

Review

Perspectives on Larval Behaviour in Biophysical Modelling of Larval Dispersal in Marine, Demersal Fishes

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Abstract: Biophysical dispersal models for marine fish larvae are widely used by marine ecologists and managers of fisheries and marine protected areas to predict movement of larval fishes during their pelagic larval duration (PLD). Over the past 25 years, it has become obvious that behaviour—primarily vertical positioning, horizontal swimming and orientation—of larvae during their PLD can strongly influence dispersal outcomes. Yet, most published models do not include even one of these behaviours, and only a tiny fraction include all three. Furthermore, there is no clarity on how behaviours should be incorporated into models, nor on how to obtain the quantitative, empirical data needed to parameterize models. The PLD is a period of morphological, physiological and behavioural change, which presents challenges for modelling. The present paper aims to encourage the inclusion of larval behaviour in biophysical dispersal models for larvae of marine demersal fishes by providing practical suggestions, advice and insights about obtaining and incorporating behaviour of larval fishes into such models based on experience. Key issues are features of different behavioural metrics, incorporation of ontogenetic, temporal, spatial and among-individual variation, and model validation. Research on behaviour of larvae of study species should be part of any modelling effort.

Keywords: dispersal; larva; marine fish; behaviour; biophysical model; swimming; orientation; vertical distribution; mortality; pelagic egg; pelagic larval duration



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1. Introduction

The large majority of demersal, marine teleost fish species, regardless of adult habitat or latitude, have a pelagic larval phase that is subject to dispersal by currents and biological processes [1,2]. We now know that the larvae of many marine teleost fishes possess behavioural and sensory abilities capable of influencing their dispersal trajectories during a major portion of their pelagic larval duration (PLD, defined herein as the time from hatching to settlement [3,4]). Several studies have shown that realistic behaviours included in models will result in dispersal outcomes that differ from assuming larvae behave as passive particles (e.g., [5–7], Figure 1). It can no longer be a justifiable simplifying assumption to ignore such abilities when attempting to model dispersal. However, a recent review of biophysical larval dispersal modelling [8] (across all marine taxa, not just fish) showed that a majority of models (56%) assumed that larvae were passive throughout their PLD, with 41% assuming some form of active behaviour for all or part of the PLD. Surprisingly, the likelihood of published marine larval dispersal models assuming passive larvae increased marginally over the period 1980–2017 [8]. Many published models continue to make the simplifying assumption of passive dispersal without justification or try to justify doing so by pleading the lack of data on the behaviour of the species being modelled (e.g., [9], p. 3). It is certainly possible that larvae of some fish species may behave in a way approximating passive particles, but this must now be demonstrated, not simply assumed.

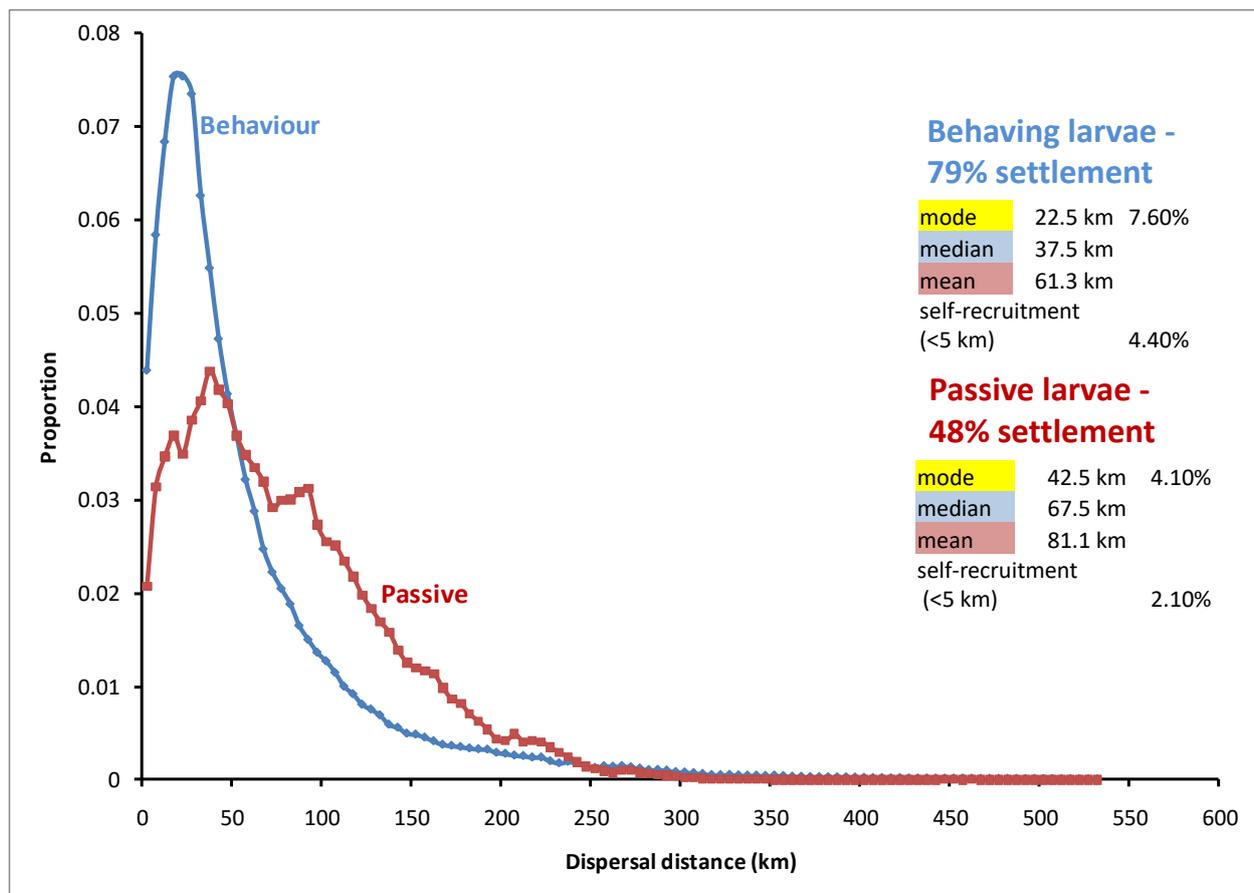


Figure 1. Dispersal kernels comparing passive larvae to larvae with behaviour (vertical positioning, swimming and orientation). These were modelled for a serranid grouper on the Great Barrier Reef for a full spawning season using a validated biophysical dispersal model (*GBR-Larvo*, [10,11]). Note differences between kernels in percentages of propagules that settled at all, and that settled within 5 km of natal reef as well as differences in mode, median and mean dispersal distance.

Calls for “a deep integration of oceanography and behavioural ecology” (e.g., [12]) in dispersal modelling are not uncommon. In spite of this, what Swearer et al. [8] call the “exemplary manual of recommended practices for biophysical modelling by North et al. (2009)” which includes explicit advice about incorporating behaviour of larvae has been cited only 76 times between 2009 and 2017, whereas the number of publications over the same period that used biophysical dispersal models was more than 700 [8]. Citations per year of North et al. [13] increased to a high of 16 in 2015, but averaged only 8.5 per year since then. This is in spite of the ready, free availability of the work of North et al. [13]. ([http://www.ices.dk/sites/pub/Publication%20Reports/Cooperative%20Research%20Report%20\(CRR\)/CRR29.pdf](http://www.ices.dk/sites/pub/Publication%20Reports/Cooperative%20Research%20Report%20(CRR)/CRR29.pdf)). Expectations that behaviour would become an integral input to dispersal modelling have not been realized.

The goal of the present paper is to encourage the inclusion of larval behaviour in biophysical dispersal models by providing practical advice and insights about obtaining and incorporating behaviour of larval fishes in an ontogenetic framework into such models. This paper focuses on larval dispersal of marine, demersal fishes—that is species with a demersal juvenile and adult life-history stage and that settle to or in association with bottom habitat after a period in the pelagic environment—although much of what is contained may also be relevant to fishes from other marine habitats. In many demersal fish species, dispersal following the larval life history stage is minimal, and dispersal is primarily during the PLD. Dispersal can take place throughout the life cycle of pelagic species, and as settlement does not take place, larval dispersal in pelagic species is not necessarily the primary mode of dispersal.

This paper is based on experience gained in studying the remarkable behavioural and sensory abilities of fish larvae, and the incorporation of these into a biophysical dispersal model for the Great Barrier Reef of Australia [10,11]. This effort has benefited from direct interactions with many excellent researchers, and from publications by them and many others, but particularly [13,14]. As my experience is limited to warm temperate and tropical systems and taxa, the present paper includes an undeniable bias, which is augmented by the very limited published work on the behaviour of larvae of colder water, demersal species. This paper does not attempt to be a complete review of all the behaviours of larvae that could be included in a dispersal model. Rather, it is an attempt to discuss the most relevant behaviours, and how to obtain data on them (with examples), and to provide suggestions on how to incorporate the behaviours into a dispersal model. Similarly, although a number of aspects of adult behaviour are needed for realistic dispersal modelling—most particularly, the time and place of spawning—these are not considered here. The physical oceanographic side of the modelling is outside the scope of this paper.

The process and implications of settlement and of post-settlement processes (mortality, movement, etc.) are also outside the ambit of this paper. In fact, few larval dispersal models for demersal fishes actually do include these things. Rather, dispersal models typically predict the movement of dispersing propagules only to the implied settlement site, however settlement habitat is defined for the purposes of the model. The reason for this is because we really know little about the process of settlement in marine fishes other than it is an abrupt period of transition between two very different environments—pelagic and demersal—with very different requirements for survival. To be successful, the settling larva must be able to very quickly make the transition to an environment it has not experienced. Mortality is expected to be very high during this transition, which involves behavioural and morphological alterations in the larva of varying degrees. To further complicate matters, a percentage of larvae of at least four families (Chaetodontidae, Lutjanidae, Pomacentridae, Serranidae) approaching coral-reef habitat from the pelagic environment may abandon attempts to settle, and swim back out to sea [15–18]. This is seemingly due to the presence of predators, or aggressive residents or inability to find acceptable settlement microhabitat [15–18], and the larvae presumably swim off to settle somewhere else. This behaviour has been found whenever appropriate observations have been made. For these reasons, a candid modeller will provide the reader with a caveat to model predictions indicating that their dispersal model does not actually predict settlement or recruitment. Rather, more likely, the model will have made the implicit assumption that settlement and post-settlement processes have spatially and temporally uniform or random effects on the model's predictions.

2. Pelagic Eggs

Relatively little attention is paid by many modellers to the attributes of the pelagic eggs which occur in the majority of marine fish families (but see [19]). Although eggs do not 'behave' in the usual sense of the word, they are usually slightly buoyant in sea water, and should be modelled as such, because if they are not, they will, by default, be considered neutrally buoyant. Pelagic eggs have a relatively short incubation time, particularly in warmer waters, compared to the PLD, so why is this relevant to dispersal? This is because eggs constitute the ontogenetic stage at the very start of development and dispersal, and until they hatch, no true behaviours on the part of the propagule exist. Buoyant eggs float upward in the water column from the depth at which they were spawned, which is rather close to the surface for many species that spawn in aggregations. Near surface waters are much more influenced by winds, and will move downwind, taking otherwise passive eggs along. Turbulence, including that induced by wind, tends to homogenize the vertical distribution of the eggs, but this effect does not extend very deep. All this means that buoyant fish eggs will tend to move downwind in surface waters, away from where they were spawned. In contrast, neutrally buoyant eggs, a large proportion of which will

be distributed deeper than the wind-influenced surface waters, will, on average, tend to remain closer to their spawning location.

In developing the *GBR-Larvo* dispersal model for the Great Barrier Reef [10], egg buoyancy was initially ignored—in this case, the eggs were about 1 mm diameter, and hatched in about 24 h. Therefore, in the model they spread by turbulence and diffusion from their spawning depth through the water column, and the test runs predicted high levels of self-recruitment (Figure 2A). With egg buoyancy included in the model, self-recruitment decreased (Figure 2B) to a level more in line with field estimates (e.g., [20]). Egg buoyancy is the result of an interaction between the specific gravity of the egg and the density of the water in which the egg floats, so an egg that is buoyant in oceanic waters may not be in lower salinity coastal or estuarine waters.

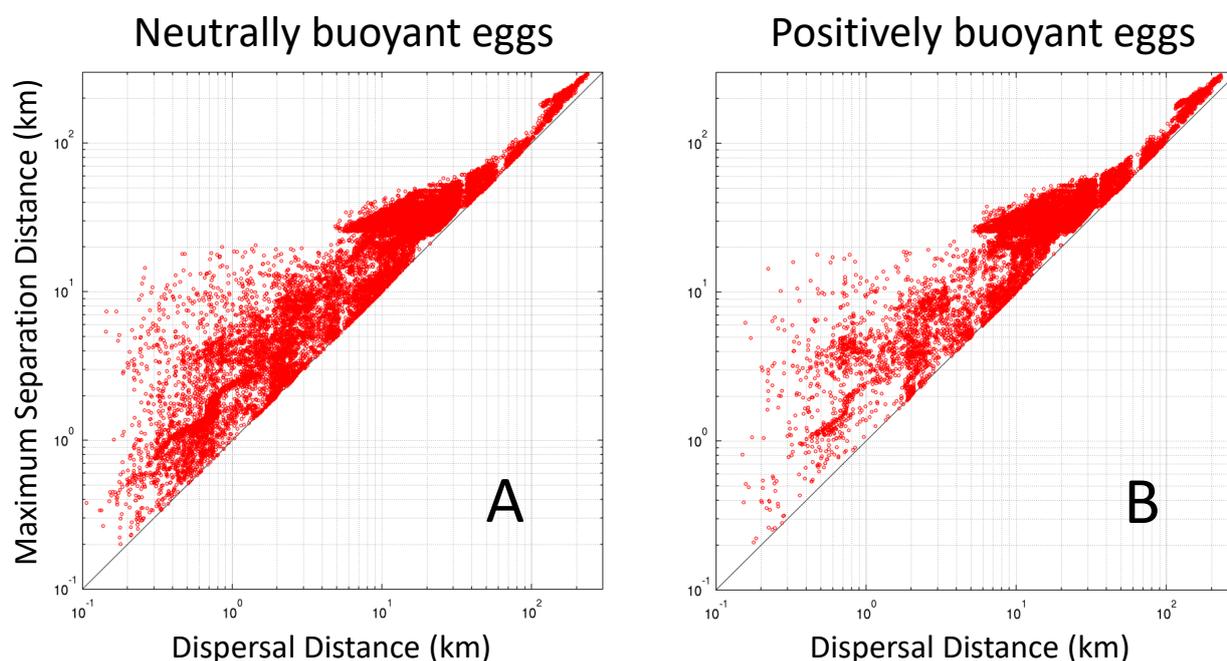


Figure 2. The effect of buoyancy of pelagic eggs on dispersal as shown by the use of *GBR-Larvo*, a validated biophysical larval dispersal model ([10,11]), for a serranid grouper species spawning in a no-take zone of the Great Barrier Reef Marine Park. The figures show the maximum distance (separation distance) from the spawning site attained by larvae during the pelagic larval duration (PLD) plotted against the straight line distance from the spawning site to the settlement location (note that some larvae settle closer to their natal site than their maximum separation distance although the model does not include explicit homing). (A) Predictions from a model run with eggs of neutral density. Note the high density of points at the lower left, indicating shorter dispersal distances, including self-recruitment. (B) Predictions from a model run with buoyant eggs. In this case, settlement near the spawning site was reduced, resulting in an overall increase in mean dispersal distance. Moreover, the proportion of propagules that settled at all or into the no-take zone decreased.

Buoyancy during egg incubation can vary ontogenetically (e.g., [21,22]), although data on this are limited. Such variation will have the most impact on dispersal of species with long incubation times, which are typically those in colder waters. However, some wild Hawaiian marine eel eggs reared in the laboratory had incubation times of 10 to 14 days and sank to the bottom of the rearing container on about the 4th day, indicating an increase in specific gravity, and still survived to hatch [23]. We do not know how widespread such changes in density of pelagic eggs are among other fish taxa, or what depth the eggs might occupy as a result, because the latter depends on the density structure of the water column. An example of how egg buoyancy can influence dispersal is [24]. Laboratory measurement of pelagic egg specific gravity is relatively straightforward [19], but egg buoyancy cannot be determined exactly unless sea-water density is known, and the latter is largely a function of

temperature and salinity [19]. In the absence of egg buoyancy data on a species of interest, the paper by Sundby and Kristiansen [19] can be very useful.

Of course, none of the above applies to species that have brooded or demersal eggs, or are live bearers [1]. In such species, dispersal of eggs is not an issue. Furthermore, as the resulting larvae may be larger and more developed at hatching than those from pelagic eggs, the truly passive phase of the PLD will be shorter, or even lacking, and the PLD may be shorter [2,25]. All of this will influence dispersal.

The PLD is most often based on counts of daily rings in otoliths, and for modelling, the PLD is often based on literature values. However, the initiation of increment formation varies among taxa: it may take place before hatching, at hatching, or at the time of yolk absorption and the start of feeding [26]. Many researchers are of the view that otolith daily rings do not form until after hatching (e.g., [27,28]), although frequently, published reports of PLD based on otolith counts do not state what assumptions or tests were made about initiation of increment formation (e.g., [25,29]). Moreover, as PLD is the pelagic *larval* duration, entomologically, it should exclude the egg period. These issues must be taken into account when determining the run time of the model. A range of PLD values will be found in most cases if the PLD has been estimated in sufficient numbers of individuals. This range can be used to determine the range of model run times and also the range of the period of settlement competence.

3. Behaviours of Larvae

The primary behaviours of larvae that could influence dispersal are vertical distribution, horizontal swimming performance, and orientation. To this should be added settlement competency, although strictly speaking, it is not a behaviour, but an ontogenetic developmental milestone. Only 6.5% of larval-fish dispersal models (and 5% of models overall) published between 1980 and 2017 reviewed by [8] included horizontal swimming by larvae. The review of [8] did not explicitly address the use of swimming orientation in dispersal models except in the context of detecting and orientating toward settlement habitat, and only 5% of all models included this behaviour. Over half (53%) of marine larval dispersal models reviewed by [8] did not include any behavioural control over vertical distribution. Of the others, 18% assumed a fixed vertical distribution throughout the PLD whereas 26% modelled vertical distribution that changed with age, stage, size or environment. So, it is clear that the inclusion of larvae behaviour of any sort in dispersal models is not the norm, and the inclusion of the full suite of possibly relevant behaviours is very rare, indeed. It could be argued that feeding behaviour and predator avoidance by larvae should also be included in dispersal modelling, but for the purposes of the present paper these are considered to be subsumed within mortality.

The fact that the PLD is also a time of morphological, behavioural and sensory development complicates attempts to model it. To put it differently, the PLD is dominated by ontogenetic changes. This means that the behavioural capabilities of a newly-hatched larval fish will almost certainly differ from that of the same larva when half-way through the PLD, and when nearing its end [30,31]. This requires that all types of behaviour are viewed, studied and modelled in an ontogenetic context (Figure 3). Ontogenetic changes in behaviour may be gradual (e.g., increases in hearing sensitivity e.g., [32]), or abrupt (e.g., orientation at the time of settlement competency e.g., [18]). Usually, these will be associated with morphological change, although some (e.g., fin development and swimming ability) may be more obvious than others (e.g., otic capsule development and hearing sensitivity). Empirical data on the ontogeny of behaviours relevant to dispersal (primarily swimming performance, orientation ability, sensory ability, and vertical distribution [7,14,31,33]) are required so they can be incorporated into the model.

Dispersal Period

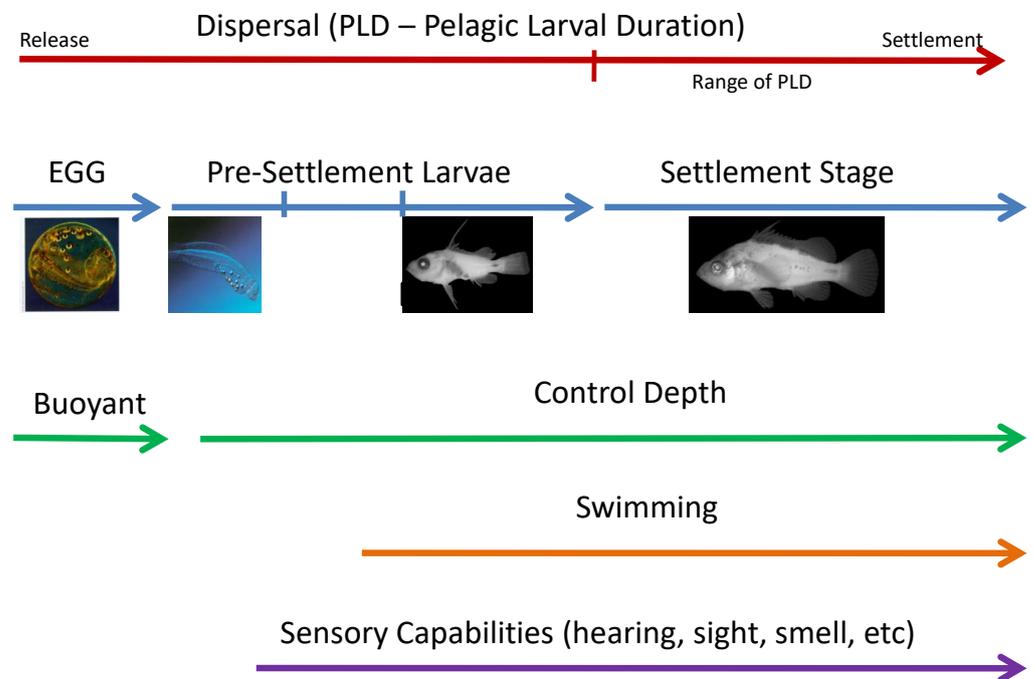


Figure 3. A visual representation of the ontogeny of morphology and behaviours relevant to dispersal in a hypothetical demersal fish. Swimming becomes important about the time the caudal fin forms, as indicated by the vertical ticks in the blue line. In each case the abilities of the larva increase, and how the behaviours are used often changes. For example, a pre-settlement stage larva may use a location independent cue for orientation, whereas a settlement stage larva may use location dependent cues.

It is important that a dispersal model includes variation in behaviours to ensure the model's dispersal predictions are not unrealistically constrained. This includes within-individual variation (e.g., standard error of an individual larva's mean swimming speed), among-individual variation (e.g., the full range of individual mean swimming speeds), diel and other temporal variation (e.g., difference between day-time and night-time swimming speed), spatial variation (e.g., different swimming speeds in different locations), ontogenetic variation (e.g., different swimming speeds at different stages of development), temperature-related variation (e.g., different swimming speed at different water temperatures) and other variation (e.g., swimming speeds that differ with swimming direction).

The general pattern is for performance to increase with the size of the larvae, and it is frequently found that size (usually expressed as length) is a better predictor of swimming performance than is age [30,34]. However, the majority of research on ontogeny of behaviour in marine fish larvae is done with reared larvae, and laboratory reared larvae often have a wider range of growth rates than do wild larvae, and often longer PLDs [35,36], even if the size at settlement is the same both in the lab and in the wild. This means that laboratory speed vs. age relationships may not accurately represent speed vs. age relationships of wild larvae. This presents a problem for dispersal modelling because one really wants ontogeny expressed as performance as a function of days since hatch. When empirical size-based relationships are used in modelling, they must be converted to age-based relationships in some manner, which requires assumptions about which there should be clarity in model documentation. A solution is to use PLD data for wild larvae,

and a size vs. age growth model over the PLD period to convert size to age in the wild for parameterizing models.

At some stage, a larva will become developmentally and behaviourally capable of leaving its pelagic environment and taking up a demersal existence, and evidence from otolith studies indicates that there is only a relatively limited window of opportunity during which this can take place, although this varies among species (e.g., labrids typically have more within-species variability in PLD, and hence window of opportunity, than pomacentrids—see collated PLD values in [27–29]). There is relatively little information on how much the width of this window depends on external factors (e.g., temperature, food availability, existence of sensory cues emanating from settlement habitat) or on internal factors (e.g., population characteristics, age, previous growth rates, current nutritional state), and in the absence of such information, the default approach can be to use the range of reported PLD values for the species or a close relative in the region of interest. During this settlement stage, the behaviour of a larva is likely to differ from that earlier in the PLD [33,37]. For example, orientation might change from swimming in a particular direction (e.g., to the west) or using a celestial cue (e.g., sun angle) to swimming toward the source of a particular habitat-specific cue (e.g., reef sounds). Some examples of ontogenetic changes in orientation are [38–40]. Initiating such ontogenetic changes in behaviour at the appropriate time is required for realistic modelling results. Once a larva is able to settle, and begins searching for a settlement site, the amount of bottom it passes over will be more important to its probability of successful settlement than the amount of water it swims through.

Ultimately, it is movement of the larva relative to the sea bottom (in other words, a combination of swimming speed and orientation plus current speed and direction) that is relevant to where larvae travel and settle. Fish larvae can swim in a highly directional way at speeds that are a similar order of magnitude to currents in which they swim, so both are essential to determine dispersal outcomes, and depending on the situation either can dominate (Figure 4). In a situation where larvae of equal swimming speed swim directionally but are equally likely to swim in different directions, some larvae will be swimming into the current, some with it and some across it. This will result in a range of speeds over the bottom, and will spread the horizontal position of the larvae compared to larvae that drift passively for the same period of time.

Furthermore, speed and direction of both swimming and water movement can vary with depth, so depth of the larva must be included in determining net movement: an average velocity of the water column is unlikely to result in accurate determination of net movement of the larva.

Behaviours are likely to vary during the day and over longer periods. A number of behaviours are known to differ on a diel basis, most particularly vertical distribution (e.g., [41,42]), but also orientation (e.g., [43]). A dispersal model must take these temporal changes into account.

In all behaviours, there is considerable variation among individual larvae. Such variation is found in both laboratory and field studies [31,44]. The variation will lead to differences in dispersal outcomes, at minimum, spreading settlement over a wider range of settlement sites than indicated by mean behavioural values alone. The question is how best to include this variation in the model. If statistics that describe the variation (standard deviation, standard error, etc.) are available, they can be used. But if, as is often the case, the values of the behavioural data are not normally distributed (see sections below), then this approach can be misleading. Perhaps a more straightforward approach is to use the behavioural data to construct a frequency distribution of values, and then randomly sample from this distribution for values to apply to the virtual larvae. Data do not need to be normally distributed for this approach.

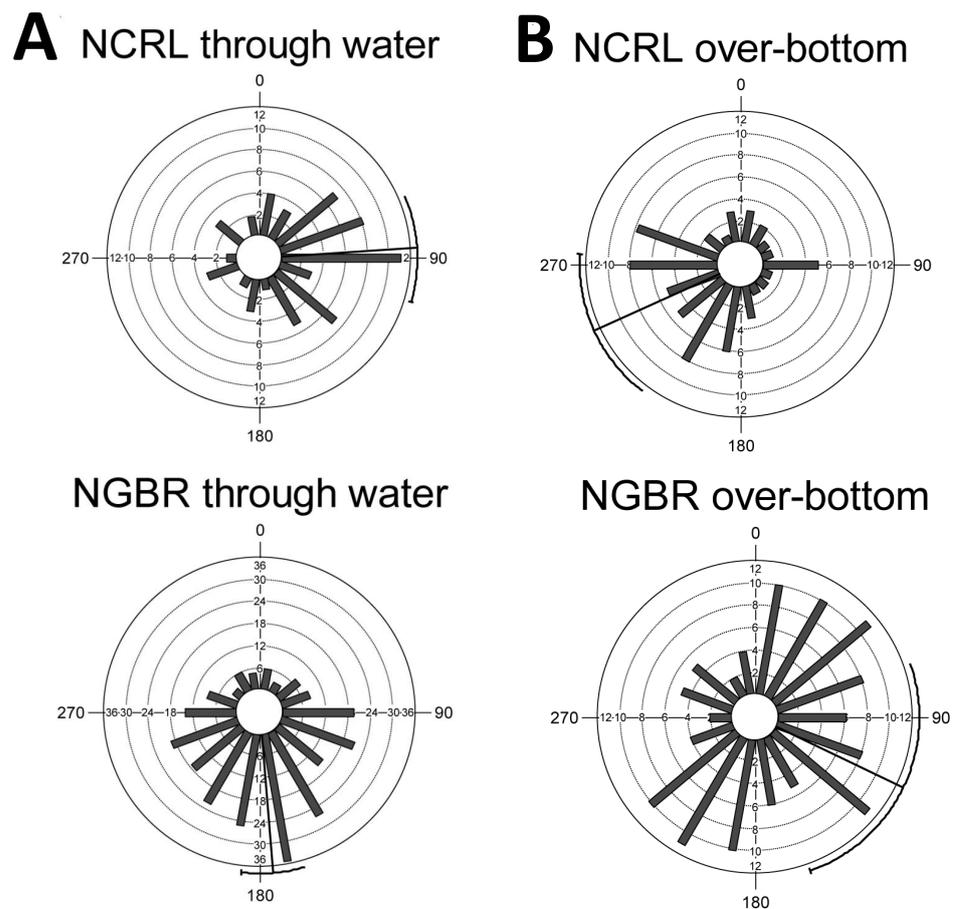


Figure 4. Frequency distributions of mean direction of movement of settlement-stage larvae of a damselfish species (*Chromis atropectoralis*) showing the result of interaction between swimming direction and current direction in two locations (NCRL—New Caledonia Reef Lagoon; NGBR—northern Great Barrier Reef: data from [45] analysed by Rayleigh Test). Note how highly directional through-water swimming at a mean speed of more than 20 cm s^{-1} by larvae can be greatly modified and even reversed by currents, resulting in very different movement relative to the bottom. The black radius is the mean bearing of many individual larvae, the arc on the outside of each circle represents the 95% CI of the mean bearing, and r is the length of the mean vector. (A) Movement through the water (i.e., swimming). NCRL mean swim direction = $87^\circ \pm 20^\circ$ ($r = 0.48$, $p < 0.0001$, $n = 62$); NGBR mean swim direction = $175^\circ \pm 11^\circ$ ($r = 0.41$, $p < 0.0001$, $n = 260$). (B) Movement relative to, or over, the bottom (i.e., combination of swimming and current). At NCRL currents were largely from the east which resulted in net over-bottom movement primarily to the west-southwest. Mean net movement = $246^\circ \pm 28^\circ$ ($r = 0.34$, $p = 0.0006$, $n = 64$). At NGBR, water movement was dominated by reversing tidal currents on the NNE-SSW axis which spread the net direction of over-bottom movement. Mean net movement = $116^\circ \pm 40^\circ$ ($r = 0.16$, $p = 0.045$, $n = 128$). Images used with permission of Inter-Research Science Publisher, Oldendorf/Luhe, Germany.

Behaviours interact with each other and with the physical environment. For example, the ability of a larva to move toward a particular goal will depend on its swimming speed through the water and on the variability (straightness) of its swim path, and on the direction and speed of the water mass through which it swims. Unlike the situation in a laboratory flume, the direction and speed of the water mass in which a larva is present are not generally evident to the larva in the sea. It is usually thought that only when a larva can sense a cue originating outside the moving water mass in which it is present—for example a view of the bottom, or perhaps a view of the sun angle, or perhaps turbulence caused by the water mass moving—that the larva will be aware that it is in moving water, and will, therefore, be

able to perform rheotaxis (swimming into a current flow). However, in some circumstances a larva's lateral-line neuromasts, which are present very early in the PLD, can detect flow velocity gradients (vorticity) and use them as cues to perform rheotaxis [46]. Furthermore, the neuromasts can distinguish water movement caused by the larva swimming from external water movement (e.g., currents or an approaching predator: [47]). So, a larva may be able to tell if it is swimming with a current, into it, or across it. These discoveries raise both interesting possibilities for larval-fish navigation [48] and challenges for modelling. More research is needed on this.

4. Swimming

Shortly after hatching from the egg, for a period of time larvae have swimming abilities that enable them to migrate vertically, capture food, and respond to predators, but morphological, physiological and hydrodynamic limitations result in horizontal swimming that is not sustainable over temporal and spatial scales relevant to dispersal outcomes [30,49]. This period ends about the time the caudal fin forms, when both speed and endurance increase markedly [31,44].

Sustainable horizontal swimming by larval fishes can greatly influence modelled (e.g., [5,6]) and real world (e.g., [11]) dispersal outcomes. Swim speeds need not be greater than the speed of the current in which a larva swims to have a major influence on where the larva ends up when it is competent to settle, regardless of which direction it swims relative to the current (e.g., [45,50]). Increasingly, measures of larval swimming ability are available to parameterize dispersal models. However, several ways of assessing swimming ability exist, and they differ in their applicability to dispersal and modelling it: this is discussed in [44], and will not be repeated here except in brief summary. Two measures of swimming speed—critical speed (U_{crit}) and in situ speed (ISS)—are most often used to parameterize dispersal models. Although many more values of the laboratory measure, U_{crit} , are available, it is generally agreed that U_{crit} is not directly relevant to dispersal [51], even though U_{crit} is sometimes, incorrectly, called a measure of sustained speed [52]. Early work based on settlement-stage larvae indicated that a value of 50% U_{crit} might be an acceptable conversion to ISS, but more recent analysis of the ontogeny of swimming speed has cast doubt on this supposed generality, concluding that there is not a broadly applicable conversion from U_{crit} to ISS [44].

It is more difficult to obtain ISS values for larval fishes because this involves divers directly measuring larvae swimming in the sea. Even when ISS data are available, further information on swimming directionality is required before it can be used in dispersal modelling. Although a large majority of fish larvae swim directionally in the sea, these larvae do not swim in a straight line, but swim in a more-or-less meandering path over the typical observation period of about 10 min [31,53]. What is required for dispersal modelling is the speed between the start to finish points of the individual larva's path. This "net" or "discounted" ISS (Figure 5) can be calculated if the swim direction of the larva is measured periodically during the observation period resulting in a within-individual directionality precision value [54,55] (Figure 6). Note that, confusingly, this precision value goes by several names, including Rayleigh's r , mean resultant length, length of the mean vector, mean vector, and vector's length. It is this net swim speed that is required for dispersal modelling. This highlights another limitation of the laboratory-based U_{crit} and attempts to use it in modelling: in the laboratory flume it is not possible to obtain the individual orientation precision values that are required to "discount" a swimming speed measure.

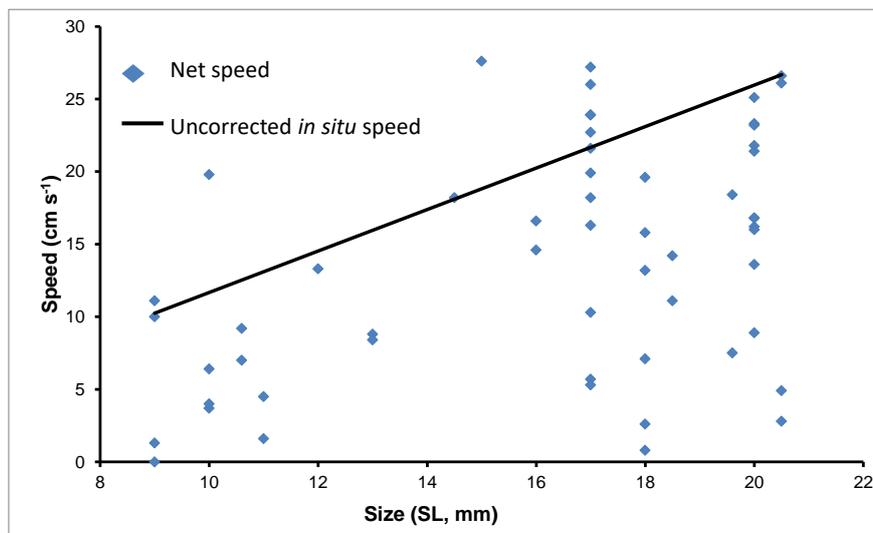


Figure 5. Ontogeny of net in situ larval swimming speed of a serranid grouper (size is standard length, SL). Plotted swimming speeds (blue diamond symbols) are discounted by the precision of within-individual directionality (r , see text and Figure 6), resulting in net speeds that are less than the corresponding swim speeds along the actual swimming path. The regression line (black) is the relationship of uncorrected in situ speed (ISS) with size ($ISS = 1.43 \cdot (SL) - 2.62$, $R^2 = 0.54$, $p < 0.001$). The net (discounted) speeds were calculated from all combinations of ISS and within-individual orientation precision of larvae from field studies of *Epinephelus coioides* (see [56]).

Within-individual *in situ* orientation precision

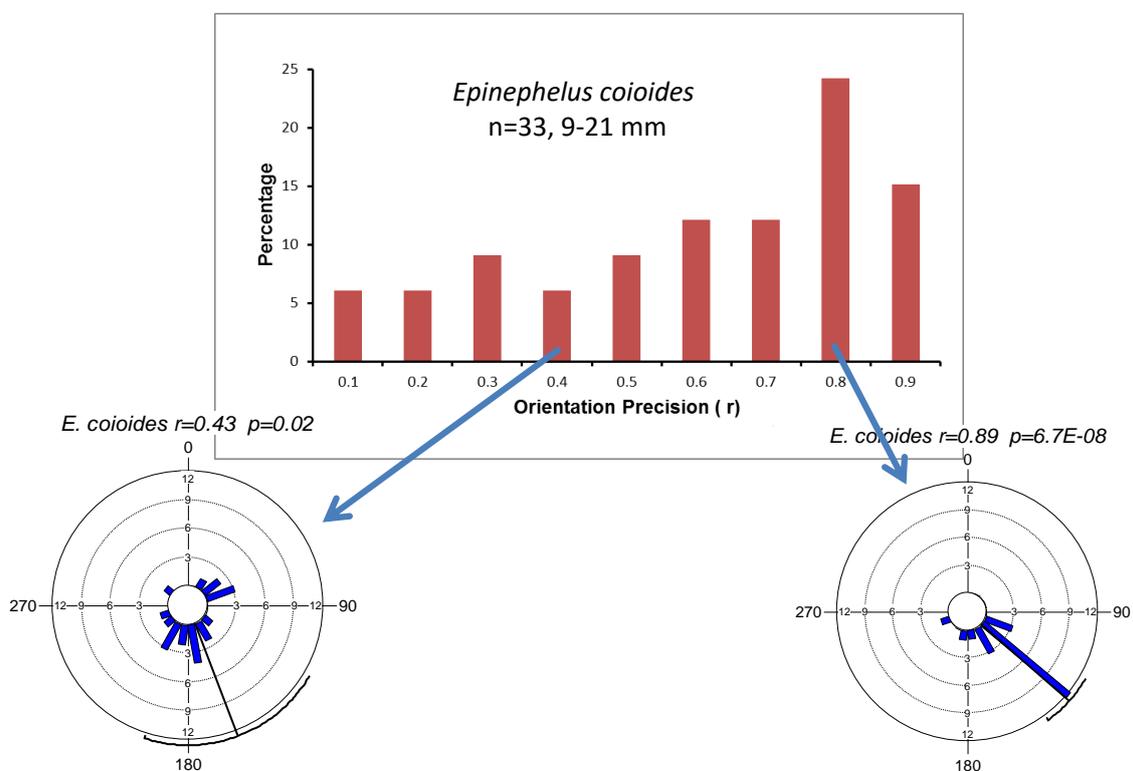


Figure 6. Frequency distribution of orientation precision of serranid grouper (*Epinephelus coioides*) larvae swimming in the ocean. Symbolism as in Figure 4. The circles contain examples of the frequency distribution of swimming directions measured every 30 s of two individuals. Both individuals had a significant mean overall bearing to the south east, but the one on the left had a more meandering (i.e., lower precision) orientation than the one on the right (data from [56]).

A second “in situ” speed measure involving the use of the Drifting In Situ Chamber (DISC, [57]) has been proposed in a recent study on herring larvae. This DISC with had an observation chamber of 20 cm diameter and 15 cm depth [58]: i.e., smaller than the 38 cm diameter of the original DISC. The reported speeds were low $0.36\text{--}0.40\text{ cm s}^{-1}$ (mean) and $3.0\text{--}3.4\text{ cm s}^{-1}$ (maximum), and given the size of the larvae (9–16 mm) and water temperature (12.0–13.5 °C), these larvae would have been swimming within a viscous hydrodynamic environment. This makes the measurements of questionable relevance to dispersal considerations (see below), but more to the point, swim speeds measured within such a small container are almost certain to be unrealistically low: in the words of the developers of the DISC, it “may allow measurements of in situ swimming speeds of the earlier stages, when swimming behaviour might not be affected by the enclosure” ([57] p. 62), but “larvae cannot maintain a sustained swim speed in a relatively small behavioural arena of 38 cm” ([59] p. 67).

Settlement-stage fish larvae of several species are known to school, shoal or otherwise aggregate in the pelagic environment prior to settlement (see summary in [60]), but most of these species also aggregate to a greater or lesser extent following settlement. So, in such species, this behaviour may be more related to what the larvae do after, rather than before, they settle [31]. However in two species, larvae are schooling before fins are completely formed, and a recent study reports aggregation by settlement-stage larvae of a cryptobenthic species (a Chilean tripterygiid [61]). Furthermore, genetic or otolith microchemistry evidence implies group dispersal over the full PLD in some situations in two species (a Red Sea pomacentrid, genus *Neopomacentrus*, that schools post settlement [62], and a New Zealand cryptobenthic tripterygiid [63]), indicating that a wider variety of species might have aggregating larvae than previously thought. In the case of the Red Sea pomacentrid, modelling indicated that schooling behaviour was necessary to achieve the patterns observed [60]. Although the model assumed an ontogenetic downward vertical migration to >25 m, the settlement-stage larvae of another species of *Neopomacentrus* are known to have modal depths of <5 m during the day [64]. How this might have influenced the conclusions of the modelling is unclear.

Nevertheless, if larvae do aggregate, this could influence both their speed and orientation, and thus their dispersal. The only study to examine the implications of schooling on larval behaviour relevant to dispersal found that schooling larvae of a pomacentrid in situ swam about 7% faster and with 15% higher directional precision than single larvae [65]. Therefore, if there is evidence of schooling, shoaling or other aggregation in the species to be modelled, and that the species behaves in the same way as the pomacentrid larva in the previous study, increasing the net speed when parameterizing the model could be justified. At the least, investigation of the influence of schooling on behaviour of the larvae of this species throughout the PLD should be considered.

Little information exists on diel variation in swimming speed of fish larvae. A single laboratory study found no diel difference in “undisturbed swimming speed” (i.e., routine speed, a laboratory measure that provides very low speed estimates [44]) averaged among larvae of four pomacentrid and one apogonid species ([34], their Table 2). Growth of tripterygiid larvae in the ocean is enhanced by lunar illumination, which indicates these larvae were actively swimming and foraging at night, at least during periods of bright lunar illumination [66]. It is clear from some field experiments that settlement-stage larvae can swim some distance at night [67,68], although their swimming speeds are unknown. However, in at least some non-perciform taxa (e.g., anchovy) larvae in laboratory tanks inflate their swim bladders at night, and simply ‘hang’ in the water with little or no swimming [69]. In the ocean, swim bladders of larvae of many species are more inflated at night than during the day [70], which implies they might be doing the same thing as anchovies, although this does not rule out nocturnal swimming by these taxa. These glimpses of fish larvae nocturnal swimming behaviour show how little we know about nocturnal behaviour of larval fishes other than their vertical distribution, and highlight the need for further research on nocturnal behaviour. In the meantime, perhaps the least worse

option is to assume that the results of [34] apply to one's study species unless evidence to the contrary exists.

The swimming performances above are all measured over relatively brief periods of time, so it is necessary to examine whether a swimming speed to be used to parameterize a dispersal model can be sustained over time periods relevant to dispersal in general, and the model in particular. Direct measurements of larval swimming endurance are helpful in this regard, although they are not directly applicable to modelling dispersal. These are typically done in a laboratory flume at a fixed speed without rest or food [71]. Relatively few such measurements across ontogeny exist, in part due to the time required to exceed the endurance of later ontogenetic stages, but the available data indicate that endurance is very limited before larvae are about 8 to 10 mm standard length and in the postflexion developmental stage. Endurance increases rapidly with size thereafter [31]. The few studies available on the effects of feeding on endurance are limited to larvae of only a few species, but show a large increase in endurance when larvae are fed [72–74]. In one of these studies of settlement-stage larvae of six species [72], no larvae reached their endurance limit in trials of up to 7 days in spite of swimming at 13.5 cm s^{-1} almost 23 h per day. The three larger species (12–14 mm) grew in both standard length (SL) and total lateral area (TLA), whereas only one of the three smaller species (10–11 mm) grew by either measure, although many individuals of all six species began to metamorphose while swimming. However, in the ocean, it is unlikely larvae swim at a fixed speed without rest, either with or without feeding. Therefore, endurance measures are useful in indicating how long fish larvae can swim in the ocean: for postflexion-stage larvae (i.e., after the caudal fin has formed) this seems to be more-or-less indefinitely as the larvae 'eat on the run' to fuel their swimming and growth [75].

Small animals swimming slowly in the ocean are likely to be swimming in a viscous hydrodynamic environment, and the colder the water, the larger the larva and/or faster the swimming must be in order to transition to an inertial hydrodynamic environment. This is relevant to dispersal modelling because the additional drag of a viscous regime results in less efficient and less sustainable swimming [49]. Modelling indicates that relatively slow swimming speeds—if sustained long enough—can influence dispersal outcomes (e.g., [76]). However, slow swimming, particularly for smaller larvae, is unlikely to be truly sustainable over time scales relevant to dispersal if the larvae are operating in a viscous regime. In such cases, direct measurements of endurance are required to determine if endurance at slow speeds is great enough to be relevant to dispersal.

Modes of swimming vary among species, and often ontogenetically. Slender-bodied fishes, such as eels, tend to swim in anguilliform mode, in which much of the body undulates at high amplitude, whereas fishes with broad tails and a narrow caudal peduncle tend to swim in carangiform mode, in which the tail undulates at high amplitude [77]. Research on adult fishes indicates that the wakes produced by these two forms of swimming differ: anguilliform swimming is more efficient at slower swimming speeds, whereas carangiform swimming is more efficient at higher speed [77]. In larvae, the continuous median fin fold—which is found in small (preflexion) larvae of nearly all taxa, and also in larger larvae of some—increases thrust, enabling increased swim speeds with the same fluid-dynamic costs [78]. This implies that for smaller larvae, transition from viscous to inertial regime might take place at slower speeds for larvae with continuous fin folds, especially if they are anguilliform swimmers. In most species, at about the time fin rays and the caudal fin form, the continuous fin fold disappears where fin rays are absent, but this loss is more than compensated by an increase in muscle mass and the increased thrust provided by the caudal fin. At present, it is unclear what the effects of these issues are on actual swimming abilities, or on the hydrodynamic environment in which larvae are calculated to be swimming. Hopefully, research can shed light on these recent developments so that the appropriate parameterization of swimming abilities can be achieved in dispersal models.

Not all larvae swim at the same speed. Swimming speed varies greatly among individuals within the same species (Figure 7 shows the variation in ISS and U_{crit} among

individual settlement-stage larvae of a damselfish), and this variation must be incorporated into a dispersal model. Simply using mean speeds will unrealistically constrain dispersal outcomes. It is worth noting that the Ucrit and ISS distributions for the species shown in Figure 7 differ, quite apart from the speed ranges. Furthermore, in most cases, ISS is more variable than Ucrit [44]. These are strong indications that attempts to convert laboratory-based Ucrit values to field-based ISS values are not straightforward (see [44]).

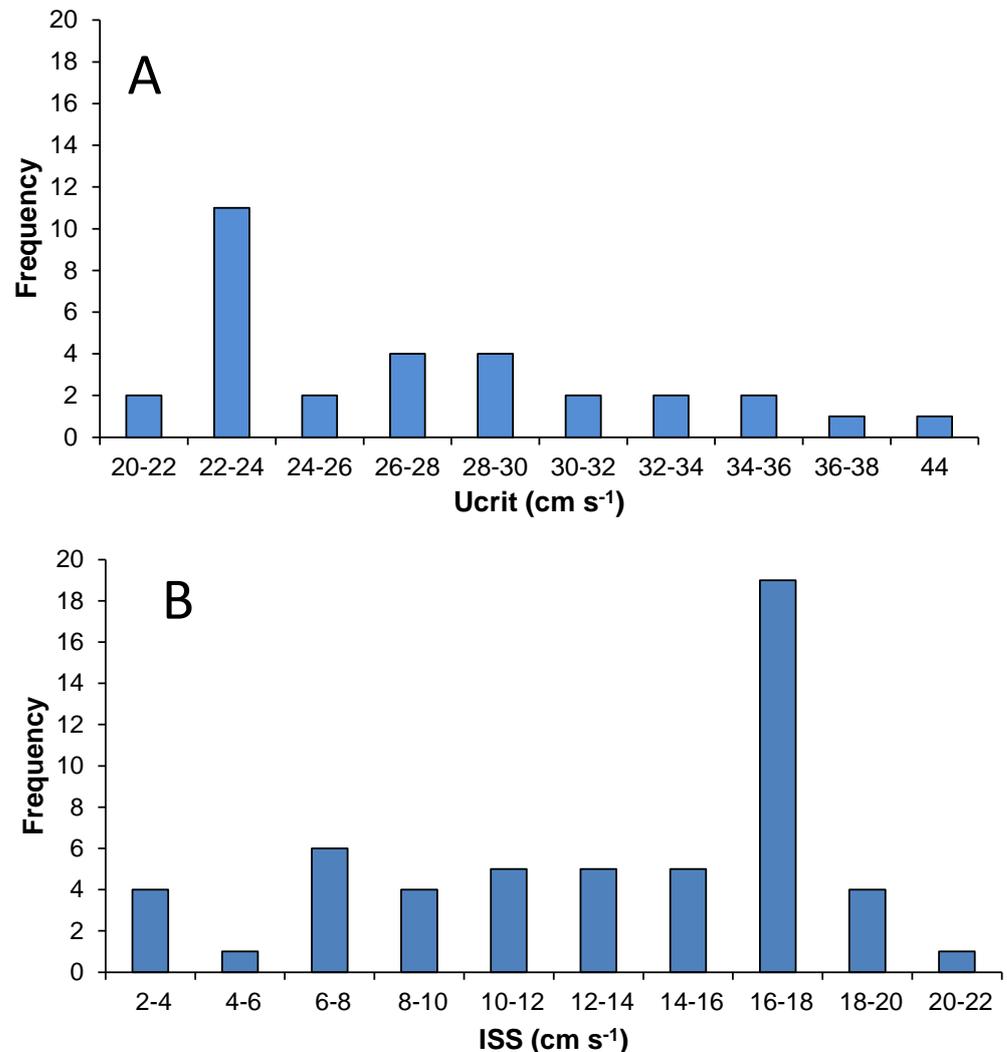


Figure 7. Variation in swimming speed in settlement-stage larvae of a damselfish (Pomacentridae) *Amblyglyphidodon curacao* (data from [64]). Larvae were 8–10 mm, Standard Length. (A) Critical Speed (Ucrit, a laboratory measure) of 31 larvae. (B) In situ speed (ISS, a field measure) of 54 larvae. Note that there is very little overlap in the ranges of the two measures.

In order to obtain swimming measurements that are representative of what competent to settle larvae do while still pelagic, it is important to make the measurements before the larvae can undergo the physiological and morphological changes that accompany settlement. This is necessary because settled larvae of some species rapidly lose swimming performance [52,79] possibly associated with their transition from open water ‘swimming machines’, with very high oxygen consumption and oxygen requirements to demersal animals with good tolerance to hypoxia [80]. Therefore, the use in dispersal modelling of swimming data from recently settled individuals would be questionable.

5. Orientation

Larvae may have good swimming abilities, but larvae with orientation abilities will have different dispersal outcomes than those lacking such abilities [7]. It is important to distinguish whether an individual is maintaining a bearing (within-individual directionality, Figure 5), from whether there is directionality among a number of individuals (among-individual directionality). Most studies show that most individual larvae swimming in the ocean do so in a directional manner, and there is little ontogenetic improvement in orientation precision [31], however, these were in situ studies limited to postflexion larvae of demersal species. A recent laboratory study on larvae of an oceanic species using both pre- and postflexion larvae showed an ontogenetic increase in orientation precision [81]. Significant directionality among individuals is not as widespread, but even when it is absent, such behaviour can have a meaningful influence on dispersal outcomes [50]. Research on sensory abilities has shown that larval fishes have good hearing, olfactory and visual capabilities to detect location-dependent cues such as reef-based sounds and odours [33], and location-independent cues such as sun position [33,43,82] (and perhaps other celestial cues) and magnetic fields [83,84]. If this kind of sensory information is available for a study species, then it is possible to use such cues to predict orientation of the modelled larvae. However, research on sensory cues and orientation has used a limited range of species and families, and most of it has been restricted to settlement-stage larvae at the end of their PLD [33,37], but see [32,85]. As a result, we know relatively little about the ontogeny of sensory abilities and orientation, so at present, the opportunities for applying to modelling this approach to orientation across the full PLD are limited. However, it may be possible to use this approach for larvae competent to settle because there is more information available on sensory cues and orientation of settlement-stage larvae. This limitation of information on sensory biology highlights a need for more research, especially on the ontogeny of larval senses, to enable orientation abilities during the PLD to be better understood.

Even if there is good evidence that larvae can detect and respond to a cue in the laboratory or over short distances in field experiments, there is no assurance that this will be possible in the sea over spatiotemporal scales (100 s of metres to 10 s of km, and days to weeks) that are relevant to dispersal and to finding settlement habitat. Current-dependent cues such as reef odours, will be inherently more difficult to model than current-independent cues such as sun position or reef sounds due to eddies, wakes, fronts and turbulence. Furthermore, larvae in the pelagic environment will have difficulty in determining where 'upstream' is, which is probably necessary for them to be able to swim upstream toward an odour source. Larvae have been shown to use olfactory cues to find settlement habitat in shallow reef habitat where detecting water movement so they can orientate upstream is relatively straightforward (see [33] for a review), but some other process, perhaps similar to "infotaxis", may be required in the pelagic environment [86]. The use of celestial cues such as sun position is most likely for larvae in the upper parts of the water column where a view of the sky is possible through Snell's Window [87]. If a larva moves deeper, the view of the sky through the Window remains the same 97°, but due to scattering and absorption, the intensity of the light becomes dimmer until the Window can no longer be discerned. Increased turbidity results in this happening at shallower depths [88], and the Window is also disrupted by waves and wind ripples on the surface. Therefore, although there is no published research on the depth to which fish larvae can use celestial cues via Snell's Window, it seems likely this will vary depending on, amongst other things, water clarity and surface conditions, but it will not extend to even moderate depths. However, larvae with the ability to detect polarized light [89] could use the e-vector (plane of polarization) distribution to locate the sun's azimuth, and utilize a sun compass to much greater depths [88]. It is expected that larvae may have the ability to switch cues and use the ones that are best at providing directional information under conditions prevailing at any time [33]. Therefore, a larva may use, say, celestial cues in calm weather, but switch to the use of auditory or magnetic cues when moderate breezes ruffle the surface. All of these variables

provide additional challenges to the modeller attempting to use sensory cues to estimate swimming orientation as an emergent property of a model.

Field experiments have demonstrated that settlement-stage fish larvae can hear and locate reef sounds [67,68,90]. Modelling sound underwater is somewhat more straightforward [91,92] than either olfactory or visual cues, although the distances over which larvae can hear and respond to sounds is not clear. The distance over which sound can provide orientation cues for fish larvae is controversial. Without going into too much detail, the disagreement boils down to whether the larva's ear can detect swim bladder vibrations caused by sound pressure waves (see [93,94]). In adult fishes, the species with the best ability to detect such vibrations have 'accessory organs' that reduce the effective distance between the swim bladder and the ear, whereas those without these organs have a poor ability to detect sound-pressure induced swim bladder vibrations. So, it is often assumed that larvae which lack accessory organs or in which they have not yet developed will be unable to detect swim bladder vibrations [95,96]. However, in small larvae, the distance between swim bladder and ear is so small in many taxa that the ear may well be able to detect (i.e., hear) swim bladder vibrations (e.g., [97]), thus increasing the distance from a sound source that a larva can detect the sound. Sound propagates well underwater, so if larvae can hear sound pressure in this way, the calculated distances over which larvae might be able to hear something like a coral reef are several kilometres [98]. Celestial and magnetic cues, in contrast, could potentially be used over very large spatial scales.

Evidence that a proportion of fish larvae settle into their natal area has led to the expectation that some sort of homing behaviour is involved, and for recommendations that explicit homing be included in dispersal models (e.g., [14]). However, with the possible exception of anemone fish larvae [99], explicit homing by larvae has not been demonstrated. Furthermore, modelling indicates that settlement at natal sites can be achieved by a portion of larvae without homing (Scott Burgess, personal communication) with larvae settling largely to the reefs located nearest to them when they achieve competence to settle (e.g., Figure 2). This can be achieved, in part, by the inclusion in models of the among-individual variability in behaviours advocated by others [14] and herein.

If insufficient information is available to use sensory cues for modelling orientation, an alternative is to use data describing orientation of the larvae in situ—over both the pre-competent and settlement-stage portions of the PLD (see, for example [39,40,56]), even if it is not clear what cues were used by the larvae to achieve the orientation. Such data can be obtained from diver observation of larvae in the ocean [53], use of the DISC [57] or some nocturnal field experiments [100–102]. Typically, it will be necessary to divide the PLD into ontogenetic stages for use in the model to accommodate ontogenetic changes in orientation behaviour.

Orientation behaviour becomes relevant to dispersal modelling when sustainable swimming abilities develop, which often coincides, at least roughly, with the completion of notochord flexion and caudal-fin formation. Therefore, the relative lack of orientation information on smaller (preflexion) larvae from in situ studies due to the difficulty of seeing very small larvae in the ocean, should not be a problem for modelling dispersal.

It is common to model swimming movement of larvae as a simple random walk [103], and more recently, in some cases, as a correlated random walk (e.g., [50,104,105]). However, recent analysis of swimming paths of marine fish larvae in situ suggests orientation should be modelled as a biased correlated random walk (BCRW: Igal Berenstien, personal communication). See [106] for a dispersal model that incorporates BCRW.

6. Vertical Distribution

A common question is: what single behaviour is most important in modelling dispersal? One is tempted to answer "vertical distribution", because it is the only behaviour present for nearly the whole PLD. Soon after hatching, fish larvae begin to control their vertical distribution and to undertake diel vertical movements (e.g., [107,108]). It is widely recognized that vertical positioning is important to larval dispersal because currents vary

in both speed and direction with depth, most often, but not always, by decreasing in speed with depth. Furthermore, it is the larval behaviour for which the most information is available. However, it is simplistic to consider a single behaviour to be the most important without qualifying the question by stating what portion or outcome of dispersal is of most concern to the questioner. One could be concerned with settlement success, or mean, median or modal distance dispersed from the natal location, or the spread of settlement locations compared with a null model of passive behaviour, or perhaps the amount of self-recruitment, or the actual dispersal pathway, or any number of other aspects of dispersal or its outcomes. Vertical distribution may be the most important behaviour in determining some of these, but it is unlikely to be the most important behaviour in all of them. Nevertheless, it is a very important behaviour to incorporate into dispersal modelling.

Different methods must be used to obtain information on vertical distributions in larvae at different sizes (or ages). Plankton nets or midwater trawls can be used day and night for larvae that are small or of medium size, respectively, and towed-net data on vertical distributions are the most readily available data suitable for parameterizing models [42,109]. Larger larvae are adept at avoiding towed nets, at least during the day and for these larger larvae, in situ observation of larvae by divers (e.g., [50,110]) is a possibility, but only during the day and in relatively shallow water. At night, light traps set at different depths can be used to study vertical distribution of larvae of species that will enter light traps (e.g., [111,112]). Unfortunately, only a relatively small proportion of species will enter light traps [113], which limits the applicability of this method. In the laboratory, use of vertical aquaria within which pressure can be regulated can provide estimates on pressures, and therefore, depths at which larvae can be expected to be found in the sea [114].

A complication in modelling vertical distribution is that vertical distribution frequently differs with water column depth or horizontal location. For example, six of seven species of settlement-stage larvae of coral-reef fishes had vertical distribution patterns that varied between windward and leeward sides of a study island and its reefs or among distances from shore (which co-varied with water column depth [110]). These sorts of location-dependent differences in vertical distribution, which occurred over horizontal scales of 100 to 1000 m from shore and water depths of 10 to 40 m, require the dispersal model to determine horizontal position of a virtual larva before assigning a vertical position to it. Another example of spatial variation in vertical distribution is larvae of four species which in the lagoon of an atoll had much shallower and less variable vertical distributions than those in the ocean close outside the lagoon [115].

As with other behaviours, simply using a mean, median or modal depth for a virtual larva without taking into account the vertical distribution pattern involved will result in dispersal outcomes that are unrealistically constrained. Again, sampling randomly from a probability distribution of vertical positions is a viable means of dealing with this variability.

7. Mortality

It is normally considered that mortality of larvae during the PLD is huge [116], and that this has strong effects on dispersal outcomes: in particular by decreasing the height of the dispersal kernel, and thus decreasing apparent dispersal distances [117]. Yet, the way mortality rates are estimated is often questionable. Some estimates are based on comparisons of female fecundity to the number of recruits [118]. Quite apart from the rather variable way that recruitment is frequently defined, this does not account for either the proportion of eggs that are not shed from the ovary, or the large number of eggs which fail to become fertilized, which is usually an external process [119,120]. Another common way of estimating mortality rate is by fitting a curve to size/frequency (or sometimes age/frequency) data of larvae captured in towed net samples (e.g., [109]). Unfortunately, size is correlated with increasing swimming and sensory abilities (Figures 3 and 5), thus resulting in an increased avoidance of towed nets with increased size and decreased catch of larger larvae. Estimates of mortality rate calculated this way are therefore confounded with increased

behavioural abilities, which as a result overestimates mortality. One solution is to estimate mortality rate using this approach, but only over a relatively narrow size range for which there is reason to expect that avoidance is not a problem, or at least constant (e.g., [109]), but this estimate should not be extended outside that narrow size (or age) range. The use of otolith increments to estimate larval-fish mortality has also been proposed [121]. A recent development for estimating mortality called the “box-balance model” [122] shows promise.

A further complication is that few larval mortality rate estimates exist [123], especially for tropical species, or species that aren't the subject of large, commercial fisheries (e.g., Cowen et al. [117] were able to compile estimates for only 42 species for their landmark paper). If the mortality rate is constant throughout the PLD, a likely result is that the shape of the dispersal kernel will not be affected, but the values in the curve will simply be lowered proportionally by mortality. If mortality rate varies with age during the PLD, the modelling becomes more complex [124]. Although it is expected that mortality rate will be greater during the early portion of the PLD than near its end [116], even fewer reliable mortality rate estimates exist to test that expectation. Furthermore, research on non-fish taxa shows mortality rates derived from ‘traditional’ methods overestimate actual larval mortality in the sea [125], thus providing further uncertainty about what mortality rates to use in modelling dispersal of fish larvae.

The longer the PLD, the greater the mortality, regardless of the shape of the mortality curve, so larvae that settle early during the window of settlement competence, will be more abundant at their time of settlement than those settling near to the window's closure. The effect this has on dispersal outcomes will be strongly influenced by the distribution of settlement habitat as well as the movement of larvae relative to the bottom, both before and after they reach settlement competence, until they reach settlement habitat. This highlights the importance of using appropriate PLD values for dispersal modelling.

Possibly the best solution in the absence of verified mortality values for the species of interest is to run the dispersal model using a range of credible mortality estimates to determine how the dispersal outcomes vary with mortality.

8. Do You Really Need to Develop Your Own Dispersal Model?

A number of papers addressing aspects of including behaviour into dispersal models should be read by anyone contemplating embarking on their own modelling. In addition to [13] mentioned previously, this includes [8,11,14,105,106,123,126].

Incorporation of larval behaviour into a dispersal model is not simple and requires access to expertise, appropriate data and a willingness to think outside the box. The goal of this paper is to help make that process somewhat easier for the biologist interested in estimating larval-fish dispersal. However, unless you have extensive experience in individual-based coupled physical-biological modelling (=biophysical modelling, see [127]), another recommendation is to find a good modeller who does, and collaborate with them. Few larval-fish biologists have the modelling talents of someone like Claire Paris, and modelling dispersal of larvae in the ocean while also incorporating all the biological variables that are necessary to approach a realistic result in an appropriate way takes an expert. Conversely, unless the expert modeller has the inputs only an experienced larval-fish biologist can provide (see the publications cited in the paragraph above), it is unlikely the model outputs will be realistic. Consider using an established modelling system, such as the Connectivity Modelling System of Paris et al. [106] which by design allows the inclusion of behaviour of larvae. However, if you do select an ‘off the shelf model’, be sure to closely examine its assumptions to make sure you are comfortable with them, and at a minimum understand how the biological inputs (especially larval behaviour) are incorporated and used by the model to generate its predictions. The same applies to a model you develop in collaboration. Many existing dispersal models are not done at a fine enough scale to effectively incorporate the biological parameters treated in this paper. Is the model you are considering using (or building in collaboration) one of these?

It is not uncommon for contemporary PhD dissertations to include a chapter on modelling larval dispersal. Or, perhaps it is more correct to say it is common for postgraduate students to attempt to build a dispersal model for their study species or system as part of their studies, but with little to no information on larval behavioural capabilities in an ontogenetic context. A more productive alternative to this approach would be to build a model that can be 'tweaked' with a range of behaviours and values and ask the question: what set of behaviours can result in the larvae of species X getting from A to B more often than not or during periods of known high recruitment success in the past? This would then provide a hypothetical starting place for the student, or someone else, to carry out behavioural research to determine just what the capabilities of the larvae of species X really are. In many cases, it may be more productive to devote limited research resources to studies of ontogeny of behaviour and sensory abilities in larvae of target species than to developing a new dispersal model.

An often-unrecognized aspect of modelling larval dispersal in the ocean is that it is usually not possible to make meaningful predictions about dispersal in the future. This is because ocean circulation (i.e., the currents with which larval behaviour interacts) depends on variables that often themselves cannot be predicted. A particular example is wind, which in coastal waters has a very important influence on current speed and direction in both horizontal and vertical planes. Coastal currents cannot be predicted with any accuracy without having data on wind velocity (speed and direction) over the period of modelling, and in most cases for some period of time before that. Therefore, any attempts to generate model outputs for larval dispersal over any period must wait until at least the end of that period. If the intent of modelling is to provide information for fishery management, this may not be much of a problem because of the inevitable delay between settlement and recruitment into the fishery, but it could limit the value of the model output for other purposes. If, however, the intent is to produce some sort of dispersal average based on averaged physical and biological conditions expected to occur over some period in the future, this could be achieved, but it is important to keep in mind just what assumptions are being made in such a case.

9. Testing and Validation

A model cannot prove or disprove. However, it can predict, in this case, where fish larvae will go during their PLD. The question then arises, how accurate will such predictions be? In most cases, peer-reviewed, published biophysical dispersal models are neither validated nor their predictions tested in an objective way [8], although it is standard procedure to validate the modelled currents by comparison with empirical data (e.g., current-meter measurements). So, the reader is left to wonder whether such models are at all useful in the real world, leading to calls for validation [8,128]. An example is the well regarded 2015 paper by Treml et al. [123] who state: "Although validation of hydrodynamic models is virtually a requirement, corroborating dispersal predictions from such models is considerably more challenging. To our knowledge, no larval dispersal model has been ground-truthed with empirical estimates of dispersal . . . This greatly limits the confidence in modelled estimates of dispersal and connectivity" (p. 14). Five years later, only a single larval-fish dispersal model incorporating larval behaviour has been able to be validated with empirical estimates of dispersal [11].

A few investigators have tried to test their model's predictions via the use of a population genetic differentiation data statistic such as F_{st} or by otolith chemistry of recruits [128]. But here, we get into just what the model is trying to portray. F_{st} is about the movement of genes over generations, and it takes only a handful of larvae each generation to successfully disperse and reproduce to maintain genetic connectivity. In other words, such genetic measures are related to the larvae in the end of the tails of a dispersal kernel curve and to dispersal over generations. Most dispersal models are developed to examine dispersal on ecological or demographic time scales (e.g., fishery or marine protected area management), so using measures such as F_{st} is inappropriate for testing them.

Otolith microchemistry can be useful to test model predictions, but the predicted identity of the natal location of the individuals tested this way may not be precise enough to be useful [128]. Otoliths should be most useful when there is a strong difference in water chemistry or temperature between spawning location, where the PLD is spent and where settlement occurs (e.g., between estuary and open coastal or oceanic waters).

Genetic parentage data provide the potential to independently test larval-fish dispersal model predictions and to determine whether a particular model provides a credible representation of real larval dispersal outcomes [11]. As such, they are perhaps the best way of testing dispersal model predictions because parentage assignments provide clear evidence of specific dispersal events [128]. However, for several reasons few attempts have been made to use this approach. First, due to constraints on the spatial and temporal scales of population sampling, only a fraction of potential dispersal pathways can be identified. Second, unfortunately, genetic parentage assignments are expensive and logistically complex to obtain at the intensity and spatial scale required to achieve the statistical power needed for rigorous testing. Third, it is challenging to produce a biophysical model at both the resolution and scale needed to match observed assignments that include both small-scale retention in and around a natal population and long-distance movements over 100 s of kilometres (e.g., [20]). Fourth, the model outputs must match the timing of the measurement of larval dispersal by parentage because of temporal variability in ocean currents. Ideally, to determine the significance of larval biology and behaviour, the parentage data should be tested against a range of different biophysical models, from passive null models to ones that incorporate biological and behavioural traits of the study species. This has been done successfully in only a few cases [11].

No model will be perfect. To paraphrase George Box: all models are wrong, but some are less wrong, and what one wants to know is if a model is illuminating and useful. Dispersal models cannot be illuminating or useful if we do not know how wrong they are.

10. Where to Next?

A minimum expectation is that contemporary larval-fish dispersal models should incorporate behaviour of the larvae (ideally based on empirical studies of swimming, orientation and vertical distribution), and that the model's predictions should be tested in a transparent way (see, for example, [11]). We need to know more about behaviour and sensory abilities of larval fishes and their ontogeny in order to parameterize models with good data. Before they are used in modelling, data from laboratory studies of behaviour should at least be contrasted with, if not rigorously compared with, studies of what larvae do in situ because behaviour may differ between the ocean and the lab, or between reared and wild larvae (e.g., [36]).

If, as will usually be the case, insufficient behavioural knowledge is available to adequately parameterize a dispersal model under construction for a particular species, it should be a standard and integral part of the modelling effort to conduct a research program on the early life-history stages of the species to obtain the needed behavioural and other biological information. If appropriate behavioural data are not available for the species of interest, use of data from a close relative (ideally, a congener or confamilial) can be considered, although this must be done with some caution as behaviour can differ among close relatives [129]. If data exist for more than one close relative, selecting the species that has an adult biology and ecology most similar to the study species, might be a logical choice.

The lack of behavioural data is not justification for assuming the larvae are passive. One has to question whether developing a model that assumes larvae are passive is worth doing, unless, of course, the purpose is to use the model's predictions to test—as described above—the assumption of passivity.

It is sometimes suggested that hypothetical behaviours can either be added stepwise to a model to perform sensitivity analyses of what behaviours to include [8,13] or varied in magnitude to assess what model predictions might be possible or realistic. However,

unless data exist to test the predictions of the model with each addition or variation, one is left with little more than the relatively uninformative conclusion that adding different behaviours results in different dispersal predictions. Although, in some cases, the relative influence different behaviours might have on dispersal can be estimated. Trembl et al. [123] describe their sensitivity analysis-based approach as “a mechanism for model parameter tuning and validation in comparison to empirical estimates. Once groundtruthed [=corroborated], simulations can be run across the full spectrum of spatio-temporal variability to generate more realistic estimates of connectivity outcomes and their impacts on metapopulation dynamics” (p. 14). In short, truly effective sensitivity analysis requires validation [123], an approach commonly used in developing the hydrodynamic portions of dispersal models [130].

We can expect dispersal models to increase in complexity and realism as we learn more about larvae, their behaviour, and their interactions with their pelagic environment. We can look forward to variables such as feeding conditions becoming emergent properties of the modelling, enabling feeding and growth likewise to be predicted as a result. This will then lead to mortality being a prediction of the model, rather than an input to it.

To help make the link between dispersal model predictions and estimates of connectivity we need to know more about settlement and post-settlement processes, particularly mortality.

Finally, validation of any dispersal model is needed to ensure its credibility, and model developers should strive to include validation as a standard part of model development. This will become increasingly important as the type of models predicted in the paragraph above come into being.

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