Three-dimensional transport of coral larvae and associated population connectivity in the coastal area of Okinawa Island, Japan

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Abstract. In recent years, global warming has intensified coral bleaching worldwide. The mesophotic zone (MPZ) at depths of 30-150 meters, where photosynthesis is viable and water temperatures are stable, is expected to serve as a refuge and gene resupply source for shallow-water corals. This study quantitatively evaluates the 3D population connectivity between shallow-water corals and MPZ corals in the potential coral habitats surrounding Okinawa Island. Utilizing a triple-nested high-resolution 3D ocean circulation model, an offline, 3D Lagrangian advection-dispersion model for planktonic coral larvae was developed. Results show that 3D intra-island coral connectivity is strongly influenced by topographically constrained residual currents around the island. Coral larvae released from shallow areas are transported in a clockwise direction around the island. While the larvae released from the west coast are transported to the east coast by crossing the northern tip of the island, their movement is significantly hindered at the southern tip by a shallow channel as a topographic barrier. Conversely, this clockwise transport is much less pronounced in the MPZ, resulting in lower connectivity between the west and east coasts. In addition, potential source areas of coral larvae were analyzed to determine an island-wide coral network that could support coral conservation efforts in Okinawa.

1 Introduction

The conservation of coral ecosystems is a critical environmental issue, as they not only provide safe habitats for juvenile fish but also contribute to carbon fixation. However, global warming and other factors are leading to coral bleaching on a global scale [1]. Shallow regions, the primary habitats for reef-building corals, experience significant bleaching due to substantial temperature fluctuations [2]. In contrast, the mesophotic zone (MPZ), located at depths ranging from 30 to 150 meters, offers a relatively stable environment, and is anticipated to act as a refuge and a source for the resupply of genes to shallow-water corals [3]. Building on the background mentioned above, this study aimed to quantitatively evaluate the connectivity between shallow-water corals and MPZ corals in the waters surrounding Okinawa Island, Japan. Specifically, the three-dimensional (3D) advection-dispersion

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processes of coral larvae were modeled using a high-resolution 3D ocean current model. Several assumptions were made in order to develop a Lagrangian model that would realistically represent the transport of larvae in the simplest possible mathematical form. The present study elucidated the horizontal and vertical transport characteristics of the coral larvae and associated population connectivity based on a Lagrangian statistical analysis.

2 Methods

A 3D flow field was obtained by reanalyzing the triply nested 3D ocean circulation model ROMS (Shchepetkin and McWilliams, 2005 [4], 2008 [5]) for the area around Okinawa Island using the JCOPE2-ROMS downscaling system [6, 7] (Figure 1a-b). To simulate coral habitats, 134 and 129 circular patches with a 1 km radius were established at shallow (approximately 2 m depth) and deep (mesophotic zone, approximately 30 m depth) locations along the coast of Okinawa Island, respectively (Figure 1b-c). The numbered patches were positioned in a counterclockwise direction, commencing at Cape Hedo, the northernmost point of the island. A total of 500 virtual coral larvae were released on a daily basis from May 1 to June 30, 2013. The 3D positions of all released Lagrangian particles were recorded at 12-hour intervals and tracked for 31 days following each release. This approach was taken to ensure consistency with the reported lifespan of floating larvae of a reef-building coral that is typical in the region. The coastal area around Okinawa Island was segmented into six subregions reflecting topographic characteristics (Figure 1c), counting counterclockwise from Haneji Inland Sea (Area 1), Nago Bay (Area 2), Ginowan Bay (Area 3), Nakagusuku Bay (Area 4), Kin Bay (Area 5), and to Gesaki (Area 6).

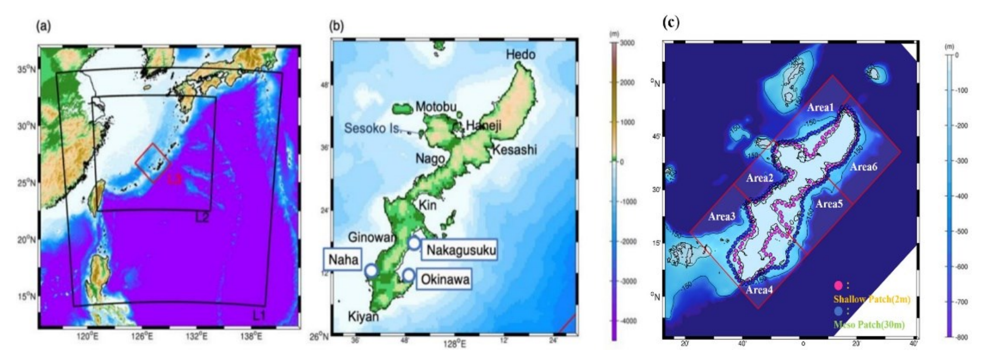

Fig. 1. (a) A hierarchy of the computational domains of the triple-nested JCOPE2-ROMS model (L1, L2, and L3). (b) An enlarged view of the coastal area of Okinawa Island with major place names. (c) Locations of source/sink patches for Lagrangian virtual coral larvae and the designated six areas, with pink circles indicating shallow source/sink patches and blue circles representing deep source/sink patches.

An attempt was made to evaluate the connectivity between these areas statistically based on the Lagrangian particle tracking model results, where the virtual larvae were assumed to be neutrally buoyant and advected passively by ambient 3D currents. In this study, the population connectivity was assessed by calculating the transport probability from the release (source) area to the arrival (sink) area using the Lagrangian Probability Density Function (LPDF) for the position vector of Lagrangian particles at each advection time, i.e., elapsed time since each release.

3 Results

3.1 3D connectivity

The results of the 3D connectivity analysis around Okinawa Island (Figure 2) indicate that clockwise larval transport is the predominant direction for the virtual larvae released from shallow areas, which is represented by a higher probability in the triangular lower right half of the depicted connectivity matrices. The connectivity between the east and west coasts is significantly reduced at Cape Kyan, situated on the southern tip of the island, in comparison to Cape Hedo, located on the northern tip. The virtual larvae released from Kin Bay (Area 5) and Nakagusuku Bay (Area 4) on the east coast exhibit strong retention (self-recruitment), while the larvae released from Nago Bay (Area 2) and Ginowan Bay (Area 3) on the west coast are transported to both shallow and deep areas of Nago Bay by the predominant clockwise transport tendency. In contrast, the clockwise transport of the virtual larvae released from deeper areas is less pronounced than that from shallower areas, leading to a limited particle exchange between the east and west coasts. Furthermore, it was found that certain larvae remained within the shallow regions of their release areas in Kin Bay and Nakagusuku Bay without drifting into deeper waters, owing to retention associated with the extensive shallow topographies. Similarly, larvae released from deeper areas in Nago Bay and Ginowan Bay tended to remain within both the shallow and deep zones of Nago Bay, exhibiting a pattern similar to that observed with shallow releases.

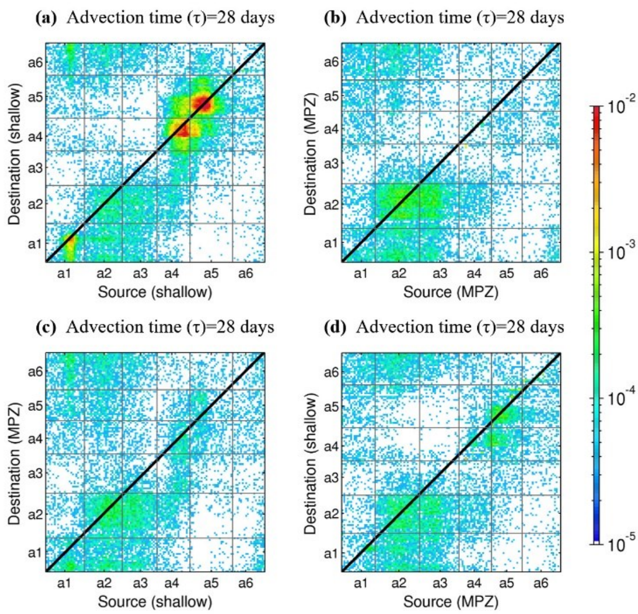

Fig. 2. Three-dimensional connectivity matrices of virtual coral larvae in the coastal areas of Okinawa Island over a 28-day advection period. The x-axis represents the source areas (a1–a6: Areas 1–6), while the y-axis indicates the sink areas (a1–a6). (a) Connectivity from shallow source areas to shallow sink areas. (b) Connectivity from deep (MPZ) source areas to deep (MPZ) sink areas. (c) Connectivity from shallow source areas to deep (MPZ) sink areas. (d) Connectivity from deep (MPZ) source areas to shallow sink areas.

3.2 Vertical Lagrangian transport

The temporal evolution of the vertical distribution of the Lagrangian Probability Density Function (LPDF) of virtual larvae released from shallow and deep patches in Areas 2 and 5 (Figure 3), respectively representing the east and west coasts of the island, shows that vertical dispersal is primarily influenced by the surface mixed layer, which develops at depths of 10–30 m during the summer season. This layer serves two primary functions: it inhibits upward vertical transport from the mesophotic zone (MPZ) to shallow areas and surface layers while facilitating larval accumulation near the surface. This mechanism is particularly evident along the east coast, intensifying self-recruitment within the region. In contrast, larval exchange between the MPZ and surface layers tends to be more pronounced on the west coast.

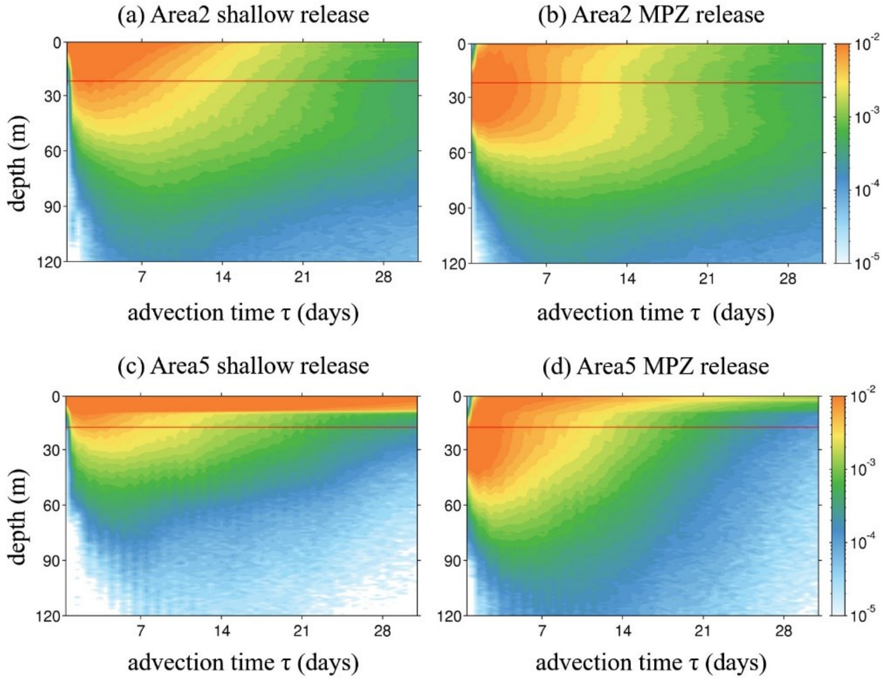

Fig. 3. Hovmöller plots of vertical distribution of Lagrangian Probability Density Function (LPDF) of virtual larvae released from Area 2 (Nago Bay) and Area 5 (Kin Bay), as a function of the advection time. (a) Shallow release in Area 2, (b) deep release in Area 2, (c) shallow release in Area 5, and (d) deep release in Area 5. The solid red line represents the time averaged depth of the surface mixed layer of each area.

3.3 Coral Network across Okinawa Island

To aid in the establishment and preservation of desirable coral ecosystems around the island, the coral network structure between shallow and deep (MPZ) habitats across Okinawa Island was investigated. Table 1 presents a summary of the recruitment rate in percent at the advection time of 28 days from all potential source areas listed in the vertical columns to (a) the shallow areas and (b) deep (MPZ) areas as sink sites, which are listed in the horizontal row. Overall, striking differences are evident between the shallow and deep sink areas. Typically, shallow habitats receive larvae released from the same area (i.e., self-recruitment) or neighboring areas. In contrast, for the deep (MPZ) habitats, the west coast (Area 1: Haneji Inland Sea and Area 2: Nago Bay) plays a critical role in supplying larvae to deep habitats across the island.

Table 1. Recruitment rate (source fraction of Lagrangian particles) in percent at the advection time of 28 days from all potential source areas to (a) the shallow areas and (b) deep (MPZ) areas as sink areas. Yellow highlights indicate the primary shallow source areas, while green highlights represent the main deep source areas to the indicated sink areas.

(a) To shallow areas

Source \ Sink		Area 1 shallow	Area 2 shallow	Area 3 shallow	Area 4 shallow	Area 5 shallow	Area 6 shallow
Area 1	shallow	28.58%	2.33%	3.21%	2.78%	3.95%	18.37%
Area 1	MPZ	7.59%	2.49%	3.44%	2.61%	3.14%	9.09%
Area 2	shallow	16.28%	20.78%	12.20%	2.96%	4.34%	14.56%
Area 2	MPZ	15.49%	21.60%	13.28%	2.45%	3.76%	13.71%
Area 3	shallow	10.33%	17.39%	13.50%	1.66%	2.08%	7.79%
Area 3	MPZ	9.71%	16.22%	13.22%	1.12%	4.37%	6.57%
Area 4	shallow	3.30%	9.23%	19.77%	57.41%	9.45%	4.23%
Area 4	MPZ	2.86%	5.26%	6.38%	3.20%	1.78%	2.90%
Area 5	shallow	1.18%	1.63%	6.79%	17.82%	60.86%	9.36%
Area 5	MPZ	1.15%	1.85%	4.54%	4.88%	5.57%	4.07%
Area 6	shallow	1.90%	0.66%	1.64%	1.48%	1.79%	3.98%
Area 6	MPZ	1.63%	0.54%	2.02%	1.63%	1.78%	5.37%

(b) To deep (MPZ) areas

Source \ Sink		Area 1 MPZ	Area 2 MPZ	Area 3 MPZ	Area 4 MPZ	Area 5 MPZ	Area 6 MPZ
Area 1	shallow	17.27%	2.79%	3.51%	11.53%	13.86%	17.12%
Area 1	MPZ	16.87%	3.80%	4.75%	15.53%	15.93%	15.36%
Area 2	shallow	16.77%	19.90%	14.52%	9.21%	12.51%	16.99%
Area 2	MPZ	18.59%	27.60%	19.64%	7.85%	11.32%	16.67%
Area 3	shallow	7.45%	15.12%	13.93%	4.55%	5.62%	7.34%
Area 3	MPZ	7.70%	18.03%	15.86%	3.46%	4.06%	6.84%
Area 4	shallow	1.72%	5.42%	10.89%	6.65%	3.22%	1.91%
Area 4	MPZ	2.01%	4.04%	5.67%	6.38%	3.54%	2.27%
Area 5	shallow	1.24%	0.83%	3.62%	8.68%	7.70%	2.97%
Area 5	MPZ	1.32%	1.17%	3.82%	9.46%	7.76%	3.33%
Area 6	shallow	4.68%	0.61%	1.64%	7.06%	6.24%	4.32%
Area 6	MPZ	4.36%	0.69%	2.16%	9.64%	8.22%	4.86%

For instance, the shallow sink site in Area 1 (Table 1a) primarily receives larvae originating from Area 1 (self-recruitment, i.e., larval transport occurred within the same area) as a shallow source and from neighboring Area 2 as a deep source. Similarly, Areas 2–6 predominantly receive larvae from either the same area or neighboring areas. In addition, it is noteworthy that intense self-recruitment (approximately 60% of the arriving larvae) occurs in the shallow sink sites in Areas 4 (Nakagusuku Bay) and 5 (Kin Bay). In contrast, for the deep sink sites (Table 1b), both the shallow and deep sites in Area 2 serve as the primary sources of larvae arriving in Areas 1, 2, 3, and 6. Likewise, the deep sink sites in Areas 4 and 5 are mostly affected by Area 1.

Although these results underscore the intricate interplay between shallow and deep coral habitats in Okinawa Island, it was observed that shallow habitats are largely influenced by self-recruitment, even from local offshore deep habitats. In contrast, the deep MPZ habitats are primarily governed by the prevailing clockwise circulation around the island, with barrier effects at the southern tip, resulting in the west coast (Areas 1–2) serving as the primary source region for the entire island.

4 Conclusions

In this study, the three-dimensional (3D) transport characteristics of hypothetical coral larvae in the coastal waters around Okinawa Island, Japan, were investigated through Lagrangian particle tracking simulations originating from both shallow and deep locations as source sites. The findings revealed an asymmetrical connectivity between the west and east coasts, influenced by the prevailing clockwise mean circulation around the island. Notably, pronounced self-recruitment was found to be enhanced in the shallow area of semi-enclosed Kin and Nakagusuku Bays. Furthermore, a significant accumulation of larvae was observed in both the shallow and deep areas of Nago Bay, which is rather an open bay as compared to the semi-enclosed bays on the east coast. These results indicate that the degree of connectivity and accumulation varies considerably depending on the topographical features of each area through the associated local 3D circulations.

These results partially elucidate the relationship between coral spawning and growth sites, strongly suggesting that gene exchange occurs extensively between shallow areas and the deep, mesophotic zones in response to the ambient 3D currents and seasonal development of the surface mixed layers. In particular, Kin Bay and Nakagusuku Bay on the east coast, along with Nago Bay on the west coast, demonstrate significant larval accumulation capacities, highlighting their roles in the conservation of island-wide coral ecosystems. Future studies should incorporate nearshore hydrodynamics, such as under-resolved turbulence and breaking wave-induced littoral currents, as well as biological mechanisms, including larval behavioural models, which were omitted in the present study, to depict more detailed and realistic larval transport processes.

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