Phalarope feeding in relation to autumn upwelling off California

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1. Abstract

A joint ship-aircraft-satellite study conducted off central and northern California examined the relationship of phalarope feeding to convergences and other physical and biological processes of upwelling. Phalaropes were most numerous where strong surface thermal gradients bordered upwelling waters. Birds collected off Point Reyes and Point Montara had fed primarily on fish eggs and euphausiids, while off Davenport copepods were the predominant prey. Thaliaceans and siphonophores dominated the zooplankton collected in shallow, oblique tows within 40 km of the coast. Copepods and euphausiids replaced these gelatinous organisms farther offshore and were especially abundant at a convergence 30 km off Davenport. Fish eggs were rare in the tows, indicating phalaropes ate them outside of the area sampled. Although phalaropes tend to be attracted to surface manifestations of ocean convergences (e.g. slicks), not all convergent areas necessarily provide the right combination of hydrographic and biological conditions for sufficient prey concentrations. Specific temporal and spatial factors may ultimately determine the value of a given convergence as a source of prey.

2. Résumé

Une étude réalisée à la fois par bateau, avion et satellite au large du centre et du nord de la Californie nous a permis d'examiner le rapport entre l'alimentation des phalaropes et les convergences et autres phénomènes physiques et biologiques de la remontée des eaux profondes. Ces oiseaux étaient plus nombreux lorsque de forts gradients thermiques de surface bordaient les eaux résurgentes. Les oiseaux recueillis au large de Point Reyes et de Point Montara s'étaient nourris surtout d'oeufs de poissons et d'euphausiides, tandis qu'au large de Davenport, les copépodes étaient la proie prédominante. Les thaliacés et les siphonophores constituaient le gros du zooplancton recueilli dans les traits de filet obliques et peu profonds effectués à moins de 40 km de la côte. Les copépodes et les euphausiides remplaçaient ces organismes gélatineux plus au large et étaient particulièrement abondants à une convergence située à 30 km de Davenport. Nous trouvions rarement des oeufs de poissons dans les prélèvements, ce qui veut dire que les phalaropes les mangeaient à l'extérieur de la zone échantillonnée. Bien que ces oiseaux avaient tendance à être attirés vers les manifestations de surface des résurgences marines (par exemple, les nappes), toutes les zones convergentes n'offraient pas nécessairement la bonne combinaison de conditions hydrographiques et biologiques pour assurer une concentration suffisante de proies. Certains facteurs spatio-temporels peuvent finalement déterminer la valeur d'une convergence donnée comme source de proies.

3. Introduction

Several successful investigations during the past decade (reviewed in Ainley 1976, Ainley 1980, Brown 1980) have demonstrated that many aspects of seabird occurrence, colony productivity, and social structure relate directly to measurable offshore hydrographic and biologic processes. The advent of remote-sensing techniques, particularly from aircraft and satellites, to oceanographic studies (Arvesen *et al.* 1973, Bernstein *et al.* 1977, Stevenson *et al.* 1979) makes possible habitat-mapping over large ocean areas in very short time intervals, i.e. "synoptic coverage." Such techniques when coupled with standardized shipboard bird observations and hydrographic measurements, allow us to document and test hypotheses about the role of *mesoscale ocean features* (tens to a few hundreds of kilometres) in seabird ecology. This is probably the spatial scale of greatest importance to many pelagic and coastal marine birds.

This paper attempts to integrate phalarope feeding ecology and distribution with the biology and hydrography of autumn upwelling systems off California. Phalaropes are particularly suitable for such studies because they are easily seen from ship or air, they do not dive for food, are not quite as mobile as some pelagic birds, and they exploit a relatively limited neustonic food source (Ainley and Sanger 1979). Furthermore, unlike birds that return to shore each day and are affected by such factors as distance to colonies or large roosts, Red Phalaropes (*Phalaropus fulicarius*) spend most of the year away from the coast and can therefore be expected to respond directly to conditions offshore.

The affinity of phalaropes for upwelling regions is well known, and their concentration at surface convergences has been noted (Murphy 1936, Lamb 1964, Martin and Myres 1969, Ashmole 1971). Brown, in studies of the Senegal upwelling system (1979) and the Labrador Sea (1980), correlated the occurrence of Red Phalarope flocks with gradients in sea surface temperature (SST) and with the location of apparent offshore convergences. Brown (1980) also found that Red Phalaropes were most numerous at a topographically induced tidal divergence that upwelled zooplankton to the surface. He postulated that these birds actually *require* convergences or divergences to concentrate their minute, patchily distributed prey to exploitable levels. Brown suggested several physical mechanisms that might concentrate planktonic prey for phalaropes, and utilized satellite imagery to map these physical features.

This paper reports the results of an experiment in which we could correlate phalarope occurrence with major habitat gradients while simultaneously examining phalarope feeding within an active upwelling system.

4. Study area and oceanographic setting

4.1. Study area

Our study area extended from the coast to 185 km offshore between Santa Barbara Channel and the California–Oregon border, comprising approximately 162 500 km^2 (Fig. 1). The continental shelf varies in width from about 10 to 75 km. Waters in in approximately 63% of the study area exceed 2000 m in depth, about 13% are shallower than 200 m, and the remainder includes continental slope waters of intermediate depth. Though the region's shelf-slope bathymetry is relatively uniform, significant anomalies in shelf topography (canyons, escarpments) exist off Point Sur, Monterey Bay, and Cape Mendocino.

4.2. Oceanographic setting

The general hydrographic characteristics of this region have been described by Reid *et al.* (1958), Bolin and Abbott (1963), and reviewed by Hickey (1979). The California Current is a wide (~ 1000 km), slow (to about 30 cm/s) current that flows equatorward, bringing cool low-arctic waters to the California coast. A poleward undercurrent (the California Undercurrent) flows along the shelf break and slope at intermediate depths (± 100–300 m), except during the late autumn and winter, when it may surface as the Davidson Current (from Point Conception to at least southern Washington). Coastal upwelling, a phenomenon near the coast related to alongshore wind stress, and farther offshore perhaps to positive wind-stress curl and cyclonic eddies, is a dominant process on the shelf during spring and summer. The strength and persistence of upwelling decline in autumn. Upwelled waters are cool, nutrient rich, and relatively saline, particularly at upwelling centres off Cape Mendocino, Point Arena, Point Sur, and Point Conception.

Upwelling is most prominent off Point Conception in late spring, occurring progressively later in the summer at higher latitudes (Bakun and Nelson 1977). At times, upwelled water may occur as plumes extending hundreds of kilometres offshore (Traganza *et al.* 1981). Steep gradients in temperature, nutrient, and biological properties often exist offshore when upwelling plumes intrude into the California Current.

5. Methods

5.1. Phalarope distribution

We counted all phalaropes within 50-m strip transects (determined by inclinometer) along 39 east–west lines surveyed from aircraft during 21–25 September 1981 (Fig. 1). A total of 3182 linear km of aerial trackline was surveyed; lines averaged 76 km in length. Transect lines were surveyed from 65-m altitude at an airspeed of 165 km/h. Two observers alternated watches while three others recorded data. Observations were recorded orally on tape; location of each bird sighting (to ± 0.1′ latitude/longitude or approximately 0.2 km) was determined with an onboard VLF navigational computer. Transcribed data were computer-processed for density analysis by location.

While travelling at 15–18 km/h aboard a research vessel along three transects on 24 and 26 September and 3 October, we recorded all phalaropes seen within 400 m to either side (Fig. 2). Two observers were located 4 m above the water. Our shipboard observation techniques and a comparison of ship and aerial survey procedures appear in Briggs, Lewis *et al.* (1981) and Briggs and Hunt (1981).

Bird behaviour was classified according to activity at first sighting (fly, swim, feed), direction of travel, associations with other organisms or physical features like slicks, flotsam, and water-colour boundaries. Feeding by phalaropes could not be discerned from the air.

5.2. Phalarope diet

We collected 58 phalaropes along the ship tracks, 53 were Red Phalaropes and five were Red-necked Phalaropes (*Phalaropus lobatus*). Birds were tagged and frozen immediately upon retrieval. Many soft-bodied prey were subsequently identified from the stomachs, so immediate freezing of specimens appears to have minimized digestion. We recorded standard measurements of the birds after thawing. Proventriculi and ventriculi were removed intact, weighed, bound in cheesecloth, fixed in buffered Formalin, and after 24 h were transferred to 10% isopropyl alcohol.

The wet weights (to nearest 0.01 g) of gut contents were measured separately after sieving through 60 or 80 mesh screens: items as small as 0.3 mm were retained on the screens. It is unlikely that phalaropes prey on organisms smaller than this. Frequency of occurrence and percent volume of each identifiable item, and the minimum number of whole prey were determined for each stomach. When possible, all crustaceans were identified to species; other taxa were identified to family or order.

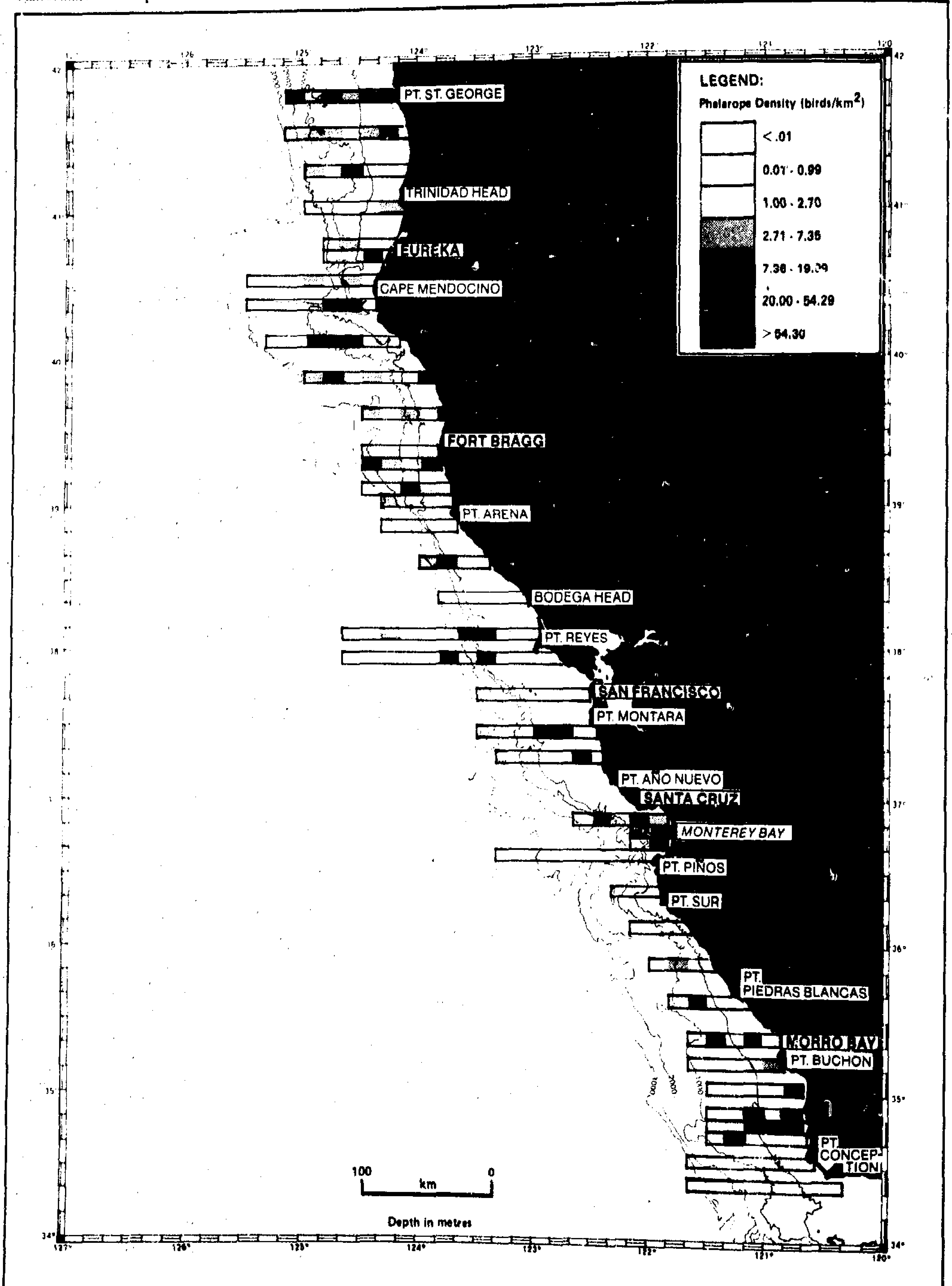
5.3. Plankton

To assess the relative composition and availability of potential planktonic prey, we made 17 oblique and 2 surface plankton tows as the ship travelled at 3–5 km/h with a 1-m-diameter net of 1-mm mesh. Oblique hauls were from approximately 40 m to the surface, a flowmeter attached to the net bridle estimated the volume of water filtered. Sampling occurred at 7–10-km intervals along ship tracks and wherever phalaropes were collected for diet analysis; waters within and on either side of moderate thermal fronts were sampled on each line as were several slicks. Samples were preserved in 10% buffered Formalin. Lab analyses of replicate subsamples from each haul included frequency of occurrence and size determinations for all major macrozooplankton taxa and enumerations of all crustacean species.

Most small zooplankton and highly motile fish larvae may have been missed at the towing speed and mesh we used, but less motile organisms in the size ranges likely to be exploited by phalaropes were probably included.

Chlorophyll *a* (Chl *a*) concentrations (an estimate of phytoplankton stocks) were measured to approximately one-third photic depth along aircraft tracklines with a differential radiometer (Arveson *et al.* 1973). Simultaneously, the photic zone chlorophyll field was measured throughout the study area by the Coastal Zone Color Scanner Satellite. Surface chlorophyll concentrations were

Figure 1
Phalarope density along aerial survey lines in central and northern California, 21–25 September 1981



measured along ship tracks by use of a flow-through fluorometer (Lorenzen 1966). Comparison of these data permitted calibration of synchronous satellite and aircraft chlorophyll values and interpolation of chlorophyll isopleths between aircraft tracklines.

5.4. Hydrographic measurements

Sea surface temperature (SST) was measured along aircraft transects with a precision radiation thermometer (accurate to ±0.2°C) coupled to a chart recorder. The entire coastal and offshore SST field was mapped at thermal infrared wavelengths (10.5–12.5 μm) on 22 September from the NOAA-6 satellite.

Along ship tracks, SST was measured continuously by a through-hull thermometer, and vertical temperature profiles were made at 20 sampling stations using 0–200 m expendable bathythermographs, 0–30 m CTD (conductivity–temperature–depth) casts, or both. Salinity was measured at the surface at 20 stations and at depths of 0–30 m at 11 stations to determine seawater density sections.

Surface concentrations of NO_3-N and PO_4-P were measured spectrophotometrically from 20 filtered samples. Nutrient concentrations and ratios provide important clues to the relative recency of nutrient regeneration from upwelling (Traganza *et al.* 1981).

6. Results

6.1. Phalarope distribution in relation to habitat

A total of 1573 phalaropes was seen in 297 sightings of 1–65 individuals during the aerial survey. Birds occurred within transects as far offshore as 115 km off Point Reyes (Fig. 1), and outside transect lines ("off transect" sightings) out to 195 km, also off Point Reyes. Phalaropes were concentrated just seaward of the shelf break and were less numerous closer to and farther from shore: 46.4% of all individuals and 48.4% of all sightings occurred in waters of the central slope (600–2000 m) although only 20.9% of survey effort was expended in waters of this depth range. By comparison, 30.0% of effort was directed into shelf waters (0–200 m), yielding 27.7 and 27.3% of individuals and sightings, respectively, while the 20.8% of effort expended in waters exceeding 2000 m resulted in only 2.8% of the individuals seen and 5.7% of the sightings. The heavily populated central slope area lies at distances ranging from 10 to 75 km offshore, averaging about 35 km.

Phalarope densities were high (exceeding 51.3 birds km^{-2}) in 13 aerial transect segments (10′ of longitude); four of these were located over the shelf and nine over the slope. Red-necked Phalaropes comprised 5–10% of all phalaropes seen during ship surveys in the Point Reyes–Monterey Bay sector; the rest were Red Phalaropes. The high numbers of birds observed over the shelf south of Point Buchon may have been predominantly Red-necked Phalaropes, because migration of that species tends to occur closer to shore than does that of Red Phalaropes (Briggs, Chu *et al.* 1981). We observed a similar distributional pattern during September–October 1980 (unpubl. data).

Because most phalaropes occurred in waters of intermediate distance from shore and of intermediate depth (median water depth of all phalarope sightings was 225 m), phalarope density was not significantly correlated with distance to shore or water depth (distance: Pearson's $r = -0.05$, $p = 0.20$; water depth: $r = 0.10$, $p = 0.07$; $N = 399$ 5′ × 5′ latitude–longitude "grid cells" for which density and physical parameters were measured). Further, phalarope density was not related linearly to surface temperature *per se*; the great majority of sightings occurred at intermediate values within the 10.0–18.0°C range that we sampled.

In contrast, most phalarope sightings occurred in areas of moderate to strong surface thermal gradients (>0.98°C/km). Figure 3 compares the strength of thermal gradients in 158 grid cells having phalarope sightings with

Figure 2
Details of sea-surface-temperature (SST) field off central California on 22–23 September 1981. Isotherms between aerial survey lines (shown on Fig. 1) are from NOAA-6 satellite images. Dashed lines indicate ship coverage on 24 (top line) and 26 (middle line) September and 3 October (bottom line)

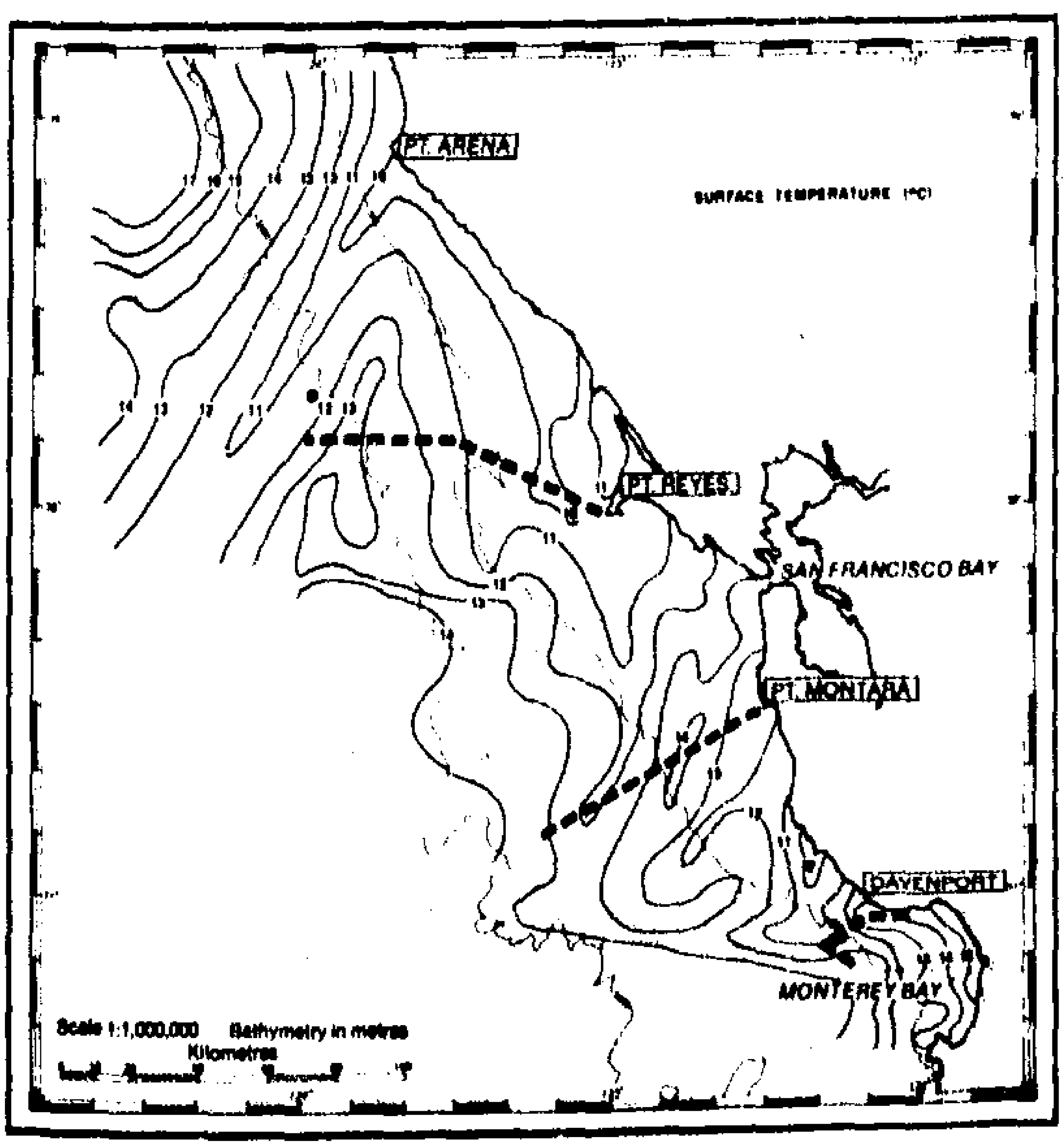
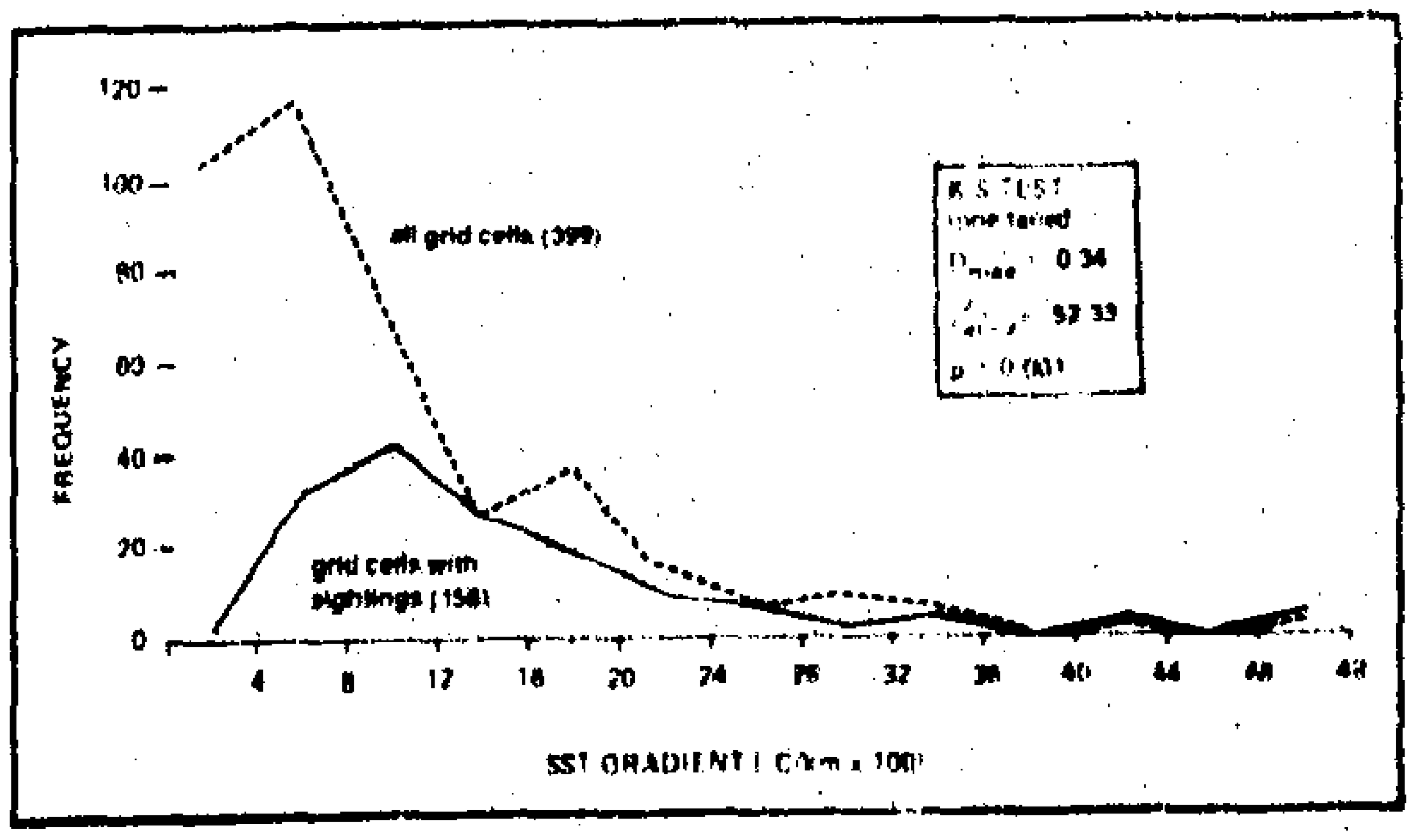


Figure 3
Frequency distributions of SST gradients in 5′ × 5′ latitude–longitude grid cells having phalarope sightings compared with SST in all grid cells. Data are from aerial surveys conducted during 21–25 September 1981. Kolmogarov–Smirnov test of goodness-of-fit shows that phalarope sightings were significantly concentrated in the grid cells having moderate to strong SST gradients



the strength of thermal gradients in the 399 grid cells surveyed. (Since bird distribution may relate to temperature gradients between surveyed lines as well as to gradients on lines, we interpolated the shape of isotherms between lines using coincident satellite infra-red (IR) imagery and assigned temperatures to ± 0.5°C by comparing satellite data with simultaneous airborne radiometer data taken on adjacent transect lines.) Thermal gradients in grid cells having phalarope sightings were significantly stronger than would be expected by chance ($p<0.001$, $\chi^2_{df=2} = 52.33$).

Steep gradients in SST occurred primarily at the boundaries between waters upwelled on the shelf and the adjacent waters of the California Current. Several very strong SST gradients were seen 100–250 km offshore in satellite IR images. Phalaropes were not especially numerous on either side of SST fronts. Instead they concentrated where SST changed rapidly with horizontal distance.

Phalarope sightings were concentrated to a significant degree in waters of low chlorophyll: grid cells with phalaropes averaged 0.19 mg Chl a/m^3 whereas all cells averaged 0.41 mg/m^3 (one-tailed K-S test of goodness-of-fit comparing frequency distributions of chlorophyll [determined by airborne radiometer] in grid cells having phalaropes with chlorophyll in all grid cells: $D_{max} = 0.257$; $\chi^2_{df=2} = 33.21$; $p<0.001$). Where Chlorophyll a was most concentrated (3–8 mg/m^3 very near the coast), phalaropes were relatively scarce.

Birds offshore (60 sightings of 329 birds >65 km from land), occurred in waters with a narrow temperature range, averaging slightly cooler than the mean of offshore grid cells (birds: range 11.1–16.2°C, $\bar{X}$ = 12.3 ± 1.3°C [SD] versus grid cells: range 11.1–17.4°C, $\bar{X}$ = 12.9°). Phalaropes frequented offshore waters where SST gradients were strong ($\bar{X}_{birds}$ = 0.14°C/km *vs* $\bar{X}_{grid\ cells}$ = 0.04°C/km) and where chlorophyll concentrations were low ($\bar{X}$ = 0.08 mg Chl a m^{-3} in cells where birds occurred).

6.2. Environmental cues for feeding

To determine the importance of visible environmental cues to foraging phalaropes, we analysed sightings of feeding flocks observed from the ship and sightings of stationary flocks (not flying) seen from the airplane. All but 66 of 500 phalaropes seen from shipboard on 24–26 September occurred in flocks feeding at slicks, as did all but about 20 of approximately 2500 seen on 3 October; no feeding flocks were seen away from slicks. Eighty-six percent of all birds seen during aerial surveys occurred in flocks (>3 birds); stationary flocks accounted for 669 birds (49.9% of the flock total). Of these, 442 phalaropes occurred in 62 stationary flocks at surface cues including slicks; colour boundaries; lines of flotsam, kelp, or foam; concentrations of baitfish; and swarms of plankton (Table 1). (The remaining phalaropes in stationary flocks may have been associated with surface cues that we failed to note due to glare, rough seas, and other conditions affecting aerial sightings.) These environmental cues are much less extensive than the thermal gradients discussed above (tens of metres to a few kilometres versus one to tens of kilometres) and all but three of the surface cues were located within strong or moderate SST gradients (>0.15°C/km or 0.08–0.15°C/km, respectively). Further, except for eight flocks comprising 64 birds, all other phalaropes in flocks (both flying and stationary) occurred within strong or moderate SST gradients. Eight of 41 discontinuities had no phalaropes; six of the eight were within 4 km of the coast and resulted from differences in suspended sediment between adjacent parcels of water, not from differences in chlorophyll concentration.

6.3. Phalarope feeding in central California upwelling systems

Phalarope feeding in relation to upwelling systems of different structure, dynamics, and apparent secondary productivity was examined from shipboard off central California. Because the development of upwelling conditions differed with area and time from 24 September through 3 October, each area is discussed separately.

6.3.1. *24 September — Point Reyes* — The 90-km ship track surveyed off Point Reyes extended into waters deeper than 3000 m. Northwest winds of 45–60 km/h during this and the preceding 3 days led to very active upwelling over the shelf. Isopycnals were upturned sharply toward the coast; the seasonal pycnocline (25.5 σT) surfaced at about 60 km offshore (Fig. 4) and coincided with a 1°C temperature gradient (0.2°C/km^2). This surface density front was within an area of elevated surface-chlorophyll concentration located 10-km seaward of a modest chlorophyll gradient (Fig. 5). The NO_3:PO_4 ratio declined from the area of the shelf seaward to the front, indicating transition from newly upwelled to more oceanic waters.

Phalaropes were found from about 47–79 km offshore, peaking in abundance at the front (Fig. 5). Thirty percent of 318 phalaropes seen were identified as reds; the rest were unidentified. Flocks totalling 106 birds visited slicks near the front. Ten Red Phalaropes, collected from flocks feeding near the front, recently had fed on euphausiids, including *Euphausia pacifica*; euphausiids totalled 47% of proventricular prey volume and 38% of prey numbers. Unidentified crustacean parts accounted for an additional 10% of volume. Other crustacean groups and plastic particles were less prominent. In contrast, fish eggs of two species (King-of-the-salmon, *Trachipterus altivelis* and Medusafish, *Ichichthys lockingtoni*), accounted for two-thirds of ventricular prey volume, whereas euphausiids comprised about a tenth. Barnacle cypris larvae, euphausiids, fish eggs, sand, and plastic each were contained in at least half of the stomachs (Table 2).

Prey items ranged in size from gastropod veliger and barnacle cypris larvae averaging 1.3–1.6 mm and 2.0 mm in length, respectively, to a 4-mm specimen of *Calanus* sp.,

Table 1
Presence of phalaropes at surface discontinuites indicative of convergences. Aerial sightings were on 21–25 September 1981

Type of discontinuity ("cues")	No. of discontinuities with (without) phalaropes	No. of birds (flocks) seen	Range of SST gradient*
A. Slicks (lacking floating material)	6 (1)	54 (11)	0.27 – 0.54
B. Slicks with kelp, foam, or flotsam	11 (0)	259 (26)	0.10 – 0.27
C. Colour boundaries	14 (7)	118 (22)	0.09 – 0.54
D. Plankton and baitfish swarms	2 (0)	11 (3)	0.18

*SST gradient in °C/km within 5′ latitude-longitude grid cell in which sighting occurred.

and 11–16 mm euphausiids. Fish eggs ranged in size from 1 to 4 mm.

Herbivorous salps (*Dolioletta* sp.) and carnivorous siphonophores together comprised 80–95% of zooplankton numbers and volume in plankton tows inshore of the front (stations 1–4). The dominant crustaceans were *Eucalanus californicus* and *Euphausia pacifica* (Table 3). Numbers of crustaceans (particularly *Calanus pacificus*) were higher in tows made at the slicks where feeding phalaropes were collected (stations 5 and 6), while *Dolioletta* sp. and siphonophores remained common (1–4 individuals/m^3). Fish eggs, so prominent within phalarope ventricular contents were quite rare in the tows, and barnacle cypris larvae (which accounted for 4% of prey volume and 36% of animal prey numbers) were completely absent. Both phalarope and *Calanus* (though not overall crustacean) abundance peaked at the front (Table 3 and Figure 5).

Table 2
Contents of the stomachs of 10 Red Phalaropes collected on 24 September off Point Reyes. Data from proventriculi and ventriculi are combined

Item	No. stomachs with item	Minimum no. whole prey	% of prey volume
Hydrozoan sp.	2	2	0.1
Gastropod sp.	5	7	0.2
Gastropod veliger	2	2	0.1
Crustacean parts	1	—	0.8
Cirriped cypris	6	230	4.0
Calanus sp.	1	1	0.4
Brachyuran zoea	1	1	0.1
Euphausiid sp.	2	6	2.1
Euphausia pacifica	5	44	28.0
Insect parts	4	—	2.2
Fish eggs	8	349	59.0
Sand grains	6	—	0.4
Plastic particles	6	—	1.1

6.3.2. *26 September — Point Montara* — Hydrographic conditions along a trackline to 80 km off Point Montara into waters 2750 m deep, changed considerably from 23 to 26 September. Measurements of SSTs from the airplane on the 23rd revealed a tongue of cool water extending from Point Reyes, intersecting the ship trackline between 40 and 70 km off Point Montara (Figs. 2 and 6). Southerly winds of 25–35 km/h on the 24th resulted in general warming of surface waters. Subsurface isotherms were only slightly upturned near shore on the 26th and SSTs offshore were 2.0 + °C warmer than when measured from the air. Offshore waters were now thermally stratified to 50 m (density sections at offshore stations showed similar stratification). Chlorophyll *a* was most concentrated within 20 km of the shore, was lowest from 40 to 60 km out and rose to 1–2 mg/m^3 farther offshore (Fig. 6). Nutrient concentrations were lower than off Point Reyes; ratios of NO_3:PO_4 were intermediate between upwelled and oceanic waters.

One hundred eighty-two phalaropes were seen along the ship track, despite the presence of dense fog for the first 20 km (airborne observers saw no phalaropes within this inshore zone on 22 September). Only 4% of the birds seen were identified to species and all were reds. Phalaropes were most numerous between 70 and 80 km from shore, with

Figure 4
Surface-layer density (σt) section for Point Reyes transect, 24 September 1981

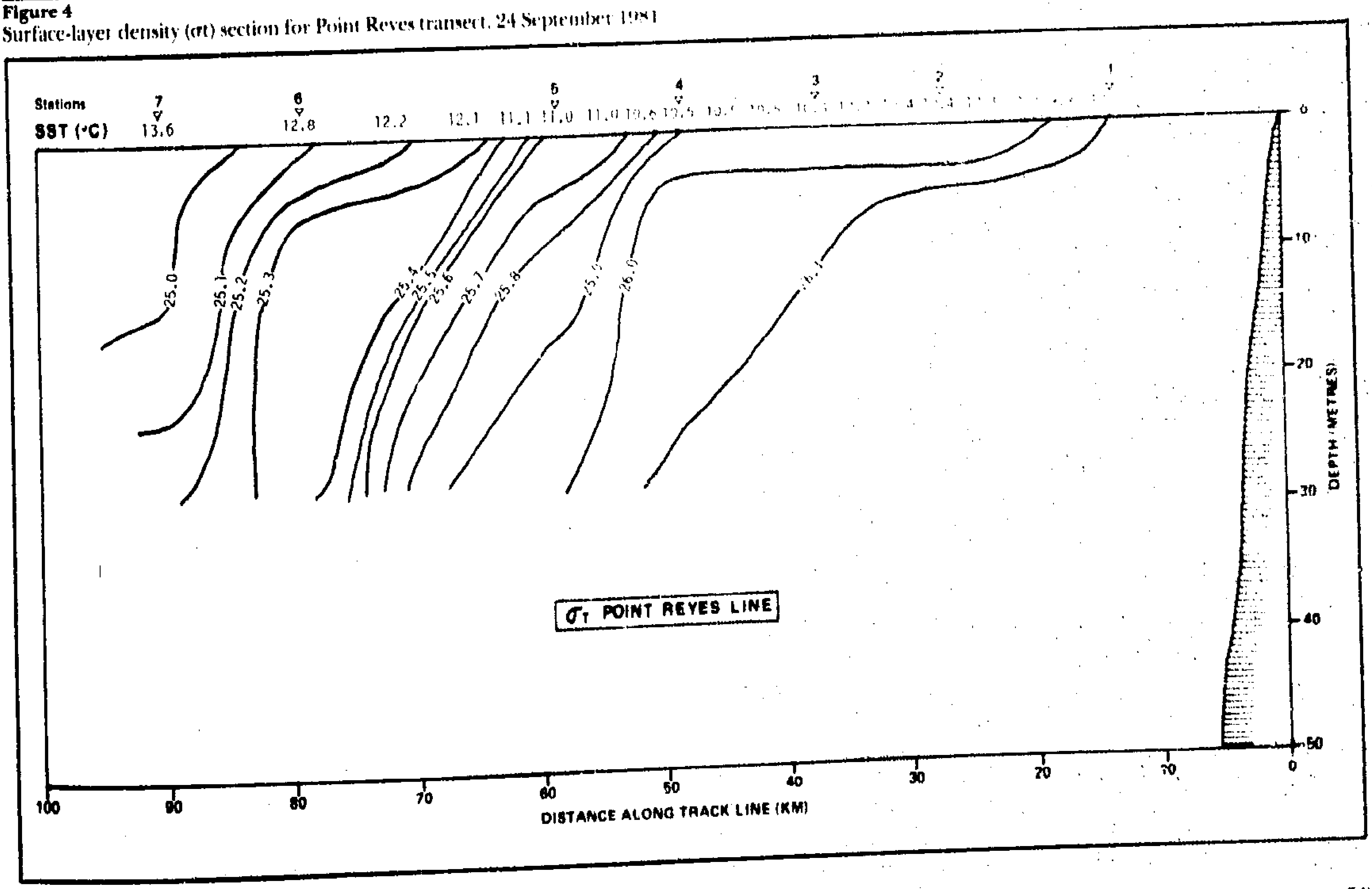


Table 3
Density (number · m^{-3}) of crustaceans, ichthyoplankton, and other macrozooplankton collected in 17 oblique and 2 surface (stations 14B and 19) tows on 24 and 26 September and 3 October, off Point Reyes, Point Montara, and Davenport, respectively (P indicates present in densities less than 0.1 m^{-3})

	Point Reyes transect							Point Montara transect										Davenport transect	
Station (km from coast)	**1 (14)**	**2 (27)**	**3 (37)**	**4 (48)**	**5 (58)**	**6 (78)**	**7 (91)**	**8 (11)**	**9 (19)**	**10 (29)**	**11 (38)**	**12 (45)**	**13 (52)**	**14A (59)**	**14B (59)**	**15 (68)**	**16 (78)**	**18 (19)**	**19 (28)**
Taxon																			
Crustacean larvae	—	—	—	—	—	—	—	—	—	1.0	1.6	0.3	0.2	P	—	0.5	0.1	0.9	0.7
Copepoda																			
Cyclopoida	—	—	—	—	P	P	P	—	—	—	—	—	—	—	—	—	—	—	—
Calanus pacificus	0.5	0.2	P	—	1.3	0.9	0.2	0.4	0.4	1.0	9.3	0.7	7.1	7.4	1.9	1.6	5.4	118.2	13.4
Eucalanus californicus	P	0.2	0.7	0.9	0.9	0.9	0.7	3.7	1.2	—	1.3	1.7	2.8	—	—	0.2	0.6	—	—
Euphausiacea																			
postlarvae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13.8	—
Euphausia pacifica	P	—	1.9	P	—	0.3	0.1	0.3	0.5	10.4	0.1	5.5	2.5	0.5	—	P	0.4	0.3	—
Thysanoessa sp.	P	P	—	P	0.4	0.2	0.1	0.3	0.3	0.2	—	—	—	—	—	—	—	—	—
Mysidae	—	—	—	—	—	—	—	—	—	P	—	—	—	—	—	—	—	—	—
Amphipoda																			
Hyperiidae	P	0.1	P	P	P	0.3	—	—	0.2	0.6	P	—	0.2	0.2	—	P	0.1	P	—
unidentified	—	—	P	—	P	—	0.1	P	—	—	—	—	0.2	—	—	—	—	—	—
Decapoda																			
Porcellanid larvae	—	—	—	—	—	—	—	—	—	—	0.3	—	—	—	—	—	—	—	—
Brachyuran larvae	P	0.3	P	—	P	—	—	1.2	0.6	—	—	—	—	—	—	0.2	P	—	—
Fish eggs/larvae	—	—	—	—	—	0.1	—	P	—	P	P	—	—	—	—	—	0.1	—	—
Unidentified egg	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	P	P	—	P	P
All other zooplankton*	0.7	3.0	69.9	5.4	2.6	8.1	4.9	3.3	2.7	42.6	19.2	4.5	16.0	15.3	0.6	2.8	3.1	0.1	2.0
Total crustacean density	0.6	0.8	2.5	1.0	2.6	2.7	1.3	6.0	3.2	13.2	12.8	8.2	12.8	7.7	1.9	2.6	6.7	133.2	14.3
Total zooplankton density	1.3	3.8	72.6	6.3	5.2	10.9	6.2	9.3	5.9	55.8	32.0	12.7	28.9	23.0	2.5	5.4	9.8	133.3	16.3
Moulted crustacean carapaces	—	—	—	—	—	—	—	—	—	10.5	—	—	—	—	439+	P	—	4.9	5.1

*Numerically important species included *Dolioletta* sp. (Thaliacia), Leptomedusae and Trachymedusae (Coelenterata: Hydrozoa), Physonectae (Hydrozoa), Cydippida (Ctenophora), and *Sagitta* sp. (Chaetognathia).

only smaller concentrations elsewhere (Fig. 6). Most birds were flying through this area; only three feeding flocks were seen, all near slicks at stations between 50 and 72 km offshore.

Six Red Phalaropes were collected from flocks in slicks at 59 and 72 km from shore. The foreguts of two birds were empty, suggesting that they had not fed recently. The foreguts of the other four birds contained primarily euphausiid parts, plus two whole *Thysanoessa spinifera* (Table 4). The hindguts of all six birds contained primarily fish eggs (accounting for 38.6% of total prey volume) and euphausiids. Euphausiids were well preserved, indicating that they were eaten recently. The sizes of prey taken by these birds were similar to those taken by birds off Point Reyes.

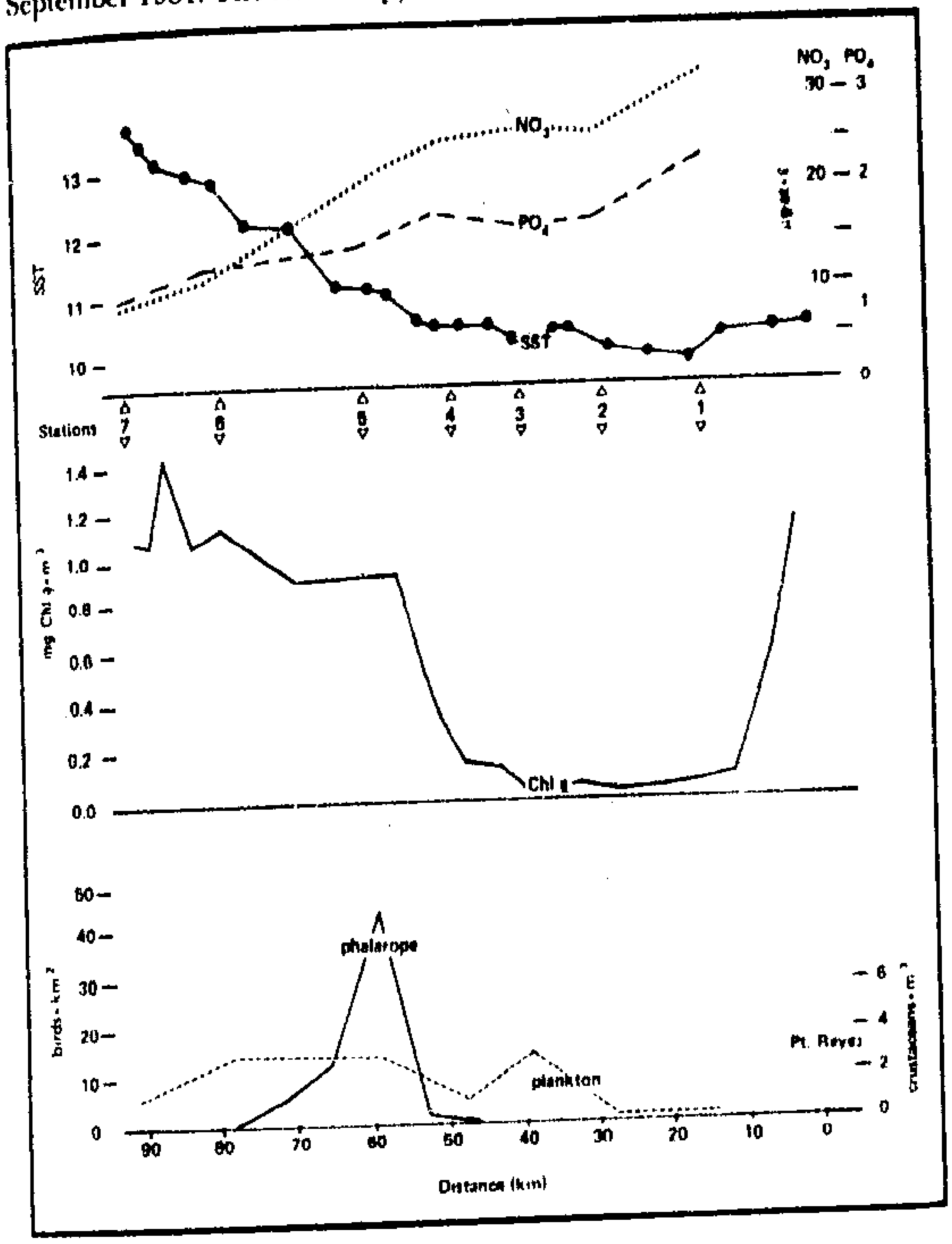
As was seen in plankton tows off Point Reyes various medusae and *Doliolетta* dominated both numbers and volume at stations out to 50 km; their abundance declined farther offshore. Crustacean density averaged much higher all along this track than off Point Reyes, owing to sizable populations of *Euphausia* and *Calanus* inshore and of *Calanus* beyond 50 km (Table 3). The phalarope flock at station 14, from which four birds were collected, was apparently attracted to extremely dense concentrations of moulted calanoid carapaces and moderate surface concentrations of live *C. pacificus*; subsurface *C. pacificus* density at station 14 was the highest encountered on this track. Small numbers of amphipods occurred all along the line while larval crustaceans were common at stations 10, 11, and 15. Euphausiids from Point Montara to station 13 were considerably larger than those farther offshore.

6.3.3. *3 October — Davenport* — Waters near the southern edge of a small upwelling plume extending southwest from Point Año Neuvo were sampled during a period of light northerly winds following the storm of the previous week. Aerial and satellite SST data taken before the storm showed intense upwelling; SSTs as low as 10°C occurred near shore (Fig. 2). Only weak upwelling was evident on this 30-km ship track on 3 October (Fig. 7), with Chlorophyll *a* and nutrient conditions much like the shelf-break section of the Point Montara transect (stations 9 and 10). Satellite images from late September through early October, consistently showed this region to be a zone of intermixing of waters upwelled to the north with warmer, oceanic waters from west of Monterey Bay.

We collected 42 phalaropes from among approximately 2500 birds in several flocks at a 0.8°C thermal front (0.14°C/km) just seaward of the shelf break. Though no direct counts of species proportions were made here, 5 of the 42 specimens collected were Red-necked Phalaropes, while the rest were reds.

In contrast to the gut contents of birds collected elsewhere, these birds had fed to a great degree (53% volume) on *Calanus* sp. (Table 5) with lesser amounts of

Figure 5
Comparison of temperature (in degrees Celsius), nutrients, and plant and animal populations at sampling stations along Point Reyes ship tract, 24 September 1981. The seasonal pycnocline (25.5 σt) surfaced near 60 km



brachyuran larvae, euphausiids and other crustaceans. Insect parts (Coleoptera) were found in about one-third of all ventriculi, and about half contained large numbers of crustacean zoea and nauplii (0.5 mm to about 1.5 mm).

Surface and oblique zooplankton tows demonstrated the extreme numerical predominance of *Calanus* among crustaceans here (Table 3). One-third of all phalaropes collected on this date were taken on a slick at station 18 where surface swarms of *Calanus* were ubiquitous. The presence at station 19 of euphausiid carapaces — indicative of active growth and moult — is noteworthy, in view of the 13% contribution this group made to proventricular prey volume. Substantial numbers of crustacean larvae were taken in plankton tows here. Clearly, conditions had been favourable for crustacean moult for some time off Davenport and perhaps also to the north, where reproductive products may have originated before drifting south.

7. Discussion

In light of recent studies of plankton ecology in upwelling regions and Brown's (1980) concept of phalarope's dependence upon physical concentrating mechanisms for successful feeding, several inferences can be drawn from our California Current data:

1. Nutrient regeneration through upwelling enhances plant production and growth, leading to relatively high standing stocks of herbivorous zooplankton. Vertically migrating zooplankton may remain in the same general location relative to the source of upwelling by alternately migrating to strata having opposite mean currents (Smith *et al.* 1981*a*, Smith *et al.* 1981*b*); but they tend to accumulate at offshore convergences because of rapid advection within the Ekman layer (~0–30 m; Huyer 1976):
a. Phalaropes feeding in convergences should encounter relatively high prey availability;
b. Foraging phalaropes should utilize visable environmental cues to locate convergences;
c. Off California, feeding flocks should be common in thermal fronts where upwelling waters converge with surface waters of the California Current;
d. Because nutrient and chlorophyll concentrations may be highest near the source of upwelling, phalarope distribution should not necessarily exhibit a positive correlation with either;

2. Unless dispersed by extreme turbulent mixing due to wind, the zooplankton found near fronts are distributed in patches (Holligan 1981, Husby and Nelson 1981). Phalarope feeding success along a convergent front may therefore be quite variable and bird occupation of such a feature should be patchy;

Table 4
Contents of the stomachs of six Red Phalaropes collected on 26 September off Point Montara. Data from proventriculi and ventriculi are combined

Item	No. of stomachs with item	Minimum no. whole prey	% of prey volume
Hydrozoan sp.	1	1	0.6
Cirriped cypris	4	13	1.8
Hyperiid amphipod	2	22	1.0
Euphausiid parts	3	3	13.0
Euphausia pacifica	1	7	13.6
Thysanoessa longipes	2	8	14.4
Thysanoessa spinifera	1	2	13.1
Insect parts	2	2	1.6
Fish eggs	6	577	38.6
Sand grains	2	—	2.2
Plastic particles	3	—	0.1

Table 5
Contents of the stomachs of 37 Red Phalaropes and 5 Red-necked Phalaropes collected on 3 October 1981 off Davenport. Data from proventriculi and ventriculi are combined*

Item	No. of stomachs with item	Minimum no. whole prey	% of prey volume
Hydrozoan sp	2	6	0.1
Thecate hydrozoan	1	1	<0.1
Gastropod sp.	2	5	<0.1
Pteropod sp.	1	1	<0.1
Crustacean parts	3		11.2
Crustacean larvae	23	4056	5.8
Cirriped cypris	9	14	1.0
Calanus sp.	30	3923	52.8
Brachyuran larvae	36	516	5.0
Euphausiid sp	8	80	4.4
Euphausiid larvae	10	167	2.0
Euphausia pacifica	2	2	0.2
Thysanoessa Spinifera	2	2	2.6
Insect parts	7		1.8
Coleoptera sp.	11	35	1.6
Halipid coleopteran	1	1	<0.1
Fish eggs	17	28	0.8
Sand grains	5		<0.1
Plastic particles	25		4.0
Seeds	2	2	0.1
Unidentifiable material	46		1.9

*One trematode (<0.1% total volume) was found; it was unknown whether it was parasitic on the bird.

does not, in the absence of high grazing plankton populations, lead to successful feeding by phalaropes. Conversely, an area with abundant zooplankton but lacking a convergence (as off Point Montara) will support few birds.

The importance of convergence-feeding by migrating phalaropes depends on the relative stability and dependability of both upwelling and convergences. Occurrence of wind conditions unsuitable to upwelling or periods of extremely strong wind might lead to adverse feeding conditions in extensive portions of the migration pathway (perhaps 500 km or more). Birds encountering such conditions might starve if they lacked sufficient energy reserves either to wait for better conditions or to pass over the unsuitable region. Bond (1971 and sources cited therein) described a mass mortality of this sort. As yet, the seasonal stability of upwellings and associated convergences off California are incompletely known. Hopefully, additional observations of phalaropes associated with coastal upwelling will provide critical data for refining and testing these ideas.

9. Acknowledgements

We thank J. Christmann and S. Davenport, who persevered through difficult ship surveys and K. Reinhard and D. Allison, who kept our aircraft flying so well for thousands of survey-hours. L.C. Breaker of NOAA–NESS and R. Austin of Scripps Institution's VisLab provided invaluable satellite coverage and interpretations. J. Arveson of NASA–Ames Research Facility loaned us a differential radiometer and other equipment while NMFS–Tiburon Lab provided an XBT recorder. Oceanographic gear and expertise were made available by M. Silver, P. DuVoll, and D. Garrison. We were assisted in the field by M. Pierson, M. Bonnell, and G. Farrens; T. Dohl provided temperature data and much logistical support. G. Moser kindly identified fish eggs from gut samples. D. Briggs and T. Smith aided us with graphics and C. Hitchman and T. Smith typed several versions of the manuscript. We are grateful for critical reviews by L.C. Breaker, E.W. Chu, R.G.B. Brown, D.G. Ainley, W.G. Pearcy, and G.A. Sanger.

This work was supported by the US Department of Interior, Bureau of Land Management under contract #AA551-CT9-33 to the regents of the University of California. This is a contribution of the Center for Coastal Marine Studies, University of California, Santa Cruz.

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