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# Phalaropes feeding at a coastal front in Santa Monica Bay, California

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## Abstract

The spinning behavior often exhibited by phalaropes when feeding at freshwater sites is rarely observed at sea. Instead, phalaropes are typically observed slowly swimming forward while foraging on marine neuston concentrated in surface convergence zones. Small-scale coastal ocean fronts, eddies and internal waves capable of generating such convergences are extremely common, albeit ephemeral, features in the Southern California Bight. This region is marked by a complex flow regime, resultant in part from its variable coastal morphology. We used satellite data (AVHRR) and in situ measurements (CTD, surface drifters) to describe and track a coastal front in Santa Monica Bay, California, centrally located in the Southern California Bight. A high number of Red-necked Phalaropes (*Phalaropus lobatus*) were associated with this feature over the course of several days. Neuston tows and gut content analyses revealed these phalaropes were primarily feeding on fish eggs and assorted debris that were abundant at the sea surface in this front. No phalaropes were observed spinning anywhere in the vicinity. Previously unpublished metabolic activity rates for phalaropes indicate that spinning is much more energetically expensive than is swimming at a comparable speed. Convergences associated with fronts (or eddies, internal waves, etc.) in the Southern California Bight apparently provide phalaropes with a rich, easily accessible and steady supply of food without having to resort to the energetically costly behavior of spinning.

*Keywords:* Phalaropes; Oceanic fronts; Convergence zones; Neuston; Surface drifters; Satellite sensing
*Regional terms:* USA; California; Santa Monica Bay

## 1. Introduction

The Red Phalarope (*Phalaropus fulicaria*) and the Red-necked Phalarope (*Phalaropus lobatus*), although classified as shorebirds in the avian order Charadriiformes, are pelagic during the nonbreeding season, foraging at sea for zooplankton on their wintering

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grounds and during their trans-equatorial migrations (Rubega et al., 2000). Wilson's Phalarope (*Phalaropus tricolor*) is exclusively New World in distribution, favoring inland aquatic habitat. All three species are buoyant, with lobed toes for swimming. Phalaropes occasionally swim in tight circles, exhibiting rapid spinning (~ 1 rps) while feeding (e.g., Obst et al., 1996). In this process, the birds vigorously kick water away from the axis of rotation with their lobed toes, generating a central upwelling vortex of water which replaces fluid displaced laterally, thus, bringing food to the surface where it is captured (Obst, 1985). Phalaropes seemingly do not spin unless the rewards are sufficiently worthwhile or else otherwise unobtainable. For example, in Mono Lake, California, Red-necked Phalaropes spin to capture brine fly larvae, but they rarely feed (let alone spin) on easily obtainable brine shrimp (Rubega and Inouye, 1994; Rubega et al., 2000). Brine flies have more calories and lipid content than brine shrimp on both an individual basis as well as per gram of dry mass (Herbst, 1986). In the laboratory, phalaropes lose weight eating up to three times their body weight in brine shrimp, but maintain or gain weight when fed brine flies (Rubega and Inouye, 1994).

At sea off the coast of California, we have never observed spinning behavior in phalaropes, though they can easily upwell food from at least 0.5 m below the surface by spinning (Obst et al., 1996). Instead, phalaropes in this region are most frequently observed foraging in linear oceanographic features (LOF) such as slicks that are surface manifestations of convergence zones, i.e., sites where neustonic organisms accumulate (Kingsford, 1990). For example, one late summer afternoon in Monterey Bay, we saw thousands of phalaropes in nonbreeding plumage (not identified to species from the ship) sitting on a long (kilometers) yet narrow (< 25 m) white scum-line presumably marking a convergence. There are numerous local oceanographic processes capable of generating such prominent surface features, including upwelling fronts and internal tidal waves and bores (e.g., Shea and Broenkow, 1982; Briggs et al., 1984; Graham et al., 1992; Graham, 1993; Breaker and Broenkow, 1994). Most of the phalaropes were feeding intensively at the center of the slick in a band about 0.5 m wide, sitting so close together that we often could not see the water surface through their plumage. On either side of this central band, a lesser number of birds were spaced about 1 m apart out to approximately 10 m from the centerline. No phalaropes were seen elsewhere; all of the birds were feeding on this LOF, and none were spinning.

Seabirds routinely occur in association with oceanographic fronts, a particular type of LOF (e.g., Schneider, 1982; Kinder et al., 1983; Bourne and Clark, 1984; Haney and McGillivary, 1985; Hunt and Schneider, 1987; Brown and Gaskin, 1988; Hunt and Harrison, 1990; Decker and Hunt, 1996; Durazo et al., 1998; Hoefer, 2000). When water masses with different densities converge in frontal zones, there is often a visible linear or curvilinear manifestation of the front in the form of a surface slick or scum-line due to the accumulation of buoyant particles, neuston and other organic material (e.g., Franks, 1992a). Near-surface zooplankton in the descending water mass swim upward at the front in order to maintain constant depth. The result is a steady accumulation of plankton and their predators at often exceptionally high densities at or near the convergence (e.g., Olson and Backus, 1985; Hamner and Schneider, 1986; Kingsford and Choat, 1986; Wolanski and Hamner, 1988; Kingsford, 1990; Hunt, 1991; Kingsford et al., 1991; Franks, 1992a,b; Graham, 1993). Seabirds can use the visual cues provided by slicks and floating debris to identify these regions filled with potential prey (e.g., Brown and Gaskin, 1988; Durazo et al., 1998). In particular, Briggs et al. (1984) noted that red and red-necked phalaropes off central and northern California use environmental cues of this type to locate offshore frontal convergences associated with upwelling. Phenomena like these appear to play a critical role in concentrating prey at the surface for phalarope consumption (Haney, 1985; Mercier and Gaskin, 1985; Brown and Gaskin, 1988).

Some fronts are thousands of kilometers long and easily observed via satellites and other means (e.g., Yoder et al., 1994). Others are spatially less extensive and/or temporally more ephemeral, particularly those generated by topographic irregularities of a coastline or by island mass effects (e.g., Alldredge and Hamner, 1980; Wolanski and Hamner, 1988). As will be discussed below, this latter class of "small-scale" features is more characteristic of those commonly observed in the Southern California Bight. We describe here oceanographic and biological conditions associated with small-scale frontal formation in and around Santa Monica Bay, California, utilizing both in situ and remote observations. We discuss how the frontal convergences provided an easily accessible and abundant supply of fish eggs and other food at the sea surface, thus, attracting Red-necked Phalaropes and apparently reducing (if not eliminating) their need to engage in spinning behavior, which previously unpublished data reveals to be energetically expensive.

## 2. Study area and methods

Fig. 1 depicts the general location of the study site. Santa Monica Bay is approximately centrally located in the region known as the Southern California Bight (SCB), which extends inshore of the Santa Rosa Ridge from Point Conception in the north to just south of San Diego. Circulation patterns within the SCB are more complex than elsewhere off the west coast of the United States (Hendershott and Winant, 1996). The colder, equatorward California Current (CC), a well-described eastern boundary current (e.g., Hickey, 1979, 1998), dominates flow offshore of the SCB. Surface flow within the SCB is predominantly poleward (except during spring), with warmer water advected from the south by the nearshore Southern California Countercurrent (SCC) (Hickey, 1979, 1992, 1993; Bray et al., 1999). There is also evidence for large-scale cyclonic recirculation within the SCB, i.e., the Southern California Eddy (e.g., Hickey, 1998; Bray et al., 1999). Unlike regions to the north, local upwelling in the SCB is minimal

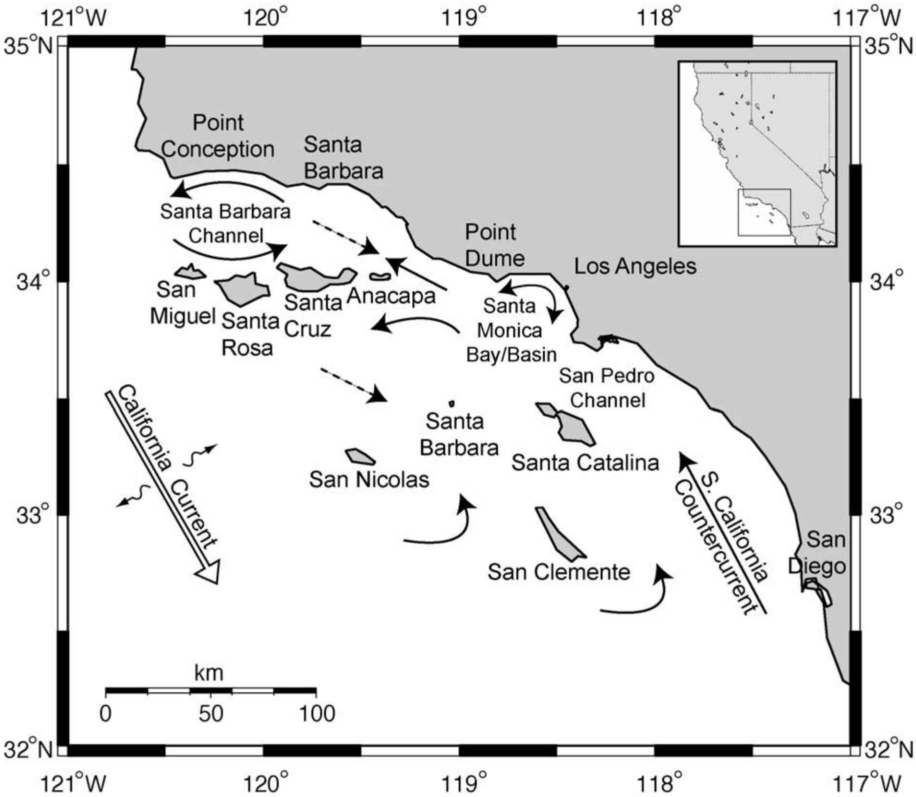

Fig. 1. The Southern California Bight (SCB). Prevailing near-surface circulation (after DiGiacomo and Holt, 2001). Solid arrows indicate general SCB pattern of poleward flow nearshore and equatorward flow offshore (i.e., California Current, migrates closer to shore in spring and summer). Dashed arrows signify a shift to bightwide equatorward flow during spring. Flow within the Santa Barbara Channel and Santa Monica Bay is complex; see DiGiacomo and Holt (2001) for a recent overview.

during summer (owing to a large reduction in wind stress) and most frequent and intense during winter and early spring (Hickey, 1992, 1998). However, upwelled waters from outside the SCB are frequently advected into this region throughout the year (Hickey, 1992). The movement and mixing within the SCB of these various water masses leads to thermal fronts of varying size, intensity and duration.

Complex coastal morphology, including eight nearshore islands, numerous promontories, submarine canyons, basins and ridges, accompanied by temporally and spatially variable local winds and remotely forced coastally trapped waves, introduces considerable variability to the large-scale SCB flow regime described above (e.g., Owen, 1980; Hickey, 1992, 1993; Hickey et al., in press). For example, DiGiacomo and Holt (2001), using high-resolution multisensor satellite and coincident field data, described the characteristics of extensive small-scale (< 50 km in diameter) coastal ocean eddies in the SCB. These eddies appeared to result from several different forcing mechanisms and likely have important biological ramifications. Relatedly, Hickey et al. (in press) discussed the formation of eddies through flow separation at the sharp upstream corners of Santa Monica Bay. In particular, poleward flow over the central SCB slope is often associated with an anticyclonic eddy that develops at the southern edge of the bay, gradually filling its entire expanse (Hickey et al., in press). There are also numerous other reports of LOF (e.g., fronts, internal waves, Langmuir cells) in the SCB (e.g., Ewing, 1950; LaFond and Lafond, 1972; Onstott and Rufenach, 1992; Hickey, 1993). As a result, sea-surface slicks marking convergences are widespread in the SCB, associated with this plethora of small-scale, ephemeral coastal ocean phenomena.

An initial cruise into Santa Monica Bay by the R/V *Sea World UCLA* was made on 30 September 1997 for purposes of field-testing a new drifter design. Drifters were constructed out of perforated 60 gallon plastic drums suspended at a depth of 3 m from a small surface float that was in turn attached by a short line to a thin, floating fiber glass pole marked with a numbered flag. Our drifter-release site was selected to coincide with an interesting, linear array of phalaropes observed sitting on the sea-surface. The birds were quite obviously feeding, but not spinning, along what appeared to be a surface convergence, visually delineated by a wide slick containing floating debris. Drifters (seven total) were released at approximately 200-m intervals in a line normal to the scum-line that marked the front, which was generally oriented east–west, with three drifters placed north of the front, one drifter placed directly in the scum-line and three drifters placed to the south. Following their release, drifter positions were determined at half-hour intervals by moving the ship to within 5 m downwind of each drifter and then recording the position of the R/V *Sea World UCLA* using differential GPS measurements. This was done for a period of 4 h, spanning from morning to early afternoon. The derived drifter rates of motion are accurate to within ± 20% due to wind drift effects.

We did not know at the time of this initial deployment that the phalaropes were apparently attracted to the strongest thermal front within Santa Monica Bay. This was subsequently determined upon our return via analysis of advanced very high resolution radiometer (AVHRR) sea-surface temperature (SST) data obtained from the NOAA CoastWatch Program. We used this satellite imagery to identify and track over a period of several days the small-scale coastal ocean front at which the phalaropes were feeding. Unfortunately, the SST coverage was intermittent at times due to the presence of clouds.

These AVHRR SST data were used to identify this same front on 3 October 1997 in the field. High numbers of Red-necked Phalaropes were still vigorously feeding at the surface slick that marked the frontal convergence. Seven drifters were once again released and tracked using a methodology similar to that described above to identify water movements associated with this coastal front, though locations were now recorded hourly (as opposed to half-hourly as on 30 September). Accompanying each drifter release on this day were CTD (SeaBird SBE-19) casts down to 100 m; these data were processed using the SEASOFT (version 4.219) software package.

The distribution of Red-necked Phalaropes in relation to the front on 3 October 1997 was determined via the standardized counting procedure of recording the number of birds seen sitting on the water during a specified amount of time (1 min) within an arc (90°) at a given distance off the bow of the ship (50 m) moving at a fixed speed (~ 3 knots). Transects of this type were made both along (west to east) and normal (north to south) to the front. Three phalaropes observed foraging on the front at this time were collected for gut content analysis under permit #801-008-01.

Neuston samples were also obtained on 3 October 1997 along the front by side-towing a 1/2-m, 0.505-mm mesh plankton net from the boom for 5 min per sample, with three samples collected. The net was weighted at the bottom so that it fished half in and half out of the water. The ship was maneuvered so that the net consistently fished the center of the scum-line along side the ship, where it was undisturbed by the ship's wake. Due to swell and the resultant periodic vertical oscillations undertaken by the net at the sea-surface, it was not possible to accurately determine the total volume of water filtered per sample, preventing quantitative analyses of the neuston samples. Nonetheless, the net effectively sampled the neustonic layer because the net was never completely submerged. Comparative neuston samples from outside the front were not collected due to increasingly rough seas that precluded further collection efforts.

## 3. Results

Fig. 2 is a schematic drawing that depicts a partial life history of the coastal front of interest here. Demarcation lines derived from five daytime (early afternoon) AVHRR SST images illustrate the front and its movement to the west–northwest as colder inshore waters were separated from warmer offshore waters. On 22 September 1997, a patch of this colder (~ 20.5 °C) water was clearly visible south of Palos Verdes Peninsula (PVP), separated from warmer (~ 23 °C) offshore waters by the front in question (Fig. 2, line a). Due to sporadic cloud coverage in the AVHRR images, it was difficult to determine the precise origin of the colder water mass, but it appears to have originated near the PVP at least several days earlier, possibly as a result of a local upwelling event. Regardless of the exact origin of this water mass, we were subsequently able to track its movements and the attendant front into the region in question. On 26 September, the front (Fig. 2, line b) had moved somewhat offshore and to the west as the colder water mass moved north around the PVP and up into Santa Monica Bay. On 29 September, the front (Fig. 2, line c) had proceeded farther west as well as north, with the colder water mass now well within Santa Monica Bay. By 2 October, the front (Fig. 2, line d) was oriented in an east–west direction, with the colder water mass north of an intrusion of warmer water from the San Pedro Channel. By 3 October, the front (Fig. 2, line e) moved somewhat closer inshore as warm poleward flow seemingly bifurcated around the colder water, apparently flowing west–northwest outside the Bay and east–northeast inside the Bay as illustrated by the AVHRR image for that day (Fig. 3). Based on these SST data, the movement (i.e., precession) of this frontal feature inside the bay appeared to be on the order of 5 km per day, or approximately 6 cm $s^{-1}$.

Corroboration for the flow regimes described above was provided by the two drifter releases on 30 September (Fig. 4a) and 3 October (Fig. 4b), whose general locations are marked in Fig. 2 as DR1 and DR2, respectively. On 30 September, all seven drifters moved southwest then west, as might be inferred from satellite images for 2–3 October (Fig. 2, lines d–e). As is also evident from Fig. 4a, the northern, colder mass of water was travelling slightly faster to the west than the warmer water to the south. Eventually, all seven drifters converged onto the slick marking the front, albeit at varying speeds over the course of their journey. Drifters 1–4, lined up on the northern side of the front (#1–3) or in it (#4), averaged 29 cm $s^{-1}$ for the first 2 h, and 26 cm $s^{-1}$ for the last 2 h. Drifter 4, initially situated in the slick, traveled back and forth across the front. Drifters 5–7, clumped together on the southern side of the front, averaged 27 cm $s^{-1}$ for the first 2 h, but only 20 cm $s^{-1}$ for the last 2 h. Based on the drifter and SST data, as well as the flow regime expected for this time of year, it would appear that the colder water mass to the north was possibly entrained and advected by the recurring Santa Monica Bay anticyclonic eddy discussed above. The warmer water mass to the south was seemingly consistent with poleward flow in slope waters outside the bay. The interaction between these two water masses led to the observed frontal convergence, which by this point was primarily east–west in orientation.

Fig. 4b details the drifter release of 3 October. The colder water to the north tracked to the west at an average speed of 12 cm $s^{-1}$ as indicated by drifters 1–3, whereas the warmer water to the south moved easterly at an average speed of 7 cm $s^{-1}$ as per drifters

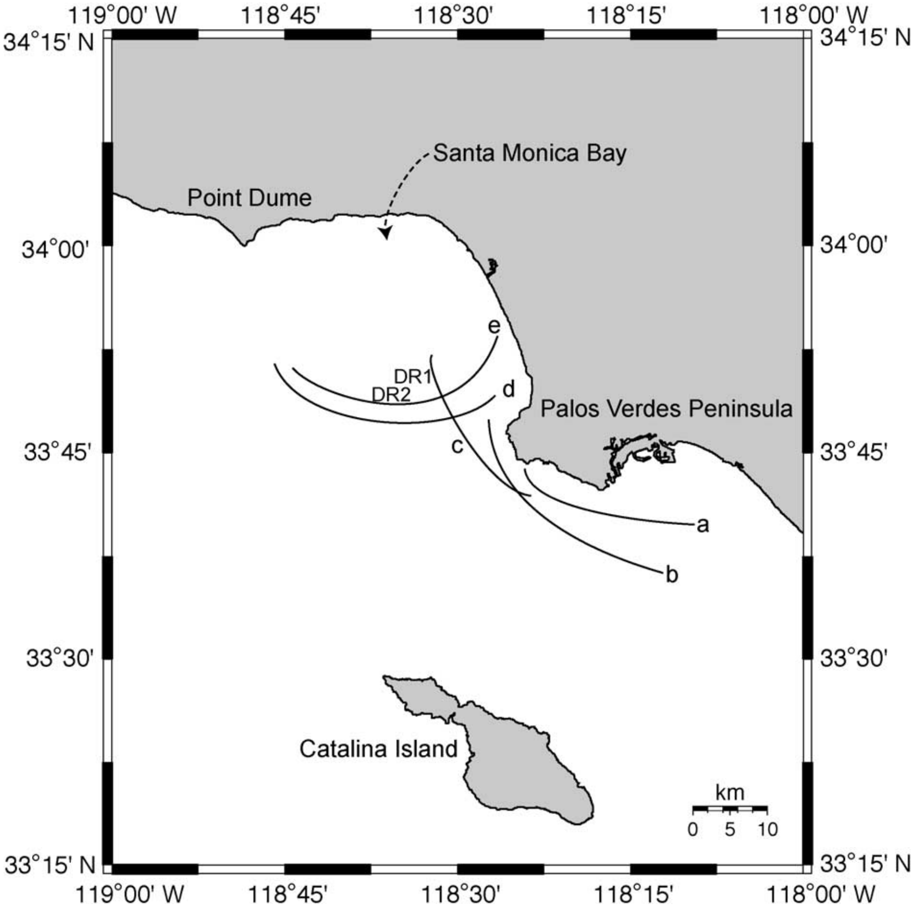

Fig. 2. Detail of Santa Monica Bay, California, and surrounding region. Approximate position of coastal front as derived from afternoon (2100–2200 UTC) advanced very high resolution radiometer (AVHRR) sea surface temperature (SST) satellite images is shown for: (a) 22 September 1997, (b) 26 September 1997, (c) 29 September 1997, (d) 2 October 1997, (e) 3 October 1997. Length of line is not necessarily indicative of length of front. DR1 signifies site of the first drifter release on 30 September (Fig. 4a). DR2 is the site of the second drifter release on 3 October (Fig. 4b).

4–7. During the first hour, drifters 4, 5 and 6 initially tracked north towards the front before eventually proceeding east; drifter 7 briefly headed west before reversing direction. These southern drifters seemed to reflect the bifurcation of the warm water flow that occurred, with part of the poleward flow diverted east and then upwards (north) into Santa Monica Bay around the cold water mass (Fig. 3). At the end of 5 h, all the drifters were aligned along the scum-line demarcating the front, oriented east–west in the western part of the drifter release region and northwest–southeast in the eastern part. The drifters, thus, revealed a lateral convergence occurring along the shear zone between these two water masses, marked by the front in question. Thus, organisms and other materials could accumulate in this region as discussed below.

Fig. 5 shows the subsurface characteristics of this front via the CTD casts of 3 October 1997. This contour plot represents a cross-section of the ocean down to 40 m across the frontal region boxed off in Figs. 3 and 4b; the arrow indicates the location of the front upon which the phalaropes were feeding (see below). The CTD casts were made to 100-m depth but there were no significant density differences deeper than 40 m across the frontal region. Temperatures increased in the surface waters by

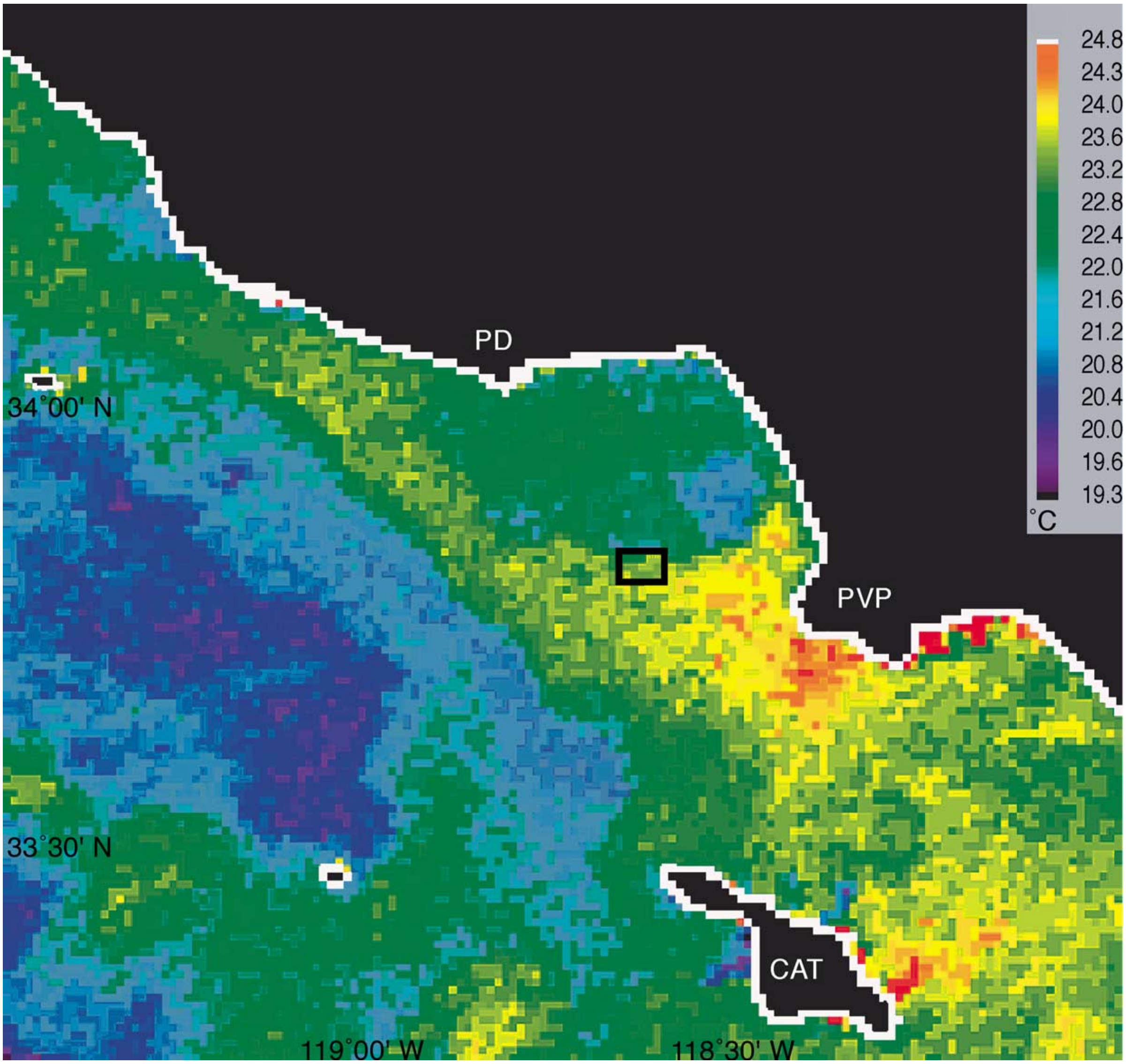

Fig. 3. AVHRR SST image of Santa Monica Bay and surrounding area for 3 October 1997 at 2134 UTC. PVP, Palos Verdes Peninsula; PD, Point Dume; CAT, Catalina Island. Black box near center indicates general site of drifter release for this day (see Fig. 4b).

more than a degree headed from north to south. Isotherms were particularly compressed around 10–15 m. Thus, at this point the observed frontal system was fairly shallow and weak, though persistent with a distinct sea-surface signature that was consistently observed in the field. It is noteworthy to mention that the front as shown in Fig. 5 perhaps manifests itself on spatial scales that are typically more characteristic of internal wave fields. This is not meant to imply that this is not an oceanographic front, however. Instead, we merely wish to note that these features are frequently intertwined; ocean fronts are often manifested by internal wave fields shoaling as part of the frontal feature.

In terms of Red-necked Phalarope distribution along the front (i.e., east–west) on 3 October 1997, 207 birds were observed sitting on the glassy water marking the front over a distance of approx-

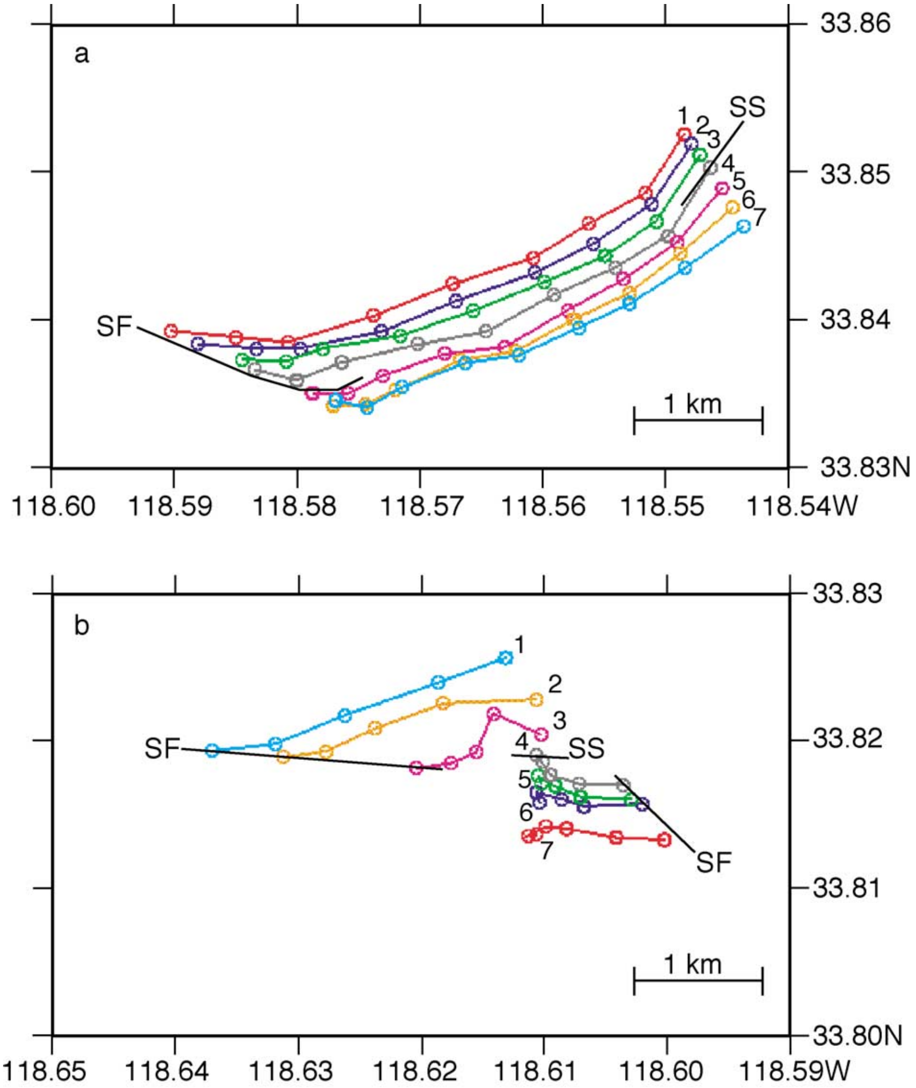

Fig. 4. Movement of drifters during 2 days of deployment: (a) 30 September 1997, (b) 3 October 1997. Drifters drifted for 4 h each day (5 h for drifter 7 in (b)), but positions were recorded half-hourly for (a) and hourly for (b). Numerals indicate drifter number and starting point. Black lines indicate approximate position of slick marking frontal convergence at start (SS) and finish (SF) relative to drifters. See Figs. 2 and 3 for approximate locations of releases.

imately 1 km, though distributed somewhat patchily (Fig. 6). On the transect normal to the front (i.e., north to south), we recorded only six birds in total over a similar distance, with all of those found just north of the front. The count of 22 birds recorded along the front some 15 min earlier was confirmed when we crossed the still clearly visible front in that same location (Fig. 6).

The three neuston samples collected on 3 October 1997 from the slick marking the frontal convergence were generally similar to one another in their composition. Each sample was characterized by large numbers of anchovy eggs, which have an approximate major axis length of 1.34 mm and a minor axis of 0.62 mm this time of year, a mean dry weight of 0.026 mg and a corresponding mean caloric value of

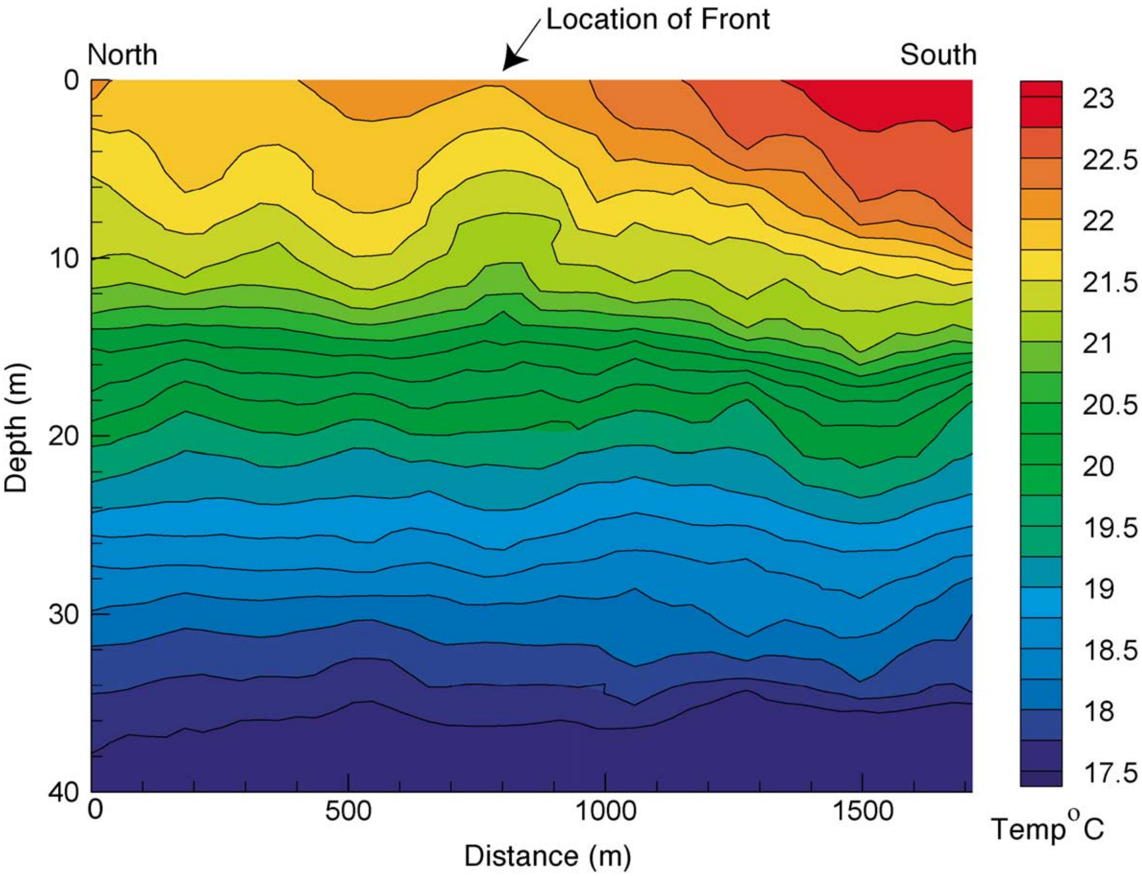

Fig. 5. Temperature section from surface to 40 m compiled from CTD casts made at site of drifter releases (see Figs. 3 and 4b) on 3 October 1997.

0.6 J per egg (Hunter and Leong, 1981). Also, small numbers of pontellid copepods (e.g., Zaitsev, 1971) were observed, as was considerable debris. This appeared to include the remnants of various vertebrate and invertebrate organisms. One week prior to these tows on 26 September 1997, CalCOFI (California Cooperative Oceanic Fisheries Investigations) Cruise 9709 conducted single, 15-min Manta (neuston) tows at two stations in close proximity to our study site. At station 87.33 inside Santa Monica Bay (~ 15 km from our tows), there were 569.2 anchovy eggs per 100 $m^3$, the highest number of anchovy eggs encountered at any station on CalCOFI Cruise 9709 (G. Moser, personal communication). This value is also large compared to the average number of anchovy eggs, ~ 35 per 100 $m^3$, found in Manta tows off southern California in September (G. Moser, personal communication). At station 87.35 just outside Santa Monica Bay (~ 1 km from our tows), however, no anchovy eggs were found during CalCOFI Cruise 9709, in striking contrast to the large number of eggs we observed in this region 1 week later. Though we were unable to obtain quantitative estimates of anchovy egg abundance from these latter tows (almost certainly significantly higher than the mean September value above), there are still relative patterns and trends that can be derived from comparisons with the CalCOFI data. In particular, the neuston data considered together clearly indicate that anchovy eggs were patchily distributed in Santa Monica Bay and offshore waters at this time, driven (at least partly) by small-scale phenomena of the type

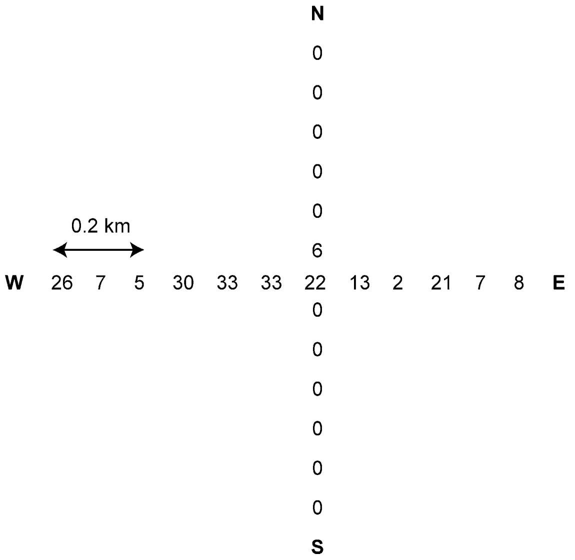

Fig. 6. Numbers of phalaropes per minute observed sitting on a front oriented west–east and along a transect oriented normal (north–south) to the front on 3 October 1997. Ship speed was approximately 3 knots. See Figs. 3 and 4b for general location of front.

described here. In this regard, it seems likely that some of the abundant anchovy eggs present nearshore at station 87.33 on 26 September 1997 were advected offshore by the prevailing oceanographic conditions discussed above and entrained in the resulting frontal system, presumably at much higher concentrations than in adjacent water masses.

Gut content analysis of the three red-necked phalaropes collected for further examination revealed one empty gut and two that primarily contained fish eggs, as well as small amounts of crustacean parts and unrecognizable material, seemingly consistent with the neuston samples described above as well as other phalarope gut content studies. For example, fish eggs appear to be a common dietary item for phalaropes foraging at sea off central and northern California (Briggs et al., 1984). Off California and elsewhere, crustaceans are also typical prey, from intact holoplankters (e.g., copepods, euphausiids, amphipods) and meroplankters (e.g., barnacle and crab larvae), to fragmented body parts (e.g., Briggs et al., 1984; Mercier and Gaskin, 1985; Brown and Harris, 1988; Obst and Hunt, 1990; Rubega et al., 2000).

## 4. Discussion

Phalaropes are exceptionally buoyant and cannot dive to capture prey. Instead, they feed at the water surface, variously, by picking plankton individually from the surface while swimming forward slowly, by pumping plankton upwards from below the surface while spinning (Obst, 1985; Obst et al., 1996), or by capturing insects, such as brine flies in Mono Lake that fly near the water surface and which the birds pluck from the air. At sea during the day, however, zooplankton larger than approximately 0.5 mm typically avoid surface waters. This is because diurnal visual predators, such as fish (e.g., anchovies) and seabirds (e.g., phalaropes), tend to preferentially select prey in this larger size class during feeding (e.g., Dodson and Egger, 1980; James, 1987; James and Findlay, 1989), creating strong selective pressures for patterns of diurnal vertical migration (DVM) of zooplankton (Hamner, 1995). Aside from hindering direct surface feeding by phalaropes, DVM could potentially reduce any benefits (i.e., prey) these birds might derive from engaging in spinning behavior, as many zooplankton might be too deep to be effectively entrained in the resulting upwelling jet (Brown and Gaskin, 1988).

Phalaropes, thus, face the dilemma of being buoyant, diurnal surface pickers in an environment where much of their potential prey migrates into deep water during the day. Nonetheless, they do find food during the day in the Southern California Bight, without resorting to spinning. Phalaropes can take advantage of the fact that numerous oceanic animals are neustonic, namely part-time or permanent residents of the sea surface fauna. Neustonic animals are always exposed to visual predators such as seabirds, and as such have various adaptations to reduce the risk of predation. Neuston often are cryptically blue, like many pontellid copepods, or extremely transparent, e.g., fish eggs and larval fish (Zaitsev, 1971; Hamner, 1995). Despite these and other adaptations, surface-seizing seabirds such as phalaropes can feed on various species of neuston with success when the sea is extremely calm or when neuston are exceptionally abundant, e.g., when concentrated in sea-surface convergence zones, or as a result of feeding activities by other predators.

Surface convergences of water (e.g., the front described here) are often marked by slicks or scumlines; these are typically only visible when wind speeds are less than 7 m $s^{-1}$ (e.g., Romano and Marquet, 1991; DiGiacomo and Holt, 2001). Two things happen at fronts that can enhance prey capture by phalaropes. First, oils and various buoyant particles become concentrated at the front when the two water masses converge. The oils spread across the sea surface at the front, dampening capillary and small gravity waves and forming the sea surface slicks that are readily seen by birds and human observers from ships, planes, and other suitable vantage points. Phalaropes can see the slicks even when flying rapidly and they routinely wheel above them, settle to the sea surface and inspect them for food. For the phalarope, the flattened sea surface provides a mirror flat viewing surface far superior to a surface ruffled by the wind, and if there are even small amounts of prey near the surface, the birds have a better optical opportunity for capturing them. When the wind is in excess of about 7 m $s^{-1}$, sea surface slicks are typically broken up by breaking waves and phalaropes that had been foraging at the front disperse when the slick disappears. Secondly, there is also a constant delivery of potential food to the front (fish eggs in this study), with the observed concentration of particulate materials in the front a function of the initial surface density of the particles, the buoyancy and/or behavior of the particles, the rate of convergence and the amount of time that the convergence has been undisturbed by predators or high winds.

Many species of fish release eggs that float at the sea surface (Zaitsev, 1971) and they, thus, become part of the neuston. The fish eggs (anchovy) found in the guts of the phalaropes here were not particularly small, but were moderately transparent and, thus, probably invisible to predators when the ocean surface is ruffled by light winds, particularly if limited in number. However, over time, even slowly converging water masses such as those observed here can result in high concentrations of food floating at the front. Fish egg (e.g., Nakata, 1989) and plankton (e.g., Kingsford, 1990) concentrations in fronts and other types of convergences can be upwards of an order of magnitude greater than concentrations in adjacent, nonslick regions. In the case of our study, anchovy eggs were apparently brought together in sufficient quantities at a front to make for a readily detectable and easily obtainable rich food source for phalaropes. While abundant here, fish eggs are by no means ubiquitous at convergences. Briggs et al. (1984), sampling convergences off central and northern California, found that fish eggs were a common prey item in the hindguts of collected red phalaropes. Surface tows revealed fish eggs to be rare in the convergences, however, indicating that phalaropes had fed on them earlier and elsewhere. In slicks, the birds had instead been feeding on the crustaceans that were abundant. Thus, phalaropes will exploit whatever type of prey is readily available at a convergence.

In a different example of opportunistic foraging, phalaropes can take advantage of the activities of other predators. Many species of zooplankton larger than 0.5 mm are herbivorous, and because their prey (i.e., phytoplankton) tend to be concentrated near the surface, these animals must ascend at night in order to feed. Alas, they are subsequently followed upward by their predators. Although visually mediated predation is obviously reduced at night, densities of both prey and predators is relatively high near the surface, with nocturnal feeding by predators presumably mediated primarily by touch and smell. Though prey often escape these predatory attacks at night, the animals that survive are sometimes damaged or disoriented. As dawn approaches, some of these individuals do not engage in normal DVM behavior, but instead remain near the surface with impaired swimming capabilities. Other individuals are even less lucky, left behind at the surface as floating carcasses or sundry fragments. During the day, phalaropes can then ingest remnants from the carnage of the previous night. Related situations have been described where surface-feeding birds consumed benthic amphipods associated with gray whale feeding (Obst and Hunt, 1990; Grebmeier and Harrison, 1992). Similarly, subsurface feeding by guillemots and murres left behind wounded, dead and fragmented euphausiids that accumulated at the sea surface where they were then fed upon by kittiwakes (Hunt et al., 1988; Schneider et al., 1990).

Thus, there are a number of behavioral and/or physical mechanisms that supply surface waters with adequate concentrations of prey for phalarope foraging. However, this does not entirely explain why spinning is not observed more frequently at sea. In fact, in some sense, this availability of food at the surface could be seen as an incentive for spinning. Presumably other factors are involved. Water depth could be important as spinning is particularly effective in bringing up particles from a shallow bottom, although spinning has also been observed in deep water (Sutton, 1932; Johns, 1969). Phalaropes do not spin in the presence of strong winds (Tinbergen, 1935; Höhn, 1971); Obst et al. (1996) speculated that wind-generated surface shear, Langmuir cells and breaking waves possibly interfere with the upwelling jets that result from spinning. This can possibly serve as a limiting factor in exposed marine environments. Spinning could also exhibit seasonal variability, associated with the availability (or lack thereof) of particular prey items (Höhn, 1971), or else wind strength as discussed above. Prey density could also be an important factor (Höhn, 1971).

An additional consideration is that of energy expenditure. Obst et al. (1996) remarked, albeit briefly, that spinning is energetically expensive, approximately four times greater than resting metabolism. Of greater relevance though is how the energetic costs of spinning compare to those of paddling (i.e., swimming). Measurements of this type were made, but not reported, as part of the Obst et al. (1996) study; we provide them here for the first time. Following are standard metabolic rates (SMR) for red-necked phalaropes, reported as the mean mass-specific rate of oxygen consumption ($V_{O_2}$) for varying states of activity (unpublished data, B. Obst, deceased): Dry, not moving, 0.03 ml $O_2$ $g^{-1}$ $min^{-1}$; Wet, not moving (i.e., floating), 0.04 ml $O_2$ $g^{-1}$ $min^{-1}$; Spinning (velocity is ~ 0.3 m $s^{-1}$; Obst et al., 1996), 0.13 ml $O_2$ $g^{-1}$ $min^{-1}$; Swimming, at speeds of 0.1–0.45 m $s^{-1}$, 0.07–0.12 ml $O_2$ $g^{-1}$ $min^{-1}$ (0.08 ml $O_2$ $g^{-1}$ $min^{-1}$ at 0.3 m $s^{-1}$). Spinning is clearly more energetically expensive, ~ 1.6 times greater, than is swimming at an equivalent velocity. The additional cost appears to be what the bird pays to set up the upward momentum jet and "lift" water to the surface (M. Rubega, personal communication). Relatedly, calculations were also made to determine what the cost is for phalaropes to inspect water for prey utilizing different methods; "inspection efficiencies" of 18.2 and 0.93 J $l^{-1}$ were found for spinning and swimming, respectively (unpublished data, B. Obst, deceased).

From the above data, it is clear that spinning as a means of foraging requires a significant expenditure of energy by a phalarope; these costs are much higher than those associated with paddling and feeding. As a result, the assumption that phalaropes should not spin unless the rewards (food) are great or otherwise unobtainable appears to have a significant energetic basis. In this regard, the ability of fronts and related oceanographic phenomena to concentrate prey at the sea surface in sufficient quantities as described here and elsewhere (e.g., Briggs et al., 1984; Haney, 1985; Brown and Gaskin, 1988) appears sufficient to satisfy the foraging requirements of phalaropes at sea. Given the widespread availability of these areas, in most cases spinning would appear to provide no additional benefits, particularly given the extra costs that would be incurred.

As discussed earlier, small-scale convergences of the type described here are extremely common features in both Santa Monica Bay and the surrounding SCB. These convergence zones result from the numerous fronts, eddies and related oceanographic phenomena that are associated with the complex morphology and flow regime found in the SCB. The presence of these recurring features provides phalaropes with a rich, easily accessible and reliable food source without having to resort to the energetically costly behavior of spinning. The occurrence, persistence and forcing of these small-scale convergence zones in the SCB and elsewhere remains poorly understood, however, due to their limited spatial extent and ephemeral nature. Relatedly, further studies are also needed to assess variability in phalarope distributions and feeding dynamics at sea, both in time (e.g., seasonally, diurnally) and space (e.g., occurrence at these convergences). For example, there can be significant diurnal variation in frontal convergence speed, especially at sunset. This variability could impact how many phalaropes forage at a front and/or their feeding behavior. Integrated, high-resolution multidisciplinary studies using in situ and remote observations are need to address these and other important questions pertaining to the marine ecology of phalaropes.

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