



**The Effect of Long-Term Alteration of in Situ Currents on the Growth of *Mercenaria mercenaria* in the Northern Gulf of Mexico**

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## The effect of long-term alteration of in situ currents on the growth of *Mercenaria mercenaria* in the northern Gulf of Mexico

**Abstract**—Water currents were experimentally manipulated for 3 months in a shallow subtidal sandflat through a series of nine channels with diverging, parallel, or converging walls (7 m long, 1.2 m high). Three treatments were chosen to bracket the ambient flow rates; vertically averaged velocities were reduced by 40%, reduced by 2%, or increased by 65%. Within the center of each channel, six *Mercenaria mercenaria* [shell length,  $36.9 \pm 2.2$  mm (mean  $\pm 1$  SD)] were placed haphazardly in 0.25-m<sup>2</sup> plots. Although water-col-

umn chlorophyll *a* levels declined near the substratum, concentrations did not differ among channel flow treatments. Mean clam lengths increased 19% during the study, but growth rates did not differ significantly among channel flow treatments. These results suggest that the natural range of flow rates (up to 27 cm s<sup>-1</sup>), in the absence of local food depletion, does not alone alter growth of this active suspension feeder.

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The role of fluid dynamics has become increasingly evident in the biology of marine organisms (Nowell and Jumars 1984; Denny 1988). Flow can affect the arrival of planktonic larvae, efficacy of chemical cues, exchange of nutrients, probability of fertilization, and morphology of many benthic organisms. Perhaps most critical to an organism's survival and reproductive output, water movement has been shown to influence growth rates in organisms as diverse as cnidarians (Sebens 1984), bryozoans

(Hughes 1989), and gastropods (Brown and Quinn 1988).

Effects of currents on growth have been studied largely in field transplant or laboratory flume experiments. Both types of experiments have exhibited successes, but each has inherent limitations. For example, when organisms are grown in field sites of presumed flow differences, a suite of other environmental parameters may also vary (e.g. food supply, temperature, and sediment characteristics) (Ginsburg and Lowenstam 1958; Eckman 1987; Grizzle and Morin 1989). Similarly, flume studies are not easily able to mimic the unsteady flows (e.g. tidal) or food concentrations normally experienced by many marine organisms (Wildish and Kristmanson 1984; Cahalan et al. 1989; Eckman et al. 1989).

Given these limitations, manipulations of the current regime in a single field location may be preferable when examining the influence of currents (and its correlates) on growth. Unfortunately, given the forces necessary to move or divert large volumes of water on long time scales, such experiments are often impractical. Although some researchers (e.g. Hughes 1989) have suggested that field alterations of water flows are easy to achieve, most growth studies have decreased water exchange only through variations in the height of roughness elements (Hughes 1989; sensu Nowell and Jumars 1984). In two studies where shear (or friction) velocities ( $u_*$ ) have been increased in situ, only short-term behavioral experiments with meiofauna (Fegley 1987) or observations of ripple migration in an intertidal sand flat (J. E. Eckman, cited by Nowell and Jumars 1984) have been conducted.

Here, we describe the results of a bivalve growth study in which the natural current regime was altered in a shallow subtidal habitat. Through a series of tapered channels, we bracketed the ambient water velocities to examine the influence of water movements on growth rates of the hard clam *Mercenaria mercenaria* (L.). Although the use of channels is not new to aquatic field research, many previous attempts (except Fegley 1987) have sought only to delimit a block of water to examine nutrient and sediment fluxes (e.g. Wolaver et al. 1985) or

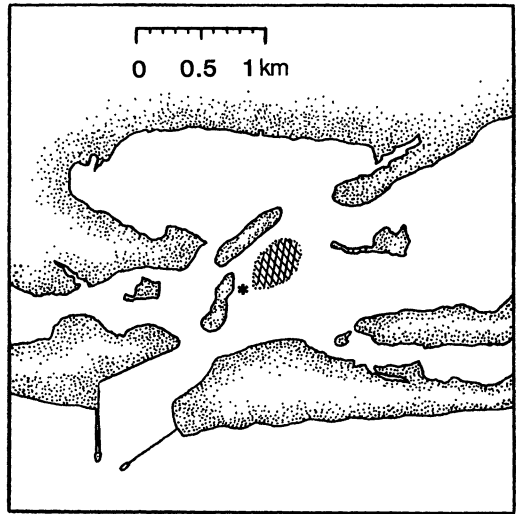


Fig. 1. Perdido Pass, Orange Beach, Alabama (30°17'N, 87°33'W). The study site (\*) is located between a small island and *Halodule wrightii* seagrass bed (indicated by hatched enclosure) in 0.6 m of water. Currents at the site are driven by winds and forced between the seagrass bed and the island.

depletion of plankton by suspension feeders (Buss and Jackson 1981). Our study differs from these earlier experiments in that in situ currents were altered for several months to study an active suspension feeder's growth response.

Field experiments designed to test the importance of water currents to growth were conducted near Perdido Pass, Alabama. Perdido Pass, a manmade opening to the Gulf of Mexico, is essentially atidal (tidal range, <15 cm) with currents driven by the wind and modified by local bottom topography (Fig. 1). Consistent field manipulations of water velocities with tapered channels require that the current direction remains parallel with the major axis of the channel. A sandy site (0.6 m deep) between an island and a shallow (0.3 m deep) seagrass bed of *Halodule wrightii* (Aschers) where currents are funneled along predictable paths was chosen for the channels. Sediments were predominately sand (>95% by wt) and <0.5% organic matter (Judge et al. in prep.).

Channel walls (7 m long × 1.2 m high) were made of 0.5-inch (1.27 cm) exterior grade, pressure-treated plywood sheets (1.2

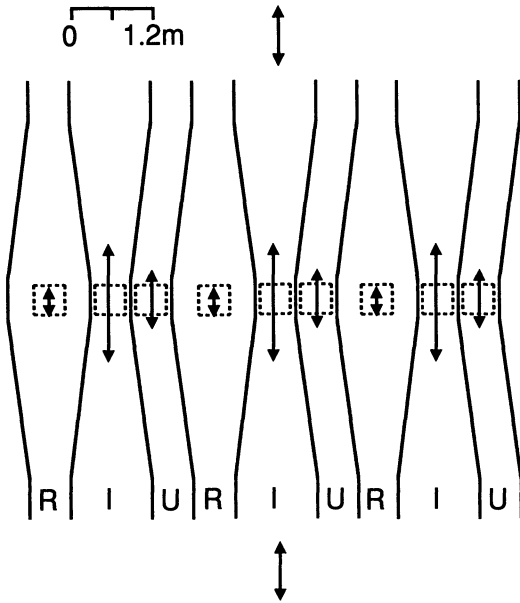


Fig. 2. Schematic representation of the nine-channel flow apparatus. Channel walls are indicated by solid lines. The apparatus of channels was aligned with the prevailing current direction. Flow velocity in the center working section was reduced (R), unchanged (U), or increased (I) by altering channels width. Flow direction and relative magnitude are indicated by arrows. Six clams were placed in each of the 0.25-m<sup>2</sup> plots (dotted boxes) and in three control plots located 5 m outside of the apparatus (not shown).

× 2.4 m) extending from 0.15 m into the sand to above the water line. Throughout the experiment, water height remained at least 30 cm below the top of the walls, ensuring that flow passed through, rather than over, the channels. Adjacent sheets were glued and bolted together and the lip created by the 15-cm overlap between the sheets was smoothed by galvanized metal flashing to reduce flow separation near the walls. Neighboring channels shared a common wall. All channels were connected above the water by 8-m, wooden crossbeams (5 × 10 cm) and secured by guy wires staked into the sand at each end. The total apparatus of nine adjacent channels had overall dimensions of 7 × 8 m.

The nine adjacent channels were allocated to one of three flow treatments: three each of reduced, unchanged, or increased flow velocity (Fig. 2). The flow treatments were created by expanding, maintaining, or

constricting channel width as the ambient currents passed through the apparatus. Marked quadrats located 5 m outside the apparatus served as an unwallled control to assess potential wall artifacts. Working sections (minimum, 0.6 m wide) were located in the channel centers 3.5 m downstream of the channel entrance. Channel entrance widths matched exit widths to maintain flow treatments if flow reversed direction. Widths along the channel's length varied between 1.2 and 0.6 m and were held fixed by the wooden crossbeams. The channels were designed to limit flow separation from the walls by keeping expansion angles below 7° (Nowell and Jumars 1987; Denny 1988). Within each working section, an experimental plot (0.25 m<sup>2</sup>) was positioned at least 5 cm from both channel walls. It was beyond the thickest boundary layer (<4 cm) expected to develop along the wall of the working section (Nowell and Jumars 1987).

All channels were calibrated systematically with a Marsh-McBirney 511 electromagnetic current meter to acquire a depth profile of velocity. Water velocities (mean over 5 min) on a typical day (i.e. modal flow speed of 10 cm s<sup>-1</sup>) were measured 10, 20, 30, 42, and 50 cm above the substratum in each channel's working section and above the three control plots located 5 m outside the channel apparatus. Flow velocities were analyzed for channel flow treatment and height above the bottom with ANOVA. Channel treatment means were compared a posteriori to ambient (control) velocities with Dunnett's test (Day and Quinn 1989). Because ambient water flows passively drive water movement through the apparatus, absolute velocities were expected to vary temporally. For example, near-surface ambient flow velocities (measured on eight occasions) were found to vary at least an order of magnitude from near zero (<2 cm s<sup>-1</sup>) to >20 cm s<sup>-1</sup> (pers. obs.).

The relative difference between channel treatments should remain roughly constant, however, over a wide range of atmospheric and hydrographic conditions. The degree of velocity change in the channel flow treatments results from the geometry of the experimental design, a factor that did not change appreciably with variations in am-

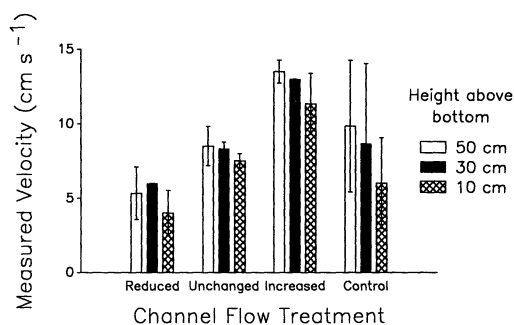


Fig. 3. Calibration of the channel flow treatments for a typical day (i.e. modal flow velocity of  $10 \text{ cm s}^{-1}$ ). Water velocities (mean over 5 min for each channel replicate  $\pm 1$  SE,  $n = 3$ ), shown only for 10, 30, and 50 cm, were measured at 10, 20, 30, 42, and 50 cm above the bottom with an electromagnetic current meter to quantify the magnitude of the flow treatment. The three treatments and control differed significantly and bracketed the ambient (control) water currents with each treatment velocity different from the other two. The unchanged treatment velocities were not significantly different from control measurements. The vertically averaged velocity profile quantified the three flow treatments as either a 40% reduction, 2% reduction, or 65% increase relative to controls.

bient current velocity or water depth. Although the channel treatments were designed to bracket the ambient flow rates by a factor of two, slight changes in water depth ( $< 10 \text{ cm}$ ) within the channel flow treatments and wall effects would make the predicted relative alterations inexact (Fegley 1987). We did not intend to create specific flow velocities—just consistent differences among channel flow treatments. Additional channel calibration periods with the Marsh-McBirney current meter at two heights (10 and 42 cm) using the same protocol during a low ambient flow condition (near-surface currents  $< 2 \text{ cm s}^{-1}$ ) and with rhodamine dye (six timed dye cloud releases measured over 50 cm) at one height (42 cm) during high-flow conditions ( $> 20 \text{ cm s}^{-1}$ ) were conducted.

Given constant relative differences among treatments, velocities at a given height can be expressed as a percentage of the measurements above the control plots. When these percentages were averaged vertically, the velocity profile provided an approximate index to quantify relative current alteration (Table 1). This relative index is largely insensitive to height above the sub-

Table 1. Comparison of the relative efficacy among channel flow treatments during periods of extreme ( $< 2$  or  $> 20 \text{ cm s}^{-1}$ ) and modal ( $10 \text{ cm s}^{-1}$ ) flow conditions. Percentage change in current velocity for each treatment relative to the control plots during low flow (mean of measurements from 10 and 42 cm above bottom) and high flow (measurements at 42 cm only) are shown with the values during the modal flow periods measured at the same height(s). The two modal-flow columns are different because some flow variations with depth exist and few heights are used for this calculation. Note that values in column 2, which averages two heights, approach the relative current alteration index values for the entire water column ( $-40\%$ ,  $-2\%$ ,  $+65\%$ ). Strictly, however, comparisons should be made only between column 1 and 2 (or 3 and 4) within a particular channel flow treatment. Velocity measurements within treatments remain different during periods of low (ANOVA,  $F_{2,12} = 6.79$ ,  $P = 0.01$ ) and high flow (ANOVA,  $F_{2,5} = 25.39$ ,  $P = 0.002$ ).

Treatment	Low flow vs. modal flow		Modal flow vs. high flow	
	(<2 cm s <sup>-1</sup> )	(10 cm s <sup>-1</sup> )	(10 cm s <sup>-1</sup> )	(>20 cm s <sup>-1</sup> )
Reduced	-25	-40	-47	-45
Unchanged	-23	-6	-37	-21
Increased	+52	+63	+36	+24

stratum (Fig. 3), except at the bottom where the “law of the wall” (Nowell and Jumars 1984) prevails, suggesting that the relative percentage change will remain similar at the feeding height of the clam. Although arithmetic averaging of nonlinear velocity depth profiles may produce a potential source of error for the flow treatment quantification, the index allowed biologically meaningful interpretation of ANOVA.

Chlorophyll *a* concentration, as an indirect assay of food quantity, was determined fluorometrically (Parsons et al. 1984) to assess potential food supply differences among channel flow treatments. At two locations within each channel (entrance and working section), Chl *a* was sampled at 1 cm above the bottom with 6.4-mm tubes at an intake velocity of  $1 \text{ cm s}^{-1}$  to match the incurrent siphon diameter and pumping rate of an individual clam (Monismith et al. 1990; Judge et al. in prep.). Active suspension feeders such as *M. mercenaria* do not sample the water isokinetically (Monismith et al. 1990) and strict attention must be paid to the sampling protocol. Departures from isokinetic sampling (intake speed matched to ambient flow velocity) can bias static

sample concentrations (Wildish and Kristmanson 1984); nonetheless food abundance must be assayed from the perspective of the clam to model growth realistically (Grizzle and Lutz 1989; Judge et al. in prep.). For comparison, simultaneous water samples were also collected similarly at 5, 15, and 45 cm above the bottom.

Samples (50 ml) were drawn by syringe and passed through filters (Whatman GF/C, 1.2- $\mu\text{m}$  pore diam). The filters were placed into 10 ml of 90% acetone in the field and held on ice in the dark for 24 h. Sample concentrations were quantified the following day with a fluorometer (Turner Designs), before and after adding two drops of 1 N HCl. Chlorophyll differences were analyzed by a three-way ANOVA for flow treatment, height above bottom, and location within the channel.

*Mercenaria mercenaria* was used to study the importance of current velocity to bivalve growth. *M. mercenaria* inhabits sandy substrates and seagrass beds near Perdido Pass. Clams were purchased from a single source population (Harbor Branch Oceanogr. Inst. Hatchery, Fort Pierce, Florida) to control for genetic variability (Peterson and Beal 1989). Juvenile clams were used to ensure that energy reserves went into growth and not reproduction. All clams were individually labeled by gluing (cyanoacrylate) numbers (Panduit Cable Co.) to the right valve and measured for shell length (longest linear dimension), shell height, and total weight. Six clams were placed in the 0.25- $\text{m}^2$  experimental plot (24 clams  $\text{m}^{-2}$ ) in the working section of each channel and in each of three control plots (72 clams total) on 10 October 1990. Although siphon nipping (i.e. cropping) by predators can decrease the individual growth rate of *M. mercenaria* (Coen and Heck 1991), clams were not protected from potential predators in this experiment. The impact of nipping was assumed to be constant across all treatments.

Clams were retrieved 3 months later on 9 January 1991, remeasured for final size, and frozen. After freezing for 1 week, clam soft tissues were separated from the shell and dried to a constant weight (48 h at 80°C) to partition total weights into tissue and shell weights for a condition index (tissue-to-shell

ratio). At least three clams were recovered in each replicate (three replicates in each of three treatments and a control) except for one replicate of the unchanged velocity treatment that was later dropped from the analysis (see below). Because individual sizes were log-normally distributed within a population, all sizes were  $\log_{10}$ -transformed to correct for these (small) variations in initial sizes (Day and Quinn 1989). Mean growth in each replicate was used as a single estimate for ANOVA to avoid pseudoreplication associated with subsampling.

Measured near-surface ambient current velocities during the 3-month study ranged from near 0 to  $>20 \text{ cm s}^{-1}$ . Flows in each channel were quantified systematically on a typical day (i.e. modal flow speed of  $10 \text{ cm s}^{-1}$ ) with the Marsh-McBirney current meter (Fig. 3). When compared with the control plot measurements, the channel apparatus successfully bracketed the ambient velocities (ANOVA,  $F_{3, 40} = 11.37$ ,  $P < 0.0001$ ) as both the increased ( $12.47 \pm 2.97 \text{ cm s}^{-1}$ , mean  $\pm$  SD) and the reduced ( $4.80 \pm 2.43 \text{ cm s}^{-1}$ ) flow treatments were different from the velocities measured in the control plots (Dunnnett's test,  $\text{MSD}_{40} = 3.27$ ,  $P < 0.05$ ) while the unchanged-velocity treatment ( $7.33 \pm 1.83 \text{ cm s}^{-1}$ ) was not significantly different from adjacent control velocities ( $8.07 \pm 6.14 \text{ cm s}^{-1}$ ) measured outside the apparatus.

To assess the biological significance of among-flow treatment differences, we further quantified the effectiveness of each treatment by taking the vertically averaged velocity as a percentage because velocities varied with height above the bottom (Fig. 3; ANOVA,  $F_{4, 30} = 7.20$ ,  $P < 0.0003$ ). Consequently, channel flow treatments were roughly categorized from the modal flow measurements (Fig. 3) as either a 40% reduction in flow velocity, a 2% reduction, or a 65% increase relative to the control plots. Thus, although the ANOVA can only detect and not quantify significant statistical differences between treatments, this index suggested that mean velocities were altered by a factor of nearly two. These proportions remained similar during periods of very high or very low ambient flow conditions at a given height above the bottom (Table 1).

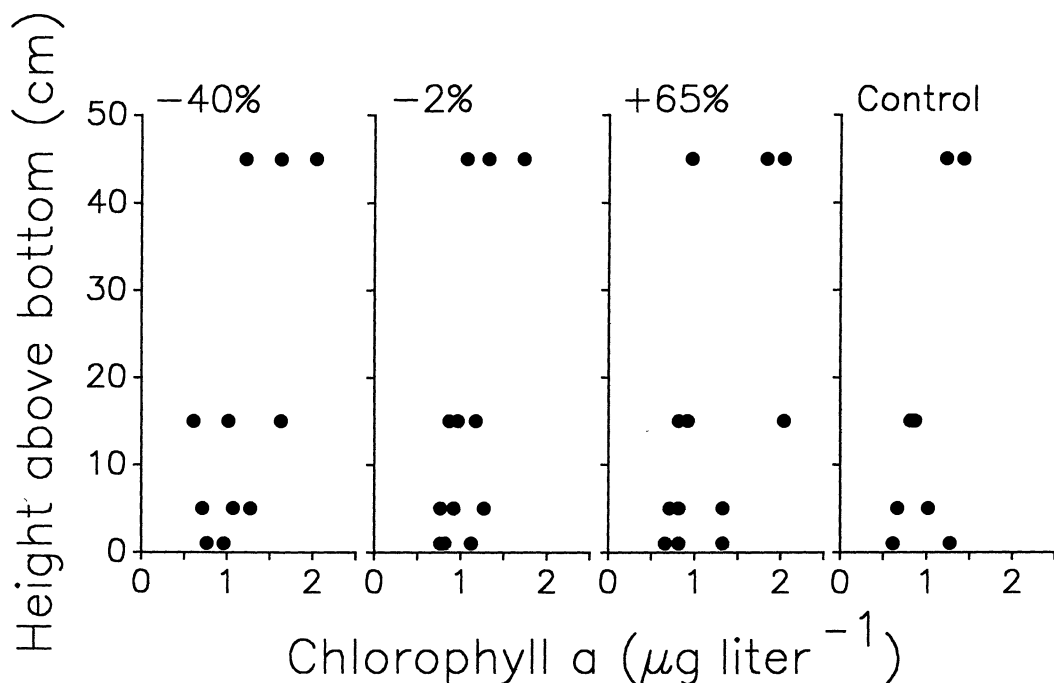


Fig. 4. Chlorophyll *a* measurements above the working section in the channel apparatus. Chlorophyll concentrations did not differ among channel flow treatments (40% reduction, 2% reduction, or 65% increase of water currents) or control (ANOVA,  $F_{3,52} = 0.87$ ,  $P = 0.46$ ) and averaged  $0.90 (\pm 0.24) \mu\text{g liter}^{-1}$  at 1 cm above the bottom. Chlorophyll abundance did vary with height above the bottom (ANOVA,  $F_{3,52} = 12.29$ ,  $P < 0.0001$ ).

Algal food abundance was assayed through Chl *a* measurements during 1 d in December 1990. Chl *a* abundances generally ranged from  $0.5$  to  $2.0 \mu\text{g liter}^{-1}$  and varied positively with height above the bottom (Fig. 4). Chlorophyll measurements did not vary among channel flow treatments or control plots (Fig. 4), however, and averaged  $0.90 (\pm 0.24) \mu\text{g liter}^{-1}$  at 1 cm above the bottom sand. Moreover, the apparatus did not cause algal abundance to change along the length of the channels [channel entrances:  $1.20 (\pm 0.49) \mu\text{g liter}^{-1}$ ; working sections:  $1.13 (\pm 0.41) \mu\text{g liter}^{-1}$ ; ANOVA,  $F_{1,52} = 0.46$ ,  $P = 0.50$ ], suggesting that water exchange through the apparatus was greater than phytoplankton production, grazing, or sedimentation. All treatment interactions were nonsignificant.

Recapture rates were high, with 71% of all clams recovered alive and no recovery-rate differences among treatments (ANOVA,  $F_{3,7} = 2.43$ ,  $P > 0.10$ ); thus, final clam densities did not differ significantly among

channel flow treatments. One replicate of the unchanged-flow treatment was dropped from the analysis because its outside wall collapsed, and no clams were retrieved at the end of the study.

Clam length averaged  $36.9 \pm 2.2$  (mean  $\pm$  SD) mm at the start of the study and increased to  $44.0 \pm 2.5$  mm in 3 months—a mean increase of  $>19\%$ . Changes in log-transformed length did not differ significantly among treatment or control plots (Fig. 5). The probability of not finding a 1-mm growth differential between flow treatments (the difference between treatments with the largest and smallest growth response) significant (i.e. type 2 error) given  $\alpha = 0.05$  is  $\sim 0.24$ . Similar results were obtained with other growth measures such as shell height or total weight—with 19 or 65% increases, respectively. Likewise, final measurements of tissue (wet or dry) weight, final shell weight, or condition index did not differ significantly among treatments (ANOVA, all values of  $P \gg 0.10$ ). Finally, log-trans-

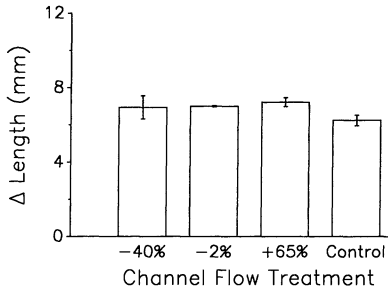


Fig. 5. Change in mean shell length ( $\pm 1$  SE,  $n = 3$ ) for *Mercenaria mercenaria* over 3 months. The average length increase of 3–6 recovered individuals provided a single growth estimate for each treatment replicate. Log<sub>10</sub>-transformed growth rates showed no significant differences among channel flow treatments (ANOVA,  $F_{3,7} = 1.21$ ,  $P = 0.38$ .)

formed growth rates in length were independent of final density ( $r^2 = 0.12$ ;  $t_9 = 1.085$ ,  $P = 0.32$ ).

Previous studies examining the relationship between flow velocity and growth rates of active suspension feeders have produced conflicting results (Kirby-Smith 1972; Eckman et al. 1989; Grizzle and Morin 1989). Unlike passive suspension feeders in which food capture, and presumably growth, has been positively correlated with particulate flux (Muschenheim 1987), active feeders are not strictly dependent on flow speed and the relationship between filtration rate and current speed is less clear (Eckman et al. 1989).

In this study, when ambient velocities (up to 20 cm s<sup>-1</sup>) were bracketed by a factor of nearly two and food concentrations remained constant, growth rates of *M. mercenaria* did not vary between treatments with different mean water velocities. The absence of a differential growth response could not be attributed to low growth during the study period because the clams exhibited substantial growth in all treatments. Clam lengths increased by 19% in only 3 months, comparable to rates found in another experiment conducted simultaneously (Coen et al. in prep.) or during the spring (9% in 2 months, Coen and Heck 1991) only 50 m away. The range of flow treatments offered by the apparatus span those used in previous field transplant experiments with *Mercenaria* (Table 2).

The lack of a clear relationship between mean current velocity and clam growth is

Table 2. Flow speeds observed in *Mercenaria mercenaria* growth experiments. Height of maximal recorded velocity (cm s<sup>-1</sup>) is not universally provided. Velocity (cm s<sup>-1</sup>) at 8–10 cm above the bottom is generally the lowest height reported.

Reference	Maximal recorded velocity	Mean velocity at 8–10 cm above sand
Kerswill 1949	>20	8
Grizzle and Morin 1989	>20	4.6–6.3
Irlandi and Peterson 1991	27	4.7
This study		
Ambient	22	6.0
High-flow channels	27.4	11.3

consistent with the observations by Pratt and Campbell (1956) who found no relationship between growth and currents in Narragansett Bay and with recent short-term flume experiments by Grizzle et al. (in prep.) for velocities >2 cm s<sup>-1</sup>. In contrast, increased growth rates have been noted for clams held in trays at progressively higher levels above the bottom (Kerswill 1949) or in regions with higher water velocities (Grizzle and Morin 1989), while others (Irlandi and Peterson 1991) have noted reduced growth rates for clams in sandy bottoms with flow speeds higher than in nearby seagrass beds.

Changes in filtration rates (rate of removal of particles from a known volume of suspension) have often been invoked as a mechanism to explain the influence of water movement on the growth rates of suspension feeders. Filtration rates in active suspension-feeding bivalves have been shown to increase (Walne 1972; Frechette et al. 1989), decrease (Wildish and Miyares 1990), or remain unchanged (Hildreth 1976) with increasing current speed. Likewise, growth in active suspension feeders has at times been increased (Kerswill 1949; Grizzle and Morin 1989) or inhibited by increased water movements (Kirby-Smith 1972; Eckman et al. 1989). Unfortunately, there are several confounding factors that preclude direct comparison of these growth studies. The first pair used siphonate bivalves in transplant experiments, while the second set used non-siphonate scallops in laboratory studies. Scallops may not be representative of other

active suspension feeders because their inhalent and exhalent pseudo-siphons may not experience the same flow fields (Eckman et al. 1989).

Even if changing water velocity alone does not influence growth, low food abundances can limit growth rates in benthic suspension feeders. Near-bottom local resource depletion under field conditions has been observed for sponges, bryozoans (Buss and Jackson 1981), and bivalves (Wildish and Kristmanson 1984; Frechette et al. 1989) and may lead to reduced growth rates (Peterson and Black 1987). For instance, the mussel *Mytilus edulis* grows more slowly at 0.05 m above the bottom than at 1 m, presumably because of levels of food (Frechette and Bourget 1985). At other times, however, food abundances near the bottom can be higher than in the water above (Muschenheim 1987; Judge et al. in prep.).

Although phytoplankton vertical distributions can be heterogeneous, water-column mixing in estuarine environments is often sufficient to eliminate any relationship between chlorophyll concentration and depth (Holligan et al. 1984; Wolaver et al. 1985). Our site adjacent to Perdido Pass is a shallow, wind-driven body of water and is generally well mixed during most of the year with chlorophyll concentrations uniformly distributed in the water above the sand (Judge et al. in prep.). Turbulence in such waters increases mixing and food supply rates to the bottom (Denny 1988; Frechette et al. 1989). Consequently, even if water velocity does not directly influence growth in these field situations, it may indirectly alter food supply through increased mixing or resuspension (Muschenheim 1987). Furthermore, because passive water flow through the clam is unlikely for *Mercenaria* (Monismith et al. 1990), food capture should depend upon the volume of the feeding zone (Grizzle and Lutz 1989) determined by the pumping rate of the clam and ambient flow velocity. The feeding zone of an active suspension feeder is more than simply the amount of water filtered and its food concentration because it incorporates the hydrodynamic processes of food particle capture (Judge et al. in prep.).

Given a well-mixed water column and

high phytoplankton productivity relative to benthic consumption rates, food consumption and growth of active suspension feeders ought to be decoupled from water velocity in the vicinity of the filtering apparatus. Our results support the contention of Eckman et al. (1989) that active suspension feeders should not be influenced by water velocity if mixing is sufficient to replenish near-bottom food supplies in the immediate vicinity of the filtering organism (i.e. no local resource depletion). Under such field conditions, growth should be dependent on food concentrations alone. Similarly, Cahalan et al. (1989), while studying scallops in a laboratory flume, found that the flux of food particles (product of concentration and velocity) was not a good predictor of growth and that the effect of food concentration was more pronounced than flow velocity.

Although sediment samples were not collected in the channels, grain size did not appear to vary with treatment (pers. obs.). Some previous correlative studies on sediment type have suggested that *Mercenaria* may grow better (Pratt and Campbell 1956), or worse (Irlandi and Peterson 1991), or no differently (Coen and Heck 1991) in sandy bottoms vs. muds, but Grizzle and Morin (1989), after correcting for local water velocity, found no strong effect of sediment type. Furthermore, it is unlikely that any unmeasured sediment-type difference between channel flow treatments would produce our observation of no differences in clam growth. Rather, potential sediment differences should serve to amplify growth differences.

There are at least two possible mechanistic explanations for the apparent lack of a growth response. First, clams may feed over only a narrow range of flow conditions and each channel experiences these feeding conditions for about the same amount of time. In both high- and low-flow environments, however, flow speeds typically vary throughout a tidal cycle and our experimental apparatus maintained some realism by allowing these natural variations to persist. Second, it can also be argued that the range of currents offered was not extreme enough to observe growth inhibition. Although we cannot rule out that growth in

*Mercenaria* may be inhibited at particular constant flow speeds (as demonstrated in flume studies, but see Table 2), clams in habitats subjected to currents that vary on lunar and meteorological time scales failed to exhibit a differential growth response when current velocities were bracketed by a factor of two over a period of 3 months. We suggest that future experiments should incorporate natural current fluctuations (rather than the constant speeds in many flume experiments) to elucidate more realistic processes affecting bivalve growth.

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## Shifts in seston characteristics after inundation of a European coastal salt marsh

*Abstract*—A microbial assay and in-source pyrolysis mass spectrometry were used to demonstrate a shift in the characteristics of sestonic particulate organic matter after tidal inundation of a coastal salt marsh in the southwest Netherlands. Analysis of seston samples collected from the main tidal creek of the marsh during a series of tidal cycles showed that an increase in microbial degradability accompanied a more pronounced lipid character of the seston after inundation. No evidence was found that the halophyte vegetation contributed to the efflux of particulate organic matter from the marsh, indicating that the vegetation of the poorly flooded European Atlantic salt marshes may be a minor contributor of particulate organic matter to adjacent bodies of water.

A long series of studies carried out on salt marshes of the Atlantic and Gulf coasts of North America has shown that these wetlands are generally sources of particulate organic C for adjacent coastal waters (Nixon

1980; Dame et al. 1986). Salt-marsh cord grass, *Spartina alterniflora*, which dominates the low intertidal zone of the marshes, is considered to be an important contributor to this carbon efflux (Odum and de la Cruz 1967). European Atlantic salt marshes lack low intertidal vascular plant species (Beefink 1977). This absence may have consequences for the flow of particulate organic matter (POM) between the marshes and adjacent waters. Whether the presence of these salt marshes affects the nature and quantity of bioavailable POM in the nearby coastal zone, and thus the functioning of the coastal food web, is unknown. Such an impact would result from changes in the POM pool in the tidal water inundating the marsh, as this water is the carrier for particulate matter between the marsh and the adjacent coastal water. To contribute to understanding C fluxes between these salt marshes and coastal waters, we investigated whether shifts in the characteristics of sestonic POM after inundation of such a marsh in the southwest Netherlands could be detected. To characterize the seston, we studied the biodegradability and chemical composition of the material.

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