

Simulated larval connectivity among Australia's southwest submarine canyons

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ABSTRACT: A biophysical dispersal model was used to simulate hydrodynamic connectivity among canyons located within Australia's southwest marine region using ophiuroid (brittlestars) larvae as a model species. The results show that exchange among canyons in this area is greatly influenced by the Leeuwin Current, transporting larvae in a unidirectional manner around Cape Leeuwin, and continuing eastwards along the Great Australian Bight. Larvae within canyons tend to remain within them; however, if they are transported above the canyon walls, they then have the opportunity to be transported significant distances (thousands of km). Analysis of the variability in connectivity patterns reveals concentrated larval flow near the shelf break, with increasing levels of variability in larval flow leading offshore from the canyons. While the average potential larval flow distance and duration (unweighted by dispersal probability values) between canyons were approximately 550 km and 33 d, respectively, the average realized larval flow distance and duration (weighted by dispersal probability values) were approximately 20 km and 5 d, respectively. This study provides the first consideration of larval connectivity among submarine canyons and will help improve management of these features by providing a better understanding of larval movement, transboundary exchange and the potential spread of invasive species.

KEY WORDS: Connectivity · Submarine canyons · Dispersal · Leeuwin Current · Southwest Australia

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INTRODUCTION

Submarine canyons are an important component of Australia's marine estate, acting as both attractors and refuges for a range of marine species (e.g. polychaetes, sponges and corals, as well as fish and whales) (Yoklavich et al. 2000, Schlacher et al. 2007, Rennie et al. 2009a, Huang et al. 2014). Submarine canyons enhance shelf-slope exchanges and generate vertical current flow, particularly in the case of shelf-incising canyons, with upwelling drawing nutrients from deeper layers to enhance productivity near the surface (Allen et al. 2001, Rennie et al. 2009b). Canyons are also complex features, topographically as well as in the range of habitat types they contain (e.g. soft, hard and mixed substrate with varying levels of wall steepness) (Schlacher et al.

2007, McClain & Barry 2010). Canyons also provide natural refuges from trawling owing to the potential for gear damage when operating in these areas (Yoklavich et al. 2000), although longlining and gill-netting are possible. For these reasons, canyons are a key area of interest for marine managers in Australia (Commonwealth of Australia 2012).

Australia has >200 identifiable submarine canyons in its southwest region, spanning almost 3000 km along Australia's continental margin and the Great Australian Bight (Fig. 1). There are many compelling reasons for effectively managing these features. The canyons are known to host a wide variety of marine species (McClatchie et al. 2006a), and contribute to a marine tourism industry worth AUS\$325 million in South Australia and AUS\$150 million in Western Australia in 2003 alone (Gardner et al. 2006). The

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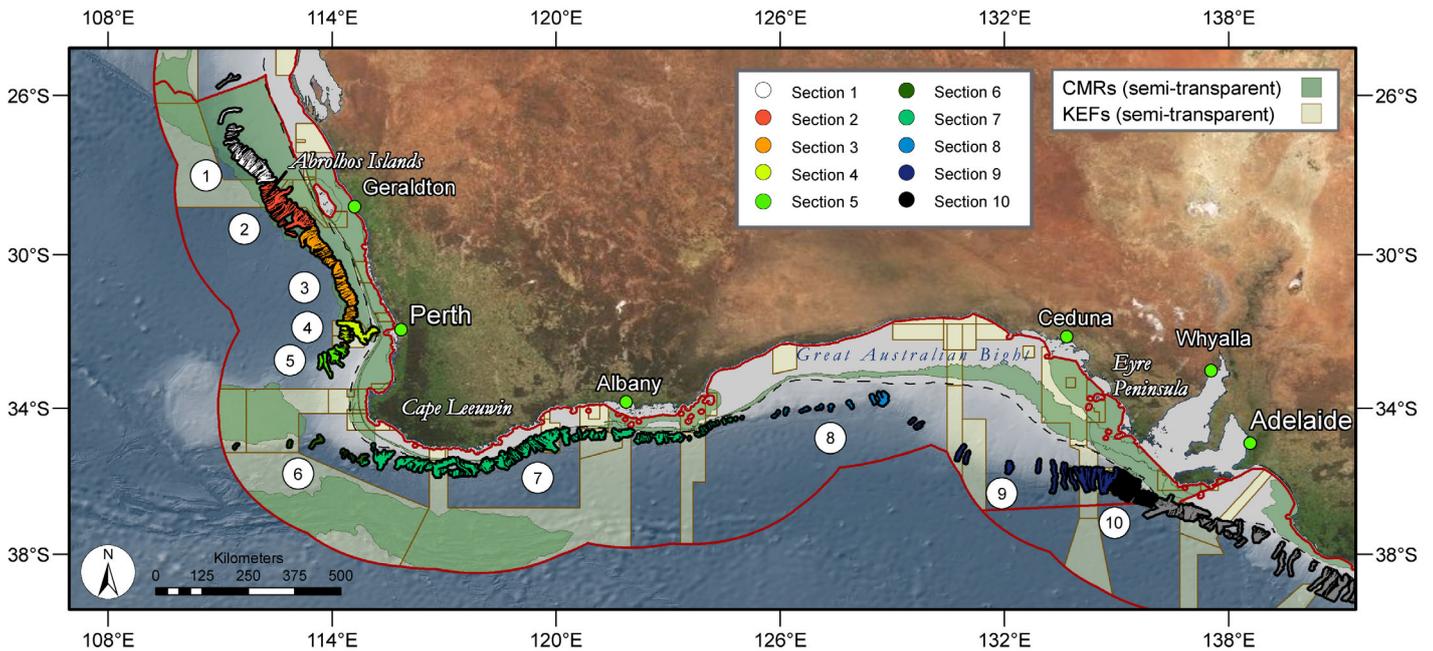


Fig. 1. Australia's southwest marine planning region (boundaries shown as red lines) (Commonwealth of Australia 2005) and associated canyons (Huang et al. 2014). Marine topography was derived from bathymetry data (Whiteway 2009), and land imagery was obtained from ESRI (see 'Acknowledgements'). Commonwealth Marine Reserves (CMRs) were taken from Commonwealth of Australia (2005) and Key Ecological Features (KEFs) from Dambacher et al. (2012). The dashed line indicates the shelf break. The outer edge of the marine planning region is coincident with the Australian Exclusive Economic Zone. Numbers and colours indicate the sections of canyons used as division points in the matrix plots (see Fig. 5)

canyons also support commonwealth-managed fisheries worth approximately AU\$140 million (gross value) (Bureau of Rural Sciences 2005) including species such as southern bluefin tuna *Thunnus maccoyii* (Patterson et al. 2008) and western rock lobster *Panillurus cygnus* (Feng et al. 2010). These areas are also known to be feeding locations for sperm whales *Physeter macrocephalus* and humpback whales *Megaptera novaeangliae* (Pattiaratchi 2007).

The degree of connectivity among Australia's southwest submarine canyons is not well known. Connectivity is a measure of the degree of dependencies among spatially or temporally separated populations (Kool et al. 2013), and can be applied to hydrodynamic flow among different areas or to demographic or genetic linkages among populations. Connectivity information is important for understanding demographic patterns, including the identification of source and sink locations, stepping-stone populations and for identifying characteristic spatial and temporal scales associated with larval connectivity. Although there have been many studies of connectivity among shallow and patchy coastal and marine populations (e.g. Kool et al. 2011, Treml & Halpin 2012, DeMartini et al. 2013), connectivity among extensive and topographically complex environments has not been as extensively studied. To address this

paucity of investigations, a 4-dimensional (3D space \times time) dispersal model was used to simulate connectivity among submarine canyons in Australia's southwest region. The results were analyzed to develop a better understanding of the interdependence of these important marine features, including the potential net direction and extent of larval transport among canyons, as well as to examine whether the size and location of canyons influence potential dispersal patterns and to identify linkages between selected connectivity and canyon metrics.

STUDY AREA

The Australian southwest marine planning region covers approximately 1.3 million km², extending from approximately 25.5° to 38.5°S and 109.2° to 137.5°E (Fig. 1). The region includes 205 submarine canyons (min. 4 km², max. 1805 km²) (Huang et al. 2014). The minimum canyon head depths in the area are at approximately 70 m (Albany canyon group, between south of Cape Leeuwin and Albany), and the maximum head depths are at approximately 3800 m (west of the Abrolhos Islands). The minimum canyon foot depth in the region is at approximately 1061 m (south of Cape Leeuwin), and the deepest

foot depth is approximately 5115 m (also west of the Abrolhos Islands). A canyon head is the shallowest part of a canyon, whereas a canyon foot is the deepest part. The depth range of the canyons spans from 641 m (between south of Cape Leeuwin and Albany) to approximately 5000 m (the Murray canyon group, south of Eyre Peninsula). The distances of the canyons from shore range from 35 km (the Albany canyon group, between south of Cape Leeuwin and Albany) to 376 km (south of the Great Australian Bight). Ten of the canyons within the studied region are shelf-incising, with incision depths ranging from 233 to 543 m (Huang et al. 2014). Incision depth refers to the average depth of the canyon area that incises into the shelf break. The Leeuwin Current is a prominent, south-flowing and stable oceanographic feature in this area, and acts as a conduit for warm, nutrient-poor water of tropical origin to approximately 300 m depth (Smith et al. 1991, Feng et al. 2003, Pattiaratchi 2006). The strength of the Leeuwin Current exhibits significant seasonal and inter-annual variations (Smith et al. 1991, Feng et al. 2003). The Leeuwin Undercurrent is also present at 300 to 800 m depth and is capable of flowing in the opposite direction to the Leeuwin Current (Waite et al. 2007). Local upwelling has been noted in the region, particularly in the vicinity of Kangaroo Island (Kämpf et al. 2004, McClatchie et al. 2006b).

METHODS

Connectivity among canyons was simulated using the 4-dimensional (3D velocities \times time) Conn4D model (Kool & Nichol 2015) using HYCOM current velocities (Chassignet et al. 2006) to drive the dispersal patterns. Particle releases were generated volumetrically (i.e. using a consistent, vertically-stratified density of release locations) and were parameterized using life history characteristics associated with brittlestar (ophiuroid) larvae. Volumetric releases provide a measurement of connectivity among water parcels, and can be subset spatially and temporally to examine connectivity values for specific aspects of interest. Ophiuroids were selected as a model species due to their prevalence in benthic marine systems and widespread distribution; however, they also play a functional ecological role as detritivores (Ponder et al. 2002) and as prey items for fish (Blaber & Bulman 1987, Ponder et al. 2002). The mortality rate for the virtual larvae was set to an exponential rate of -0.06 d^{-1} (Rumrill 1990, Lefebvre et al. 2003), with a maximum pelagic larval duration of approximately

90 d (Mercier et al. 2013). Ophiuroid larvae are generally considered to be passive and neutrally buoyant drifters (Banse 1986). To structure the arrangement of release locations, a 9 km^2 mesh grid was constructed with an extent of -2.6×10^3 to $2.85 \times 10^3 \text{ km}$ in the horizontal, and -5.15×10^3 to $1.075 \times 10^3 \text{ km}$ in the vertical using the World Cylindrical Equal Area projection (central meridian 135° , standard parallel -25°). This mesh grid was then intersected with the Australian exclusive economic zone (EEZ) boundary such that the majority of the cell had to lie within the EEZ and also had to be entirely within the water column (i.e. if the 3D cell [voxel] intersected the benthic layer, it was excluded as a starting box). Thirty-one depth ranges were used ranging from 0–10 m to 5000–5500 m, resulting in a total number of 360 975 voxels (Fig. 2). From each voxel, 100 larvae were released every 30 d commencing 1 January 2009 through until 31 December 2012 resulting in more than 1.7 billion individual releases. Larvae were tracked up to a limit of 90 d, and their position was recorded on a daily basis (simulation time) into binary output files before being transferred into a PostGResQL 9.2 (PostGResQL Global Development Group 2014) database.

Canyon locations (Fig. 1) and their associated characteristics were taken from Huang et al. (2014) and include information on 30 different canyon metrics, including measurements on shape, location and morphometric complexity (for the complete list of parameters and their description see Huang et al. 2014). The canyons were spatially intersected with the larval point locations in the database to extract larvae and tracks to and from the canyon locations. Larval particle tracks were animated to show the dispersal patterns from the canyons and summarized by taking the point density over a given time and/or depth window. The variability of the data can also be used to identify areas of consistent larval flow, corresponding to the marine analogue of terrestrial corridors (Kool & Nichol 2015).

The total numbers of larvae exchanged among the canyons were summarized into a matrix of connection values, which were then analysed to identify source and sink patterns. Contributions to canyons located outside the Australian southwest marine planning region were considered when determining source strength. Two types of connectivity were analysed: (1) full water-column connectivity where exchange among canyons and the water column above them was considered, and (2) canyon-restricted releases tracking larvae released within a canyon and ending either within or above a canyon. The connec-

Depth bins in metres

D0	D1	D2	D3	D4	D5	D6	D7	D8	D9	D10	D11	D12	D13	D14	D15	D16
0	10	20	30	50	75	100	125	150	200	250	300	400	500	600	700	800
10	20	30	50	75	100	125	150	200	250	300	400	500	600	700	800	900

D17	D18	D19	D20	D21	D22	D23	D24	D25	D26	D27	D28	D29	D30	D31
900	1000	1100	1200	1300	1400	1500	1750	2000	2500	3000	3500	4000	4500	5000
1000	1100	1200	1300	1400	1500	1750	2000	2500	3000	3500	4000	4500	5000	5500

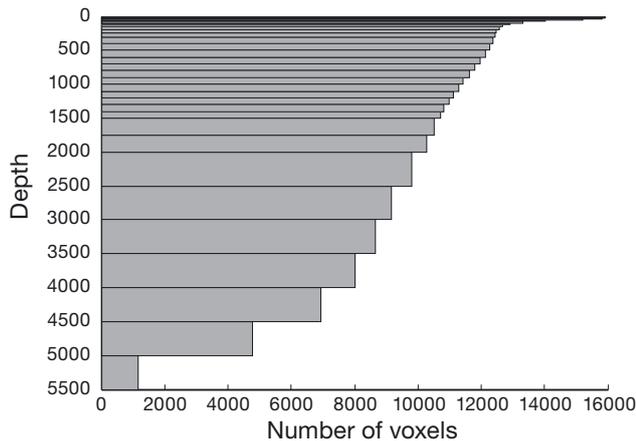


Fig. 2. Histogram of the number of voxels per release depth bin (m). Depth values increase positively downwards from the sea surface

tivity data was also binned to generate instantaneous and cumulative kernels on the basis of potential and realized dispersal. We use the term ‘dispersal’ following Pineda et al. (2007) to highlight that post-settlement processes are not being considered here. We define potential dispersal (ϕ) as the sum total of all connections that are accessible among populations or patches with respect to a given measure (e.g. larval dispersal/flow distance, time), whereas realized dispersal (ρ) is calculated on the basis of the number of larvae successfully transitioning among canyons relative to the same measures. These can be formally written as:

$$\phi_{ij} = [n_{ij} > 0] \quad \text{and} \quad \rho_{ij} = \frac{n_{ij}}{\sum_{j=1}^c n_{ij}}$$

with n indicating the number (count) of individual larvae dispersing from source population j to destination population i , and c is the total number of source populations. The square brackets are Iverson brackets (Iverson 1962) where $[P] = \begin{cases} 1 & \text{if } P \text{ is true} \\ 0 & \text{if } P \text{ is false} \end{cases}$.

Kernels were also created to show the percent of connected area with respect to distance from shore and the continental shelf break through generating buffers around these features (i.e. shoreline and shelf break) and tabulating the proportion of dispersed larvae intersecting the buffered area.

A redundancy analysis with forward selection was performed to determine the multivariate relationship between the connectivity metrics (source and sink capacity, diversity) and canyon metrics from Huang et al. (2014) using Canoco 5 (Šmilauer & Lepš 2014) based on percent of variability explained, using a cutoff improvement threshold of 1% to reduce the number of variables shown in the ordination figure. Source capacity was calculated as the vector of column sums of the dispersal matrix, and sink capacity was calculated as the vector of row sums of the dispersal matrix. Source diversity was calculated using the numbers-equivalent Gini-Simpson index (Jost 2007), calculated as $H = 1 / (1 - \sum p_j^2)$, where p_j is the probability of receiving larvae from source j . Sink diversity can equivalently be calculated by substituting source j with destination i .

The data were partitioned into seasonal and release depth groups to investigate the sensitivity of the model to seasonality and release depth. For season, groups consisted of austral spring (September–November), summer (December–February), autumn (March–May) and winter (June–August). The release depth groups consisted of 0–50, 50–120, 120–200, 200–700, 700–1500, 1500–3000 and >3000 m. Statistical differences resulting from partitioning of the data set were tested using randomization-based ANOVA (Manly 1997). For individual connections where at least one of the values was not zero (i.e. connections where all connectivity values were zero were not considered in the analysis), a standard sample-based F -statistic was calculated on the basis of grouped data, weighted by sample size. The F -statistic was calculated as the ratio of the between group variability to the within group variability. The equation for within-group variance with unequal sample sizes is $\sum_{i=1}^I \frac{(n_i - 1)s_i^2}{N - I}$ and between-group variance is $\sum_{i=1}^I n_i \frac{(x_i - \bar{x})^2}{I - 1}$, where x_i is the mean value for group i , \bar{x} is the pooled mean over all observations, n_i is the number of observations for group i , s_i is the sample variance of group i , N is the total number of observations, and I is the total number of groups. Observed F -statistics were compared against data generated by randomizing on the axis of interest with replacement (e.g. season, depth) but using the identical sample structure (i.e. number of samples and configuration for each group). This was performed 4999 times (plus the observed value = 5000). The frequency with which the randomized F -statistics equalled or exceeded the observed statistics was then used to generate p -values.

RESULTS

The general pattern of larval dispersal appears to be heavily dominated by the flow of the Leeuwin Current, which transports the simulated larvae from the area offshore of Carnarvon and Geraldton southwards before rounding Cape Leeuwin and continuing eastward (Fig. 3A). This pattern is consistent with observations made by Maxwell & Cresswell (1981) who made note of the transport of tropical species into the Great Australian Bight, and is also comparable to results observed by Ridgway & Condie (2004) and Domingues et al. (2007). Eddies routinely transport near-surface larvae offshore (e.g. westwards from the Western Australian coast and southwards from the Great Australian Bight; Fig. 3A), but also loop back towards shore, frequently returning the larvae near to their release points (Fig. 3A,B). Although there is some transport of the simulated larvae from canyons south of Cape Leeuwin northwards, the larvae typically do not pass over canyons north of Cape Leeuwin. Instead larvae tend to be retained by a persistent mesoscale gyre west of Cape Leeuwin (Fig 3A). Aggregating the data as a dispersal surface (Fig 3B) shows that the larvae are expected to remain near their source canyon and the shelf margin, although it is possible to have longer, albeit more unlikely, dispersal trajectories as well. This general pattern is consistent with other simulations of connectivity (Domingues et al. 2007, Condie et al. 2011), as well as field observations which suggest that larvae tend to remain near to their source population, and the potential does exist for longer distance dispersers (Eble et al. 2010). In general, simulated larvae positioned near the surface were transported greater distances than those deeper in the water column (Fig. 4). Plotting of larval flow variability (Fig. 3C) indicates that a consistent stream of larvae, supplied by canyons, is expected to travel shoreward from the shelf break as revealed by the lower variability values (lighter colour) in this area. Seaward from the shelf break, the larval dispersal pattern is more variable, with the degree of variability being similar to that of the dispersal intensity (Fig. 3B).

The matrix results suggest that Australia's southwest submarine canyons are connected as a series of gradients in canyon dispersal strength (Fig. 5), indicated by the relatively consistent bandwidth along the diagonal of the connectivity matrix. Gradients in canyon dispersal strength indicate continuous, overlapping zones of local exchange, suggesting the influences of exponential larval mortality over time (and consequently distance) as well as larval reten-

tion through recirculation. A notable exception to this pattern occurs near Cape Leeuwin (sections 6 and 7; Fig. 1), evidenced by asymmetric blocking, suggesting that once larvae are transported around the Cape, they are unlikely to be able to return back north due to the influence of the Leeuwin Current and possibly the presence of the persistent eddy mentioned above. The simulations indicate that some counter current flow is expected north of Cape Leeuwin, as well as some westward transport into the Great Australian Bight. The canyons located near Adelaide also appear to be relatively isolated from the other southwestern Australian canyons (section 10; Fig. 1). Limiting releases to those that originated within the confines of the canyons resulted in a much more restricted larval connectivity pattern (Fig. 5B), although some exchange was still evident. The results suggest that if larvae are able to escape the confines of canyons, then they have the potential to be transported significant distances.

Plotting the relative degree to which canyons act as sources and sinks (Fig. 6) also highlights the graded nature of connections among canyons (i.e. connection strength as a function of distance has a smooth gradient). For example, canyons located south of the Eyre Peninsula are expected to be high source areas to other canyons, as are the canyons situated between Geraldton and Perth (Fig. 6A). Again, this appears to be largely the result of the Leeuwin Current transporting larvae around Cape Leeuwin and over intercepting canyons off the southern coast, or by contributing larvae to immediately adjacent canyons. The Albany canyons (east of section 7; Fig. 3A) act as moderate source areas (Fig. 6A), losing larvae due to offshore transport and a relative lack of suitable destination canyons in the Great Australian Bight. In general, the sink capacity of southwestern canyons mirrored the source capacity, with areas south of the Eyre Peninsula and along the west coast ranking highly as sink areas (Fig. 6B). Some differences can be seen, however, with a slight eastward shift in the strength of the sink values relative to the source values south of the Eyre Peninsula, as well as increased sink capacity in the clustered canyons northwest of Perth.

On the basis of larval flow distance, peak potential larval dispersal occurs at a distance of approximately 225 km with 50% of larval connectivity occurring within approximately 550 km, and 95% of larval connectivity occurring within approximately 2000 km of the point of origin (Fig. 7A). With respect to duration, peak potential larval dispersal occurs at 30 d, with 50% of larval connectivity occurring within approximately 33 d and 95% within approximately 69 d

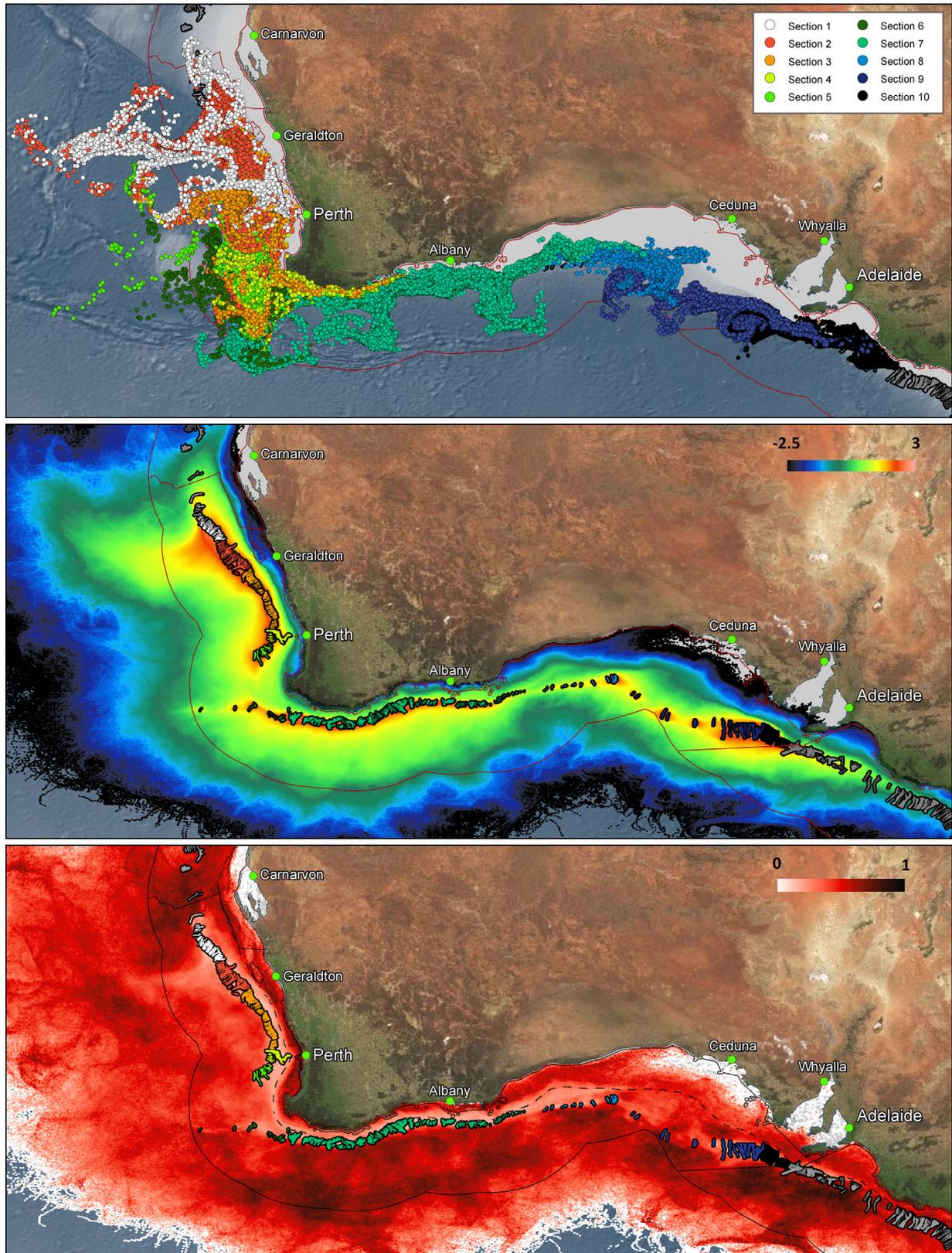


Fig. 3. (A) Simulated ophiuroid larval dispersal pattern after 46 d (16 February 2012) with releases occurring both within canyons and in the water column above canyons. The animation (www.int-res.com/articles/suppl/m539p077_supp/) shows monthly releases in 2012. (B) Particle density of simulated ophiuroid larvae. Values are \log_{10} simulated ophiuroid larval densities (unitless) for a 4 km radius around a 250 m cell, and are integrated over the time interval January 2009 to December 2012. (C) Variability of simulated ophiuroid larvae. All values are calculated as the standard deviation of the \log_{10} simulated ophiuroid larval densities for a 4 km radius around a 250 m cell over the interval January 2009 through December 2012. Numbers and associated colours indicate the sections of canyons investigated. The red (A,B) and black (C) lines indicate the outer edge of the marine planning area coincident with the Australian Exclusive Economic Zone. The dashed line denotes the shelf break

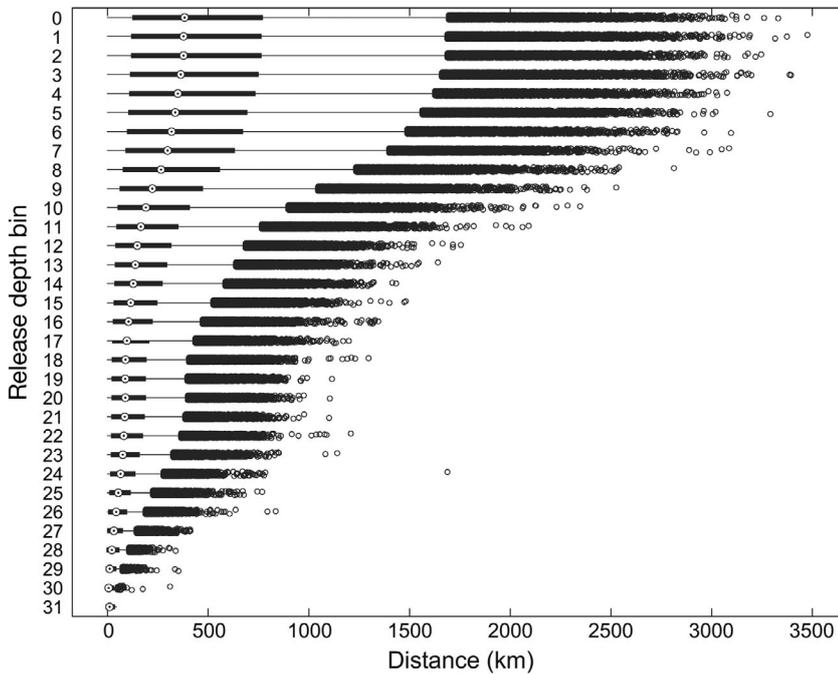


Fig. 4. Box plots of ophiuroid larval transport distances stratified by release depth (for depth bin ID see Fig. 2). Median values are indicated by the circle and dot, box edges are the 25th and 75th percentiles, and whiskers extend to $\pm 1.5 \times$ the interquartile range within the bounds of the data values. Outliers beyond the limits of the whiskers are plotted as hollow circles

(Fig. 7B). Peak realized larval dispersal occurred between 10 to 20 km with 50% occurring within approximately 20 km and 95% within approximately 150 km (Fig. 7C). Realized larval dispersal decreased exponentially with respect to time from the initial release, with 50% of successfully transitioning larvae having durations of less than approximately 5 d, and 95% within approximately 25 d (Fig. 7D). The larval dispersal kernel showing expected levels of larval connectivity to canyons with respect to distance from shore indicates that the peak connectivity levels occur a little less than 100 km offshore (70–80 km), coinciding with the average distance of the canyons from shore, and then tapering into a long tail, extending out to distances of 500 km or more (Fig. 7E). The peak distance of 100 km offshore coincides with observations of the average location of the Leeuwin Current (Huang & Feng 2015). Simulated larvae released within or above canyons remained

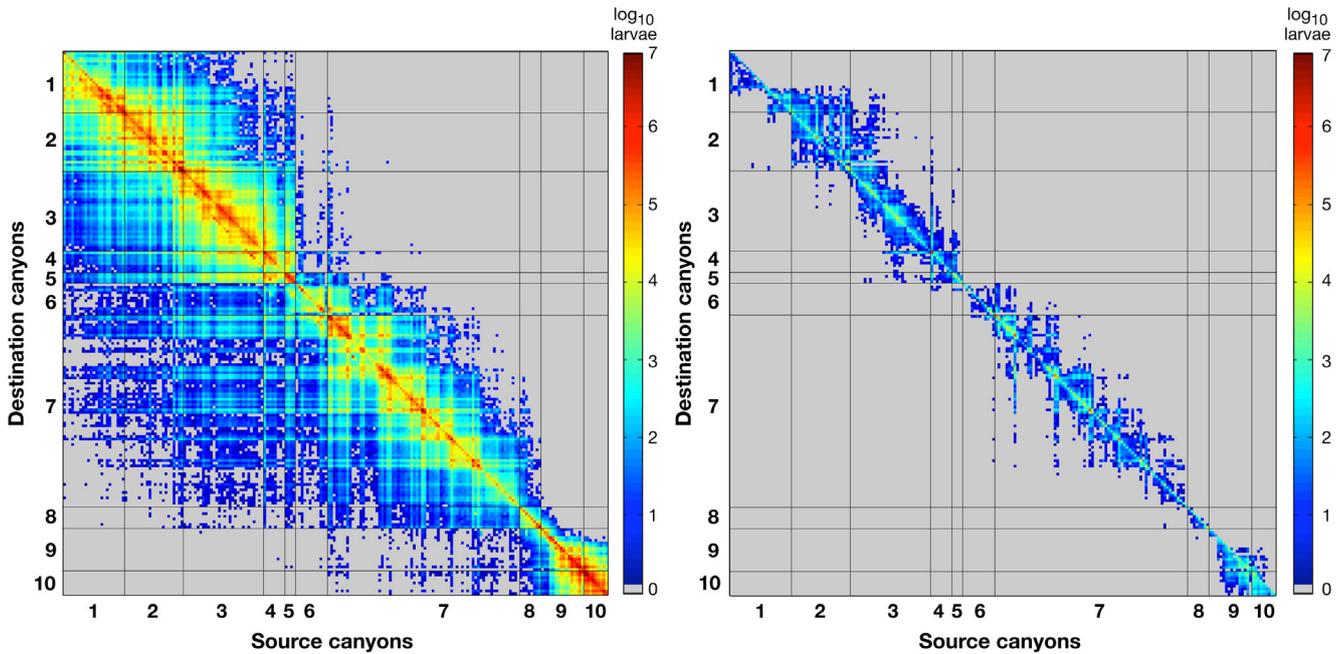


Fig. 5. Connectivity matrices between southwest submarine canyons defined by Huang et al. (2014). Results are aggregated across all release depths (0–5500 m) and release times (January 2009 to December 2012). Connectivity values are based on volumetric releases using characteristics associated with ophiuroid larvae. (A) Connectivity values derived using the entire water column above the canyons for both source and destination locations. (B) Connectivity values derived using larvae released within the confines of the canyon and intercepting the water column above canyons as a destination. Numbers along axes denote sections of geographic canyon regions shown in Fig. 1. Higher ophiuroid larval densities at a point on the diagonal axis indicate strong local connectivity, and continuity of these values along that axis indicates strong connectivity within a geographic region

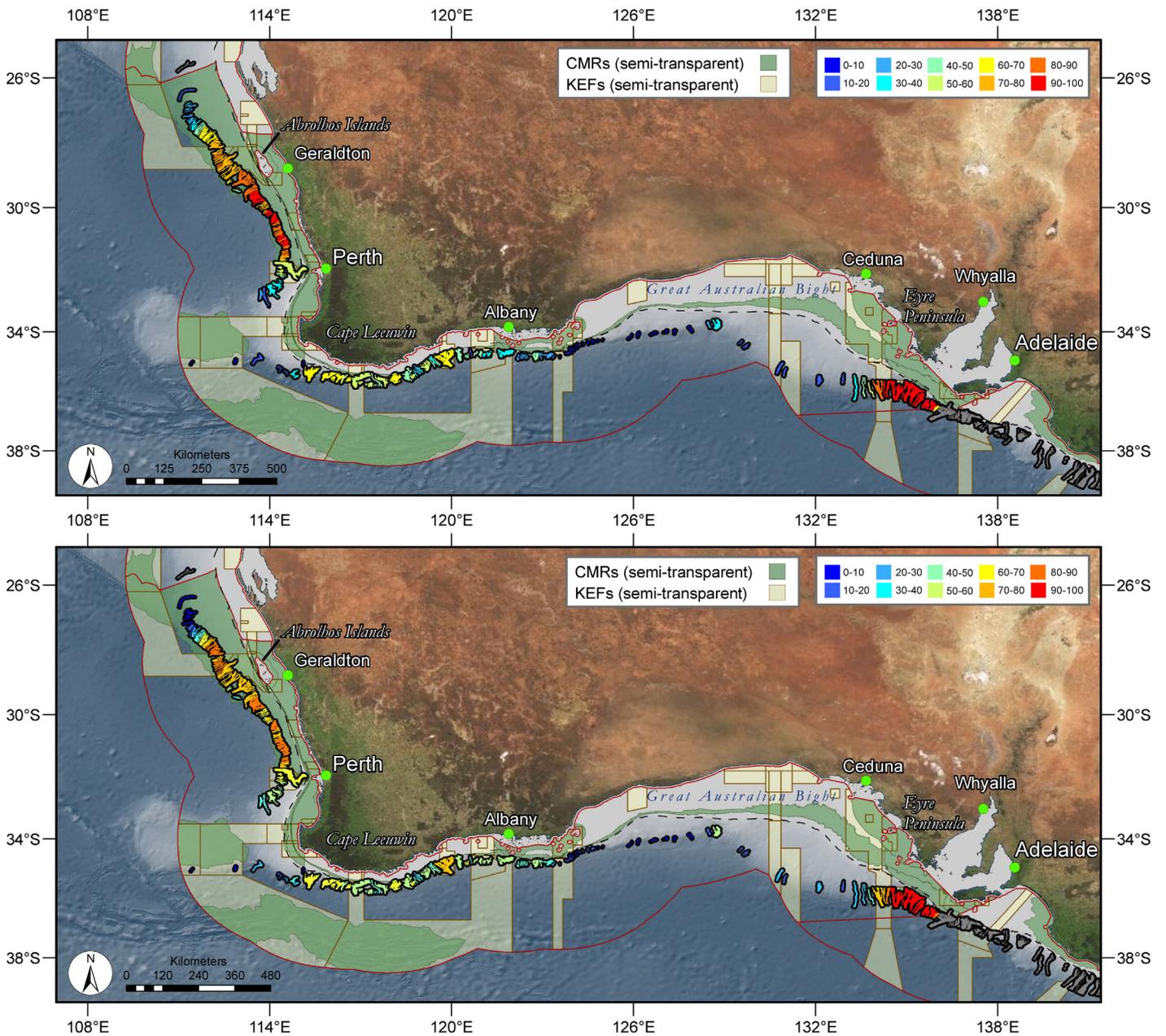


Fig. 6. (A) Larval source and (B) sink capacity of southwest Australian submarine canyons based on total larval count, standardized on canyon area, expressed as a percentile. See Fig. 1 for map details

within Australia's EEZ with a probability of nearly 98%. Generating a larval dispersal kernel using the shelf break as the point of reference generates similar results, but with the mode of the distribution nearer to zero (Fig. 7F). Plotting the mean ratio of the larval flow distance to the Euclidean distance travelled by larvae with respect to their point of origin reveals that as duration and distance travelled increase, the differences in these values can reach factor values of 6 or greater (Fig. 8).

Partitioning the modelled connectivity patterns according to depth revealed significant differences be-

tween depth layers, with the greatest differences occurring between shallow and deep layers (Table 1). Seasonality did not appear to have a major influence on larval connectivity patterns in southwest Australia, in contrast with simulations carried out for Australia's north and northwest, which were influenced by seasonal monsoon patterns in the Arafura Sea (Kool & Nichol 2015). Larval connectivity patterns also did not appear to be significantly different between shelf-incising and non-shelf incising canyons, or between canyons within versus outside Commonwealth Marine Reserves. A slightly greater difference in larval

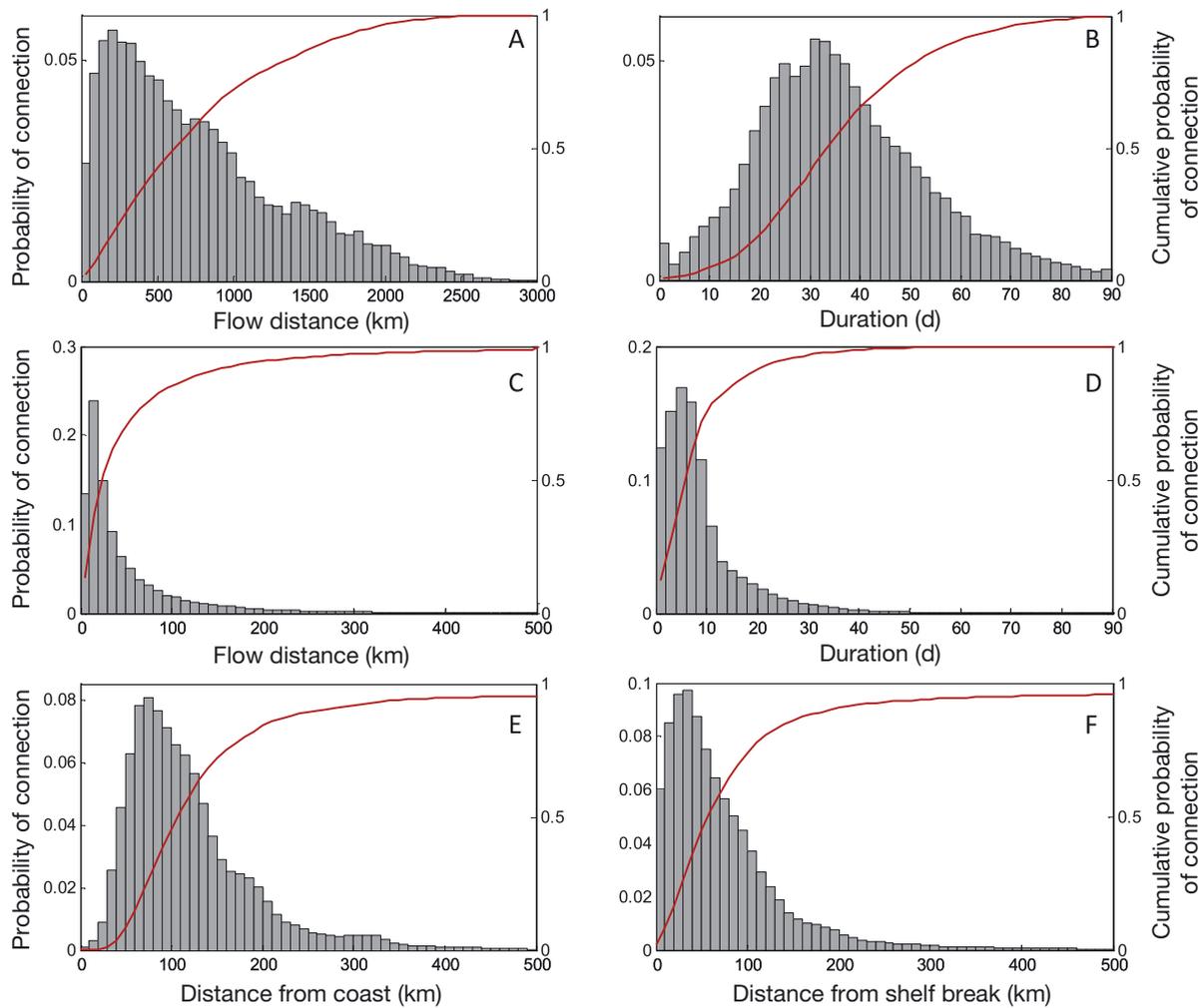


Fig. 7. Ophiroid larval connectivity kernel plots (single generation). Bars indicate probability/frequency of connection at the specified interval (left axes), lines indicate cumulative probability of connection at the specified interval (right axes): (A) Flow distance (km) versus proportion of canyons connected at that distance through potential dispersal. (B) Duration (d) of larvae in the water column versus proportion of canyons connected at that interval through potential dispersal. (C) Flow distance (km) versus proportion of larvae intersecting canyons encountered at that distance through realized dispersal. (D) Duration (d) of larvae in the water column versus proportion of larvae intersecting canyons encountered at that duration through realized dispersal. (E) Distance from coast (km) versus proportion of larval dispersal captured at the given distance interval. (F) Distance from the shelf break (km) versus proportion of dispersal captured at the given distance interval

connectivity values appears to exist between within versus outside key ecological features compared with the other groupings (Table 1), though these values were not close to reaching a 0.05 level of significance.

The likelihood that a canyon will act as a source was negatively associated with canyon longitude, which is likely due to the influence of the Leeuwin Current transporting the larvae in an eastward direction (i.e. westerly canyons are more likely to be sources) as indicated by the redundancy analysis (Fig. 9). Source capacity was negatively associated with distance from canyon to the coastline, indicating that canyons located closer to the coast are more likely to act as a

larval source location. Source capacity was also positively associated with focal variety (the number of unique larval dispersal values for each voxel within a canyon) and a large head to foot gradient, suggesting that canyon clustering (high focal variety) with steep depth changes are likely to act as providers to other canyons. The degree to which a canyon was likely to act as a sink was positively associated with factors that measure canyon shape and sink capacity such as minimum bounding rectangle width (the most significant factor, Table 2), compactness and slope range, and negatively associated with a high canyon length to width ratio. These associations suggest that wider

and larger canyons will be expected to have a higher sink capacity for larvae. Source and sink diversity were negatively associated with canyon source and sink capacity respectively, reflecting the fact that a diverse number of canyon connections will split the flow of larvae and thereby reduce the larval concentration coming from a given source or arriving at a given destination.

DISCUSSION

The Leeuwin Current is clearly a dominant influence with regards to canyon connectivity in Australia’s southwest marine region (Fig. 1). The break in connectivity at Cape Leeuwin suggests that while canyons north of the cape would be expected to contribute to canyons to the south and east, the reverse would be comparatively rare. This hypothesis could be experimentally

Table 1. Randomization-based ANOVA statistics showing the sensitivity of the connectivity matrices to seasonality and release depth. The likelihood that the observed value would have been encountered by random chance, as determined through permutation of the observed values on the basis of the variable of interest are indicated by p-values. Significant values ($p < 0.05$) are indicated in **bold**. Seasonal groups were: spring (September–November), summer (December–February), autumn (March–May) and winter (June–August). Release depth groups were 1: 0–50 m, 2: 50–120 m, 3: 120–200 m, 4: 200–700 m, 5: 700–1500 m, 6: 1500–3000 m, and 7: >3000 m. CMRs: Commonwealth Marine Reserves, KEFs: Key Ecological Features

Season	Spring	Summer	Fall	Winter			
Spring	–						
Summer	0.35	–					
Fall	0.32	0.32	–				
Winter	0.35	0.35	0.38	–			
Depth	1	2	3	4	5	6	7
1	–						
2	0.24	–					
3	0.20	0.26	–				
4	0.08	0.10	0.17	–			
5	0.07	0.10	0.16	0.15	–		
6	0.10	0.08	0.10	0.15	0.18	–	
7	0.04	0.03	0.03	0.08	0.08	0.04	–
Within/outside CMRs					Source = 0.30, Sink = 0.31		
Intersecting/not intersecting KEFs					Source = 0.27, Sink = 0.26		
Shelf-incising/non-incising					Source = 0.41, Sink = 0.41		

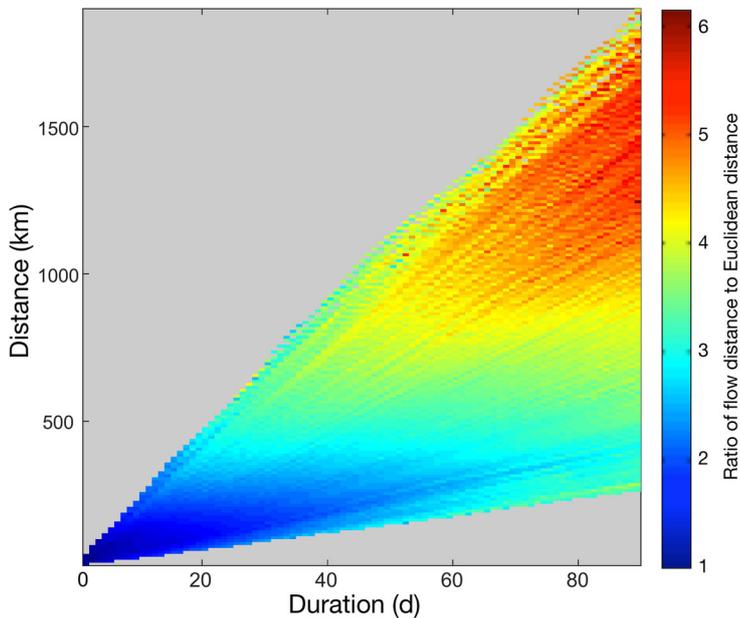


Fig. 8. Mean ratio of flow distance to Euclidean (straight line) distance relative to initial release location for simulated particles, partitioned by flow distance (km) travelled and duration (d) of larval transport

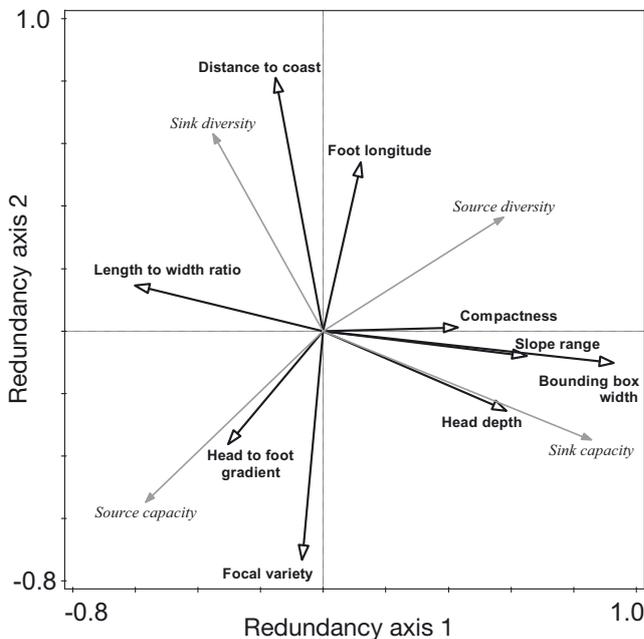


Fig. 9. Redundancy analysis showing the ordination of canyon metrics from Huang et al. (2014) (hollow black arrows and bold labels) versus the ordination of ophiuroid larval connectivity metrics (solid grey arrows and italic labels). For the redundancy analysis, ophiuroid larval counts were normalized against the number of larvae released from their point of origin. Longer arrows indicate a stronger relationship with the canonical axes. Smaller angles between arrows indicate greater correspondence between factors in the context of the ordination

Table 2. Relative contributions (%) of the different parameters towards the explained relationship between the canyon metrics from (Huang et al. 2014) and the larval connectivity metrics (this study) as determined by the redundancy analysis (Fig. 9)

Name	Explains %	Cumulative %
Bounding box width	33.2	33.2
Distance to coast	15.6	48.8
Foot longitude	6.4	55.2
Head depth	4.1	59.3
Focal variety	2.2	61.5
Slope range	1.9	63.4
Head to foot gradient	1.8	65.2
Compactness	1.2	66.4
Length to width ratio	1.0	67.4

tested using population genetics by looking for a greater number of private alleles (versions of a gene that are only found in a single population among a larger number of populations) (Neel 1973, Slatkin 1985) in southern canyon ophiuroid populations as compared with western canyon ophiuroid populations. Some counter-current transport is also expected to occur in the Great Australian Bight and along the western coast of Western Australia, indicating capacity for collective re-seeding in these regions. This expectation could also be experimentally tested by analysing metrics of population genetic subdivision such as Φ_{ST} (Excoffier et al. 1992), G'_{ST} (Hedrick 2005), Jost's D (Jost 2008), or other similar measures. These subdivision metrics show the degree of genetic exchange taking place among sampled populations which will correspond with demographic exchange. Although the strength of the Leeuwin Current has a significant seasonal cycle (Feng et al. 2003), the simulated larval transport patterns did not appear to have a strong seasonal component. This observation corresponds well with satellite image-based data which indicate that while the Leeuwin Current is known to shift both its position and shape between summer and winter, its general form does remain relatively consistent (Huang & Feng 2015). This consistency is also reflected in the connectivity variability map (Fig. 3C), which suggests a steady stream of larvae rounding Cape Leeuwin and entering the Great Australian Bight. The consistent larval flow revealed by the variability map can also be regarded as the marine analogue of corridor pathways as observed in terrestrial systems (Kool & Nichol 2015).

Differences in larval dispersal due to different release depths were significant (Table 1), with simu-

lated larvae in shallow depths being conveyed much greater distances on average. The depths at which the larvae are positioned as well as the depth of their target habitats have the potential to significantly influence larval transport patterns. This pattern is also reflected in the differences between the matrix of dispersers originating in the entire water column above canyons and the matrix of dispersers originating solely within the confines of the canyons (Fig. 5). Together, the results suggest that larvae that are positioned within canyons are likely to stay either within their natal canyon or within close proximity to it; however, small changes in vertical position due to behaviour or upwelling events, for example, have the potential to generate opportunities for long-distance larval transport.

The dispersal kernels provide information regarding some of the general characteristics of larval canyon connectivity in southwest Australia (Fig. 6). The results can be used to generate heuristic estimates of spacing between management areas, as well as the time interval expected between a perturbation or intervention and the appearance of its corresponding downstream effects. For example, here, the dispersal kernels suggest that although canyons have an average spacing of approximately 550 km, over 50% of the realized larval dispersal occurs within 10 to 20 km. This has important consequences for setting spacing requirements when managing a network of reserves. Although suitable habitat may be available, it may not necessarily be accessible. Similarly, the results also suggest that while the system of canyons in the southwest of Australia are potentially connected on average over 30 d of larval transport, functionally speaking, most larval connectivity is actually expected to occur over less than 5 d in this system. This information helps with understanding the scale of marine larval dispersal among Australia's southwest marine canyons. Downstream effects can be expected to be observed on the order of hundreds of km and 1 to 2 mo for ophiuroid-based larval dispersal from canyons in the southwest region. Note however, that these scales apply to demographic (single-generation) connectivity. Reproduction over multiple generations and chains of connections between populations will make it possible for organisms or the effects of disturbances to have consequences that reach beyond their immediate local environment (Dunstan & Bax 2007).

The results of this study also quantitatively demonstrate the difference between straight-line (Euclidean/geographic) distance measurements and current flow-based distance measurements, reaching a greater than

5-fold difference over a period of 90 d, demonstrating the need to either use flow-based distance measurements to ensure accurate representation of isolation due to current flow patterns, or to correct for this bias accordingly, for example, by factoring in additional mortality if warranted when using Euclidean distances.

The ordination results highlight how different canyon metrics correspond with the derived connectivity metrics (Fig. 7). The results indicate that the size and location of canyons do influence larval dispersal patterns. Fig. 7 suggests that the source and sink capacity of a canyon is mainly related to its location and shape (size), respectively. Canyons northwest of Perth are located at the upstream of the Leeuwin Current, which are more likely to act as sources to the canyons downstream. In addition, canyons that are closely spaced together have more opportunities to act as sources to distant canyons. On the other hand, the sink capacity of a canyon is mainly related to shape characteristics that enhance the ability for larvae to enter into and remain in them. Therefore, large, wide and deep canyons are more likely to be destinations for the simulated larvae. For example, the Leeuwin Current flows across the southwest Australian canyons so that wider canyons are longer exposed to the flow of simulated larvae. This pattern helps to explain the strong significance of the minimum bounding rectangle width as an explanatory variable.

The hydrodynamic data used by the dispersal model need to be complete and consistent across the study domain, and at continental scales, this prerequisite requires using current information that is either regional or global in nature. The state-of-the-art in hydrodynamic modelling at this scale has been approximately 7 to 8 km (e.g. 1/10° resolution BLUELink, Schiller & Smith 2006; 1/12° resolution HYCOM, Chassignet et al. 2006). Given that the mean centre line length of canyons in southwest Australia is approximately 50 km with 70% having less than that value, it is almost certain that intra-canyon dynamics will not be well-resolved by these models, although aggregating canyon results might be an option for improving the power of the data. Although higher-resolution (1/25°) models covering large extents are being developed (e.g. OzROMS, HYCOM global 1/25°), there is still a need to investigate and incorporate fine-scale benthic interactions, especially in order to accurately represent processes such as canyon-driven upwelling. The collection of consistent, continuous, and high-resolution bathymetric data will be required to enable the development of

fine-scale oceanographic models. Having this information will also make it possible to study fine-scale processes, such as intra-canyon capture and retention of larvae, and will help with simulating and testing fine-scale benthic interactions.

The results were generated using brittlestar larval life history characteristics, but other organisms are likely to have very different life history traits and behaviour, potentially leading to different connectivity outcomes. While the model can accommodate a range of individual characteristics and behaviours or even distributions of characteristics (Kool & Nichol 2015), it is impossible to generate comprehensive results that will be applicable to all species. Some post-processing can be carried out with the results (e.g. increasing mortality, decreasing pelagic larval duration, weighting number of individuals released); however, changes that would result in a potential change in trajectory would involve re-running the model which would require corresponding computing resources. Thus it is important to identify key species of management interest in advance, as well as necessary to collect individual-level life history trait data, which will require developing and maintaining active monitoring and observation programs. Programs of this nature will also facilitate the collection of demographic information, which will help in developing a better understanding of the dynamic factors influencing larval survival.

With limited resources to effectively set aside for management and conservation, it is essential to have a strong understanding of which components would contribute most effectively to the overall condition and resilience of the marine reserve network as a whole. Developing an understanding of the manner and degree to which canyons act as sources and sinks will make it possible to identify which areas provide a net positive contribution to the system, and thereby are able to provide a rescue effect (Gotelli 1991) when needed, enhancing the overall resilience of the network (Cowen et al. 2007, Cowen & Sponaugle 2009). Understanding connectivity patterns will also help in predicting and preventing the potential spread of invasive species through identifying critical spread locations and vulnerable destinations (Dunstan & Bax 2008). Allocation of transboundary resources is another potential area of application, which in this case pertains to the 6 marine regions within Commonwealth waters around mainland Australia. The importance of upstream management has been recognized when managing river environments (Hellegers 2005), but the same considerations also hold true in the marine environment in that there can

be a spatial separation between the care of ecosystems (and the associated costs) and the benefits that they provide. Although there may be a significant local cost associated with a management activity, the overall net benefit may justify taking collective action. For example, in this study, canyons located offshore of Western Australia upstream of the Leeuwin Current have the potential to contribute over time to canyons offshore of South Australia, and consequently improved management of the Western Australian canyons may generate benefits for South Australia in terms of improvements to larval supply which in turn would have the potential to generate benefits for fisheries in terms of improved potential for recruitment of juveniles. Determining the degree to which improved management of upstream canyons will affect downstream canyons will also require a clear understanding of the demographic and environmental conditions in these areas and the particular life-history characteristics and behaviour for individual species of interest; however, recognizing that the potential for these kinds of transboundary exchanges exists is a key first step in enhancing management effectiveness.

CONCLUSIONS

This study provides the first assessment of connectivity among submarine canyons, focusing on the southwest Australian marine planning region. The Leeuwin Current is clearly a dominant factor in this area, although there does appear to be some opportunity for counter-current exchange. Canyons demonstrate the capacity to retain larvae, although if they are able to leave the confines of the canyon, they can potentially be transported significant distances (thousands of km). Improving our knowledge of canyon connectivity will help to make better-informed conservation planning decisions, and also demonstrates the importance of taking into account subsurface information and having good submarine topographic information.

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LITERATURE CITED

- Allen SE, Vindeirinho C, Thomson RE, Foreman MGG, Mackas DL (2001) Physical and biological processes over a submarine canyon during an upwelling event. *Can J Fish Aquat Sci* 58:671–684
- Banse K (1986) Vertical distribution and horizontal transport of planktonic larvae of echinoderms and benthic polychaetes in an open coastal sea. *Bull Mar Sci* 39:162–175
- Blaber SJM, Bulman CM (1987) Diets of fishes of the upper continental slope of eastern Tasmania: content, calorific values, dietary overlap and trophic relationships. *Mar Biol* 95:345–356
- Bureau of Rural Sciences (2005) Socio-economic impact assessment toolkit: a guide to assessing the socio-economic impacts of Marine Protected Areas in Australia. Bureau of Rural Sciences, Canberra
- Chassignet EP, Hurlburt HE, Smedstad OM, Halliwell GR, Hogan PJ, Wallcraft AJ, Bleck R (2006) Ocean prediction with the Hybrid Coordinate Ocean Model (HYCOM). In: Chassignet EP, Verron J (eds) *Ocean weather forecasting: an integrated view of oceanography*. Springer, Dordrecht, p 413–426
- Commonwealth of Australia (2005) National marine bioregionalisation of Australia. Summary. Australian Government, Canberra
- Commonwealth of Australia (2012) Marine bioregional plan for the south-west marine region. Department of Sustainability, Environment, Water, Population and Communities, Australian Government, Canberra
- Condie SA, Mansbridge JV, Cahill ML (2011) Contrasting local retention and cross-shore transports of the East Australian Current and the Leeuwin Current and their relative influences on the life histories of small pelagic fishes. *Deep-Sea Res II* 58:606–615
- Cowen RK, Sponaugle S (2009) Larval dispersal and marine population connectivity. *Annu Rev Mar Sci* 1:443–466
- Cowen RK, Gawarkiewicz G, Pineda J, Thorrold SR, Werner FE (2007) Population connectivity in marine systems: an overview. *Oceanography* 20:14–21
- Dambacher JM, Hayes KR, Hosack GR, Lyne V and others (2012) Project summary: national marine ecological indicators. Department of Sustainability, Environment, Water, Population and Communities, Australian Government, Hobart
- DeMartini EE, Wren JLK, Kobayashi DR (2013) Persistent spatial patterns of recruitment in a guild of Hawaiian coral reef fishes. *Mar Ecol Prog Ser* 485:165–179
- Domingues CM, Maltrud ME, Wijffels SE, Church JA, Tomczak M (2007) Simulated Lagrangian pathways between the Leeuwin Current System and the upper-ocean circulation of the southeast Indian Ocean. *Deep-Sea Res II* 54: 797–817
- Dunstan PK, Bax NJ (2007) How far can marine species go? Influence of population biology and larval movement on future range limits. *Mar Ecol Prog Ser* 344:15–28
- Dunstan PK, Bax NJ (2008) Management of an invasive marine species: defining and testing the effectiveness of

- ballast-water management options using management strategy evaluation. *ICES J Mar Sci* 65:841–850
- Eble JA, Rocha LA, Craig MT, Bowen BW (2010) Not all larvae stay close to home: insights into marine population connectivity with a focus on the brown surgeonfish (*Acanthurus nigrofuscus*). *J Mar Biol* 2011:518516
- Excoffier L, Smouse PE, Quattro JM (1992) Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. *Genetics* 131:479–491
- Feng M, Meyers G, Pearce A, Wijffels S (2003) Annual and interannual variations of the Leeuwin Current at 32° S. *J Geophys Res* 108:C11 3355, doi:10.1029/2002JC001763
- Feng M, Caputi N, Penn J, Slawinski D and others (2011) Ocean circulation, Stokes drift, and connectivity of western rock lobster (*Panulirus cygnus*) population. *Can J Fish Aquat Sci* 68:1182–1196
- Gardner S, Tonts M, Elrick C (2006) A socio-economic analysis and description of the marine industries of Australia's south-west marine region. Department of the Environment and Water Resources. Australian Government, Canberra
- Gotelli NJ (1991) Metapopulation models: the rescue effect, the propagule rain, and the core-satellite hypothesis. *Am Nat* 138:768–776
- Hedrick PW (2005) A standardized genetic differentiation measure. *Evolution* 59:1633–1638
- Hellegers PJGJ (2006) The role of economics in integrated river basin management. *Irrig Drain* 55:157–163
- Huang Z, Feng M (2015) Remotely sensed spatial and temporal variability of the Leeuwin Current using MODIS data. *Remote Sens Environ* 166:214–232
- Huang Z, Nichol SL, Harris PT, Caley MJ (2014) Classification of submarine canyons of the Australian continental margin. *Mar Geol* 357:362–383
- Iverson KE (1962) A programming language. John Wiley & Sons, New York, NY
- Jost L (2007) Partitioning diversity into independent alpha and beta components. *Ecology* 88:2427–2439
- Jost L (2008) G_{ST} and its relatives do not measure differentiation. *Mol Ecol* 17:4015–4026
- Kämpf J, Doubell M, Griffin D, Matthews RL, Ward TM (2004) Evidence of a large seasonal coastal upwelling system along the southern shelf of Australia. *Geophys Res Lett* 31:L09310, doi:10.1029/2003GL019221
- Kool JT, Nichol SL (2015) Four-dimensional connectivity modelling with application to Australia's north and northwest marine environments. *Environ Model Softw* 65:67–78
- Kool JT, Paris CB, Barber PH, Cowen RK (2011) Connectivity and the development of population genetic structure in Indo-West Pacific coral reef communities. *Glob Ecol Biogeogr* 20:695–706
- Kool JT, Moilanen A, Treml EA (2013) Population connectivity: recent advances and new perspectives. *Landsc Ecol* 28:165–185
- Lefebvre A, Ellien C, Davoult D, Thiébaud E, Salomon JC (2003) Pelagic dispersal of the brittle-star *Ophiothrix fragilis* larvae in a megatidal area (English Channel, France) examined using an advection/diffusion model. *Estuar Coast Shelf Sci* 57:421–433
- Manly BFJ (1997) Randomization, bootstrap, and Monte Carlo methods in biology. CRC Press, Boca Raton, FL
- Maxwell J, Cresswell G (1981) Dispersal of tropical marine fauna to the Great Australian Bight by the Leeuwin Current. *Mar Freshw Res* 32:493–500
- McClain CR, Barry JP (2010) Habitat heterogeneity, disturbance, and productivity work in concert to regulate biodiversity in deep submarine canyons. *Ecology* 91: 964–976
- McClatchie S, Middleton JF, Pattiaratchi C, Currie D, Kendrick G (2006a) The south-west marine region: ecosystems and key species groups. Department of the Environment and Water Resources, Australian Government, Hobart
- McClatchie S, Middleton JF, Ward TM (2006b) Water mass analysis and alongshore variation in upwelling intensity in the eastern Great Australian Bight. *J Geophys Res* 111:C08007, doi:10.1029/2004JC002699
- Mercier A, Sewell MA, Hamel JF (2013) Pelagic propagule duration and developmental mode: reassessment of a fading link. *Glob Ecol Biogeogr* 22:517–530
- Neel JV (1973) 'Private' genetic variants and the frequency of mutation among South American Indians. *Proc Natl Acad Sci USA* 70:3311–3315
- Patterson TA, Evans K, Carter TI, Gunn JS (2008) Movement and behaviour of large southern bluefin tuna (*Thunnus maccoyii*) in the Australian region determined using pop-up satellite archival tags. *Fish Oceanogr* 17:352–367
- Pattiaratchi C (2006) Surface and sub-surface circulation and water masses off Western Australia. *Bull Aust Meteorol Oceanogr Soc* 19:95–104
- Pattiaratchi C (2007) Understanding areas of high productivity within the south-west marine region. Department of the Environment, Water, Heritage and the Arts. Australian Government, Canberra
- Pineda J, Hare JA, Sponaugle S (2007) Larval transport and dispersal in the coastal ocean and consequences for population connectivity. *Oceanography* 20:22–39
- Ponder W, Hutchings P, Chapman R (2002) Overview of the conservation of Australian marine invertebrates. Environment Australia, Australian Museum, Sydney
- PostgreSQL Global Development Group (2014) PostgreSQL version 9.2.10. www.postgresql.org
- Rennie S, Hanson CE, McCauley RD, Pattiaratchi C and others (2009a) Physical properties and processes in the Perth Canyon, Western Australia: links to water column production and seasonal pygmy blue whale abundance. *J Mar Syst* 77:21–44
- Rennie SJ, Pattiaratchi CB, McCauley RD (2009b) Numerical simulation of the circulation within the Perth Submarine Canyon, Western Australia. *Cont Shelf Res* 29: 2020–2036
- Ridgway KR, Condie SA (2004) The 5500-km-long boundary flow off western and southern Australia. *J Geophys Res* 109:C04017, doi:10.1029/2003JC001921
- Rumrill SS (1990) Natural mortality of marine invertebrate larvae. *Ophelia* 32:163–198
- Schiller A, Smith N (2006) BlueLink: large-to-coastal scale operational oceanography in the southern hemisphere. In: Chassignet EP, Verron J (eds) Ocean weatherforecasting: an integrated view of oceanography. Springer, Dordrecht, p 427–439
- Schlacher TA, Schlacher-Hoenlinger MA, Williams A, Althaus F, Hooper JNA, Kloser R (2007) Richness and distribution of sponge megabenthos in continental margin canyons off southeastern Australia. *Mar Ecol Prog Ser* 340:73–88
- Slatkin M (1985) Rare alleles as indicators of gene flow. *Evolution* 39:53–65

- Šmilauer P, Lepš J (2014) Multivariate analysis of ecological data using CANOCO 5, 2nd edn (revised). Cambridge University Press, Cambridge
- Smith RL, Huyer A, Godfrey JS, Church JA (1991) The Leeuwin current off western Australia, 1986–1987. *J Phys Oceanogr* 21:323–345
- Trembl EA, Halpin PN (2012) Marine population connectivity identifies ecological neighbors for conservation planning in the Coral Triangle. *Conserv Lett* 5:441–449
- Waite AM, Thompson PA, Pesant S, Feng M and others (2007) The Leeuwin Current and its eddies: an introductory overview. *Deep-Sea Res II* 54:789–796
- Whiteway TG (2009) Australian Bathymetry and Topography Grid. Geoscience Australia, Canberra
- Yoklavich MM, Greene H, Cailliet G, Sullivan D, Lea R, Love M (2000) Habitat associations of deep-water rockfishes in a submarine canyon: an example of a natural refuge. *Fish Bull* 98:625–641

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