SCENARIO OF SCLERACTINIAN LARVA DISPERSAL IN SULAWESI WATERS FROM A HYDRODYNAMIC MODELING PERSPECTIVE

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ABSTRACT

Scleractinian coral such as Lobophyllia corymbosa that reproduce by external fertilization have an extended planktonic phase in their life cycle during which they "drift" in the water column. This life cycle phase is an advantage in itself because it increases the capacity of propagules to disperse far from their place of origin. In this hydrodynamic model study, secondary data on bathymetry and tides for the western monsoon period (represented by November 2017) were input into the Surface Water Modelling System SMS 8.1 to simulate the surface current circulation model. In running this program there are 2 important stages, namely GFGEN (Geometry File Generation) and RMA2 (Resources Management Associates-2). The simulation of surface current direction during the west monsoon, which is the reproductive period of L. corymbosa in Indonesia, shows the complexity and distraction of current vectors that occur in the coastal waters around Sulawesi Island. The model results indicate the possibility of spatial and temporal biological networks forming in waters around Sulawesi. The current patterns forming in Sulawesi waters during the west monsoon tend to circulate from north to south due to the higher volume of water mass originating from the Pacific Ocean flowing to the southern part of Sulawesi which is also the entry point for the Indonesian Throughflow (ITF). The larval dispersion model scenario produced for each location (Manado, Toli-Toli, Palu, Mamuju, Spermonde, Sinjai, Wakatobi, and Luwuk Banggai) tended to follow the water movement patterns, with most propagules leaving the location where they were spawned.

Keywords: Larval dispersal, Modelling, SMS 8.1, Spawning corals.

INTRODUCTION

Hard corals or often referred to as scleractinian corals, are coral reef-forming organisms in waters that have symbiosis with zooxanthellae. Corals have a bipartite life cycle that attaches to the aquatic reef substrate during the adult phase and floats during the pelagic phase, allowing the organism to spread to other reef areas (Adame et al., 2017). The dispersal of coral larvae in waters is affected by current movements and the geography of an area. Good coral distribution can be seen from the diversity and percentage of coral cover (Hutabarat, 2001). In Indonesia, the largest coral reefs are in the eastern part of the country, especially in Sulawesi waters, which cover an area of 862,267 ha (Giyanto et al., 2017) and are also one of the waters that have quite good biological potential. Currently, Sulawesi Waters can be said to be the heart of the Coral Triangle Area because of its geographical location in the middle of the CTA. Apart from that, the strategic geographical location of its region, which intersects with the Java Sea, Flores Sea, and the waters between the Sulawesi Sea, Pacific Ocean, and Banda Sea, means that the Sulawesi waters area is said to have a high contribution of biological material. It is recorded that 73% of the world's hard coral species are in the eastern region of Indonesia, none other than this area being in the waters of Sulawesi.

In terms of distribution, there are several limiting factors that cause coral distribution in Indonesia to be uneven. Pelagic larva duration (PLD), anthropogenic activities, habitat, pollution, and of course the physical dynamics of waters, in this case currents (Connolly and Baird, 2010). Currents are the main factor and directly influence the distribution of coral larvae in waters, which also contribute to coral genetic connectivity (Nathan and Muller-Landau, 2000; Strathmann et al., 2002). The islands in Sulawesi waters are generally close to each other and can be a stopover or attachment area for coral larvae during their distribution. The larvae of these sessile animals can move, following the flow of water currents, from their spawning location to areas where they will live and grow. This movement can take place over a distance of several to thousands of kilometres, depending on the duration of the coral larvae's pelagic as well as the oceanographic conditions in the area (Vollmer, 2007; Lequeux et al., 2018).

Information on current patterns in Sulawesi waters could be used as a basis for obtaining data on movement or spatial distribution that occurs in a type of hard coral. The distribution patterns obtained have an important role in providing understanding for basic applications in water conservation management.

This research is the first to examine the potential of coral reef networks formed in Sulawesi waters. Information regarding the characteristics and behaviour of coral larvae is still limited; therefore, model predictions will also experience imperfections in building assumptions. Direct measurements of larval distribution in the field are still very rarely carried out and still require effective and efficient technological support (Krueck et al., 2017). Currently, the physical oceanographic modeling approach is considered to be representative for providing an overview of larval distribution when considering the design of conservation areas.

MATERIAL AND METHOD

At this stage, our data is obtained from secondary data sources from relevant agencies.

Secondary Data-Collection and Determining Model Areas

Secondary data used for the construction of current modeling are bathymetry and tidal data obtained from Hydro and Oceanography Service (DISHIDROS) Lantamal VI Makassar, South Sulawesi, and Meteorology, Climatology, and Geophysics Agency, Makassar (BMKG), as well as online data collected from ESA GlobCurrent (http://www.globcurrent.org/) and the General Bathymetric Chart of the Oceans (GEBCO). This data recording was collected during the reproductive period of the target coral, such as in the western season (representative period in November 2017). It is reasonable to collect data for this period to investigate the dominant direction of movement that occurs at the coral sampling location so that it can accurately illustrate the movement of coral larvae based on the circulation scenario that occurs.

Hydrodynamics Modelling

The current pattern model is the initial stage needed before proceeding to the simulation stage of the coral larvae distribution model. At this initial stage, the secondary data obtained will be input into the SMS 8.1 (Surface Water Modeling System) software, which is a numerical analysis and modeling tool developed to simulate surface current circulation. In this program, there are two important stages for hydrodynamic simulation, namely GFGEN (Geometry File Generation) and RMA2 (Resources Management Associates-2). In the run process, GFGEN functions to create geometry and mesh files therefore, they can be programmed in RMA-2. Meanwhile, RMA-2 is used to complete the hydrodynamic settings for

the geometric arrangement that has been built previously.

Data Input

At this stage, the numerical data used is tidal dynamics and also depth (bathymetric conditions). Tidal data is obtained from the BIG website (tides.big.go.id/pasut/index), which is then validated with annual data issued by the Indonesian Navy's Hydrographic and Oceanographic Service. The input data is tabulated in Microsoft Excel based on time lines and water level fluctuations in the study area. Tidal data was used for 15 days (360 hours) within the range of the highest spawning period of the targeted sample. The sorted numeric input is then formatted in an a.txt file, and then the file will be read in the SMS software. It should be noted that tidal data collection only uses secondary data available on the BIG website and does not take direct measurements in the field. Apart from limited time and facilities, validation was carried out by research previously conducted by Affandy (2017), and the bias that occurred was not very significant.

Apart from tidal data, available bathymetric data obtained from the GEBCO website (http://www.gebco.net) is downloaded in partitions or segments. Downloading segments based on sampling points is intended so that the hydrodynamic simulation process is not too heavy and the size of the grid used is no more than 2000 m with the model design using a triangular mesh so that small islands around the location are still taken into account. The downloaded depth data is in the form of a TIFF file format, which is then extracted into the Global Mapper 17 software. The data obtained is in the form of xyz coordinates and depth points and formatted in.txt form. The file format is then ready to be sorted in Excel according to the processing needs in SMS.

GFGEN Modul and RMA-2

The input data that has been entered into the SMS will then form a grid on the bathymetric map. The model design uses a triangular mesh, which has high resolution. The bathymetric map that has been depicted is built from a collection of nodes or points that are connected and form grid elements. Apart from that, the average length and area of the coastline towards the sea is around 150 m x 2020 m and does not ignore the small islands around the study area. For model stability, a time step of 360 steps is used according to the input tidal data.

The geometry and elements of the modeled location have been created, then the geometry and mesh program become input data for the system program and SMS modeling, then proceed to the GFGEN running stage. In this process, the GFGEN program will check for possible errors that could occur in the mesh being built before going to a further stage so that they can be anticipated. The next method to build a model of flow direction and speed is RMA-2. RMA-2 numerical modeling is specifically designed to simulate changes in elevation and the distribution of current flow velocity, which is then integrated into a vector scenario. At this stage, the input that has been generated after the GFGEN process is used for the RMA-2 program. The control model in RMA-2 is run based on tidal numerical data, which is dynamic or influenced by certain time periods. After running the RMA-2 module, you can see the speed vector display and the color gradient contour of the vector quantity and water level elevation in the ".sol" file format.

SED2D

The hydrodynamic simulation that was obtained from the running results of RMA-2 was then used in the SED2D stage as a method to determine the distribution of particles. Basically, SED2D is used as a mass transport model, and in this study, this approach was used to determine the distribution of coral larvae based on the potential for dispersal of these organisms through currents. Therefore, the SED2D program is used, which is still in one SMS software unit. This program will calculate the displacement of particle positions from the velocity input resulting from the hydrodynamic modeling output at any time. The position of the source or particle source is assumed to be at the sampling

location, and then the particles from the source

will move according to the displacement that has been formed based on the oceanographic input data provided. The principal method at this stage is determining the initial concentration value. The initial concentration value used is 0.05 mm3. This value is the number of larvae contained in a unit volume of water in a body of water.

In this larval distribution model, there are several condition scenarios created in the simulation of larval distribution using the SED2D program, including [1]. In this simulation, the larval object used is L. corymbosa coral, which is a representative of the order Scleractinia, which is the main component that forms reefs. [2] The dispersal of larvae only depends on the movement of ocean currents, which are generated by tidal dynamics, and the movement of objects is considered passive particles with low mobility and does not distract the direction of dispersal. [3] Migration is formed only in the horizontal zone and ignores vertical migration. [4] The duration of larval drift was demonstrated to be 39 hours (more than 1 tidal wave), and alternating current was not taken into account. [5] During the simulation run, the assumption applies that no larvae will experience incidents of predation, mortality, or other external factors that will affect larval durability.

Image Registration and Overlay

Merging or overlapping registered maps in the RMA-2 and SED2D output results were done in SMS software. SHP (shapefile) maps throughout Indonesia were downloaded from the Geospatial Info page in .rar format and then edited into ArcGIS 10.3. The map is registered, which means that the coordinate position matches the output results. The coordinate system used for this modeling map is the hemisphere coordinate system, or Universal Transverse Mercator (UTM).

RESULTS AND DISCUSSION

Simulation of surface currents during the west monsoon, which is the reproductive period of the scleractinian corals in Indonesia, shows the complexity and distraction of current vectors that occur along Sulawesi waters. The current pattern that is formed tends to flow from north to south; however, clockwise rotation or recirculation occurs in the northern part of Sulawesi Waters, which is a refraction of the flow from the Sulawesi Sea-Pacific Ocean, thus forming a north-west trajectory towards the Makassar Strait and north-east towards the Maluku Sea. In the western part of Sulawesi, right in the Makassar Strait channel, there is a tendency to divert towards the north and south in the waters around the Mamuju coast. Refraction also occurs around the waters of Luwuk Banggai on the east coast of Sulawesi. This location experiences an intensification of current rotation, which occurs due to the presence of cold and warm currents from the Banda Sea when the bottom water mass rises upwards. It is comprehensively presented in the next explanation through the results of hydrodynamic modeling scenarios.

Larval Dispersal

Numerical modeling of finite difference elements of 2D hydrodynamic functions This modeling provides information in the form of visualized images of the distribution process of coral sediment and planula over time. This modeling is considered quite representative in determining the distribution of coral larvae in a body of water by assuming that the density of its considered to be the same as the density of clay sediment, so SED2D modeling is used.

The simulation of the distribution of coral larvae is divided into two parts: at the first prediction of larval release or spawning event (1st hour) and at the 39th hour following the scenario of 1 cycle hydrodynamic data (tidal) in the field. In addition, this period is used as the initial planktonic period for coral larvae. The following are the results of the simulations that have been carried out for each study sites:

Toli-Toli

In this first hour, the simulation model for the distribution of coral larvae, which is significantly influenced by current dynamics, shows a distribution that tends to the northeast with a concentration of coral larvae ranging from 1.7 to 3.3 kg/m³. Sampling was carried out on the east side of Kabetan Island, which is on the west coastline of Sulawesi Waters, quite influencing the simulation of the spread of coral larvae in that area. Furthermore, at the 39th hour, the predicted distribution of larvae continued to move away from the sampling location. Then simultaneously, this simulation was carried out for up to 15 days according to the input made and obtained predictions of larval dispersal up to 6.5 km to the east-northwest in the waters of and Tumpangan Islands with Buol concentrations ranging from 0.5 to 1.7 kg/m^3 .



Figure 1. Distribution model of coral larvae during the 1st hour (left) and the 39th hour (right) in Toli-Toli.

This distribution pattern is largely determined by the characteristics of the tidal current pattern in the study area, where the tidal current pattern tends more towards the east and spreads towards the northwest. The distance traveled by the target also shows an indication that the alternating current that occurs slightly limits the distance the object spreads to surrounding locations.

Palu Bay

The geographical condition of Palu Bay, which is semi-isolated, shows that the predicted dispersal pattern of coral larvae in the first hour tends to be only a short distance from where the originates. The object larvae group concentration in the scenario is around 0.540 kg/m³. After the 39th hour, the coral larvae were seen starting to disperse, but they were not widespread and were only around the bay. In the simulation process of up to 15 days, the distribution of planula is predicted to move around the waters of Palu Bay as far as ±2.3 km to the east and 1.6 km to the west and southwest and not leave the water area. Conditions limiting the movement and distribution of larvae due to the geographical location of the bay make hydrodynamic dynamics very small.



Figure 2. Distribution model of coral larvae during the 1st hour (left) and the 39th hour (right) in Palu Bay.

Mamuju

In Figure 3, a dispersed simulation of coral larvae in Mamuju Waters (Karampuang Island) shows that the movement is not very widespread in the first hour of prediction. On the first day of the simulation, the distribution pattern shown tended to be east to southeast with a distance of 1.8 km and a southerly direction of around 0.9 km. The assumed average concentration over 24 hours is 0.561 kg/m³. In contrast to the 39^{th} hour, the movement of larvae spread around the waters was visible, and on the 15^{th} day, the simulation distance was measured as far as 4.8 km to the north and east, 1.8 km to the southeast and west, and 2 km to the north. Northwest.



Figure 3. Distribution model of coral larvae during the 1st hour (left) and the 39th hour (right) in Mamuju.

Spermonde

Figure 4 (left) shows the distribution of coral larvae during the first hour to 24 hours, with an average concentration of around 0.554 kg/m³. The distribution of this planula is diffused 2.2 km to the southwest, west, and northwest, with depths ranging from 5 to 6 m. The

distribution of planula continues to diffuse with time and depth. Furthermore, from the 39th hour onwards (15-day limit), the distribution of coral planulae diffused in all directions up to 2 km to the north and 4 km to the west, southwest, 1.5 km to the east, and southeast.



Figure 4. Distribution model of coral larvae during the 1st hour (left) and the 39th hour (right) in Spermonde.

Sinjai

The simulation of the distribution of coral larvae presented in Figure 5 shows that the distribution of coral planula during the 1st hour has an average coral planula concentration of 0.56 kg/m³. Apart from that, the spread on the first day tended to be north to northeast, with a

distance of 1.8 km. After the 39th hour, the spread of coral larvae moves in all directions according to the pattern of tidal currents. This distribution continued to be recorded for 15 days, and a dispersion distance of 2.9 km to the east and southeast and 4.5 km to the west and northwest was recorded.



Figure 5. Distribution model of coral larvae during the 1st hour (left) and the 39th hour (right) in Sinjai.

Wakatobi

Based on Figure 6, it shows that the distribution of coral larvae during the first hour on Hoga Island (Wakatobi) was distributed as far as 1 km to the northeast to the southeast, with an average concentration level of 0.52 kg/m³. Then, the distribution distance of coral planula

during the 39^{th} hour is estimated to have expanded until the 15th day, reaching 3.2 km to the east, 3.78 km to the southeast, and 3.4 km to the south. This distribution has a concentration level between 0.95 and 3.25 kg/m³.



Figure 5. Distribution model of coral larvae during the 1st hour (left) and the 39th hour (right) in Hoga Island (Wakatoi).

Luwuk Banggai

The distribution of coral larvae in Luwuk Banggai waters based on figure 6 shows that the distribution model in the first hour had an average concentration of 1.38 kg/m³ and was towards the east to the north of Luwuk Banggai

beach with a distance of 5.2 and 3.2 km to the southeast, west, and southwest. Furthermore, for the 39th hour, the spread diffused over time in all directions and further away from the

source point, with decreasing concentration levels. Its spread over 15 days was recorded as far as 8.1 km to the east, north, and southeast and 5.3 km to the south and west.



Figure 6. Distribution model of coral larvae during the 1st hour (left) and the 39th hour (right) in Luwuk Banggai.

Manado

Figure 7 shows the distribution of coral larvae during the first hour on day 1; the average concentration was around 0.97 kg/m³. It can be seen that the spread tends to be north to southwest, with a distance of 0.5 km. Coral larvae continue to diffuse over time with an increasing distribution area and decreasing

concentration levels. Figure 7 (right) is presented, showing the distribution area up to a distance of 4.4 km to the northeast, 4.7 km to the southwest, and 3.3 km to the east and west, with concentrations of coral planula ranging from 1.7 to 3.3 kg/m³ at the last time of the simulation, from the 39th hour to the 15th day.



Figure 7. Distribution model of coral larvae during the 1st hour (left) and the 39th hour (right) in Manado.

Discussion

The coral larvae (Scleractinia) dispersal scenario from the results of this study appears to show quite varied spatial and temporal patterns. The distribution of larvae, whose movements are strongly influenced by water dynamics, was sampled during the mass spawning period in the west monsoon for the Sulawesi waters area. The pattern formed indicates that the process of spreading the object is strongly influenced by hydrodynamic conditions during the spawning period until the phase attached to the substrate.

Apart from oceanographic aspects, the distribution of coral larvae is also influenced by the PLD period of the organism, which generally occurs 7–24 days for corals with internal fertilization and 54–100 days for coral types with external fertilization (Graham et al., 2008; Connoly, 2010). PLD is one of the fundamental variables in the context of population connectivity (Cowen et al., 2009), which depends

on the environmental conditions encountered and the biological transitions of organisms. Sometime after the larvae are released into the water column and fertilization occurs, the larvae will float to the surface of the water because of the fat reserves contained in their bodies and positive buoyancy, so that the tendency to float generally occurs, and it is in this phase where the role of oceanographic conditions will influence movement of larvae.

The dispersal pattern of coral larvae in western Sulawesi waters (Kapoposang Island) has previously been documented by Affandy et al. in 2017 biogeographically. However, basically, there is still limited information on temporal and spatial patterns in Sulawesi waters. The consistency of meteorological and oceanographic influences in research conducted in Hawaiian waters (Storlazzi et al., 2006) is one of the factors that influence the flow of larvae in an area, apart from several other factors including the release and length of time the larvae float (Cowen and Sponagule, 2009) as well as spawning locations (Tay et al., 2012), which of course will also apply to the study area in Sulawesi waters. The dispersal pattern of coral larvae based on a biophysical approach in Sulawesi waters is quite fluctuating, as seen from the hydrodynamic model simulation results that have been obtained. The geography of Sulawesi waters is quite complex and dynamic, influencing the potential distribution routes for coral larvae at each attachment point, which will become their habitat. The results of modeling the distribution of coral larvae show the possibility of spatial and temporal biological networks occurring in Sulawesi waters. The current pattern formed in Sulawesi waters during the west season has a tendency to circulate from north to south due to the higher volume of water mass coming from the Pacific Ocean to the southern part of Sulawesi, which is also the entry point for ITF flow, as stated by Gordon et al. in 1999 and 2010.

The larval distribution model scenario seen at each location tends to follow the movement of currents and is quite far from the location where the spawning process originates. The trend of movement centered towards the southern part of Sulawesi is in accordance with the current trajectory of the Pacific Ocean during the west monsoon. According to Wyrtki (1987), the difference in surface height that occurs during the west monsoon will be lower in the south, so that water masses from the Pacific Ocean will move towards the Indian Ocean. The route to the Indian Ocean will of course pass through the Sulawesi Waters corridor, which in principle will have an influence on the physical oceanographic movement model of the area through which it passes.

The particle tracking model to determine predictions of coral larvae dispersion spatially shows that the predicted distance of distribution of objects from the source point to the open waters as a whole is recorded as 0.9 km–8.1 km in the 1 to 15-day simulation period. The larval distribution distance capacity is followed by the predicted rate of surface currents generated by tidal dynamics in Sulawesi waters. Fluctuations in current speed recorded ranged from 0.004 m/s to 0.50 m/s, where the model shows that generally the current speed at low tide is greater than at high tide. This happens because of the influence of the earth's gravity and the principle of balance (Dobrovolskis and Ingersoll, 1980).

The direction of surface current vectors and coral larvae in the model tends to follow the oceanographic dynamics at the study location. The northern part of Sulawesi Waters is clearly visible as movement occurs towards the west of Sulawesi in the Toli-Toli model area, which will cross the Makassar Strait corridor, which is strengthened by the push of water masses originating from the Pacific Ocean passing through the southern entrance of Tanjung Mindiano, while the Manado model area tends to the east of Sulawesi. Along the route through the Makassar Strait area, greater water movement flows south towards the Flores Sea. This flow is the dominant movement path for larvae carried by the current. The flow trajectory also represents the ITF current circulation axis.

Not only is it caused by surface currents generated by tides, but the distribution of coral larvae is also indirectly influenced by density currents. In the western waters of Sulawesi (Mamuju) and the eastern part (around Luwuk Banggai), there is a visible disturbance in the area. This distraction is caused by vertical flow from the ITF, which exerts pressure on the surface waters, resulting in a deflection of surface currents and affecting the dispersion pattern of coral larvae.

Exponential larval density and mortality (Peliz et al., 2007) are not calculated and measured directly in the field, making it possible to overestimate connectivity in the results of larval distribution models (Tay et al., 2012). Thus, the depiction is descriptive and assumptive based on the visualization shown by the model. Previous studies (Wolanski et al., 1989) stated that the drifting period (drifters) of coral larvae is more or less accurate from hydrodynamic data in the area where the larvae are released and strongly follows the movement patterns that occur in a body of water. Thus, the model results can still be used as a basic basis for seeing the path that is formed.

REFERENCES

- Adame MCG, Batchelder HP, and Spitz YH. (2017). Modeling Larval Connectivity of Coral Reef Organisms in the Kenya-Tanzania region. Front. Mar., Sci. 4:92.
- Affandy Z, Damar A, Agus SB. (2017). Kajian Konektivitas Ekologi Karang pada Kawasan Konservasi Perairan (Studi Kasus: Taman Wisata Perairan Kapoposang. Thesis. Institut Pertanian Bogor.
- Connolly SR and Baird AH. (2010). Estimating dispersal potential for marine larvae: dynamic models applied to scleractinian corals. Ecology, 91, 3572– 3583. DOI: 10.1890/10-0143.1.
- Cowen RK, Sponaugle S. (2009). Larval dispersal and marine population connectivity. Annual Review of Marine Science, 1(1):443–466.
- Dobrovolskis AR, and Ingersoll AP. (1980). Atmospheric tides and the rotation of Venus: I. Tidal theory and the balance of torques, Icarus, 41, 1–17, doi:10.1016/0019-1035(80)90156-6.
- Giyanto, Abrar M, Hadi TA, Budiyanto A, Hafitz M, Salatalohy A. dan Iswari MY. (2017). Status Terumbu Karang Indonesia 2017. COREMAP-CTI. Pusat Penelitian Oseanografi-LIPI. Jakarta.
- Gordon AL, Sprintall J, van Aken HM, Susanto RD, Wijffels S, Molcard R, Ffield A, Pranowo W, Wirasantosa S. (2010). **The Indonesian Throughflow during 2004– 2006 as observed by the INSTANT program.** Dyn. Atmos. Oceans 50, 115– 128.

- Gordon AL, Susanto RD and Ffield A. (1999). **Throughflow within Makassar Strait.** Geophys. Res. Lett. 26, 3325–3328.
- Graham NAJ, McClanahan TR, MacNeil MA, Wilson SK, Polunin NVC, Jennings S. et al. (2008). **Climate warming, marine protected areas and the ocean-scale integrity of coral reef ecosystems.** PLoS ONE, 3, e3039.
- Hutabarat S. (2001). **Pengaruh Kondisi** Oseanografi Terhadap Perubahan Iklim, Produktivitas dan Distribusi Biota Laut. Pidato Pengukuhan Guru Besar. Fakultas Perikanan dan Ilmu Kelautan. Universitas Diponegoro. Serang.
- Krueck NC, Ahmadia GN, Green A, Jones GP, Possingham HP, Riginos C, Treml EA, and Mumby PJ, (2017). Incorporating larval dispersal into MPA design for both conservation and fisheries. Ecological Applications 27: 925–941.
- Lequeux BD, Ahumada-Sempoal MA, López-Pérez A, et al. (2018). **Coral connectivity between equatorial eastern Pacific marine protected areas: A biophysical modeling approach,** PloS one, 13(8), DOI:10.1371/journal.pone.0202995.
- Nathan R and Muller-Landau HC. (2000). **Spatial** patterns of seed dispersal, their determinants, and consequences for recruitment. Trends in Ecology & Evolution, 15, 278-285.

- Peliz A, Marchesiello P, Dubert J, Marta-Almeida M, Roy C and Queiroga H. (2007). **A study** of crab larvae dispersal on the Western Iberian Shelf: physical processes J. Mar. Sys. 68 215–36.
- Storlazzi CD, McManus MA, Logan JB, and McLaughlin BE. (2006). Cross-shore velocity shear, eddies, and heterogeneity in water column properties over fringing coral reefs: West Maui, Hawaii. Cont. Shelf Res. 26, 401–421. doi: 10.1016/j.csr.2005.12.006.
- Strathmann RR, Staver RM, and Hoffman JR. (2002). Risk and the evolution of cellcycle durations of embryos. Evolution, 56: 708 – 720.
- Tay Y, Todd P, Rosshaug P, et al. (2012). Simulating the transport of broadcast coral larvae among the Southern Islands of Singapore, Aquatic Biology, 15:283-29.
- Vollmer SV and Palumbi SR. (2007). Restricted Gene Flow In The Caribbean Staghorn Coral Acropora cervicornis: Implications For The Recovery Of Endangered Reefs. J Hered 98: 40–50.
- Wolanski E, Asaeda T and Imberger J. (1989). **Mixing across a Iutocline.** Limnology and Oceanography. 34 (5), 931-8.
- Wyrtki K. (1987). **Indonesian through flow and the associated pressure gradient.** Journal of Geophysical Research 92: doi: 10.1029/JC092iC12p12941. issn: 0148-0227.