I feel that! Fluid dynamics and sensory aspects of larval settlement across scales

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Abstract

A commonality among oceanic life cycles is a process known as settlement, where dispersing propagules transition to the sea floor. For many marine invertebrates, this transition is irreversible, and therefore involves a crucial decision-making process through which larvae evaluate their juvenile habitat-to-be. In this chapter, we consider aspects of the external environment that could influence successful settlement. Specifically, we discuss water flow across scales, and how larvae can engage behaviors to influence where ocean currents take them, and enhance the likelihood of their being carried towards suitable settlement locations. Next, we consider what senses larvae utilize to evaluate their external environment and properly time such behavioral modifications, and settlement generally. We hypothesize that larvae integrate these various external cues in a hierarchical fashion, with differing arrangements being employed across ontogeny and among species. We conclude with a brief discussion of the future promises of larval biology, ecology and evolution.

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Introduction

Standing on a wave swept shore, it's tempting to imagine that the myriad microscopic larvae beneath the surface are simply at the mercy of oceanic forces, so-called 'passive particles' being hurled to and fro by the tremendous energy of tides, waves and currents. In this conception, a larva that eventually would settle in the nearshore has three key tasks:

1) to survive long enough and be lucky enough to be passively carried to a suitable adult habitat;
2) to recognize such a habitat when it arrives there; and
3) to attach or burrow into that habitat so as not to be swept away by impinging flows.

In this sense, even a larva that might appear 'passive' with respect to typical flow regimes could be in some ways master of its own fate. For example, engaging larval defenses could increase its odds of survival in the presence of predators, adjusting its feeding mechanisms could allow it to grow faster and more efficiently, detecting conspecifics or a favored adult food source could increase its likelihood of settling in an appropriate location, and quickly deploying well-developed adhesive structures could allow it to withstand agents of dislodgment when it arrives there. Furthermore, our larva's mother (and in some cases its father) could have stacked the deck in its favor. For example, she might have protected the embryo and larva for a time, endowed it with extra energy in the form of yolk, or provided it with chemical defenses to deter planktonic predators. She may also have released her offspring during a specific season, lunar phase or time of day that could offer it the maximum available planktonic food, fewest potential predators, and most favorable oceanic flow conditions to retain it near to shore.*

But a growing body of evidence indicates that larvae are best considered as other than passive particles (see Morgan 2014). Although the maximum swimming speed of the larvae of most invertebrates (<1cm • sec^{-1} or far less; Chia et al. 1984, Fuchs & Gerbi 2016) are too slow to make headway in strong oceanic currents (10s of cm • sec^{-1}) or within wave-driven flows (meters • sec^{-1}), these larvae nevertheless have a behavioral repertoire that they can exploit to increase their odds of finding food, avoiding predators, and being carried back to shore when they are ready to settle into benthic habitat. Stronger swimming larvae of crustaceans and fish can swim against and at least partially resist such currents, and are thus even less passive.

Based on the notion that larvae of benthic species have an underappreciated capacity to influence their locations in space and thus their arrival into specific habitats, in this chapter we will draw upon examples from disparate marine invertebrates to describe:

- the fluid environment that larvae experience in the pelagic and benthic realms;
- what larvae can sense in their fluid environment and how they do so; and
- what cues larvae utilize, and how their responses to such cues vary depending on the scale relative to suitable settlement locations.

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*References related to these topics as well as numerous auxiliary references throughout can be found in the *Supplementary Material* associated with this chapter. It is appended here after the primary reference list (i.e., following page 43).

The main focus in this chapter is to review these topics from the perspective of larvae maximizing their chances of surviving to settle at an appropriate time and place. While addressing these issues, we will often connect to subjects of other chapters in this volume, which we will cross-reference for their more extensive consideration of such material. We also will highlight the tremendous progress made in larval ecology in the last 50 years, and in particular in the two decades since the publication of *Ecology of Marine Invertebrate Larvae* (1995, L.R. McEdward, ed.), the multi-authored work that inspired the current edited volume. And, finally, we will look to the future of the field, where new techniques and interdisciplinary integration offer the promise of deeper understanding of the surprisingly common yet remarkably diverse complex life cycles of marine organisms.

What does it feel like to be a larva?

Although we do not know the complete answer to this question, fluid dynamics offers some clues. A bottlenose dolphin swimming through the water experiences its fluid environment much differently than does a coral planula larva. At the scale of the dolphin, inertial forces predominate (think of a boat continuing to glide long after the engine is cut); at the scale of the planula, the dominant forces are viscous (akin to a human swimming in a vat of honey). The relative importance of inertial and viscous forces can be described in terms of a parameter called the **Reynolds number (Re)**:

$$\mathrm{Re} = \frac{(\rho U l)}{\mu}$$

The factors in the numerator contribute to larger inertial forces (ρ – the density of the fluid; U – the fluid velocity; and l – a characteristic length of the organism in flow), whereas the surrounding fluid's dynamic viscosity μ is in the denominator. The units cancel one another out, so the Reynolds number is a dimensionless metric, useful across scales from planktonic (mm's or less) to oceanic (1000s of km's), whereby two organisms with the same Re can be thought of as experiencing a similar fluid dynamic environment.

Because Reynolds number depends on a length scale, two organisms that differ vastly in size but occupy the same habitat (like a bottlenose dolphin and a coral planula in a tropical lagoon) will experience quite distinct fluid dynamic environments: while the density and viscosity of the ambient seawater are more or less the same for the two organisms, the length of the dolphin (~3 m) is four orders of magnitude greater than the length of the planula (~0.3 mm), and the swimming speeds of these two animals also differ by about three orders of magnitude (~3 m • sec^{-1} versus ~3 mm • sec^{-1}, respectively). At the scale of the dolphin, the value in the numerator of the Re equation is thus very large, and the inertial forces override the viscous ones. At the scale of the larva the opposite is true (see Vogel 1994; and for a recent review, Weissburg et al. 2014).

In terms of the relative flow experienced by each of these animals, this difference could not be more profound. Flow at the scale of a dolphin (Re ~ 10^6) is chaotically turbulent: as it swims through the water the dolphin leaves a wake with swirling eddies behind it (Vogel 1994). In fact, the streamlined body of the dolphin is well adapted to limit the size of the eddy-filled wake since it increases drag, and thus impedes forward progress. By contrast, the planula (Re ~ 1 or less), due to its small size, does not create a turbulent wake as it moves through the lagoon by ciliary propulsion. Instead, the larva's movement induces strong local gradients in velocity that are characterized by adjacent layers of fluid slipping smoothly past one another, with little mixing-type motions (Fig. 1). Less well studied are flow fields surrounding organisms operating at intermediate Reynolds numbers (Re in the 1-100 range), which is relevant for many larger larvae (such as in fish, ascidians, and some crustaceans; McHenry et al. 2003) as well as during certain burst swimming modes in smaller larvae, such as in diving bivalves (e.g., Fuchs et al. 2015). At such intermediate Re values, the flow characteristics transition from viscous-dominated to a domain where inertial forces are more prominent, and the particular shapes of the larvae can have an increasing effect on the flow characteristics compared to what is seen in lower Re conditions (see, e.g., Koehl 1995, McHenry et al. 2003).

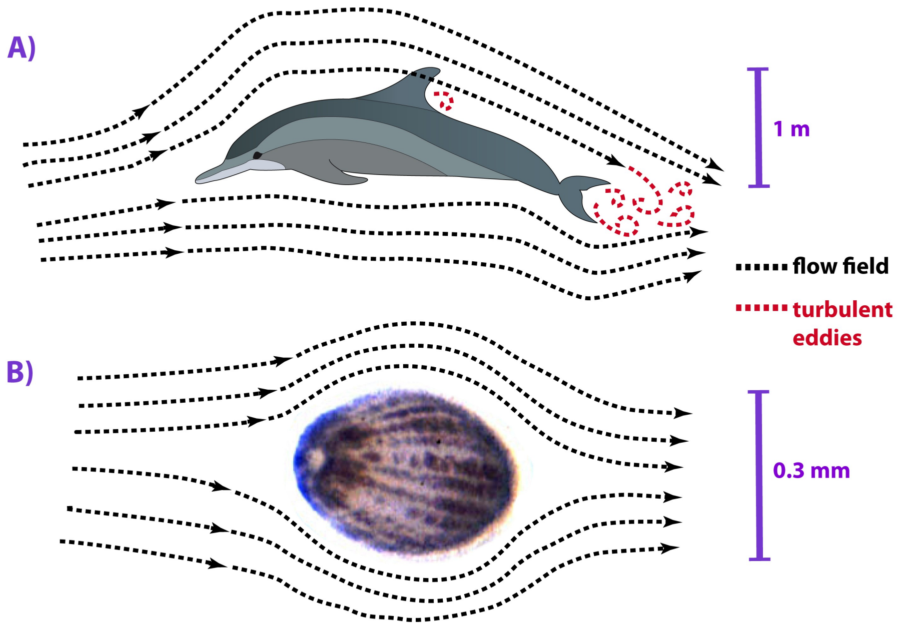

Figure 1. Turbulent and laminar flow at different Reynolds numbers (Re). As discussed in the text, a bottlenose dolphin (A) and a coral planula larva (B) in the same habitat experience very different flow regimes, due to their vastly different sizes and corresponding Re. (A) At high Re, flow (dashed black lines) even around a streamlined organism like a dolphin is broken up by turbulent eddies (dashed red lines) in its wake, which impedes forward progress. (B) At low Re, by contrast, typical flow around the larva is smooth with no turbulent eddies. As such, any turbulent intrusion (e.g., due to wave action) into the larval flow field would stand out against the background flow regime. Figure modeled after Weissburg et al. 2014. *Pocillopora damicornis* planula photo by Bob Richmond.

The former example of eddies produced by flow around larger and faster moving objects is representative of **turbulent flow**: parcels of water moving in random directions on average relative to that of the mean flow. The smooth flow around smaller objects is an example of **laminar flow**. Or put another way: at larger organism sizes and higher Re (as in dolphins) flows are typically turbulent, whereas at smaller organism sizes and smaller Re (as in planulae) flows tend to be more laminar. Characterization of laminar versus turbulent flow regimes (and the transitions between them) based solely on Re should be undertaken cautiously, as local geometries and boundary conditions modulate such regime shifts (see, Denny 1988, Vogel 1994). In general, however, flows at Re $>10^5$ tend to be turbulent, while flows at Re < 10 tend to be laminar.

For the purposes of this chapter, the characteristics of the flow regime at the larval scale have several implications. But to appreciate these implications, we first need to consider one more concept: that of the boundary layer (reviewed in Nowell & Jumars 1984, Butman 1987). Flow over smooth surfaces creates a boundary effect, where flow speed decreases on average the nearer that flow is to the surface. This principle holds across scales: it is why taller wind turbines are more efficient (wind speed is slower near the ground), and it is why so many benthic filter feeders –from tube worms to barnacles to brittle stars– extend their feeding appendages above the substrate into the flow to increase the rate of encounter with particles. Fast flow, especially over rough surfaces, creates turbulent vortices that enhance transport of materials across the boundary layer, and can expose organisms within the boundary layer to instantaneous bursts in velocity (Nowell & Jumars 1984).

Given the above trends, a problem would emerge for a larval-sized organism that relies on material exchange from the surrounding fluid, that operates at low Re, and where surrounding flow is slow and turbulent mixing is absent: such an organism itself has a boundary layer. This boundary layer would tend to interfere with its ability to interact with more distant portions of its surrounding fluid environment. For our larva, then, such limitations could cause significant challenges: the unicellular algae that our larva needs to eat, the oxygen that it needs to absorb and the cue molecules that it would use to locate a suitable settlement location can be rapidly depleted adjacent to its body, and could take considerable time to replenish via diffusion alone. However, larvae have evolved mechanisms to counter such limitations, in particular behaviors to ensure mixing across their boundary layers (see Strathmann 1995, Karp-Boss et al. 1996). In many feeding larvae (see, Pernet this volume) –such as in echinoderms, mollusks and annelids– ciliary action creates currents and locomotory movements that replenish the water alongside the larval body in a manner much more efficient than diffusion alone (Gilpin et al. 2016). Likewise, larvae with movable appendages –such as in arthropods, ascidian tadpoles and possibly brachiolaria-stage sea stars (Bashevkin et al. 2016)– can also break up the boundary layers around their bodies, aiding in fluid and material exchange.

A second implication of larval-scale flow, this one more beneficial for our larva, relates to its entry into the **benthic boundary layer** that forms over the seafloor. This boundary layer becomes relevant when our larva attempts to settle at the end of its pelagic life. In this context, solid surfaces within the boundary layer – near which average flow speeds are slower and (in the case of turbulent benthic boundary layers) lulls in velocity occur with more regularity– could afford precious refuge to our larva so that it can attach strongly and reduce its chances of being dislodged (e.g., Mullineaux & Butman 1991, Crimaldi et al. 2002).

A third implication for our larva of the predominantly laminar flow that moves past its body (Fig. 1) is that any turbulent eddies that impinge upon it, could, in a sense, “stand out” above the typical smooth background flow regime. Such turbulence could come from flow across rough substrates, as mentioned above, from wind-generated white-capping at the ocean surface, from the water movement created by potential predators, and could also come from crashing waves in the surf zone. The chaotic water movement produced from each of these processes is translated down through ever smaller eddies to the smallest scales of fluid motion where that turbulent energy is “dissipated” (i.e., converted into heat) due to viscosity: more intense turbulent flows result in higher levels of energy dissipation and a broader energy cascade that sustains eddies of tinier size. Under the exceptionally intense turbulence of the surf zones of rocky shores (Gaylord et al. 2013), and to a somewhat lesser extent in the other turbulence-generating contexts mentioned above, the smallest turbulent eddies operate at scales that are smaller than that of a typical larva. As a consequence, such flow structures could conceivably be sensed by larvae as gradients in velocity across the dimensions of their bodies (Jumars et al. 2009, Fuchs & Gerbi 2016). Furthermore, because turbulence is so strong in shoreline areas where waves break, the local level of turbulence could be potentially utilized by larvae as a reasonable –though not entirely diagnostic– proxy for their approach to benthic habitat (Gaylord et al. 2013, Fuchs & Gerbi 2016). This ability would have profound implications for larvae settling into nearshore locations, and we will return to this point in some detail below.

A fourth implication of flow for our larva also relates to boundary layers, but at much broader scales. Unlike our previous examples of flow around individual larvae, we here scale up to consider flow that can affect the transport of entire cohorts of larvae, thus possibly impacting connectivity among populations. Adjacent to coastlines, there is an area of slower alongshore flow known as the **coastal boundary layer (CBL)**. Several kilometers offshore, depending on the bathymetry, the along-shore ("free-stream") flow is the fastest; nearer to the coastline, the prevailing alongshore flows decrease markedly due to the CBL. Larvae released on the shoreline can also be retained near to shore by reduced cross-shore mixing within the CBL (Nickols et al. 2013), representing one possible mechanism of the 'larval retention' that data from recent years (e.g., Morgan et al. 2009) has suggested is much more common than previously thought.

In sum, understanding what it feels like to be a larva involves understanding fluid dynamics at multiple scales. As we will see, larvae are not always purely at the mercy of these flows. In some situations they can manipulate the local flow regime to their advantage, and in others they can utilize specific behaviors which increase the likelihood that prevailing flows will carry them to suitable settlement habitat: a critical need for every larva with a benthic adult.

What can a larva sense in its fluid environment and how does it do so?

The ocean is a rich sensory environment for the organisms within. Sound, gravity, pressure, organic and inorganic chemicals, flow, light, salinity, pH and temperature are sensed by marine organisms (Dusenbery 1992, Young, 1995). In many cases, evidence for the sensory response of marine organisms to these cues, and the cellular mechanisms by which they do so, come from studies on adults (and in some cases their terrestrial relatives, such as insects and nematodes). But whether larval forms in animals predated the origin of their corresponding adult body plans or the reverse (Strathmann 1985), adults and their larvae share the same genomes. As such, it seems reasonable to hypothesize that selection could efficiently lead to the acquisition of sensory modalities in larvae that are known to occur in adults.

A full exploration of the sensory capabilities and fluid dynamics of marine larvae –much less so their adults– is beyond the scope of the current review (see, Crisp 1974, Young 1995, Yen 2000, Kingsford et al. 2002, Epifanio & Cohen 2016, Fuchs & Gerbi 2016). Instead, we will focus on well-studied examples where larvae utilize characteristic features of the fluid environment to either identify potential settlement locations, or determine their location relative to flow features that might preferentially carry them to such settlement locations. While doing so, we will briefly describe some of the cellular mechanisms that larvae use or might use to monitor their external environment. We will conclude this section by speculating how these cellular mechanisms might be integrated hierarchically not only to maximize the probability of successful settlement, but indeed to prevent the kinds of errors that would often be fatal for larvae making what is usually their irreversible decision to leave the plankton (see Table 1 for definitions of terms).

Table 1. Metamorphosis, attachment, settlement, recruitment and "continuous settlement".

TERM	DEFINITION
Metamorphosis	is a more or less drastic morphological change between two multicellular phases (e.g., larva and juvenile), often involving major changes in physiology and feeding. As such, the process can take from days to weeks to complete, and can begin while the larva is still swimming (Chia 1978).
Settlement	is the point at which the dispersive larval period ends in those marine organisms that undergo a shift between the plankton and the benthos. As such, settlement is rapid

	(minutes to hours) and generally irreversible (though there are a few exceptions to this; e.g., Richmond 1985). The notion that metamorphosis is distinct from settlement is exemplified by crabs, whose metamorphosis occurs between the zooeal and megalopal stages, before settlement occurs.
Attachment	is typically the first step in the settlement process (though infaunal juveniles may burrow at settlement, not attach). Care should be taken in using attachment as a proxy for settlement, since unlike settlement, attachment can be and often is reversible. Larvae sampling the substrate might attach and release repeatedly before finally settling.
Recruitment	is an ecological term describing the successful entry of a settled juvenile into a population of conspecifics. The distinction between settlement and recruitment can be exemplified as follows: a larva that either settles in a totally inappropriate location, far away from any conspecific adults –or a newly settled larvae that is immediately eaten– will never successfully recruit. A complication with the use of this term in the literature is that recruitment is defined relative to a particular census time following settlement, which varies among studies.
Continuous settlement-relocation	is a term proposed by Navarrete and colleagues (2015) to describe their observation of mussel "postlarvae" settling in one location and then tumbling along the substrate until they encounter their definitive adult (i.e., potential recruitment) location.

Note: We here provide definitions of key terms involving the planktonic-benthic transition in marine invertebrates. We are compelled to do so due to the widely varied (and often contradictory) definitions of these terms that have characterized the literature for over a hundred years right up to the present day.

Planktonic animals in general –and larvae specifically– have been shown to have the ability to detect a wide range of environmental stimuli (Fig. 2). The majority of this evidence comes from crustaceans (reviewed by Yen 2000, Epifanio & Cohen 2016); however, several other phyla have been studied as well (reviewed by Young 1995, Kingsford et al. 2002). In many cases, these cues have been hypothesized or demonstrated to be employed by larvae to assist them in locating settlement locations, and these are the ones we will briefly describe here.

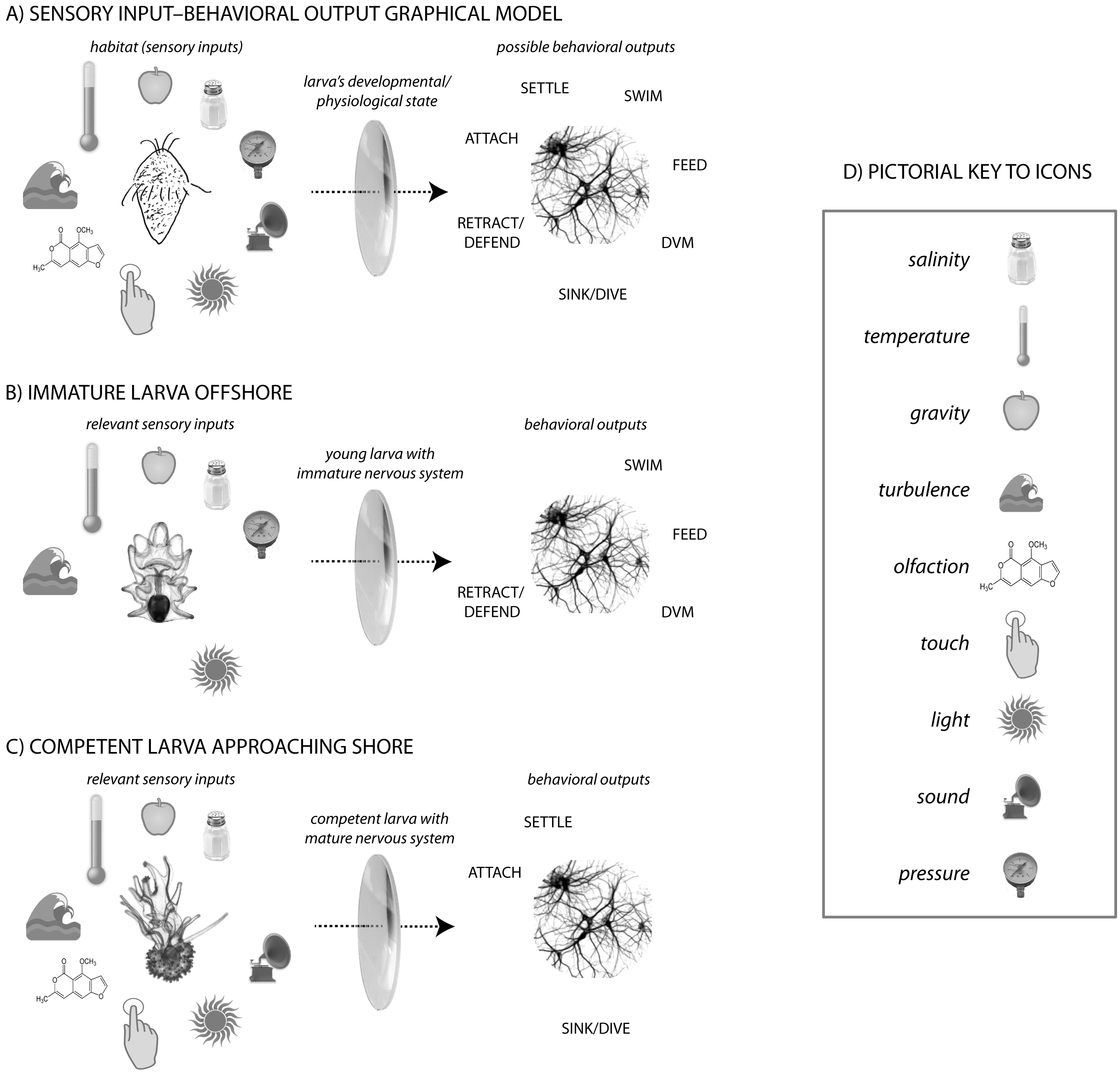

Figure 2. Graphical model of multi-sensory inputs and behavioral outputs as they relate to settlement. Here we consider only those sensory modalities and larval behaviors that have direct relevance to settlement itself, or that increase the likelihood that larvae get retained near or carried to suitable settlement locales. (A) In the basic model, a generic larva (here a *trochophore*) can detect a wide range of sensory inputs – the combination of those inputs can be thought of as a representation of the habitat that the larva is in. The physiological and developmental state of the larva can be thought of as a *lens* (pictured in the center) through which the larva interprets these inputs. The *larval nervous system* (pictured at right) then integrates those sensory inputs to elicit specific behavioral outputs. (B) An example of ▶

As mentioned earlier, most larvae swim too slowly to be able to control their horizontal position directly: their main strategy is to enter and exit horizontal flows by adjusting their vertical position. Larvae can detect their depth by sensing pressure (Young 1995), and can potentially tell if they are sinking, stable or rising by monitoring light intensity, pressure, and their acceleration relative to gravity vectors over time (Fig 2). Although there is widespread behavioral evidence for these sensory capabilities across phyla, direct physiological / morphological evidence is more limited (Kingsford et al. 2002, Epifanio & Cohen 2016). To adjust their vertical position in response to these cues, larvae can either swim upward or downward, sink passively if they are negatively buoyant, adjust their buoyancy, or deploy or retract devices –like threads or mucus– or appendages to either increase or decrease resistance to sinking.

Using one or a combination of these mechanisms, many larvae undergo daily migrations (so-called **diel vertical migrations; DVM)** from depths up into surface waters at night, at a time when visual predators are less of a problem, and prevailing winds tend to blow towards the shore, and hence potentially carry larvae there (reviewed in Queiroga & Blanton 2005). Other larvae undergo **reverse DVM** into surface waters during the day, which would tend to offer higher levels of their phytoplanktonic food and a potential refuge from non- visual invertebrate predators undergoing

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(Fig. 2 legend continued) ▶ an immature larva (here, a *sea star bipinnaria*) detecting a series of sensory cues that inform upon its depth, flow regime, and position relative to fronts and clines. Integration of those cues can provoke specific swimming behaviors that could increase its likelihood of arriving at suitable settlement locations later in ontogeny. (C) An example of a mature, competent larva (here a *sea star brachiolaria*, with a very well developed juvenile rudiment) ready to settle in a favorable locale. Now, additional cues can aid the larva in making the final phase of its journey to settlement on the sea floor, via specific behaviors such as sinking and attaching in flow. (D) Pictorial key to the *sensory icons* shown in the left half of panels A-C.

DVM, but could simultaneously expose larvae to visual predators and potentially wind-driven offshore flows (e.g., Ohman et al. 1983, Pennington & Emlet 1996). It may be that larvae undergoing reverse DVM are well defended against visual predators, though we are aware of no compelling evidence that tests this idea in a comparative context. Larvae in estuaries are known to undergo **tidal migrations**, which is best studied in various crabs (reviewed in Queiroga & Blanton 2005). Depending on the species and developmental stage, these migrations can either retain or flush larvae from estuaries on ebb tides, and carry them up-estuary on flood tides. Finally, many larvae undergo so-called **ontogenetic migrations**, in which earlier stages behave differently than later ones (Queiroga & Blanton 2005). Such ontogenetic shifts may manifest as distinct tidal or DVM/reverse-DVM behaviors, or the ontogenetic patterns might be consistent at a given stage throughout the day or tidal cycle. The classic ontogenetic migration is to sink at late stages, which is considered an adaptation for approaching potential settlement habitat (e.g., McCarthy et al. 2002).

It should be noted that late stage larvae of many taxa (e.g., echinoderms, gastropods, cladocerans, brachiopods, bryozoans, crustaceans) acquire shells or skeletal structures that are retained as these organisms enter the benthic juvenile stage. At some point, such structures are likely (and in a few cases have been shown) to make these larvae negatively buoyant (Chia et al. 1984; but see Pennington & Emlet 1986). If so, we would argue that this is likely an example of an exaptation (sensu Gould & Vrba 1982; often, but less precisely called "cooption"): the likely selective advantage of pre-settlement skeletal development is protection from predators, either in the benthos (e.g., newly-settled echinoderms) or in both the plankton and benthos (e.g., gastropod larvae and corresponding juveniles). The usefulness of such shells in helping larvae sink would, in this conception, be a beneficial side effect.

After depth regulation, the next best studied behavioral capacity of larvae is **olfaction** (Fig 2). Detecting and responding to dissolved chemicals could be useful to some larvae in feeding and avoiding toxicants (see Corsi and Marques-Santos, this volume; Yen 2000, Zimmer & Butman 2000), but the most intensively researched olfactory behavior of larvae is surely in identifying potential settlement cues and deterrents (reviewed in Pawlik 1992, Young 1995). In the cases where the existence and activity of such dissolved cues have been demonstrated, larval behavior in response to such cues can be quite complex. For example, in the coral-grazing sea slug *Phestilla sibogae*, entering and exiting plumes of the dissolved coral-derived cue causes larvae to sink and resume swimming respectively (Koehl et al. 2007). Interestingly, larval responses to settlement-inducing olfactory cues are modulated during ontogeny: they manifest more or less suddenly when a larva becomes “competent” to settle. Indeed, response to settlement cues is the way competence has been traditionally defined (see Table 1, Hodin et al. 2015).

The cellular and molecular mechanisms of olfaction are very well studied in fish and terrestrial organisms, including flies, roundworms and mammals. The similarities in olfactory mechanisms among these taxa (e.g., the involvement of G-protein coupled receptors; Kaupp 2010) make it plausible that similar mechanisms are used by aquatic organisms in general, and diverse larvae at settlement in particular (Baxter and Morse 1992, Amador Cano et al. 2006).

Whatever are the cellular mechanisms, the aforementioned observation –across marine phyla– of the sudden acquisition of competence and hence responsiveness to olfactory settlement cues is most consistent with the following scenario: olfactory responsiveness is actively repressed in immature and pre-competent larvae. This is sensible, given that de-repressing (or "unmasking" *sensu* Chia 1978) an intact olfactory signaling system is more efficient than assembling the transcripts and proteins involved *de novo*. Indeed, one potential global regulator of settlement is nitric oxide/cyclic guanosine monophosphate (NO/cGMP) signaling, which is an active repressor of settlement in multiple phyla (reviewed in Bishop & Biggers 2014). Inhibition of NO/cGMP signaling then represses the repressor, thus uncovering the capacity of a larva to settle, possibly in part via unmasking an already intact olfactory response. In sea urchins, histamine has been identified as another such regulator of settlement (Swanson 2007, Sutherby et al. 2012) and, in the context of fertilization, has been shown to activate NO signaling (Leguia & Wessel 2006).

A few notes of caution about larval olfaction are warranted. First, the majority of studies of larval responses to settlement inducers are undertaken in dishes in the laboratory in still water. This is a highly artificial situation (see, e.g., Metaxas 2013), and there is evidence that the olfactory system integrates with the larval response to water motion in natural settings (Woodson et al. 2007, Zimmer & Butman 2000). As such, more studies examining olfactory and other settlement responses under realistic flow conditions would surely be welcome. Second, the levels of inducer that are needed to stimulate settlement are often orders of magnitude higher than concentrations measured in the field (but, e.g., see Swanson et al. 2007). In such cases, we should be circumspect in ascribing ecological relevance to those cues and/or the mechanisms by which larvae respond to them. And third, it has been argued by several authors that dissolved chemical cues are unlikely to be effective in most natural settings (and especially in high flow environments) beyond a few centimeters from the source of the cue (e.g., Denny & Shibata 1989, Koehl et al. 2007). Therefore, if larvae are responding to dissolved cues, this is typically only going to be effective once they have already managed to arrive extremely close to potential settlement habitat. This is one of the reasons that we maintain the *a priori* expectation that larvae also respond to other (non-olfactory) types of cues that would be effective at scales from cm's to km's.

A third class of sensory modalities that larvae could use to aid in their successful settlement –and one that could potentially act at much broader scales than dissolved chemical cues– relates to water movement. Larvae being carried in horizontal flows of a given velocity would generally have no frame of reference to detect that flow. By contrast, attached larvae on the benthos are in some cases known to react to different rates of flow going past them, and this can influence their decision to either settle permanently in that location or to continue their search (see Table 1; Fig. 2). In addition, some larvae are known to respond to **turbulence**, and because turbulence and wave motions are often stronger in shoreline regions they could be useful indicators to larvae attempting to return to nearshore settlement habitats, as we discuss in more detail below. The mechanisms by which larvae detect turbulence and wave motions are unknown, and furthermore, there are several aspects of water motion to which larvae could be responding (e.g., Fuchs et al. 2015), including translational acceleration, fluid rotation (via statocysts), various gradients in velocity (via deformation of cilia or activation of stretch receptors) or some combination (Fuchs & Gerbi 2016).

Additional sensory capabilities of larvae that could aid their progression towards settlement are the abilities to detect and monitor **sound**, **touch**, **temperature** and **salinity** (Fig. 2). Response to temperature (e.g., via transient receptor potential [TRP] channels) and salinity (via sodium and potassium channels) are widespread and likely generic features of marine larvae. Behaviorally, responding to temperature and salinity can be adaptive for larvae entering or avoiding estuaries, or for entraining into or exiting upwelling (colder, higher salinity) versus downwelling (warmer, lower salinity) flows, as we will discuss briefly below. Mechanosensation is also likely generic, even if it has not been widely studied. Examples include some fouling organisms like colonial ascidian larvae, as well as some non-animal propagules (e.g., kelp spores), which will seemingly settle when contacting virtually any solid surface (Grosberg 1981, Gaylord et al. 2006). Sound has only recently been appreciated as an important cue that larvae can use to recognize the overall features of their adult habitat. In the last few years, compelling evidence has been presented that some larval reef fish and invertebrate larvae respond positively to sound recordings of waves impacting coral reefs, and late stage oyster larvae likewise respond specifically to recordings made over an intact oyster habitat, but not to control recordings from other nearby locations (see, Lillis et al. 2013).

We expect that larvae deciding where to irreversibly settle would draw on a rich and diverse array of sensory information that could provide details about the suitability of its potential adult habitat. In this sense, our larva might be expected to use a process akin to an Analytic Hierarchy Process (*sensu* Saaty 2008), in which larval experience could modulate the relative importance and strength of certain cues. For example, the presence of planktonic predators might lower a larva's threshold sensitivity to a dissolved chemical inducer. More to the point, we might expect different taxa in different types of habitats to prioritize certain cues over others. For example, larvae settling in high energy habitats might prioritize turbulence cues over chemical cues, those settling in mangrove estuaries might prioritize salinity and temperature cues over turbulence cues, and those settling on a specific species of coral might prioritize a specific dissolved chemical cue even in the temporary absence of characteristic reef sounds. In particular, the hypothesized hierarchically-arranged signaling pathways might be more or less organized in a fashion parallel to the scale over which the cue acts (Fig. 3). For example, turbulence, sound, and salinity cues could operate at a broader "habitat" scale of meters to kilometers, dissolved chemical cues and turbulent flows over rough surfaces at millimeters to centimeters, and mechanosensory cues like surface topography on sub-millimeter scales (e.g., Whalan et al. 2015). Presently, the evidence for such hierarchical cue strategies for settlement is limited (Kingsford et al. 2002), and their arrangement by scale is pure speculation. Still, it seems a fruitful area for future comparative investigations.

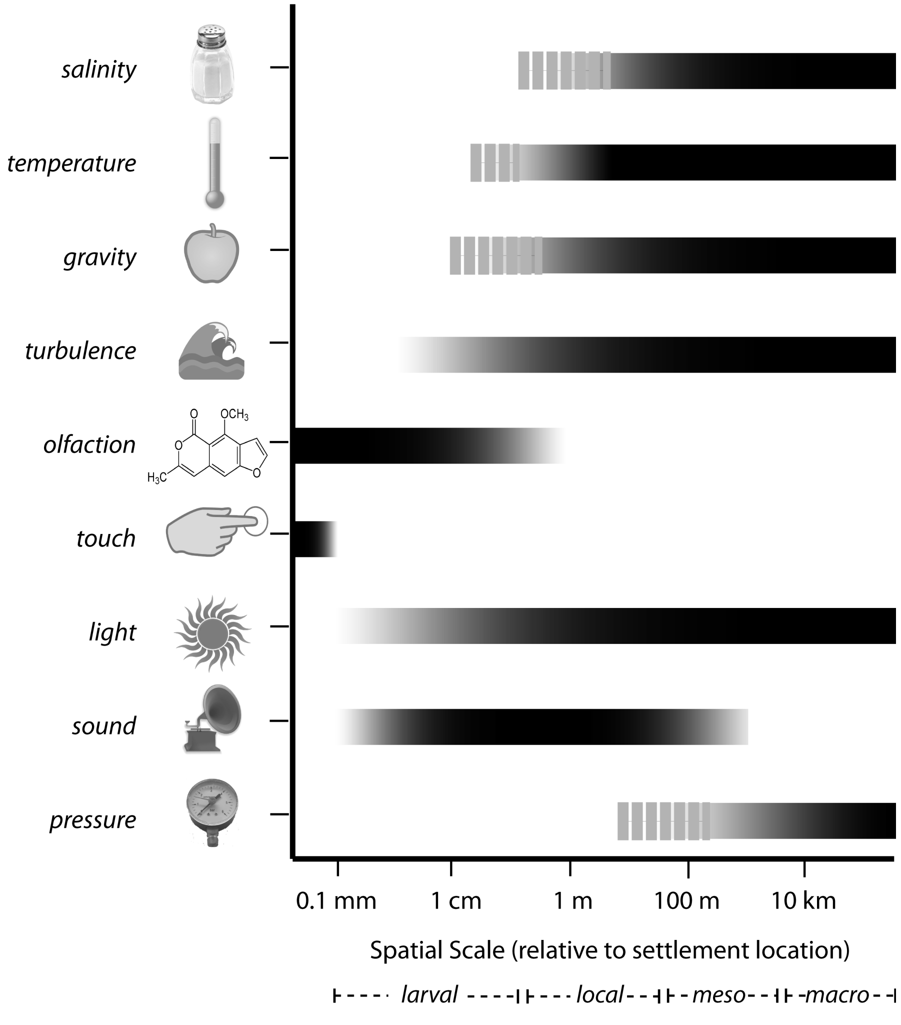

Figure 3. Relevant scales of sensory input for settlement. As in Fig. 2, we here specifically focus on those sensory modalities that larvae might use to identify suitable settlement locations or that might trigger behaviors that would increase the likelihood that they are retained near or carried to such sites. For example, we do not here consider the many sensory inputs that larvae use (or likely use) for feeding. Note the logarithmic distance scale on the x-axis, denoting the larva's distance from a suitable settlement site. The four scale bins shown below the x-axis (*macro*, *meso*, *local* and *larval*) mirror our treatment of these scales in the text. *Grey scale gradients* indicate our approximation of the relative importance of a given sensory modality at a range of scales; *dashed regions* indicate probable gaps in our knowledge of the importance of specific sensory inputs for settlement at those scales.

In more general terms, the behavioral integration of multiple sensory modalities (multisensory integration) is a concept that has received much attention in vertebrates and insects in recent years. It is, in brief, the interaction or synergy among the different senses and the compilation of their information content (Stein et al. 2014). In mammals, such integration can typically be coordinated at multiple levels of the nervous system (Stein et al. 2014). In flies, the integration between olfactory, visual and mechanosensory input guides flight in three dimensions (Duistermars et al. 2009), but the underlying mechanisms of this integration remain to be explored. Similarly, planktonic organisms maneuver in a three-dimensional environment rich with sensory cues, such as those outlined above (e.g., Woodson et al. 2007). Although larval nervous systems are generally less centralized (and certainly less well studied) than those of vertebrates and insects, larvae from disparate phyla have concentrated neuronal structures which in some cases are thought to function in sensory integration during settlement via the action of familiar neurotransmitters, which act on single target cells, and neuromodulators, which can have multiple targets (e.g., Hadfield 2011, Bishop & Biggers 2014, Sutherby et al. 2012).

The small size of marine larvae makes functional neurophysiological studies challenging. Nevertheless, modern methods examining the full complement of proteins and metabolic profiles (proteomics and metabolomics, respectively) that are expressed over time and under different conditions can and are being employed in studies of larvae and their metamorphoses (e.g., Song et al. 2016; Williams & Carrier, this volume). Furthermore, targeted gene manipulation methods have begun to be applied to metamorphic stages of marine larvae as well (e.g., Heyland et al. 2014). As such, the coming years offer great promise for further elucidating the detailed mechanisms of sensory perception in larvae, and how –on a mechanistic level– settlement decisions are made.

How larvae find their way home: scales of flow and larval behavior

We have considered the flow regimes that larvae experience as well as the sensory capacities that larvae use to detect cues in their environment. Now we move back out to larger scales to try to address the following question: where do larvae go, and how do they find their way back?

In recent decades, our understanding of where larvae go and how they find their way back to shore has grown enormously, with literally hundreds of papers each year published on various aspects of this topic. Nevertheless, there remain surprisingly fundamental disagreements in the field about the predominant oceanographic mechanisms that deliver larvae to coastal habitats (reviewed in Pineda et al. 2010). Are the numbers of larvae in the plankton (the so-called **larval supply**) a good predictor of the number of eventual settlers or not? Do larvae by and large get advected far off shore by large-scale coastal processes like **upwelling**, only to be returned to shore on the occasional reversal events? Or are most larvae actually retained very close to shore throughout their entire larval life (Morgan et al. 2009)? If so, is this pattern of **nearshore retention** due to active larval behaviors or passive responses to oceanographic forces beyond their control? Do larvae concentrate in clinal fronts, oceanographic eddies or even flotsam as a possible means of remaining close and/or transporting to shore? Do larvae easily transit through the surf zone? Or do they remain in the waters just seaward of the surf –like a sailing ship becalmed within sight of port– with the surf zone as a **semi-permeable barrier** (*sensu* Rilov et al. 2008) to onshore delivery?

We will not attempt to offer definitive answers to any of these questions, we instead defer to Pineda and Reyns (this volume), who treat these questions in much greater detail. For our purposes, we will briefly describe some of these oceanographic mechanisms of transport as they relate to the likelihood of larvae returning successfully to settlement locales, and we will provide some of the evidence for and against them from specific case studies. Finally, we will indicate where we think there are gaps in the literature that could enrich our understanding of how disparate larvae in discrete geographic or oceanographic situations might enhance the probability of surviving to settle in the right place and time. In so doing, we will follow our larva across multiple scales from offshore waters back to the nearshore, stressing the behavioral adjustments that larvae could make to maximize the likelihood of successful settlement in suitable habitats.

1. The macro scale: ~1-100 kilometers

Much effort in recent decades has been directed at developing increasingly realistic oceanographic circulation models, and using them to predict the dispersal patterns of larvae, other propagules and the plankton in general. With respect to settlement and the delivery of larvae to the shoreline, many of these aforementioned models have made the optimistic assumption that sampling of larvae at various distances from the shoreline will give direct insight into their settlement on the shore. Or to put it another way: larval supply is the main driver dictating settlement and ultimately recruitment. This view is not without support (see, Pineda et al. 2010; Pineda & Reyns, this volume), but many additional studies have shown that the patterns are not quite so simple, revealing situation specific disconnects between larval supply and recruitment. For example, pre-settlement processes like density dependence of settlement itself and the association between tidal height and settlement timing can profoundly impact recruitment success and location (e.g., Grosberg 1981, 1982). Post settlement processes such as secondary movement of settled larvae and heavy predation or environmental stress on settlers can also break the simple connection between larval supply and recruitment (reviewed in Pineda et al. 2010).

With respect to larval transport, the following question seems deceptively simple, but is fraught with complexity and controversy: where do larvae go? One attractive scenario in upwelling dominated regions such as the Eastern Pacific and West coast of South Africa is that predictable wind-driven currents cause large scale, coordinated movements of larvae on a seasonal time scale. For example, along the California coast the prevailing California Current flows from the North in the Spring. Coriolis forces (driving **Ekman transport**) deflect the prevailing currents offshore, with these displaced waters being subsequently replaced through upwelling of deep, nutrient rich waters up onto the continental shelf. These upwelled nutrients drive famous seasonal plankton blooms, and Ekman transport is predicted to send these plankton –and the larvae therein– offshore. Occasional relaxations in the prevailing winds cause temporary reversals in the direction of the cross-shore currents, transporting larvae shoreward.

Many observations have substantiated the predictions of this **upwelling-relaxation hypothesis** (Roughgarden et al. 1991), finding enhanced settlement and/or recruitment (see Table 1 for the distinction) associated with relaxation conditions and lower settlement/recruitment with upwelling events. Nevertheless, there have also been numerous studies in recent decades finding just the opposite: no association between upwelling-relaxation events and onshore recruitment (see, Pineda et al. 2010; Pineda & Reyns, this volume). Instead, these and other studies have identified or proposed additional oceanographic mechanisms for onshore transport, including internal tides, fronts, wave-driven flows, and even suspended materials like flocs, flotsam, and surface slicks.

In some cases, the seemingly contradictory results outlined above could simply be due to differing sampling methodologies and intervals (Pineda et al. 2010; Pineda & Reyns, this volume). Nevertheless, there are a growing number of studies in which the same species at different times or locations, or, more commonly, different species sampled in the same location and time period yield conflicting support for relaxation-associated settlement, even within the same publication. In one recent example from an upwelling region of Brazil, Mazzuco et al. (2015) found contrasting results for mussel and barnacle settlement: barnacles settled in association with times of predicted relaxation events, whereas mussel settlement patterns showed no such relationship.

One particular set of observations that runs counter to a central prediction of the upwelling-relaxation hypothesis is the surprising finding that many larvae are not advected far offshore at all. Instead, through various oceanographic and behavioral mechanisms (such as the coastal boundary layer and vertical migration patterns, respectively, as discussed above), larvae in multiple locations and contexts appear to complete all or most of their planktonic period very close to the shore at which they were released. Thus a new paradigm has emerged regarding so-called **larval retention**, which would of course seem to make it far more likely that larvae could make their way back to appropriate settlement locations (presumably using the onshore transport mechanisms referenced above; see, Pineda et al. 2010; Pineda & Reyns, this volume).

One caveat with the majority of studies that have addressed these issues to date is that they have generally taken a rather limited taxonomic focus, with barnacles and other crustaceans, mussels, and fishes as the subject of nearly all of this published work. In certain respects, this focus is understandable. First, most heavily studied taxa either have associated fisheries (crustaceans, mussels, fishes) or are dominant in fouling communities (barnacles) as adults. Second, studying larvae in the plankton can be painstaking work, as larvae of many taxa appear highly episodically in the plankton and in recruitment events. By contrast, mussels, crabs, and barnacles, in particular, are dominant shoreline and estuarine invertebrates in many locales, and likewise dominate larval zooplankton assemblages in corresponding offshore regions. Nevertheless, an expanded taxonomic focus seems necessary to give a more complete picture of where larvae go and when.

But research focused even within the well-studied taxonomic groups has yielded contradictory findings, as mentioned above. It may be that the taxonomically, spatially and temporally diverse responses of larvae to a given set of oceanographic conditions is consistent with the Sweepstakes Reproductive Success (SRS) hypothesis (see, Hedgecock and Pudovkin 2011). The SRS hypothesis posits that larvae within populations demonstrate physiological and behavioral diversity with respect to their context-dependent growth and survival in the plankton, and that successful recruitment can be seen as a process akin to winning a sweepstakes, where all of the right circumstances come together for that improbable win. In a variable environment, no one "strategy" would be consistently favored, thus maintaining diversity in the way larvae respond to oceanographic conditions. Such diversity might be predicted to manifest in inconsistent geographic and temporal patterns of larval dispersal mechanisms both among and within species.

Whether or not the SRS hypothesis is supported, we conclude that biological and physical factors that vary geographically, seasonally, tidally, daily and taxonomically can and do impact the relationship between supply and recruitment, and therefore we are still seeking a holistic understanding of these processes that might offer predictive power. For example, we await a comprehensive meta-analysis of the myriad published studies on larval supply and recruitment to help illuminate the path forward for the field.

2. The meso scale: < 0.1 – 1 kilometers

At this point, by whatever mechanism has brought or retained our larva in the coastal zone, the difficulties are far from over. A larva seeking shoreline habitat still needs to traverse the surf zone to arrive on shore, and once it does so, to recognize that it has indeed arrived there. Is it possible that the surf zone itself can provide such cues to larvae?

Recent and growing evidence suggests that the answer is 'yes' (Fig. 3). First, larvae of multiple taxa have recently been shown to respond to recordings of habitat sounds by increasing their likelihood to settle (see Lillis et al. 2013). Likewise, there may be chemical cues in some specific situations that are enhanced in broader scale habitats, like breakdown products of kelp in the nearshore, and mangrove-derived chemicals in tropical estuaries. Finally, the surf itself may be a cue. Studies by Gaylord et al. (2013) and Hodin et al. (2015) show that sea urchin and sand dollar larvae with nearshore adults exhibit enhanced settlement in response to high levels of turbulence: specifically, levels indicative of those seen under crashing waves. Interestingly, turbulence is not a settlement "cue" per se, since it does not directly induce larvae to settle. Instead, exposure to turbulence primes these larvae to settle: a greater proportion of turbulence exposed larvae will settle when subsequently provided with a strong localized (i.e., chemical) settlement inducer. Because such settlement inducers are how competence is traditionally defined, these results lead to the intriguing conclusion that turbulence exposure actually causes larvae to become competent to settle. Other studies demonstrate that exposure to turbulence and waves can have another seemingly advantageous impact on late stage larvae in some taxa: it causes them to either actively or passively sink (see, e.g., Fuchs et al. 2015; but see Wheeler et al. 2013). This behavior could provide a selective advantage for nearshore-destined larvae in the water column by increasing their chances of contacting the seafloor (Denny & Shibata 1989), or at least of arriving nearby.

3. The local scale: 10s of centimeters – 10s of meters

Our larva has now –through what was likely a combination of luck and directed behaviors (such as sinking in turbulence or association with surface slicks)– arrived tantalizingly close to potential settlement sites. What larval behaviors in association with the properties of the fluid environment at these local scales might make the difference between reaching such benthic sites or being advected away?

Here our larva is approaching the benthos, and much research effort has been directed at how flow over complex substrates can impact the likelihood of larvae –and non-animal propagules such as seaweed spores– entering the benthic boundary layer and contacting the substrate. In one classic modeling study, Denny and Shibata (1989) showed that on wave swept shores, turbulence alone (in the absence of directed larval behaviors) can carry larvae efficiently and quickly to the substrate, and that rapid (>1 mm • sec^{-1}) sinking or downward swimming of larvae can enhance this effect (Fig. 3). Likewise, multiple studies have shown that realistic flow over complex surfaces (including conspecific adults) can increase the likelihood of larvae contacting the substrate, though in very high flows, larvae may not be able to effectively attach (Crimaldi et al. 2002). Manipulation of flow dynamics in field settings show that increasing flow over settlement plates can increase recruitment rates (Palardy & Whitman 2011), but it is unclear if this result is due to settlement or post-settlement processes.

In estuaries, salinity and temperature can vary on the local scale, and competent larvae are known to adjust their swimming behavior in response, for example, to drops in salinity (Epifanio & Cohen 2016; Fig. 3). Also, characteristic habitat sounds (such as urchins scraping the substrate; Radford et al. 2010) may indicate to larvae that they have arrived close to preferred habitat. Although most studies on larval sound perception and settlement responses to date have considered the meso scale to be the effective scale, studies contrasting more localized sound cues seem warranted.

With respect to olfaction, as at the meso scale, there are certain flow regimes in which one could imagine larvae detecting and responding to local-scale chemical signatures associated with specific settlement sites, but definitive evidence is scant. In some reef fish, larvae are known to settle in response to the smell of conspecific adults, and in one case (the Humbug damselfish, *Dascyllus aruanus*) previous eye contact of the adults with the juveniles changes the nature of the adult odor to make it more inductive to larvae: these adults thus actively recruit conspecific larvae (Roux et al. 2015).

There are other classes of potential local cues that remain unexplored or largely so. For example, tide pools are known to undergo dramatic diurnal fluctuations in pH (Daniel & Boyden 1975; Jellison et al. 2016). The possibility that larvae settling in the intertidal zone might respond positively to such pH shifts has not to our knowledge been directly addressed experimentally. Likewise, although temperature can also fluctuate dramatically in intertidal habitats, only a few studies have examined the potential modulatory effect of temperature on other classes of settlement cue (Pechenik 1984).

4. The larval scale: < 1 milimeter – a few centimeters

This is the spatial scale over which a larva experiences its environment on short time scales (seconds to minutes). At this point, our larva has successfully been carried to benthic habitat that –based on cues already received at broader scales– seems like a potentially beneficial place to settle. But the final decision about whether or not to irreversibly commit to this settlement location could still be modulated by the environment on very fine, even microscopic scales (Fig. 3).

Based on modeling of odor dispersion, this is the scale at which dissolved chemical cues would likely exist at sufficient concentrations to be detected above background by –and thus elicit a behavioral response in– larvae (Koehl et al. 2007). Furthermore, many chemical inducers of settlement have been shown to be substrate bound, including what is perhaps the most generic chemical cue used by disparate marine larvae: chemicals associated with surface biofilms (reviewed in Hadfield 2011); it is therefore only at the scale of the larva that such cues are available to them. On the other hand, chemical deterrents of settlement (such as toxic compounds or the smell of a predator) could also be detected at the larval scale, and may effectively inhibit the settlement process before it is too late (Woodin 1991).

There are also several other classes of cues that could inform our larva at the larval scale, including light, fluid shear, and microtopography (Crisp 1974). For example, certain coral and sponge larvae preferentially settle on settlement tiles that have holes drilled in them: tiles with 0.4 mm holes (approximately the width of the larvae) show enhanced settlement relative to flat plates or those with 0.7-1.0 mm holes (Whalan et al. 2015). Other corals settle on the undersides of experimental settlement surfaces, and clever manipulative experiments demonstrated that this was due to specifically to the inhibitory nature of red (but not blue/green) spectrum wavelengths striking the upper surfaces (Strader et al. 2015). Finally, decisions on the larval scale could be important for our larva to avoid being carried away by currents and strong, turbulent flows during the initial stages of making its attachment permanent (e.g., Reidenbach et al. 2009)

In sum, by the time our larva reaches the larval scale in a potential settlement location, it likely has already received broader scale indicators of suitable habitat. Depending on the resulting juvenile's ability to move post-settlement –as well as its vulnerability to predation, grazing or fouling soon after settlement– cues at the larval scale might not only provide valuable information to enhance growth and survival (see Pechenik, this volume), but may indeed be the last chance that our larva has to abort the settlement process and seek purchase elsewhere.

Conclusion

These are exciting times for larval ecology and evolution. Oceanographic models and survey methods are greatly improving our ability to determine where larvae go and how they return to coastal regions (see Pineda & Reyns, this volume). Barcoding methods will soon make it possible to obtain rapid information on plankton assemblages that previously required painstaking manual sorting (see Marko & Hart, this volume). Laboratory methods can challenge larvae with increasingly realistic flow conditions and sensory experiences, coupled with imaging techniques to visualize resulting behaviors. And molecular methods are making it possible, in almost any taxa, to interrogate and manipulate the detailed cellular and neurophysiological mechanisms underlying complex behaviors like larval settlement (see Williams & Carrier, this volume).

Thus there is great promise for addressing issues in larval ecology that have puzzled and inspired researchers for many decades. For example, examining the sensory context of settlement behaviors in realistic environmental conditions would give important insight into the evolution of contrasting settlement strategies, how disparate larvae prioritize diverse sensory inputs, and what this prioritization means neurophysiologically. Elucidating the predominant migration pathways that larvae undertake may inform on a second generation of marine protected area design, one that more deliberately couples critical nearshore locales to their offshore "nursery" grounds (see, Weissburg et al. 2014). More generally, as we hope to have demonstrated, settlement in marine invertebrates is an ideal subject for integrative biology: combining oceanography, fluid dynamics, sensory ecology, animal behavior, developmental, cellular and molecular biology. Furthermore, the likely independent origins of larvae in diverse phyla, as well as the sometimes extreme contrasts in settlement locales even among closely related species, offer abundant comparative material for detailed evolutionary studies into this key life stage transition for animals and non-animals alike.

Summary

1. Flow at the larval scale is fundamentally different than flow at the scale of larger organisms (such as ourselves): the former is dominated by viscous forces, the latter is dominated by inertial forces.
2. Larvae are not merely 'passive particles': although many larvae cannot make headway against strong oceanic currents, they can adjust their vertical position in the water column, and this can have profound influences on where larvae go and how they can find their way back towards suitable settlement locations.
3. Larvae engage a wide range of sensory modalities in order to ascertain and advantageously adjust their vertical position in the water column, as well as their proximity to potential settlement locations; an overlapping but unique set of sensory inputs characterizes their habitat at different scales.
4. We hypothesize that larvae integrate these various cues in a hierarchical fashion, and disparate taxa in different contexts will demonstrate alternative arrangements and strengths of the cues that they use to locate settlement sites.
5. Modern techniques offer the promise of answering several long-standing, vexing questions in larval ecology that bear on topics as wide ranging as mechanisms of metamorphosis, life history evolution, conservation biology and the origins (and losses) of larvae.

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SUPPLEMENTARY ONLINE MATERIAL FOR:

HODIN ET AL. 2017, CHAPTER 13 IN *ECOLOGY AND EVOLUTION OF MARINE INVERTEBRATE LARVAE*

The following document proceeds through the manuscript on a page by page basis, listing additional citations for the topics discussed. These citations are not intended to be comprehensive, but we hope will prove sufficient to give the interested reader an entree into these various topics. The full reference list for all such auxiliary citations is found at the end of this document. Note that we do not here repeat the reference(s) cited in the main text on the page/topic in question.

PAGE 3

Larvae as "passive particles"

Eckman 1990, Hannan 1984, Hill 1990, Roberts 1997, Roughgarden et al. 1988, Williams et al. 1984

Larval defenses

Vaughn & Allen 2010 (review)

Phenotypic plasticity of feeding

McAlister & Miner, this volume (review)

Responding to settlement cues indicative of adult habitat

Perhaps first proposed explicitly by Crisp 1974.

Newly-settled juvenile adhesion in flow

Crisp 1955, Eckman 1996, Harlin & Lindbergh 1977, Koehl 2007, Jonsson 2005

Paternal effects on offspring life history (maternal-offspring conflict)

Chapman 2006, Eberhard 2005, Guillaume et al. 2016

Maternal protection, encapsulation, brooding

Castro & Podolsky 2012, Doherty 1983, Edmunds et al. 2010, Emlet et al. 1987, Epifanio & Garvine 2001, Queiroga & Blanton 2005, Forward 2009, Himmelman 1978, Levin & Bridges 1995, Mandal et al. 2010, Moran & Emlet 2001, Morgan & Christy 1994, Reitzel et al. 2004, Russell-Hunter et al. 1972, Starr et al. 1993, Strathmann & Strathmann 1982; but see Hill et al. 1996, Medeiros-Bergen & Ebert 1995, Pechenik 1999

Lecithotrophy as a strategy for increased larval survival

Marshall et al. 2012, Pechenik 1999, Pringle et al. 2014, Strathmann 1985

PAGE 4

Chemical defenses of embryos/larvae

McClintock & Baker 1997, Vaughan & Allen 2010 (review)

Timing of offspring release to enhance settlement likelihood

Morgan & Christy 1994

Comparative swim speeds of invertebrate and non-invertebrate larvae

Cobb et al. 1989, Massel 1999, Queiroga & Blanton 2005

PAGE 5

Reynolds number in the ocean

Levinton 2013 (basic review), Massel 1999, Purcell 1977

PAGE 6

Swim speeds of planulae and dolphins

Fadlallah 1983, Fish & Hui 1991

PAGE 7

Intermediate Re

Massel 1999, Nawroth & Dabiri 2014, Wang & Ardekani 2015, Yen 2000

PAGE 9

Breaking up boundary layer around a larva

Margalef 1978, McDonald 2007, Gemmell et al. 2016

Benthic boundary layer flow and larval attachment

Crisp 1955, Eckman 1996, Harlin & Lindbergh 1977, Jonsson 2005, Koehl 2007

PAGE 10

Turbulence detection by plankton

Fuchs et al. 2015a, Fuchs et al. 2015b, Kiørboe 2011 (review), Koehl & Strickler 1981, Yen 2000 (review)

Turbulence and settlement

Carrillo 2015, Crimaldi et al. 2002, Grassle et al. 1992, Denny & Shibata 1989, Fuchs et al. 2010, Fuchs & DiBacco 2011, Fuchs et al. 2013, Fuchs et al. 2015a, Fuchs et al. 2015b, Hodin et al. 2015, Hubbard & Reidenbach 2015, Koehl et al. 2013, Koehl & Cooper 2015, Manriquez & Castilla 2011, Navarrete et al. 2015, Pernet et al. 2003, Pineda et al. 2010 (review), Mullineaux & Butman 1990, Mullineaux & Butman 1991, Wheeler et al. 2015, Pawlik et al. 1991, Pawlik & Butman 1993, Koehl 2007; but see Naegel et al. 2003

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Coastal Boundary Layer

Csanady 1972, Nickols et al. 2012

Larval retention

Almany et al. 2007, Becker et al. 2007, Brown et al. 2016, Cowen et al. 2006, Drake et al. 2013, Fuchs & DiBacco 2011, López-Duarte & Tankersley 2007, Montoya-Maya et al. 2016, Nickols et al. 2013, Paris & Cowen 2004, Pineda et al. 2010 (review), Poulin et al. 2002, Sammarco & Andrews 1988, Sponagule et al. 2002 (review), Swearer et al. 2002 (review), Teodosio & Garel 2015, Trindade et al. 2016

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"...efficient acquisition of sensory modalities in larvae that are known to occur in adults."

The idea here is that if an adult has the cellular and neurophysiological capacity to respond to a given stimulus, then this capacity already resides in the genome. Therefore, in this case, the evolutionary origin of such a capacity in their larvae would simply be a matter of activating that capacity early in ontogeny. This is thus evolutionarily much more efficient than evolving the genomic capacity *de novo*. See also Marshall & Morgan 2011.

Table 1: Terminology & definitions

The reader will note that definitions of these terms do not always agree in the literature, and in many cases, such definitions differ subtly or not-so-subtly from the definitions that we have provided in Table 1. For example, the Bishop et al. 2006a reference listed below presents more than a dozen different definitions for "metamorphosis" within a single multi-authored publication! Therefore, we here provide an array of references that presents a subset of this definitional diversity, and encourage all writing on these subjects to provide their own definitions (and/or give a citation) whenever using such terms.

Campos et al. 2016, Bishop et al. 2006a, Burke 1980, Capinpin 2015, Dobretsov & Wahl 2008, Hadfield et al. 2001, Highsmith & Emlet 1986, Hodin 2006, Knight-Jones 1951, Lamare and Barker 2001, Manriquez & Castilla 2011, Naegel et al. 2003, Noble et al. 2015, Pineda et al. 2010, Swanson et al. 2007

"Continuous settlement-relocation", evidence: Dobretsov & Wahl 2008, Lane et al. 1985, De Nesnera 2016, Porri et al. 2016

PAGE 14

Figure 2: Sensory systems as filters

Reviews: Warrant 2016, Zimmer & Butman 2000

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Depth sensing in larvae and other plankton

Digby 1977, Forward & Wellins 1989, Knight-Jones & Morgan 1966, Naylor 2006 (review), Sulkin 1984, Young & Chia 1987

Plankton abilities to sense light intensity and gravity

Forward 2009, Miller & Hadfield 1986, Naylor 2006, Queiroga & Blanton 2005, Tankersley et al. 1995

Buoyancy adjustments in larvae and other plankton

Alexander 1990, Bidigare & Biggs 1980, Kahn & Swift 1978, Molloy & Cowling 1999, Power 1989, Sanders & Childress 1988

Diel vertical migration (DVM), Reverse DVM

Transport: Bonicelli et al. 2016, Christy & Morgan 1998, Cohen et al. 2014, Emlet 1986, Forward 2009, Garland et al. 2002, Hoffmann et al. 2012, Koehl et al. 1997 (review), Lloyd et al. 2012, Mariani et al. 2006, Naylor 2006 (review), Sulkin et al. 1980, Trindade et al. 2016
Predator avoidance: Christy & Morgan 1998, Cohen et al. 2014, Forward 2009, Garland et al. 2002, Levinton 2013, Lloyd et al. 2012, Morgan 1990, Ohman 1990
Salinity: Conley & Uye 2014, Sulkin et al. 1980

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Tidal migrations

Christy & Morgan 1998, Naylor 2006 (review), Tankersley et al. 2002

Ontogenetic migrations

Carriker 1951, Gallager et al. 1996, Morgan et al. 2009, Naylor 2006 (review), Paris et al. 2007, Pennington & Emlet 1986, Romero et al. 2012, Tankersley et al. 2002

PAGE 17

Olfaction in planktonic existence

Heuschele & Selander 2014, Kaupp 2010, KiØrboe 2011, Yen 2000

Olfaction in settlement specifically

Reviews: Crisp 1974, Hadfield & Paul 2001, Zimmer & Butman 2000

Molecular mechanisms of olfaction in invertebrates

Leal 2013 (review)

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NO/cGMP

Biggers et al. 2012, Bishop & Brandhorst 2001, Bishop et al. 2001, Bishop et al. 2006b, Bishop et al. 2008, Hens et al. 2006, Romero et al. 2013, Wang et al. 2016, Zhang et al. 2012; but see Ueda & Degnan 2013

Histamine

Hoekstra et al. 2012, Jin et al. 2014a, Jin et al. 2014b, Swanson et al. 2012

Olfaction integration with hydrodynamics

Ellrich & Scrosati 2016, Franco et al. 2016, KiØrboe 2011 (review), Koehl & Strickler 1981, Koehl & Cooper 2015, Pawlik & Butman 1993, Tamburri et al. 1996, Yen 2000 (review)

Dissolved cues yes

Browne & Zimmer 2001, Elbourne & Clare 2010, Ellrich & Scrosati 2016, Ferrier et al. 2016, Hadfield & Koehl 2004, Krug & Manzi 1999, Morello & Yund 2016, Tamburri et al. 1996, Wheeler 2016, Zimmer et al. 2016, Zimmer-Faust & Tamburri 1994; *c.f.* Webster & Cardé 2016

Dissolved cues no

Crimaldi & Koseff 2001, Toth et al. 2015

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Turbulence detection by plankton

Fuchs et al. 2015a, Fuchs et al. 2015b, Kiørboe 2011 (review), Koehl & Strickler 1981, Yen 2000 (review)

Turbulence and settlement

Carrillo 2015, Crimaldi et al. 2002, Grassle et al. 1992, Denny & Shibata 1989, Fuchs et al. 2010, Fuchs & DiBacco 2011, Fuchs et al. 2013, Fuchs et al. 2015a, Fuchs et al. 2015b, Gaylord et al. 2013, Hodin et al. 2015, Hubbard & Reidenbach 2015, Koehl et al. 2013, Koehl & Cooper 2015, Manriquez & Castilla 2011, Navarrete et al. 2015, Pernet et al. 2003, Pineda et al. 2010 (review), Mullineaux & Butman 1990, Mullineaux & Butman 1991, Wheeler et al. 2015, Pawlik et al. 1991, Pawlik & Butman 1993, Koehl 2007; but see Naegel et al. 2003

Temperature

Forward 2009, Kingsford et al. 2002, Young 1995

Salinity

Forward 2009, Hughes 1969, Kingsford et al. 2002, Mann et al. 1991, Tankersley et al. 1995, Young 1995

Touch

Schmidt & Ache 1996 (mechanism in spiny lobster adults)

Sound

Butler 2016, Eggleston et al. 2016, Hinojosa et al. 2016, Jolivet et al. 2016, Kaplan & Mooney 2016, Lillis et al. 2016, Pine et al. 2012, Rossi et al. 2015, Rossi et al. 2016

PAGE 20

Hierarchical arrangement of cues

Franco et al. 2016, Fuchs et al. 2010, Von der Meden et al. 2015, Morgan & Christy 1994, Welch & Forward 2001, Woodson et al. 2007, Zimmer et al. 2009; *c.f.* Webster & Cardé 2016; but see Morello & Yund 2016

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Figure 3: Cross-scale perspective on plankton, sensory systems and settlement

Kingsford et al. 2002, Prairie et al. 2012, Zimmer & Butman 2000

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Apical organs and neuronal concentrations in larvae

Byrne et al. 2007, Marlow et al. 2014, Voronezhskaya et al. 2004

Neurophysiology on larvae

Barlow 1990, Braubach et al. 2006, Burke 1983, Satterlie and Cameron 1985

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Larval supply

Barbosa et al. 2016, Hoffmann et al. 2012, Hurlbut 1992, Keough 1989, Mandal et al. 2010, Ross 2001, Hughes et al. 2000, Witman et al. 2010

Upwelling-Relaxation Hypothesis

Connolly & Roughgarden 1999, Connolly et al. 2001, Dudas et al. 2009, Epifanio & Garvine 2001, Garland et al. 2002, Mazzuco et al. 2015, Menge et al. 2004, Menge et al. 2015, Miller & Emlet 1997, Roughgarden et al. 1988, Roughgarden et al. 1991, Pfaff et al. 2015, Shanks et al. 2014, Wing et al. 1995, Wing et al. 2003, Witman et al. 2010

Active nearshore retention

Almany et al. 2007, Becker et al. 2007, Brown et al. 2016, Cowen et al. 2006, Drake et al. 2013, López-Duarte & Tankersley 2007, Montoya-Maya et al. 2016, Morgan et al. 2009, Nickols et al. 2013, Paris & Cowen 2004, Poulin et al. 2002, Sammarco & Andrews 1988, Sponagule et al. 2002, Teodosio & Garel 2015, Trindade et al. 2016

Passive nearshore retention

Epifanio & Garvine 2001, Hill et al. 1996, Queiroga & Blanton 2005, Shulzitski et al. 2016, Trindade et al. 2016, Teske et al. 2016

Larvae not retained close to shore

Becker et al. 2007, Doherty 1983, Hadfield & Koehl 2004, Jackson & Strathmann 1981, Pennington & Emlet 1986, Richmond 1987, Scheltema 1971, Williams et al. 1984, Wood et al. 2016, Young et al. 2012

Fronts, eddies, flotsam as phenomena that concentrate larvae

Jarvis 2014, Manriquez & Castilla 2011, Shanks 1983, Zimmer et al. 2012

Surf zone as semi-permeable barrier

Morgan et al. 2016, Nickols et al. 2013, Pfaff et al. 2015, Shanks et al. 2010, 2016

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Oceanographic circulation models

e.g.: Mitarai et al. 2009, Sundelof & Jonsson 2012

Larval supply as dictator of settlement/recruitment patterns

Barbosa et al. 2016, Hoffmann et al. 2012, Hurlbut 1992, Keough 1989, Mandal et al. 2010, Ross 2001, Hughes et al. 2000, Witman et al. 2010

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Pre-settlement processes as determinants of settlement/recruitment

Bierne et al. 2003, Gorospe & Karl 2015, Hunt & Scheibling 1996, Jenkins 2005, Pineda et al. 2010 (review)

Post-settlement processes as determinants of settlement/recruitment

Bohn et al. 2013a, Bohn et al. 2013b, Dalby & Young 1992, Franzitta et al. 2016, Gorospe & Karl 2015, Guy-Haim et al. 2015, Jones & Ricciardi 2014, Nasrolahi et al. 2013, Nickols et al. 2013, Palma et al. 2006, Shanks 2009, Tomanek & Somero 2000

Ekman Transport

Ekman 1905, Massel 1999

Upwelling-relaxation hypothesis, and evidence for

Connolly & Roughgarden 1999, Connolly et al. 2001, Dudas et al. 2009, Epifanio & Garvine 2001, Garland et al. 2002, Mazzuco et al. 2015, Menge et al. 2004, Menge et al. 2015, Miller & Emlet 1997, Roughgarden et al. 1988, Roughgarden et al. 1991, Pfaff et al. 2015, Shanks et al. 2014, Wing et al. 1995, Wing et al. 2003, Witman et al. 2010

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Evidence against

Almany et al. 2007, Becker et al. 2007, Brown et al. 2016, Cowen et al. 2006, Drake et al. 2013, Epifanio & Garvine 2001, Hill et al. 1996, López-Duarte & Tankersley 2007, Montoya-Maya et al. 2016, Morgan et al. 2009, Nickols et al. 2013, Paris & Cowen 2004, Poulin et al. 2002, Queiroga & Blanton 2005, Sammarco & Andrews 1988, Shulzitski et al. 2016, Sponagule et al. 2002, Teodosio & Garel 2015, Trindade et al. 2016, Teske et al. 2016

Other mechanisms of onshore transport (e.g., internal tides, fronts, wave-driven flows, flocs, flotsam, surface slicks)

Jarvis 2014, Manriquez & Castilla 2011, Metaxas 2001, Pfaff et al. 2015, Rasmuson & Shanks 2014, Shanks 1983, Shanks 1995, Shanks & McCulloch 2003, Shanks & Wright 1987, Shanks et al. 2014, Valencia-Gasti & Ladah 2016, Vargas et al. 2004, Wilderbuer et al. 2016, Zimmer et al. 2012; but see Queiroga & Blanton 2005

Different species, different transport mechanisms

e.g.: Bonicelli et al. 2016, Shanks et al. 2014, South 2016

Larval retention

Almany et al. 2007, Becker et al. 2007, Brown et al. 2016, Cowen et al. 2006, Drake et al. 2013, Epifanio & Garvine 2001, Hill et al. 1996, López-Duarte & Tankersley 2007, Montoya-Maya et al. 2016, Morgan et al. 2009, Nickols et al. 2013, Paris & Cowen 2004, Poulin et al. 2002, Queiroga & Blanton 2005, Sammarco & Andrews 1988, Shulzitski et al. 2016, Sponagule et al. 2002, Teodosio & Garel 2015, Trindade et al. 2016, Teske et al. 2016

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Episodic appearance of larvae in plankton

e.g.: Reitzel et al. 2004, Dayton et al. 2016

"Sweepstakes Reproductive Success" (SRS) hypothesis, evidence

Note, we are here including several papers that do not directly address the SRS hypothesis, but that provide evidence for multiple mechanisms of onshore transport, which would seem consistent with the scenario envisioned in the SRS hypothesis, as argued in the text.

Dayton et al. 2016, Hedgecock 1994, Knights et al. 2012, Lloyd et al. 2012, Menge et al. 2015, Moberg & Burton 2000, Pfaff et al. 2015, Pineda et al. 2010, Sammarco 1991, van Montfrans et al. 1990, Wing et al. 2003, Watts et al. 1990

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Sounds and settlement

Butler 2016, Eggleston et al. 2016, Hinojosa et al. 2016, Jolivet et al. 2016, Kaplan & Mooney 2016, Lillis et al. 2016, Pine et al. 2012, Rossi et al. 2015, Rossi et al. 2016

"Meso scale" olfactory cues

Note that the scale of these cues has not been explicitly studied in most of these cases.

Gerlach et al. 2007, Dixson et al. 2008, Dixson et al. 2011, Trapido-Rosenthal & Morse 1985

Turbulence and settlement

Carrillo 2015, Crimaldi et al. 2002, Grassle et al. 1992, Denny & Shibata 1989, Fuchs et al. 2010, Fuchs & DiBacco 2011, Fuchs et al. 2013, Fuchs et al. 2015a, Fuchs et al. 2015b, Hubbard & Reidenbach 2015, Koehl et al. 2013, Koehl & Cooper 2015, Manriquez & Castilla 2011, Navarrete et al. 2015, Pernet et al. 2003, Pineda et al. 2010 (review), Mullineaux & Butman 1990, Mullineaux & Butman 1991, Wheeler et al. 2015, Pawlik et al. 1991, Pawlik & Butman 1993, Koehl 2007; but see Naegel et al. 2003

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Turbulence and larval behaviors that may enhance settlement prospects

Fuchs et al. 2010, Fuchs & DiBacco 2011, Fuchs et al. 2013, Fuchs et al. 2015a, Fuchs et al. 2015b, Kiørboe 2011 (review), Koehl & Strickler 1981, Pawlik 1992, Yen 2000 (review); but see Welch et al. 1999, Wheeler et al. 2013

PAGE 30

Flow in benthic boundary layer, and settlement of larvae

Crisp 1955, Eckman 1990, Eckman 1996, Franco et al. 2016, Gambi et al. 1990, Gaylord et al. 2002, Harlin & Lindbergh 1977, Jonsson 2005, Koehl 2007, Koehl & Cooper 2015, Larsson et al. 2016, Leonard et al. 1998, Mullineaux & Butman 1990, ç lafsson et al. 1994, Quinn & Ackermann 2014, Reidenbach et al. 2009, Walters et al. 1997, Zimmer & Butman 2000

Temperature as local cue

Forward 2009, Kingsford et al. 2002, Young 1995

Salinity as local cue

Forward 2009, Hughes 1969, Kingsford et al. 2002, Mann et al. 1991, Tankersley et al. 1995, Young 1995

Local scale olfactory cue evidence

e.g.: Browne & Zimmer 2001, Dixson et al. 2008, Dixson et al. 2011, Knight-Jones 1953, Toonen 2005, Toonen & Pawlik 1994, Toonen & Pawlik 2001, Trapido-Rosenthal & Morse 1985

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Settlement impacts of acidification

The specific hypothesis mentioned in this section (that larvae might use diurnal shifts in pH as a proxy for the nearshore environment, and thus such treatments might increase settlement rates in nearshore taxa) has not to our knowledge been addressed. However, there have been several studies that have examined the settlement of larvae under various ocean acidification scenarios. For example:

Crim et al. 2011, Doropolous et al. 2012, Uthicke et al. 2013

Temperature fluctuations and settlement

Saunders & Metaxas 2007, Vargas et al. 2004

Odor dispersion and plumes

Ellrich & Scrosati 2016, Franco et al. 2016, Koehl & Cooper 2015, Pawlik & Butman 1993, Zimmer & Butman 2000

Biofilms

Hadfield et al. 2014, Shikuma et al. 2014, Whalan & Webster 2014

PAGE 32

Settlement deterrants

Abelson & Denny 1997, Abelson et al. 1994, Butman & Grassle 1992, Jonsson et al. 2004, Krug 2006, Larsson & Jonsson 2006, Morello & Yund 2016, Mullineaux & Butman 1991, Pawlik 1992, Turner et al. 1994, Young 1995

Microtopography

Crisp & Barnes 1954, Crisp & Ryland 1960, Koehl 2007, Le Tourneux & Bourget 1988

Light as local cue/deterrant

Baird et al. 2003, Queiroga & Blanton 2005, Webster et al. 2015

Fluid shear as local cue/deterrant

Crimaldi et al. 2002, Crisp 1955, Eckman 1990, Eckman 1996, Franco et al. 2016, Gambi et al. 1990, Gaylord et al. 2002, Harlin & Lindbergh 1977, Jonsson 2005, Koehl 2007, Koehl & Cooper 2015, Larsson et al. 2016, Leonard et al. 1998, Mullineaux & Butman 1990, ç lafsson et al. 1994, Palardy and Witman 2011, Quinn & Ackermann 2014, Walters et al. 1997, Zimmer & Butman 2000

Settlement cues as indicators of suitable adult habitat

Perhaps first proposed explicitly by Crisp 1974.

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Recreating oceanic flow conditions in laboratory

Review: Zimmer & Butman 2000

Imaging techniques for organisms in flow

Fuchs et al. 2015a, Fuchs et al. 2015b, Neu & Genin 2014, Wheeler et al. 2016

Marine protected area design and larvae

Brown et al. 2016, Shulzitski et al. 2016

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