

I Feel That! Fluid Dynamics and Sensory Aspects of Larval Settlement Across Scales

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13.1 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 (see Online Supplementary Material).

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 ($<1 \text{ cm}\cdot\text{sec}^{-1}$ or far less; Chia et al., 1984; Fuchs and Gerbi, 2016) are too slow to make headway in strong oceanic currents (10s of $\text{cm}\cdot\text{sec}^{-1}$) or within wave-driven flows ($\text{meters}\cdot\text{sec}^{-1}$), 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 following:

- the fluid environment that larvae experience in the pelagic and benthic realms;

- what larva 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.

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* (McEdward, 1995), 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.

13.2 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):

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

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 (millimeters or less) to oceanic (1000s of kilometers), whereby two organisms with the same Re can be thought of as experiencing a similar fluid dynamic environment.

Because the 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 vs. ~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 more 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 ~10⁶) 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 (Figure 13.1). 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

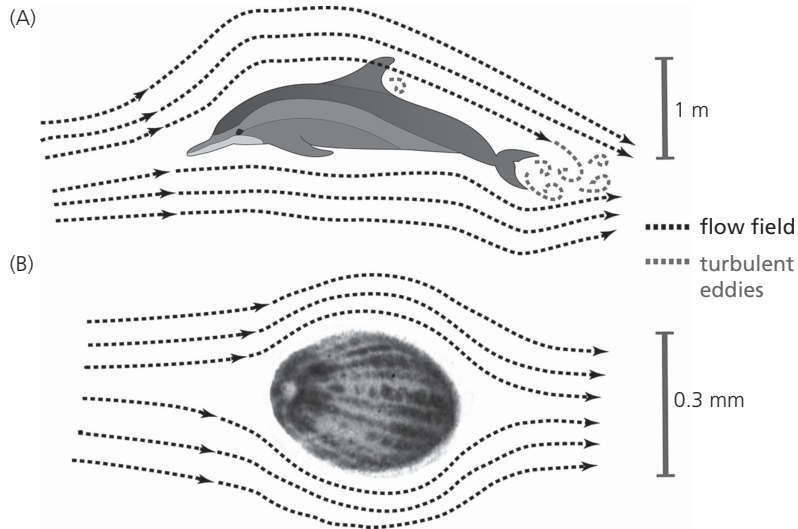


Figure 13.1 Turbulent and laminar flow at different Reynolds numbers (Re). As discussed in the text, a bottlenose dolphin (A) and a coral planula larva (B) in the same habitat experience very different flow regimes, due to their vastly different sizes and corresponding Re . (A) At high Re , flow (dashed black lines) even around a streamlined organism like a dolphin is broken up by turbulent eddies (dashed gray 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. (see Plate 13)

compared to what is seen in lower Re conditions (see, e.g., Koehl, 1995; McHenry et al., 2003).

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 vs. 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 and

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 and Jumars, 1984).

Given these 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, molluscs, 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 (Mullineaux and Butman 1991, Crimaldi et al., 2002).

A third implication for our larva of the predominantly laminar flow that moves past its body (Figure 13.1) 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 earlier, 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 earlier, 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 and 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 and Gerbi, 2016). This ability would have profound implications for larvae settling into nearshore locations, and we will return to this point in some detail later.

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 alongshore (“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.

13.2.1 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 and Cohen, 2016; Fuchs and 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 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 13.1 for definitions of terms).

Planktonic animals in general—and larvae specifically—have been shown to have the ability

Table 13.1 Metamorphosis, Attachment, Settlement, Recruitment and “Continuous Settlement”.

| Term | Definition |
|----------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Metamorphosis | 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 | 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; Richmond 1985). The notion that metamorphosis is distinct from settlement is exemplified by crabs, whose metamorphosis occurs between the zoeal and megalopal stages, before settlement occurs. |
| Attachment | 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 | 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 larva 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 | A term proposed by Navarrete et al., (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.

to detect a wide range of environmental stimuli (Figure 13.2). The majority of this evidence comes from crustaceans (reviewed by Yen, 2000; Epifanio and 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.

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

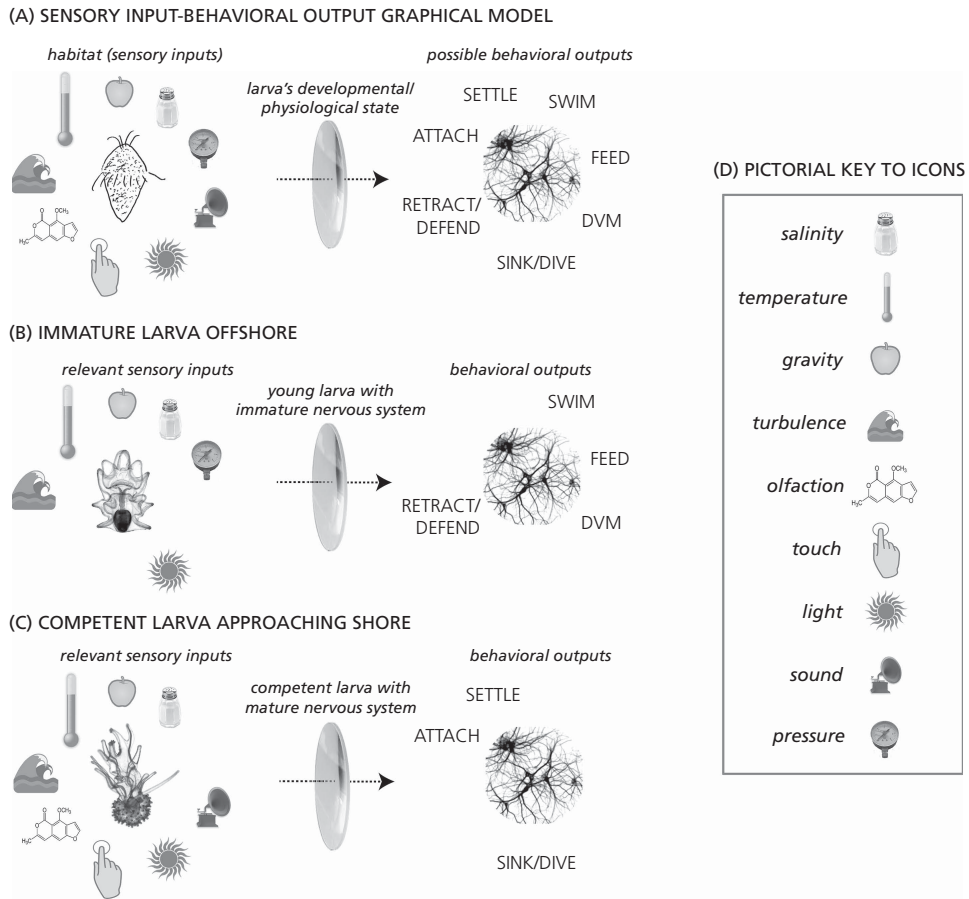


Figure 13.2 Graphical model of multisensory inputs and behavioral outputs as they relate to settlement. Here we consider only those sensory modalities and larval behaviors that have direct relevance to settlement itself, or that increase the likelihood that larvae get retained near or carried to suitable 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 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 seafloor, 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.

sinking, stable, or rising by monitoring light intensity, pressure, and their acceleration relative to gravity vectors over time (Figure 13.2). Although there is widespread behavioral evidence for these sensory capabilities across phyla, direct physiological and morphological evidence is more limited (Kingsford et al., 2002; Epifanio and 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 toward the shore, and hence potentially carry larvae there (reviewed in Queiroga and 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 DVM, but could simultaneously expose larvae to visual predators and potentially wind-driven offshore flows (Ohman et al., 1983, Pennington and 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 and 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 (reviewed in Queiroga and 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 thought to be an adaptation for approaching potential settlement habitat (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 and Emlet, 1986). If so, we would argue that this is likely an example of an exaptation (in the sense of Gould and Vrba, 1982; often, but less precisely, called “co-option”): 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 (Figure 13.2). 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 and 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 traditionally been defined (see Table 13.1; 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 precompetent larvae. This is sensible, given that de-repressing (or “unmasking”; 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 and 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 and 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 (Zimmer and Butman, 2000; Woodson et al., 2007). 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 see, e.g., 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. 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 and 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 a 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 centimeters to kilometers.

A third class of sensory modalities that larvae could use to aid 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 13.1; Figure 13.2). 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 later. 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 (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 and Gerbi, 2016).

Additional sensory capabilities of larvae that could aid their progression toward settlement are the abilities to detect and monitor sound, touch, temperature, and salinity (Figure 13.2). Response to temperature (e.g., via transient receptor potential 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) vs. downwelling (warmer, lower salinity) flows, as we will discuss briefly later. 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 (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 (Figure 13.3). For example, salinity, turbulence, and sound cues could operate at a broader "habitat" scale of meters to

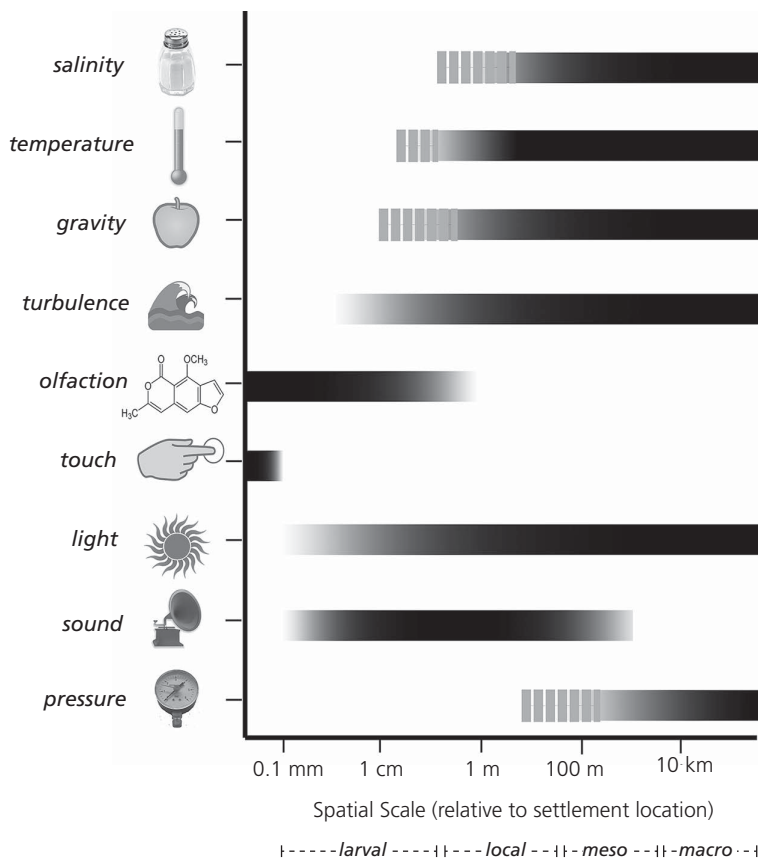


Figure 13.3 Relevant scales of sensory input for settlement. As in Figure 13.2, we focus on those sensory modalities that larvae might use to identify suitable settlement locations or that might trigger behaviors that would increase the likelihood that they are retained near or carried to such sites. 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. Grayscale 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.

kilometers, dissolved chemical cues and turbulent flows over rough surfaces at millimeters to centimeters, and mechanosensory cues like surface topography on sub-millimeter scales (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.

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 earlier (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 (Hadfield, 2011; Bishop and 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 (Song et al., 2016; Williams and Carrier, this volume). Furthermore, targeted gene manipulation methods have begun to be applied to metamorphic stages of marine larvae as well (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.

13.3 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 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 (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 Reynolds (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.

13.3.1 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 and Reynolds, 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 (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 timescale. 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 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 13.1 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 and Reynolds, 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 just outlined could simply be due to differing sampling methodologies and intervals (Pineda et al., 2010; Pineda and Reynolds, 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 earlier), 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 previously referenced; see Pineda et al., 2010; Pineda and Reynolds, 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 the 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 earlier. 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.

13.3.2 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” (Figure 13.3). 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 and Shibata, 1989), or at least arriving nearby.

13.3.3 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 ($>1 \text{ mm} \cdot \text{sec}^{-1}$) sinking or downward swimming of larvae can enhance this effect (Figure 13.3).

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 and 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 and Cohen, 2016; Figure 13.3). 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 and 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).

13.3.4 The Larval Scale: <1 Millimeter–A Few Centimeters

This is the spatial scale over which a larva experiences its environment on short timescales (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 (Figure 13.3).

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 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 (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.

13.4 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 and Reynolds, this volume). Barcoding methods will soon make it possible to obtain rapid information on plankton assemblages that previously required painstaking manual sorting (see Marko and 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 and 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, and 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.

13.5 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 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 toward 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; 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 longstanding, 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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