



Original Articles

System level indicators of changing marine connectivity

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ABSTRACT

Spatial connectivity has long been recognized as a key process for sustaining healthy ecosystems and robust ecosystem services. However, system-level metrics that capture environmentally significant aspects of connectivity at appropriate temporal and spatial scales have not previously been identified. Using a major industrial harbour adjacent to Australia's Great Barrier Reef as a test case, we developed a consistent and comprehensive set of connectivity indicators associated with waterborne dispersal that transparently relate to water quality, spread of contaminants, and potential for recruitment of planktonic larvae to nursery habitats. Results indicate all measures of connectivity are variable across management zones and likely to influence water quality and breeding success at these scales. Connectivity indicators also reveal environmental and ecological trade-offs. For example, while reduced flushing of creeks and estuaries may negatively impact local water quality, it can benefit ecological connectivity through more effective upstream transport of larvae to nursery habitats.

1. Introduction

While spatial connectivity is one of the most fundamental processes in the functioning of ecosystems, it is also one of the most difficult to measure and characterise at a system level (Crook et al., 2015; Kindlmann and Burel, 2008; Moilanen and Nieminen, 2002). In aquatic environments, connectivity can take many forms including exchanges between freshwater and marine environments (Andutta et al., 2014; Gillanders et al., 2011; Raimonet and Cloern, 2017); exposure to waterborne contaminants and pathogens (Andutta et al., 2014; Kough et al., 2015; McCallum et al., 2003; Uncles et al., 1988); and dispersal of eggs, larvae and other planktonic organisms (Bunn and Arthington, 2002; Clark et al., 2005; Condie et al., 1999; Condie et al., 2011; Jones et al., 2009; Kool et al., 2013; Mumby, 2006; Vasconcelos et al., 2011). Monitoring these processes in coastal and marine systems can provide information critical to maintaining water quality, evaluating exposure risks, and ensuring the sustainability of species of high economic, social or conservation value.

Understanding connectivity is critical to identifying the underlying causes of environmental and ecological change, and therefore should be a high priority when developing effective management actions (Bunn and Arthington, 2002; Crook et al., 2015). For example, deterioration in water quality may be primarily associated with changes in water circulation and therefore a management response aimed at reducing

terrestrial nutrient loads may be ineffective (Condie et al., 2012; Wild-Allen and Andrewartha, 2016). Similarly, if reduced catches within a fishery are associated with changes in the transport of eggs and larvae from spawning grounds to nursery habitats, then imposing catch restrictions may again be an ineffective strategy (Gaines et al., 2010; Kough et al., 2013; Mcleay et al., 2016).

While there are numerous studies and reviews that describe aquatic connectivity in relation to particular sources of contaminants or the lifecycle of particular species, the scientific literature provides limited guidance on practical indicators of system level connectivity that are both comprehensive and relevant to environmental or ecosystem-based management. If considered at all, system level indicators of marine connectivity have used either indirect physical measures, such as the strength of major currents or upwelling flows (Hayes et al., 2015); relative measures of retention such as residence time, exposure time, or flushing time, (de Brauwere et al., 2011; Delhez et al., 2004; Sandery and Kampf, 2007); or species-level molecular or micro-chemical measures (Burgess et al., 2014).

While the importance of connectivity has been broadly acknowledged, development of indicators has been limited by the lack of a conceptual framework that relates connectivity metrics to ecosystem processes and associated management issues (Fig. 1). Establishing this relationship is critical in determining appropriate spatial and temporal scales over which connectivity should be defined (Calabrese and Fagan,

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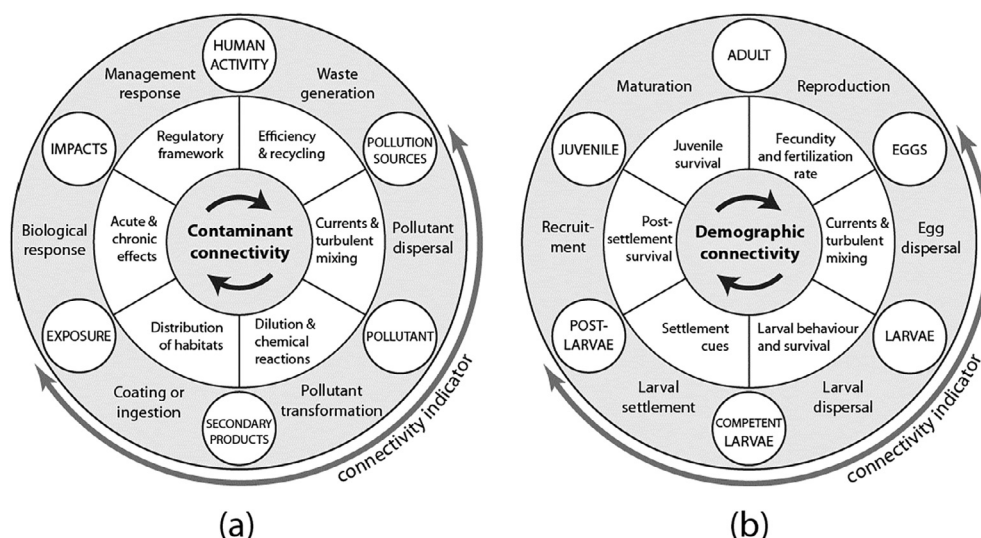


Fig. 1. (a) Elements contributing to the dispersal and impacts of contaminants. (b) Demographic connectivity elements contributing to successful recruitment of marine species (right; adapted from Steneck et al. 2009). Simple connectivity indicators can capture critical aspects of these cycles related to dispersal of contaminants and larval transport (outer arrows).

2004; Steneck et al., 2009). By developing a framework that explicitly includes such relationships we aim to provide a context for interpreting indicator trends and defining meaningful targets and thresholds.

A second barrier to the development of connectivity indicators has been the availability of relevant information. Data on the distributions of contaminant inputs, habitats and aquatic populations are still limited in many coastal systems, and our understanding of relevant chemical transformations and ecological processes may be almost non-existent. On the other hand, exchange and movement of water is a pervasive influence on most aspects of aquatic connectivity (Fig. 1) and the availability of sophisticated hydrodynamic models is expanding rapidly through more automated implementation and validation (Kourafalou et al., 2015). Here we show that it is feasible to combine detailed hydrodynamic models with limited data on contaminant inputs and habitat distributions to generate indicators of systemic connectivity. The outcome is a set of practical system level connectivity indicators with clear links to key biophysical processes and coastal management issues.

2. Methods

The methodology uses outputs from a calibrated hydrodynamic model to generate dispersal pathways that can then be combined with other relevant system properties (contaminant inputs and nursery habitat distributions) to produce indicators of systemic connectivity (Fig. 2). The approach is demonstrated here within a complex coastal harbour environment, but is applicable to any aquatic system.

2.1. Study area

Gladstone Harbour is a major industrial port on the east coast of Australia that opens onto the Great Barrier Reef (Fig. 3a). It is a macrotidal estuary containing extensive tidal flats, stands of fringing mangroves, sea-grass beds and coral reefs. These habitats support numerous aquatic fauna and flora including iconic species such as dugongs and turtles, as well as important commercial and recreational fish species. Anthropogenic influences in the harbour are extensive, being the site of major production facilities for aluminium, cement, chemicals, liquid natural gas, and electricity.

Environmental health is managed spatially at the scale of harbour zones (Fig. 3a), which range in area from 1 to 177 km². Connectivity patterns in the harbour are strongly influenced by physical drivers such as winds, tides, river discharges and offshore ocean conditions. However, there are concerns that port developments such as dredging and land reclamation may be impacting on ecological connectivity processes (Crook et al., 2015) and a recent global analysis has identified

this as a region of large and increasing pollution pressure (Partelow et al., 2015).

2.2. Hydrodynamic modelling, particle tracking and network analyses

A three-dimensional hydrodynamic model was implemented for Gladstone Harbour and the adjacent marine environment (see Appendix for details). It used a three-dimensional curvilinear grid with 21 vertical layers and horizontal resolution of 100–250 m within the harbour. This grid resolved 11 of the 13 harbour management zones, excluding only two small creeks. The model was forced by realistic winds, tides and offshore conditions over the period September 2010 to June 2016.

Every 20 days the 11 harbour management zones were randomly seeded horizontally and vertically with 2000 neutrally buoyant particles that were individually tracked as a proxy for water parcels containing dissolved substances or particulates (see Appendix for details). Particle trajectories (Fig. 3b) were used to compute connectivity matrices, with each matrix element corresponding to the probability of directed exchange between pairs of harbour zones based on the seed locations and final destinations of all particles. It was assumed that the particles moved passively with currents over a 20-day dispersal period, which is broadly consistent with available data on pelagic larval durations of the three most important commercial and recreational fisheries species in the region – barramundi (Yahaya et al., 2011), yellow bream (Clark et al., 2005) and mud crab (Nurdiani and Zeng, 2007). However, the methodology can easily be extended to include alternative dispersal times or more complex larval behaviours.

Network metrics were then used to estimate the relative importance of each zone to overall connectivity within the harbour. A composite measure called *weighted degree centrality* used both the flux of particles and the number of regions affected in estimating whether a zone could be considered a source or a sink of particles in the harbour (Hock et al., 2014). Specifically, the *weighted out-degree* for each *source zone* and each 20-day dispersal period was the fraction of particles transported to all other zones. It excluded particles retained within the source zone as well as those transported entirely out of the harbour. The *weighted in-degree* for each *sink zone* and each 20-day dispersal period was the fraction of particles arriving in the zone from all other zones. It excluded particles that started within the sink zone. Weighted out-degree was combined with information on contaminant sources and weighted in-degree was combined with information on habitat distributions to generate connectivity indicators as described below (Fig. 2).

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