Converging approaches for modeling the dispersal of propagules in air and sea

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Abstract

Terrestrial plants seeds, spores and pollen are often dispersed by wind. Likewise, most eggs and

10   larvae of marine organisms are dispersed by oceanic currents. It was historically believed that the spatial scale at which dispersal occurs was orders of magnitude smaller for plants than for fish. However, recent empirical estimates of seed and larval dispersal suggest that these dispersal scales are more alike than previously thought. The modeling approaches used to simulate aerial and aquatic dispersal are also converging. Similar biophysical models are developed, in which outputs

15   of Eulerian models simulating the main physical forcing mechanism (wind or currents) are used as inputs to Lagrangian models that include biological components (such as seed terminal velocity or larval vertical migration). These biophysical models are then used to simulate trajectories of the biological entities (seeds, larvae) in three dimensions. We reflect on these converging trends by first putting them into an historical perspective, and then by comparing the physical and biological

20   processes represented in marine larva vs. terrestrial seed dispersal models, the data used for the models output corroboration, and the tools available to perform simulations. We conclude that this convergence offers the opportunity to bridge the gap between two scientific communities which are currently largely disconnected. More broadly, we also see our comparison across systems as a

useful way to strengthen the links between aquatic and terrestrial ecology by sharing knowledge,

25   methods, tools, and concepts.

Keywords

propagule dispersal, aquatic dispersal, oceanic dispersal, marine dispersal, aerial dispersal, wind

dispersal, atmospheric dispersal, biophysical model, Eulerian model, Lagrangian model

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Introduction

Denny (1995) published an inspiring book on the comparative physics of air and water and the

consequences for life in these two media, including movement. Movement is fundamental to life

and therefore widely studied to determine why, when, where, and how organisms move (Holyoak et

35   al., 2008). How organisms move depends on their own internal state drivers (such as gain energy or

look for safety) and navigation ability but also on external factors such as the media in which they

move (Nathan et al., 2008a). External factors may have predominant impact on the movement, as,

e.g., for terrestrial seed dispersal in the air and larval dispersal in the water. Terrestrial plant seeds,

spores, pollen, fungi and insects are typically dispersed by wind (Bakker et al., 1996) together with

40   other bioaerosols (Fröhlich-Nowoisky et al., 2016) but can also be dispersed by water or animals.

Similarly, most aquatic organisms have planktonic early life stages (eggs and larvae) which are

transported by oceanic currents from spawning to nursery habitats during the larval dispersal stages

(Pineda et al., 2007; Secor, 2015). There are many natural parallels between aerial and aquatic

dispersal. In both cases dispersal occurs in three dimensions and is largely influenced by a physical

45   process, wind or ocean currents, respectively. However, until recently it was believed that one of the

significant differences between dispersal of plants and fish was the spatial scale at which dispersal

occurs. According to Kinlan and Gaines's (2003) comparative review of propagule dispersal in

marine and terrestrial environments, the genetically-estimated dispersal scales of demersal fish

species (in the range 1–1000 km) is typically orders of magnitude larger than the estimated

50   dispersal scale of terrestrial plants species (0.1 m–10 km). This lead to the view of marine systems

tending to be "open" and terrestrial systems being more "closed" (Carr et al., 2003). This view was

challenged (Dawson and Hamner, 2008) and direct estimates of fish dispersal gave a more nuanced

view (Levin, 2006). For example, Buston et al. (2011) reported a five-fold decrease of successful

dispersal over a distance from 0 to 1 km for clown anemone fish larvae. Similarly, Almany et al.

55   (2013) showed that 50% and 95% of coral grouper larvae settled within ~10 and 30 km of the

spawning aggregation, respectively. D'Aloia et al. (2015) found that the spatial scale of dispersal

for a reef fish was one order of magnitude smaller than previously thought. There are several other

examples reported in Bode et al. (2018).

60   The modeling approaches being developed to simulate propagule dispersal in air and sea have also

become similar. As an illustration of these converging approaches, the schematic views proposed by

Lett et al. (2009) and by Trakhtenbrot et al. (2014) for modeling larval and seed dispersal,

respectively, are essentially the same. In both cases, outputs of a Eulerian model simulating the

main physical forcing mechanism (currents or wind) serve as inputs to a Lagrangian model that

65   include biological components (e.g., larval vertical movement, seed terminal velocity). In the

Eulerian model the set of equations governing the dynamics of the ocean or the atmosphere are

solved numerically on a spatially-discrete domain to provide velocity fields of water or air in

(generally) three dimensions over time. In the Lagrangian (or individual-based) model the

biological entities (eggs and larvae or seeds) are represented as distinct virtual individuals. These

70   individuals are tracked over space and time while being transported by the simulated currents or

wind. The main biological parameters and processes potentially interacting with the physical

transport are also explicitly considered in the Lagrangian model. The resulting Eulerian-Lagrangian

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(or biophysical) model is used to simulate the trajectories of the larvae or seeds over the spatial

domain (Figure 1). In this study, we reflect on these converging modeling approaches by first

75   putting them into an historical perspective, and then by comparing the physical and biological

processes represented in marine larva vs. terrestrial seed dispersal models, the data used for the

models output corroboration (sensu Augusiak et al., 2014), and the tools available to perform

simulations. We finally discuss the opportunity that this convergence offers to bridge the gap

between two scientific communities which are currently relatively disconnected. More broadly, we

80   also see our comparison across systems as a useful way to strengthen the links between aquatic and

terrestrial ecology (Stergiou and Browman, 2005) by sharing knowledge, methods, tools, and

concepts, highlighting similarities and differences against which each system can be better

evaluated (Rotjan and Idjadi, 2013).

85   ## *Historical perspective*

Theoretical developments in terrestrial and marine ecology started from the same general concepts

that internal ecological dynamics (such as density-dependent relations and competitive interactions)

determined the persistence of populations and communities (Steele, 1991a, 1991b). But the large

and rapid fluctuations observed in fish stock abundance and fish recruitment lead to the alternative

90   view that external physical processes (such as advective and mixing processes in the ocean) could

actually determine the persistence of marine populations (Steele, 1991b). This hypothesis was

initially raised by Hjorth (1914) but most studies on the links between ocean variability and

fluctuations in fish populations remained qualitative until the 1970's (Werner and Quinlan, 2002).

In the 1970's and 1980's several hypotheses (such as the match-mismatch, stable ocean, member-

95   vragrant, and optimal environmental window hypotheses) were raised to conceptualize these links

(Houde, 2008). It is in that context that Bartsch et al. (1989) developed the first broadly published

physical-biological model (Miller, 2007) in order to simulate the dispersal of herring larvae in the

North Sea. Bartsch et al.'s model was still a Eulerian model, in which the concentration of larvae was simulated over time on a regular spatial grid. The Eulerian-Lagrangian modeling approach, as illustrated in Figure 1a, was developed from the mid 1990's (Hermann et al., 1996; Hinckley et al., 1996) within the broader context of individual-based modeling in ecology (Huston et al., 1988; DeAngelis and Gross, 1992). In this approach, eggs and larvae were represented as virtual individuals and tracked while being transported (Lagrangian) by the simulated ocean currents delivered on a fixed spatial grid (Eulerian). It has been referred to as biophysical model from the start (Hermann et al., 1996; Hinckley et al., 1996), although other terms, coupled physical-biological model in particular, were also used later (e.g., Miller, 2007; Werner et al., 2007; precisely the physical model is used as a forcing to the biological model). Both terms emphasize the interdisciplinary nature of the approach, requiring to take into account biological and physical processes and parameters. Miller (2007) published the first review of biophysical models of marine larval dispersal, which has just been updated (Swearer et al., 2019).

The Eulerian-Lagrangian approach for modeling terrestrial seed dispersal has been applied since 2002 (Nathan et al., 2002) and reviewed by Kuparinen (2006) and Nathan et al. (2011). This approach has also been referred to as biophysical model by Zimmer at al. (2009). Before that, models of seed dispersal were mostly phenomenological, using dispersal distributions fitted to data collected at fixed locations (Eulerian approach) or using mark-recapture and tracking techniques (Lagrangian approaches) (Nathan et al., 2012). The main objective of using biophysical models rather than phenomenological models was to understand and represent explicitly the mechanisms leading to the observed dispersal distributions instead of fitting theoretical distributions to data (Nathan and Muller-Landau, 2000). Biophysical models of seed dispersal benefited much from the Lagrangian stochastic models developed in the 1980's and 1990's by the atmospheric community (as detailed below). By contrast, it is the development of biophysical models of marine organisms

dispersal that lead to an increased use of Lagrangian stochastic models in oceanography in the 2000's (Brickman and Smith, 2002). This development has generated nearly 100 publications on marine larval dispersal modeling studies every recent year (Swearer et al., 2019). The large majority of these models are Eulerian-Lagrangian although fully Eulerian approaches are still being used. We refer to Runge et al. (2005) and Kuparinen (2006) for a discussion of Lagrangian vs. Eulerian models of oceanic and wind dispersal, respectively.

Journals which published at least 10 papers citing Bartsch et al.'s (1989) seminal work or Miller's (2007) review are all aquatic sciences journals (Table 1). Journals which published at least 15 papers citing Nathan et al.'s (2002) seminal work, Kuparinen's (2006) or Nathan et al.'s (2011) reviews are generalist, not plant-specific, ecological journals (Table 1). There is therefore no journal in common between these two sets. However, Ecological Modelling published 6 papers citing Bartsch et al. (1989) or Miller (2007) and 18 papers citing Nathan et al. (2002), Kuparinen (2006) or Nathan et al. (2011). Among the 685 publications that cited at least one of these 5 papers, only one (Fraker et al., 2015) cited Bartsch et al. (1989) or Miller (2007) and Nathan et al. (2002), Kuparinen (2006) or Nathan et al. (2011). Fraker et al. (2015) indeed briefly discussed the applicability of dispersal models to both marine and terrestrial organisms. None of the 94 publications citing Miller (2007) had the word "terrestrial" in their title, abstract or keywords. Three papers (Bonte et al., 2012; Knights et al., 2012; Moritz et al., 2013) among the 81 citing Nathan et al. (2011) had the word "marine" in their abstract or keywords. Bonte et al. (2012) is a general review on the costs of dispersal, whereas in the two other papers Nathan et al. (2011) was cited as a general reference for terrestrial or seed dispersal, not specifically modeling. In conclusion, this quick analysis of the literature suggests that the methods used to model larva and seed dispersal converged largely independently of each other.

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Table 1

Of particular interest for our analysis are two publications (van Dijk et al., 2009; Corell et al., 2012) among the three identified in Table 1 that were published in an aquatic sciences journal (Marine Ecology Progress Series), cited Nathan et al. (2002) but not Bartsch et al. (1989) nor Miller (2007). Instead, they referred to Cowen et al. (2000, 2006), the two most cited publications using biophysical models of larval dispersal. Indeed, a total of 1,357 papers referred to one or both Cowen et al.'s (2000, 2006) paper(s). Although these papers were predominantly published in aquatic sciences journals, a significant number of these were published in generalist or ecological journals (Table 2). Still, we found only 13 publications (the two already identified at the beginning of this paragraph and Denny and Benedetti-Cecchi, 2012; Gaylord et al., 2012, 2006; Jacobi et al., 2012; Kool et al., 2010; Macfarlane et al., 2013; Nathan et al., 2012, 2003; Nickols et al., 2015; Trakhtenbrot et al., 2005; Zimmer et al., 2009) citing one of Cowen et al.'s(2000, 2006) papers and Nathan et al. (2002), i.e., < 1% of all (22 papers cited one of Cowen et al.'s (2000, 2006) papers and one of Nathan et al's (2002; 2006; 2008b) highly cited papers). Some of these papers focused on the dispersal of seaplants (van Dijk et al., 2009) or seaweeds (Gaylord et al., 2006, 2012). Some papers outlined similarities or differences between dispersal of organisms in sea and air (Corell et al., 2012; Gaylord et al., 2012, 2006; Jacobi et al., 2012; Macfarlane et al., 2013; Nathan et al., 2012; Nickols et al., 2015; Zimmer et al., 2009). Four papers (Nathan et al., 2003; Trakhtenbrot et al., 2005; Kool et al., 2010; Denny and Benedetti-Cecchi, 2012) identified premises of the converging approaches in modeling dispersal in both media (see also Dawson and Hamner, 2008), which we emphasize here.

Table 2

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Figure 1

Physical processes and models

Lagrangian dispersal of organisms are simulated by wind or current velocity fields. These velocity

175   fields are obtained by solving the Geophysical Fluid Dynamics (GFD) equations on a discretized

spatio-temporal grid. GFD equations include (EOM.1-EOM.4, Vallis, 2006):

- the mass continuity equation, which is the mathematical derivation of mass conservation of a fluid

parcel;

- the momentum equation, which is the derivation of Newton's second law for a fluid. It is based on

180   the Navier-Stokes equations, to which is added the Coriolis force to account for the Earth rotation;

- the thermodynamic equation, which is the mathematical derivation of energy conservation of a

fluid parcel;

- the equation of state, which provides the density of a fluid parcel as a function of the fluid

properties.

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The mass continuity and momentum equations are identical for both the atmosphere and the ocean,

but the thermodynamic and state equations are different between the two fluids. These differences

originate from the fact that the air is a compressible fluid, whereas seawater can be considered as

incompressible. Indeed, the density of an air parcel depends on pressure and temperature, following

190   the perfect gas law (equation 1-1, Marshall and Plumb, 2008), whereas the density of a seawater

parcel depends on temperature and salinity, not pressure. Noteworthy, there is no exact equation of

state for seawater (i.e., there is no oceanic counterpart to the perfect gas law), which rather follows

semi-empirical equations (IOC et al., 2010).

195   Interestingly, despite these differences, Mashall et al. (2004) showed that providing variables

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changes, the equations that represent atmospheric and oceanic fluid motions are isomorphic, meaning that they can be written following a common framework. For instance, in the incompressible ocean, the flow is non divergent, leading to the following equation:

$$\frac{\partial u}{\partial x}+\frac{\partial v}{\partial y}+\frac{\partial w}{\partial z}=0 \quad (1)$$

200   with (u, v, w) the zonal, meridional and vertical flow velocities and (x, y, z) the spatial coordinates. The above relationship is not true in the compressible atmosphere. Nevertheless, by changing the vertical coordinate from depth to pressure (p), and by assuming that the hydrostatic assumption is valid, the continuity equation can be rewritten as follows (equation 6-12, Marshall and Plumb, 2008):

$$\frac{\partial u}{\partial x}+\frac{\partial v}{\partial y}+\frac{\partial w}{\partial p}=0 \quad (2)$$

205   Therefore, the main equations that approximate the circulation of the atmosphere and the ocean are very similar, although some additional processes are specific to one fluid or another. In addition, most work done in atmospheric dispersion are within the so-called atmospheric boundary layer, where the flow can be assumed to be incompressible (Garratt, 1994).

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Still, there is a large number of Atmosphere and Ocean General Circulation Models (AGCMs and OGCMs, respectively), which simulate the same physical phenomena but in different ways. The models may use different horizontal grids (rectilinear, curvilinear, tripolar, tiled, unstructured mesh) and vertical coordinates systems (z-coordinate, sigma-coordinate, s-coordinate, z*-coordinate). For

215   instance, the MITgcm model, which exploits the isomorphism between the ocean and the atmosphere, is discretized on a cubed-sphere grid (Ronchi et al., 1996). This discretization method, which divides the Earth sphere into 6 faces, is used to better simulate the atmosphere and ocean of the two poles, despite their singularities. Other AGCMs, such as NICAM (Satoh et al., 2014), use a icosahedral grid. A tripolar grid is used in the NEMO ocean model (Madec and Imbard, 1996); it

220 allows to overcome the sole North-Pole singularity and therefore to simulate the circulation of the

Arctic ocean. The models may also use different numerical schemes to integrate the partial

derivative equations in both time (Euler scheme, Leapfrog scheme) and space (depending on the

relative positions of the U/V/T points, Arakawa and Lamb, 1977). A last important difference

concerns the scientific assumptions that are made during the model construction. Circulation

225 models that have been constructed for global studies (e.g., NEMO, HYCOM for the ocean,

ARPEGE, NICAM for the atmosphere) have a coarser resolution than circulation models that have

been constructed for regional studies (e.g., ROMS, MARS for the ocean, RAMS, WRF for the

atmosphere). As a consequence, physical processes of small spatial and temporal scales, such as

cloud formation, turbulence, and ocean mesoscale eddies, can be represented explicitly in regional

230 models. But they need to be parameterized in global models, because they are smaller that the

model horizontal resolution.

In order to solve numerically the above equations on a discrete spatiotemporal computational grid,

initial conditions and boundary conditions are needed. In ocean simulations, the initial conditions

235 are usually the mean temperature and salinity 3D fields derived from observational based datasets

(such as World Ocean Atlas, https://www.nodc.noaa.gov/OC5/woa18/), whereas ocean current

velocities are initialized from rest. In atmospheric models initial conditions include the air

temperature and relative humidity, and wind velocities are initialized from rest. Boundary

conditions are also required since the ocean and the atmosphere form a coupled system interacting

240 at the air-sea interface. In ocean simulations, surface boundary conditions are the turbulent fluxes of

heat (latent and sensible) and momentum (wind stress), the shortwave and longwave solar fluxes

and the freshwater fluxes (evaporation, precipitation, and runoff). In atmospheric models, surface

boundary conditions include the land and sea-surface temperature, the land composition (such as

sand, vegetation, etc.) and the surface albedo. These surface boundary conditions are usually

245   provided by observation based data reanalyzes. For regional configurations, information about the

system at the domain boundaries are also required. These lateral boundaries can either be closed

(i.e., the domain is surrounded by virtual walls; not suitable for atmospheric models) or open (i.e.,

prescribed values encompassing a bigger domain are used).

250   Despite the common physical basis on which they are based, there are therefore differences in the

implementation of GCMs which explain the large number of physical models that have been used in

biophysical models (Swearer et al., 2019). The choice of a specific model and configuration then

depends on the question being addressed, in particular its spatial extent (global or regional study),

the domain (open or closed) and time period (climatological, interannual, hindcast, forecast) of

255   interest, and the scales (synoptic, mesoscale, submesoscale) of the important physical processes to

resolve.

Lagrangian particle dispersion models

Lagrangian dispersion models were first introduced and studied by the atmospheric community with

260   the aim of predicting the evolution of plumes of pollutants in the atmosphere. First well-known

references for Lagrangian stochastic models (LSM) include Wilson et al. (1981), Sawford (1985)

De Baas et al. (1986), and the classic landmark paper Thomson (1987). The reader is also referred

to Rodean (1996) for a comprehensive review of works and improvements in LSM for atmospheric

purposes. Developments of LSM also came from other fields such as turbulent combustion or

265   single-phase flow turbulence modeling (Pope, 1985, 1991, 1994) and recent works (Bahlali, 2018;

Bahlali et al., 2018) aimed at bridging these developments with atmospheric dispersion

applications.

Broadly, Lagrangian models reproduce the transport of a large number of particles whose evolution

270   of velocities is governed by Newton's second law. These equations generally involve the Eulerian

instantaneous fluid velocity fields. However, due to computational costs, these velocity fields (and

other fields such as pressure, temperature, turbulence, depending on the problem addressed) are

most often averaged, based either on Reynolds' statistical averaging method or on spatial and/or

temporal averages. Consequently, in order to close the system of equations, the fluctuating part of

275   these fields must be reconstructed. This is precisely where LSM come into play. Lagrangian

methods are indeed most often associated with stochastic dispersion models governing the evolution

of velocity fields associated with particles. This idea was originally proposed by Langevin in 1908

who, given the random nature of turbulence, represented the motion of particles through a stochastic

differential equation, called the Langevin equation (Lemons and Gythiel, 1997).

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Brickman and Smith (2002) and Van Sebille et al. (2018) are two reviews of Lagrangian modeling

applied to oceanography. The fundamental principles are identical to those of the atmospheric

domain, although sometimes the models used are zeroth-order Markov models, in which the

stochastic term is added to the particle positions, rather than to their velocities in first-order Markov

285   models. Fundamentally, one of the main practical implications of using a zeroth- or a first-order

Markov lies in the time (or space) scales that are considered. A first-order Markov model shows

rapid diffusion near the source (short times) and then tends to follow the diffusive law in the far-

field (long times). Zeroth-order models do not have this property and model the whole dispersion

process through a diffusive law. In consequence, if one is interested in near-source modeling, i.e., in

290   the region corresponding to the short-time limit where the fully diffusive regime has not been

reached yet, then the use of a first-order Markov model is recommended. In atmospheric studies,

this occurs when focusing on the local-scale pollutant dispersion around industrial sites for

example. Oceanic dispersion studies generally focus more on the long-range transport (Brickman

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and Smith, 2002), which is why zeroth-order Markov models are more commonly used, as they are

295 computationally less demanding. Döös et al. (2011) is an example of both approaches being used in

order to compare trajectories of simulated particles and oceanographic drifters.

Starting from a common base, Lagrangian models can then be developed for several applications

according to their own specific properties. Hence, for the dispersal of propagules, the relevant

300 biological processes included in the models are described in the following section, with a focus on

marine larvae and terrestrial seeds.

Biological processes and models

Once the wind or current velocity fields are available from the atmospheric or oceanic model

305 simulations, the minimum information required to set up a biophysical model of terrestrial seed or

marine larva dispersal is the time and location of individuals release and the duration of their

tracking. For terrestrial seeds, the duration of transport is the "seed passage time" (Nathan et al.,

2008b), which depends on seed terminal velocity and atmospheric stability (see below) but is often

fixed in models based on the duration of experiments conducted jointly with modeling, e.g. 35 days

310 in Nathan et al. (2002). For marine larvae, this duration corresponds to the planktonic larval

duration (PLD), which typically ranges from days to months depending on species (Shanks, 2009)

but is relatively well-established because the end of the PLD often corresponds to the

metamorphosis of individuals into a stage where they are able to settle. This point actually

illustrates a major difference between seed dispersal and larval dispersal: during their dispersal

315 phase most aquatic organisms develop into different life stages. Hence, most fish develop from egg

to yolk-sac larva where individuals carry their own food reserves, to early larva where they have

developed a functional jaw and pigmented eyes that allow them to catch food, to late larva where

they have fins and are therefore able to swim (Figure 1b). During this development the growing

larvae also progressively acquire more abilities to move vertically (e.g., performing diel vertical

320   migration) and horizontally (e.g., searching for food), and therefore to interact with the physical

dispersal processes (Cowen and Sponaugle, 2009; Leis, 2010). This complexity of the marine larval

life (Pineda et al., 2009) is reflected by the generally large number of biological parameters and

processes included in the biophysical models of larval dispersal, such as egg buoyancy, larval

vertical migration, growth, mortality, and a time period at the end of the PLD during which larvae

325   are able to settle (Figure 1b). Garavelli et al. (2016), for example, showed how the successive

inclusion of larval growth, vertical migration, and mortality significantly changed the simulated

patterns of larval settlement for a marine gastropod along the Chilean coast. Swimming (Willis,

2011) is less frequently taken into account. The onset of schooling also begins early in marine larval

development (Hunter and Coyne, 1982; Nakayama et al., 2007; Fukuda et al., 2010) but has not

330   been directly included in biophysical dispersal models, to our knowledge. The biological parameters

included in biophysical models of seed dispersal are comparatively fewer: release height, and

terminal velocity (Figure 1c). Uplift is the most crucial process to represent adequately in these

models in order to simulate long-distance dispersal events (Nathan et al., 2002; Wright et al., 2008).

Damschen et al. (2014) formulated the probability of a seed to be uplifted above the forest canopy

335   as a function of canopy height, seed height, seed terminal velocity, mean and standard deviation of

the vertical component of wind velocity.

User-friendly tools have been developed to customize and perform marine larva dispersal

simulations easily, including Ichthyop (Lett et al., 2008), LTRANS (North et al., 2008) and CMS

340   (Paris et al., 2013). These tools are often compatible with several oceanic model outputs (e.g.,

ROMS, MARS, NEMO, etc., for Ichthyop). They have proven useful to the scientific community,

as the relatively high number of publications using Ichthyop shows (10 to 20 every year since 2012;

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references at http://www.ichthyop.org/publications), for simulating marine larval dispersal at various scales ranging from a local lagoon (Cuif et al., 2014) to a whole ocean (Putman and Naro-

345 Maciel, 2013). Similarly, for atmospheric dispersal simulations, tools such as RAFLES (Bohrer et al., 2009), HYSPLIT (Rolph et al., 2017) and others (Tesson et al., 2016) exist. Although HYSPLIT, for example, was mostly designed to simulate the dispersal of atmospheric pollutants, it has also been used extensively to simulate the dispersal of insects (see Makra et al., 2018 and the references therein), seeds (Liu et al., 2018), spores (e.g. Grinn-Gofron et al., 2016), pollen (e.g. García-Mozo

350 et al., 2017) and microbes (Mayol et al., 2014) in the air. The most recent and spectacular example is the use of HYSPLIT to simulate the overnight wind-dispersed trajectories of malaria mosquitoes (Huestis et al., 2019). We are not aware of applications to arthropod aerial dispersal using silk, where pre-ballooning and ballooning behaviors were described as ways to some extent "control" the wind dispersal (Bell et al., 2005).

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Biophysical model outputs corroboration

A direct corroboration of simulated dispersal trajectories is still challenging because it is currently possible to track *in situ* only a limited number of seeds on land (Skarpaas et al., 2004) and even less larvae in the sea (Leis et al., 2006). The physical part of the biophysical models can be evaluated by

360 comparing trajectories of real vs. simulated oceanographic drifters in the sea (e.g. Fossette et al., 2012) and atmospheric balloons in the air (e.g. Riddle et al., 2006). The complete, biophysical, models outputs have been corroborated using similar trapping experiments for larvae (e.g. Sponaugle et al., 2012) and seeds (e.g. Nathan et al., 2002; Stephenson et al., 2007; Skarpaas et al., 2011; Liu et al., 2018). Alternatively, artificial objects mimicking propagules were also used in the

365 sea (Hrycik et al., 2013) and in the air (Damschen et al., 2014) to compare observed and simulated dispersal kernels. Empirical estimates of ecological connectivity (sensu Leis et al., 2011) using parentage analysis (Jones et al., 2005; Planes et al., 2009) or chemical marking of calcified

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structures such as fish otoliths (Jones et al., 2005; Thorrold et al., 2006) have only recently been compared to marine larva biophysical model outputs (Cuif, 2014; Nanninga et al., 2015; Klein et

370   al., 2016; Calò et al., 2018). By contrast, empirical estimates of evolutionary connectivity (sensu Leis et al., 2011) have been extensively used in conjunction with biophysical models of marine larva dispersal in the last 15 years (e.g. Gilg and Hilbish, 2003; Gerlach et al., 2007; Putman and Naro-Maciel, 2013; Buonomo et al., 2017). Genetic (e.g. García et al., 2007; Ismail et al., 2017) and chemical (Herrmann et al., 2016) marking methods have also been used to estimate dispersal on

375   land, and some of these methods are particularly useful to assess rare long-distance dispersal events (Ouborg et al., 1999; Cain et al., 2000). Back-tracking the putative origin of collected organisms using a biophysical model is also an approach used for both marine (Mariani et al., 2010; Holliday et al., 2012; Bauer et al., 2013; Fraker et al., 2015; Calò et al., 2018) and terrestrial (Grinn-Gofron et al., 2016; García-Mozo et al., 2017; Huestis et al., 2019) individuals, often as a complement to

380   other genetic or chemical marking methods in recent studies (Fraker et al., 2015; Grinn-Gofron et al., 2016; Calò et al., 2018).

Conclusion

Our analysis shows that the methods used to model and measure marine larva and terrestrial seed

385   dispersal are converging largely independently of each others. More broadly, similar biophysical modeling approaches are now largely applied to simulate aquatic and aerial dispersal. The physical parts of these models are similar to the extent that the main equations that approximate the circulation of the ocean and the atmosphere are very much alike. Hence, the geostrophic balance between the pressure gradient force and the Coriolis force implies that currents follow sea surface

390   height contours in the ocean in the same way as winds follow isobars in the atmosphere. The biological parts of the biophysical models depend on their application to marine eggs and larvae or

terrestrial seeds, spores, pollen, and insects, but the main assumption of weak motion capacity of

the biological entities compared to the fluid velocity applies to all. The two scientific communities

using these approaches are currently still largely disconnected, although high-impact publications

395   (Cowen et al., 2000; Nathan et al., 2002; Cowen et al., 2006) contributed to sharing knowledge

between them. Sharing methods and tools could also help bring these two communities together.

For example developing a common simulation tool for larval and seed dispersal (e.g. a Lagrangian

model using outputs from RAMS for seed dispersal or from ROMS for larval dispersal), using the

same methods for identifying subpopulations (Jacobi et al., 2012) or ecological neighbours (Treml

400   and Halpin, 2012), and deriving similar graph metrics (Treml et al., 2008; Urban et al., 2009;

Thomas et al., 2014) and connectivity indices (Kool et al., 2013) from dispersal simulations. Hence,

OpenDrift was recently proposed as an open-source generic Lagrangian tool for modeling

trajectories in the ocean and in the atmosphere (Dagestad et al., 2018). It has just been used to

simulate the transport of environmental DNA in the ocean (Andruszkiewicz et al., 2019) and could

405   be equally applied to simulate the transport of eDNA in the air as both media can transport eDNA

over long distances (Barnes and Turner, 2016). Measuring the same quantities in the field like

connectivity, self-recruitment, and local retention (Kool et al., 2013; Burgess et al., 2014; Lett et al.,

2015) would also be helpful for comparative studies. There are a number of similar perspective

objectives outlined by the two scientific communities that would legitimate common work,

410   including linking the biophysical dispersal models to population dynamics models (e.g. Carson et

al., 2011; Nuttle and Haefner, 2005) and assessing the value of these models to evaluate spatial

managements plans like marine reserves (White et al., 2014) and terrestrial corridors (Damschen et

al., 2014). Biophysical models applied to plants dispersed by ocean currents, such as in mangroves

(Van der Stocken et al., 2019) and coastal dunes, or by overland flows (Thompson et al., 2014),

415   could play a critical role in bringing these two communities together. Hence, a promising modeling

approach combining oceanic and aerial dispersal was recently applied to simulate trajectories of

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mangrove propagules for species with different sensitivities to wind (Van der Stocken and

Menemenlis, 2017). Similarly, our comparative study across systems is particularly relevant for

driftwood and other drifting vegetation debris hosting both terrestrial and marine dispersers (de la

420   Peña et al., 2011; Rotjan and Idjadi, 2013) for bioparticles of marine origin dispersing into the

atmosphere (Wilson et al., 2015; Fröhlich-Nowoisky et al., 2016; Mayol et al., 2017). There is also

an opportunity to aggregate other scientific communities that begin using biophysical models to

study the dispersal of aquatic or aerial plankton, e.g. in freshwater lakes (Ludsin et al., 2014). We

hope that our study highlighting the converging approaches used to model the dispersal of

425   propagules in marine and terrestrial environments will also contribute to the development of closer

ties between these scientific communities in the future, and thereby participate to a unified research

on movement ecology (Nathan et al., 2008a). In line with previous calls (Stergiou and Browman,

2005; Menge et al., 2009; Webb, 2012; Rotjan and Idjadi, 2013), we also expect this study to

strengthen the links between marine and terrestrial ecologists.

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List of abbreviations

AGCM: Atmosphere General Circulation Model

GFD: Geophysical Fluid Dynamics

LSM: Lagrangian Stochastic Model

435   OGCM: Ocean General Circulation Model

PLD: Planktonic Larval Duration

Declarations of interest

None

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Author contributions

CL analyzed and interpreted the WoS citations data, NB was the major contributor of the "Physical processes and models" section of the manuscript, MB was the major contributor of the "Lagrangian particle dispersion models" section, CL was the major contributor of the "Historical perspective",

445 "Biological processes and models" and "Biophysical model outputs corroboration" sections. All authors read and approved the final manuscript.

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Journal	Number of publications citing	
	Bartsch et al. (1989) or Miller (2007)	Nathan et al. (2002), Kuparinen (2006) or Nathan et al. (2011)
Fisheries Oceanography	19	0
Marine Ecology Progress Series	16	3
ICES Journal of Marine Science	16	0
Progress in Oceanography	14	0
Canadian Journal of Fisheries and Aquatic Sciences	11	0
Continental Shelf Research	11	0
Journal of Ecology	0	33
Ecology	0	18
Ecological Modelling	6	18
Oikos	0	16
Total	204	482

Table 1: Journals with at least 10 publications citing Bartsch et al. (1989) or Miller (2007) or with at least 15 publications citing Nathan et al. (2002) , Kuparinen (2006) or Nathan et al. (2011) (source Web of Science 16/11/2018). The 10 and 15 threshold values were used to get a similar limited number of journals in both cases.

Journal	Number of papers citing Cowen et al. (2000) or Cowen et al. (2006).
Marine Ecology Progress Series	138
Plos One	77
Marine Biology	54
Molecular Ecology	53
Coral Reefs	43
Fisheries Oceanography	29
Bulletin of Marine Science	26
Ecology	26
Canadian Journal of Fisheries and Aquatic Sciences	24
ICES Journal of MarineScience	22
Ecological Modelling	21
Journal of Experimental Marine Biology and Ecology	21
Proceedings of the National Academy of Sciences USA	20
Estuarine Coastal and Shelf Science	20
Total	1,357

Table 2: Journals with at least 20 papers citing one or both Cowen et al.'s (2000, 2006) paper(s) (source Web of Science 16/11/2018).
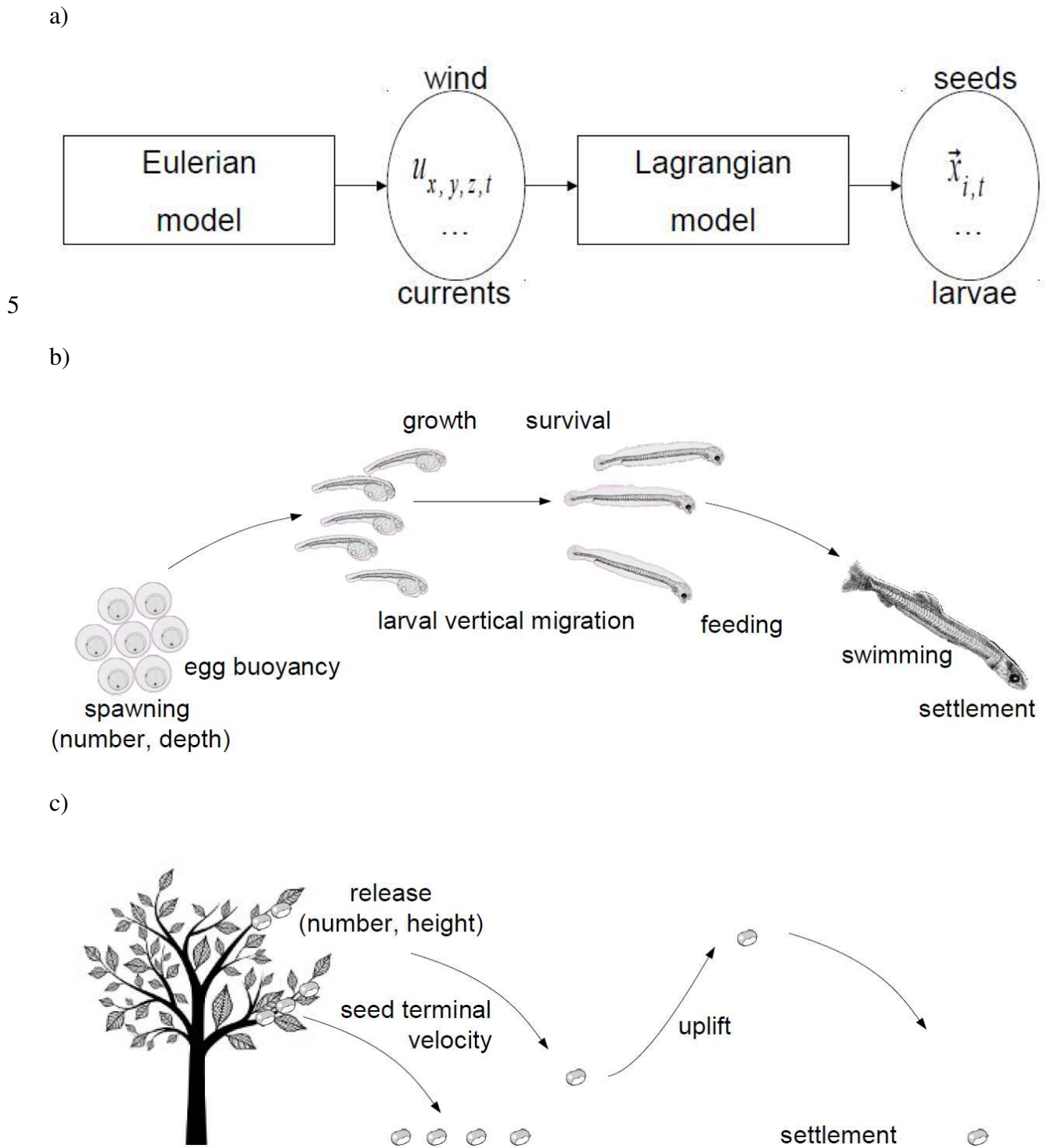
a)

5

b)

c)

Figure 1: The same general biophysical approach tends to be used to model terrestrial seeds dispersed by wind or marine larvae dispersed by currents. A Eulerian model provides three-dimensional dynamic fields of wind or current velocities u to a Lagrangian model that tracks the location x of a collection of seeds or larvae over time. Differences between the two applications reside mainly in the parameters and processes included in the models, as illustrated in b) for larvae and in c) for seeds.