Connectivity as a Management Tool for Coastal Ecosystems in Changing Oceans

Nicolas Le Corre[1], Frédéric Guichard[2] and Ladd E. Johnson[1]
[1]Université Laval,
[2]McGill University,
Québec
Canada

1. Introduction

Recent theoretical management research has focused on systems from species to ecosystem at large scales (i.e., metapopulations and meta-ecosystems), and the links between habitats patches and subpopulations are of crucial importance to understand, predict, and manage resource dynamics. One of the key characteristics affecting the dynamics and demography of metapopulations is thus connectivity (Hanski, 1999; Kritzer & Sale, 2004; Moilanen & Nieminen, 2002), the exchange or flux of material between different locations (Cowen & Sponaugle, 2009). Because of its broad definition and growing relevance, "connectivity" is now employed in a number of fields, including metapopulation ecology. Consequently, several definitions of connectivity exist with the main differences between them lying in the spatial scale of study (Kadoya, 2009). In this review, we consider connectivity in its broadest sense of demographic or population connectivity: the exchange of individuals among geographically separated subpopulations in a metapopulation (Cowen & Sponaugle, 2009).

1.1 Connectivity in marine ecology

In a marine context, metapopulation structure is defined as populations occupying discrete patches, demographically connected according to a dispersal kernel (the function of propagule abundance vs. distance from the parental source) and potentially affecting the dynamic of the entire ecosystem (Kritzer & Sale, 2004). The main difference from equivalent terrestrial systems is that local extinctions rarely occur in marine systems (Kritzer & Sale, 2004) as the diverse regulation processes operating in the ocean and their inherent stochasticity lead to lower extinction rates (Hixon et al., 2002). Connectivity is one of these processes and tends to operate over larger spatial scales in marine metapopulations, due to fewer dispersal barriers and a more favorable medium for long distance movement of propagules. However, the potential for self-recruitment, i.e., the retention of propagules within a population, has recently been highlighted in many marine systems and may act as an additional mechanism to prevent extinction (Almany et al., 2007; Cowen et al., 2006; Levin, 2006).

In marine ecology, ideas have historically ranged from the extremes of demographically-open systems (fully connected) to closed populations (not connected) (Hixon et al., 2002).

For example, fisheries stock recruitment models generally ignored connectivity among populations, and local density-dependent factors were considered the most important parameter in the regulation of the populations. At the other end of the spectrum, recruitment into local populations was thought to occur from a general pool of propagules with new settlers arriving from unknown source populations. These simplifications of immigration and emigration processes were imaginable due to the spatial scales of studies that were either large enough (in the former case of some fisheries) or sufficiently small enough (open populations) to avoid dealing with the more realistic intermediate situations that characterize most marine systems. Connectivity is now, however, recognized to be a primary driver of most large-scale marine population dynamics. This is particularly true for the large number of marine species that are bentho-pelagic, with a stationary phase (e.g., sessile or sedentary juveniles and adults) and a planktonic stage (e.g., larvae, spores) during which dispersal occurs. Thus, marine ecologists have more recently focused on the dispersing agents (i.e., propagules) themselves and how they serve to connect populations. Here we focus on coastal marine invertebrate species with both a stationary and planktonic (dispersive) phase although the principles apply as well to reef fish and seaweeds.

Generally, connectivity is assumed not only to be a function of larval dispersal but also of post-larval survival (Pineda et al., 2007). It implies a large range of scales of connectivity, which are variable between and within species and locations (Cowen & Sponaugle, 2009; Kritzer & Sale, 2004). Thus, for a species in a specific area, once one knows the pattern of dispersal (i.e., dispersal kernels) and post-settlement processes, patterns of connectivity can then be derived. Unfortunately, this is often more simply said than done as dispersal parameters, such as pelagic larval duration (PLD) and post-settlement processes, that were historically considered to be stable over time (i.e., implying invariant connectivity) can be, in fact, quite variable. Indeed, several recent genetic studies have shown substantial spatial heterogeneity between life stages and temporal variability in genetic structure with metapopulations (Hogan et al., 2010; Selkoe et al., 2010). Likewise, several studies have explored hypotheses of oceanographic variability to explain fine-scale genetic patchiness (Banks et al., 2007) or chaotic genetic patchiness (Hogan et al., 2010), and certain larval transport models suggest that large variations in PLD and recruitment patterns could even be linked to hydrodynamic variability (Bolle et al., 2009; Connolly & Baird, 2010). Indeed, even knowledge of the PLD is not sufficient to predict scales of dispersal and gene flow among populations (Mitarai et al., 2009; Weersing & Toonen, 2009). Regardless, all these studies emphasize the importance of variation in larval dispersal on the resulting spatial patterns observed in different systems, and consequently, we should investigate connectivity as a varying feature of natural systems. Levels of variation (seasonality, annual variation, and periodicity) need to be examined in depth, and methods to assess connectivity should take these variations into account. Connectivity then should be thought of as the net result of all dispersal that has been observed over a given period, and the actual connectivity of the system will arise from the integration of all dispersal processes (Jacobson & Peres-Neto, 2010).

1.2 Measurement of connectivity

As the awareness of connectivity as a crucial characteristic for understanding ecosystems has emerged, a number of methods have been developed to explore and estimate connectivity within metapopulations and meta-ecosystems . These can differ, however, in their ability to

assess variability in connectivity and can be further distinguished by their specificity in measuring dispersal between subpopulations and their applicability to other systems (Cowen et al., 2006; Cowen & Sponaugle, 2009; Jones et al., 2009; Levin, 2006). Other reviews about connectivity have adopted a classification based on two main categories: direct and indirect methods (Jacobson & Peres-Neto, 2010) or natural & artificial markers (Thorrold et al., 2002). Because each method targets a different goal and is often applied to a specific scale, we have chosen instead to classify methods by assessing their specificity to a species or system. The former concentrates on the connectivity of a specific species, giving information on dispersal patterns of the species in the study area. The latter focuses on the dispersal processes (e.g., hydrodynamics) and its variations in a specific study region and can thus be applied to co-occurring species having similar characteristics. Both types can include methods for assessing connectivity over multiple years (integrative) or for a single event (punctual).

Although using different methods to assess patterns of connectivity of a species in a particular system inevitably leads to different estimates, such predictions should ideally be similar. Regardless, to compare results among methods, the scale at which connectivity is evaluated ought to be the same for all methods (Palumbi, 2004; Weersing & Toonen, 2009). For example, dispersal distance of blue mussel larvae has been estimated through different methods in various systems and ranges from <5km to <100km (Gilg & Hilbish, 2003; McQuaid & Phillips, 2000; Smith et al., 2009). A part of this variability is inherent to the analysis of distinct systems with different methods; more significantly, however, these methods did not estimate the connectivity at the same spatiotemporal scale. For example, Gilg and Hilbish (2003) used a genetic method that averaged over several generations whereas Smith et al. (2009) estimated the pattern of connectivity within a single year. Consequently, when connectivity estimates are compared, attention should be given to the temporal scale employed in the method. The use of multiple methods at different temporal scales may be necessary, however, to completely understand a system, and the application of several methods in a given system should permit measures at different spatiotemporal scales and lead to a better knowledge of the crucial connections between populations.

When comparing different methods of measuring connectivity, it is important to evaluate not only differences in mean connectivity, but also how to measure variability in the pattern of connectivity within a specific system. Such variation can arise from biotic or abiotic factors and can affect the connectivity and the dynamics of the system at different scales. Depending on the system, variability of connectivity can result in periodicity, stationarity or more complex behavior of individual populations or the entire ecosystem. Therefore, the range of variation in dispersal patterns needs to be better understood to improve model predictions and management strategies, ideally using a single method over different temporal scales (e.g., day, season or year). However, because assessing connectivity employs newly developed tools, most efforts concentrate on simply evaluating the principal patterns of connectivity; only a few studies have tried to empirically estimate the variability of connectivity itself (Botsford et al., 2009; Jones et al., 2009). Moreover, in spite of the vast choice of methods, only a few are appropriate to assess potential variability of connectivity.

Beyond academic interest in ecosystem functioning, knowledge of connectivity and its variability is essential for applied environmental problems. It is particularly important for the design of marine protected areas (MPAs) to preserve biodiversity. As reserves integrate many species, it becomes important to consider the dispersal networks of all targeted species to improve coastal management. In this case, multi-scale studies are necessary because of the potential for different species to disperse at different scales, and respond differently to settlement variation.

In this chapter, we examine recent progress in our understanding of population connectivity in coastal marine systems and discuss the implications of variability of connectivity in the persistence of populations and ecosystems over large temporal and spatial scales. We hope to demonstrate how understanding connectivity and its variability can help the long-term sustainable management of entire ecosystems in a variable world. We divide our treatment into three parts. Firstly, we review the recently developed tools from different scientific disciplines concerned with connectivity and classified them as species- or system-specific as well as on their scale of applicability. Secondly, we examine evidence on the variability of observed patterns of connectivity and its causes. Finally, we discuss considerations for management and conservation of ecosystems. In particular, we review different theories and strategies related to populations and ecosystem dynamics that integrate the variability of connectivity in the context of marine protected areas.

2. Methods to assess variability in connectivity

As the interest in population connectivity has grown, so too has the number of methods to estimate connectivity patterns. Several scientific disciplines, including physics, genetics, and microchemistry, have contributed to our improved understanding of dispersal in marine systems. These approaches were originally developed for other reasons, but they can also be applied to estimate the dispersal of individuals and the flux between populations. However, as mentioned above, the diverse life histories, PLD and mobility of different species require that temporal and spatial scales are taken into account, making comparisons among methods tenuous.

The high mortality rate and high diffusion of larvae during the dispersive stage make direct measurements of larval dispersal nearly impossible. Therefore most methods measure dispersal patterns indirectly, e.g., through successful settlers (recruits). Previous reviews of the methodology used to measure connectivity distinguished between direct or indirect, or artificial or natural methods (Jacobson & Peres-Neto, 2010; Thorrold et al., 2002). Rather than following these dichotomies, we classify connectivity methods according to their applicability to different species or other systems. The first category groups methods that provide results for a particular species. The second includes techniques relevant to particular systems (e.g., bay, reef, or shoreline), and can be applied to other species. For each category, we briefly describe several methods that allow the measurement of variability in connectivity among populations, describe their scale of applicability, and discuss their potential utility. To conclude, we discuss scenarios where several complementary methods can be used within the same system.

2.1 Species-specific methods

Methods presented here have been developed recently to evaluate the dispersal kernel of individual key or representative species. They can be applicable to other species, but require further development to fit the species of interest. Both of the main methodological approaches rely on sampling individuals for genetic or geochemical markers.

2.1.1 Parentage analysis and assignment tests

Population genetics is the most widely used approach for making inferences about dispersal and connectivity in marine organisms (Hellberg, 2009). Traditionally, spatial variation in frequencies of alleles and genotypes (F_{st} and G_{st}) was the most common indirect method to

genetically assess genetic divergence and long-term connectivity among populations (Hedgecock, 2010). However, limitations in the resolution of temporal scales, especially the inherent integration of dispersal over multiple generations, made it impossible to assess connectivity patterns over shorter ecological scales (Hedgecock et al., 2007). Recently new more direct genetic methods such as population and parentage analysis have been developed to more precisely estimate connectivity among populations (Christie et al., 2010b; Hedgecock, 2010; Manel et al., 2005). These methods are based on the multilocus genotype of individuals at different locations (Manel et al., 2005). Assignment tests provide the probability that an individual originated from one of a number of different known source populations. However, precise assignment of a given individual to a population requires that populations are genetically distinct and is unsuccessful when populations are too similar (Christie et al., 2010a; Saenz, 2009). Parentage analysis is a particular type of assignment test used to determine the parents of an individual or group of individuals based on shared alleles between individuals (Manel et al., 2005). As populations of marine invertebrates are usually comprised of large numbers of individuals with possibly long dispersal phases, the fraction of sampled individuals is usually too small for precise parental assignment (Hedgecock et al., 2007), and a persistent challenge associated with these techniques is the necessity for genotyping many individuals, both adults and recruits, from all of the different populations within the metapopulation. However, a promising new technique of parentage assignment (Christie et al., 2010a) requires fewer individuals from a given population than previous techniques. Using a Bayesian classification approach for the kind of organisms, this approach has been used successfully to document connectivity patterns of marine organisms with long PLD (Christie et al., 2010b; Richards et al., 2007; Underwood et al., 2007).

The spatial scale over which these methods can be used depends on the characteristics of the species (e.g., PLD, larval behaviour) and of the system (e.g., currents, topography) in question. In addition, the temporal scale of the sampling will depend on the frequency of reproduction of the species and on the variability of the oceanographic conditions encountered by the larvae. Consequently, the assessment of the variability of connectivity pattern necessitates an extensive sampling of all the potentially connected populations over different cohorts. Despite the high costs of these methods, they offer very precise techniques to measure connectivity pattern. Unfortunately, estimating the variability of connectivity requires multi-year studies.

2.1.2 Geochemical signatures in calcified structures

While genetic assignment tests measure connectivity by determining the natal origin of juveniles that are collected from different sites within a region, calcified structures (e.g., otoliths, statoliths or shells) can retain chemical traces of the environment (due to spatial and temporal variations of seawater) encountered by individuals during their entire life. Researchers are using such chemical signatures (e.g., isotope ratios, trace elements) of calcified structures formed during early development to identify the region or site of origin of individuals (Thorrold et al., 2002; Zacherl, 2005). These structures are either naturally marked by the environment or artificially "tagged" by transgenerational isotope labelling (TRAIL) at their origin. Natural markers can be found in the otoliths of fish, the statoliths or shells of molluscs. This process is usually bipartite – first the microchemistry of the calcareous parts corresponding to early life is analysed to define the trace elemental profile

of a location of interest. Then, the trace elemental fingerprint of post-dispersal individuals is compared with the elemental profiles of individuals from which the original location is known (Becker et al., 2005; Becker et al., 2007). The source identification is obviously more reliable when differences in elemental composition are great among possible source locations (Thorrold et al., 2007). However, this method necessitates identifying the elemental profiles from all potential sources (Berumen et al., 2010), and moreover, it can be variable in time (seasonally, yearly) (Cook, 2011; Fodrie et al., 2011; Walther & Thorrold, 2009). Even though some statistical methods can be used to increase the precision of assignments (White et al., 2008), some limitations of this method appear for marine organisms because chemical distinctions among origin areas are sometimes too small to enable accurate assignment of individuals (Berumen et al., 2010), and the processes of integration of these trace elements in the hard parts of these organisms is not fully understood (Thorrold et al., 2007; Warner et al., 2005). The applicability of these techniques over multiple years has been shown recently and has provided new insights on the variability in connectivity. In particular, multi-year studies on fish otoliths (Clarke et al., 2010), oyster and mussel shells (Carson, 2010) have revealed seasonally and yearly variations in connectivity and the importance of self-recruitment in different systems. This variability underscores the need to identify the source elemental profiles over appropriate temporal scales if needed.

The second approach involves directly tagging individuals with enriched isotopes at possible source populations (Thorrold et al., 2006). Stable isotopes at concentrations an order of magnitude higher than those found in nature are injected into gravid females and are subsequently incorporated into internally developing embryos, thereby acting as unequivocal tags (Thorrold et al., 2006). This method permits the marking of many individuals at one time, and at low doses does not alter larval and juvenile behaviour (Williamson et al., 2009). TRAIL has been used mostly to assess the self-recruitment hypothesis in cephalopods (Pecl et al., 2010) and reef fishes (Almany et al., 2007; Planes et al., 2009). However, because of high mortality rates during the larval dispersal stage, this technique cannot be employed to assess connectivity at large scales. Moreover, as a large part of the population needs to be marked at one time, it is almost impossible to use this method with benthic invertebrates or large populations of reef fishes. Finally, the use of this method is limited by the different markers available and questions regarding the incorporation process of markers (Pecl et al., 2010). Thus, this method appears to be most useful in assessing variability of connectivity at limited spatial scales of dispersal in system where larval retention and self-recruitment are thought to be important.

2.1.3 Invasive species

The establishment and subsequent spread of non-indigenous species ("invasive species") is an emerging environmental problem of global extent, but a "silver lining" of biological invasions is a relative easy opportunity to examine rates and patterns of dispersal (Johnson & Padilla, 1996). Estimates of rates of spread can be made from sequential observations at the edge of the range (Grosholz, 1996; Lyons & Scheibling, 2009; McQuaid & Phillips, 2000) assuming that sampling efforts are reasonably constant over time. Such information has already been used in the planning for MPA (Shanks et al., 2003) for comparison with range shifts associated with climate change (Sorte et al., 2010). Unfortunately, the monitoring of most past invasions has been a rather piecemeal affair with different observers using different techniques and/or efforts to document the distribution of the invasive species over

time. Current interest in aquatic invasive species has, however, provided better information and interest in documenting the secondary spread of established invaders.

Measures of the rates of spread of invasive species are not, however, exact equivalents of either dispersal or connectivity in metapopulations. First, invasive species often spread by both natural (e.g., currents) and human-mediated (boat hull fouling) vectors (Goldstien et al., 2010), and the latter can give artificially high estimates of dispersal. Second, population densities at the edge of an invader's range are likely to be lower than in sites where the species is well established. This attribute may reduce the propagule supply available for dispersal and lead to underestimates of the normal dispersal that occurs within a fully developed metapopulation. Finally, given the number of propagules that are likely to settle will diminish with increasing distance from the edge of an invader's range, there are likely to be sites where populations will not become established due to demographic limitations such as "Allee effects" (Leung et al., 2004) which would not exist if dispersal was simply occurring between populations within a metapopulation. Thus, again estimates of range expansion for either invasive or native species are likely to underestimate dispersal distances. Such measures can serve, however, as first approximations for dispersal within metapopulation of similar species and provide information on pathway of transport within coastal ecosystems.
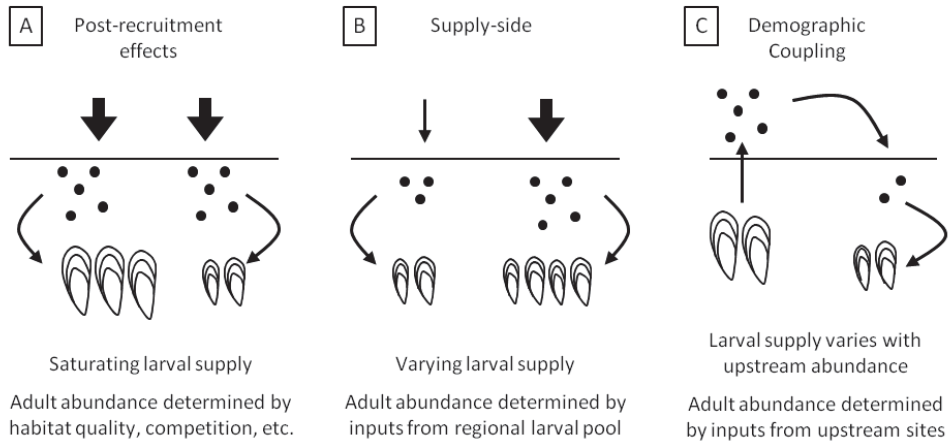
2.2 System specific methods

System-specific approaches depend primarily on properties of the physical system to assess connectivity patterns in the study area. These methods are developed to fit to a specific system but can be adapted to other systems and to a range of species. Two such methods are particularly useful in evaluating variability in connectivity: geostatistics and biophysical models.

2.2.1 Geostatistics

Geostatistics, the statistical analysis of spatially-referenced data over large spatial extents, represents a powerful new tool to assess connectivity in marine ecosystems. These analyses are based on estimates of the adult abundance and the number of recruits at different sites within the study area. Significant coupling between sites at a particular spatial scale gives an estimate of the distance over which a given source population has an impact on recruitment in a recipient population (Fig 1.). Appropriately oriented and homogeneous coastal systems (e.g., estuaries, rivers, straight shoreline) are currently the preferred systems for the application of this method because such coastal configurations facilitate the detection of significant signals between adult populations and their impact on juvenile recruitment.

This method has already been used to estimate the distance of demographic coupling of blue mussels in the St. Lawrence estuary (Fig. 2; Smith et al., 2009). Depending on the different dispersal properties of the species, distinct signals can be distinguished, ranging from no association at all to significant relationships at a given distance between adults and recruits. Different theories can be tested (e.g., post-recruitment effects, supply-side limitations, demographic coupling), and the covariogram developed from the data provides a system specific estimation of the dispersal characteristics of the species. Also, this approach can avoid difficulties in separating different kind of variability (e.g., environmental variations among sites versus pure connectivity variations) by using detrended data to partition the variance (Le Corre et al., unpublished).

1. Three alternative hypotheses (A, B and C):

| A | Post-recruitment effects | B | Supply-side | C | Demographic Coupling |

Saturating larval supply   Varying larval supply   Larval supply varies with upstream abundance

Adult abundance determined by habitat quality, competition, etc.   Adult abundance determined by inputs from regional larval pool   Adult abundance determined by inputs from upstream sites

2. Expected plots of covariance (cross-covariance) against lag distance for two variables (adult abundance and recruits) at multiple sites:

Adults covary positively with recruits only at short distances   Positive cross-covariance at coupling distance
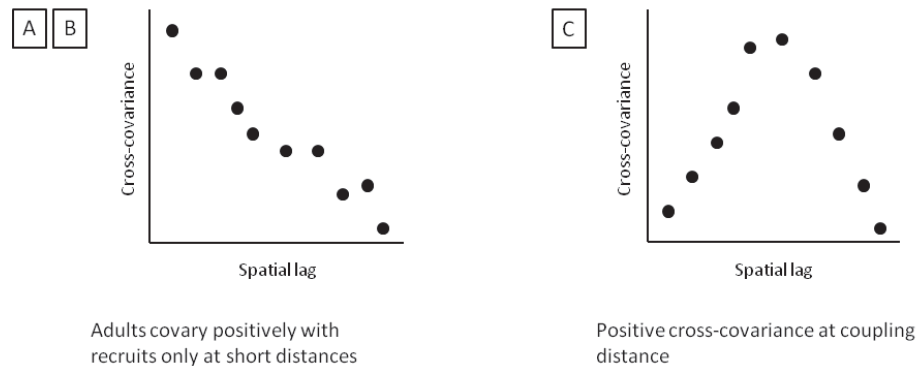
Fig. 1. (1) Different scenarios of mussel recruitment (A, B, and C) that can be tested using cross-covariance geostatistics. (2) Expected cross-covariograms for each scenarios.

Although system-specific by nature, this method is less expensive as the data are relatively easy to collect and analyse. Consequently, it permits the repeated sampling necessary for evaluating the temporal variability of the connectivity pattern of the study species. Depending on the frequency of reproductive/dispersal events, the analysis can be repeated yearly or even seasonally to estimate the effective scale of connectivity, to infer dispersal patterns, and to capture the temporal variability of connectivity. This method is particularly useful for estimating the scale of connectivity and the variability in dispersal pattern, and be used to complement other methods, such as genetic analyses that provide longer spatial and temporal scale information.
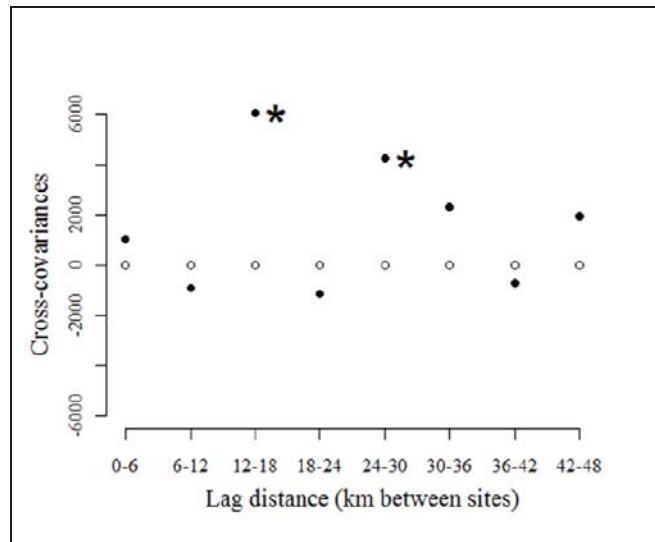
Fig. 2. Example of demographic connectivity in marine mussel metapopulations: significant cross-covariances (filled circles with asterisk) were observed between upstream adult mussels and downstream recruitment, indicating spatial connectivity between sites at 12-18km and 24-30km apart from one another. Open circles indicate mean values of a random process in that system. This figure is modified from Smith et al. 2009 (Copyright (2009) by the Association for the Sciences of Limnology and Oceanography, Inc.).

2.2.2 Coupled biophysical models

With advances in computational abilities, many three-dimensional hydrodynamic models have been developed to better understand geochemical processes, hydrology, and sedimentology. In recent years, ecologists have started exploring the power of these tools to better comprehend dispersal of larvae which are almost impossible to track directly (Cowen et al., 2007; Thorrold et al., 2007; Werner et al., 2007). These powerful tools can model entire coastal ecosystems, incorporating diverse attributes such as coastal geometry and the influence of wind. The spatial scale of the model is a key parameter for coastal marine species because of the important interaction between dispersing larvae and of nearshore physical processes, but depending on the complexity required, their spatial resolution can be adjusted accordingly (Greenberg et al., 2007). For example, models with high resolution are preferred to simulate coastal processes like eddies or waves.

The best way to model the dispersal of larvae appears to be the Lagrangian dispersal process (Siegel et al., 2003), particularly through the use of Individual Based Modeling (IBM) (Werner et al., 2007). At its simplest, Lagrangian dispersal assumes that larvae are transported advectively as passive particles (Mitarai et al., 2009; Siegel et al., 2003), and thus the process consists of following a parcel of water that is characterized by a particular set of conditions (e.g., initial density, PLD). Movements of the Lagrangian particles are then viewed as proxies for passively dispersing larvae and the analysis of the trajectories of several particles (used to create probability density functions) allows the estimation of dispersal kernels, the connectivity matrix, or potential connectivity (Cowen et al., 2006;

Siegel et al., 2003; Watson et al., 2010). Recently, IBMs have also been able to integrate behavioural traits of organisms (e.g., diel migration, mortality, feeding).

In a context of marine coastal species, the most important factors influencing dispersal, in addition to physical currents, are species properties such as timing of spawning, PLD, and competence, i.e., development to a stage able to settle back into the benthic environment (Mitarai et al., 2009). Integration of the interaction between individuals and their physical environment into physical oceanographic models, including the addition of specific larval behaviours, will certainly increase the precision of estimates of dispersal kernels and connectivity. IBMs have already permitted researchers to explore and integrate the role of specific behaviours during the dispersal phase and better explain diverse phenomena such as self-recruitment and limited dispersal (Werner et al., 2007). Depending on the species, the incorporation of processes such as the relationship between growth and water temperature (O'Connor et al., 2007), diel migration (Ayata et al., 2010; Cowen et al., 2006), chemical cues (Gerlach et al., 2007), and attraction by turbulence and waves (Fuchs et al., 2007) can have large impacts on resulting dispersal patterns. The added complexity due to the integration of such processes can be mitigated by the judicious identification and selection of behaviours that are found to be most critical in the dispersal of the individual species in question.

The development of 3-D hydrodynamic models necessitates high level programming capacities, good calibration before and after development of the model, and extensive validation before they are used by ecologists to run simulations. Also larval behaviours require considerable effort to be properly integrated into the model and a strong understanding by the programmer of the processes most critical for accurately describing the behaviour. Consequently, the development of a good hydrodynamic model requires substantial time and associated costs. However, once appropriately developed and validated, these models offer a powerful tool to explore a given system and enable researchers to test hypotheses with increasing realism. In particular, the low costs associated with exploring different environmental scenarios provide a fantastic tool to assess population connectivity and its variability across different spatiotemporal scales. The modeled patterns can then be used to generate testable hypotheses regarding connectivity which can, with the use of targeted experiments, provide data critical for model refinement, increasing our ability to understand the mechanisms driving patterns of connectivity. Ultimately, such coupled biophysical models will permit ecologists to test implications of different scenarios of climate change for population connectivity and persistence.

2.3 Use of multiple methods

Given the inherent limitations of any given approach, attempts have been made to compare different methodologies. In particular, several studies have confirmed predictions of biophysical models with genetic analysis (Galindo et al., 2010; White et al., 2010) or the inverse (Gilg & Hilbish, 2003), and the comparison of these tools has permitted researchers to verify predictions and to identify the main genetic processes involved in marine dispersal. Perhaps more importantly, mismatches between theoretical predictions and empirical data have directed researchers to explore further the mechanisms involved (Galindo et al., 2010). A good example is that of Gilg and Hilbish (2003) who combined simulated hydrodynamic data (2D) and allele frequencies in a region with strong differentiation among populations to estimate the geographic scale of larval dispersal. The use of 3 years of averaged simulation data in combination with the genetic allele frequencies

data enabled them to define dispersal distance. They were not, however, able to assess the temporal variability in their estimate because the temporal resolution of connectivity assessed by these methods was too different. In the future, the use of multiple methodologies should provide more robust estimates of connectivity patterns by incorporating newly developed methods. As previously mentioned, it remains important to use multiple complementary methods with similar temporal resolution, especially when assessing the variability of connectivity patterns.

3. Variability of connectivity for populations: Causes and consequences

As discussed above, variability in estimates of connectivity can be attributed to methodology alone, i.e., due simply to technical artifacts. However, there are many natural processes that result in connectivity being truly and inherently variable. At larger spatial and temporal scales, this variability has important impacts on different characteristics (e.g., demography, genetics) of populations, communities, and ecosystems. In this section we review the primary processes affecting and causing variability in connectivity and then discuss the implications of these variations in dispersal patterns over larger spatiotemporal scales.

3.1 Main factors causing variability of connectivity

Dispersal, which underlies connectivity, involves three distinct sequential steps – it begins with the release of propagules (e.g., gametes, spores or larvae), is followed by a pelagic dispersal phase and ends with settlement to an appropriate habitat (Cowen & Sponaugle, 2009; Pineda et al., 2010). Each of these phases represents a potential source of variability because of the distinct suite of biological, physical, and biophysical processes involved in each period (Fig. 3). Depending on species, region, and timing of a particular study, these phases of connectivity may differentially impact dispersal and consequently produce variability in connectivity patterns.

3.1.1 Spawning

The first phase, release of propagules, can be affected by variation in the abiotic environment (e.g., temperature), maternal condition, food availability, and local oceanographic conditions. All of these parameters can influence the timing and location of spawning (Levitan, 2005). The importance of spawning, and its influence on connectivity depends greatly on the study species and their various modes of reproduction. Species-specific variation in offspring size reflects evolutionary strategies to deal with unpredictable variation of the environment (Marshall et al., 2008) and represents a compromise between quantity and quality as reflected by the number, size, and feeding strategy (e.g., lecithotrophic vs. planktotrophic) of propagules produced. Maternal condition can also be an important factor in terms of brood quality and is likely linked to the food available to parents prior to the spawning event. Spawning is influenced by both intrinsic (e.g., gonadal condition) and extrintic (e.g., spawning cues) properties of the system (Starr et al., 1990), and as local oceanographic features are highly variable at small spatial and temporal scales (i.e., due to topography, bathymetry, waves, and tides), the timing of spawning will be a key factor influencing fertilization in broadcast spawners and larval dispersal trajectories of planktotrophic and lecithotrophic species (Largier, 2003).
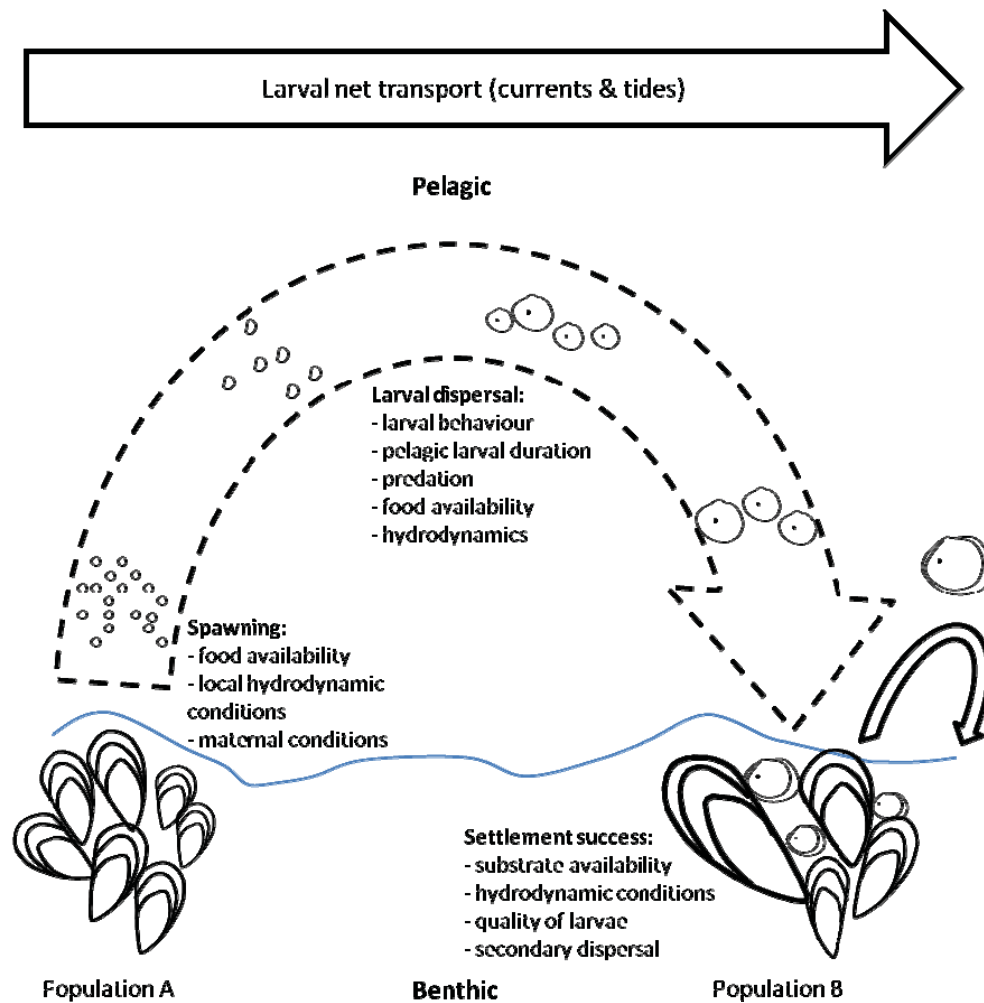
Fig. 3. Overview of the different processes contributing to the variability in connectivity among populations (e.g., marine mussels).

3.1.2 Larval dispersal

Once the planktonic phase begins, the spatial and temporal scales over which connectivity varies increase relative to the spawning phase. During this phase, many features influence larval dispersal: hydrodynamics of the system, larval behavior, prey availability, PLD and predation (Levin, 2006). In the simplest case, many larvae can be thought of as passively dispersing particles subject to oceanographic dynamics (see above), but these complex processes vary enormously over all spatial and temporal scales. Certain hydrodynamic conditions may increase larval dispersal distances (e.g., alongshore currents, wind driven surface current), while others may act to reduce dispersal distance (e.g., eddies, waves,

tides) (Largier, 2003; McQuaid & Phillips, 2000; Mitarai et al., 2009; Sponaugle et al., 2005). More realistically, larval behaviour, especially vertical swimming, can influence dispersal. Indeed, the swimming ability of many pelagic larvae often increases with ontogeny enabling complex swimming behavior in both horizontal and vertical directions; which in turn has associated impacts on dispersal trajectories (Cowen et al., 2006; Fuchs et al., 2007; Gerlach et al., 2007). Likewise, because many species have planktotrophic larvae which must feed and develop during the dispersive phase, there is an obligatory pelagic period (the PLD) of days to weeks during which dispersal is occurring. PLD can vary greatly both within and among species (Kinlan & Gaines, 2003; Kinlan et al., 2005; Shanks & Eckert, 2005), depending on abiotic and biotic conditions. In particular, temperature and prey availability play key roles in larval development due to their high spatiotemporal variability, resulting in large variation in mean PLD and mortality among cohorts (O'Connor et al., 2007). In addition, if a suitable substratum is not available when larvae become competent to settle down to benthic habitat, organisms can even delay metamorphosis, so that the PLD can extend significantly beyond the mean pelagic larval duration (Pechenik et al., 1990). Consequently, the dispersal phase can last a relatively long time with concomitant increases in possible dispersal trajectories. All of these factors, in addition to direct predation on larvae, result in very high mortality during the pelagic larval phase (Houde, 1997).

3.1.3 Settlement
Even if larvae do survive the challenges of the pelagic realm and find suitable substrata, post-settlement processes can dramatically influence the chances of these "recruits" becoming part of the local population. First, post-settlement survivorship is closely tied to larval quality (Pechenik et al., 1998), and thus the diverse factors influencing larval life (see above) can produce variation as well in the quality of settlers (e.g., size, physiological conditions). This variability in quality has important demographic impacts, particularly on the growth and survival rate of individuals (Pechenik et al., 1998; Phillips, 2002). Various selection processes occur early in the development of juveniles because high quality metamorphosed larvae have a higher probability of recruiting to the adult population (Cowan & Shaw, 1988). Nevertheless, favorable larval traits do not necessary produce successful juveniles because the benthic environment can require different traits for survival. Quality of settlers then, as with quantity and quality of larvae, appears to be highly variable over spatial and temporal scales and consequently contribute to produce heterogeneous and highly variable recruitment patterns across locations (e.g., sink locations, areas of low recruitment). At smaller spatial scales, some species aggregate during the dispersal phase because of currents and differences among water masses (Natunewicz et al., 2001); larval delivery appears to be highly variable at spatial scales less than one hundred meters and necessitates additional sampling effort to characterize the population (Pineda et al., 2010; Siegel et al., 2008). Even if most long distance dispersal occurs during the pelagic larval stage of invertebrates, dispersal has been observed as post-larvae, juveniles and adults, which also contributes to variability exhibited across the three stages of the connectivity process (Bayne, 1964; Petrovic & Guichard, 2008).

3.2 Ecological implications of variability in connectivity.
All the phenomena described above can produce variability in connectivity. Therefore, the ecological consequences at larger spatiotemporal scales (metapopulation and ecosystem) are

diverse. Only a few theoretical studies have been conducted to assess these impacts (e.g., variable dispersal kernels). In this section, we discuss the general implications of considering variable connectivity patterns on large scale demography and genetics.

As previously emphasized, marine systems are characterized by variability in environmental conditions. Stochasticity of dispersal kernels or the connectivity matrix is often used to incorporate this variability in models. When stochasticity of connectivity is increased, large increases occur in the mean abundance of individuals in the metapopulation as well as in its variance (Aiken & Navarrete, 2011). Moreover, persistence of the metapopulation is logically enhanced by adding dispersal variability corresponding to what is observed in empirical studies (Aiken & Navarrete, 2011). In practice, strong variations in recruitment occur at a regional scale due to variation in bathymetry and winds. Because of this, some areas can be identified as "hot spots" where recruitment is always higher than the regional average (Siegel et al., 2008), in spite of the large variation in recruitment observed among years (Shima et al., 2010). Since some species are reproducing all year round, important variations can be observed in the number of recruitment events. Depending on seasonality, certain patterns of dispersal at different scales can emerge during a given year (Siegel et al., 2008). Some systems are strongly oriented by ocean currents, causing asymmetrical dispersal, and higher sensitivity to climate change has been observed in simulations (Aiken & Navarrete, 2011). The metapopulation system can then shift continually between stable and unstable states, according to variability in recruitment (Aiken & Navarrete, 2011). However, long-term empirical evidence for variability in connectivity is rare, so the long-term analysis of its impact on the demography of populations remains unknown. However, some methods developed recently (e.g., biophysical model, geostatistics; see above) should allow a better assessment of connectivity patterns with previously collected data and permit better validation of theoretical work.

Variability in dispersal distance also leads to different levels of gene flow between populations; parent populations of different cohorts of recruits at a given location are therefore variable and gene flow may occur, in time, over various distances (O'Connor et al., 2007). High variability in connectivity can lead to unstable genetic structure at seasonal and annual temporal scales in adults and juveniles (chaotic genetic patchiness), each site consisting of an admixture of cohorts from multiple sources. Chaotic genetic patchiness provides stability to the entire metapopulation and operates as a buffer against strong fluctuations in population size (Hogan et al., 2010).

4. Implications for management and conservation of biodiversity and ecosystems

Management of biodiversity and conservation of ecosystems, often through the establishment of marine protected areas (MPAs), has been well studied in past decades, and agreement has been reached on the necessity of a solid knowledge of population size, genetic diversity, representativeness to the entire system, and connectivity pattern across the area for effective management (O'Connor et al., 2007; Sundblad et al., 2011). However, different goals exist in species management, so benefits are different depending on the adopted strategy (e.g., specific fisheries protection or biodiversity conservation), opportunities, budget, and number and types of species targeted by the MPA network (e.g., homing or sessile vs. migratory species) (Kritzer & Sale, 2004; McCook et al., 2010). Goals of MPA networks are evaluated and chosen by policy decisions and are often established

according to the opportunities present in the region, rather than following strict ecological analysis (Kritzer & Sale, 2004; Sundblad et al., 2011). In spite of the recent interest and extensive research on fisheries management on an ecosystem level, the effectiveness of MPAs to protect ecosystems and their biodiversity has unfortunately received relatively little attention (Jones et al., 2007).

4.1 Design of MPA networks

MPAs are generally established to help a given metapopulation or an ecosystem persist demographically. When defining a network of protected areas, the determination of the size and structure (e.g., a single or several areas, spacing, location) requires a good knowledge of the scale of dispersal and the size of discrete local populations (Jones et al., 2007; Kritzer & Sale, 2004). In MPAs where the goal is to preserve biodiversity, several areas are normally required; if the goal is to protect a single species (e.g., fishery), fewer and larger areas are generally used (Fogarty & Botsford, 2007; Jones et al., 2007). Size of reserves also depends on the effective number of individuals surviving to the next generation (Almany et al., 2009). With regard to the distance among reserves, the greater the dispersal range, the larger the protected areas should be and the longer the distances among them can be (Jones et al., 2007). For example, if the goal is the persistence of species, Moffitt et al. (2011) recommended increasing the size of MPAs and diminishing distances among them to allow a higher number of species to persist via network connectivity rather than self-replenishment, particularly species with long dispersal. Additionally, the spacing among reserves to protect a given species is variable among regions because of local differences in larval development time. For example, because water is warmer in tropical regions relative to temperate ones, PLD is generally shorter and thus spacing among reserves in networks should be smaller in tropics to ensure connectivity (O'Connor et al., 2007).

Because low levels of larval exchange limit success of MPAs (Bell, 2008), networks of protected areas should be designed as a function of observed connectivity patterns, but can also include potential connectivity among areas that can be linked and where suitable substrata exist. Consequently, some of the methods described above (section 2) to assess variability in connectivity can be used in determining locations that are potentially connected and can reinforce the MPA network. Moreover, a good description of the demography of the population through statistical methods (Aiken & Navarette 2011) or source/sink population analysis (Almany et al., 2009) will help to define sectors of the coast that would have a greater impact if protected. For example, isolated populations or retention areas, which have high conservation values, should be preferred because they ensure the persistence of the metapopulation (Almany et al., 2009; White et al., 2010). However, in retention zones, connectivity is less important, but sensitivity to stochastic disturbances might be higher. Therefore, such populations could go extinct, endangering the whole network because of its weaker connectivity (White et al., 2010). Generally, Jones (2007) suggests protecting source populations, isolated populations and spawning aggregation sites.

4.2 Management of biodiversity

When applied to whole ecosystems, management becomes more complex and reserves should be designed differently. Metacommunity levels should be considered in spatially-explicit models to manage effectively reserves in MPAs network (Guichard et al., 2004).

More recently, MPAs have been designed to be large enough to protect a suite of populations and have emphasized the importance of protecting different functional groups in ecosystems (McLeod et al., 2009). Also, the protection of vulnerable or fragile species may necessitate focussing on the other species upon which they depend, perhaps at multiple spatial and temporal scales (Almany et al., 2009). As dispersal distances occur at different scales among species, variability in spacing between reserves is desirable to reduce dependence of the system to a specific distance and better protect diverse groups of species (Kaplan, 2006).

When a MPA network is designed, population genetics also need to be considered. Because panmictic populations are rare, it is important to study direction and strength of the gene flow (von der Heyden, 2009). Gene flow should be maintained by frequent, medium and rare (long distance) dispersal of individuals among populations and its inclusion in MPA network designs is highly recommended (O'Connor et al., 2007). Also, von der Heyden (2009) recommends favoring multiple MPAs to avoid excessive population genetic structuring and population isolation; spacing of reserves should be designed to ensure adequate demographic connectivity and maintenance of genetic diversity (Almany et al., 2009). Even if substantial self-recruitment has been observed in dispersal analyses and may permit the persistence of specific populations, the exchange of individuals among populations remains crucial from a perspective of genetic diversity.

Because high environmental variability is an inherent part of marine systems, conservation strategies have to be developed to reduce its impacts on biodiversity and ecosystems. For example, in a context of global climate change, McLeod et al. (2009) suggested "spreading the risk" to avoid coral reef extinction by protecting several replicates of all kinds of habitats. To identify potential habitats, they proposed to use past incidents of coral bleaching and sea surface temperature. Another risk-spreading strategy that limits the impact of variability of connectivity patterns and strong fluctuations in MPAs networks involves using more, but smaller reserves (Almany et al., 2009; Hogan et al., 2010). Also, under high environmental variability, Baeza & Estades (2010) have shown that enhancement of the habitat quality in small reserves has better effects on surrounding landscapes than large and costly enhancement of large reserves.

5. Conclusion

Limited connectivity and the resulting metapopulation dynamics are now recognized features of coastal ecosystems. This overview of connectivity has revealed both the inherent shortcomings and future potential of applying this approach to the understanding and management of coastal ecosystems. There is clearly an emerging set of techniques that can now be applied to estimate and document dispersal between populations and the concomitant effects on metapopulation connectivity. There are, however, biases in these techniques in terms of the temporal and spatial scales over which they can be applied, and future effort will need to strive for the integration of these different approaches to better understand the role of connectivity in maintaining demographic stability and genetic diversity within metapopulations across scales. Moreover, connectivity can no longer be considered a static, invariant property of metapopulations. It too is inherently variable, subject to intrinsic and extrinsic factors that can affect the dispersal and survival of propagules. The importance of documenting and incorporating this variability in our theoretical and empirical understanding of metapopulation dynamics and ecosystem

function is a new challenge, but one that must be met to address the environmental challenges associated with the sustainable management of ecosystems threatened by overexploitation and climate change.

6. Acknowledgments

7. References

Aiken, C. M. & Navarrete, S. A. (2011). Environmental fluctuations and asymmetrical dispersal: generalized stability theory for studying metapopulation persistence and marine protected areas. *Marine Ecology-Progress Series*, 428, pp. 77-88, 0171-8630

Almany, G. R.; Berumen, M. L.; Thorrold, S. R.; Planes, S. & Jones, G. P. (2007). Local replenishment of coral reef fish populations in a marine reserve. *Science*, 316, 5825, (May), pp. 742-744, 0036-8075

Almany, G. R.; Connolly, S. R.; Heath, D. D.; Hogan, J. D.; Jones, G. P.; McCook, L. J.; Mills, M.; Pressey, R. L. & Williamson, D. H. (2009). Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. *Coral Reefs*, 28, 2, (Jun), pp. 339-351, 0722-4028

Ayata, S. D.; Lazure, P. & Thiebaut, E. (2010). How does the connectivity between populations mediate range limits of marine invertebrates? A case study of larval dispersal between the Bay of Biscay and the English Channel (North-East Atlantic). *Progress in Oceanography*, 87, 1-4, (Oct-Dec), pp. 18-36, 0079-6611

Baeza, A. & Estades, C. F. (2010). Effect of the landscape context on the density and persistence of a predator population in a protected area subject to environmental variability. *Biological Conservation*, 143, 1, (Jan), pp. 94-101, 0006-3207

Banks, S. C.; Piggott, M. P.; Williamson, J. E.; Bove, U.; Holbrook, N. J. & Beheregaray, L. B. (2007). Oceanic variability and coastal topography shape genetic structure in a long-dispersing sea urchin. *Ecology*, 88, 12, (Dec), pp. 3055-3064, 0012-9658

Bayne, B. L. (1964). Primary and secondary settlement in *Mytilus edulis* L. (Mollusca). *Journal of Animal Ecology*, 33, 3, pp. 513-523, 0021-8790

Becker, B. J.; Fodrie, F. J.; McMillan, P. A. & Levin, L. A. (2005). Spatial and temporal variation in trace elemental fingerprints of mytilid mussel shells: a precursor to invertebrate larval tracking. *Limnology and Oceanography*, 50, 1, (Jan), pp. 48-61, 0024-3590

Becker, B. J.; Levin, L. A.; Fodrie, F. J. & McMillan, P. A. (2007). Complex larval connectivity patterns among marine invertebrate populations. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 9, (Feb), pp. 3267-3272, 0027-8424

Bell, J. J. (2008). Connectivity between island marine protected areas and the mainland. *Biological Conservation*, 141, 11, (Nov), pp. 2807-2820, 0006-3207

Berumen, M. L.; Walsh, H. J.; Raventos, N.; Planes, S.; Jones, G. P.; Starczak, V. & Thorrold, S. R. (2010). Otolith geochemistry does not reflect dispersal history of clownfish larvae. *Coral Reefs*, 29, 4, (Dec), pp. 883-891, 0722-4028

Bolle, L. J.; Dickey-Collas, M.; van Beek, J. K. L.; Erftemeijer, P. L. A.; Witte, J. I. J.; van der Veer, H. W. & Rijinsdorp, A. D. (2009). Variability in transport of fish eggs and larvae. Iii. Effects of hydrodynamics and larval behaviour on recruitment in plaice. *Marine Ecology-Progress Series*, 390, pp. 195-211, 0171-8630

Botsford, L. W.; White, J. W.; Coffroth, M. A.; Paris, C. B.; Planes, S.; Shearer, T. L.; Thorrold, S. R. & Jones, G. P. (2009). Connectivity and resilience of coral reef metapopulations in marine protected areas: matching empirical efforts to predictive needs. *Coral Reefs*, 28, 2, (Jun), pp. 327-337, 0722-4028

Carson, H. S. (2010). Population connectivity of the Olympia oyster in southern California. *Limnology and Oceanography*, 55, 1, (Jan), pp. 134-148, 0024-3590

Christie, M. R.; Johnson, D. W.; Stallings, C. D. & Hixon, M. A. (2010a). Self-recruitment and sweepstakes reproduction amid extensive gene flow in a coral-reef fish. *Molecular Ecology*, 19, 5, (Mar 10), pp. 1042-1057, 0962-1083

Christie, M. R.; Tissot, B. N.; Albins, M. A.; Beets, J. P.; Jia, Y.; Ortiz, D. M.; Thompson, S. E. & Hixon, M. A. (2010b). Larval connectivity in an effective network of marine protected areas. *Plos One*, 5, 12, (Dec 21), pp. 1932-6203

Clarke, L. M.; Munch, S. B.; Thorrold, S. R. & Conover, D. O. (2010). High connectivity among locally adapted populations of a marine fish (*Menidia menidia*). *Ecology*, 91, 12, (Dec), pp. 3526-3537, 0012-9658

Connolly, S. R. & Baird, A. H. (2010). Estimating dispersal potential for marine larvae: dynamic models applied to scleractinian corals. *Ecology*, 91, 12, (Dec), pp. 3572-3583, 0012-9658

Cook, G. S. (2011). Changes in otolith microchemistry over a protracted spawning season influence assignment of natal origin. *Marine Ecology-Progress Series*, 423, pp. 197-209, 0171-8630

Cowan, J. H. & Shaw, R. F. (1988). The distribution, abundance, and transport of larval sciaenids collected during winter and early spring from the continental-shelf waters off west Louisiana. *Fishery Bulletin*, 86, 1, (Jan), pp. 129-142, 0090-0656

Cowen, R. K.; Paris, C. B. & Srinivasan, A. (2006). Scaling of connectivity in marine populations. *Science*, 311, 5760, (Jan 27), pp. 522-527, 0036-8075

Cowen, R. K.; Gawarkiewic, G.; Pineda, J.; Thorrold, S. R. & Werner, F. E. (2007). Population connectivity in marine systems: an overview. *Oceanography*, 20, 3, (Sep), pp. 14-21, 1042-8275

Cowen, R. K. & Sponaugle, S. (2009). Larval dispersal and marine population connectivity. *Annual Review of Marine Science*, 1, pp. 443-466, 1941-1405

Fodrie, F. J.; Becker, B. J.; Levin, L. A.; Gruenthal, K. & McMillan, P. A. (2011). Connectivity clues from short-term variability in settlement and geochemical tags of mytilid mussels. *Journal of Sea Research*, 65, 1, (Jan), pp. 141-150, 1385-1101

Fogarty, M. J. & Botsford, L. W. (2007). Population connectivity and spatial management of marine fisheries. *Oceanography*, 20, 3, (Sep), pp. 112-123, 1042-8275

Fuchs, H. L.; Neubert, M. G. & Mullineaux, L. S. (2007). Effects of turbulence-mediated larval behavior on larval supply and settlement in tidal currents. *Limnology and Oceanography*, 52, 3, (May), pp. 1156-1165, 0024-3590

Galindo, H. M.; Pfeiffer-Herbert, A. S.; McManus, M. A.; Chao, Y.; Chai, F. & Palumbi, S. R. (2010). Seascape genetics along a steep cline: using genetic patterns to test predictions of marine larval dispersal. *Molecular Ecology*, 19, 17, (Sep), pp. 3692-3707, 0962-1083

Gerlach, G.; Atema, J.; Kingsford, M. J.; Black, K. P. & Miller-Sims, V. (2007). Smelling home can prevent dispersal of reef fish larvae. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 3, (Jan), pp. 858-863, 0027-8424

Gilg, M. R. & Hilbish, T. J. (2003). Patterns of larval dispersal and their effect on the maintenance of a blue mussel hybrid zone in southwestern England. *Evolution*, 57, 5, (May), pp. 1061-1077, 0014-3820

Goldstien, S. J.; Schiel, D. R. & Gemmell, N. J. (2010). Regional connectivity and coastal expansion: differentiating pre-border and post-border vectors for the invasive tunicate *Styela clava*. *Molecular Ecology*, 19, 5, (Mar), pp. 874-885, 0962-1083

Greenberg, D. A.; Dupont, F.; Lyard, F. H.; Lynch, D. R. & Werner, F. E. (2007). Resolution issues in numerical models of oceanic and coastal circulation. *Continental Shelf Research*, 27, 9, (May), pp. 1317-1343, 0278-4343

Grosholz, E. D. (1996). Contrasting rates of spread for introduced species in terrestrial and marine systems. *Ecology*, 77, 6, (Sep), pp. 1680-1686, 0012-9658

Guichard, F.; Levin, S. A.; Hastings, A. & Siegel, D. (2004). Toward a dynamic metacommunity approach to marine reserve theory. *Bioscience*, 54, 11, (Nov), pp. 1003-1011, 0006-3568

Hanski, I. (1999). Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. *Oikos*, 87, 2, (Nov), pp. 209-219, 0030-1299

Hedgecock, D.; Barber, P. H. & Edmands, S. (2007). Genetic approaches to measuring connectivity. *Oceanography*, 20, 3, (Sep), pp. 70-79, 1042-8275

Hedgecock, D. (2010). Determining parentage and relatedness from genetic markers sheds light on patterns of marine larval dispersal. *Molecular Ecology*, 19, 5, (Mar), pp. 845-847, 0962-1083

Hellberg, M. E. (2009). Gene flow and isolation among populations of marine animals. *Annual Review of Ecology Evolution and Systematics*, 40, pp. 291-310, 1543-592X

Hixon, M. A.; Pacala, S. W. & Sandin, S. A. (2002). Population regulation: historical context and contemporary challenges of open vs. closed systems. *Ecology*, 83, 6, (Jun), pp. 1490-1508, 0012-9658

Hogan, J. D.; Thiessen, R. J. & Heath, D. D. (2010). Variability in connectivity indicated by chaotic genetic patchiness within and among populations of a marine fish. *Marine Ecology-Progress Series*, 417, pp. 263-U289, 0171-8630

Houde, E. D. (1997). Patterns and trends in larval-stage growth and mortality of teleost fish. *Journal of Fish Biology*, 51, (Dec), pp. 52-83, 0022-1112

Jacobson, B. & Peres-Neto, P. R. (2010). Quantifying and disentangling dispersal in metacommunities: How close have we come? How far is there to go? *Landscape Ecology*, 25, 4, (Apr), pp. 495-507, 0921-2973

Johnson, L. E. & Padilla, D. K. (1996). Geographic spread of exotic species: ecological lessons and opportunities from the invasion of the zebra mussel *Dreissena polymorpha*. *Biological Conservation*, 78, 1-2, (Oct-Nov), pp. 23-33, 0006-3207

Jones, G. P.; Srinivasan, M. & Almany, G. R. (2007). Population connectivity and conservation of marine biodiversity. *Oceanography*, 20, 3, (Sep), pp. 100-111, 1042-8275

Jones, G. P.; Almany, G. R.; Russ, G. R.; Sale, P. F.; Steneck, R. S.; van Oppen, M. J. H. & Willis, B. L. (2009). Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. *Coral Reefs*, 28, 2, (Jun), pp. 307-325, 0722-4028

Kadoya, T. (2009). Assessing functional connectivity using empirical data. *Population Ecology*, 51, 1, (Jan), pp. 5-15, 1438-3896

Kaplan, D. M. (2006). Alongshore advection and marine reserves: consequences for modeling and management. *Marine Ecology-Progress Series*, 309, pp. 11-24, 0171-8630

Kinlan, B. P. & Gaines, S. D. (2003). Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology*, 84, 8, (Aug), pp. 2007-2020, 0012-9658

Kinlan, B. P.; Gaines, S. D. & Lester, S. E. (2005). Propagule dispersal and the scales of marine community process. *Diversity and Distributions*, 11, 2, (Mar), pp. 139-148, 1366-9516

Kritzer, J. P. & Sale, P. F. (2004). Metapopulation ecology in the sea: from Levins' model to marine ecology and fisheries science. *Fish and Fisheries*, 5, 2, (Jun), pp. 131-140, 1467-2960

Largier, J. L. (2003). Considerations in estimating larval dispersal distances from oceanographic data. *Ecological Applications*, 13, 1, (Feb), pp. S71-S89, 1051-0761

Leung, B.; Drake, J. M. & Lodge, D. M. (2004). Predicting invasions: propagule pressure and the gravity of allee effects. *Ecology*, 85, 6, (Jun), pp. 1651-1660, 0012-9658

Levin, L. A. (2006). Recent progress in understanding larval dispersal: new directions and digressions. *Integrative and Comparative Biology*, 46, 3, (Jun), pp. 282-297, 1540-7063

Levitan, D. R. (2005). Sex-specific spawning behavior and its consequences in an external fertilizer. *American Naturalist*, 165, 6, (Jun), pp. 682-694, 0003-0147

Lyons, D. A. & Scheibling, R. E. (2009). Range expansion by invasive marine algae: rates and patterns of spread at a regional scale. *Diversity and Distributions*, 15, 5, (Sep), pp. 762-775, 1366-9516

Manel, S.; Gaggiotti, O. E. & Waples, R. S. (2005). Assignment methods: matching biological questions techniques with appropriate. *Trends in Ecology & Evolution*, 20, 3, (Mar), pp. 136-142, 0169-5347

Marshall, D. J.; Bonduriansky, R. & Bussiere, L. F. (2008). Offspring size variation within broods as a bet-hedging strategy in unpredictable environments. *Ecology*, 89, 9, (Sep), pp. 2506-2517, 0012-9658

McCook, L. J.; Ayling, T.; Cappo, M.; Choat, J. H.; Evans, R. D.; De Freitas, D. M.; Heupel, M.; Hughes, T. P.; Jones, G. P.; Mapstone, B.; Marsh, H.; Mills, M.; Molloy, F. J.; Pitcher, C. R.; Pressey, R. L.; Russ, G. R.; Sutton, S.; Sweatman, H.; Tobin, R.; Wachenfeld, D. R. & Williamson, D. H. (2010). Adaptive management of the Great Barrier Reef: a globally significant demonstration of the benefits of networks of marine reserves. *Proceedings of the National Academy of Sciences of the United States of America*, 107, 43, (Oct), pp. 18278-18285, 0027-8424

McLeod, E.; Salm, R.; Green, A. & Almany, J. (2009). Designing marine protected area networks to address the impacts of climate change. *Frontiers in Ecology and the Environment*, 7, 7, (Sep), pp. 362-370, 1540-9295

McQuaid, C. D. & Phillips, T. E. (2000). Limited wind-driven dispersal of intertidal mussel larvae: in situ evidence from the plankton and the spread of the invasive species *Mytilus galloprovincialis* in South Africa.a. *Marine Ecology-Progress Series*, 201, pp. 211-220, 0171-8630

Mitarai, S.; Siegel, D. A.; Watson, J. R.; Dong, C. & McWilliams, J. C. (2009). Quantifying connectivity in the coastal ocean with application to the Southern California Bight. *Journal of Geophysical Research-Oceans*, 114, (Oct), pp. 0148-0227

Moffitt, E. A.; White, J. W. & Botsford, L. W. (2011). The utility and limitations of size and spacing guidelines for designing marine protected area (MPA) networks. *Biological Conservation*, 144, 1, (Jan), pp. 306-318, 0006-3207

Moilanen, A. & Nieminen, M. (2002). Simple connectivity measures in spatial ecology. *Ecology*, 83, 4, (Apr), pp. 1131-1145, 0012-9658

Natunewicz, C. C.; Epifanio, C. E. & Garvine, R. W. (2001). Transport of crab larval patches in the coastal ocean. *Marine Ecology-Progress Series*, 222, pp. 143-154, 0171-8630

O'Connor, M. I.; Bruno, J. F.; Gaines, S. D.; Halpern, B. S.; Lester, S. E.; Kinlan, B. P. & Weiss, J. M. (2007). Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 4, (Jan), pp. 1266-1271, 0027-8424

Palumbi, S. R. (2004). Marine reserves and ocean neighborhoods: the spatial scale of marine populations and their management. *Annual Review of Environment and Resources*, 29, pp. 31-68, 1543-5938

Pechenik, J. A.; Eyster, L. S.; Widdows, J. & Bayne, B. L. (1990). The influence of food concentration and temperature on growth and morphological differentiation of blue mussel *Mytilus edulis* L. larvae. *Journal of Experimental Marine Biology and Ecology*, 136, 1, pp. 47-64, 0022-0981

Pechenik, J. A.; Wendt, D. E. & Jarrett, J. N. (1998). Metamorphosis is not a new beginning. *Bioscience*, 48, 11, (Nov), pp. 901-910, 0006-3568

Pecl, G. T.; Doubleday, Z. A.; Danyushevsky, L.; Gilbert, S. & Moltschaniwskyj, N. A. (2010). Transgenerational marking of cephalopods with an enriched barium isotope: a promising tool for empirically estimating post-hatching movement and population connectivity. *ICES Journal of Marine Science*, 67, 7, (Oct), pp. 1372-1380, 1054-3139

Petrovic, F. & Guichard, F. (2008). Scales of *Mytilus* spp. Population dynamics: importance of adult displacement and aggregation. *Marine Ecology-Progress Series*, 356, pp. 203-214, 0171-8630

Phillips, N. E. (2002). Effects of nutrition-mediated larval condition on juvenile performance in a marine mussel. *Ecology*, 83, 9, (Sep), pp. 2562-2574, 0012-9658

Pineda, J.; Hare, J. A. & Sponaugle, S. (2007). Larval transport and dispersal in the coastal ocean and consequences for population connectivity. *Oceanography*, 20, 3, (Sep), pp. 22-39, 1042-8275

Pineda, J.; Porri, F.; Starczak, V. & Blythe, J. (2010). Causes of decoupling between larval supply and settlement and consequences for understanding recruitment and population connectivity. *Journal of Experimental Marine Biology and Ecology*, 392, 1-2, (Aug), pp. 9-21, 0022-0981

Planes, S.; Jones, G. P. & Thorrold, S. R. (2009). Larval dispersal connects fish populations in a network of marine protected areas. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 14, (Apr), pp. 5693-5697, 0027-8424

Richards, V. P.; Thomas, J. D.; Stanhope, M. J. & Shivji, M. S. (2007). Genetic connectivity in the Florida reef system: comparative phylogeography of commensal invertebrates with contrasting reproductive strategies. *Molecular Ecology*, 16, 1, (Jan), pp. 139-157, 0962-1083

Saenz, A. (2009). Estimating connectivity in marine populations: an empirical evaluation of assignment tests and parentage analysis under different gene flow scenarios. (vol 18, pg 1765, 2009). *Molecular Ecology*, 18, 11, (Jun), pp. 2543-2543, 0962-1083

Selkoe, K. A.; Watson, J. R.; White, C.; Ben Horin, T.; Iacchei, M.; Mitarai, S.; Siegel, D. A.; Gaines, S. D. & Toonen, R. J. (2010). Taking the chaos out of genetic patchiness: seascape genetics reveals ecological and oceanographic drivers of genetic patterns in three temperate reef species. *Molecular Ecology*, 19, 17, (Sep), pp. 3708-3726, 0962-1083

Shanks, A. L.; Grantham, B. A. & Carr, M. H. (2003). Propagule dispersal distance and the size and spacing of marine reserves. *Ecological Applications*, 13, 1, (Feb), pp. S159-S169, 1051-0761

Shanks, A. L. & Eckert, G. L. (2005). Population persistence of california current fishes and benthic crustaceans: a marine drift paradox. *Ecological Monographs*, 75, 4, (Nov), pp. 505-524, 0012-9615

Shima, J. S.; Noonburg, E. G. & Phillips, N. E. (2010). Life history and matrix heterogeneity interact to shape metapopulation connectivity in spatially structured environments. *Ecology*, 91, 4, (Apr), pp. 1215-1224, 0012-9658

Siegel, D. A.; Kinlan, B. P.; Gaylord, B. & Gaines, S. D. (2003). Lagrangian descriptions of marine larval dispersion. *Marine Ecology-Progress Series*, 260, pp. 83-96, 0171-8630

Siegel, D. A.; Mitarai, S.; Costello, C. J.; Gaines, S. D.; Kendall, B. E.; Warner, R. R. & Winters, K. B. (2008). The stochastic nature of larval connectivity among nearshore marine populations. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 26, (Jul), pp. 8974-8979, 0027-8424

Smith, G. K.; Guichard, F.; Petrovic, F. & McKindsey, C. (2009). Using spatial statistics to infer scales of demographic connectivity between populations of the blue mussel, *Mytilus* spp. *Limnology and Oceanography*, sous presse, pp.

Sorte, C. J. B.; Williams, S. L. & Carlton, J. T. (2010). Marine range shifts and species introductions: comparative spread rates and community impacts. *Global Ecology and Biogeography*, 19, 3, (May), pp. 303-316, 1466-822X

Sponaugle, S.; Lee, T.; Kourafalou, V. & Pinkard, D. (2005). Florida current frontal eddies and the settlement of coral reef fishes. *Limnology and Oceanography*, 50, 4, (Jul), pp. 1033-1048, 0024-3590

Starr, M.; Himmelman, J. H. & Therriault, J. C. (1990). Direct coupling of marine invertebrate spawning with phytoplankton blooms. *Science*, 247, 4946, (Mar), pp. 1071-1074, 0036-8075

Sundblad, G.; Bergstrom, U. & Sandstrom, A. (2011). Ecological coherence of marine protected area networks: a spatial assessment using species distribution models. *Journal of Applied Ecology*, 48, 1, (Feb), pp. 112-120, 0021-8901

Thorrold, S. R.; Jones, G. P.; Hellberg, M. E.; Burton, R. S.; Swearer, S. E.; Neigel, J. E.; Morgan, S. G. & Warner, R. R. (2002). Quantifying larval retention and connectivity in marine populations with artificial and natural markers. *Bulletin of Marine Science*, 70, 1, (Jan), pp. 291-308, 0007-4977

Thorrold, S. R.; Jones, G. P.; Planes, S. & Hare, J. A. (2006). Transgenerational marking of embryonic otoliths in marine fishes using barium stable isotopes. *Canadian Journal of Fisheries and Aquatic Sciences*, 63, 6, (Jun), pp. 1193-1197, 0706-652X

Thorrold, S. R.; Zacherl, D. C. & Levin, L. A. (2007). Population connectivity and larval dispersal using geochemical signatures in calcified structures. *Oceanography*, 20, 3, (Sep), pp. 80-89, 1042-8275

Underwood, J. N.; Smith, L. D.; Van Oppen, M. J. H. & Gilmour, J. P. (2007). Multiple scales of genetic connectivity in a brooding coral on isolated reefs following catastrophic bleaching. *Molecular Ecology*, 16, 4, (Feb), pp. 771-784, 0962-1083

von der Heyden, S. (2009). Why do we need to integrate population genetics into South African marine protected area planning? *African Journal of Marine Science*, 31, 2, (Sep), pp. 263-269, 1814-232X

Walther, B. D. & Thorrold, S. R. (2009). Inter-annual variability in isotope and elemental ratios recorded in otoliths of an anadromous fish. *Journal of Geochemical Exploration*, 102, 3, (Sep), pp. 181-186, 0375-6742

Warner, R. R.; Swearer, S. E.; Caselle, J. E.; Sheehy, M. & Paradis, G. (2005). Natal trace-elemental signatures in the otoliths of an open-coast fish. *Limnology and Oceanography*, 50, 5, (Sep), pp. 1529-1542, 0024-3590

Watson, J. R.; Mitarai, S.; Siegel, D. A.; Caselle, J. E.; Dong, C. & McWilliams, J. C. (2010). Realized and potential larval connectivity in the Southern California Bight. *Marine Ecology-Progress Series*, 401, pp. 31-48, 0171-8630

Weersing, K. & Toonen, R. J. (2009). Population genetics, larval dispersal, and connectivity in marine systems. *Marine Ecology-Progress Series*, 393, pp. 1-12, 0171-8630

Werner, F. E.; Cowen, R. K. & Paris, C. B. (2007). Coupled biological and physical models present capabilities and necessary developments for future studies of population connectivity. *Oceanography*, 20, 3, (Sep), pp. 54-69, 1042-8275

White, C.; Selkoe, K. A.; Watson, J.; Siegel, D. A.; Zacherl, D. C. & Toonen, R. J. (2010). Ocean currents help explain population genetic structure. *Proceedings of the Royal Society B-Biological Sciences*, 277, 1688, (Jun), pp. 1685-1694, 0962-8452

White, J. W.; Standish, J. D.; Thorrold, S. R. & Warner, R. R. (2008). Markov Chain Monte Carlo methods for assigning larvae to natal sites using natural geochemical tags. *Ecological Applications*, 18, 8, (Dec), pp. 1901-1913, 1051-0761

Williamson, D. H.; Jones, G. P. & Thorrold, S. R. (2009). An experimental evaluation of transgenerational isotope labelling in a coral reef grouper. *Marine Biology*, 156, 12, (Nov), pp. 2517-2525, 0025-3162

Zacherl, D. C. (2005). Spatial and temporal variation in statolith and protoconch trace elements as natural tags to track larval dispersal. *Marine Ecology-Progress Series*, 290, pp. 145-163, 0171-8630