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A perspective on the importance of oceanic fronts in promoting aggregation of visitors to seamounts

Alternative title: **Do oceanic fronts promote aggregation of visitors on seamounts? A perspective**

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Running title: Fronts promote aggregation on seamounts?

Abstract

Recent evidence has demonstrated that not all seamounts are areas where productivity, biomass and biodiversity of marine life thrive. Therefore, understanding the drivers and mechanisms underlying seamount productivity is a major challenge in today's seamount research. Incorporating oceanographic data in future analyses has been suggested to be of paramount importance to unveil many of the seamount ecology paradigms. Persistent hydrographic features, such as oceanic fronts, have been recognised to enhance biological activity and to drive marine animal distributions and migration patterns. However, the importance of oceanic fronts in driving aggregations of visiting animals on seamounts has not been understood yet. Here, we analysed a dataset of seamounts in the Pacific Ocean alongside satellite-derived maps of strong, persistent and frequently occurring oceanographic features, to evaluate if oceanic fronts promote aggregation of visitors on seamounts. Our analyses suggest that seamounts with a higher front frequency were more likely to aggregate tuna catch than average seamounts. However, it appears that fronts may be driving factors for aggregation only if present above a certain threshold. These results highlight the importance of environmental conditions in general, and oceanic fronts in particular, in promoting seamount productivity. We therefore argue that a thorough examination of the oceanographic conditions promoting seamount productivity at various temporal and spatial scales is warranted in future seamount research agendas.

Keywords: Oceanic fronts, pelagic biodiversity, remote sensing, seamount ecology, species aggregations

Introduction

Seamounts have been found to be hotspots of pelagic biodiversity, productivity and biomass (Morato *et al*. 2010a; Kvile *et al*. 2014). These generalisations originated from observations of large aggregations of demersal or benthopelagic fish on seamounts (Morato *et al*. 2006; Morato and Clark 2007), but also of visiting pelagic predators such as tunas, billfishes, pelagic sharks, marine mammals, sea-turtles and sea-birds (Gilman *et al*. 2012; Morato *et al*. 2010a,b; Morato and Clark 2007; Amorim *et al*. 2009; Holland and Grubbs 2007; Kaschner 2007; Santos *et al*. 2007). However, seamounts have very diverse morphological characteristic and are subject to distinct oceanographic settings, and these aggregating properties do not hold true for all submarine features in the world's oceans (Kvile *et al*. 2014).

It is now recognized that the diverse oceanographic and morphological properties of seamounts affect patterns of biological diversity and production of resident and associated organisms (Genin *et al.* 1986; Morato *et al.* 2010b; McClain and Lundsten, 2015). The reasons that certain seamounts host abundant populations of fish and other marine predators are still unclear, neither are the mechanisms promoting or sustaining these aggregations (Kvile *et al*. 2014). Understanding the drivers and mechanisms underlying seamount productivity is a major challenge in today's seamount research (Clark *et al*. 2012). Incorporating detailed oceanographic data along with better seamount morphological information is considered to be of paramount importance to reveal new insights in seamount ecology (Clark *et al*. 2012).

Persistent hydrographic features, such as fronts, have been recognised to enhance biological activity and to create hotspots for mobile marine vertebrates (Scales *et al*. 2014a). Mixing at the boundary between two water bodies of distinct oceanographic properties can enhance primary and secondary production (Franks 1992; Samuelsen *et al*. 2012) and as a result promote species aggregations at higher trophic levels. Many marine animals' distribution and migrating patterns are associated with oceanic fronts (reviewed by Scales *et al*. 2014b) and there has been particular interest in understanding how oceanic fronts influence the distribution of commercial fish species (Klemas 2013; Prants et al. 2014). Fronts have been shown to be both direct and indirect drivers for the distribution of many tuna species in the Pacific (Sund *et al*. 1981; Zainuddin *et al*. 2006, 2008), bluefin tuna (*Thunnus thynnus*, Scrombidae) in Gulf of Mexico (Teo and Block 2010) and Gulf of Maine (Schick *et al.* 2004). In the Pacific Ocean the annual migrations of albacore tuna have been related to the position of the Transition Zone Chlorophyll Front (TZCF; Polovina *et al*. 2001) and the Subtropical Convergence Zone (Jones 1991; Hoyle *et al*. 2012) in addition to higher catches being associated with finer-scale frontal features (e.g. in the California Current; Laurs *et al*. 1984; Fiedler and Bernard 1987; and Tasman Sea; Reddy *et al*. 1995). However, the importance of oceanic fronts in driving aggregations on seamounts has not yet been fully understood. Given the aggregating nature of some seamounts and the influence of sea-surface temperature fronts on species' distributions, we seek here to take a first step toward teasing out possible interactions between the two, namely by evaluating if oceanic fronts promote aggregation of visitors on seamounts.

Aggregating seamounts

We build upon the work of Morato *et al*. (2010b) that identified seamounts in the Pacific Ocean where tuna longline catch rates were significantly higher close to seamount summits when compared to further away. They analysed the tuna longline catch and effort database in the Western and Central Pacific Ocean, from 1960 to 2007 and for the area 50°N-50°S and 105°E-95°W, in relation to the location of 1,649 seamounts. Morato *et al*. (2010b) used generalized linear models (GLM) to evaluate the ocean-basin scale patterns of tuna association with seamounts and to model individual seamounts to identify those where aggregating effects were significant. They found support for significantly higher catch rates of tuna close to seamount summits on 602seamounts throughout the study area, representing 36% of all screened seamounts. This begs the question: Why did some seamounts have an aggregating effect while others did not? The resulting dataset containing the geographical location and the summary statistics for the GLM analyses for each seamount is available for further exploration in Table S2 of Morato *et al*. (2010b). Here, we use this dataset to test the correlation between seamounts with a significant aggregation effect and sea surface temperature front frequency.

Oceanic front metrics

Satellite infrared measurements of sea surface temperature (SST) are obscured by cloud, which limits their application to large scale studies of open ocean environments. Alternatively, passive microwave sensors can estimate SST through clouds, although at a much lower resolution. Here, we employed a SST dataset that applies optimal interpolation on a 9 km grid to merge 25 km passive microwave and 1 km infrared data (Gentemann *et al.*, 2009). Thermal fronts were detected on every daily map between 2006 and 2012, with a minimum step of 0.6°C across the front determined from a bimodal histogram within a moving window of 32x32 pixels (Miller, 2009). These maps were accumulated over 8 days to reveal stronger fronts (mean gradient F_{mean} >= 0.1 °C km^{-1}), which were aggregated over all years to calculate a front frequency map for the study area (Miller *et al.*, 2013), as shown in Fig. 1.

Oceanic fronts at seamounts

To test whether there was a difference in oceanic frontal frequency between seamounts that were significant aggregators of tuna catch and those that were not, we first tested whether frontal frequency was normally distributed for each seamount type (aggregating and non-aggregating) using a Shapiro-Wilk test of normality. This test indicated that frontal frequency was not normally distributed for either seamount type, so we used a non-parametric two-sample Kolmogorov–Smirnov test (K–S test) to test the null hypothesis that the samples from aggregating and non-aggregating seamounts were drawn from the same distribution. Although this did not reject the null hypothesis that the samples were drawn from the same distribution, there appeared to be differences in both sides of the tails of these distributions (Fig. 2), suggesting a possible non-linear threshold effect of high frontal frequencies which could not be examined with the K-S test. All statistical tests were conducted using the base stats package in R and plots were generated using the ggplot2 package (Wickham, 2009).

To test whether seamounts with higher frontal frequency were more likely to have a significant aggregating effect and to begin to identify possible threshold values, we applied two methods. First we ran a permutation test comparing seamounts sorted by highest front frequency to lowest frontal frequency with 1000 randomly labelled iterations (Fig. 3a). We used a one-sided test and considered values above the 95% of the distribution of permuted values ($\alpha = 0.05$) to reject the null hypothesis of no difference in the likelihood of seamounts with higher frontal frequency being significant aggregators of tunas. This permutation test was repeated for every possible sample size (n = 1 to 1,649), progressively including lower front frequencies, to identify possible threshold values of front frequency leading to increased likelihood of aggregation around seamounts. The permutation test does not permit us to determine significance, so we also applied a one-sided binomial test ($\alpha = 0.05$) at each sample size to test the null hypothesis that the ratio of significant to non-significant seamounts in the sorted dataset was greater than the overall ratio in the full dataset of 0.36 (Fig. 3a).

The permutation and binomial tests suggested that seamounts with a higher front frequency, greater than 0.44 (n= 95), were more likely to aggregate tuna catch than average seamounts. These results support our hypothesis that differences in the upper tails (> ~0.45) of the distributions of thermal front frequency may indicate an aggregating seamounts effect at high frontal frequencies.

We have repeated this methodology to investigate the tails of the distributions at low front frequency. In this case, we ran the permutation and binomial test comparing seamounts sorted by lowest to highest frontal frequency (Fig. 3b). Some significant differences were observed however with no particular pattern. Therefore, differences observed at low front frequency might be related to local effects, not a potential threshold effect of front frequency as was detected in the upper tail..

Although, we do not aim to provide a definitive answer, our results highlight the possible importance of oceanic fronts in aggregating pelagic visiting animals around seamounts. However, it appears that fronts may be driving factors for aggregation only if present at above a certain threshold. Here we provide a baseline exploratory analyses that oceanic fronts may act as one of multiple drivers of seamount productivity. We therefore argue that a thorough examination of the oceanographic conditions promoting seamount productivity at various temporal and spatial scales is warranted in future seamount research agendas.

However, there are many potential caveats in this first analysis that need to be carefully addressed in future research. For example, although high front frequency seamounts that significantly aggregate tuna catch are seemingly randomly scattered over the region, it is likely that there is a spatial pattern between front frequency and the density of seamounts which could confound our results. Therefore, future research should take these spatial patterns into account and should be based on more accurate non-linear analysis.

Setting the future research agenda

Scales et al. (2014b) suggested that predictable and productive frontal zones associated with bathymetric features, such as seamounts, attract marine vertebrates from diverse trophic levels. Yet, the reasons why seamounts with higher oceanic front frequency aggregate pelagic visitors remain elusive. Fronts may create enhanced allochthonous productivity at seamounts that can be trapped due to retention mechanisms. Therefore, fronts may create enhanced foraging opportunities; easier to locate due to seamounts' specific "signatures", more persistent due to seamount retention mechanisms, and accessible for a larger array of trophic guilds. However, such hypotheses have not yet been considered for this seamount dataset.

Future work should address such hypotheses and clarify interactions between seamount morphology, front frequency and aggregation potential. For example, given the depth of mixing generated by oceanic fronts it is likely that the depth of the seamount summit will influence the interaction between the two, and consequently productivity both at the front and the seamount. However, this and other hypotheses have not been tested yet at a large scale because information on the morphology of most seamounts, such as depth of the summit, height or slope is lacking or not accurately measured preventing any detailed analyses (Morato *et al*. 2010b).

Improvements in front detection algorithms are also needed to support a finer scale analyses necessary to better answer the question posed in our study. For example, although the merged 9km resolution SST dataset was appropriate and practical for covering the large region of interest, it does place a significant limitation on the scale of ocean fronts that can be detected and hence also on the size and separation of seamounts that can be studied individually. Future work should focus on generating front frequency maps at higher resolution (e.g. 1 km) from both thermal and ocean colour data. This will enable important research questions to be tackled, for example relating the aggregating nature of certain seamounts to their depth, morphology, and primary productivity.

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Figure Legends

Figure 1 Thermal ocean front frequency map for the study area from 2006 to 2012 (percentage of time for which a strong front was observed, based on 8-day periods). White dots represent the location of seamount considered in this study and the colour scale bar represents front frequency.

Figure 2 Thermal ocean front frequency density plot for seamounts aggregating and non-aggregating tuna catch. The smooth density estimates were calculated using ggplot2 stat_density.

Figure 3 Permutation analyses comparing the proportion of tuna aggregating seamounts for 1,649 seamounts sorted by (a) highest to lowest frontal frequency, and (b) lowest to highest frontal frequency. The sorting allows for analysis of the upper and lower tail, respectively, of the distribution of aggregating seamounts to frontal frequency. The permutation envelope was generated from 1000 randomly sorted iterations. Red dots show significantly greater ratios of aggregation to non-aggregating seamounts in the sorted dataset compared to the overall ratio in the full dataset. Sample sizes less than n = 10 were excluded as being too small to allow confidence in their results.

Figures

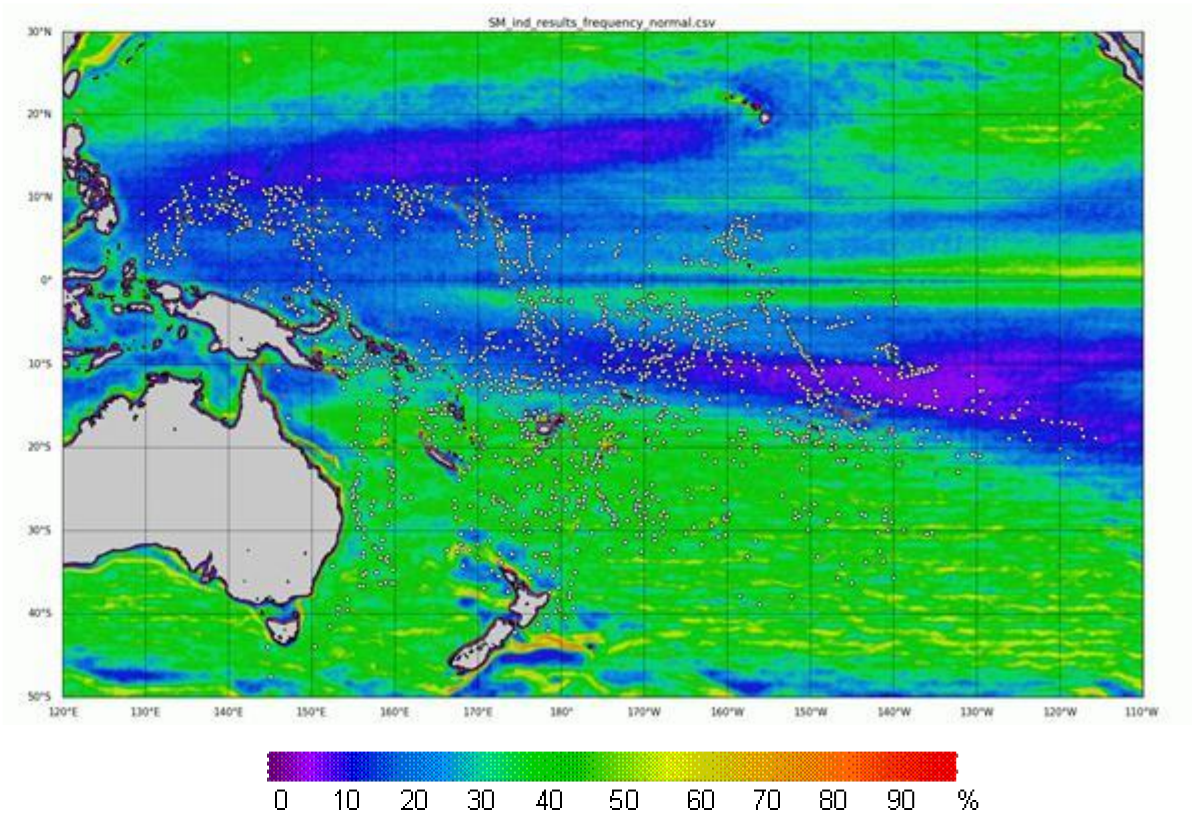
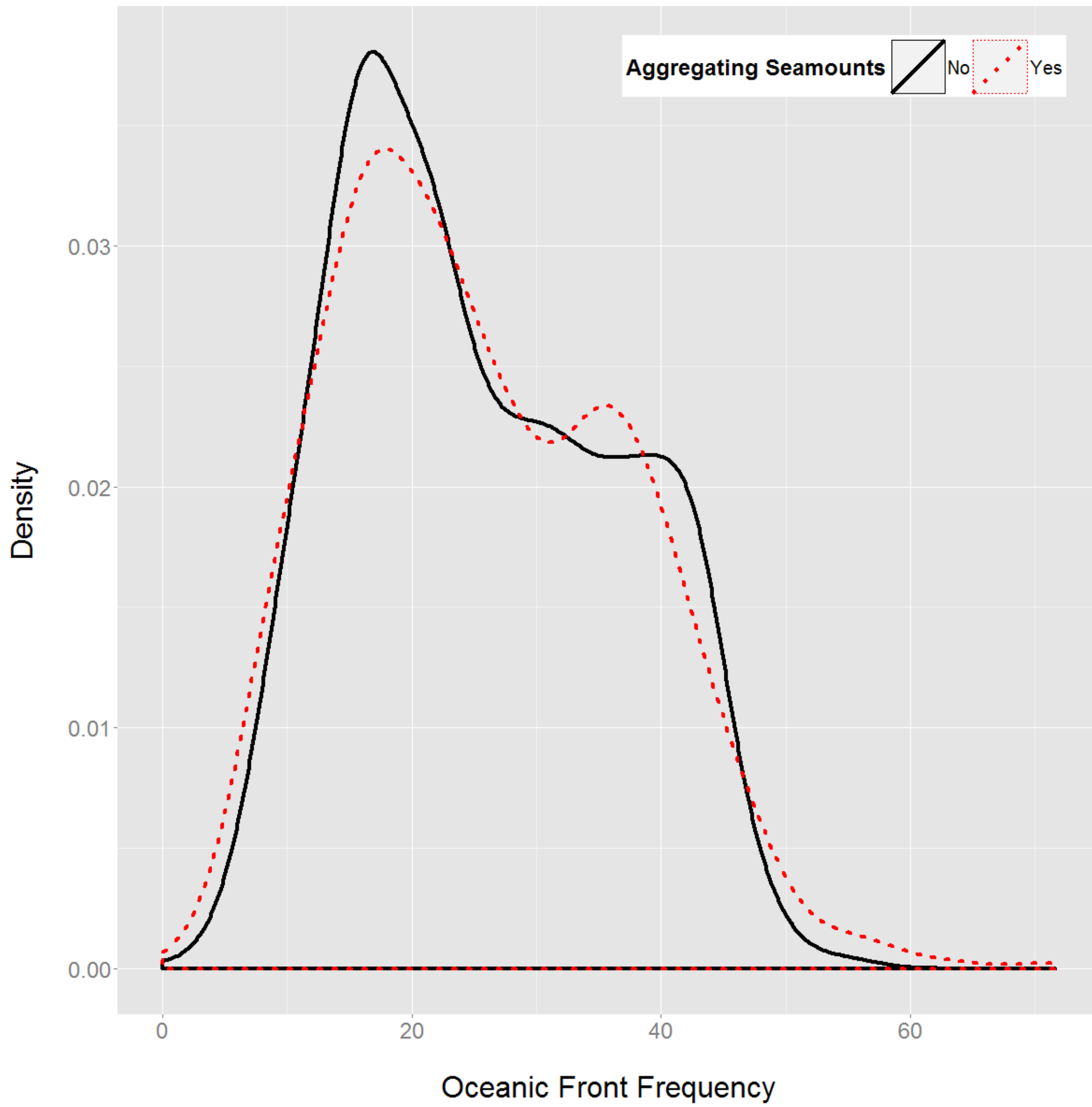


Figure 1.


Aggregating Seamounts
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Yes
0.03
0.02
0.01
0.00
Density
0
20
40
60
Oceanic Front Frequency

Figure 2.

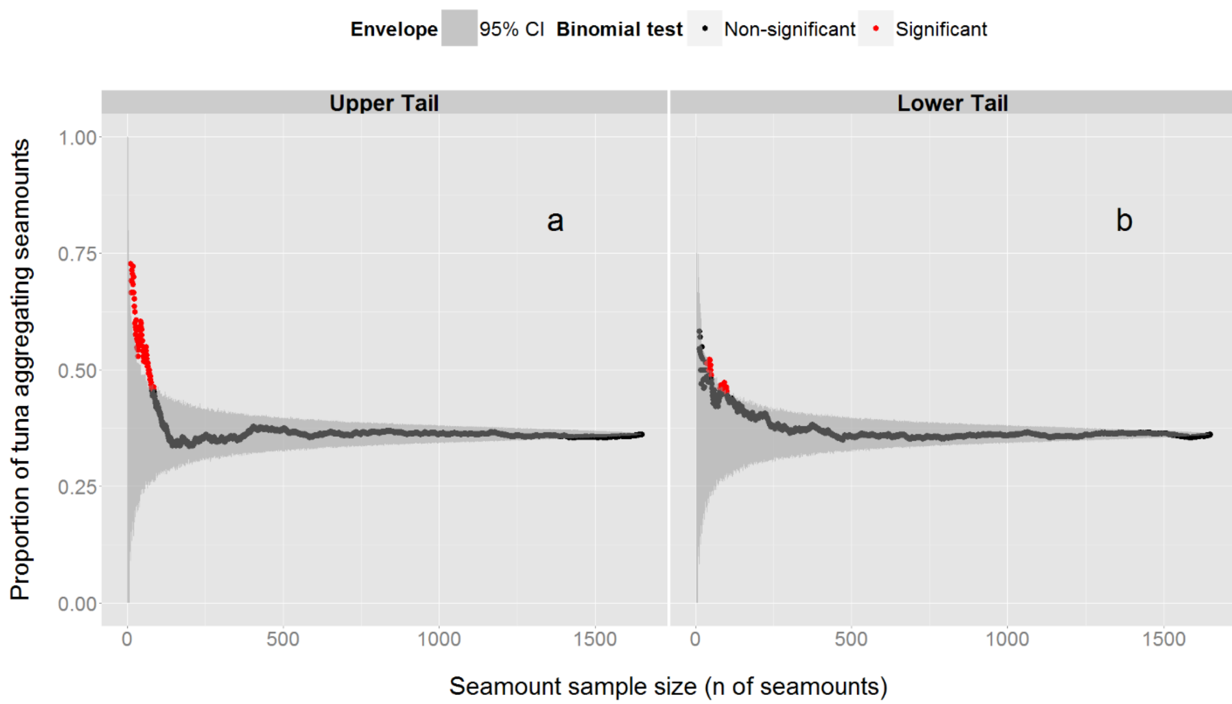
Envelope
95% CI
Binomial test
Non-significant
Significant
Upper Tail
Lower Tail
a
b
Proportion of tuna aggregating seamounts
1.00
0.75
0.50
0.25
0.00
0
500
1000
1500
Seamount sample size (n of seamounts)

Figure 3.