

AN ABSTRACT OF THE THESIS OF

Ladd Irvine for the degree of Master of Science in Oceanography presented on December 18, 2007.

Title: Characterizing the Habitat and Diving Behavior of Satellite-Tagged Blue Whales (*Balaenoptera musculus*) off California.

Abstract approved:

Bruce R. Mate

This study was designed to identify and characterize areas of concentrated use and diving behavior of blue whales (*Balaenoptera musculus*) off the California coast. During the summer of 2004, thirteen blue whales were tagged with implantable Telonics ST-15 Argos satellite-monitored radio tags and five were tagged with Telonics ST-21 Argos satellite-monitored depth of dive tags. Tag duration averaged 100 d with a total of 2159 locations recorded. Whales generally remained near the continental slope and were most often found at the west end of the Santa Barbara Channel, near the Gulf of the Farallones, or between Cape Mendocino and Cape Blanco. Analysis of the 95% kernel density distributions of whale locations showed a one degree increase in sea surface temperature (SST) was correlated with a decrease in whale density by 7% ($p < 0.0001$) while density was highest at a surface chlorophyll level of 4.5 mg/l and a water depth of 1573 m

($p < 0.001$ each). These results show that tagged whales were most likely to be found in areas of strong upwelling along the slope edge. Dive data from 414 summary periods showed whales spent at least 50% of their time in the top 50 m of the water column and up to 94% of their time there at night. Daytime average dive depth was 2.3 times deeper than during the night, probably due to the vertical migration of some euphausiid species upon which blue whales feed. Differences in mean number of dives and mean maximum dive duration suggest a behavior change during the night, possibly a period of rest. Whales dove less frequently as swim speed increased, and more frequently as water depth increased. No significant variation in daytime average dive depth was observed between clustered and linear location types, however fewer total dives were made during linear location types suggesting whales were making exploratory dives to foraging depths while traveling.

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Characterizing the Habitat and Diving Behavior of Satellite-Tagged Blue Whales
(*Balaenoptera musculus*) off California

by
Ladd Irvine

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APPROVED:

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Dean of the Graduate School

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.

Ladd Irvine, Author

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CONTRIBUTION OF AUTHORS

Dr. Mate assisted with data collection and revisions of this manuscript.

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Characterizing the Habitat and Diving Behavior of Satellite-Tagged
Blue Whales (*Balaenoptera musculus*) off California

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Introduction

At the beginning of the 20th century, blue whales (*Balaenoptera musculus*) were abundant throughout the world's oceans (Rice 1998; Yochem and Leatherwood 1985). Growing up to 33m in length and weighing up to 150 tons, they are the largest animals ever to have roamed the earth. Commercial whaling during the first half of the century devastated the global population, with over 325,000 blue whales removed from Antarctic waters alone (IWC 1996; Small 1972). An estimated 5000-12,000 blue whales remain in the world today (Sears and Calambokidis 2002). One of the largest and best studied blue whale populations is the eastern Pacific blue whale, which winters off Central America and spends summers feeding in the productive waters of the California Current off the coasts of California and Oregon. Photo-ID and line-transect methods estimated the population at 2000-3000 with possible, but inconclusive evidence that the population is growing (Calambokidis and Barlow 2004; Sears and Calambokidis 2002).

The California Current System (CCS) is the collective term for the region of high seasonal primary productivity spanning the continental margin from Washington to Baja California. Prevailing northerly (alongshore) winds from April – September drive upwelling, which brings cool, nutrient rich water to the surface, making this an extremely productive region. Upwelled water is transported south by a seasonal jet which forms near the coast early in the upwelling season, and moves offshore as the summer progresses into fall (Strub

and James 2000). The strength of the seasonal jet has been shown to influence zooplankton abundance over interannual timescales (Chelton *et al.* 1982; McGowan *et al.* 1998). The many capes and underwater geographic features along the continental margin augment primary production by adding nutrients to the photic zone through increased vertical mixing and can create circulation patterns which have been shown to aggregate euphausiids into locally dense patches which can then be exploited by higher trophic level predators (Fiedler *et al.* 1998; Ressler *et al.* 2005).

Eastern Pacific blue whales feed almost exclusively on swarms of euphausiids, primarily *Euphausia pacifica* and *Thysanoessa spinifera* (Croll *et al.* 2005; Croll *et al.* 1998; Fiedler *et al.* 1998; Yochem and Leatherwood 1985). They must consume an estimated 2-4 tons per day to maintain their enormous size. Dense swarms of *E. pacifica* and *T. spinifera* are associated with upwelling centers like the Channel Islands, Monterrey Bay, and the Gulf of the Farrallones/Cordell Bank (Croll *et al.* 2005; Croll *et al.* 1998; Fiedler *et al.* 1998; Schoenherr 1991; Smith and Adams 1988) and, therefore, blue whales tend to congregate in these highly productive areas (Calambokidis and Barlow 2004). The larger and more coastal *T. spinifera* is typically found at daytime depths of 50 – 150 m over the shelf, although it will form swarms at the surface, possibly related to reproduction (Schoenherr 1991; Smith and Adams 1988). *E. pacifica* is typically found at the shelf edge and extending off it at typical daytime depths of 200-400 m (Brinton 1976). Both species undergo significant diel vertical

migrations to the surface at night (Bollens *et al.* 1992; Brinton 1962; 1976; 1981; Greenlaw 1979).

Studies of blue whales are complicated by the difficulty of monitoring them while underwater, and their ability to range widely over relatively short periods of time (108 km/d, Mate *et al.* 1999). Satellite monitored radio tags are capable of tracking blue whales for periods of months (Mate *et al.* 2007; Mate *et al.* 1999), allowing locations from satellite tagged whales to define important habitat using the areas where they spend the most time. By transmitting every day, or every other day, these tags can provide relatively high resolution data on the movements of individual whales at lengthy timescales. Satellite tags are also capable of monitoring the diving behavior of blue whales allowing insight into potential foraging behavior in addition to movements (Lagerquist *et al.* 2000).

This study uses a large data set of satellite tagged blue whale locations to determine their diving behavior and the characteristics of high use areas across the entire summer feeding grounds. The work is broken into two components: The first component uses the satellite locations to identify high use areas and the environmental characteristics of those areas are subsequently characterized. The second component uses a subset of the satellite tagged whales to describe their diving behavior as they move around the summer feeding grounds. The results are then summarized at the end of the paper.

Characterizing the Habitat of Satellite-Tagged Blue Whales
(*Balaenoptera musculus*) off California

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Introduction

Studies of blue whale habitat are complicated by their ability to range widely over relatively short periods of time (108 km/d, Mate *et al.* 1999). They have, therefore, mostly been limited to either high resolution studies in relatively small areas (Croll *et al.* 2005; Croll *et al.* 1998; Fiedler *et al.* 1998; Schoenherr 1991), or broad scale methods like line transect surveys (Calambokidis and Barlow 2004; Tynan *et al.* 2005) and acoustic monitoring from fixed hydrophone arrays (Burtenshaw *et al.* 2004). Of the three methods, acoustic monitoring has the greatest temporal resolution, but the lowest spatial resolution due to gaps in the locations of the fixed acoustic array, and the unknown number of calling whales as a percentage of the whole population.

Satellite monitored radio tags are capable of tracking blue whales for periods of months (Mate *et al.* 2007; Mate *et al.* 1999), allowing locations from satellite tagged whales to define important habitat using the areas where they spend the most time. Locations from tagged whales can be used to create Utilization Distributions (UD) which are probability functions that quantify an individual or group of whales' relative use of space (Kernohan *et al.* 2001). Each cell of the resulting distribution represents the probability of a whale being in that cell based on the smoothed function of the locations used (Figure 1). Phrased differently, it represents the probability that a pixel was used by a whale. The UD is usually estimated using nonparametric procedures such as fixed kernel techniques (Seaman and Powell 1996). With the primary assumption that space

use relates to resource use, UD's have been used to describe habitat use of Steller's Jays (Marzluff *et al.* 2004; Millspaugh *et al.* 2006) and cow elk (Millspaugh *et al.* 2006). The UD analysis offers increased sensitivity over other habitat analysis methods by using a continuous rather than discrete (presence/absence) measure of use. This allows for variations in the intensity of resource use within an area rather than assuming the locations represent use, and all other areas are not used. UD's have the added benefit of reducing the impact of location error as each location is spread over an area, rather than being used as a discrete point. A more detailed discussion of the properties and uses of UD's can be found in Marzluff *et al.* (2004) and Millspaugh *et al.* (2006).

This chapter identifies the environmental characteristics of high use areas across the entire summer feeding grounds. I hypothesize the whales will most likely be found in regions with strong upwelling near the slope edge.

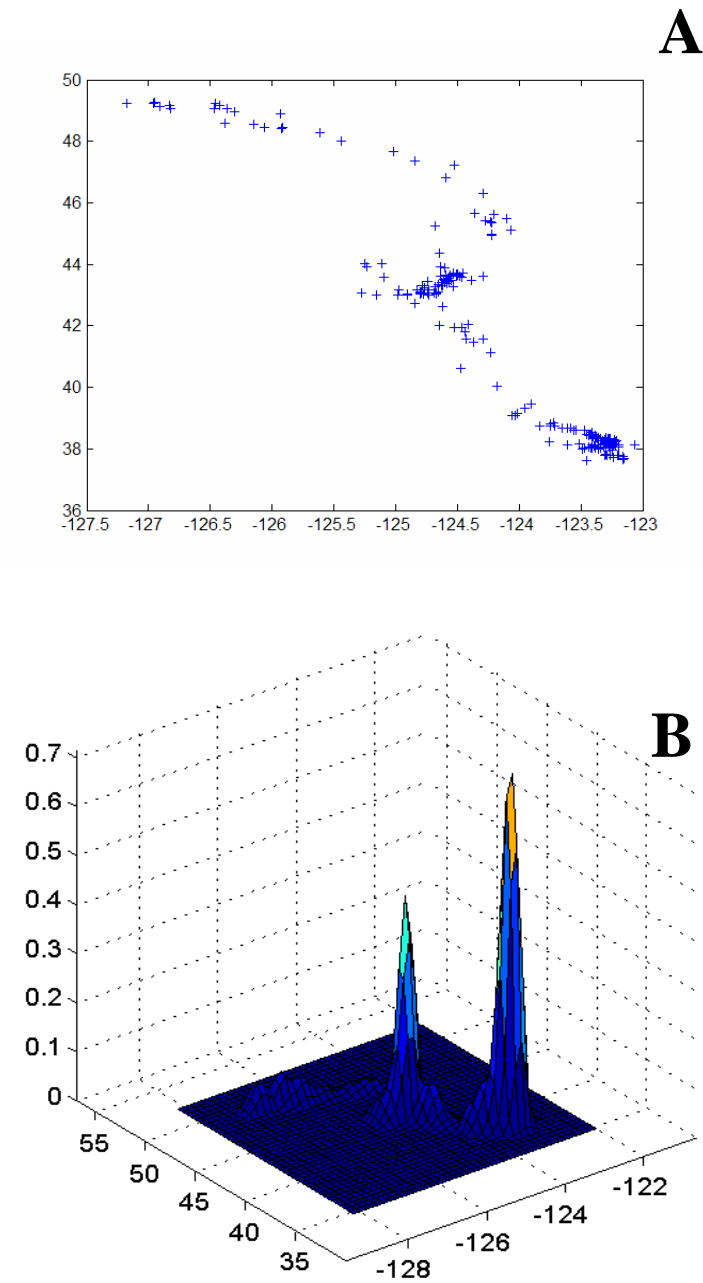


Figure 1: An example of a fixed kernel utilization distribution (B) created from tagged whale locations (A)

Methods

Eighteen satellite monitored radio tags were attached to blue whales off the California coast during August, 2004. Nine whales were tagged at the west end of the Santa Barbara Channel near San Miguel Island, and nine were tagged in the Gulf of the Farrallones near Cordell Bank. The tags were deployed 1-3m forward of the dorsal fin, near the midline, from a 6.4m rigid hulled inflatable boat using the ARTS system, a modified line throwing gun using compressed air (Heide-Jørgensen *et al.* 2001). The tags consisted of a Telonics ST-15 UHF radio transmitter and two Duracell 2/3A lithium batteries housed in an implantable stainless steel cylinder covered in part with a long dispersal antibiotic coating. Further details about tag design and deployment can be found in Mate *et al.* (2007).

Satellite Data/Environmental Variables

Pathfinder version 5.0 SST data and Sea-viewing Wide Field-of-View Sensor (SEAWIFS) chlorophyll-a data were used for this project. Eight day composites of each data type were downloaded from the Coastwatch West Coast Regional Node (<http://coastwatch.pfeg.noaa.gov/coastwatch/CWBrowser.jsp>). Sequential composites were combined using the simple arithmetic mean between the corresponding non-cloud obscured pixels to produce two week (16 d) composites for each data type. Composites were used to reduce the number of cloud obscured pixels in the image.

The Pathfinder data set was developed by the University of Miami's Rosenstiel School of Marine and Atmospheric Science (RSMAS) and the NOAA

National Oceanographic Data Center (NODC). It is a high quality, 4 km resolution SST product of the NOAA Advanced Very High Resolution Radar (AVHRR) aboard the NOAA Polar Operational Environmental Satellites (POES). Pixels are flagged with one of eight possible quality flags using a hierarchical series of tests (Kilpatrick et al. 2001) and SST values are accurate to within 0.3 degrees C. Only the highest quality pixels were used in this study. SEAWIFS data are a 4.5 km resolution chlorophyll-a product of the SeaWiFS instrument onboard the OrbView-2 spacecraft. The data are produced by OrbImage (now GeoEye) and have an accuracy of approximately +/- 35%.

Two minute gridded relief bathymetry data (ETOPO2v2) were downloaded from the National Geophysical Data Center (NGDC, <http://www.ngdc.noaa.gov/>). The data were produced by satellite radar altimetry and high resolution ship surveys with a vertical accuracy of 1 m.

SST, chlorophyll-a, and bathymetry gradients were calculated using a 3 x 3 pixel moving window Sobel Gradient method (Etnoyer *et al.* 2006). Once the grid of gradient values was calculated, a new grid of gradient densities was made for SST and Chlorophyll by counting the number of pixels in a 40 km (10 pixel) radius from each pixel, whose gradient values exceeded the top 10% of all gradient values.

Location Data

Locations were calculated by Service Argos from Doppler shift data when three or more messages reached a satellite (Argos 1990) during a “pass”. Multiple

locations for an individual on the same day were averaged if both location classes were 0 or better, otherwise, the better quality location was used.

The deployment of tags in two localized areas on the feeding grounds could bias some of the data toward tagging locations. The potential range of movement of a tagged whale is relatively limited for the first day or two after tagging (100 km/d) which would lead to over sampling of data from the tagging locations, compared to the rest of the summer feeding grounds, during that time. After whales have had time to disperse, tag location bias is much less of a factor because whales are providing locations from places they chose to visit, not a place they happened to be when the tag was attached. Ideally tags would be deployed at random locations throughout the summer feeding grounds to avoid this problem, but this is not possible logistically.

This study used only tags which lasted more than one week to avoid short duration tags skewing the data to the tagging areas. No further effort was made to account for tagging bias in the data. The tagging locations were chosen because they are regions where large numbers of blue whales are regularly observed and, in the case of the Channel Islands, have been shown to produce euphausiids in large enough quantities to sustain them (Croll *et al.* 1998; Fiedler *et al.* 1998). Therefore if the early data is biased toward these locations, it is biased toward the type of habitat we are trying to identify.

Locations from all tags on whales lasting longer than one week were combined, and divided by date into two week (16 d) periods ranging from July 29, 2004 to Jan 20, 2005. A utilization distribution (UD) was calculated using fixed

kernel methods for the locations in each two week period using the Wave Analysis for Fatigue and Oceanography (WAFO) toolbox for Matlab (available at www.maths.lth.se/matstat/wafo/documentation/wafodoc/index.html). Each pixel was given a value based on the number of locations within a given distance, known as the smoothing factor, from the cell. Separate smoothing factors for the x and y directions were calculated using either the smoothed cross validation, or normal scale estimate of the smoothing. The grid size of the UD was calculated to match the size of the satellite data grids. All values of the UD smaller than the 95th percentile were removed.

UD's were overlaid on satellite data composites of the same timeframe so that each pixel of the UD corresponded to a pixel from the grid of each environmental variable. Mixed effects regression was used to test what effect the environmental variables had on the density of tagged whales. Differences between two week periods were accounted for by an indicator variable in the random effects. Change in AIC was then used to determine the best model. The size of the data set (over 100,000 data points) prevented analysis in its entirety as all variables would show a statistically significant effect (due to the large sample size) even if they were not biologically significant. Instead, regressions were run on 10 groups of 1000 randomly selected points from the data set. The resulting coefficients were averaged and used as the results of the analysis.

Results

Fifteen of the eighteen tags lasted longer than one week and were used to create kernel density estimates. Tag duration ranged from 9 to 502 d ($\bar{x} = 100$ d) providing a total of 2159 locations (1048 after averaging multiple locations). Two tags transmitted beyond the Jan 20, 2005 range of this study, but not enough locations (< 30) were recorded in the subsequent two week periods to create accurate kernel density estimates. The number of locations (after averaging) received per two week period of a tag's life was relatively consistent for the life of each tag ($\bar{x} = 10.1$ locations, $SD = 2.0$) with fewer locations typically received during the first and last two week periods of a tag's life.

From August to late November the whales ranged from Point Conception to the central Oregon coast, with one whale going as far north as Vancouver Island (Figure 2). During this period, whales were located mostly over the slope edge, within approximately 50km of shore. Three whales made offshore excursions in the area between Monterrey Bay and Point Conception, with one whale (ptt number 10843) moving over 600km offshore, before turning south to begin its southerly migration for the winter. Otherwise, offshore activity appeared to be limited to southerly migrations, and over wintering areas near Baja California, Mexico.

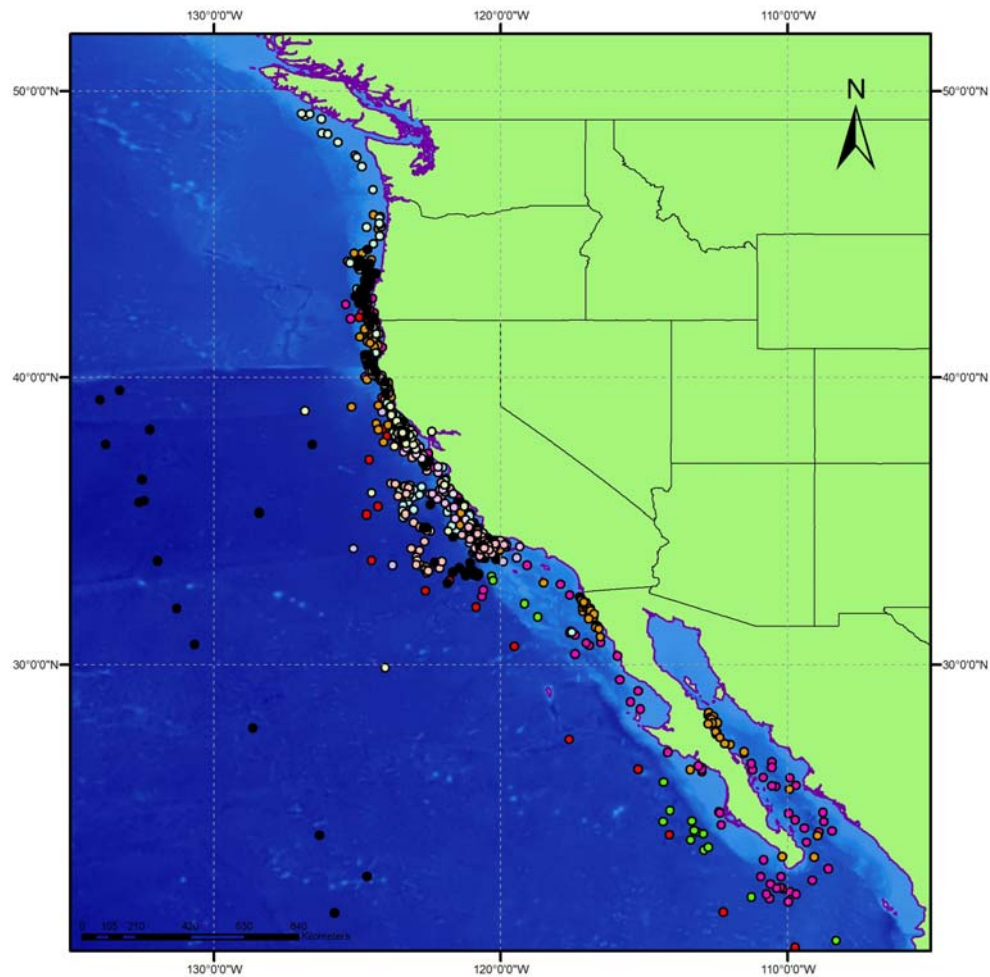


Figure 2: Locations from all blue whales tagged during the summer of 2004. Different colors represent different individual whales.

A histogram of the number of locations by latitude (Figure 3) shows high numbers of whale locations in three distinct modes at latitude ranges: 33-36°, 37-39°, and 40-44° latitude. A UD plot using all locations shows an area of high use at the west end of the Channel Islands near Point Conception (latitude 34° N), and a more continuous distribution of use to the north, with peaks near the Gulf of the Farrallones/Cordell Bank (latitude 38° N) and between Cape Mendocino and

Cape Blanco (latitude 41° N, Figure 4). Whales moved northward during the summer feeding season, with the 50% UD core area of locations shifting from the Gulf of the Farrallones to southern Oregon/northern California in mid-to late-September (Figure 5). By October 12 tags were still transmitting, six from each tagging location. One of the 12 whales was south of the Mexican border, six were north of the Gulf of the Farrallones, three were in the Gulf of the Farrallones, and only two were located near the Channel Islands.

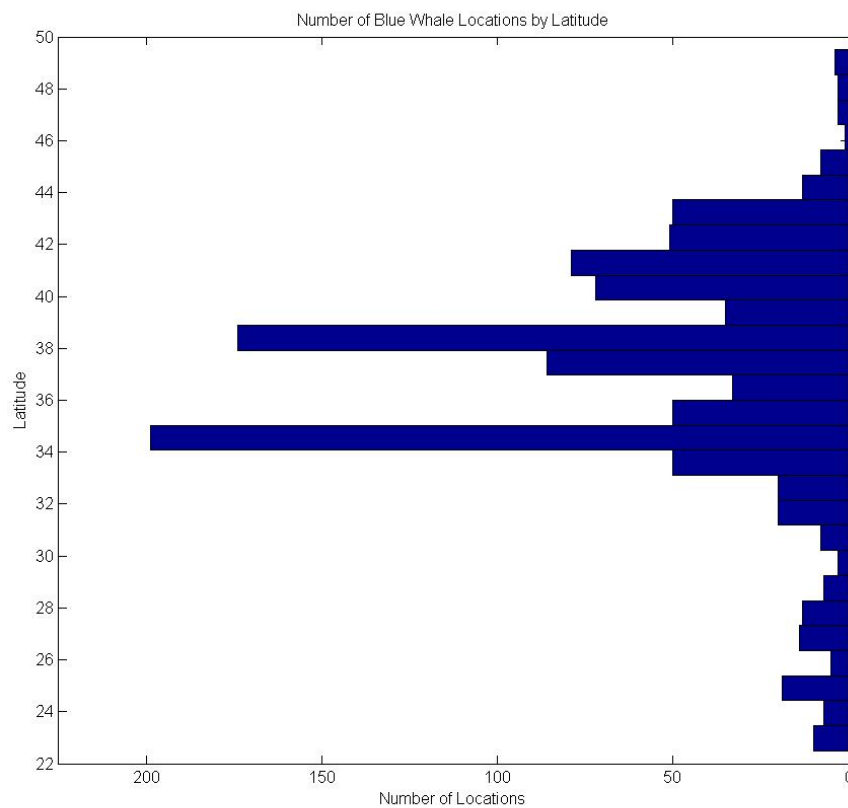


Figure 3: Number of blue whale locations by latitude for whales tagged off California during the summer of 2004.

Probability of use was log transformed as the response variable in the regression after a residual plot showed a cone shaped distribution. Transformed regression results showed sea surface temperature (SST), chlorophyll concentration, SST gradient density, chlorophyll gradient density, and water depth all significantly affected median probability of use (Table 1). Significant quadratic effects were also observed for Water Depth and Chlorophyll ($p < 0.001$ for both). A one degree increase in SST was correlated with a decrease in the

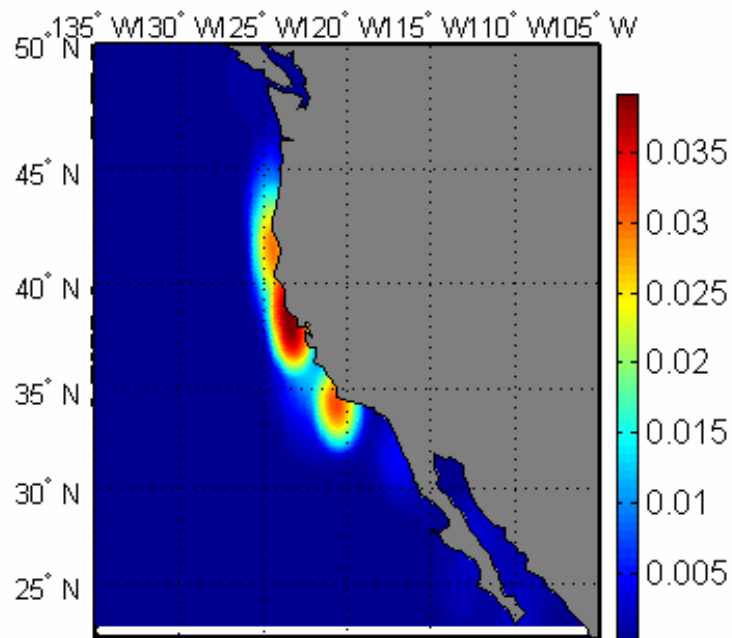


Figure 4: Utilization Distribution of all tagged blue whale locations during the summer and early winter of 2004.

median whale density by 7% (95% conf 6-8%, $p < 0.0001$). Ten unit increases in SST gradient density and Chlorophyll gradient density both showed small, but significant multiplicative effects on median whale density after accounting for the other variables in the model (95% conf 1 – 3%, $p = 0.015$ and 95% conf 1 – 2%, $p = 0.048$ respectively). The positive slope term and negative quadratic term for both Water Depth and Chlorophyll means their effect on whale density can be visualized as a concave curve. The peak of the curve representing the effect of Water Depth ($-b/2a$) was 1573m so mean whale density increased with increasing water depth until 1573m, when whale density declined with any further increase in water depth. Chlorophyll concentration showed a similar quadratic effect. The peak of the curve was 4.5 mg/l, after which, whale density decreased with increasing chlorophyll.

Table 1: Mixed effects regression coefficients for the habitat analysis using log transformed probability of use as a response.

| Coefficient | Value | Std Error | p-value |
|---------------|-----------|-----------|----------|
| intercept | -9.16 | 0.398 | < 0.0001 |
| sst | -0.072 | 0.0079 | <0.0001 |
| chlorophyl | 0.41 | 0.068 | <0.0001 |
| sstGradDens | 0.0019 | 5.23E-04 | 0.011 |
| chlorGradDens | 0.0013 | 4.22E-04 | 0.039 |
| waterDepth | 2.13E-04 | 5.52E-05 | 0.0008 |
| waterDepth^2 | -6.76E-08 | 1.34E-08 | <0.0001 |
| chlorophyl^2 | -0.046 | 0.0093 | <0.0001 |

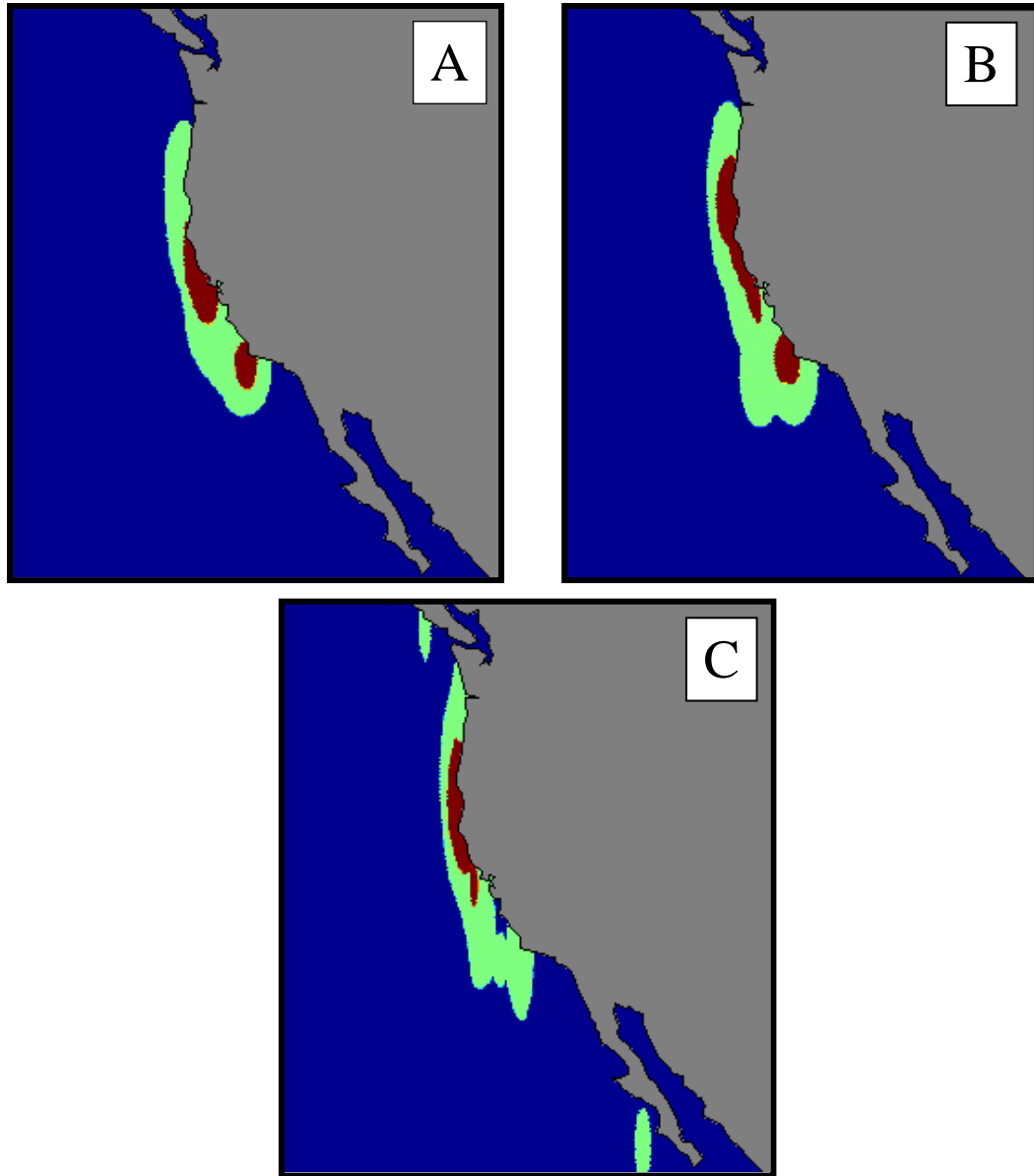


Figure 5: 95% (green) and 50% (red) utilization distribution plots of blue whale locations during A) Aug 31 – Sept 15, B) Sept 16 – Oct 2, and C) Oct 3 – Oct 18 2004

The final model was:

$$\begin{aligned} \log(\text{probability of use}) \sim & -9.2 - 0.072 * \text{SST} + 0.413 * \text{Chlorophyll} + 0.00188 * \\ & \text{SSTGradDens} + 0.00128 * \text{ChlorGradDens} + 0.000213 * \text{WaterDepth} - \\ & 0.000000068 * \text{WaterDepth}^2 - 0.046 * \text{Chlorophyll}^2. \end{aligned}$$

Discussion

The whales in this study were most likely to be found in cold, productive water along the edge of the continental slope. These types of ocean conditions have the potential to support high densities of prey. Studies performed in Monterey Bay and at the Channel Islands showed that cold, upwelled water in those areas was advected off the shelf break providing sufficient nutrients and subsequently phytoplankton blooms to attract swarms of zooplankton (*Euphausia pacifica* and *Thysanoessa spinifera*) which were concentrated by topographic breaks in the shelf at high enough densities to support blue whales (Croll *et al.* 2005; Croll *et al.* 1998; Fiedler *et al.* 1998). It was proposed by Croll *et al.* (2005) that blue whales are attracted to areas of predictably high prey density and that movements of the whales are related to seasonal patterns in productivity at different areas. While it is not possible from the data collected to know the actual prey densities in areas frequented by whales in this study, the results appear consistent with this hypothesis as, over an average of three months, tagged whales were most likely to be found in ocean conditions very similar to those which created areas of high prey density in the Channel Islands and Monterey Bay.

The significant quadratic effect of chlorophyll in the final model is interesting because it suggests whales were less likely to use regions with the highest chlorophyll levels. Rather than being attracted to areas at the onset of a phytoplankton bloom, blue whales may be keying in on a peak in secondary productivity, which can lag peak primary productivity by 1-4 months (Hayward and Venrick 1998; Croll *et al.* 2005).

Blue whales have been observed in abyssal waters > 4000 m deep (Calambokidis and Barlow 2004; this study), however, the result showing highest whale density at 1573 m was surprising because they are more typically found (and were tagged) at the shallower part of the continental slope and onto the shelf in 125 – 500 m of water (Croll *et al.* 2005; Croll *et al.* 1998; Fiedler *et al.* 1998; Schoenherr 1991; Mate pers. Observation). While some whales did venture into deep water, the deeper than expected result is likely due to the density distributions being spread over the continental slope, where the water depth rapidly drops from 200 m to > 4000 m. Ultimately, the result is shallower than the middle depth of the slope (~ 1800 m), and therefore, could be interpreted as the whales preferring the shallower portion of the slope, as is commonly accepted.

Movements of tagged whales showed a northward progression as the feeding season progressed. By October, an equal number of tags deployed in each tagging area had stopped transmitting, so it is unlikely that the move north is an artifact produced by variations in tag life from each location. This northward movement is strong corroborating evidence of the work of Burtenshaw *et al.* (2004), who used acoustic localizations of blue whale calls from 1993-2000 to

infer a northward migration to Vancouver Island, BC by blue whales during the feeding season. While most of the tagged whales in this study did not pass north of Oregon, one did briefly venture up to Vancouver Island, before returning to Oregon/northern California. This difference may be due to year to year variation in productivity, or differences between calling and non-calling whales.

The high use of the west end of the Channel Islands, and the Gulf of the Farrallones/Cordell Bank area by tagged whales was expected based on observations from a number of other studies. (Calambokidis and Barlow 2004; Croll *et al.* 1998; Fiedler *et al.* 1998; Mate *et al.* 1999). The dramatic peaks in the number of observed locations at latitude 34-35° N and 38-39° N are likely an artifact of the tags being deployed in those areas. While this may be interpreted as a bias in the results, the areas would need to have high densities of prey for the whales to remain for any period of time, therefore, it is unlikely to have significantly influenced the results.

Tagged whales also heavily used the area from Cape Mendocino to Cape Blanco, moving northward from the original tagging locations as time progressed. Were it not for the peaks in locations at the tagging areas, this northern area would have recorded an equal, if not greater number of locations than either of the two more well known aggregation sites.

The area around Cape Blanco, Oregon has been studied in great detail, and is a region of high productivity (Batchelder *et al.* 2002). The interaction between the seasonal equatorward upwelling jet and the coastal topography of the headland creates zones of plankton retention which produce locally dense patches

of euphausiids (Ressler *et al.* 2005). A number of surveys have been conducted in this region with none reporting a large number of blue whale sightings (Calambokidis and Barlow 2004; Tynan *et al.* 2005). Burtenshaw *et al.* (2004) did not frequently detect blue whale calls off Oregon during their acoustic study, and it was hypothesized that whales were passing through, enroute to Vancouver Island. This suggests that the high use of the Cape Blanco area observed in this study may not have been a regular occurrence.

Plots of the NOAA Environmental Research Division (ERD) coastal upwelling index anomaly for southern and central California show that upwelling was much lower than normal from June – August of 2004 (Figure 6 b&c). The index anomaly between Cape Mendocino and Cape Blanco (Figure 6 a) showed average upwelling, so the northward movement of the whales may represent an effort by the whales to find more productive feeding areas as euphausiid populations in southern/central California were depleted. The northern California/southern Oregon coast may not typically produce zooplankton swarms dense enough to draw blue whales in large numbers, but it appears, in 2004, it was more productive relative to the Channel Islands and the Gulf of the Farrallones.

The result of this collective information supports the hypothesis of Croll *et al.* (2005), that the migratory movements of blue whales probably reflect seasonal patterns in productivity in various foraging areas. Whales moved north to an area with stronger upwelling than the areas they typically frequented. The timing of the northward move (approximately three months after the decline in upwelling anomaly) is on the same scale as the lag between peak primary productivity and

zooplankton production observed by Croll *et al.* (2005) in Monterey Bay (three to four months). If peak zooplankton production lags peak primary productivity by three to four months, it is reasonable to assume a drop in primary productivity will similarly lead to a drop in euphausiid populations by a similar time span, and

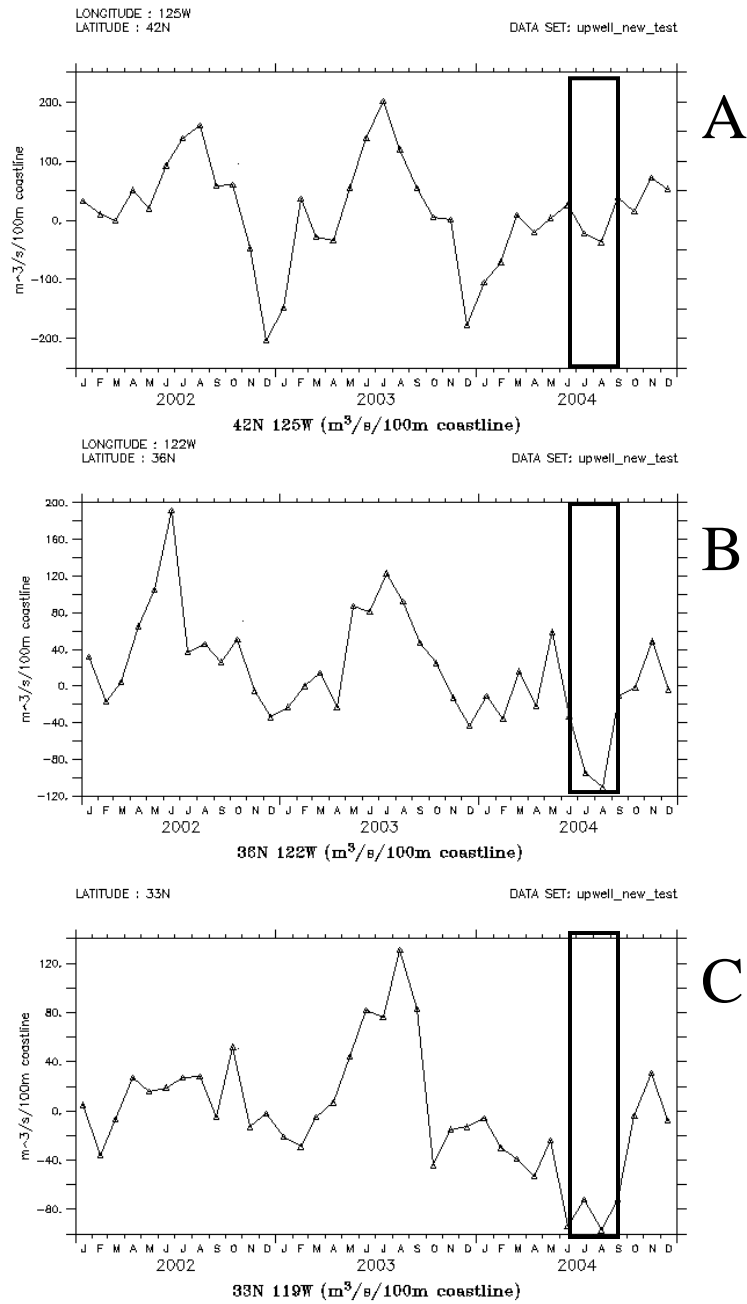


Figure 6: Upwelling Index Anomaly at A) 42 N B) 36 N C) 33N latitude along the California coast from January 2002 – December 2004. The outlined area refers to the time discussed in this study

therefore, the whales left because there were no longer high enough densities of krill to sustain them.

The results of this study show that blue whales frequent the continental slope waters off the western United States, and congregate in regions with decreased sea surface temperature and elevated chlorophyll-a levels. These characteristics are consistent with highly productive upwelling regions which concentrate zooplankton in high densities on the slope edge. A northward shift of whale locations as the feeding season progressed suggests that changes in whale distribution were related to variation in prey density at different locations.

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Introduction

The diving behavior of most of the great whales has been described using one of two techniques: 1) monitoring the duration between surfacing intervals through visual observations, or recorded surfacings by a satellite monitored radio tag (Kopelman and Sadove 1995; Lagerquist *et al.* 2000; Mate *et al.* 2000; Mate *et al.* 1998; Mate *et al.* 1999; Mate *et al.* 1997), or 2) monitoring the actual depth of the whale during each dive using a time depth recorder (TDR, (Baumgartner and Mate 2003; Croll *et al.* 2001; Croll *et al.* 2005). Visual observations and especially TDR data provide a wealth of information, but technical limitations (darkness, whale re-identification, suction cup attachment) usually limit them to periods of operation less than 12 hrs long during daylight hours. Most satellite monitored radio tags allow the monitoring of dive intervals 24 hrs/day for weeks or months at a time, but they are not able to provide any information on the depth to which the whale was diving. This study used a new type of satellite tag, capable of monitoring dive depths of whales for weeks and offering a unique look at the general diving behavior of whales over a previously unreachable timescale.

Methods

Five Argos monitored depth of dive tags were attached to blue whales off the California coast during August, 2004. The tags were deployed 1-3m forward of the dorsal fin, near the midline, from a 6.4m rigid hulled inflatable boat using the ARTS system, a modified line throwing gun using compressed air (Heide-

Jørgensen *et al.* 2001). The tags consisted of an Entran model pressure transducer, a Telonics controller board, ST-21 UHF radio transmitter and two Duracell 2/3A lithium batteries housed in an implantable stainless steel cylinder covered in part with a long dispersal anti-biotic coating. Further details about tag design and deployment can be found in (Mate *et al.* 2007).

Dives were monitored by a salt water conductivity switch. Any submergence longer than 7 s was recorded as a dive. The tags continuously recorded data from the pressure transducer during each dive. Dive data were summarized into four 6-h summary periods (period1 19:00 - 01:00, period2 01:00 - 07:00, period3 07:00 - 13:00, period4 13:00 - 19:00 all times local) and consisted of percent time spent in nine depth ranges (bins: 0-50 m, 50-100, 100-150, 150-200, 200-250, 250-300, 300-400, 400-500, 500+), the total number of dives (dive count), and the duration of the longest dive (max dive duration). Because dives were defined as submergences of longer than 7 s, the first 7 s of each dive was not included in the dive information, causing the depth bin values add up to less than 100%. Seven seconds was added to the 0-50 m bin for each dive recorded. The remaining difference in the total percent time recorded by the depth bins and 100% was reported as Percent Time at the Surface. Average Dive Depth per summary period was calculated as:

$$\text{Average Dive Depth} = \sum \text{bin}_i * (\text{percent time}_i / \text{total percent time})$$

for $i = 1-8$

Where ‘ bin_i ’ is the middle of depth bin_i , ‘percent time _{i} ’ is the percent time spent in depth bin_i , and total percent time is the sum of time spent in all depth ranges.

Tags transmitted data during four 1-h periods each day with one transmission period scheduled during each 6-h summary period. The transmission periods were scheduled to coincide with the most likely times a satellite was overhead. The salt water conductivity switch assured that the tags would only transmit when they were out of the water. Each transmission carried data for the previous three summary periods to reduce message error by redundancy and to account for missed transmissions during previous summary periods.

Locations were calculated by Service Argos from Doppler shift data when three or more messages reached a satellite. Water depths at each location were taken from the NOAA Geophysical Data Center digital bathymetry maps. A conservative swim speed was calculated as the minimum distance between two consecutive locations divided by the elapsed time between the locations. Locations were classified as one of two movement types (‘Transit’ or ‘Meander’) based on concepts explained by (Stern 2002). Transit move types have also been called “commuting” and “ranging” and tend to be more linear in nature. Meandering movement is often characterized as “foraging,” however, since we do not have direct evidence that this movement pattern is related to feeding activity, we refer to it more generally as “meandering.” Three conditions were used to determine the movement type of a location (i):

a) Change of squared displacement (dD/dm , (Turchin 1998) for the movement between locations i and $i+1$ was less than the 95th percentile of the distribution of dD/dm (59121 km^2)

b) Distance between location i and location $i+1$ was less than or equal to the upper 95% confidence interval of the mean move length (25.18 km)

c) Linearity between moves i and $i+2$ was less than 0.90. Linearity (l) was calculated as:

$$l = C/(A+B) \quad \text{where,}$$

A = Distance between location i and location $i+1$

B = Distance between location $i+1$ and location $i+2$

C = Distance between location i and location $i+2$

If the change in squared displacement (a) and the distance between locations (b) were true, or if all three conditions were true, the location was considered “meandering.”

Two mixed effects linear regressions were fit to the data using dive count or max dive duration as the response variable. Summary period, water depth, swim speed, and movement type were used as explanatory variables for both models. Each model included whale ID number to account for random effects between individuals and variation in the duration of tag operation. Variables were tested for significance using the extra sum of squares F test. Average dive depth could not be analyzed using mixed effects regression because of unequal variance between the summary periods even after transformation. A non-parametric Kruskal-Wallis test was therefore used to test for differences between individuals using untransformed data, and a Wilcoxon rank-sum test was then used to test for diel differences in average dive depth. A series of two sample t-tests were then used to test for differences between the two daytime periods, and differences

between the two night time periods as the variances were equivalent within the night and day time periods. A serial correlation coefficient was calculated to account for possible lack of independence in the data, and a Bonferroni correction was made to the confidence intervals to account for the multiple comparisons. A logistic regression was fit using Movement Type as the response and Average dive depth as an explanatory variable to test if movement type had any effect on the diving behavior. A binary Day/Night explanatory variable was also included to account for any observed diel variation.

To increase sample size for further analysis, data for the two longest running tags (10831 & 10833) were combined after a Kruskal-Wallis test showed no significant difference between the whales. Clustered data identified as meandering from four different latitude ranges (1: 33.5-35°, 2: 37.5-39°, 3: 42.8-43.5°, 4: 48.2-49.5° Figure 1) were compared using a series of one way ANOVAs and two sample t tests. Due to a limited sample size the data were combined from the four 6-h summary periods (two daytime and two nighttime) into two 12-h summary periods (Day: 07:00 – 19:00 and Night: 19:00 – 07:00 local time). Sample size for the northernmost cluster (Location 4) was too small for analysis (four daytime, three night time locations), so it was left out of the analysis, but included in the graphs for reference.

Results

The two whales tagged at the west end of the Channel Islands (ptt 10820 and 10825) remained in a localized area near the tagging location for the duration of the tag life (Figure 7). Two of the other three tagged whales (ptt 10831 and

10833), which were all tagged NW of the Farallon Islands, exhibited both transiting and meandering locations while ranging widely along the coast of California, Oregon, Washington, and Vancouver Island.

Tag duration was highly variable from 3-70 d with a mean of 28.6 d (Std Dev = 28.006). Tags transmitted for a total of 150 d, providing data for 414 summary periods and 249 locations. Two tags (ptt 10831 and 10833) accounted for 78 % of the total transmissions.

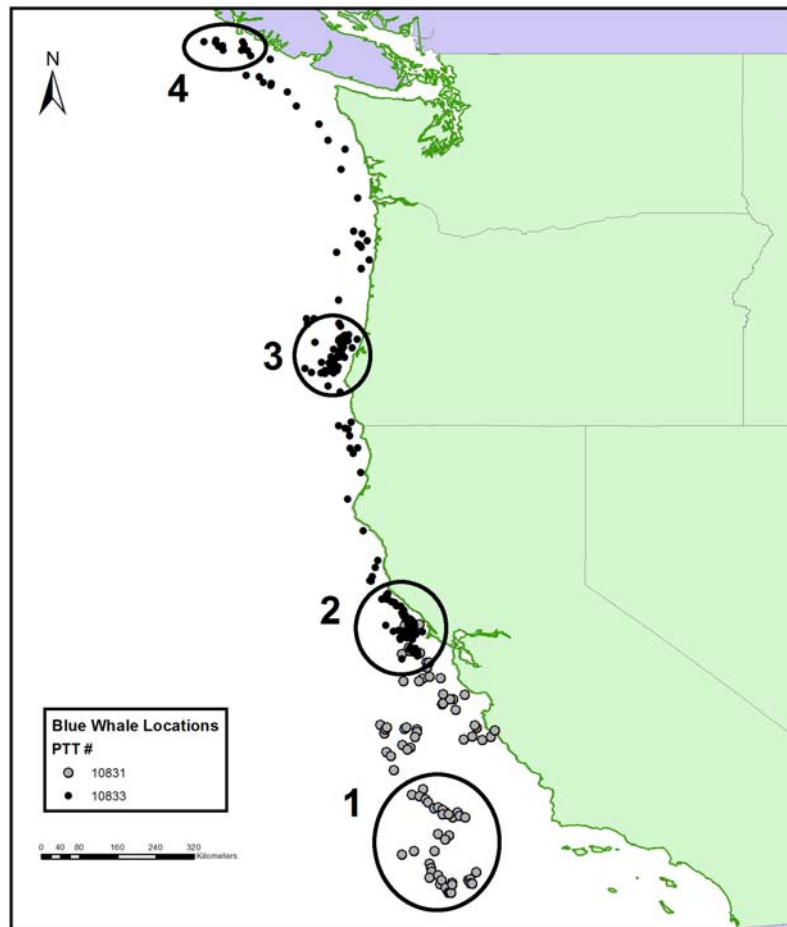


Figure 7: Tagged blue whale locations for whales tagged during the summer of 2004. Highlighted areas are clustered locations used in the analysis.

Whales spent at least 50% of their time during all summary periods in the top 50 m of the water column (Figure 8) and up to 94% of their time there at night (periods 1&2). Whales spent more time deeper in the water column during the day (periods 3&4) than at night. Dives below 200m were recorded during only seven

of 200 (4%) ‘Night’ periods, compared to 68 of 214 (32%) during ‘Day’ periods, including three records between 300 and 400 m.

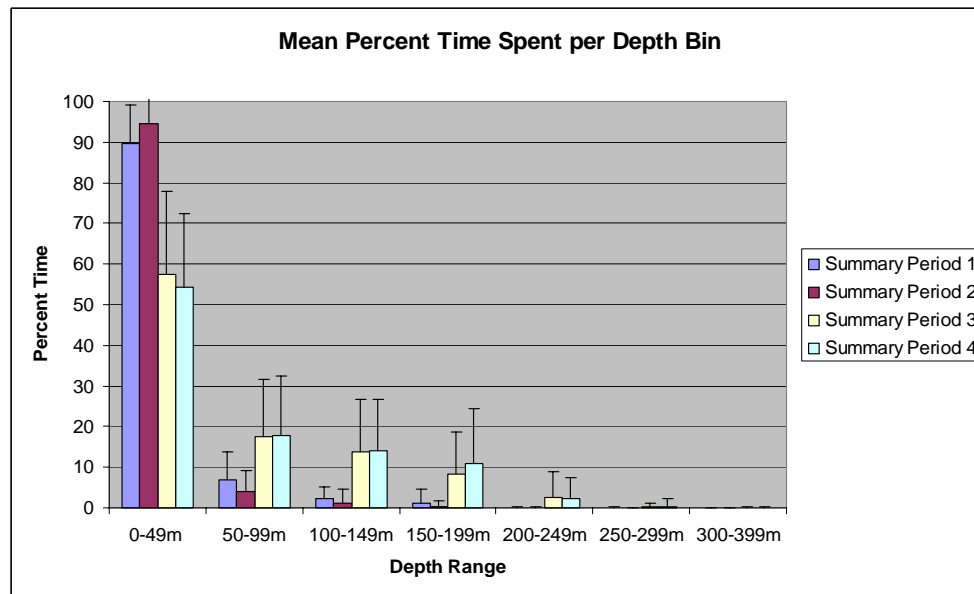


Figure 8: Average percent time spent in each depth bin by blue whales tagged off California during the summer of 2004 separated by summary period (1&2=Night, 3&4=Day).

No significant difference in average dive depth of individual whales was found ($p = 0.232$), so data from all whales were grouped together. The largest serial correlation coefficient of the grouped data was 0.23 (Summary period 1) indicating the data were relatively independent.

Average dive depth was deeper and much more variable during the day (Figures 9 & 10A; $p < 0.0001$) than at night. The median Average Dive Depth of Summary period 1 was significantly deeper than Summary period 2 ($p < 0.0001$). Summary period 3 was significantly deeper than Summary period 1 ($p < 0.0001$), but there was no significant difference between the median average dive depth of

Summary period 3 and Summary period 4 ($p = 0.27$).

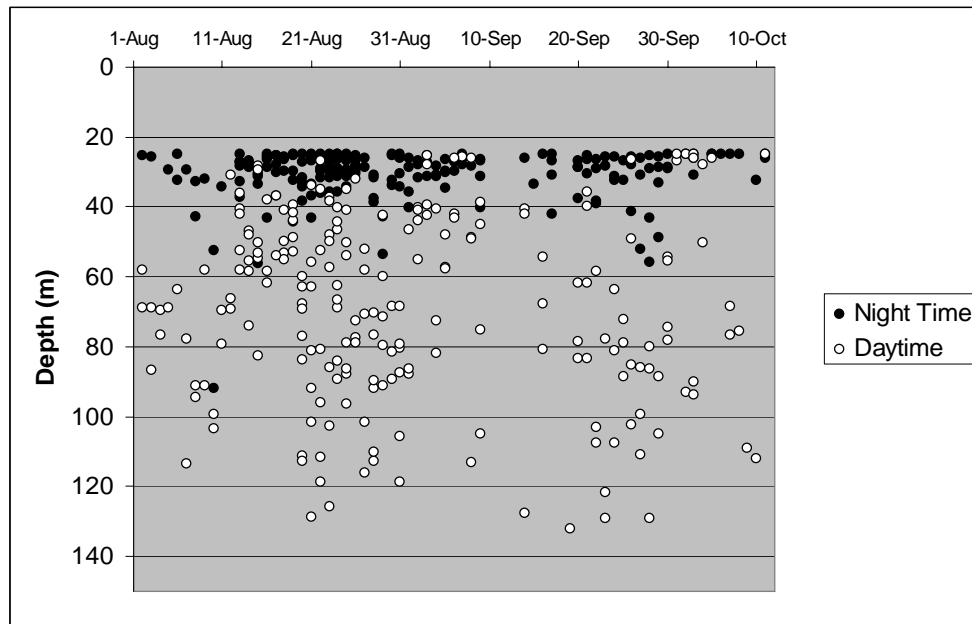


Figure 9: Average dive depth of all blue whales tagged off California in 2004 for all recorded summary periods. (25m minimum depth due to the Average dive depth calculation)

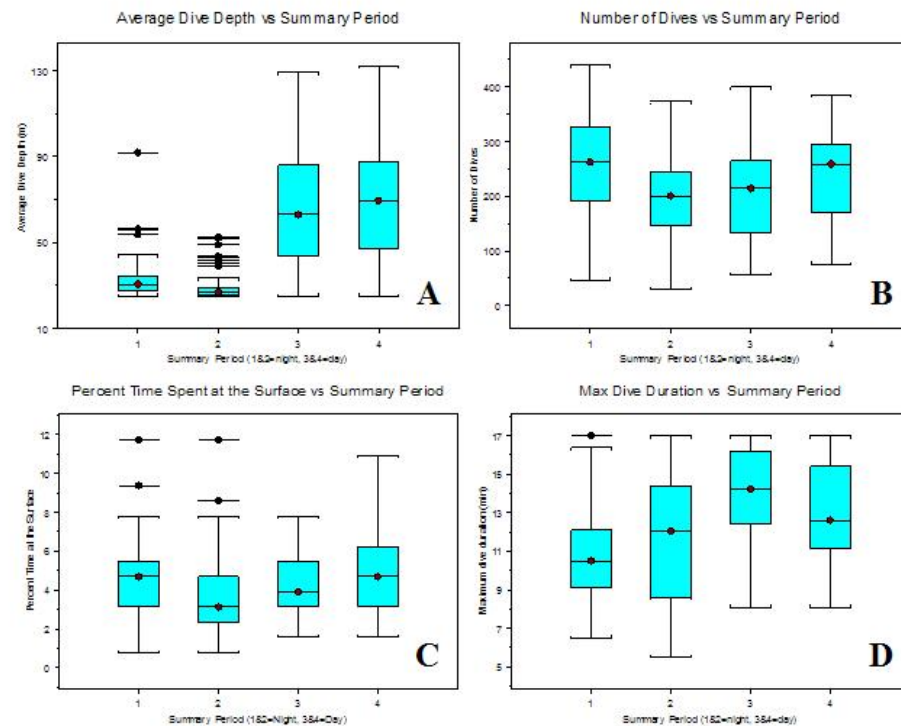


Figure 10: A) Average dive depth by summary period. B) Number of dives by summary period. C) Percent time spent at the surface by summary period. D) Maximum dive duration by summary period of blue whales tagged off California during the summer of 2004. Boxes are the first and third quartiles of the data. Whiskers are 1.5 * the inter-quartile distance or to the next closest point.

The logistic regression of movement type revealed no significant interaction between Average Dive Depth and Day/Night ($p = 0.174$), and also showed no effect of Average Dive Depth ($p = 0.127$) between transit or meandering location types.

The average number of dives made per period (dive count) was greatest during Summary period 1 ($\bar{x} = 248.91$, Figure 10B). Summary period 2 recorded the lowest average number of dives ($\bar{x} = 193.08$), with periods 3 and 4 each having more dives recorded than the previous period. A mixed effects linear

regression showed that Summary period, water depth, swim speed and movement type all had separate significant effects on the number of dives made in a summary period (Table 2). There were no significant interaction terms. Whales made 24.22 fewer dives in period 2 than in period 1 ($p = 0.0003$, 95% conf. -36.96- -11.48) and 7.51 fewer dives during summary period 3 ($p = 0.045$, 95% conf. -14.83- -0.20). Summary period 4 showed no significant difference from period 1 ($p = 0.398$). A 100 m increase in water depth resulted in a significant increase of 1.53 dives ($p = 0.0009$, 95% conf. 0.90-2.42) and a 1 km/h increase in swim speed resulted in a significant decrease of 5.01 dives ($p = 0.005$, 95% conf. -8.48- -1.55). Locations designated as transit reduced the number of dives by 12.84 ($p = 0.0105$, 95% conf. -22.60- -3.08).

Table 2: Mixed effects regression results for total number of dives

Model :

Fixed effects: divecount ~ Summary.period + Depth + Speed + Transit.meander

| | Value | Std.Error | DF | t-value | p-value |
|-----------------|--------|-----------|-----|---------|---------|
| (Intercept) | 270.1 | 14.03 | 239 | 19.2 | <.0001 |
| Summary.period2 | -24.2 | 6.55 | 239 | -3.70 | 0.0003 |
| Summary.period3 | -7.5 | 3.73 | 239 | -2.01 | 0.0453 |
| Summary.period4 | 2.1 | 2.52 | 239 | 0.85 | 0.3976 |
| Depth | 0.015 | 0.0045 | 239 | 3.38 | 0.0009 |
| Speed | -5.013 | 1.77 | 239 | -2.83 | 0.0050 |
| Transit.meander | -12.84 | 4.99 | 239 | -2.58 | 0.0105 |

Average percent time spent at the surface was highest during summary period 4 ($\bar{x} = 4.95$, Figure 10C), and lowest during summary period 2 ($\bar{x} = 3.55$). The number of dives made during a summary period was very strongly

correlated to percent time spent at the surface ($\text{cor} = 0.650$, $p < 0.0001$ from a Spearman's correlation test). For the remainder of this paper, the number of dives will be used to describe both variables.

The mean maximum dive duration was lowest during Summary period 1 (10.88 min, Figure 10D) and reached a maximum during Summary period 3 (14.11 min). Summary period was again strongly significant in the regression equation ($p < 0.0001$), while water depth and movement type had no significant effect ($p = 0.584$ and $p = 0.429$ respectively). Swim speed was modestly linked to maximum dive duration ($p = 0.0357$). As with Dive Count, there were no significant interaction terms. Three of the four summary periods had separate significant effects on max dive duration. Summary period 2 had no significant effect after accounting for Summary period 1 ($p = 0.390$) meaning the maximum dive duration during the night was constant. Maximum Dive Duration during period 3 showed a significant increase of 1.10 min ($p < 0.0001$, 95% conf 0.85-1.36) over period 1, and period 4 was 0.26 min longer ($p = 0.0030$, 95% conf 0.090-0.43). A 1 km/h increase in swim speed resulted in an increase of 0.13 min ($p = 0.0357$, 95% conf. 0.0092-0.25) after accounting for Summary period. Maximum dive duration was correlated to Average dive depth ($\text{cor} = 0.631$, $p < 0.0001$ from a Spearman's correlation test).

Significant diel variations in average dive depth ($p < 0.01$) were present at all latitude ranges (Figure 11A). No significant difference in night time average dive depths was observed at any of the locations ($p = 0.22$ from a one way ANOVA) with a mean value of 30.7 m. Mean daytime average dive depth at

locations 1 and 2 were equal ($\bar{x} = 71.8$ m, $p = 0.41$), while location 3 recorded significantly deeper daytime dives ($\bar{x} = 90.5$, $p = 0.0034$).

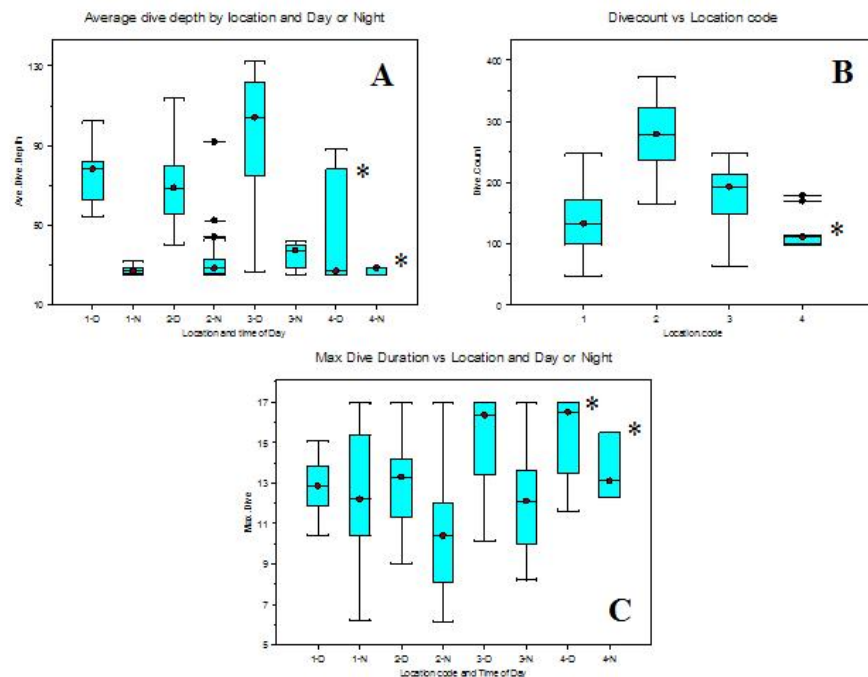


Figure 11: A) Average dive depth vs location. B) Dive count by location. C) : Maximum dive duration by location (1: 30-35° (33.5-35°), 2: 35-40° (37.5-39°), 3: 40-45° (42.8-43.5°), 4: 45-50° (48.2-49.5°), 'D' = Daytime, 'N' = Night) for blue whales tagged off California during the summer of 2004. Boxes are the first and third quartiles of the data. Whiskers are 1.5 * the inter-quartile distance or to the next closest point.

There was no significant diel effect on the number of dives at any of the latitude ranges ($p = 0.518$ from a one way ANOVA). Location 2 recorded more dives than all other locations ($\bar{x} = 277$, Figure 11B). Mean number of dives at

Location 3 (187) was less than Location 2 but greater than Location 1 (136).

Differences in number of dives at all locations were significant ($p < 0.0001$, from a one way ANOVA).

Significant diel variation in maximum dive duration was observed at Locations 2 and 3 ($p < 0.0001$), but not Location 1. (Figure 11C). There was no significant difference between daytime maximum dive durations at Locations 1 and 2 ($\bar{x} = 13.0$ min, $p = 0.62$), but Location 3 recorded significantly longer daytime maximum dive durations than the two southerly locations ($\bar{x} = 15.3$ min, $p = 0.0005$). Night time maximum dive durations were significantly shorter for Location 2 ($\bar{x} = 10.5$ min, $p = 0.012$) than Locations 1 ($\bar{x} = 12.6$ min) and 3 ($\bar{x} = 12.1$ min)

Discussion

This study represents only the second time satellite-telemetered information on the dive depths of blue whales has been collected (Lagerquist *et al.* 2000), and is by far the largest data set in terms of number of days transmitting, locations received, and summary periods reported. The large number of summary periods reported allows for robust statistical analysis, however, because the data came from only five individuals, with two individuals accounting for 78% of the total days of transmission, any inferences must be made with caution.

The overall time at depth distribution was strongly skewed to the shallow depth ranges. This is likely the result of non-feeding activity and short duration recovery dives which occur close to the surface (Croll *et al.* 2001), as well as

surface feeding activity. The comparatively large amount of time spent at shallow depth is in agreement with the literature. Lagerquist *et al.* (2000) reported that 75% of all dives by a satellite-tagged blue whale were less than or equal to 16 m deep, and Croll *et al.* (2001) reported blue whales diving with suction cup attached TDR's to an average of 67.6 m during non-foraging dives. Recovery time between foraging dives for both blue and fin whales has also been shown to increase with number of lunges (Acevedo-Gutierrez *et al.* 2002) and is expected to increase with increased dive duration (Houston and Carbone 1992; Kramer 1988) which would also contribute to increased time spent near the surface.

Daytime average dive depth was much greater, and showed a much larger variance than average dive depth during night summary periods. The primary prey of blue whales off California are *Euphausia pacifica* & *Thysanoessa spinifera* (Fiedler *et al.* 1998; Yochem and Leatherwood 1985). Both species undergo significant diel vertical migrations, moving to the surface at night from typical daytime depths of 200-400 m at the shelf edge for *E. pacifica*, and 50-150 m on the shelf for *T. spinifera* (Brinton 1967; 1981). The increase in daytime average dive depth is likely the result of blue whales following the vertical migrations of their prey. The small variance of night time data suggests the whales were almost never diving deeply at night. Either they were not feeding, or, more likely, they were feeding very close to the surface. The high variance in daytime average dive depth most likely resulted from the data encompassing the shallower, non-foraging dives mentioned earlier, as well as deeper foraging dives.

Studies have reported large euphausiid concentrations typically occurring at depths exceeding 100m (Croll *et al.* 2005; Croll *et al.* 1998; Sardou *et al.* 1996), (Croll *et al.* 2001), using suction cup attached TDR's, reported blue whales diving to an average of 140m during foraging dives, and 113m overall, and (Lagerquist *et al.* 2000) reported a blue whale diving to an average of 105m for all dives > 16m. These values are much greater than the calculated average dive depths of this study. However, if recovery dives and other shallow dives are excluded by removing the 0-50 m bin from the average dive depth calculation, the daytime dive depths are close to the overall dive depths reported (\bar{x} = 117.2 m, SD = 33.4, \bar{x} = 120.4 m, SD = 34.2 for summary periods 3 & 4 respectively).

Energetic models predict a positive relationship between dive duration and dive depth (Houston and Carbone 1992; Kramer 1988), which was observed in the correlation between maximum dive duration and average dive depth. Average daytime maximum dive durations (14.12 & 13.08 min) were very close to values reported by Croll *et al.* (2001) (14.7 min) and Lagerquist *et al.* (2000) (10-18min) and similar to other values reported in the literature (16.4-26.9 min, Donovan 1984 and Strong 1990). Average nightly maximum dive durations were much lower than most of the literature values (10.86 & 11.97 min), however it is likely that most of the literature values were collected primarily during the day as the primary data collection methods were either visual observations or short duration (3 – 4 hr max) suction cup attached tags. Lagerquist *et al.* (2000) reported three of four tagged whales recorded no dives longer than 10 minutes during at least half

of the summary periods. The fourth whale had maximum durations as short as 10 min which would agree with the observed data. The maximum possible duration that could be recorded for our study was 17.5 minutes. This value was recorded 54 times (out of 414 summary periods), with 62% of the maximum values recorded during the day and 58% recorded during 'meandering' location types. The large number of maximum dive durations exceeding the threshold value leaves open the possibility that the whales were making dives approaching their theoretical aerobic dive limit of 31.2 min (as defined by Croll *et al.* 2001).

Surface time has been used to approximate the energetic costs of dives (Acevedo-Gutierrez *et al.* 2002). The nature of blue whale surfacing behavior, typically one breath per surfacing, allows the total number of dives to be used to approximate surface time, and therefore, to also be used as an estimate of diving energetics. The strong correlation we found between percent time at the surface and total number of dives supports this idea.

The range of average total number of dives per summary period observed in this study (193 – 245) is in very close agreement to literature values (83-128 per three hour period, Lagerquist *et al.* 2000). Most dives were recorded during the first night period, with significantly fewer dives being made during the second night period, then progressively more during each of the daytime periods. The number of dives made during the two daylight summary periods (3&4) appears to be inversely related to the maximum dive duration. As dive duration increased, fewer dives could be made during each summary period. The significant decline in number of dives made between the first and second summary periods was not

similarly reflected in maximum dive duration. Acevedo-Gutierrez *et al.* (2002) showed that surface time (and therefore number of dives made) is related to the number of lunges made during foraging, therefore, it would appear that the reduction in number of dives between the first and second summary periods is due to a reduction in the number of lunges being made. This implies that the whales were either not making typical foraging lunges or not foraging for all or part of the second summary period.

It seems unlikely that blue whales would not feed when their prey is most accessible, close to the surface, however a study of *E. pacifica* in an inlet off British Columbia showed the euphausiids were more dispersed after migrating to shallower water at night (DeRobertis 2002). Since the major energetic cost of foraging for a blue whale is in the lunge/engulfing of prey, rather than the dive to reach a prey concentration (Acevedo-Gutierrez *et al.* 2002), it is possible that a decrease in prey density during the second summary period, would cause a whale to modify its foraging technique to a less energetically costly method. Another study showed that the timing of the downward migration of *E. pacifica* is related to food satiation, rather than a specific time of the morning (Nakagawa *et al.* 2003). This means that prey would be spread throughout the water column during the second half of the night, rather than in the upper 50 m because of the differing times to satiation of individuals. Prey would be very diffuse compared to all other times of the day, and, in such a case, it may be more energetically efficient for whales to rest, or socialize, rather than forage.

The ‘movement type’ classification attempts to distinguish between potential foraging behavior, and movement between food patches. Fewer dives were recorded during ‘Transit’ locations, implying that the energetic cost of transit behavior is lower than that of meandering behavior. This was emphasized by the observed decrease in the number of dives as swim speed increased. Higher swim speeds have been reported during migratory behavior in blue whales (Mate *et al.* 1999). Studies have shown that the energetic cost of foraging is much greater than the cost of traveling (Acevedo-Gutierrez *et al.* 2002), which suggests that foraging was occurring during the ‘meandering’ movement types. The lack of a significant difference in daytime average dive depth between ‘meandering’ and ‘transit’ location types suggests the whales were diving to similar depths during both movement types, but the reduction in total dives during transit locations suggests they were not expending as much energy. Acevedo-Gutierrez found that the energetic costs of single lunge foraging dives were similar to that of non-foraging dives, and hypothesized that single lunge dives may represent exploratory dives to assess prey concentration. One possible interpretation of the results, therefore, is that the whales were searching for food while traveling by diving to depths where euphausiids aggregate. It is also a possibility that the whales gain a hydrodynamic advantage by diving to a certain depth while traveling, allowing them to spend less energy.

The variance in daytime average dive depth by latitude is most likely explained by variation in the depth of prey aggregation at the different locations. Historic ranges of both *T. spinifera* and *E. pacificus* are known to include all

locations (Brinton 1981), but it is possible that the increased average dive depth at location 3 could represent a foraging focus on the deeper dwelling *E pacificus* at that location. Maximum dive duration by latitude showed the strong correlation to average dive depth described earlier except for a lack of a diel difference at location 1.

The results of this study indicate that tagged blue whales employed two distinct dive strategies and likely foraging strategies depending on the time of day. Long duration dives with long recovery periods were made during the day when prey is known to be deep in the water column, which would maximize their time in the prey field after expending the energy to reach it. Shorter dives were made at night, when prey is known to be near the surface and easily accessible. Whales appeared to change their foraging behavior during the second half of the night, either using a less energetically costly method, or not foraging at all. Differences in diving behavior between transit and meandering movement types also suggest distinct diving strategies which minimize the energetic cost of each movement type.

Summary

The whales tagged in this study heavily used the waters over the continental slope from the Channel Islands, CA to Cape Blanco, OR. Some whales made offshore excursions while on the feeding grounds, however most locations in deep water occurred during the southerly migration. Tagged whales generally moved north as the feeding season progressed, suggesting the whales were seeking out productive areas as prey density varied during the feeding

season. The areas where tagged whales spent the most time were characterized by decreased sea surface temperature and elevated surface chlorophyll-a levels indicating regions where nutrient rich, upwelled water was advected off the slope edge.

Tagged whales appeared to forage during all daylight hours and the first half of the night. Daytime dives were much deeper than night time dives, mimicking the diel vertical migration of their prey. During the night, the whales appeared to switch from normal lunge feeding behavior to a less energetically demanding behavior that may or may not include foraging. Differences in diving behavior between transit and meandering movement types suggest distinct diving strategies which minimize the energetic cost of each movement type. Whales appeared to make exploratory dives to foraging depths while transiting from one location to another.

The information presented in this study greatly expands the existing knowledge of blue whale habitat and diving behavior and how it may change during the course of the feeding season. This is valuable information for wildlife management officials to use as they attempt to identify critical habitat, and make accurate population surveys to aid the recovery of this endangered species.

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