A Characterization of the Habitat of *Charcharodon carcharias* Between Hawaii and the Line Islands:

To What Extent is Productivity a Determining Factor in Habitat Choice?

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Abstract:

This study attempted to describe the distribution patterns of great white sharks, C. carcharias, in the geostrophic eddy field between Hawaii and the Line Islands in relation to primary and secondary productivity in the water column. To do so, in situ *chl-a fluorescence measurements as well as zooplankton net tows were taken along a cruise track between Hawaii the Line Islands. This data was analyzed together with an equivalent dataset collected in 2005 by Markman and Schwartz. Also, Pop Up Satellite Archival Tag (PSAT) data for white shark movements in the vicinity of Hawaii was used to determine the degree of correlation between white shark distribution and eddy locations. The results of this study tentatively suggest that firstly, geostrophic currents seem to boost primary and secondary productivity in a largely predictable manner, and secondly, that white sharks may take advantage of this by focusing on these relatively productive eddies during their aggregation period offshore of Hawaii.*

Introduction:

Much of the research on the predator-prey interactions of great white sharks to date has focused on coastal pinneped colonies. Researchers such as Peter Klimley in the Farallon Islands, for example, have demonstrated that predictable aggregations of white sharks occur on an annual or biannual cycle following the appearance of pinniped colonies in the area. (Klimley and Anderson, 1996) Yet in contrast to this, little research has been carried out concerning the significance of open ocean prey abundance on the ecology and distribution of *C. carcharias*. This lack of research is particularly significant when it is considered that white sharks appear to spend only a relatively minor portion of their life along the coasts, with over half of their time spent instead in the pelagic open seas. (Weng *et al*, in press) This study attempts to offer some insight into this relatively unknown area of the white shark life history through an analysis of productivity as a proxy for potential prey abundance in relation to known areas of *C. carcharias* aggregation in the pelagic ocean. Specifically, this paper will attempt to assess the significance of patterns in primary and secondary productivity between Hawaii and the Line Islands on *C. carcharias* habitat choice by describing these characteristics between the islands as they relate to the occurrence of mesoscale eddy systems.

The Biology of Eddy Systems

Mesoscale eddies in the pelagic habitat are relatively stable oceanographic features that appear to be prime areas of aggregation for oceanic predators. Most open-ocean eddy systems off the southern coast of Hawaii are generated by the force of strong surface trade winds that flow across the Hawaiian island chain. Immediately to the lee of these islands, turbulent patterns of current flow create “eddy fields”, with a high density of spinning eddies that each may span over a hundred kilometers and create mesoscale oceanographic features that are clearly visible from satellite data. Budding off from the islands that created them, such eddies may travel thousands of miles, taking many weeks to cross entire ocean basins. Importantly, current systems within the eddy often cause water to move vertically as well as horizontally. This can raise new nutrients from below the thermocline to shallow euphotic zones, stimulating primary production in the area. In particular, the two types of eddies – cyclonic and anticyclonic systems – have distinct characteristics. Cyclonic eddies in the northern hemisphere are largely organized around upwelling centers, which bring cold nutrient rich water closer to the surface of the eddies. These eddies typically are associated with an increase of primary production. Anticyclonic eddies, on the other hand, are organized around downwelling centers. Although eddies still appear to contribute to primary production rates, their effect is not as strong as with cyclonic eddies. (Markman and Schwartz, 2005)

Sources of Data

A number of approaches can be taken when studying the predator-prey interactions of *C. carcharias* in the pelagic habitat. One recent method of data collection has been the use of Pop Up Satellite Archival Tags (PSAT) to track white shark movement through their pelagic migrations. In 2001 for example, Boustany et al recorded a nearly 4,000 km migration in an adult white shark between the coast of California and the vicinity of the Hawaiian Island chain. (Boustany *et al*, 2002) Since then, tagging efforts by TOPP (Tagging of Pacific Pelagics, www.toppcencus.org) scientists have shown what appears to be a seasonal migration route for *C. carcharias*. Five white shark tracks have been recorded departing the California current in winter to early spring then spending the spring to early summer months near Hawaii before returning to the North American coastline. (See Figure 1) These tracks provide indications of *C. carcharias* distribution on multiple planes. On a horizontal plane, anecdotal data suggests that a comparison of white shark tracks with sea surface altimetry data shows a high degree of association between white shark distribution and the location of the Hawaiian eddy field. This area of *C. carcharias* distribution is bounded on its southern extreme by the location of the North Equatorial Current, where as yet no white shark tracks have been recorded.

On a vertical plane, the detection of short, deep dives of 300-600m on a diel cycle suggests that daytime foraging may be occurring during these pelagic migrations. (Weng *et al*, in press) The tagging efforts of Kerstetter et al on deepwater Opah also provide evidence of the presence of foraging in these areas. Temperature and light readings from this satellite tag data suggests that a tagged Opah was ingested by an endothermic lamnid shark, such as a white shark or shortfin mako, at a depth of 400 m offshore of the island of Hawaii, a similar depth to that where two submersibles sightings of white sharks occurred slightly earlier off the coast of Oahu. (Kerstetter *et al*, 2004) Similarly, it is worth noting that Worm *et al* used longlining observer data to establish a worldwide census of pelagic species abundance and diversity in which he described an area corresponding to the Hawaiian eddy field as one of the five large predator hot spots in the world (See Figure 2). (Worm *et al*, 2003 and 2005) This suggests that great white shark migration to this area may be linked to the aggregation of large pelagic prey items, such as tuna and smaller sharks, to the vicinity of the eddy field.

An additional avenue for analysis is the use of *in situ* surveys of prey abundance within the eddy field to generate indications of prey availability in the area. In this case, by taking advantage of the characteristics of trophic interactions in the pelagic food web, relatively small datasets can produce indications of relative biomass in the higher trophic levels. Some key species, such as squid and myctophids in the open ocean, often serve as “energy transfer” organisms, where a large quantity of energy enters this group from lower trophic levels, while at the same time much of this energy is quickly transferred to higher trophic levels through predation. (Olson and Watters, 2003) Myctophids, for example, make up an average of some 60-90% of mesopelagic fish biomass in net tows worldwide, and, while they are predators of a large variety of micro and macro zooplankton, they are also prey items for many pelagic predators. (Gjosaeter and Kawaguchi, 1980) Similarly, cephalopods, particularly squid species of the genus ommastrephidae, have been shown to be significant prey items for dolphins, tuna, blue sharks, and white sharks through various stomach content analyses. Figure 3 illustrates the concept that location of these species within a “bottleneck” of the trophic food web makes the abundance of these species critical for the aggregation of many of the principle white shark food sources, including dolphins, albacore, bluesharks, shortfin mako sharks, and opah. (Olson and Watters, 2003) The energy available to this trophic bottleneck can be assessed via indices of secondary productivity in the pelagic ocean environment. Such an assessment serves as an extension of a similar study by Markman and Schwartz done in this area in 2005. The data obtained in the current analysis was collated with this prior dataset to serve as a source of replicates between years.

Methods:

Study Site

Sampling locations were determined on the basis of mesoscale sea surface height data provided by NOAA as well as on-site observations of sea surface temperature and current direction. In particular, one eddy pair on the northern edge of the offshore aggregation area was selected for sampling, as this eddy system showed both a strong anticyclonic and a relatively strong cyclonic eddy in close proximity to each other. Station 1 was located within an area of high anticyclonic eddy activity as predicted by the satellite altimetry data. Station 2, with only a chl-a fluorescence cast, was between the two eddies. Station 3, slightly further to the Southeast, was more characteristic oceanographically of a cyclonic eddy. Finally, Station 4, the southernmost station, was located in an area indicated by on site current measurements to have little eddy presence.

Materials

AVISO Satellite high-resolution sea surface height data for our cruise track.

Acoustic Doppler Current Profiler (ADCP)

Conductivity, Temperature and Depth profiler (CTD)

Tucker trawl

Meter Net

Neuston Tow

PSAT satellite tagging data of white sharks in the Hawaiian eddy field

Census Methodology

The census was focused on the following indicators of prey abundance, assuming potential prey items as those defined in the introduction:

1. Phytoplankton abundance – an indicator of primary productivity in the water column.

3. Volume of plankton mass – previous studies of stomach content analysis in the area have established crab megalops as a primary food source for tuna species in the area, (Scharf, 2003) a known prey item for C. *carcharias.* Similarly, euphasids are significant prey species for *Prionace glauca* and *Lampris guttatus*, both food items of white sharks. (Martin, 2003) This was especially targeted in the deep scattering layer where zooplankton abundance is highest, and where satellite tracks seem to indicate that white sharks are reaching on their dives.

All data collection at the eddy sites was carried out in a limited timeframe between 0730 and 0900, to standardize for light penetration into the water column at the time of collection.

At each chosen sampling site, the following datasets were collected:

1. Conductivity, temperature, and depth.

The CTD profiler was deployed to 600m of depth, with data points taken every four seconds for temperature, conductivity, and fluorescence. This provided an indication of phytoplankton abundance in the area, and also created a profile of oceanographic features at the station.

2. Tucker Trawl.

Tucker trawls (mesh size 333μ) were deployed at each station. Of the three nets in the trawl, the first and the third nets were kept open from the surface to the deep scattering layer, and the second net was opened over a discrete depth in the deep sonic scattering layer. Trawl speed was approximately 2.5 knots for all collection trials. Once retrieved, all nets deployed underwent a standardized procedure for analysis. Any teleost fishes in the trawl, any identifiable biomass of crab megalops, as well as any species of interest were removed and counted by species. Finally, the volume of the sampled organisms was measured via a graduated cylinder to produce both a total biomass estimate. Organism density for the different samples was then be normalized through trawl distance measurements obtained from flow meter readings on the net.

3. Meter Net

2-meter diameter nets (mesh size 333μ) were deployed to just below the thermocline for in each station to obtain a profile of zooplankton density throughout the water column. Net processing followed the procedure used in the Tucker trawls.

4. Neuston Tow

A Neuston net (mesh size 333μ) was deployed at the surface at each station. Net processing also followed the procedure for the Tucker trawl.

Beyond these four stations, the ADCP was kept running on a 24-hour schedule during the days on which sampling occurred. In addition to providing on-site current profiles to confirm satellite derived eddy locations, this allowed for the tracking of the deep water scattering layer to allow targeting by the net samples.

Also, Arcview the white shark tracks obtained from PSAT tag data in the Hawaiian eddy field was analyzed with GIS mapping software to calculate kernel densities for three tracks. In particular, 95%, 50%, and 25% kernel densities were generated to provide an indication of centers of white shark activity. This was qualitatively compared to contour maps of monthly-averaged sea surface height obtained from satellite altimetry data (see Figure 12 a, b, c). The distance of each tag location in the dataset from the nearest major eddy centers were then calculated to provide an index of the degree of association between white shark distribution and eddy locations. Major eddy centers were defined as local maximums of minimums of sea surface height that either exceeded 18cm or were less then -22cm in height.

Results

In Situ Fluorescence Data

An interpolated depth-by-latitude plot of the fluorescence data between Hawaii and the Line Islands is shown in Figure 8. Local peaks in chl-a fluorescence at depth can be clearly seen between 19-16 degrees latitude, corresponding to the eddy systems chosen for sampling on this cruise. Figure 9 compares fluorescence profiles at the different eddy stations. Two replicates were considered for each station: one from current research data and another from a similar dataset collected in the area in 2005 by Markman and Schwartz. Table 1 provides summary information for the fluorescence data obtained.

Net Tow Data

The net tows returned a range of organism types, from myctophids and crab larvae to euphausids and gelatinous organisms. Analysis of relative species densities in the different stations, however, revealed few consistent patterns. Similarly, a scarcity of larger mesopelagic organisms such as fish and squid made an analysis of their distributions impractical. Instead, general patterns of zooplankton density, taken as a proxy for productivity, were analyzed for trends. Figures 8 and 9 show gear-specific as well as overall zooplankton density data for the four sample stations. Similarly, Table 2 provides summary information for the trawl data.

White Shark Tag Data:

A qualitative assessment of white shark distribution was done with respect to eddy centers, as illustrated in Figure 10. A more quantitative analysis can be seen in Figure 11, which shows a histogram of white shark distance away from areas of major eddy activity. This method of analysis calculated a mean distance of 230km, and a mode distance of 120km for the white shark tracks as a whole from the nearest eddy feature, as summarized in Table 3.

Discussion

The data obtained largely supports the hypothesized prey-driven mechanism for habitat selection in great white sharks. Firstly, measurements of chl-a fluorescence in the Hawaiian eddy field revealed a predictable pattern in primary productivity between the eddy types. Secondly, zooplankton density between the eddy systems showed a trend of organism abundance that appears to be coupled to the primary productivity of the eddies. Finally, preliminary analysis of satellite tagging data on white sharks with respect to these eddy locations showed a strong correlation between shark location and eddy activity. In all counts, however, a scarcity of replicates precluded the achievement of statistical significance in these patterns.

Fluorescence

Chl-a fluorescence data as an index of primary productivity across the Hawaiian eddy field corresponded strongly to the hypothesized pattern. Figure 9 shows the highest fluorescence peak as being observed in the upwelling areas of the cyclonic eddies, with a gradient sloping to the comparatively lower fluorescence of the downwelling, anticyclonic eddy station and then to the lowest fluorescence peak of the control station. It is interesting to note that in comparison to the fluorescence values reported by Markman and Schwartz in 2005, the values obtained on this cruise show a two to three-fold decrease in overall chl-a fluorescence. This gives an indication of the scale of the interannual variability that occurs in this system with respect to productivity. Within a limited timescale, however, the identical trend patterns observed between the sampling stations themselves in both years suggested that the effect of eddy activity on the relative productivity of the Hawaiian eddy field may be comparatively constant.

One final aspect of the fluorometry data obtained in this study that is worth discussing is the much wider scale latitudinal variation in the study area. Figure 8 interestingly shows that the zone stretching from 20 to approximately 12° of latitude has a relatively low fluorescence value when compared to the fluorescence spike that occurs at 12° and continues until the end of the dataset at 3° Lat. Significantly, this “low productivity zone” which encompasses the Hawaiian eddy field also corresponds to the primary zone of white shark distribution as indicated by current tagging records. A question for further study is to investigate what factors - whether physiological limitations, a decoupling between primary productivity and white shark prey abundance, or simply a lack of data - determine this apparent reluctance of white sharks to take advantage of these large scale patterns of productivity.

Secondary Production

Indications of production in higher trophic levels, through measurements of zooplankton abundance, showed similar but not identical trends. Figure 11, which displays mean zooplankton abundance for all tow data across the stations, shows a clear trend from the high zooplankton density of the cyclonic eddy to the low density of the anticyclonic eddy station, indicating that differences in primary production lead to changes in energy availability among the zooplankton. Similarly, as in the fluorometry data, zooplankton densities in the cyclonic and border stations showed higher values to those obtained in the control station. A significant departure from the fluorometry data, however, is that the anticyclonic eddy data showed a lower zooplankton density than the control station. Due to a lack of samples, it is difficult to know if this was due to eddy activity or simply to chance variation in the data. Figure 10 displays some of the variability in this data, with different tows producing dissimilar trend lines. The comparative lack of data in the control station, shown as a lack of gear types in this station even relative to the other stations, makes a comparison of the control station and the anticyclonic station especially difficult in this dataset.

In the future, one avenue of further investigation to resolve these issues is the use of Hawaiian longlining data with respect to eddy location to determine whether this trend is reflected in the highest trophic levels of the large pelagic predators. This would both serve as a more extensive dataset for analysis, and it would also give a much more direct analysis of white shark prey abundance in the Hawaiian eddy field.

White Shark Distribution

A qualitative comparison of white shark kernel densities relative to sea surface altimetry data shows an apparent correlation between areas of high kernel density and centers of eddy activity. In particular, considering that the monthly averaged sea surface altimetry data used in Figure 12 was compared to white shark track data that could span several months, the degree of correlation observed is surprising. Both tracks P132 and P059 appear to focus on areas just southwest of the Hawaii, where the range of the 25% kernel density contours overlap with the edges of a cyclonic and anticyclonic eddy, respectively. Similarly, track P160 shows a 95% kernel density contour that envelops a weak pair of cyclonic and anticyclonic eddies just east of Hawaii, as well as an arm of this same contour that appears to envelop a weak cyclonic eddy at 11° of latitude also southwest of Hawaii. These results both confirm anecdotal information on the possible correlation between white shark distribution and eddy location in this area, as well as support research on other large pelagic predators such as Albacore, which were argued in

Zainuddin et al, 2006, to be targeting areas of high eddy kinetic energy in the central Pacific open ocean.

An important exception to this trend is the 25% kernel density contour for P160, which focuses on an area of seemingly low eddy activity at approximately 15° of latitude. The source of this deviation from the expected trend is unclear.

An analysis of the distance of white shark locations from major eddy centers (defined quantitatively as local maxima or minima of sea surface height with a value greater than 10 cm or less then -25cm) shows a large difference in the mean value (230km) from that expected assuming no treatment effect. However, mean distance values with respect to the tracks analyzed in this study, where long migrations are carried out between limited areas of slower travel, are expected to generate a skewed interpretation of the preferred distance from an eddy. This is because a misleadingly large number of outlying datapoints generated when tracks are en route from one preferred area to the next will lead to an overestimation through the mean value of the optimum location for white sharks relative to eddy features. Thus, a more significant index of white shark association with the eddies is the mode of the distance, calculated at 120km in a frequency distribution histogram, which provides an indication of the most preferred relative position of the sharks to the eddies. In comparison with the expected value assuming no treatment effect (360km), this value shows an almost a three-fold decrease.

In future investigations, it is suggested that the analysis use sea surface height data that is time-synced with the individual tag data points. Such an analysis should provide the resolution necessary to both more rigorously test the degree of correlation between white shark distribution and eddy activity, as well as to distinguish between preferred eddy types for the white sharks.

Conclusion:

These results of this study suggest that white shark distribution may be coupled to mesoscale current features. White sharks that migrate to the Hawaiian aggregation area appear to be seeking out eddies that raise primary productivity and may indicate a potential for high prey abundance. Such findings corroborate those reported by researchers such as Zainuddin *et al*, who used satellite data and the distribution of albacore catches by longliners in the north Pacific to suggest that a significant correlation existed between albacore aggregation, eddy kinetic energy, and primary productivity. (2006) However, the sparseness of this dataset makes these conclusions far from robust. More extensive investigation is required to better understand white shark biology in this area.

Figures With Captions:

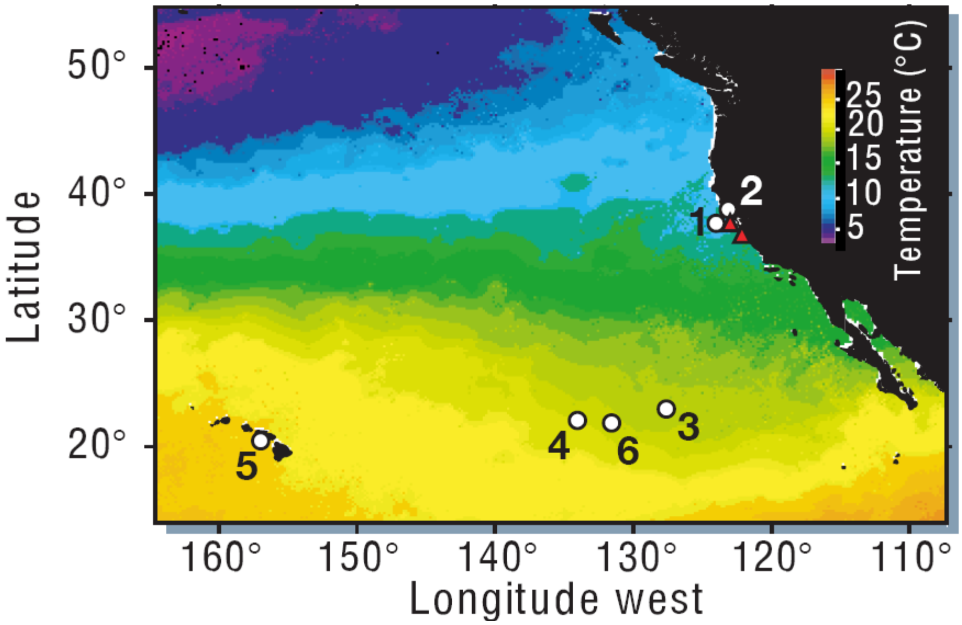


Figure 1: A sample of tagging data from Boustany et al 2002. Red triangles show tag deployment sites, white circles show tag recovery locations.

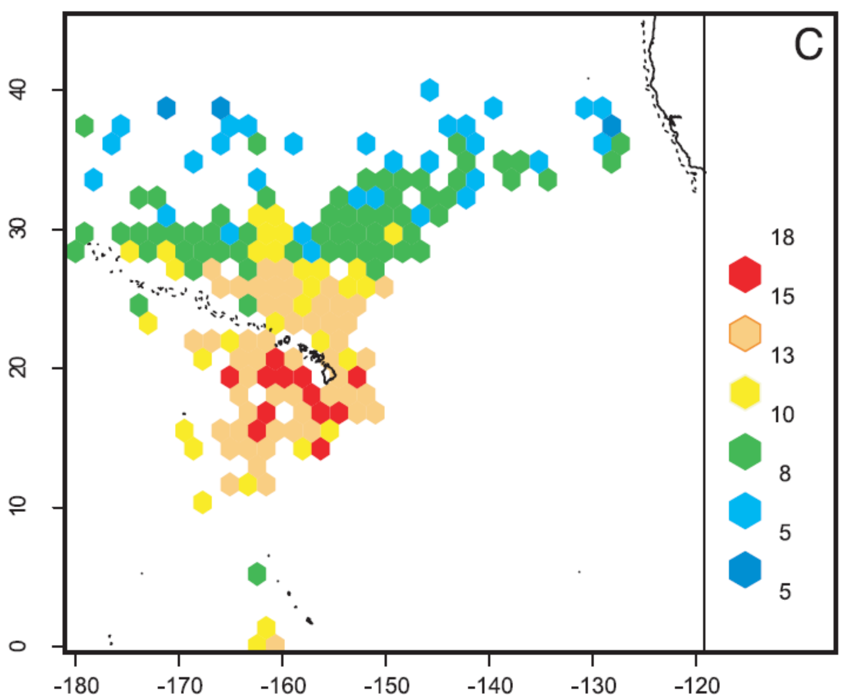


Fig 2: Predator diversity in the ocean predicted from Hawaiian longline observer data. Latitude and longitude on the x and y-axes, the legend shows an index of diversity. (Worm et al 2003)

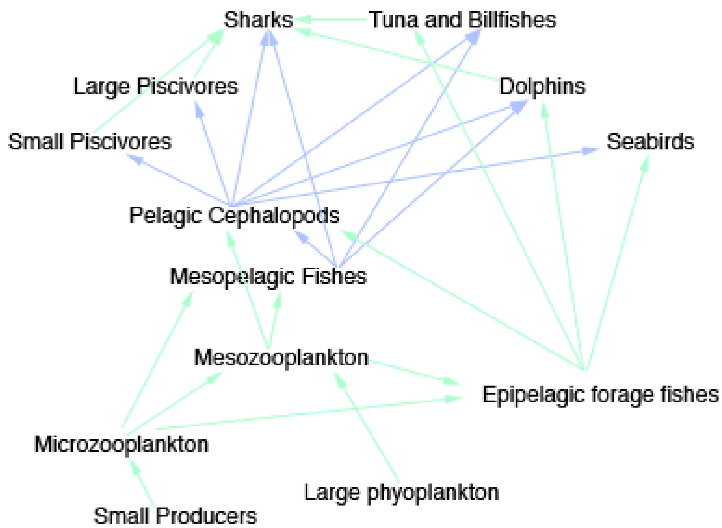


Figure 3: Simplified food web for the pelagic open ocean in the Eastern Tropical Pacific, adapted from Olson and Watters, 2003. Paths of energy intake through predation on cephalopods and myctophids are shown in blue.

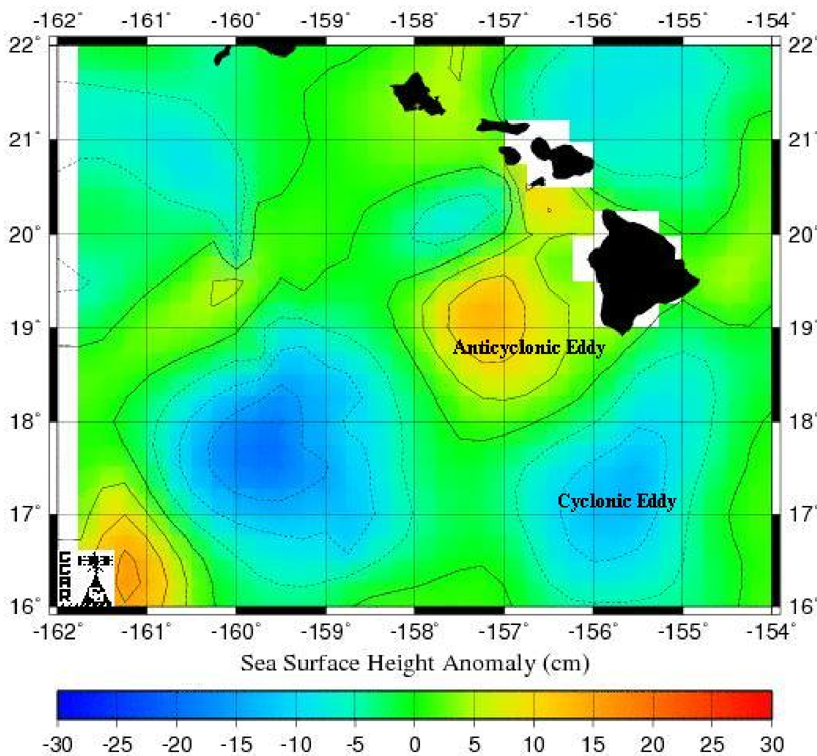


Figure 4: Satellite altimetry data for the northern portion of the study site on May 12, 2007, showing the eddy pair chosen for sampling. Collected on cruise S-211

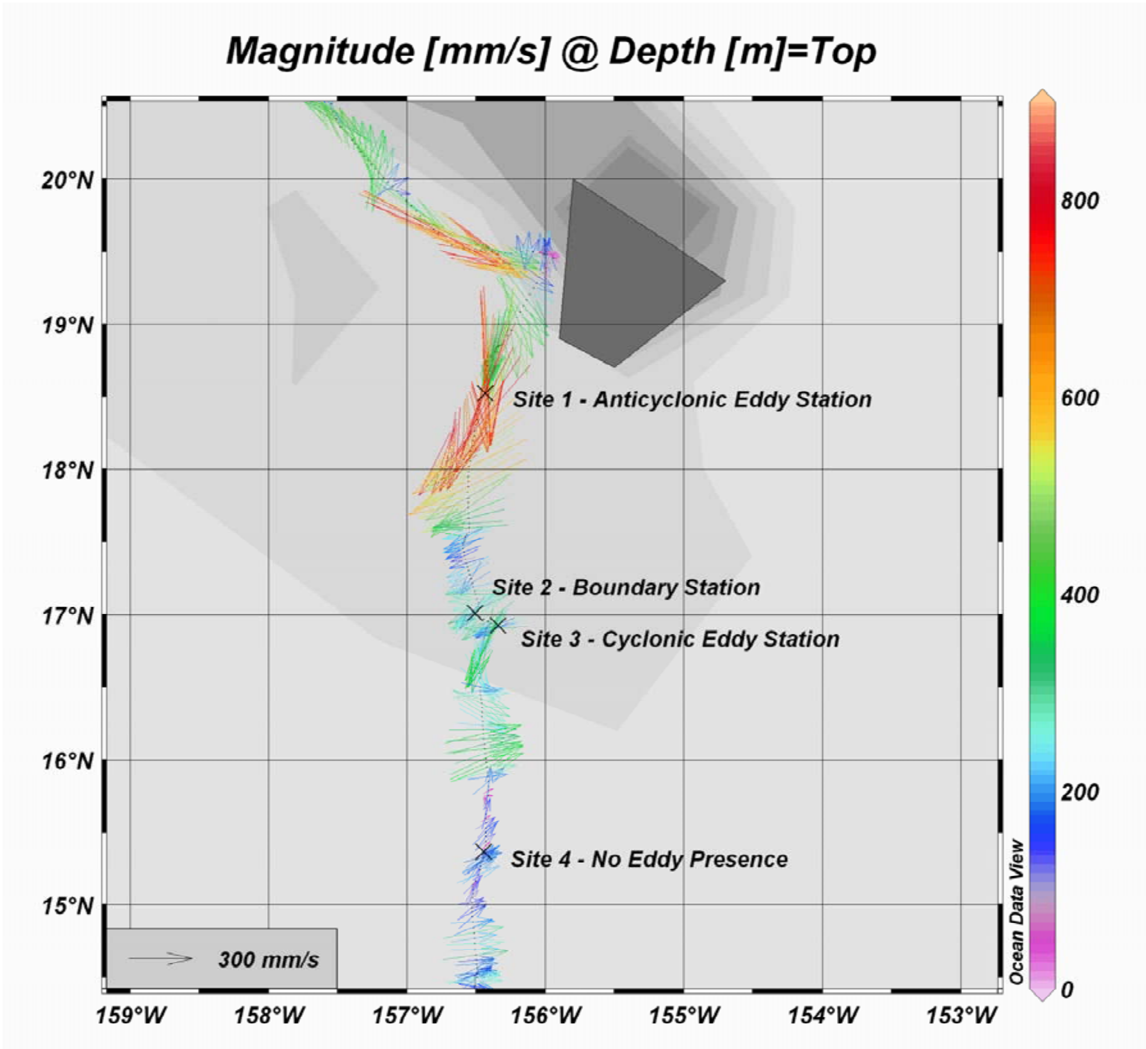


Figure 5: On site current data during the research cruise, showing the locations of the sites chosen for sampling. May 15-17. Color bar denotes current magnitude, arrows represent current magnitude and direction. Collected on cruise S-211

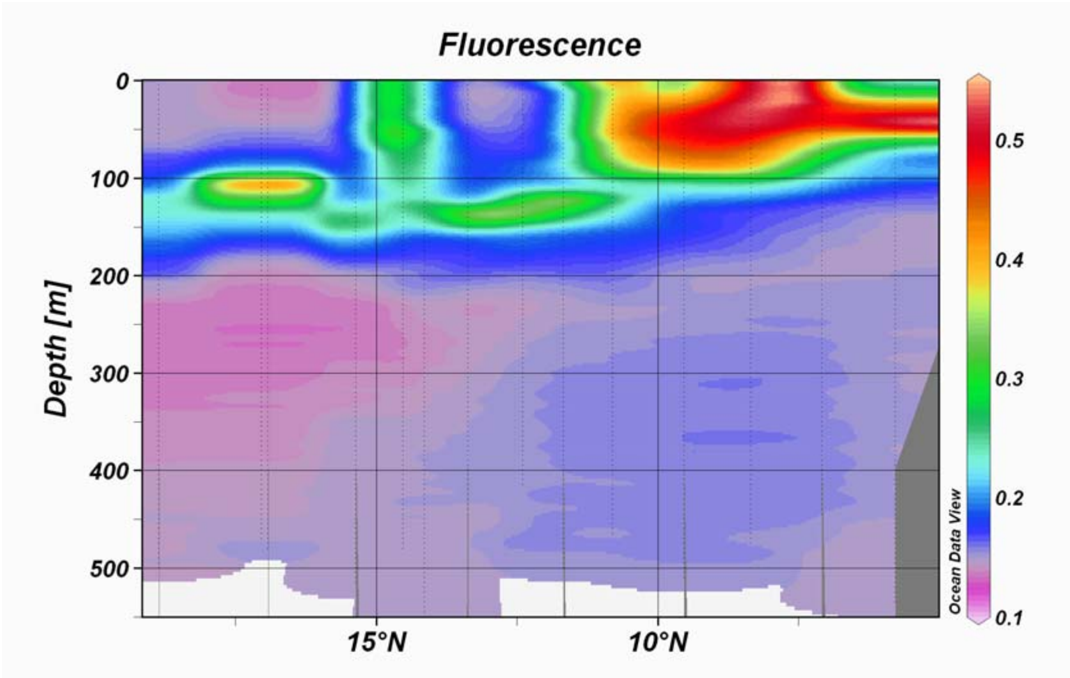


Figure 6: Patterns of Chl-a flourescence by depth and latitude between Hawaii and the Line Islands. May 13-Jun 6. Collected on cruise S-211.

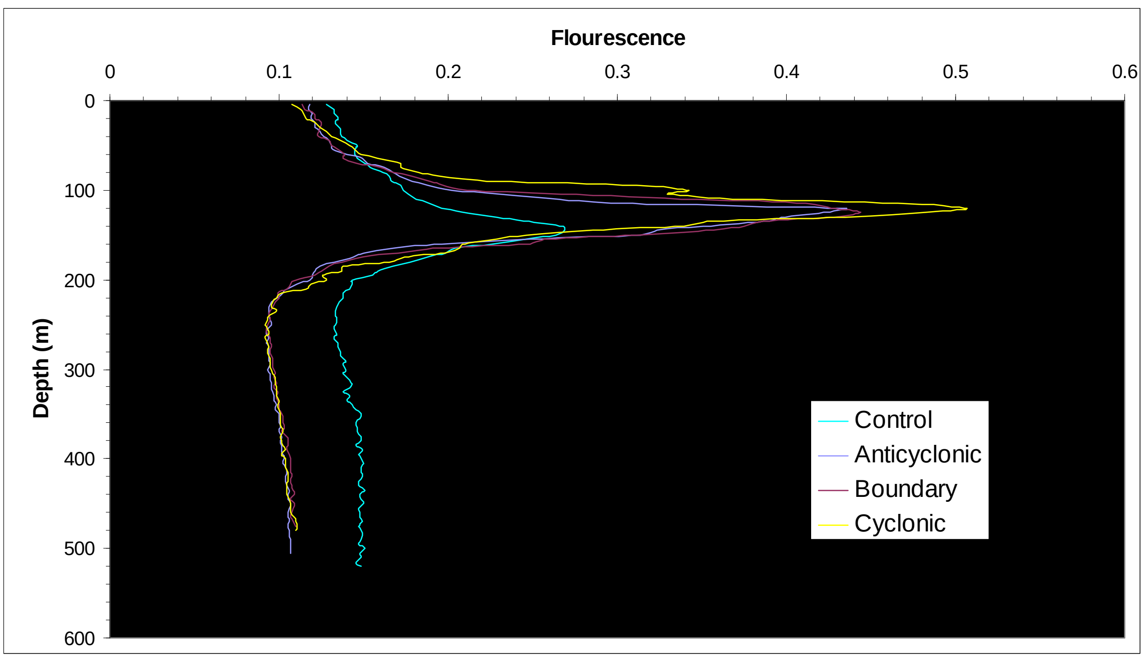


Figure 7: Chl-a flourescence versus depth as an index of phytoplankton abundance within geostrophic eddies (n=2). Times: 07:22 on May 13, 07:57 on May 14, and 08:47 on May 15, 2007. Collected on cruises S-199 (Markman and Schwartz, 2005) and S-211.

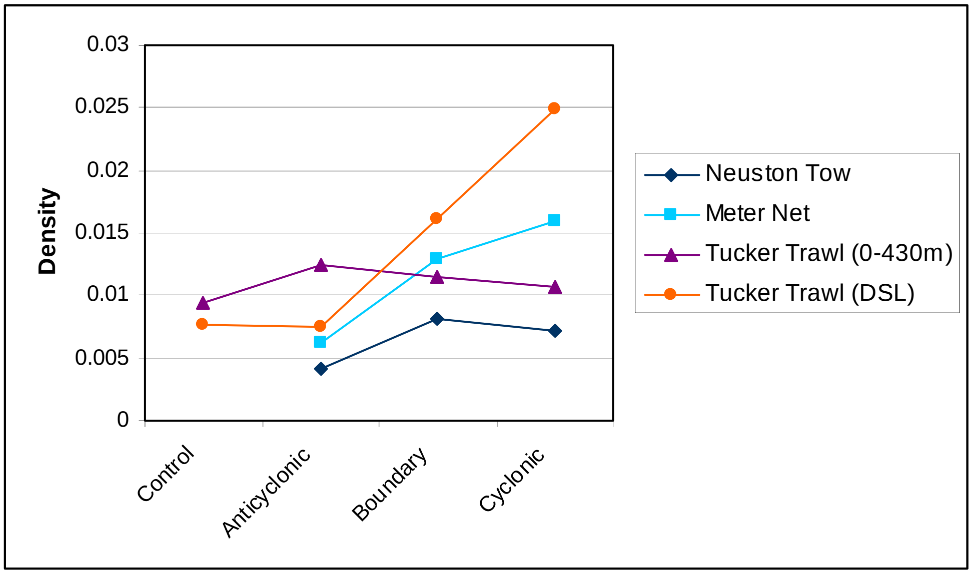


Figure 8: Zooplankton density by gear type and eddy category over the sample stations (n=2). Times: 07:22 on May 13, 07:57 on May 14, and 08:47 on May 15, 2007. Collected on cruises S-199 (Markman and Schwartz, 2005) and S-211.

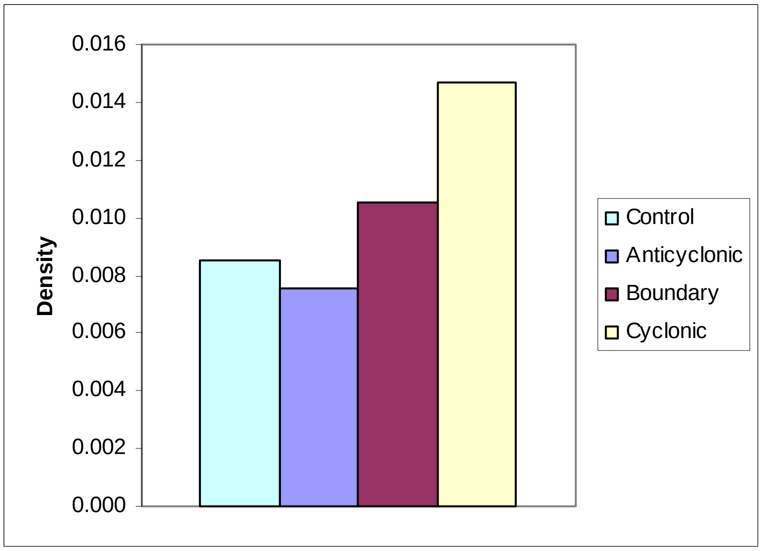
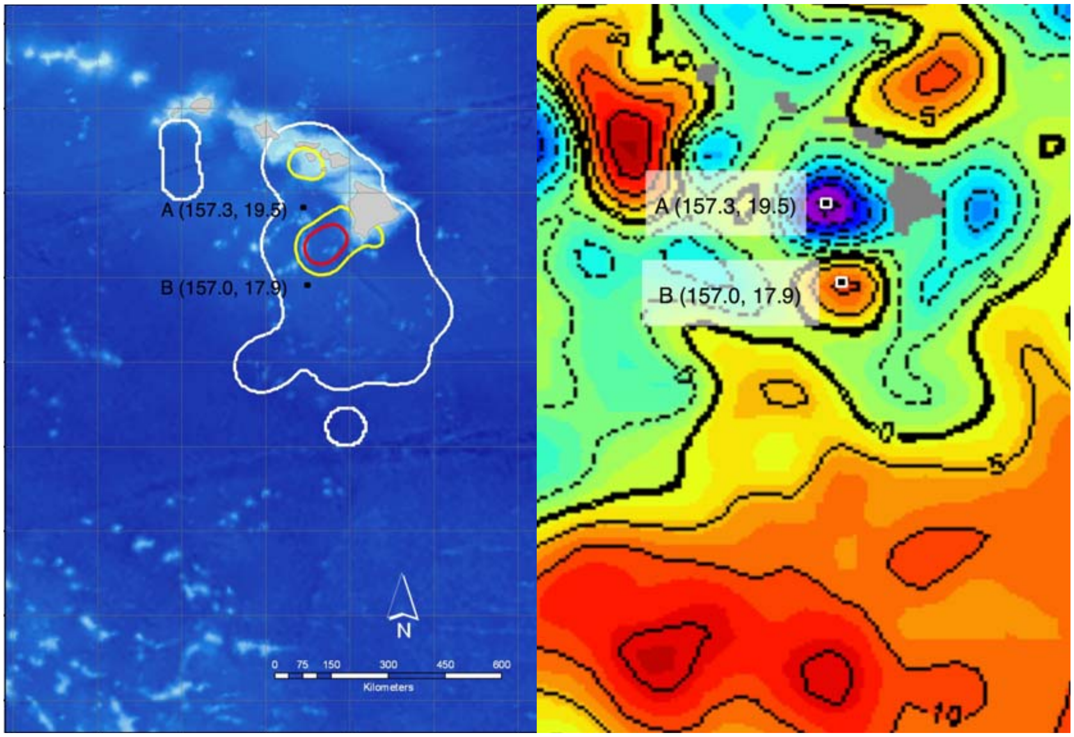
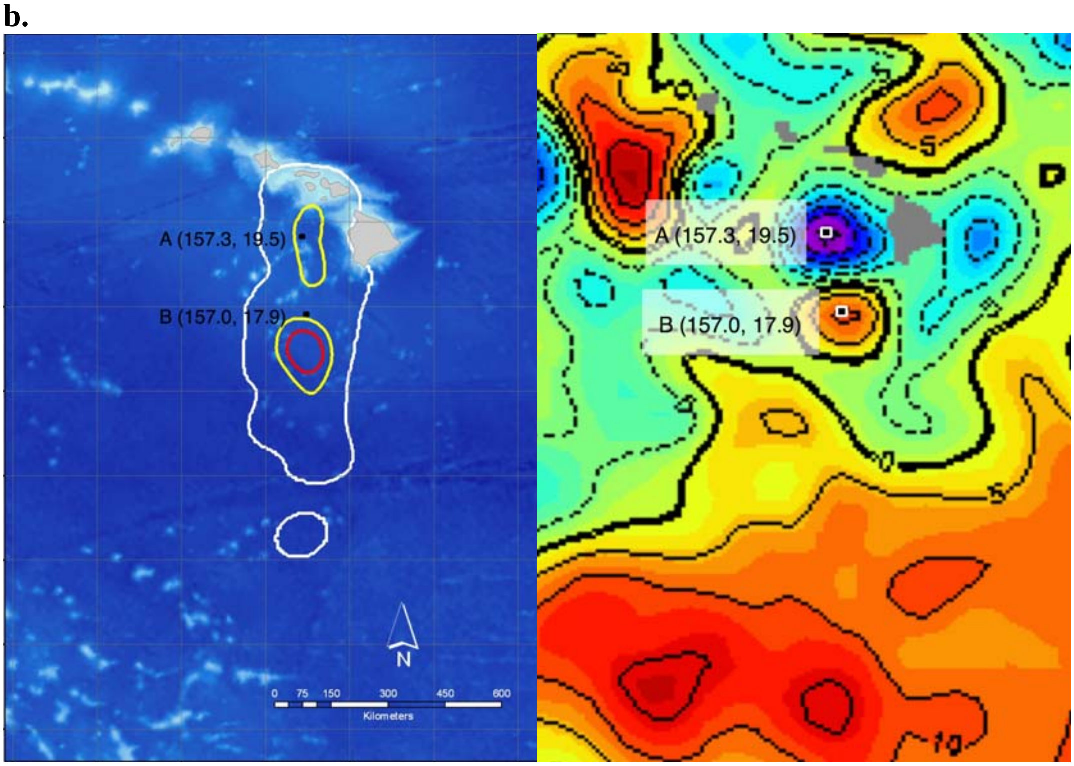


Figure 9: Mean zooplankton density in geostrophic eddies from all tow data combined (n=2). Times: 07:22 on May 13, 07:57 on May 14, and 08:47 on May 15, 2007. Collected on cruises S-199 (Markman and Schwartz, 2005) and S-211.

a.


A (157.3, 19.5)
B (157.0, 17.9)
N
0 75 150 300 450 600
Kilometers
A (157.3, 19.5)
B (157.0, 17.9)

b.


A (157.3, 19.5)
B (157.0, 17.9)
N
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Kilometers
A (157.3, 19.5)
B (157.0, 17.9)

c.

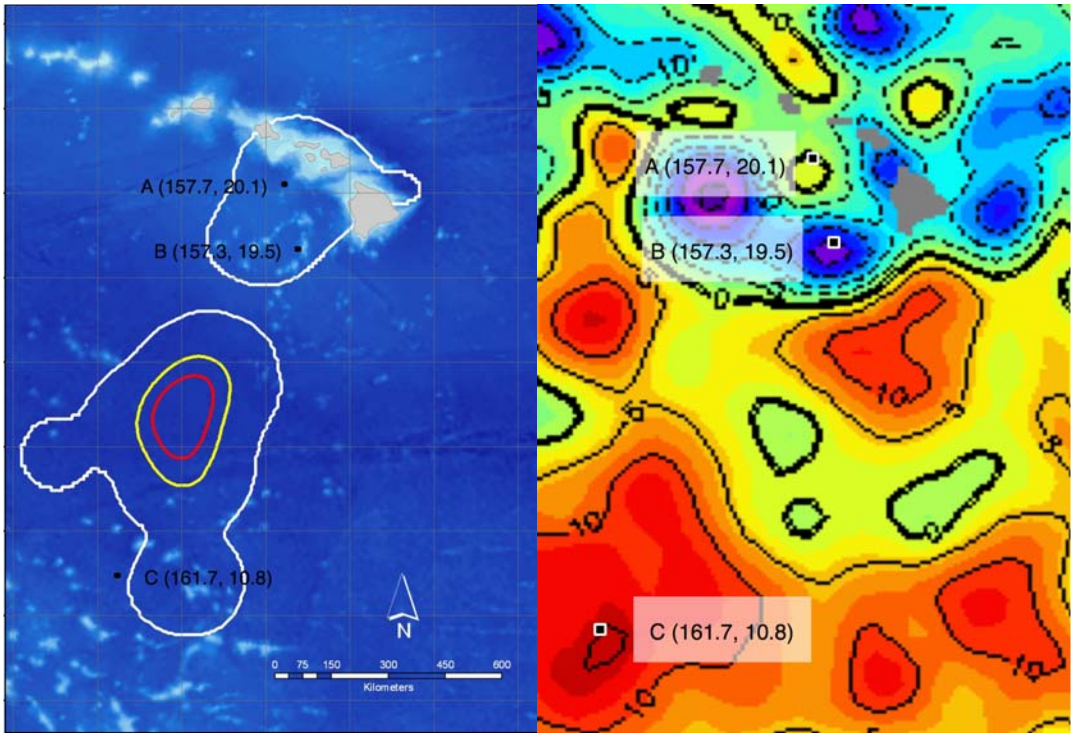

Figure 10: Kernel Densities of white shark distribution for tracks P132, P059, and P160 compared with monthly-average sea surface altimetry data. a) Track P132, March through June 2006. b) Track P059, June through August 2006. c) Track P160, March through June 2005. Points A, B, and C denote local maximums of sea surface height extremes as plotted on both kernel density and sea surface height representations. Colors on the left hand graph: white represents 95% kernel density contours, yellow represents 50% density contours, and red represents 25% density contours. Colors on the right hand graph: warm colors represent high sea surface height and cool colors represent lower sea surface height. Contour lines denote height in cm.

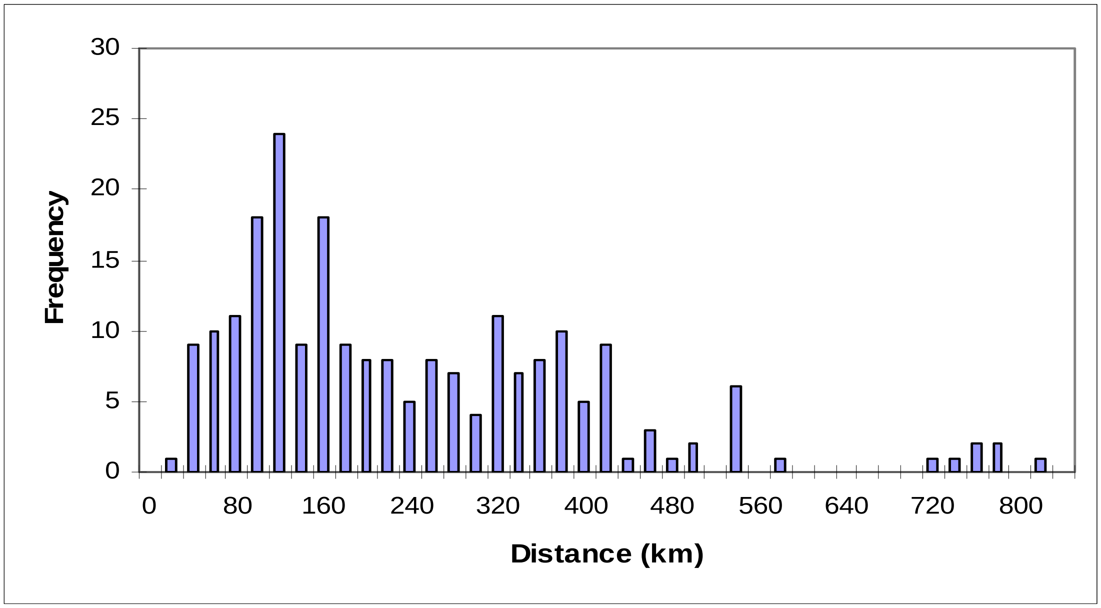

Figure 11: Distance of tag locations in 20km bins from average monthly locations of major eddy features (n=3). The distance from the nearest major eddy center in 20km bins on the x-axis, and the frequency of these distances on the y-axis. March 2005 to March 2006.

Tables With Captions:

Table 1: Zooplankton density as indicated by tow data with respect to eddy type (n=2). Sampling information: Collected May 13, 14, 15 between 07:22-08:47.

	Zooplankton Density (g/m±0.001 g/m³			
Gear Type	Control	Anticyclonic	Boundary	Cyclonic
Neuston Tow	0.000	0.004	0.008	0.007
Meter Net	0.000	0.006	0.013	0.016
Tucker Trawl (0-430m)	0.009	0.012	0.012	0.011
Tucker Trawl (DSL)	0.008	0.008	0.016	0.025
Mean for all tows	**0.008**	**0.011**	**0.015**	**0.009**

Table 2: Depth and strength of the deep chlorophyll maximum (DCM) layer in relation to eddy type as indicated by *in situ* fluorometry (n=2). Sampling information: Collected May 13, 14, 15 between 07:22-08:47

Station	Depth of DCM (m±5)	Fluorescence (volts±0.001)
Control	*120*	*0.145*
Anticyclonic	*125*	*0.144*
Border	*120*	*0.146*
Cyclonic	*145*	*0.269*

Table 3: Mean and Mode distance from the nearest eddy center for white shark PSAT data in the Hawaiian eddy field (n=3). March 2005-March 2007.

	Distance (km±20)
Mean	230
Mode	120

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Appendix A:

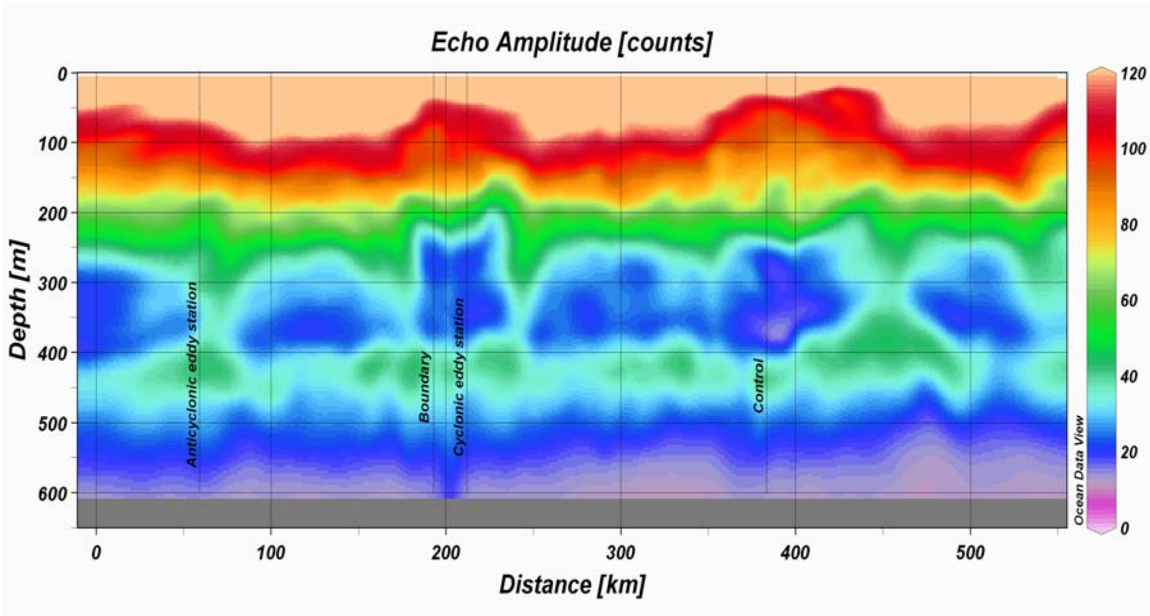

Figure 6: Images of the deepwater scattering layer over the study site as taken by ADCP. This data was used to target the deep scattering layer with the Tucker Trawls.