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REVIEW

Patterns and trends in marine population connectivity research

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ABSTRACT: Research into marine population connectivity (MPC) — the rate of transfer of organisms between locations — is important for our understanding of how marine systems operate as well as our ability to conserve them effectively. The large body of research in this field has never been quantitatively assessed to identify the manner in which research effort has been expended. We conducted an extensive quantitative literature review of >1000 studies and analysed the 'What?' and the 'How?' of MPC research. Publication rates increased dramatically in the mid-2000s, due to a surge of studies utilising genetic techniques and assessing larval dispersal, but studies assessing post-larval movement have not increased at the same rate. The MPC literature is dominated by bony fish, ~3 times more prevalent than the next most common taxonomic class (malacostracan crustaceans). The dispersal of some habitat-forming organisms (e.g. seagrasses, kelps) have been studied extensively (particularly corals), whereas other groups have received minimal attention (e.g. mangroves and saltmarshes). Spatially, studies have been concentrated around Europe, North America and Australia, in contrast to regions such as eastern and southern Asia and western Africa. These taxonomic, habitat and geographic biases are likely to impact our ability to predict and manage for connectivity in these systems due to the large variance in life-history traits and abiotic conditions between well-studied and under studied systems. We recommend that researchers refocus efforts towards under-studied regions, taxa and habitats to obtain a more representative understanding of the scales of connectivity and connectivity's role in maintaining populations.

KEY WORDS: Larval · Post-larval · Dispersal · Movement · Literature · Review

INTRODUCTION

Population connectivity, the exchange of individuals between distinct populations, is an important aspect of the ecology, evolution and conservation of marine populations. Connectivity influences, for example, the flow of energy and materials (Boström et al. 2011), metapopulation dynamics (e.g. Puckett & Eggleston 2016), resistance to threats (e.g. Tett et al. 2013), and evolutionary divergence (D'Aloia et al. 2015). Over the past few decades, new technologies have allowed researchers to track the cryptic dispersive stages of marine organisms. Both the increase in research interest and the advancement of new technologies have resulted in the first decade of the 2000s being known as the 'decade of connectivity' (Hixon 2011).

In the marine realm, population connectivity has been studied intensively, with many research articles assessing the factors which influence marine population connectivity (MPC) (e.g. Le Port et al. 2014, D'Aloia et al. 2015) as well as the importance and

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*Corresponding author: dale.bryan-brown@griffithuni.edu.au practical application of MPC (e.g. Roberts et al. 2003, McCook et al. 2009, Boero et al. 2016, Magris et al. 2016). This body of literature represents a substantial research effort and has been quantitatively summarised in part on a few occasions (e.g. Jones et al. 2009, Berkstrom et al. 2012, Hussey et al. 2015). Each of these reviews is limited to particular methodological practices (e.g. Levin 2006, Hussey et al. 2015) or ecosystems (e.g. Jones et al. 2009, Boström et al. 2011, Berkstrom et al. 2012). The narrower focus of these reviews has allowed them to exhaustively investigate the methodological trends and specific insights garnered from particular study designs. What is still lacking, however, is an overall assessment of MPC research effort to identify how research gaps may have biased our understanding of MPC.

Previous reviews have highlighted how our understanding of MPC has changed as research progresses. The reviews of larval dispersal by Levin (2006) and Jones et al. (2009) highlight the changing perception among the research community that dispersive larval stages are not merely passive plankton, that the scale of larval dispersal is far smaller and that self-recruitment is a far more prominent process than was previously thought (self-recruitment is here defined as in Jones et al. 2009 [p. 310] as 'the proportion of recruitment to a local population that is derived from adults in that population'). Levin (2006) postulates that larval dispersal studies are severely limited by the fact that most studies identifying the larval traits of invertebrates have been conducted using echinoderm and bivalve larvae, while most work using chemical signatures has been conducted with fish. Similarly, Jones et al. (2009) reported that studies of larval dispersal on coral reefs have been dominated by fish and coral, with considerably smaller effort given to other invertebrate taxa. Quantitative reviews of post-larval movements have advanced our understanding of connectivity by identifying no positive relationship between body size and migratory distances (Hussey et al. 2015).

These previous reviews have highlighted MPC research achievements and future areas of research for specific aspects of MPC. These include larval dispersal research (Levin 2006), larval dispersal of coral reef fish and corals (Jones et al. 2009), the ecological consequences and patterns of movement of organisms within and through tropical seascapes (Berkstrom et al. 2012) or the use of electronic tagging in understanding the movement of organisms (Hussey et al. 2015). The limited scope of these reviews, however, does not advance a comprehensive view of MPC across life stages, taxa and habitats.

Here we assess methodological trends in the field of MPC as a whole. In contrast to previous quantitative assessments of MPC we applied no limitations to our dataset, incorporating any paper that has assessed MPC. MPC is here defined as 'the transfer of individuals between discrete locations (suitable for post-larval life stages) through the marine realm'. This broad definition of MPC allowed us to conduct the first unbiased assessment of the state of the research effort expended in this important field. We have enabled MPC researchers to take a step back from their research to assess whether current research trajectories are in line with both, conservation and scientific needs. This research intends to summarise the methodological trends present within MPC research by conducting an extensive, unbiased literature review of this discipline.

METHODS

Database acquisition

To gain a representative sample of the literature, 2 databases (ISI Web of Science [http://wokinfo.com] and Scopus [https://www.scopus.com]) were searched, using default search settings and the following terms (the following search example is for ISI, for Scopus the term 'Near/' is to be replaced with 'W/'):

(Marine OR Ocean* OR Coastal) AND

(Connectivity OR (Larv* Near/5 sink) OR (Larv* Near/5 source) OR Linkag* OR (Population Near/5 sink) OR (Population Near/5 source) OR Recruit* OR Self-recruit* OR (source AND sink) OR subsid*) AND

((larva* NEAR/2 dispers*) OR Migration OR (migration AND diel) OR (migration AND ontogenet*) OR (migration AND seascape) OR (dispersal AND migration) OR (dispersal AND diel) OR (dispersal AND ontogenet*) OR (dispersal AND seascape) OR (habitat AND seascape))

The search terms were chosen to narrow the results to MPC without incorporating systematic bias in the search results. The first section of the search term ensured that the bulk of the literature obtained related to marine studies. The second set of search criteria was designed to capture alternative terms for 'connectivity'. The third list of terms was intended to further enhance results to include papers that were explicitly concerned with the movement of organisms. The searches were conducted on January 4, 2016. Detailed methods for the paper processing are supplied in Supplement 1 (all Supplements are located at www.int-res.com/articles/suppl/m585p243_supp.pdf). These search terms and later processing excluded all non-English papers. It is unlikely that this bias will have a substantive impact on the dataset (Morrison et al. 2012).

Papers that were included in the dataset after individual examination needed to contribute novel research (i.e. general reviews were not included but meta-analyses were) to the field of MPC. For the purposes of this review, an MPC study (1) assesses the movement of organisms through the marine realm, and (2) assesses the transfer of individuals between ≥2 distinct (although not necessarily explicit) geographic locations. Once papers were gathered they were assessed on several criteria. Papers were assessed in alphabetical order by the surname of the first author to ensure no systematic bias was accidentally incorporated into the dataset. The final dataset consisted of 1023 papers.

Database analysis

The literature review intended to identify 2 factors, effectively, the 'How?' and the 'What?' of each study. The 'how' component considered the scientific intentions underpinning the study, the dispersive stage considered in the work and the specific methodology used. The 'what' component assessed the study organism(s) and their general relationship to society, the habitats explicitly considered in the experimental design and the geographical region in which the study was conducted. Publication metadata were also collected.

How have they been studied?

Intention was identified by categorising the goals of each study into 6 general categories: (1) larval dispersal (e.g. Jones et al. 1999), (2) post-larval movements (e.g. Dorenbosch et al. 2005), (3) dispersal without a defined life stage under investigation (e.g. Muths et al. 2015), (4) population structure of a putative meta-population (e.g. Portnoy et al. 2014), (5) technique validation (e.g. Dufour et al. 1998) or (6) high-level ecological theory (where a study has assessed population connectivity to answer a higher-order question, such as the influence of kin selection, e.g. Buston et al. 2009).

The dispersive stage under investigation was divided into 3 categories: larval, post-larval and ambiguous. Studies assessing larval dispersal are conducted in such a manner that post-larval processes can be effectively ignored (e.g. a study of fish otoliths only assessing chemical signatures occurring before the formation of the settlement mark, e.g. Standish et al. 2011), or a genetic study conducted at a scale at which post-larval dispersal is extremely unlikely (e.g. Burden et al. 2014). In contrast, studies assessing post-larval movement are conducted so that larval processes are inconsequential (e.g. genetic assessments of an organism without a larval stage, e.g. Wiszniewski et al. 2010, or fish size distribution across a seascape indicating ontogenetic movements, e.g. Aguilar-Perera & Appeldoorn 2007). Finally, ambiguous studies of dispersal are conducted so that larval and post-larval processes are likely working in tandem to influence the results obtained (e.g. a genetic study of a large potentially migratory organism with a larval stage, e.g. Côté et al. 2013, or pelagic organisms, e.g. Aglieri et al. 2014).

Finally, the specific methodologies utilised were divided into 4 categories: genetics, biophysical modelling, tagging and simple observation (Table 1). Predictive techniques often lack empirical evidence but can provide highly detailed information about realistic scenarios. Inferential tools allow researchers to obtain large amounts of empirical evidence, which is, however, limited by an array of necessary assumptions (such as genetic equilibrium, Hellberg et al. 2002, or accurate isoscapes, McMahon et al. 2013). Direct tools allow researchers to unambiguously identify dispersal pathways, but these tools often have low replication and are expensive (although costs are decreasing, Hussey et al. 2015).

What has been studied?

All organisms studied were categorised using 2 criteria, taxonomic status (phylum, class, family, genus, species, subspecies) and significance to society. Societal significance was grouped into: fished (culinary), fished (ornamental), pest, habitat-forming (e.g. *Porita* corals, *Avicennia* mangroves), culturally significant, NA (particle in biophysical model) and NA (organism of no economic consequence) (Table 2). Note that the definition of societal significance excludes species that provide supporting services, such as ecosystem engineers, but it was beyond the scope of this review to identify all possible services provided by the studied species.

Table 1. Descriptions of methodological classification

Methodology	Class	Definition	Sub-categorisations	Examples
Genetics	Inferential	Using inherited markers to infer the rate of exchange of individuals between putative populations	NA	Nuclear/Plastid genetic markers, allozymes, parentage analyses
Modelling	Predictive	Using computer-based models to predict connectivity between populations	NA	Hydrodynamic biophysical modelling
Tagging	Direct (artificial) / inferential (natural)	Using indicators (either natural or artificial) to discriminate the identity of organisms	(1) Electronic (artificial) (2) Simple (artificial) (3) Passively acquired (natural) (4) Dietary analysis (natural)	(1) Satellite tracking, PIT tagging (2) ID tags, photography (3) Otolith chemistry (4) Gut content analysis
Simple observation	Inferential	Inferring dispersal events by assessing changing community/population dynamics or the use of simple surrogates for estimating movement	(1) Extractive sampling (2) Non-extractive sampling (3) Physical oceanography	(1) Trawling (2) Underwater visual census (3) Drifter studies

A study was deemed to have included a particular habitat in its experimental design if the authors: (1) explicitly stated the habitats that their organisms utilise (e.g. Andreakis et al. 2012), (2) contextualised study sites by describing the habitats within sampling sites (e.g. Acosta 1999) or (3) considered the spatial arrangement of habitats outside of their study site (e.g. Aguilar-Perera & Appeldoorn 2007). Twenty-three distinct habitats were identified in the literature. Biogenic habitats included algae, shallow coral reefs, deep corals, mangroves, mussel reefs, oyster reefs, saltmarsh, seagrass beds, worm reefs and other biogenic habitats (e.g. endo-commensals). Abiotic habitats included the deep sea (>1 km depth), hydrothermal vents, sea-mounts, estuarine, freshwater (e.g. assessing connectivity between catadromous organisms, such as Hughes et al. 2014), terrestrial (e.g. assessing movement between intertidal and terrestrial habitats, e.g. Hübner et al. 2015), marine lagoons, hard bottom, soft bottom, soft intertidal, rocky intertidal, open pelagic and man-made.

Study region was defined by assessing which geographic province (as defined in Spalding et al. 2007) the study was conducted in. If, however, the sampling regime was deeper than 200 m or did not explicitly use shelf habitats, the Spalding system could not be used and the general oceanic basin was identified.

Data analysis

Data were analysed by assessing trends in different aspects of MPC as a proportion of the entire MPC literature. The use of proportional trends as a method of data analysis is valid provided that research effort results in a proportional increase in both publications and knowledge. If analysing proportional trends is valid, the number of papers produced will give an indication of how well-studied the phenomena being researched are. It must be noted that it is impossible to identify systems which are (in)sufficiently studied for conservation practice or for which we have good knowledge simply by assessing the number of papers produced. Accordingly, this work is not meant to provide the definitive guide on where research investment is required, rather it seeks to highlight where research has been invested and question whether or not there are important gaps that should be a priority to address in future research.

Due to the way papers were obtained, a temporal bias likely exists in the dataset. Firstly, papers published recently are more likely than older works to

Table 2. Definitions of the practical significance of study organisms

Significance to society	Description	Example
Fished (culinary)	An organism subject to a commercial fishery with the intention of being eaten by humans	Snapper (Sparidae) Abalone (Haliotidae)
Fished (ornamental)	An organism subject to a commercial fishery with the intention of being viewed by humans either dead or alive	Clown anemonefish (Pomacentridae) Yellow tang (Acanthuridae)
Pest	An organism responsible for economic loss to society	Atlantic lionfish (*Pterois* spp.) Invasive ascidians (Ascidiaceae)
Habitat-forming	An organism which is a major component of the physical structure of the environment	Mangrove trees (Avicenniaceae) Reef-forming Corals (Poritidae)
Culturally significant	An organism which society cares about, for cultural, spiritual etc. reasons, xnot economic	Whales (Balaenopteridae) Turtles (Cheloniidae)
NA (particle in biophysical model)	Particles in a biophysical model which have not been parameterised to simulate an actual organism	NA
NA (organism of no economic consequence)	An organism that society has little direct interest in, regardless of any ecosystem functioning it may be involved in	Worms (Sabellariidae) Periwinkles (Littorinidae)
	The classification given to any study subject featured in a study that was not intentionally sought after	A study assessing differences in fish community composition

be available online and, secondly, the search terms potentially reflect contemporary, not historical, MPC vocabulary. Accordingly, when assessing the number of papers produced, it is important to apply multipliers to accurately reflect the historical investment of research effort. The first multiplier was obtained by modelling the proportion of papers that appeared online, but for which no PDFs were available as a function of year. The second multiplier was modelled as the proportion of papers rejected at the manual check stage as a function of year. These 2 multipliers correspond to Stages 4 and 5, respectively, see Supplement 1. PDF acquisition rates were highly correlated to year (a 3rd order polynomial, $R^2 = 0.92$) and paper acceptance rates were also correlated to year (a linear relationship, $R^2 = 0.42$). These corrections only affect results shown in Fig. 1.

RESULTS

Database description

The earliest paper in the dataset was published in 1987 and the dataset included papers published in all years until 2015, with a substantial increase in studies in 2005 (Fig. 1). Primary research papers were published in 141 journals, with Marine Ecology Progress Series (17%), Molecular Ecology (10%), Marine Biology (8%) and PLOS ONE (7%), collectively publishing ~40% of all papers. For a list of all papers included in the study see Supplement 2.

How have they been studied?

Intention. Most papers in this dataset (~60%) aimed to understand larval dispersal through either predicting (~20%) and/or assessing (~48%) patterns of larval dispersal. Post-larval movement studies were assessed in approximately 30% of studies, with comparatively few predictive studies (~2% predictive and ~29% assessing). Another major aim of these studies was to assess population structure with ~48% of all studies assessing the characteristics of genetic (e.g. Hughes et al. 2014), morphological (e.g. Beck & Styan 2010) or social (Garland et al. 2015) markers between putative metapopulations. Only a small proportion of the literature was dedicated to identifying higher-level ecological theories (0.5%).

Dispersive stage. The majority (~62%) of papers assessed larval dispersal whilst the dispersal of post-larval stages was studied in approximately 29% of studies (Fig. 2). Studies assessing 'ambiguous' dispersal formed a relatively small component of the literature (~13%). Among the highly influential papers (>10 citations per year), 83% of papers studied larval dispersal, while ~13% focussed on post-larval movements. Ambiguous dispersal was assessed in 10% of the studies.

Methodology. Genetic and modelling techniques were the methods dominating the literature, constituting 48 and 24% of studies, respectively (Table 3). Within inferential observation studies (~19% of all studies), an equal split exists between extractive and non-extractive techniques, both of which were ap-

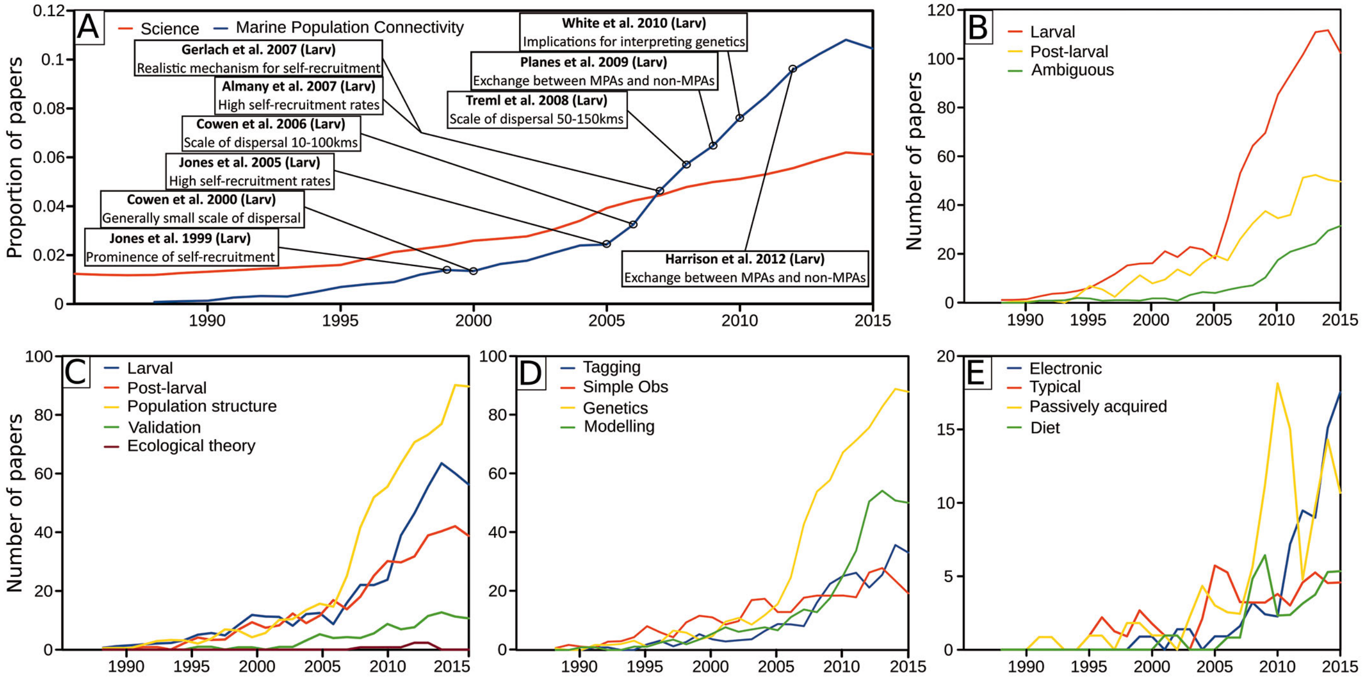

Fig. 1. Temporal patterns in the data. (A) The rate of increase in connectivity studies versus the rate of papers accruing in science in general (general 'science' papers obtained by searching 'marine OR coast* OR ocean' in Scopus). The 10 most cited papers (measured in citations per year) are also plotted along with a major conclusion of each paper. Panels (B), (C) and (D) show temporal changes in the dispersive stage investigated, intention behind papers and methodologies employed, respectively. Panel (E) expands panel (D) specifically for temporal variation in tagging studies

proximately 5 times more common in the literature than observations of physical oceanography. Tagging studies (~17% of all studies) could be divided into passively acquired (43%), electronic (30%), simple (21%) and dietary tagging studies (14%); see Table 1 for methodological details.

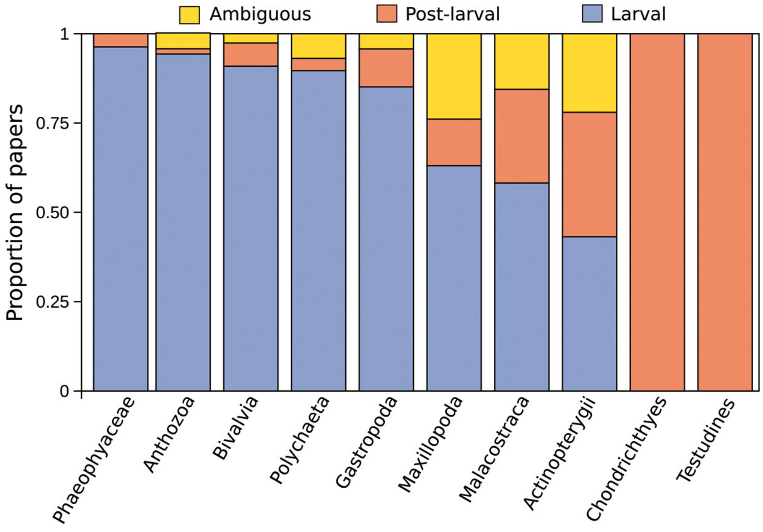

Fig. 2. Research investment into understanding larval dispersal and post-larval movements by taxonomic classification shown in descending order of the number of larval studies relative to other studies

Temporal patterns. The methodologies employed, dispersive stage investigated and intention behind the research varied significantly over time. An example of this is the relatively stable period prior to 2005, where no single technique dominated. This was followed by a sudden spike in genetic studies. Similarly, the intention and dispersive stage of studies conducted prior to 2005 were relatively similar among sub-categories. After 2005, studies assessing and intending to assess larval dispersal greatly increased. By 2010, modelling studies also began to increase. Within tagging studies, different techniques appear to come in and out of favour (Fig. 1).

What has been studied?

Study species. A huge variety of organisms have been studied, representing 21 phyla, 46 classes and 380 families. These organisms included taxa as disparate as barnacles, whales, viruses and penguins. Although there was a great variety in taxonomic representation, cer-

Table 3. Methodological trends in the literature. Below the diagonal: the observed and expected (in parentheses) number of studies using methodological combinations. Along the diagonal (in **bold**): the number of studies using the methodology both exclusively and in concert with other methods and the number of studies using the methodology exclusively (in parentheses). Above the diagonal: (Observed–Expected)^2 / Expected for each methodological combination (negative and positive values indicate less and more studies than expected, respectively)

Technique	Electronic Tag	Passively acquired marker	Diet	Typical tag	Physical oceano-graphy	Extractive sampling	Non-extractive sampling	Genetic	Modelling
Electronic tag	**52 (38)**	1.23	3.85	32.66	–0.99	0.00	0.40	–0.50	–3.78
Passively acquired marker	2 (0.93)	**74 (58)**	3.07	0.01	–1.12	–2.23	2.11	7.48	–0.38
Diet (total)	2 (0.93)	2 (1.05)	**25 (16)**	0.01	–1.12	0.02	0.01	–1.99	–4.28
Typical tag (total)	6 (0.82)	1 (0.93)	1 (0.55)	**37 (23)**	–0.99	0.00	0.01	–0.02	–3.78
Physical oceanography	0 (0.99)	0 (1.12)	0 (0.66)	0 (0.99)	**21 (5)**	–2.36	–3.43	0.00	4.40
Extractive sampling	2 (1.97)	0 (2.23)	2 (1.31)	2 (1.97)	0 (2.36)	**95 (63)**	16.30	–3.02	2.69
Non-extractive sampling	1 (1.86)	0 (2.11)	2 (1.24)	2 (1.86)	5 (2.23)	13 (4.47)	**99 (72)**	–2.65	–0.04
Genetic	2 (3.28)	9 (3.72)	1 (2.19)	3 (3.28)	4 (3.94)	3 (7.88)	3 (7.45)	**490 (432)**	26.18
Modelling	0 (3.78)	3 (4.28)	0 (2.52)	0 (3.78)	9 (4.53)	14 (9.07)	8 (8.56)	35 (15.11)	**249 (186)**

tain taxa dominated the literature (Fig. 3). For instance, of the 9 phyla represented in >1% of papers (Chordata:523 studies; Mollusca: 163; Arthropoda: 153; Cnidaria: 70; Echinodermata: 37; Annelida: 28; Heterokontophyta: 27; Plantae: 16; Porifera: 14), chordates, molluscs and arthropods dominated, constituting 77.7% of all papers (see Supplement 3 for a full list of taxa used in the dataset).

The functional classification of organisms (see Table 2) also shows a bias (Fig. 3). The most studied group of organisms were those that are fished for culinary reasons (~40% of studies) and the least studied were pest species (~4% of all studies). Organisms fished for ornamental reasons constituted ~10% of the dataset while those forming habitats were studied in ~12% of studies. Culturally significant organisms were studied in ~8% of studies. Within habitat-forming organisms, there was a clear bias towards certain habitats, particularly corals, algae and seagrass (Fig. 4).

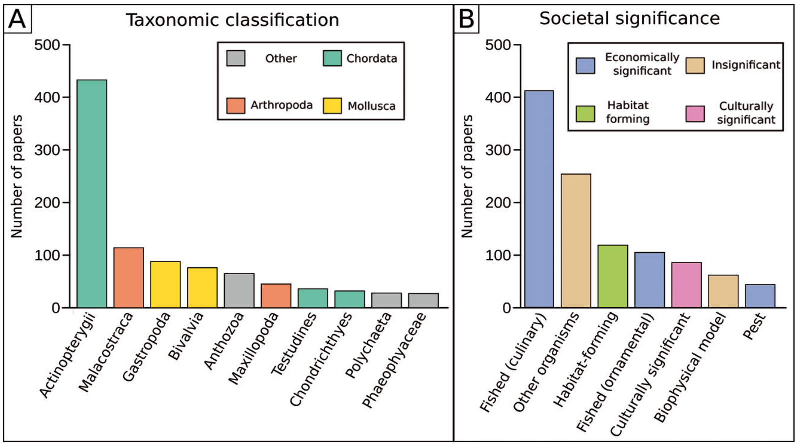

Fig. 3. Proportional investment of research effort into (A) taxonomic and (B) societal classifications

Habitats. The habitat in which an organism dwells is considered of marginal significance in many studies. Papers that do not mention habitat attributes constitute ~24% (246) of all studies. For those papers explicitly considering habitat connectivity, coral reefs (~23%), freshwater habitats (~15%) and the rocky intertidal zone (~12%) constitute the largest portion of the literature (see Supplement 4 for a full list of habitats).

Region. All ecoregional provinces (Spalding et al. 2007) were represented in the database, with the exception of the Amsterdam-St Paul Island group in temperate southern Africa (Fig. 5). Of the 10 provinces studied in ≥50 papers, 9 were located near North America, Europe and Australia (Fig. 5). Of the 62 ecoregional provinces, 32 were considered in < 20 (2%) of studies each, with areas around the northern Indian Ocean, western Africa, South America and isolated landmasses (such as oceanic islands and Antarctica) generally under-studied.

DISCUSSION

Influential papers

Over the past 2 decades, new technologies allowing researchers to track the cryptic dispersive larval stages that many marine organisms possess have been made accessible. Historically, the dominant paradigm in MPC research was that marine populations were well connected by the exchange of larval stages through the dispersive and appar-

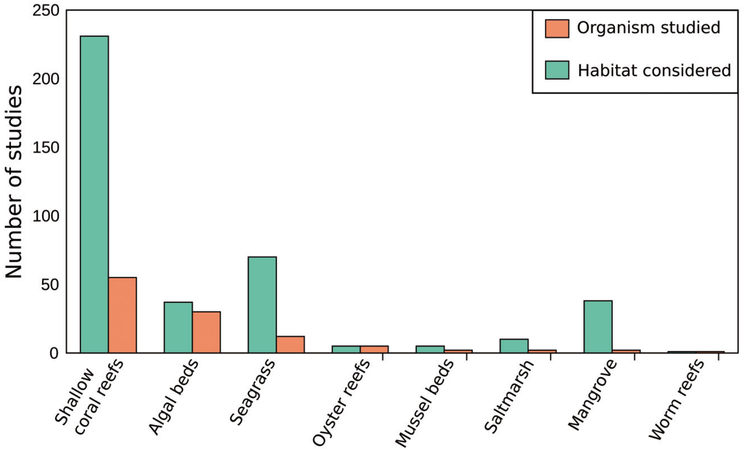

Fig. 4. Difference between the number of studies produced that explicitly consider the habitat in their study design and those that study connectivity between populations of the organisms that form these habitats

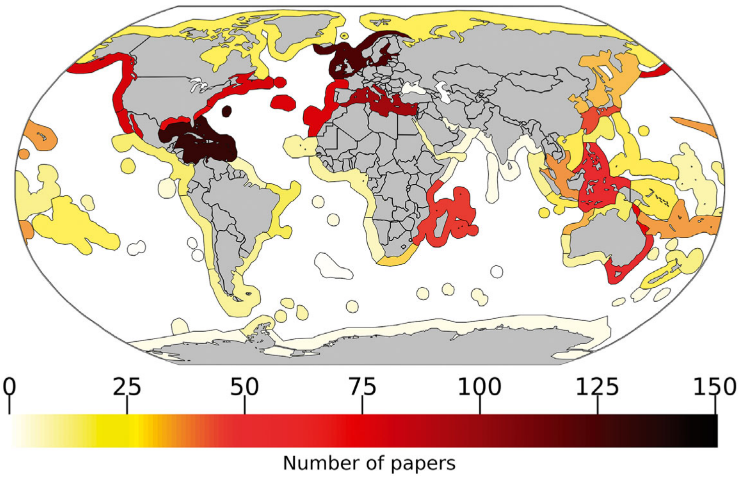

Fig. 5. The geographic partitioning of the research effort expended on understanding marine population connectivity. Colour scale represents the number of studies in bioregions (defined by Spalding et al. 2007)

ently barrier-free marine realm. However, some of the most influential papers produced, especially in the first half of the 2000s, challenged this paradigm by identifying self-recruitment as an important process influencing marine population dynamics (Jones et al. 1999, 2005, Almany et al. 2007). Self-recruitment was found to be far more frequent than previously thought and the scale of dispersal far smaller, with larval dispersal typically between 10 and 150 km (Cowen et al. 2006, Treml et al. 2008) (Fig. 1).

The 10 most cited papers in our dataset all studied larval dispersal (Fig. 1). When we assess all highly influential papers (>10 citations per year, 30 papers total) we find that the majority of these studies assess larval dispersal (see Supplement 2), implying that the need to understand larval dispersal patterns has been driving this discipline. The most influential post-larval dispersal papers have identified large-scale movements of great white sharks *Carcharodon carcharias* (Bonfil et al. 2005) or Atlantic bluefin tuna *Thunnus thynnus* (Rooker et al. 2008) or identified the global population structure of a culturally significant organism, the scalloped hammerhead shark *Sphyrna lewini* (Duncan et al. 2006). These papers did not (as some of the early larval papers did) provide any sort of new methodological framework to their field, but applied well-established techniques to organisms of interest at large scales.

How?

The temporal patterns in the dataset demonstrate how research trends often reflect the availability of technologies. This is exemplified by an increase in studies assessing larval movements since the advent of accessible (and increasingly advanced) genetic techniques (approximately the year 2005) and biophysical modelling (in vogue since 2010) (Fig. 1). Similarly, studies on post-larval movements are benefitting from increasing affordability of electronic tags (Hussey et al. 2015). Although electronic tagging is currently not the dominant technique, it is the only technique to have shown an increase in recent years (Fig. 1), implying that a revolution in our understanding of post-larval movements may now be underway (see Hussey et al. 2015).

Most research papers utilise a single methodology, as opposed to multiple methods in unison (see Table 3). This is potentially problematic as single techniques often have inherent limitations, which can be ameliorated if used together. The use of multiple techniques in concert, particularly between the 3 previously defined methodological classifications (predictive, inferential and direct), can provide more robust results as inherent limitations within a single method may be addressed by the other methods. It is evident, however, that methodological integration within studies is not normal, being conducted in only ~12 % of studies. Studies that integrate methods appear to have a predisposition to utilise certain methodologies together (see Table 3). In particular, genetics (an inferential technique) is often used with either passively acquired markers (e.g. otolith chemical composition, an inferential technique) or predictive models (i.e. oceanographic models of particle dispersal). There is no indication that predictive models have been integrated with direct measures (such as mark-recapture). Finally, techniques which are simple to use together (such as applying simple tags and electronic tags) are often used in conjunction (for instance, simple tags may be used to build upon data generated from more expensive electronic tags, e.g. Stokes et al. 2014).

Combining techniques can show how individual behavioural cues drive seascape-level population connectivity. For instance, a combination of direct (acoustic telemetry) and inferential (grouper calling signal—indicating courting behaviour) techniques were used to map patterns of grouper movement in the southern Caribbean (Rowell et al. 2015). The use of the 2 techniques meant researchers were able to identify the movement of groupers through fished areas to reach protected breeding sites and that individual groupers follow acoustic signals produced by conspecifics to reach spawning locations. This provides a compelling example of how integrating multiple techniques can overcome the inherent limitations of individual techniques and realise far greater insights into the functioning of marine systems.

What?

Regional patterns. It is known from more broad geographic patterns of scientific effort that general economic strength correlates with scientific output (Pyšek et al. 2008, Archer et al. 2014). A similar bias is found in the MPC literature (Fig. 5). All biogeographic provinces studied in >50 papers are located near affluent nations (Canada, USA, Northern/Western European nations or Australia).

If research effort had been expended economically (i.e. where the financial investment of research is proportional to the magnitude of the problem to be addressed, see Nelson 1959) then we would expect that the investment of connectivity research in different biogeographic provinces would roughly reflect the anthropogenic threats to the biodiversity of the province. Contrasting the patterns of biodiversity in marine systems and the associated threats (Selig et al. 2014) with the geographic distribution of research effort in this study, shows that there are mismatches between where research effort has been expended historically and where it is required for science to inform conservation management. Areas that have been heavily studied generally merit the attention. For example, although the Caribbean seas have been studied more thoroughly than any other region, this region is heavily threatened and possesses many range-restricted species. Similarly, the Mediterranean Sea is highly threatened and has a very high proportion of species with restricted ranges. Areas such as north-eastern Australia, however, have been heavily studied despite, historically, being under less anthropogenic pressure. Conversely, there are threatened areas where connectivity research is lacking. These include the areas associated with the west African transition, South China Seas and southern Kuroshio (Spalding et al. 2007). Two regions, the western Indian Ocean and the western Coral triangle, where there has been extensive investment of international conservation funding, have been studied intensively, despite being located near poorer nations (see Fig. 5).

Each province defined in Spalding et al. (2007) constitutes a unique system differentiated by distinctive biotic and abiotic conditions. The provinces that are well-studied for MPC (such as the tropical northwestern Atlantic) have had their (a)biotic conditions well-characterised. Accordingly, it is possible to derive important lessons about the impact of biological traits and abiotic conditions on patterns of MPC. However, due to the variability in biological traits between closely related species (e.g. Pires et al. 2013) and their unique interaction with abiotic conditions (e.g. dos Santos et al. 2008), it is probably erroneous to assume that the conclusions garnered from affluent areas can simply be applied to less affluent areas. This is typified by the fact that ecologically and geographically similar congeners can have disparate population structures, indicating that neither ecological, geographic nor taxonomic similarity is a sufficient proxy for population connectivity (Crandall et al. 2012).

Study species. There is a strong taxonomic bias within the literature towards studying fish. This does not, however, indicate a deficit within the MPC literature for other taxa. Many important questions in MPC, such as the influence of pelagic larval duration on connectivity metrics, will be broadly applicable across many taxa (see Selkoe & Toonen 2011). However, some questions will be influenced by taxonomic classification (such as the scale of post-larval movements, Acosta 2002) or the influence of swimming capabilities on planktonic dispersal (Chia et al. 1984, Le Port et al. 2014). In this review we find that the proportional dominance of larval or post-larval dispersive stages reflects how often those stages are studied in the literature (see Fig. 2). For example Actinopterygii fish have an approximately even split between larval and post-larval studies (Green et al. 2015), in contrast to Polychaetes and Chondrichthyes, which have been primarily studied for larval and post-larval dispersal, respectively.

There is also bias in the research effort expended on organisms of significance to society. The most and least intensively studied organisms (those which are fished for food (>40%) and those which are pest species (~4%), respectively) both have immediate substantial economic impacts on society. Tracking and predicting the advance of invasive organisms is often touted as a major advantage of having a proper understanding of MPC (Levin 2006, Cowen et al. 2006, Pineda et al. 2007). Predicting invasions, and quantifying local spread of invasive species, however, does not appear to be one of the major applications of research. Invasive species pose a major threat to human health, economic infrastructure, native organisms and habitats by disrupting natural chemical cycling pathways, and changing community structure and food webs (Molnar et al. 2008). Predicting the invasion of such potentially deleterious organisms should receive more attention, equivalent to that directed at identifying patterns of connectivity between populations of organisms that are significant to society for aesthetic reasons, such as marine turtles and cetaceans.

The distribution of research effort expended on understanding patterns of connectivity in habitat-forming organisms (studied ~12% of the time) does not show an even spread across different habitats. For instance, ~45% of all these studies focus on shallow-water corals, while a further 36% consider species which form algal and seagrass habitats. The dispersal of mangroves and saltmarsh plants (2 important and extremely valuable habitats, de Groot et al. 2012), which are known to be under intense anthropogenic pressures (Gedan et al. 2009, Polidoro et al. 2010), has collectively been assessed in only ~3% of these studies. It is unlikely that the in-depth knowledge obtained regarding coral population connectivity is transferable to other habitat forming organisms. Many aspects of coral reproductive behaviour, including mass spawning events, parental and larval behaviour, are absent in some other groups of habitat forming organisms like mangroves, saltmarsh, seagrass and algae. Mangrove and saltmarsh propagules are completely passive, are found only inconsistently in the medium through which they disperse (in the case of intertidal populations), and have highly variable propagule morphologies (e.g. Clarke et al. 2001). Further, other habitat types (algae, oysters, seagrasses, etc.) are formed by organisms with substantially different reproductive biologies to corals, further highlighting the lack of applicability of these studies to other habitats.

There is a trade-off between obtaining in-depth knowledge by working in well-studied systems and our confidence to extrapolate this knowledge to unstudied systems. For example, *Stegastes partitus* (the bicolour damselfish), a model species, has been the focus of 14 studies all of which have been conducted in the Caribbean Sea. The in-depth understanding of the processes which govern patterns of population connectivity of *S. partitus* in this area are likely transferrable to other systems (Puebla et al. 2012). However, the unique abiotic (e.g. currents, pollution, geological structures) and biotic (e.g. larval attributes, predation pressures, parental care) attributes of other systems are likely to interact with the principles yielded in these studies and cause the predicted patterns of connectivity to be different. For example, population genetic structure is often different between species which are ecologically similar as adults and are co-distributed, indicating different patterns of connectivity (e.g. Ayre et al. 2009). Factors such as habitat tolerance (Ayre et al. 2009), spawning time (Veale & Lavery 2011) and larval behaviour (Pires et al. 2013) all have an impact on the connectivity of populations, highlighting the depth of species-specific knowledge required to properly predict patterns of population connectivity between otherwise similar organisms.

Habitats studied. Inherent in the definition of population connectivity given earlier is the notion that organisms are transported between areas, often featuring different habitats. Approximately 25% of studies in this review, however, did not discuss the habitats under investigation in any manner (see Supplement 4). Although population connectivity is observable at the population level (irrespective of habitat attributes), the spatial arrangement of populations (determined by the arrangement of habitats) has profound impacts on both larval and post-larval (Olds et al. 2012, Brown et al. 2016) movements and, as such, population connectivity.

Ecosystem valuation studies reveal that coral reefs are the most valuable of all habitats per hectare (Costanza et al. 2014). Furthermore, tidal wetlands (mangroves and saltmarsh) and shallow marine habitats (marine systems up to 200 m depth excluding tidal wetlands and coral reefs, e.g. seagrass beds, kelp forests, rocky intertidal) are the second and third most valuable ecosystems per hectare, respectively. If research effort has been expended economically, we would expect to see the number of studies produced in any given system roughly reflecting the proportional value of said system (see Lubchenco 1998). The number of papers produced which contextualise the study by the geographical arrangement of the habitats should roughly reflect the value that the habitat carries as an entity in the seascape (e.g. for organisms performing ontogenetic migrations), while the number of papers produced assessing connectivity between organisms which form the habitat should reflect the importance of maintaining the habitat's viability. However, the proportional investment of research effort found in this review does not reflect major ecosystem valuations (de Groot et al. 2012, Costanza et al. 2014) (Fig. 6).

Research investment into connectivity between habitats does not match the economic values of those habitats. For example, intertidal wetlands have the highest value of all habitats as nursery habitat (de Groot et al. 2012), implying that understanding how organisms use these habitats during different life stages is a critical research area that needs to be addressed. However, the way in which organisms use these habitats while dispersing is studied, proportionally, far less than connections between other habitats such as coral reefs (Fig. 6). Furthermore, the connections between the organisms that form these extremely valuable habitats is studied less than organisms that form habitats that are considerably less valuable economically, such as oyster reefs.

The studies that have been conducted in these under studied systems have led to interesting conclusions regarding how these systems operate. For instance, historically, mangroves were thought to be important for fish because they provided foraging areas. However, through assessing the manner in which fish use these habitats across 5 continents, it was shown that fish typically utilise mangroves as highly structured habitat (Igulu et al. 2013). This conclusion furthers our understanding of how highly mobile organisms use different habitats during migration events. Another example is the transfer of energy and materials between the marine and terrestrial zones. The movement of intertidal crabs between saltmarsh and terrestrial forest was sex-dependant, giving important information about the flow of materials between these 2 realms, allowing greater conservation of ecosystem processes (Hübner et al. 2015). These novel insights into how these habitats operate are good examples of what can be gained through investigating patterns of movement in various marine systems.

Systematic geographic, habitat and taxonomic biases in MPC research effort may affect the ability of managers to conserve natural systems. Conservation decisions, such as where to place marine reserves, should be influenced by knowledge of local population connectivity (Jones et al. 2007, Burgess et al. 2014, Olds et al. 2016). Therefore, our lack of knowledge of the patterns of connectivity in different ecological contexts hampers our ability to effectively conserve marine environments. For example, the layout of habitats within a seascape is highly variable with some seascapes naturally more condensed than others. This variable distribution of habitats influences the distance at which habitat proximity facilitates connectivity (Martin et al. 2015).

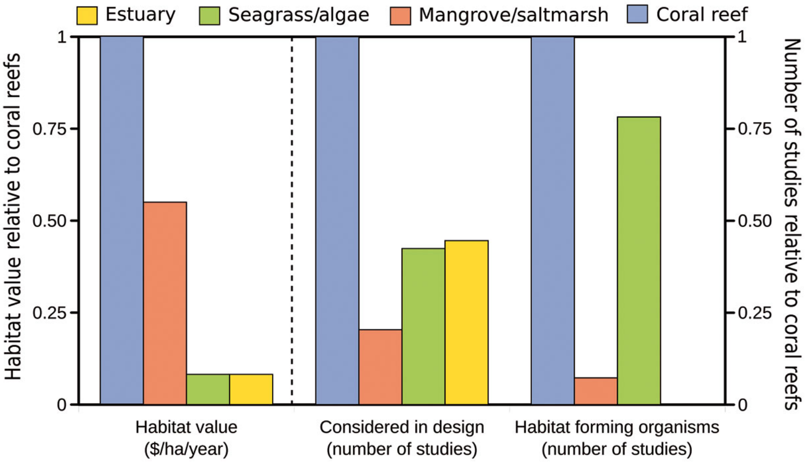

Fig. 6. Economic assessment of the expended research effort. Habitat values derived from deGroot et al. (2012). Scaling is relative to the value of coral reefs for each metric

CONCLUSIONS

Research, as an industry, represents an investment from private individuals, organisations and governments (and, by extension, citizens) with the specific aim of filling important knowledge gaps and ultimately providing a return on the investment made (Lubchenco 1998). We demonstrate that the huge research effort expended on understanding MPC has been systematically biased and, as such, needs to be realigned with research priorities. There are understandable biases detected in the regions under investigation, organisms under investigation and habitats considered explicitly in study designs. Connectivity research is distinctly lacking in southern and eastern Asia, as well as in western Africa. It is impossible to 'over-study' a system, it is, however, possible to disproportionately assign research priority to well-researched groups. This review suggests that taxonomic groups outside of the Actinopterygii are under studied and require further research as there are many ecologically and economically significant species in these groups. Similarly, among organisms that form habitats, shallow-water corals have received a disproportionally large investment of the research effort, whilst other highly important ecosystems (particularly mangrove and saltmarsh) have not been considered at a comparable rate. The investment of research into marine population connectivity has greatly increased our understanding of how these systems operate and how to manage them better. However, the generalities obtained from these well-studied systems should be validated in less-studied systems in order to ensure we are managing our marine systems correctly.

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