

Conditional density dependence: The flow trigger to expression of density-dependent emigration in bay scallops

Abstract—Understanding how biological interactions vary under different water flow regimes is important in systems that are known to exhibit fluctuations in flow due to storms, tidal forcing, or variation in habitat structure. We performed a series of experiments to determine the migratory response of bay scallops, *Argopecten irradians concentricus* Say, to changes in intraspecific density under two different, tidally oscillating flow regimes in the field: 0–0.10 m s⁻¹ and 0–0.28 m s⁻¹. Despite the bay scallop's ability to swim actively and achieve unaided bursts of motion covering distances on the scale of 0.5 m, the expression of density-dependent emigration was dependent on the presence of higher flows. In the low-flow regime, there was negligible emigration during 24 h at any density level (12, 25, or 62 m⁻²); however, emigration rate increased with density (0% at 12 m⁻², 60% at 25 m⁻², and 71% at 62 m⁻²) under the higher flow regime. These results demonstrate that flow can facilitate biological interactions, creating conditional density dependence.

Benthic organisms depend on flows of overlying water for food or nutrient supply, growth, respiration, and reproduction. The integration of hydrodynamics and biology is thus critical for understanding the processes that determine individual physiology and behavior, control population patterns, and structure communities on the sea floor. Variation in hydrodynamic regime has been used to explain differential patterns in growth (e.g., Eckman et al. 1989), fertilization success (e.g., Levitan et al. 1991), recruitment (e.g., Eckman 1983), feeding behavior (e.g., Levinton 1991), and functional morphology (e.g., Denny et al. 1985) of benthic invertebrates. There is also evidence (Sih and Wooster 1994; Power et al. 1995) that differences in current velocities may alter intra- and interspecific interactions; however, few studies have addressed this type of interaction in marine systems (but see Palmer 1988). In this paper, we describe a series of experiments conducted in field flumes within otherwise natural habitat to test whether changing the water flow regime alters the migratory response of a common epifaunal bivalve, the bay scallop *Argopecten irradians concentricus* Say, to manipulations of intraspecific density. We use these results to hypothesize more generally about how flow regime may facilitate biological interactions.

Scallops represent one of the more motile groups of “sedentary” benthic invertebrates, and their swimming behavior has been well studied. Swimming in scallops is described as a two-stage process comprised of an initial active vertical ascent followed by passive horizontal displacement (Carsen et al. 1996). For smaller scallops, the ability to move horizontally may be greatly enhanced by increases in current velocities (Carsen et al. 1996). As scallops grow larger (>50 mm), they are capable of more sustained swimming and can supplement the passive horizontal displacement with bursts

of active swimming, thus increasing horizontal distance moved.

Swimming in scallops (*Placopecten*, *Pecten*, *Argopecten* spp.), as well as in some other families of bivalves (Ammussidae, Cardidae, and Limidae), is viewed primarily as an escape response from predators (Peterson et al. 1982). Levinton (1979) provided evidence for an alternative cause of the swimming response in a benthic mollusc when he demonstrated a density-dependent floating response that allowed emigration from crowded conditions in the deposit-feeding gastropod *Hydrobia ventrosa*. Peterson et al. (1982) tested for an analogous response in bay scallops but were unable to detect any change in emigration rate in response to increasing local density of intraspecific or interspecific (i.e., *Mercenaria mercenaria*) competitors inside 1-m² plots. Based on their successful demonstration of enhanced emigration from plots containing foraging predatory whelks (*Busycon carica*), they concluded that the stimulus from close approach by or actual contact with the predator was the primary factor inducing swimming behavior of adult bay scallops. Similar results were reported by Winter and Hamilton (1985), who found that the threat of predation by two other gastropods (*Fasciolaria tulipa* and *Murex pomium*) was the primary stimulus for rapid swimming in bay scallops. Their study showed that habitat also influenced the probability of swimming: bay scallops in seagrass were less likely to initiate swimming than those on clean sand. Such habitat dependence may reflect an evolutionary response to habitat-dependent risk of predation, in that predation on bay scallops is lower in seagrass beds than in unvegetated areas (Prescott 1990). Alternatively, the low flows underneath canopies of seagrass may not provide the advective energy required for bay scallops to achieve sufficient distances to make swimming excursions useful. Given the evident swimming ability of bay scallops and the induction of food depletion by other suspension-feeding bivalves at similar densities in this system (Peterson and Beal 1989), it seems odd that scallops would continue to reside in high densities. Peterson et al. (1982) speculated that any competitive interaction between scallops may require greater time or greater densities than those tested (experiments were conducted for 6 h with scallop densities of 10 and 25 m⁻²).

We designed our experiments in part as a test of this suggestion concerning duration of the experiments and density level: Our experiments were conducted over 24 h using a greater range in density than that of Peterson et al. (1982), 12 to 62 m⁻² versus 10 to 25 m⁻². Even more importantly, our experiments were conducted under two different, tidally oscillating flow regimes: a low-flow regime (0–0.10 m s⁻¹) and a higher flow regime (0–0.28 m s⁻¹), both within the range naturally occupied by bay scallops (Peterson et al. 1984). We presumed that horizontal movement of a fixed

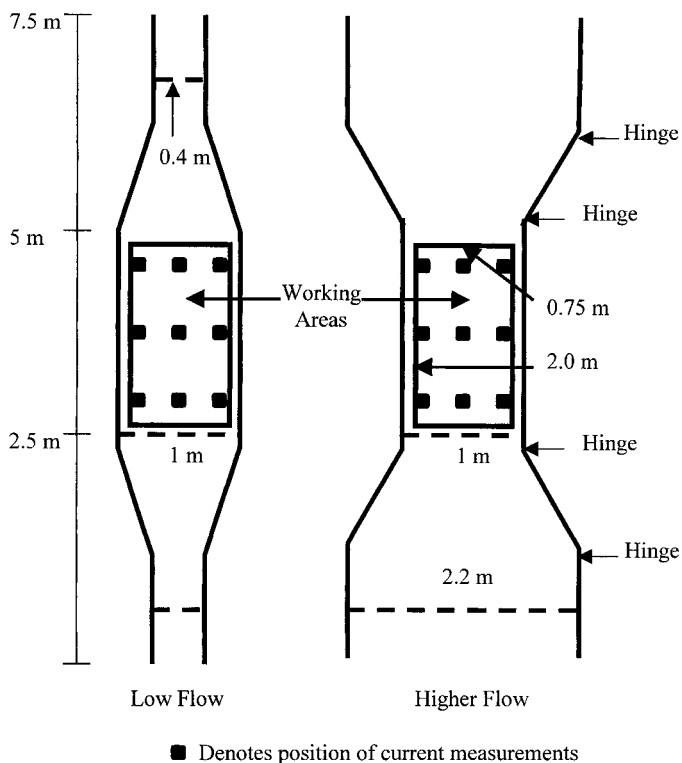


Fig. 1. Design of channels, with sampling locations for flow measurements indicated by filled squares.

distance would be passively enhanced and thus energetically less costly in the higher flow than in the low-flow regime. Consequently, we hypothesized that flow enhancement might interact with density by allowing bay scallops to express density-dependent emigration behavior when flows are enhanced.

Flow regimes were manipulated in situ by use of large plywood channels (Judge et al. 1992). Conducting such flow manipulations at a single field site avoids potential artifacts of site differences common in many comparative studies and avoids the artificiality of simplified environments of laboratory flumes. By varying the width of the channel opening relative to the width of the working section (the area where scallops were placed), flow over an unvegetated bottom was modified in a repeatable fashion. Our channels measured 7.5 m in length, 0.8 m in height, and 1.0 m in width at the center. Actual widths of the opening were 2.2 m for the higher flow treatment and 0.4 m for the low-flow treatment. The working section of the channel measured 0.75 m in width by 2.0 m in length. Walls were made of 1.25-cm pressure-treated plywood that was hinged in four places, resulting in five sections for each wall. Each channel could thus be configured to either reduce or increase flow (Fig. 1). Minimizing the angles at the hinged joints along the walls decreased the amount of flow separation at the hinge points (Nowell and Jumars 1987; Judge et al. 1992). Walls of the channels were anchored by 1.4-m-long, 5-cm-diameter galvanized fence posts inserted outside the walls to a depth of 0.7 m in the sediments. Each wall was attached to six posts using 5-cm-diameter wall fasteners. Walls were inserted 10 cm into the

Table 1. Results of a two-factor ANOVA testing whether current velocities varied in response to location (inside the low-flow channel, inside the higher-flow channel, or in the unmodified areas), time of measurement (relative to the tidal stage), or their interaction.

Source of variation	df	MS	F	P
Location of measurement	2	0.060	36.939	<0.001
Time	6	0.067	33.223	<0.001
Location of measurement \times time	12	0.004	0.398	0.009
Residual	92	0.002		

sediments. To stabilize the sediments along the channel walls, sandbags (2-m-long tubes with a 0.25-m diameter) were completely buried against the outer edges of the walls and along the first section of the inner edge.

To quantify the effect of each channel design on water flow, we measured current velocities within the channel and in adjacent unmodified areas during the experiments. Current velocities were measured at nine positions (Fig. 1) within the working section of both channel designs on six dates under either ebb (3 d) or flood tides (3 d). Measurements were taken hourly over each 6-h cycle. Current velocities were measured with a Marsh-McBirney model 201 portable water flow meter. The probe, 3-cm diameter at its widest point and 6.5-cm long, was attached to a standard wading rod. Two measurements were taken at heights of 5 cm (measured from the bottom of the probe) above the sediment and 8 cm below the water surface. Readings were visually averaged from the panel readout over a 5-s interval after initial calibration; values were then recorded by hand into field notebooks. After all nine positions were measured, the entire process was repeated twice: The averages of the three measurements for each position were then used in the analysis. Bottom current velocities were analyzed with a two-factor analysis of variance (ANOVA) with location of measurement (low-flow channel, higher flow channel, or ambient) and time of measurement (standardized to tidal stage from 0 to 6 h) as fixed factors. Date was initially treated as a blocking factor, but the effect was nonsignificant (using the conservative P value of 0.25: Underwood 1981) so the data were pooled from the different dates to serve as replication in the two-factor ANOVA. We used the average bottom current velocity of the nine positions per each hourly measurement as the dependent value in the analysis. Current measurements were similar over the nine positions, with a range of only ± 0.01 – 0.02 m s⁻¹. Cochran's test showed that variances were homogeneous at $\alpha = 0.05$, so analysis was performed on untransformed data. The ANOVA revealed significant effects of location, time of measurement, and their interaction (Table 1). Student-Newman-Keuls (SNK) post hoc contrasts (Day and Quinn 1989) demonstrated that current velocities taken at 0 and 6 h (slack tides) did not differ between locations ($P > 0.05$). Current velocities taken at 1 and 5 h differed between the low- and higher flow treatments ($P < 0.05$), but neither differed from the ambient velocity measurements ($P > 0.05$). Measurements taken at 2, 3, and 4 h differed between low- and higher flow treatments, and each treatment differed from ambient velocities ($P < 0.05$). Overall, current velocities (Fig. 2) were 42% below ambient

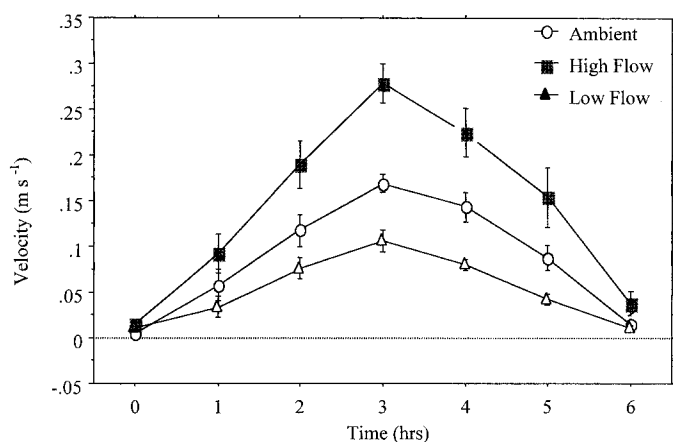


Fig. 2. Average current velocities (\pm SE) in the low-flow channel, higher flow channel, and unmodified areas (ambient) over six dates.

readings in the low-flow channel and 65% above ambient in the higher flow channel over the 1- to 5-h stages and were similar during slack flow periods (0 and 6 h).

To stock our experiments, we collected 120 adult (4.5–5.0 cm in height) bay scallops by hand from seagrass beds in Bogue Sound, NC, during early November 1998. Because epiphytic and epizootic growth affect drag forces on organisms and may influence their movement (Winter and Hamilton 1985), we chose scallops that had only minor fouling of the shell. After collection, scallops were placed out of water in large plastic trays, stored in shaded areas of the boat, and covered with moist towels for transport (thus following successful handling methods of Peterson et al. 1996). In the laboratory, scallops were held in flowing seawater tanks at the Institute of Marine Sciences until initiation of the experiment (1–4 wk). Then, scallops were placed in large mesh bags and transported to the site under handling conditions described above. Scallops were allowed to acclimate to ambient conditions within the channels for 2 h prior to initiation of experimental trials.

Experiments were performed in Middle Marsh in Back Sound, NC (see Prescott 1990 for a complete site description). One pair of channel flumes (1 low-flow, 1 higher flow) had been erected during low tides on a shallow subtidal (5- to 80-cm depth), unvegetated sand/mud flat within Middle Marsh along a channel oriented NE-SW. The channel was surrounded by dense stands of *Spartina alterniflora* and protected from wave action by the marsh shelter. Both channel flumes were set up along the axis of tidal flow and spaced about 5 m apart, separated from the nearest shoreline by 10 m. We conducted experiments in pairs on each date (same initial density, but under the two flow regimes) and achieved replication over 11 dates between 11 November and 12 December 1998. Density treatments per date were randomized in time (62, 25, 62, 25, 12, 25, 12, 12, 25, 12, and 62 m^{-2}). Experiments were limited to dates that shared similar wind patterns (5–10 mph S or SW wind) and tidal amplitudes (65 to 75 cm). Water temperature ranged from 11 to 14°C and salinity remained constant at 34‰ throughout the experiment. To control for any intrinsic site-specific effects, we

Table 2. Results of a two-factor ANOVA testing whether proportion (p) of scallops (transformed by $2 \arcsin \sqrt{p}$) emigrating from the 0.4×0.4 -m center plot varied in response to flow regime, initial density, or their interaction.

Source of variation	df	MS	F	P
Initial density	2	0.222	12.698	<0.001
Flow regime	1	0.681	38.889	<0.001
Initial density \times flow regime	2	0.181	10.317	0.003
Residual	12	0.210		

exploited the hinged design of the weirs to reverse the flow treatments: On two dates during the study period, we converted low flow to high and vice versa.

To test whether emigration rate of large bay scallops varied in response to local scallop density, flow regime, or their interaction, we designed a two by three factorial experiment in which every possible combination of two flow regimes (low and higher) and three density levels (12, 25, 62 m^{-2}) was replicated at least three times. Density levels were chosen to represent the range of maximum average scallop densities in Back and Core Sound, 12.3 m^{-2} (Peterson et al. 1996), 25 m^{-2} , and 62 m^{-2} (Peterson unpubl. data). Experiments began by placing the appropriate number of scallops within a 0.4×0.4 -m area (2, 4, or 10 scallops) in the middle of the working section of each weir during daylight hours 30 min after the low tide minimum. When placing the scallops in the plot, we were careful to vary the orientation of the scallops because orientation may affect both growth (Eckman et al. 1989) and flow over the shell (Wildish and Kristmanson 1997). After 24 h, we noted the final position of each scallop, its condition (all survived), the number missing, and the presence of potential predators or signs of predator activity (e.g., mud trails left by *Busycon* whelks). In all but two cases (when two scallops were recovered outside the flume), all scallops were recovered within the flume and showed no shell damage indicative of predator attack (i.e., chipped or unhinged shells). Proportions of scallops emigrating from the original plot after 24 h were then computed for each flume run on each date. Angular transformed proportions (p) ($2 \arcsin \sqrt{p}$) of scallops emigrating from the original plot after 24 h were analyzed by a two-factor ANOVA with both initial scallop density and flow regime as fixed crossed factors. Cochran's test detected no heterogeneity of variances at $\alpha = 0.05$ after transformation.

Originally, four replicates of each possible combination were planned; however, before the last pair of trials could be conducted, the weather pattern changed drastically and remained unfavorable for the next month. The consequence was an unbalanced design ($n = 4$ for 12 m^{-2} ; $n = 4$ for 25 m^{-2} ; and $n = 3$ for 62 m^{-2} at each flow regime). We performed two separate ANOVAs, one on a balanced data set and one on the full, but unbalanced, data set. The data set was balanced by randomly choosing one set of replicates at each of the two lower densities and excluding them from analysis (Underwood 1981). The ANOVA for the balanced data set revealed significant effects of initial density, flow regime, and their interaction ($P < 0.01$ for all tests; Table 2), as did the ANOVA on the unbalanced data set ($P < 0.02$

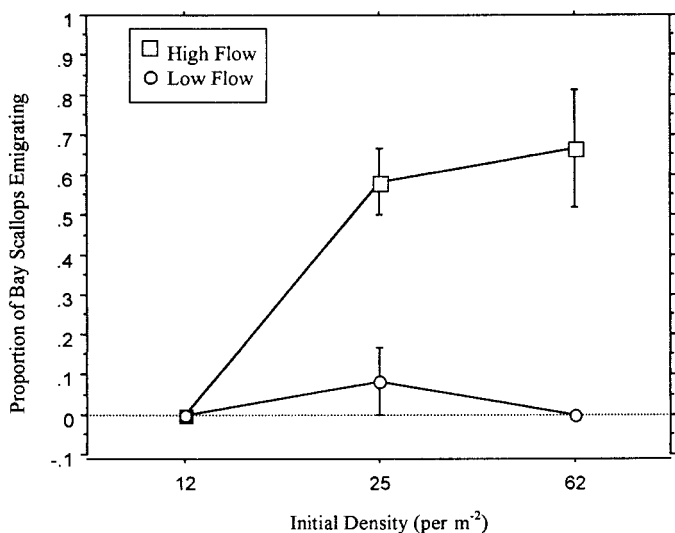


Fig. 3. Proportion of scallops emigrating from the 0.4×0.4 -m center plot (mean \pm SE) at three densities under two flow regimes.

for all tests). SNK post hoc contrasts revealed that under the higher flow treatment, a larger proportion of scallops emigrated from the original plot (Fig. 3) in the 25 m^{-2} and 62 m^{-2} than in the 12 m^{-2} densities ($P < 0.01$ for both tests), but that emigration did not differ significantly between these two higher densities, 25 and 64 m^{-2} ($P > 0.05$). Emigration under the low-flow treatment rarely occurred and did not differ among density levels ($P > 0.05$ for all SNK comparisons).

We conclude from our experiments that rate of emigration of adult bay scallops increases with density but that this response is dependent on the presence of some flow threshold. Higher flow regimes could facilitate net movement of scallops either by inducing more swimming events or by enhancing the horizontal displacement achieved during swimming. Induction of swimming events could represent either a passive, erosive response to enhanced flow or an active behavioral response to initiate swimming, whereas the enhancement of distance traveled is more likely to represent an exclusively passive response of advective transport.

Observational data collected during the experiments resolved the question of active versus passive initiation of movement. On six dates, the same days when current velocities were measured, scallops were observed for 5–6 h at the start of the trials. We observed a total of 10 swimming events, one in the low-flow and nine in the higher flow regime. This difference is significant ($P < 0.01$) in a sign test. In no case was a scallop observed to be slipping passively along the sediment surface. Swimming was always initiated actively by an abrupt change in position from horizontal reclining to an almost vertical position (hinge on the sediment surface). Within a few seconds of this change, the scallop rapidly opened and closed its valves, expelling water out of the hinged area and entering the water column. Scallops were then transported in the direction of flow for at least 0.5 m and up to 1.25 m. All 10 swimming events occurred during the maximum tidal flow. The swimming event that did occur in the low-flow treatment resulted in no large displace-

ment ($< 0.25 \text{ m}$). At the end of the 24-h experiments, the majority of scallops (90%) was found with the lower valve recessed in the sediment. Thus, our visual observations support the conclusions that higher flows induce more frequent swimming behavior in adult bay scallops, and in the rare instances that swimming is initiated at low flow, the net movement is small. Consequently, there emerges an evolutionary hypothesis to explain the scallop's failure to express density-dependent enhancement of swimming behaviors under low flows: Such behavior is a futile expenditure of energy without sufficient flow to transport the swimming bivalve across some ecologically meaningful distance before gravity returns it to the sea floor.

In the absence of the observations of active swimming behavior, one could propose a feasible alternative explanation for the interaction between flow regime and scallop density. In theory, erosion and subsequent transport of scallops might be enhanced at higher scallop densities, because scallops on a sandy bed could act as isolated roughness elements to produce areas of increased shear and instability due to vortex shedding and flow constriction (Eckman et al. 1981). However, this explanation does not fit with either the pattern in emigration (Fig. 3) or our observations of active initiation of swimming. If increased vortex shedding were responsible for increased emigration at the 25 m^{-2} and 62 m^{-2} densities in the higher flow regime, we would expect that emigration would be significantly higher at the 62 m^{-2} density compared to the 25 m^{-2} density; however, post hoc testing revealed no difference between these two densities. Furthermore, at the 25 m^{-2} density, each scallop was at least 25 cm away from its nearest neighbor, and no scallop was in a direct flow stream of another scallop, so it is unlikely that the hydrodynamic wake from one scallop reached other scallops (see Eckman et al. 1989) or that any instability in the bed could propagate over this distance. The only viable explanation for the specific interactive effect of flow regime and crowding in our study is that active swimming behavior was enhanced by the joint stimulus of crowding and higher flow fields.

Our experiments represent the first in situ demonstration that differences in water flow regime can facilitate a density-dependent dispersal response of animals. In laboratory flumes, Fonseca and Hart (1996) demonstrated that density-dependent dispersal of black fly, *Simulium vittatum*, neonates was mediated by flow regime. Interestingly, the response of black flies is the opposite of the one that we report. Dispersal increased in a density-dependent manner but was lower in higher flow regimes. Presumably, higher flow rates could support higher densities of animals because the flux of food to this passive suspension feeder increased with increasing flow. Our results are intriguing in that it would seem that crowded scallops would also receive more benefit from dispersing in low flow conditions than under higher flows. Although crowding does not directly affect survivorship, growth of even active suspension-feeding bivalves can decline with local density due to local depletion of suspended foods (Peterson 1982; Peterson and Black 1987). Nevertheless, swimming to avoid food depletion would need to achieve some distance from competitors, a distance that may not be likely in the absence of strongly advective current flows.

The response of any animal to encountering unfavorable conditions may be generally understood as a function of expected net costs incurred by inaction and net gain to be expected from taking action. Taken together, these two components of decision making constitute inspiration. Yet, our experiments imply that another factor can play a significant role: opportunity. The bay scallop's response to crowding at low and high flows runs counter to a prediction based solely on motivation by food depletion, in that bay scallops should experience greater food depletion at lower than at higher flows (Wildish and Kristmanson 1997). While the inspiration to emigrate may be stronger in low flows, the opportunity for an effective move is much reduced. If the scallop were confronted with an immediate threat to its survival, such as consumption by a predator, the inspiration for movement would be maximized; thus, the issue of opportunity may be much less important. Under immediate threat of loss of life, even desperate movements may be successful often enough to be adaptive. For example, bay scallops will swim to try to avoid consumption by predatory whelks even under low flow conditions, when distance traveled may often be insufficient to provide protection (Peterson et al. 1982). For many juvenile and adult benthic invertebrates, secondary dispersal is tightly coupled to water flow patterns. For example, many already metamorphosed and settled bivalves will secrete byssal threads and extend these into the water column as water sails to facilitate transport and movement. If flow speeds are adequate, the resulting drag on the threads allows the bivalve to be passively transported above the sea floor into a new area (Sigurdsson et al. 1976). In Levinton's (1979) experiments, no mention is made of flow regime; however, given that horizontal displacement for hydrobiid snails is surely a function of horizontal advection, one would expect greater displacement distances with higher flows. Consequently, while the inspiration for movement may be held in common by many of these species to avoid resource depletion experienced under crowding, sufficient flow speeds in the overlying water are required for expression of the inspiration. This limitation creates an example of what we term conditional density dependence in emigration behavior, in which the density-dependent response is expressed only under higher flows. We presume that the failure to express density-dependent emigration under low flows has the effect of prolonging another density-dependent response, reduced energy acquisition and growth under crowded conditions, but we did not run our experiments long enough to test for this response.

For both freshwater and marine habitats, heterogeneous flow regimes are common as a result of such factors as hydrological cycles, storm events, habitat heterogeneity, the presence of structure, bottom topography, and tidal variation; however, studies that have been conducted under multiple flow regimes in natural settings are rare, particularly in marine systems. Here, we present a clear example of how changes in water flow affect one type of intraspecific biological interaction. The way that bay scallops exploit opportunity provided by the energy subsidy inherent in high flows to trigger the swimming behavior that leads to dispersal is somewhat analogous to the role of heat energy in promoting certain chemical reactions between reagents that

form stable mixtures in the absence of sufficient activation energy. By further extending this analogy, additional tests are needed of whether energy subsidies in water flow catalyze a larger suite of biological interactions in aquatic systems.

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Total phosphorus–chlorophyll *a* size fraction relationships in southern Québec lakes

Abstract—The study is a first attempt to generate a series of Total Phosphorus–Chlorophyll *a* (TP–Chl *a*) predictive models relating the quantitative responses of four algal size fractions to phosphorus gradients. The study was carried out in 27 glacial lakes from two regions in southern Québec, the Laurentians and the Eastern Townships, and covered a relatively modest range of trophic conditions (TP, 3–34 $\mu\text{g P L}^{-1}$; Chl *a*, 0.3–7.6 $\mu\text{g L}^{-1}$). Algal biomass was estimated using measurements of Chl *a*, and the total Chl *a* was divided into four operational size fractions: picophytoplankton <3 μm , nanophytoplankton 3–20 μm , nanophytoplankton plus picophytoplankton <20 μm (edible fraction), and microphytoplankton >20 μm (inedible fraction). We tested the hypothesis that the slopes of the TP–Chl *a* regression models developed for algal size fractions would increase consistently from the smallest to the largest algal size fraction, as suggested by the first half of the sigmoidal TP–Chl *a* models. Although there was no consistent trend in the magnitudes of the slopes of TP–Chl *a* relationships for picophytoplankton (slope = 1.14), nanophytoplankton (0.93), and microphytoplankton (1.22), Chl *a* concentrations in the largest size fraction increased more rapidly with phosphorus enrichment than in either of the smaller fractions. When included as an additional variable, lake water alkalinity improved the prediction of Chl *a* and presented differential effects on size fractions. The effect of TP enrichment on microphytoplankton is more pronounced in well-buffered lakes, whereas TP enrichment has a stronger effect on nanophytoplankton in low-alkalinity lakes. The effects of alkalinity may be the result of either a pH influence on phytoplankton carbon uptake or a stronger top-down grazing effect on small algae in well-buffered lakes.

Empirical Total Phosphorus–Chlorophyll *a* (TP–Chl *a*) models have been developed and used successfully worldwide in the management of lake eutrophication (e.g., Schindler 1978; Cooke et al. 1993). However, TP–Chl *a* models result from the combined responses of several algal groups or size classes to nutrient enrichment, as shown by several studies (McCauley et al. 1989; Watson et al. 1992; Chow-Fraser et al. 1994). Significant shifts in algal species composition and functional attributes typically occur across a lake trophic state gradient (e.g. Smith 1990; Watson et al. 1992; Seip and Reynolds 1995). As a result of these shifts in taxonomic composition, pronounced changes in algal size structure also occur with nutrient enrichment. Several studies have indicated size-specific responses of algae to nutrient enrichment (Kalff and Knoechel 1978; Watson and Kalff 1981; Watson and McCauley 1988; Watson et al. 1992) and related them to changes in phytoplankton functional attributes such as phytoplankton cell volume and growth rate with lake trophic gradients (Seip and Reynolds 1995). Algal nutrient uptake is a surface phenomenon (Smith and Kalff 1983), and any increase in cell surface:volume ratio will confer a competitive advantage to small phytoplankton in oligotrophic lakes, which are relatively dilute. Also, their positive buoyancy, photopigment spectrum, and potential for rapid growth make small algae well adapted to the low-nutrient euphotic zones of oligotrophic ecosystems (Smith and Kalff 1983). Small algae are more efficiently used by zooplankton (Gelin and Rippl 1978). This could explain the relative loss of competitive advantage of small algae in more