Does flow speed also have a direct effect on growth of active suspension-feeders: An experimental test on oysters

Abstract—The direct effects of flow velocity on growth of juvenile American oysters *Crassostrea virginica* (Gmelin) were tested without confounding by indirect effects of vertical mixing by measuring growth inside pipes, varying average flow over five levels (0, 0.5, 2.5, 4, and 7 cm s\(^{-1}\)) at each of two food concentrations. Growth increased with food concentration and increased monotonically with flow velocity over all flows tested for both food treatments. In this experiment, food concentration and flow velocity acted independently in their effects on growth, with a multiplicative term (flux) not making any significant contribution beyond the independent, additive contributions of food and flow. Thus, the apparent positive response of growth in this active suspension-feeder to external flux of food is best interpreted as a coincidental by-product of the action of two separate responses to the terms that comprise flux.

Benthic suspension-feeders harvest particulate food materials from the surrounding water and thereby provide an important coupling between the pelagic and benthic environments, especially in shallow waters (Dame et al. 1980; Officer et al. 1982; Peterson and Black 1987). Although individual growth rates, production, and energy transfers vary strongly with seasonally changing water temperatures, metabolic rates, and reproductive status (Vahl 1980; Bayne and Newell 1983), growth of suspension-feeders over finer temporal and spatial scales seems to be controlled by complex interactions among feeding physiology, food availability, and hydrodynamics in the region of the benthic boundary layer (e.g. Vogel 1981; Jørgensen 1983; Fréchet et al. 1989).

Suspension-feeders can be divided into two basic feeding modes: passive and active. Passive suspension-feeders intercept particles that advect past the organism and thus are directly responsive to food flux—the product of concentration and flow speed (Patterson 1980; Muschenheim 1987); growth increases with increasing food concentration and flow speed (Muschheim 1987; Sanford et al. 1994), although excessively high flow speeds threaten damage to the food capture organs and can inhibit feeding and growth (e.g. Okamura 1984). Active suspension-feeders, such as bivalve molluscs, pump water from the external environment to internal cavities thereby creating their own internal feeding currents (Jørgensen 1983; Newell and Langdon 1995). Although it seems clear that growth of active suspension-feeders should depend on food con-
centration, a point that has been confirmed (e.g. Widdows et al. 1979), it is not so obvious why growth of an active suspension-feeder should be affected by flow speed in its external environment (Eckman et al. 1989). Yet, several previous studies have shown growth of active suspension-feeders to respond to external flow velocity, although in complex ways (Kirby-Smith 1972; Grizzle and Morin 1989; Grizzle et al. 1992).

Processes that might relate current velocity to growth rate in active suspension-feeders can be categorized as indirect or direct. Growth of active (and also passive) suspension-feeders can be enhanced at higher flow speeds because of enhancement of turbulent vertical mixing. In faster flows, greater vertical mixing reduces the intensity of vertical gradients in food concentration created by feeding of benthic suspension-feeders and minimizes the resultant depletion of foods near the sea floor (Wildish and Kristmanson 1979; Fréchette et al. 1989; Skilleter and Peterson 1994). This enhancement of vertical mixing by flow increases represents an indirect effect of flow velocity on growth, acting through the mechanism of enhancing food concentrations around feeding animals. Increased bottom shear stress associated with higher flow velocity also can influence growth indirectly by resuspending deposited materials and thus altering food quantity and quality (Bricelj and Malouf 1984; Emerson 1990; Turner and Miller 1991).

Alternatively, flow velocity might also act directly on the feeding rate of active suspension-feeders, with the most compelling mechanism involving the influence of hydrostatic pressure generated by the external flow field on the rate of movement (pumping velocity) of food-bearing water through the organism. This process is most clearly suggested in studies of scallops, especially studies demonstrating that the influence of external flow varies with the orientation of the feeding animal to the direction of flow. When the inhalant opening to the mantle cavity is directed into the flow, growth rates of scallops are enhanced with increasing flows over a range of relatively slow current velocities, whereas if the exhalant opening is pointed into the flow, the unfavorable pressure gradient inhibits feeding and reduces growth (Wildish et al. 1987; Eckman et al. 1989; Wildish and Saulnier 1993). Despite this evidence of direct effects of flow on feeding and growth of scallops, general models of feeding by active suspension-feeders do not incorporate any direct effect of flow speed on feeding rate (Fréchette et al. 1989; Monismith et al. 1990; O'Riordan et al. 1993), and Fréchette et al. (1994) have argued that the apparent relationship of growth in active suspension-feeders to flow and food flux is illusory (an “epiphenomenon”), driven only by the indirect effects of flow on food concentration.

We designed our experiment as an explicit test of the role of direct effects of flow and external flux of food particles on growth of an active suspension-feeder. We chose to test responses inside pipes with a Kirby-Smith (1972) flow-tube apparatus. Our intent in using pipes was not to mimic natural flow but rather to separate the direct effects of flow from the indirect effects acting on food concentrations. Such confounding of the effects of flow speed and food concentration accompanies virtually any field or laboratory experiment with an overlying water column (e.g. Fréchette et al. 1989). We selected the American oyster Crassostrea virginica (Gmelin) so as to extend tests of the direct effects of flow on active suspension-feeders beyond scallops and mussels. Furthermore, the information collected in this study is of immediate value to restoration and management of a species whose decline has probably greatly affected the partitioning of energy between the pelagic and benthic realms and thereby the ecology of entire estuaries (Newell 1988). Proper oyster management is likely to include restoring and maintaining the now badly degraded reef habitat, which should provide the topography to elevate the oysters above the estuarine sea floor and thereby enhance flow velocities and particle fluxes around them (Rothschild et al. 1994).

We designed and conducted an experiment measuring growth of juvenile oysters inside pipes such that food concentration (two levels) and flow velocity (five levels) were varied in a factorial design. Juvenile oysters, provided by a shellfish hatchery to ensure genetic and historical identity among individuals (10 weeks old; shell width, 6–8 mm; shell height, 10–12 mm; total wet wt, 0.3–0.5 g), were exposed to current speeds of 0, 0.5, 2.5, 4, and 7 cm s⁻¹ for 45 d (1 September–15 October 1993) in a Kirby-Smith (1972) flow-tube apparatus virtually identical to that used by Eckman et al. (1989). The flow-tube apparatus consisted of 12 4-m-long PVC pipes (5.1-cm i.d.) extending from the base of a rectangular head box (0.75 × 0.75 × 2 m long). Water was pumped continuously from nearby Bogue Sound into the head boxes to keep them overflowing and always full; water flowed out through the pipes into a surrounding seawater pond, in which the pipes were submerged at 3-cm depth. Two replicates of each of the five flow velocities were produced by fitting pipes with stoppers containing holes of different sizes. A zero flow rate was produced by using stoppers without holes. This zero flow treatment experienced some sluggish, circulating flow within the pipes and the head box, as indicated by both survival and some growth of oysters. Average flow rate in pipes was calculated by dividing the measured volumetric discharge rate by the pipe cross-sectional area. Flow speeds at the centerline of each pipe where oysters were positioned were in theory twice the mean flow rate calculated for each pipe (Vogel 1981). Pipes were cleaned of deposits weekly by removing the stopper and allowing rapid flow for a brief time. Pipes were shaded with opaque cloth to minimize algal growth within them and reduce heat stress to oysters.

Twenty-four oysters were placed in each replicate pipe by gluing animals individually onto 1.7-mm-diameter glass rods. Oysters were positioned at the centerline of each pipe by fixing the glass rods to rubber disks and inserting them into a hole in the pipe wall. The rubber disks sat flush with the inside wall of the pipe. This design (see Eckman et al. 1989) minimized induction of turbulence within pipes. The left valve of each oyster was glued to the glass rod so that the umbo faced downward and the anterior, inhalant side of the mantle faced upstream. Oysters were spaced at 10-cm intervals with the first oys-
ater positioned 1.6 m downstream of the entrance of the pipe.

To evaluate the direct influence of flow velocity under differing food conditions and to test the influence of food flux on growth by using different combinations of food concentration and flow velocity, we used two head boxes with different food concentrations—ambient and reduced. Reduced food concentration was produced by filtering the inflowing water of one box through an 80-μm mesh, thereby reducing mean chlorophyll a concentration by 57% (2.36 ± 0.02 vs. 1.02 ± 0.01 μg Chl a liter⁻¹; n = 2), measured by fluorometry (Parsons et al. 1984) as a food quantity index at both the beginning and end of the experiment (ANOVA, effect of filtration: \( F_{1,4} = 1.15 \times 10^4, P < 0.001 \); effect of time: \( F_{1,4} = 1.25 \times 10^{-3}, P \gg 0.05 \); interaction of filtration and time: \( F_{1,4} = 1.25 \times 10^{-5}, P \gg 0.05 \)). Two replicates of 10 food fluxes were thus created: 0, 1.2, 5.9, 9.4, and 16.5 μg Chl a cm⁻² s⁻¹ in the ambient concentration treatment and 0, 0.5, 2.6, 4.1, and 7.2 μg Chl a cm⁻² s⁻¹ in the reduced concentration treatment. Filters were replaced every 8 h. Although filtration through 80 μm selectively eliminates chainlike and colonial phytoplankters, as well as blue-greens and large detrital particles, concentrations of POM (particulate organic matter) (0.11 ± 0.03 g liter⁻¹; n = 2) and PIM (particulate inorganic matter) (0.01 ± 0.005 g liter⁻¹; n = 2) were the same in both food concentration treatments and did not change between the beginning and end of the experiment (ANOVA for POM, difference between food concentration treatments: \( F_{1,4} = 0.62 \); time: \( F_{1,4} = 1.10 \); interaction: \( F_{1,4} = 0.00 \); all with \( P \gg 0.05 \); ANOVA for PIM, concentration: \( F_{1,4} = 0.00 \); time: \( F_{1,4} = 1.10 \); interaction: \( F_{1,4} = 1.10 \); all with \( P \gg 0.05 \)). Consequently, although filtration doubtless altered food quality as well as quantity, the bulk of the particulate matter must have been <80 μm.

The response variable in this experiment was growth of the oysters. Growth was measured for each individual oyster by comparing starting and ending shell heights and widths and total wet weights. Linear sizes were measured to 0.1 mm by vernier calipers and wet weights were calculated on an electronic balance to 0.01 g after towel drying the oysters. We report here only the response in shell width for the 45-d period because all three response variables revealed the same response patterns and growth in shell width proved to be measured with least error. Initial shell width did not vary significantly among treatments (ANOVA; \( F_{19,354} = 1.02; P \gg 0.05 \)), so there was no need to use a size covariate in any analysis. To test whether oysters within a pipe were exposed to the same food conditions or whether, alternatively, foods were depleted by upstream oysters (cf. Kirby-Smith 1972; Wildish and Kristmanson 1985), we performed separate linear regressions of individual oyster growth on position (distance from the beginning of each pipe). Subsequently, a two-way, crossed model ANOVA with five levels of current speed and two levels of food concentration was conducted on untransformed growth data to test whether average growth in shell width varied with average external current speed, food concentration, or their interaction. Cochran's test detected no heterogeneity of variances at \( \alpha = 0.05 \). Our design was pseudo-replicated at the level of concentration because we had only one head tank for each concentration, but this feature does not influence interpretation of the test of flow velocity, which is the primary focus of our study. Post hoc multiple comparisons were made with SNK tests. Finally, the growth results were further explored by multiple linear regression to evaluate whether food flux (the product of flow speed and food concentration) contributed significantly to explaining the growth responses after separate and independent effects of both flow speed and food concentration were already taken into account.

The regressions of individual growth on position along the pipe failed to detect a significant effect of position in any of the 20 pipes (Fig. 1). In the pipe with the best fit, position along the pipe could not explain even as much as 10% of the variability in growth among replicate individuals, and position, on average, explained only 2.3% of this variation (\( r^2 \)-values given in Fig. 1). The plots of individual growth along the pipes do not suggest reduced growth with distance nor do they indicate a stronger effect of distance at the lowest flow speeds, as would be predicted if depletion were occurring.

Both main factors, flow speed and food concentration, exhibited highly significant effects (\( P < 0.001 \)) on growth in the two-factor ANOVA, but there was no significant interaction between these factors (Table 1). For each food concentration treatment, average growth of oysters increased monotonically with average pipe flow speed over the range tested (Fig. 2). The post hoc SNK tests at \( \alpha = 0.05 \) showed that growth was significantly greater at the two highest average flow speeds, 4 and 7 cm s⁻¹, than at the two lowest flow speeds, 0 and 0.5 cm s⁻¹. Growth at 2.5 cm s⁻¹ was also significantly greater than at 0 cm s⁻¹. The effect of reducing food concentrations by filtration was to reduce growth of juvenile oysters at every flow velocity (Fig. 2).

The multiple linear regression analyses revealed that in a full model containing all four terms, food concentration, flow velocity, flow², and flow × concentration, only food concentration and flow velocity were significant in partial \( F \)-tests (Table 2). Together, food concentration and flow velocity accounted for 67% of the variance in average growth among pipes and inclusion of the two higher order terms explained only 6% more variance and depressed the \( P \)-value relative to a reduced model containing only the two main factors (Table 2). We included the quadratic (squared) term for flow in this full model to account for the apparent asymptotic reduction in growth at higher flows (Fig. 1) and the product of flow velocity and food concentration so as to have a direct measure of food flux in the model. A plot of average growth of juvenile oysters with changing food flux in this experiment does reveal that growth increased with flux of food (as must be true if growth increased with increases in both component factors) such that a plateau appears to be attained above ~10 μg Chl a cm⁻² s⁻¹ (Fig. 3). However, inclusion of the direct measure of flux could not explain significantly more variance in growth than is explained
by the independent, additive combination of food concentration and flow velocity.

Our primary motivation here was to answer two questions to help resolve a fundamental debate about active suspension feeding. First, do observed relationships between growth in active suspension-feeders and either flow velocity or external flux of food particles represent a direct effect of velocity or of flux (e.g. Grizzle et al. 1992)? Al-
Table 1. Results of a two-factor ANOVA testing whether growth of juvenile oysters varied in response to food concentration, flow speed, and their interaction. Data are given in Fig. 1. ANOVA was conducted on untransformed data because variances were homogeneous (Cochran’s test, $C_{crosstab} = 0.62; C = 0.20; df = 10, 1; P > 0.05$).

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>MS</th>
<th>$F$-ratio</th>
<th>$P$</th>
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</thead>
<tbody>
<tr>
<td>Food concn</td>
<td>1</td>
<td>37.26</td>
<td>28.66</td>
<td>0.0003</td>
</tr>
<tr>
<td>Flow speed</td>
<td>4</td>
<td>16.18</td>
<td>12.45</td>
<td>0.001</td>
</tr>
<tr>
<td>Food concn $\times$ flow speed</td>
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<td>0.88</td>
<td>0.68</td>
<td>0.62</td>
</tr>
<tr>
<td>Residual</td>
<td>10</td>
<td>1.30</td>
<td></td>
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Alternatively, does this relationship between growth and flow velocity exist only because of indirect effects of flow velocity acting on food concentration by enhancing vertical mixing and reducing near-bed depletion of foods (e.g., Fréchette et al. 1994)? There is little doubt that over some range of concentrations from zero up to some rather high concentration, growth and production of active suspension-feeders will generally increase with increasing food concentrations. This positive relationship between food concentration and growth of active suspension-feeders makes sense arguing from first principles and is supported by observational and experimental evidence (e.g., Widows et al. 1979). Beds of suspension-feeders clearly can deplete food concentrations near the sea floor sufficiently to reduce their own growth (Peterson 1982; Peterson and Black 1987) and turbulent mixing induced by increased flow speeds acts to break down the vertical gradient in food concentration (Fréchette et al. 1989; O’Riordan et al. 1993; Skilleter and Peterson 1994). Thus, there is an excellent basis for believing that indirect effects of flow velocity are important contributors to the transfer of energy and materials from the water column to active and passive suspension-feeders in the benthos.

The presence of potentially important indirect effects of flow velocity on growth of active suspension-feeders, however, does not imply the absence of additional direct effects of flow velocity. In field conditions and even in laboratory flumes with a proper vertical dimension to the overlying water column, the indirect effect of flow on vertical mixing interferes with detection of any possible direct effect of flow on feeding. This confounding of direct and indirect effects of flow on suspension-feeder growth in nature and in flumes motivated us to establish our test of oyster feeding response inside pipes, where despite complex flow regimes steady flows can be maintained and flow character is generally predictable. Furthermore, the absence of a vertical dimension to the water column in pipes prevents establishment of vertical concentration gradients (Kirby-Smith 1972; Wildish and Kristmanson 1985; Eckman et al. 1989). Our intent was not to duplicate natural boundary-layer flows, but rather to artificially isolate the direct effects of flow on feeding and growth from the indirect effects that are typically confounded in nature so that food depletion would not interfere with a test of this one component of response to flow. Indeed, detailed examination of growth of individual oysters by location along the pipes revealed a convincing lack of any horizontal food depletion in our experimental system (Fig. 1). Consequently, our test of the effects of flow velocity under two separate food concentrations appears not to confound indirect effects with direct effects of flow.

Analysis of the growth of juvenile oysters inside pipes showed an unambiguous, direct effect of flow velocity, which enhanced growth monotonically over the full range of flows tested under both sets of food conditions (Fig. 2). This result is consistent with those of Wildish and Kristmanson (1985) for blue mussels and of Wildish et al. (1987), Eckman et al. (1989), and Wildish and Saulnier (1993) for two species of scallops. Among these studies, direct effects of flow were detectable, although the pattern of response of growth to increasing flow differed. Here, we tested responses to rather slow average pipe flows up to only 7 cm s$^{-1}$, which represent realistic conditions for oysters in nature (Lenihan unpubl. data), but we did not explore the potential inhibition of feeding at high flows. Our study thus extends previous tests of the direct effects of flow velocity from mussels and scallops to oysters. More importantly, the factorial design and analysis of the tests of whether flow and flux have a direct effect on growth of an active suspension-feeder permit enhanced understanding of the first-principles processes affecting feeding and growth of active suspension-feeders.
Table 2. Results of multiple regressions performed on oyster growth data. Model 1 is the full model including all four terms. Model 2 is the reduced model presenting the regression with the best fit; all factors in model 1 with insignificant effects on growth were removed. Terms in the upper portion of each model are for the complete model. Terms in the lower portion are for the partial F-tests performed on the separate factors of the model.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F-ratio</th>
<th>Partial F-ratio</th>
<th>P</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
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<td></td>
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</tr>
<tr>
<td>Width = 0.96 + 2.52(food concn) + 1.72(flow) − 0.10(flow)² − 0.19(food concn × flow)</td>
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</tr>
<tr>
<td>Regression</td>
<td>4</td>
<td>25.42</td>
<td>10.20</td>
<td>0.0003</td>
<td>0.73</td>
<td></td>
</tr>
<tr>
<td>Residual</td>
<td>15</td>
<td>2.49</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>19</td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Food concn</td>
<td></td>
<td></td>
<td>10.30</td>
<td>0.006</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Flow</td>
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<td></td>
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<td>0.01</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Flow²</td>
<td></td>
<td>2.47</td>
<td>0.14</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Flow × food concn</td>
<td></td>
<td>0.87</td>
<td>0.37</td>
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<td></td>
<td></td>
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<tr>
<td><strong>Model 2</strong></td>
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<td></td>
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<tr>
<td>Width = 2.41 + 1.98(food concn) + 0.67(flow)</td>
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<td></td>
</tr>
<tr>
<td>Regression</td>
<td>2</td>
<td>46.68</td>
<td>17.36</td>
<td>0.0001</td>
<td>0.67</td>
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<tr>
<td>Residual</td>
<td>17</td>
<td>2.69</td>
<td></td>
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<tr>
<td>Total</td>
<td>19</td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Food concn</td>
<td></td>
<td></td>
<td>13.03</td>
<td>0.002</td>
<td></td>
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<tr>
<td>Flow</td>
<td></td>
<td>21.69</td>
<td>0.0002</td>
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</table>

We did not investigate the specific mechanistic basis by which flow velocity affected oyster growth in our experiments, but we can propose two possible hypotheses to explain the response. Oysters are active suspension-feeders that rely on internally generated flow to remove particulate foods from the water (Newell and Langdon 1995). Oysters utilize steep shear gradients between internal water currents produced by cilia located along their gill lamellae to position particles close to other cilia, which then capture and transport them to the mouth. It seems reasonable to hypothesize that application of the low flows used in our study could serve as a passive enhancement of the oyster’s ability to move water through the mantle cavity and thereby improve the efficiency of its own ciliary pump (cf. Vogel 1981). This explanation is consistent with the observation that direct effects of flow velocity on scallop feeding and growth vary with orientation of the inhalant opening to the flow direction, with growth enhanced when flow strikes the inhalant opening and depressed when it strikes the exhalant opening (Wildish et al. 1987; Eckman et al. 1989). Alternatively, increasing flow velocity may have actively enhanced oyster growth because of complex fine-scale hydrodynamics. It is conceivable that at very low flows, individual oysters create localized envelopes of depleted water, thereby depressing growth (a process also proposed by Wildish and Saulnier 1993). Increased flow could inhibit formation of these depletion envelopes.

Because oyster growth increased with both increasing food concentration and also with increasing flow velocity in our study, there necessarily exists an apparent relationship between growth and food flux (Fig. 3) because flux is the product of concentration and flow velocity. This relationship appears from our analyses to be a consequence of the independent influences of food concentration and flow velocity, each acting in different ways. We make this argument based on results of both the ANOVA and the multiple regressions. The ANOVA revealed that the two main factors (food concentration and flow velocity) each had positive effects on oyster growth over the ranges tested, but the absence of any significant interaction between the main effects shows that these contributions were independent (Table 1). If growth were

Fig. 3. Mean growth in shell width of juvenile oysters inside pipes plotted as a function of mean food (Chl a) flux through the pipes. Error bars represent ±1 SE around the mean of two replicate pipes each containing 16–21 surviving oysters. Although this plot reveals an apparent relationship between growth of this active suspension-feeder and external flux of food, the relationship is misleading because analyses (Tables 1, 2) imply that it derives from a coincidental consequence of separate, independent responses to the two components of flux—food concentration and flow speed.
responding directly to changes in flux, the main effects should interact, given that flux is the product not the sum of these two variables. This conclusion that the variables contribute separately and independently is further supported by the regression results, showing that the best model to explain the variance in average growth of oysters among treatments includes only the two separate main effects and not the explicit flux term (Table 2). Consequently, we conclude that the apparent relationship between oyster growth and food flux (Fig. 3) is fundamentally misleading and coincidental.

The danger in perpetuating the notion that growth of active suspension-feeders responds to flux (e.g. Grizzle and Lutz 1989) as opposed to responding separately to its individual components is twofold. First, because this relationship is coincidental, it is likely to fall apart as the range in variables is increased or as another species is examined. This contention that the monotonically increasing relationship between flux of food and growth in active suspension-feeders is limited to a narrow range of conditions is especially true for increasing flow velocities, which seem unlikely to cause further direct enhancement of feeding and are likely to inhibit feeding when above ~10 cm s⁻¹ (Grizzle et al. 1992). Second, relating growth of active suspension-feeders to food flux instead of the two apparently causative factors inhibits understanding of the underlying mechanisms, which are doubtless based on feeding physiology and fine-scale hydrodynamics.

The development of a mechanistic understanding of the role of flow velocity in affecting growth of oysters and other active suspension-feeders has practical significance to habitat restoration, conservation, and management in estuaries. Oysters have been greatly depleted in the estuaries of the mid-Atlantic coast, where they previously transferred a large percentage of pelagic primary production to the benthos (Newell 1988; Baird and Ulanowicz 1989). This loss of the ecological vehicle for energy transfer between the water column and the benthos has been blamed for a fundamental shift in the food webs of the Chesapeake Bay ecosystem, favoring the development of pelagic consumers including the noxious sea nettle (Newell 1988). Removal of a dominant suspension-feeding bivalve may conceivably open an ecological niche that could promote successful establishment of exotic ecological analogs. The ongoing alteration of the San Francisco Bay ecosystem by expansion and cascading effects of the introduced suspension-feeding bivalve, Potamocorbula (Nichols et al. 1990), may be a partial consequence of the rarity of the native west coast oyster. The success of invasions of the asiatic clam Corbicula and the zebra mussel Dreissena in freshwater aquatic systems may also relate to declines in native suspension-feeding mussels within those water bodies.

Along the Atlantic and Gulf Coasts, where estuarine fisheries production is such a valuable ecosystem service, protection and restoration of oyster reef habitat and dependent populations is a priority of environmental management. Knowledge of the complete relationship of oyster growth and production to flow velocity will be of practical value. Oyster reefs project above the sea floor, thereby influencing the local flow environment and potential growth and production of oysters (Rothschild et al. 1994). Our results in combination with studies of the larger scale hydrodynamic effects of altering reef size and shape will help direct reef restoration and management based upon a mechanistic understanding of the consequences of flow alteration.

Hunter S. Lenihan
Charles H. Peterson
Jennifer M. Allen

University of North Carolina at Chapel Hill
Institute of Marine Sciences
Morehead City 28557

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