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# Paradigm shifts in community ecology: Open versus closed units, challenges and limits of connectivity studies

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**Abstract**

Due to the presence of the complex life cycles involving a benthic adult and a pelagic larval phase, the study of benthic community dynamics cannot ignore investigations of the processes occurring in the water column. Current investigations focus mainly on larval dispersal from an evolutionary and a biogeographic perspective, taking into account also population connectivity, conservation planning and coastal management. In the present paper we underline the need to improve knowledge of the main traits of marine invertebrate life cycles, highlighting the limits and challenges of current approaches. Firstly, we summarized the changing approaches within community studies, following the paradigm shifts found in recent marine ecological research, from supply-side ecology to connectivity, and involving the concepts of open and closed populations. Secondly, we analysed the main larval traits influencing dispersal, paying particular attention to pelagic larval duration in light of the few available data for connectivity studies. The difficulty in estimating many of the main traits of larval ecology make numerical simulation fundamental for a better understanding of the relationship between propagule dispersal and seawater dynamics, both being highly variable. We conclude that some essential biological information is still lacking for the proper integration of the modeling approaches. Thus it is necessary to further investigate the life-cycle traits and physiological and ecological characteristics of each species, an approach known as autecology or natural history. All too frequently modern ecologists ignore such reductionist approaches, although they are essential for a full understanding of processes, such as connectivity and metapopulation dynamics.

**KEYWORDS**
biophysical models, dispersal, larval supply, larval transport, population connectivity, recruitment

## 1 | INTRODUCTION

One of the main goals of marine ecology is to understand factors regulating the distribution and abundance of organisms, taking into account benthic–planktonic coupling. Many benthic organisms in fact have a complex life cycle involving a benthic adult and a pelagic larval stage enabling them to be transported for long distances. This means that no study of benthic community dynamics is complete without investigating the processes occurring in the water column. Sexual propagules (e.g., zygotes, larvae or juveniles) can either remain near their parents or, more often, disperse by currents to sites with varyingly favorable conditions for settlement and metamorphosis. The success of each developmental stage in different habitats affects population dynamics, demography and genetic structure, and, in turn, the composition of the communities (Cowen & Sponaugle, 2009; Lowe & Allendorf, 2010; Weersing & Toonen, 2009). Although dispersal can also occur during the juvenile and adult stages (Giangrande, Geraci, & Belmonte, 1994), the larval phase is the dominant dispersal stage for most benthic species. For this reason, considerable focus has been placed on larval ecology in addressing issues of marine population dynamics.

Since the 1950s many studies have focused on the great diversity of larval development (see Giangrande et al., 1994 for a review). Many papers have also dealt with structural adaptation and functional significance of invertebrate larvae, as well as various traits of their ecology (Levin, 2006). That various types of larval development have differing durations of pelagic life has been recognized as one of the main traits of life-history strategies in marine benthic invertebrates, and is now considered an essential element in the dynamics of benthic communities (Giangrande et al., 1994). Dispersal influences the geographic ranges of species (Scheltema, 1986), the demography of marine species over ecological time (e.g., Caswell, Neubert, & Hunter, 2011), and species longevity over geological time (Jablonski, 1986). Consequently, dispersal is critical to the understanding of population dynamics and of biogeography in the marine realm (Botsford et al., 2009; Cowen, Gawarkiewicz, Pineda, Thorrold, & Werner, 2007; Cowen, Paris, & Srinivasan, 2006; Cowen & Sponaugle, 2009; McClain & Hardy, 2010). In virtually all species, dispersal is implicated as an important mechanism of connectivity and is a key element in all discussions about ecological resiliency and marine ecosystem conservation (Brown, Harborne, Paris, & Mumby, 2016; Cowen, 2002; White, Louis, Botsford, & Largier, 2010; Wood, Paris, Ridwell, & Hendy, 2014).

The importance of larval supply in driving the structure of the adult populations of marine organisms, although hinted at for at least 90 years (Young, 1990) has only become fully recognized since the 1980s (Hughes, 1990; Hunt & Scheibling, 1997; Menge & Sutherland, 1987; Morgan, 2001; Roughgarden, Gaines, & Possingham, 1988; Roughgarden, Iwasa, & Baxter, 1985; Sale, 1990). This is because, as in other ecological fields, marine benthic community research, although not dominated by true paradigm shifts, has been considered along the lines of favored themes or transient foci of interest (Paine, 2002). Consequently, notwithstanding their pivotal importance in explaining patterns of local biodiversity, biological traits, such as reproductive ones, have yet to receive their due degree of attention, as different approaches have come and gone (Giangrande et al., 1994; Levin, 2006; Menge, 1978, 1983; Menge & Sutherland, 1987).

At present, investigations about larval dispersal are also linked to the development of new fields of interest such as the configuration and determination of the optimal size and placing of marine protected areas (MPAs), restoration of habitats, understanding and control of invasive species, recognition of species range alteration by climate change, and the maintenance of regional and local biodiversity. Today, research focuses mainly on the physical and biotic processes that determine larval transport. What is still lacking is a full knowledge of life cycles, life histories and reproductive traits of species, despite these factors' importance in understanding species distributions and population connectivity. In light of this, the study of larval dispersal is crucial, both from a theoretical (evolutionary, bio-geographic) viewpoint and an operational one (populations' connectivity, conservation planning, coastal management).

This paper aims to promote further discussion about connectivity and larval dispersal, both hot topics in marine ecology. We set out to consider the life-cycle traits of marine organisms, including larval transport, larval ecology, and recruitment, all in the context of a paradigm shift in community ecology. We will focus on insights into supply-side ecology provided by connectivity studies, highlighting the limitations and the prospects of current approaches.

## 2 | FROM SUPPLY-SIDE ECOLOGY TO CONNECTIVITY

The recognition of the importance of larval transport in determining the dynamics of invertebrate populations dates back to Thorson (1950), who reviewed the most important biological traits and behaviors in the larval phase of benthic invertebrates, mainly focusing on pre-settlement events. Subsequently, especially during the 1970s, the theoretical basis of benthic ecology shifted from life-cycle-based theories to theories of density-dependent population regulation, in which benthic communities were considered closed units in equilibrium, mostly regulated by competition and predation (Diamond, 1978; Paine, 1974; Peterson, 1979). Post-settlement factors were emphasized in benthic community development models, taking for granted that larval supply was always enough to replace the populations. In this context, ecologists examined local populations with little reference to the interactions with distant populations of the same species and seldom considered the potential roles of pre-settlement events. Lottery models and the equal changes hypothesis of Sale (1977) were exceptions to this trend.

Since the 1980s, increased interest in non-equilibrium processes has led to a recognition of the key role of larval supply in adult population dynamics. As a result, studies of larval stages have become a central aspect of marine ecology (Fairweather, 1991; Gaines & Roughgarden, 1985; Lewin, 1986; Young, 1987), developing the idea of open (i.e., requiring propagule inputs from other populations) versus closed (i.e., producing their own propagule supply) populations (Gaines & Lafferty, 1995; Gaines & Roughgarden, 1985; Palmer, Allan, & Butman, 1996; Underwood & Fairweather, 1989). Supply-side ecology is the term to describe advances in this field (Lewin, 1986), initially considered novel by ecologists, but in fact a rediscovery of ideas first proposed much earlier by Thorson and others (Young, 1987, 1990), thus earning the description of "old wine in new bottles." This theory had a strong impact on research, focusing interest on the export and import of larvae and their effects on local communities. In open systems, propagules may be dispersed within and among metapopulations, obscuring any relationship between reproductive output and propagule abundance on a local scale (Strathmann et al., 2002; Swearer, Caselle, Lea, & Warner, 1999). As a result, the maintenance of a local population can depend not only on local reproductive success, but on larval supplies from other metapopulations. Supply-side interpretations of community dynamics have been applied to inter-tidal rocky-bottom communities so successfully that the open system hypothesis, albeit difficult to demonstrate, has rapidly become a new paradigm in ecological studies (Booth & Brosnan, 1995; Caley et al., 1996; Cowen, Lwiza, Sponaugle, Paris, & Olson, 2000; Hughes et al., 1999; Roughgarden et al., 1985, 1988; Warner & Cowen, 2002).

With this shift of paradigm, from the equilibrium to non-equilibrium viewpoint, the metapopulation theory (Hanski & Simberloff, 1997) replaced the dynamic theory of island biogeography (MacArthur & Wilson, 1967), becoming the rule in conservation biology, as well as in studies on patchily distributed benthic populations with high dispersal rates and high gene flows (Hellberg, Burton, Hedgecock, Neigel, & Palumbi, 2002; Sale, Hainski, & Kritzer, 2006; Weersing & Toonen, 2009). From this perspective, spatially fragmented populations are singled out as "sources" or "sinks" depending on the balance of individuals' input (birth and immigration) and output (death and emigration) (Bode, Bode, & Armsworth, 2006; Dias, 1996; Pulliam, 1988). In the era of supply-side ecology, propagules were thought to be carried by ocean currents far from their site of hatching and controlled by the same forces that act on sediment particle deposition (Butman, 1987). Given the assumed existence of this extensive dispersal and massive export for most benthic species, marine populations were considered open and with such a high degree of exchanges as to render the metapopulation approach less applicable in a marine environment than when applied to land systems (Grimm, Reise, & Strasser, 2003; Sale et al., 2006). For some taxa found in deep Mediterranean ecosystems, the existence of pseudo-populations was also hypothesized. These populations are entirely dependent on external larval supply from the Atlantic, as they are unable to reproduce in the oligotrophic Mediterranean waters (Bouchet & Taviani, 1992).

The degree of exchange of individuals among populations is a critical factor for the stability of populations and their capacity to exploit new areas and/or re-colonize areas after local extinction or extirpation (Hellberg et al., 2002). A major goal of ecologists currently is to assess the larval exchange among marine populations and to answer questions such as: What proportion of recruits is produced locally? What is the source of recruits for a local population, and where do the propagules produced in a local population go? How far do larvae travel? What are the factors that influence their transport? What are the physical processes affecting their transport? What are the roles of developmental traits, timing, location of release, nutrition, and larval behavior? All these features are key components of the modern concept of connectivity (Moilanen & Hanski, 2001).

Connectivity deals with the degree of relatedness between local populations (Cowen et al., 2000, 2006, 2007). The exchange of individuals among metapopulations affects the gene pool, regulates population size and function, and mitigates recovery from natural or anthropogenic disturbances. Low levels of exchange per generation can be linked to evolutionary (genetic) connectivity responsible for maintaining genetic similarity among populations, but having no measurable demographic effects. By contrast, demographic (ecological) connectivity, which often involves higher rates of exchange, can have a measurable impact on population dynamics (Cowen et al., 2007).

The assessment of connectivity among populations of marine invertebrates requires a knowledge of larval transport (Gawarkiewicz, Monismith, & Largier, 2007). To this end, the dispersal distances covered by larvae are expected to be closely correlated with the pelagic larval duration (Shanks, 2009; Shanks, Grantham, & Carr, 2003). This trait is unknown for many species; moreover, the distance covered by

larvae remains notoriously difficult to measure directly. In the past, larval dispersal was inferred to be extensive, due to larvae of coastal species being collected far out at sea (Scheltema, 1992); by contrast, some recent surveys have estimated a great difference in the distances covered, from tens to hundreds of kilometers for many fish species and still shorter distances for coastal invertebrates (Kinlan, Gains, & Lester, 2005), although thousands of kilometers have been reported for some decapods and sipunculans (Fogarty & Botsford, 2006; Young et al., 2012).

The present knowledge of genetic connectivity and/or isolation among populations shows contrasting levels of differentiation between species with high and low dispersal potential (Haye et al., 2014), with higher levels of differentiation in species with low potential for dispersal (Palumbi, 2001, 2003). By contrast, species with relatively long-lived and broadly dispersing larvae may show a surprising number of genetic breaks over even small spatial scales (Costantini, Fauvelot, & Abbiati, 2007). Therefore, contrary to some previous interpretations, dispersal ability may appear unusually low even for species with relatively long pelagic larval phases (Levin, 2006). This indicates that knowledge on population connectivity is still at an initial phase and that the paradigm is still changing.

## 3 | LARVAL ECOLOGY AND RECRUITMENT

The closed versus open population debate has made a significant impact on the concept that recruitment together with propagule availability and success regulate population density, as they are all fundamental factors in the replacement of individuals and in community persistence.

In determining the success of recruitment of any species an important unanswered question concerns the degree of self-recruitment in populations, especially the means of separating mortality occurring in the water column from that occurring in the benthos.

The duration of the pelagic larval phase influences their chances of long-distance dispersal, colonizing new areas and of moving away from overcrowded habitats. Indeed, in connectivity studies the pelagic larval duration is one of the fundamental traits examined and, as already pointed out, larval duration may be correlated to distance covered (Cowen et al., 2000; Kinlan et al., 2005; Shanks et al., 2003).

The features of larval development and many traits from larvae production to metamorphosis can influence dispersal and in turn the degree of larval export and import. A large array of life-cycles exists among marine invertebrates (see Giangrande et al., 1994 for a review). The period spent in the water column can be null, or can range from hours to months, leading to different probabilities of dispersal (Chia, Buckland-Nicks, & Young, 1984; Thiébaut, Lagadeuc, Olivier, Dauvin, & Retiere, 1998). The pelagic larval duration can vary widely not only among different taxa, but also between closely related ones. For example, with the exception of the long-lived mitraria larvae of *Owenia fusiformis*, polychaete larvae seldom exceed months in the plankton (Giangrande, 1997); the duration of crustacean larvae can take 12 months (Fogarty & Botsford, 2006), while larval life lasts

up to 2 years in a deep-sea starfish (Young et al., 2012) and more than 4 years in some teleplanic gastropod veligers (Strathmann & Strathmann, 2007). The feeding mode can influence the developmental duration and in turn the distance covered. Non-feeding (lecithotrophic) larvae depend on the energy stored by parents, and some can undergo metamorphosis in a short time; by contrast, planktotrophic larvae reach the size for metamorphosis by utilizing a different source of energy from parents and have a longer development in the plankton (Strathmann, 1977, 1985). Most planktotrophic larvae are capable of dispersing long distances from their site of release. However, the time spent in the water column is highly dangerous (Rumrill, 1990; Thorson, 1950) and larval mortality strongly influences dispersal. Some larvae have been shown to be able to delay their final metamorphosis for a few days or weeks (Pechenik, 1990). As shown by Knight-Jones (1953) and later by Marshall and Keough (2003, 2008), non-feeding larvae often become less selective in their choice of settlement substratum. Species that produce such larvae can affect the dispersal of their offspring by manipulating larval size (Marshall & Keough, 2008).

Although available data on larval duration are still too scant for a broad generalization, by examining an empirical data set on larval dispersal distances and propagule duration, Shanks (2009) found that the distance covered by larvae was often lower than that predicted by Lagrangian models of dispersion. Often a bimodal distribution was observed, with long propagule duration exhibiting both long and short dispersal distances. The causes of such results can be ascribed to the different reproductive and larval behaviors (Fiksen, Jørgensen, Kristiansen, Vikeb, & Huse, 2007). Larvae, in fact, have been shown to exhibit different behavioral responses to cues in the water column (Kingsford et al., 2002). It is well known that the cues are important during the competent period, when the larvae search for a substratum on which to metamorphose into benthic juveniles (reviewed by Pawlik, 1992), and that larval behavioral responses to settlement cues significantly affect transport to the benthos (Eckman, Werner, & Gross, 1994; Metaxas & Saunders, 2009). Such cues, however, act during the whole period of pelagic existence. Although the larvae of marine invertebrates are weak swimmers, swimming speeds being in the order of millimeters to centimeters per second (Chia et al., 1984), they cannot be regarded as simply passive particles carried by currents. The larvae, in fact, exhibit typical behaviors: they are able to regulate their vertical position; they can stay in the deep layer of the water column where speed is minimal; or they can migrate up to the surface layers; or, again, they can be carried in different directions by water flow according to the period when they are released (Queiroga & Blanton, 2005). *Mytilus* larvae, for instance, have been observed to change their vertical distribution according to the tidal conditions (Knights, Crowe, & Burnell, 2006); moreover, in various invertebrates, different larval behaviors have been found to explain different adult distributions under the same hydrodynamic regime (Pineda, 1999).

The fact that some larvae, despite their potential for covering long distances, are collected within the parental area supports the idea that they metamorphose near the adults because the site is more suitable than others further away (Thiébaut et al., 1998). Retention near the release site increases with increasing mortality in the water column;

conversely, dispersal away from the source decreases, (Speirs & Gurney, 2001; Swearer et al., 1999). The progeny of a permanent population, so as not to be swept downstream, need to develop a behavior enabling them to oppose the current (Byers & Pringle, 2006; Warner & Cowen, 2002). Many estuarine species exhibit swimming rhythms of reverse tidal vertical migration to aid their transport away from the hatching site. These species can exhibit tidal vertical migrations to re-enter the estuary when they metamorphose, enabling them to settle, as shown by a study on blue crab in the Delaware system. This estuary is the source area for the entire Southern system enabling the majority of larvae recruited to the Delaware system to be hatched in Delaware Bay (Epifanio & Garvine, 2001).

One of the obstacles for larval dispersal assessment is the difficulty in measuring post-settlement mortality. Recruitment limitation is, in fact, the sum of pre- and post-settlement events. Primary recruitment limitation (i.e., pre-settlement events) depends on water-column processes and involves pelagic larval mortality, a process affecting larval supply, and can be considered identical to supply-side ecology. Secondary recruitment limitation (i.e., post-settlement events) is due to benthic settler mortality, affecting early post-larval supply, or realized recruitment (Chesson, 1998; Swearer et al., 2002; Victor, 1986, 1991).

Supply-side ecology has proposed recruitment models based on the assumption of open versus closed populations and has drawn generalizations largely from studies on inter-tidal sessile species. These latter are highly dependent on larval import from the water column and thus, pre-settlement events appear particularly important (Gaines & Bertness, 1992; Roughgarden et al., 1985; Underwood & Fairweather, 1989). Typically, rocky shore species are distributed patchily and are clearly described by metapopulation processes, although very few study cases show the adult-recruitment relationships, as pre-settlement and post-settlement processes are often studied separately (Johnson, 2006). Moreover, the mortality after settlement, often caused by predation and inter-specific competition, can have a differing impact in soft- and hard-substrate communities, depending on differences in both life-cycle features and environmental factors (Fraschetti, Giangrande, Terlizzi, & Boero, 2003). However, a clear relationship between recruitment rates and adult density has rarely been found. Investigations of benthic–planktonic coupling at a specific level are generally impossible, even if the small recruits of a target species can be identified and sampled. To identify larvae to the species level is often too difficult, even using molecular tools (Shanks & Halanych, 2007; Webb, Barnes, Cark, & Bowden, 2006), while meroplankton abundance can often be only quantified at a high taxonomic level (Highfield et al., 2010). Benthic–planktonic coupling becomes easier in confined areas where species show larval retention with a very low degree of exchange with the sea (Ayata, Stolba, Comtet, & Thiébaut, 2011; Thiébaut et al., 1998), enabling these environments to be considered as islands separated by the sea. Most of the species inhabiting these environments show, however, direct development. Thus these areas are also interesting for studying the relationships between developmental type and stability of the population. The notion that species with dispersive larvae show greater density fluctuations than those lacking a free-drifting larval stage has

been questioned by several authors (Levin & Huggett, 1990; Olafsson, Peterson, & Ambrose, 1994). Examining adult density variation in a large number of invertebrates, Eckert (2003) found that species with no pelagic development exhibited the greatest coefficients of variation, whilst benthic populations with short (<3 days), intermediate (3–10 days) and long (>2 weeks) pelagic periods did not differ greatly in variability. Such evidence supports the idea that a greater pelagic larval duration may decrease, rather than promote, variability, probably by spreading larvae over different suitable environments.

## 4 | LARVAL DISPERSAL AND BIOPHYSICAL MODELS

Different methods have been developed to measure exchanges among populations. Larval transport and connectivity can be estimated by in situ observations of the individual propagules; mapping their trajectories; tagging propagules at release and then recapturing; examining the microchemistry of the otoliths of larval fishes, or other hard structures in invertebrates (Zacherl et al., 2003; see Levin, 2006 for a review of methods). Among biological approaches, the use of genetic markers remains the best method for measuring patterns of isolation by distance (Galindo, Olson, & Palumbi, 2006; Hellberg et al., 2002; Lowe & Allendorf, 2010; Weersing & Toonen, 2009). Despite this, the interpretation of the meaning of small genetic signals remains difficult because even reduced genetic structure implies a demographic exchange between populations even if very limited. Genetic connectivity depends primarily on the absolute number of dispersers among populations, whereas demographic connectivity depends on the relative contributions to population growth rates of immigrants rather than local recruitment.

The inherent difficulty in measuring larval dispersal in the field has led to an increasing use of numerical simulations to solve related problems. Biophysical models are increasingly being used to both evaluate larval transport and assess its role in regulating population connectivity (Aiken, Navarette, Castillo, & Castilla, 2007; Metaxas & Saunders, 2009). These models can be either general circulation models with particle-tracking subroutines, or simpler advection–diffusion models (Metaxas & Saunders, 2009).

The focus is often on the development of dispersal kernels (Aiken et al., 2007), estimation of self-recruitment rates, generation of site-specific data for MPA design and the construction of null hypotheses for connectivity studies (Siegel, Kinlan, Gaylord, & Gaines, 2003). Circulation models may be used to study the consequences of specific hydrographic features and are often combined with realistic estimates of mortality and behavior. The development of biophysical models entails an inter-disciplinary approach that integrates larval biology and physical oceanography, two disciplines with different sampling approaches at different temporal and spatial resolutions. Understanding the drivers of larval dispersal is, in fact, an inherently biophysical problem: it is biological in the sense of processes that influence offspring production, growth, development, and survival; it is physical in the sense of advection and diffusion

properties of water circulation. Resolving the mechanisms controlling larval dispersal involves understanding the relevant physical processes and how the organisms mediate the physical processes. From the physical viewpoint, the complexity of ocean movement has become increasingly evident with the development of more sophisticated ocean observation instruments, and the patterns of connectivity among locations correlated with water movements. However, a model's successful validation requires the incorporation of the species' biological traits. These include pelagic larval duration, larval mortality, and behavior and abundance of larvae after larval transport just before settlement, all of which remain, however, unknown for most organisms.

When biological information is available, biophysical models have been successfully applied, fitting the demographic traits with hydrographic data such as in the cases of population connectivity of the polychaetes *O. fusiformis* and *Sabellaria alveolata* (Barnay, Ellien, Gentil, & Thiébaut, 2003; Bush, Balestrini, Robins, & Davies, 2015). Connections being a central topic in the ecological functioning of coastal habitats and in the production of environmental goods and services, most present knowledge on connectivity comes from economically important exploited species, for whose management knowledge of spatial distribution is important. Examples are available for Mediterranean abalone and sea urchin (Morgan & Shepherd, 2006), but especially for species associated with tropical coral reefs (Sale et al., 2010). These studies show that settlement of larvae occurs in many different ways among fishes and invertebrates. Connectivity among populations of reef species is primarily, or exclusively, due to dispersal during larval life. For the majority of reef species studied, demographic connectivity has been shown to act on scales to tens of kilometers, rather than hundreds of kilometers or more. Therefore, the concept of a demographically well-connected population does not apply. Genetic (evolutionary) connectivity operates at larger spatial scales because larvae are only occasionally transported far beyond their usual dispersal range. If MPAs are to play a role in fisheries management, the smaller scale of demographic connectivity should be taken into account in the design of MPA networks (White et al., 2010). Connectivity estimates (self-recruitment and network centrality) have in fact already been incorporated into the design of marine reserves (Hilário et al., 2015; White, Schroeger, Drake, & Edwards, 2014). Information within spatially explicit population models can improve reserve design algorithms; however, to evaluate species' population dynamics it is essential to determine which species will benefit from a given reserve network. Biophysical models utilized in analysing large-scale connectivity among Mediterranean Protected Areas showed that they are far from constituting a true, well-connected network (Andrello et al., 2013; Melià et al., 2016).

Finally, one of the best examples of simulation trajectories comes from a large-scale study of dispersal of some bathyal species in the Caribbean and the Atlantic Ocean (Young et al., 2012). The model was successfully supported by the availability of at least some biological information (e.g., spawning times), but could be greatly refined in future by the addition of detailed information about actual depths of dispersal.

# 5 | CONCLUSIONS

The dramatic increase of knowledge and the changes of paradigm occurring in marine ecology during the last half century highlight the progress in understanding the mechanisms and processes that connect populations, the concept of which has shifted from closed to open populations. By contrast, life-history research has shown a highly complex relationship between larval life traits and dispersal. What is emerging is that the basic assumption of the passive nature of larval dispersal and massive export in the past was mainly due to the absence of information about behavior of larvae (Young, 1995). Many empirical data have shown that the retention of larvae in the natal habitat is more frequent than suspected, even in species with long larval duration phases (Byers & Pringle, 2006; Epifanio & Garvine, 2001). Moreover, results from genetic studies suggest a discrete relationship between connectivity and larval phase duration. This has led to a re-assessment of marine metapopulation models involved in conservation, fisheries management, marine reserve designs and biodiversity monitoring, and also to a revision of ideas about the mechanisms of marine speciation (Pinsky, Palumbi, Andréfouët, & Purkis, 2012; Strathmann et al., 2002; Swearer et al., 2002; Thorrold et al., 2002; Warner & Cowen, 2002).

Larval transport results from complex interactions of biological traits highly variable at a spatial and temporal scale (Pineda, Hare, & Sponaugle, 2007), while the actual dispersal distance is difficult to measure due to the lack of both biological information and of an appropriate larval tracking method for most marine invertebrates. This, coupled with the difficulty in estimating larval and post-settlement mortality, has led to problems in addressing self-recruitment and pelagic–benthic coupling for most marine populations.

To face such overwhelming complexity, numerical simulation approaches, aided by advanced computing power and circulation physical models, can be considered fundamental for better understanding the relationship between propagule dispersal and seawater dynamics, both highly variable. Biophysical models can provide effective explanations, especially on a large scale. However, the predictive power of biophysical models of larval transport can be ascertained only through proper validation by also using biological information, this being no small problem given the difficulty in measuring biological traits. Ontogenetic vertical migration, buoyancy of embryos, predation, food availability, developmental rate and physiological tolerances all play roles in determining dispersal patterns. Pelagic larval duration is an important parameter for all dispersal models, albeit the estimation and use of this parameter are fraught with potential errors, especially when information is lacking. In addition, even when pelagic larval duration is known, it is easy to make serious errors in estimating dispersal potential unless realistic oceanographic data are used, while the real transport of larvae cannot be extrapolated without knowledge about larval behavior (Shanks, 2009). More data are required to enhance accuracy and address the high variability between and within taxonomic groups (Hilário et al., 2015).

There are many challenges posed when validating the connectivity models, such validation being based on information about each species' biological traits. These traits are variable and species specific; furthermore, the elements for larval stage identification are often far from complete, while the biological traits of one species may not be necessarily extended to other congeneric and similar species. In brief, many basic elements of the biology of marine invertebrates remain unclear.

According to Boero et al. (2016), who defined the cell-ecosystem units, the connectivity must be the basis for the definition of management and conservation units, but these units should be established considering a large number of organisms and using synergistically different methods as a measure of connectivity. Contrastingly, most simulation models are still based on biological data of very few species, mostly fish and crustaceans with well-known biological traits. Obviously these models show different results, according to the different biological traits of the species considered (Claudet et al., 2010). Therefore, these target species should not be used as descriptors of the whole community. The existence of a large amount of data from field studies in fish and crustaceans derives not only from their economic importance, but also from the fact that their larvae are larger and easy to investigate compared to those of other invertebrate groups (Fogarty & Botsford, 2006; Hilário et al., 2015; Planes, Geoffrey, & Thorrold, 2009; White et al., 2014). By contrast, for most benthic invertebrates the small size of their propagules, coupled with the vastness of the pelagic environment and its complex fluid dynamics, hampers our ability to quantify dispersal and connectivity. Paradoxically, it seems that the connectivity of spatially fragmented deep-sea benthic populations is better known than those of populations in shallow areas (Etter & Bower, 2015).

Although we are aware that complex ecological systems cannot be considered the simple sum of the single components, knowledge of each species' autecology has become of paramount importance in understanding their functioning. This is also shown by the increase in the number of articles addressing larval dispersal in recent years (e.g., Cowen & Sponaugle, 2009; Levin, 2006; Nanninga & Berumen, 2014; Shanks, 2009).

Nevertheless, a large proportion of the data used in current models derives most from old literature and when data are not available, often broad generalizations are produced. This is because most of today's investment is towards the development of analytical methods to create sophisticated computational models whose successful application, however, could be compromised by the poor data quality available. By contrast, we need new biological data to increase our data set for the proper integration of the biological and modeling approaches; therefore, many resources must still be devoted to increase our basic knowledge.

A similar trend occurred in the past in other ecological fields, for instance in the choice of using surrogates as a measure for biodiversity, and so diminishing the role of taxonomic specialists (Giangrande, 2003), or in the feeding guild approaches, where entire families have been considered as belonging to a particular group based on studies conducted on only a small number of species (Giangrande, Licciano, & Pagliara, 2000).

Thus, in the context of ecological studies, in order to better understand the complexity and functioning of ecological systems, further investigation into the features of each individual species involved is

also needed. The central problem, therefore, is that for most marine species the biology remains unclear, including life-cycle traits and physiological and ecological requirements. What is called natural history (Guidetti, Parravicini, Morri, & Bianchi, 2014) probably went out of fashion much too early; however, we have now come to understand that such reductionist research is also indispensable when studying holistic processes. Thus, this is the moment for natural history's reinstatement, if not renaissance.

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