

# Epipelagic fish distributions in relation to thermal fronts in a coastal upwelling system using high-resolution remote-sensing techniques

Douglas C. Reese<sup>1\*</sup>, Robert T. O'Malley<sup>2</sup>, Richard D. Brodeur<sup>3</sup>, and James H. Churnside<sup>4</sup>

<sup>1</sup>Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, USA

<sup>2</sup>Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331, USA

<sup>3</sup>Northwest Fisheries Science Center, NOAA, Hatfield Marine Science Center, Newport, OR 97365, USA

<sup>4</sup>NOAA Earth System Research Laboratory, 325 Broadway, Boulder, CO 80305, USA

\*Corresponding Author: tel: +1 541 740 3693; fax: +1 541 737 3590; e-mail: [dreese@lifetimer.oregonstate.edu](mailto:dreese@lifetimer.oregonstate.edu).

Reese, D. C., O'Malley, R. T., Brodeur, R. D., and Churnside, J. H. 2011. Epipelagic fish distributions in relation to thermal fronts in a coastal upwelling system using high-resolution remote-sensing techniques. – ICES Journal of Marine Science, 68: 1865–1874.

Received 23 October 2010; accepted 10 May 2011; advance access publication 13 July 2011.

Coastal upwelling systems are characterized by substantial spatial and temporal variability with respect to surface conditions, with fauna patchily distributed and high abundances in localized areas. Examining habitat associations on finer spatial scales than previous studies have been able to achieve would advance the understanding of important marine coastal ecosystems. This study evaluates the spatial and temporal relationships of single fish and fish schools with sea surface temperature (SST) fronts in the northern California Current upwelling system, using lidar (light detection and ranging) from an aircraft to sample surface waters over the continental shelf. High-resolution data were collected on the distribution of surface nekton and SST, then the locations of fish were analysed with respect to their proximity to SST fronts using GIS spatial analyses. Both fish schools and solitary fish were located significantly closer to fronts than would be expected by chance. The association of fish to fronts varied with the progression of the upwelling season such that fish associated less with fronts under stronger upwelling conditions. The relationships observed indicate the importance of thermal features to fish as a habitat component in a variable upwelling environment and have implications for management and conservation.

**Keywords:** California Current, coastal ecosystem, front, habitat, lidar, pelagic fish, sea surface temperature, spatial analysis, upwelling.

## Introduction

Identifying species distributions and their associations with specific habitat features is necessary for conservation and wise management. Recent studies in marine ecosystems, however, have highlighted the complexities involved in such associations within these heterogeneous environments (Etnoyer *et al.*, 2004; Ainley *et al.*, 2009). Hence, considerable attention has been directed at identifying marine biological hotspots and the biophysical relationships associated with these ecologically important areas (Hughes *et al.*, 2002; Piatt *et al.*, 2006; Reese and Brodeur, 2006; Sydeman *et al.*, 2006). Within terrestrial and coral reef systems, biological hotspots have traditionally been defined in terms of biodiversity (Myers, 1997; Hughes *et al.*, 2002). In contrast, biological hotspots in pelagic systems are typically defined as areas of high chlorophyll concentration (Valavanis *et al.*, 2004), areas where highly mobile species spend considerable time foraging (Piatt *et al.*, 2006; Polovina *et al.*, 2006), or in terms of community characteristics such as species richness, abundance, and biomass (Reese and Brodeur, 2006).

Eastern boundary currents (California, Canary, Humboldt, and Benguela) are some of the most biologically productive regions of the world's oceans as a consequence of the upwelling of nutrient-rich waters there (Carr and Kearns, 2003). Despite the

small proportion of ocean surface upwelling areas cover (~0.1% of the total ocean area), they support up to 50% of the global fish catch (Lalli and Parsons, 1993). Fish catches are good in these regions because of the high rates of production and because large numbers of fish can be harvested in proximity to the coast. Undoubtedly, such regions are of great ecological and economic value, but they are at risk of environmental change and overexploitation (Jackson *et al.*, 2001; Myers and Worm, 2003; Planque *et al.*, 2010).

Fish congregate in areas of sharp physical gradients, but the key forcing mechanisms causing variability in the distribution of such congregations are poorly understood. Recent tagging studies and visual observations have provided insight into important habitat features of highly mobile species (Schick *et al.*, 2004; Etnoyer *et al.*, 2006; Doniol-Valcroze *et al.*, 2007). Most of these studies demonstrate that sea surface temperature (SST) fronts are important habitat features that influence the distributions of pelagic species. SST fronts have long been of interest to marine ecologists because of the increased production typically associated with them.

Previous innovative studies employing remotely sensed data to identify thermal features typically used averaged SST values over some period (e.g. a week or a month) to determine the locations of SST fronts (e.g. Belkin and Cornillon, 2003; Hardman-Mountford and McGlade, 2003; Wang *et al.*, 2007).

The locations of SST fronts in areas characterized by pulsed, upwelling events, however, tend to be ephemeral and change over relatively short time-scales. The strength of the upwelling event will also influence the distribution of food resources, such that stronger upwelling and horizontal transport across the shelf distributes and disperses prey (Chavez and Messié, 2009). Therefore, a method of determining the fine-scale locations of fish while obtaining synoptic coverage of SST in these areas would be of great utility. Upwelling regions are often difficult to map from ships because of their spatial extent and the dynamic nature of the aggregations that do not allow ships to sample the area of interest completely within a reasonable time. Alternatively, airborne lidar (light detection and ranging) is effective at detecting fish and zooplankton in the ocean (Churnside *et al.*, 2001; Churnside and Thorne, 2005), with high correlations between lidar and echosounder measurements (Churnside *et al.*, 2009). Aerial surveys and lidar imaging provide a good combination of sampling tools with which to describe and explain the spatial distributions and habitat characteristics of marine life in high-resolution spatial and temporal detail.

The primary goal of this study was to evaluate the spatial and temporal relationships between both solitary fish and fish schools and the physical environment using a GIS-based method on synoptic measurements with improved spatial and temporal resolution of observations. We then test the hypothesis that daylight distributions of surface-dwelling fish are related to thermal fronts within the coastal upwelling region by comparing the distances of both fish schools and solitary fish from SST fronts with points selected randomly along the tracklines. Further, we examine how this relationship changes as the upwelling season progresses and productivity increases over the shelf, which may make it less likely that fish will associate with fronts given the increased availability of food resources away from the fronts.

## Methods

The study was conducted along the coast of Oregon and Washington in the northern California Current (Figure 1). The shelf is relatively narrow, extending 14–64 km offshore, so studies conducted there allow for sampling over the entire shelf plus oceanic waters far off the shelf. The region encompasses the Columbia River plume, the largest ocean plume of freshwater on the west coast of North America, as well as offshore banks, many submarine canyons, and persistent eddy features (Hickey and Banas, 2003).

## Upwelling

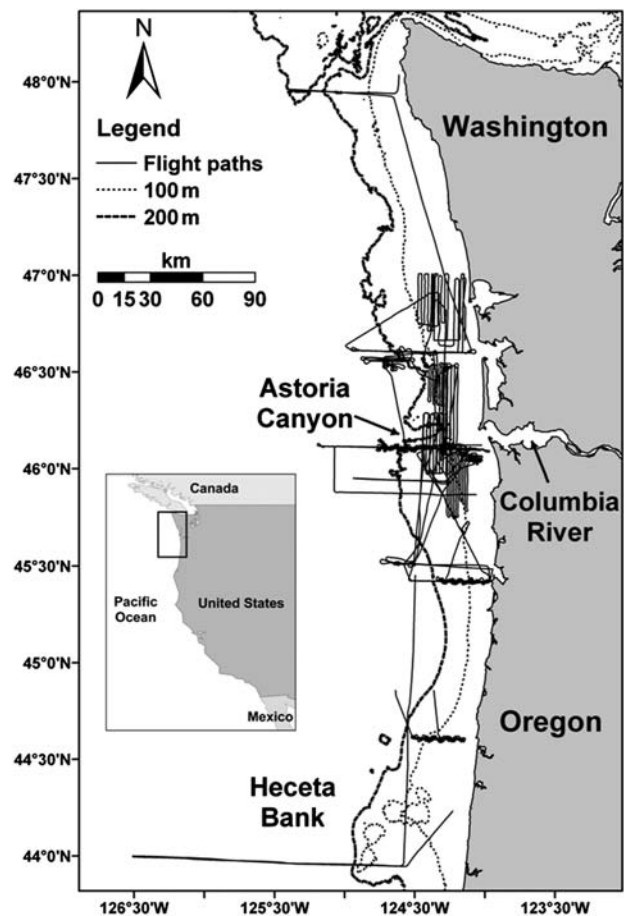
The physical oceanographic processes within the study region are dominated by seasonal wind-driven upwelling, with considerable horizontal structure with respect to SST. During summer, flow along the coast is generally from the north, with meanders and jets associated with topographic features (Barth *et al.*, 2005). Along the west coast of North America, equatorward wind supplies frictional stress to the surface of the ocean, and along with the earth's rotation, results in surface waters moving away from the coast. This displaced water is then replaced by deeper, nutrient-rich, colder water that is upwelled to the surface from depths of ~50–100 m. The upwelling season in the area typically starts in May and ends in September/October. Seasonal upwelling is highly variable along the coast of North America. The region is characterized by pulsed upwelling events and, even during the upwelling season, periods of downwelling. Daily upwelling

indices at 45°N 125°W were obtained from the NOAA/NMFS Pacific Fisheries Environmental Laboratory website (<http://www.pfeg.noaa.gov>). For this study, we used the daily upwelling indices to interpret the presence and abundance of SST fronts within the study area.

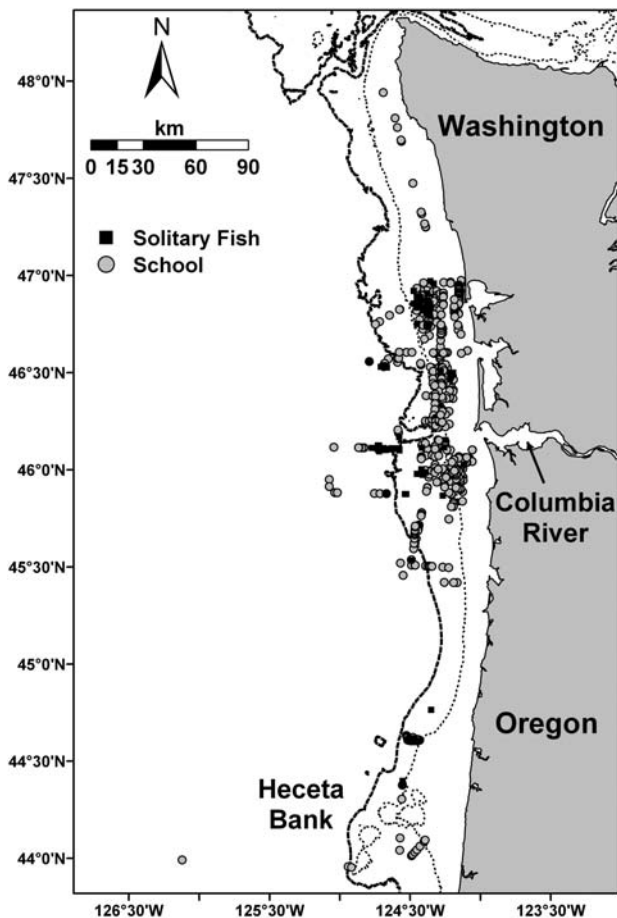
## Lidar survey data

Data were collected during three periods, 9–17 July 2003, 16–29 August 2005, and 25 May – 11 June 2006, in an attempt to capture the seasonal progression of upwelling and related physical and biological responses. Sampling was along the coast of northern Oregon and southern Washington and included the Columbia River plume (Figures 1 and 2). During each year, 6–9 flight surveys were conducted during daylight; however, only flights with adequate spatial coverage, fish, and SST data were used in the analyses. Several flights were eliminated from the analyses because of a lack of good spatial coverage or poor weather.

Aerial sampling was conducted with the NOAA fish lidar, which is a non-scanning, profiling system that operates much like an echosounder (Churnside *et al.*, 2001; Carrera *et al.*, 2006). The lidar transmitted about 100 mJ of linearly polarized green (532 nm) light in a 12-ns pulse at a rate of 30 pulses  $s^{-1}$ . Instruments were mounted on a twin-engine aircraft and pointed ~15° off nadir to minimize the specular reflection from the sea surface. The flight altitude was ~300 m, and the airspeed was 60–90  $m s^{-1}$ ,



**Figure 1.** The study area, showing the flight-track coverage over all 3 years of the study.



**Figure 2.** Distribution of fish schools and solitary fish over the 3-year observation period.

depending on the area to be covered in a single flight. The laser beam diameter at the surface was 5 m, large enough for the power density at the surface to be safe for humans (ANSI, 1993) and marine mammals (Zorn *et al.*, 2000). At the same time, it is small enough for the background sunlight to be a small part of the overall signal. The scattered light from the water column was collected by a telescope with a field of view matched to the laser-beam divergence. The light collected by the telescope was detected by a photomultiplier tube, logarithmically amplified to increase the dynamic range, and digitized at a rate of  $10^9$  samples  $s^{-1}$ . A polarizer on the telescope was used to detect only light linearly polarized in the plane orthogonal to that of the transmitter to increase detectability (Lewis *et al.*, 1999). The resulting profile of scattering in the water column had a depth resolution of 11 cm. The maximum depth of these profiles varied with water clarity, from  $\sim 15$  m near the shore to 45 m in the clearer waters off the shelf. Schools and individual fish returns were identified manually in the data. For schools, the start and the end of the school were identified, and the along-track length was calculated as the distance between these points. The position was taken as that at the centre of the school. Processing for individual fish was similar to that for schools, except that no length was estimated. Depending on water clarity, we estimated the smallest solitary fish size detectable by the lidar to be some 30–50 cm long.

The SST was measured from the aircraft with a Heitronics KT 15.85 D pyrometer pointing straight down. The instrument

measures brightness temperature over a wavelength range of 8–14  $\mu\text{m}$ , and the temperature was used without correction.

### Front detection

A two-dimensional edge-detection algorithm (Cayula and Cornillon, 1992) is used commonly as a front-detection tool for satellite data (see Belkin *et al.*, 2009). We used the algorithm by applying it to our high-resolution aerial SST trackline data and converting from a two-dimensional routine to a one-dimensional routine to account for the linear nature of the flight path. All statistical criteria and tests were implemented; only the cohesion test was relaxed slightly to take into account the smaller sample sizes. The one-dimensional version of the algorithm was tested on windows of varying lengths, and a 24-point window was selected as the preferred size. For a given window of data, the algorithm was tested to evaluate where it would be most likely to detect the presence of two distinct groups in terms of SST, as indicated by the variances. When the variance test was successful (indicating a bimodal distribution), we examined (i) the signal-to-noise ratio to verify that it was sufficient, (ii) the size of the two subsets to verify that they were sufficient, and (iii) whether there was sufficient cohesion on both sides of the statistically determined front. If successful based on the three criteria, the front was marked and the window shifted over one point to start the analysis again. The process continued until all points along the trackline had been evaluated.

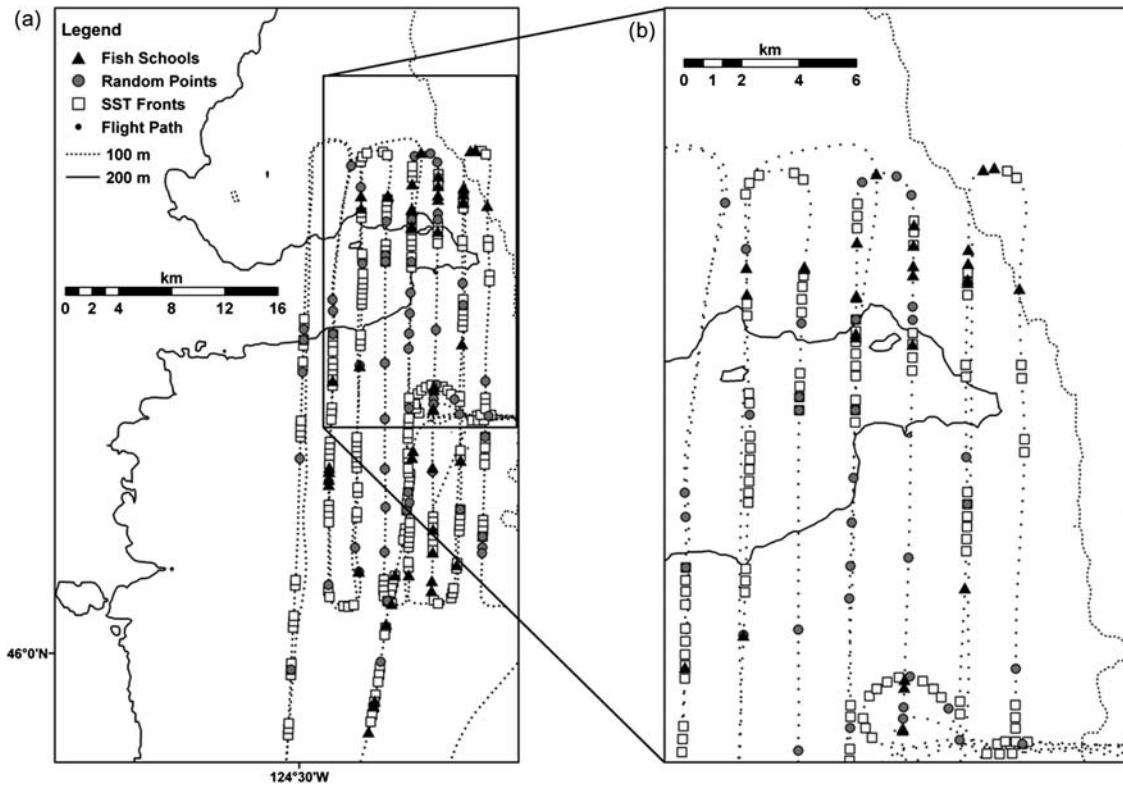
### Trawl data

Night-time trawl sampling was conducted during July 2003 (Churnside *et al.*, 2009) and daylight fish sampling during August 2005 and June 2006, using a chartered fishing vessel. At each trawl station, fish collections were made with a Nordic 264 rope trawl (Nor'Eastern Trawl Systems, Inc., Bainbridge Island, WA) towed in the surface layer for 30 min at a speed of  $6 \text{ km h}^{-1}$  (see Brodeur *et al.*, 2004, for additional sampling detail). The net measured 30 m wide by 18 m deep, and its mesh size was 162.6 cm in the throat and 8.9 cm in the codend, with a 6.1-m long, 0.8-cm mesh liner sewn into the codend. In 2005, 31 trawls were conducted in daylight, in 2006, 9 trawls in daylight, and in 2003, 12 night-time trawls. Trawl data were used for ground-truthing and to aid interpretation of the lidar data as a means of determining the species of schooling fish present in the water at the time of the aerial surveys.

### Spatial data analyses

A front is commonly defined as a rapid change in SST over a short distance as a result of the interface between two water masses. Once SST fronts had been identified by the method described above, the distances between the fish schools or solitary fish locations and the nearest front were calculated. For each day, an equal number of points along the flight path was selected randomly using Hawth's Analysis Tools for ArcGIS ([www.spatial ecology.com/htools](http://www.spatial ecology.com/htools)). The distances to SST fronts were then compared between random points along the flight path and the observed fish school and solitary fish locations (Figure 3).

To test the hypothesis that fish were closer to SST fronts than would be expected from random locations along the flight tracks, a one-sided standard *t*-test ( $\alpha = 0.05$ ) was used. In some instances, equal variances were not assumed, because of heteroscedasticity in the data that was not improved with



**Figure 3.** Locations of fish schools relative to SST fronts compared with the locations selected randomly along the flight path on 16 August 2005 at two spatial scales: (a) larger scale, and (b) finer spatial scale. Note that the 200 m isobath represents the edge of the continental shelf (shelf break).

log-transformation. In those cases, a  $t$ -test for unequal variances (Ruxton, 2006) was used. In that test, the unequal variance  $t$ -test still involves the calculation of a  $t$ -statistic, which is then compared with the appropriate value in standard  $t$ -tables, but the calculation of the degrees of freedom differs (Moser and Stevens, 1992).

To test for seasonal differences in the association of SST fronts based on the upwelling season an ANOVA followed by a Tukey honestly significant difference *post hoc* multiple comparison test was used. As it was not possible to conduct all flights during a year to cover the entire upwelling season, it was assumed that the month sampled was representative of the typical conditions experienced in the region during that period. A one-sided Pearson's correlation was used to examine the relationship between daily mean fish distances to fronts and the daily upwelling index to test specifically whether fish distances to fronts increased with increased upwelling, as predicted. Data were log-transformed when necessary to meet the normality and homoscedasticity assumptions of parametric tests. To test for violation of independence in the data (spatial autocorrelation), Moran's  $I$  was used to evaluate whether the pattern of distances to SST fronts was clustered, dispersed, or random (Fortin et al., 2002). A Moran's  $I$  value near  $+1.0$  indicates clustering and positive spatial autocorrelation, whereas a value near  $-1.0$  indicates dispersion. Values near zero indicate an absence of spatial autocorrelation. The Moran's  $I$  function calculates a  $z$ -score value that indicates whether the spatial patterns (e.g. clustering or dispersion) could be the result of random chance or are statistically significant.

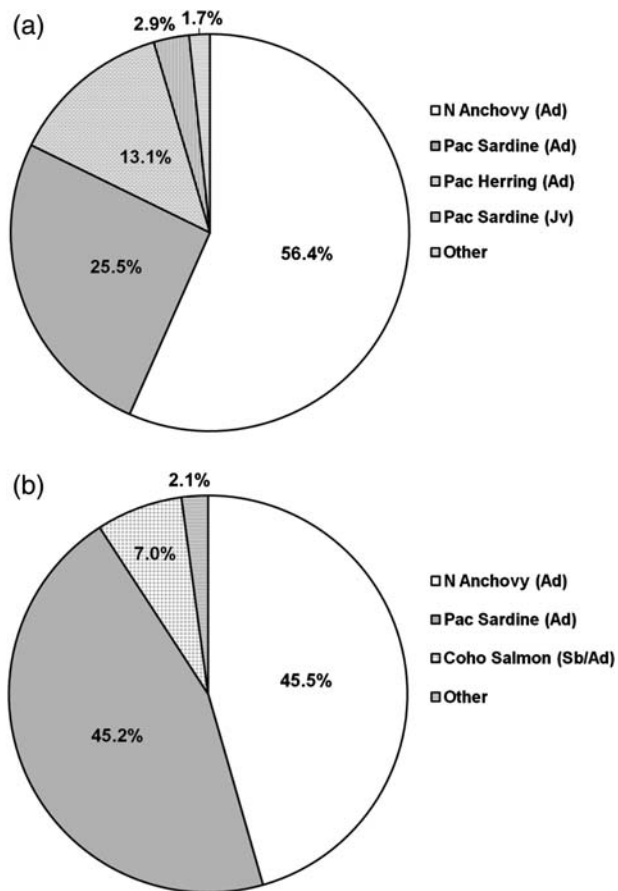
## Results

### Catch statistics for trawl surveys

Pacific sardine (*Sardinops sagax*), followed by adult Pacific herring (*Clupea pallasii*) and northern anchovy (*Engraulis mordax*), were numerically the dominant species caught at night in 2003 (see Churnside et al., 2009, for more catch detail). During both 2005 and 2006 surveys, adult northern anchovy (*E. mordax*) were numerically the dominant fish species in surface trawls taken during the aerial surveys, accounting for approximately half of all the fish caught (Figure 4). Adult Pacific sardine (*S. sagax*) were the second most abundant species caught during both years. Adult Pacific herring (*C. pallasii*) were the third most abundant species caught during August 2005, but were not abundant during the June 2006 trawls (Figure 4). Conversely, subadult/adult coho salmon were taken during June 2006 trawls in moderate abundance, yet were not frequently encountered during the August 2005 trawls (Figure 4). Each remaining species/age class was much less abundant and individually accounted for  $<3\%$  of the total catch during each year.

### Upwelling

During the July (early summer) 2003 aerial surveys, upwelling was relaxed both immediately before and during the initial days of the study (Figure 5a). Upwelling-favourable winds occurred briefly during the study, but the magnitude of upwelling was moderate and at the end of the study. Upwelling was strongest during August (late summer) 2005, with relatively strong upwelling



**Figure 4.** Fish species composition of nekton surface tows taken during the aerial observations for (a) August 2005 and (b) June 2006. Ad, adults; Jv, juveniles; Sb, subadults. See Churnside *et al.* (2009), for trawl catches made during the July 2003 flights.

events immediately preceding the study period, followed by a period of relaxation over the first few days of sampling (Figure 5b). There was a brief but relatively strong, pulsed upwelling event in the middle of the study period that was followed by a relaxation of upwelling-favourable wind towards the end of the surveys. Upwelling was the weakest of any survey period during the May/June (late spring) 2006 sampling period (Figure 5c). Upwelling events were sporadic during the month before the 2006 surveys, but there was a strong downwelling event at the onset of the sampling and again in the middle of the sampling period, resulting in fewer prominent SST fronts. Towards the end of the study period, there was again a moderate upwelling event.

### Fish distances to SST fronts

Many more fish schools were encountered than solitary fish during the daylight aerial surveys (Table 1, Figure 2). A greater proportion of schools (94.1%) than of solitary fish (68.4%) was found closer to shore over the shelf, whereas solitary fish were encountered more frequently beyond the shelf break (200 m isobath) than fish schools. As a result, 31.6% of solitary fish were found offshore beyond the shelf break, compared with only 5.9% of the fish schools.

Fish schools were consistently closer to SST fronts (mean  $\pm$  s.e.,  $0.69 \pm 0.04$  km) than would be expected from a random

distribution ( $0.97 \pm 0.08$  km) over the 3 years of the study ( $t_{1014} = -3.229$ ,  $p < 0.001$ ). The pattern was the same each year despite the increased distance to fronts associated with the time of year during the upwelling season (Figure 6). During 2003, fish schools on average were approximately half the distance to SST fronts compared with points selected randomly ( $t_{76} = -1.918$ ,  $p = 0.030$ ; Figure 6). Fish schools were farthest from SST fronts during the 2005 survey, but again were significantly closer than random points ( $t_{677} = -2.723$ ,  $p = 0.004$ ). Fish schools were closest to SST fronts during the 2006 survey (Figure 6) and were again significantly closer to SST fronts than points chosen randomly ( $t_{329} = -3.131$ ,  $p = 0.001$ ).

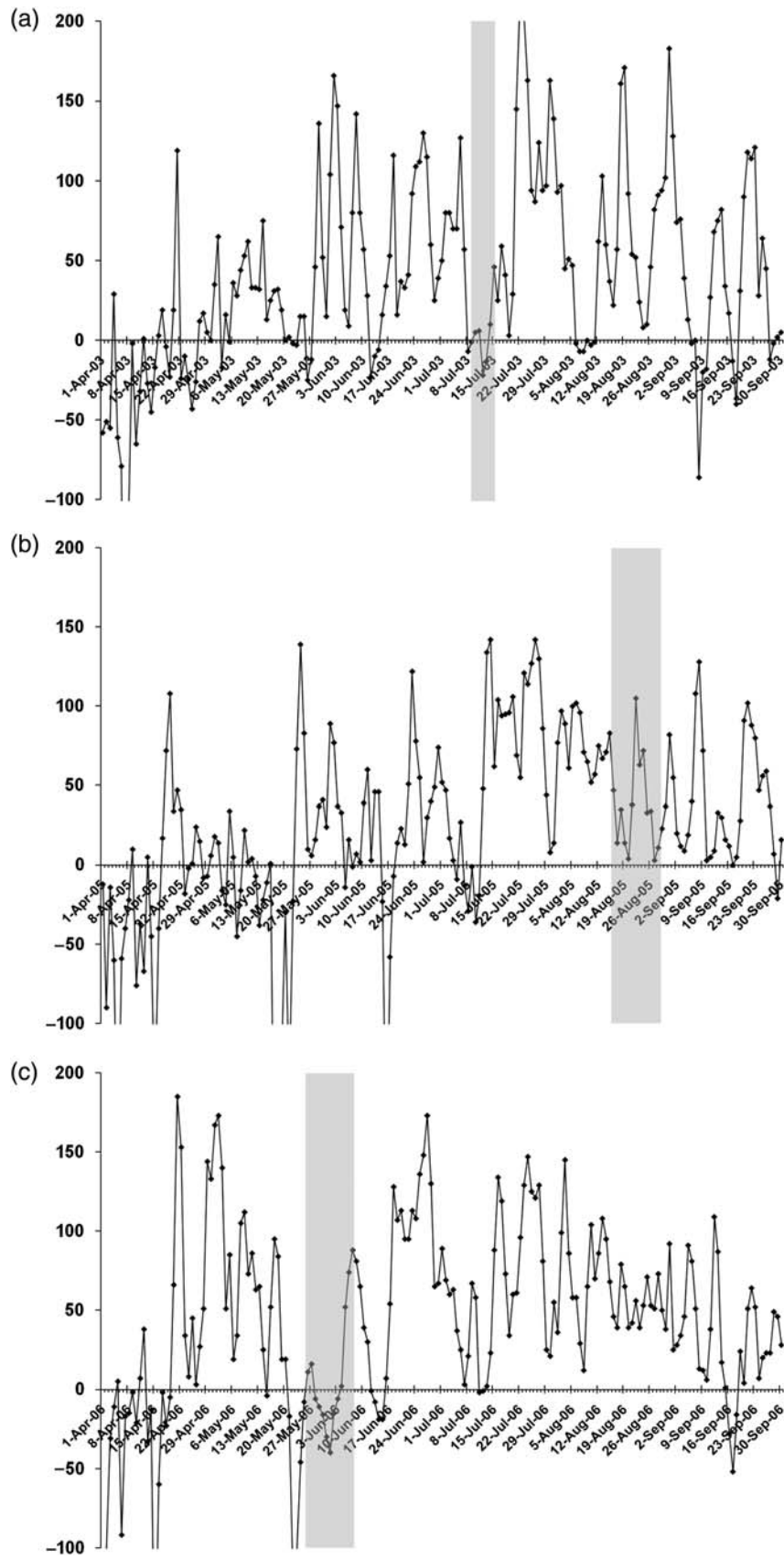
The observed spatial distributions and associations with SST fronts were similar for solitary fish (Figure 7). Overall, solitary fish were significantly closer to SST fronts ( $0.61 \pm 0.09$  km) than an equal number of points selected randomly ( $1.02 \pm 0.20$  km;  $t_{210} = -1.876$ ,  $p = 0.031$ ). However, only during 2006 (late spring) were daylight observations of solitary fish statistically closer to SST fronts than points selected randomly along the flight path ( $t_{98} = -2.405$ ,  $p = 0.009$ ; Figure 7).

Although spatial autocorrelation was not prevalent in the analyses, a moderate degree of spatial autocorrelation was found when distances to SST fronts for all schools were combined for the 3 years of study (Moran's  $I = 0.381$ ,  $z$ -score = 2.278,  $p = 0.011$ ) and for distances to SST fronts for fish schools in 2005 (Moran's  $I = 0.652$ ,  $z$ -score = 2.876,  $p = 0.002$ ). A lack of independence in data can increase type I error such that some relationships appear to be significant when they are not; however, we found only a moderate degree of autocorrelation in just two analyses. Given the high degree of significance obtained from the  $t$ -tests for the fish schools in these two cases, we chose to maintain the use of the parametric test despite the moderate degree of autocorrelation, because the degree of autocorrelation was not likely to affect the highly significant results of the  $t$ -test notably. Nonetheless, results for those two analyses should be interpreted with caution. No other significant spatial autocorrelation was detected for schools or solitary fish.

### Seasonal fish association with SST fronts

Fish school distance to SST fronts differed with respect to the time during the upwelling season (ANOVA;  $F = 35.268$ ,  $p < 0.001$ ; Figure 6). *Post hoc* tests indicated a significantly shorter distance between fish schools and SST fronts for August 2005 (late summer) than during either July 2003 (early summer,  $p = 0.029$ ) or May/June 2006 (late spring,  $p < 0.001$ ; Figure 6). The pattern was not as dramatic for solitary fish, but a significant difference in the distance to SST fronts was observed depending on the time during the upwelling season ( $F = 10.114$ ,  $p < 0.001$ ; Figure 7). *Post hoc* tests showed that for solitary fish, the shortest distance to SST fronts was in late spring (May/June) of 2006, when the fish were significantly closer to fronts than they were in late summer (August) 2005 ( $p < 0.001$ ), when the distances were greatest.

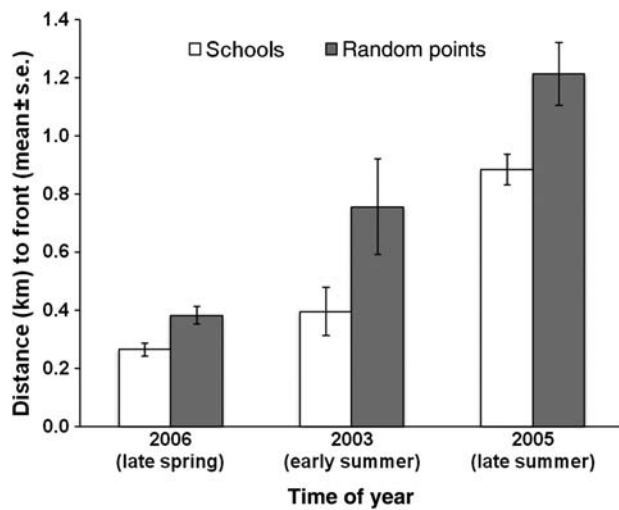
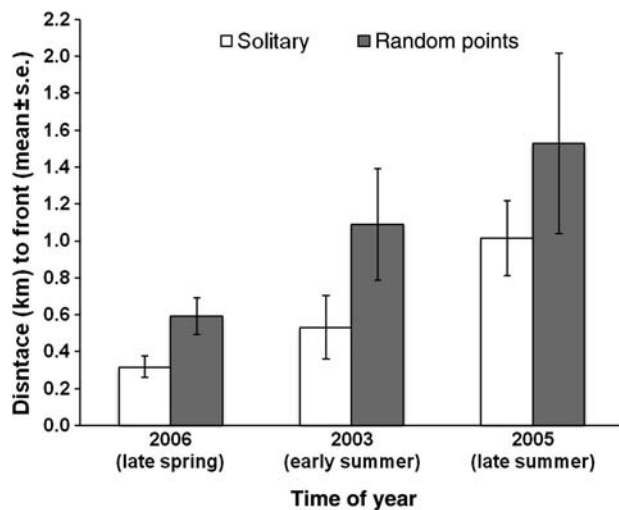
If the time during the upwelling season, as related to the magnitude of SST fronts, is responsible for the differences observed in distances to SST fronts for both fish schools and solitary fish, then it is predicted that the same patterns would be observed for random points along the flight paths. For an equal number of points selected randomly as fish schools, the pattern was the same, with a significant difference with respect to distance to SST fronts according to the time during the upwelling season



**Figure 5.** Daily upwelling indices from 1 April to 30 September for (a) 2003, (b) 2005, and (c) 2006. The y-axis represents the upwelling index where upwelling units are in  $\text{m}^3 \text{s}^{-1} 1000 \text{ m}^{-1}$  coastline, and shaded bars represent the survey dates. Positive values are upwelling and negative values downwelling events.

**Table 1.** Number of suitable observation days and lidar-detected fish in aerial surveys for each of the years of study.

Year (season)	Number of flights	Number of schools	Number of solitary fish
2003 (early summer)	3	39	16
2005 (late summer)	7	471	40
2006 (late spring)	3	183	50
Total	13	693	106

**Figure 6.** Mean ( $\pm$  s.e.) distance (km) of fish schools and random points along the flight paths to SST fronts for each year (season) of study.**Figure 7.** Mean ( $\pm$  s.e.) distance (km) of solitary fish and random points along the flight paths to SST fronts for each year (season) of study.

( $F = 11.874$ ,  $p < 0.001$ ; Figure 6). *Post hoc* tests showed significantly shorter distances of points selected randomly to SST fronts during May/June 2006 (late spring) than for August 2005 (late summer;  $p < 0.001$ ). Although the overall pattern was the same between random points and fish schools with increased

distance to fronts with the progression of the upwelling season, there were no other statistically significant differences. Similarly, for an equal number of points selected randomly as solitary fish, the pattern was generally the same, with the shortest distances to fronts during late spring (May/June 2006) and the greatest distances during late summer (August 2005), with intermediate distances during early summer (July 2003). However, no statistically significant difference was found (Figure 7).

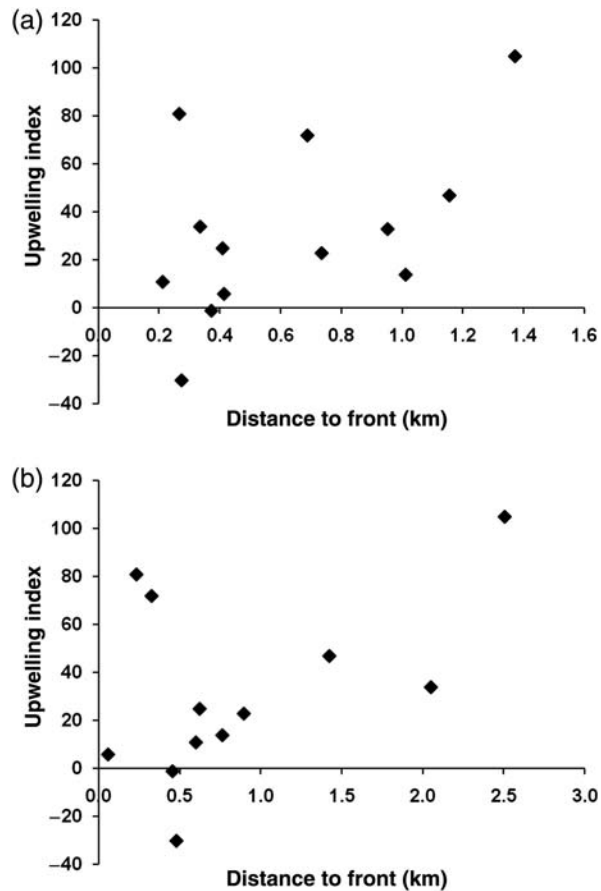
We also examined the relationship between the daily upwelling index and the mean daily distances to fronts for both fish schools and solitary fish, to determine whether fish do not associate as closely with stronger fronts. There was a positive correlation between fish school distance to fronts and the upwelling index, demonstrating that the distance of fish schools to SST fronts increases with the magnitude of the upwelling index (one-sided Pearson's correlation coefficient 0.504,  $p = 0.040$ ; Figure 8a). Although the trend was similar for solitary fish, the result was not statistically significant (correlation coefficient 0.460,  $p = 0.066$ ; Figure 8b).

## Discussion

A novel technique was used for this work, employing aerial sampling with lidar and other instrumentation to sample large areas in the coastal upwelling environment of the Pacific Northwest at high spatial and temporal resolution. The results showed that the daylight distributions of schooling fish (most likely northern anchovy and Pacific sardine) consistently depended on SST fronts, yet the association was complex in that it was related to the timing and magnitude of upwelling events. A similar pattern was observed for solitary fish, but solitary fish tended to be farther offshore and in general farther from fronts than fish schools.

Fronts are biologically active areas in the ocean (Belkin, 2002; Bakun, 2006). Phytoplankton and zooplankton accumulate in frontal zones offering a localized area of concentrated food particles for feeding organisms (Bakun, 2006). The increased productivity in those areas attracts a wide variety of fish, bird, and mammal predators (Sims and Quayle, 1998; Hofer, 2000; Etnoyer *et al.*, 2006; Doniol-Valcroze *et al.*, 2007; Wang *et al.*, 2007; Ainley *et al.*, 2009). In the Oregon coastal upwelling region, cross-shelf zonation in the spatial distribution of zooplankton is typically associated with SST (Reese *et al.*, 2005). Zooplankton concentrations are spatially patchy, with highest concentrations nearshore in cooler upwelled water (Reese *et al.*, 2005). In addition, there is typically cross-shelf variation in the sizes and life stages of euphausiids, a primary food source for many fish species, with higher densities and biomass of larvae and juveniles nearshore, and of older, larger stages offshore (Gómez-Gutiérrez *et al.*, 2005).

Optimal foraging theory predicts that organisms should seek out food items at locations where there is a higher probability of finding prey, hence reducing the energy expended in searching for prey. As predicted, schooling fish were consistently closer to SST fronts and in greater concentration over the shelf (<200 m), where zooplankton concentration is highest. The results from the trawls made at the same time as the aerial surveys demonstrated that schooling fish being observed with the lidar were most likely northern anchovy and Pacific sardine. In the region, both species feed on plankton (Miller and Brodeur, 2007), which aggregate at fronts. Northern anchovy feed primarily on phytoplankton and euphausiids, and Pacific



**Figure 8.** Relationship between the daily upwelling index and the distance to SST fronts (km) for (a) fish schools and (b) solitary fish. The y-axis represents the upwelling index where upwelling units are in  $\text{m}^3 \text{s}^{-1} 1000 \text{ m}^{-1}$  coastline. Positive values represent upwelling and negative values downwelling events.

sardine primarily on phytoplankton, copepods, and to a lesser extent, euphausiids (Miller and Brodeur, 2007).

The same general pattern was observed for solitary fish. These were encountered more frequently farther offshore than fish schools and were overall quantitatively closer to SST fronts than random points. Distances to fronts were not statistically different among years for solitary fish, but they were for fish schools, which were significantly closer only during late spring (May/June 2006) than random points along the flight path. There are three potential reasons for the lack of detection of significant differences for solitary fish. The first is that there may have been too few data on solitary fish ( $n = 106$  solitary fish vs. 693 fish schools) to determine a statistical difference. The second explanation could be that solitary fish were farther offshore, beyond the shelf break, where the magnitude of pulsed upwelling fronts diminishes as the colder, upwelled water heats and becomes less discernible from the warmer offshore water. The large, solitary fish beyond the shelf break were most likely highly mobile albacore (*Thunnus alalunga*), because there was an active fishery for that species going on, particularly during the August period, that could be seen from the aircraft (RDB, pers. obs.). We are less certain of the species of solitary fish observed over the shelf. Assuming them to be tuna, the lack of a spatial relationship with

SST fronts is unsurprising. In the Gulf of Maine, Schick *et al.* (2004) found an inconsistent relationship between visual aerial surveys of bluefin tuna and satellite-derived SST fronts, suggesting that some other environmental feature, such as prey density, was important in predicting the distribution of the fish. The third explanation could be that large solitary organisms (e.g. tuna, sharks, or another large fish or mammal) utilize SST fronts but do not spend extensive periods associated with them in the region. As the productive, upwelled coastal water is transported offshore and becomes less discernible from the surrounding water, the patches of upwelled water likely become smaller, requiring larger solitary fish to travel between patches more frequently than fish schools located on the shelf, where productivity is more ubiquitous. Laurs *et al.* (1984) and Reddy *et al.* (1995) found the best catch rates for tuna near temperature fronts. It is believed that tuna aggregate near fronts and use the areas as feeding sites (Fiedler and Bernard, 1987). However, Laurs *et al.* (1984) and Reddy *et al.* (1995) relied on fishery catch data, so their relationships were based on where the fish were aggregating, resulting in the best catches. Schick *et al.* (2004) used aerial visual surveys coupled with satellite imagery, so had better spatial and temporal resolution than the other studies. Moreover, just as in this study, they recorded the fish locations wherever they were encountered, not just where they were aggregating to feed. This suggests that highly mobile tuna utilize temperature fronts, but not for lengthy periods, possibly just to feed or thermoregulate. A larger sample size of solitary fish identified utilizing the methods of this study would likely yield more conclusive results, however.

Coastal upwelling systems are well known for their high levels of productivity and are some of the most important regions on earth in terms of resource potential (Lalli and Parsons, 1993). The coastal region along the west coast of the United States is characterized by variable, pulsed, upwelling events throughout the upwelling season. The pulsed nature of upwelling leads to daily fluctuations in the distribution and abundance of SST frontal structures, yet schooling fish species are consistently found closer to them than would be expected by chance, suggesting that schooling fish can detect the slight changes in thermal gradients and select to associate with them.

A seasonal relationship was found for schooling and solitary fish, as well as for random points along the flight path, in terms of distance to SST fronts. All showed increasing distance to SST fronts as the upwelling season progressed (late spring, early summer, later summer; Figures 6–8). As the upwelling season progressed, upwelling events tended to be more frequent, with fewer periods of relaxation (Figure 5). As upwelling frequency increased, more nutrient-rich water was upwelled, resulting in greater primary production over larger areas of the shelf. Moreover, stronger upwelling and horizontal transport acts to distribute and disperse prey (Chavez and Messié, 2009), so it is unsurprising that fish schools, solitary fish, and even the points selected randomly tended to be farther from SST fronts as the upwelling season progressed. Although our seasonal sampling was not conducted over the course of a full year, we would expect the same results simply based on seasonal progression in upwelling activity and the horizontal transport of resources making food more ubiquitous across the shelf. With more food resources available across the shelf, and not just at fronts, fish could find food away from the fronts. This would have the added benefit to fish of allowing them to forage in locations where there were fewer predators if



the predators (e.g. seabirds and mammals) concentrate at the prominent fronts. The result of this would be that fish schools and solitary fish associated more closely with SST fronts during the periods of little upwelling. In such an instance, food resources may be scarce, requiring the fish to associate more closely at fronts where the food particles were concentrated.

Previous studies have shown the importance of thermal fronts to fish distributions (Reddy *et al.*, 1995; Sims and Quayle, 1998; Wang *et al.*, 2007). To assess the relationship between fish distributions relative to environmental features, such as SST fronts, fully, however, requires synoptic, high-resolution data. To date, most fish studies have utilized ship-based acoustic data, collection of which is limited by the speed that the ship can travel. In addition, environmental data are typically obtained *in situ* by sampling at stations spaced widely apart. Alternatively, some studies used satellite SST data to determine the locations of fronts (Fiedler and Bernard, 1987; Zainuddin *et al.*, 2006; Wang *et al.*, 2007), but those data are not obtained at the same time as information on the distributions of fish and often indicated the presence of more permanent frontal features such as those associated with the shelf break or convergence zones. To examine more ephemeral frontal features, which may be important habitat features to many marine species, and to obtain actual distances to thermal fronts, requires synoptic coverage of fish distributions and SST data. In this study, we acquired nearly synoptic coverage with the use of instruments mounted on an aircraft that sampled a large area of ocean surface over a relatively short period while identifying the locations of fish schools and solitary fish and collecting SST data.

To conclude, this study has confirmed that SST fronts in a coastal upwelling system, although ephemeral in time and space, provide an important habitat feature for schooling fish, in our region most notably northern anchovy and Pacific sardine, and to a lesser extent, solitary fish. To further understand the relationship of solitary fish with SST fronts would require additional data and sampling farther offshore. Alternatively, more solitary fish tend to be observed over the shelf at night as a result of the disbanding of schools and the presence of species migrating vertically. Nonetheless, lidar seems to be a cost-effective approach to examining the biophysical relationships between ecologically and commercially important fish species and the environment, at high spatial and temporal resolution (Gauldie *et al.*, 1996). Management and conservation efforts for marine fish species could benefit by examining the locations and persistence of thermal features in coastal waters. Such areas could be further evaluated as potential locations for marine protected areas (Game *et al.*, 2009).

As the era of decreasing fish stocks and rapidly changing environmental conditions extends, identifying and monitoring important environmental features and incorporating them into management and conservation practices would lead to better-informed decisions about coastal resources. Under favourable environmental conditions, heavy fishing pressure may be sustainable, but when conditions change, such fishing pressure may become unsustainable (Hofmann and Powell, 1998). Moreover, the understanding and identification of environmental fluctuations can be delayed easily by 1–5 years before it is realized that a change has occurred, so management decisions that do not consider environmental changes early can inadvertently harm a resource (Hofmann and Powell, 1998). Hence, a more complete and detailed understanding of the biophysical

relationships between marine species and their environment is required. Environmental features, such as upwelling-induced SST fronts, are important habitat components for ecologically and economically important fish species in coastal upwelling regions. Such features can be monitored easily by the use of remotely sensed data coupled with readily available upwelling indices.

## Acknowledgements

We thank Bob Emmett and the scientists and crew of the FV “Frosti”, who participated in the cruises and helped process the fish catch data, and the pilots of the NOAA Twin Otter aircraft for providing flight support. We also thank Igor Belkin for providing helpful guidance in our front-detection method and Alix Gitelman for help and advice on statistical analyses. The work was supported partially by the National Ocean Partnership Program and the NOAA Office of Ocean Exploration (grant #N000140510669, BAA number 04-022: a novel technique to detect epipelagic fish populations and map their habitat). Funding for the trawl collections came from the Bonneville Power Administration and the Northwest Fisheries Science Center.

## References

- Ainley, D. G., Dugger, K. D., Ford, R. G., Pierce, S. D., Reese, D. C., Brodeur, R. D., Tynan, C. T., *et al.* 2009. Association of predators and prey at frontal features in the California Current: competition, facilitation, and co-occurrence. *Marine Ecology Progress Series*, 389: 271–294.
- ANSI. 1993. Safe use of lasers: standard Z-136.1. American National Standards Institute, New York. 120 pp.
- Bakun, A. 2006. Fronts and eddies as key structures in the habitat of marine fish larvae: opportunity, adaptive response and competitive advantage. *Scientia Marina*, 70(Suppl. 2): 105–122.
- Barth, J. A., Pierce, S. D., and Cowles, T. J. 2005. Mesoscale structure and its seasonal evolution in the northern California Current system. *Deep Sea Research II*, 52: 5–28.
- Belkin, I., and Cornillon, P. 2003. SST fronts of the Pacific coastal waters and marginal seas. *Physical Oceanography*, 1: 90–113.
- Belkin, I. M. 2002. New challenge: ocean fronts. *Journal of Marine Systems*, 37: 1–2.
- Belkin, I. M., Cornillon, P. C., and Sherman, K. 2009. Fronts in large marine ecosystems. *Progress in Oceanography*, 81: 223–236.
- Brodeur, R. D., Fisher, J. P., Teel, D. L., Emmett, R. L., Casillas, E., and Miller, T. W. 2004. Juvenile salmonid distribution, growth, condition, origin and environmental and species associations in the northern California Current. *Fishery Bulletin US*, 102: 25–46.
- Carr, M-E., and Kearns, E. J. 2003. Production regimes in four eastern boundary current systems. *Deep Sea Research II*, 50: 3199–3221.
- Carrera, P., Churnside, J. H., Boyra, G., Marques, V., Scalabrin, C., and Uriarte, A. 2006. Comparison of airborne lidar with echosounders: a case study in the coastal Atlantic waters of southern Europe. *ICES Journal of Marine Science*, 63: 1736–1750.
- Cayula, J-F., and Cornillon, P. 1992. Edge detection algorithm for SST images. *Journal of Atmospheric and Oceanic Technology*, 9: 67–80.
- Chavez, F. P., and Messié, M. 2009. A comparison of eastern boundary upwelling ecosystems. *Progress in Oceanography*, 83: 80–96.
- Churnside, J. H., Demer, D. A., Griffith, D., Emmett, R. L., and Brodeur, R. D. 2009. Comparisons of lidar, acoustic and trawl data on two scales in the Northeast Pacific Ocean. *CalCOFI Reports*, 50: 118–122.
- Churnside, J. H., Sawada, K., and Okumura, T. 2001. A comparison of airborne lidar and echo sounder performance in fisheries. *Journal of the Marine Acoustics Society of Japan*, 28: 46–61.

- Churnside, J. H., and Thorne, R. E. 2005. Comparison of airborne lidar measurements with 420 kHz echosounder measurements of zooplankton. *Applied Optics*, 44: 5504–5511.
- Doniol-Valcroze, T., Berteaux, D., Larouche, P., and Sears, R. 2007. Influence of thermal fronts on habitat selection by four rorqual whale species in the Gulf of St Lawrence. *Marine Ecology Progress Series*, 335: 207–216.
- Etnoyer, P., Canny, D., Mate, B., and Morgan, L. 2004. Persistent pelagic habitat in the Baja California to Bering (B2B) ecoregion. *Oceanography*, 17: 90–101.
- Etnoyer, P., Canny, D., Mate, B. R., Morgan, L. E., Ortega-Ortiz, J. G., and Nichols, W. J. 2006. Sea-surface temperature gradients across blue whale and sea turtle foraging trajectories off the Baja California Peninsula, Mexico. *Deep Sea Research II*, 53: 340–358.
- Fiedler, P. C., and Bernard, H. J. 1987. Tuna aggregation and feeding near fronts observed in satellite imagery. *Continental Shelf Research*, 7: 871–881.
- Fortin, M.-J., Dale, M. R. T., and ver Hoef, J. 2002. Spatial analysis in ecology. *In* *Encyclopedia of Environmetrics*, pp. 2051–2058. Ed. by A. H. El-Shaarawi, and W. W. Piegorsch. John Wiley & Sons, New York. 2502 pp.
- Game, E. T., Grantham, H. S., Hobday, A. J., Pressey, R. L., Lombard, A. T., Beckley, L. E., Gjerde, K., *et al.* 2009. Pelagic protected areas: the missing dimension in ocean conservation. *Trends in Ecology and Evolution*, 24: 360–369.
- Gauldie, R. W., Sharma, S. K., and Helsley, C. E. 1996. Lidar applications to fisheries monitoring problems. *Canadian Journal of Fisheries and Aquatic Sciences*, 53: 1459–1468.
- Gómez-Gutiérrez, J., Peterson, W. T., and Miller, C. B. 2005. Cross-shelf life-stage segregation and community structure of the euphausiids off central Oregon (1970–1972). *Deep Sea Research II*, 52: 289–315.
- Hardman-Mountford, N. J., and McGlade, J. M. 2003. Seasonal and interannual variability of oceanographic processes in the Gulf of Guinea: an investigation using AVHRR sea surface temperature data. *International Journal of Remote Sensing*, 24: 3247–3268.
- Hickey, B. M., and Banas, N. S. 2003. Oceanography of the US Pacific Northwest coastal ocean and estuaries with application to coastal ecology. *Estuaries*, 26: 1010–1031.
- Hoefler, C. J. 2000. Marine bird attraction to thermal fronts in the California Current system. *The Condor*, 102: 423–427.
- Hofmann, E. E., and Powell, T. M. 1998. Environmental variability effects on marine fisheries: four case histories. *Ecological Applications*, 8(Suppl.): S23–S32.
- Hughes, T. P., Bellwood, D. R., and Connolly, S. R. 2002. Biodiversity hotspots, centres of endemism, and the conservation of coral reefs. *Ecology Letters*, 5: 775–784.
- Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., *et al.* 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science*, 293: 629–638.
- Lalli, C. M., and Parsons, T. R. 1993. *Biological Oceanography: an Introduction*. Pergamon Press, Oxford. 301 pp.
- Laurs, R. M., Fiedler, P. C., and Montgomery, D. R. 1984. Albacore tuna catch distributions relative to environmental features observed from satellites. *Deep Sea Research*, 31: 1085–1099.
- Lewis, G. D., Jordan, D. L., and Roberts, P. J. 1999. Backscattering target detection in a turbid medium by polarization discrimination. *Applied Optics*, 38: 3937–3944.
- Miller, T. W., and Brodeur, R. D. 2007. Diets of and trophic relationships among dominant marine nekton within the northern California Current ecosystem. *Fishery Bulletin US*, 105: 548–559.
- Moser, B. K., and Stevens, G. R. 1992. Homogeneity of variance in the two-sample means test. *The American Statistician*, 46: 19–21.
- Myers, N. 1997. The rich diversity of biodiversity issues. *In* *Biodiversity*, 2, pp. 125–138. Ed. by M. L. Reaka-Kudla, D. E. Wilson, and E. O. Wilson. Joseph Henry Press, Washington DC. 551 pp.
- Myers, R. A., and Worm, B. 2003. Rapid worldwide depletion of predatory fish communities. *Nature*, 423: 280–283.
- Piatt, J. F., Wetzel, J., Bell, K., DeGange, A. R., Balogh, G. R., Drew, G. S., Geernaert, T., *et al.* 2006. Predictable hotspots and foraging habitat of the endangered short-tailed albatross (*Phoebastria albatrus*) in the North Pacific: implications for conservation. *Deep Sea Research II*, 53: 387–398.
- Planque, B., Fromentin, J.-M., Cury, P., Drinkwater, K. F., Jennings, S., Perry, R. I., and Kifani, S. 2010. How does fishing alter marine populations and ecosystems sensitivity to climate. *Journal of Marine Systems*, 79: 403–417.
- Polovina, J., Uchida, I., Balazs, G., Howell, E. A., Parker, D., and Button, P. 2006. The Kuroshio extension bifurcation region: a pelagic hotspot for juvenile loggerhead sea turtles. *Deep Sea Research II*, 53: 326–339.
- Reddy, R. V., Lyne, R., Gray, R., Easton, A., and Clarke, S. 1995. An application of satellite-derived sea surface temperatures to southern bluefin tuna and albacore off Tasmania, Australia. *Scientia Marina*, 59: 445–454.
- Reese, D. C., and Brodeur, R. D. 2006. Identifying and characterizing biological hotspots in the northern California Current. *Deep Sea Research II*, 53: 291–314.
- Reese, D. C., Miller, T. W., and Brodeur, R. D. 2005. Community structure of near-surface zooplankton in the northern California Current in relation to oceanographic conditions. *Deep Sea Research II*, 52: 29–50.
- Ruxton, G. D. 2006. The unequal variance *t*-test is an underused alternative to Student's *t*-test and the Mann–Whitney *U* test. *Behavioral Ecology*, 17: 688–700.
- Schick, R. S., Goldstein, J., and Lutcavage, M. E. 2004. Bluefin tuna (*Thunnus thynnus*) distribution in relation to sea surface temperature fronts in the Gulf of Maine (1994–96). *Fisheries Oceanography*, 13: 225–238.
- Sims, D. W., and Quayle, V. A. 1998. Selective foraging behaviour of basking sharks on zooplankton in a small-scale front. *Nature*, 393: 460–464.
- Sydesman, W. J., Brodeur, R. D., Grimes, C. B., Bychkov, A. S., and McKinnell, S. 2006. Marine habitat “hotspots” and their use by migratory species and top predators in the north Pacific Ocean: introduction. *Deep Sea Research II*, 53: 247–249.
- Valavanis, V. D., Dapantagakis, A., Katara, I., and Palialexis, A. 2004. Critical regions: a GIS-based model of marine productivity hotspots. *Aquatic Sciences*, 66: 139–148.
- Wang, J., Pierce, G. J., Sacau, M., Portela, J., Santos, M. B., Cardoso, X., and Bellido, J. M. 2007. Remotely sensed local oceanic thermal features and their influence on the distribution of hake (*Merluccius hubbsi*) at the Patagonian Shelf edge in the SW Atlantic. *Fisheries Research*, 83: 133–144.
- Zainuddin, M., Kiyofuji, H., Saitoh, K., and Saitoh, S.-I. 2006. Using multi-sensor satellite remote sensing and catch data to detect ocean hot spots for albacore (*Thunnus alalunga*) in the northwestern North Pacific. *Deep Sea Research II*, 53: 419–431.
- Zorn, H. M., Churnside, J. H., and Oliver, C. W. 2000. Laser safety thresholds for cetaceans and pinnipeds. *Marine Mammal Science*, 16: 186–200.