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Oceanographic chaos and its role in larval self-recruitment and connectivity among fish populations in Micronesia

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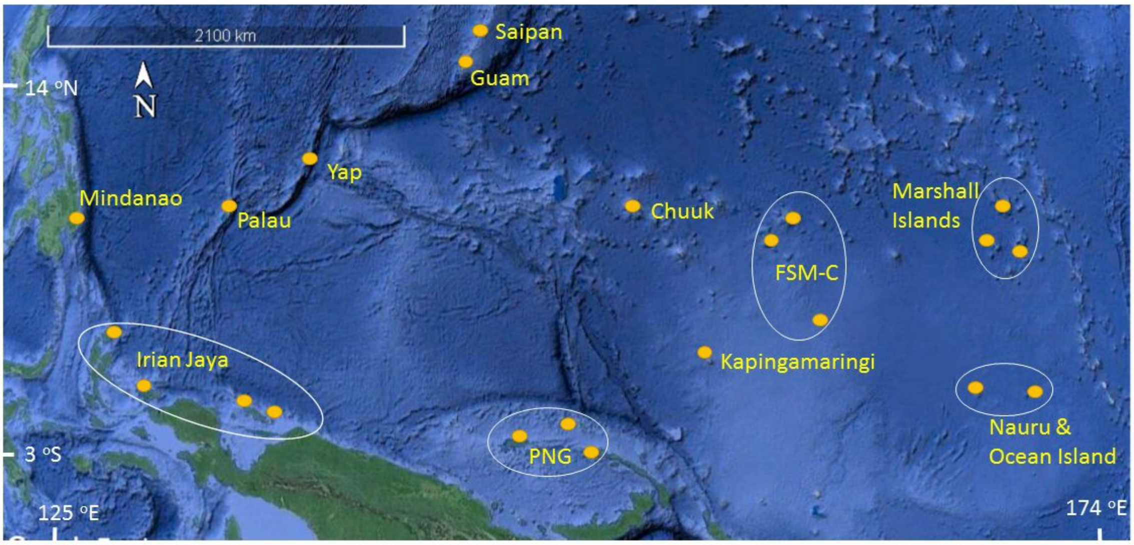
Abstract

A 30-year time series of the recruitment of rabbit fish, an herbivorous coral reef fish, on the island of Guam in the tropical western Pacific, showed variability that ENSO alone does not explain. To help explain this variability, a high-resolution biophysical model that includes directional swimming reveals how mesoscale turbulence and ENSO-driven changes in the ocean circulation control the self-recruitment of rabbit fish. ENSO drives island wakes that enhance the capacity to retain locally spawned larvae, and mesoscale turbulence generates much variability and promotes seaward dispersion at time scales larger than the Pelagic Larval Duration. The same processes are predicted to occur for the self-recruitment of grouper fish, a carnivorous coral reef fish, in Palau, Micronesia. The models suggests that 99% of these fish larvae are exported seaward from Guam and Palau. Those larvae are the ones that could provide connectivity between reefs and islands in Micronesia. This connectivity for the grouper fish was predicted using an altimetry-driven advection-diffusion oceanography model for 40 mass spawning events spread over 10 years. The mesoscale turbulence, and not the mean oceanographic currents, is the dominant process controlling the connectivity, which is thus chaotic. This finding applies also in the Galapagos archipelago and the Coral Sea fringing the Great Barrier Reef.

Keywords: Eddies; Southern Oscillation Index; coral reef fish; self-recruitment; connectivity.

1. Introduction

The Pacific Islands have been described politically as Small Island Developing States, but the regional perspective is that they are large ocean states, taking into account their extensive, and sometimes overlapping, Exclusive Economic Zones (EEZs). Micronesia includes a number of islands in the central and western Pacific. In this study, Micronesia is defined as the area from Mindanao to the West and the Marshall Islands to the east, PNG to the South and Saipan to the North (Figure 1a). These islands have numerous and highly diverse coral reefs of critical economic, cultural and ecological value to island communities (Figure 1b).



(a)

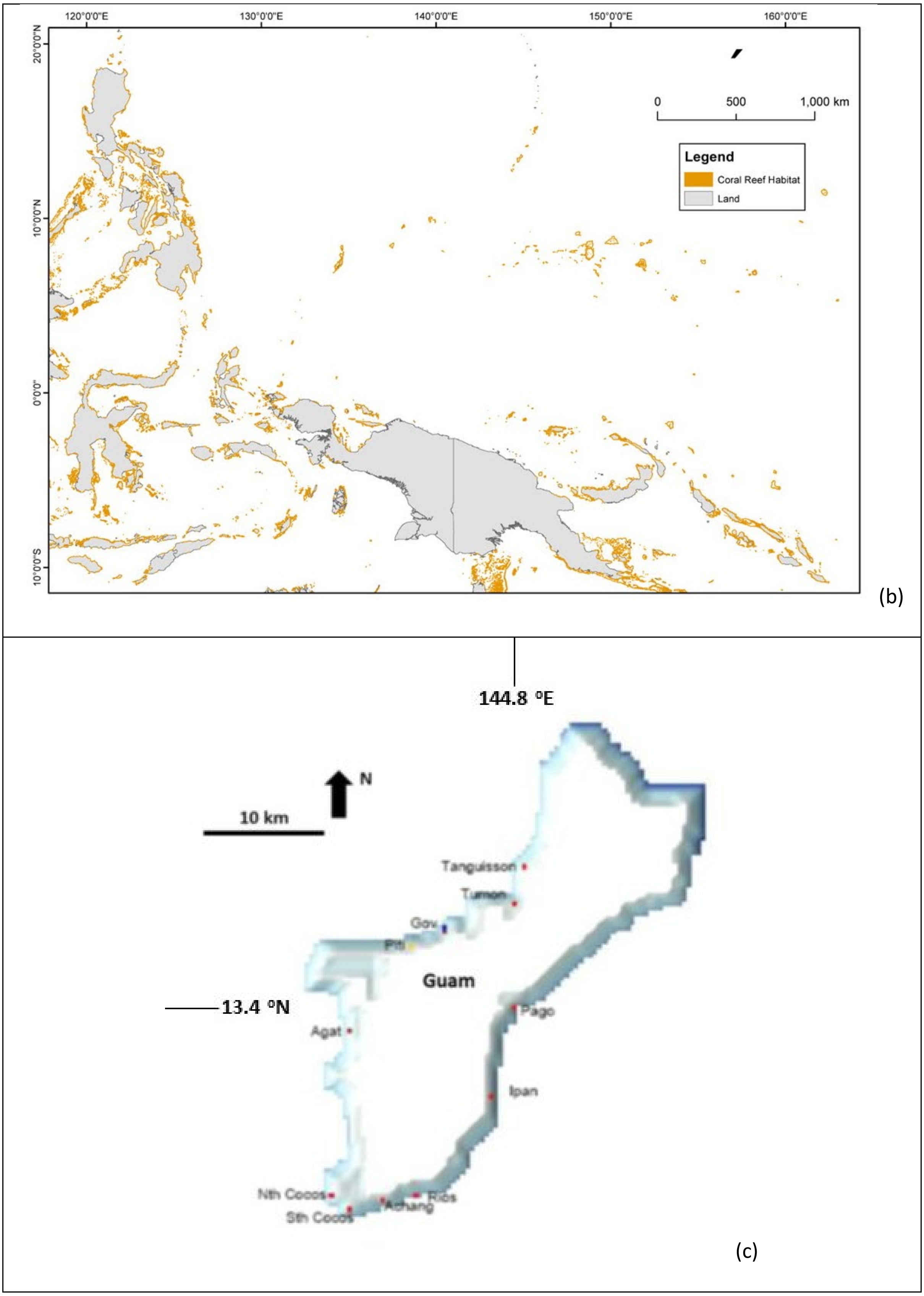


Figure 1. (a) A location map of Micronesia. The FSM is spread over a vast area; to introduce some

spatial resolution, various islands are distinguished, within the core area of the Federate States of

Micronesia (FSM) referred to as FSM-C and Papua New Guinea referred to as PNG. (b) Coral reef habitats in Micronesia (Source: K. Critchell). (c) Map of Guam and the rabbit fish spawning sites; Dr. A. Halford kindly provided these locations.

Fish, such as the rabbit fish species, *Siganus spinus* and *S. argenteus*., as well as other species such as the snapper (*Lutjanus* sp.) and the grouper (*Epinephelus fuscoguttatus, E. polyphekadion* and *Plectropomus areolatus)*, are important economically, ecologically and culturally in Micronesia. For instance, in Guam (Figure 1c) the juveniles, referred to locally as mañahak, recruit to the reefs and shallow water bays. During these periods, special accommodation is made for fishers, such as limiting jet ski activity in areas where the juveniles aggregate, to allow them to capture the immature fish, primarily via throw net. The large numbers of these small herbivores are also ecologically significant, as they rapidly graze down several species of fleshy and filamentous algae. While there are recognized annual timing patterns for the fish recruitment events, year-to-year variation has not been adequately studied, particularly with regards to El Niño – Southern Oscillation events. Due to their ecological, cultural and economic importance, there clearly is a need to understand the relationship between local and regional current patterns and fish distribution and recruitment patterns. These patterns are due to both self-recruitment (i.e. the larvae recruiting at their spawning sites) and to connectivity between islands (i.e. the larvae recruiting at a different island than their natal island). This information is of great value to fishers and resource managers of islands in Micronesia.

There has been no biophysical modeling of reef fish recruitment and connectivity in Micronesia. There have been however a few biophysical modeling studies of the distribution of coral larvae following spawning events within the archipelago of Palau (e.g. Golbuu et al., 2012; Gouezo et al., 2019). These studies show that there is self-seeding of coral larvae to local reefs as well as connectivity among reefs from different sites within island archipelago. These studies also suggest that some coral larvae are exported to the surrounding ocean, where their fate remains largely unknown. It is expected that the water currents will carry these exported larvae to other reefs and islands within Micronesia, provided that the transport occurs at a time scale less than the pelagic larval duration (PLD), or competency period, during which they are capable of successful settlement and metamorphosis (Richmond, 1987). If successful, this transport creates connectivity among different islands of Micronesia and regionally. From genetic studies, this connectivity was demonstrated to occur for corals across Micronesia (e.g. Davies et al., 2014). Cross et al. (2016) in their genetic studies on a single coral species suggested that Palau coral populations could have been reseeded by larvae from the neighbouring island of Yap (see a location map in Figure 1a) and other more distant populations that were mixed with larvae from local populations. Ma et al. (2018) found from an examination of their mitochondrial control region and microsatellite markers, evidence of hot spots (clusters), and a possible weak connectivity between them, across Micronesia for three aggregating grouper species.

For the case of Guam, we analysed of a 30-year time series of the catch of rabbit fish, an herbivorous coral reef fish. We show that ENSO events generate island wakes that enhance the capacity to retain locally spawned larvae; however, mesoscale turbulence promotes seaward dispersion. The same processes are predicted to occur for the self-recruitment of grouper fish, a carnivorous coral reef fish, in Palau, Micronesia. The models suggests that 99% of these fish larvae are exported seaward from Guam and Palau. Those larvae are the ones that could provide connectivity between reefs and islands in Micronesia. To estimate this connectivity, a biophysical model of reef connectivity in Micronesia is proposed. We show that present oceanographic models of Micronesia are not able to describe with proper resolution the velocity data at the surface because of meso-scale turbulence. We show that the same meso-scale turbulence prevails in the Galapagos archipelago and in the Coral Sea fringing the Great Barrier Reef. We incorporated meso-scale turbulence by using NOAA altimetry data averaged over 5 days and at 1/3 of a degree horizontal resolution. They are used in input for the biological model. The biological model is driven by an oceanography submodel with fine resolution around islands. This connectivity was modeled and it was found to be chaotic. A few porous clusters of high internal connectivity are predicted in Micronesia, with a small connectivity between them, and this pattern suggests the existence of biogeographic boundaries.

2. Methods

2.1 Reef fish self recruitment in an island setting

To estimate the self-recruitment at typical Micronesia islands, fine-scale models must be used. The best example for island self-recruitment for which data are available is the rabbit fish in Guam. Yearly Guam rabbit fish catch data, comprising both settled fryes and aduts, were provided by the Department of Agriculture, Division of Aquatic and Wildlife Resources, Guam. The fish were assumed to spawn at the sites shown in Figure 1c, as sites where adult populations exist and these are thus likely spawning sites. The biophysical model has an oceanography submodel that provides the surface currents to the larval dispersal advection-dispersion submodel. The oceanography submodel was that of Golbuu et al. (2012); for Guam it had a mesh size of 259 m, it was forced by the tides, the wind, and the altimetry-derived mean oceanic current offshore Guam at the open boundaries. The 5-days averaged near surface currents facing Guam were obtained from the NOAA satellite altimetry database. The influence of ENSO in these data was parameterized using the Southern Oscillation Index (SOI), whose monthly data were obtained from the Australian Bureau of Meteorology.

The larval dispersal submodel moved the larvae using a Lagrangian scheme, assuming a sub-grid scale horizontal eddy diffusion parameter of 0.1 $m^2 s^{-1}$. The fish larvae are assumed to move passively with the water currents at pre-flexion, when they cannot swim, and to swim horizontally and directionally following sound and smell cues towards Guam at post-flexion following the method of Wolanski and Kingsford (2014). The virtual fish larvae were passive at pre-flexion until day 15, when they become capable of directional motion. At that time they started swimming, the swimming speed increased linearly with time to reach a swimming cruise speed of 0.15 m s^{-1} on day

25 and they maintained that speed until day 32. There are uncertainties in all these estimates and they all somewhat affect the results (Fisher, 2000, 2005; Junker et al., 2006; Leis, 2006, 2020, 2021; Soliman et al., 2010; Staaterman et al., 2012).

A number of scenarios, which are typical in the altimetry data, were modeled to help explain the fish recruitment observations. Three of them are described here. In scenario 1, the mean oceanic current, following the altimetry data, was large (0.27 m s^{-1} westward and 0.02 m s^{-1} northward) with no oceanic eddy. In scenario 2, the mean oceanic current was large (0.27 m s^{-1} westward and 0.02 m s^{-1} northward) and there was an anticyclonic oceanic eddy northwest of Guam generating an additional peak velocity of 0.08 m s^{-1}, and this is a realistic scenario based on the altimetry data (Wolanski et al., 2003). In scenario 3, there was a small mean oceanic current (0.09 m s^{-1} westward and 0.02 m s^{-1} northward) and no oceanic eddy.

2.2 Surface ocean currents

Meso-scale turbulence occurs a speeds larger than the mean current, and these meso-scale turbulent events last as long as the fish PLD. Altimetry-derived currents are compared with predicted currents and this shows that present oceanographic models underestimate the meso-scale turbulence in Micronesia, the Galapagos, and the Coral Sea facing the Great Barrier Reef.

2.3 Connectivity within Micronesia

What is important for a larva is the actual currents following the spawning events. As the classical oceanographic models fail to reproduce the meso-scale turbulence in Micronesia where meso-scale turbulence is dominant, we chose not to use the currents predicted by the oceanographic models. Instead, we used the altimetry-derived currents. The reason is simple: without meso-scale turbulence, a reef will systematically seed downstream reefs (downstream in terms of the mean currents) while with meso-scale turbulence a reef can seed areas well away from a mean downstream direction. Therefore, to capture this spatial and temporal variability, the biophysical advection-diffusion model of Wolanski et al. (2020) that relies on altimetry-measured currents for the advection submodel, was used to calculate the connectivity between islands in Micronesia. The model runs with a time step of 5 days at a horizontal scale of 1/3 degree. The altimetry data are corrected, but no correction is perfect, for noise and errors for geoid and poor atmospheric conditions and for the 5° band near the equator (Cheney,2001; Taburet et al., 2019; https://www.aviso.altimetry.fr/es/data/data-access/las-live-access-server/lively-data/2007/january-23-2007-the-equator-against-the-current.html).

The model was seeded with virtual larvae at spawning sites. Temperature and salinity were not included in the model because their gradients across Micronesia are very small, typically less than 0.5 °C for temperature 0.2 psu for salinity between Uwe at the far east of Micronesia and Colonia at the far west of Micronesia (http://www.salinityremotesensing.ifremer.fr/sea-surface-salinity/salinity-distribution-at-the-ocean-surface). The advection-dispersion processes were modelled as being uniform along the vertical column following the diel migration field studies of reef fish larvae of Irisson et al. (2010) who found no difference in mean depth or spread of the reef fish larvae between day and night, except for *Serranidae*.

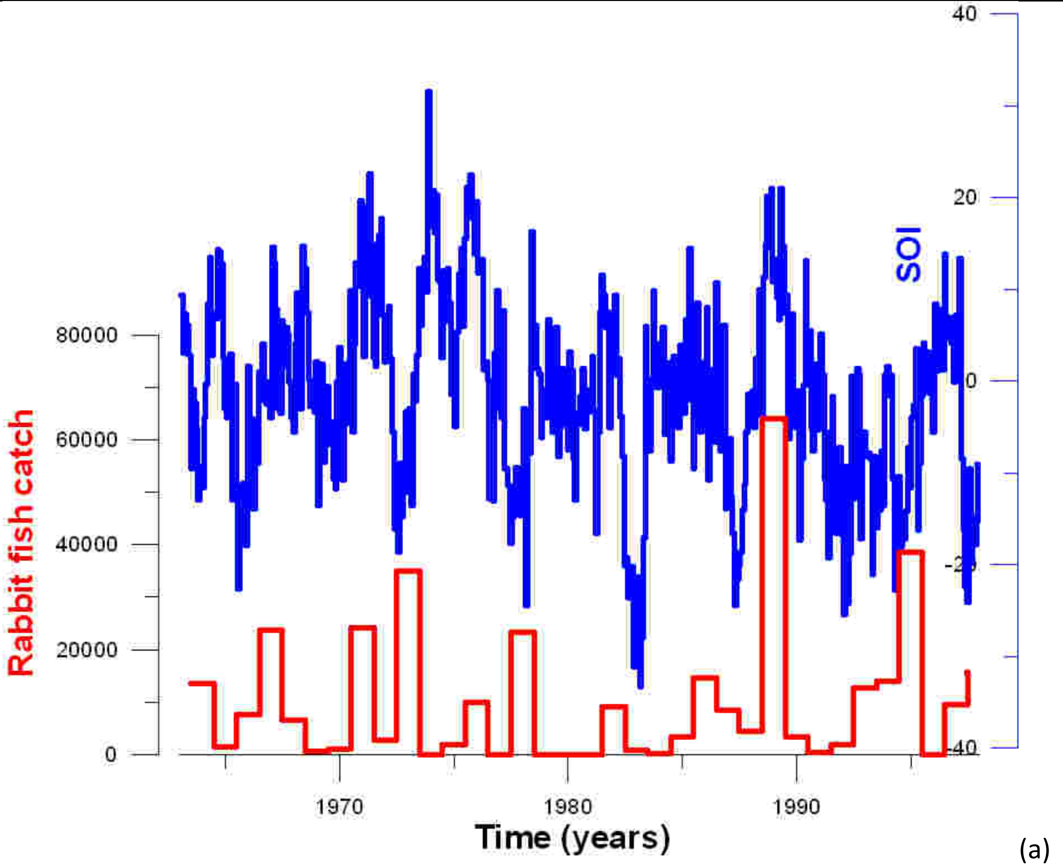
The fish larvae in the Micronesia biophysical model were assumed to remain in the top 30 m of the water column (that satellite altimetry measures), they are transported by the surface currents as measured by altimetry, and they recruit if they reach a recruitment site within a time period less than their PLD. The model used the grouper fish family as the fish to model. Based on their spawning behavior in Palau, groupers spawn during the new moon in April, May, June and July of each year. At each of the spawning (sites shown in Figure 1c), 5000 virtual larvae were released, so that there were 110,000 virtual larvae in the model for each spawning event. The larvae were transported by the actual currents at that time and space. Each monthly spawning event was considered separately from the others to avoid superimposing fish larvae of different ages. The fish PLD was taken to be 80 days as deduced from examining the otolith increment (Lester and Ruttenberg 2005). Even the finest scale (5 km resolution) oceanographic models are too coarse to reliably predict the precise location of recruitment sites. This is because the currents around oceanic islands generate shear layers, eddies, jets and stagnation zones at scales much smaller than 5 km and these complex currents determine the location of the recruitment sites (e.g. Dietrich et al., 1996; Wolanski et al., 2003; Merrifield et al., 2019). Thus, the recruitment sites were assumed to be the cells touching an island or the coast. Altimetry data for the years 2010 to 2019 were used. Thus, the connectivity of fish larvae in Micronesia was studied for 40 spawning events spread over 10 years.

3. Results

3.1 Self recruitment in Guam and Palau

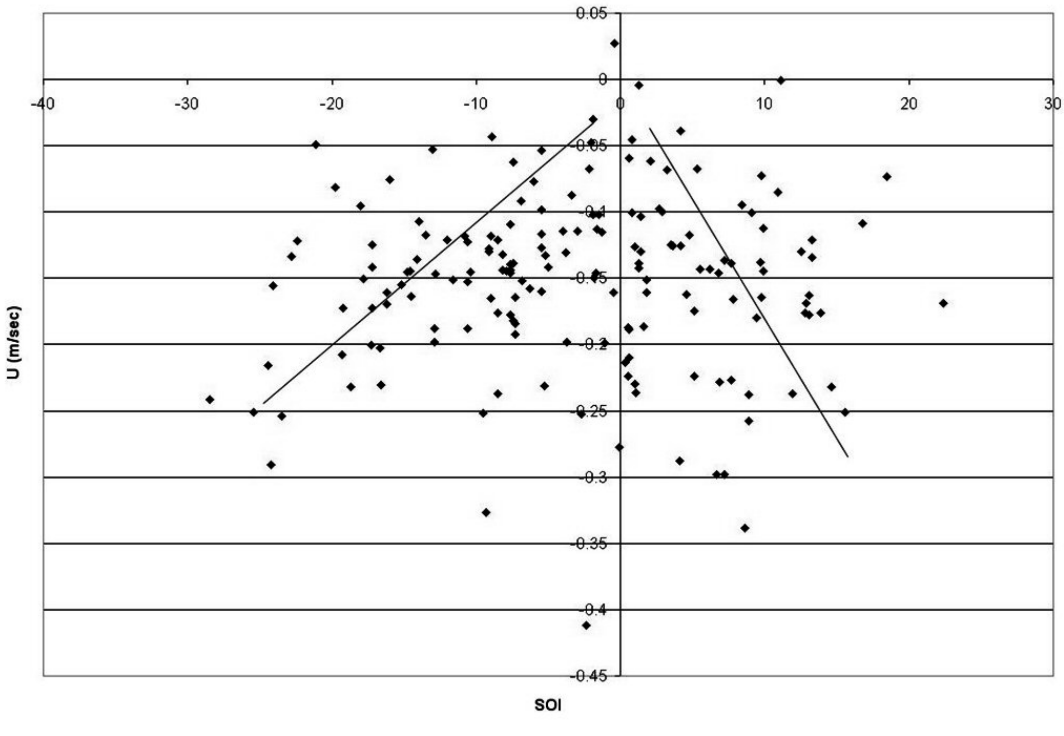
Guam

The rabbit fish catch data show a large inter-annual variability (Figure 2a). At times, high fish catch occurred during years with a large absolute value of the Southern Oscillation Index (|SOI|) but not always; no high fish catch values occurred during years with a small |SOI|. The time-series of the annual fish catch and the mid-year value of the SOI were not correlated (R^2 =0.003). It is known (Wolanski et al., 2003) that the flow field around Guam is commonly disturbed by eddies, with some eddies being meso-scale oceanic eddies, while other eddies are generated by the island disturbing the oceanic circulation. There are no altimetry-derived data before 1992. Figure 2b shows, for the period 1992-1995, that the altimetry-derived surface currents facing Guam was the largest for large values of |SOI| and the smallest for small values of |SOI|, while there was considerable scatter due to the meso-scale turbulence.



Rabbit fish catch
SOI
Time (years)
80000
60000
40000
20000
0
1970
1980
1990
40
20
0
-20
-40

(a)



U (m/sec)
SOI
0.05
0
-0.05
-0.1
-0.15
-0.2
-0.25
-0.3
-0.35
-0.4
-0.45
-40
-30
-20
-10
0
10
20
30

(b)

Figure 2. (a) Time-series plot of the yearly rabbit fish catch (in pounds) in Guam and the monthly Southern Oscillation Index. (b) A scatter plot of the altimetry-derived east-west monthly-averaged near-surface oceanic current (<0 if westward) off Guam and the Southern Oscillation Index (SOI) for the period 1996-2010. The straight line is the suggested linear trend line. The scatter is generated by the meso-scale turbulence.

In scenario 1 (large mean westward current with no oceanic eddy, as shown in Figure 3 (left column), the strong oceanic currents generated an island-driven recirculating flow downstream of Guam that kept pre-flexion larvae within a boundary layer, i.e. within swimming distance from the island; on reaching post-flexion, these larvae were able to successfully swim directionally and recruit. The recruitment rate was 1 % (Figure 4a). For scenario 2 (large mean westward current and an oceanic eddy), the larvae were swiftly flushed away from this boundary layer and only a few stragglers managed to recruit on the southwest tip of the island (Figure 3, middle column). We found the same process of swift flushing when the eddy was cyclonic (not shown). The recruitment rate for scenario 2 was less than 0.02 % (not shown). For scenario 3 (weak mean oceanic current and no oceanic eddy), there was no island-driven recirculating flow trapping pre-flexion larvae; the larvae were swiftly exported offshore (Figure 3, right column). The recruitment rate for scenario 3 was about 0.02% (Figure 4a). The only successful recruitment event for all the scenarios studied occurred for a large mean oceanic current and no eddy. In that best-case scenario, 99% of the larvae do not self-recruit in Guam; instead, they are exported at sea. These findings offer an explanation for the observations (Figure 2a) that the fish catch in Guam is chaotic, because it depends on at least two independent variables controlling the currents (Figure 2b), namely the SOI and the meso-scale turbulence, in addition to fishery effort and demand. As sketched in Figure 4b, the successful self-recruitment of rabbit fish in Guam requires at the time following spawning a strong incoming current that generates an island-generated eddy, no oceanic eddy, and directional swimming by the post-flexion fish larvae.

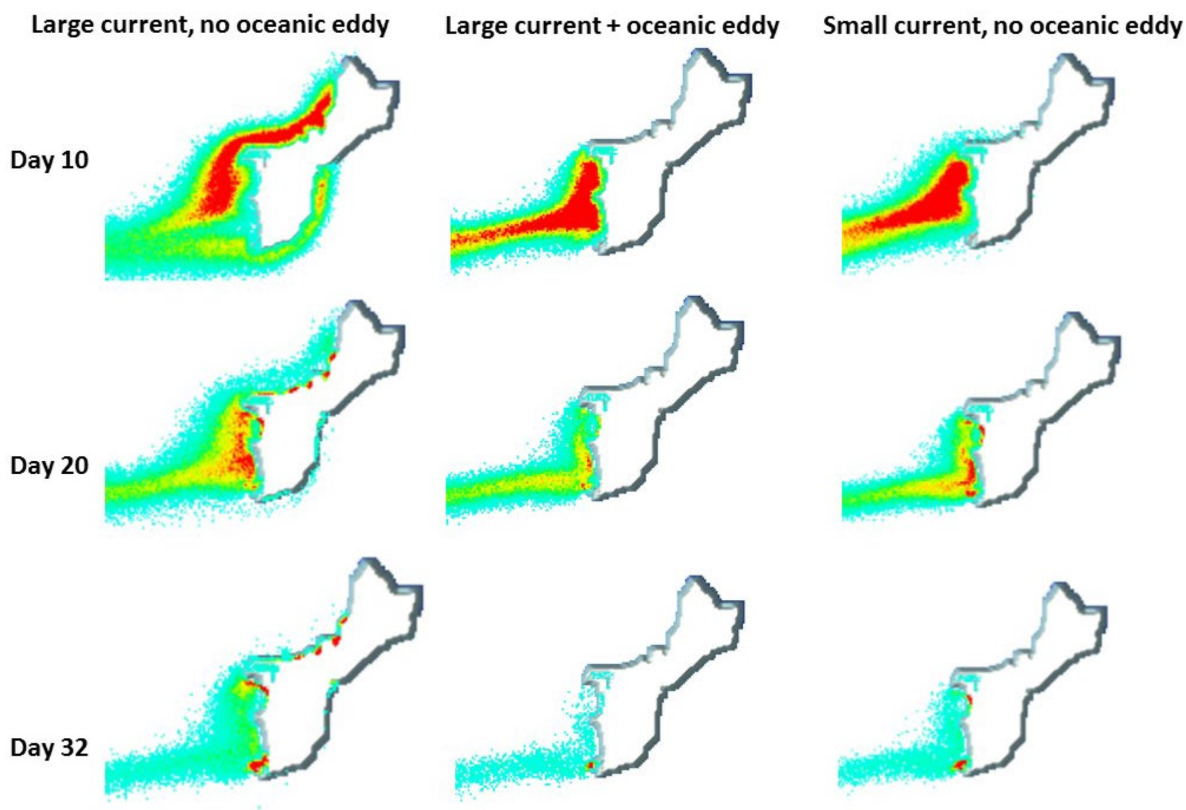
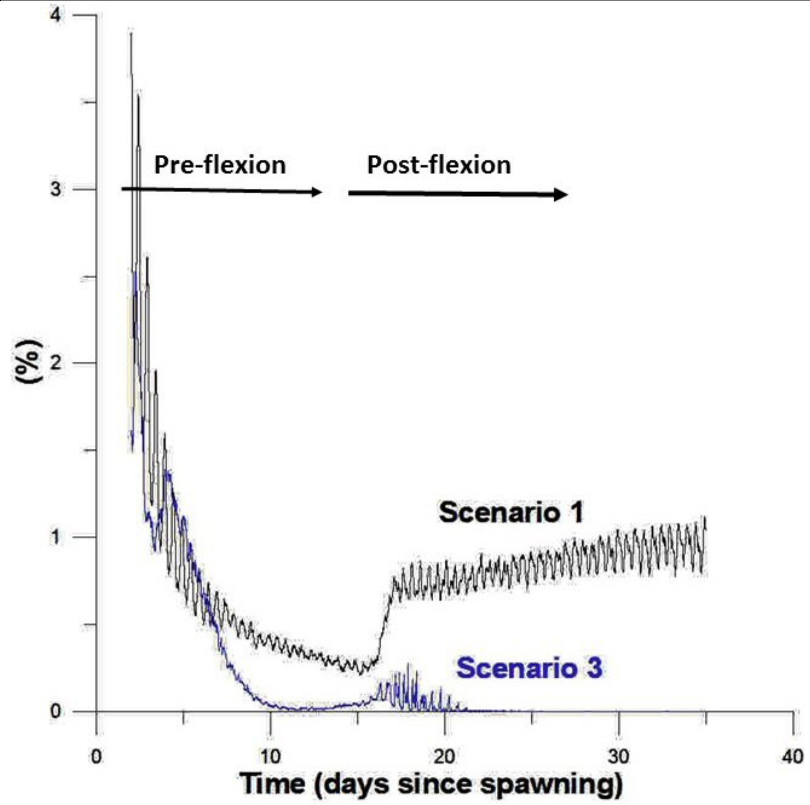
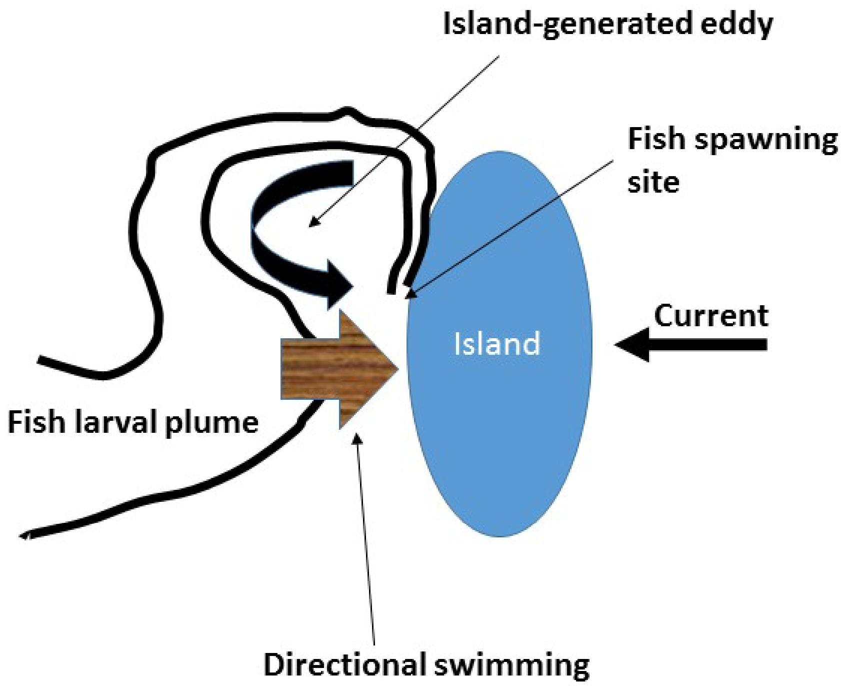


Figure 3. Rabbit fish larval plumes around Guam on (lines) days 10, 20 and 32 after spawning for a large mean oceanic current and no oceanic eddy (left column), a large mean oceanic current and an oceanic eddy (middle column), and a small mean oceanic current and no eddy (right column). All these current scenarios for the water currents are commonly observed in the altimetry data. The colours show the concentration of fish larvae, with red being the highest. The range of the PLD of these fish larvae is 20-32 days.



Pre-flexion
Post-flexion
(%)
Scenario 1
Scenario 3
Time (days since spawning)
0
1
2
3
4
0
10
20
30
40

(a)



Island-generated eddy
Fish spawning site
Current
Island
Fish larval plume
Directional swimming

(b)

Figure 4. (a) Time-series plot of the capture of rabbit fish larvae in Guam for scenario 1 (strong mean oceanic currents and no oceanic eddy) and scenario 3 (weak mean oceanic currents and no oceanic eddy). The high-frequency oscillations are due to the tides. Recruitment starts at post-flexion. (b) A sketch of the processes necessary for self-recruitment of rabbit fish in Guam.

Palau

Mass spawning of groupers occurs in Palau, in Ebiil Passage (Figure 5a). The timing is known (the new moon of April, May, June and July) but the movement of larvae after spawning was not known. To understand the movement of the larvae, the Guam biophysical model was applied to Palau. The model results suggest that, for the usual westward flowing oceanic currents facing Palau, the fish larvae initially disperse seaward to be entrained in an eddy. If, at post-flexion, they do swim directionally to sound and smell cues, then a small fraction of them will recruit to Palau reefs; the rest of the larvae are 'lost' at sea (Figure 5a). This scenario prevails for most currents observed around Palau, except that the recruitment sites will be different for different net oceanic currents facing Palau (Figure 5b). In Figure 5a, the larvae recruit in the Western Passage, an historical grouper fish spawning ground now much degraded, and in Figure 5b they recruit in the historical SE corner grouper fish spawning ground, now depleted due to overfishing. Thus the historical spawning grounds were all connected. In all cases the majority of the fish larvae is 'lost' at sea. The next section of this paper on island connectivity attempts to quantify to which reefs 'downstream' do these 'lost' larvae recruit and what is the relative importance of such recruitment.

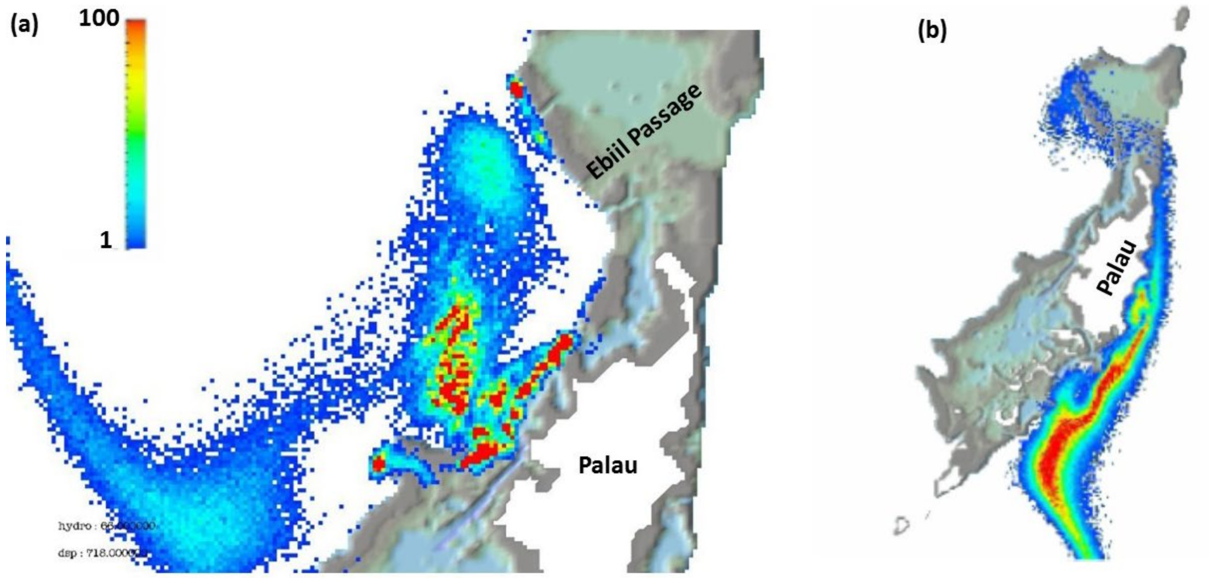
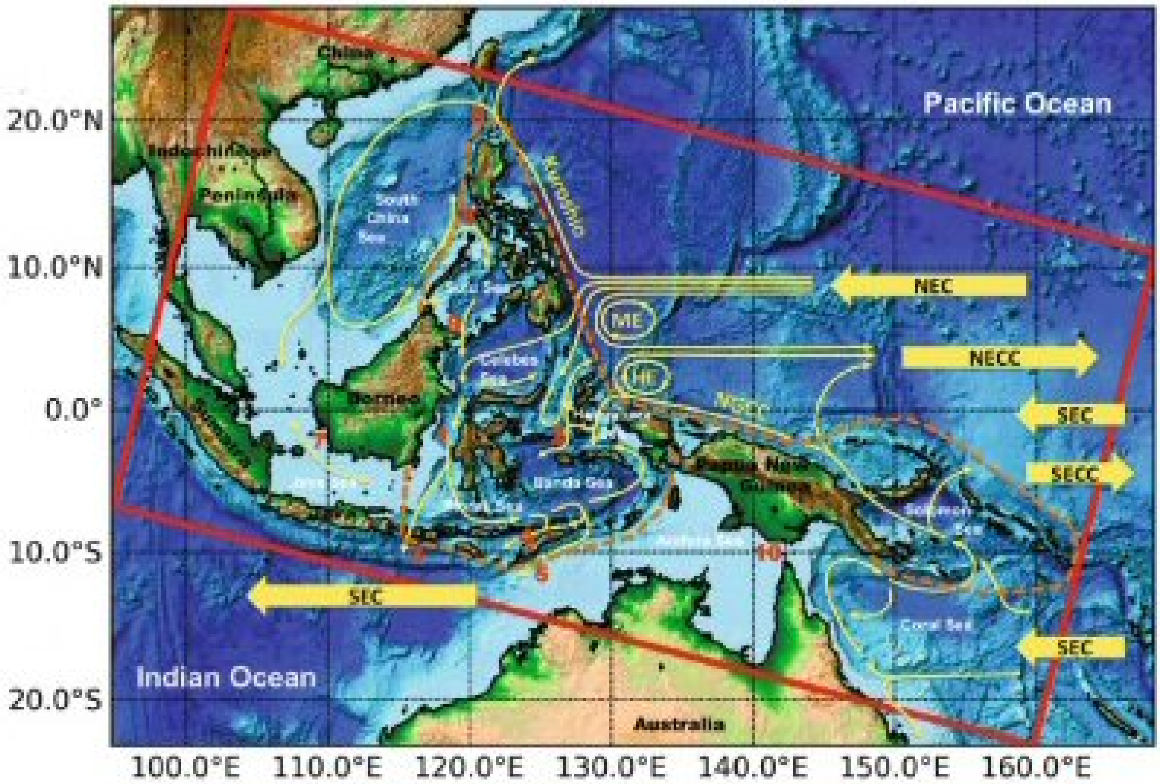


Figure 5. Grouper larval plume at the end of their PLD after spawning at Ebiil Passage in Palau for (a) the usual westward flowing net oceanic currents facing Palau and (b) during the 2005 El Nino oceanographic event. The colours show the concentration of fish larvae, with red being the highest.

3.2 The surface water circulation in Micronesia

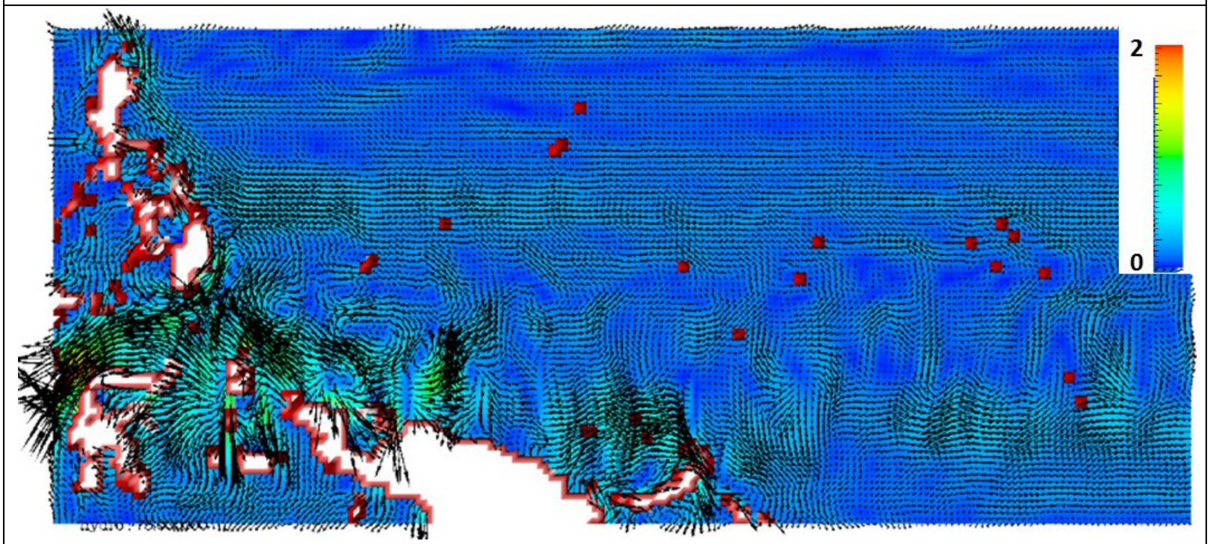
The net, near-surface water circulation in Micronesia is complex (Figure 6a). It includes the North Equatorial Current (NEC), the South Equatorial Current (SEC), the North Equatorial Counter Current (NECC), the Mindanao eddy (ME), the Halmahera eddy (HE), the Kuroshio Current, and the southward flowing Mindanao current along the east coast of Mindanao, and the Indonesian Throughflow (Thompson et al., 2018). The altimetry data reveal that this actual water circulation is much more complex and it has a very large inter-annual variability (Figure 6b-c).

For instance, the mean NECC, the mean NEC, the mean Indonesian Through flow, the mean southward Mindanao Current and the mean northward Kuroshio Current around Luzon, all varied greatly from year to year.



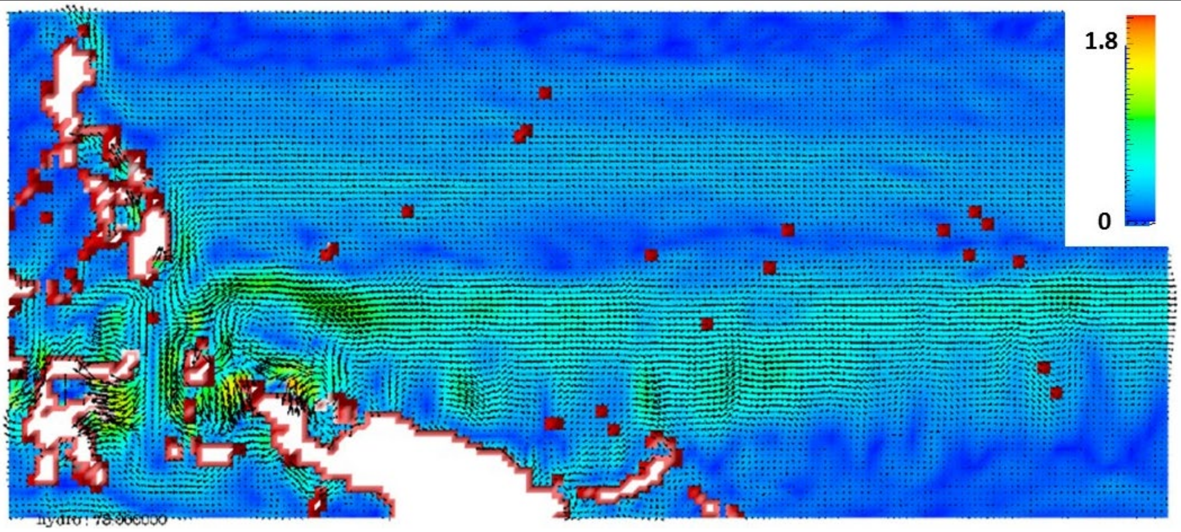
China
Pacific Ocean
Indochinese
Peninsula
South China Sea
Sulu Sea
Celebes Sea
Borneo
Banda Sea
Papua New Guinea
Arafura Sea
Solomon Sea
Coral Sea
Indian Ocean
Australia
NEC
NECC
SEC
SECC
ME
HE
20.0°N
10.0°N
0.0°
10.0°S
20.0°S
100.0°E
110.0°E
120.0°E
130.0°E
140.0°E
150.0°E
160.0°E

(a)



2
0

(b)

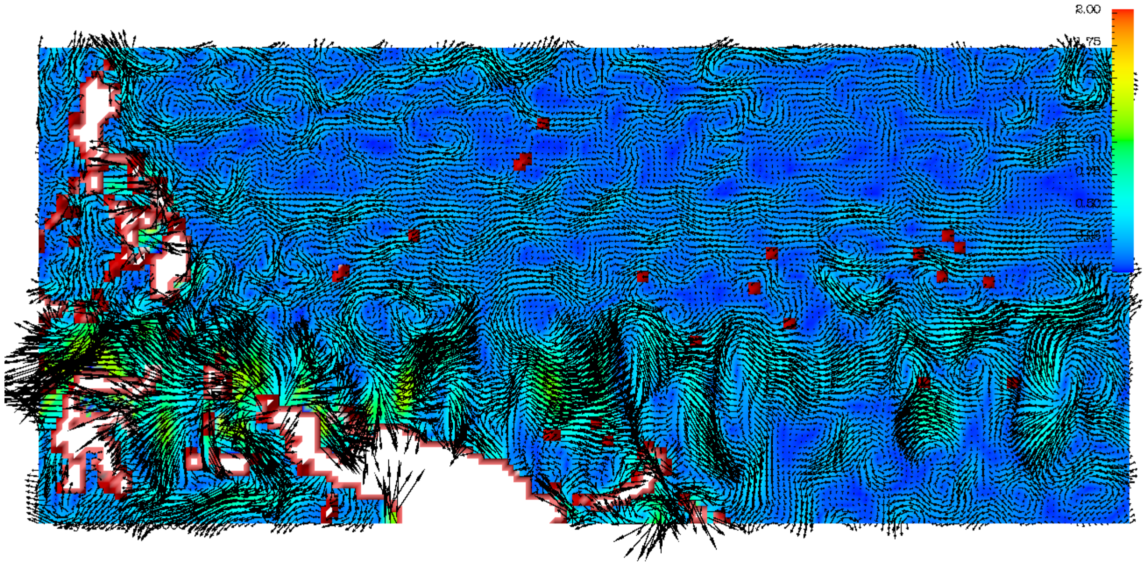


(c)

Figure 6. (a) The net, near-surface water circulation in Micronesia following Thompson et al. (2018). SEC=South Equatorial Current; NEC=North Equatorial Current; NECC=North Equatorial Counter Current; SECC=South Equatorial Counter Current; ME=Mindanao Eddy; HE=Halmahera Eddy. The yearly-averaged, altimetry-derived, near-surface water circulation in (b) 2013 and (c) 2015. The colour bar shows the speed (m s^{-1}).

Recently publications document finer scale oceanographic models of the water circulation in Micronesia (e.g. Heron et al., 2006; Davies et al., 2015; Thompson et al., 2012); these finest scale models have a mesh size of 5 km. How good are these oceanographic models at reproducing the observed currents? The surface currents in Micronesia are meso-scale turbulent (i.e. they are chaotic, i.e. they are full of eddies, jets, and other unsteady events). Two snapshots of the near-surface currents one month apart in mid-2013 are shown in Figure 7a-b. To illustrate in two figures what oceanographic chaos looks like is not possible. Therefore, in the Supplementary Material an animation is provided of the altimetry-derived surface currents in Micronesia from January to December 2013 at 5 days interval. This animation clearly shows the meso-turbulence at temporal scales similar to the PLD of the fish larvae, and the chaos that results. Clearly, the currents were highly meso-scale turbulent, so much so that some features of the NEC, NECC, SEC, ME and HE are not apparent in these data. In one month, the currents have changed drastically. Figures 7a, b and the animation show the prevailing intense, meso-scale turbulence that occurs all the time. The currents power spectra shows that the currents are energetic in all regions at periods of 30-90 days, with a number of peaks that vary with location and the largest peak occurs everywhere at a period of about 80 days (Wang et al., 2016). These periods are the same ballpark as the PLD of many fish larvae, implying that the fate of the fish larvae within the time scale of their PLD is controlled mainly by the meso-scale turbulence and not so much by the mean flow as predicted by classical advection-diffusion models. Thus, it is not possible when modeling the connectivity of fish populations within Micronesia, to use the classical assumption for modeling advection-diffusion in turbulent flows of using the mean flow as the advective component and using an empirical diffusion coefficient for the diffusion component. Instead, it is necessary to include the meso-scale turbulence in the advective component.

(a)



(b)

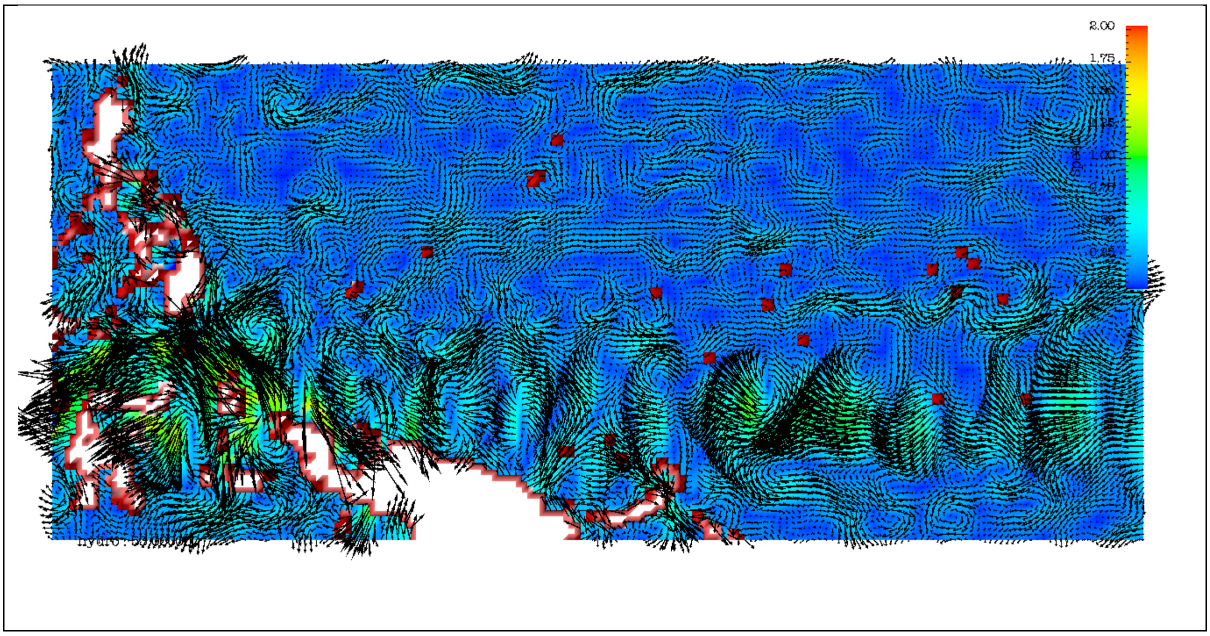


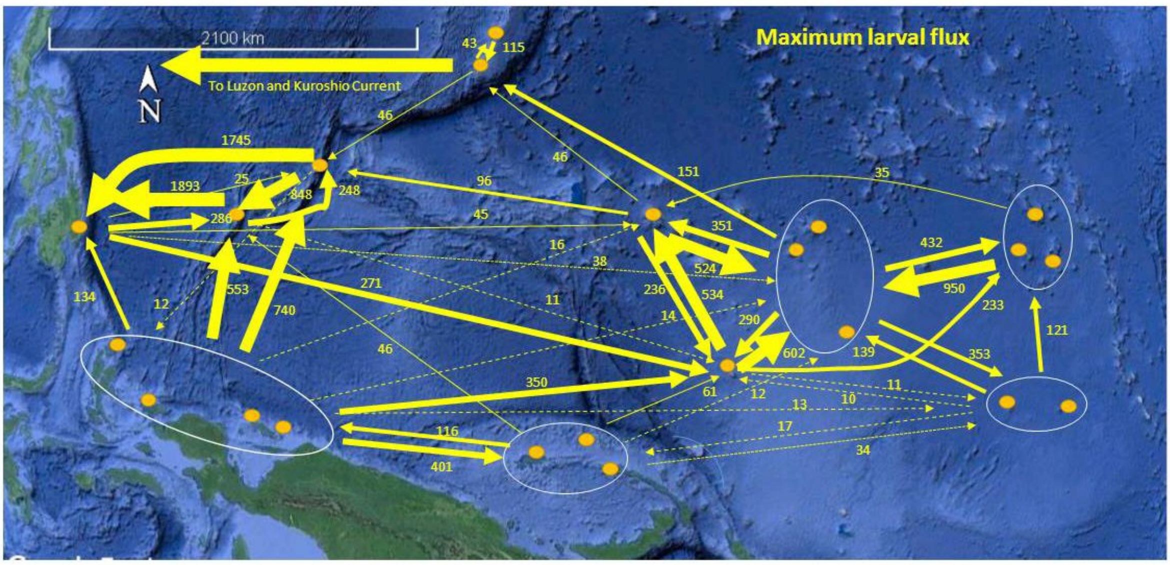
Figure 7. (a, b) Two snapshots, one month apart, of the 5-days averaged, altimetry-derived, currents in Micronesia in 2013, showing the dominance of the meso-scale turbulence. The coordinates are shown in Figure 1a. The colour bar shows the speed in m s^{-1}.

How good are the oceanographic models in the presence of this intense meso-scale turbulence? Heron et al. (2006) were apparently the only researchers who published data showing the accuracy of their models against the altimetry-derived current data. They found that the model largely fails to reproduce this meso-scale turbulence. Indeed, they compared the predicted currents with the observed currents measured during oceanographic cruises from January 1993 to September 2000, and the average correlation coefficient was 0.52 (±0.17; number of observations=16; max=0.71; min=0.26).

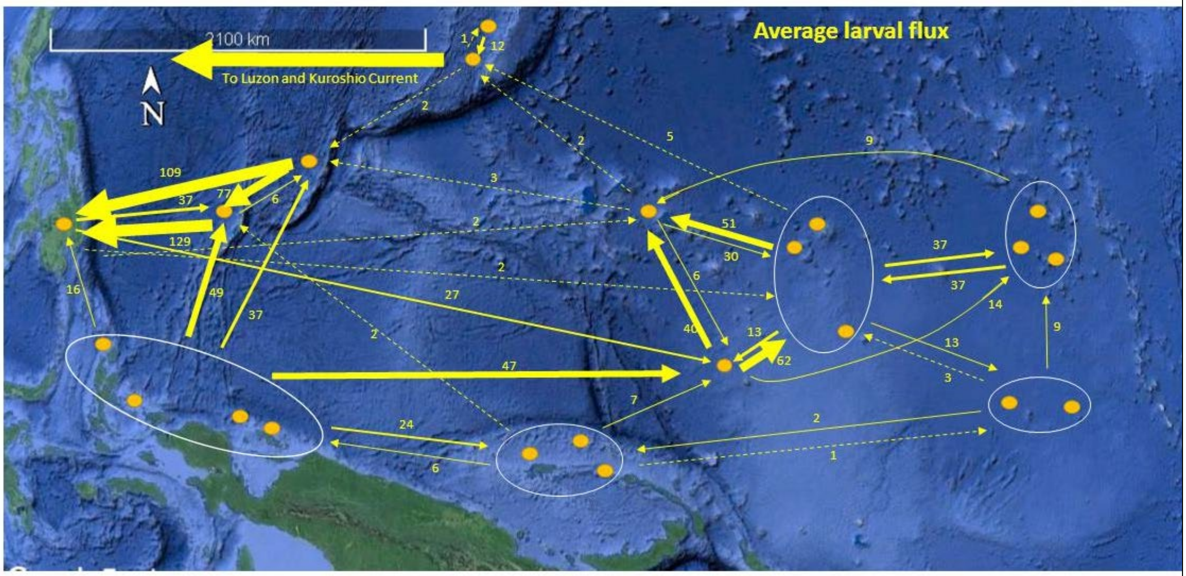
3.3 Connectivity within Micronesia

To become operational, the model, though driven by the observed water currents, still needs to be validated using genetic parentage data. The only such data are from Ma et al. (2018) who found evidence of localised connectivity interrupted by hot spots (clusters) across Micronesia for three aggregating grouper species. Can the model explain this? The model suggests that, because of the chaotic flow, the fish larval plumes took different pathways after each spawning event. There are three likely interpretations of the results. Firstly, the fish larval connectivity is driven by the occasional massive inflow of larvae in one event even if it is rare; Figure 8a is the result. This shows the maximum number of larvae recruited after a spawning event from 2010 to 2019 (40 spawning events). This interpretation assumes that the recruitment of sub-adult reef fish is sporadic and intermittent and that recruitment does not occur after each spawning event; indeed, for snappers, several years of zero recruitment can occur until a recruitment event takes place (Schlaefer et al., 2018). Secondly, the fish connectivity may also be controlled by the long-term averaged larval inflow. This was calculated by averaging the larval connectivity data from the 40 spawning events from 2010 to 2019. The result is shown in Figure 8b. Thirdly, the fish connectivity may also be influenced by the number of times that a spawning site and a recruitment site connect. This is shown in Figure 8c.

(a)



(b)



(c)

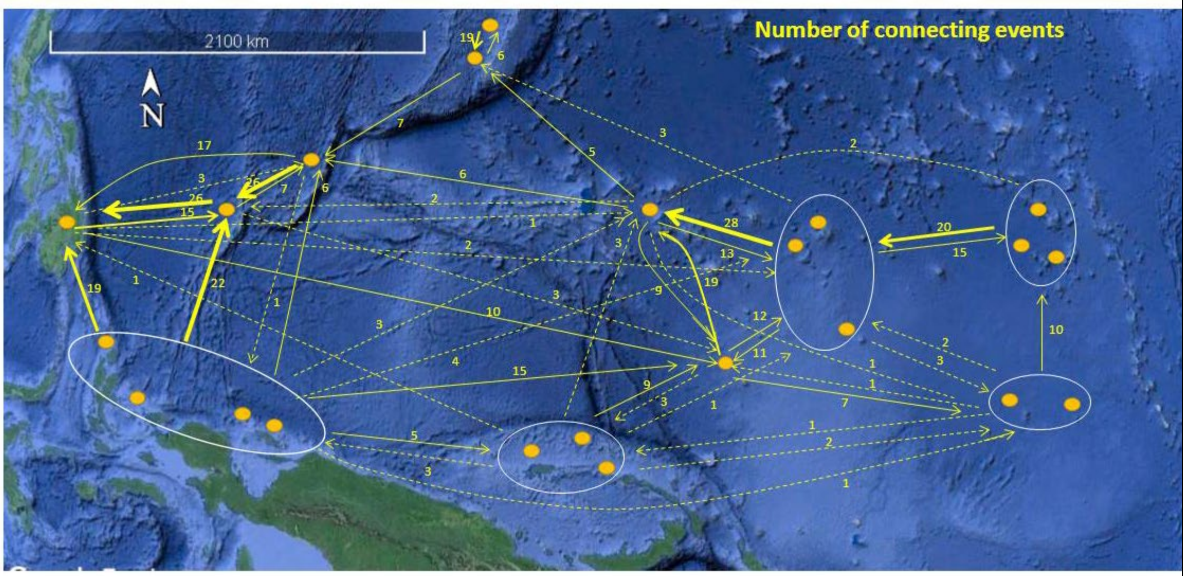


Figure 8. (a) The maximum number of virtual fish larvae transported in one event from 2010 to 2019. (b) The average number of virtual fish larvae transported from 2010 to 2019. Values < 1 are not shown. (c) The number of connecting events (out of 40) from 2010 to 2019.

From Figure 9 it is visually apparent that the connectivity is chaotic, as there is no apparent correlation of recruitment success with the SOI, nor are there overall ‘good’ years and ‘bad’, nor are there overall ‘good’ and ‘bad’ spawning events for all reefs at the same time in Micronesia (Figure 9). For instance, the two high connectivity events from Yap to Palau occurred for small values of |SOI| but there were also 15 events of zero to very small connectivity events between those two islands for similarly small values of |SOI|. However, Figure 8 suggests the existence of porous clusters of reefs with a high connectivity between them, with a smaller connectivity between these clusters. In general, a connection between two sites in Micronesia occurs in less than 30% of the spawning events. There are two major connectivity clusters, one cluster being Irian Jaya-Palau-Yap-Mindanao, and the other cluster being the FSM-C and surrounding islands. Irian Jaya is a major source of fish larvae. The larvae from Guam and Saipan are mainly exported towards Luzon and the Kuroshio. There are some keystone transit reefs such as Kingamaringi and Chuuk. Pohnpei and surrounding islands are also transit areas, largely receiving larvae from Irian Jaya and providing larvae to Chuuk, Guam and the Marshall Islands. PNG reefs provide little to the connectivity in Micronesia. Palau and Yap receive a net inflow from Irian Jaya, Yap has a net export to Palau and both Yap and Palau have a net export to Mindanao. The Marshall Islands connect mainly with FSM-C and receive much more than they provide. Saipan is a net, but small, provider of fish larvae to Guam. Nauru and Ocean Island provide and receive little.

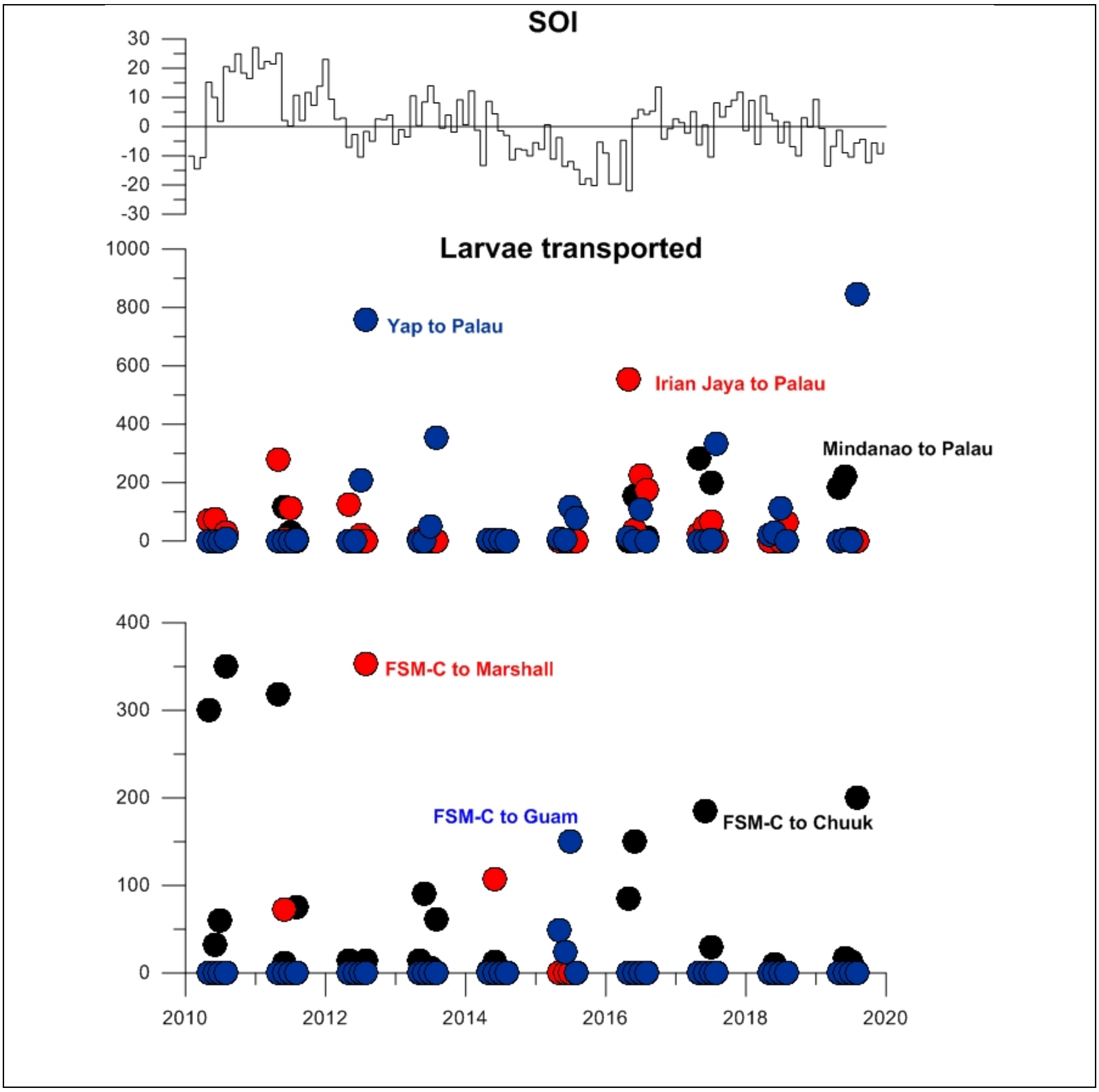
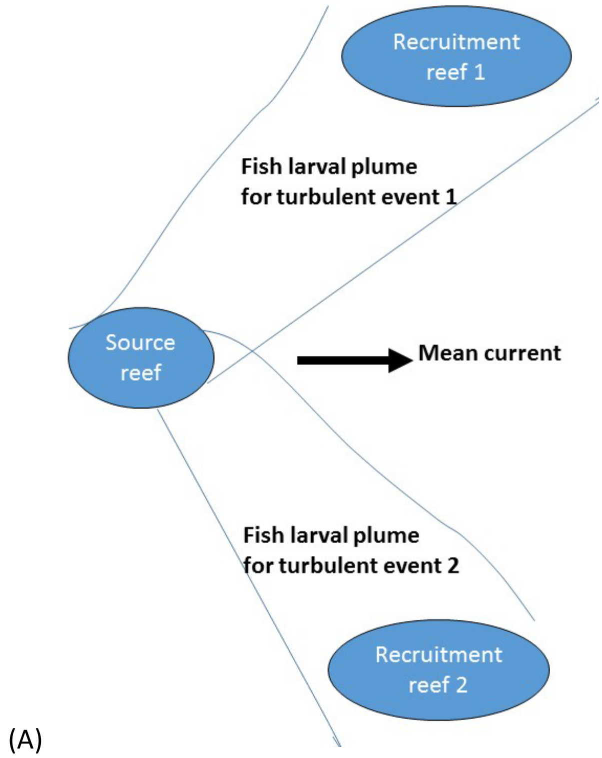


Figure 9. Time-series plot from 2010 to 2019 of the Southern Oscillation Index (SOI) and the number of larvae recruited in each of the 40 spawning events for two clusters (inflow to Palau and outflow from the FSM-C) as examples of the chaotic results. El Nino events occur during high negative values of the SOI, and La Nina events during high positive values of the SOI.

4. Discussion

Previous studies have shown the importance of both auditory and chemical cues for attracting post-flexion fish larvae to reefs, which leads to recruitment (e.g. Wolanski et al., 1997; Carleton et al., 2001; Gerlach et al., 2007; Atema et al., 2012; Paris et al., 2013; Wolanski and Kingsford, 2014). This present modeling study demonstrates the importance of the variability of the oceanic currents due to oceanic meso-turbulence and ENSO. The scale of effects can be broad, depending on pre-El Niño conditions, including the strength and duration of south westerly winds that precede the Kelvin Wave that results from the accumulation of water in the western Pacific region, as it moves back, eastward when the winds abate (Richmond, 1990). Strong ENSO events can affect both local and Pacific-wide distributions of a variety of fish and invertebrate larvae, and can be important for introductions over both ecological and geological time scales. However, we were able to determine that ENSO events are not the only process affecting juvenile rabbit fish recruitment on Guam; indeed, meso-scale turbulence near the surface also plays a key role in the recruitment process. The resulting recruitment is chaotic. A sketched in Figure 10a, the recruitment sites depend on the meso-scale turbulence that entrain the fish larvae and generate fish larval plumes. These follow the currents due to the sum of meso-scale turbulence and the mean flow to form fish larval plumes. Reefs not aligned at all with the long-term average flow downstream of a source reef can still be recruitment sites (Figure 10a). Therefore, there is also a certain dependence on 'mean' currents depending on the relative strength of the turbulent and the mean currents. The rabbit fish recruitment in Guam and the grouper fish recruitment process in Micronesia are chaotic because they are driven by at least two independent parameters, namely the intense meso-scale turbulence and ENSO, and possibly other processes. The meso-scale turbulence is incoherent temporally and spatially, thus the self-recruitment and the connectivity is incoherent from spawning event to spawning event and from site to site. Scientifically what we did, to find a simple way to predict connectivity in a chaotic flow field in the ocean, is novel. The likely connectivity of reef fish populations among Micronesian Islands demonstrated by this study supports government efforts at regional cooperation in implementing conservation initiatives. Most notable of this regional example is the establishment of the Micronesia Challenge, with the different government in Micronesia coming together and agreeing to effective conserve their marine resources. It is encouraging that the various governments and communities in Micronesia are striving for sustainability of their reef and fishing resources, the opposite of what is happening now in the South China Sea located just on the other side of the Philippines (Wolanski et al., 2020).

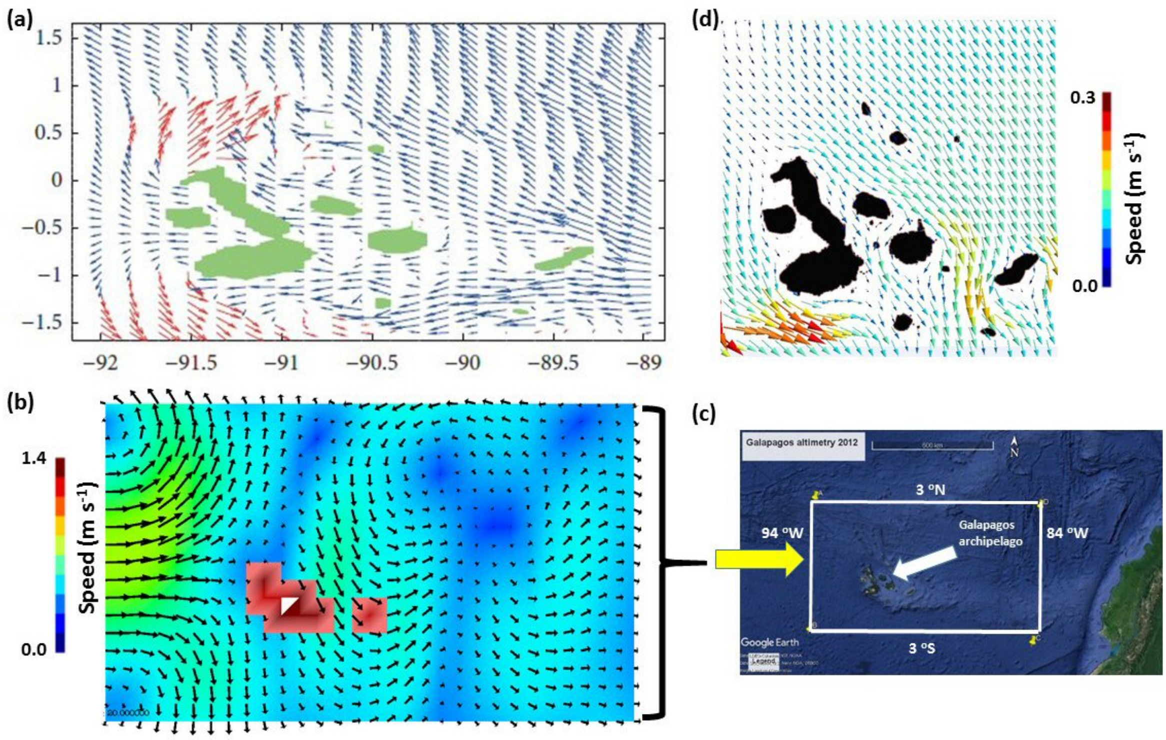
As coral reefs continue to decline worldwide, it is important to recognize that it is not only corals that are affected by local (sedimentation, pollution, overfishing) and global level (climate change) stressors, but other constituents of these complex ecosystems are affected as well. Such ecosystem level losses affect human communities reliant on the associated resources of economic, cultural and ecological value. While local and regional current patterns can be drivers of recruitment, and such information help guide management-directed activities, more localized cues are also critically important. The data presented in this paper can be used to support communities in efforts at resource sustainability, and add to the information upon which policies and management planning can be developed and implemented.



Recruitment reef 1
Fish larval plume
for turbulent event 1
Source reef
Mean current
Fish larval plume
for turbulent event 2
Recruitment reef 2

(A)

(B)



(a)
1.5
1
0.5
0
−0.5
−1
−1.5
−92
−91.5
−91
−90.5
−90
−89.5
−89
(d)
0.3
0.0
Speed (m s-1)
(b)
1.4
0.0
Speed (m s-1)
(c)
Galapagos altimetry 2012
3 °N
94 °W
84 °W
Galapagos archipelago
3 °S
Google Earth

(C)

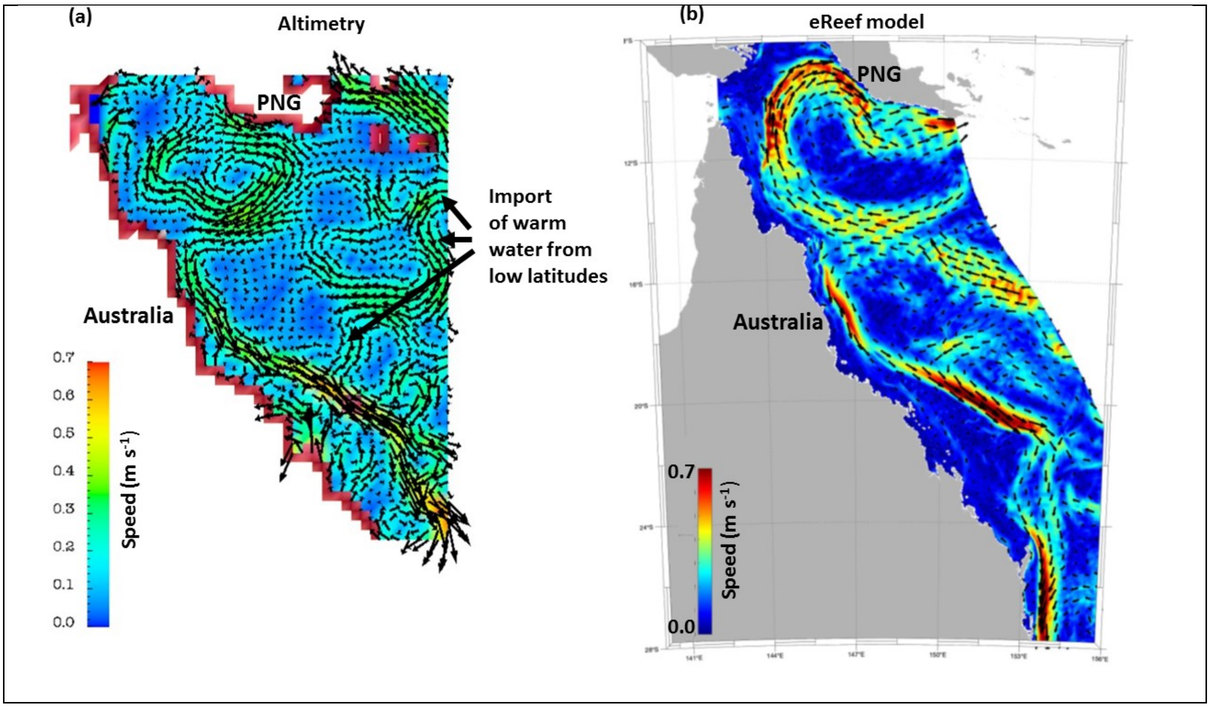


Figure 10. (A) A sketch explaining the role of meso-scale turbulence in the connectivity between reefs in Micronesia. (B) (a) Predicted surface currents in and around the Galapagos archipelago in March 2005 following Liu et al. (2014) and (b) the altimetry-derived surface currents in the domain shown in (c),and (d) the predicted currents using the model of Golbuu et al. (2012) forced at the open boundaries by the altimetry data. In (a) the figure was distorted by using a different horizontal scale for the x and y-axes. (C) (a) The altimetry-derived surface currents in the Coral Sea fringing the Great Barrier Reef on February 5, 2020 and (b) the eReef model predicted surface currents. Dr. S. Choukroun kindly provided the latter figure.

What is the future for biophysical modeling of connectivity between islands and reefs in the oceans such as Micronesia, the Galapagos and the Coral Sea? Our findings for Micronesia is that the classical oceanography models need to significantly improve to reproduce the intense meso-scale turbulence in Micronesia in order for these models to be able to reliably predict the biological connectivity between islands and reefs. We undertook a similar comparison of observed and predicted currents in the Galapagos (Figure 10B) and the Coral Sea fringing the Great Barrier Reef (Figure 10C) and we arrived at the same conclusion. In the Galapagos, the oceanographic model of Liu et al. (2014) greatly underpredicted the meso-scale turbulence that resulted in great sweeping motions mainly northward and southward at periods of typically 3-8 weeks. An example of such a southward motion is shown in Figure 10Bb-c while the predicted currents were of opposite direction. Using such predictions would be misleading when modeling the connectivity of reef fish larvae in the Galapagos. The other example of the importance of meso-turbulence is for the Coral Sea. In February 2020, altimetry revealed the existence of a transient month-long jet of warm water originating from low latitudes and impinging on the southern Great Barrier Reef (Figure 10Ca). The eReef oceanographic model https://research.csiro.au/ereefs/) did not predict this jet (Figure 10Cb). This warm water jet was ecologically important because it contributed to a heat-induced bleaching of corals in the Southern Great Barrier Reef in March 2020, the 1st recorded bleaching event in that area (https://theconversation.com/we-just-spent-two-weeks-surveying-the-great-barrier-reef-what-we-saw-was-an-utter-tragedy-135197). Meso-turbulence was also shown to be the dominant process controlling the connectivity of fish larvae in the Spratly Island archipelago, South China Sea (Wolanski et al., 2020). Therefore, it appears that the classical oceanography models are probably not quite ready yet to answer important biophysical questions of self-recruitment, connectivity and coral bleaching in a number of archipelagos. Further, the problem of incorporating the turbulent cascade in advection-diffusion models remains unsolved. Indeed, there may be intense turbulent events at a scale less than the resolution of the SLA maps (5 days, 1/3 degree). The resolution of this problem needs to be addressed in future research on the use of satellite data.

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