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. Thalassacans and siphonophores dominated the zooplankton collected in shallow, oblique tows within 10 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 phalâropes 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 étaient nourris surtout d'œufs de poissons et d'euphausiides, tandis qu'au large de Davenport, les copepodes étaient la proie prédominante. Les thalassacans 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 copepodes et les euphausiides remplacèrent ces organismes gelatinés plus au large et étaient particulièrement abondants à une convergence située à 30 km de Davenport. Nous trouvions rarement des œufs de poissons dans les prélèvements, ce qui veut dire que les phalaropes les mangeaient à l'extérieur de la zone de remontée. Bien que ces oiseaux aient 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 spatiaux-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 kilometers) 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 192 500 km² (Fig. 1). The continental shelf varies in width from about 10 to 75 km. Waters in it approximately 65% 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 (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 (~200–300 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 (Truganze 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 transect 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 21 and 28 September, and 3 October, we recorded all phalaropes seen within 100 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 (1984).

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. 13 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. Proventriculus and ventriculus were removed intact, weighed, bound in cheese cloth, dried in buffered formalin, and after 24 h were transferred to 10% isopropyl alcohol.

The wet weights (to nearest 0.1 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 phalarope 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 80-μm mesh. Oblique hauls were from approximately 10 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 analyses; waters within and on either side of moderate thermal fronts were sampled on each line as were several stacks. Samples were preserved in 10% buffered formalin. 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 transects with a differential radiometer (Arvinsen 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 NO₃-N and PO₄-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 995 sightings of 1-05 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 further from shore. 36.4% of all individuals and 39.4% 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, 31.8% 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 28.0% of the individuals seen and 57.7% 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 5-5 birds km⁻²) in 13 aerial transect segments (10% of longitude, 10% of these were located over the shelf, and 34% over the slope. Red-necked Phalaropes comprised 5% 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, C. 1976). We observed a similar distribution pattern during September-October 1980 and 1981.

Because most phalaropes occurred in waters of intermediate distance from shore and of intermediate depth, median water depth of all phalarope sightings was 22.3 m. Phalarope density was not significantly correlated with distance to shore or water depth. Distance to shore r = 0.05, p = 0.20; water depth r = 0.04, p = 0.21. N = 399.5 = 2.5 latitude-longitude grid cells for which densities and physical parameters were measured. Further, phalarope densities were not related linearly to surface temperature for, 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 (0-0.9°C km⁻¹). Figure 3 compares the strength of thermal gradients in 158 grid cells having phalarope sightings with
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 simultaneously 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 ($p < 0.001$, $X^2 = 52.93$).

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 numer-
ous on either side of SST fronts. Instead they concentrated
where SST changed rapidly with horizontal distance.

Phalarope sightings were concentrated to a signifi-
cant degree in waters of low chlorophyll; grid cells with
phalaropes averaged 0.19 mg Chl a/m$^2$ whereas all cells
averaged 0.11 mg Chl a/m$^2$ (two-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: $D_{max} = 0.257$

$$X^2 = 133.21$ ($p < 0.001$). Where Chlorophyll a was
most concentrated (3.8 mg Chl a/m$^2$ very near the coast), phala-
ropes 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, $X = 12.3 ± 1.3$°C [n=159]
versus grid cells: range 11.1–17.4°C, $X = 12.9$°C. Phalaropes
frequented offshore waters where SST gradients were
strong ($X_{max} = 0.14$°C/km in $X_{max} = 0.01$°C/km) and
where chlorophyll concentrations were low ($X = 0.08$ mg
Chl a/m$^2$ in cells where birds occurred).

6.2. Environmental cues for feeding

To determine the importance of visible environ-
mental 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 oc-
curred 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 exten-
sive 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 phala-
ropes; 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 chlor-
ophyll 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 Cali-
ifornia. 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 ± 1°C) surfaced at about 60 km
offshore (Fig. 4) and coincided with a 1°C temperature
gradient (0.2°C/km). 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 eupha-
siids, including Euphausia pacifica; euphausiids totalled
47% of provencultral 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 alvii and
Medusafish, Ichthychys 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>
<thead>
<tr>
<th>Type of discontinuity</th>
<th>No. of discontinuities</th>
<th>No. of birds (flocks) seen</th>
<th>Range of SST gradient*</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Slicks (lacking floating material)</td>
<td>6 (1)</td>
<td>54 (11)</td>
<td>0.27 – 0.54</td>
</tr>
<tr>
<td>B. Slicks with kelp, foam, or flotsam</td>
<td>11 (0)</td>
<td>259 (20)</td>
<td>0.10 – 0.27</td>
</tr>
<tr>
<td>C. Colour boundaries</td>
<td>14 (7)</td>
<td>118 (22)</td>
<td>0.00 – 0.54</td>
</tr>
<tr>
<td>D. Plankton and baitfish swarms</td>
<td>2 (0)</td>
<td>11 (5)</td>
<td>0.18</td>
</tr>
</tbody>
</table>

* 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 (*Doliolita* 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 *Doliolita* sp. and siphonophores remained common (1–4 individuals/m²). 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 38% 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).

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 Montara, intersecting the ship trackline between 10 and 70 km off Point Montara (Figs. 2 and 6). Southerly winds of 25–35 knots 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.

Surface 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 10 to 60 km out and rose to 1–2 mg/m³ further offshore (Fig. 6). Nutrient concentrations were lower than off Point Reyes; ratios of NO₃:PO₄ 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 (barbore observers saw no phalaropes within this inshore zone on 22 September). Only 17% of the birds seen were identified to species and all were reds. Phalaropes were most numerous between 70 and 80 km from shore, with

<table>
<thead>
<tr>
<th>Item</th>
<th>No. stomachs with item</th>
<th>Minimum no. whole prey</th>
<th>% of prey volume</th>
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<tr>
<td>Hydrozoan sp.</td>
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<td>2</td>
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<tr>
<td>Gastropod sp.</td>
<td>5</td>
<td>7</td>
<td>0.2</td>
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<tr>
<td>Gastropod veliger</td>
<td>2</td>
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<td>0.1</td>
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<tr>
<td>Crustacean parts</td>
<td>1</td>
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<td>0.8</td>
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<tr>
<td>Carried cypris</td>
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<td>200</td>
<td>4.0</td>
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<tr>
<td><em>Calanus</em> sp.</td>
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<td>1</td>
<td>0.1</td>
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<tr>
<td>Brachyuran zoa</td>
<td>2</td>
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<td>0.1</td>
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<tr>
<td>Euphausiids sp.</td>
<td>2</td>
<td>6</td>
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<tr>
<td><em>Euphausia pacifica</em></td>
<td>5</td>
<td>44</td>
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<td>Insect parts</td>
<td>4</td>
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<td>Fish eggs</td>
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<td>349</td>
<td>70.0</td>
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<tr>
<td>Sand grains</td>
<td>6</td>
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<td>0.1</td>
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<tr>
<td>Plast particles</td>
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<td>—</td>
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Table 3

<table>
<thead>
<tr>
<th>Station (km from coast)</th>
<th>Point Reyes transect</th>
<th>Point Montara transect</th>
<th>Davenport transect</th>
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<tr>
<td></td>
<td>1 2 3 4 5 6 7</td>
<td>8 9 10 11 12 13 14A 14B 15 16 17 18 19</td>
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</tr>
<tr>
<td>Taxon</td>
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<tr>
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</tr>
<tr>
<td>copepodites</td>
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<tr>
<td>Copepods</td>
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<tr>
<td>Calanus propinquus</td>
<td>0.5 0.2 P</td>
<td>1.3 0.9 0.2</td>
<td>0.3 0.2 P</td>
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<td>Euphausiids</td>
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<td>0.9 0.9 0.7</td>
<td>3.7 1.2</td>
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<td>Phyllospinae</td>
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<td>Mestida</td>
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<tr>
<td>Amphipods</td>
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<tr>
<td>unidentifed</td>
<td>P 0.01 P</td>
<td>0.09 P</td>
<td>0.3 0.2 P</td>
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<td>Eubostracida</td>
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<tr>
<td>Phyllospinae</td>
<td>P 0.03 P</td>
<td>0.2 P</td>
<td>1.2 0.2</td>
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<tr>
<td>Phyllospinae</td>
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<tr>
<td>Unidentified</td>
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<tr>
<td>Total zooplankton*</td>
<td>0.7 3.0 0.99 0.54</td>
<td>2.6 0.8 2.1</td>
<td>3.3 2.7 42.6 19.2</td>
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<tr>
<td>Crustacean density</td>
<td>0.6 0.8 2.3 1.0</td>
<td>2.6 2.7 1.3</td>
<td>6.0 3.2 13.2 12.8</td>
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<tr>
<td>Zooplankton density</td>
<td>1.3 3.8 72.6 63</td>
<td>5.2 10.9 6.2</td>
<td>9.3 5.9 35.8 32.0</td>
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<td>Mestida-Calanoid</td>
<td></td>
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<tr>
<td>carcasses</td>
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</tbody>
</table>

*Numbers lack important species included: Daleolites sp. (Thaliacea), Lepidodana eurisphera (Calanoida: Hyperiidae), Phyllospinae (Heteropoda), Caulliodora (Euphausiidae), and Sagittaria (Oithonidae).

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 euphausiids part plus two whole Thyasius sp., but 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, or by those off, Point Reyes.

As seen in plankton tow off Point Reyes various medusae and Didemnella dominated both numbers and volume at stations out to 50 km; their abundance declined farther offshore. Crustacean density averaged much higher 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 Nuevo were sampled during a period of light northwesterlies 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 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, 6 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 (93% volume) on Calanus sp. (Table 5) with lesser amounts of
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 pre-ventricullar 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

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

<table>
<thead>
<tr>
<th>Item</th>
<th>No. of stomachs</th>
<th>Minimum no. whole prey</th>
<th>% of prey volume</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hydrozoan sp.</td>
<td>1</td>
<td>1</td>
<td>0.6</td>
</tr>
<tr>
<td>Gribble Evans</td>
<td>4</td>
<td>13</td>
<td>18</td>
</tr>
<tr>
<td>Hyperid amphipods</td>
<td>2</td>
<td>22</td>
<td>10</td>
</tr>
<tr>
<td>Euphausiid parts</td>
<td>3</td>
<td>35</td>
<td>13</td>
</tr>
<tr>
<td>Euphausia pacifica</td>
<td>1</td>
<td>7</td>
<td>13</td>
</tr>
<tr>
<td>Thyasiroidea longipes</td>
<td>2</td>
<td>8</td>
<td>14</td>
</tr>
<tr>
<td>Thyasiroidea longipes</td>
<td>1</td>
<td>2</td>
<td>12</td>
</tr>
<tr>
<td>Insect parts</td>
<td>2</td>
<td>2</td>
<td>16</td>
</tr>
<tr>
<td>Fish eggs</td>
<td>6</td>
<td>577</td>
<td>96</td>
</tr>
<tr>
<td>Sand grains</td>
<td>2</td>
<td>2</td>
<td>22</td>
</tr>
<tr>
<td>Plastic particles</td>
<td>3</td>
<td>1</td>
<td>0.1</td>
</tr>
</tbody>
</table>

Table 5
Contents of the stomachs of 37 Red Phalaropes and 3 Red-necked Phalaropes collected on 30 October 1981 off Davenport. Data from pre-ventricullar and ventricullar are combined.

<table>
<thead>
<tr>
<th>Item</th>
<th>No. of stomachs</th>
<th>Minimum no. whole prey</th>
<th>% of prey volume</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hydrozoan sp.</td>
<td>2</td>
<td>6</td>
<td>0.1</td>
</tr>
<tr>
<td>Thracetum hydroid</td>
<td>1</td>
<td>1</td>
<td>0.1</td>
</tr>
<tr>
<td>Gasteropod sp.</td>
<td>2</td>
<td>2</td>
<td>0.1</td>
</tr>
<tr>
<td>Pteropod sp.</td>
<td>1</td>
<td>1</td>
<td>0.1</td>
</tr>
<tr>
<td>Crustacean parts</td>
<td>3</td>
<td>3</td>
<td>1.2</td>
</tr>
<tr>
<td>Crustacean larva</td>
<td>6</td>
<td>40</td>
<td>5.8</td>
</tr>
<tr>
<td>Copepod sp.</td>
<td>4</td>
<td>11</td>
<td>1.1</td>
</tr>
<tr>
<td>Calanus sp.</td>
<td>9</td>
<td>92</td>
<td>13.8</td>
</tr>
<tr>
<td>Branchiopod larva</td>
<td>2</td>
<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td>Euphausid larva</td>
<td>2</td>
<td>0.5</td>
<td>0.8</td>
</tr>
<tr>
<td>Phyla, holothurian</td>
<td>2</td>
<td>2</td>
<td>2.6</td>
</tr>
<tr>
<td>Thysanura, benthica</td>
<td>2</td>
<td>1</td>
<td>1.8</td>
</tr>
<tr>
<td>Insect parts</td>
<td>5</td>
<td>15</td>
<td>1.6</td>
</tr>
<tr>
<td>Coleoptera sp.</td>
<td>1</td>
<td>1</td>
<td>0.1</td>
</tr>
<tr>
<td>Halipid coleoptera</td>
<td>5</td>
<td>1</td>
<td>0.5</td>
</tr>
<tr>
<td>Fish eggs</td>
<td>17</td>
<td>1</td>
<td>0.1</td>
</tr>
<tr>
<td>Sand grains</td>
<td>4</td>
<td>2</td>
<td>0.8</td>
</tr>
<tr>
<td>Plastic particles</td>
<td>25</td>
<td>25</td>
<td>1.0</td>
</tr>
<tr>
<td>Seeds</td>
<td>3</td>
<td>3</td>
<td>0.1</td>
</tr>
<tr>
<td>Unidentifiable material</td>
<td>16</td>
<td>16</td>
<td>1.0</td>
</tr>
</tbody>
</table>

*One trematode (c. 0.15 mm length) was found; it was unknown whether it was parasitic on the bird.

migrating to strata having opposite mean currents (Smith et al. 1984), Smith et al. 1981(b), but they tend to accumulate at offshore convergences because of rapid advection within the Ekman layer (c. 0–30 m; Huerv 1975). a. Phalaropes feeding in convergences should encounter relatively high prey availability;

b. Foraging phalaropes should utilize visible 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;
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 upwelling and associated convergences off California is incompletely known. Hopefully, additional observations of phalaropes associated with coastal upwelling will provide critical data for refining and testing these ideas.

9. Acknowledgements

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10. Literature cited


