

Species-specific effects of fluid shear on grazing by sea urchin larvae: comparison of experimental results with encounter-model predictions

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ABSTRACT: Small-scale turbulence can alter the rate of plankton predator–prey encounters. Encounter models predict that prey ingestion by slow-swimming zooplankton is enhanced at low levels of turbulence. We investigated whether small-scale turbulence increases ingestion for the slow-swimming, suspension-feeding pluteus larvae of the white urchin *Lytechinus pictus* and the purple urchin *Strongylocentrotus purpuratus*. Model predictions of the critical level of turbulence, ϵ_{cr} , above which encounters due to turbulence are greater than those due to behavior (swimming or suspension feeding) alone, were experimentally tested using short- and long-term grazing treatments. Because urchin larvae are smaller than the smallest eddy scales of turbulence and thus experience turbulence as laminar shear, larvae were exposed to flow conditions using a simple laminar shear flow with dissipation rates, ϵ , of 0, 0.1, 0.4, and 1 cm² s⁻³. Short-term ingestion of beads by *L. pictus* larvae was unaffected by $\epsilon < 1$ cm² s⁻³ but was 30% greater at this level, which was greater than ϵ_{cr} based on flow speeds produced in suspension feeding. Long-term flow treatments with algal prey had no significant effect on grazing or growth. Short-term ingestion of beads by *S. purpuratus* larvae was unaffected by $\epsilon < \epsilon_{cr}$ based on suspension feeding; the effect of long-term flow exposure on ingestion and growth could not be investigated because of high mortality, suggesting greater sensitivity to flow exposure compared to *L. pictus*. Experimental results are consistent with model predictions that ϵ_{cr} is high, and thus levels of turbulence in the ocean are not expected to significantly increase ingestion and reduce food limitation in suspension-feeding urchin larvae.

KEY WORDS: Grazing · Larvae · Turbulence · Urchin · Encounter model

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INTRODUCTION

The encounters between plankton predators and prey are influenced by small-scale turbulence (Rothschild & Osborn 1988) due in part to the velocity difference between predator and prey (Denman & Powell 1984, Tett & Edwards 1984, Rothschild 1986). Turbulence increases this velocity difference, resulting in encounter rates that increase with turbulence level (Kiørboe & Saiz 1995, Shimeta et al. 1995, Kiørboe 1997).

The effect of turbulence on predator–prey encounters is species specific (Shimeta et al. 1995). The critical turbulence level, ϵ_{cr} , determines whether encoun-

ters are dominated by turbulence or behavior. Below ϵ_{cr} , encounter rates are primarily determined by the feeding behavior and swimming or feeding current speed of the predator (Kiørboe & Saiz 1995, Shimeta et al. 1995, Kiørboe 1997). Above ϵ_{cr} , fluid motion dominates over behavioral processes. For some non-motile and slow-swimming organisms, such as the slowest-swimming flagellates and ciliates (swimming speed ~ 20 $\mu\text{m s}^{-1}$), ϵ_{cr} is low and turbulence is important because the velocity difference between predator and prey is small relative to turbulence (Saiz & Kiørboe 1995, Shimeta et al. 1995). Experimental results are also consistent with predator–prey encounter theory that turbulence has no significant ef-

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fect on contact rates for fast-moving or suspension-feeding predators, such as copepods and fish larvae, because the velocity difference between predator and prey is large relative to turbulent velocity fluctuations and ϵ_{cr} is very high (Rothschild & Osborn 1988, Kiørboe & Saiz 1995, Saiz & Kiørboe 1995).

Prey ingestion typically exhibits a dome-shaped response as turbulence intensity increases (Holling 1961, MacKenzie et al. 1994, Kiørboe & Saiz 1995). The rising phase of the response is due to enhanced encounters resulting in increased ingestion up to a maximum level. Higher turbulence levels can result in decreased ingestion despite predicted increases in encounter rates. Turbulence levels greater than those resulting in maximum ingestion can negatively affect feeding by eroding the hydromechanical signal of a prey detected by the predator or change prey or predator behavior (Alcaraz et al. 1994, MacKenzie et al. 1994, Kiørboe & Saiz 1995). Ingestion can also decrease when the local velocity imposed by turbulence is greater than the feeding current speed or reaction time of the predator (MacKenzie et al. 1994, Kiørboe & Saiz 1995, MacKenzie & Kiørboe 1995, 2000, Shimeta et al. 1995).

This study focused on sea urchin larvae, representative of the slow-swimming planktotrophic larvae of benthic marine invertebrates for which the effects of turbulence on encounters and ingestion are unknown. Small-scale turbulence could affect food availability; if larvae are food limited in the ocean (Paulay et al. 1985), then changes in food availability will affect larval survival, larval development time (Meyer et al. 2007), and post-metamorphic juvenile survival (Jarrett 2003, Pineda et al. 2007), all of which are important for recruitment success, reproductive population connectivity, and fisheries management. Additionally, it is important to understand grazing in larvae because they feed on phytoplankton and protists and are grazed upon by other zooplankton, especially copepods and fish larvae, providing an important component of the planktonic food web (Hansen et al. 1994). Finally, larvae can also contribute to biogeochemical cycles by converting phytoplankton into carbon for metabolic energy or export to deep water as biomass or detritus (Sterner et al. 1992, Cloern 1996). Thus, an understanding of larval grazing is important to modeling the ocean carbon cycle (Six & Maier-Raimer 1996).

One formulation (Kiørboe & Saiz 1995) of predator-prey encounter theory was used to calculate a critical turbulence level, ϵ_{cr} , for urchin larvae. ϵ_{cr} determines whether encounters are dominated by behavior or turbulence, and is dependent on predator swimming

or feeding current speed and perceptive radius (Kiørboe & Saiz 1995). Although urchin larvae use ciliary currents to swim and have relatively lower swimming speeds compared to other zooplankton such as copepods and fish larvae, they are also suspension feeders that can sense and capture individual particles (Strathmann 2007). Additionally, urchin larvae first detect particles at the tips of their 20 μm long cilia and then move the particles towards their mouth using reversal of ciliary beat (Strathmann 1971, 2007). Thus, because the local velocity at the tips of the cilia is low, larvae can react to the prey and turbulence may not decrease ingestion.

A unique experimental approach was used to test these predictions. At the small scale of larvae, viscosity dominates and turbulence is experienced as laminar shear (i.e. fluid rate of strain; Lazier & Mann 1989). Thus, the effects of small-scale turbulence on ingestion in urchin larvae were studied using a laminar shear-generating laboratory apparatus not previously used with marine invertebrate larvae. This approach is powerful because the flow field is fully characterized and the shear level can be quantified to determine the exact levels of shear that are important for grazing in sea urchin larvae.

MATERIALS AND METHODS

Test organisms

Adults of the purple urchin *Strongylocentrotus purpuratus* (Stimpson 1857) and white urchin *Lytechinus pictus* (Verrill 1867) were held at ambient temperature in flow-through aquaria at the Experimental Aquarium Facility at the Scripps Institution of Oceanography. Adults were injected with 0.5 M KCl to induce spawning. For each experiment, the eggs from 1 female were then fertilized with the sperm of 1 male. Two days after fertilization, prism-stage larvae were transferred to 3 l glass jars filled with 0.45 μm filtered seawater (FSW) at a temperature of 20°C for *L. pictus* and 16°C for *S. purpuratus*, to achieve a concentration of 2 larvae ml^{-1} unless stated otherwise. The antibiotic penicillin was added to the cultures at a concentration of 50 mg ml^{-1} to prevent bacterial growth. Larvae were fed the alga *Rhodomonas lens* (Pascher 1913) at an initial concentration of 300 cells ml^{-1} . This prey species was chosen for its high nutritional value to urchin larvae (Strathmann 1975, Schiopu et al. 2006). Experiments were conducted 3 d after fertilization, when pluteus larvae were at the early 4-armed stage of development in *L. pictus* and late prism stage in

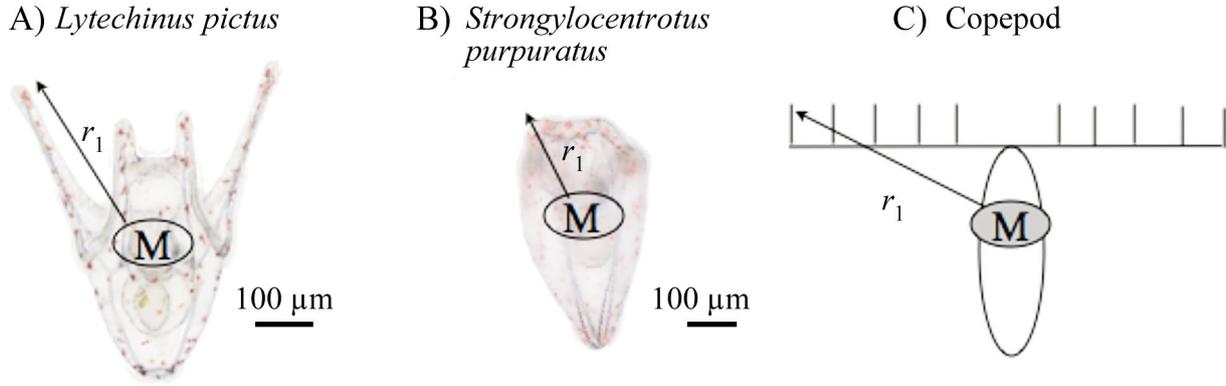


Fig. 1. Parameters included in the encounter model for urchin larvae are similar to those for copepod-based models. The perceptible radius (r_1) is the distance from the mouth (M) over which particles can be sensed. (A) *Lytechinus pictus* 4-armed stage larva. (B) *Strongylocentrotus purpuratus* late prism stage larva. (C) Schematic representation of a copepod, modified from Kjørboe & Saiz (1995)

S. purpuratus. These are critical stages of development when larvae become fully competent to feed; food-limited larvae during this time have a lower likelihood of recovering and surviving to metamorphosis (Fenaux et al. 1988, Kelly et al. 2000).

Parameters for the encounter model

The predator–prey encounter model proposed by Kjørboe & Saiz (1995) states that the encounter rate, E , per predator is based on the behavioral encounter kernel, β_{beh} , the encounter kernel due to turbulence, β_{turb} , and the concentration of prey, C_{prey} :

$$E = (\beta_{\text{beh}} + \beta_{\text{turb}}) C_{\text{prey}} \quad (1)$$

β_{beh} and β_{turb} quantify the different behavioral and physical processes that can cause a velocity difference between predator and prey to result in an encounter. They are dependent on the perceptible radius of the predator, r_1 , radius of the prey, r_2 , and the swimming velocity or the speed of the feeding current generated by a suspension-feeding predator, u_1 , so that:

$$E = [\pi(r_1+r_2)^2 u_1 + 4.2\pi \epsilon^{0.5}(r_1+r_2)^2] C_{\text{prey}} \quad (2)$$

where ϵ is the turbulence level expressed as the dissipation rate of kinetic energy ($\text{cm}^2 \text{s}^{-3}$). When $\beta_{\text{turb}} > \beta_{\text{beh}}$, turbulence is predicted to dominate prey encounters. This is used to calculate a critical turbulence level, ϵ_{cr} , above which encounters due to turbulence are greater than those due to behavior alone (Kjørboe & Saiz 1995):

$$\epsilon_{\text{cr}} = 0.057 (u_1^2 / r_1^2) \quad (3)$$

In this study, we tested model predictions incorporating both swimming speed and feeding current.

The first parameter for the encounter model, perceptible radius, the distance at which particles are sensed, is based on the length of the urchin larval arms (Fig. 1A,B), because particles are sensed at the tips of cilia that run in bands along the larval arms and moved towards the mouth using a local reversal of ciliary beat (Strathmann 2007). A perceptible radius of 0.28 mm for *Lytechinus pictus* larvae and 0.18 mm for *Strongylocentrotus purpuratus* larvae was used (Table 1). For modeling purposes, the larval arms are equivalent to the antennules in copepods, the lengths of which are used as the perceptible radius (Fig. 1C).

The second parameter for the behavioral encounter kernel is speed, u_1 , of the prey particle relative to the urchin larvae. Urchin larvae swim using bands of cilia arranged along the larval arms. Larval swimming speeds were determined experimentally; u_1 was 0.4 mm s^{-1} for *Lytechinus pictus* and 0.2 mm s^{-1} for *Strongylocentrotus purpuratus* (Maldonado 2009). Calculations based on swimming speed indicated that $\epsilon_{\text{cr}} = 0.11 \text{ cm}^2 \text{ s}^{-3}$ for *L. pictus* larvae and $\epsilon_{\text{cr}} = 0.07 \text{ cm}^2 \text{ s}^{-3}$ for *S. purpuratus* larvae (Table 1).

Table 1. *Lytechinus pictus* and *Strongylocentrotus purpuratus*. Estimates of critical turbulence level, ϵ_{cr} , based on perceptible radius, r_1 , and swimming or feeding current speed, u_1

	r_1 (cm)	u_1 (cm s^{-1})		ϵ_{cr} ($\text{cm}^2 \text{ s}^{-3}$)	
		Swimming	Feeding current	Swimming	Feeding current
<i>L. pictus</i>	0.028	0.04	0.1	0.11	0.7
<i>S. purpuratus</i>	0.018	0.02	0.1	0.07	1.7

Urchin larvae are also suspension feeders that use a feeding current with sensing and capture of individual particles (Strathmann 2007). In this case, u_1 is the velocity of the prey in the feeding current as it enters the perceptive radius (Kiørboe & Saiz 1995). Feeding current speeds are 0.98 mm s^{-1} for 4-armed *Strongylocentrotus purpuratus* larvae (Hart 1996). Although feeding current speeds are not available for *Lytechinus pictus* larvae, feeding current speed does not depend on ciliary band length (Hart 1996). For example, the feeding current speed of 1.16 mm s^{-1} for *Dendraster excentricus* pluteus larvae is similar to that of *S. purpuratus* larvae, even though they have longer ciliary bands (Hart 1996). Thus, an average feeding current speed of 1 mm s^{-1} was used for both *S. purpuratus* and *L. pictus* larvae. Calculations based on feeding current indicated that $\epsilon_{\text{cr}} = 0.7 \text{ cm}^2 \text{ s}^{-3}$ for *L. pictus* larvae and $\epsilon_{\text{cr}} = 1.7 \text{ cm}^2 \text{ s}^{-3}$ for *S. purpuratus* larvae (Table 1).

The lowest values represent levels present near the surface of the ocean on a stormy day, while the highest levels are much higher than what occurs in the coastal zone of the ocean (Soloviev et al. 1988, Gargett 1989, Thomas & Gibson 1990, Granata & Dickey 1991, MacKenzie & Leggett 1991, Jiménez 1997). Thus, ϵ_{cr} based on feeding current is higher than turbulence generally experienced by urchin larvae, and leads to the prediction that ocean turbulence will not increase ingestion in urchin larvae.

Flow apparatus

Larvae were subjected to either still conditions or constant shear using simple Couette flow generated in the gap between concentric cylinders with only the outer cylinder rotating at constant speed. This flow field is characterized by a linear velocity gradient in the seawater-filled gap between the 2 cylinders, resulting in nearly constant shear throughout the chamber volume (Coles 1965). Thus, larvae within the gap experience a uniform flow environment. Simple Couette flow has been used previously to study the effect of shear on the growth (Thomas & Gibson 1990, Juhl et al. 2000, Juhl & Latz 2002), bioluminescence (Latz et al. 1994, Maldonado & Latz 2007), and suspension feeding (Shimeta et al. 1995) of planktonic protists.

The flow chambers used in this study were the same previously used in growth studies (Juhl et al. 2001, Latz et al. 2009). They were constructed of clear acrylic with the following dimensions: inner radius (r_i) = 20.5 mm; outer radius (r_o) = 24 mm; height

of fluid (h) = 200 mm; fluid volume in gap = 265 ml. The bottom end cap of the outer cylinder was mounted to a pulley system with plastic chain to couple 4 replicate chambers to a Silvermax servomotor (QuickSilver Controls). Motor speed was controlled by custom software on a personal computer (Latz et al. 2009). The mean shear rate, G , within the gap is calculated as:

$$G = [(2\omega_o r_o r_i)/(r_o^2 - r_i^2)] \quad (4)$$

where ω is the angular velocity ($\omega = 2\pi N/60$, where N is the rotational speed in rpm; Schlichting 1979). The rotation rate of the outer cylinder in all experiments was either 0, 1.5, 6, or 15 rpm, representing shear rates of 0 (still control), 1 ('low'), 4 ('moderate'), and 10 ('high') s^{-1} , respectively. Dissipation rate, ϵ , is related to shear as:

$$\epsilon = G^2 \nu \quad (5)$$

where ν represents the fluid kinematic viscosity ($\text{cm}^2 \text{ s}^{-1}$). Thus, the tested shear levels are equivalent to dissipation rates, ϵ , of 0, 0.1, 0.4, and $1 \text{ cm}^2 \text{ s}^{-3}$, which represent oceanic conditions in near-surface waters under the influence of moderate to strong winds (Soloviev et al. 1988, Gargett 1989, Thomas & Gibson 1990, Granata & Dickey 1991, MacKenzie & Leggett 1991, Jiménez 1997).

Short-term grazing experiments

Short-term grazing studies to determine the effect of flow on encounters between urchin larvae and prey were performed with beads rather than algal prey. Urchin larvae have low ingestion rates compared to fish larvae, making it difficult to extrapolate changes in cell concentration over short periods of time using indirect estimates of grazing. Thus, direct estimates of ingestion rates were made by counting prey particles in the larval stomachs. Fluorescent or non-fluorescent beads are commonly used as prey mimics to obtain short-term grazing rates in a wide variety of suspension-feeding planktonic and benthic organisms (Børsheim & Andersen 1987, Hall et al. 1993, Appelmans 1994, Pedrotti 1995, Hart 1996, Shimeta 2009, Riisgard & Larsen 2010). In this study, beads were chosen because algal cells disintegrate immediately upon ingestion, so that methods based on the counting of prey cells and measuring chlorophyll fluorescence of the prey are not feasible (Maldonado 2009). Specifically, urchin larvae ingest beads that are 'flavored', or soaked in algal filtrate (Podolsky 1994). Based on initial preference tests,

Lytechinus pictus larvae were incubated with beads flavored with the green alga *Dunaliella tertiolecta* (Butcher 1959) CCMP strain 1320, and *Strongylocentrotus purpuratus* were incubated with beads flavored with the red alga *Rhodomonas lens* CCMP strain 739. To flavor beads, 1.5 ml of the *D. tertiolecta* or *R. lens* culture in exponential growth phase was added to an Eppendorf tube and centrifuged for 15 min at $13\,000 \times g$ to pellet the cells. The supernatant was removed and combined with 1.0 ml of autoclaved FSW that contained a 60 μl volume of 20 μm polystyrene DVB microspheres (SPI) that had been rinsed twice in autoclaved FSW. The beads were soaked overnight in the algal exudate.

At the beginning of each experiment, 85 larvae were added to 170 ml of FSW in each flow chamber and acclimated in the chambers for 30 min. After this time, each chamber was inoculated with beads to achieve an initial concentration of 300 or 2500 ml^{-1} . These 2 concentrations were chosen to determine whether the flow conditions can help larvae overcome food limitation. Larval growth rates are lower and development time is longer, suggesting food limitation, when larvae are raised on 300 cells ml^{-1} compared to 2500 cells ml^{-1} food concentration (Hart & Strathmann 1994). Larvae were then exposed to a flow condition with ϵ values of 0 (still control), 0.1, 0.4, or 1 $\text{cm}^2 \text{s}^{-3}$ for 30 min. Preliminary experiments indicated that greater ingestion was achieved in 30 min compared to 10 and 20 min. After the 30 min incubation, larvae were removed from the chambers, fixed in formalin, and observed under a compound microscope to count the number of beads in the stomach and intestine. There were 4 replicate chambers for each shear treatment, and each experiment was performed twice.

Values of ingestion rates (no. beads ingested $\text{larva}^{-1} \text{h}^{-1}$) and clearance rates ($\text{ml larva}^{-1} \text{h}^{-1}$), obtained by dividing the ingestion rate by the concentration of beads, were expressed as means + SD, with n equaling the number of larvae per treatment. Data were log-transformed for statistical testing.

Long-term growth experiments

Ingestion rates during long-term experiments were determined based on the depletion of prey. To calculate grazing rates using the equations of Frost (1972), the intrinsic growth rate of *Rhodomonas lens* in the absence of larvae was measured at each turbulence level. Although *Lytechinus pictus* larvae preferred the taste of *Dunaliella tertiolecta*, a unialgal diet of

this species is insufficient to support larval growth (George et al. 2004). *R. lens* was chosen because they are sufficient to support larval growth. They are also motile, promoting a homogeneous prey spatial concentration. *R. lens* was added to each chamber at an initial concentration of 300 cells ml^{-1} and grown on a 12:12 h light:dark cycle. After 4 d, a 20 ml sample was removed from each chamber, and cell concentration was measured using an Elzone II particle counter (Micromeritics). There were 4 replicate chambers for each shear treatment, and each experiment was performed twice. The exponential net growth rate (k) was calculated based on the change in prey concentration over 4 d and expressed as the mean with SD.

To test the effects of flow on ingestion and growth, larvae were incubated with algal cells and exposed to laminar shear flow for 12 h d^{-1} for 8 d during their night phase. The daily duration of flow exposure simulated diel variability in turbulence due to wind stress or convective mixing. It was also insufficient to cause larval mortality, which occurred for longer flow exposure. Extensive preliminary tests with *Lytechinus pictus* larvae determined that the time of day of flow exposure had no effect on growth, and that an 8 d experiment duration avoided significant mortality, which occurred for longer experiment durations. Larvae were added to 250 ml of FSW in each chamber. To optimize the experimental conditions, extensive preliminary experiments tested the effects of larval concentrations of 0.5, 1, 2, and 3 ml^{-1} on grazing and survival of larvae after 4 and 8 d. The goal was to use the lowest concentration that caused a measurable decrease in prey concentration while minimizing density-dependent effects on grazing and mortality. Based on these initial tests, optimal larval concentrations that produced consistent grazing and survival rates across shear treatments were 0.5 larvae ml^{-1} for *L. pictus* and 2 ml^{-1} for *Strongylocentrotus purpuratus*. Larvae were fed *Rhodomonas lens* at a food-limiting initial concentration of 300 cells ml^{-1} (Hart & Strathmann 1994). Higher concentrations were not tested due to density-dependent effects, based on preliminary experiments with concentrations of 2500 cells ml^{-1} , which increased mortality by 70%. Preliminary experiments also examined ingestion rates every 24 h, and revealed that a 4 d period was the shortest that could resolve changes in prey concentrations given low ingestion rates by larvae and low larval concentrations. Every 4 d, 20 ml samples were removed from each chamber to determine the concentration of *R. lens* using the particle counter. There were 4 replicate chambers for each flow treatment, and each experiment was performed

twice. Ingestion rates were calculated using the equations of Frost (1972) for the 4 to 8 d period.

To determine the effect of flow on growth, postoral (PO) arm length was measured using an ocular micrometer attached to a compound microscope. PO arm length is typically considered in studies on the effects of food limitation on growth of urchin larvae (Strathmann et al. 1992, Hart & Strathmann 1994). Specifically, early in development, PO arm length relative to body length is greater in starved compared to satiated larvae. After several days, however, satiated larvae develop faster and have larger overall PO arm lengths compared to starved larvae (Strathmann et al. 1992, Hart & Strathmann 1994). For each experimental condition, measurements from 20 larvae were made to the nearest 10 μm . PO arm length was expressed as a mean and SD, with n equaling the number of larvae per treatment.

Finally, the concentration and developmental stage of larvae were also determined for each 20 ml sample. Developmental stages in *Lytechinus pictus* and *Strongylocentrotus purpuratus* were defined as follows: late prism stage = gut fully formed, postoral and antero-lateral arms not fully formed; early 4-armed pluteus = postoral and anterolateral arms fully formed, obvious gut; late 4-armed pluteus = with 'bud' of postdorsal arms; 6-armed pluteus = fully formed PO, anterolateral, and postdorsal arms; and 8-armed pluteus = fully formed preoral arms (Lamare & Barker 1999, Sewell et al. 2004). The proportions of larvae at each developmental stage were arcsine transformed for statistical analysis.

Statistical analyses

Unless otherwise stated, data were tested for statistical significance using a 1-way analysis of variance (ANOVA) with Tukey's test used for post hoc paired comparisons. Statistical differences were based on an $\alpha = 0.05$ criterion. All statistical analyses were performed using Prism (GraphPad Software).

RESULTS

Short-term grazing experiments

Ingestion rates of *Lytechinus pictus* larvae fed a concentration of 300 beads ml^{-1} , equivalent to a limiting prey concentration, were similar for flow treatments with $\epsilon < 1 \text{ cm}^2 \text{ s}^{-3}$; the pooled average ingestion rate was 3.7 ± 2.6 beads $\text{larva}^{-1} \text{ h}^{-1}$ and clearance

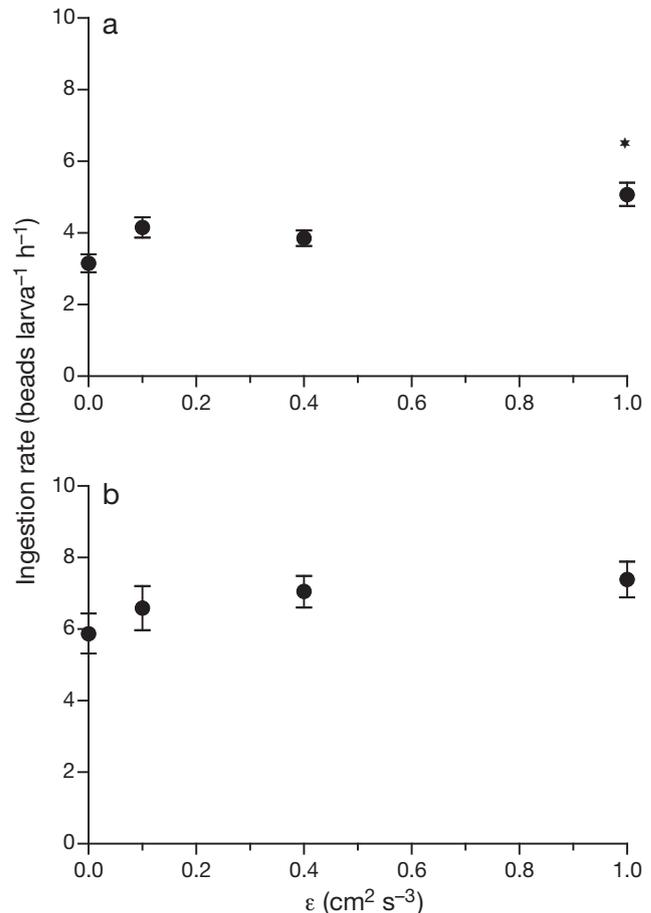


Fig. 2. *Lytechinus pictus*. Effect of flow (where ϵ represents the turbulence level) on ingestion of flavored glass beads by early 4-armed stage larvae. Symbols represent mean \pm SE of observed ingestion rates. (a) Bead concentration of 300 ml^{-1} , equivalent to a limiting prey concentration. Asterisk for the 1 $\text{cm}^2 \text{ s}^{-3}$ treatment represents a significant difference of observed ingestion rate from that at other flow levels based on Tukey post hoc comparisons. (b) Bead concentration of 2500 ml^{-1} , equivalent to a satiating prey concentration

rate was $0.01 \pm 0.009 \text{ ml larva}^{-1} \text{ h}^{-1}$ ($n = 327$; Fig. 2a). For the 1 $\text{cm}^2 \text{ s}^{-3}$ flow treatment, the ingestion rate of 5.1 beads $\text{larva}^{-1} \text{ h}^{-1}$ and clearance rate of 0.02 $\text{ml larva}^{-1} \text{ h}^{-1}$ ($n = 144$) were significantly different (Tukey's test; $t_{220} = 0.96$; $p < 0.001$) and 30% greater compared to the pooled average for the lower flow treatment results.

Lytechinus pictus larvae fed a concentration of 2500 beads ml^{-1} , equivalent to a satiating prey concentration, showed a different pattern. Observed ingestion rate was not significantly different ($F_{3,530} = 1.12$; $p = 0.34$) among flow treatments, with a pooled average ingestion rate of 6.7 ± 5.9 beads $\text{larva}^{-1} \text{ h}^{-1}$ and clearance rate of $0.02 \pm 0.02 \text{ ml larva}^{-1} \text{ h}^{-1}$ ($n = 533$; Fig. 2b).

In *Strongylocentrotus purpuratus* larvae fed a concentration of 300 beads ml^{-1} , equivalent to a limiting prey concentration, there was no significant difference ($F_{3,217} = 1.714$; $p = 0.16$) among flow treatments (Fig. 3). The pooled ingestion rate was 4.3 ± 3.3 beads $\text{larva}^{-1} \text{h}^{-1}$ and clearance rate was 0.014 ± 0.01 $\text{ml} \text{larva}^{-1} \text{h}^{-1}$ ($n = 220$). The ingestion rate was not significantly different from the pooled ingestion rate for *Lytechinus pictus* ($\text{df} = 6$; $t = 0.5$; $p = 0.64$).

Long-term growth experiments

Net population growth of the prey *Rhodomonas lens* was similar for the tested ϵ levels ($F_{3,12} = 0.138$, $p = 0.94$). Mean growth rates of *R. lens* between 4 and 8 d were 0.125 d^{-1} in the $0 \text{ cm}^2 \text{ s}^{-3}$ (still control), 0.244 d^{-1} in the $0.1 \text{ cm}^2 \text{ s}^{-3}$, 0.187 d^{-1} in the $0.4 \text{ cm}^2 \text{ s}^{-3}$, and 0.182 d^{-1} in the $1 \text{ cm}^2 \text{ s}^{-3}$ flow treatments. These growth rates were used to calculate ingestion and clearance rates in the 4 d grazing experiments using the equations of Frost (1972).

There was no significant difference ($F_{3,19} = 0.704$; $p = 0.56$) among flow treatments (Fig. 4) for grazing of food-limited *Lytechinus pictus* larvae on *Rhodomonas lens* prey over Days 4 to 8. Mean ingestion rate was 13.0 ± 8.9 cells $\text{larva}^{-1} \text{h}^{-1}$ in the $0 \text{ cm}^2 \text{ s}^{-3}$ (still control), 23.2 ± 19.4 cells $\text{larva}^{-1} \text{h}^{-1}$ in the $0.1 \text{ cm}^2 \text{ s}^{-3}$ treatment, 17.0 ± 9.2 cells $\text{larva}^{-1} \text{h}^{-1}$ in the $0.4 \text{ cm}^2 \text{ s}^{-3}$ treatment, and 15.5 ± 5.7 cells $\text{larva}^{-1} \text{h}^{-1}$ in the $1 \text{ cm}^2 \text{ s}^{-3}$ flow treatment. The pooled ingestion rate was 16.8 ± 10.6 cells $\text{larva}^{-1} \text{h}^{-1}$. There was also no significant difference ($F_{3,75} = 1.636$; $p = 0.19$) in growth with

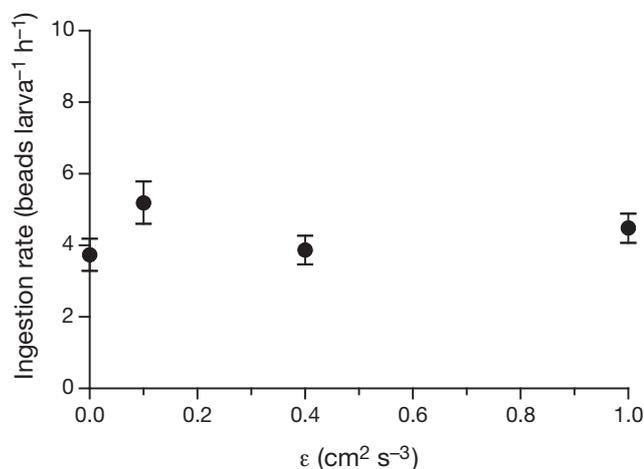


Fig. 3. *Strongylocentrotus purpuratus*. Effect of flow (where ϵ represents the turbulence level) on ingestion of flavored glass beads by early 4-armed stage larvae at a concentration of 300 beads ml^{-1} , equivalent to a limiting prey concentration. Symbols represent mean \pm SE of observed ingestion rates

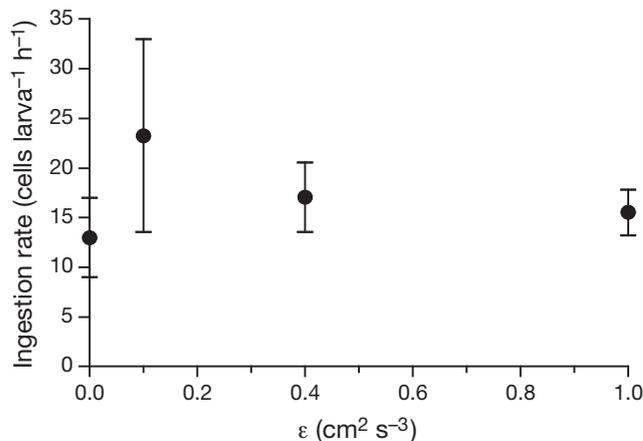


Fig. 4. *Lytechinus pictus*. Effect of flow (where ϵ represents the turbulence level) on ingestion of the alga *Rhodomonas lens* by 4-armed stage larvae at a limiting concentration of 300 cells ml^{-1} over Days 4 to 8. Symbols represent mean \pm SE

flow treatment. On Day 4 at the beginning of the experiment, mean PO arm length of *L. pictus* was $390.5 \pm 9.1 \mu\text{m}$ in the $0 \text{ cm}^2 \text{ s}^{-3}$ (still control) treatment, $375.4 \pm 7.8 \mu\text{m}$ in the $0.1 \text{ cm}^2 \text{ s}^{-3}$ treatment, $371.1 \pm 7.3 \mu\text{m}$ in the $0.4 \text{ cm}^2 \text{ s}^{-3}$ treatment, and $395.6 \pm 14.9 \mu\text{m}$ in the $1 \text{ cm}^2 \text{ s}^{-3}$ flow treatment. Pooled PO arm length on Day 4 was $383.2 \pm 9.8 \mu\text{m}$ ($n = 95$). On Day 8, mean PO arm length was $465.6 \pm 19.3 \mu\text{m}$ in the $0 \text{ cm}^2 \text{ s}^{-3}$ (still control) treatment, $437 \pm 18.4 \mu\text{m}$ in the $0.1 \text{ cm}^2 \text{ s}^{-3}$ treatment, $487.6 \pm 14.8 \mu\text{m}$ in the $0.4 \text{ cm}^2 \text{ s}^{-3}$ treatment, and $465 \pm 15.9 \mu\text{m}$ in the $1 \text{ cm}^2 \text{ s}^{-3}$ flow treatment. Pooled postoral arm length on Day 8 was $461.6 \pm 21.4 \mu\text{m}$ ($n = 79$). There was no significant difference ($F_{3,14} = 0.820$; $p = 0.51$) in developmental stage with flow treatment. On Day 8, 87% of the larvae were at the early 4-armed stage in the $0 \text{ cm}^2 \text{ s}^{-3}$ (still control) treatment, 100% in the $0.1 \text{ cm}^2 \text{ s}^{-3}$ treatment, 100% in the $0.4 \text{ cm}^2 \text{ s}^{-3}$ treatment, and 90% in the $1 \text{ cm}^2 \text{ s}^{-3}$ flow treatment. These results confirm that a concentration of 300 cells ml^{-1} of *R. lens* was limiting, because in preliminary tests, 80% of the larvae reached the 6-armed stage after 8 d when fed a satiating concentration of 5000 cells ml^{-1} of *R. lens*.

Long-term flow exposure caused high mortality in *Strongylocentrotus purpuratus* larvae. The concentration of *S. purpuratus* larvae surviving after 8 d was significantly different ($F_{3,10} = 7.034$; $p = 0.007$) in the flow treatments compared to the still control. Mortality was 19% for the $0.1 \text{ cm}^2 \text{ s}^{-3}$, 22% for the $0.4 \text{ cm}^2 \text{ s}^{-3}$, and 53% for the $1 \text{ cm}^2 \text{ s}^{-3}$ flow treatments compared to 5% for the still control. As extensive initial tests showed that feeding was strongly density dependent (data not shown), it was not possible to obtain reliable ingestion rates for this species.

DISCUSSION

Comparisons to model predictions

Encounter theory predictions of ϵ_{cr} based on swimming speed were lower than when suspension feeding was taken into account. Encounter model predictions of ϵ_{cr} based on swimming speed were $0.11 \text{ cm}^2 \text{ s}^{-3}$ for *Lytechinus pictus* and $0.07 \text{ cm}^2 \text{ s}^{-3}$ for *Strongylocentrotus purpuratus*. Even though urchin larvae are slow swimmers, they are also suspension feeders. When feeding current speed was incorporated, ϵ_{cr} was much higher, ranging from $0.7 \text{ cm}^2 \text{ s}^{-3}$ in *L. pictus* to $1.7 \text{ cm}^2 \text{ s}^{-3}$ in *S. purpuratus*. As a result, turbulence would not be predicted to dominate over feeding behavior unless higher levels of turbulence were present.

The results of short-term grazing experiments were consistent with encounter model predictions based on suspension feeding. For *Lytechinus pictus* larvae, flow levels with $\epsilon < 1 \text{ cm}^2 \text{ s}^{-3}$ had no net negative or positive effect on observed ingestion or growth. However, in short-term feeding experiments, ingestion rates were 30% greater in food-limited larvae exposed to flow with $\epsilon = 1 \text{ cm}^2 \text{ s}^{-3}$. For *Strongylocentrotus purpuratus* larvae, short-term exposure to any of the tested flow conditions did not significantly affect ingestion, which is also consistent with model predictions of ϵ_{cr} based on suspension feeding. Long-term exposure caused mortality, suggesting greater sensitivity of *S. purpuratus* larvae to turbulence compared to *L. pictus* larvae. Overall, these results are consistent with encounter model predictions based on feeding current speed and suggest that ϵ_{cr} is high for suspension-feeding urchin larvae. The increase in ingestion for flows with $\epsilon > \epsilon_{cr}$ occurred only for food-limited, not satiated, *L. pictus* larvae; at satiating prey concentrations, turbulence does not enhance ingestion, despite higher encounters, due to limited room in the gut (Frost 1972).

Echinoderm pluteus larvae are thought to inhabit shallow depths based on their tendency to congregate near the surface in laboratory conditions (Sameoto & Metaxas 2008, Sameoto et al. 2010). The highest levels of turbulence, outside of the surf zone or narrow surge channels, occur in near-surface waters of the coastal zone of the ocean that experience physical forcing from wind and surface waves, with an ϵ of 10^{-3} to $1 \text{ cm}^2 \text{ s}^{-3}$ (Soloviev et al. 1988, Gargett 1989, Thomas & Gibson 1990, Granata & Dickey 1991, MacKenzie & Leggett 1991, 1993, Jiménez 1997). The ϵ_{cr} of 0.7 to $1.7 \text{ cm}^2 \text{ s}^{-3}$ for the urchin larvae studied represent the highest values of turbulence

present in the ocean; it is unlikely that larvae will experience turbulence levels $> \epsilon_{cr}$ under natural conditions. Thus, model and experimental results suggest that levels of turbulence present in the ocean are insufficient to increase ingestion by urchin larvae.

The greatest increase in clearance rates is predicted for nonmotile and slow-swimming organisms exposed to low levels of turbulence typically present in the coastal zone of the ocean (Rothschild & Osborn 1988, Kiørboe & Saiz 1995). In the nonmotile helioflagellate *Ciliophrys marina*, clearance rates increase 3-fold when exposed to a turbulence level of $0.1 \text{ cm}^2 \text{ s}^{-3}$, which is greater than $\epsilon_{cr} = 0.004 \text{ cm}^2 \text{ s}^{-3}$, compared to the still control (Shimeta et al. 1995). Urchin larvae are slow swimmers, which would suggest that their grazing rate would increase due to turbulence dominating their swimming behavior. *Lytechinus pictus* larvae have swimming speeds of 0.4 mm s^{-1} and *Strongylocentrotus purpuratus* have swimming speeds of 0.2 mm s^{-1} (Maldonado 2009). However, they are also suspension feeders that can sense and capture individual particles (Strathmann 2007). In this study, ϵ_{cr} based on suspension-feeding behavior was equivalent to the highest turbulence levels found in the coastal zone of the ocean. Short-term exposure to turbulence levels $< \epsilon_{cr}$ had no effect on clearance and ingestion rates in *L. pictus* and *S. purpuratus* larvae. Similarly, the copepod *Acartia tonsa* feeding in suspension mode experiences no significant increase in ingestion when exposed to turbulence with $\epsilon > 10^{-3} \text{ cm}^2 \text{ s}^{-3}$, the ϵ_{cr} when ambush feeding, because the velocity difference generated relative to turbulence is large (Saiz & Kiørboe 1995). Thus, results from this study are consistent with previous work in which suspension feeders and fast-swimming predators are not predicted to benefit from low levels of turbulence (Kiørboe & Saiz 1995).

Turbulence levels above an optimal level can result in decreased ingestion rate due to post-encounter processes (MacKenzie et al. 1994). For example, ingestion rates are lower in the copepod *Acartia tonsa* feeding in suspension mode exposed to a turbulence treatment with dissipation rate of $\epsilon = 10 \text{ cm}^2 \text{ s}^{-3}$ compared to the still control (Saiz & Kiørboe 1995, Kiørboe 1997). After a prey particle is encountered, it can be advected out of the predator's perceptive radius before it can be ingested because the local turbulent velocity fluctuation is greater than the predator reaction speed (MacKenzie et al. 1994, Kiørboe & Saiz 1995, MacKenzie & Kiørboe 2000). However, in short-term experiments in the present study, ingestion rates were not lower in *Lytechinus pictus* and *Strongylocentrotus purpuratus* larvae exposed to

flow with $\epsilon < 1 \text{ cm}^2 \text{ s}^{-3}$ compared to the still control. Unlike copepods, which detect prey using relatively long antennae, urchin larvae first detect particles at the tips of their 20 μm long cilia and then move the particles towards their mouth using reversal of ciliary beat (Strathmann 1971, 2007). At the scale of the cilia, the local turbulence-induced velocity may be sufficiently low that larvae can react to the prey. As a result, on short time scales, turbulence equivalent to the highest levels found in the coastal zone of the ocean may not negatively affect post-encounter processes because urchin larvae feed on very small scales.

Species comparisons

Flow sensitivity was species specific. Early 4-armed stage *Strongylocentrotus purpuratus* larvae were more sensitive to long-term flow exposure than *Lytechinus pictus* larvae. While there was low mortality in *L. pictus* larvae for an 8 d exposure at all flow conditions, there was no significant increase in ingestion at the highest flow level as observed in the short-term experiments. This could be due to sublethal effects on grazing from long-term exposure to high flow conditions. Larvae may reject more particles or spend less time feeding, resulting in lower ingestion despite predicted increases in encounter rates, when exposed to turbulence levels $> \epsilon_{\text{cr}}$ for long periods of time. In other zooplankton, feeding under high levels of turbulence requires more energy compared to lower levels of turbulence (Alcaraz et al. 1994). Thus, ingestion rates would reach a maximal level without causing mortality. However, further

work is needed to determine the mechanism. Long-term exposure to turbulence caused high mortality in *S. purpuratus* larvae despite the similarity in short-term grazing rates with *L. pictus*. Species differences in mortality were most likely due to physiological differences rather than the experimental chamber. Larval size was $< 20\%$ of the gap width of 3.5 mm based on a total length of 600 μm for *L. pictus* larvae and 400 μm for *S. purpuratus* larvae. If differences were caused by wall effects due to the size of the Couette flow chamber, greater mortality would be expected in *L. pictus* larvae compared to *S. purpuratus* larvae because they are larger in size with longer postoral arms, but the opposite was true. Because *S. purpuratus* larvae have smaller ciliary bands than *L. pictus* larvae, *L. pictus* larvae may have a lower specific clearance rate, or clearance rate per unit length of ciliated band (Hart 1996), compared to *S. purpuratus* larvae. Echinoderm larvae with low specific clearance rates have higher metabolic efficiencies because they metamorphose earlier compared to species with high specific clearance rates (Hart 1996). Higher metabolic efficiency could be an explanation for the greater survival of *L. pictus* larvae exposed to flow compared to *S. purpuratus* larvae, but further work on physiological features such as clearance and metabolic rates in larvae exposed to flow is needed.

Urchin larvae demonstrate preferences for size and flavor of prey when suspension feeding in still water (Table 2; Rassoulzadegan et al. 1984, Appelmans 1994, Pedrotti 1995). This suggests that larvae selectively filter particles out of a dilute suspension in the ocean, which is important for modeling plankton population dynamics and the ocean carbon cycle

Table 2. Summary of clearance rates of echinoderm pluteus larvae in still water. Clearance rate values are means \pm SD. PO: postoral; na: not available

Species	PO arm length (μm)	Developmental stage	Temp. ($^{\circ}\text{C}$)	Species or bead 'flavor'	Concentration (ml^{-1})	Bead diameter (μm)	Clearance rate ($\text{ml larva}^{-1} \text{h}^{-1}$)		Source
							Beads	Live cells	
<i>Dendraster excentricus</i>	500	Late 4-arm	22	<i>Dunaiella tertiolecta</i>	2000	20.0	0.05	na	Appelmans (1994)
<i>Paracentrotus lividus</i>	557	Early 4-arm	20	<i>Crichosphaera elongata</i>	300	18.5	0.18 ± 0.09	na	Pedrotti (1995)
	810	6-arm	20	<i>C. elongata</i>	1500	18.5	0.53 ± 0.15	na	
<i>Arbacia lixula</i>	338	Early 4-arm	20	<i>C. elongata</i>	300	18.5	0.09 ± 0.06	0.01 ± 0.06	Pedrotti (1995)
	569	6-arm	20	<i>C. elongata</i>	1500	18.5	0.22 ± 0.10	0.02 ± 0.01	
<i>Strongylocentrotus purpuratus</i>	NA	Early 4-arm	9–14	Unflavored	1000–2400	20	0.06	na	Hart (1996)
<i>Lytechinus pictus</i>	380	4-arm	20	<i>D. tertiolecta</i>	300	20.0	0.01 ± 0.01	0.04	This study
					2500	20.0	0.02 ± 0.02	na	
<i>Strongylocentrotus purpuratus</i>	180	Late prism	16	<i>Rhodomonas lens</i>	300	20.0	0.01 ± 0.01	na	This study

(Appelmans 1994). Clearance rates measured in the still controls in this study are consistent with previous observations because *Lytechinus pictus* and *Strongylocentrotus purpuratus* larvae preferentially ingested particles of 20 μm diameter, ingested more particles that were 'flavored' (i.e. incubated with algal exudate) compared to 'unflavored' (i.e. particles soaked in FSW), and clearance rates depended on concentration of prey. Any differences in clearance rates between this and previous studies (Table 2) are most likely due to differences in experimental conditions. For example, greater ingestion rates in short-term experiments compared to long-term experiments were expected, as observed by Pedrotti (1995) (Table 2), because long-term experiments average feeding rates over time. However, lower ingestion rates were observed in short-term experiments compared to long-term experiments. We used 2 different species to flavor beads in the short-term experiments and to feed larvae in the long-term experiments, whereas Pedrotti (1995) used 1 species. The differences in grazing rates observed in this study could reflect preferences of larvae for live *Rhodomonas lens* cells compared to flavored glass beads. However, this prediction could not be tested because *R. lens* cells disintegrate immediately upon ingestion in short-term experiments. Another difference between our study and that of Pedrotti (1995) is that we measured ingestion rates after 4 d, whereas she measured ingestion rates after 15 to 24 h. We conducted extensive preliminary experiments in which ingestion rates were measured every 24 h. Ingestion rates were lower and more variable after 24 h, and we found that a 4 d period was the shortest that could resolve changes in prey concentrations given low ingestion rates of larvae and low larval concentrations. This is the first time that grazing rates have been calculated after this amount of time for sea urchin larvae, so it is difficult to predict results given differences in experiment duration and prey species.

SUMMARY

Overall, the contribution of our study is that we investigated suspension feeding in urchin larvae under conditions of fluid motion, which are more representative of ocean conditions than still conditions. Urchin larvae are representative of planktotrophic marine invertebrate larvae, most of which clear particles from suspension using a ciliary feeding current (Strathmann 1971). Additionally, marine invertebrate

larvae are found throughout the water column (see Metaxas 2001 for review). Thus, most planktotrophic marine invertebrate larvae would not be expected to benefit from turbulence in the ocean.

The use of simple Couette flow is but 1 step towards investigating the effects of ocean turbulence on plankton. While simple Couette flow is fully characterized and all organisms experience similar conditions, it does not capture the unsteady nature of vorticity and turbulent intensity (Peters & Marrasé 2000, Jumars et al. 2009). This deficiency can be addressed by conducting grazing studies using flow fields that better approximate the statistical properties of ocean turbulence, such as the T-box isotropic turbulence chamber (Webster et al. 2004, Yen et al. 2008). Additionally, imaging the instantaneous velocity of urchin larvae and their prey in isotropic turbulence using the T-box would allow direct measurement of the encounter rate between urchin larvae and their prey, to correlate the encounter rate with the velocity gradient at the same location.

The results of laboratory experiments suggest that turbulence in the ocean does not increase ingestion in suspension-feeding planktotrophic marine invertebrate larvae. Even though these larvae are slow swimmers, suspension feeding dominates and they do not experience turbulence-induced increases in ingestion as in other slow-swimming plankton. However, experimental approaches that more closely mimic ocean conditions are needed to determine the ecological relevance of turbulence effects on urchin larvae and other plankton.

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