

Plankton Biomass Models Based on GIS and Remote Sensing Technique for Predicting Marine Megafauna Hotspots in the Solor Waters

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Abstract. Geographic information system and remote sensing techniques can be used to assist with distribution modelling; a useful tool that helps with strategic design and management plans for MPAs. This study built a pilot model of plankton biomass and distribution in the waters off Solor and Lembata, and is the first study to identify marine megafauna foraging areas in the region. Forty-three samples of zooplankton were collected every 4 km according to the range time and station of aqua MODIS. Generalized additive model (GAM) we used to modelling zooplankton biomass response from environmental properties. Thirty one samples were used to build a model of inverse distance weighting (IDW) (cell size 0.01°) and 12 samples were used as a control to verify the models accuracy. Furthermore, Getis-Ord Gi was used to identify the significance of the hotspot and cold-spot for foraging area. The GAM models was explain 88.1% response of zooplankton biomass and *percent to full moon*, *phytoplankton biomass* being strong predictors. The sampling design was essential in order to build highly accurate models. Our models 96% accurate for phytoplankton and 88% accurate for zooplankton. The foraging behaviour was significantly related to plankton biomass hotspots, which were two times higher compared to plankton cold-spots. In addition, extremely steep slopes of the Lamakera strait support strong upwelling with highly productive waters that affect the presence of marine megafauna. This study detects that the Lamakera strait provides the planktonic requirements for marine megafauna foraging, helping to explain why this region supports such high diversity and abundance of marine megafauna.

1. Introduction

Numerous scientific publications have reported marine megafauna population declines in recent decades, largely due to fisheries and other anthropogenic threats [1]. As a result, there have been an increasing number of studies focused on establishing marine megafauna spatial models to identify key habitat and conservation priority areas. Geographic information system (GIS) and remote sensing (RS) techniques can be applied to assist with distribution or habitat modelling of highly migratory marine megafauna [2, 3]. Moreover, GIS can be a useful tool that assists with the strategic design and development of both terrestrial and marine conservation planning. Three components are fundamental to develop species distribution or habitat models; (i) biotic, which are related to ecological



communities and the role of each species in the food web, (ii) abiotic, which are the physical environment requirements of a species, and (iii) movement, which is the opportunity a species has to reach a suitable location for their abiotic and biotic requirements [4].

Firstly, biotic components are important in understanding how different species interact with each other and the resulting consequences; for example, many marine megafauna species (e.g. cetaceans) feed on high densities of small animals such as krill and small fish [5]. As a result, understanding zooplankton biomass is critical in modelling marine megafauna distribution and behaviour [6-7], and many studies have documented positive correlations between the occurrence of cetaceans and the distribution and abundance of zooplankton [9, 10]. These related ecological system, which are zooplankton transfer energy from primary producers to consumers at higher trophic levels, such as fish and marine mammals [8]. Secondly, abiotic components (i.e. temperature, bathymetry,) are important in understanding the environmental requirements of marine megafauna species, which move actively both horizontally and vertically throughout the water column. For example, species may have specific thermal requirements needed to support their metabolic process [11]. Thirdly, it is important to understand species capability and opportunity to move and reach their required biotic and abiotic conditions. This is particularly important to determine given the current climate change situation that is altering ocean temperatures. Zooplankton are poikilothermic, which means that their physiological processes are highly sensitive to temperature [8, 12, 13], therefore changing ocean temperatures is likely to impact the distribution and composition of zooplankton, which in turn will impact the movement and distribution of marine megafauna that prey upon them.

This study was focused in the Savu Sea off Solor Island (SI) and Lembata Island (LI) in the East Nusa Tenggara province of Indonesia. The region is known for its complex, high-energy currents, and temperature variation and is an important corridor for cetaceans, mobulids rays and other marine megafauna [14, 15]. The waters of SI and LI is critical habitat for marine megafauna, which migrate through this region to find high density prey [16]. However, the villages of Lamakera (Solor) and Lamalera (Lembata) are traditional and commercial megafauna fishing communities that primarily target mobulids, whales, and dolphins and are arguably the biggest artisanal megafauna fisheries in the world [17, 19]. Extremely high international demand for mobulids gill plates, and protein needs from marine megafauna meat has been driving these fisheries and is likely to have caused an estimated 75% decline in catch rate of mobulids in Lamakera over the last 10 years [19]. In an effort to conserve vulnerable marine megafauna, the Indonesian government declared full protection for cetaceans in 1999, whale sharks (*Rhincodon typus*) in 2013, and most recently manta rays (*Manta alfredi* and *Manta birostris*) in 2014. To support the effective conservation and management of marine megafauna in the waters of SI and LI, identifying key habitat of marine megafauna in this region is critical. The aim of this pilot study was to develop a model for determining plankton biomass and distribution in order to help predict key foraging habitat for marine megafauna in SI and LI. We expected that our models would provide the following information; (i) predictions for zooplankton biomass as an ecological response, (ii) the approaches of using GIS and RS techniques to build spatial models to determine key habitat of marine megafauna.

2. Study site and sampling design

The study was conducted in the waters off SI and LI, East Nusa Tenggara province of Indonesia, including the Solor Strait and the Lamakera Strait (Figure 1). This region was chosen as the study site due to its known abundance of marine megafauna and highly productive waters, in addition the threat from targeted megafauna fisheries makes it important from a conservation perspective. Peak season for productivity and marine megafauna occurrence is during the eastern monsoon, from June through to September, when upwelling divergence in flow transport through the straits (and Ekman pumping) is large [20]. Plankton sampling surveys were conducted over five boat trips between the 5th to 18th January 2016. Zooplankton was sampled every 4km over the entire the study area (Fig. 1a).

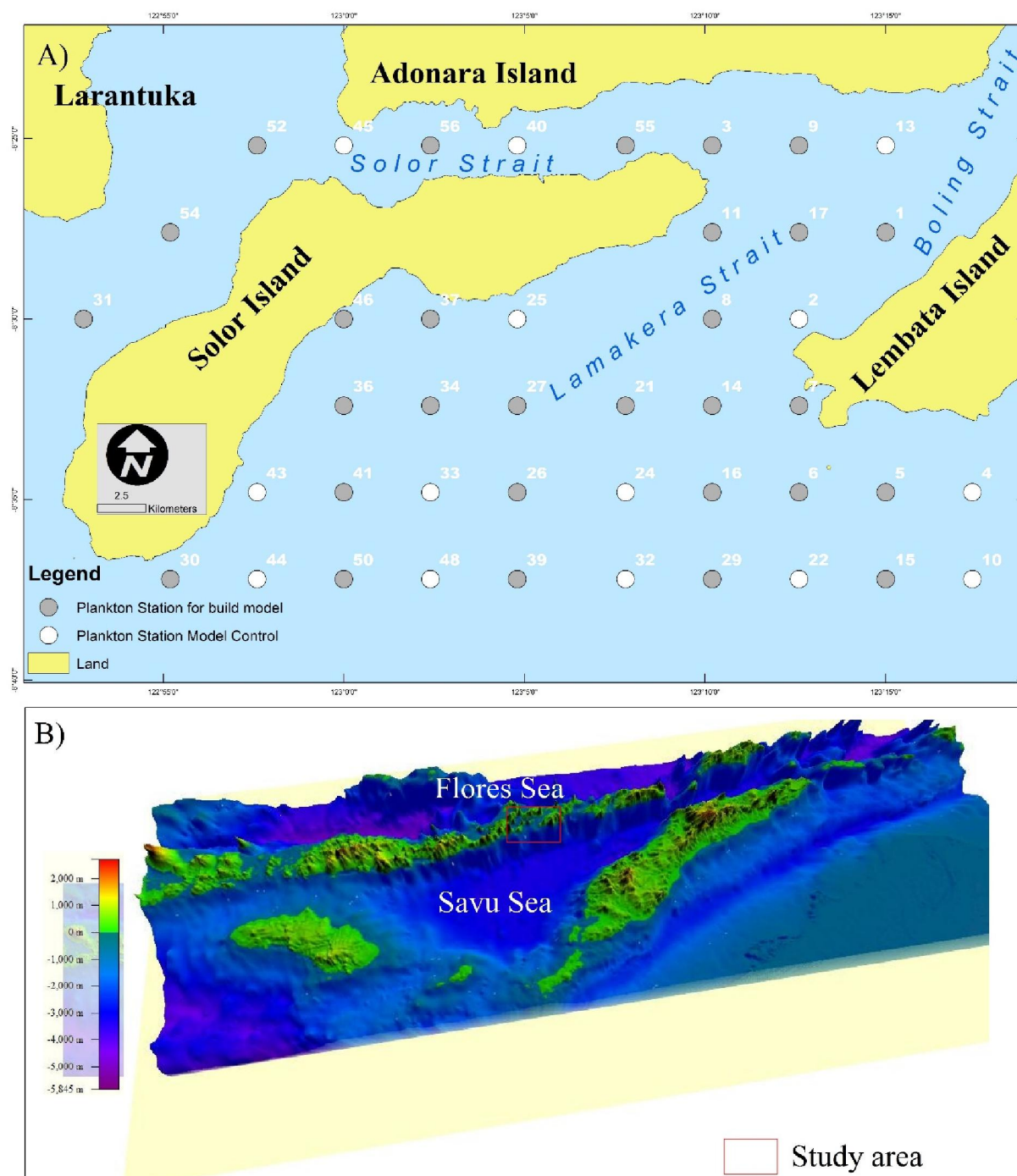


Figure 1. Maps of the study site showing a) the location of the zooplankton sampling stations (each station is 4km apart), and b) 3D bathymetric visualization of the Savu Sea.

3. Materials and Methods

3.1. Data collection

3.1.1. Zooplankton sampling

Zooplankton was collected using a 300 μm (mesh size) SEAGEAR net with a 30cm mouth diameter and 100cm length plankton net, which was trawled behind a speedboat. Trawls were conducted every 4km (Fig. 1) according to the range time and station of aqua MODIS record in the day we sampled.

During each trawl, the plankton net was towed ten meters behind the boat for 10 minutes at the surface waters. Mean distance towed was 1340 meters (± 222.5 SD), mean speed towed was 7.75 km/hours (± 1.3 SD), and mean sampling time was 9:50 AM (± 0.1 SD) such potential time for zooplankton in the surface waters. Five percent formaldehyde was used to preserve zooplankton samples until laboratory analyses, which was conducted in May 2016. The GPS position was recorded at the start and end of each trawl to determine the distance of each plankton toward the volume of water filtered.

3.1.2. Marine megafauna observations

A Rapid ecological assessment (REA) method was used to investigate the distribution and relative abundance of marine megafauna. GPS position are planned to exploring the marine megafauna sighting during survey trip [21]. Double platform visual observation method [22] was applied, and 2 groups of observers were scanning the area using Bushnell binocular marine series with optical distance 5km during every REA. A total of five REA trips were conducted on the same day/trip that the plankton sampling was conducted. Data collected included; start time and finish time of survey trips, marine megafauna sighting time, peak marine megafauna encounter time, GPS location of sighting, species, behaviour, and approximate number of individuals. In addition, the weather conditions during the REA was recorded using a modified Beaufort scale [23].

3.1.3. Biophysical satellite oceanography approach

Satellite oceanography is a crucial tool used for monitoring the dynamics and productivity of water masses. Moderate Resolution Imaging Spectroradiometer (MODIS) level 3 from NASA was used to derive sea surface temperature and chlorophyll-a concentration at a 4km spatial resolution for the dates of our survey period. Chlorophyll-a concentration as a photosynthetic pigment $\text{mg} \cdot \text{m}^{-3}$, is commonly used as a proxy for phytoplankton biomass in the surface waters (oceancolor.gsfc.nasa.gov).

3.2. Data analysis

3.2.1. Plankton biomass

In the laboratory, we filtered out 800 ml of each zooplankton sample from every sampling station/location using laboratory filter paper with a mesh size $< 300 \mu\text{m}$. The zooplankton samples were then dried in an air-conditioned room for 3 days until the dry weight of the zooplankton samples were constant. Analytic weight was used to measure the dry weight of zooplankton, and $\text{mg} \cdot \text{m}^{-3}$ was used as the dry weight unit of zooplankton based on the following equation:

Filtered volume

$$\text{Zooplankton biomass } \text{mg} \cdot \text{m}^{-3} = \frac{\text{dry biomass mg}}{\text{water filtered } \text{m}^3} \quad (1)$$

3.2.2. Modelling Approach

Conventionally, linear regression has been used to determine the relationship between zooplankton and phytoplankton, and in some cases there have been strong positive correlation, likely due to a food chain structure of zooplankton feeding upon phytoplankton. However, coastal and pelagic ecosystems are vast, dynamic and complex systems that will be more challenging for modelling linearity. We used generalized additive models (GAMs the mgcv R-package [24]) to address the issues, as they are powerful tools for modeling nonlinear relationships between zooplankton biomass and environmental properties. The final model was chosen based on the determination value (R^2) and Akaike Information Criterion (AIC) values, where the lowest AIC and highest determination values show better performance in prediction.

3.2.3. Inverse distance weighting (IDW)

GIS modelling tools are used to conduct spatial interpolation, which estimates the values of unsampled points or data gaps in the study area. This approach is extremely useful when studying the vast marine environment, where limits such as time and money prevent data collection throughout the whole study area. Spatial interpolation is a prediction of a variable at an unmeasured location based on samples at

known locations. We used local interpolators of inverse distance weighting because the concept of computation is relevant for phytoplankton and zooplankton, where closer points are thought to be similar as result of the food web. All feature data was calculated using ArcGIS 10.2.2[25], using the following equation:

$$Z_j = \frac{\sum_i \frac{Z_i}{d_{ij}^n}}{\sum_i \frac{1}{d_{ij}^n}} \quad (2)$$

Where, Z_j is the estimated value for the unsampled point (j), d_{ij} is the distance between the known sample (i) and the unsampled point(j), Z_i is the value of the known sample (i), and n is the user-defined exponent for weighting.

3.2.4. Model Verified

The IDW biomass models of phytoplankton and zooplankton, which we applied, are tested to measure the accuracy prior to conducting further analyses to identify the foraging area of marine megafauna in the study region. 12 samples were used and the following equation was applied:

$$RE = \frac{(X-C)}{X} \times 100 \% \quad (3)$$

$$MRE = \sum_{i=0}^n \frac{RE}{n} \quad (4)$$

Where, X is the field data, C is the model data. Relative error (RE) is the percentage error of the model's result compared with the field data, and mean relative error (MRE) is the mean percentage error from the 12 samples that were tested.

3.2.5. Hot spot analysis (Getis-Ord G_i^*)

We used clustering biomass models of phytoplankton and zooplankton every 0.01° (100 meters to 100 meters) to identify marine megafauna foraging sites in our study area. This analysis used the Getis-Ord G_i^* [26] to identify statistically significant high values (hotspots) and low values (cold-spot) for foraging requirement of marine megafauna. Since its development in the mid-1990s the *Getis-Ord G_i^** has been applied to analysing clustering in spatial data (point or area) and can be used to identify explicit areas of high use based upon specific test criteria, independent of the magnitude of abundance. The *Getis-Ord G_i^** has been used substantially in recent years in various research areas [27-28]. The Getis-Ord statistic is given by the following equation:

$$G_i^*(d) = \frac{\sum_{j=1}^n W_{i,j} X_{i,j} - \bar{X} \sum_{j=1}^n W_{i,j}}{S \sqrt{\frac{(n \sum_{j=1}^n W_{i,j}^2 - (\sum_{j=1}^n W_{i,j})^2)}{n-1}}} \quad (5)$$

$$\bar{X} = \frac{\sum_{j=1}^n x_j}{n}$$

$$S = \sqrt{\frac{\sum_{j=1}^n x_j^2}{n} - (\bar{X})^2}$$

G_i^* is calculated by the attribute value for feature (j), $w_{i,j}$ is the spatial weight between features i and j , n is equal to the total number of features and the G_i^* statistic calculated in this way is a Z-score (no further calculations are needed). Statistical significance of hot-spot and cold-spot are a measure from the Z-score and *p-value* which tell us whether or not to reject the null hypothesis, feature by feature. We applied a fixed distance band to get conceptualization of the spatial relationship and

Euclidean to measure the distance method. Statistical test result of significant hot and cold spots are showing (+/-) 3 bins reflect statistical significance with a 99 percent confidence level; (+/-) 2 bins reflect a 95 percent confidence level; (+/-) 1 bins reflect a 90 percent confidence level; and the clustering for features in bin 0 is not statistically significant. All calculation were carried out using ArcGIS 10.2.2[25].

4. Results and Discussion

4.1. Marine megafauna sighting

Marine megafauna was sighted 83% of the time during marine megafauna observation and zooplankton trawling surveys. A total of six observation survey days were conducted with a mean observation time of nine hours per trip, from 7am to 5pm. Most observation survey trips covered the whole study area around SI and LI. The majority of dolphin sightings occurred in the morning between 9am and 10am, with peak encounter time 09:20am. Tidal phase significantly affected dolphin occurrence with most sightings (61%) occurring during an ebb tide. A similar pattern was found in Lady Elliot Island (LEI), Australia for reef manta ray (*Manta alfredi*), where feeding manta rays were observed more frequently during an ebb tide, due to a higher abundance of prey (zooplankton) accumulating around LEI during this tidal phase [29-30]. Tidal current is highly driven by the moon and during our surveys, waning crescent was the most frequent moon phase. Results from the GAMs models (figure 2), show that the waning crescent moon phase with the percent of full moon between 2.3% - 27.8% has significant correlation with zooplankton biomass, thus driving the occurrence of higher tropic level species such as small fish and dolphins. Furthermore, weather appeared to affect the present or absence of marine megafauna in the waters of SI and LI. We observed that marine megafauna were most commonly sighted when the weather conditions were calm to slight wind and wave (see Table 1).

During the entire survey period the mean number of dolphins observed was 29 individuals (± 15 individuals SD, $n=6$), and 88% of the time they were observed feeding, and were frequently observed with large schools of fish and on occasion sharks were also observed hunting on the same school of fish. This usually occurred in the morning when productivity was higher.

Marine megafauna was commonly present in locations that showed higher productivity. These higher productivity locations showed a mean biomass of 0.18 mg.m^{-3} ($\pm 0.03 \text{ mg.m}^{-3}$ SD) for phytoplankton, and a mean biomass of 0.7 mg.m^{-3} ($\pm 0.25 \text{ mg.m}^{-3}$ SD) for zooplankton. Although, significant upwelling currents did not occur during the January survey period, which is outside of the peak productivity months, our results indicate that certain marine megafauna species such as dolphins still utilise the region, particularly higher productivity spots. Moreover, bathymetry maps of the channel between SI and LI (Lamakera Strait) are showing in figure 6a, show that the region is characterized by complex continental slope between $0^\circ - 90^\circ$, and the area in which dolphins were frequently observed was over a slope of 46° (± 27 SD). It has been reported that gentle continental slopes support strong upwelling currents and thus highly productive waters that affect the presence of marine megafauna. In the Gulf of Mexico, Risso's dolphins were regularly sighted along the step of the upper continental slope, an area that provides high productivity [31]. The authors (MIH Putra and S Lewis, Persobs) have observed high diversity and abundance of marine megafauna (including, whales, dolphins, manta rays, whale sharks and ocean sunfish) using the Lamakera strait at other times of the year outside of the study period, suggesting that this area is a key habitat for marine megafauna. Both dolphins and whales have been observed resting in surface waters (logging behaviour), and also hunting on schools of small fish in the Lamakera Strait approximately 4.75 km ($\pm 2.3 \text{ km}$ SD) from land (figure 6), this indicates that the area is likely to be important cetacean habitat for both feeding and resting.

During our observation surveys, we were also successful in identifying hawks bill turtles, which were observed actively swimming in surface waters most commonly in the morning. Sea turtles are grazers of macro algae and also predation on some invertebrates. Hawksbill turtles were sighted in a high productivity location (figure 6), Phytoplankton biomass in this location was 0.16 mg.m^{-3} and

zooplankton biomass was 0.67 mg.m^{-3} . It is likely that the relative high productivity in this area is a driver in turtle occurrence at this location, as the high productivity suggests that there are greater feeding opportunities here compared to areas with lower productivity. Turtles in Ningaloo Reef, Western Australia, have also shown a similar pattern with peak sightings occurring in March, which is a time of high productivity for the region [32]

Table 1. Marine megafauna survey results with environmental condition during observation

Parameters	Explanation	Parameter range	Dolphin	Turtle
Trophic guilds ^(a,b)	Prey items	N/A	Fish/cephalopods feeders	Invertebrates/macro-algae feeders
Relative abundance in total (%) ^(b)	Number of marine megafauna abundance during survey	0 – 100	99	1
Beaufort scale ^(b)	Wheatear condition during encounters	1 - 5	1 (99%), 2 (1%)	2
Peak encounter time ^(b)	The most species encountered	7 AM – 17 PM	09:20	08:00
Feeding behavior (%) ^(b)	Percentage behavior of marine megafauna are indicated feeding	0 - 100	88 %	0 %
Tide condition ^(c)	Tide condition during encountered with marine megafauna	ebb, flood, high tide, low tide	Flood (13%), ebb(61%), high (13%), low (13%)	Ebb (100%)
Moon phases ^(d)	Moon phases during encountered with marine megafauna	Third quarter moon, waning crescent, new moon, waxing crescent, first quarter moon, waxing gibbous, full moon, waning gibbous	Waningcrescent (67 %), New moon (17 %), waxing gibbous (17 %)	Waningcrescent (100 %)
Phytoplankton biomass mg. ^{m-3(e)}	Phytoplankton biomass mg. ^{m-3(d)} (31 d mean)	Mean 0.16 (± 0.01 SD) range 0.14 – 0.25	0.18 (± 0.03 SD)	0.16
Zooplankton biomass mg. ^{m-3(b)}	Zooplankton biomass mg. ^{m-3(b)} (during field survey)	Mean 0.56 (± 0.01 SD) range 0.36 – 1.45	0.7 (± 0.25 SD)	0.67
Bathymetry Slope (°) ^(f)	Slope degree of bathymetry in marine megafauna sighting	0° – 90°	46° (± 27 SD)	30°
Distance to the near coast (km) ^(b)	Distance between marine megafauna sighting and coast	N/A	4.75 (± 2.3 SD)	3

^(a)Literature
^(b)Field observation
^(c)WXTide32

^(d)NASA Horizons
^(e)NASA's MODIS
^(f)GEBCO

4.2. Environmental drivers on predicting zooplankton biomass response

The GAMs for zooplankton biomass and environmental predictor was tested in 2 model scenarios, which are shown in figure 2. The first model examines zooplankton biomass as a response of the predictors (*percent to full moon, distance of sampling station to the coast, sea surface temperature, and phytoplankton biomass*) and was explained as 87.7% of the deviance of zooplankton biomass in the waters of SI and LI. Results from the first model shows that moon phase ($F = 3.6$, $edf = 5.6$, $p < 0.05$) and phytoplankton biomass ($F = 9.3$, $edf = 7.85$, $p < 0.05$) were a more significant predictor for zooplankton biomass response than sea surface temperature ($F = 4.9$, $edf = 1.8$, $p < 0.05$). Zooplankton biomass was not significantly related to distance of sampling station to the coast ($F = 0.4$, $edf = 1$, $p > 0.05$). The second model shows the zooplankton biomass as the response of predictors (*percent to full moon, phytoplankton biomass, sea surface temperature, and time of sampling to high tide*) was 88.8 % of the deviance of zooplankton biomass, which was higher than model 1. Model 2 identified moon phase ($F = 4.9$, $edf = 7.6$, $p < 0.05$), phytoplankton biomass ($F = 4.6$, $edf = 6.4$, $p < 0.05$) and sea surface temperature ($F = 11.54$, $edf = 1$, $p < 0.05$) as the most important predictor. However, time of sampling to high tide ($F = 1.8$, $edf = 2.2$, $p > 0.05$) which were not significant predictors.

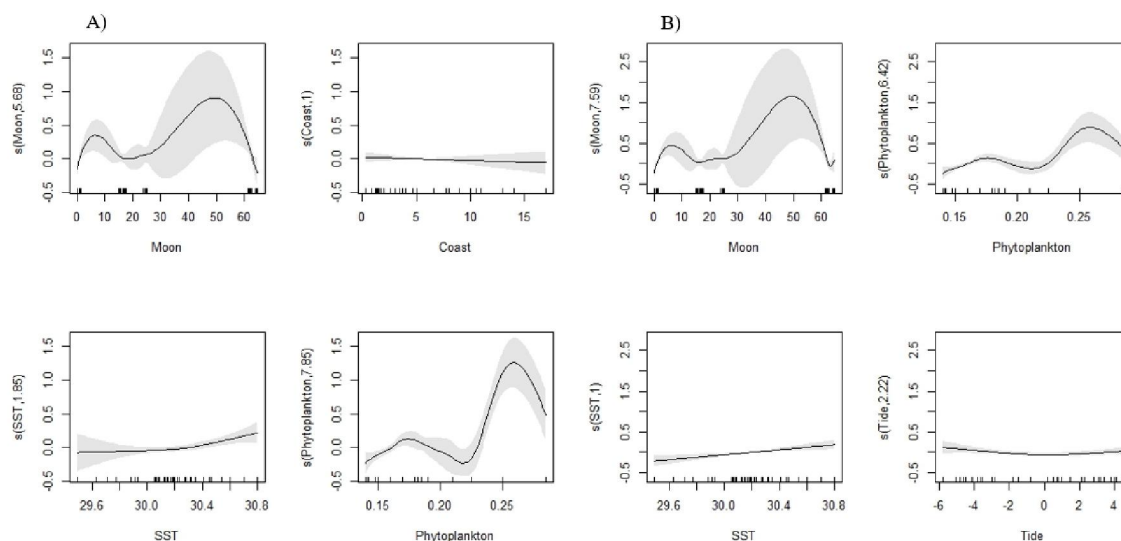


Figure 2. Generalize adaptive models final output of zooplankton biomass as the response of a) *percent to full moon, distance to coast, sea surface temperature, and phytoplankton biomass*; b) *percent to full moon, phytoplankton biomass, sea surface temperature, and time of sampling to high tide*. Zero on the y axis indicates no effect of the predictor. The magnitude reflects the importance of variable. Shade lines and error bars represent 95% confidence intervals.

The first predictor, which was the fraction of moon illumination (*percent to full moon*) was the most significant predictor for both model 1 and model 2, which showed a higher zooplankton biomass response than the other predictors. Waxing gibbous and waning gibbous are the moon phases with the highest response of zooplankton biomass (figure 2), the magnitude of zooplankton biomass significantly increased during these moon phases. A similar pattern was observed in 2015, where catch rate of the planktivore feeder, *Manta birostris*, was three times higher during waxing gibbous and waning gibbous moon phase (Misool Baseft in *unpublished data*). However, studies in Komodo National Park (KNP) and Lady Elliot Island (LEI) showed a different pattern. Manta rays were more abundant in KNP and LEI during the new moon and full moon when the tidal flux was highest [29, 33]. In contrast, the waters of SI and LI showed that during the full moon and new moon mobulids ray catch (i.e. *Manta birostris*, *Mobula japonica*, and *Mobulatarapacana*) in Lamakera were the lowest. The fraction of moon illuminated (*percent to full moon*) is a key factor that Lamakeran fisherman use to determine a potential hunting period, which reportedly starts two-four days after the new moon, i.e. a waxing crescent moon [19]. GAMs models indicate that the beginning of a waxing crescent moon (0-

10 percent to full moon) significantly influences the response of zooplankton biomass, and thus drives the occurrence of higher trophic level species such as manta rays, dolphins and other marine megafauna in the waters of SI and LI. The second predictor, phytoplankton biomass, also significantly correlated with zooplankton biomass in both model 1 and model 2. Since satellite-derived chlorophyll-a concentration appears to be a proxy for biomass of zooplankton, satellite data is an important predictor for studying marine megafauna [29, 34]. The third predictor, sea surface temperature, is commonly reported as being a critical predictor for modelling zooplankton. Several studies have documented that zooplankton biomass will be higher in cooler temperatures [30]. However, in this study both model 1 and model 2 found that there was a positive correlation between warmer SST and zooplankton biomass. However, this result does not necessarily signify that higher zooplankton biomass will be found in warmer temperatures, this is because in the study region there is very little temperature variation in January with temperature range generally between 29°C – 30°C. Further analysis throughout the entire year is needed to determine the effect of SST on zooplankton biomass.

Table 2. Candidate generalized additive models for predicting zooplankton biomass as the function of various candidate explanatory variables, with a comparison of the model's goodness-of-fit in terms of coefficient of determination value (R^2) and Akaike Information Criterion (AIC) values. Model 2 was the better candidate model, which more lower AIC value and highest determination value.

Model	R^2	GCV Score	AIC	Deviance explained
Model 1 = Zooplankton ~s(Moon)+s(Coast)+s(SST)+s(Phytoplankton)	0.79	0.012	-71.33	87.7%
Model 2 = Zooplankton ~s(Moon)+s(Phytoplankton)+s(SST)+s(Tide)	0.81	0.012	-73.69	88.8%

The fourth predictor, tide cycle, has been found by several studies to be another important predictor for modelling zooplankton and thus planktivores [29-30]. Results from our GAMs output showed that tide cycle did not significantly effect zooplankton biomass in this study. This is contradictory to other studies that have shown a strong relationship between tide and zooplankton biomass. However, this is a similar case to that of reef manta rays and whale sharks in southern Mozambique that showed a weak relationship with the time to high tide [35]. Our fifth predictor, distance of sampling station to the coast, showed no significant correlation to zooplankton biomass. This result is similar to a study in Oman, which showed no strong correlation between distance to the coast and cetacean habitat.

Based on coefficient of determination value (R^2) and Akaike Information Criterion (AIC) values in Table 2. Model 2 was the most comprehensive and showed better performance in explaining zooplankton response to different oceanographic predictors in the waters of SI and LI.

4.3. Plankton spatial modelling

Spatial biomass distribution of both phytoplankton and zooplankton was completed (final) using IDW with search radius using variable method, and cell size 0.01⁰ (100 meters to 100 meters). Twelve station we used to assess the accuracy of models. Both models of phytoplankton biomass and zooplankton biomass was performance in high accuracy. Phytoplankton biomass of IDW models was the higher accuracy with mean relative error 4.23% than zooplankton biomass 12.14 % (see Table 3). Spatial interpolation of IDW as a part of deterministic interpolation which calculate from measured point that are closely and give most influence, than IDW assume that a distance each sampling point as critical role on build high accuracy models [36-37]. In this case, phytoplankton and zooplankton was sampled each 4 km according a station sample of Aqua MODIS (4km or level 3) for this region as figure 1 showed. Sampling effort which was conducted show that the plankton distribution was affected by sampling density and distance each sampling station. Although, spatial interpolation are available in several method such as kriging and spline, some researcher was found that no significant differences between method. The most significant for build a high-resolution spatial models is sampling density [38].

Spatial analysis of plankton distribution in this study was show that are both phytoplankton (0.14 mg.m^{-3}) and zooplankton (1.45 mg.m^{-3}) was higher in Lamakera strait and west part of SI. The spatial patterning was get smooth on colouring transition as results from density and distance station sample which showing Figure 1, 3a and 3d. Based on results of GAMs models, the phytoplankton biomass is a strong predictor for modelling zooplankton biomass and that are was approved by spatial models which was recognise that are phytoplankton biomass drives zooplankton biomass distribution. Although, in some cases there are not positive correlate as effects of role from other predictor such as tidal current which drives and accumulate zooplankton in sheltered and shallow waters location such in SI bay area (Figure 3a). Study in Kilindoni Bay off Mafia Island, Tanzania was found there are tidal current play a critical role in accumulate zooplankton in this area and motivate whale sharks to feeding in regularly [39-40].

Table 3. Accuracy assessment of inverse distance weighting models (0.01°) of zooplankton biomass and phytoplankton biomass. (RE %) is relative error between models output and field data each station “control”, and (MRE %) mean relative error is relative error for full model.

Station ID	Field data zooplankton biomass mg.m^{-3}	IDW model zooplankton biomass mg.m^{-3}	RE (%)	MRE (%)	Satellite data phytoplankton biomass mg.m^{-3}	IDW model phytoplankton biomass mg.m^{-3}	RE	MRE
2	0.78	0.65	16.59	12.14	0.17	0.17	0.00	4.23
13	0.82	0.78	4.34		0.28	0.21	26.32	
22	0.49	0.54	11.08		0.15	0.15	0.00	
24	0.66	0.51	22.57		0.15	0.15	0.00	
25	0.51	0.55	8.23		0.16	0.16	0.00	
32	0.44	0.48	9.22		0.14	0.15	5.63	
33	0.81	0.54	33.60		0.16	0.16	0.00	
40	0.52	0.55	6.41		0.18	0.18	2.70	
43	0.53	0.54	1.65		0.15	0.16	6.67	
44	0.44	0.47	7.45		0.15	0.15	0.00	
45	0.42	0.50	19.97		0.18	0.17	8.11	
48	0.45	0.47	4.57		0.14	0.15	1.35	

4.4. Detecting the foraging area of marine megafauna in the waters of Solor

Based on spatial interpolation output, 129014 station data with spatial resolution 0.01° was we test using *Getis-Ord Gi** spatial statistical analysis to generate area which identify as hotspots (high productivity) and cold-spot (low productivity) both phytoplankton and zooplankton. Four map were generate to identify foraging area of marine megafauna in the waters of SI and LI: Figure 3c and 3f are visualize from a Z-score to determining confidence thresholds of hotspots and cold-spot both phytoplankton and zooplankton. Moreover, to identify foraging area we classify the significances hotspot of biomass threshold as 90%, 95%, and 99% or 99.9%. Statistical significant 90% of phytoplankton biomass hotspots was (lowest Z-score 1.645, p-value 0.099, phytoplankton biomass 0.177 mg.m^{-3} ; highest Z-score 1.957, p-value 0.05, phytoplankton biomass 0.188 mg.m^{-3}), 95% of hotspots (lowest Z-score 1.977, p-value 0.047, phytoplankton biomass 0.179 mg.m^{-3} ; highest Z-score 2.573, p-value 0.01, phytoplankton biomass 0.189 mg.m^{-3}), 99% and or 99.9% of hotspots (lowest Z-score 2.581, p-value 0.0098, phytoplankton biomass 0.194 mg.m^{-3} ; highest Z-score 13.66, p-value 0.00, phytoplankton biomass 0.25 mg.m^{-3}). Zooplankton biomass threshold for statistical significant of 90% hotspots (lowest Z-score 2.543, p-value 0.01, zooplankton biomass 0.662 mg.m^{-3} ; highest Z-score

2.872, p -value 0.004, zooplankton biomass 0.676 mg.m^{-3}), 95% hotspots (lowest Z -score 2.876, p -value 0.004, zooplankton biomass 0.677 mg.m^{-3} ; highest Z -score 3.504, p -value 0.0004, zooplankton biomass 0.754 mg.m^{-3}), 99% and or 99.9% hotspots (lowest Z -score 3.51, p -value 0.0004, zooplankton biomass 0.755 mg.m^{-3} ; highest Z -score 23.01, p -value 0.00, zooplankton biomass 1.445 mg.m^{-3}). Figure 3b and 3e is spatial clustering based on Z -score and p -value, a highest Z -score and smallest p -value are indicated as hotspots for both phytoplankton biomass and zooplankton biomass. Then, a low negative Z -score and smallest p -value are indicated as cold-spot for both phytoplankton biomass and zooplankton biomass. Z -score near zero will classify as no clustering.

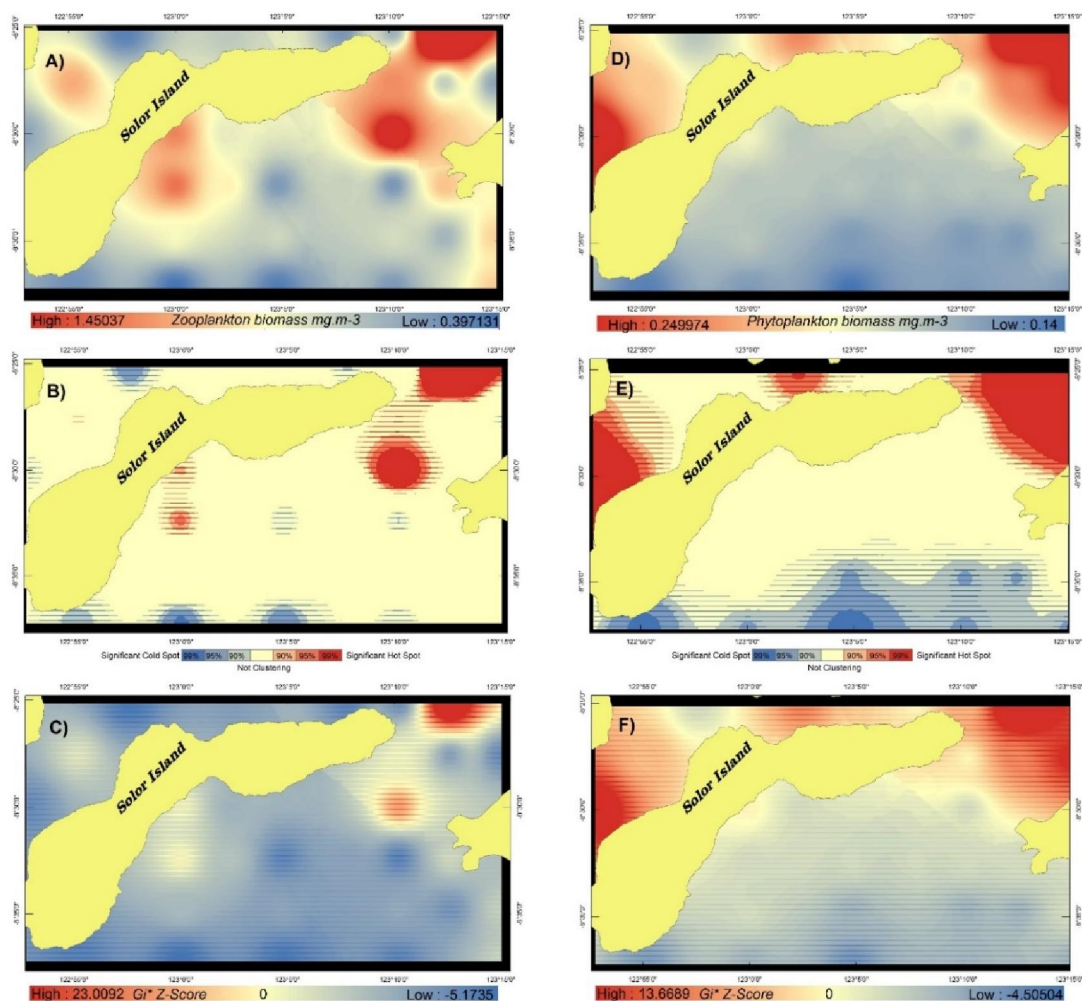


Figure 3. Spatial analysis of biomass distribution models of IDW (row 1); statistical significant hotspot and cold-spot *Getis-Ord G_i^** (row 2); G_i^* Z-score statistical significance threshold values; column right as zooplankton and column left as phytoplankton. Red colour as indicated high value (hotspots), blue colour as indicated low value cold-spot.

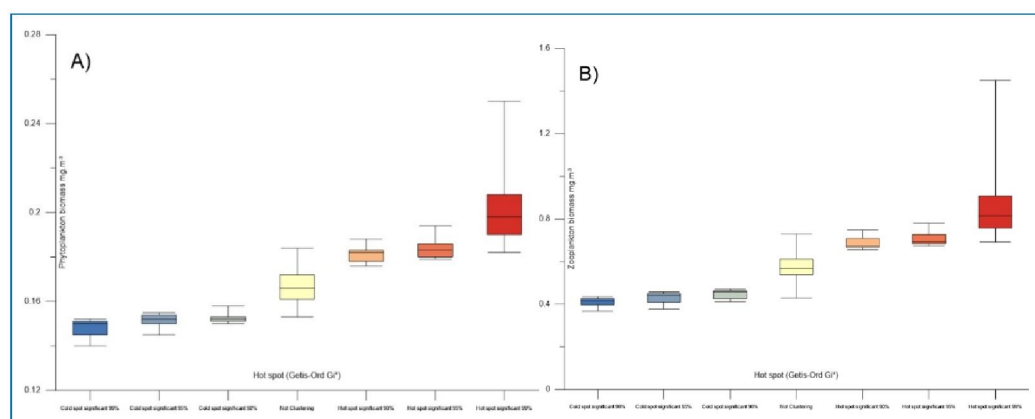
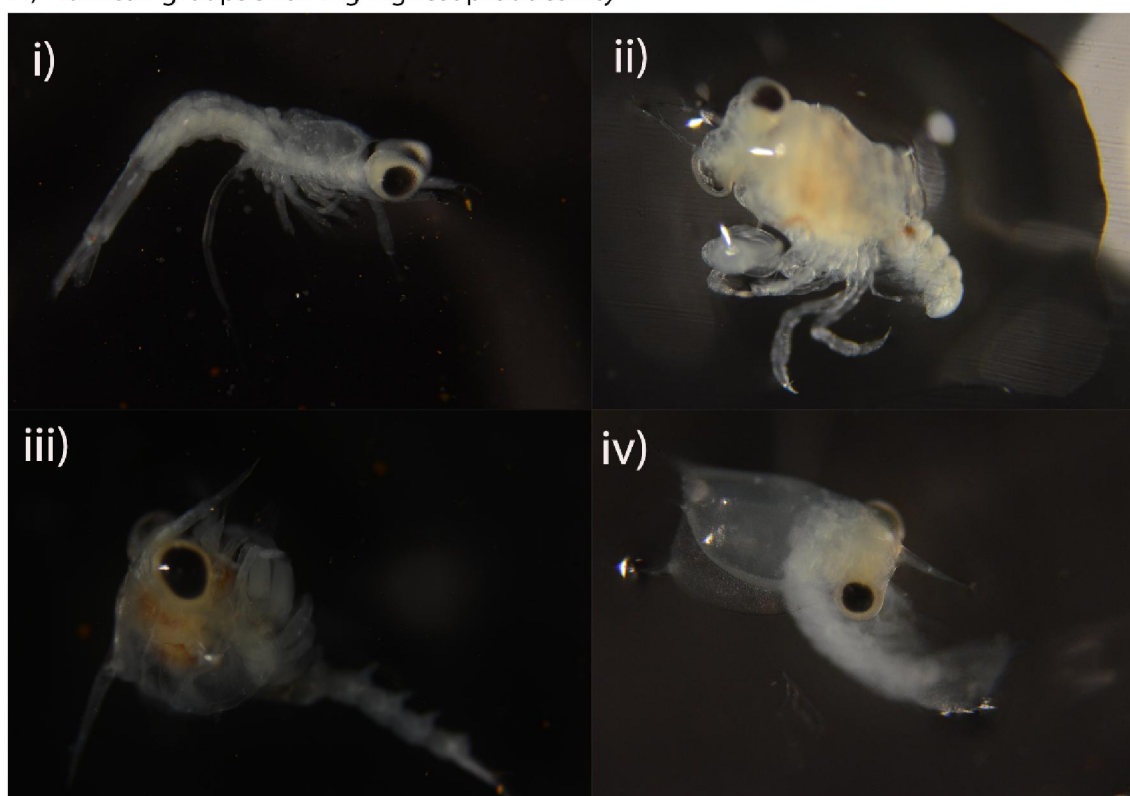


Figure 4. Comparison biomass by statistical significant clustering of *Getis-Ord Gi** a) phytoplankton mg.m⁻³, b) zooplankton mg.m⁻³.

A) Plankton groups showing highest productivity



B) Plankton groups showing lowest productivity

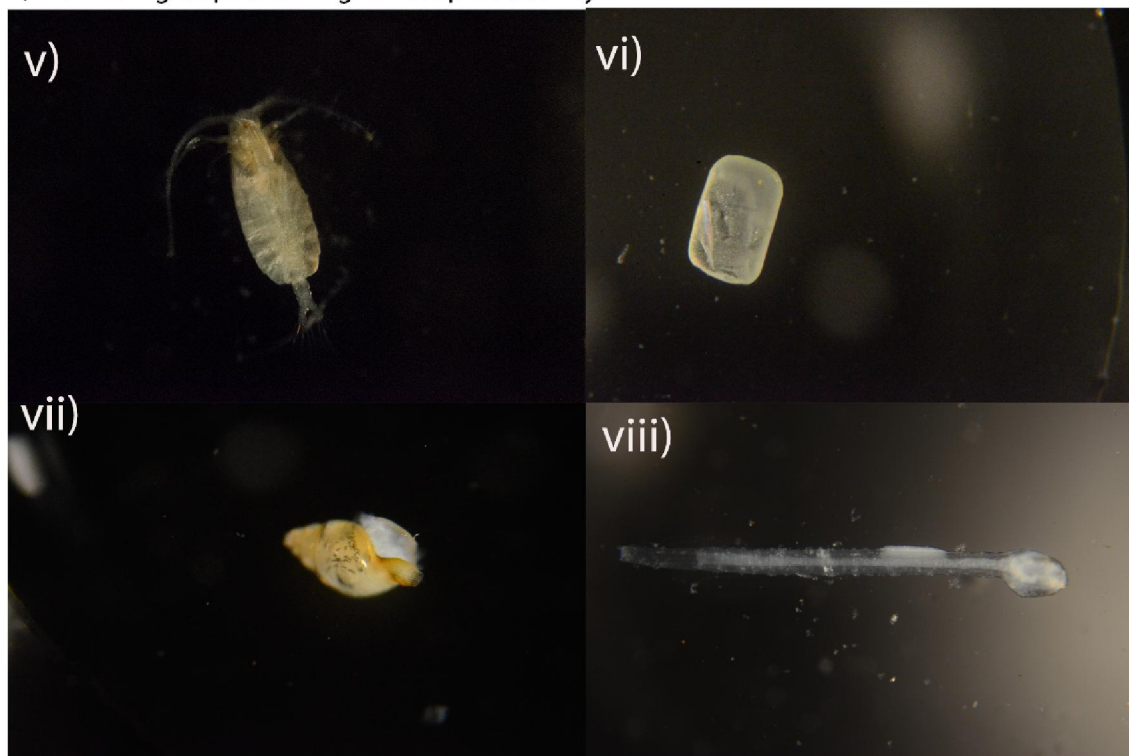


Figure 5. zooplankton group composition in different station; location with the highest productivity are dominated with *macro zooplankton* such i) shrimp, ii) crab, iii) crab, iv) crab; and location with lowest productivity are dominated with v) copepods, vi) egg vii) mollusca, vii) chaetognatha.

Overall, *Getis-Ord Gi** spatial statistical analysis was identify a potential hotspots for foraging area based on plankton biomass modelling which are distribute in high dense patch in Lamakera strait. A high dense patch of hotspots are exist in small area an approximately 15% - 30% of total waters off SI and LI. Plankton biomass was higher in specific location which has characterize by oceanographic process in this region. Combined by tidal currents surrounding straits of Solor, Lamakera, and Bolinghas driving zooplankton from various direction to the same place in Lamakera strait. Bathymetric across this channel are quite shallow in the north part and extremely slope in the south part off SI and south west of LI, which has provide a strong upwelling and drives a water masses from Savu Sea with high productivity in Lamakera strait (see Figure 6). Interestingly, that combination has resulting current turbulence and accumulate high dense patch of zooplankton biomass in this area. Shrimp and crab has dominate the zooplankton composition in the waters with high productivity, which mean there are is main key on transferring energy to marine megafauna in trophic ecology (Figure 5) [41]. Environmental drives has strong explanatory for the dynamics of zooplankton in this area. A comparison biomass by statistical significances as Figure 4 showed we used to approving this theory. Statistical test was show that are 99% significant hotspot are have high range than other classify, that indicated something exceptionally unusual has happened at this location in terms of the spatial concentration of biomass was higher in Lamakera strait as results environmental drives. Statistical one t-test we used to generalize a significances of hotspot analysis. The results was showed the foraging behavior was significantly related to plankton biomass hotspots (see Figure 6), which were two times higher compared to plankton cold-spots of phytoplankton (0.2 ± 0.01 SD vs 0.14 ± 0.003 SD mg.m^{-3}) and zooplankton (0.87 ± 0.17 SD vs 0.41 ± 0.01 SD mg.m^{-3}). Whale sharks in Kilindoni Bay, off Mafia Island, Tanzania was show same pattern that the foraging area was characterize by high dense patch zooplankton which 10 times higher (25 vs. 2.6 mg m^{-3}) [40].

Table 4. Statistical summary and sample one t-test of plankton biomass *Getis-Ord Gi** output.

Plankton	<i>Getis-Ord Gi*</i>	Mean biomass mg.m ⁻³	SD	CV	<i>p-value</i>	95% confidence interval (mg.m ⁻³)
Phytoplankton	Cold spot 99%	0.148	0.003	0.02	<0.05	0.1482 – 0.1484
	Cold spot 95%	0.151	0.002	0.01	<0.05	0.1516 – 0.1517
	Cold spot 90%	0.152	0.002	0.01	<0.05	0.1528 – 0.1529
	Not clustering	0.165	0.006	0.60	<0.05	0.1653 – 0.1654
	Hot spot 90%	0.180	0.002	0.01	<0.05	0.1803 – 0.1805
	Hot spot 95%	0.183	0.003	0.01	<0.05	0.1833 – 0.1835
	Hot spot 99%	0.200	0.010	0.06	<0.05	0.2004 – 0.2009
Zooplankton	Cold spot 99%	0.41	0.01	0.04	<0.05	0.408 – 0.411
	Cold spot 95%	0.43	0.02	0.05	<0.05	0.431 – 0.433
	Cold spot 90%	0.44	0.02	0.04	<0.05	0.446 – 0.448
	Not clustering	0.55	0.05	0.09	<0.05	0.554 – 0.555
	Hot spot 90%	0.68	0.02	0.03	<0.05	0.685 – 0.687
	Hot spot 95%	0.70	0.02	0.03	<0.05	0.701 – 0.703
	Hot spot 99%	0.87	0.17	0.19	<0.05	0.865 – 0.876

4.5. Applied modelling for management and conservation of marine megafauna

Our models provide fine-scale of the biomass distribution and highlight the importance of prey availability on driving a distribution of marine megafauna. The potential of foraging area was characterized by environmental properties such as phytoplankton biomass, sea topographic, sea surface temperature and tidal current, which provide their environmental requirement for feeding and thermoregulation. Three dimensional models of bathymetry in Figure 6a and 6b help us to understand the distribution of marine megafauna related characteristic and complexity of sea topographic. Extremely steep slope, which characterizes Lamakera strait, has strong support for upwelling and thus highly productive waters that influence the presence of marine megafauna. Even though, in several observations, dolphins have sighted in the location which are not characterized as plankton biomass hotspots, but field observation was found that dolphins move from the south part/open Ocean to Lamakera strait which is characterized by high productivity. The dolphin moves such an indication has response to the area with high productivity. Several animal movement studies have documented that animals move as a response to exploring food, reproduction, and climate change [42].

Pervious study was found that this region is such a critical habitat for some cetaceans (i.e. spinner dolphin and pantropical spotted dolphin) which can be observed every year [43]. This study detects that the Lamakera strait provides the planktonic requirements for marine megafauna foraging, helping to explain why this region supports such high diversity and abundance of marine megafauna. Modelling approaches are powerful to help studying marine environmental, which are large area, dynamic, and complex. Then, this study has identified that this location is a key habitat for marine megafauna and is a priority location for conservation.

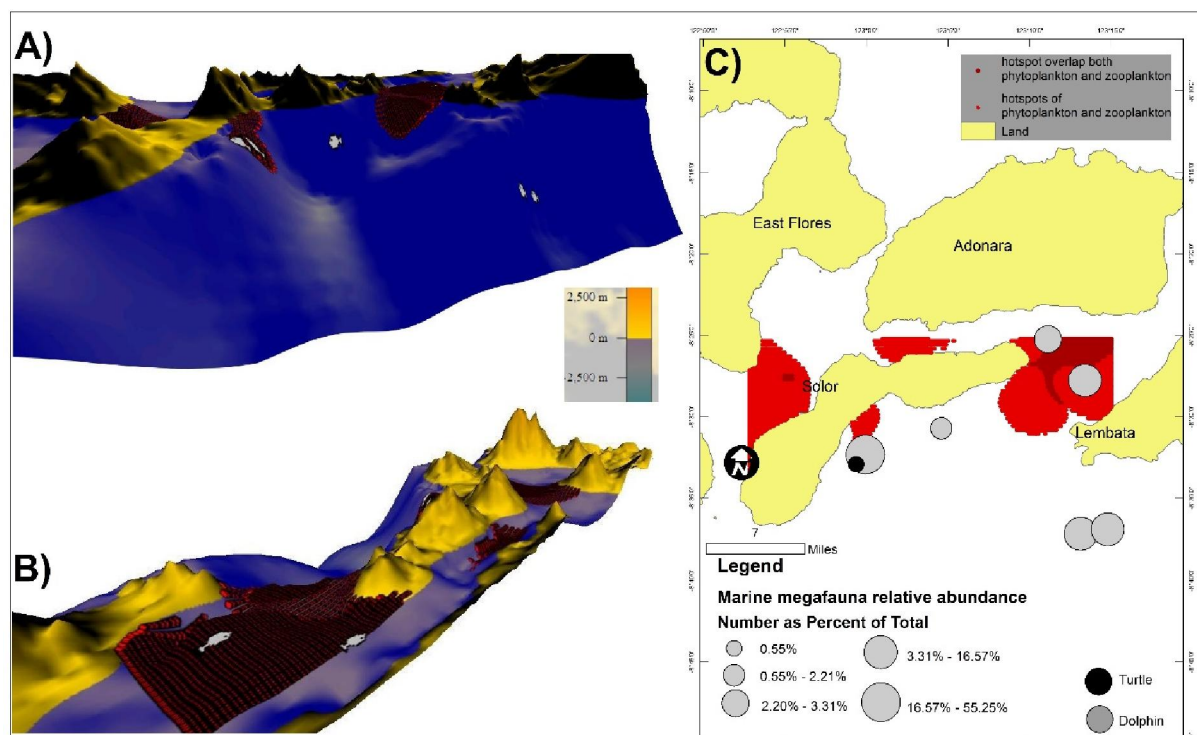


Figure 6. Productivity hotspot as indicated foraging area in this region during field survey in January 2015. 3D visualization topography models GEMCO of Solor region; a) south part of Solor and b) northeast of Solor. Red dots indicated plankton hotspot as statistically significant test of *Getis-Ord Gi** 99%, 95%, 90%. Fish symbol indicated marine megafauna sighting during study. C) 2D visualization; red color indicated hotspots of phytoplankton and zooplankton; dark red indicated hotspot overlap both phytoplankton and zooplankton.

5. Conclusion

Here we present GIS and remote sensing approach to modelling a plankton biomass hotspots which together triggered the marine megafauna feeding aggregation in the waters of SI and LI. Our GAMs model found that zooplankton biomass was driven by environmental properties such as moon phase and phytoplankton as a higher predictor for zooplankton biomass response. Linking environmental dynamic in understanding the plankton biomass distribution is helpful to figure out the response of trophic level above such as small fish which will drive a dolphin. Our spatial statistical analysis examined that a potential foraging area was 2 times higher of plankton biomass than other locations which identify as cold-spot. Including zooplankton biomass in predicting critical habitat of marine megafauna habitat is important to build a high accuracy model, and several studies have examined that incorporating prey items can improve cetacean habitat models [2]. Moreover, spatial analysis approaches are useful tools that help managers to recognize a critical habitat for marine megafauna, especially endangered species, and further to build strategic design and management plans for MPAs.

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References

- [1] Schipper J, Chanson, JS, Chiozza F, Cox NA, Hoffmann M, Katariya V, Lamoreux J, Rodrigues, AS, Stuart SN, Temple HJ and Baillie J 2008 The status of the world's land and marine mammals: diversity, threat, and knowledge *Science* **322** (5899) pp.225-230
- [2] Lambert C, Mannocci L, Lehodey P, Ridoux V 2014 Predicting Cetacean Habitats from Their Energetic Needs and the Distribution of Their Prey in Two Contrasted Tropical Regions. *PLoS ONE* **9**(8): e105958. doi:10.1371/journal.pone.0105958
- [3] Mannocci L, Catalogna M, Dore'mus G, Laran S, Lehodey P, et al 2014 Predicting cetacean and seabird habitats across a productivity gradient in the South Pacific gyre *Prog Oceanogr* **120** 383–398
- [4] Peterson AT 2011 *Ecological niches and geographic distributions*(MPB-49) (No. 49). Princeton University Press
- [5] Preen A R, Marsh H, Lawler, IR, Prince RIT and Shepherd R 1997 Distribution and abundance of dugongs, turtles, dolphins and other megafauna in Shark Bay, Ningaloo Reef and Exmouth Gulf, Western Australia *Wildlife Research* **24** 185–208. doi:10.1071/WR95078
- [6] Bradshaw JA, Higgins J, Michael K, Wotherspoon SJ and Hindell MA 2004 At-sea distribution of female southern elephant seals relative to variation in ocean surface properties *ICES Journal of Marine Science* **61** 1014–1027. doi:10.1016/J.ICESJMS.2004.07.012
- [7] Littaye A, Gannier A, Laran S and Wilson JPF 2004 The relationship between summer aggregation of fin whales and satellite-derived environmental conditions in the northwestern Mediterranean Sea *Remote Sensing of Environment* **90** 44–52
- [8] Richardson AJ 2008 In hot water: zooplankton and climate change *ICES Journal of Marine Science: Journal du Conseil* **65**(3) 279–95
- [9] Kideys AE, Kovalev AV, Shulman G, Gordina A and Bingel F 2000 A review of zooplankton investigations of the Black Sea over the last decade *Journal of Marine Systems* **24** 355–371. doi:10.1016/S0924-7963(99)00095-0
- [10] Wilson SG, Pauly T and Meekan MG 2002 Distribution of zooplankton inferred from hydroacoustic backscatter data in coastal waters off Ningaloo Reef, Western Australia. *Marine and Freshwater Research* **53** 1005–1015. doi:10.1071/MF01229
- [11] Sims DW 2003 Tractable models for testing theories about natural strategies: foraging behaviour and habitat selection of free-ranging sharks *Journal of Fish Biology* **63** 53–73
- [12] Mauchline J 1998 The biology of calanoid copepods *Advances in Marine Biology* **33** 710 pp
- [13] McKinnon AD, Richardson AJ, Burford MA and Furnas MJ 2007 *Vulnerability of Great Barrier Reef plankton to climate change. In Climate Change and the Great Barrier Reef* Great Barrier Reef Marine Park Authority. p 121–152
- [14] Kahn B, Pet J 2003 Long-term visual and acoustic cetacean surveys in Komodo National Park, Indonesia 1999-2001: Management implications for large migratory marine life. In: *Proceedings and Publications of the World Congress on Aquatic Protected Areas 2002*. Australian Society for Fish Biology. Murdoch, WA.
- [15] DeVantier LM, Turak E, Allen G 2008 Lesser Sunda ecoregional planning coral reef stratification. Reef and seascapes of Lesser Sunda ecoregion. The Nature Conservancy, Arlington, VA.
- [16] Kahn B 2010 *Seismic Surveys and Offshore Exploration in Highly Sensitive Marine Areas: Regulatory Guidelines and Best Practices for Contractors and Operators Working in the Indonesian Seas*. Bali: Apex Environmental. p
- [17] Mustika PLK 2008 *Marine mammals in the Savu Sea (Indonesia): indigenous knowledge, threat analysis and management options*. PhD Thesis (James Cook University)
- [18] Setiasih N *Manta Ray of Hope Indonesia Fishery Investigation*. Shark Saver and WildAid.
- [19] Lewis SA, Setiasih N, O'Malley MP, Campbell SJ, Yusuf M and Sianipar AB 2015 Assessing Indonesian manta and devil ray populations through historical landings and fishing community interviews (No. e1642). *PeerJ PrePrints*.
- [20] Potemra JT, Sprintall J, Hautala SL and Pandoe W 2003 Observed estimates of convergence in the Savu Sea, Indonesia *J. Geophys. Res* **108**(C1), 3001, doi:10.1029/2002JC001507.
- [21] Khan B 2003 *Solor-Alor visual and acoustic cetacean survey: interim report April-May 2003*

- survey period*. The Nature Conservancy South East Asia Center for Marine Protected Area. Bali. Indonesia.
- [22] WWF-Hongkong 2003 *Marine Mammals*. In *Marine Mammals Survey Technique. Proceeding of the workshop on cetacean species identification, Marine Mammals survey Technique and Review of Regional Knowledge, 29-30 Januari 2003, Indonesia*. Departemen Kelautan dan Perikanan dan WWF-Indonesia, Jakarta, Indonesia.
 - [23] Khan B 2001. *Komodo National Park: A Rapid Ecological Assessment of Cetacean Diversity, Abundance, and Distribution: Monitoring Report April 2001. 1999-2000 Synopsis*. TNC Indonesia Program. Coastal and Marine Conservation Center. Bali, Indonesia.
 - [24] R Core Team 2012 R: a language and environment for statistical computing. Vienna, Austria: R Foundation or Statistical Computing. Available: <http://www.R-project.org/>.
 - [25] ESRI 2011 *ArcGIS Desktop: Release 10*. Redlands, CA: Environmental Systems Research Institute.
 - [26] Ord JK, Getis A 1995 Local spatial autocorrelation statistics: distributional issues and an application *Geogr. Anal* **27** (4), 286–306.
 - [27] Rud R, Shoshany M, Alchanatis V 2013 Spatial–spectral processing strategies for detection of salinity effects in cauliflower, aubergine and kohlrabi *Biosyst. Eng* **114** (4), 384–396.
 - [28] Kuletz KJ, Ferguson MC, Hurley B, Gall AE, Labunski EA and Morgan TC 2015 Seasonal spatial patterns in seabird and marine mammal distribution in the eastern Chukchi and western Beaufort seas: Identifying biologically important pelagic areas *Prog Oceanogr* **136** (2015) 175–200. <http://dx.doi.org/10.1016/j.pocean.2015.05.012>
 - [29] Jaine FRA, Couturier LIE, Weeks SJ, Townsend KA, Bennett MB, Fiora K, Richardson AJ 2012 When Giants Turn Up: Sighting Trends, Environmental Influences and Habitat Use of the Manta Ray *Manta alfredi* at a Coral Reef *PLoS ONE* **7**(10): e46170. doi:10.1371/journal.pone.0046170
 - [30] Armstrong AO, Armstrong AJ, Jaine FRA, Couturier LIE, Fiora K, Uribe-Palomino J, Weeks SJ, Townsend KA, Bennett MB, Richardson AJ 2016 Prey Density Threshold and Tidal Influence on Reef Manta Ray Foraging at an Aggregation Site on the Great Barrier Reef *PLoS ONE* **11**(5): e0153393. doi:10.1371/journal.pone.0153393
 - [31] Baumgartner MF 1997 The distribution of Risso's dolphin (*Grampus griseus*) with respect to the physiography of the northern Gulf of Mexico *Mar Mamm Sci* **13**(4):614–638
 - [32] Sleeman JC, Meekan MG, Wilson SG, Jenner CK, Jenner MN, Boggs GS, Steinberg CC and Bradshaw CJ 2007 Biophysical correlates of relative abundances of marine megafauna at Ningaloo Reef, Western Australia. *Marine and Freshwater Research* **58**(7), pp.608-623.
 - [33] Dewar H, Mous P, Domeier M, Muljadi A, Pet J, Whitty J 2008 Movements and site fidelity of the giant manta ray, *Manta birostris*, in the Komodo marine park, Indonesia *Mar Biol* **155** 121–133.
 - [34] Richardson AJ 2004 Climate impact on plankton ecosystems in the northeast Atlantic *Science* **305** 1609–1612. doi:10.1126/science.1100958.
 - [35] Rohner CA, Pierce SJ, Marshall AD, Weeks SJ, Bennett MB and Richardson AJ 2013 Trends in sightings and environmental influences on a coastal aggregation of manta rays and whale sharks *Marine Ecology Progress Series* **482** pp.153-168.
 - [36] Apaydin H, Sonmez FK and Yildirim YE 2004 Spatial interpolation techniques for climate data in the GAP region in Turkey *Climate Research* **28**(1) pp.31-40.
 - [37] Earls J and Dixon B 2007 Spatial interpolation of rainfall data using ArcGIS: A comparative study *In Proceedings of the 27th Annual ESRI International User Conference* **31**
 - [38] Dirks KN, Hay JE, Stow, CD, Harris D 1998 High-resolution studies of rainfall on Norfolk Island. Part II: Interpolation of rainfall data *J Hydrol* **208**(3-4):187–193
 - [39] Thums M, Meekan M, Stevens J, Wilson S and Polovina J 2012 Evidence for behavioural thermoregulation by the world's largest fish *Journal of The Royal Society Interface* **rsif20120477**.
 - [40] Rohner CA, Armstrong AJ, Pierce SJ, Prebble CE, Cagua EF, Cochran JE, Berumen ML and Richardson AJ 2015 Whale sharks target dense prey patches of sergestid shrimp off Tanzania. *Journal of plankton research*, p.fbv010.

- [41] McClellan CM, Brereton T, Dell'Amico F, Johns DG, Cucknell A-C, Patrick SC, Penrose R, Ridoux V, Solandt JL, Stephan E, Voiter SC, Williams R, Godley BJ 2014 Understanding the Distribution of Marine Megafauna in the English Channel Region: Identifying Key Habitats for Conservation within the Busiest Seaway on Earth *PLoS ONE* **9**(2): e89720. doi:10.1371/journal.pone.0089720
- [42] Jaine, FAD 2013 *The movement ecology of the reef manta ray Manta alfredi in eastern Australia PhD Thesis* School of Geography, Planning and Environmental Management, The University of Queensland.