave-exposed coasts is likely due to direct competition with *M. californianus* during juvenile stages when velocities are high. This suggests that access to food resources may be more important to benthic invertebrates, especially suspension feeders, than has been considered previously. We, therefore, conclude that fluid dynamic factors are significant in determining the growth, competition, and evolutionary ecology of blue mussels.

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