REPORT

Assessing coral reef conservation planning in Wakatobi National Park (Indonesia) from larval connectivity networks

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Abstract Wakatobi National Park (WNP), located in the heart of the Coral Triangle in Indonesia, is one of the most biodiverse marine habitats on Earth. Coral ecosystems within the park, however, are threatened by anthropogenic stressors such as coral diseases, coral mining, blast fishing, invasive species and pollution. This led the Government of Indonesia to establish marine protected zones (MPZs) over 2% of the WNP, but the efficiency of these MPZs to support coral reef resilience against anthropogenic disturbances remains poorly documented. Here this gap was filled by evaluating coral connectivity within the WNP at the sub-reef scale and assessing how the MPZs contribute to coral resilience on other reefs within the WNP. The larval dispersal of the coral species *Acropora millepora* and *Acropora gemmifera* were simulated during eight spawning seasons in 2014–2021 using a multi-scale ocean model that achieves a local resolution finer than 100 m. The coral connectivity matrices were then analysed using Google's PageRank algorithm to identify the sub-reefs that act as major sources and sinks, as well as sub-reefs best suited for protection and restoration planning. The interannual and interspecific variability of these indicators were assessed and identified sub-reefs that were consistently ranked high for all eight years and for both species. Both El Niño and La Niña events were found leading to a significant increase in larval exchanges across the WNP for both species. Overall, the results suggest that, under the current WNP zoning, there is limited overlap between MPZs and the reefs identified as best candidates for reef protection and restoration based on acroporid larval connectivity. The current restoration site of Ou Tooge was unlikely found to be a significant larval supplier to adjacent reefs in the WNP. Based on the high-resolution coral connectivity analysis, a list of reefs that were proposed should be prioritised for maximising the broad-scale impact of coral reef conservation and restoration planning in the WNP.

Keywords Wakatobi National Park · Coral connectivity · Biophysical modelling · Reef management

Introduction

Ecological connectivity is a crucial consideration in the design of marine protected zones (MPZ) networks to enhance the preservation of ecological functionality and productivity (Balbar and Metaxas 2019). Assessing connectivity between reefs can be achieved through direct examination of genetic (Hedgecock et al. 2007) or demographic connectivity (Lowe and Allendorf 2010). Genetic connectivity, for instance, can be observed by extensively collecting data around the reefs in the region of interest and analysing DNA sequence clustering patterns to assess gene flow, genetic drift, selection, and mutation. It enables the identification of populations with high connectivity as well as breaks in connectivity between and within populations or sub-populations, helping to identify source and sink populations (Umar et al. 2019; Leis 2006). However, it should be noted that genetic homogeneity between geographic populations does not unequivocally indicate strong demographic

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connectivity, nor do genetic differences necessarily imply poor connectivity (Hedgecock et al. 2007). Genetic or demographic connectivity, on the other hand, focus on measuring the exchange rate of individuals between neighbouring populations, which can significantly impact demographics and population dynamics (Lowe and Allendorf 2010). Factors such as biological traits, larval competency, buoyancy and spawning dates of spreading infividuals may influence connectivity in this context (Lowe and Allendorf 2010).

Coral organisms (in particular Scleractinia) generally have a bipartite life cycle. They remain attached to the reef substrate during the adult phase and disperse during the pelagic larval phase (Mayorga-Adame et al. 2017). Ocean currents are the main factor that control their spatial and temporal distribution (Strathmann et al. 2002). These currents transport larvae from their spawning to their settlement locations. The transport can cover distances of several to hundreds of kilometres, depending on the duration of the pelagic phase and the oceanographic conditions in the area (Vollmer and Palumbi 2007; Lequeux et al. 2018). Larval dispersal can be simulated and the strength of the connectivity between reef habitats can be quantified using a biophysical model that simulates both the ocean circulation and the larval dispersal dynamics. With a proper parameterisation and model design, the results can be considered as an acceptable approximation to study connectivity and inform reef management (McCook et al. 2009; King et al. 2023; Krueck et al. 2017; Bode et al. 2019).

The WNP, situated in the heart of the Coral Triangle is one of the most diverse marine habitats on Earth (Bell and Smith 2004; Marlow et al. 2020). It is the second-largest marine national park in Indonesia, with atolls, patch reefs, and extensive fringing coral reefs around the four main islands that are home to highly biodiverse scleractinian coral communities (Clifton, Unsworth, and Smith 2013). The name Wakatobi is an abbreviation of the four main islands in the archipelago, i.e. Wangi-Wangi Island with an area of 448 km², Kaledupa Island with an area of 104 km², Tomia Island with an area of 115 km², and Binongko Island with an area of 156 km². Conservation areas in the WNP are managed through a zoning system, namely: core zone, marine protected zone, and the limited utilisation zone, which is divided into the general use zone, local use subzone, and tourism subzone (Fig. 1). About 396 hermatypic coral species and about 590 fish species live in the area (Pet-Soede and Erdmann 2004). Large-scale studies on biodiversity
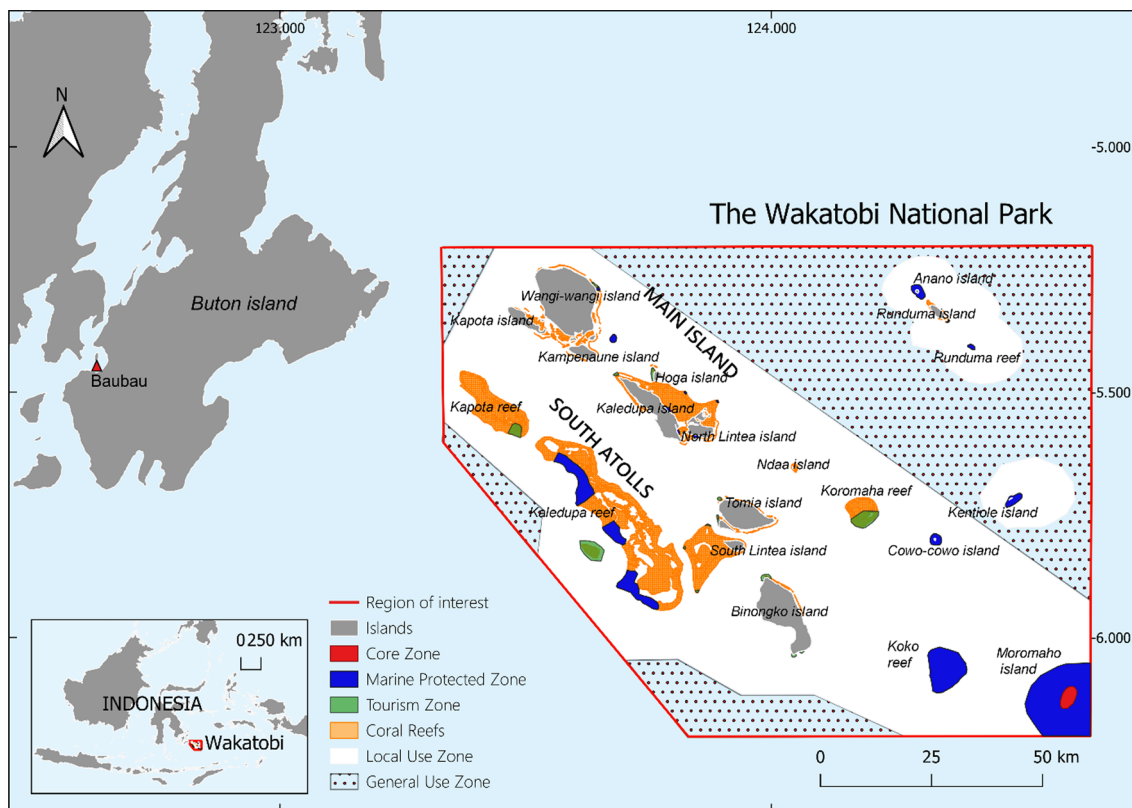

Fig. 1 The map shows the region of interest. The coral larvae dispersal simulation focused on the area within the red polygon. The red triangle indicates the validation point located in Baubau, Buton Island. The blue arrows represent the seasonal transport of water masses by the Indonesian Throughflow (ITF), originating from the Pacific Ocean and moving towards the Indian Ocean through the WNP, Flores, and Banda Seas. This phenomenon, known as the reversed ITF or ITF eastward phase, typically occurs from around March to July

using multiple criteria have placed the WNP among the areas critical to conserving global marine ecosystem diversity (Green and Mous 2008). In addition, the WNP has been designated as a world biosphere reserve by UNESCO (UNESCO 2019). Furthermore, as claimed by Operation Wallacea, the WNP (in particular, Hoga island) is one of the most studied areas in the Coral Triangle (Operation Wallacea 2023).

In recent decades, WNP coral reef ecosystems have been endangered by several threats, including coral diseases (Muller et al. 2012; Haapkylä et al. 2007), coral mining (Caras and Pasternak 2009), blast fishing (Von Heland and Clifton 2015), invasive species (Roth et al. 2018), and pollution (BBC 2018; Nur, Kantun, and Kabangnga 2021, Phelan et al. 2020). Therefore, the WNP has become a national conservation priority. In 2018, the Indonesian Ministry for Maritime Affairs and Investment of Indonesia launched the Indonesia Coral Reef Garden restoration program, with the WNP as one of the target sites (Biro Komunikasi Kemenko Marves RI 2021). However, the effectiveness of the marine protected zones (MPZs) within the WNP has not yet been properly evaluated. The restoration projects have also been implemented without considering key ecological factors, in particular coral connectivity. Consequently, the usefulness of the current MPZs in preserving coral reefs is still unknown, and the artificial reefs might not be placed in the most relevant locations for connectivity.

Larval connectiviy has not been considered for the design and zonation of the WNP. The marine park was designed in 1989 based on literature reviews and biophysical surveys, and then declared as a marine protected zone in 1996 (Lommen 2011). In 2003, the WNP zonation was redesigned to integrate environmental conservation priorities and local community needs (Wisesa 2010; Lommen 2011). The new design divides the WNP into five management zones: core, marine protection, tourism, local use, and general use zones. The possibility of redesigning the WNP zonation will remain open until 2030 because the Government of Indonesia's roadmap aims to achieve 32.5 million hectares of MPZs by that year (Rusandi 2019).

Given the importance of marine connectivity in informing conservation planning, this study aims to evaluate the effectiveness of the MPZs in the WNP and identify priority sites for reef protection and restoration based on a larval dispersal model. To achieve that objective, the ocean circulation within the WNP was simulated at a fine resolution of less than 100 m. The simulated currents then used to model the larval dispersal of two scleractinian corals (*Acropora millepora* and *Acropora gemmifera)* during the west monsoon season over the 8-years period 2014–21. The effect of El Niño and La Niña events on larval dispersal was considered by studying connectivity over multiple years. Larval dispersal simulations yield large connectivity matrices that

were analysed with different graph-theory algorithms to identify reefs maximising larval export and import, as well as those that would maximise the benefits of reef protection and restoration programs. The results of this study were then compared with the current WNP zonation and proposed as an alternative MPZ design.

Materials and methods

Hydrodynamic model

The two-dimensional (2D) depth-integrated version of the Second-generation Louvain-la-Neuve Ice-Ocean Model (SLIM) (Lambrechts et al. 2008) was used to simulate ocean circulation in the area of interest (see Appendix Fig. 6). SLIM is a multi-scale coastal ocean model, which has already been successfully applied and extensively validated in reef systems such as the Great Barrier Reef (Thomas et al. 2015; Figueiredo et al. 2022) and the Florida Reef Tract (Frys et al. 2020; Dobbelaere et al. 2020). The model solves the nonlinear shallow water equations:

$$\frac{\partial \eta}{\partial t} + \nabla.(H\mathbf{u}) = 0, \tag{1}$$

$$\begin{aligned}
\frac{\partial \mathbf{u}}{\partial t} + \mathbf{u}.\mathbf{\Delta u} + f\mathbf{e_z} \times \mathbf{u} &= -g\Delta\eta + \frac{\tau}{\rho H} + \gamma\left(\mathbf{u_*} - \mathbf{u}\right) \\
&+ \frac{1}{H}\nabla.[Hv(\nabla\mathbf{u})] - \frac{C_d||\mathbf{u}||\mathbf{u}}{H},
\end{aligned} \tag{2}$$

where η is the water level, $H = h + \eta$ is the water column height, h is the bathymetry and $\mathbf{u}$ is the depth-integrated velocity, f is the Coriolis factor, $\mathbf{e_z}$ is a unit vector pointing vertically upwards, and g is the gravitational acceleration, $\boldsymbol{\tau}$ is the surface wind stress that depends quadratically on the wind velocity 10 m above sea level and uses the Smith and Banke (1975)'s wind drag parameterization, ρ is the seawater density, γ is a flow relaxation coefficient, and $\mathbf{u_*}$ is velocity from the global ocean model NEMO towards which SLIM is relaxed in the deep ocean, v is the nonlinear Smagorinsky horizontal eddy viscosity, and C_d is the bulk bottom-drag coefficient.

The domain bathymetry was retrieved from the General Bathymetry Chart of the Oceans (GEBCO) at 15 arc-second intervals (GEBCO 2020). To guarantee that the entire domain was always underwater, the minimum depth was set to 3 m. The wind velocity was obtained from the European Centre for Medium-Range Weather Forecast (ECMWF) ERA5 reanalysis, with a 30 km spatial resolution and hourly temporal resolution (ECMWF 2019). The 3D velocity field is computed on a 1/12° horizontal grid with 50 vertical levels to calculate the flow relaxation term. NEMO model

outputs are distributed by Mercator Ocean, the French centre for analysis and forecasting of the global ocean. Mercator Ocean operates global forecasting systems and produces global and regional reanalysis, all based on the NEMO ocean model, coupled to a data assimilation system. Finally, to calculate the ordinary momentum diffusion, the bulk bottom drag coefficients were set, $Cd = 2.5 \times 10^{-3}$, for sandy-muddy ocean beds (Safak and Marti 2016) and $Cd = 5 \times 10^{-2}$ over coral reefs (Rosman and Hench 2011; Kunkel et al. 2006).

In this study, the choice of a 2D model over a 3D model was made due to its lower computational cost, which allows for an increase in the horizontal resolution without exceeding computational limitation. Although a 2D barotropic model is well suited for shallow region, such as those where reefs are situated, it does not include all the physical processes that drive larger scale ocean circulation. To address this, we have coupled it with a 3D baroclinic ocean model, NEMO, using a flow relaxation term when the water depth exceeds 50 m. This coupling enables us to indirectly represent baroclinic phenomena. The region of interest was discretised by using the seamsh (Lambrechts 2023) unstructured mesh generator. The mesh is made of 122,858 triangular elements, with a resolution varying from about 50 m around the islands and reefs of WNP and Baubau to 12 km in the open ocean.

To assess the performance of the hydrodynamic simulation, the simulated sea surface elevation was validated against the data from the tide gauge located at the Baubau station (−1.951°N, 124.382°W). A harmonic analysis was used for the model output and the observational data to determine the respective tidal constituents using the R library oce (Dan, Clark, and Chantelle 2021) implemented in R version 3.6.1 (R Core Team 2020). The two sets of tidal constituents were then compared (harmonics).

Hydrodynamics of the WNP

As part of the Indonesian Seas, the WNP is flanked by the Pacific Ocean and the Indian Ocean and traversed by a branch of the Indonesian Throughflow (ITF) (Van Sebille et al. 2014; Sprintall and Révelard 2014). Additionally, it is affected by large-scale forcings from the El Niño Southern Oscillation (ENSO) and Indian Ocean Dipole (Susanto et al. 2006). The ENSO is related to the large-scale variability in sea surface height anomalies, wind and sea surface temperature (Susanto et al. 2006), and can thus be expected to induce variability in coral larval dispersal.

In the simulation, coral larval dispersal was simulated during March-July, coinciding with the first monsoonal transition period (Hung and Hsu 2008). Previous studies have demonstrated that this period is characterised by seasonal wind variability and the passage of the ITF through the WNP (Sprintall and Révelard 2014). The ITF transports water masses from the Pacific Ocean towards the Indian

Ocean (Fig. 1), bringing relatively cool and low salinity water through the Flores and Banda Seas (Schneider 1998; Baumgart et al. 2003; Sprintall et al. 2014; Sprintall and Révelard 2014). Meanwhile, Pacific subtropical water (relatively high salinity) and the North Pacific intermediate water (relatively low salinity) mix vertically in the Banda Sea (Sprintall et al. 2014).

Larval dispersal model

The dispersal of virtual coral larvae was simulated using a depth-averaged Lagrangian particle tracker (LPT) (Spagnol et al. 2002), which runs on top of the hydrodynamic model output. Virtual larvae were uniformly released over each coral reef at the time of spawning and then subject to both physical and biological processes. The former is driven by the ocean currents simulated by the hydrodynamic model and by the turbulent diffusion, which is represented as a random walk. The latter include larvae life history traits such as mortality/acquisition/loss rate and settlement age. Larvae transported beyond the WNP boundaries were assumed to be lost and no longer considered in the analysis. The LPT computes the position and state of individual larvae based on their biological characteristics. Enabling the tracking of trajectories of coral larvae from spawning to settlement at the end of their dispersal stage yields estimates of the number of virtual larvae transported between all the sub-reefs composing the area of interest. More details on the coral larvae transport model can be found in Thomas et al. (2014).

In this study, *A. millepora* and *A. gemmifera* coral larvae were considered as these species are among the main coral species found in the WNP (Salinas-de-León et al. 2013). These species have also been observed in the Spermonde Islands, which, like the WNP, are located in the southern hemisphere of Sulawesi and relatively similar latitudes (van der Ven, Heynderickx and Kochzius 2021; Baird et al. 2021). Their larval mortality rate can be parameterized with a generalised Weibull distribution:

$$m(t) = \frac{\left(\lambda n (\lambda t)^{n-1} \right)}{1 - (\lambda t)^n}, \qquad (3)$$

where λ and ν are the independent distribution parameters that were estimated by Connolly and Baird (2010) from the larvae survival proportion curves (Table 1). Other larvae life history traits include pre- and post-competency periods, as well as competence acquisition and loss rates. In the model, the pre-competency period refers to the stage when coral larvae develop before they can settle and become sessile organisms. The duration of this period varies among species and is influenced by factors like larval age, size, health, and environmental cues. In the simulation, it is assumed that larvae would settle on the initially encountered reef after a

Table 1 Biological parameters used to estimate the dispersal potential of *A. millepora* and *A. gemmifera* based on Connolly and Baird (2010)

	A. millepora	*A. gemmifera*
Mortality Rate		
λ	4.3×10^{-2} [d^{-1}]	6.6×10^{-2} [d^{-1}]
ν	5.7×10^{-1} [−]	1.08 [−]
Pre-competency period	3.293 [d]	3.471 [d]
Post-competency period	100 [d]	100 [d]
Competence acquisition rate	1.8×10^{-1} [d^{-1}]	3.9×10^{-1} [d^{-1}]
Competence loss rate	5×10^{-2} [d^{-1}]	1.45×10^{-1} [d^{-1}]

pre-competency period of 3.47 d for *A. gemmifera* and 3.24 d fo/r *A. millepora* (Connolly et al., 2010), unless they perish or leave the designated area beforehand. The post-competency period is when larvae have acquired the competence to settle and undergo metamorphosis. Its length depends on the species and environmental conditions. The competence acquisition rate measures how quickly larvae gain settlement ability. A higher rate leads to faster development, earlier settlement, and shorter dispersal distances (Connolly et al., 2010). Conversely, competence loss rate refers to the decline in settlement ability over time. A higher rate results in extended dispersal periods and potentially longer distances (Connolly et al., 2010). They are represented by constant parameters (Table 1) that were also taken from the study by Connolly and Baird (2010). These variables impact larval dispersal and settlement patterns. The duration of the pre-competency period, competence acquisition and loss rates, and the post-competency period influence the timing and success of settlement. Understanding these variables helps reveal the dynamics of larval dispersal, distances travelled, and potential population connectivity and recruitment to different reef locations.

Larval dispersal was simulated from 2014 to 2021 to account for the interannual variability of ocean circulation. The hydrodynamic simulation was consistently conducted over a three-month period, from March to July. To determine the spawning dates for the WNP, the observed spawning dates in the Spermonde islands was used as a reference. In 2014, *A. millepora* spawned in April, 14 d before the full moon, while *A. gemmifera* spawned in March, 14 d after the full moon (Baird et al. 2021). However, the exact start date of the spawning event varied each year based on the occurrence of the full moon (Table 2, Baird et al. 2021). As a result, the maximum duration of larval dispersal simulation ranged from 108 to 134 d. At the end of the simulation, almost all of the simulated larvae had either settled, perished, or moved away from the designated area. The reef map from UNEP World Conservation Monitoring Centre and the WorldFish Centre, in collaboration with the World Resources Institute and The Nature Conservancy (UNEP-WCMC, WorldFish Centre, WRI, TNC 2021), was used to seed all reefs with a density of 1.6×10^3 particles per km^2 of reef, resulting in approximately 7.3×10^4 particles per simulation. To enhance the resolution of the estimated larval settlement patterns, the extensive coral reefs were divided into $0.004° \times 0.004°$ (about 400 m × 400 m) sub-reefs, resulting in a total of 6623 sub-reefs in the WNP. Since specific information on the distribution of the modelled coral species in the Wakatobi islands was not available, both species were assumed to be present in all sub-reef habitat grid sections.

Connectivity indicators

The LPT yielded a potential connectivity matrix (with entries M_{ij}) that represent the exchanges among all sub-reefs in the WNP. The row index i represents the source reef, and the column index j represents the sink reef. Total larval exchanges here denote the collective count of larval movements among various reef locations depicted in the connectivity matrix. It serves as a quantitative measure of the overall larval exchange between reefs, offering valuable information about the patterns and scale of larval dispersal within coral reef ecosystems. The formula for calculating the total larval exchange in connectivity matrices of coral larval dispersal is determined by summing up the values in the connectivity matrix, which represent the larval exchange

Table 2 Modelled coral spawning periods based on spawning date records (Baird et al. 2021) relative to the full-moon (FM) period

Species	*Acropora millepora* (− 14 FM)				*Acropora gemmifera* (+ 14 FM)			
Year	Month	Days	Start hour	End hour	Month	Days	Start hour	End hour
2014	04	01–03	19:00:00	23:00:00	03/04	31–02	20:00:00	24:00:00
2015	03	21–23	19:00:00	23:00:00	03	20–22	20:00:00	24:00:00
2016	04	08–10	19:00:00	23:00:00	04	06–08	20:00:00	24:00:00
2017	03	28–30	19:00:00	23:00:00	03	26–28	20:00:00	24:00:00
2018	04	16–18	19:00:00	23:00:00	04	14–16	20:00:00	24:00:00
2019	04	05–07	19:00:00	23:00:00	04	04–06	20:00:00	24:00:00
2020	03	25–27	19:00:00	23:00:00	03	24–26	20:00:00	24:00:00
2021	04	13–15	19:00:00	23:00:00	04	12–14	20:00:00	24:00:00

rates or probabilities between different reef locations. This summation provides the cumulative measure of larval movements and represents the total larval exchange $\left(\sum_{ij} M_{ij} \right)$.

In this study, four connectivity metrics were considered based on Google's PageRank algorithm (Page et al. 1999) introduced by Frys et al. (2020) to study coral connectivity in the Florida Reef Tract. Unlike more standard connectivity metrics, such as in- and out-degree that consider only the direct incoming/outgoing connections to a reef, metrics based on Google's PageRank take the entire connectivity graph topology into account (Frys et al. 2020). They thus can identify robust multi-generational source and sink reefs. Here, we considered the incoming and outgoing PageRank metrics, and also their combination suggested by Frys et al. (2020) to derive protection and restoration PageRank metrics. The incoming and outgoing metrics measure the sink and source potential of a reef by considering the complete upstream and downstream topology of the connectivity graph. A reef with a high incoming PageRank metrics score will thus receive many larvae from many reefs that also receive many larvae from reefs further upstream. Such a reef will be particularly resilient to disturbances. A reef with a high outgoing PageRank score will supply many larvae to many other reefs that also supply larvae to other reefs further downstream. It will thus be particularly useful to the rest of the reef system. The PageRank protection metric is calculated by normalising the difference between the outgoing and incoming metrics with their sum, thereby identifying reefs that are good larval exporters but that do not receive many larvae from other reefs. Reefs with a high protection score are thus, at the same time, useful to other reefs and vulnerable to disturbances. They should therefore be protected in priority. Finally, the PageRank restoration metric is calculated by multiplying the outgoing and incoming metrics. It identifies reefs that are both good larval sources and larval sinks. By being at the same time resilient to disturbances and useful to the rest of the system, they are good candidates for restoration projects by minimising the risk of being disturbed while maximising the positive impact of restoration on downstream reefs.

Results

Hydrodynamic model validation

Firstly, the hydrodynamic model outputs were validated against sea surface elevation at Baubau (see Fig. 1 and Appendix Fig. 6. The simulated elevation agreed well with the field measurements (see Appendix Fig. 7), as confirmed by the relatively small values of the root mean square error (11 cm), as

well as by the high correlation coefficient (0.967), and the high agreement index value (0.983). The amplitude and phase of each tidal constituent in the modelled and observed time series were then extracted and compared (see Appendix Fig. 8). The main tidal constituents were M2 (principal lunar semidiurnal constituent), K1 (lunar diurnal constituent), S2 (principal solar semidiurnal constituent), and O1 (lunar diurnal constituent). Overall, the agreement between modelled and observed tidal components was excellent, with an average RMSE of 8 mm for the amplitude.

Inter-annual variability of larval exchanges

It is well known that the Indonesian region, including the WNP, was affected by the ENSO (Susanto et al. 2006). The ENSO was responsible for numerous anomalies in weather patterns, sea surface temperature, and oceanic currents (Richmond 1984). Meanwhile, ocean current velocity and direction were considered as conduits for the dispersal of coral larvae (Urban and Pratson 2008; Richmond 1984), so that coral larval dispersal patterns could be highly impacted by El Niño and La Niña phenomena. These results revealed that the total larval exchanges $\left(\sum_{ij} M_{ij} \right)$ of both *A. gemmifera* and *A. millepora* in the study area significantly increased during the strong El Niño event in 2015 and the weak La Niña event in 2021 (see Appendix Fig. 9) and slightly increased during pre-El Niño years (2014, 2018) and during the weak El Niño event in 2019. The increased total larval exchanges in 2015 and 2021 could be attributed to a greater number of connections among reefs, resulting in a higher overall larval exchange.

Previous research has shown the influence of the El Niño Southern Oscillation on coral connectivity, with increases in overall connectivity across the Pacific (Urban and Pratson, 2008). During the El Niño phase the Lombok Sea and the Flores Sea, located south-east of the WNP, generally have more significant water mass transport than in neutral years (Van Sebille et al. 2014). These phenomena will affect the dispersal of larvae within the WNP and may explain why in Pre-El Niño, El Niño and La Niña years, the surface waters flow over greater distances/areas, resulting in a significantly higher number of larval exchanges. By considering the interconnected dynamics of ENSO, IOD, monsoonal transitions, and the Indonesian Throughflow, the complex factors influencing larval dispersal patterns within the WNP can be better understood.

Connectivity metrics

How often each sub-reef was among the top 25% best larval exporters or importers (as defined by the outgoing and incoming PageRank metrics) was evaluated over the eight simulated years and for both coral species. Sub-reefs with a

score of 16 out of 16 were therefore always among the best performing reefs and were thus very stable larval sources or sinks. Those best performing reefs were mapped for frequencies of 10, 13 and 16 out of 16 (Fig. 2). On the one hand, the best source sub-reefs were concentrated around Wangi-Wangi and Kaledupa islands and smattered over the central southern atolls, Koko reef, Koromaha reef, and Anano Island (Fig. 2a). These were the best larval suppliers, and hence played a crucial role in supporting the WNP coral reef ecosystems. On the other hand, the top importing sub-reefs were predominantly found around the North Lintea Island, South Lintea Island, Kapota Reef, and Koko reef (Fig. 2b). These sub-reefs consistently received many larvae from adjacent reefs and were thus particularly resilient to perturbations.

Similarly, the sub-reefs with PageRank protection metric values that were consistently ranked among the top 25% were identified. Those reefs were considered good candidates for reef protection programmes. They were mostly located northeast of North-Lintea Island (Fig. 3). It is interesting to note that there was little overlap between the existing MPZs (dark blue areas in Fig. 1, Balai Taman Nasional Wakatobi 2020) and the reefs that were identified from the multi-year and multi-species connectivity analysis. This discrepancy was confirmed when highlighting current MPZs within the PageRank protection index histogram of all reefs in the WNP (Fig. 4). The reefs that currently benefited from the largest level of protection were mostly within the lower and medium ranges of the protection index histogram. These reefs were therefore either moderate larval suppliers and/or were naturally resilient to disturbances thanks to a robust larval supply from neighbouring reefs. This means that few of the reefs that were good larval suppliers but received low volumes of larvae from upstream reefs benefited from protection under the current WNP zonation plan.

Reefs that consistently had the highest PageRank restoration score were located around the southern atolls (Kaledupa reef and Kapota reef), the main islands, and the South-Lintea Island (Fig. 5). Some outer reefs such as Koko and Koromaha reefs, and Ndaa, Kentiole, Moromaho, and Runduma Islands, also had a high restoration potential. Those reefs both supplied larvae to downstream reefs and received larvae from upstream reefs. They were the most robust stepping stones in the 16 connectivity networks derived for 8 different years and 2 different species. Coral reefs at the Ou Tooge-Waha site, where a restoration program had been underway since 2017 (Asuhadi et al. 2021), had a consistently low restoration score. These sub-reefs were not included in the top 25% of reefs for either the protection or the outgoing connectivity scores. However, they were among the top 25% of reefs for the incoming connectivity score. Coral reefs that were part of the current reef restoration planning were therefore unlikely to be good larval suppliers and hence had a limited impact on the other reefs. However, since they received

many larvae from other reefs, they were likely to be quite resilient to disturbances.

Discussion

This study aims to support coral reef conservation and restoration programs within the WNP based on the modelling of reef connectivity. On a larger scale, multispecies connectivity studies have shown that the Coral Triangle, particularly the WNP, is an essential connectivity hub for anemonefishes, damselfishes, and corals (Treml and Halpin 2012). On a global scale, Wood et al. (2014) modelled the dispersal of generic broadcast spawning coral species, showing that the Coral Triangle, including the WNP, scored highly in terms of source-potential indices. In addition, due to its rich biogenic habitats and protected species, the WNP is categorised as a high biodiversity site and should be protected and restored (Asaad et al. 2018). Therefore, high-resolution information on connectivity within the WNP, such as that provided in this study, will be valuable to support future protection and restoration programs in the park.

This connectivity study enabled us to identify coral dispersal patterns within the WNP and recognise critically important coral reef areas that need to be conserved. The effectiveness of the existing zonation plan was also evaluated, especially with respect to the most heavily protected areas, to propose amendments where they seem to be needed. Using Google's PageRank algorithm, a protection score for every sub-reef in the study area was calculated. Here the protection and conservation priority reefs as those with protection PageRank scores in the top 25% was defined. Unfortunately, the results show that most reefs in the existing protected zones are not within this top 25% category. This finding suggests a mismatch between the current WNP zoning plan and the coral reef ecosystems that are most in need of protection. Several coral reef areas with high protection scores are not included in the existing MPZs, such as the reefs around the main islands of Wangi-Wangi and Kaledupa and southern atolls (e.g. Kaledupa reef). Therefore, the re-zoning of these high-value reefs in future revisions of the WNP zonation plan was urge. Nonetheless, the recommended amendments are conveniently presented in Table 3, which offers a comprehensive overview with two distinct lists: high-value sites lacking enhanced protection and existing protected sites with poor connectivity scores.

The areas with a high potential for restoration programs were also evaluated by identifying sub-reefs that supply and receive many larvae, and are therefore the most suitable sites for transplanting corals. Coral reef restoration projects require systematic planning, and choosing suitable locations for restoration programs is critical to the successful recovery of coral reefs (Precht and Robbart 2006). The PageRank
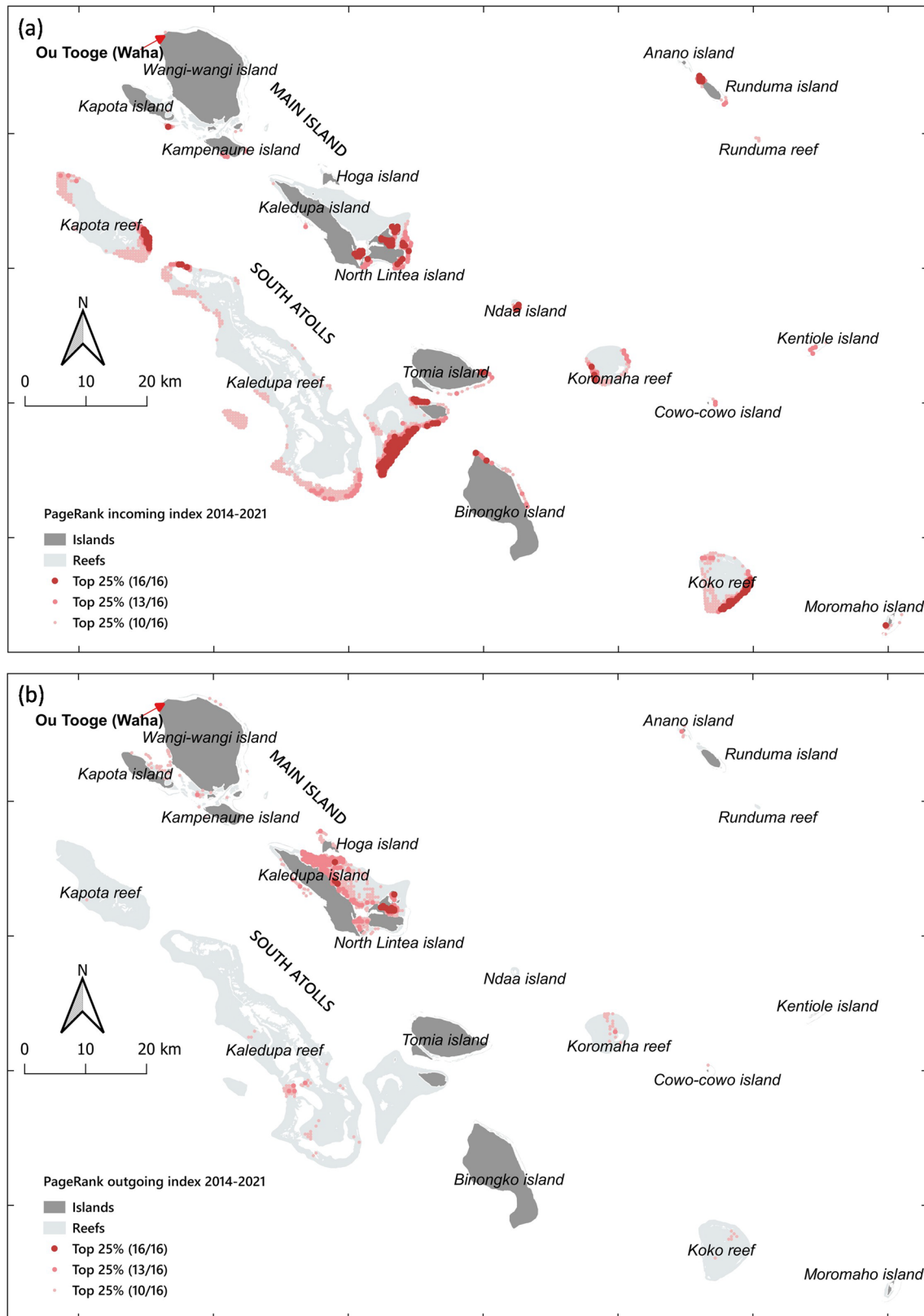
Fig. 2 Top 25% PageRank (**a**) incoming and (**b**) outgoing (**b**) index value over the period 2014–2021 based on the coral larval dispersal of two scleractinian coral species obtained with the PageRank algo- rithm. 16/16 means the sub-reefs appeared in the top 25% outgoing- incoming PageRank index values in all eight simulated years and for both species
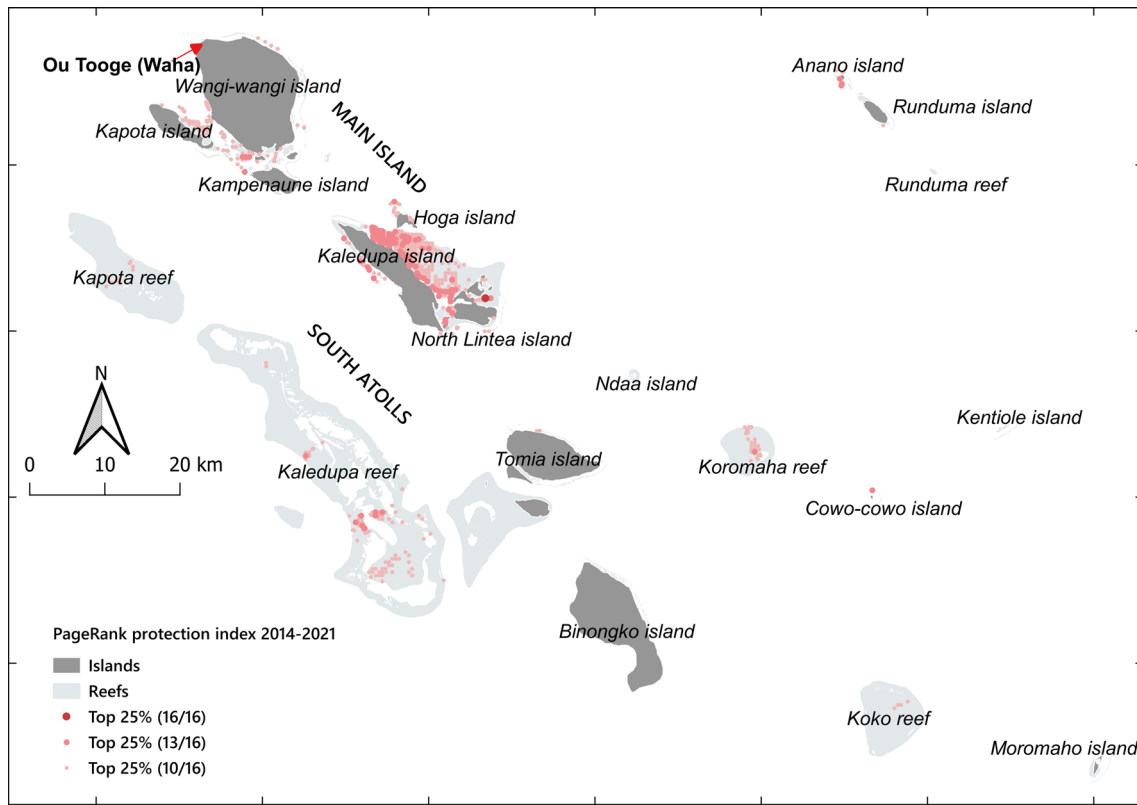
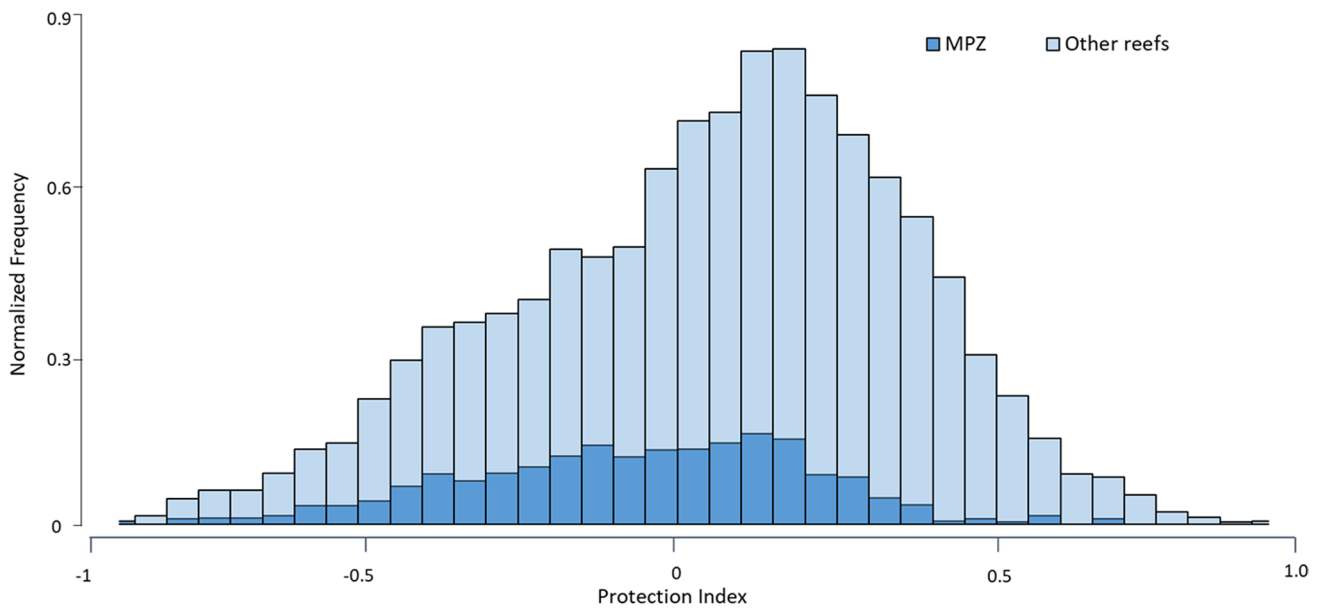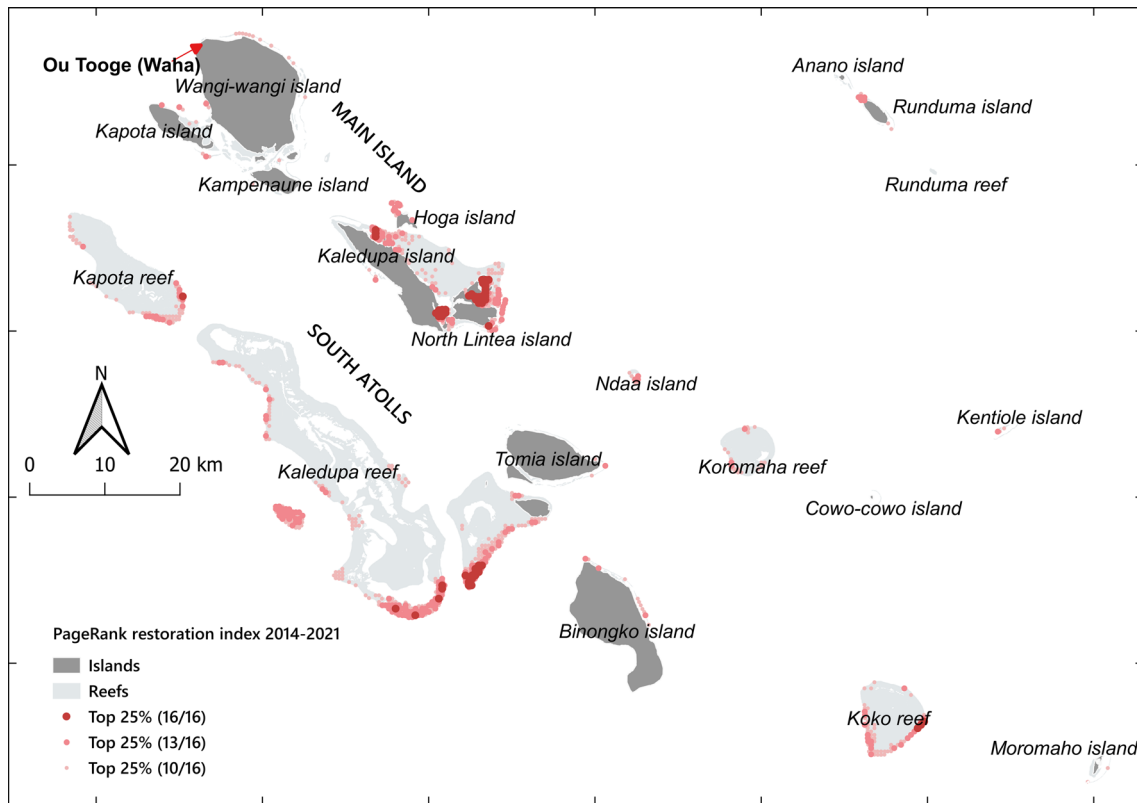**Fig. 3** Top 25% PageRank protection index values over the period 2014–221 based on the coral larval dispersal of two scleractinian coral species obtain with the PageRank algorithm. 16/16 means the sub-refs appeared in the top 25% PageRank protection index values in a all eight simulated yeas and for both species

Fig. 4 Histogram of average Protection PageRank index scores overlaid by existing marine protection zones (MPZs) in the WNP for the period 2014–2021

Fig. 5 Top 25% PageRank restoration index values over the period 2014–2021 based on the coral larval dispersal of two scleractinian coral species obtained with the PageRank algorithm. 16/16 means the sub-reefs appeared in the top 25% PageRank restoration index values in al eight simulated years and for both species. The current restoration project site in the WNP of Ou Tooge (Waha) has a low restoration index score

Table 3 Comprehensive overview of high-value sites lacking enhanced protection and protected sites with poor connectivity scores

High-value sites not currently under enhanced protection	Protected sites with poor connectivity scores
Lat −5.56, Lon 123.86 between Lintea Tiwolu and Darawa island	Moromaho island
Lat −5.39, Lon 123.58 and Lat −5.39, Lon 123.57 Southwest side of Wangi-wangi island	Kentiole island
Lat −5.4, Lon 123.57 Northwest side of Komponaone island	Some west-side of Kaledupa reefs
Between Kaledupa and Hoga Island and Northwest of Kaledupa island	Runduma Reef
Some reefs in Kaledupa reefs	Southeast Wangi-wangi island (Lat -5.39, Lon 123.67)
Lat −5.74, Lon 124.192, Koromaha reef	

restoration index was calculated for every sub-reef in the study area and pinpointed potential restoration program sites with the highest index scores. In 2017, the relevant government unit in the Indonesian Ministry of Marine Affairs and Fisheries (LPTK BRSDM KP) designated Ou Tooge, located on the north-west coast of Wangi-Wangi Island, as one of the areas to be restored through the deployment of the artificial substrate and *Isis hippuris* (sea bamboo) cuttings. Ou Tooge became the site of an 8.82 ha Community-Based Biodiversity Garden (Combbity) in the coastal waters of Wangi-Wangi Island. Ou Tooge was chosen for several reasons; this sites was under pressure, especially from destructive fishing; it is the largest lagoon in the coastal waters around Wangi-Wangi Island; it is located near a coastal community; and conservation practices had been ongoing for more than a decade (Asuhadi et al. 2021). Unfortunately, these results show that the restoration index score for Ou Tooge is low. This means that reefs in this area are not major

stepping stones (i.e. both significant larval exporters and importers) in the connectivity network; therefore, this site is not ideal for a coral reef restoration program. Other reefs with a high PageRank restoration index value that were identified —dispersed over the southern atolls, main islands, and outer reefs—for consideration as potential sites for future restoration projects.

Geophysical conditions determine the pattern of larval dispersal in the WNP, both directly and indirectly. Previous studies have shown that Indonesian surface current flows passing through the WNP are associated with seasonal wind variability (Sprintall and Révelard 2014). Furthermore, they have connections to the ITF, a system responsible for transporting water masses from both the North Pacific and South Pacific Oceans into the Indian Ocean. This process introduces comparatively fresher, and cooler water to the WNP as it traverses the Flores and the Banda Seas (Schneider 1998; Baumgart et al. 2003; Sprintall et al. 2014; Sprintall and Révelard 2014). Pacific subtropical water (high salinity) and the North Pacific intermediate water (low salinity) mix vertically in the Banda Sea (Sprintall et al. 2014), also impacting the hydrodynamics of the area and indirectly affecting the larval dispersal. As a result of these ocean currents, surface waters flow south-eastward along the east side of the main island and south-westward along the west side of the southern atolls. Additionally, tides play a role in the dispersal, causing some larvae to oscillate back and forth through inter-island straits and southern atolls.

However, it is important to acknowledge certain limitations in this study. Firstly, the study does not account for the potential effects of elevated temperatures during El Niño events, which can lead to earlier spawning and accelerated larval development, as well as the impact of cooler temperatures during La Niña events, which could result in delayed spawning and slower larval growth (Edmunds 2017; Toth and Aronson 2019). Furthermore, this study does not consider other factors such as nutrient availability, oxygen levels, and salinity, which can interact with temperature changes and potentially modify the observed connectivity patterns (Toth and Aronson 2019). To gain a comprehensive understanding of larval responses to multiple environmental stressors, it is crucial for future research to investigate the complex and nonlinear physiological responses exhibited by larvae.

These results are model-based and await validation with empirical data; nonetheless, they represent the most comprehensive information to date on coral reef connectivity in the WNP. However, it should be noted that natural systems are complex, and many factors which can influence larval connectivity in the real world were not considered in this study. For example, this study considered two broadcast-spawning acroporid corals, and a broader range of species would be required for a more accurate and complete assessment. Connectivity patterns can vary significantly among species due to differences in reproductive strategies, larval behaviours, and environmental conditions. Including additional species with different spawning seasons or larval durations would likely result in different connectivity patterns and may require revised recommendations. Despite the above limitations, the results of this assessment provide spatial information regarding areas WNP managers should prioritise for protection and restoration. These data can help to design improvements to the zonation plan and inform restoration program planning in the WNP.

Conclusion

This study provides quantitative information on coral connectivity within the WNP at the individual reef scale. This connectivity information can help marine managers select the best-suited locations for protection and restoration to maximise ecosystem resilience within the WNP. The results suggest a mismatch between the existing marine protected zones and the reef areas that should be protected for maximum conservation effectiveness, as most of the existing marine protected zones are not in the top 25% of reefs based on protection index scores. The current restoration area of Ou Tooge is unlikely to be a significant larval supplier to adjacent reefs. Based on these results, there are reef connectivity hotspots that were recommended should be prioritised to improve the effectiveness of future conservation and restoration programs in the WNP.

Appendix

Additional result analysis

This appendix offers supplementary data that reinforce the analysis of the results discussed in the main article. The included figure and data serve to enhance the comprehensive understanding of the phenomena under investigation Figs. 6, 7, 8, 9.
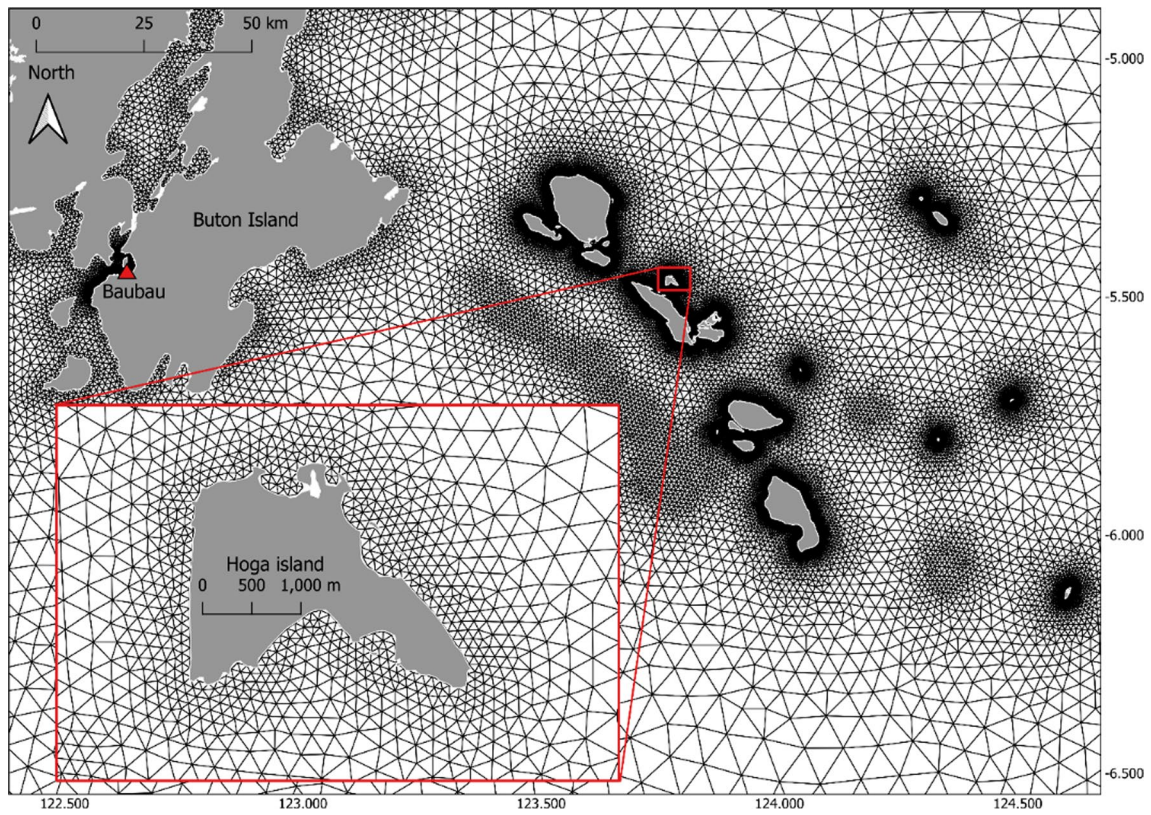
Fig. 6 The computational domain, which covers the area of interest, was discretised with an unstructured mesh. The mesh resolution was the highest (50 m) around the Wakatobi islands, over the reefs, and near the tide gauge at Baubau. It decreased to 12 km in the open ocean, far from the region of interest
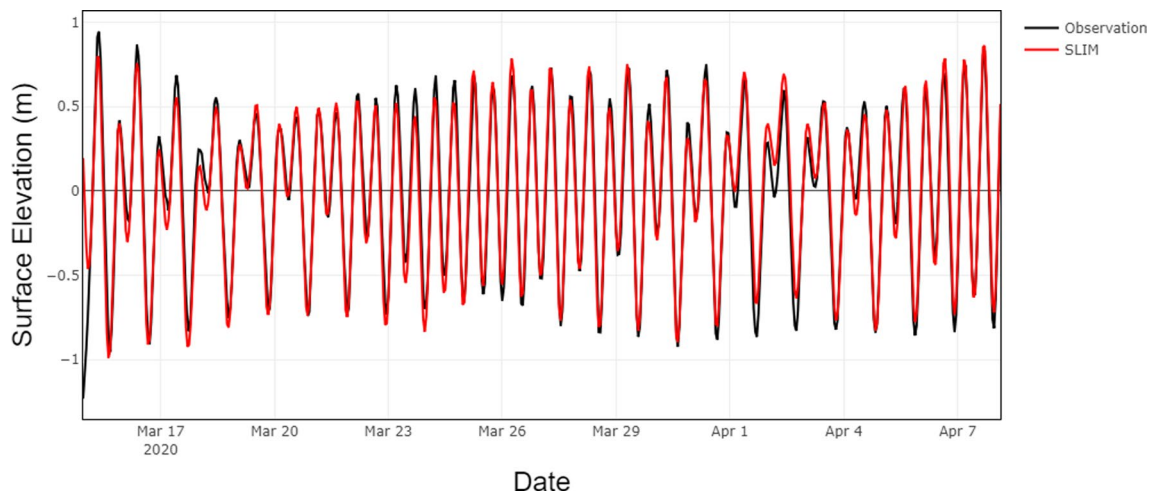

Fig. 7 Time-series plot of observed (black) and predicted (red) sea surface elevations at the Baubau station, from 18 March to 8 April 2020
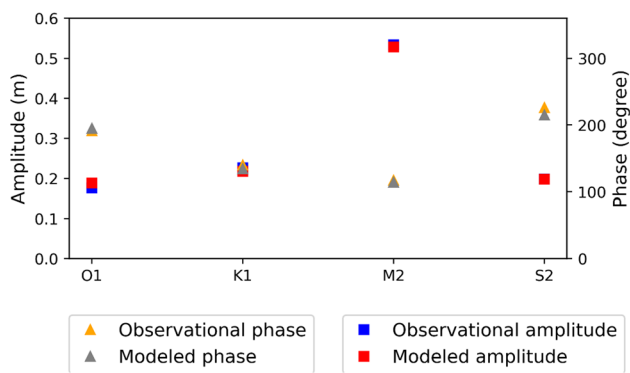
Fig. 8 Observed and modelled amplitude (left axis) and phase (right axis) of the most energetic (principal) tidal constituents
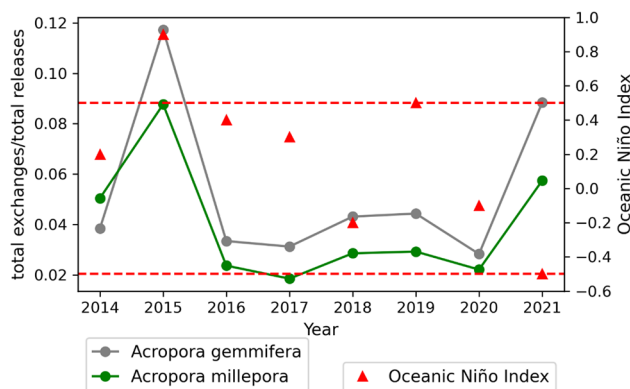

Fig. 9 The dynamics of the ratio between total larval exchanges and total larval releases in the region of interest for two species, *A. gemmifera* and *A. millepora*, were compared to the Oceanic Niño Index from 2014 to 2021. The analysis revealed a significant increase in the ratio during strong El Niño events (2015) and La Niña events (2021). The red dashed lines indicate the thresholds of the Oceanic Niño Index for the occurrence of El Niño (0.5) and La Niña (−0.5)

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