AN ABSTRACT OF THE THESIS OF

Robyn S. Matteson for the degree of Master of Science in Oceanography presented on October 22, 2009

Title: The Costa Rica Dome: A Study of Physics, Zooplankton and Blue whales

Abstract approved:

Bruce R. Mate

At the Costa Rica Dome (CRD), upwelling associated with cyclonic circulation and the presence of a shallow thermocline support a highly productive biological habitat, exploited by marine fauna at several trophic levels. During January 2008, a cruise to the CRD by the R/V Pacific Storm was conducted to relocate blue whales tagged off California in September 2007. In the process of relocating these whales, and others in the region, shipboard measurements of physical and biological parameters were taken with a goal of exploring how patterns of physical oceanography influence marine life in this area, particularly the distribution of blue whales and their prey. Conductivity-Temperature-Depth (CTD) casts were used to describe the physical habitat, while acoustic measurements and net tows were used to examine the distribution and behavior of zooplankton, and visual surveys and satellite tagging were used to examine habitat use by blue whales. CTD profiles showed a high level of physical variability in the water column. Tagged whales were selective in their movements for chlorophyll but not surface temperature. Prey and whales were both affected by subsurface temperature structure, not always reflected in satellite data. Acoustic backscatter data illustrated both layers and distinct, dense patches of zooplankton at various depths. These patches seemed most important to the distribution of blue whales with the total acoustic scattering from patches being a key feature in predicting blue whale proximity. Cluster analysis of acoustic regions revealed two types of patches, one of which was found only in the presence of blue whales. Collection of fecal samples from whales at the CRD confirmed their feeding in this region. Foraging during the winter reproductive season is not typical of baleen whales, but year-around forging may be an important element in the survival and recovery of blue whale populations. The data collected on this cruise demonstrate that the aggregation characteristics of prey are clearly important in determining the distribution of blue whales at the Costa Rica Dome during the northern hemisphere winter season.

The Costa Rica Dome:
A Study of Physics, Zooplankton and Blue Whales

by
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APPROVED:

Major Professor, representing Oceanography

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Robyn S. Matteson, Author

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This thesis is dedicated to my friend Lina Kitin, age 7, who wants to be a scientist
when she grows up.

1. INTRODUCTION

The Costa Rica Dome is a 300-500 km shoaling of the generally strong and shallow thermocline of the eastern tropical Pacific, about 300 km off the Gulf of Papagayo (Ballance, Pitman, & Fiedler, 2006). This cyclonic circulation feature has a mean position is at 9°N and 90°W (Fiedler, 2002). Localized cyclonic wind stress curl here causes upwelling (Hofmann, Busalacchi, & O'Brien, 1981), creating an interesting biological habitat, with increased phytoplankton and zooplankton biomass, and increased cetacean abundance (Fiedler, 2002).

Blue whales (*Balaenoptera musculus)* are found at the Dome year-round, yet we know very little about which populations utilize this area, or which oceanographic features are most important in determining their distribution while there. In this study, shipboard measurements of physical and biological parameters within this region were taken with a goal of exploring patterns of physical oceanography and how they influence marine life, in particular the distribution of blue whales and their prey. Conductivity-Temperature-Depth (CTD) casts were used to describe the physical habitat, acoustic measurements and net tows were used to examine the distribution and behavior of zooplankton, and visual surveys and satellite tagging were used to examine habitat use by blue whales.

2. Literature Review

The eastern tropical Pacific (ETP) has some of the highest productivity waters of the world oceans (Fiedler, Philbrick, & Chavez, 1991), supporting approximately 50 species of seabirds and 30 species of cetaceans as regular residents (Ballance, Pitman, & Fiedler, 2006). At these low latitudes, thermocline shoaling and upwelling are the main sources of nutrients to the surface waters causing increased primary production (Pennington et al., 2006). At the Costa Rica Dome, an upwelling region within the eastern Pacific warm pool at the eastern terminus of the 10°N thermocline ridge, nutrients are rarely depleted (Thomas, 1979). A shallow doming of the thermocline in this area, often to within 10 meters of the surface (Wyrtki, 1964), allows vertical advection to bring higher salinity, nutrient-rich water to the surface, maintains saturating concentrations of NO_3 and results in high levels of new production (Chavez & Barber, 1987). The long-term mean of the 20° isotherm, which closely tracks the thermocline, is only 30m deep (Xie, Xu, Kessler, & Nonaka, 2005). Up to 70% of the inter-annual variation in chlorophyll-a at the dome, more than any of the world oceans, can be explained by the effects of the sea level anomaly, an indicator of upwelling (Kahru, Fiedler, Gille, Manzano, & Mitchell, 2007). Upwelling is patchy here, and surface temperature at the center of the dome has an irregular pattern with patches of water less than 25°C in close proximity to patches higher than 27°C (Wyrtki, 1964). There is a fairly steady state of productivity with high standing stocks from nutrients through micronekton (Blackburn, 1966). This high productivity likely influences the distribution of cetaceans in the region by increasing prey availability (Fiedler, 2002).

Blue whales (*Balaenoptera musculus*) are found in every world ocean, inhabiting and feeding within both coastal and pelagic environments. They have been protected internationally since 1965 (Leatherwood & Reeves, 1983), with current population estimates around 2000 to 3000 individuals (Calambokidis & Barlow, 2004). A population of blue whales inhabits the northeast Pacific, from Central America up to the Gulf of Alaska. These links have been established through photo-ID, satellite-tag data, and passive acoustics (Bailey et al., 2009; Calambokidis, Rasmussen, & Steiger, 1999; Mate & Lagerquist, 1999; Stafford, Nieukirk, & Fox, 1999). Annual migration of this species is cyclic, associated with intensive feeding at mid- to high-latitudes during the summer and fall followed by migration to tropical regions for reproduction in winter and spring (Burtenshaw et al., 2004). It has been commonly assumed that blue whale distribution is governed mostly by food requirements and that they migrate (like other baleen whales) toward warmer waters during the winter to reduce their energy expenditure while fasting and engaging in reproductive activities (Lockyer & Brown, 1981; Reeves, Clapham, Brownell Jr, & Silber, 1998). Warm waters at the lower latitude breeding grounds are not likely to be advantageous to adult whales, which with their extensive blubber may have problems staying cool, not warm, but newly born calves probably benefit from birth in higher temperature waters before they have built up their blubber (Lockyer & Brown, 1981).

The eastern tropical Pacific traditionally has been described as a wintering ground for the North Pacific blue whale population (Berzin, 1978). Blue whales are found in this area year round with a peak in abundance at the dome in the winter months (Reilly & Thayer, 1990; Stafford, Nieukirk, & Fox, 1999) and individual whales have been tracked from mid-latitude eastern north-Pacific feeding areas to the Costa Rica Dome with satellite-monitored radio tags (Mate & Lagerquist, 1999). Ecological aspects of blue whale distribution and feeding have not been studied extensively at these lower latitudes (Gaskin, 1982). However, Wade and Friedrichson (1979) noted that a high standing stock of zooplankton at the dome might allow feeding. Blue whales have a coarse baleen mesh and feed on dense swarms of plankton (Lockyer & Brown, 1981). Euphausiids, or krill, found throughout the ETP are the predominant prey of blue whales. Several authors have in the past suggested that whales may fast during migration to the wintering areas but engage in foraging once they arrive (Reilly & Thayer, 1990; Wade & Friedrichsen, 1979).

Ocean processes are likely to greatly influence the distribution and behavior of cetaceans and other ocean predators. However, especially in the tropics, mechanisms which underly species-habitat relationships are not well known (Ballance, Pitman, & Fiedler, 2006). There is a growing amount of literature describing the distribution of cetaceans relative to environmental features, using whale catch data (Nasu, 1974) acoustic detections (Hastie, Swift, Slesser, Thompson, & Turrell, 2005), and tag data of various types (Etnoyer et al., 2006). Unfortunately, most of these studies rely solely on physical environmental features, not including direct measures of the organisms' prey. Some studies have incorporated knowledge of associations with primary productivity or prey (e.g. Baumgartner et al. 2003; Murase et al. 2002; Tynan et al. 2005; Woodley and Gaskin 1996). However many of these studies use environmental variables at very coarse spatial or temporal scales that may not be relevant to an individual predator. The goal of this study was to explore species-habitat relationships of blue whales in this productive area of the tropical ocean, using a combination of approaches that would allow study at multiple scales and incorporate direct measurements of blue whale prey.

3. Materials and Methods

Environmental and visual survey data were collected from the 25 m long R/V *Pacific Storm* between 3 and 29 January, 2008. Oceanographic sampling was opportunistically conducted around the primary goal of the voyage, which was to re-locate tagged whales, thus sampling was somewhat biased toward areas used by blue whales. However, much area was also covered without the presence of blue whales. Our goal was to sample in areas with and without blue whales, observing physical and biological parameters that might affect whale distribution. CTD casts were used to measure the hydrography of the study area. Echosounder data were collected to assess the distribution and abundance of krill, the primary prey of blue whales, with net tows to ground-truth those measurements. Visual surveys and whale tagging were used to assess habitat use by blue whales.

3.1 Visual survey efforts

Visual surveys for blue whales were conducted using a rotation of 10 observers with goals of both finding individuals to tag and observing the location of blue whales relative to environmental parameters. Two observers at a time, rotating in 1 hour shifts were stationed at either side of the front of the ship. Binoculars were available for species identification. Observations included individuals up to 4 km from the vessel. All cetacean species were noted but only blue whales were included in this analysis.

3.2 Satellite tagging

Fifteen whales were tagged with Telonics ST-15 satellite transmitters near the Channel Islands in 2007, to study the movements of individuals. These whales were approached by small boat and sub-dermal tags were attached to the whale using barbs.

Three of these individuals made their way south to the dome area. Three further whales were tagged at the Costa Rica Dome in 2008. Two of the three tags deployed at the CRD successfully transmitted their positions.

Satellite transmitted whale positions were retrieved from the Argos data collection and location system. Locations were edited using the Argos-assigned accuracies of 150 m, 350 m, and 1 km for high-quality locations (LC3, LC2, and LC1 respectively as radial errors, and using an 11.5 km error around poor-quality locations (LC0, LCA, LCB and LCZ), based on results from previous tests (Mate, Nieukirk, & Kraus, 1997). Locations on land further than the assigned error distance from the ocean were not used. Poor-quality locations within one hour of high-quality locations were not used, nor were LC1 locations received within 10 minutes of LC2 or LC3 locations. If two poor-quality locations were received less than an hour apart, or if two LC1 locations were less than 10 min apart, only the location providing the shortest distance between previous and subsequent locations of acceptable quality was used. Minimum distances and speeds were then calculated between acceptable locations, and additional locations were eliminated if the estimated swimming speed of the whale between a location and the prior one was greater than 15 km h^{-1} (after adjusting for radial error).

3.3 CTD data collection and processing

A Seabird 19 CTD was used to measure temperature, salinity and pressure at depths up to 200m. Casts were opportunistically carried out in 38 locations as ship time allowed. Locations of CTD casts are shown in Figure 1. A calibration of the CTD was done by Seabird just prior to the cruise (Nov 2007) and these calibrations were applied to all data collected. Temperature and salinity casts were smoothed to remove spikes using a 5-point moving average for the temperature and a 20-point moving average for salinity. Thermocline depths were calculated based on a maximum gradient function of temperature.

3.4 Acoustic data collection and processing

A 120 kHz Simrad EK60 echosounder, ideal for the detection of krill and other large zooplankton that are potential prey for blue whales (Medwin, 2005) was used to measure acoustic scattering in the water column. The transducer had a conical beam with a 3-dB beamwidth of approximately 7 degrees and was mounted to a rigid pole over the side of the vessel at a depth of about 1 m below the surface of the water. Data were collected at vessel speeds of up to 6 knots. The echosounder was calibrated immediately following data collection using a 36.8 mm diameter tungsten carbide reference sphere as described by Foote et al. (1987).

Initial analysis of data was conducted using Myriax’s Echoview Software (version 4.7). All data below 300 m or above 5 m were excluded from analysis and a minimum volume scattering threshold of -75 dB was applied. Remaining data were visually assessed to identify acoustic regions of interest that were at least 5 m in vertical extent. The edges of features that were consistent in depth across a large distance were selected manually. The edges of features that were small in horizontal extent and were more irregular in shape were selected using Echoview’s school detection tools (Diner, 2001). Criteria used for school detection included a minimum total school length of 5 m, minimum total school height of 5m, minimum candidate length of 2 m, minimum candidate height of 2 m, maximum vertical linking distance of 5 m (greatest vertical distance allowed between two school candidates being linked to form a school), and maximum horizontal linking distance of 5 m (greatest horizontal distance allowed between two school candidates being linked to form a school). An integrated analysis was exported for each acoustic feature, with variables of mean scattering volume (S_v mean) and standard deviation, nautical area scattering coefficient (NASC), thickness mean, depth mean, longitude and latitude exported.

A primary assessment of the acoustic data was carried out using a visual approach to classify aggregations within the acoustic data called “patches” and “layers”, where patches were dense, horizontally finite features and layers were thin, horizontally broad features. In addition to the characteristics listed above, horizontal extent was exported for each of the patches. Horizontal extent was not exported for layers, as they were not horizontally finite. The horizontal extent values for the patches were corrected for beam width effects in cases where the uncorrected horizontal extent of the patch was larger than the calculated beam width at the mean depth of the patch.

In addition to visual categorization, cluster analysis on characteristics of acoustic regions was carried out in SPSS to look for statistically similar groupings within the data. To explore the relationship between whale positions and cluster types, for each cluster, the distance to the nearest tagged whale position was calculated. These distances, classified by cluster 1, 2 and 3, were compared using an ANOVA and Tukey’s Honestly Significant Difference (HSD) test in SPSS.

Total water column NASC was compared by time of day, split into day, night and crepuscular time periods using sunrise, sunset and civil twilight definitions from the US Naval Observatory database for an average position within the study area. ANOVA and post-hoc Tukey's HSD test were done in SPSS to compare these vertically integrated NASC values. Overall movement of biomass as a function of time of day was observed by binning data into 10m vertical by 1 hour horizontal bins and averaging the NASC across all days. NASC values were also integrated in hour increments but within each of two aggregation types (patches and layers) separately to explore the possibility of individuals from one aggregation type converting to another aggregation type at a different time of day.

3.5 Net tow collection and processing

Targeted vertical net tows were carried out in 15 locations (Figure 1) using a 0.75 m diameter, 1 mm mesh, weighted plankton net equipped with a General Oceanics double trip mechanism. All vertically integrated casts were conducted within the upper 200 m. At each opportunity, the net was dropped in the closed position to the approximate depth of an acoustic scattering region, then a weighted messenger was sent down to open the net, and it was pulled through the layer. A second messenger was then sent to reclose the net before pulling it to the surface. Samples were preserved in 10% buffered formalin in seawater for later analysis. All krill found in samples were identified to genus and their length measured to the nearest mm using an ocular micrometer. Samples were also examined to check for any other organisms that were large or might be strong acoustic scatterers.

These net data were used in estimating krill density from acoustic data. Using counts of krill from the net samples to estimate proportions of each genus one might expect in the acoustic data, paired with length specific estimates of target strengths for each group using the equations of Greene et al (1991), which is considered the standard biomass equation for krill (Demer & Conti, 2005), krill densities for each genus were estimated for the patches in the acoustic data using Echoview.

3.6 Environmental data from satellites

All satellite environmental data was acquired through the Thematic Real-time Environmental Distributed Data System (THREDDS) at the Pacific Fisheries Environmental Laboratory. Sea surface temperatures are from the Pathfinder v5 5.5 km data set. Chlorophyll values are from the MODIS aqua 0.05 degree ocean color data set. Stepwise multiple linear regressions relating whale proximity to environmental factors were run using S-plus 16.0 software. Paths of satellite tagged individuals were compared to surrounding temperature data using a moving box approach. At each whale position the temperature and chlorophyll at that precise location were recorded as well as the mode of the surrounding environment for each at scales of 40, 60 and 100km. Point values at the tagged whale locations were compared to the surrounding environment using partial correlation, controlling for scale.

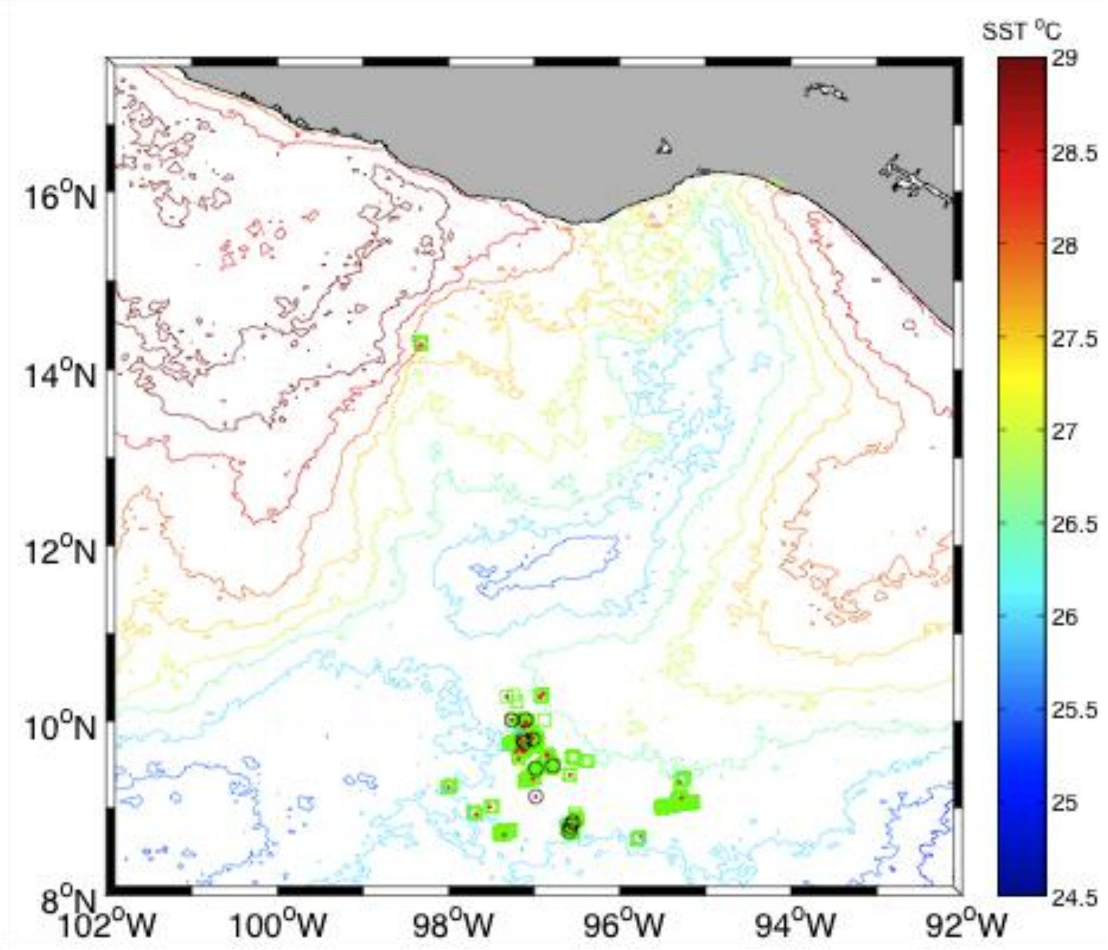

Figure 1. Data collection points overlayed on contour of Pathfinder for January 2008 v5 5.5km SST month long composite. CTD cast locations are shown as red points. Echosounder data collection regions are shown as green squares. Net samples locations are shown as black circles.

4. RESULTS

4.1 Hydrography

Conditions varied considerably during the study period. Surface water temperatures within the study area increased over the four weeks, as shown in Figures 2 and 3a, starting at a mean of 26.0 and ending at a mean of 26.5°C. Satellite-derived chlorophyll a, shown in Figures 2 and 3b, decreased over the study time period, starting at a mean of 0.53 and ending at a mean of 0.38 mg/m^3.

CTD casts show subsurface structure in the water column beyond what is seen in characteristics visible by satellite. Although areas of upwelling (shallower thermocline) roughly correspond to areas with lower temperature at the surface and areas with deeper thermocline generally correspond to areas of higher surface temperature, there is a great deal of variation around this pattern, with peaks and troughs in thermocline depth inconsistent with this general trend (Figure 4).

4.2 Zooplankton

Within the acoustic data, there were two visually discernable feature types: “layers” and “patches”. "Layers" were visually distinguishable from "patches" in the analysis, as layers were usually shallower, less acoustically intense with mean S_v< -58dB, and horizontally spread across distances of one half nautical mile or more, while remaining fairly constant in height. Patches were usually deeper, had higher acoustic scattering with mean S_v >-58dB, and had more irregular vertical shapes. Using this visual categorization of acoustic features, an ANOVA was used to examine the differences in the scattering and geometric characteristics of these zooplankton features. Many differences were found between them. Patches had a greater nautical area scattering coefficient (NASC) than layers (ANOVA F=211.59, $p < 0.0001$). NASC is the acoustic backscatter per unit area in m^2/nmi^2 and thus is an integrated proxy of zooplankton biomass. Patches had a higher mean scattering volume (S_v) than layers (ANOVA F = 5262.07, $p < 0.0001$); S_v is roughly proportional to the number of animals per unit volume given consistent patch composition. Patches were generally thinner than layers, with patches having a mean thickness of 5.8 m vertically, and layers varying in thickness with a mean of about 23m. Patches had greater heterogeneity in S_v than layers. In their depth distribution, patches were deeper than layers, and exhibited differing diel behaviors. While layers had a fairly constant depth through the diel cycle, patches migrated toward the surface at night. A comparison of the two classifications of acoustic scattering types is shown in Table 1.

Using the statistical software SPSS, a two step cluster analysis was run on the acoustic patches and layers with the continuous variables ‘mean S_v’, ‘NASC’, ‘thickness mean’, ‘depth mean’, and ‘standard deviation of the S_v’. Schwarz's Bayesian criterion was used for clustering with the number of clusters determined automatically. All acoustic scattering regions identified fell into one of three clusters. Compared with the visually sorted acoustic scattering regions, 73% of visually identified "patches" were assigned to cluster 2, and 91% of visually identified "layers" were assigned to cluster 3. Cluster 1 was comprised mostly (98%) of the remaining patches.

Cluster 1 was comprised mostly of patches, was only apparent during daylight hours, in close proximity to whales, and only within upwelling centers. Cluster 2 (92%

patches) was present during both day and night, was sometimes found where whales were not, and was not exclusively found within upwelling regions (Figure 5). S_v mean (ANOVA, F = 1337.27), NASC (ANOVA, F=853.93), mean thickness (ANOVA, F=190.32), mean depth (ANOVA, F =5.38), and standard deviation of the S_v (ANOVA, F= 1303.04) of clusters 1 and 2 were all significantly different at the 0.05 level. A Tukey's post hoc tests indicated that cluster 1 had greater S_v than cluster 2 ($p<0.05$), was more heterogeneous ($p<0.05$), had greater NASC ($p<0.05$), had greater thickness ($p<0.05$), and was found slightly deeper ($p<0.05$). The horizontal extents of the cluster 1 and cluster 2 acoustic features were not significantly different (ANOVA, F=0.167, $p>0.05$).

In exploration of the relationship between the three cluster types and tagged blue whale positions, the distribution of distances from the clusters to the nearest whales were significantly different (ANOVA, F=34.2, $p<0.05$). Tukey's honestly significant difference test showed significant differences between each pair of cluster types ($p<0.005$ in all cases). Cluster 1 had the shortest mean distance to nearest whale at 2.33 km, cluster 2 had a mean of 5.87 km to the nearest whale, and cluster 3, comprised mostly of layers, had the longest distance to nearest whale with a mean of 9.62 km.

Integrated water column NASC showed significant differences between day, night and crepuscular time periods (ANOVA, F= 10.8, $p<0.05$). Tukey's HSD test showed that the daytime NASC values were significantly different from both the nighttime values and the crepuscular values; night values were not significantly different from crepuscular values. Daytime values of NASC were the smallest, with a mean of 4908 m^2/nmi^2, nighttime values were larger with a mean of 7463 m^2/nmi^2, and crepuscular values were the highest with a mean of 9309 m^2/nmi^2. Overall movement of acoustically determined biomass examined by binning the data into 10m by 1 hour bins and averaging across all days showed the greatest NASC values within the top 50m at night and between 250 and 300 m during the day, with migration periods around 6am and 6pm. An inverse relationship in NASC between aggregation types with time was observed, with nearly all of the patches disappearing at night time while layers increased in NASC.

Total calculated density values for each patch were on average 8.32×10^{10} krill/nmi^2, or given average patch thicknesses of 5.84 m, approximately 4,149 krill/m^3. The least dense patches had about 47 krill/ m^3 while the most dense patches observed had an estimated 312,100 krill/m^3. The mean krill density was 13,539 krill/m^3. Under this scenario, an individual krill has 74 cm^3 of water space within the swarm while under the most dense conditions observed an individual krill has 3.2 cm^3 of water space within the swarm.

4.3 Blue whales

A total of 54 sightings of 87 blue whales were made during on-effort visual surveys. Three of fifteen blue whales tagged off southern California in September 2007 went to the CRD and two of these were sighted while there. Whales were observed diving over patches of krill. Brick-red feces were observed on several instances and on one occasion collected from a pair of animals, providing a strong suggestion of blue whale feeding at the Dome (John Calombokidis, personal communication).

Of tagged blue whales, median distance traveled per day was 45.5 km. Three of the 2007 whales went directly south from the tagging location near the Channel Islands toward the Costa Rica Dome, arriving there in 2-4 months time. In January 2008, the two whales which had been tagged at the CRD headed north toward Baja following 2-3 months further time at the Dome, arriving at the southern tip of Baja by June.

Visually sighted blue whales and tagged whales were both examined for any correlation with the surrounding environment. An association was observed between thermocline structure measured in situ with CTD and blue whale sightings. Comparison of the thermocline depths where whales were found and the thermocline depths throughout the entire study area showed a significant difference (ANOVA, F= 47.8, $p< 0.001$) with whales found in areas with shallower thermoclines (Figure 6). In the data from satellite-tagged individuals, comparison of animal paths to the surrounding sea surface temperature environment at multiple scales of 40, 60 and 100 km revealed that whales were not selective for surface temperature (Partial correlation controlling for scale, slope not significantly different from 1, $p < 0.05$, $R^2 = 0.99$). Comparison of animal paths to the surrounding chlorophyll environment at multiple scales revealed that whales were selective for chlorophyll distribution (Partial correlation controlling for scale, $R^2 = 0.56$) and were on average found in areas with higher surface productivity (Figure 7). A stepwise (both directions) multiple linear regression was used to explore relationships between the various environmental measurements available and the locations of the visually surveyed whales (Figure 8). Acoustic patches and layers were taken as the reference point, and distance of the nearest sighted blue whales from these locations was the response. NASC, thermocline depth, mean depth of the patch or layer, sea surface temperature mean and chlorophyll mean, as well as all possible interactions were used as predictors. When both patches and layers were included in the analysis, the p value was very small ($p<0.001$) however the explanatory capability was quite low ($R^2 = 0.19$). However when layers were removed from the analysis, the predictive capability of the model improved greatly ($R^2 = 0.97$, $p<0.001$) (Table 2). The most important factors predicting blue whale proximity to acoustically identified patches were NASC and interactions involving NASC.

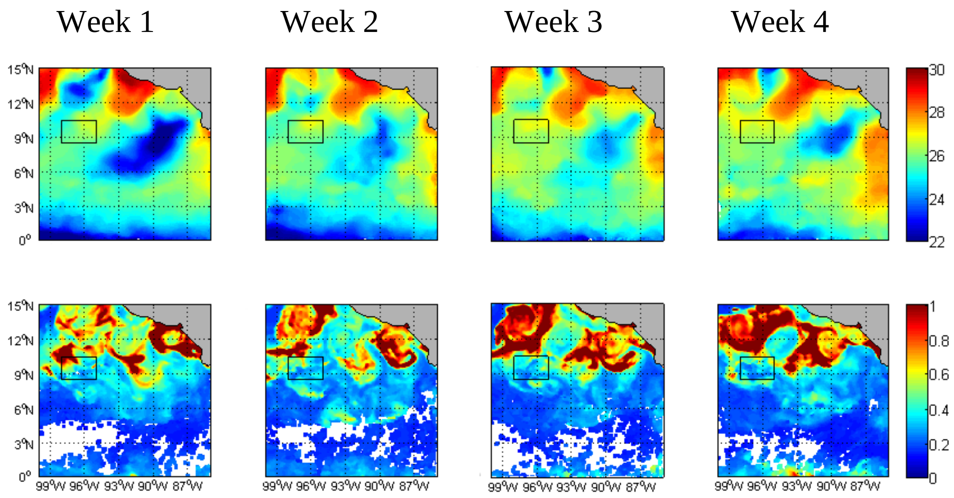

Figure 2. Sea surface temperature (Pathfinder, upper row) and Chlorophyll (Modis Aqua 0.05 degree, lower row) within study area, shown in black box, and surrounding waters for weeks 1 through 4.

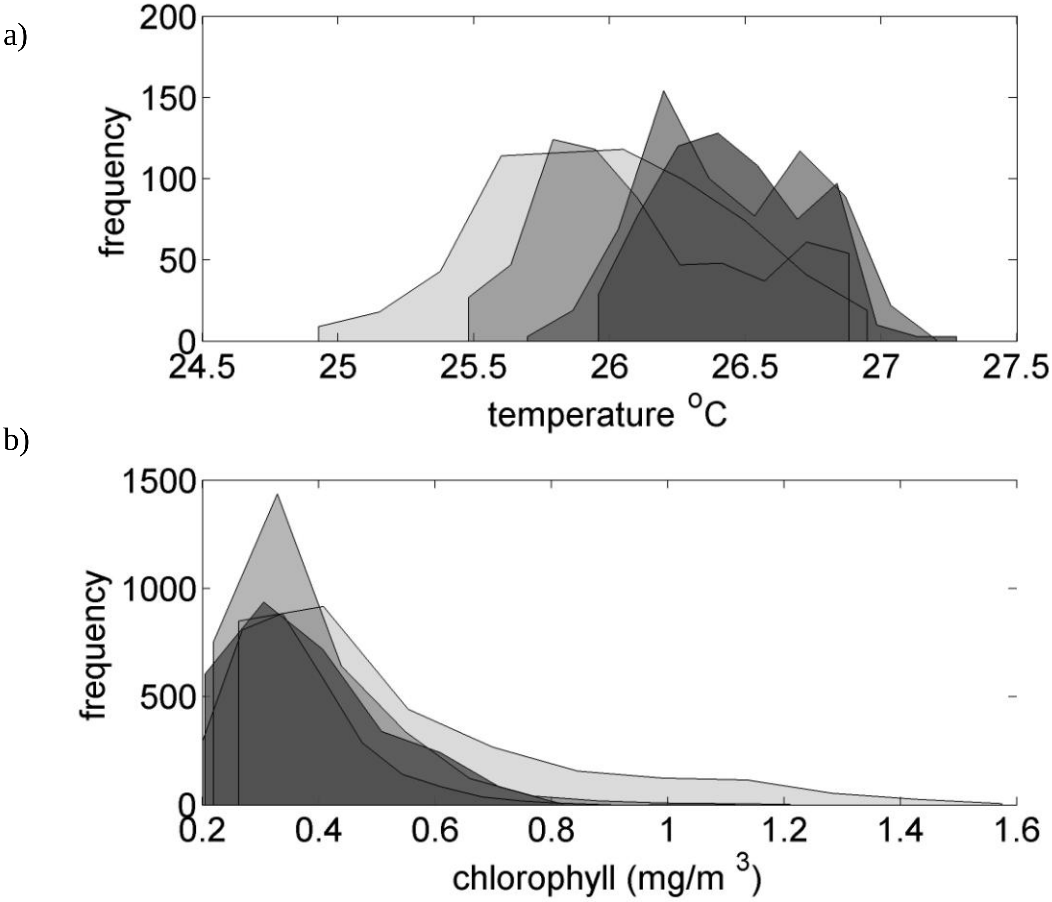

Figure 3. Sea surface temperature and chlorophyll observations within the study area over the study time period. (a) frequency of temperature observations in the satellite data with lighter greys representing earlier weeks and darker greys representing later weeks. (b) frequency of chlorophyll observations in the satellite data over time with light grey representing earlier weeks and dark grey representing later weeks.

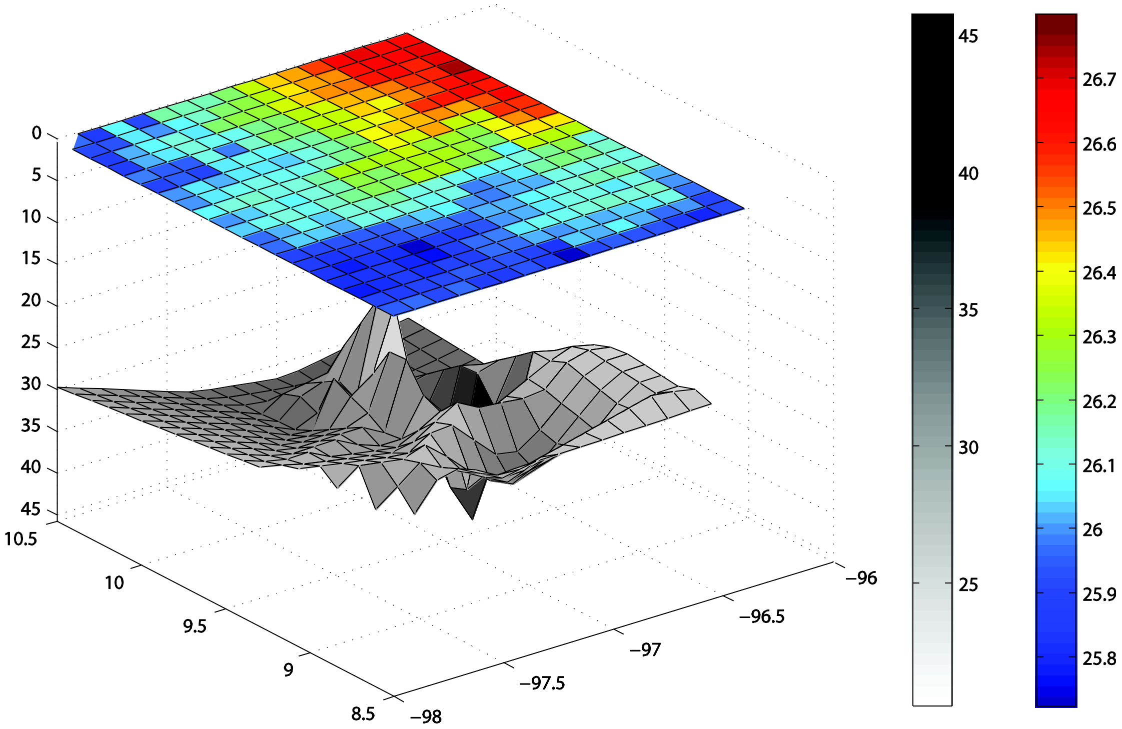

Figure 4. Variations in thermocline depth. Mean sea surface temperature within the study area is shown in color with thermocline depth shown in relief and gray scale.

Table 1. Comparison of characteristics of patches and layers. Values are mean +/- SD..

	Patches	Layers	ANOVA
Sv	-58.76 +/- 5.7	-73.65 +/- 3.6	F = 5262.07 p < 0.0001
Std (Sv) "heterogeneity"	5.59e-006 +/- 9.26e-006	5.76e-007 +/- 3.6856e-006	F = 261.99 p < 0.0001
NASC	923.0 +/- 1.85e+003	71.09 +/- 208.6135	F = 211.59 p < 0.0001
Thickness (m)	5.84 +/- 6.49	22.97 +/- 12.36	F = 1765.3 p < 0.0001
Depth (m)	209.33 +/- 55.24	67.89 +/- 67.76	F = 2956.8 p < 0.0001
Diel behavior	Migration toward surface at night	Fairly constant depth	

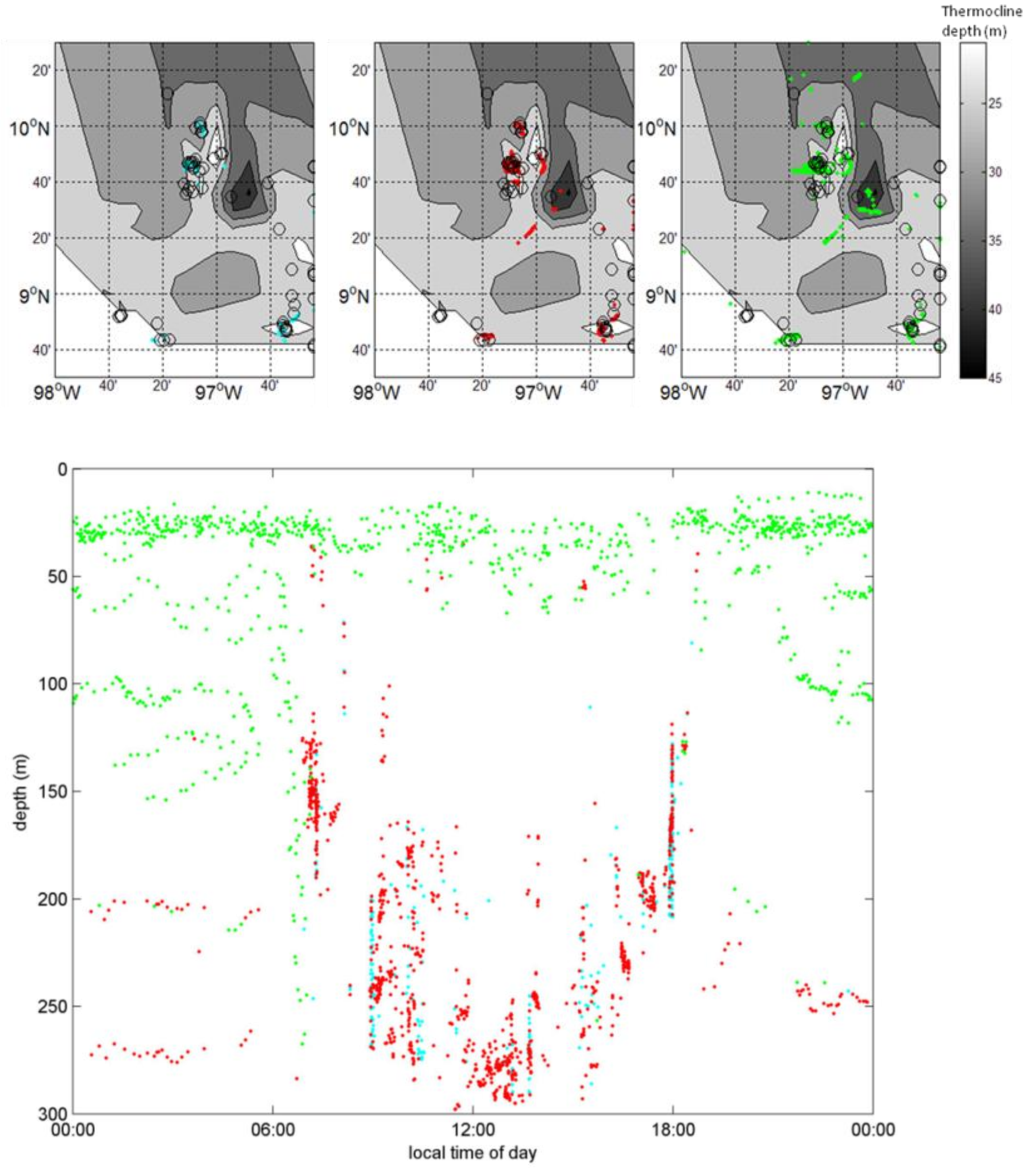

Figure 5. Cluster analysis results shown on maps and by time of day. Cluster 1 is cyan, cluster 2 ("patches") is red and cluster 3 ("layers") is green.

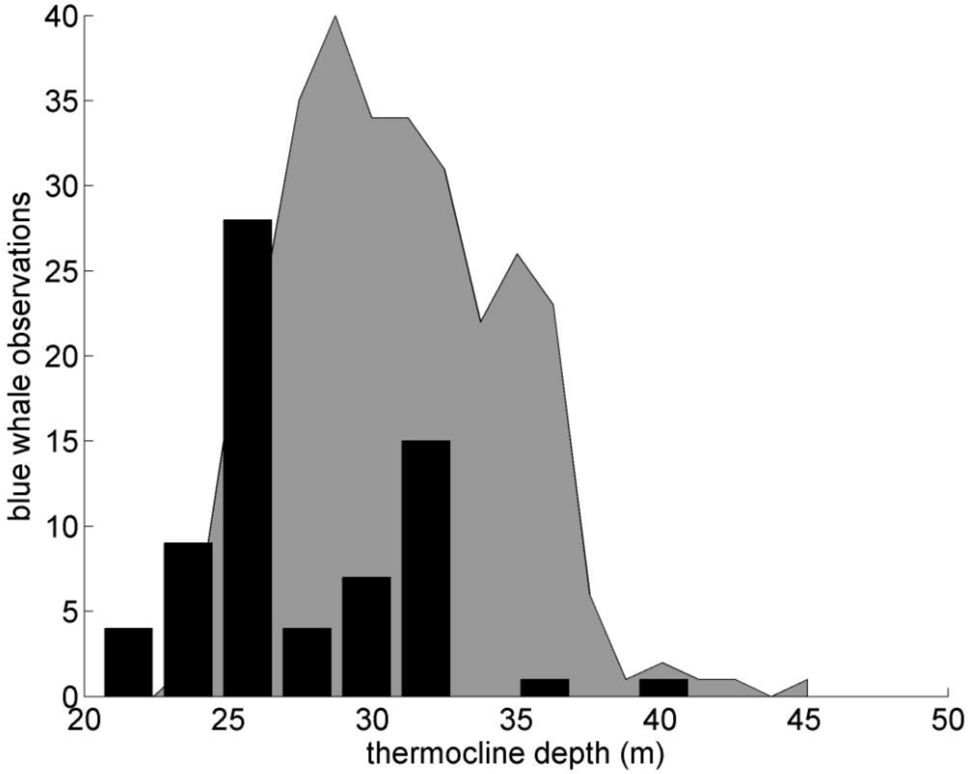

Figure 6. Thermocline depths at observed blue whale positions (visual survey) (black) versus total interpolated thermocline field within the study area (gray).

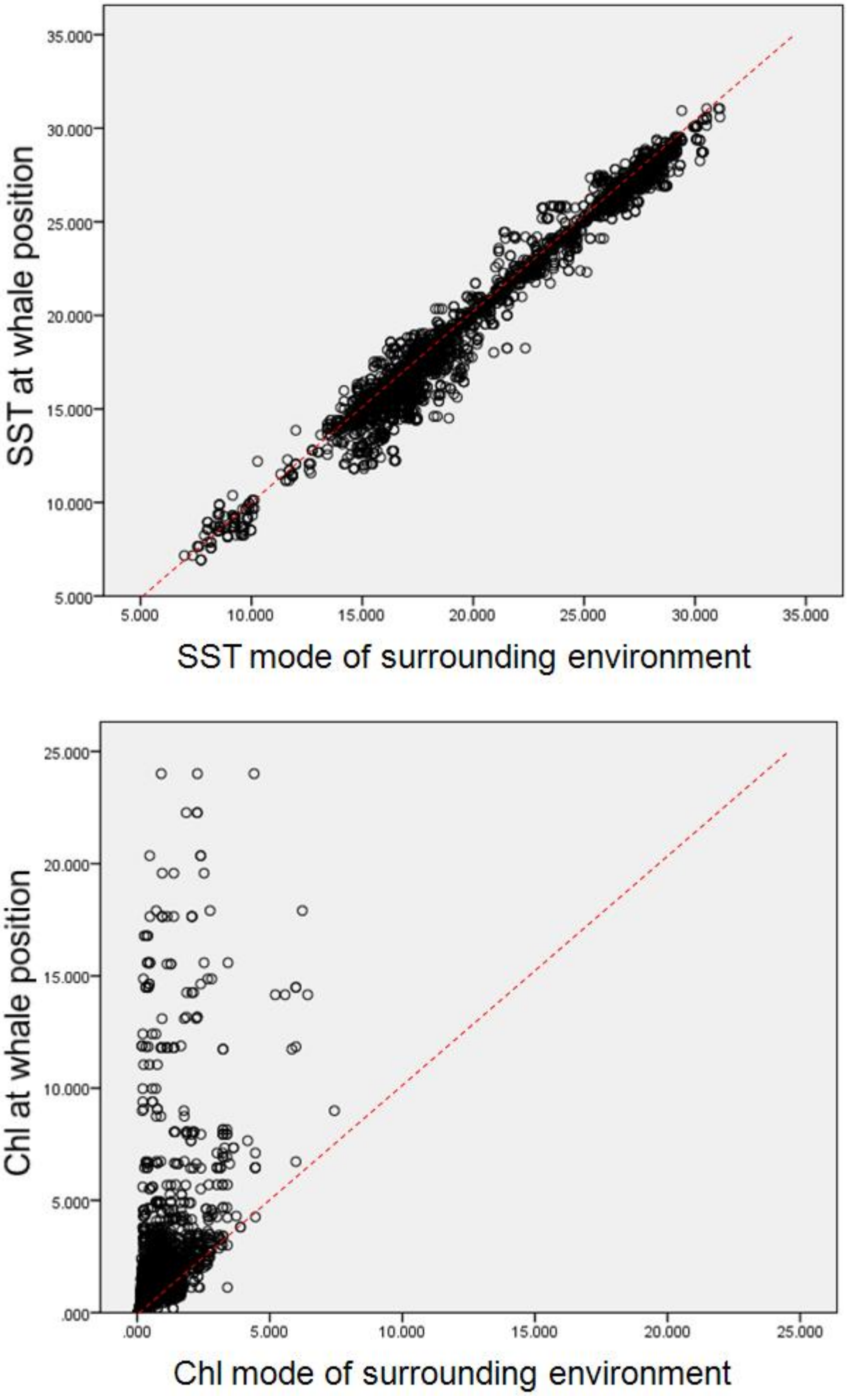

Figure 7. Comparison of tagged whale paths to mode of surrounding for both temperature and chlorophyll at the 40km scale.

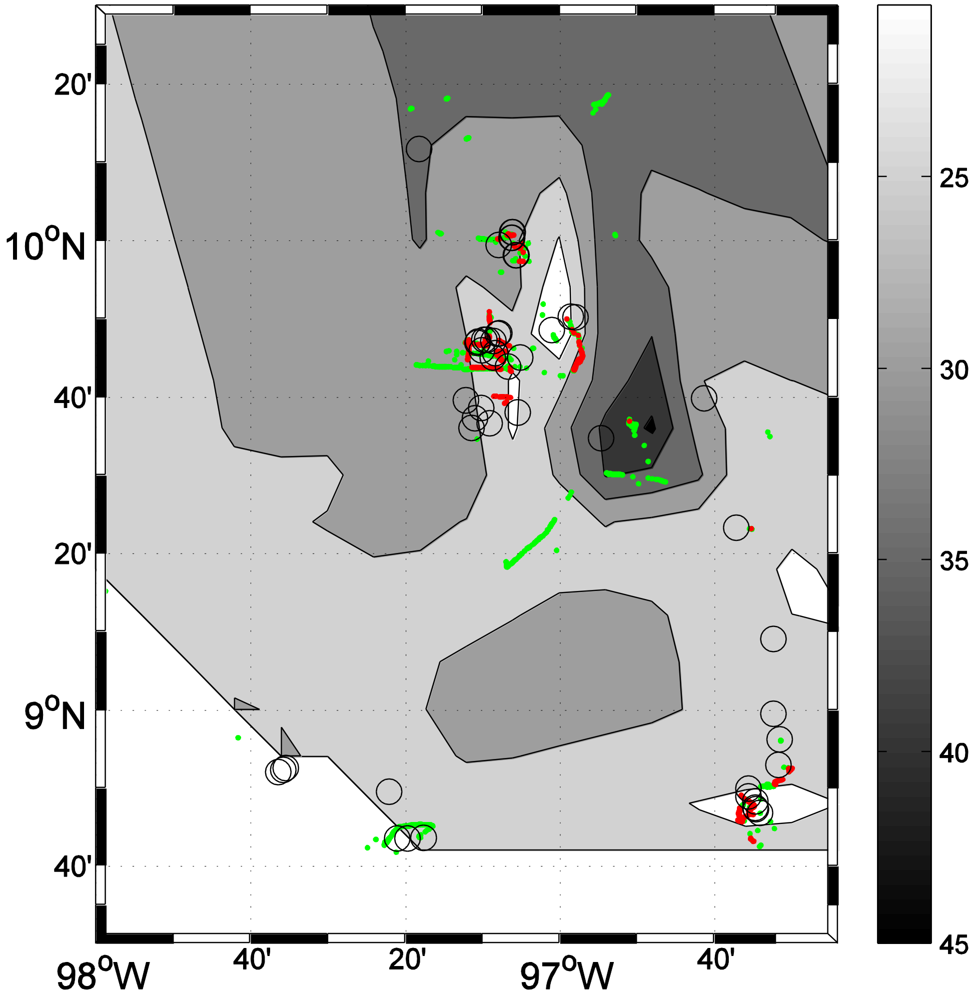

Figure 8. Locations of layers and patches relative to upwelling and whale sightings.Thermocline depth in meters is shown in the filled contours in the background, with layers in green, patches in red, and whale sightings shown as black circles.

Table 2. Results of stepwise linear regression with distance to nearest whale as the response variable and NASC, thermocline depth (TD), mean depth of layer, SST mean at that point, Chl mean at that point, and all possible interactions as predictors.

	Patches & Layers		Patches only	
Value	t value	Pr(>|t|)	t value	Pr(>|t|)
(Intercept)	2.2898	<.05	10.3338	<.05
nasc	0.5413	NS	2.2843	<.05
TD	0.5353	NS	-0.328	NS
meandepth	0.5398	NS	-0.3309	NS
SSTmean	-0.4405	NS	-1.8423	NS
CHLmean	-0.4071	NS	-0.2773	NS
nasc:TD	-0.5442	NS	-2.2736	<.05
nasc:meandepth	-0.21	NS	-2.1033	<.05
TD:meandepth	-0.571	NS	0.5707	NS
nasc:SSTmean	0.7761	NS	1.5163	NS
TD:SSTmean	0.0059	NS	1.127	NS
meandepth:SSTmean	-0.5792	NS	-0.9809	NS
nasc:CHLmean	2.2103	<.05	0.0226	NS
TD:CHLmean	0.4975	NS	0.2963	NS
meandepth:CHLmean	1.7932	NS	0.3259	NS
SSTmean:CHLmean	0.3065	NS	0.7991	NS
nasc:TD:meandepth	0.4621	NS	1.856	NS
nasc:TD:SSTmean	-1.2455	NS	-1.1784	NS
nasc:meandepth:SSTmean	-0.2781	NS	-1.3432	NS
TD:meandepth:SSTmean	0.5411	NS	1.0207	NS
nasc:TD:CHLmean	-2.6806	<.05	-0.0215	NS
nasc:meandepth:CHLmean	-2.7226	<.05	-0.0271	NS
TD:meandepth:CHLmean	-2.1518	<.05	-0.3413	NS
nasc:SSTmean:CHLmean	-2.2439	<.05	-2.2003	<.05
TD:SSTmean:CHLmean	-0.3928	NS	-0.9916	NS
meandepth:SSTmean:CHLmean	-1.7645	NS	0.7374	NS
nasc:TD:meandepth:SSTmean	0.6385	NS	0.973	NS
nasc:TD:meandepth:CHLmean	3.1661	<.05	0.0261	NS
nasc:TD:SSTmean:CHLmean	2.716	<.05	2.0282	<.05
nasc:meandepth:SSTmean:CHLmean	2.75	<.05	2.3042	<.05
TD:meandepth:SSTmean:CHLmean	2.1114	<.05	-0.6804	NS
nasc:TD:meandepth:SSTmean:CHLmean	-3.1838	<.05	-2.0483	<.05
	R-squared 0.1904		R-squared 0.9704	
	P-value < 0.0001		P-value < 0.0001	

5. DISCUSSION

Movement of 3 of 15 blue whales tagged off of California toward the Dome and at least 2 of 3 blue whales tagged at the Dome back toward California corroborates the findings of Calambokidis et al (1999), Mate et al (1999), and Stafford et al (1999) that North Pacific blue whales do use the Dome area on a regular basis. At the same time it is interesting that only 20% of the blue whales tagged at higher latitudes went to the Costa Rica Dome in 2008. Other whales made it only as far south as Baja.

Comparison of the paths of satellite-tagged individuals to environmental features suggested that at large scales, the movements of blue whales are correlated with higher chlorophyll values. Although the movements seem selective for chlorophyll values, they are not selective for surface temperature. It is likely that the higher chlorophyll values also lead to higher prey densities in those areas. Diving of individuals over patches of krill suggest feeding at the Dome but collection of fecal material confirms it.

Baleen whales, when feeding, require dense and predictable prey aggregations (Moore, Waite, Friday, & Honkalehto, 2002). Prey at the Dome was found in two distinct types of aggregations, called here patches and layers. Whales were more abundant in areas where patches were present versus just layers, suggesting their food source might lie within these patches. Patches were readily distinguishable from layers in their greater mean volume scattering, suggesting higher prey densities, and higher integrated scattering, indicating a greater total abundance of prey in those features.

This may account for the whales' increased proximity to them rather than the less acoustically dense layers, which may be less efficient forage.

Acoustically detected potential prey was significantly affected by subsurface temperature structure, and was concentrated within upwelling regions. However, this important subsurface structure was not always reflected in satellite (surface image) data which may account for the lack of a relationship between sea surface temperature and locations of tagged whales despite the association of zooplankton with lower temperature, upwelled water. Hydrographic features like the subsurface upwelling features observed here that can aggregate prey may increase the foraging efficiency of blue whales, accounting for the observed association. Regression of the visually surveyed whales against available environmental data further supported the feeding hypothesis suggesting that acoustic patches were more significant determinants of whale proximity than layers, and in particular the integrated acoustic scattering, as a measure of the total prey abundance in the patches appeared to be important for whales.

Krill densities within the patches were on average 4,149 krill/m^3 while the most dense patches observed acoustically had an estimated 312,100 krill/m^3. For comparison, in Antarctic waters, density estimates vary, with early visual estimates given at 64,000/m^3 (Marr, 1962) and later visual estimates at 20,000 to 30,000 individuals/m^3 (Hamner et al 1983). In the Gulf of California, krill densities within swarms are quite variable with densities ranging from 9 to 9,394 individuals/m^3 (Ladron et al 2008). Mauchline (1980) noted that krill aggregate over a wide range of densities, proposing a classification with schools and swarms of krill have the highest local densities at 1,000 to 100,000 krill/m^3, shoals having 1-100 krill/m^3, and what he called patches and breeding aggregations being the least dense at 1-10 krill/m^3. Under this classification scheme, patches at the CRD were at densities comparable to Mauchline's "schools" or "swarms" and on average had higher numbers of euphausiids per cubic meter than seen in the Gulf of California but less than seen in the Antarctic.

Cluster analysis of the acoustic regions revealed a third type of acoustic scattering region not identified visually, a distinct subset of patches that was only found in close proximity to whales within upwelling centers. Other visually identified patches (cluster 2) were sometimes found where whales were not and outside of upwelling regions. However, the unique (cluster 1) patches identified by the cluster analysis were different from the other patches, with more intense acoustic scattering that was also more variable, higher integrated acoustic scattering (NASC) with more overall variation, greater thickness, and a deeper distribution. Unlike other patches, these cluster 1 patches were only seen during daylight hours. Coupled with the fact that these cluster 1 patches were always found in the presence of whales, this might suggest that blue whales feed only during the day at the Dome or that they feed differently during the day than at night. From these data, there is no way of knowing if whales were picking these unusual patches or if the patches were unusual because of the whales. Cluster 1 patches might be composed of different species or size class of prey than the normal patches or they could be the same animals arranging themselves into denser, thicker, deeper and more heterogeneous aggregations. They could be doing this in response to the presence of the whales or, alternatively, the whales could be picking these unique patches that make foraging more efficient.

The distribution and patterns of the acoustically measured zooplankton were interesting beyond their significance for whales. The difference seen in total water column acoustic scattering between day, night and crepuscular time periods, with less total acoustic scattering during the day could indicate that krill are too loosely distributed during the day in some cases to be detected acoustically, or that they migrated from below the 300m limit of our acoustic sampling to increase the total acoustic scattering at night. The inverse relationship in total acoustic scattering between aggregation types with time suggests that patches took on layer characteristics at night time. At the Dome during the daytime, the greatest acoustic scattering was seen between 250 and 300 m, well below the thermocline depth. Within the California current, several species are also known to migrate 300 m daily, rising to the surface at night similar to at the Dome (Brinton, 1967).

6. CONCLUSION

The objective of this study was to describe the physical and biological characteristics of blue whale habitat at the Costa Rica dome by exploring relationships between environmental variables and the distribution of whales. While retrospective analysis of tagging or sighting data for various predators against satellite-remote sensing data is a common approach, direct measures of prey for inclusion in these analyses has been limited. In this study with both approaches taken, the strongest correlations were found between predator locations and direct acoustic measures of their prey. At larger scales measured by satellite, tagged whales appear to select for chlorophyll but not temperature. Caution should be used in interpreting results of studies that only use satellite data as a basis of comparison between predators and environmental cues, as there can be considerable spatial or temporal lag between chlorophyll and higher trophic levels and features visible to the satellites at the surface may not be representative of the remainder of the water column. In cases where there is an apparent lack of correlation between predator distribution and hydrographic variables (e.g. Davis and Fargion 1996; Davis et al. 1998) incorporation of direct measures of prey as well as subsurface hydrographic features would likely prove helpful in explaining the distribution of these predators. It is important in these ecological studies to understand the process driving the pattern in order to evaluate the importance of a correlation between predators and prey; in this study zooplankton are correlated with upwelling and whales are correlated with zooplankton. Aggregation characteristics of prey are clearly important in determining the distribution of blue whales at the Costa Rica Dome, providing further evidence that feeding is an important driver of their overall behavior even during the winter “breeding season”.

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