Experimental results of turbulence-exposed sand dollar Dendraster excentricus larvae and their response to a variety of settlement cues

Website: https://www.bco-dmo.org/dataset/740414
Data Type: experimental
Version: 1
Version Date: 2018-07-19

Project

» Turbulence-spurred settlement: Deciphering a newly recognized class of larval response
(Turbulence-spurred settlement)

Contributors	Affiliation	Role
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Abstract

Experimental results of turbulence-exposed sand dollar Dendraster excentricus larvae and their response to a variety of settlement cues.

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Coverage

Spatial Extent: **N**:48.6944 **E**:-121.8891 **S**:36.6017 **W**:-122.8951
Temporal Extent: 2015-07-23 - 2017-05-22

Dataset Description

These data are presented in Hodin et al (2018).

Adult Dendraster excentricus were collected from two geographically distinct populations: 1) a subtidal population (~ 100 m offshore and 1.5m below the surface at mean lower low water) approximately 30m east of Municipal Pier 2 in downtown Monterey CA, USA; 2) an intertidal population on Crescent Beach in East Sound, Orcas Island, WA, USA. Adults in Monterey were collected by snorkeling and transported to Hopkins Marine Station ("HMS"; Pacific Grove CA, USA). Adults in East Sound were collected at low tide and transported to Friday Harbor Labs ("FHL"; Friday Harbor, WA, USA). In both locations, the sand dollars were partially buried within fine sediments (collected from the adult beds) in flowing seawater aquaria until spawning. (Hodin et al, 2018). These adults served as sources for the larvae used in the experiments.

We raised larval sand dollars (Dendraster excentricus) through their feeding larval stage using standard methods [Strathmann, 1987 and 2014], and on various days after larvae had become competent to settle, we subjected a subset of them to a brief turbulence exposure of a specified high intensity (6 W/kg) conforming to that measured on wave-exposed rocky coasts. Immediately after exposure, we transferred the larvae into different settlement inducing media: Millipore-filtered seawater (MFSW), extracts of sand from inside or outside sand dollar beds, or excess potassium chloride in MFSW. We then quantified settlement as it relates to turbulence exposure and settlement medium. For more detail refer to Hodin et al (2018) and prior papers [Gaylord et al, 2013; Hodin et al, 2015].

Acquisition Description

Figure 1: Early competent sand dollar larvae do not display 'desperate' behaviors at settlement, with or without turbulence exposure. We either exposed D. excentricus larvae 10 day post fertilization (dpf) (reared at ~20°C) to 3 min of 6 W/kg turbulent shear or did not. Then, we transferred exposed and control larvae into one of two settlement conditions: 24 hrs in MFSW

alone (left side of graph) or a 1 hr exposure to 40mM excess KCl in MFSW –to assess competence– followed by a 24 hr recovery in MFSW. We detected an effect both of turbulence exposure ($F_{1,12}=5.36$, $p<0.02$) and settlement medium ($F_{1,12}=228.93$, $p<0.001$) on proportion of larvae settled, but no clear interaction ($F_{1,12}=3.41$, $p=0.09$).

Figure 2: Fully competent sand dollar larvae exposed to turbulence are less choosy about settlement substrate, and thus behave like 'desperate' larvae. We either exposed D. excentricus larvae 11 dpf (reared at ~20°C) to 3 min of 6 W/kg turbulent shear or did not ("no turbulence"). Then, we transferred exposed and control larvae into one of two settlement conditions: 0% extract of sand from sand dollar aquaria (MFSW; no inducer) or 40% extract of sand from sand dollar aquaria (strong natural inducer), and counted the numbers settled at 1 and 16 hrs. We also exposed a separate set of control (no turbulence) larvae for 1 hr to 40mM excess KCl in MFSW, followed by recovery in MFSW. More than 95% of these latter larvae settled, confirming that the larvae in this experiment were indeed fully competent.

Figure 3: Fully competent sand dollar larvae exposed to turbulence are less choosy about settlement substrate, and thus behave like 'desperate' larvae. We either exposed D. excentricus larvae 40 dpf (reared at ~14°C) to 3 min of 6 W/kg turbulent shear or did not ("no turbulence"). Then, we transferred exposed and control larvae into one of two settlement conditions: 0% extract of sand from sand dollar aquaria (MFSW; no inducer) or 200% extract of sand from a beach without sand dollars (poor quality natural inducer), and counted the numbers settled at 1.5, 3, 7.5 and 19 hrs. We also exposed a separate set of control (no turbulence) larvae to a strong natural inducer (30% extract of sand from sand dollar aquaria; right side of graph). This treatment not only confirms that the larvae were fully competent (100% of larvae settled by 8 hrs), but indicates the expected rate of settlement response in a strong cue as a basis of comparison to the sub-optimal cues described above.

We performed all statistical analyses using R (version 3.4.2) and the lme4 package.

Processing Description

BCO-DMO Processing:
- added conventional header with dataset name, PI name, version date, reference information
- renamed parameters to BCO-DMO standard
- replaced blank cells with '-' ('not applicable')

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Related Publications

Bates, D., Maechler, M., & Bolker, B. (2013). lme4: Linear mixed-effects models using S4 classes. R package version 0.999999-2.

Denny, M. W., Nelson, E. K., & Mead, K. S. (2002). Revised Estimates of the Effects of Turbulence on Fertilization in the Purple Sea Urchin, Strongylocentrotus purpuratus. The Biological Bulletin, 203(3), 275–277. doi:10.2307/1543570

Gaylord, B., Hodin, J., & Ferner, M. C. (2013). Turbulent shear spurs settlement in larval sea urchins. Proceedings of the National Academy of Sciences, 110(17), 6901–6906. doi:10.1073/pnas.1220680110

Hodin, J., Ferner, M. C., Ng, G., & Gaylord, B. (2018). Turbulence exposure recapitulates desperate behavior in late-stage sand dollar larvae. BMC Zoology, 3(1). doi:10.1186/s40850-018-0034-5

Hodin, J., Ferner, M. C., Ng, G., Lowe, C. J., & Gaylord, B. (2015). Rethinking competence in marine life cycles: ontogenetic changes in the settlement response of sand dollar larvae exposed to turbulence. Royal Society Open Science, 2(6), 150114. doi:10.1098/rsos.150114

Strathmann, M. F. (2017). Reproduction and development of marine invertebrates of the northern Pacific coast: data and methods for the study of eggs, embryos, and larvae. University of Washington Press.

Strathmann, R. R. (2014). Culturing larvae of marine invertebrates. In Developmental Biology of the Sea Urchin and Other Marine Invertebrates (pp. 1-25). Humana Press, Totowa, NJ.

Parameters

Parameter	Description	Units
figure	figure number from BMC Zoology publication	unitless
competence	readiness of the larvae to settle	unitless
date_expt	date of experiment formatted as yyyy-mm-dd	unitless
species	species name	unitless
rpm	rotations per minute of the Taylor-Couette cell; unmanip = no rotation applied	rotations per minute
replicate	replicate number	unitless
dpf	days post fertilization	days
cue	settlement inducing media; MFSW = Millipore-filtered seawater; KCl = potassium chloride in seawater	unitless
number_larvae	number of larvae in experiment	larvae
number_settled	number of settled larvae	larvae
number_settled_0hr	number of settled larvae at time 0	larvae
number_settled_1hr	number of settled larvae at 1 hour	larvae
number_settled_16hr	number of settled larvae at 16 hours	larvae
number_on_bottom	number of settled larvae	larvae
number_settled_1_5hr	number of settled larvae at 1.5 hours	larvae
number_settled_8hr	number of settled larvae at 8 hours	larvae
number_settled_18hr	number of settled larvae at 18 hours	larvae

Instruments

Dataset-specific Instrument Name	
Generic Instrument Name	Taylor–Couette system
Dataset-specific Description	To generate turbulence intensities (quantified in terms of the energy dissipation rate, in units ofWkg−1) ranging from those found in open ocean waters to those arising on wave-battered coasts, we employed a Taylor–Couette cell [29], an apparatus composed of two vertically oriented, coaxial cylinders separated by a 3.5mm gap that contains seawater (described in greater detail in [1]). We held the stationary inner cylinder, and thus the water in the gap, at 19–21∘C by means of a circulating water stream from a temperature-controlled water bath passing through the cylinder's interior. During operation, the outer cylinder rotated at a prescribed speed causing relative motion between the cylinders and thereby shearing the seawater between them. At rotation speeds employed for testing sand dollar larvae, the sheared flow was turbulent [1]. [1]Gaylord B, Hodin J, Ferner MC. 2013 Turbulent shear spurs settlement in larval sea urchins. Proc. Natl Acad. Sci. USA 110, 6901–6906. (doi:10.1073/pnas. 1220680110)
Generic Instrument Description	An apparatus composed of two vertically oriented, coaxial cylinders separated by a gap that contains seawater. During operation, the outer cylinder rotates at a prescribed speed causing relative motion between the cylinders and thereby shearing the seawater between them.

Deployments

Gaylord_Turb-Settlement

Website	https://www.bco-dmo.org/deployment/640417
Platform	lab Bodega Marine Laboratory
Start Date	2014-06-01
End Date	2014-08-31
Description	sand dollar settlement studies

Project Information

Turbulence-spurred settlement: Deciphering a newly recognized class of larval response (Turbulence-spurred settlement)

Coverage: Northeast Pacific

Description from NSF award abstract: With this award the investigators will explore a habitat-scale oceanographic process that has the potential to integrate studies of larval delivery with an understanding of how larvae respond to substrate-associated cues. This work will build on published and preliminary data indicating that turbulent shear characteristic of high-energy near shore environments primes larvae to initiate settlement and to transform into the juvenile stage. These prior findings suggest that: 1) Because turbulence intensity varies predictably as a function of the strength of wave breaking and other factors, turbulence could operate as an indicator for larvae of their approach to suitable habitat, providing a link between larger-scale dispersal phenomena, and near-bottom search and selection behaviors; and 2) The larval response to turbulence acts in an unprecedented fashion. In contrast to typical cues, turbulence does not induce settlement directly, but rather spurs otherwise "pre-competent" larvae that are refractory to chemical cues to become "competent", thereby causing them to acquire responsiveness to such cues and undergo settlement. The interdisciplinary team has combined expertise in larval biology, sensory ecology, and organism-flow interactions necessary to address this topic. They will employ a phylogenetically robust approach to explore the scope and adaptive significance of the turbulence response in a widespread and ecologically important class of organisms (echinoids; sea urchins and their relatives), and will determine whether the response is aligned with environmental conditions characteristic of these organisms' adult habitat. They will also test for ecologically important functional consequences of precocious, turbulence-induced settlement. This work will provide a detailed look at an entirely new class of settlement inducer, one with strong potential for changing current conceptualizations of dispersing larval stages, their ability to detect signatures of habitat across multiple scales, and the ways in which organism-level traits might influence population connectivity. How organisms with dispersing life stages find their way back to adult habitat is a fundamental question in marine ecology. Considerable research has explored links between transport, delivery, settlement, and recruitment, with important advances in knowledge. However, a complete understanding of the larval recruitment process remains elusive. Standard tools for estimating dispersal (e.g., numerical circulation models) have

limited spatial resolution, which prevents them from predicting at scales below a few hundred meters how larvae will interact with the shore. Studies investigating larval attachment have focused on chemical, tactile, or near-bottom hydrodynamic cues active across microns to centimeters. The novelty of the present project is that it will focus on processes at habitat scales -- between transport and settlement -- where there is a gap in the understanding of processes. This project will provide a framework for integrating key concepts of propagule dispersal and settlement, two fundamental but largely disjunct themes in marine science. The understanding that will come from this study will provide key information for ecosystem based management of coastal marine resources. The investigators will develop a "Surfing to Settlement" virtual lab activity based on their research that will be incorporated into the VirtualUrchin web platform, a widely exploited educational resource at Stanford that gets thousands of unique users per month. Through connections to the San Francisco Bay National Estuarine Research Reserve, they will integrate the "Surfing to Settlement" activity into one of NERRs professional development workshops for central California educators, thus disseminating this resource to and gaining valuable feedback from dozens of teachers and thousands of students.

Funding

Funding Source	Award
NSF Division of Ocean Sciences (NSF OCE)	OCE-1356966
NSF Division of Ocean Sciences (NSF OCE)	OCE-1357033
NSF Division of Ocean Sciences (NSF OCE)	OCE-1357077