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Introduction to the Themed Section: ‘Beyond ocean connectivity: new frontiers in early life stages and adult connectivity to meet assessment and management’

Introduction

Advancing the link between ocean connectivity, ecological function and management challenges

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“Ocean connectivity” is a dynamic and rapidly evolving field of research in marine science, partly because there is an increasing demand for information on connectivity that informs effective assessment and management of marine resources. Achieving this will require a better alignment between ocean connectivity tools and developments and the needs and challenges of assessments and conservation. For these reasons, the *ICES Journal of Marine Science* solicited contributions to the article theme set (TS), “Beyond ocean connectivity.” We briefly summarize the nine articles that appear herein, grouping them into four general topics: methodological advances, population dynamics and assessment implications of connectivity, spatial and management implications, and connectivity in ecosystem processes. We also discuss the challenges facing ocean connectivity research if it is to effectively support advancing fisheries assessment frameworks and integrated ecosystem approaches. We hope that the contributions included in this TS serve to convince managers and fisheries scientists of the need to incorporate results from research on connectivity.

Keywords: animal movement, ecosystem-based management, fisheries assessment, larval dispersal, marine protected areas, marine spatial planning, metacommunity, metapopulation, ocean connectivity, spatial modelling.

Background and motivation for this article theme set

“Ocean connectivity” is a rapidly evolving field in marine science. This is attributable to advances in ocean modelling, the availability of more spatially and temporally explicit environmental information from ocean information systems, and technical developments in our ability to track the movement or determine the origin of fish and other taxa. The increasing demand for information on connectivity to inform effective assessment and

management of marine resources and the conservation of marine ecosystems is also driving this research forward. With this in mind, a theme session entitled, “Beyond the connectivity in the ocean: bridging forefront advances on early life stages and adults connectivity to assessment and management challenges”, was convened at the 2015 ICES Annual Science Conference to provide a scientific platform to present theoretical, modelling and empirical studies on ocean connectivity (<http://www.ices.dk/news-and-events/asc/ASC2015/Pages/Theme-Session-E.aspx>).

Resolving mismatches between biological and management science continues to be a key challenge in fisheries science (Kerr *et al.*, 2017). This complex issue has two related elements. First, the still problematic question of spatial delineation of fish stocks and, second, the more recent recognition of the significant sub-structuring within stocks, with spatial subunits having different ecological and/or demographic functions (Cadrin and Secor 2009, Secor 2015). In order to address these challenges, a better understanding of the coupling between short spatial and temporal scale demographic connectivity and large-scale evolutionary/genetic connectivity is needed. This perspective of marine connectivity is consistent with the classic view of seeing it as a structural driver (i.e. structural connectivity). However, it is also important to link these structural implications to their consequences for ecological functions (i.e. functional connectivity). This leads to a more integrated ecosystem perspective on the impact of ocean connectivity in marine systems, developing integrative studies that combine tools and information across temporal and spatial scales. Ocean connectivity spans a broad range of spatial and temporal scales, from sub-reef to global scales, and from daily to decadal time scales (e.g. Cowen and Sponaugle 2009, Jönsson and Watson, 2016). Studies at different scales are needed to provide a complete view of the structural and functional complexity of marine ecosystems and inform effective resource management. Achieving this will require a combination of continued development of cutting-edge modelling tools, with cross-disciplinary applications from empirical population, community and ecosystems studies (e.g. ICES 2016, Pita *et al.*, 2016).

For all these reasons, the *ICES Journal of Marine Science* solicited contributions to the article theme set (TS), “*Beyond ocean connectivity: new frontiers in early life stages and adult connectivity to meet assessment and management challenges*”, which follows from the theme session convened at the 2015 ICES ASC. This TS includes contributions on novel advances in the study of early life history stages and adult movements; population dynamic implications of connectivity, e.g. related to demographic and spatial implications for assessment of population persistence; anthropogenic pressures altering connectivity pathways; management strategies accounting for ocean connectivity; and ecosystems connectivity—spatial transport or dispersion of ecosystem properties and services. The contributions to this TS provide evidence of how novel tools and methods, as well as multi-disciplinary approaches, are already being applied to provide efficient solutions for assessment and management.

About the articles in this TS

Methodological advances

Mark-recapture (MR) studies are commonly applied to assess the movements of adults of a broad range of organisms but, mainly for practical reasons, have until recently been applied less often to assess connectivity of larvae (Jones *et al.*, 1999, Kaplan *et al.*, 2010, Secor *et al.*, 2017). Despite recent advances in estimating patterns of larval transport from spawning areas to settlement sites, the level of uncertainty in these estimates has received little attention. Kaplan *et al.* (2017) developed probabilistic statistical methods for estimating uncertainty of a broad range of larval MR connectivity estimators, including otolith microchemistry and genetic parentage analysis. The methods integrate uncertainty associated with small sample size and the identification of settlers as well as variability in egg production. These new methods were

applied - to data extracted from the marine larval connectivity literature - using an R package (ConnMatTools). The analysis showed that estimation uncertainty due to small sample size is often considerable and that there is a need for more precise reporting of experimental procedures and more accurate characterization of the reproductive modes of the target populations. The tools provided by this study will improve the accuracy of ocean connectivity estimates which could, for example, inform the design of networks of marine protected areas (MPAs).

The use of larval MR experiments to estimate marine connectivity is explored in two studies, one using artificial chemical tagging of larval otoliths (Secor *et al.*, 2017), the other applying genetic approaches to assign recruits to source populations (Christie *et al.*, 2017). Secor *et al.* (2017) used artificial chemical tagging of otoliths to study the early life stages of striped bass (*Morone saxatilis*) in the tidal Nanticoke River (Chesapeake Bay). They identified environmental factors that had important impacts on larval retention and survival, including the role of the salt front in limiting dispersal of juvenile striped bass out of the river and high river flow rates enhancing juvenile survival. They also identified interactions between the main drivers and constraints affecting the total production of larvae such as nursery volume, water quality and meteorological events. This study helps to characterize the role that small-scale retention processes play in structuring populations and how this interacts with population productivity.

There are a broad range of statistical tools to estimate patterns of connectivity based on genetic information, each with pros and cons with respect to the type and amount of sampling needed. Christie *et al.* (2017) applied a forward-time agent-based model of genetic information to Kellet's whelk (*Kelletia kelletii*) in southern California, incorporating key life history and physical oceanographic information, to assess the advantages and disadvantages of two commonly used methods to assign individuals back to their natal origin. The study compared parentage analysis, which directly links parents to their offspring, and assignment tests, which associate a probability to each recruit originating in each of a set of source populations. This study clarifies common misconceptions by demonstrating the trade-offs of applying these two techniques in terms of the sensitivity to the proportion of a metapopulation sampled and the genetic differentiation among local subpopulations. They also highlight the need for methodological advances to improve the low rate of true assignments between real and estimated connectivity matrices.

Empirical approaches to estimate larval connectivity have greatly advanced recently, as have numerical modelling techniques. Monroy *et al.* (2017) present an assessment of one such tool, Lagrangian Flow Networks (LFN; Ser-Giacomi *et al.*, 2015). This approach designates ocean sub-areas as nodes in a network interconnected by weighted links that represent the passive transport of eggs and larvae by currents. From all modelled virtual trajectories, LFN builds high-resolution connectivity matrices between all possible origin and destination nodes. An advantage of the LFN framework is its spatial coverage and flexibility as each of the matrices is post-processed to discard specific sites and various spatial scales can be simultaneously examined without the need to re-compute trajectories. Monroy *et al.* (2017) assessed the sensitivity and robustness of commonly used connectivity metrics derived from LFN to a number of important larval life history parameters: the density of released particles, the pelagic larval duration (PLD) and the frequency of spawning. They show that

connectivity estimates for long PLDs are more robust to biological uncertainties, as well as the need for daily release of particles when working with broadcast spawners that release gametes over short periods (~2–10 days). Because these sensitivity/robustness analyses are not species-specific, they provide general guidelines that are applicable to a broad range of connectivity experiments that are based on particle tracking models.

Population dynamics and assessment implications of connectivity

Kerr *et al.* (2017) present a review of approaches applied to resolve mismatches between the scale of biological populations and spatially defined stock units. First, they consider stocks for which a management status quo is maintained simply because of a lack of sufficient information to make any connectivity-related modifications. Atlantic bluefin tuna (*Thunnus thynnus*), which migrates across the Atlantic (Block *et al.*, 2005; Secor *et al.*, 2015) but is currently assessed as two stocks assuming no stock mixing, is used as a case study. The second management scenario examined is “weakest link” management, a practical approach aimed at preserving critical spawning components when limited data are available to assess mixing or yield for each subunit. This accounts for biological complexity of the population and was applied in the case of North Sea autumn spawning herring (*Clupea harengus*) by protecting the weakest stock component, the Downs spawning component (Dickey-Collas *et al.*, 2010). The third management approach involves temporal and spatial closures to protect spawning populations, something that has been applied to the Gulf of Maine stock of Atlantic cod (*Gadus morhua*) (Zemeckis *et al.*, 2014, 2017). Fourth, stock composition analyses in which there is enough knowledge of stock mixing but insufficient quantitative information to include in models of intra-stock connectivity within assessment frameworks. This is the case for Eastern and Western Baltic cod, for which geographic stock boundaries cannot delineate sympatric populations (Hüssy *et al.*, 2016). Fifth, when there is clear information about population structure that allows revision of stock boundaries to improve the match between biological populations and management units (e.g. sandeel, *Ammodytes spp.*, in the North Sea, Frederiksen *et al.*, 2005; redfish, *Sebastes mentella*, in the Irminger Sea, Cadrin *et al.*, 2010). These studies, and those cited by Kerr *et al.* (2017), highlight the growing realisation among fishery scientists that loss of biological and spatial complexity can impact the resilience and stability of exploited marine populations (Secor *et al.*, 2009; Kerr *et al.*, 2010).

Mismatches between biological and management scales can be particularly complicated when international boundaries are involved. For instance, for transboundary species that exhibit clear connectivity across national boundaries, an integrative assessment of shared stocks is needed to obtain realistic population estimates and efficient management measures (e.g. Caribbean spiny lobster, *Panulirus argus*, Kough *et al.*, 2013; or Atlantic halibut, *Hippoglossus hippoglossus*, in the United States and Canada, Shackell *et al.*, 2016).

Spatial and management implications

The study of marine connectivity and its influence on population dynamics has been developed largely in the context of species whose adults are sedentary or inhabit nearshore systems where local management is pertinent, e.g. the implementation of coastal

MPAs. Most research and management efforts have focused on fish or large crustaceans. The study by Gallego *et al.* (2017), expands this to epi-benthic species, such as benthic cnidarians, mollusks or echinoderms, which are often of special importance for conservation. These authors investigated the connectivity of these organisms as a part of the Scottish nature conservation MPA designation process. The study reveals that connectivity between MPAs is possible even for species with short PLDs, and that there is potential for large scale advection across eco-regions. However, the authors also stress that although the potential to exchange larvae at the region level is guaranteed for species with short PLD and low replication over MPAs, these species may be more vulnerable to local, regional and global stressors. This study identifies which focal species may be more vulnerable, providing additional support to the MPA designation process in Scotland.

Spatial management can be an effective approach for data limited fishery resources. Particle tracking models have provided detailed spatial connectivity information for the design and assessment of spatial management measures. However, the efficiency and efficacy of spatial management may increase when biophysical models are supported and complemented with information from additional sources. Nicolle *et al.* (2017), examined great scallop (*Pecten maximus*) dispersal pathways and the patterns of connectivity between fishing grounds in the English Channel. This study makes extensive use of complementary sources of information, including fisher knowledge, unpublished scientific surveys, grey literature, and VMS data, to define the main fishing grounds and the spawning stock biomass (using landing data) of each current stock. The starting position of drifters fundamentally controls the direction and distance of their drift paths demonstrating that the spatio-temporal distribution of spawners (when, where and how many) is crucial for initializing particle-tracking models (Hidalgo *et al.*, 2012). The study by Nicolle *et al.*, (2017) reveals that management should be based on assuming a connected metapopulation, rather than independent spatial management units.

Zemeckis *et al.* (2017) investigated the seasonal movements and connectivity of the spring spawning component of Atlantic cod in the western Gulf of Maine. Measures of the habitat occupancy and movement patterns provided evidence of both spawning site fidelity and connectivity among spawning areas, which has a considerable but differential impact on the metapopulation dynamics in the Gulf of Maine region, including fine- and broad-scale population structure. This study demonstrates that small spatiotemporal scale movements of marine fishes can considerably impact their population dynamics and, therefore, including such information into management plans can increase the efficiency of spatial management.

Connectivity in ecosystem processes

Most of the research in the field of “applied oceanic connectivity” focuses on how exchange of individuals, by advection or migration, affects temporal dynamics and the spatial patterns of distribution. However, few studies go beyond this to investigate the influence of connectivity processes on ecological function and ecosystems services, which is often referred to as “functional connectivity.” For instance, cross-system transportation of lipids (i.e. key fatty acids) occurs from herring feeding grounds in the North Sea to cod livers in the Western Baltic where resident cod prey on herring that have migrated into the system (van Deurs

et al., 2016). This study provides an example of marine ecosystem connectivity through cross-system fluxes of trophic subsidies and migrant-resident interactions. However, functional connectivity also relates to the suite of biological or behavioural responses, as well as ecological interactions, of dispersing individuals (Gerber *et al.*, 2014). For example, several studies suggest that climate change may reduce larval dispersal distance mainly because of shorter developmental time and, thereby, also reduce functional connectivity (e.g. Andrello *et al.*, 2015). In this sense, Lough *et al.* (2017), illustrated how prey selection by juvenile pelagic cod for zooplankton of different size (*Centropages spp.* vs. *Pseudocalanus spp.*) under different climatic regimes can affect growth and survival rates.

Conclusions and future challenges

The studies included in this TS demonstrate that tools and methods commonly used to investigate ocean connectivity are increasingly being applied to address challenges in fisheries assessment and management. However, despite these advances, progress in integrating connectivity information (of early life stages) into spatial management and population assessments has been slow. For instance, numerical ocean models are becoming mature enough to explore the spatiotemporal variability of larval connectivity over several years (e.g. Ospina-Álvarez *et al.*, 2015, Kough *et al.*, 2016). However, these simulated connectivity metrics are rarely compared to observed population estimates (but see Hidalgo *et al.*, 2012, Stige *et al.*, 2014) or incorporated into fisheries assessment frameworks (but see Rochette *et al.*, 2013) besides general comparisons with the fishery management context (e.g. Kough *et al.*, 2013, Huwer *et al.*, 2016). In contrast to early life stages, the incorporation of connectivity estimates obtained from adult movement is in a much more mature state of development and is now commonly used to integrate the complexity of population spatial structure into assessment frameworks (e.g. Goethel *et al.*, 2015). The latest generation of fisheries assessment models enables new and innovative approaches that include complexity of spatial structure and ecosystem information, including metrics of key ecological processes spatially structured and shaped by environmental drivers, connectivity processes and ecosystem drivers.

Several of the studies included in this article TS illustrate the main methodological challenges faced by ocean connectivity research, while providing innovative and efficient solutions for incorporating connectivity into management via: (i) robust statistical and modelling frameworks for connectivity estimation (Kaplan *et al.*, 2017, Monroy *et al.*, 2017), (ii) better assessment of the merits and weaknesses of different tools to provide the most informative response to known management challenges (Christie *et al.* 2017, and (iii) development of novel cross-disciplinary frameworks that combine information from different sources to respond to current assessment and management demands (Pita *et al.*, 2016; Nicolle *et al.*, 2017). There is also general agreement that detailed behavioural and ecological information is needed to initialize biophysical coupled models and to interpret their outcomes. Including standard life history information, such as growth, reproduction and ontogeny data, is a common requirement of marine science and management, but the studies in this TS also highlight the relevance of other poorly known life history characteristics important for the assessment of connectivity pathways. For instance, processes affecting larval orientation (e.g. Staaterman and Paris, 2014, Faillettaz *et al.*, 2015) or other

trait-mediated interactions that shape the final success of settlement (e.g. phenotype-environment mismatch, Marshall *et al.*, 2010) and, thus, the realized connectivity. Similarly, details of a species' reproductive strategy are essential for empirical estimation of connectivity patterns (Kaplan *et al.*, 2017) as they affect the initial parameterization of biophysical models (Monroy *et al.*, 2017).

Ocean connectivity research is addressing a variety of demands emerging from ecosystem based management. This is encouraging tighter links between connectivity research and its ecological implications and, consequently, increasing its relevance and applicability to the management of marine resources. This includes (i) a more complete view of all taxa (e.g. from benthic to pelagic; Gallego *et al.*, 2017), and (ii) a better knowledge of a limited number of controlling processes (ecological and/or oceanographic) that will improve the way that we understand ecosystem functioning, acknowledging the complexity of marine ecosystems in a comprehensive and balanced manner. This is consistent with marine policies that mandate integrated ecosystem assessments, and call for the incorporation of temporally intensive and spatially extensive predictions of key populations and ecosystem processes and services. In this sense, ocean connectivity must embrace rapid methodological developments such as the capacity to retrieve information from ocean observing systems (Hidalgo *et al.*, 2016). This is necessary to advance and improve the operationalization and implementation of ecosystem-based management (Link and Browman, 2017).

One of the most significant challenges in the coming years will be to understand how anthropogenic activities will alter natural connectivity pathways. Besides the impact of man-made physical structures, climate change is anticipated to have profound impacts on both structural and functional connectivity (Gerber *et al.*, 2014). For instance, temperature changes will impact physiological and behavioural traits (e.g. spawning phenology, larval growth or vertical migration) that will alter dispersal (Andrello *et al.*, 2015). However, there is still high uncertainty about the relative role of phenotypic plasticity and genetic adaptation to such climate-induced changes (Merilä and Hendry, 2014).

We anticipate that the output of ocean connectivity research will be progressively more integrated into fisheries assessment tools and management policies. Applications developed from that science will then evolve towards a more interactive, communicative and efficient platform for applied research. Future research should include improved coupling of demographic and evolutionary/genetic connectivity at short and large spatiotemporal scales.

We hope that the contributions included in this TS serve to convince managers, fisheries modellers and scientists developing applied research on marine ecosystems of the need to incorporate results from research on connectivity.

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