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## Review 7

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### A Review of Biophysical Models of Marine Larval Dispersal

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## A REVIEW OF BIOPHYSICAL MODELS OF MARINE LARVAL DISPERSAL

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### Abstract

Larval dispersal is arguably the most important but least understood demographic process in the sea. The likelihood of a larva dispersing from its birthplace to successfully recruit in another location is the culmination of many intrinsic and extrinsic factors that operate in early life. Empirically estimating the resulting population connectivity has been immensely difficult because of the challenges of studying and quantifying dispersal in the sea. Consequently, most estimates are based on predictions from biophysical models. Although there is a long history of dispersal modelling, there has been no comprehensive review of this literature. We conducted a systematic quantitative review to address the following questions: (1) Is there any bias in the distribution of research effort based on geographical or taxonomic coverage? (2) Are hydrodynamic models resolving ocean circulation at spatial scales (resolution and extent) relevant to the dispersal process under study? (3) Where, when and how many particles are being tracked, and is this effort sufficient to capture the spatiotemporal variability in dispersal? (4) How is biological and/or behavioural complexity incorporated into Lagrangian particle tracking models. (i.e. are key attributes of the dispersal process well captured.)? Our review confirms strong taxonomic and geographic biases in published work to date. We found that computational ‘effort’ (i.e. model resolution and particle number) has not kept pace with dramatic increases in computer processor speed. We also identified a number of shortcomings in the incorporation of biology, and behaviour specifically into models. Collectively, these findings highlight some important gaps and key areas for improvement of biophysical models that aspire to inform larval dispersal processes. In particular, we suggest the need for greater emphasis on validation of model assumptions, as well as testing of dispersal predictions with empirically derived data.

### Introduction

Marine ecosystems cover nearly 75% of the Earth’s surface and harbour over 25% of global biodiversity (Scheffers et al. 2012), with recent estimates suggesting a total number of marine species in the range of 700,000 to 1 million (Appletans et al. 2012). At present, there are nearly 200,000 accepted species of marine animals (>80% of currently described marine biodiversity; WoRMS Editorial Board 2017). Developing a broad understanding and appreciation for this diversity is daunting, particularly as research effort in biological disciplines is terrestrially focussed (Lawler et al. 2006, Caliman et al. 2010, Trimble & van Aarde 2012) and the limited transfer of scientific knowledge across the land-sea interface has hampered the growth of marine biology and ecology as disciplines, despite calls for greater collaboration and integration (e.g. Menge et al. 2009). As Steele

(1991) so clearly articulated over a quarter century ago, the physical characteristics of marine and terrestrial environments operate over different spatiotemporal scales, with important consequences for how organisms interact with each other and the environment. The question of whether these environmental differences result in contrasting biological or ecological outcomes across systems requires explicit recognition and testing (Webb 2012).

### *The ubiquity of complex life cycles in the sea*

One example of how environmental differences lead to dissimilar ecological outcomes is in the nature of complex life cycles. Although many terrestrial animals exhibit complex life cycles in which different developmental stages occupy different niches and/or habitats (Wilbur 1980), this life-history pattern is more common and striking in the ocean, particularly in the context of benthic marine animals where relatively sedentary adult stages give rise to pelagic larvae. For these animals, transitions between life stages coincide with transitions not just among benthic habitat patches (e.g. coral and rocky reefs) but also with the overlying pelagic environment. The terrestrial analogy is those species that spend time in air, yet this habitat transition is usually temporary, as air provides almost none of the resources needed for survival. In contrast, benthic marine species that produce planktotrophic (feeding) larvae can spend weeks to months feeding and developing while in the pelagic environment (Keough & Swearer 2007).

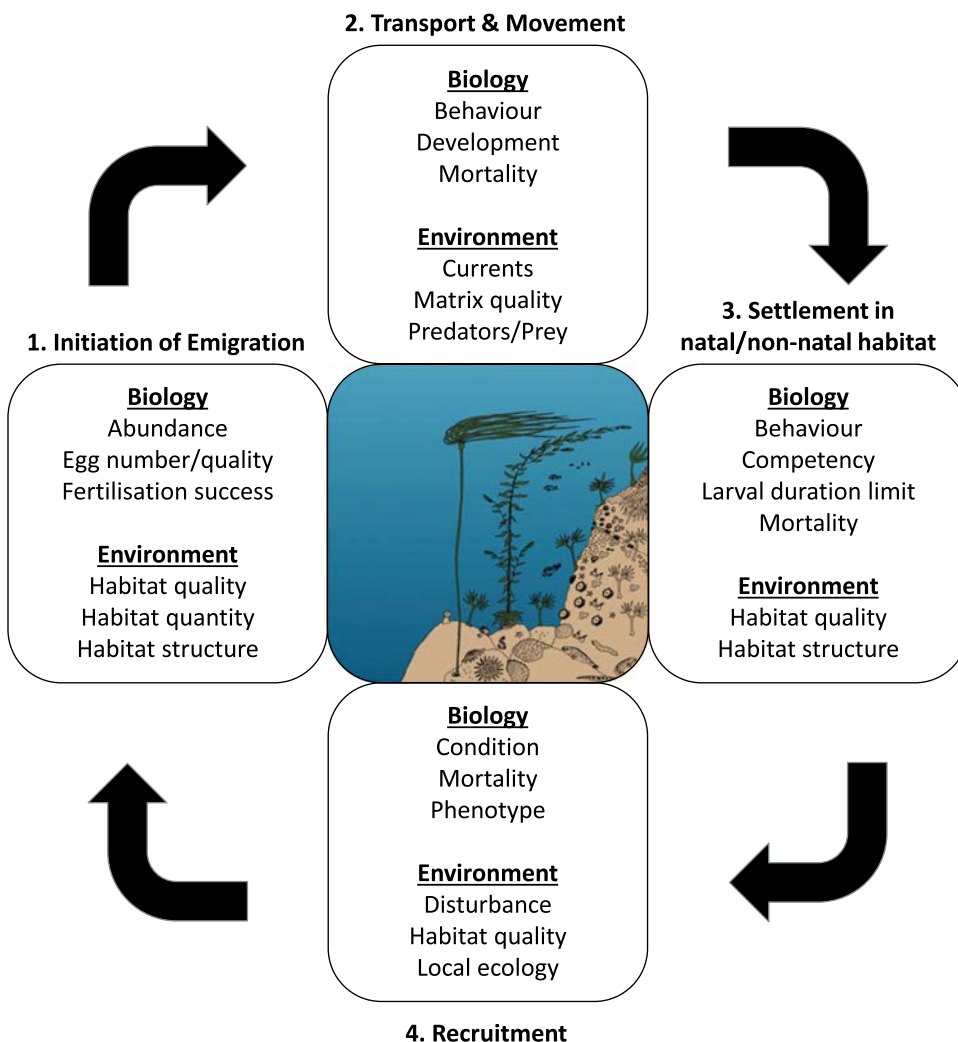
Pelagic larval development is the dominant developmental mode among benthic marine species (Young 1990). Out of the thirty phyla of marine animals, there are only four phyla with benthic lifestyles (Gastrotricha, Gnathostomulida, Nematoda and Tardigrada) that lack species with pelagic larvae (Pechenik 1999). While there has been some debate over the ultimate drivers for the evolution of pelagic larval stages (e.g. Pechenik 1999, Burgess et al. 2016), the prevalence of this development mode combined with the dynamic nature of ocean currents means dispersal, the movement of individuals away from their birth location, over ecologically relevant scales is likely to be characteristic of the great majority of benthic marine animals most of the time.

### *The importance of dispersal and population connectivity*

Despite its fundamental importance to understanding the ecology and evolution of benthic marine organisms, dispersal is arguably the least-understood demographic process in the sea. Because most marine species spawn large numbers of tiny pelagic offspring that suffer extreme mortality while being dispersed by ocean currents (Thorson 1950, Cowen & Sponaugle 2009, Metaxas & Saunders 2009, White et al. 2014, Johnson et al. 2015), small changes in survival and ocean circulation can have profound consequences to the dynamics of marine populations. Successful dispersal, the movement of individuals from their birth to their recruit location, can lead to large recruitment pulses (e.g. Hjort 1914) that are capable of sustaining populations of long-lived species for decades (i.e. the storage effect, *sensu* Warner & Chesson 1985). Successful dispersal can also connect groups of local populations (population connectivity—the dispersal of individuals among populations) into a metapopulation (i.e. a population of populations, *sensu* Levins 1969), with the dynamic nature of marine environments causing widely varying demographic rates within and among subpopulations (Bertness et al. 1991, Phillips 2005). How such demographic heterogeneity influences marine metapopulations depends on knowledge of the spatiotemporal scales over which populations are connected via larval dispersal (e.g. Hjort 1914, Gaines and Bertness 1992, Kinlan et al. 2005, Noonburg et al. 2015, Shima et al. 2015). Identifying these scales has important management implications, as it sets the spatial scales for assessing, among other things, environmental impacts and recovery from disturbances (Reed et al. 2000), the spatial structure of exploited fisheries (Botsford et al. 2009), broad-scale conservation planning (Trakhtenbrot et al. 2005, Trembl & Halpin 2015) and the design of marine reserve networks (Roberts 1997, Shanks et al. 2003, Gaines et al. 2010).

*The components of successful dispersal*

Whether an individual larva is ultimately successful in dispersing from its birthplace to its recruit location depends on the culmination of a suite of intrinsic and extrinsic processes operating in early life (Pineda et al. 2009). In a previous study, Trembl et al. (2015a) presented a framework for describing the four stages of population connectivity—the three stages of dispersal (Clobert et al. 2009) and the final stage of recruitment (post-settlement survival to reproduction), which determines reproductive population connectivity, dispersal of individuals that survive to reproduction (Pineda et al. 2007, Shima & Swearer 2010), and is important in evolutionary models of dispersal (Travis et al. 2012). This framework outlines the key drivers acting upon each stage of connectivity, capturing the biophysical complexity of this process for benthic marine species with biphasic life cycles (Figure 1). Stage 1 is the initiation of emigration in which some number of propagules (gametes, larvae or spores) are spawned. The parameters important in this stage are related to reproductive output (i.e. adult abundance, fecundity, egg quality and fertilisation success). Stage 2 is transport and movement,



**Figure 1** The four stages of successful larval dispersal, resulting in population connectivity in benthic marine organisms. (Modified from Trembl, E.A. et al. 2015a.)

where the disperser's trajectory is determined both by the potential advection and turbulence of currents and the motility and behaviour of individuals. Transition through this stage depends on larval survival and development rates, particularly sensory and motility capabilities that determine behaviour, and the extrinsic roles of currents and the spatial structure of the pelagic environment (i.e. the quality of the ocean matrix and the abundance of predators and prey). Stage 3 is settlement, which marks the end of the dispersal period and occurs when dispersers actively settle into some suitable habitat patch, either within the natal source site or in a non-natal location. This stage can also be biophysically complex and governed by intrinsic (settlement competency window—from competency to duration limit of the larval period, behaviour, motility and sensing) and extrinsic (habitat quality and structure) factors, which all influence the likelihood of survival during this habitat transition. Stage 4 is recruitment, which occurs when some settlers survive and mature to reproduce, thereby contributing to subpopulation demographics and gene flow. Recruitment into the adult stage is determined by individual growth and survival to maturation, which are influenced by habitat quality (including nursery grounds), disturbance, local ecology (competition and predation) and individual condition and phenotype. Together, these four stages capture the full biophysical complexity of the processes determining population connectivity.

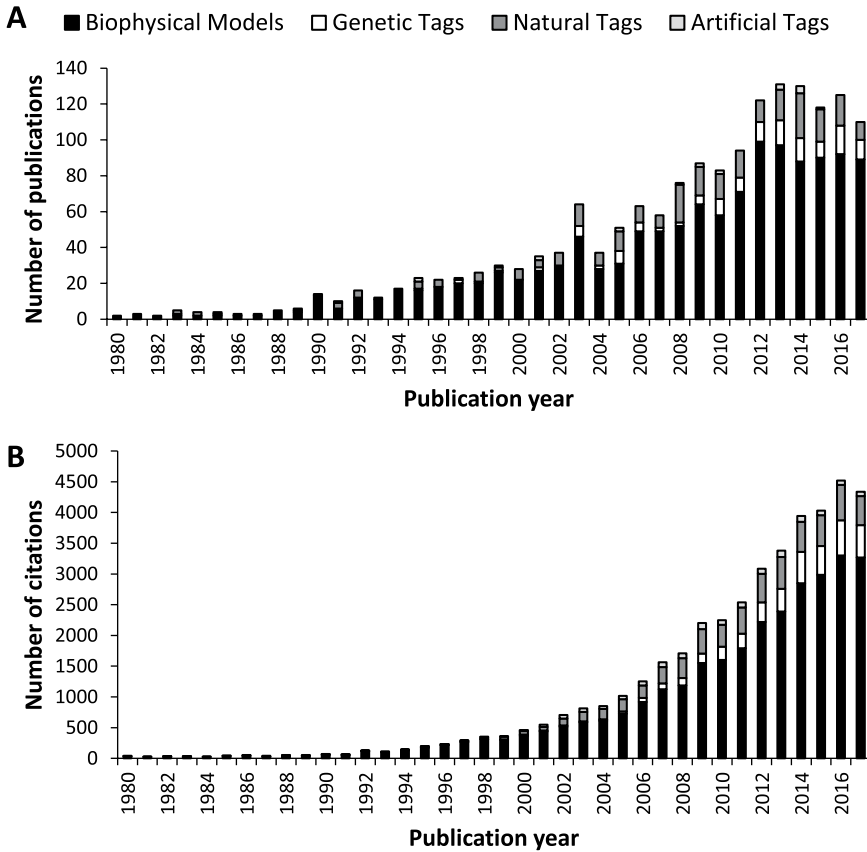
### *Methods for estimating dispersal: The rise of the machines*

Empirically generating this level of insight into the connectivity process, even for a handful of species, has been immensely difficult because of the challenges of studying and quantifying dispersal in the sea. Not only do most marine animals produce large numbers of minuscule larvae that suffer high mortality and that can be difficult to identify to the level of species, but they typically spend days to months developing in the water column, where they are subject to transport by ocean currents, potentially over large distances away from their natal population (Swearer et al. 2002, Cowen & Sponaugle 2009). These spatiotemporal scales make the tracking of larvae virtually impossible, except in the rare cases where it is possible to follow larvae *in situ* (e.g. the short-lived and large larvae of ascidians; Olson 1985). As such, most estimates of dispersal are based either on indirect empirical methods (e.g. parentage analysis, genetic assignment tests, fluorescent staining, enriched stable isotope labelling, and assignment tests using environmental markers) that rely on the collection of successful dispersers to determine where they came from [and usually not how they got there, but see Shima & Swearer (2009, 2016) for applications of fish otolith elemental time series to reconstruct dispersal histories] or on theoretical estimates of potential dispersal trajectories based on biophysical models (for reviews of these methods, see Levin 2006, Cowen & Sponaugle 2009, Jones et al. 2009, Leis et al. 2011).

Although these approaches have different strengths and weaknesses depending on the spatial and temporal scales of interest, empirical approaches for quantifying demographic connectivity are often logistically and financially costly and provide only snapshot estimates of dispersal, usually for a few sample sites and over limited geographical scales. Consequently, biophysical models have long been the dominant approach for estimating potential dispersal patterns and resulting connectivity outcomes in marine systems, even with the development of new methods and technologies fueling the rapid rise in empirical marine larval dispersal research over the past fifteen years (Figure 2; see also Jones 2015). Since 1980, 77% of marine larval dispersal research per year has been modelling studies (mean [95% confidence interval (CI)] annual proportion of studies: 0.766 [0.791–0.812]), and this pattern has remained constant over time (linear regression of proportion of modelling studies against publication year: slope parameter estimate (95% CI) =  $-0.0007$  ( $-0.0051$ – $0.0036$ ),  $n = 38$ ,  $p = 0.724$ ).

### *Horizon scan—How well are we doing?*

Given the long history of coupling Eulerian ocean circulation models with Lagrangian particle tracking models to predict patterns of larval dispersal, it seems to be an appropriate time to assess



**Figure 2** Temporal trends in (A) publication and (B) citation rates for the principal theoretical (biophysical models) and empirical (genetic, natural and artificial tags) methods for estimating contemporary marine larval dispersal. Data are based on an ISI WoS publication search and citation report (performed on 1 May 2018) using the following Boolean search terms, with additional refining based on article titles and abstracts: *Biophysical Models*—(larv\* OR propagul\* OR egg\*) AND (transport\* OR retention OR dispers\* OR connectivity OR ‘residence time\*’) AND (hydrodynamic\* OR numerical OR biophysical OR lagrangian) AND (model\* OR simulation\*); *Genetic Tags*—(larv\* OR propagul\* OR egg\*) AND (transport\* OR retention OR dispers\* OR connectivity OR ‘residence time\*’) AND (parentage OR ‘genetic assignment’); *Natural Tags*—(larv\* OR propagul\* OR egg\*) AND (transport\* OR retention OR dispers\* OR connectivity OR ‘residence time\*’) AND (microchemistry OR ‘natural tag\*’ OR ‘natural mark\*’ OR ‘natural signature\*’ OR ‘natural composition\*’ OR ‘chemical tag\*’ OR ‘chemical mark\*’ OR ‘chemical signature\*’ OR ‘chemical composition\*’ ‘elemental tag\*’ OR ‘elemental mark\*’ OR ‘elemental signature\*’ OR ‘elemental composition\*’ OR ‘environmental tag\*’ OR ‘environmental mark\*’ OR ‘environmental signature\*’ OR ‘environmental composition’ OR ‘geochemical tag\*’ OR ‘geochemical mark\*’ OR ‘geochemical composition\*’ OR ‘geochemical signature\*’ OR ‘multielemental mark\*’ OR multielemental signature\*’ OR multielemental tag\*’ OR ‘multielemental composition’); *Artificial Tags*—(larv\* OR propagul\* OR egg\*) AND (transport\* OR retention OR dispers\* OR connectivity OR ‘residence time\*’) AND (artificial OR fluorescent OR calcein OR \*tetracycline OR alizarin OR ‘enriched stable isotop\*’ OR ‘isotop\* ratio’) AND (mark\* OR signature OR tag). Given the differences in publication history among methods and incomplete reporting for 2018 at the time of analysis, trends were trimmed to cover the 37-year period from 1980 to 2017.

our efforts at incorporating biological complexity into such modelling efforts and what consequences this might have for our understanding of actual dispersal and population connectivity. Although several studies have assessed sensitivities of modelled dispersal patterns to both particle-tracking (e.g. Simons et al. 2013) and biological-input parameters (e.g. Paris et al. 2007, Peck & Hufnagl 2012, Robins et al. 2013, Trembl et al. 2015a), there has been no specific review of this extensive body of research (however, see Bryan-Brown et al. 2017 for a broad review of marine population connectivity studies across empirical approaches).

To address this knowledge gap, we conducted a systematic quantitative review of studies that used hydrodynamic models and Lagrangian particle tracking with at least some level of biological relevance to investigate larval dispersal in marine environments. The resulting database was then used to answer the following questions:

- Is there any bias in the distribution of research effort based on geographical or taxonomic coverage?
- Are hydrodynamic models resolving ocean circulation at spatial scales (resolution and extent) relevant to the dispersal process under study?
- Where, when and how many particles are being tracked, and is this effort sufficient to capture the spatiotemporal variability in dispersal?

## **A systematic quantitative review of marine larval dispersal studies using Lagrangian biophysical models**

### *Development of the database*

We performed a literature search on 31 October 2017 using the ISI Web of Science and the following Boolean search term: (larv\* OR propagul\* OR egg\*) AND (transport\* OR retention OR dispers\* OR connectivity OR ‘residence time\*’) AND (hydrodynamic\* OR numerical OR biophysical OR Lagrangian) AND (model\* OR simulation\*). This resulted in an initial list of 1089 references. No additional references were identified through other sources. The titles and abstracts of all references were screened to eliminate irrelevant studies ( $n = 594$ ). As the purpose of the review was to evaluate biophysical models of larval dispersal, we excluded references that only modelled ocean circulation, with no particle tracking ( $n = 25$ ) and references that were not conducted on animals with pelagic larval development ( $n = 8$ ). Overall, this resulted in a final data set of 524 records (from 462 references—see Appendix).\*

### *Criteria used to evaluate studies*

A range of information was extracted from each study that can be broadly grouped into seven categories: geographical context, study animal, hydrodynamic model, particle-tracking model and the three stages of dispersal (initiation of emigration, transport and movement and settlement in natal/non-natal habitat) (Table 1). These criteria were chosen in order to answer the questions posed in our review.

## **The distribution of research effort**

Geographical and taxonomic bias in research efforts can limit inference and obscure a general understanding of larval dispersal.

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\* Access to this database is available to potential collaborators—contact the lead author for more information.



**Table 1** Criteria used to characterise biophysical modelling studies of marine larval dispersal

| Category                 | Data                                    | Description   |
|--------------------------|---|---|
| Geographical context     | Year of publication                     |   |
|                          | Country of author                       | Country of lead author at time of publication   |
|                          | Country of study                        | Left blank if the study was across multiple countries   |
|                          | Ocean/major sea of study                | Arctic Ocean, Atlantic Ocean (Baltic Sea, Mediterranean Sea, North Atlantic, South Atlantic), Indian Ocean, Pacific Ocean (North Pacific, South Pacific), South China Sea, Southern Ocean   |
| Study animal             | Type of dispersal environment           | Continental shelf, deep sea, embayment, open coastline  |
|                          | Taxonomic details                       | Class, phylum, genus, species; generic categories include generic benthic animal, coral, fish, particle, reef animal, reef fish   |
|                          | Habitat type of adult life stage        | Animal (parasitic), benthic (demersal), pelagic; left blank if study was on a 'generic' species   |
|                          | Habitat type for benthic species        | Coral reef, estuary, rocky reef, reef/soft sediment, soft sediment; left blank if study was on a 'generic' species  |
| Hydrodynamic model       | Commercial relevance                    | Fished, not fished, unknown   |
|                          | Software used                           | Name of programme, proprietary, unstated  |
|                          | Dimensionality                          | 2-dimensional, 3-dimensional  |
|                          | Area of model domain (km <sup>2</sup> ) | Calculated by drawing polygons in Google Earth and calculating the area of the polygon using <a href="http://www.earthpoint.us/Shapes.aspx">http://www.earthpoint.us/Shapes.aspx</a> . Three methods were used to determine the polygons: (1) If boundary coordinates were available, points were plotted as place-marks, and a polygon drawn using the place-marks and the coastlines as boundaries. (2) If only maps were available, boundaries were extrapolated from latitude and longitude coordinates. (3) In cases where maps were provided but with no grid references, then boundaries were inferred from the coastline shapes and any textual references provided. This was done separately for small and large domains in studies that used nested models. |
|                          | Horizontal cell type                    | Fixed, variable, unstated   |
|                          | Horizontal cell resolution (m)          | Maximum (finest) and minimum (coarsest)   |
|                          | Maximum depth of model domain (m)       | Calculated as follows: (1) the maximum modelled depth, or (2) if whole water column was modelled, the maximum depth of the modelled domain, with values taken from <a href="http://webapp.navionics.com/">http://webapp.navionics.com/</a>  |
|                          | Vertical cell type                      | Fixed, variable, unstated   |
|                          | Vertical cell number (if fixed)         | N/A   |
|                          | Vertical cell thickness                 | Fixed, variable, unstated   |
| Particle-tracking model  | Vertical cell resolution (m)            | Maximum (finest) and minimum (coarsest)   |
|                          | Software used                           | Name of programme, proprietary, unstated  |
|                          | An IBM?                                 | Yes, no   |
|                          | Model run duration (days)               | N/A   |
| Initiation of emigration | Total number of larvae released         | N/A   |
|                          | Release location                        | Constant spacing, even spread over a specified area, habitat as proxy for populations, known populations, unstated  |
|                          | Release amount/location                 | Constant, scaled to habitat area, scaled to observed number of dispersers, scaled to population size, unstated  |

(Continued)

**Table 1 (Continued)** Criteria used to characterise biophysical modelling studies of marine larval dispersal

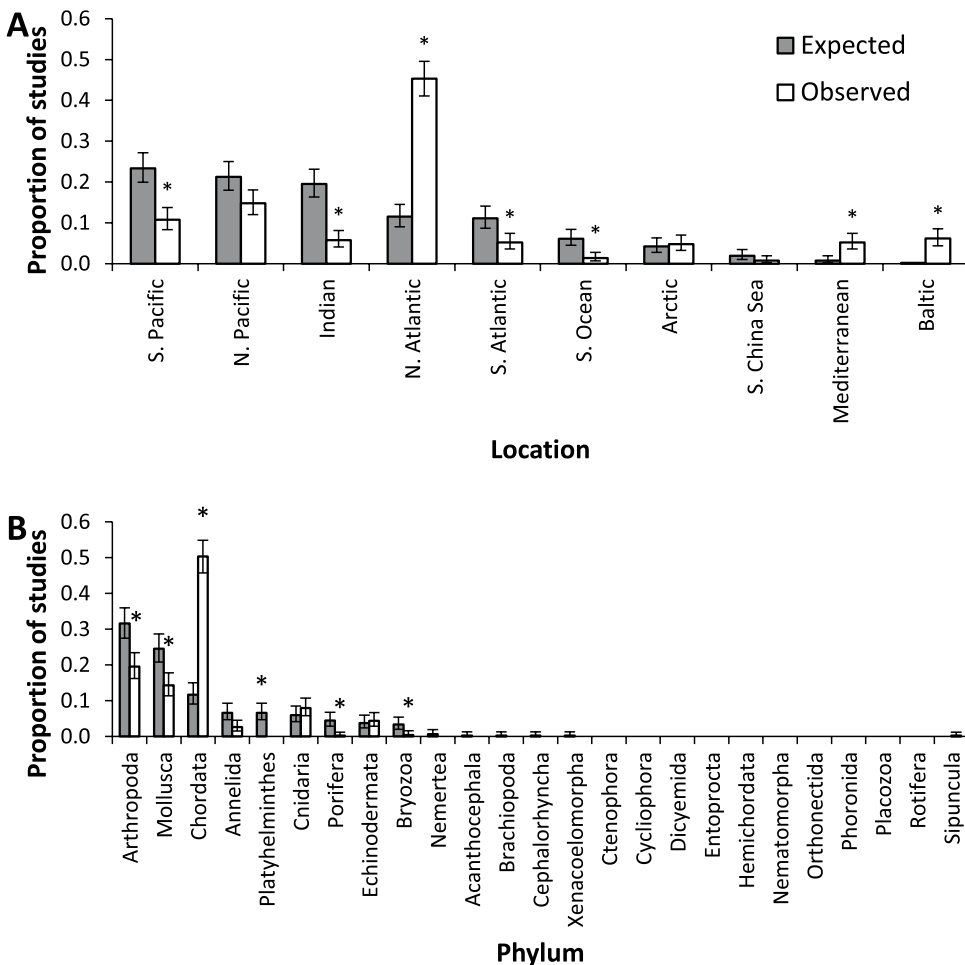
| Category                              | Data  | Description  |
|---------------------------------------|---|--|
|                                       | Release times                                       | Single, multiple at constant rate over arbitrary window, multiple with known times   |
|                                       | Released during known spawning season?              | Yes, no  |
|                                       | If single release, number/location                  | N/A  |
|                                       | If single release, duration of release (min)        | N/A  |
|                                       | If multiple releases, release frequency (h)         | N/A  |
|                                       | If multiple releases, total release duration (days) | N/A  |
| Transport and movement                | Larval mortality?                                   | Yes, no, unstated  |
|                                       | Larval mortality type                               | Fixed-generic, fixed-species specific, variable-environmentally dependent, variable- state dependent   |
|                                       | Behaviour mode                                      | Active, passive only for an initial period, passive throughout development, unstated   |
|                                       | Vertical movement?                                  | Yes, no, unstated  |
|                                       | Vertical movement type                              | Constant, constant buoyancy, variable with age/size  |
|                                       | Vertical swimming speed used (cm/s)                 | Minimum and maximum  |
|                                       | Horizontal swimming?                                | Yes, no, unstated  |
|                                       | Horizontal swimming type                            | Constant, variable with age/size   |
|                                       | Horizontal swimming speed used (cm/s)               | Minimum and maximum  |
|                                       | PLD   | Fixed, fixed competency window, set by duration of model run (unlimited), unstated, variable- modelled, variable- from collected settlers  |
| Settlement in natal/non-natal habitat | Time to competency (min PLD) (days)                 | N/A  |
|                                       | Maximum PLD (days)                                  | N/A  |
|                                       | Settlement type                                     | If within habitat zone/detection distance before end of model run, if within habitat zone/detection distance at end of PLD, if within habitat zone/detection distance before end of PLD, if within habitat zone/detection distance and competent to settle, location at end of PLD, location at end of run, no settlement, other, unstated |
|                                       | Habitat detection present?                          | No, yes—fixed, yes—variable  |
|                                       | Habitat detection distance (km)                     | Minimum and maximum  |

### *Geographical coverage*

We used sea-surface area (of oceans or other predefined regions) to generate an expected distribution of research effort (i.e. the predicted distribution of published studies in the absence of any bias) and found a clear and striking pattern of over-representation of published studies from European/North American waters (i.e. the North Atlantic Ocean and Mediterranean and Baltic seas) and an under-representation of studies in the Southern Hemisphere (South Pacific and Southern oceans) and the Indian Ocean [ $n = 521$  (three global scale studies were removed),  $df = 9$ ,  $X^2 = 1749.466$ ,  $p < 0.0001$ ;

Figure 3A]. This pattern is qualitatively similar to that observed by Bryan-Brown et al. (2017). Given the global distribution of leading research universities ([www.timeshighereducation.com](http://www.timeshighereducation.com)), this pattern is unsurprising, and others have observed similar geographical distributions of ecological research (Lawler et al. 2006, Trimble & van Aarde 2012, Hale & Swearer 2016). Research efforts are concentrated closer to shore (76% of studies), with 12% of them from coastal embayments and 64% from open coastlines. A total of 18% of studies are from the continental shelf, and 6% are from the deep sea. Although we are unable to evaluate these against an expected distribution, it seems clear that more studies are needed for more offshore and/or deepwater taxa.

These clear geographic biases in research efforts may skew our perceptions of the relevant scales and processes that shape dispersal. For example, islands that are more than 5 km apart (effectively, habitat patchiness for many benthic and demersal marine species) are two to three times more abundant in the tropics than in temperate latitudes (Leis et al. 2013). Because scales of habitat patchiness



**Figure 3** Distribution of research effort based on study (A) location and (B) phylum. The expected numbers of studies by location were based on a frequency distribution of surface ocean area (in km<sup>2</sup>) among the 10 major oceans and seas. (Data from Eakins & Sharman 2010.) The expected numbers of studies by phylum were based on a frequency distribution of accepted species among the 25 marine animal phyla with pelagic larvae. (Data from the World Register of Marine Species; accessed 1 December, 2017.) Error bars are 95% CI based on the Wilson score interval method for sample proportions. (\*indicates significant deviation from expected.)

relative to dispersal potential have important ecological consequences (e.g. Pinsky et al. 2012), an over-representation of studies from certain latitudes could lead to perceptions about dispersal and connectivity that do not necessarily hold for other areas. Also, regional variations in ocean circulation can lead to different predictions of dispersal trajectories and distances. For example, differences in amplitude, rotational speed and direction of eddies in the Northern and Southern hemispheres (Chelton et al. 2011), as well as regional differences in geostrophic velocities among major ocean basins (Gray & Riser 2014), are likely to result in variable dispersal outcomes. Dispersal outcomes will also be a function of larval life histories, which vary considerably among biogeographic regions (e.g. Marshall et al. 2012). In short, dispersal and patterns of population connectivity are likely to be context-dependent, and if the goal is to achieve a more general understanding, then this requires a widening of the geographical coverage in dispersal modelling studies.

### *Taxonomic coverage*

Most studies (78%) have been conducted on species with benthic adult life stages; 20% focus on species with pelagic adults, and 2% target species with parasitic adult life stages (51 out of the 524 studies modelled generic particles/taxa). Of the 369 studies conducted on a benthic species, most (43%) focussed on reef-associated species (coral reefs: 24%; rocky reefs: 19%), with a further 28% looking at sediment-associated species, 12% at estuarine species (split evenly between rock- and sediment-associated species) and 17% at generalist (reef and sediment) species. This distribution of research effort reflects a bias towards reef-associated species, given that the majority of benthic habitat is sedimentary. Based on the frequency distribution of currently accepted marine species among animal phyla with larval development, there is also a taxonomic bias in research effort, with considerable overrepresentation of chordate (i.e. fish) studies and under-representation of studies on arthropods, molluscs, flatworms, sponges and bryozoans [ $n = 455$  (sixty-nine studies of generic taxa were excluded),  $df = 24$ ,  $X^2 = 803.618$ ,  $p < 0.0001$ ; Figure 3B]. In part, this bias is driven by a strong focus on commercially important species (79.8% fished versus 20.2% not fished;  $df = 1$ ,  $X^2 = 126.247$ ,  $p < 0.0001$ ), with 93% of chordate studies on fished species. Again, as with other reviews of ecological research, taxonomic biases are not uncommon (e.g. Caliman et al. 2010, Bryan-Brown et al. 2017). Nonetheless, these biases almost certainly mean that the great diversity of larval developmental modes, morphologies, behaviours and life histories (e.g. Young et al. 2002) is unevenly represented. For example, this has resulted in spurious differences in estimates of marine larval dispersal based on different methods (e.g. Kinlan & Gaines 2003). If the goal is a more holistic understanding of dispersal across the full spectrum of marine biodiversity, then broader taxonomic coverage is clearly needed.

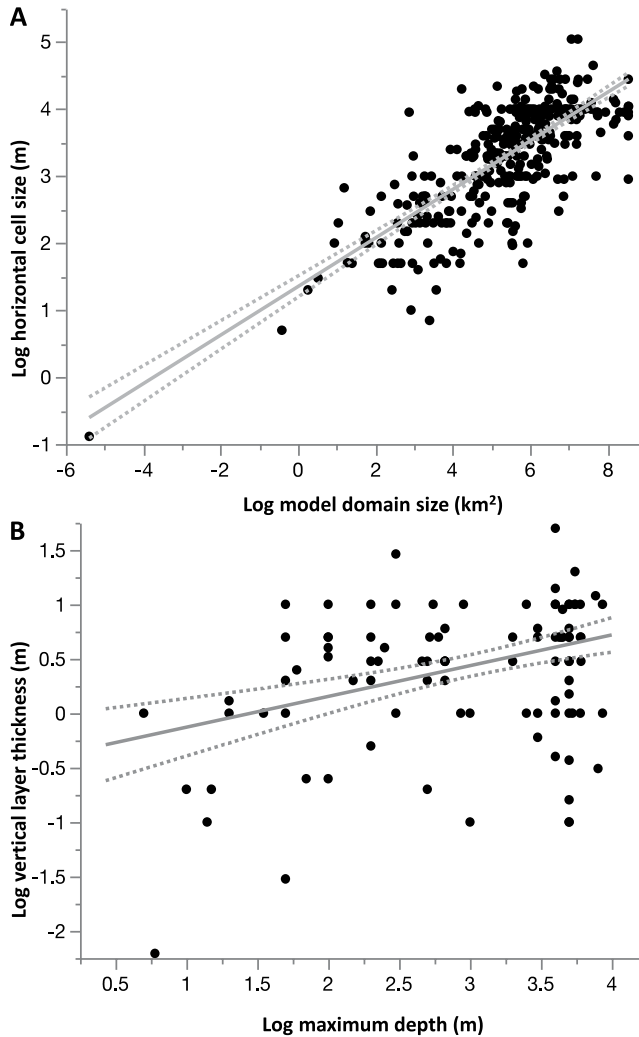
### **Matching the physics to the biology**

Although there exists a long and rich history of observations and, more recently, modelling of open ocean circulation (see Semtner 1986 and Talley et al. 2011 for historical perspectives), most of the research efforts on dispersal and connectivity appear to be driven by the interests of benthic ecologists (this is an inference based upon the over-representation of studies on benthic species and nearshore habitats). We contend that many of these research efforts use models that may be better suited to offshore regions (which has remained a strong focus of oceanographers), and in at least some instances, the models may fail to capture important features of the nearshore coastal zone where larvae of many benthic marine species are born, settle, and may even complete their entire development (e.g. Morgan et al. 2018a). Modelling the nearshore environment is notoriously difficult, as hydrographic features of the coastal zone (e.g. breaking waves, tides, runoff, and upwelling) result in ocean circulation dynamics that operate at finer temporal and spatial scales than are typically observed or modelled (Largier 2003, Nickols et al. 2012, Morgan et al. 2018b, Shanks and Morgan 2018). In situations where dispersal outcomes are largely driven by physical transport, this

spatiotemporal mismatch means that the underlying modelled ocean circulation patterns (which advect Lagrangian particles) may often fail to capture dispersal at the relevant scales for many marine species (Largier 2003, Nickols et al. 2012).

*Dimension and resolution of the model domain*

Overall, most (84%) of the 524 studies used 3-dimensional hydrodynamic models. Model domain extent varied enormously, ranging from  $4 \times 10^{-6}$  to  $3.5 \times 10^8$  km<sup>2</sup> in area and going to maximum depths of 2.7–10,000 m. Across studies with reported information, model resolution varied by eight orders of magnitude in the horizontal dimension (median cell size: 3.5 km; range: 13 cm to 110 km;  $n = 498$  studies) and was strongly correlated with model domain size (Figure 4A). Most models used fixed regular grids (67%), with a moderate number of studies using curvilinear or variable mesh



**Figure 4** Relationships between (A) horizontal model cell size and model domain size ( $R_{\text{adj}}^2 = 0.564$ ,  $F_{1,494} = 640.397$ ,  $p < 0.0001$ ), and (B) minimum vertical layer thickness (i.e. discretisation) and maximum depth ( $R_{\text{adj}}^2 = 0.133$ ,  $F_{1,128} = 20.707$ ,  $p < 0.0001$ ). When nested and/or terrain-following models were used, we used the highest (finest) resolution reported. Model fits are linear regressions (with 95% CI).

sizes (20%) or nested models (9%), with the remaining 4% unstated. For studies using 3-dimensional models, 77% used a fixed number of vertical layers; a further 6% used variable (dynamic) layers and 17% were unstated. For studies using a fixed number of layers, they ranged from 2 to 128 layers (median: 30). Most studies used variable layer thicknesses (e.g. 59% were terrain following); a further 12% used fixed thicknesses, and the remainder (29%) did not provide this information. Vertical resolution varied by three orders of magnitude (median layer thickness: 5 m; range: 1 cm to 50 m) and was only weakly related to the model's maximum depth (Figure 4B). What these results clearly show is a lack of consistency in how well resolved oceanographic models are, even when accounting for differences in domain size (residual unexplained variance: 43% horizontally, 90% vertically).

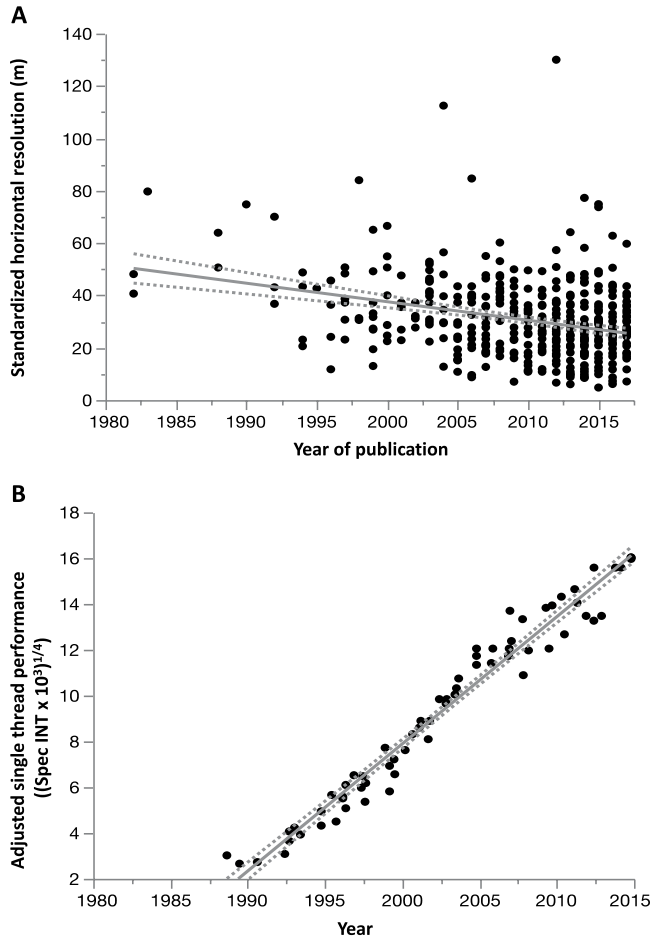
### *Are we keeping pace with computational advancements?*

Although downscaling models will likely improve the representation of velocity flow fields, particularly along topographically complex coastlines, substantial computational costs are incurred. Computational costs scale in proportion to the number of cells and the number of time steps in the model (Kim et al. 2014); for example, increasing a 3-dimensional model resolution by a factor of two (i.e. twice the number of meridional cells, zonal cells and depth cells and twice the number of time steps) would increase the computational requirements by approximately sixteen times (or even more, depending on maximum velocities and model stability). Over the past 35 years of larval dispersal modelling, advancements in computer technology [e.g. processor power, cache, random access memory (RAM), graphics processing units (GPUs)] mean that these computational costs, in terms of time and money have decreased and are continuing to decrease. This begs the question of whether hydrodynamic model resolution has increased over time, and if so, whether the rate of increase is proportional to increases in computational speed (after accounting for the scaling of computational costs).

After adjusting for the effect of model domain size on horizontal resolution (see Figure 5), model resolution has been getting finer (on average) with time (Figure 5A), a decrease in cell size of 49% over the 35 years of published studies. Over a comparable time period (26 years), computational speed (based on a single-thread performance of CPUs) has increased by over 800% (Figure 5B). If downscaling is beneficial because it usually leads to better representation of fine-scale current velocities acting on larvae (particularly nearshore), then the rate at which this has occurred over the past three decades has not been limited by computing power. This, of course, does not account for the fact that downscaled models may necessarily include more equations, more parameters, and therefore more memory requirements, which may contribute to this slower-than-expected increase in resolution.

### *Is the tail still wagging the dog?*

Although more coarsely resolved velocity fields have been shown to realistically capture long-distance dispersal pathways, particularly among offshore islands where oceanic conditions can lead to greater spatial coherence in velocity fields (e.g. Davies et al., 2015; Trembl et al. 2015b; Liggins et al. 2016), there is the possibility that they can lead to biases in characterising the spread of particles from release locations in more coastally dominated environments and for more local-scale questions. Several recent simulation studies have shown that both estimates of transport distances and direction, as well as the relative dispersion of particles, are very sensitive to model resolution, over both short (50–800 m, 1–12 h; Lyngé et al. 2010) and long (0.8°–0.56°, 1–30 days; Putman & He 2013) length and time scales, respectively. In the case described in Putman & He (2013), finer-resolved models more closely matched *in situ*, near-surface drifter trajectories. Small-scale flow conditions, such as those found in coastal boundary layers, can lead to greater particle retention times and a reduction in the mean but an increase in the variance of dispersal distances (e.g. Nickols et al. 2012). These findings are intriguing and suggest that future efforts at downscaling models in coastal ecosystems may lead to more evidence for greater local retention times for some particles, as well as greater maximum dispersal distances.



**Figure 5** (A) Relationship between standardised horizontal model resolution (cell size) and year of publication ( $R_{\text{adj}}^2 = 0.090$ ,  $F_{1,494} = 49.948$ ,  $p < 0.0001$ ), and (B) trends in computer processing efficiency (as measured by single-thread performance (SpecINT × 10<sup>3</sup>) of CPUs) over time ( $R_{\text{adj}}^2 = 0.964$ ,  $F_{1,64} = 1740.411$ ,  $p < 0.0001$ ). Horizontal model resolution was standardised to account for the effect of domain size. This was done by saving the residuals of the linear regression in Figure 4A, adding those residuals to the mean log horizontal resolution and back-transforming to the original units. The single-thread performance data were downloaded from <https://www.karlsruhp.net/2015/06/40-years-of-microprocessor-trend-data/>. These computer processing efficiencies were adjusted by a 1/4-power weighting, as computational costs for a 3-dimensional hydrodynamic model generally increase with model resolution in proportion to cell size<sup>-4</sup> (e.g. Kim et al. 2014). Model fits are linear regressions (with 95% CI).

### *Characterising the dispersal process*

Because of the computation costs associated with estimating velocity fields, Lagrangian particle-tracking models run most efficiently when they are run offline or independent to the ocean model (e.g. Jones et al. 2016). Determining how many particles to release and from how many locations represent trade-offs between computational time and precision. Releasing too few particles, from too few locations within a source area/patch or all at once can result in poor characterisation of the underlying variability in potential dispersal trajectories from that source (Brickman & Smith 2002). Although the optimal number of particles to release will depend (at least in part)

on what question is being asked, the findings of Jones et al. (2016) suggest that releasing <1000 particles per location is likely to result in considerable error in estimates of dispersal and population connectivity. In contrast, Simons et al. (2013) found the minimum number of particles per location in their model domain ranged from 2800 to 5900 for tracking times of 15 and 30 days, respectively.

Relevant studies in our database ( $n = 299$  with reported data) released between 72 and  $4.9 \times 10^{17}$  particles (median: 464,495 particles) in total, with particles being released over a period of 0.15 to 2,523,744 days (median: 365 days). 38% of studies released particles in a single event/location (Figure 6A). The remainder implemented multiple releases, either within a fixed window (43%), a predicted spawning window (2%), or a known spawning window (11%); 6% of studies provided no information on timing of particle release. For the studies that used a single release ( $n = 110$ ), the number released ranged from 1 to  $1 \times 10^7$  particles (median = 1000), with 90% of studies releasing simultaneously. For studies with multiple releases ( $n = 168$  out of 327, with reported details), the number of particles released from each location ranged from 1 to  $4.2 \times 10^7$ , with a median of 178. Release intervals ( $n = 252$ ) ranged from 1 second to 1 year (median: 72 h). Surprisingly, the number of particles released has not increased over time, suggesting that computational power is an unlikely limiting factor [linear regression of the log number of particles released per location against publication year: slope parameter estimate (95% CI) = 0.013 (-0.026–0.051),  $n = 167$ ,  $p = 0.514$ ].

Taken together, these findings raise the possibility that in some instances, the shape of the potential or realised dispersal kernel is not effectively being described: more than one-third of studies released only at a single time and about 50% of studies released fewer than 1000 particles per location. Avoidance of error due to undersampling will require careful consideration of sample size, release locations and times, duration of tracking, biophysical complexities in relation to the questions of interest and the precision required to answer them. These model parameter values will be system specific and should be informed by a sensitivity analysis (as has been suggested by others, including North et al. 2009 and Simons et al. 2013).

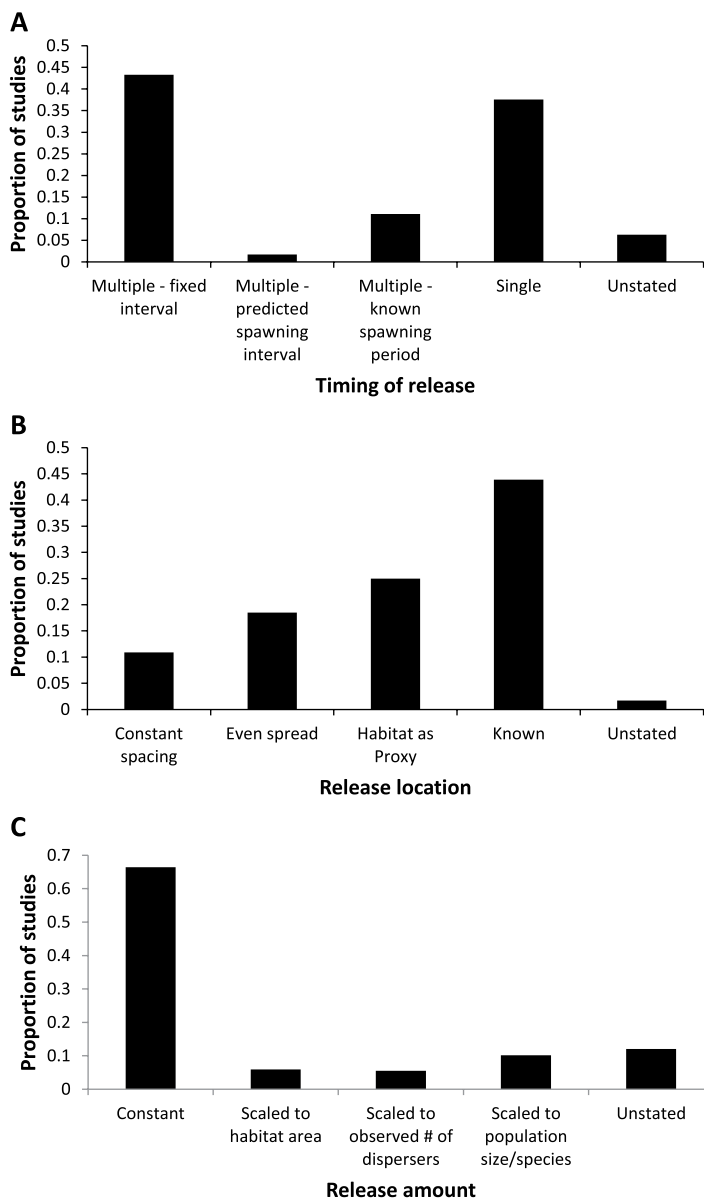
## Initiation of emigration

Benthic marine invertebrates and fishes are some of the most fecund animals on Earth. Given the stochastic nature of larval transport in coastal oceans (e.g. Siegel et al. 2008), the precise locations and timings of spawning can profoundly affect dispersal outcomes (e.g. Treml et al. 2012, Robins et al. 2013, Treml et al. 2015a).

### *Location, location, location*

Although the majority (44%) of studies released particles from known spawning/population locations (Figure 6B), the remainder either used habitat as a proxy (25%) or distributed releases evenly (19%) or with constant spacing (11%) within a target area (with a further 1% unstated). Spawning locations can strongly affect dispersal distributions due to differences in local oceanographic conditions, particularly along topographically complex coastlines. For example, it is well known that many marine species migrate to spawn in areas that are more favourable for larval retention (the member-vagrant hypothesis, Sinclair 1988). We recently showed that estimates of a range of dispersal and metapopulation metrics were strongly influenced by the location of larval release (Treml et al. 2015a), even when known release locations were only tens of kilometers apart. For species that are common and strongly associated with a particular habitat type (e.g. reef-associated), the habitat is likely to be a suitable proxy for spawning location. For species that are more mobile, however, knowing where spawning occurs will be important.





**Figure 6** The distribution of modelling studies based on (A) how and when particles were released, (B) where particles were released and (C) the number of particles released from each location and event (for studies with multiple releases), as described in Table 1.

*Timing is everything*

Only 13% of studies released particles during a known (11%) or predicted (2%) spawning period (Figure 6A). Reproductive timing in marine invertebrates and fishes exhibits tremendous diversity over diel, lunar, seasonal and annual time scales, with many of the adaptive explanations for particular spawning times related to offspring transport/dispersal (e.g. Robertson 1991, Morgan & Christy 1995). Using an environmental marker approach, Carson et al. (2010) detected consistent

seasonal differences in directionality of alongshore transport of larvae of two mussel species in southern California due to seasonal changes in the dominant current direction. As each species spawns primarily in different seasons, this led to differences in the predominant dispersal direction and resulting connectivity patterns, highlighting the importance of knowing the phenology of a species. Several recent modelling studies corroborate this conclusion by illustrating that both the timing (Romero-Torres et al. 2017) and frequency (Kough & Paris 2015) of spawning can have profound impacts on dispersal and population connectivity predictions. Given these findings, there is a clear need for models to incorporate more realistic spawning patterns.

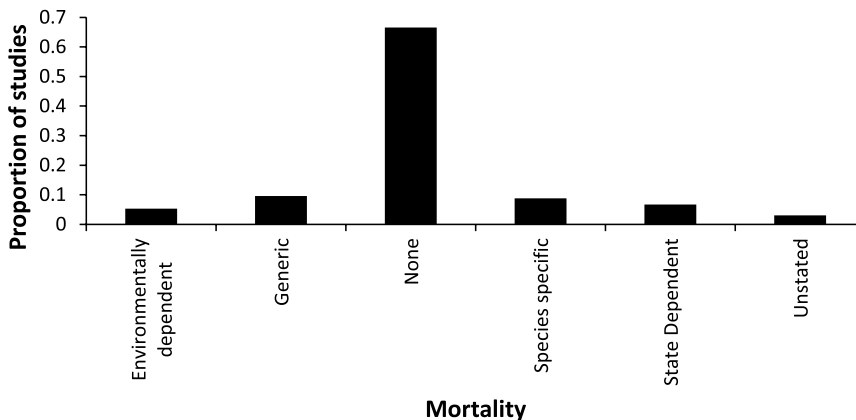
### *Accounting for spatial variability in production*

Successful dispersal between populations is not simply dependent upon a non-zero probability of larval transport from spawning to settlement locations (potential connectivity—the probability of dispersing between populations); it also requires that a sufficient number of larvae are spawned to result in at least some settlement (realised connectivity—the product of larval production and potential connectivity or the number of individuals that disperse between populations) (Watson et al. 2010). To date, most (66%) modelling studies released the same number of particles per location to estimate a probability of potential connectivity, with only 16% rescaling this relative probability to a realistic dispersal rate using population size (10%) or habitat area (6%) as an estimate of reproductive output (Figure 6C). This is likely because most studies are focussed on estimating the potential for dispersal/connectivity. These potential connectivity predictions, however, may not represent realistic dispersal rates and connectivity strengths because they do not account for the effects of larval production. Thus, they cannot be directly compared to empirical estimates (which, are by definition, measures of realised connectivity). Accounting for spatiotemporal variability in propagule production rates can result in fundamentally different predictions about dispersal and connectivity (e.g. Hameed et al. 2016, Castorani et al. 2017). Modelling efforts that can incorporate such information will be more ecologically relevant and should be a priority for future work.

## Transport and movement

### *Larval mortality*

Estimates of realised connectivity require consideration of both the numbers of propagules released and their chances of survival. Surprisingly, 70% of models did not consider mortality. Of those that did, only 29% (8.7% overall) used a species-specific mortality rate (Figure 7). Furthermore, the



**Figure 7** The distribution of modelling studies based on the parameterisation of mortality, as described in Table 1.

likelihood of models including a mortality rate has actually marginally decreased over time (logistic regression:  $R^2 = 0.03$ ; likelihood-ratio  $X^2 = 18.499$ ,  $df = 1$ ,  $p < 0.0001$ ). This limitation is, in part, a consequence of the fact that empirical estimates of mortality in the wild are rare, and those that are available are highly variable and uncertain even within taxa, ranging by more than two orders of magnitude (White et al. 2014). Most estimates suggest a mortality rate of approximately 20% per day, but several recent studies suggest this may be an overestimate (e.g. White et al. 2014, Johnson et al. 2015). Coincidentally, the 30% of models that incorporated mortality used a median rate of 18% per day (range: 0.1%–95%).

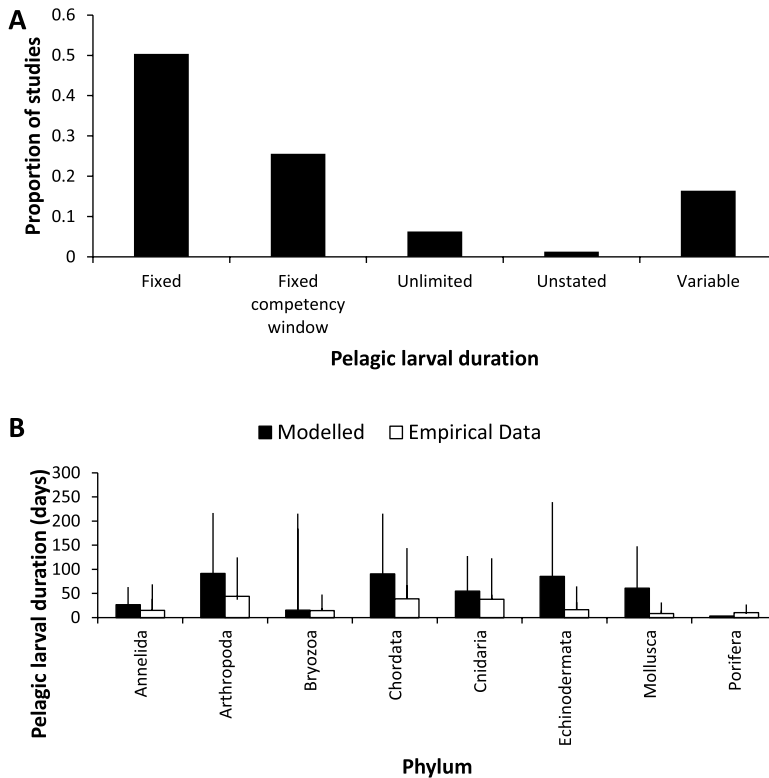
There is also ample empirical evidence that mortality rates are not constant during larval development (e.g. Cushing 1975, Leggett and DeBlois 1994, Houde 1997). However, only 7% of models allowed mortality to vary as a function of age, size or stage (e.g. stage duration hypothesis, Cushing 1975; bigger-is-better hypothesis, Bailey & Houde 1989). Regardless of the shape of the function, mortality is one of the biggest biological drivers of variation in modelled dispersal patterns and connectivity outcomes (e.g. Cowen et al. 2000, Paris et al. 2007, Treml et al. 2015a). Over the past two decades, there has been considerable development in coupling individual based models (IBMs) to hydrodynamic and particle-tracking models to investigate the drivers of variation in larval mortality (see Peck & Hufnagl 2012 for a recent review). Such approaches seem to be a fruitful avenue for improving mortality functions, including time- and space-varying components, in future dispersal modelling research.

### *Duration of the settlement window*

In most marine species, settlement can occur only once a larva becomes developmentally competent. Competency can arise from very early to quite late in the larval dispersal phase, and it continues up to the point when a larva dies or loses its capacity to settle (Anderson 1988, Leggett and DeBlois 1994). The maximum length of the pelagic larval phase [pelagic larval duration (PLD)], or the limit of competency, is arguably the most well studied biological trait that influences the dispersal potential of marine animals. Despite considerable evidence that many species exhibit high variability in age at settlement (e.g. Victor 1986), 50% of studies used a fixed larval duration (i.e. ‘the music stops’ — individual either settles or dies when PLD reached), 26% used a fixed competency window (i.e. a range over which an individual could settle), and 16% used a variable PLD (i.e. individuals took varying times to reach the PLD), with the remainder either unlimited (4%) (i.e. until the end of the model run) or unstated (1%) (Figure 8A). For studies that modelled a particular species (as opposed to a generic disperser), modelled PLDs were on average 30 days (170%) longer than observed durations for a given phyla (range: 7 days shorter to 69 days longer; 70% less to 642% more). These differences, however, were not statistically significant, given the high among-species variation within taxa (Figure 8B). This suggests that modelled dispersal distances could be overestimates for most marine species. This possibility is supported by empirically derived relationships between PLD and dispersal distance (e.g. Shanks 2009; but see D’Aloia et al. 2015) and genetic metrics (e.g. Selkoe & Toonen 2011), and because modelled predictions of dispersal and population connectivity are sensitive to variation in larval duration (e.g. Treml et al. 2015a, Defne et al. 2016).

### *Behaviour*

The past three decades of efforts to model marine larval dispersal have coincided with an increasing appreciation for the important role that behaviour can play in larval transport (Kingsford et al. 2002, Queiroga & Blanton 2005, Levin 2006). Particles have evolved from being entirely passive, to vertically migrating, and more recently, to active swimming, with the capacity for independent movement and decision-making (see Leis 2006 for a comprehensive review of the role of behaviour in the biology of larval fish).



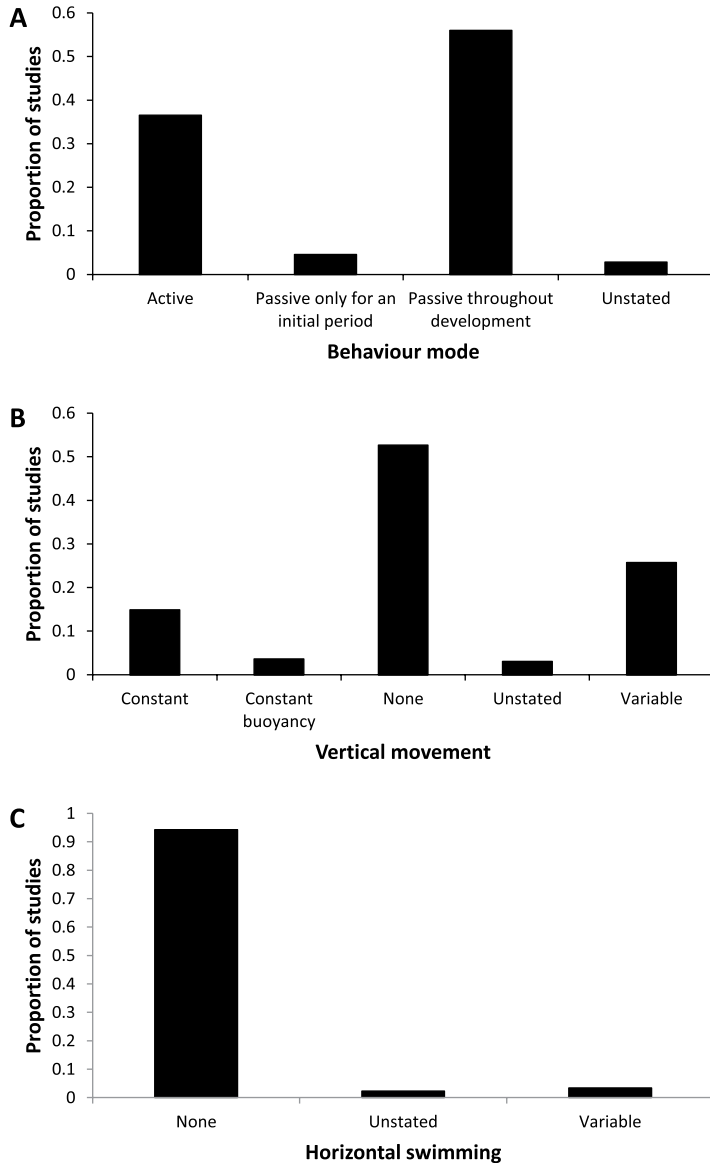
**Figure 8** The (A) distribution of modelling studies based on the parameterisation of pelagic larval duration (PLD), as described in Table 1; and (B) mean (95% CI) PLD from modelling ( $n = 454$ ) and empirical ( $n = 383$ ) studies across eight phyla. (Data from empirical studies were redrawn from Figure 1 in Bradbury et al. 2008.)

### *Dispersal as a passive or active process*

The pervasive viewpoint for many years was that larvae were planktonic, subject to the vagaries of ocean currents, with active movements operating at much smaller scales and in relation to foraging and predator avoidance (e.g. Blaxter 1969). This perspective also dominates biophysical modelling, surprisingly not changing over time, as the likelihood of models assuming passive larvae has actually marginally increased based on the year of publication (Logistic regression:  $R^2 = 0.006$ , Likelihood-ratio  $X^2 = 4.116$ ,  $df = 1$ ,  $p = 0.0425$ ). Overall, 56% of studies assumed that larvae were passive throughout development, 41% of studies modelled active behaviour throughout the larval period (36%) or after an initial passive period (3%), with a further 3% not reporting this detail (Figure 9A). Like larval mortality, larval behaviour is notoriously difficult to observe and measure, particularly in the field, and is currently an active area of research.

### *Vertical movement*

It is well recognised that small changes in vertical position of larvae can have a large influence on horizontal transport (e.g. Fortier & Leggett 1983, Queiroga & Blanton 2005, Huebert et al. 2011), and that some animals actively modify their vertical position to avoid predators, find food and take advantage of directional changes in currents (e.g. selective tidal-stream transport; Forward and Tankersley 2001, Kunze et al. 2013). Despite this fact, more than half of models (53%) only had passive dispersal (i.e. no behavioural control over the vertical position in the water column), with the remainder of the models incorporating fixed (18%: 15% swimming and 3% buoyancy) or variable



**Figure 9** The distribution of modelling studies based on the parameterisation of (A) behaviour mode, (B) vertical movement and (C) horizontal swimming, as described in Table 1.

(26%; i.e. changing with stage, age, size or environment) speeds of active dispersal (3% of studies were unstated) (Figure 9B). Given the sensitivity of modelled predictions to even small changes in vertical positioning (e.g. Fiksen et al. 2007, Robins et al. 2013), this indicates a clear need for species-specific knowledge of the biophysical processes that influence the depth distributions of larvae during development.

#### *Horizontal swimming*

There is considerable evidence, particularly for coral reef fishes, that at least late-stage larvae are capable of swimming *in situ* at speeds that exceed mean currents (e.g. Leis et al. 2009) and thus

have the capacity to behaviourally modify their transport, both in terms of advection and diffusion. Nevertheless, 95% of studies (Figure 9C) did not incorporate horizontal swimming (93.5% when only considering studies on fishes), and of the 18 known studies that did, over 70% were published in the past five years. The challenge now is gaining a better understanding of why larvae actively move (see Allen et al. 2018 for a recent review of movement ecology of marine animals with complex life cycles) so that appropriate, rule-based behavioural algorithms can be incorporated into biophysical dispersal models (see Willis 2011, Staaterman & Paris 2014 for reviews and discussion of modelling approaches).

### Settlement in natal/non-natal habitat

Settlement, the transition from pelagic to benthic environments and subsequent metamorphosis into the benthic juvenile stage, is a critical period in the life of marine animals with complex life cycles. Choosing a suitable settlement location has important consequences for future growth, survival and reproduction.

#### *Competency*

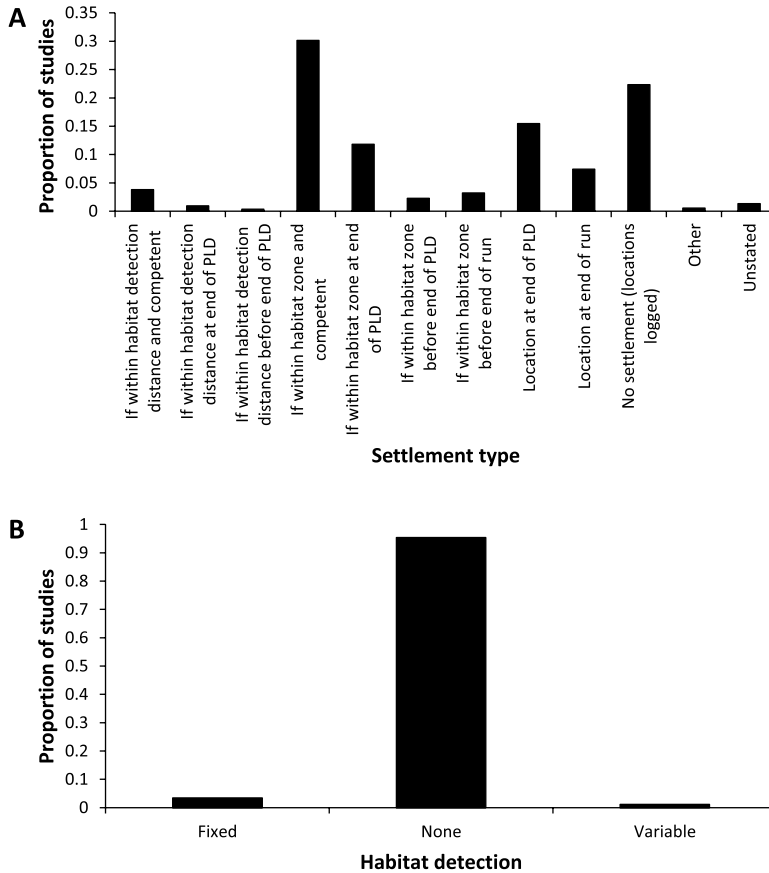
The transition between pelagic and benthic habitats can occur only if larvae are developmentally competent to settle. Species can vary considerably in how long they can remain competent (e.g. Scheltema 1971, Hadfield & Strathmann 1994), with evidence that in some species, individual larvae can delay settlement to exploit more favourable settlement times (e.g. Forward et al. 2001, Robertson et al. 1999, Shima et al. 2018) or until encountering more favourable settlement habitat (e.g. Pechenik 1990, Raimondi & Keough 1990). However, only 40% of published studies modelled some form of a competency window (e.g. using an age range or variable cutoff, Figure 10A). For the remaining studies, settlement was either simply defined by the end of the PLD (28%) or model run (8%), not modelled explicitly (22%), or imposed using a different and/or unspecified criterion (2%). We recommend greater consideration of parameters related to competency periods, as these can affect the likelihood of both local retention and long-distance dispersal (e.g. Kinlan and Gaines 2003, Connolly & Baird 2010, Treml et al. 2015a).

#### *Habitat detection and settlement*

The settlement stages of benthic marine invertebrates and fishes use a variety of sensory cues (e.g. auditory, olfactory, mechanical and visual) to detect and orientate towards settlement habitat (Crisp and Ryland 1960, Rodriguez et al. 1993, Thompson et al. 1998, Montgomery et al. 2001, Kingsford et al. 2002, Fuchs et al. 2018). This ability, combined with vertical and horizontal swimming capacity, means that behaviourally mediated habitat detection, selection and settlement is probably characteristic of most marine species, particularly fishes, and at distances that can influence dispersal patterns (e.g. Montgomery et al. 2006, Gerlach et al. 2007). However, this trait has not been incorporated into biophysical dispersal models; only 5% of published studies included either a fixed (4%) or varying (1%) ability to detect settlement habitat from some distance away (Figure 10B). Algorithms that probabilistically implement active settlement behaviours (e.g. integrating realistic horizontal and vertical swimming and habitat detection distances; Staaterman & Paris 2014, Treml et al. 2015a) may be a useful way forward.

### Recruitment

Realised dispersal and population connectivity depend on whether dispersers survive to exert some demographic influence on local populations.



**Figure 10** The distribution of modelling studies based on the parameterisation of (A) settlement type and (B) habitat detection capability, as described in Table 1.

*You have to survive to be counted*

Post-settlement mortality of benthic marine animals is variable, and rates may exceed 30% (Gosselin & Qian 1997) or even be up to 95% (Doherty et al. 2004) within the first 24 h. Mortality rates may be even higher when dispersers settle into poor-quality habitats (e.g. Burgess et al. 2012), or when they are phenotypically mismatched to settlement habitat (i.e. when an individual that is specialised to one environment settles to an alternative environment where it incurs a reduction in fitness; Marshall et al. 2010). Additional studies—particularly ones that evaluate the spatiotemporal variation of habitats and phenotype-environmental interactions, as well as for species that also transition between juvenile nursery and adult breeding habitats—would be valuable.

*Dispersal history and condition matter*

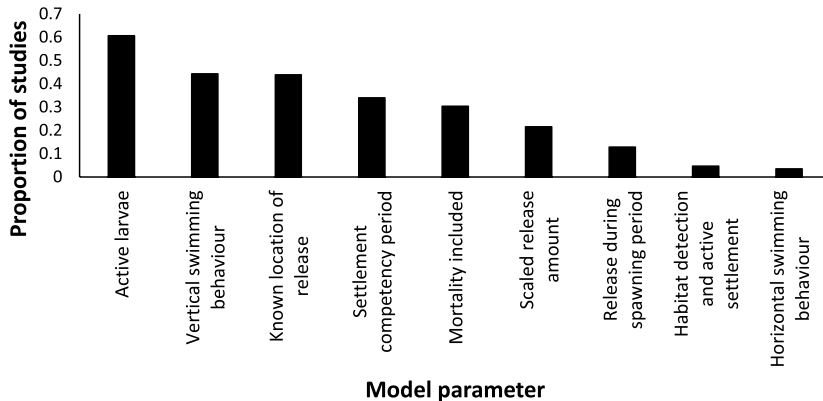
Metamorphosis is not a new beginning (Pechenik 2006), and dispersal history and the resulting impacts on larval quality can carry over into the juvenile stage (Phillips 2004) and cause differential effects (Fischer and Phillips 2014), such as selective mortality (Shima & Swearer 2010), with important consequences for population stability (Noonburg et al. 2015) and metapopulation persistence (Shima et al. 2015). As far as we are aware, these effects have not yet been incorporated into biophysical models of dispersal and population connectivity.

## Conclusions and future directions

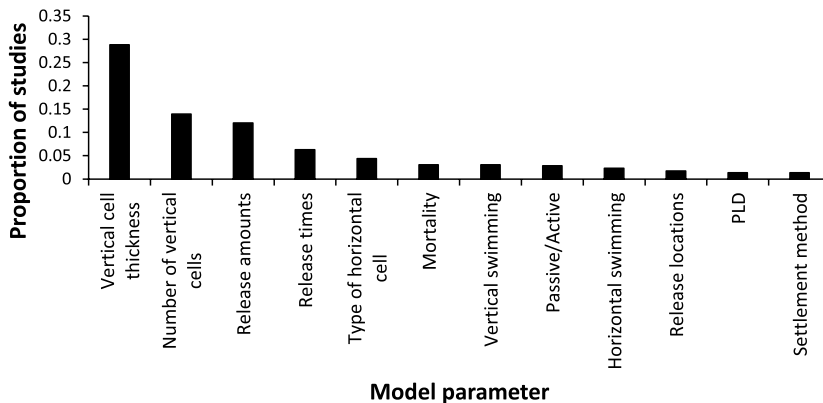
Over 75% of all marine larval dispersal studies have been based on biophysical models, and this trend is likely to continue for the foreseeable future. Our synthesis of this body of literature indicates that while models are improving in their biological realism, incorporating the bio-complexity of the four stages of successful dispersal, as outlined in [Figure 1](#), has only been realised in 2 out of the 524 studies reviewed (Tremblé et al. 2015a,b). Fewer than 50% of studies considered any single key biological parameter other than larval behaviour (61%, [Figure 11](#)). In part, this is due both to the limitations of the model platforms used and a lack of empirical data for model parameterisation.

### Reporting standards

A major challenge in compiling the data for this review was the lack of a standard way of reporting, particularly in relation to hydrodynamic model details and particle release statistics ([Figure 12](#)). While only 6% of studies failed to provide details for any individual parameter, on average, 38% of studies were missing details for at least one. One of the primary bottlenecks in the utilisation of ecological models, in general, is the lack of proper documentation (e.g. Hoch et al. 1998). We suggest



**Figure 11** The proportion of studies that included each of the key biological traits related to realised dispersal as outlined in stages 1–3 of [Figure 1](#). Traits are arranged in decreasing proportion of studies. Proportions were calculated separately for each trait.



**Figure 12** The proportion of studies that did not report details or settings of key model parameters.



that the exemplary manual of recommended practices for biophysical modelling by North et al. (2009) could serve as a template for developing such standards for documentation.

*One model to rule them all*

A striking outcome of this review was documenting just how many hydrodynamic and particle-tracking models have been used in studies of marine larval dispersal (Figure 13). Some of this diversity reflects the evolution of available modelling platforms, but many are proprietary or commercial in nature, limiting their accessibility to and uptake by a broader research community.

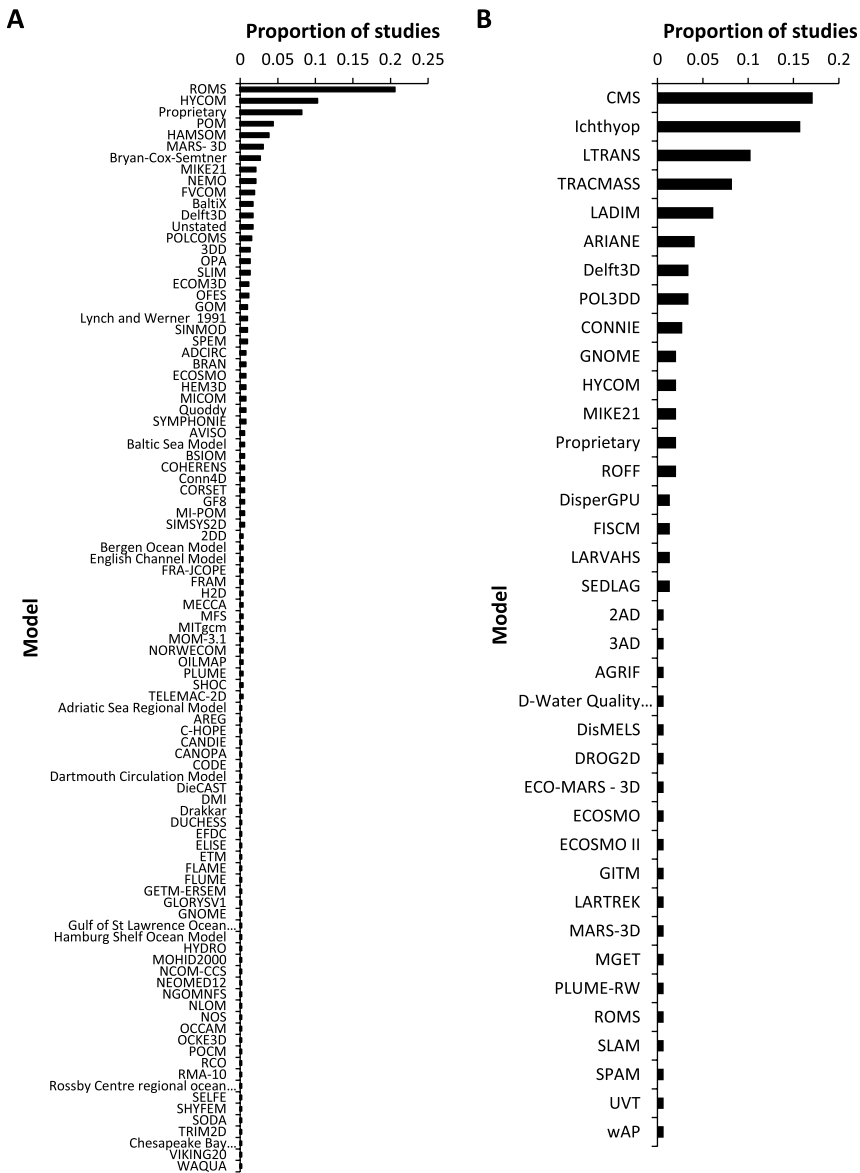


Figure 13 The distribution of studies based on the (A) hydrodynamic and (B) particle-tracking model used.

Increasingly, researchers are using open-source hydrodynamic models (e.g. regional ocean modelling system [ROMS], hybrid coordinate ocean model [HYCOM]) and making offline Lagrangian particle tracking models with increasing levels of biological complexity (e.g. connectivity modelling system [CMS], Ichthyop, lagrangian transport model [LTRANS], Tracmass, marine geospatial ecology tool [MGET]) available to other users. However, most of the innovation remains siloed to particular models or research groups instead of a collective effort being invested into one or a few platforms. We suggest that the value of biophysical models in studies of marine larval dispersal and its broader implications will be enhanced through more coordinated and collaborative efforts among researchers.

### *Data limitations*

Despite previous requests (e.g. Metaxas & Saunders 2009), we continue to need more empirical research to make models of marine larval dispersal better. In relation to some complexities (e.g. mortality), there simply are not enough field-based estimates. This is problematic when interactions between life-history traits, such as the timing and duration of propagule release, the numbers of larvae spawned, the onset and duration of settlement competency and the magnitude and variability in mortality, can lead to wildly varying dispersal outcomes. For other traits, we have gained considerable insights, such as larval locomotory and sensory capabilities (reviewed in Chia et al. 1984, Montgomery et al. 2001, Queiroga & Blanton 2005, Leis 2006). In this context, the issue is not so much a lack of empirical data, but in how such behavioural knowledge can and should be incorporated into models of dispersal. Yes, larvae can swim and detect benthic habitat from afar, but the question of whether these capabilities influence dispersal and settlement patterns directly or indirectly, such as in response to ocean physics, particularly in the coastal zone (Pineda & Reynolds 2018) or as a by-product of responses to predators and prey (Woodson & McManus 2007), remains a major challenge. It also raises an important caveat about how models can be improved to more realistically capture the dispersal process in light of data limitations. As Sir Robert May (2014) sagely said in his concluding remarks on the uses and abuses of mathematical models:

Perhaps the most common among abuses, and not always easy to recognize, are situations where mathematical models are constructed with an excruciating abundance of detail in some aspects, whilst other important facets of the problem are misty or a vital parameter is uncertain to within, at best, an order of magnitude. It makes no sense to convey a beguiling sense of ‘reality’ with irrelevant detail, when other equally important factors can only be guessed at. Above all, remember Einstein’s dictum: ‘models should be as simple as possible, but not more so’.

### *Model validation*

Models generate predictions about larval dispersal and population connectivity, which should be tested and validated against empirical observations. To date, only 33 studies have generated estimates of dispersal from biophysical models that have been combined (in all cases) with genetic data. In none of these studies were genetic estimates used (or intended) to validate model predictions. Instead, biophysical models were largely used to generate estimates of oceanographic distance to feed into models of gene flow (see the Supplementary Information 1 in Nolasco et al. 2018).

To our knowledge, Nolasco et al. (2018) is the only study to explicitly compare modelled versus observed dispersal estimates for the purpose of model testing and evaluation. They show that connectivity matrices generated from the chemistry of larval mussel shells and a biophysical model became more concordant when uncertainties in larval origins were accounted for appropriately. What is clearly needed are more empirical observations of dispersal and population connectivity that can be used to compare against simulations from biophysical dispersal models with varying levels of biological complexity and parameter settings (Pineda et al. 2007).

*Downscaling the physics and upscaling the behaviour*

Many hydrodynamic models do not capture a variety of the coastal oceanographic features (e.g. coastally trapped waves and boundary flows, frontal convergences and divergences, internal waves, etc.) that larval biologists have long known to exert important influences on larval transport. This is because many models do not extend into the nearshore, but also because resolving the structure of advective currents depends on the physics of the model, which is limited by the grid resolution of the model. As models move into the nearshore environment, downscaling will be important in order to capture smaller-scale physical processes, but these models will also need extensive field observations for model testing and validation (e.g. Taebi et al. 2012). Small-scale, subgrid processes are usually approximated using stochastic models for diffusion, which often assume a constant rate to approximate the random (and passive) spread of larvae. This is problematic as many of these processes result in spatial heterogeneity; for example, areas of convergence (fronts, thin layers) will reduce rates of diffusion.

Although most research has focussed on how larval behaviour affects advection, there is growing awareness of its relevance to diffusion as well. Several recent studies suggest that at least larval fishes can have shared dispersal histories, suggesting that they travel in cohesive groups (e.g. Ben-Tzvi et al. 2012, Shima & Swearer 2016). Given this can happen from a very early age, it suggests a significant level of behavioural control on the rate of diffusion. Larvae travelling in groups has important implications for dispersal. There is compelling theoretical and empirical evidence that animals travelling in groups are better able to navigate than individuals (Berdahl et al. 2018), and this has been recently shown for larval fishes (Irisson et al. 2015). This finding suggests that behavioural interactions among larvae can scale up to influence dispersal, but this sort of dynamic has yet to be incorporated into particle-tracking algorithms.

*The ghost in the machine?*

*The Concept of Mind* (Ryle 2000), originally published in 1949, is a critique of René Descartes, who believed in dualism, the idea that the human mind is not physical—that it exists independent of the human brain. Its author, Gilbert Ryle, referred to this idea as the “ghost in the machine.” We suggest that this idiom is a useful metaphor for the dualism in our modelling of dispersal—that behaviour exists independently of the physical state of a larva (i.e. its body). Much of the early modelling assumed that larvae were passive; only the physical state was relevant to dispersal outcomes. In recent decades, models have begun to incorporate behavioural algorithms in recognition of the fact that larvae are active participants in their dispersal. However, much of this effort has occurred independent of the physical state of the larva. There is, however, growing evidence that the movement decisions made by individual animals are informed by their local environment (context dependence) and internal state, such as its growth, age or condition (phenotype dependence; Clobert et al. 2009). Biophysical dispersal models that break through this dualism will be an important innovation moving forward.

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