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Local connections and the larval competency strongly influence marine metapopulation persistence

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Abstract. The relationship between metapopulation stability and connectivity has long been investigated in ecology, however, most of these studies are focused on theoretical species and habitat networks, having limited ability to capture the complexity of real-world metapopulations. Network analysis became more important in modeling connectivity, but it is still uncertain which network metrics are reliable predictors of persistence. Here we quantify the impact of connectivity and larval life history on marine metapopulation persistence across the complex seascape of southeast Australia. Our work coupled network-based approaches and eigenanalysis to efficiently estimate metapopulation-wide persistence and the subpopulation contributions. Larval dispersal models were used to quantify species-specific metapopulation connectivity for five important fisheries species, each summarized as a migration matrix. Eigenanalysis helped to reveal metapopulation persistence and determine the importance of node-level network properties. Across metapopulations, the number of local outgoing connections was found to have the largest impact on metapopulation persistence, implying these hub subpopulations may be the most influential in real-world metapopulations. Results also suggest the length of the pre-competency period may be the most influential parameter on metapopulation persistence. Finally, we identified two major hot spots of local connectivity in southeast Australia, each contributing strongly to multispecies persistence. Managers and ecologists would benefit by employing similar approaches in making more efficient and more ecologically informed decisions and focusing more on local connectivity patterns and larval competency characteristics to better understand and protect real-world metapopulation persistence. Practically this could mean developing more marine protected areas at shorter distances and supporting collaborative research into the early life histories of the species of interest.

Key words: degree centrality; eigenvalue; eigenvector; larval dispersal; network analysis; out-degree; resilience; self-recruitment.

INTRODUCTION

Many terrestrial and marine populations can be viewed as metapopulations due to their fragmented distribution, as a result of natural habitat characteristics or because of anthropogenic landscape changes (Hanski 1998). Understanding metapopulation persistence in these patchy landscapes is critical for conservation planning where the identification of vulnerable, as well as the most influential, subpopulations is fundamental in the development of cost-effective and ecologically meaningful management decisions (Hanski and Ovaskainen 2000, 2003). Conservation biologists and wildlife managers can estimate population persistence and viability through mathematical models to quantify the effectiveness among a suite of alternative management options

(Fieberg and Ellner 2001). In metapopulation theory, metapopulations can persist when there is stability between the loss of subpopulations and the establishment of new subpopulations in unoccupied areas (Hanski 1998). In spatially structured metapopulations, patch size and the rate of movements among patches, or connectivity, are fundamental to determining persistence in fragmented landscapes (Hanski 1998). In this context, metapopulation persistence largely depends on the dispersal dynamics between each pair of patches or subpopulations (Adler and Nuernberger 1994, Figueira and Crowder 2006).

Metapopulation persistence can be estimated through various numerical approaches, such as the metapopulation mean lifetime (Frank and Wissel 1998, Kininmonth et al. 2010) or estimating local extinction and colonization rates (Etienne and Heesterbeek 2001). Another common approach estimates the metapopulation growth rate through a matrix population model (Caswell 2001). The dominant eigenvalue, or spectral radius (λ), of the Leslie matrix represents the persistence condition, where

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growing (i.e., persisting) metapopulations have values >1 (Hanski and Ovaskainen 2000, Hanski and Gaggiotti 2004). This metapopulation growth rate estimate has been regularly used to quantify persistence in many aquatic (Mari et al. 2014, Bertuzzo et al. 2015), terrestrial (Saikkonen et al. 2002, Touloumis and Stamou 2009), and marine (Armsworth 2002, Williams and Hastings 2013) systems.

In many cases, persistence estimates for age-structured metapopulations rely on models where subpopulation viability was based on the intrinsic growth rate of the individual patches alone (Hastings and Botsford 2006a, b). Yet, to develop a more realistic estimate of subpopulation persistence in complex landscapes, the implications of immigration and emigration dynamics on persistence must also be considered. As a result, more recent work in metapopulation dynamics has evolved to include realistic dispersal and migration estimates between subpopulations explicitly (Hanski and Ovaskainen 2003, Figueira and Crowder 2006, Figueira 2009, Shima et al. 2010, Puckett and Eggleston 2016). Metapopulation models, now including local and non-local dispersal dynamics can be summarized in an appropriately structured migration matrix, representing the proportion of individuals that successfully settle to a patch that came from each source patch (Artzy-Randrup and Stone 2010). In this dispersal-dominated context, the strength of persistence is controlled by the magnitude of the dominant eigenvalue (λ) of the connectivity matrix (Artzy-Randrup and Stone 2010).

The continuous marine environment provides the potential for long-distance dispersal among marine populations, yet the intensity of realized dispersal and the spatial scale of connectivity is often more local and highly context dependent (Cowen et al. 2000, Mora and Sale 2002, Bode et al. 2019). For many coastal species, the larval stage dominates the dispersal dynamics, determining the connections among patches. As a result, understanding the early life history characteristics is essential for determining the dynamics of population connectivity. Here, we explicitly refer to connectivity as the movement of individuals, as larvae, among habitat patches or subpopulations (Cowen and Sponaugle 2009), a critical process contributing to subpopulation growth or decline and metapopulation persistence.

Many biological and physical processes drive larval dispersal patterns (Cowen and Sponaugle 2009, Shanks 2009, Treml et al. 2015a). In marine systems, larval dispersal outcomes are strongly influenced by the extent of pelagic larval duration (PLD) and competency window (Baums et al. 2006, Levin 2006, Shanks 2009). In addition, larval mortality, and post-settlement mortality is critical as it causes significant fluctuations in settlement and recruitment (Houde 1989, White et al. 2014). Experimental and laboratory work has also shown that behavior during the larval stage may alter dispersal trajectories, depending on the local seascape setting and larval traits (Paris et al. 2007). Yet larval biology alone is

not enough to understand realized dispersal patterns in marine environments, as ocean currents act on the larvae and can greatly influence outcomes (Largier 2003).

Numerous approaches exist to quantify and summarize larval connectivity for real-world metapopulation networks (Botsford et al. 2009, Burgess et al. 2014, Holstein et al. 2014, Samsing et al. 2017); among them, graph theory was used to analyze and visualize the network-based connectivity (Treml et al. 2008, Thomas et al. 2014). Graph theory is an appropriate framework to use to quantify the spatial and temporal patterns in larval connectivity because it can efficiently accommodate complex real-world networks (Urban and Keitt 2001, Treml et al. 2008). Metapopulation connectivity summarized in the migration matrix can be visualized and analysed through these network-based algorithms. An important insight from the study of metapopulations is that the dominant eigenvalue of this matrix estimates metapopulation persistence (Artzy-Randrup and Stone 2010, Shtilerman and Stone 2015). The relationship between the metapopulation network structure and metapopulation persistence has been extensively investigated to understand the ecological significance of network metrics. For example, asymmetry is a network characteristic that quantifies the probability that two nodes in a network are equally connected in both directions (Shtilerman and Stone 2015). Real-world metapopulations are frequently asymmetric, especially in marine systems, where dispersal is driven by directional current, with asymmetric metapopulations being more vulnerable to extinction (Bode et al. 2008, Vuilleumier et al. 2010, Kleinhans and Jonsson 2011, Shtilerman and Stone 2015). Directed networks are often heterogeneous where the rate of immigration and emigration to/from a habitat patch is not equal. Heterogeneity has been shown to have mixed effects on metapopulation persistence (White et al. 2010, Shtilerman and Stone 2015). Similarly, network cycles have been shown to influence metapopulation persistence, where loops of connections provide multigenerational (and multipatch) pathways of recruitment back to the origin patch (Artzy-Randrup and Stone 2010). Various centrality measures have also been explored to quantify patch-level importance in metapopulation dynamics (Bodin and Norberg 2007, Bode et al. 2008, Estrada and Bodin 2008, Watson et al. 2011). Self-seeding has a fundamental role in local metapopulation dynamics (Hastings and Botsford 2006a,b), and network metrics accounting for self-connections are better predictors of metapopulation persistence for real-world networks (Pascual-Hortal and Saura 2006, Zamborain-Mason et al. 2017).

Much of this previous work was based on theoretical models, however real-world applications are required to help us understand real system dynamics and how to best inform marine conservation and management decisions. Here, we used network models to represent connectivity of several complex real-world marine metapopulations, where a mosaic of habitat patches,

defined as nodes or vertices, are connected through dispersal linkages, called edges (Urban et al. 2009). The dispersal linkages are determined by the presence of ecologically significant larval dispersal and settlement. As a result, our realistic and geographically referenced metapopulation networks were characterized by directional dispersal linkages, each connection with a dispersal strength. These resultant marine metapopulation networks are broadly representative of many other real-world networks in marine environments where the movements of larvae are strongly influenced by biological traits and ocean currents (Bode et al. 2008, Mitarai et al. 2009, Berglund et al. 2012).

The primary aim of this study is to understand the link between metapopulation persistence and connectivity, from patch-level properties to network-wide metrics. In addition, we identify the relative importance of subpopulations or patches that contribute the most to metapopulation persistence within the seascape of southeast Australia. Finally, we also explore the influence of species-specific life history traits on the network measures and metapopulation persistence. We illustrate a powerful and straight-forward approach to evaluating patch contribution to metapopulation persistence for five real-world marine metapopulations. We combined network-based and matrix-based approaches for quantifying metapopulation persistence and identifying species-specific habitat patches critical to this persistence. These priority sites, as well as the multispecies geographic hot spots can help inform marine management efforts throughout this complex seascape.

METHODS

Study area

The South-east Marine Region of Australia is one of the six marine managed regions in Commonwealth waters around Australia. This region extends from the south of New South Wales (NSW) through the coast of Victoria (VIC) and Tasmania (TAS) to Kangaroo Island in South Australia (SA). It consists of a mosaic of habitat, from hard to soft bottom habitat, populated by a range of diverse species, and includes the biodiversity hot spot of Wilsons Promontory marine park (Bax and Williams 2000, Department of the Environment 2015). The spatial domain for this study (Fig. 1) was defined by buffering this Marine Region along South Australia and New South Wales coasts by 200 km to include subpopulations beyond our focal seascape to avoid edge effects in the analysis and results.

Study species

For this study, we selected five representative and economically important species of the south-eastern Australian coast, also representing a broad range of dispersal capacities. We selected species across a wide

range of life history characteristics to build a broad understanding of the relationship between network characteristics and metapopulation persistence, yet focus on locally important taxa to maximize local relevance. The blacklip abalone, *Haliotis rubra*, long-spined sea urchin, *Centrostephanus rodgersii*, and purple sea urchin, *Heliocidaris erythrogramma*, are three important marine invertebrates inhabiting rocky reefs, characterized by differences in larval traits and spawning seasons traits, and are widely distributed throughout the region. *H. rubra* also represents one of the most important species for Australian commercial fisheries, producing 2,578 tons of abalone for export, for a value of 174 million dollars each year (Savage 2015). Both *C. rodgersii* and *H. erythrogramma* are extensively studied for their role as ecosystem engineers in the nearshore rocky reef kelp systems throughout Australia (Pederson 2003, Pecorino 2012). They also represent two growing fishery species in this area (King et al. 1994, Blount and Worthington 2002). We also modeled two species of fish, the snapper, *Chrysophrys auratus* formerly known as *Pagrus auratus*, and the King George whiting, *Sillaginodes punctatus*; the former fish species with somewhat limited larval dispersal, the latter with greater dispersal capability. *C. auratus* and *S. punctatus* are widely distributed across the South-East Marine Region of Australia, where both are important taxa in commercial and recreational fisheries (Hamer et al. 2011, Jenkins et al. 2016).

Quantifying marine metapopulations connectivity

A series of 1,441 larval dispersal simulations, for a total of 788 habitat patches, were completed for the study species. We used an existing spatially explicit biophysical model (Treml et al. 2012) to simulate larval dispersal for all species using the University of Melbourne high performance computing cluster, Spartan (Lafayette et al. 2016). The data requirements of this model are (1) a map of habitat patches or subpopulations; (2) data describing the ocean currents; and (3) information on species demographic parameters and dispersal strategies (e.g., spawning timing, larval competency, and mortality rates). Each of these are described in detail in the following subsections.

Habitat patches.—Spatial information on the distribution of the metapopulation within the seascape is necessary to define the habitat patches where each subpopulation resides within the model (Treml et al. 2012). Habitat data for this study were developed using ArcGIS 10.5.1 software (ESRI 2017) and environmental data from various sources. The extent of the area is 1,990 × 1,850 km using 5 × 5 km cell size, consistent with the resolution of best-available hydrodynamic data.

Species distribution models (SDMs) were used to estimate habitat suitability for *H. rubra*, *H. erythrogramma*, and *C. rodgersii* and to identify unique habitat patches. We built the habitat suitability maps using species

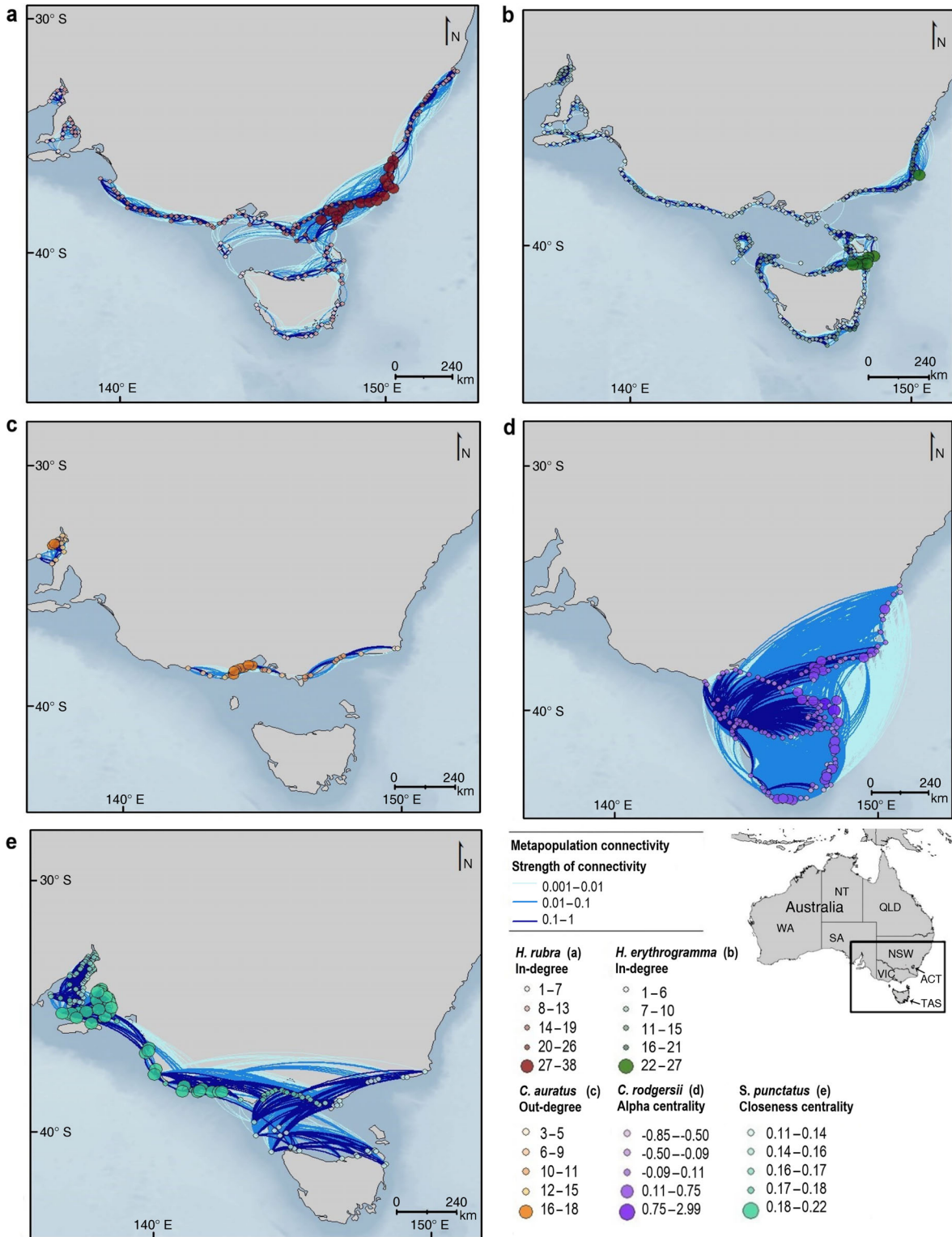


FIG. 1. Spatial distribution of metapopulation connectivity and a variety of node-level metrics across study area. *Haliotis rubra* (a) and *H. erythrogramma* (b) in-degree, *Chrysophrys auratus* out-degree (c), *C. rogersii* alpha centrality (d) and *Sillaginodes punctatus* closeness centrality (e). The weight of the connections is indicative of the strength of dispersal and the directionality is implied by following the arcs in a clockwise direction. The study area of South-east Marine Region of Australia includes waters off Victoria (VIC), southern New South Wales (NSW), Tasmania (TAS), and eastern South Australia (SA). See Table 1 for full species names. All maps in Transverse Mercator projection, Geocentric Datum of Australia (GDA2020).

presence data from the Atlas of Living Australia occurrence data (*available online*).⁴ Environmental parameters for the SDMs consisted of bathymetry (data available online),⁵ chlorophyll concentration, monthly average sea surface temperature, and the magnitude of currents, all freely available from the AODN portal (Beggs et al. 2010, Johnson et al. 2013; data *available online*).⁶ Other habitat data used to build the SDMs were seabed gravel and sand content, *available online* for the entire Australian Exclusive Economic Zone.⁷

We modeled *C. auratus* and *S. punctatus* habitat patches by mapping the species-specific location of spawning and settlement (Fowler et al. 2000; Jenkins et al. 2000; 2016; Fowler and Jennings 2003; Hamer et al. 2011; Hamer and Conron 2016). Despite the wide distribution in adult stages, snapper's spawning and settlement locations are concentrated in the Spencer Gulf region for South Australia and Victorian estuaries and bays, available from the Estuary Watch Victoria database (*available online*).⁸ The identification of source patches for the King George whiting was derived from published spawning areas (Fowler et al. 2000; Jenkins et al. 2000; 2016), while destinations patches were identified based on settlement habitat preferences and mapped using data on presence of seagrass beds, available through Seamap Australia National Benthic Habitat Classification Scheme (Butler et al. 2017; data *available online*).⁹ Further details on habitat patches maps and SDMs can be found in Appendix S1.

Oceanographic model.—We modeled the larval movements between patches using ocean current data derived from a global circulation model (HYCOM; *available online*).¹⁰ Data are available from 1992 to 2012 at a 3-h time-step; all available data were used in this study. We simulated the dispersal of each species' spawning season for all years of data. In the model, clouds of larvae were released from source patches and the likelihood of larval settlement to all destination patches was estimated based on the species' biological parameters (see *Species' parameters*). Further details on the larval dispersal model can be found in Appendix S1.

Species' parameters.—The biological parameters included in the biophysical larval dispersal model were maximum PLD, the larval competency window, larval mortality, the species' spawning period based on previously published data (Williams and Anderson 1975; Prince et al. 1987; Laegdsgaard et al. 1991; Francis 1994; Jenkins and May 1994; McShane 1995; Fowler

et al. 1999; Fowler and Jennings 2003; Litaay and De Silva 2003; Huggett et al. 2005; 2008; Swanson et al. 2012; Hamer and Conron 2016), larval settlement rates, and other biophysical parameters such as sub-scale turbulence (Table 1). Other parameters were held constant across species due to unknown or unjustifiable differences such as homing behaviors and vertical migration strategies. For a review of sensitivities and further modeling details, see Trembl et al. (2012).

Larval production within habitat patches was scaled by available habitat area, where the patch size was the explicit proxy for reproductive output from the subpopulation (Bunn et al. 2000, Urban and Keitt 2001, Trembl et al. 2012). Larval mortality was incorporated into the model as a Weibull function, capable of representing variants on the exponential decay function, believed to be common in many species (Connolly and Baird 2010), and informed by previous studies on similar taxa (Houde 1989, Rumrill 1990, Lamare and Barker 1999).

Connectivity matrices and metapopulation persistence

The output of the marine connectivity model for each species was a dispersal matrix, recording the cumulative quantity of larvae released from each source patch that survive and settled to each destination patch, summarizing across all modeled dispersal events and years. The dispersal matrices were converted to migration matrices, **M**, entries of which represent the proportion of settled larvae arriving at each destination, *j* (column), that came from each source patch, *i* (row), and the diagonal of the matrix represents self-recruitment. Matrices diagonals were included in the analysis. A threshold of 0.001 was applied to the migration matrices, setting any value below this threshold to zero. This focuses the analysis on only ecologically meaningful connections that contribute more than 0.1% of total settlement of larvae to a destination, a level also robust to a range of fisheries stock-recruitment dynamics (Myers et al. 1999). We used these migration matrices to visualize and analyze the network structure of the metapopulations in relation to persistence, which was summarized by the matrices' dominant eigenvalue (Artzy-Randrup and Stone 2010, Shtilerman and Stone 2015). We quantified metapopulation persistence at the component level (or fully connected subgraph), a condition required to satisfy the Perron-Frobenius Theory (Li and Schneider 2002). The approach used in Artzy-Randrup and Stone (2010) defines metapopulation persistence as the product of the largest eigenvalue and the reproductive output, using a symmetric adjacency matrix to describe connectivity. We modified this approach and maintained the asymmetries to preserve directions in connectivity, yet convert the strong ecological migration matrices into binary adjacency matrices as per Artzy-Randrup and Stone (2010), thereby focusing the analysis on the topology or structure of the ecological metapopulation networks. The elements in the adjacency matrix are one when the nodes are strongly

⁴ <https://www.ala.org.au>

⁵ <https://www.gebco.net>

⁶ <http://imos.aodn.org.au/oceancurrent>

⁷ data.gov.au

⁸ <http://www.estuarywatch.org.au>

⁹ <https://seamapaustralia.org>

¹⁰ <https://www.hycom.org>

TABLE 1. Demographic species-specific parameters included into the marine connectivity model.

Parameter	<i>Haliotis rubra</i> (blacklip abalone)	<i>Heliocidaris erythrogramma</i> (purple sea urchin)	<i>Centrostephanus rogersii</i> (long spined sea urchin)	<i>Chrysophrys auratus</i> (Australasian snapper)	<i>Sillaginodes punctatus</i> (King George whiting)
Depth (m)	0–10 ¹	0–35 ⁵	0–30 ⁹	0–50 ¹²	0–200 ¹⁶
Max PLD (d)	12 ²	5 ⁶	155 ¹⁰	32 ¹³	170 ¹⁷
Competency period (d)	6.5–12 ³	3–5	105–155 ¹⁰	27–32 ¹⁴	75–170 ¹⁷
Pre-competency period (d)†	2.5–6.5 (4) ³	1.5–3 (1.5) ⁶	77–105 (28) ⁷	18–27 (9) ¹⁴	45–75 (30) ¹⁷
Spawning period	Aug–Jan ⁴	Dec and Mar ⁸	Jun–Sep ¹¹	Nov–Feb ¹⁵	Mar–May ¹⁸
Diffusivity (m ² /s)	100 ¹⁹	100 ¹⁹	100 ¹⁹	100 ¹⁹	50 ¹⁹
Larval settlement likelihood (%)	90	90	98	90	98
Larval mortality (% per d)	5 ²⁰	16 ²⁰	16 ²⁰	26 ²¹	25 ²¹

Note: Max PLD, maximum pelagic larval duration.

Sources: 1, Morgan and Sheperd (2006); 2, McShane (1995); 3, Prince et al. (1987); 4, Litaay and De Silva (2003); 5, Huggett et al. (2008); 6, Williams and Anderson (1975); 7, Swanson et al. (2012); 8, Williams and Anderson (1975), Laegdsgaard et al. (1991); 9, Pecorino (2012); 10, Huggett et al. (2005); 11, King et al. (1994), Byrne et al. (1998), Huggett et al. (2005); 12, Kailola et al. (1993), Froese and Pauly (2000) <http://www.fishbase.org>; 13, Francis (1994); 14, Fowler and Jennings (2003); 15, Hamer and Conron (2016); 16, Jenkins et al. (2016); 17, Jenkins and May (1994); 18, Fowler et al. (1999); 19, Okubo (1971); 20, Rumrill (1990), Lamare and Barker (1999); 21, Houde (1989).

†Length of period (d) in parentheses.

connected and zero in the absence of an ecologically significant connection (Artzy-Randrup and Stone 2010, Shtilerman and Stone 2015). With this assumption we omitted the strength of connectivity, represented by the edge weight, but we maintained edges directions. As a result, our migration matrices focus exclusively on strong ecologically significant connectivity to and from all patches in the system. With this required generalization, our matrices were non-column stochastics, resulting in informative dominant eigenvalues, often >1 , allowing the species' migration matrix eigenvalues to be quantitatively compared.

Network analysis

To identify the most critical subpopulations influencing metapopulation persistence we performed network analysis in R version 3.6.2 (R Core Team 2019) and the *igraph* package (Csardi and Nepusz 2006). We built graphs from these matrices, where nodes in our networks represented the habitat patches and linkages quantified the dispersal likelihood between all sources and destinations. We used a suite of node-level and network-level metrics to quantify the influence of patches on metapopulation persistence (Appendix S1: Table S1). We calculated a variety of centrality measures. Degree centrality, quantifies the number of outgoing (out-degree) and/or incoming (in-degree) linkages to a subpopulation or node, extended to weighted in-degree and weighted out-degree for analyzing weighted networks. Betweenness centrality is a measure based on the number of shortest paths going through a node (Newman 2005), which identifies critical habitat stepping stones within the

networks (Urban and Keitt 2001, Bodin and Norberg 2007, Bode et al. 2008, Estrada and Bodin 2008). Closeness centrality, quantified as the reciprocal of the sum of the shortest paths between all nodes and all other nodes (Freeman 1978), was used to identify core or central subpopulations (Gonzalez et al. 2010, Cabral et al. 2016). Eigenvector centrality (Bonacich 1987), which identifies centrally important nodes, assigning relative scores based on the connections with other high-scoring node, has been shown to strongly correlate with metapopulation persistence in a benthic boundary current system (Watson et al. 2011). Alpha centrality as an eigenvector-like measure of centrality for asymmetric networks (Bonacich and Lloyd 2001) was also calculated.

We also quantified network-level metrics such as network asymmetry using asymmetry gamma, γ , an index of the pairwise difference in directionality among each pair of subpopulations defined as the ratio of symmetric connections among all connections (Kleinhans and Jonsson 2011). We estimated network heterogeneity as the coefficient of variation of degree (Zamborain-Mason et al. 2017) measuring the unbalance between incoming vs. outgoing connections to/from a patch. Finally, we quantified the number of cycles (of length three) in the networks counting the cycle occurrence in each graph (Fischer et al. 2015) to help evaluate the influence of these feedback loops on metapopulation persistence (Artzy-Randrup and Stone 2010).

To explicitly quantify the influence of these network-based proxies on metapopulation persistence, we removed the top 5%, 10%, and 20% of the most important nodes as determined by patch area and by each node-level metric and recalculated metapopulation

persistence (largest eigenvalue). The impact of important subpopulations (e.g., those with high degree or high eigenvector centrality) in terms of the decrease in metapopulation persistence was summarized as the ratio between the largest eigenvalue of the adjacency matrix after and before removing the top 5%, 10%, and 20% of these key nodes. This ratio should be interpreted as the magnitude of decline in metapopulation persistence resulting from the removal of these focal subpopulations.

An additional node removal exercise was performed to quantify the patch-level influence on metapopulation persistence. All nodes were removed iteratively (with replacement), and the matrix eigenvalue was recalculated to quantify the magnitude in the decrease in metapopulation persistence. This method allows nodes to be ranked, thereby assisting managers in identifying important habitat patches that may represent conservation priorities or opportunities for management actions.

Finally, we investigated the role life history traits may have on metapopulation persistence through changes in the network structure and emergent properties. Clearly, species-specific traits such as larval duration influence the dispersal potential among subpopulations and therefore contribute significantly to metapopulation dynamics and persistence. Yet, this functional link between life history and persistence may be through emergent network properties, which also integrate system-wide habitat characteristics and spawning patterns. To explore this potential link, we summarized the species-specific network properties and node-level results, and the correlation between persistence and life history parameters. In this exploratory analysis, we included habitat size (a proxy for reproductive output), number of sources patches, extent of the spawning season, length of pre-competency window (the period of time larvae are capable of settlement), and larval mortality (see online Appendix S1 for further details). This analysis has the potential to highlight the life history traits that influence network-level metapopulation persistence.

RESULTS

After completing 1,441 dispersal simulations across five species and all years, we mapped the species-specific metapopulation networks. Mapping connectivity allowed us to visualize and investigate the geographic structure of the dispersal pathways, and provided the seascape context for network analysis. Note that the total area of habitat, the area of individual patches, and the total number of patches varied among species due to the species-specific habitat requirements. Metapopulation network maps (Fig. 1) show presence and strength of dispersal connections among source and destination subpopulations, as defined by the migration matrices. Networks varied in the number of dispersal connections (graph size), dependent on the species-specific attributes: 2,205 dispersal links for *H. rubra*, 2,086 for

H. erythrogramma, 861 for *S. punctatus*, 542 for *C. auratus*, and 8,736 for *C. rodgersii*.

Network-level metrics

Network-level metrics calculated for all species are listed in Table 2. The *S. punctatus* network was fully asymmetric, with a degree of asymmetry of 0, *C. rodgersii* was strongly asymmetric; while the other species' networks (*H. rubra*, *C. auratus*, *H. erythrogramma*) revealed a low level of asymmetry (Table 2) with gamma indices close to 1, due to a nearly symmetric exchange of larvae among habitat patches.

A heterogeneity index was calculated from each node's in-degree and out-degree connections, and is based on the coefficient of variation of degree per matrix (Table 2). These indices allowed us to compare heterogeneity across species, where values between 0 and 1 indicate that the in-degree or out-degree are under-dispersed, values larger than 1 indicate high variability or heterogeneity. In species with limited dispersal capacity (e.g., *H. rubra*, *C. auratus*, *H. erythrogramma*), the heterogeneity in in-degree and out-degree was similar. There were differences between in-degree and out-degree heterogeneity for two species; a small difference for *C. rodgersii* (in-degree heterogeneity of 0.25 and out-degree of 0.65) and a strong difference for *S. punctatus* (in-degree of 0.31 and out-degree index of 8.74).

In all species, we found many three-node cycles (Table 2), with the only exception of *S. punctatus*, which was an acyclic network. Though the number of cycles appears large, these values are far from the maximum possible number of cycles in theoretical networks (Gerbner et al. 2018, Arman and Tsaturian 2019) that might contribute to increased metapopulation persistence and stability (Artzy-Randrup and Stone 2010).

Node-level metrics

Each species' node-level properties and network metrics (Appendix S1: Table S2), and degree distribution (Appendix S1: Fig. S1) were quite variable due to species-specific characteristics and habitat requirements (Minor and Urban 2008). For species with somewhat restricted dispersal capabilities (*H. rubra*, *H. erythrogramma*, and *C. auratus*), areas of the seascape with large in-degree and out-degree were largely aligned. The metapopulation network for *H. rubra*, highlighting patterns of in-degree, is shown in Fig. 1a. High degree nodes for *H. rubra* are clustered on the eastern coast of Victoria and New South Wales while more isolated nodes are concentrated along the Tasmanian coast. In *H. erythrogramma* (Fig. 1b), we found hubs of connectivity in Victorian and New South Wales subpopulations but also across northeast Tasmania. In *C. auratus* (Fig. 1c), central Victoria had a large concentration of well-connected nodes. For species with a greater dispersal capacity, areas of strong local connectivity (in- and

TABLE 2. Result for network-level metrics: asymmetry index (γ), heterogeneity index, and the number of cycles.

Species	Asymmetry index γ	Heterogeneity index				Cycles (three connections)
		In-degree edges	Out-degree edges	Weighted in-degree edges	Weighted out-degree edges	
<i>H. rubra</i>	0.65	0.42	0.45	0.39	0.45	4,674
<i>H. erythrogramma</i>	0.74	0.29	0.31	0.45	0.39	3,346
<i>C. rogersii</i>	0.35	0.25	0.65	0.32	0.51	37,609
<i>C. auratus</i>	0.86	0.09	0.1	0.12	0.14	1,583
<i>S. punctatus</i>	0	0.31	8.74	0.41	9.77	0

out-degree) were much more variable. *C. rogersii* showed high in-degree in eastern Tasmanian coast subpopulations while habitat patches across the northwest coast of Tasmania were strong sources (high out-degree). *S. punctatus* had different spawning and settlement areas, and degree data denoted that South Australian spawning grounds can reach more settlement areas (higher out-degree) than Victorian and Tasmanian grounds, due to the potential of larvae generated in South Australia to reach patches in the whole model domain. Other centrality measures such as betweenness centrality, closeness centrality, eigenvector centrality, and alpha centrality, were calculated at a component level for disconnected graphs for three species, *H. rubra*, *H. erythrogramma*, and *C. auratus*, (see Appendix S1: Table S2 for species and component-level data).

Metapopulation stepping stones were identified by patches with a high betweenness centrality. The most central and most influential subpopulations were identified by those with high values of closeness, eigenvector, and alpha centrality. Mapping these network-level centrality measures across all species, revealed no strong geographic trends with each species displaying different key stepping-stone patches and central nodes.

We found geographic consistency between alpha centrality (Fig. 1d) and degree centrality for *C. rogersii*, *C. auratus*, and *H. rubra*. In *S. punctatus*, closeness centrality is shown in Fig. 1e, with largest values along the western Victorian coast and St. Vincent Gulf. In *C. auratus*, the distribution in betweenness centrality was opposite to closeness centrality, nodes with large closeness centrality were found in the South Australian component, while betweenness centrality identified most of species' stepping stones around Victoria.

Network structure, as well as the spatial pattern in node-level metrics appeared to be influenced by species-specific life history traits (see traits in Table 1). In general, species characterized by greater dispersal capacities and longer competency periods tended to have higher mean in-degree and out-degree, as well as a greater range across in-degree and out-degree nodes. Mean centrality statistics did not show a clear pattern with respect to species' traits. For detailed species-specific summary statistics across networks, see Appendix S1: Table S2, and the supporting data contained in DataS1: Node-

level_metrics.csv (supplementary material for all node-level metrics results).

Eigenanalysis and network-based metrics influence on persistence

All species satisfied the condition of persistence with eigenvalues larger than the persistence threshold of 1 (Artzy-Randrup and Stone 2010, Shtilerman and Stone 2015). Across species, persistence was most impacted by removing subpopulation "hubs" of connectivity (Fig. 2 and further details in Appendix S1: Fig. S2), or those with the largest out-degree (13% drop in persistence when removing 5% of top out-degree nodes, 29% drop in persistence for 10% node removed, and 43% drop in persistence for 20% of nodes removed). Other common centrality measures appeared to have a more limited impact on metapopulation persistence. Patch area also had an important role, with an overall impact on persistence lower than the degree metrics, but above all other centrality metrics, as the loss of available habitat (and therefore lower population sizes and reproductive output) has a direct negative impact on metapopulation persistence. All other node-level network metrics revealed variable impacts on system-wide metapopulation persistence across species. For each species, we also progressively removed all nodes to identify species-specific estimates of metapopulation resilience. *C. rogersii* emerged as the most resilient species where the metapopulation started to be significantly affected only after more than 25% of the most important subpopulations were removed, after which it suffered a severe decline in persistence. *S. punctatus*, on the other hand, was the most vulnerable species, where a precipitous decline in persistence was immediately revealed with only 5% of important nodes removed (Appendix S1: Fig. S3).

We mapped the out-degree metric, the most influential metric, across all species to reveal geographically consistent hot spots of important nodes identified by this network metric proxy (Fig. 3). After intersecting all species and using a moving window to summarize the density of linkages, the northwest coast of Tasmania was revealed as a critical multispecies hot spot where many species have important subpopulation hubs. Secondary hot spots appear along the northeast coast of Tasmania, as

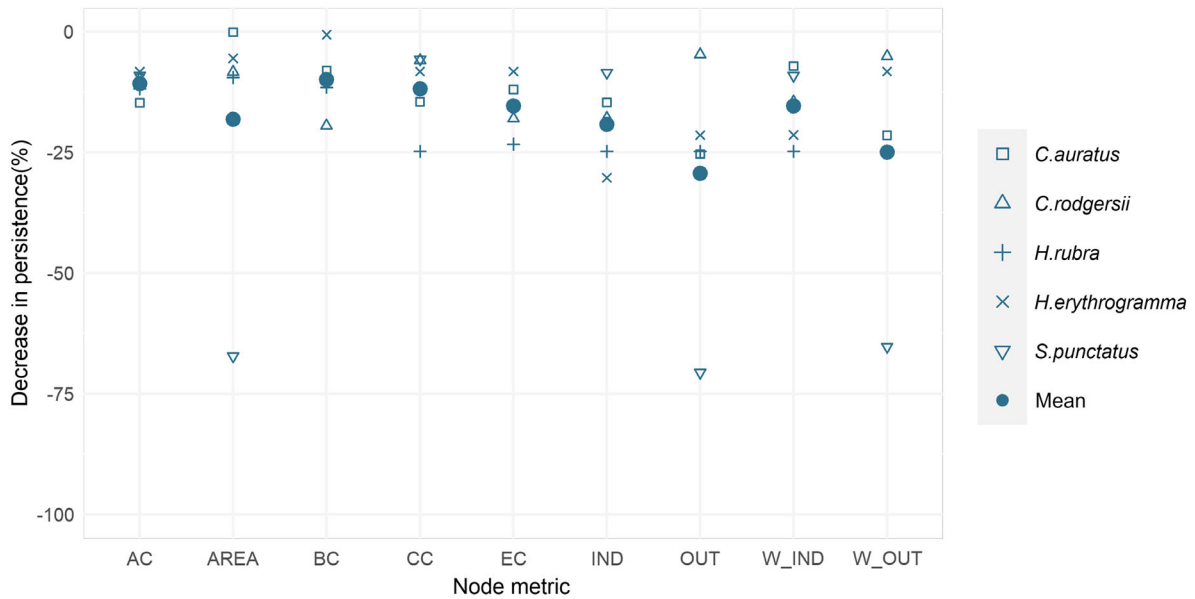


FIG. 2. Decrease in persistence by network metric. Decrease in metapopulation persistence (%) when removing top 10% of nodes determined by each node-level network metric for each species and mean across species. Metrics used to select nodes to remove from the graphs include AC (alpha centrality), Area, BC (betweenness centrality), CC (closeness centrality), EC (eigenvector centrality), IND (in-degree), OUT (out-degree), W_IND (weighted in-degree), and W_OUT (weighted out-degree). See Table 1 for full species names.

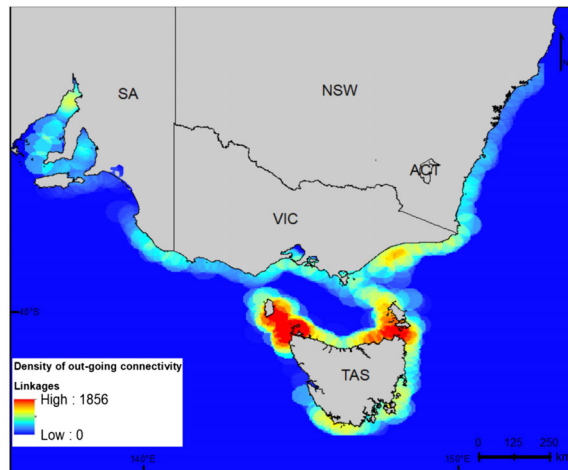


FIG. 3. Local connectivity hot spot map. Map showing the density of outgoing connections across all species modeled. Densities are displayed using a linear stretch within the upper and lower limit defined by the third standard deviation value. Map is in Transverse Mercator projection, Geocentric Datum of Australia (GDA2020).

well as in eastern Victoria. Each node's influence on metapopulation persistence was individually quantified for each species and mapped across the study area (Appendix S1: Fig. S4). Species-specific spatial patterns are largely consistent with the multispecies geographic hot spot found by out-degree, although revealing species-specific clusters of critical nodes, broadly distributed across the north coast of Tasmania and east coast of Victoria.

Finally, the investigation of the relationship between early life history characteristics and habitat on metapopulation persistence revealed mixed results. Habitat quality parameters, such as source habitat area and number of habitat sources, did not show consistent trends in metapopulation decline or impacts. In contrast, traits such as the length of the competency window, and particularly the duration of the pre-competency larval stage (Fig. 4), displayed a negative relationship with

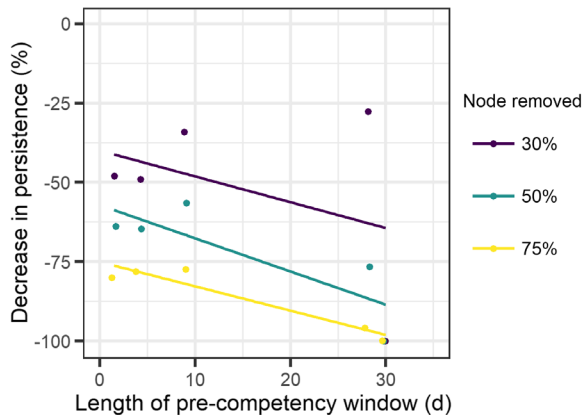


FIG. 4. Length of pre-competency window and decrease in persistence correlation. Relationship between length of pre-competency window (d) and change in persistence. Respectively at 30%, 50%, and 75% change in persistence $R = -0.39$, $n = 5$, $P = 0.52$; $R = -0.83$, $n = 5$, $P = 0.08$; $R = -0.96$, $n = 5$, $P = 0.01$.

metapopulation impact (see Appendix S1: Fig. S5 for further details). As the pre-competency period gets larger, metapopulation persistence appears to drop quickly with the removal of habitat, particularly at levels of 20–25% nodes removed.

DISCUSSION

Degree centrality, measured by out-degree, proved to be the most informative node-level metric when quantifying the impact on metapopulation persistence (Fig. 2). Other centrality measures common in the literature (e.g., eigenvector centrality, betweenness centrality) showed a limited influence on metapopulation persistence through this analysis. Out-degree was observed to be the most significant network metric with the strongest impact on metapopulation persistence (more than 10% decline in persistence after removing the top 5% of these hubs), although the size of habitat patches was also important for persistence. Habitat patches with large out-degree are important sources of larvae to many neighboring subpopulations, creating local hubs sustaining the population. Source habitats with great dispersal capacity are critical to ensure persistence of metapopulations since these habitats have an important role in ensuring successful reproduction and increasing the gene pool size, dispersing across a wide area. The network analysis suggested protecting hubs of local-scale connectivity as an important strategy in ensuring long-term persistence.

Knowing how node-level characteristics, such as size and degree centrality, impact persistence helps us identify which subpopulations or patches are vital to metapopulation persistence. This site-specific information is important for conservation scientists, as it provides an effective and ecologically meaningful way to value and prioritize areas for management or

conservation efforts. Although prioritizing hubs of connectivity in conservation is not new (Kininmonth et al. 2011), the methods and results presented here reinforce the importance of these hubs, and put this in context with other common (and less effective) connectivity measures.

Multispecies hubs of important connectivity (out-degree) are clustered across the coast of Tasmania, particularly in the northwest and northeast (Fig. 3). Among the species modeled here, marine invertebrates showed similar distribution of high out-degree hubs, mostly located across northern Tasmania. It appears these habitat patches in northern Tasmania may be essential for ensuring connectivity between Tasmania and Victoria coasts. Eastern Tasmanian hot spots have also been identified as a key ecological feature in the South-east Marine Regional Profile (Dambacher et al. 2012). In this area, subantarctic water masses driven by westerly winds interact with eddies from the East Australian current. This oceanographic mixing zone enhances productivity and experiences phytoplankton blooms and mass aggregations of coastal temperate taxa (Hosack and Dambacher 2012, Department of the Environment 2015). These areas are also recognized as significant for their conservation value; critical habitats in northern and eastern Tasmania are classified by the Tasmanian government as Conservation Areas, which mostly protect the coastal zone as regulated under the Nature Conservation Act 2002. We also found that some connectivity hubs correspond to Australian Marine Parks of the South-east Network, such as Freycinet Marine Park in the southeast and Boags Marine Park in northwest Tasmania. Other important hubs of multispecies connectivity appear to exist in eastern Victoria. Several sites in this region have also been previously identified as associated with biogeographic breaks for many taxa (Colton and Swearer 2012). Breaks have been located in some cases at Wilsons Promontory (O'Hara and Poore 2000) or in the vicinity of Ninety Miles Beach (Hidas et al. 2007, Gomon et al. 2008). These biogeographic breaks are often associated with changes in species range and assemblages (e.g., due to temperature gradients or local of habitat), and can potentially limit broadscale dispersal connections (Colton and Swearer 2012). Waters surrounding Wilsons Promontory correspond to Protected areas, such as the Beagle Marine Park, part of the South-east Network of the Australian Marine Parks, and the Wilsons Promontory Marine Park and Wilsons Promontory Marine Reserve.

Network-based approaches can be a powerful tool to help understand metapopulation structure, particularly when studying species where dispersal dominates metapopulation dynamics, like many marine taxa. Connectivity has recently been shown to be an important criterion to better design protected area networks, possibly more important or efficient than habitat quality or quantity alone (Berglund et al. 2012). Network-level metrics can also help managers understand the overall

geographic structure of a metapopulation, efficiently identifying where hubs and barriers exist. These metrics store information on network symmetry or heterogeneity, where a very asymmetric or heterogeneous network can be an indicator of a vulnerable metapopulation (Shtilerman and Stone 2015). Similarly, node-level metrics help identify core areas important for building optimal management strategies (Kininmonth et al. 2011, Watson et al. 2011, Berglund et al. 2012). Broad-scale spatial management often involves many diverse agencies, often leading to programmatic challenges in funding and implementation (Cowan et al. 2012). This can be alleviated to a degree by identifying local-scale areas of interest, such as multispecies connectivity hubs or consistent biogeographic zones, thereby aligning management with these ecologically meaningful scales. In other circumstances, managers may benefit from disconnecting hubs of connectivity to optimizing invasive species management (Perry et al. 2017, Samsing et al. 2017). This can be an option for *C. rodgersii* and *H. erythrogramma* management, which are spreading across the South-east Marine Region of Australia causing dramatic habitat alterations (Ling et al. 2015).

Identifying node-level metrics that strongly influence metapopulation persistence, provides opportunities to more directly investigate the influence of life histories and location on persistence (Dallas et al. 2019). Network structure and node metrics were influenced by species-specific differences, associated with species-specific life history traits, and were mostly evident for in-degree and out-degree results. Identifying key life history traits and the associated species, may help quickly redirect funds and research to these vulnerable species and locations. From our preliminary analysis of species-specific life-history traits, we found the pre-competency period to be the most influential parameter (Fig. 4), where metapopulation persistence declines with an increase in the pre-competency period; the relationship is driven by the species with the longest pre-competency period. However, a significant relationship with the pre-competency period is only found when 75% of the important nodes are removed. Extended pre-competency periods may be associated with greater dispersal ability downstream (Heyward and Negri 2010), lower local retention (Trembl et al. 2015b), and may make larvae more vulnerable to mortality and starvation (Jenkins and May 1994). Further research is required to investigate the potential relationship between life history traits and metapopulation persistence and to identify vulnerable species and habitat patches and locations.

Despite the fact that this approach is flexible and applicable to many species and habitat, the model presented here has several limitations. Our analysis on persistence was based on averaged data across years, and temporal variability was not considered, but it might be important to explore the consistency of node importance through time and whether the network structure itself

changes through time. In addition, our model assumes the habitat quality is homogeneous (i.e., quality/density is the same per suitable habitat cell) and habitat patches vary only in individual patch sizes and locations. Ignoring spatial heterogeneity will impact predictions of connectivity, particularly where the relationship between patch size and reproductive output does not hold, and therefore might change results. Finally, there is limited availability of empirical data on the early life history of most coastal species (e.g., swimming, sensing, and mortality), and virtually no data describing how these parameters might vary across the seascape. Improving our understanding with field- and laboratory-based research is critical to produce more accurate predictions around metapopulation connectivity and persistence.

In conclusion, larval dispersal modeling and network analysis provides an efficient approach in studying real-world marine metapopulation persistence. Degree centrality, identifying hubs of outgoing connections, was shown to be a major predictor of persistence. Multispecies hubs of connectivity highlight important hot spots for management and conservation consideration. In this seascape, these connectivity hot spots occur where tropical and temperate currents merge and in regions surrounding known biogeographic breaks. Finally, a preliminary analysis suggests that the length of the pre-competency phase may be a predictor of local-scale connectivity (i.e., out-degree) and have a strong influence on metapopulation persistence. Together, these species-level attributes and important hot spots in south-east Australia can assist managers in making more efficient and more ecologically informed decisions regarding priorities to ensure persistent metapopulation of fished and/or threatened species.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2302/full>

DATA AVAILABILITY

Data generated during the study are available in Data S1. Underlying source data are available as follows. The species occurrence data that supports the findings of this study are available from the Atlas of Living Australia website: *H. rubra*, species page, <http://biocache.ala.org.au/occurrences/search?&q=lsid%3Aurn%3Aalsid%3Abiodiversity.org.au%3Aafd.taxon%3A614956ef-f4ef-4f78-90cc-e3bf82f47258> accessed on August 24, 2017; *C. rogersii*, species page, <https://biocache.ala.org.au/occurrences/search?&q=lsid%3Aurn%3Aalsid%3Abiodiversity.org.au%3Aafd.taxon%3A11322f4a-3442-4129-a8bb-57d8e42d739a> accessed on February 19, 2018; *H. erythrogramma*, species page, <https://biocache.ala.org.au/occurrences/search?&q=lsid%3Aurn%3Aalsid%3Abiodiversity.org.au%3Aafd.taxon%3Aa83c96b0-64d5-4b14-97ec-894a158ee417> accessed on February 19, 2018. The environmental data sets were derived from multiple public domain resources (see *Methods* for additional details): General Bathymetric Chart of the Oceans, GEBCO (<https://www.gebco.net/>); HYCOM (<https://www.hycom.org/>); Estuary Watch Victoria (http://www.estuarywatch.org.au/estuary_watch_map.php); Seamap Australia National Benthic Habitat Classification Scheme (<https://seamapaustralia.org/>); Geoscience Australia (<https://data.gov.au/data/dataset/seabed-gravel-content-across-the-australian-continental-eez-2011>); <https://data.gov.au/data/dataset/seabed-sand-content-across-the-australian-continental-eez-2011>); AODN (<https://portal.aodn.org.au/>).