



# Modeling of the larval response of green sea urchins to thermal stratification using a random walk approach

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## ABSTRACT

Larval transport in the ocean can be affected by their vertical position in the water column. In biophysical models that are often used to predict larval horizontal dispersal, generally larval vertical positions are either ignored or incorporated as static parameters. Here, we evaluate the ability of one dimensional random walk based model to predict larval vertical distribution of *Strongylocentrotus droebachiensis* in response to thermal stratification. Vertical swimming velocities were recorded at various temperatures and used to parameterize the model. Data from a previous laboratory study on the effects of thermal stratification on larval vertical distribution of *S. droebachiensis* were compared to the model results to evaluate the predictive ability of the model. The model predicts general trends in vertical distribution fairly well, but has a systematic bias which can be explained by un-quantified larval behaviors at the boundaries of the experimental water column. Overall, our behavioral model successfully reproduces the mechanism which regulates larval vertical distribution in response to thermal structure. Collectively, the findings suggest that simple behavioral models parameterized using simple lab experiments can prove useful in estimating the vertical distributions of invertebrate larvae in the laboratory and likely in the ocean. Such models can then be linked to bio-physical models to more accurately predict larval dispersal.

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## 1. Introduction

For larval marine benthic invertebrates, horizontal swimming speeds are generally considered to have a negligible effect on larval transport since they are much smaller than the velocity of the prevailing currents (Largier, 2003). However, larvae are able to alter their vertical position behaviorally, and even weak swimmers, such as gastropods and bivalves, display vertical migration (Lloyd et al., in press). This vertical migration can be in response to numerous biological and physical cues such as salinity, temperature, turbulence, predators and food (Boudreau et al., 1992; Fuchs et al., 2007; Gallager et al., 1996; Metaxas and Burdett-Coutts, 2006; Metaxas and Young, 1998; Sameoto and Metaxas, 2008a; Young, 1995). By vertically migrating, the dispersal pattern of larvae can be altered since different water layers can flow in different directions. Consequently, determining the relative importance of these cues, as well as the mechanism and timing of the response, is important in making predictions of larval dispersal.

While it is possible to quantify realized dispersal using geochemical tracers or genetics, bio-physical modeling is the only method currently used to predict trajectories of larval dispersal (Cowen and Sponaugle, 2009; Levin, 2006). Bio-physical models are either general circulation

models or advection–diffusion models used to quantify the effects of the physical properties of the ocean (e.g. general circulation patterns, tides, wind-driven circulation) on larval dispersal (Metaxas and Saunders, 2009). Ideally, these studies should incorporate the best available biological parameters, such as pelagic larval duration, mortality and vertical migration, which, are often unknown or inaccurately quantified.

Currently, most bio-physical models do not incorporate vertical migration (Metaxas and Saunders, 2009) except in a handful of studies, where it affected the larval dispersal potential across a number of species (Banas et al., 2009; Deksheniaks et al., 1996; DiBacco et al., 2001; North et al., 2008). An early attempt using the shrimp *Penaus latisulcatus* did not model swimming behavior, but rather evaluated the effect of actual vertical position on dispersal (Rothlisberg et al., 1983). In that study, an ontogenetic shift in diel vertical migration resulted in offshore dispersal of younger larvae, and onshore transport of older ones. However, the framework used by Rothlisberg et al. (1983) fixed larvae to a certain water layer at any given time, and the lack of simulated swimming precluded any interaction with vertical advection. Similarly, Banas et al. (2009) showed that diel and tidal vertical migration affected the larval dispersal of *Carcinus maenas*. However, the role of larval swimming was less important than seasonal differences in hydrodynamics in explaining the difference in dispersal between spring and summer spawnings. Other studies have shown that the larval dispersal of *Crassostrea virginica* can be affected by vertical distributions, which were in turn modulated by salinity gradients and temperature (Deksheniaks et al., 1996; North et al., 2008). However, in

Abbreviations: ZCM, the center of larval mass; SL, simulated larvae; MPA, Marine Protected Areas; PDF, probability distribution functions.

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both these studies, “idealized” swimming behaviors were generated through mean swimming and sinking velocities to model vertical migration. If changes in larval vertical position can be accurately modeled based on pattern of cues such as temperature, salinity or light, behavioral outcomes of these models could be then incorporated into bio-physical models of larval transport.

Random walks are useful in numerically simulating the trajectory of an animal that makes successive random steps. Initially developed to study the irregular movements (Brownian motion) of plant pollen (Brown, 1828), models based on random walks are now widely used to study movement of many organisms, such as slime molds, insects and even large mammals (Bartumeus et al., 2005; Benhamou, 1989; Codling et al., 2008). In the ocean, such models have been used to study the aggregation of copepods in turbulence (Yamazaki, 1993), encounter rates of zooplankton (Cianelli et al., 2009), and the relative importance of swimming in a turbulent medium (Porch, 1998) among others. Porch (1998) suggested that horizontal diffusion of larvae was not affected by random swimming, which, however, can affect vertical diffusion since vertical turbulence is much weaker than horizontal turbulence.

In the present study, we created a random walk model that simulated larval swimming behavior in the green sea urchin, *Strongylocentrotus droebachiensis*, in response to thermal stratification of the water column. The modeled vertical distributions were compared with the observed vertical distributions from a previous study on the vertical distribution of real sea urchin larvae in relation to thermoclines generated in the laboratory (Daigle and Metaxas, 2011). The movement of organisms can result from 2 main types of responses to a stimulus or cue. Klinokinesis refers to the sinuosity of the organism's path or the rate of change of directions, whereas orthokinesis refers to the modulation of speed (Codling et al., 2008). Since the model described here only considers the vertical dimension, klinokinesis (path sinuosity), which generally operates in 2 or more dimensions, would not be a relevant means of adjusting position; therefore, we simulated orthokinesis. To parameterize the model, we examined the effect of temperature on larval vertical swimming speed experimentally in the laboratory. An organism can sense and react to either an absolute or a differential stimulus (Benhamou, 1989). Since the vertical scale of the thermoclines simulated in the laboratory experiments (Daigle and Metaxas, 2011), and consequently those in the model domain, were exaggerated with respect to those found in nature, the use of temperature gradients (differential mode) as the sensory stimulus in the model was inappropriate. Rather, the absolute mode of stimulus, where only the temperature in the immediate area will affect the behavior of the simulated larvae (SL), was preferred. Additionally, since bio-physical models often have gradients that are less steep than those found in nature, the absolute mode of stimulus avoids the use of non-biologically derived gradient thresholds, as was done in North et al. (2008). This allows us to use biologically derived data and apply it directly to a bio-physical model by using a modified random walk model. The physiological condition of invertebrate larvae can affect the behavioral response to a cue and consequently their vertical distribution (Chan and Grünbaum, 2010; Metaxas and Young, 1998). For the sand dollar *Dendraster excentricus*, diet did not affect larval swimming speed or vertical swimming velocity, but it affected the helical width of their swim path (Chan and Grünbaum, 2010). In this study, we examined the role of thermal conditioning on larval swimming speed and vertical velocity. We evaluated the ability of one dimensional random walk-based models with various degrees of complexity (mean vertical swimming velocity, unbiased random walk, or the full model with the probability distribution function of vertical swimming velocities) at predicting the vertical distribution of *S. droebachiensis* larvae in response to thermal stratification. Data from a previous laboratory study on the effects of thermal stratification on the vertical distribution of *S. droebachiensis* (Daigle and Metaxas, 2011) were compared to the model results to evaluate the predictive ability of the model.

We used the green sea urchin as a model species because its behavior has been studied extensively and is well documented (Burdett-Coutts and Metaxas, 2004; Daigle and Metaxas, 2011; Sameoto and Metaxas, 2008a; Sameoto and Metaxas, 2008b; Strathmann, 1971). Additionally, it is the dominant herbivore in the rocky subtidal habitats in our region and is also a commercially harvested species. The use of model organisms allows predictions to be made about the behavior of other related species that may be of ecological or commercial interest, such as invasive or threatened species. The insights into larval behavior gained in this study combined with the predictive ability of our model would allow for better predictions of larval vertical distributions. Combining these distributions with general circulation models or advection–diffusion models would ultimately produce more accurate estimates of dispersal than a bio-physical model which does not consider vertical distributions. For example, the effect of behavior on dispersal distance is important in the design networks of Marine Protected Areas (MPA), created with the intent to conserve biodiversity. If a greater functional diversity of behaviors is considered in the MPA design phase, the MPA network could be scaled more appropriately to allow dispersal between individual MPAs and provide protection for a broader range of species.

## 2. Methods

### 2.1. Fertilization and larval rearing

Adults of *S. droebachiensis* were collected from the shallow subtidal zone at Bear Cove, NS, in Mar 2009 and Mar 2010. They were maintained in ambient seawater flow-through tanks in the Aquatron facility at Dalhousie University and fed kelp (*Saccharina latissima* and *Laminaria digitata*) *ad libitum*. Spawning was induced by injecting 2–4 ml of 0.55 M KCl through the peristomial membrane. Eggs and sperm from a total of 22 parental pairs (15 in 2009 and 7 in 2010) were combined in 0.45  $\mu\text{m}$ -filtered seawater. Fertilization success, determined as the proportion of eggs with elevated perivitelline membranes, ranged between 96 and 100% ( $n = 50$ ).

All zygotes and larvae were transferred into 4-L culture jars containing 0.45- $\mu\text{m}$  filtered seawater, which were maintained either in a temperature-controlled room at  $9 \pm 1$  °C or in a water bath at  $5 \pm 1$  °C. Water was gently stirred with slowly rotating paddles and was changed every other day. Larvae were kept at a maximum density of 4 larvae  $\text{ml}^{-1}$  and were fed a mixture of *Isochrysis galbana* (from Tahiti) and *Chaetoceros muelleri* at a total concentration of 5000 cells  $\text{ml}^{-1}$ . Larvae were used in the experiments once they reached the 4-arm (6-day old at 9 °C or 8-day old at 5 °C) stage. This larval stage was chosen because it represents the dominant early dispersal stage for this species.

### 2.2. Quantifying larval swimming

In the laboratory, larval swimming was recorded using a Panasonic WV-3170 camera with a 12.5–75 mm (f 1:1.4) TV Zoom Lens in order to quantify swimming speed ( $s$ ), vertical swimming velocity ( $w$ ), as well as the temporal covariance of the latter. Plexiglas columns (10  $\times$  10  $\times$  30 cm, L  $\times$  W  $\times$  H) were filled with 2.95 L of 0.45- $\mu\text{m}$  filtered seawater, and placed in a 55-L water bath to maintain the desired water temperatures. For larvae reared in 9 °C, swimming was measured in 3, 5, 10, 15 and 20 °C, while for those reared in 5 °C, it was measured in 5, 10 and 20 °C. Larvae from 4 randomly selected parental pairs were used for each of the 3 replicates at each experimental temperature. The 3 °C treatment was done in 2010 with a different batch of larvae, but the large number of parental pairs and the random mixing of offspring used should make the results comparable between years. Larvae were introduced to within 1 cm from the bottom of the experimental tank by gently pouring 50 ml of seawater containing 8–10 larvae  $\text{ml}^{-1}$  into a funnel attached to a small tube (2-mm inner diameter), yielding a

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