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Title:

Connectivity networks and delineation of disconnected coastal provinces along the Indian coastline using large-scale Lagrangian transport simulations

Running Title:

Lagrangian simulations of connectivity along the Indian coastline

Authors:

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Abstract

Ocean circulation is the engine of dispersal and population connectivity in marine ecosystems, knowledge of which is essential for conservation planning. Understanding connectivity patterns at a large scale can help define the spatial extent of metapopulations. In this study, we built connectivity networks from Lagrangian transport simulations of neutrally buoyant particles, released along the Indian coastline, a significant region in the Indian Ocean. We assessed the variation in connectivity networks across release periods for the major drivers of oceanography including the two monsoonal seasons, El Niño–Southern Oscillation (ENSO) years and for the entire range of region-specific pelagic larval durations (PLD) for marine invertebrates. We detected well-connected communities, mapped frequent connectivity breaks and assessed the functional role of coastal areas within the connectivity network using node metrics. Network characteristics did not differ based on the ENSO year, but varied with season and PLD. Connectance for the Indian coastline was relatively low, ranging from 0.5% to 3.4%, and increased significantly for PLD larger than 20 days. The number of cohesive coastal communities decreased gradually from 60 (PLD <4 days) to 30 (PLD >20 days) with increasing PLD. Despite variation in the location of connectivity breaks with the time of particle release within a monsoonal season, four disconnected provinces were consistently identified across the entire PLD range, which partially overlapped with observed genetic and biogeographic breaks reported along the Indian coastline. Our results support the adoption of coordinated management framework within each of the four provinces delineated in the present study.

Keywords: biophysical model, dispersal, connectivity, Indian Ocean, marine biogeography

Introduction

Marine populations have traditionally been described as ‘open’, with high exchange of propagules between spatially distant populations owing to oceanic transport of pelagic life stages (Roughgarden et al., 1988). However, it is the interaction between oceanographic features, habitat distribution and species-specific traits that determines if a population falls in the continuum from ‘open’ to ‘closed’, within a meta-population framework (Levin, 2006). Biophysical modelling, which combines ocean circulation simulations with larval traits and habitat information, is a useful tool to explore patterns of larval transport in the ocean (Swearer et al., 2019). Ocean flow and pelagic larval duration (PLD) are the minimum parameters required to assess seascape connectivity (North et al., 2009), though biological parameters related to larval behaviour can strongly influence dispersal patterns (Robins et al., 2013).

Biophysical simulations of larval transport based on coarse-resolution global ocean circulation simulations can serve as a foundation for regional ecological studies by delineating large-scale disruptions in connectivity (Jacobi et al. 2012; Rossi et al., 2014). Identifying the extent of well-connected regions, within which spatially distinct populations exchange individuals to give rise to a metapopulation (Hanski & Gagiotti, 2004), is essential for coordinating biodiversity management (Halpern & Warner, 2003; Mertens et al. 2018). This is especially important for tropical continental coastlines, which have received less attention in marine ecology studies (Partelow et al., 2018). Since management policies are a national prerogative, it is also important to include all the regions falling within the boundaries of marine resource governance. Identifying the extent and strength of connectivity

spanning regional and national boundaries can help in focusing conservation efforts leading to more effective management (Treml & Halpin, 2012).

The Exclusive Economic Zone (EEZ) of India includes (1) a coastline of over 5400 km that divides the northern Indian Ocean into two basins – the Arabian Sea in the west and the Bay of Bengal in the east, (2) the Lakshadweep archipelago located in the Arabian Sea, and (3) the Andaman and Nicobar archipelago located in the Bay of Bengal. Sri Lanka is an island located in the Bay of Bengal, which is separated from India by the narrow Palk Strait, where both countries have contiguous EEZs (Figure 1). There is an absence of large-scale connectivity studies from the northern Indian Ocean (see George et al., 2011 and Gaonkar et al., 2012 for local-scale studies) despite a large body of physical oceanography research from this region (reviewed in Schott et al., 2009).

The upper ocean circulation along the coasts of India is driven by seasonally reversing monsoon winds (Schott & McCreary, 2001). During the summer (south-west) monsoon from June to September, the West India Coastal Current (WICC) flows towards the equator along the west coast of India (Shetye & Gouveia, 1998, Amol et al., 2014) and merges with the South-West Monsoon Current (SMC). It turns around the southern tip of India bringing saltier water into the Bay of Bengal, and joins the northern branch of the Sri Lanka Dome (Vinayachandran & Yamagata, 1998) flowing poleward as the East India Coastal Current (EICC) (Mukherjee et al., 2014) (Figure 1). During this period, coastal upwelling events of varying intensity occur along the west coast of India (Luis & Kawamura, 2004; Hood et al., 2017), with weak upwelling along the eastern coast of India, and the Andaman and Nicobar islands (Varkey et al. 1996; Vinayachandran et al., 2021).

During the winter (north-east) monsoon from November to February, the circulation along the east coast of India reverses direction to flow equatorward (EICC) (Shetye & Gouveia, 1998, Mukherjee et al., 2014), turns around the southern tip of India (Winter Monsoon Current) and flows poleward along the west coast (WICC), bringing fresher water into the Arabian Sea (Figure 1, Shetye & Gouveia, 1998; Amol et al., 2014). Together with alongshore flow reversal, upwelling reverses into downwelling events within a 40 km wide band along the east coast of India (Varkey et al. 1996) and along the north-west coast of India (Luis & Kawamura, 2004).

The seasonal wind-driven circulation described above is modulated at several time-scales (Schott et al. 2009) ranging from intra-seasonal to inter-annual variation. Intra-seasonal atmospheric oscillations act at time-scales ranging from a week (northward propagating precipitation anomalies) to 30-60 days (Madden-Julian Oscillation, Madden & Julian 1972). Inter-seasonal variation in circulation arises from both El Niño Southern Oscillation, leading to a year-long basin-scale warming after El Niño events, and Indian Ocean Dipole events, with cool (warm) and dry (wet) anomalies in the eastern (western) Indian Ocean (Vinayachandran et al. 2009). In such a complex oceanographic context with large to meso-scale structures, it is difficult to a priori anticipate how biological filters such as the time of larval release and PLD might shape connectivity along the vast Indian coastline.

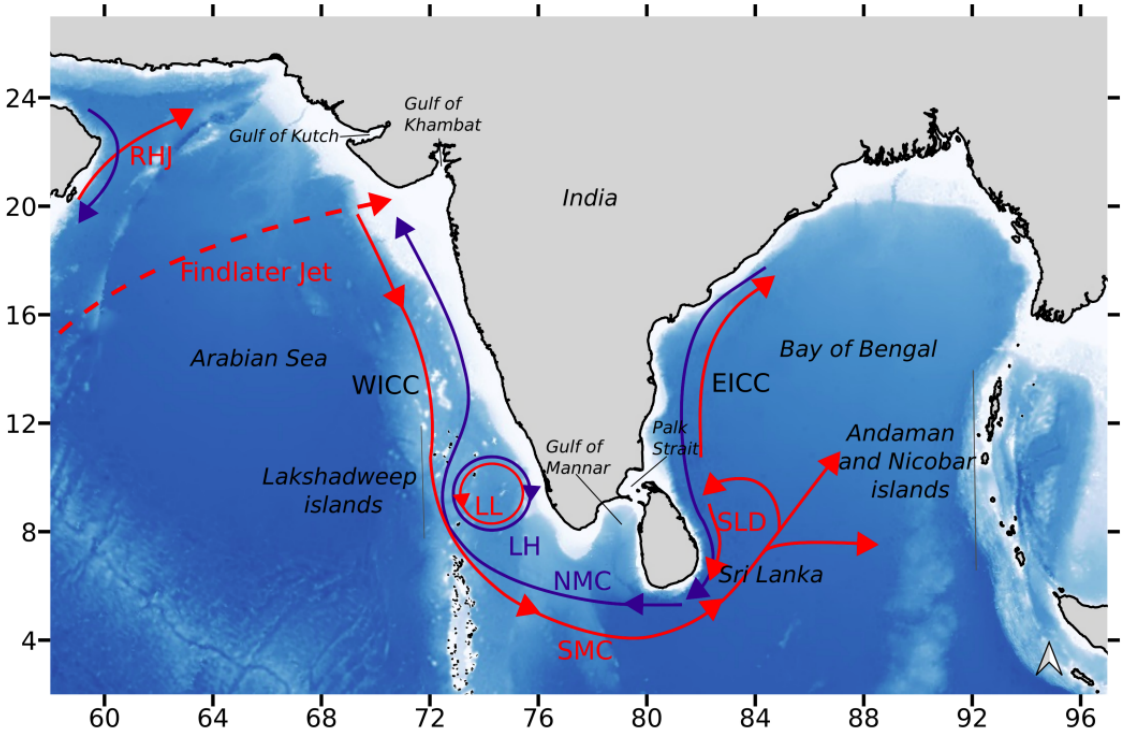


Figure 1. Schematic illustration of major currents along the Indian coastline. From west to east – Ras al Hadd Jet (RHJ), West India Coastal Current (WICC), Lakshadweep Low (LL), Lakshadweep High (LH), South-West Monsoon Current (SMC), North-East Monsoon Current (NMC), SLD (Sri Lanka Dome) and East India Coastal Current (EICC). Findlater Jet is an atmospheric jet observed in the northern Arabian Sea during the summer monsoon. Processes associated with the summer monsoon are in red and those associated with the winter monsoon are in blue. WICC and EICC occur in both monsoons but differ in direction as indicated by the coloured arrows.

In the current study, we aim to describe patterns of oceanographic connectivity along the Indian coastline. To do so, we carried out Lagrangian transport simulations of neutrally buoyant particles released along the coastline during the two major seasons – summer and winter monsoon, for three years and across a wide range of PLD. Transport simulations were post-processed to build coastal connectivity networks for different combinations of season, year and PLD. The specific aims of our study were to (1) identify breaks in oceanographic connectivity and analyze their stability across years, seasons and PLD, and (2) examine the implications of these connectivity breaks for biodiversity management.

Materials

Ocean circulation data

We used HYCOM (Chassignet et al., 2007) global ocean circulation reanalysis data (https://www.hycom.org/dataserver/gofs-3pt0/reanalysis) for running particle tracking simulations. HYCOM reproduces the main circulation features around the Indian peninsula (Supplementary Information 1), and simulations at various resolutions have validated its application in operational oceanography (George et al. 2010, Joseph et al. 2018). We acquired HYCOM output at 0.08° horizontal spatial resolution, 40 z-levels in depth and 3-hour temporal frequency for the spatial extent ~30°N-10°S, 50°W-100°E and the years 2008-2011. This temporal range captures the variation in ocean circulation presented by various states of the El Niño–Southern Oscillation (ENSO), as 2009-2010 represents an El Niño year, while 2011 was a La Niña year (https://psl.noaa.gov/enso/past_events.html). Particle transport in the vertical, which is particularly important in coastal areas with upwelling or downwelling,

was accounted for after reconstructing vertical velocity values (not available in the HYCOM repository) using the continuity equation of mass conservation. This was done for the upper 27 depth levels from surface, i.e. down to 400 m deep, to avoid anomalies that can arise in reconstruction at further depths.

Particle tracking procedure

We ran three-dimensional neutrally buoyant particle tracking simulations with the Connectivity Modeling System (Paris et al., 2013). Particles were released along the Indian subcontinent, Sri Lanka, Lakshadweep islands and the Andaman and Nicobar islands. Release locations were placed at a distance of 12 km from the coastline to avoid unresolved flow velocities at the coast and to ensure at least 3 vertical levels of ocean flow input (bathymetry ranging from 4 m to 2500 m, Supplementary Information 2). Particles were released 1 m below the surface, every 5 km along the coastline (2136 release locations) during the summer (June to September) and the winter (November to February) monsoons, in release periods spanning ten days each. Successive particle positions were calculated using a time-step of 20 minutes and recorded every three hours, for over six million particles in each season. Particles were tracked for a period of 50 days, informed by the distribution of PLD for marine invertebrates found in this region (Supplementary Information 3).

In the present study, we chose to scan a wide range of species by varying dispersal duration and release timing to model large-scale connectivity that is generalizable across taxa. Our use of neutrally buoyant particles assumes limited larval behaviour and does not capture the

174 effect of species-specific variation in larval motility (e.g. nychtemeral vertical migration),
175 which can influence connectivity estimates between species.
176
177 *Connectivity networks*
178
179 The coastal area was divided into 528 coastal polygons, ~200 km^2 in area, overlaid over
180 particle release locations (Supplementary Information 4). Connectivity matrices of particle
181 transfer (278,784 possible connections) were built by calculating the proportion of particles
182 released in a source coastal polygon that successfully dispersed to a destination coastal
183 polygon. Particle transfer per unit surface was obtained by scaling particle transfer values
184 with the the area of the destination polygon. This was done to correct for the differences in
185 area between destination polygons, which can influence the probability of a particle reaching
186 it (Fig 2). Instead of using a representative subset of PLDs, and to make our results
187 generalizable across all possible dispersal durations, we analyzed connectivity matrices
188 across PLDs ranging between 2 to 50 days, with an interval of 2 days. Based on the
189 frequency distribution of PLDs for marine invertebrates collated for the Indian Ocean
190 (Supplementary Information 3), connectivity matrices were averaged into four PLD-classes
191 for each release period – 2-4 days, 6-12 days, 14-20 days and 22-50 days (4 PLD-classes × 2
192 seasons × 12 release periods × 3 years = 288 connectivity matrices).
193
194 Each connectivity matrix defined a directed weighted graph (called connectivity network
195 hereafter), where nodes were coastal polygons and directed weighted edges between each
196 pair of source and destination nodes were values of particle transfer per unit surface between
197 them (Figure 2). Various metrics were used to describe the connectivity network.

Connectance is a global property of a network, which measures the overall network density (number of realized connections in comparison with all possible connections), and is calculated as the proportion of non-zero edges within a network. The number of singleton nodes is the count of isolated nodes (with no connection), which indicates the extent of the network. To further understand the structure of the network density indicated by connectance, we identified and counted two kinds of network components. A weak subgraph consists of nodes that are connected to each other irrespective of direction and indicates weak connectivity between nodes. On the other hand, a strong subgraph is more well-connected network component where each pair of nodes is connected in both directions, and reflects strong bidirectional connectivity.

Particle release locations and coastal polygons were created using the packages *'raster'* (Hijmans, 2020), *'rgeos'* (Bivand & Rundel, 2020), *'sp'* (Pebesma & Bivand, 2005; Bivand et al., 2013) in R version 3.6.1 (R Core Team, 2019), and further edited in QGIS 3.14.0-Pi (QGIS.org, 2021).

Community detection

Each connectivity network was individually processed to detect communities using the Infomap algorithm (Rosvall & Bergstrom, 2008) (Figure 2) by applying the *'cluster_infomap'* function in the *'igraph'* package (Csardi & Nepusz, 2006) in R version 3.6.1 (R Core Team, 2019). This algorithm uses information-theoretic principles to define a community based on the ease of flow between nodes of a directed weighted network. A community is detected when a random walker visits a set of nodes within the network more

often than nodes outside it and is likely to get trapped between them (Rosvall & Bergstrom, 2008).

The significance of a detected community was estimated using its coherence ratio – the proportion of particles that originate from nodes within a community and remain within the same community (Rossi et al., 2014). A coherence ratio greater than 0.5 was applied to detect well connected communities, and the location of community boundaries (referred to as community breaks henceforth) was identified. Community breaks were classified based on their frequency of occurrence across release periods within a PLD-class. Those occuring with a frequency greater than 50% were termed ‘frequent’ and those with a frequency greater than 90% were termed ‘persistent’. Persistent community breaks were used to identify connectivity provinces along the Indian coastline. Connectivity between island groups and connectivity provinces was evaluated by analyzing their co-occurrence in detected communities using the Bray-Curtis similarity measure, while accounting for variation in the number of coastal polygons between regions (Baselga, 2017) using the *‘betapart’* package (Baselga & Orme, 2012) in R version 3.6.1 (R Core Team, 2019).

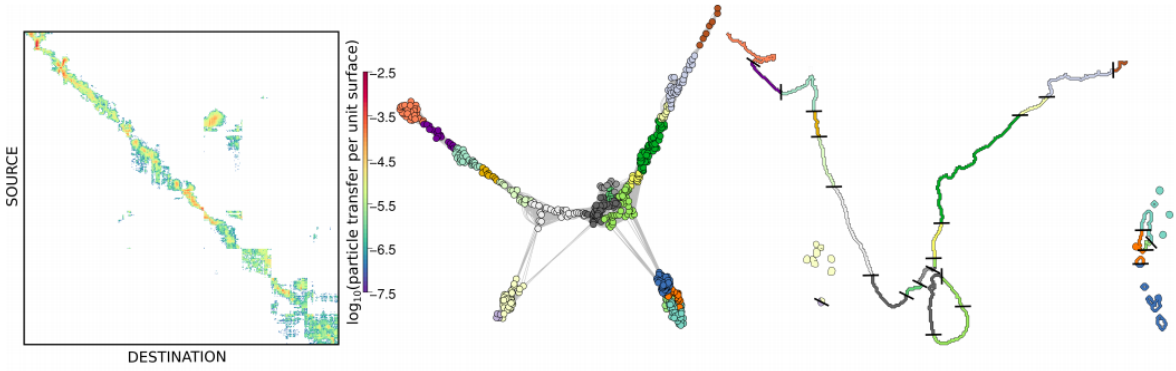


Figure 2. Schematic figure depicting the various stages in connectivity analysis, which include (left) connectivity matrix obtained from particle trajectories, (center) connectvity network with nodes coloured based on Infomap communities and (right) connectivity breaks derived from Infomap community boundaries. The figures shown here are derived from a mean connectivity matrix across release periods and years for the PLD-class 14-20 days during the summer monsoon.

Statistical tests

The significance of the variation in the distributions of connectance, the number of singleton nodes, weak and strong subgraphs and Infomap communities with >1 membership, with PLD-class, year and season was evaluated using non-parametric Kolmogorov-Smirnov test in R version 3.6.1 (R Core Team, 2019).

Nodes descriptors

Apart from network-level metrics, we also calculated node-level metrics of connectivity to understand the variation in the number of connections (degree) and flux intensity of connections (strength) to or from a node (coastal polygon). The total node degree and strength can be used to compare the contribution of different nodes to the overall connectivity in a network. Proportion in-degree is the relative magnitude of incoming connections with respect to total connections at a node, and indicates its influence in comparison to other nodes in the network. High in-degree indicates a node under the influence of other nodes, while low in-degree indicates that the node influences other nodes in the network. Proportion of in-strength indicates the relative magnitude of import with respect to total traffic through a node, and can be associated with its role as a source or a sink location. These measures were calculated using functions implemented in R version 3.6.1 (R Core Team, 2019).

Results

There was no significant variation in most connectivity network characteristics between years, while their variation between release periods within a year was large (Supplementary Information 5). Based on these results, variability of all the network metrics was estimated after pooling 36 connectivity matrices across 12 release periods for each PLD-class and season across three years.

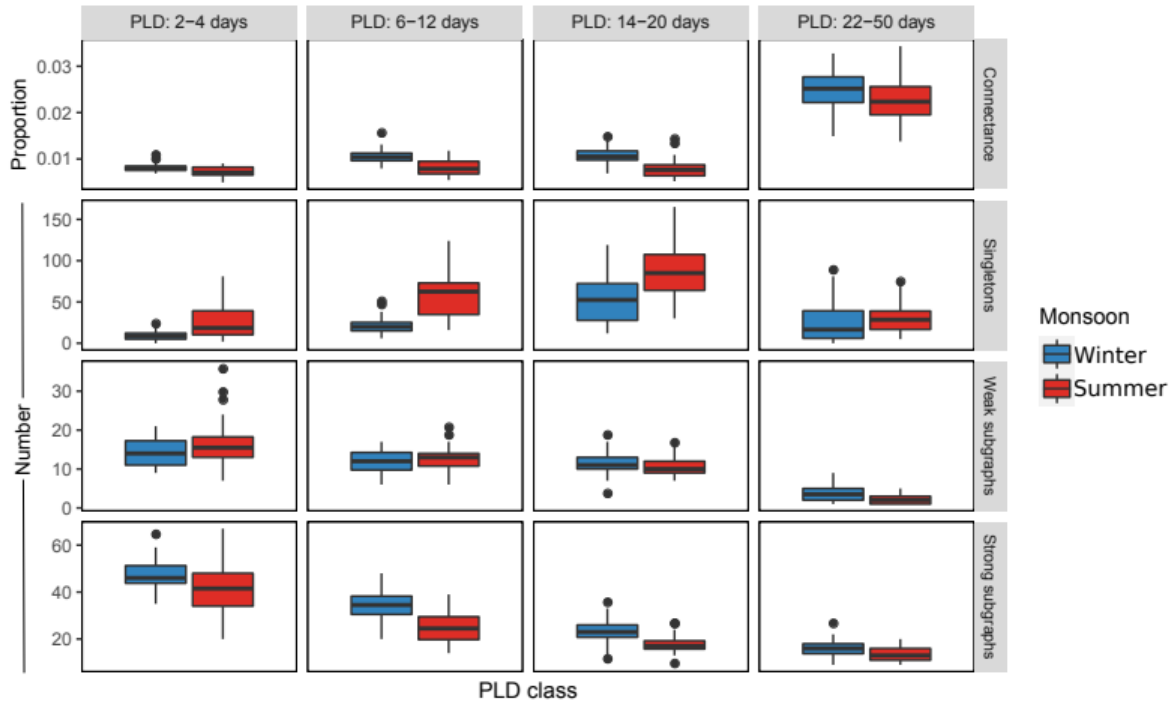
Network descriptors

Connectance ranged from 0.5% to 3.4% across PLD-class and season, and showed the greatest significant difference between PLD less than 20 days and PLD greater than 20 days in both seasons (Figure 3). A significant increase in connectance indicates that a PLD of 20 days is pivotal to ensure siginificant transport farther than 2-5 km (range of shortest distance between a release location and adjacent coastal polygon) along the coastline.

There were less than 30% disconnected singleton nodes across PLD-classes and seasons (Figure 3). The number of singleton nodes increased till a PLD of 20 days (Supplementary Material 5), indicating that local connections with neighbouring coastal polygons seen at shorter PLDs disappeared as particles dispersed away from the coast at intermediate PLDs.

The number of weak subgraphs largely remained unchanged for PLD less than 20 days (4-36), while the number of strong subgraphs significantly decreased between the PLD less than 6 days (20-67) and the PLD greater than 20 days (9-27) (Supplementary Material 5). This indicates that there was an increase in the number of bi-directional connections within subgraphs with increasing PLD. This densification of subgraphs, for PLD up to 20 days, was

more pronounced in the summer monsoon as compared to the winter monsoon (Supplementary Information 5).



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295 **Figure 3.** Summary characteristics of connectivity networks.

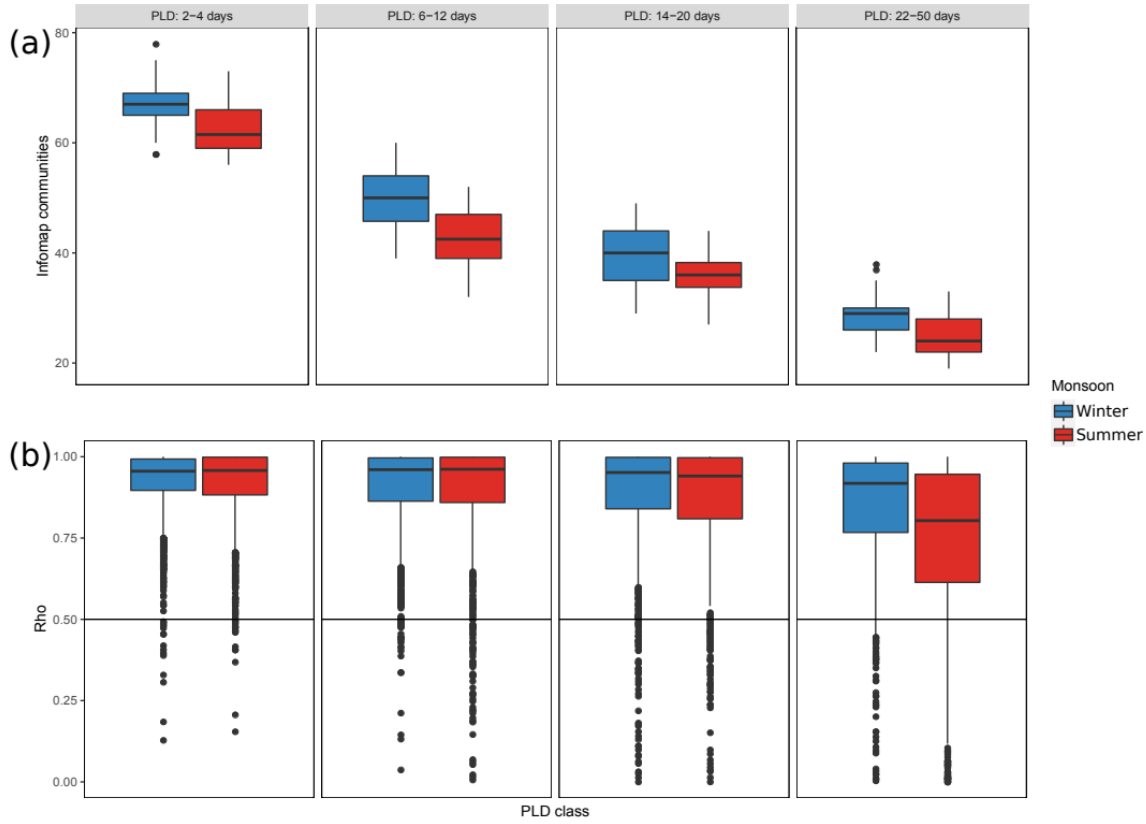
Infomap communities

Similar to the trend observed with strong subgraphs, the number of Infomap communities (communities hereafter) decreased with an increase in PLD (Figure 4a). Except for the PLD-class 6-12 days, the number of communities detected for the same PLD-class was not significantly different between seasons (Supplementary Material 5). The coherence ratio of the detected communities showed little variation for PLD classes less than 20 days, but showed the greatest variability for PLD larger than 20 days and during the summer monsoon (Supplementary Material 5) (Figure 4b). The decrease in coherence ratio indicates a decrease in the exchange of particles within a community through losses outside it.

The location of community breaks varied with PLD, season and release period (indicated by the variation in the consistency of breaks within a PLD-class). However, a few locations frequently appeared as community breaks across release periods (>50% frequency), with some occuring persistently with a frequency greater than 90% (Figure 5). These community breaks were found along the north-west coast of mainland India (south of the Gulf of Khambhat 21°N, and Gulf of Kutch), Palk Strait (a narrow channel separating the Indian landmass from Sri Lanka) and north-east India, across both seasons (Figure 5). In the summer monsoon, a persistent community break appeared at the southern tip of India for all PLDs. Additional breaks also appeared along the west and east coast of India for PLD less than 20 days, but were not consistent across season and PLD.

Based on PLD and season, the island groups varied in their connectivity with the coastal provinces along mainland India defined by the community breaks described above. In

general, median community similarity was greater at the larger PLD-class and during the summer monsoon. While Sri Lanka was well connected with most regions except the north-west coast, the Lakshadweep islands and the Nicobar islands were limited in their connectivity to the linear west coast and the Andaman islands respectively (Supplementary Information 6).



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326 **Figure 4.** (a) Number of Infomap communities and (b) their coherence ratio.

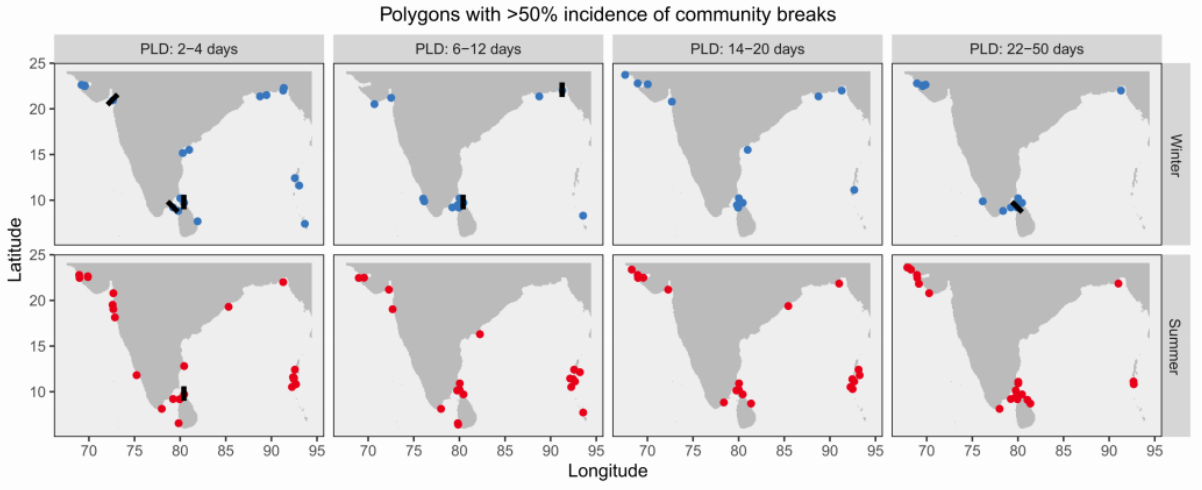


Figure 5. Distribution of Infomap community breaks. Blue and red circles indicate breaks with frequency >50% across release periods for the winter and summer monsoon respectively. Black bars indicate breaks with frequency >90% across release periods.

Node descriptors

As observed with connectance and the number of Infomap communities, node degree increased with PLD as a longer transport duration promoted variability in transport (Figure 6). The increase in node degree was not uniform in the study region, and was observed to be higher in the east coast of India and the Lakshadweep islands during the winter monsoon, southern tip of India during the summer monsoon, and Sri Lanka and the Andaman and Nicobar islands during both the seasons (Figure 6). A consequence of transport over longer durations was the loss of particles from the coastal zone as observed from a decrease in the node strength in both seasons (Figure 6). However, in the winter monsoon, node strength showed lesser spatial variability and decreased more gradually with longer PLD as compared to the summer monsoon (Figure 6). The proportion of total node degree and strength contributed by incoming edges did not show stark large-scale spatial patterns, which may be associated with prominent source or sink populations.

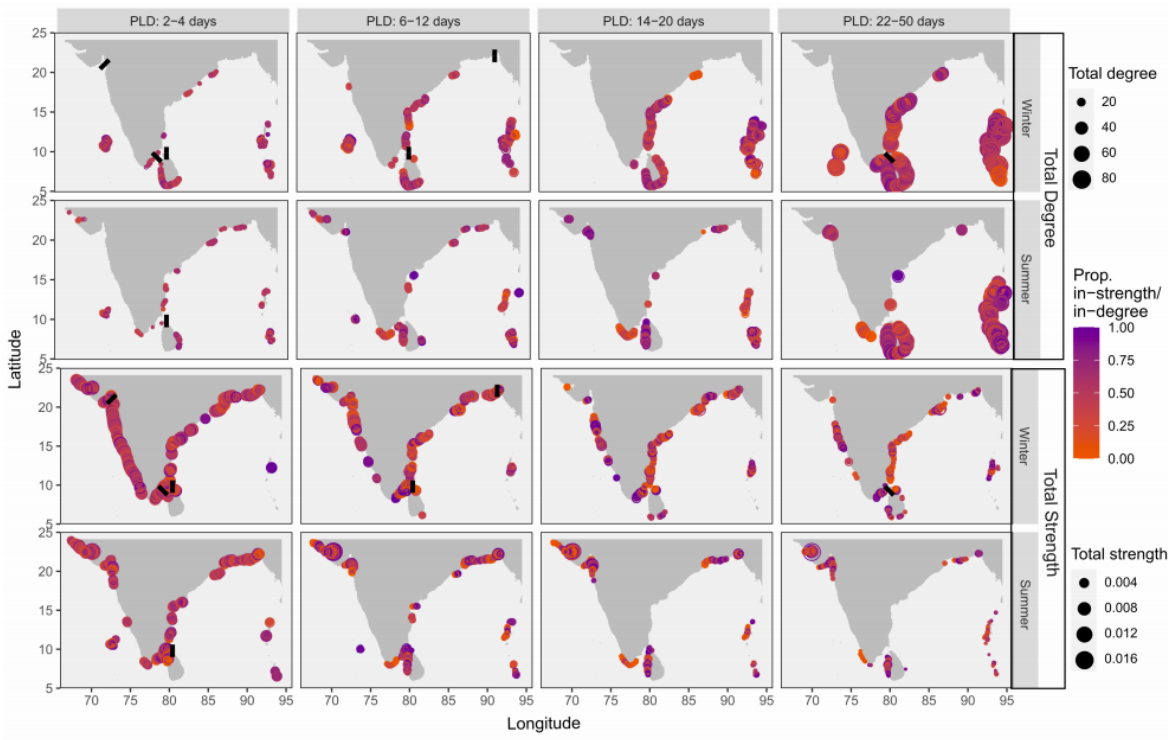


Figure 6. Spatial distribution of total strength (sum of incoming and outgoing edge weights) and degree (sum of number of incoming and outgoing edges). Nodes presented here have strength/degree values greater than the median atleast 75% times across release periods in a given PLD-class. The colour of a node ireflects the magnitude of proportion in-strength/degree, ranging from orange (source) to blue (sink). At each node, the size of the filled circles represent the median and the concentric open circles represent the 75th quantile of degree/strength. Infomap community breaks with >90% incidence are shown as black bars.

Discussion

This is the first broad-scale study to use ocean flow data and particle tracking models across a wide range of pelagic larval duration (PLD) and temporal scales to describe patterns of coastal connectivity along the Indian subcontinent and the adjacent island groups. We find that properties of connectivity networks exhibited large intra-seasonal and moderate inter-seasonal variability, but were comparable across years. Though connectance was relatively low within the Indian coastline connectivity network (0.5 to 3.4%) as compared to other regions (4.8% to 25.8%) (Andrello et al., 2013; Agostini et al., 2015; Crochelet, et al., 2016), a PLD of 20 days was pivotal in ensuring significant transport farther than 2-5 km along the coastline, resulting in a few large well-connected coastal communities.

Connectivity provinces and biogeography

Despite seasonal differences in the location of community breaks, particularly for PLD less 20 days, four persistent disconnected provinces were identified along the mainland coast (Figure 8a). From west to east along the coastline of the Indian subcontinent, the first province extended across the Gulf of Khambat and the coast of Gujarat (southern boundary at 21°N), the second province was found along the west coast of India (~21°N to 8°N), the third province observed in the summer monsoon extended from the southern tip of India to the Palk strait (8-11°N, Gulf of Mannar, between Sri Lanka and mainland India) and the fourth province was observed along the east coast of India (~11°N up to 22°N). The island groups differed in their connectivity with these provinces, where Sri Lanka was well connected to

most regions, while the Lakshadweep and Nicobar islands were more isolated from the mainland connectivity provinces.

Three of the four coastal provinces delineated in our study remained stable across seasons despite the striking seasonal reversal of the upper ocean circulation along the Indian coastline. The extent of the observed provinces is congruent with two oceanographic features – the salinity front north of 20-21°N in the Arabian Sea (Luis & Kawamura, 2004) and the deviation in coastal circulation around Sri Lanka near the southern tip of the Indian coastline (Schott & McCreary, 2001).

Flow separation around 21°N in the northern Arabian Sea likely leads to the predicted connectivity break and the stability of a salinity front in this region, which is the southern limit of the Arabian Sea High Salinity Water Mass in the winter monsoon (Kumar & Prasad, 1999). This salinity front is also associated with greater productivity in the water column as a result of upwelling (Madhupratap et al., 1996). While pelagic species distributions can be influenced by connectivity breaks, environmental differences or both, the composition of benthic invertebrates aligns more closely with the predicted connectivity province (Sivadas & Ingole, 2016; Figure 8b) in comparison to ecological units defined using climatological parameters (Sayre et al., 2017; Figure 8c). The present study encourages the incorporation of additional parameters that integrate ocean dynamics with climatology to delineate biogeographic units..

Despite some mismatch in the precise location of the predicted connectivity breaks and observed biogeographic boundaries, the connectivity provinces delineated in the north-west

coast and southern India overlap with divisions recognized using benthic and pelagic biogeography, supporting a relationship between ocean flow, environmental properties and species distributions (Spalding et al., 2007; Sivadas & Ingole, 2016, Figure 8c). Other biogeographic subdivisions that have been proposed along the east coast were recovered as community breaks for a specific subset of PLD-class and season (Figure 5 and Figure 8c), pointing to the importance of biotic filters of connectivity.

Oceanographic drivers of connectivity

Interestingly, though the monsoon is a key driver of the circulation around the Indian peninsula, its inter-annual variability, related to the El Niño–Southern Oscillation had a lower influence on all descriptors of coastal connectivity. In comparison, there was a larger effect of atmospheric intra-seasonal oscillations that result in short-lived upwelling/downwelling events along the Indian coastline (Varkey et al., 1996; Luis & Kawamura, 2004; Durand et al., 2009). When spawning time interacts with such intra-seasonal oscillations, dispersal descriptors can show intra-seasonal variability for PLDs shorter than the temporal scale of flow variability (Guizien et al., 2012). In the Indian Ocean, these atmopsherical oscillations span over a wide range of time-scales ranging from a week to 60 days (Madden & Julian, 1972; Fu et al., 2003), which likely explains why intra-seasonal variability was not averaged out across the PLD range of 2 to 50 days considered in the present study.

Studies from other ocean basins have found regional differences in the relative influence of intra-seasonal, inter-seasonal and inter-annual flow variability on connectivity patterns. Connectivity metrics are determined by geography more than seasonal and inter-annual

variability in circulation in the northern Indo-West Pacific (Pata & Yñiguez, 2019), while in Southern California, intra-seasonal variation alone contributes to half of the uncertainty in connectivity across temporal scales (Mitarai et al., 2009). In contrast, seasonal variation in circulation has a more significant influence on the structure of hydrodynamical provinces in the Mediterranean Sea (Rossi et al., 2014), and interacts with inter-annual variability in driving the spatial extent of connectivity along south-east Australia (Roughan et al., 2011). The absence of a strong seasonal influence in our study can be related to short-lived connectivity between a range of sites promoted by strong intra-seasonal flow variability leading to variation in connectivity breaks along shallow coastal regions, which has also been reported in other regions (Vaz et al., 2013; Rossi et al., 2014).

These results advocate for fine-tuning connectivity studies in the future to include a better description of short-lived atmospheric processes and to down-scale flow modelling within each of the provinces delineated in the present study.

Genetic connectivity and future sampling effort

Connectivity disruptions observed using genetic divergence among populations has only been tested in a few species along the Indian coastline. The extent of the observed genetic breaks broadly coincide with connectivity breaks predicted around the north-west coast, southern India and the Palk Strait (Figure 8b). However, many of these studies have low sampling effort along the coastline, which limits the accurate detection of genetic breaks and the ability to differentiate between isolation by distance and dispersal barriers in shaping population genetic structure (Audzijonyte & Vrijenhoek, 2010). Future population genetics studies using

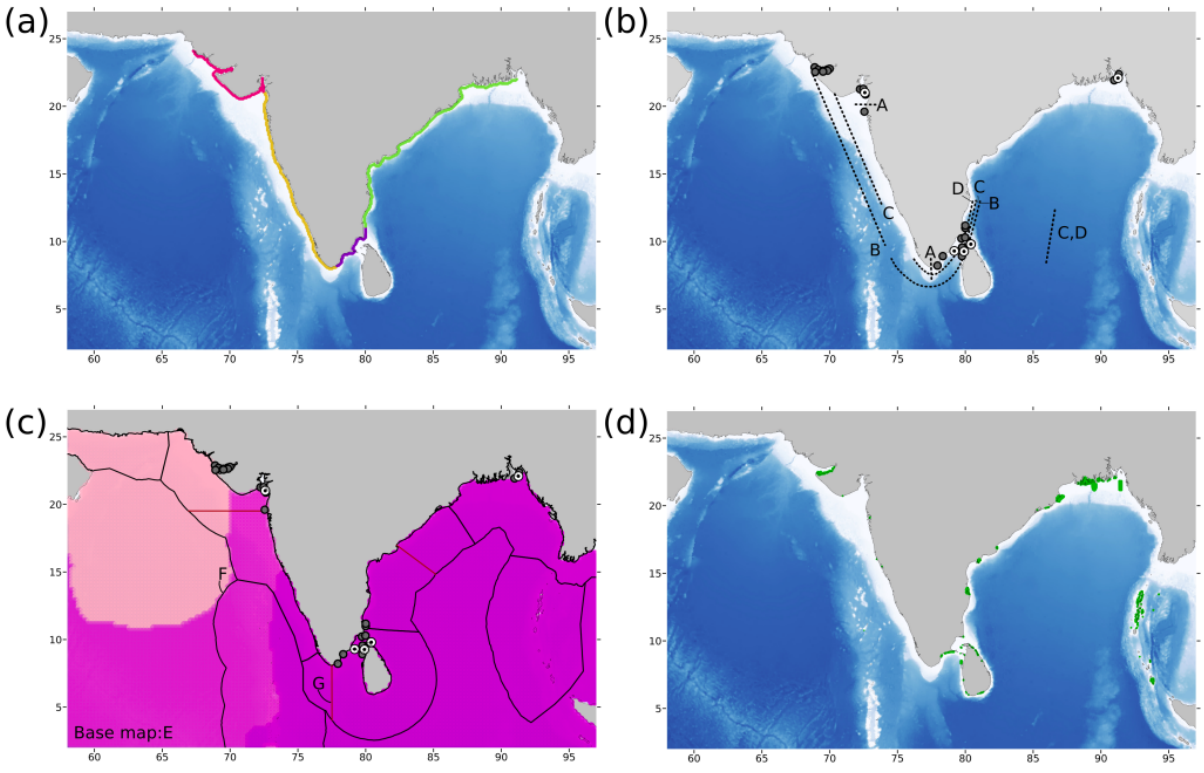
448 a more continuous sampling strategy along the coastline will be necessary to evaluate the
449 influence of ocean flow disruptions predicted here in shaping patterns of genetic connectivity.
450
451 Traits related to release timing and PLD act as biotic filters over connectivity patterns by
452 determining the time-dependent ocean flow scenarios experienced by larvae. By combining
453 information on spawning season and PLD range of the species of interest (Supplementary
454 Information 3) with connectivity descriptors from the present study, it is possible to propose
455 taxa-specific predictions of connectivity breaks, which could be empirically tested. For
456 instance, in the case of taxa with likely summer spawning such as anthozoans (PLD < 7 days)
457 and holothurians (PLD > 20 days), important connectivity breaks would be predicted to occur
458 around the southern tip of India, Palk Strait, south-west Sri Lanka and ~20-21°N on the west
459 coast of India. In contrast, likely winter spawners such as crustaceans (PLD < 20 days) and
460 gastropods (PLD = 12-45 days), connectivity breaks would be predicted to occur around the
461 Gulf of Khambat, Palk Strait and the north-east Indian coastline. For other taxonomic groups,
462 which show a large variability in their spawning period (bivalves) or PLD (non-holothurian
463 echinoderms), using species-specific traits to obtain predictions can help in guiding sampling
464 effort for comparison with genetic estimates of connectivity (PLD and spawning information
465 for benthic invertebrated from the Indian Ocean summarized in Figure S3.4, Supplementary
466 Information 3).
467
468 However, large-scale transport simulations using neutrally buoyant particles with PLD and
469 release period as the only biological parameters, can fail to predict taxa-specific connectivity
470 breaks for various reasons. The transport of neutrally buoyant particles may considerably
471 differ from that of buoyant or swimming larvae (Robins et al., 2013), especially in complex

flow scenarios (Condie & Condie, 2016) and in taxa with efficient larval swimmers (Condie et al. 1999). In addition, ocean flow simulations, with a coarse spatial resolution are inadequate to describe the fine-scale connectivity patterns in fragmented and spatially complex coastal habitats (Padrón et al. 2018; Frys et al., 2020). Finally, biotic filters acting pre- and post-transport (sensu Pineda et al. 2007), which are not accounted for in biophysical models, are likely to explain additional breaks at the level of demographic or genetic connectivity.

Implications for biodiversity conservation

The community breaks identified from our study mark the scale and extent of metapopulation connectivity along the Indian coastline, and can be used to guide the management of marine biodiversity. Currently, Marine Protected Areas (MPAs) are located within each of the provinces delineated by our study, though large protected areas, including national parks, are missing along the linear west coast of India (Figure 8d). The identified connectivity provinces define the spatial extent within which high-resolution biophysical models can be developed to capture fine-scale population connectivity and source-sink dynamics within a metapopulation. This is especially important in evaluating the role of MPAs occurring in areas with recurrent connectivity breaks such as the Gulf of Mannar, Palk Strait, Andaman and Nicobar islands and the Gulf of Kutch. In these regions with complex coastal bathymetry, where connectivity breaks were detected at small spatial distances, spatially and temporally refined transport studies are key in accounting for the effect of fine-scale ocean features on flow connectivity (Briton et al. 2018, Guizien et al. 2012, 2014).

The wide extent of the predicted connectivity provinces also suggests the need for coordinated management of coastal biodiversity across regional jurisdictional, and transnational boundaries. Two of the Indian MPAs listed under the IUCN Transboundary Protected Area programme with Bangladesh and Sri Lanka, as well as MPAs and sites identified as Important Coastal and Marine Areas (Sivakumar et al., 2013) need to be evaluated for effectiveness of spatial and temporal connectivity in the future.



503

504 **Figure 8.** (a) Connectivity provinces predicted in the current study; (b) location of genetic
505 breaks in A. intertidal snails (Bharti, 2019), possible extent within which genetic breaks may
506 occur in B. a marine fish *Rachycentron canadum* (Divya et al., 2017), C. a shrimp *Penaeus*
507 *indicus* (Sajeela et al., 2019) and D. a mussel *Perna viridis* (Divya et al., 2020); (c)
508 classification corresponding to F. Ecological Marine Units (purple and pink) (Sayre et al.,
509 2017), E. Marine Ecoregions of the World (black outline) (Spalding et al., 2007), and G.
510 Ecoregion subdivisions from benthic community composition (red lines) (Sivadas & Ingole,
511 2016); (d) marine protected areas (wiienvis.nic.in). In sub-figures (b) and (c) community
512 breaks detected in this study are depicted using grey (>50% frequency) and concentric black
513 (>90% frequency) circles.

To conclude, the present study provides a coarse prediction of connectivity provinces valid in both monsoon regimes that fulfil a gap in marine biogeography studies from this region. Our results can guide the spatial scales at which future biophysical models should be set up. Based on the frequency of community breaks, we advocate for refining transport studies based on flow modelling and species habitat mapping at the appropriate resolution along the Gujarat coastline, around the southern tip of India and Sri Lanka, over two large areas extending along the western and eastern coasts of the Indian subcontinent, and within each of the island groups.

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