



ELSEVIER

Deep-Sea Research II ■ (■■■■) ■■■-■■■

DEEP-SEA RESEARCH  
PART II

www.elsevier.com/locate/dsr2

# Sea-surface temperature gradients across blue whale and sea turtle foraging trajectories off the Baja California Peninsula, Mexico

Peter Etnoyer<sup>a,\*</sup>, David Canny<sup>b</sup>, Bruce R. Mate<sup>c</sup>, Lance E. Morgan<sup>d</sup>,  
Joel G. Ortega-Ortiz<sup>c</sup>, Wallace J. Nichols<sup>c</sup>

<sup>a</sup>Aquanautix Consulting, 3777 Griffith View Dr., LA, CA 90039, USA

<sup>b</sup>National Marine Protected Areas Center Science Institute, 99 Pacific Street, Suite 100-F, Monterey, CA 93940, USA

<sup>c</sup>Department of Fisheries and Wildlife, Oregon State University, Hatfield Marine Science Center, Newport, OR 97365, USA

<sup>d</sup>Marine Conservation Biology Institute, 14301 Arnold Dr. Suite 25, Glen Ellen, CA 95442, USA

<sup>e</sup>Department of Herpetology, California Academy of Sciences, 875 Howard Street, San Francisco, CA 94103, USA

Received 15 March 2005; accepted 5 January 2006

## Abstract

Sea-surface temperature (SST) fronts are integral to pelagic ecology in the North Pacific Ocean, so it is necessary to understand their character and distribution, and the way these features influence the behavior of endangered and highly migratory species. Here, telemetry data from sixteen satellite-tagged blue whales (*Balaenoptera musculus*) and sea turtles (*Caretta caretta*, *Chelonia mydas*, and *Lepidochelys olivacea*) are employed to characterize 'biologically relevant' SST fronts off Baja California Sur. High residence times are used to identify presumed foraging areas, and SST gradients are calculated across advanced very high resolution radiometer (AVHRR) images of these regions. The resulting values are compared to classic definitions of SST fronts in the oceanographic literature.

We find subtle changes in surface temperature (between 0.01 and 0.10 °C/km) across the foraging trajectories, near the lowest end of the oceanographic scale (between 0.03 and 0.3 °C/km), suggesting that edge-detection algorithms using gradient thresholds > 0.10 °C/km may overlook pelagic habitats in tropical waters. We use this information to sensitize our edge-detection algorithm, and to identify persistent concentrations of subtle SST fronts in the Northeast Pacific Ocean between 2002 and 2004. The lower-gradient threshold increases the number of fronts detected, revealing more potential habitats in different places than we find with a higher-gradient threshold. This is the expected result, but it confirms that pelagic habitat can be overlooked, and that the temperature gradient parameter is an important one.

© 2006 Elsevier Ltd. All rights reserved.

**Keywords:** Oceanic fronts; Blue whales; Sea turtles; Northeast Pacific; Remote sensing; Temperature gradients

## 1. Introduction

Sea-surface temperature (SST) frontal features can be used to define pelagic habitat (Laurs et al., 1984; Podesta et al., 1993; Block et al., 2003), to

\*Corresponding author.

E-mail address: peter@aquanautix.com (P. Etnoyer).

identify biological hotspots (Worm et al., 2003), to discern migration corridors (Polovina et al., 2000), and to set marine conservation priorities (Yen et al., 2003; Etnoyer et al., 2004), but one outstanding problem for marine biologists is that the classic definitions of a front originate in physical oceanography. In oceanography, fronts are an interface between two dissimilar water masses, often characterized by a steep temperature gradient. High biological productivity is attributed to these features, due to density-driven aggregation, and increased vertical flux resulting in high primary and secondary production (Owen, 1981; Roughgarden et al., 1988; Franks, 1992; Olson et al., 1994; Bakun, 1996; Genin et al., 2005). However, we still have an incomplete understanding of the way marine species define their own ‘biologically relevant’ temperature gradients and some fundamental questions remain unanswered. For example, what sort of SST front is likely to be important to whales and turtles? How do SST fronts for whales and turtles compare to oceanographic definitions of a temperature front? Temperature gradients are important parameters in analyses of SST data because this parameter *defines* a frontal feature in an edge-detection algorithm. Gradient values less than this threshold may be overlooked, so the threshold value must be carefully considered.

In this study, we utilize transmission coordinates from satellite-tagged animals and satellite-derived SST data in a marine geographic information system (GIS) to calculate temperature gradients across the trajectories of 16 whales and sea turtles off the Baja California (BC) Peninsula (Fig. 1) between 1995 and 2002. We consider these gradients against a background of regional surface temperatures, chlorophyll, and upwelling conditions during times in which whales and sea turtles actively forage offshore, and we compare these gradients to descriptions of SST fronts in the oceanographic literature.

Our satellite surveys examine the character and distribution of temperature gradients in the Northeast Pacific at two extents. A regional extent (15–35N, 105–125W; Fig. 1) uses animal tracks with 9 km Advanced Very High Resolution Radiometer (AVHRR) SST to determine the character of fronts near foraging animals. A continental extent (12–72N, 90–180W; Fig. 6) uses 18 km interpolated multi-channel SST (MCSST) values to examine the distribution of these fronts in the Northeast Pacific.

Waters off BC Sur have long been known as a hotspot for commercial fisheries (McHugh, 1952; Alverson, 1960; Sosa-Nishizaki and Shimizu, 1991; Squire and Suzuki, 1991), and a region of complex meander and eddy formation for oceanographers (Griffiths, 1965; Legeckis, 1978). Large concentrations of SST fronts persist offshore BC Sur in both phases of the El Niño/La Niña Southern Oscillation, a quality shared with less than 1% of the Northeast Pacific Ocean (Etnoyer et al., 2004). Yet, the origin, character, and contents of these frontal features remain almost completely unknown. Satellite-tagged animals have been shown to meander along frontal features in the region for prolonged periods of time, including blue whales *Balaenoptera musculus* and several species of sea turtles. These animals are presumably foraging, so the region provides a good opportunity to study the interactions between marine species and oceanographic features.

## 2. Background

### 2.1. Classic definitions of frontal features

Japanese oceanographer Kitahara first proposed the principle of fish assemblage along lines of convergence in 1918 (Uda, 1959). Since that time, many researchers have described the regions of convergence and divergence, floating objects, plankton, and abundant sealife that characterize *siome*, or rip-currents, along the swift fluid boundaries between different water masses we know as a front. Uda (1938) described *siome* with rates of change in temperature between 0.5 and 0.05 °C/km in high-latitude temperate waters of the Kuroshio Current off Japan. Kuroshio gradients are remarkable, and extreme, so this definition is broad. More recently, Fedorov (1986) defined a frontal zone and a frontal interface or *front* as one and two orders of magnitude over background conditions (e.g., mean meridional temperature), respectively. In the Northeast Pacific, for example, the mean meridional temperature is 0.003 °C/km (Fedorov, 1986), so technically, a frontal zone is 0.03 °C/km and a frontal interface or *front* is 0.3 °C/km by this definition. Subtler fronts are on record. The Ensenada Front off BC Peninsula exhibits a 0.36 °C/km maximum gradient, with 99% of values less than 0.22 °C/km (Haury et al., 1993). We follow Fedorov’s terminology when gradient information is available, but use the term *frontal feature* when

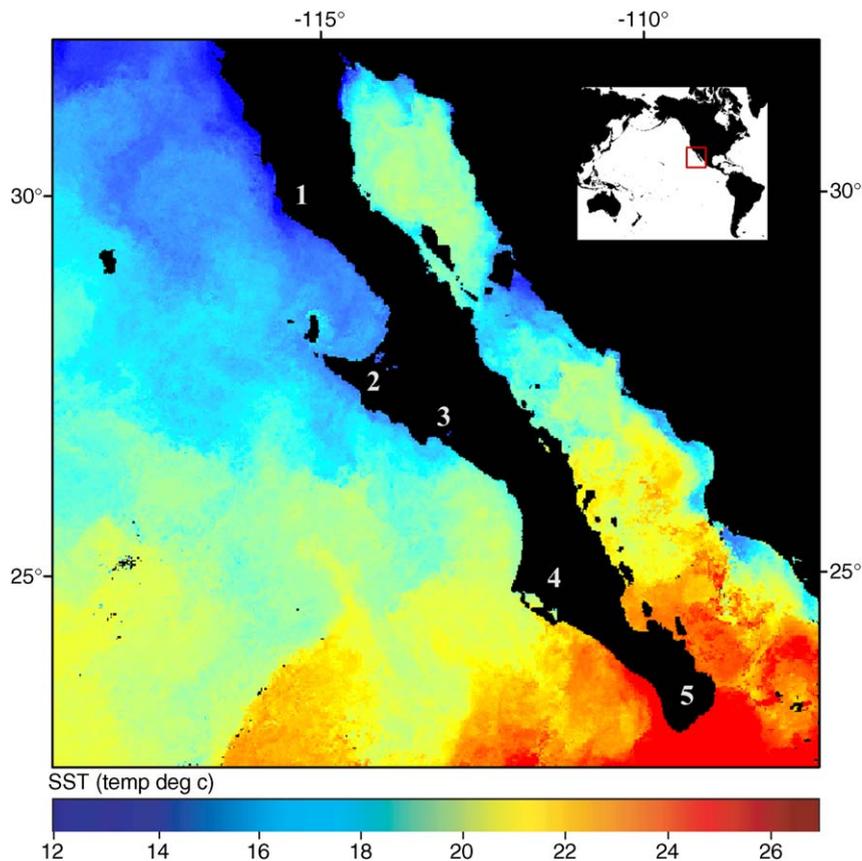


Fig. 1. Sea-surface temperature from November 2000 is shown here off the Baja California Peninsula in 2.5 km resolution Coastwatch data from NOAA Pacific Marine Environmental Laboratory. Numbers indicate places mentioned in the text: (1) Punta San Antonio, (2) Punta Eugenia, (3) Bahia de Ballenas (to the west) and Laguna San Ignacio (to the south), (4) Magdalena Bay, and (5) Cabo San Lucas.

gradients are less than these definitions, or no gradient information is available.

## 2.2. Satellite definitions of frontal features

The first global satellite survey of temperature fronts used very high resolution radar (VHRR) to identify 22 globally significant regions of frontogenesis using qualitative visual interpretations (Legeckis, 1978), but more quantitative approaches have developed along with recent advances in satellite and computer technology. Many interpretations of SST fronts are based on the relative intensity of gradients across a broad spatial extent. Histograms of gradients in the North Atlantic Gulf Stream from Advanced Very High Resolution Radar (AVHRR) show most gradient values fall between 0.1 and 0.3 °C/km (Ullman and Cornillon, 1999) and most gradients across swordfish landings are higher than 0.5 °C/km (Podesta et al., 1993).

Other recent interpretations of frontal features in Pacific waters were also relative, based on the highest 10% of slope values. These found recognizable gradients off the BC Peninsula an order of magnitude finer than many definitions, near 0.02 °C/km. (Etnoyer et al., 2004). None of these studies used animals to define a gradient biologically, and this must be done in order to determine whether physical oceanographic definitions of a significant gradient can be used to identify biological ‘hotspots’ in satellite derived data products.

Physical oceanographers traditionally map temperature gradients at intermediate spatial scales (100–1000 km) using shipborne continuous underway recorders (e.g., Fedorov, 1986; Yoder et al., 1994; Archer et al., 1997), but satellite-derived SST products permit near global analyses at resolutions of 18, 9, and lately, 4 km. However, the quality of these data products varies. Low resolution obscures the finescale structure of thermohaline gradients

(Fedorov, 1986), and much of the world remains obscured by cloud cover. Algorithms can be employed to mask clouds or to interpolate cloud covered temperature values with time-averaged data and in-situ measurements from ships and buoys (see Ullman and Cornillon, 1999). However, in-situ temperature recordings are critical to our best understanding of oceanic gradients.

Recently, biologists have proposed that marine animals be employed to supplement and calibrate satellite data (see Block et al., 2003; Polovina, 2006) but only some marine species known to aggregate along frontal features breach the surface often enough to transmit accurate ( $\pm 1$  km) daily geositions (e.g., whales and turtles). Other species (e.g., fishes) can be tracked using pop-up tags that archive oceanographic conditions until their tags release. These species are slightly less useful for interpreting surface temperature values, because they run deep and their coordinates are only accurate within 100 km. Geositions are calculated retroactively, using temperature values to estimate latitude and light attenuation values to estimate longitude (Block et al., 2001; Teo et al., 2004). Therefore, satellite telemetry data from whales and sea turtles provide the best available opportunity to characterize biologically relevant temperature gradients off the BC Peninsula.

### 2.3. Oceanographic setting

The waters off BC Sur were first described as an Eastern Pacific Subtropical Front (EPSF) with complex meanders and eddies extending westward off the coast of Baja California (Legeckis, 1978). The extent of the EPSF was defined as 20–50N, 105–135W, but these coordinates bound a region that is very dynamic and broad. The southern part of the EPSF was called the California Current—Eastern Tropical Pacific transition zone (Brinton, 1979) and the Baja California Frontal System (Etnoyer et al., 2004) but no less than five different water masses and half a dozen subfeatures persist within these lower latitudes. The transition zone south of 25N is a major feeding and growth area in the North Pacific (Squire and Au, 1990) but relative to others, the dynamics of this frontal region are still poorly understood.

This is a zone of abrupt transition with intense seasonal upwelling (Walsh et al., 1974) and sharp gradients in temperature, salinity, dissolved oxygen, nutrients, and plankton biomass. This is also the

northernmost extent of a shallow oxygen-minimum layer ( $<0.25$  ml/l) in the Eastern Tropical Pacific and a biogeographic boundary between maximum densities of the northern *Euphausia eximia* southern *E. distinguenda* species of krill (Brinton, 1979). Strong subsurface gradients in salinity and temperature fields also are known to occur between 23 and 25N (Blanton and Pattullo, 1970).

Near Magdalena Bay and Cabo San Lucas, researchers describe exceptional surface temperature anomalies (Reid et al., 1958; Lynn, 1980), coupled with swift geostrophic flows (Bailey et al., 1982), ‘indistinguishable’ onshore and offshore flows (Hickey, 1979), and remarkable 13-year ranges in temperature and salinity 120–180 km offshore (Lynn, 1980). The region has been called a “persistent pelagic habitat” and a “hotspot” for black marlin, swordfish and blue whales, based on exceptional billfish landings (Sosa-Nishizaki and Shimizu, 1991; Squire and Suzuki, 1990), long residence times for whales, and a persistent concentration of SST frontal features (Etnoyer et al., 2004). Longhurst (2004) suggested the red crab *Pleuroncodes planipes* was at the root of this productivity because they are abundant in filaments of upwelled water that reach as far as 1000 km offshore.

### 2.4. Sea turtles off Baja California Sur

Baja California waters provide foraging habitat for all five of the sea turtle species found in the Pacific basin. Two species, the leatherback *Dermochelys coriacea* and the olive ridley *Lepidochelys olivacea*, nest regularly on Baja California beaches. Yet, the green turtle *Chelonia mydas* and the loggerhead turtles *Caretta caretta* are the most common species of sea turtle in the region (Nichols, 2003). Loggerhead turtles are rare in the NE Pacific except near the BC coast (Olson et al., 2001). Along the BC Peninsula, most turtles are found between the Vizcaino Peninsula and the southern end of Bahía Magdalena.

The surveys here focused primarily on the offshore regions between Punta Abreojos and Bahía Magdalena. These waters are considered foraging grounds for green turtles because the closest nesting grounds are remote, 1500-km to the south on the Mexican mainland (Nichols, 2003). These are also considered foraging grounds for loggerhead turtles. There is no loggerhead turtle nesting activity known in the eastern Pacific Ocean.

Five turtle species off BC Peninsula are listed as endangered on the IUCN Redlist of Threatened Species. If foraging habitat can be mapped using satellites we could limit some impacts to sea turtle populations, but we must also understand turtle diet and prey. Olive ridley turtles and loggerhead turtles off BC are thought to feed primarily, if not exclusively, on *Pleuroncodes planipes*, a.k.a red crabs, tuna crabs, or “langostilla” (Marquez, 1990; Villanueva, 1991; Peckham and Nichols, 2003). Stomach content samples of stranded or incidentally captured loggerhead turtles from offshore of Bahía Magdalena contained only red crabs, except for one stomach, which contained a fragment of *Callinectes* sp. (Nichols, 2003). Green turtles are also known to feed on *P. planipes*, but less so during the benthic stage, when they are thought to be primarily herbivorous, consuming sea grasses and algae. Food items for green turtles vary among feeding grounds, and include a variety of marine animals (Mendilaharsu et al., 2005). Molluscs, crustaceans, sponges, jellyfishes and echinoderms are among the known prey (Marquez, 1990). All the turtle tracks analyzed here, including the pelagic-stage green turtle, are therefore assumed to represent foraging trajectories.

### 2.5. Blue whales off Baja California Sur

Two new blue whale tracks are presented, and four others are reintroduced in a new context. The new tracks (1910831 and 200840) are from blue whales satellite tagged in the Gulf of California in 2001 and 2002. Their migration pattern differs markedly from southbound blue whales tagged off Southern California (see Mate et al., 1999). Thorough reviews of the Northeast Pacific leviathan migration patterns are available elsewhere (see Fiedler et al., 1998; Mate et al., 1999; Burtenshaw et al., 2004), but these studies focus mostly on blue whale behaviors in subtropical waters. Etnoyer et al. (2004) describe blue whale behavior off the BC Peninsula specifically, noting long residence periods along clearly discernable frontal features.

Blue whales migrate in relatively low densities. Their calving grounds remain unknown. Eastern Pacific aggregations are known to occur in the Gulf of Alaska, Channel Islands, both sides of the BC Peninsula, and the Costa Rica Dome (Reilly and Thayer, 1990). In the Channel Islands, blue whales concentrate their feeding on swarms of euphausiids (*Thysannoessa spinifera* and *Euphausia pacifica*),

demonstrating preferences for specific taxa (*T. spinifera*) (Fiedler et al., 1998; Schoenherr, 1991). Blue whales have been observed feeding on euphausiids *Nyctiphanes simplex* in the Gulf of California (Gendron, 1992) and red crabs offshore (P. Colla, pers. comm), but there is some debate whether *P. planipes* reaches abundance levels that could sustain foraging blue whales, like they sustain turtles (Marquez, 1990; Peckham and Nichols, 2003) and yellowfin tuna (Alverson, 1960). Anecdotal evidence shows them feeding on red crabs and subsequently excreting red colored material (B. R. Mate, pers. obs.), but the blue whales are thought to persist on krill. The mysticete gray whale *Eschrichtius robustus* has also been observed feeding on red crabs in the region (F. Ollervides, pers. comm.).

We assume that high residence times (>10 days within 100-km radius) represent foraging periods for blue whales, and we overlay their telemetry on AVHRR data, generating 250-km transects across presumed foraging trajectories in order to calculate ‘biologically relevant temperature gradients’ off Baja California Sur. We compare these gradients to classical definitions from physical oceanographers to better calibrate and better understand our edge detection algorithm. Then, we employ those values in the frontal density technique, and identify persistent concentrations of biologically relevant SST fronts in the Northeast Pacific 2002–2004 using a sensitive edge detection model. We compare the outcome with a less sensitive model.

## 3. Materials and methods

### 3.1. Materials

#### 3.1.1. Satellite tags on sea turtles

Researchers and fishermen from Grupo Tortuguero attached instruments to 23 sea turtles along the BC Peninsula between 1996 and 2001. Ten of these crossed or meandered within the EPSF region. Model ST-3 backpack transmitters manufactured by Telonics, Inc. (Mesa, AZ, USA) were attached to the second vertebral scute (counting from the anterior) of each turtle’s carapace using a modified version of the attachment technique described by Balazs et al. (1995), substituting a thin layer (<1 cm) of tinted two-part marine epoxy (Marine-Tex; Montgomeryville, PA, USA) for Silicone Elastomer. Epoxy also was used to create a small faring on the leading and trailing edges of the transmitter to reduce drag (Watson and Granger,

1998). The transmitter was programmed with a duty cycle of 6 h on, 6 h off. Tags transmit ultra-high frequency (UHF) radio signals (401.650 MHz) to Argos receivers on National Oceanic and Atmospheric Administration (NOAA) Television Infra-Red Observation Satellite (TIROS)-N weather satellites in sun-synchronous polar orbits.

All turtle data were subset to select fields for the best single transmission per day (to normalize transmission effort), nearest to mid-morning (when more than one high-quality record was available), in order to create daily records. Almost all categories of LCs (A, B, 0, 1, 2 and 3, but not Z) were included in the analysis. LCs of 1 or greater have known error factors of <1 km and accuracy increases with location class (LC = 2, accuracy within 350 m; LC = 3, within 150 m). To improve overall data quality when transmissions were sparse, two records were selected on a day when numerical LC values were separated for 10 h or more. Records include fields for tag number, name, longitude, latitude, date, time, and dive depth. Files were converted to “time series points” in ArcGIS 9.2’s Geodatabase, analyzed using Spatial Analyst and Animal Tracking extensions, then mapped over 9 km AVHRR SST data for the period during which the animal was foraging. A chart of turtle tags numbers, names, species, start coordinates, transmission end coordinates, and dates is given in Table 1.

### 3.1.2. Satellite tags on blue whales

Surface-mounted tags (Mate et al., 1997) and implantable tags (Mate, in press) were deployed with a crossbow and an air-powered applicator

from a small rigid-hulled inflatable boat in order to monitor southbound blue whale migration patterns. The tags consisted of Telonics transmitters (ST-15s), housed in stainless steel (SS) cylinders (19 cm long by 1.9 cm in diameter). The implantable tags had a Methacrylate coating of long-dispersant (5–8 month) Gentomycin antibiotic. This technique is described more fully by Mate et al. (1997, 1999).

Blue whales also were tracked through the Argos Data Location and Collection System. To conserve power, transmissions were limited to select times (four 1-h periods) with high probabilities of satellites overhead. We use six blue whale tracks to calculate temperature gradients, with two new whales (blu1910831 and blu2300840), and four previously described whales (blue 323040 (Mate et al., 1997), blu400823, blu404175, and blu404174 (Etnoyer et al., 2004). These telemetry results have not been evaluated systematically for satellite temperature gradients across their trajectories.

### 3.1.3. Satellite derived sea surface temperature (SST) data

Satellite-derived AVHRR and MCSST data products have precedent in studies of North Pacific blue whales (Moore et al., 2002; Burtenshaw et al., 2004). AVHRR has a global extent, and a 9-km resolution, but the radiometer is non-cloud penetrating. AVHRR data are available as a daily product, but clouds are diminished in weekly and monthly binned and averaged products. AVHRR data are an accepted scientific standard for identifying temperature fronts in the North Atlantic (Ullman and Cornillon, 1999). The approximate root

Table 1  
Summary of sea turtle tags provided by El Grupo Tortuguero

Tag	Name	Species	Age	Start transmit	End transmit	Days travel	No. of records	Coverage	Accuracy
7667	Adelita	Loggerhead	Adult	8/18/1996	8/13/1997	361	235	0.65	0.41
5521	Manuela	Olive Ridley	Adult	9/3/1997	2/16/1998	167	71	0.43	0.86
1085	Xiomara	Loggerhead	Juv	9/11/1997	6/5/1998	268	88	0.33	0.85
5524	Lupita	Loggerhead	Juv	7/5/1998	10/9/1998	97	33	0.34	0.97
3851	Yamilet	Loggerhead	Adult	3/23/1999	9/1/2000	529	265	0.50	0.68
70780	Urashima Taro	Loggerhead	Juv	7/25/1999	10/8/1999	76	20	0.26	0.60
20750	Carla	Loggerhead	Juv	7/26/1999	11/3/2000	467	115	0.25	0.49
20779	Hasekura	Loggerhead	Juv	7/31/1999	5/9/2000	284	78	0.27	0.58
20622	Sabina	Green	Juv	8/6/1999	9/9/1999	35	18	0.51	0.72
21217	Max	Loggerhead	Juv	7/28/2000	11/11/2000	107	65	0.61	0.75

The field for coverage represents the percentage of travel days with successful transmissions, and the field for accuracy represents the percentage of days with transmission accuracy better than 1 km.

mean square (rms) error of the AVHRR SST retrievals is approximately  $0.5^{\circ}\text{C}$  (Brown et al., 1985; Minnett, 1991), with a mean  $0.15^{\circ}\text{C}$  difference from buoys in the North Atlantic across all NOAA 9, NOAA 11, and NOAA 14 satellites. Weekly AVHRR data were matched with dates of transmission from ARGOS and used to calculate the gradients across the animal telemetry off BC Peninsula.

The MCSST product is a global 18-km grid of interpolated values derived from AVHRR measurements processed by University of Miami, Rosenstiel School of Marine and Atmospheric Sciences. Missing (cloud-covered) values are interpolated from measured values where possible, to create the highest possible coverage of MCSST values. Global comparisons between satellite retrievals and drifting buoy measurements of sea surface temperature show a minor bias of  $0.3\text{--}0.4^{\circ}\text{C}$ , and standard deviations of  $0.5\text{--}0.6^{\circ}\text{C}$  (McClain et al., 1985). MCSST is available through January 2001. NAVOCEANO data are available exclusively beginning September 2001. NAVOCEANO data use the MCSST algorithm. NAVOCEANO was used to calculate persistence (in weeks per year) for the years 2002–2004 between 12 and 72N, 90 and 180W, but not to calculate temperature gradients across animal telemetry. A year is defined climatologically, from June to May. SST data were downloaded from NASA's Jet Propulsion Laboratory (JPL) Physical Oceanography Distributed Active Archive Center (PO.DAAC) using their PO.DAAC Ocean ESIP tool (POET: <http://poet.jpl.nasa.gov/>).

#### 3.1.4. Additional data resources

The focus of this study is on SST gradients, but chlorophyll fronts also are known to influence the distribution of highly migratory species (Laurs et al., 1984; Polovina et al., 2001), so we examined monthly Sea-viewing Wide Field-of-View Sensor (SEAWIFS) data for three turtles and three whales between the years 1996–1999. Chlorophyll blooms can occur in wind-driven upwelling zones that transport deep nutrients to an enriched photic zone, so we also plotted regional upwelling indices from Pacific Environmental Marine Laboratory. These indices are based on estimates of offshore Ekman transport driven by geostrophic winds derived from 6-hourly synoptic and monthly mean surface atmospheric pressure fields. The pressure fields are provided by the U.S. Navy Fleet Numerical Meteorological and Oceanographic Center.

Topographic features also are considered biologically important because they influence regional circulation patterns, contributing to upwelling patterns, enhanced productivity, and/or larval retention (Wolanski and Hamner, 1988). We mapped the seamounts and the shelf break (200-m isobath) around the BC Peninsula using 100-m resolution bathymetry and seamount coordinates from the Baja California to Bering Sea (B2B) Marine Conservation Initiative's B2B 1.1 CD-ROM- Information for Marine Conservation Planning (Etnoyer et al., 2003) to estimate the relative importance of these features. We quantify three chlorophyll<sub>a</sub> gradients for each of six trajectories in units of  $\text{mg/l/km}$ , and make qualitative observations regarding the relative contribution of these features to observed animal behaviors.

### 3.2. Methods

#### 3.2.1. Calculating mean meridional temperature in SST data

Fedorov's definition of a temperature front is based upon the mean meridional temperature gradient, which he defines as  $0.003^{\circ}\text{C/km}$  in the North Pacific. To revisit this estimation using satellite data, we measured cell values from fixed coordinates at the northern (145W, 58N) and southern (145W, 12N) extremes of our Northeast Pacific study area, using monthly averaged MCSST and AVHRR for the years 1996–1999, because the coverage for these years is most complete. We compare cell values and slope values between months, years, and data products.

#### 3.2.2. Calculating temperature gradients across telemetry

To identify temperature gradients across animal trajectories, we use the 3D Analyst extension in ArcGIS 9.2 to run 250-km 'virtual transects' over weekly (8 day) 9-km AVHRR data, perpendicular to presumed foraging trajectories. The 250-km transect length provides for 10 grid cells on either side of the trajectory, minimizing the effect of positional variables like SST data shifts, minor distortions due to geographic projection, and transmission errors. An example of the method is shown in Fig. 2. The number of transects varied by the length and breadth of the trajectory. We purposely sought the most intense gradients within the 250-km transects, and we calculated the steepest rate of change across a minimum of three cells, so



to the center cell, and moves to the next cell in the grid.

The slope for the center cell  $e$  within that window is calculated by

$$\text{percent slope} = \text{SQRT}(\text{SQR}(dz/dx) + \text{SQR}(dz/dy))$$

$a$  through  $i$  represent the  $z$  values in the window.

$a b c$

$d e f$

$g h i$

and the deltas are calculated

$$(dz/dx) = \frac{(a + 2d + g) - (c + 2f + i)}{8^* \times x\_mesh\_spacing},$$

$$(dz/dy) = \frac{(a + 2b + c) - (g + 2h + i)}{8^* \times y\_mesh\_spacing}.$$

The result is a new grid of slope values. Values are selected from this grid based on the aforementioned threshold value. These cells become vertices. Nearby vertices (within 10-cell radius, or 180 km) are connected into a line that represents a frontal feature in Euclidean space. Following this, we use another moving window calculation to create a new grid of line density, assigning each cell a value that represents the density of frontal features in units of line length per unit of area. For example, one  $3 \times 3$  window around an 18-km cell ( $2916 \text{ km}^2$ ) may have 300 linear km of fronts intersecting there, for a density value of  $300 \text{ km}/2916 \text{ km}^2$  or  $0.10 \text{ km}/\text{km}^2$ , or only one single front of 30 km, for  $0.01 \text{ km}/\text{km}^2$ .

Finally, we calculate a grid of values for persistence, in weeks per year, by summing weekly binary plots of density, where low density ( $<0.02 \text{ km}/\text{km}^2$ ) = 0 and high density  $>0.02 \text{ km}/\text{km}^2$  = 1. The resulting persistence grid is a grid of values representing the number of weeks per year that a given cell has a high concentration of frontal features. These persistence values are mapped into the Pacific Basin using ArcGIS version 9.2.

## 4. Results

### 4.1. Sea turtle telemetry

Sea turtles spent many months off the BC Peninsula along SST gradients between  $0.005$  and  $0.11 \text{ }^\circ\text{C}/\text{km}$ . Of the 70 gradients discerned from the satellite imagery, 82% were less than  $0.05 \text{ }^\circ\text{C}/\text{km}$ .

The mean SST gradients for individual turtles ranged from  $0.016$  to  $0.059$ . The most intense gradients ( $0.10 \text{ }^\circ\text{C}/\text{km}$ ) were relatively nearshore, but four turtles transited west– southwest along identifiable frontal features (gradients between  $0.025$  and  $0.06 \text{ }^\circ\text{C}/\text{km}$ ) occurring almost 200-km offshore between  $115$  and  $120\text{W}$ , and between  $20$  and  $25\text{N}$  (Fig. 2—“Carla”). Geoposition data were available for an average 40% of total days transmitting, with coverage values ranging from 25% for “Carla’s” long southward arc to 65% for Adelita’s remarkable trans-Pacific migration (Nichols et al., 2000). Location codes (LCs) from eight of the ten turtles indicate that  $>50\%$  of transmission coordinates were accurate within 1 km, and four turtles’ transmission were accurate within 1 km  $>75\%$  of the time (Table 1).

The ten turtle tracks can be classified into three general patterns of activity-offshore meandering near Magdalena Bay, westward transit, and southern transits far offshore. “Max” and “Hasekura” meandered offshore for periods between 107 and 284 days, and “Urashima Taro” meandered offshore for 60 days before beginning a southern transit. SST fronts across these trajectories were the highest gradients observed for sea turtles (Table 1).

Six other turtles migrated offshore, as shown in Fig. 3, following either a direct route west for periods between 33 and 60 days, or a long extended arc to the south for periods between up to 200 days after meanderings in the nearshore between 100 days and more. “Lupita”, and “Yamilet” undertook direct western transits along  $27\text{N}$  latitude (Fig. 3). “Sabina” spent a month 100-km southwest of Magdalena Bay. The steepest SST gradients across these westward transits ranged from  $0.03$  to  $0.06 \text{ }^\circ\text{C}/\text{km}$  in temperatures between  $20$  and  $23 \text{ }^\circ\text{C}$ .

“Xiomara”, “Carla”, and “Manuela” all transited in long similar extended arcs, eventually heading almost due south in near linear trajectories between  $116$  and  $118\text{W}$  (Fig. 3, top). The loggerhead turtle “Xiomara” spent February, March, and some of May 1998 500-km offshore BCS at  $116\text{W}$  along a  $22 \text{ }^\circ\text{C}$  isotherm that forms a fairly weak frontal zone of  $0.03 \text{ }^\circ\text{C}/\text{km}$ . A graph of SST values along one of the six ‘virtual transects’ across “Xiomara’s” telemetry is shown in Fig. 5. Generally, the steepest gradients across sea turtle trajectories were between  $0.03$  and  $0.05 \text{ }^\circ\text{C}/\text{km}$  in temperatures between  $20$  and  $24 \text{ }^\circ\text{C}$ . A list of maximum, mean, and minimum SST gradients is given in Table 2.

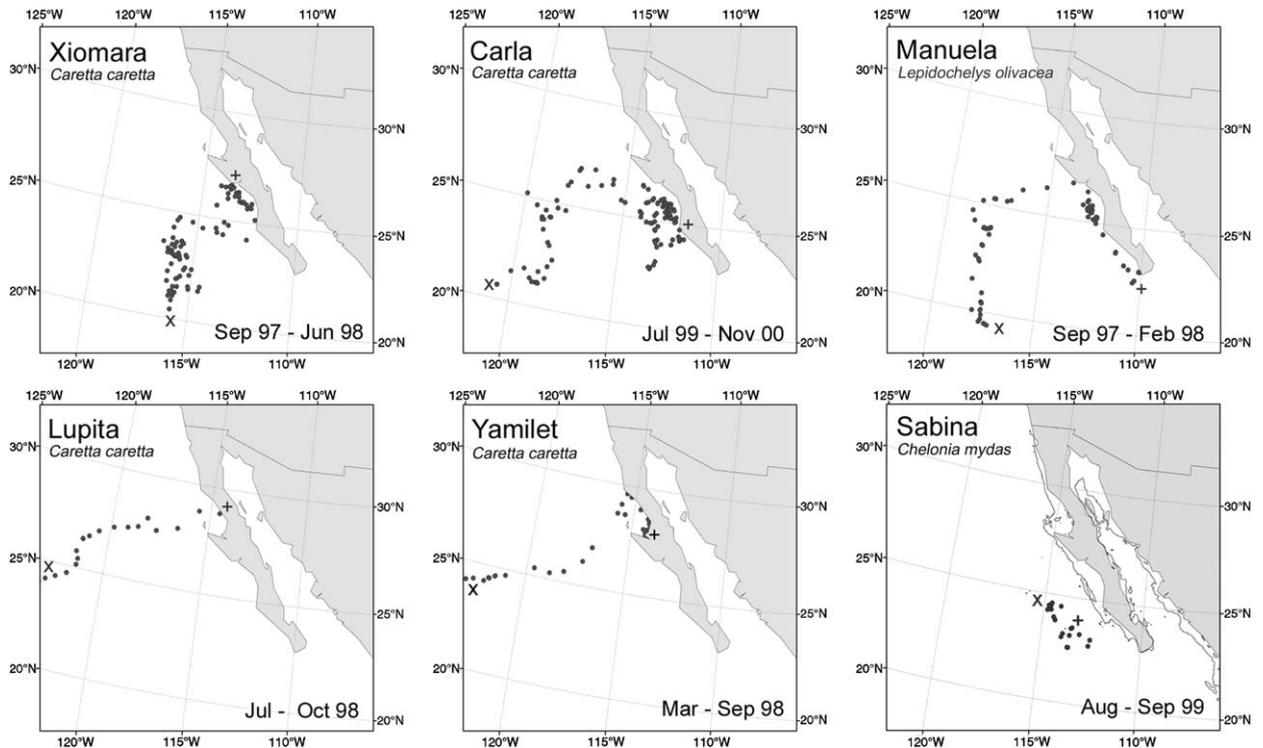


Fig. 3. Satellite telemetry data show migration patterns from four tagged loggerhead turtles, one olive ridley turtle, and one green sea turtle off the Baja California Peninsula. “+” indicates start, and “O” indicates end. The 200 m isobath is shown in the lower right panel.

Table 2

SST gradients across sea turtle trajectories, where  $N$  represents the number of transects

Sea turtle	Max slope (°C/km)	Mean slope (°C/km)	Min slope (°C/km)	$N$
Hasekura	0.11	0.059	0.013	10
Urashima	0.08	0.028	0.009	9
Taro				
Adelita	0.06	0.031	0.014	7
Sabina	0.06	0.034	0.017	7
Max	0.06	0.040	0.020	5
Carla	0.05	0.022	0.010	11
Xiomara	0.04	0.024	0.005	6
Lupita	0.03	0.018	0.007	11
Manuela	0.03	0.016	0.005	5
Yamilet	0.03	0.018	0.013	6

#### 4.2. Blue whale telemetry

Blue whale tag numbers and residence periods are shown in Table 3, and gradients are shown in Table 4. Whales spent weeks and months offshore Baja California along SST gradients between 0.011 and 0.072 °C/km. Of the 69 gradients discerned

from the satellite imagery, 78% were less than 0.05 °C/km. The mean SST gradients for individual whales ranged from 0.022 to 0.05. The most intense gradients (0.07 °C/km) were seen in three whales (Fig. 4—4000823, 404174, 404175) well offshore Baja California Sur in the fall of 1998, 125 km west of the shelf break. Whales spent between 2 and 4 weeks near this open ocean frontal feature in temperatures ranging from 20 to 26 °C. Elsewhere, to the south of Cabo San Lucas, two whales (2300840 and 1910831) spent 2–4 weeks transiting along frontal features (0.05 and 0.06 °C/km) between 20 and 23 °C. Griffiths (1965) described a front south of Cabo San Lucas formed from boundary water between the Gulf of California and California Current, at isotherms between 21 and 23 °C.

Two general migration patterns are evident in the six whales shown in Fig. 4. The first pattern is shown in whales 400823, 404175, and 404174 from 1998. This is a fairly linear southbound offshore migration that tracks the coastline of the Peninsula for one or two weeks, punctuated by a residential period of similar duration 125 km offshore at 113W. Whale 323040 also exhibits a similarly brisk

Table 3  
Summary of blue whale *Balaenoptera musculus* tags provided by the Bruce Mate laboratory

Tag	Start transmit	Enter frame	Residence times				Exit frame	Days in frame	End transmit	Total days
			Period	Days	Start	End				
323040	9/18/1995	9/28/1995	A	18	10/18/1995	11/4/1998	11/9/1995	43	12/8/1995	82
410823	9/1/1998	10/25/1998	NA	NA	NA	NA	12/2/1998	39	2/14/1999	225
404174	8/25/1998	9/14/1998	A	29	10/4/1998	11/1/1998	11/7/1998	55	11/7/1998	75
			B	13	9/18/1998	9/30/1998				
404175	10/11/1998	11/16/1998	A	16	11/25/1998	12/10/1998	12/10/1998	25	12/10/1998	61
400823	10/10/1998	11/3/1998	A	27	11/12/1998	12/8/1998	12/10/1998	38	12/10/1998	62
1910831	3/26/2001	3/26/2001	A	39	5/22/2001	6/29/2001	10/26/2001	215	10/26/2001	215
			B	13	5/4/2001	5/17/2001				
			C	72	7/6/2005	9/15/2001				
			D	27	9/17/2001	10/13/2001				
2300837	3/23/2002	5/28/2002	NA	NA	NA	NA	6/28/2002	32	6/28/2002	98
2300840	3/21/2002	3/21/2002	A	15	4/6/2002	4/20/2002	10/1/2002	185	10/1/2002	195
			B	50	5/14/2002	7/2/2002				
			C	91	7/3/2002	10/1/2002				

The information here corresponds to trajectories shown in Fig. 5. Residence periods are defined as >10 days within <100 km radius.

Table 4  
SST gradients across blue whale trajectories, where  $N$  represents number of transects

Whale tag	Max slope (°C/km)	Mean slope (°C/km)	Min slope (°C/km)	$N$
404175	0.07	0.05	0.030	6
400823	0.07	0.037	0.018	11
404174A	0.07	0.046	0.032	6
323040	0.06	0.037	0.023	13
2300840A	0.06	0.044	0.032	7
404174B	0.05	0.042	0.026	5
1910831A	0.05	0.029	0.020	7
2300840C	0.05	0.031	0.013	5
2300840B	0.04	0.022	0.011	5
1910831C	0.04	0.031	0.018	3

migration in 1995, closer to shore, punctuated by a singular residential period of 18 days along a (max. 0.060 °C/km) frontal feature 100-km to the east of the max. 0.070 °C/km frontal feature seen in 1998. Of these four whales, only one showed a secondary residence period, along a 0.067 temperature gradient off Punta Eugenia. These residential periods are identified by the letter A in Fig. 4, and their dates are shown in Table 3.

A second pattern is evident in the new whale tracks (1910831, 2300837, and 2300840) from 2001 and 2002. These whales spent 3–4 times as many days along Peninsula as the earlier set, and they stayed closer to shore, with residential periods

between 2 and 3 months off Punta Eugenia along an oft-clouded gradient between 0.013 and 0.049 °C/km. Residential periods between 2 and 7 weeks were concentrated in and around the Bahía de Ballenas between Punta Abreojos and Laguna San Ignacio. Intense cloud cover during these residential periods obscured the temperature gradients here and to the north off Punta San Antonio where 1910831 spent 27 days in September and October 2001.

The first pattern is remarkable because the blue whale residence periods are far offshore, and four different whales meander for prolonged periods in this same place in two different years. A graph of SST values along one of the eleven 'virtual transects' across telemetry data from this offshore residential period is shown in Fig. 5. Blue whale 400823 spent 25 days in November of 1998 along the leading edge of the mean 0.04 °C/km gradient in 23 °C waters west of Magdalena Bay (Fig. 4). Blue whale 404175 also spent at least 15 days (transmission lost in mid-December 1998) along the cool side (21 °C) of a similar 0.05 °C/km temperature gradient at 113 W, between 21 and 23 °C. Blue whale 404174 traversed a mean 0.05 °C/km gradient for 20 days near the same place and time, with a more west–southwest orientation. The origin of the gradient appears to be a warm northward pulse of the northern equatorial current 3 months after the cessation of one of the most intense upwelling periods on record (Schwing et al., 2000). In 1995, Blue whale 323040 meandered for a similar period at the same latitude along a

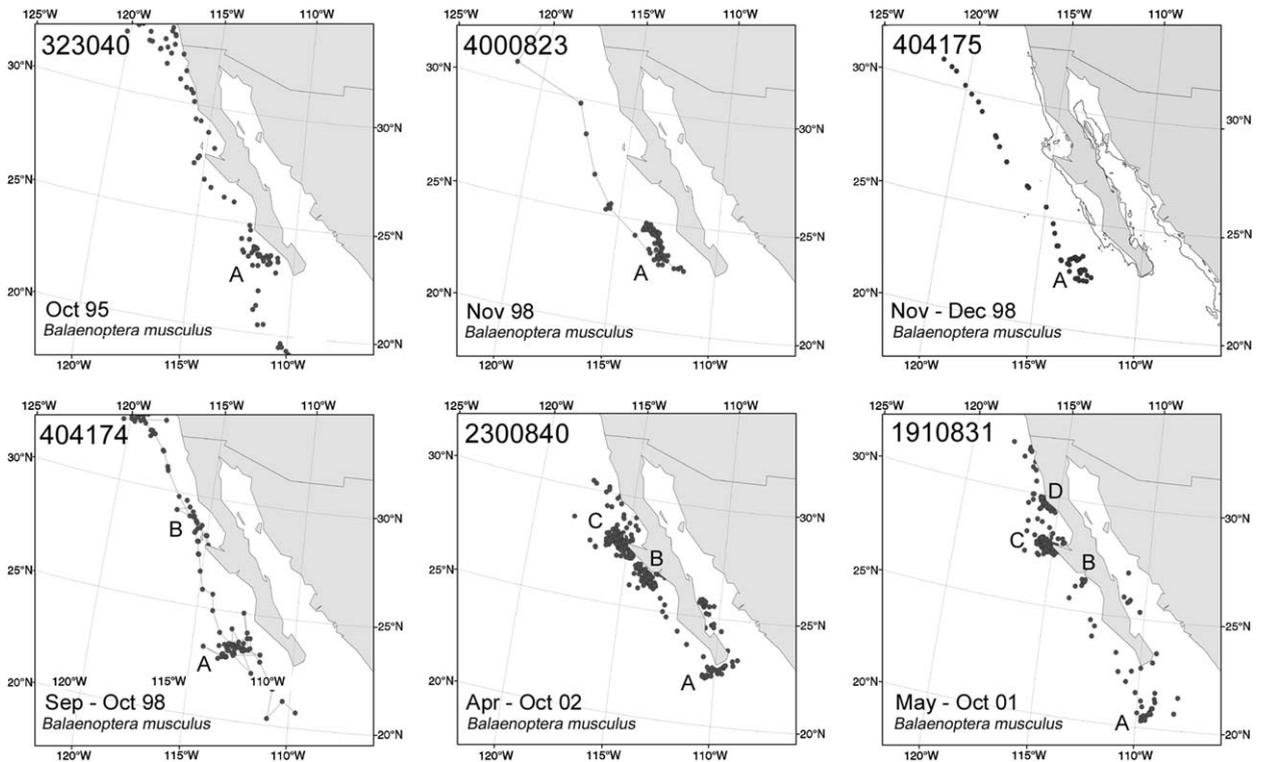


Fig. 4. Satellite telemetry data from six blue whales off the Baja California Peninsula. Dates reflect time period whales spent within the image frame. Letters represent residence periods and transects described in Tables 3 and 4. The 200 m isobath is shown in the upper right panel.

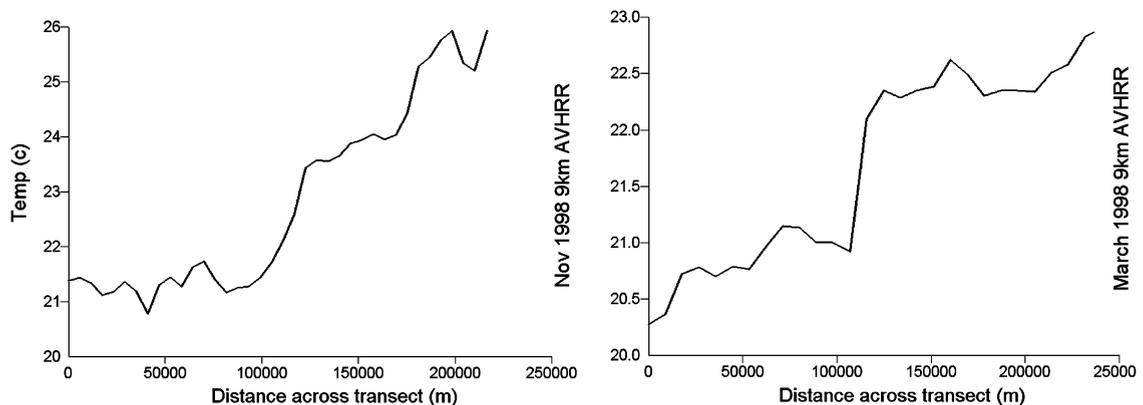


Fig. 5. Example plots of 9 km AVHRR SST data across the foraging trajectories of a blue whale (400823, left) and a loggerhead sea turtle (“Xiomara”, right) off the Baja California Peninsula.

0.60 °C/km gradient, but 100-km to the east, closer to the continental shelf.

The second pattern is remarkable because it shows the whales tagged in the Gulf of California. They show a slower migration, with more residence periods in more places closer to shore. Furthermore,

the second pattern shows that 1910831 spent 7 months (April through October 2001) in residence along the Pacific coast of the BC Peninsula. Foraging effort in the early summer was focused off Cabo San Lucas, while effort in August and September was confined to a 60-km radius west of

Punta Eugenia (Fig. 4). These are the first records of blue whales spending the summer feeding season south of California. If these records are typical of migratory behavior in Gulf of California blue whales, then their northward migration is limited to the BC Peninsula, and the whales can forego abundant resources elsewhere.

Blue whale 2300840 spent the summer of 2001 (July, August, and September) off Punta Eugenia. Other whales (404174, 2300831, and 2300840) meandered along this Ensenada Front in September 1998 and May 2002. Clouds often obscured this point, but the few gradients we recovered ranged between 0.013 and 0.050 °C/km. This gradient is more subtle than shipboard measurements of the gradient across the Ensenada Front (~0.22 °C/km, Haury et al., 1993). Blue whale 2300840 was one of two whales shown to transit along the shelf break. Again, both of these were tagged in the Gulf of California. Others were tagged off Southern California.

#### 4.3. Satellite oceanography

The mean meridional gradient (or average rate of change across the basin) in the Northeast Pacific 1996–1999 = 0.0030 °C/km, according to both AVHRR and MCSST, with no significant difference within or between years. This is consistent with Fedorov's (1986) mean meridional temperature gradient of 0.003 °C/km. We used fixed coordinate measurements to calculate this gradient monthly over 4 years, so this allows us to compare cell values in clouded AVHRR and cloudless MCSST. In the MCSST interpolated data, we find an RMS difference less than or equal to 0.5 °C at low latitudes compared to AVHRR, consistent with published accuracy estimates. At high latitudes, we calculate an RMS difference between 0.7 and 1.9 °C. This is higher than published estimates.

We find some major discrepancies between AVHRR and MCSST in Gulf of Alaska in the Fall of 1999, between 2.5 and 5 °C. We found some minor discrepancies in Gulf of Alaska in the Fall of 1998, about 1 °C. This partly confirms some earlier concerns about temperature gradients derived from MCSST at latitudes higher than 50N (Etnoyer et al., 2004). Contrary to our expectation that edge detection in MCSST might underestimate fronts in the Gulf of Alaska due to frequent cloud cover, it appears the opposite is also likely, and edge detection may overestimate frontal features in the

north because cloud-covered interpolated values can differ markedly from AVHRR-derived surrounding values.

The threshold for the highest 10% in AVHRR predicted by the slope calculation is ~4.5 °C change over 100 km, or 0.045 °C/km. The highest individual AVHRR gradient off BC Sur was 0.22 °C/km. This occurred in a Nov 1998 transect at 113 W, 23 N but the value failed to meet the 3 cell rule we established in our methods. As an exercise, we sought out the highest gradient we could find with three cell values in high-resolution (2.5 km) Coastwatch data off BCS, detecting a 2 °C change over 8.5 km, or 0.235 °C/km. Higher resolution SST data like the Coastwatch product could be extremely valuable to future investigations of pelagic habitat, especially if it could be ground-truthed and calibrated with instruments attached to ships, buoys, and/or marine animals. High-resolution cloudless data could be even more valuable to these investigations, but this would require a cloud penetrating technique, or an instrument flown below the cloud layer to observe SST gradients around foraging whales and turtles.

Transects across SEAWIFS data showed small, discernable spikes in chlorophyll concentrations across most of the animal trajectories. One near-shore chlorophyll gradient (0.5–1.5 mg/l over 100 km, or 0.01 mg/l/km) and one offshore chlorophyll gradient (0.125 mg/l–0.35 mg/l over 100 km, 0.002 mg/l/km) were the two highest gradients observed. Both spikes were seen in the same track from the olive ridley “Manuela”. The highest chlorophyll gradient observed across a blue whale trajectory offshore was 0.001 mg/l/km, or 0.12–0.18 mg/l over 60 km. The highest chlorophyll gradient observed *independent* of a turtle or whale trajectory was 0.02 mg/l/km across a long filament extending 100 km or more off Magdalena Bay in August of 1999. Persistently high chlorophyll values (~3–5 mg/l chl<sub>a</sub>) occurred off Magdalena Bay, off Bahia de Ballenas (seen as residence period B in whales 19100831 and 2300840), and south of Punta San Antonio (seen as residence period D in whale 1910831). Chlorophyll clearly plays some factor in the distribution of these turtles and whales, but the role of topographic features like the shelf break, and seamounts are less clear. Besides the two whales mentioned earlier, few animals spent any appreciable period of time meandering along the narrow shelf break, or above seamount features known to the region. Turtle meanderings lagged upwelling peaks by 6 months, and offshore whale meanderings

lagged upwelling peaks by 3 months, but tagging effort and very long residence times obscure any clear relationship (see Fig. 7).

#### 4.4. Persistence

The apparent breadth of persistent pelagic habitat in the Northeast Pacific increases dramatically when the edge detection algorithm is sensitized to detect more subtle temperature gradients (Figs. 6 and 7). The BC Peninsula and the North Pacific Transition Zone are still epicenters of frontal activity based on their persistent concentration of steep temperature gradients, but the margins of the activity are increased with the sensitive algorithm, to the point where nearly one third of the Pacific sub-basin plays host to active temperature gradients 6 months of the year and more. Secondary concentrations of fronts are shown again in the California's Channel Islands, and off Point Conception, consistent with earlier findings from 1996 to 1999.

It should be noted that the NAVOCEANO interpolated data differ dramatically from Miami MCSST, though it seems to share the problem of cloud contamination between the Gulf of Alaska and the central Northeast Pacific. These 2002–2004 NAVOCEANO data can show “no data” values in

this cloud-covered region, whereas 1996–1999 MCSST showed interpolated temperature values. As mentioned earlier, these discrepancies will register false fronts. In order to run these analyses more effectively in the future, either more complete coverage will be required from these interpolated data, the analysis extent will need to be restricted to less cloudy regions, or a better cloud mask will need to be developed and employed.

## 5. Discussion

Sea turtles and blue whales spend considerable amounts of time off the BC Peninsula in waters that exhibit SST gradients higher than the Northeast Pacific background gradient. Meandering behaviors and linear trajectories frequently occur along the edges of subtle gradients (0.01–0.10 °C/km) when compared to the classic definitions of a front in the Northeast Pacific (0.03–0.30 °C/km). These gradients are apparent in satellite imagery, and edge-detection algorithms can identify these as frontal features. The extended presence of whales and sea turtles in and around a region with high density of frontal features suggests that these offshore gradients are important foraging habitats for turtles and

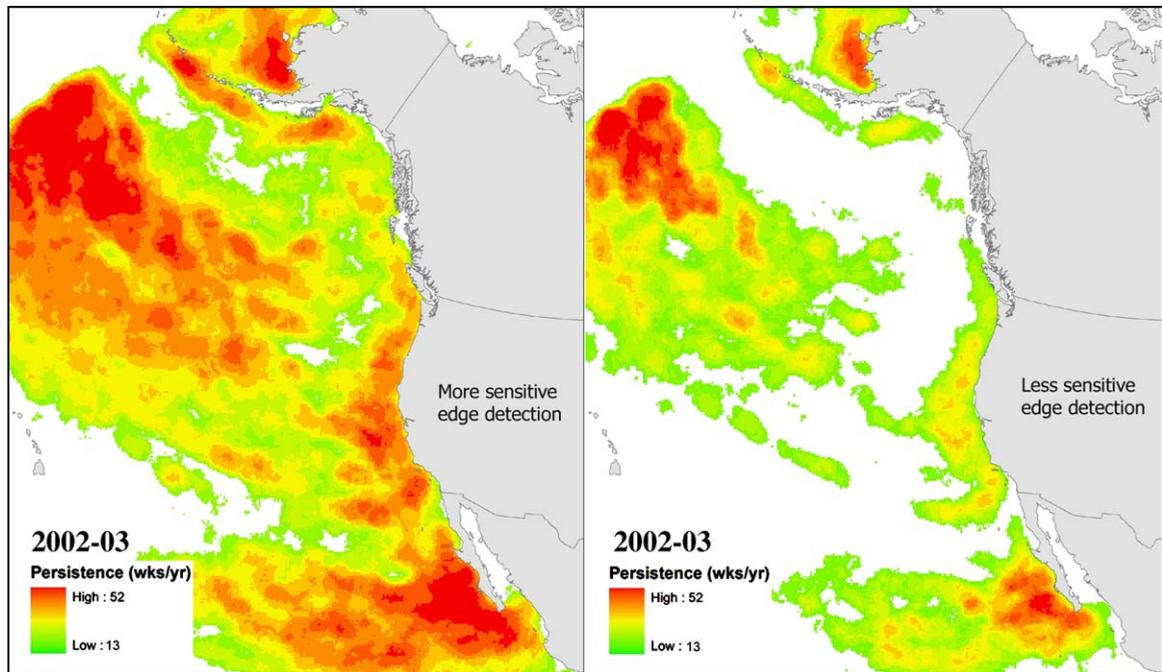


Fig. 6. A comparison of persistence values for high densities of temperature fronts in the Northeast Pacific using a sensitive edge-detection algorithm (left—slope 0.015%) and a strict edge detection algorithm (right—slope 0.020%) in NAVOCEANO 18-km interpolated SST.

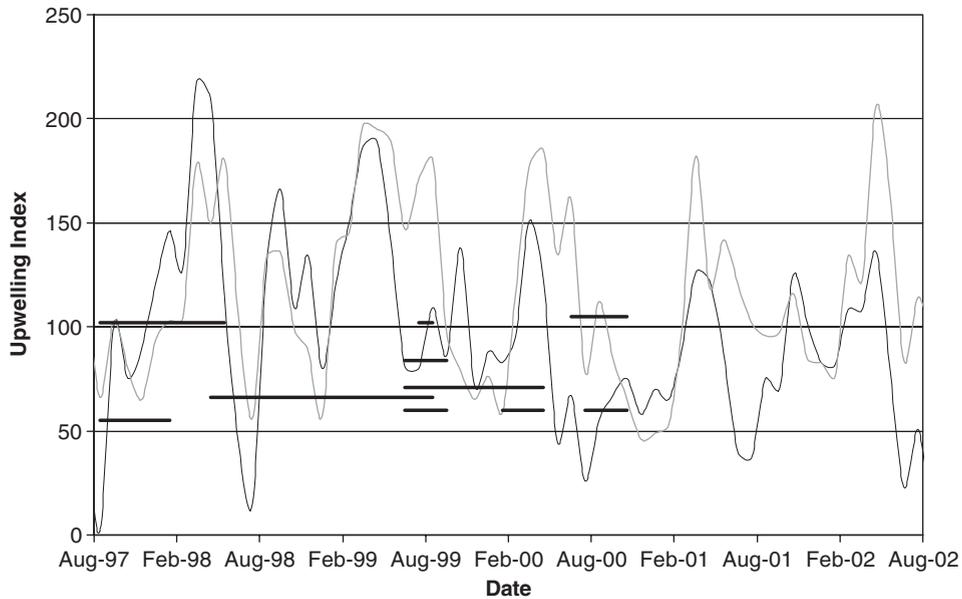


Fig. 7. Upwelling indices (dark line is 24N latitude and gray line is 27N latitude) from Pacific Fisheries Environmental Laboratory, NOAA are shown here with residence periods for sea turtles east of 120W longitude (thick dark lines) in coastal waters of Baja California Sur. <http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/upwelling.html>

whales. A single frontal feature can persist 3 months or more, and attract conspecific individuals.

There is clearly something happening at the front, but the true nature of the attraction is difficult to discern. We assume these fronts represent some form of optimal foraging habitat, but loggerhead turtles and olive ridley turtles prefer red crabs, green turtles prefer algae, and whales are thought to prefer krill in their diets, so lumping these species together is problematic from a trophic perspective. However, the similar gradients across these trajectories and the similar concentrations of effort offshore are very interesting. Fronts have been characterized by high levels of biomass across trophic levels, so a variety of resources may be concentrated into a dense pelagic ecosystem along this frontal interface. However, an abundant single-species prey may also account for the high residence times we see along these subtle fronts. Large groups of olive ridley turtles have been reported in lines of debris as far as 120W (Arenas and Hall, 1992), and olive ridleys feed exclusively on the pelagic red crab *Pleuroncodes planipes* off the Baja California Peninsula.

Longhurst (2004) invoked *P. planipes* as a shared resource for blue whales and many other species off Baja California Sur, but it remains unknown whether the frontal features we describe here have a high abundance of phytoplankton, zooplankton,

or red crabs, because no net samples were taken near the animals while they were in the region. We can only infer the contents of these features from other studies. Plankton tows off the BC Peninsula in 1974 showed that *P. planipes* comprised almost half the zooplankton biomass in three stations (Brinton, 1979) that correspond closely to the residence zones shown as “A” in all six blue whale trajectories shown in Fig. 4. Humboldt squid (*Dosidicus gigas*) were found engorged with red crabs off Baja California Sur in the fall of 1998 (Nichols, 2003), while some of these blue whales foraged offshore. It is plausible that blue whales and sea turtles (olive ridley, loggerhead, and to a lesser extent green turtles) might also forage on red crabs at these fronts, and anecdotal evidence suggests this, but a fully integrated, well-coordinated approach coupling telemetry, satellites and hydrographic surveys (see Croll et al., 1998) will be required to confirm the prey groups entrained within these frontal features.

The geophysical origin of these fronts is also unclear. Waters between 20 and 35N include mixes of northern and southern waters from the California Current in the North Pacific gyre (Sverdrup and Fleming, 1941), Northern Equatorial Currents (Blanton and Pattullo, 1970), upwelled abyssal waters (Bakun and Nelson, 1977), and a near-shore stream flowing westerly from the Gulf of California

(Griffiths, 1965; Brinton, 1979). These frontal features therefore may develop in response to seasonal upwelling, develop in response to boundary flows between the Gulf of California and the Pacific, or form as a result of the convergence between cool southbound waters from the California Current System (CCS) and northward-flowing warm equatorial waters. The orientation and topography of the Baja California Peninsula must also perturb these geostrophic flows.

The origin of these ubiquitous frontal features is doubtless complex, but a persistent concentration of temperature fronts off Baja California Sur is clearly evident between 2002 and 2004, as it was 1996–1999 (Etnoyer et al., 2004). Persistent concentrations of temperature fronts are also shown to occur off the Channel Islands, another region where blue whales meander. However, these edge detection models are very sensitive to the gradient definition. A lower-gradient threshold will increase the number of fronts detected offshore, revealing more potential habitats in different places than we find with higher gradient thresholds. This is the expected result, but it confirms that many biologically relevant temperature fronts can go undetected, and that the temperature gradient parameter is an important one.

The strongest gradients observed across blue whale ( $0.070\text{ }^{\circ}\text{C}/\text{km}$ ) and sea turtle ( $0.10\text{ }^{\circ}\text{C}/\text{km}$ ) foraging trajectories are on par with the steepest gradient in 13 years of CalCOFI data ( $6\text{ }^{\circ}\text{C}$  in  $120\text{ km}$  or  $0.05\text{ }^{\circ}\text{C}/\text{km}$  (Lynn, 1980)). However, these barely qualify as fronts by classic definitions, or by temperate North Atlantic standards (Ullman and Cornillon, 1999). They occur at the lowest end of those gradient scales. The fronts occurring off BC Sur are one order of magnitude over the mean meridional temperature, but less than two. Technically, they qualify as frontal zones by Fedorov (1986).

The maximum value for an in-situ recording of the Ensenada Front ( $0.36\text{ }^{\circ}\text{C}/\text{km}$  max) qualifies that feature as a front, but 99% of shipboard values were less  $0.22\text{ }^{\circ}\text{C}/\text{km}$  (Haury et al., 1993) suggesting maximum values are appropriate metrics. Few Fedorov fronts ( $\text{grad} > 0.3\text{ }^{\circ}\text{C}/\text{km}$ ) were observed in the BCS region, but many frontal features between  $0.01$  and  $0.1\text{ }^{\circ}\text{C}/\text{km}$  were seen along pelagic animal trajectories.

Generally, whales and turtles appear to be foraging along subtle gradients, at the low end of the physical oceanographic spectrum. It is remark-

able that satellites can detect and track these subtle features, despite obstacles like cloud cover, limited resolution, and limited extent. However, it is important that we recognize the subtlety of these gradients because an insensitive edge detection algorithm will underestimate the abundance of biologically relevant oceanographic features and important pelagic habitat. A slope calculation across a temperature grid in a GIS is sensitive enough to reveal and quantify these features, so these methods can be replicated in other regions. SST data are freely available worldwide, but greater attention must be paid to the strengths and limitations of each of the myriad SST data types. Cloud cover can render false fronts, and low-resolution satellite data will obscure changes in temperature over small distances. Some “lines in the sea” in the central Pacific have been described as discrete surface expressions less than  $20\text{-km}$  across (Yoder et al., 1994). Future researches should pursue the best attainable SST data to supplement animal distribution studies.

The temperature gradients we have shown also may be subtle enough to invite the possibility that these animals are not feeding along surface features at all. In this case, turtles and whales would focus effort on these regions off the BC Peninsula due to some other phenomenon, like a subsurface gradient or a benthic resource. Subtle surface temperature gradients may be surface expressions of steeper subsurface gradients, and subtle gradients may indicate a dynamic three dimensional mixing process that might retain plankton at depth (Roughan et al., 2005). Some biologically relevant subsurface gradients may also be unrelated to temperature, like salinity gradients (halocline), the depth of the mixing layer, or the oxygen minimum zone. All these characteristics are known to occur off BC Peninsula (Blanton and Pattullo, 1970), especially where zooplankton biomass is highest (Brinton, 1979), so much remains to be explored in this regard.

Despite 50 years of surveys along the California Cooperative Fisheries Investigations (CalCOFI) grid, several Eastern Tropical Pacific (EASTROPAC) expeditions (1967–1968), and other Scripps Tuna Oceanography Research (STOR) group researches in the 1960s, there remains a need to better understand the complex three-dimensional oceanographic structure west of Baja California Sur. These results support a shallow water phenomenon, because whales in California’s Channel Islands dive

100–200 m depth, to target submerged concentrations of euphausiid krill (Fiedler et al., 1998) on the continental shelf. The blue whales shown here had no depth recorders, but zooplankton volume and euphausiid biomass off BC Peninsula were concentrated in the first 100 m of the water column 25 years earlier, in 1974 (Brinton, 1979), at a station very near the 1998 blue whale “hot spot” we have shown as residential zone A, 125 km southwest of Magdalena Bay. The accumulated circumstantial evidence supports Longhurst’s (2004) hypothesis that upwelled pelagic stage *P. planipes* red crabs are entrained in these frontal features far offshore, and this is the primary reason endangered and highly migratory species are drawn to the pelagic marine hotspot off Baja California Sur.

## 6. Conclusion

Blue whales and sea turtles meander for extended durations along subtle temperature gradients off Baja California Sur, a region known for an unusually persistent concentration of these gradients. The temperature gradients measured by satellite across whale and turtle trajectories off Baja California Peninsula are finer and more delicate than fronts defined in other regions by other means. The most obvious explanation for this is that marine species are more sensitive to the temperature gradients than oceanographers are, but it is also possible that satellites are too poorly resolved to register high rates of change, or that stronger gradients lie below, and other factors entice these animals. However, satellite technologies can identify very subtle frontal features. Satellite measures reinforce the importance of field measurements, and the synergy of these technologies offers great promise. Continued support of satellite tagging programs, hydrographic surveys, data processing efforts, and data distribution initiatives should help to make this information more complete, more available, and more broadly applicable to better management of the world’s oceans.

We have shown that endangered marine species can be tracked for long periods of time with good coverage and high levels of accuracy as they meander along subtle temperature gradients. Some of these frontal features are fairly stable and predictable, and they may be integrated into spatial management regimes, especially when they persist within federal boundaries, as they do in the Mexican waters off the Baja California Peninsula.

## Acknowledgements

Special thanks to the *North Pacific Marine Science Organization*, the Marine Conservation Biology Institute, Commission for Environmental Cooperation, and NOAA’s National Marine Protected Areas Center Science Institute for making this research possible. We deeply appreciate the shared tagging and tracking efforts of Jeffrey Seminoff, Hoyt Peckham, Louise Brooks, Grupo Tortuguero, and Seaturtle.org, and we wish them continued success with this unique community outreach effort in Baja California. Funding for sea turtle tracking was from Wallace Research Foundation, US Fish and Wildlife Service, and David and Lucile Packard Foundation. Funding for blue whale tracking was from the Office of Naval Research contract #9310834 and from donors to the Oregon State University endowed Marine Mammal Program. Dave Foley of the Pacific Marine Environmental Laboratory contributed the stunning image of temperature gradients observed in Coastwatch SST off BC Peninsula. Maria Montoreano graciously assisted with the preparation of the manuscript while mothering Clara Lynn Etnoyer, to whom the manuscript is dedicated. Drs. Larry Crowder, Pat Halpin, and Andy Read of Duke University Marine Lab and Dr. Barbara Block of Hopkins Marine Station at Stanford University were a great source of inspiration.

## References

- Alverson, F.G., 1960. The food of yellowfin and skipjack tunas in the eastern tropical Pacific. *Inter-American Tropical Tuna Commission Bulletin* 7, 295–396.
- Archer, D., Aiken, J., Balch, W., Barber, R., et al., 1997. A meeting place of great ocean currents: shipboard observations of a convergent front at 2N in the Pacific. *Deep-Sea Research II* 44, 1827–1849.
- Arenas, P., Hall, M., 1992. The association of sea turtles and other pelagic fauna with floating objects in the eastern tropical Pacific Ocean. In: M. Salmon, J. Wyneken (compilers), *Proceedings of the Eleventh Annual Workshop on Sea Turtle Biology and Conservation*, U.S. Dep. Comm., NOAA Tech. Memo. NMFS-SEFSC-302, 195pp.
- Bailey, K.M., Francis, R.C., Stevens, P.R., 1982. The life history and fishery of Pacific whiting *Merluccius productus*. *California Cooperative Oceanic Fisheries Investigations Reports* 27, 109–112.
- Bakun, A., 1996. *Patterns in the Ocean. Ocean Processes and Marine Population Dynamics*. California Sea Grant, 323pp.
- Bakun, A., Nelson, G., 1977. Climatology of upwelling related processes off Baja California. *California Cooperative Oceanic Fisheries Investigations Reports* 19, 107–127.

- Balazs, G.H., Miya, R.K., Beaver, S.C., 1995. Procedures to attach a satellite transmitter to the carapace of an adult green sea turtle, *Chelonia mydas*. In: Keinath, J.A., Barnard D.E., Musick J.A., Bell, B.A., (compilers). Proceedings of the Fifteenth Annual Workshop on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSE-387, pp. 21–26.
- Blanton, J.O., Pattullo, J.G., 1970. The subsurface boundary between Subarctic Pacific water and Pacific Equatorial water in the transition zone off Southern California. *Limnology and Oceanography* 15, 606–614.
- Block, B.A., Dewar, H., Blackwell, S.B., Williams, T.D., Prince, E.D., Farwell, C.J., Boustany, A., Teo, S.L.H., Seitz, A., Walli, A., Fudge, D., 2001. Migratory movements, depth preferences, and thermal biology of atlantic bluefin tuna. *Science* 293, 1310–1314.
- Block, B.A., Costa, D., Boehlert, G.W., Kochevar, R.E., 2003. Revealing pelagic habitat use: the tagging of Pacific pelagics program. *Oceanologica Acta* 25, 255–266.
- Brinton, E., 1979. Parameters relating to the distributions of planktonic organisms, especially Euphausiids in the eastern tropical Pacific. *Progress in Oceanography* 8, 125–189.
- Brown, O.B., Brown, J.W., Evans, R.H., 1985. Calibration of advanced very high resolution radiometer infrared observations. *Journal of Geophysical Research* 90, 11667–11677.
- Burtenshaw, J.C., Oleson, E.M., Hildebrand, J.A., McDonald, M.A., Andrew, R.K., Howe, B.M., Mercer, J.A., 2004. Acoustic and satellite remote sensing of blue whale seasonality and habitat in the Northeast Pacific. *Deep Sea Research II* 51, 967–986.
- Croll, D.A., Tershy, B., Hewitt, R., Demer, D., Fiedler, P., Smith, S., Armstrong, W., Popp, J., Kiekhefer, T., Lopez, V., Urban-Ramirez, J., 1998. An integrated approach to the foraging ecology of marine birds and mammals. *Deep-Sea Research II* 45, 1353–1371.
- Etnoyer, P., Canny, D., Morgan, L.E., 2003. B2B 1.1 CD-ROM-Information for marine conservation planning from Baja California to the Bering Sea. Marine Conservation Biology Institute, Redmond, WA.
- Etnoyer, P., Canny, D., Mate, B., Morgan, L.E., 2004. Persistent Pelagic habitat in the Baja California to Bering Sea (B2B) Ecoregion. *Oceanography* 17 (1), 90–101.
- Fedorov, K.N., 1986. the physical nature and structure of oceanic fronts. lecture notes on coastal and estuarine studies, Vol. 19. Springer, Berlin.
- Fiedler, P.C., Reilly, S.B., Hewitt, R.P., Demer, D., Philbrick, V.A., Smith, S., Armstrong, W., Croll, D.A., Tershy, B.R., Mate, B.R., 1998. Blue whale habitat and prey in the California channel islands. *Deep-Sea Research II* 45, 1781–1801.
- Franks, P.J.S., 1992. Swim or sink: accumulation of biomass at fronts. *Marine Ecology Progress Series* 82, 1–12.
- Gendron, D., 1992. Population structure of daytime surface swarms of *Nyctiphanes simplex* (Crustacea, Euphausiacea) in the Gulf of California, Mexico. *Marine Ecology Progress Series* 87, 1–6.
- Genin, A., Jaffe, J.S., Reef, R., Richter, C., Franks, P.J.S., 2005. Swimming against the flow: a mechanism of zooplankton aggregation. *Science* 308, 860–862.
- Griffiths, R.C., 1965. A study of ocean fronts off Cape San Lucas, Lower California. U.S. Fisheries and Wildlife Service Special Scientific Report Fisheries, vol. 499, pp. 1–54.
- Haury, L.R., Venrick, E., Fey, C.L., McGowan, J.A., Niler, P.P., 1993. The Ensenada Front: July 1985. California Cooperative Oceanic Fisheries Investigations Reports 34, 69–88.
- Hickey, B.M., 1979. The California current system: hypotheses and facts. *Progress in Oceanography* 8, 191–279.
- Lauris, R.M., Fiedler, P.C., Montgomery, D.R., 1984. Albacore tuna catch distributions relative to environmental features observed from satellites. *Deep-Sea Research* 31, 1085–1099.
- Legeckis, R., 1978. A survey of worldwide sea surface temperature fronts detected by environmental satellites. *Journal of Geophysical Research* 83 (C9), 4501–4522.
- Longhurst, A., 2004. The answer must be red crabs, of course. *Oceanography* 17 (2), 6–7.
- Lynn, R.J., 1980. Seasonal variation of temperature and salinity at 10 m in the California Current. California Cooperative Oceanic Fisheries Investigations Progress Reports, vol. 11, July 1963–June 1966.
- Marquez, M.R., 1990. Sea turtles of the world. An annotated and illustrated catalogue of sea turtle species known to date. FAO Species Catalog, FAO Fisheries Syn. 11 (125) 81pp.
- Mate, B.R., in press. The evolution of large whale radio tags: one laboratory's experience. *Deep-Sea Research II*.
- Mate, B.R., Nieukirk, S.L., Kraus, S.D., 1997. Satellite-monitored movements of the northern right whale. *Journal of Wildlife Management* 61, 1393–1405.
- Mate, B.R., Lagerquist, B.A., Calambokidis, J., 1999. The movements of North Pacific blue whales off Southern California and their southern fall migration. *Marine Mammal Science* 15 (4), 1246–1257.
- McClain, E.P., Pichel, W.G., Walton, C.C., 1985. Comparative performance of AVHRR-based multichannel sea surface temperatures. *Journal of Geophysical Research* 90, 11587–11601.
- McHugh, J.L., 1952. The food of albacore (*Germon alalunga*) off California and Baja California. *Scripps Institute of Oceanography Bulletin* 6 (4), 161–172.
- Mendilaharsu, M.L., Gardner, S.C., Seminoff, J.A., Rodriguez, R.R., 2005. Identifying critical foraging habitats of the green turtle (*Chelonia mydas*) along the Pacific coast of the Baja California peninsula, Mexico. *Aquatic Conservation of Marine and Freshwater Ecosystems* 15, 259–269.
- Minnett, P.J., 1991. Consequences of sea surface temperature variability on the validation and applications of satellite measurements. *Journal of Geophysical Research* 96 (C10), 18,475–18,489.
- Moore, S.E., Watkins, W.A., Daher, M.A., Davies, J.R., Dahlheim, M.E., 2002. Blue whale habitat associations in the northwest Pacific: analysis of remotely sensed data using Geographic Information System. *Oceanography* 15 (3), 20–25.
- Nichols, W.J., 2003. Biology and conservation of sea turtles in Baja California, Mexico. Ph.D. Dissertation. The University of Arizona.
- Nichols, W.J., Resendiz, A., Mayoral-Rousseau, C., 2000. Biology and conservation of loggerhead turtles in Baja California, Mexico. In: Kalb, H.J., Wibbels, T. (compilers), Proceedings of the Nineteenth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS-SEFSC-443, pp. 169–171.
- Olson, D.B., Hitchcock, G.L., Mariano, A.J., Ashjan, C.J., Peng, G., Nero, R.W., Podesta, G.P., 1994. Life on the edge: marine life and fronts. *Oceanography* 7 (2), 52–60.

- Olson, P.A., Pitman, R.L., Ballance, L.T., Hough, K.R., Dutton, P.H., Reilly, S.B., 2001. Summary of seabird, marine turtle, and surface fauna data collected during a survey in the eastern tropical Pacific Ocean, July 28–9 December 2000. U.S. Department of Commerce. NOAA Technical Memorandum. NOAA-NMFS-SWFSC-304.
- Owen, R.W., 1981. Fronts and eddies in the sea: mechanisms, interactions and biological effects. In: Longhurst, A.R. (Ed.), Analysis of Marine Ecosystems. Academic Press, New York, pp. 197–231.
- Peckham, S.H., Nichols, W.J., 2003. Why did the turtle cross the ocean? Pelagic red crabs and loggerhead turtles along the Baja California coast. In: Seminoff, J.A. (compiler). Proceedings of the Twenty-Second Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-503, 308pp.
- Podesta, G.P., Browder, J.A., Hoey, J.J., 1993. Exploring the association between swordfish catch rates and thermal fronts on U.S. longline grounds in the western North Atlantic. Continental Shelf Research 13 (2/3), 253–277.
- Polovina, J.J., Kobayashi, D.R., Parker, D.M., Seki, M.P., Balazs, G.H., 2000. Turtles on the edge: movement of loggerhead turtles (*Caretta caretta*) along oceanic fronts spanning longline fishing grounds in the central North Pacific, 1997–1998. Fisheries Oceanography 9, 1–13.
- Polovina, J.J., Howell, E., Kobayashi, D.R., Seki, M.P., 2001. The transition zone chlorophyll front, a dynamic global feature defining migration and forage habitat for marine resources. Progress in Oceanography 49, 469–483.
- Polovina, J.D., Uchida, I., Balazs, G., Howell, E., Parker, D., Dutton, P., 2006. The Kuroshio extension current bifurcation region: a pelagic hotspot for juvenile loggerhead sea turtles. Deep-Sea Research II, this issue [doi:10.1016/j.dsr2.2006.01.006].
- Reid Jr., J.L., Roden, G.I., Wyllie, J.G., 1958. Studies of the California current system. California Cooperative Oceanic Fisheries Investigations Reports 6, 28–56.
- Reilly, S.B., Thayer, V.G., 1990. Blue whale (*Balaenoptera musculus*) distribution in the eastern tropical Pacific. Marine Mammal Science 6 (4), 265–277.
- Roughan, M., Mace, A.J., Largier, J.L., Morgan, S.G., Fisher, J.L., Carter, M.L., 2005. Subsurface recirculation and larval retention in the lee of a small headland: a variation on the upwelling shadow theme. Journal of Geophysical Research 110, C10027.
- Roughgarden, J., Gaines, S., Possingham, H., 1988. Recruitment dynamics in complex life cycles. Science 241, 1460–1466.
- Schoenherr, J.R., 1991. Blue whales feeding on high concentrations of euphausiids around Monterey Submarine Canyon. Canadian Journal of Zoology 69, 583–594.
- Schwing, F.U., Moore, C., Ralston, S., Sakuma, K.M., 2000. Record coastal upwelling in the California current, 1999. California Cooperative Oceanic Fisheries Investigations Reports 41, 148–160.
- Sosa-Nishizaki, O., Shimizu, M., 1991. Spatial and temporal CPUE trends and stock unit inferred from them for the Pacific swordfish caught by the Japanese tuna longline fishery. National Research Institute for Far Seas Fisheries. Bulletin 28, March 1991.
- Squire, J.L., Au, D., 1990. Management of striped marlin (*Tetrapturus audax*) resources in the northeast Pacific a case for local depletion and core area management. In: Proceeds of the International Billfish Symposium, Part II, Kailua-Kona, Hawaii, 1–5 Aug 1988, pp. 199–214.
- Squire, J.L., Suzuki, Z., 1991. Migration trends of Striped Marlin (*Tetrapturus audax*) in the Pacific Ocean In: Stroud, R.H. (Ed.), Planning the Future of Billfishes—Research and Management in the 90s and Beyond, Part 2, Contributed papers.
- Sverdrup, H.U., Fleming, R.H., 1941. The waters off the coast of southern California. Scripps Institute of Oceanography Bulletin (4), 261–387.
- Teo, S.L.H., Boustany, A., Blackwell, S., Walli, A., Weng, K.C., Block, B.A., 2004. Validation of geolocation estimates based on light level and sea surface temperature from electronic tags. Marine Ecology Progress Series 283, 81–98.
- Uda, M., 1938. Researches on “*siome*” or current rips in the seas and oceans. Geophysical Magazine 11 (4), 307–372.
- Uda, M., 1959. Fisheries oceanography in Japan, especially on the principles of fish distribution, concentration, dispersal, and fluctuation. California Cooperative Oceanic Fisheries Investigations Reports 8, 25–31.
- Ullman, D.S., Cornillon, P.C., 1999. Satellite-derived sea surface temperature fronts on the continental shelf off the northeast U.S. coast. Journal of Geophysical Research 104, 23,459–23,478.
- Villanueva, D., 1991. La tortuga perica, *Caretta caretta gigas* (Deraniyagala, 1939), en la costa del Pacifico de Baja California Sur, Mexico. Departamento de Biología Marina. Universidad Autonoma de Baja California Sur. La Paz, BCS, Mexico, 68pp.
- Walsh, J.J., Kelly, J.C., Whitley, T.E., MacIssac, J.J., Huntsman, S.A., 1974. Spin-up of the Baja California upwelling ecosystem. Limnology and Oceanography 19, 553–572.
- Watson, K.P., Granger, R.A., 1998. Hydrodynamic effect of a satellite transmitter on juvenile green turtle (*Chelonia mydas*). Journal of Experimental Biology 201, 2497–2505.
- Wolanski, E., Hamner, W.H., 1988. Topographically controlled fronts in the ocean and their biological importance. Science 241, 177–181.
- Worm, B., Lotze, H.K., Myers, R.A., 2003. Predator diversity hotspots in the blue ocean. Proceedings of the National Academy of Sciences USA 100, 9884–9888.
- Yen, P., Sydeman, W.J., Hyrenbach, K.D., 2003. Marine bird and cetacean associations with bathymetric habitats and shallow-water topographies: implications for trophic transfer and conservation. Journal of Marine Systems 50, 79–99.
- Yoder, J., Ackleson, S., Barber, R., Flament, P., Balch, W., 1994. A line in the sea. Nature 371, 689–692.