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HISTORICAL CHANGES IN THE ABUNDANCE AND DISTRIBUTION OF THE AMERICAN AVOCET AT THE NORTHERN LIMIT OF ITS WINTER RANGE

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ABSTRACT: Humboldt Bay, California, is the northern limit of the winter distribution of the American Avocet (*Recurvirostra americana*) on the Pacific coast. After the first record in 1935, avocets were uncommon (17 observations) until the early 1960s, when a wintering population of <100 birds became established in North (Arcata) Bay. Numbers increased to approximately 1000 by the early 1990s but have since declined to approximately 500. From 1968 to 1985, avocets consistently used intertidal habitats and oxidation ponds in the northeast quarter of Arcata Bay. Beginning in the mid-1990s they expanded their use of Arcata Bay and into South Bay. During February and March 1998 and February 2000, up to 32 occasionally fed in flooded pastures adjacent to the bay; only two avocets had been observed there in the previous 40 years. At low tide, avocets aggregated in intertidal habitats of Arcata Bay and South Bay. We hypothesize that they increased because of a rangewide population increase and that in Humboldt Bay they concentrate where small particle size of sediments makes for better feeding habitat. Altered habitat quality, especially during wet years (late 1990s), may have changed avocet distribution in Humboldt Bay.

Understanding changes in the abundance and distribution of a species is a central theme of animal ecology, and research at the limits of an organism's range can provide valuable insight into factors limiting a species' distribution, especially when conducted over a long period. The American Avocet (*Recurvirostra americana*) winters in intertidal and freshwater habitats along the Atlantic, Gulf, and Pacific coasts of North America (Robinson et al. 1997). Along the Pacific coast, Humboldt Bay, California represents the northern extreme of the species' winter range (Evans and Harris 1994, Robinson et al. 1997); there are no winter records from the Pacific Northwest (Paulson 1993). Evans and Harris (1994) showed that avocets were a recent addition to the wintering avifauna of the northern California coast, first recorded in 1935. Beginning in the 1960s, a growing population of wintering avocets concentrated in the northeast quarter of

Humboldt Bay (Evans and Harris 1994). Since 1989, we have collected information on avocet abundance and distribution at Humboldt Bay and have noticed changes in the patterns reported by Evans and Harris (1994). Here, we summarize changes in avocet distribution and abundance on Humboldt Bay and discuss possible reasons for these changes.

STUDY AREA

Humboldt Bay (40° 46′ N, 124° 14′ W) is the largest bay between San Francisco Bay, California, 370 km south, and Coos Bay, Oregon, 335 km north (Barnhart et al. 1992). Costa (1982) characterized the bay as a tidal coastal lagoon with limited freshwater input. The bay consists of three sections, each of which is at the end of a different tributary. The largest section, Arcata Bay, receives fresh water from Jacoby and Freshwater creeks. Broad intertidal habitats of Arcata Bay consist of sediments varying from clayey silts of intertidal flats to sandy substrates lining main channels. Much of the lower intertidal reaches of the center of Arcata Bay supports eelgrass (*Zostera marina*), but the extent of this habitat has been reduced by oyster culture (Barnhart et al. 1992). Oxidation ponds of the Arcata marsh and sewage-treatment facility lie on the northeast shore of Arcata Bay. A narrow shipping channel connects Arcata Bay to Entrance Bay. The channel and Entrance Bay are dredged to provide access to ships, hence most intertidal habitats have steep banks and coarse substrates. The Elk River empties into the main channel and provides some intertidal flats, which are partially covered by eelgrass. South Bay consists of extensive intertidal habitats and substrates varying from sand to clayey silt. Large relatively pristine eelgrass beds cover much of the lower intertidal reaches of South Bay. Salmon Creek enters the southeast corner of South Bay through Humboldt Bay National Wildlife Refuge (HBNWR). Since 1850, people have converted much of the bay's salt marsh and intertidal habitats to agricultural lands, especially pasture. Barnhart et al. (1992) described Humboldt Bay in detail.

METHODS

Our examination of avocet population size and distribution relies on several independent sources of data collected over the last 50 years. The quality of this information varies with the different objectives of researchers and unequal sampling effort.

Field notes. Harris has kept regular field notes on bird distribution and abundance around Humboldt Bay since 1959. From these notes, we collated maximum annual estimates and locations of avocets.

Christmas Bird Counts. Two CBC circles cover virtually all intertidal habitats of Humboldt Bay and abut at the harbor entrance. The Centerville CBC, conducted for 41 years, covers all of South Bay. Harris has coordinated this count and collated data since 1973. To the north, the Arcata CBC, conducted since 1984, covers all of Arcata Bay and the main channel leading to the bay entrance. Because we were able to identify most locations at which observers recorded avocets, CBC data offer an important historical perspective on the species' use of the bay.

Graduate theses. Two graduate theses provided data on avocet distributions. In 1968 and 1969, Gerstenberg (1972) surveyed all shorebirds at nine locations on Humboldt Bay. Evans (1988) summarized avocet distribution baywide during three winters (1982–83 through 1984–85); he made 76 surveys at 11 sites within Arcata Bay and 42 surveys from 11 locations in South Bay. Since each used different survey methods and collated data differently, we summarized their information as follows. Using Gerstenberg's (1972) maximum winter count of avocets at each of his survey locations, we summed all avocet observations at the nine locations and calculated the proportion at each site (yielding a proportional abundance). Evans (1988) summarized his results as the average monthly high- and low-tide count at each location. We used the maximum average winter (October–February) count for each location to represent use of a site. Next, we calculated the proportion of these summed maximum counts for each location.

Baywide shorebird surveys. From 1989 to 1994 and again in 1998, Colwell coordinated multiple observers who surveyed Humboldt Bay simultaneously to estimate seasonal use by shorebirds (Colwell 1994). Surveys were shore-based counts of intertidal habitats of the bay, adjacent pastures and freshwater sloughs, and ocean beaches fronting the bay. The survey protocol entailed four sequential half-hour scans (Altmann 1974) during which observers estimated the number of shorebirds using an area. The start of each half-hour scan was synchronized among observers to reduce the likelihood that birds moving between areas would be counted by more than one observer. We surveyed shorebirds during rising tides so that foraging birds were pushed by the advancing tide toward shore, improving observers' estimates of abundance (Colwell and Cooper 1993). Observers conducted surveys from prominent observation points around the bay to maximize observation area and minimize overlap between adjacent observers (further details in Colwell and Cooper 1993, Colwell 1994).

During the five years of surveys, sampling effort varied greatly with weather and the number of observers (Colwell 1994); many locations were not surveyed every year, although some sites received regular coverage, often by the same observers. Consequently, we selected the single maximum count of avocets at each site from 10 winter survey dates (November and February, 1989–1994). We summed these maximum counts and calculated the proportional abundance of observations at each location. In this form, data were corrected for possible changes in avocet population size at Humboldt Bay. We summarized 1998 survey data separately by the same method.

Winter 1998–1999 surveys. At 19 locations around the bay, we used a protocol similar to that of the shorebird surveys to esitmate winter (November 1998–January 1999) shorebird numbers. Unlike baywide surveys (see above), which took place during flood tides, we did these surveys during ebb tides, when intertidal flats were exposed. Areas surveyed varied from 3.5 to 52.1 ha; we based their boundaries on edges of channels, salt marsh, and other prominent habitat features. We summarized these data as the maximum count of four surveys at each site and present data as the proportion at each location of total avocet observations (Danufsky 2000).

Low-tide avocet mapping. At five tides <0.33 m (January, February, and October 1999; January and February 2000), we mapped avocets on high-

resolution images of the bay, overlaid by a UTM-based grid system. Observers mapped avocets from the same shoreline observation points used in the baywide surveys (see above) and from boats moving through the bay's main channels. We marked the location of avocets on images by means of topographic features like channels, islands, and saltmarsh points and we recorded the number of avocets observed within each 500-m grid. We standardized data by calculating the number of avocets in a grid cell within five observation periods (January and February 1999 and 2000, October 1999). For cells including intertidal habitats exposed at low tide, we calculated the average number of avocets per grid cell and variance. We compared observed avocet distributions to a random model by using the index of dispersion (I, variance-to-mean ratio; Krebs 1989). If avocets were randomly distributed among grid cells, this ratio equaled one; if they were aggregated it was greater than one; if they were evenly distributed it was less than one. We compared each survey's I value to a random distribution by means of a two-tailed t test.

RESULTS

Population estimates. Over 40 years, avocet numbers have varied significantly (Kruskal–Wallis test, $\chi^2 = 36.4$, $P = 0.00002$) among the five-year intervals (Figure 1). Beginning in the 1950s, a small population established itself at Humboldt Bay. Numbers nearly doubled over the next two decades.

Figure 1. Estimates (maximum counts) of American Avocets wintering at Humboldt Bay, California, from 1955 to 1999, based on field notes (1955–1967; 1970–1981; 1995–1997), graduate theses (1968–1969; 1982–1985), shorebird surveys (1989–1994; 1998) and baywide mapping of avocet distributions (1999–2000).

Table 1 Estimates of the Number and Spatial Distribution of Nonbreeding American Avocets at Humboldt Bay, California, Based on Bay-wide Mapping During Diurnal Low Tides

	30–31 Jan 1999	27–28 Feb 1999	23 Oct 1999	29–30 Jan 2000	13 Feb 2000
Number of avocets	543	343	182	475	479
Mean (per grid cell)	1.65	1.04	0.55	1.44	1.45
Variance (per grid cell)	62.33	21.97	17.43	90.89	70.97
Dispersion index	37.9	21.1	31.6	63.1	48.9
t value	758.1	261.6	217.2	1118.1	869.0
P	<0.01	<0.01	<0.01	<0.01	<0.01
Observed low tide (m)	−0.31, −0.51	−0.02, −0.10	0.10	0.55, 0.49	0.63
Time of low tide	1712, 1748	1618, 1724	1642	1300, 1424	1212

By the early 1990s, estimates ranged from 850 to 1200 birds, after which numbers declined during the late 1990s. During January/February low-tide mapping in 1998–1999 and 1999–2000, we estimated an average of 460 ± 84 (range 343–543) avocets on Humboldt Bay (Table 1).

Historical distributions in Humboldt Bay. Avocets occurred on 20% of Centerville CBCs over the count's 41-year history; 98% of the 372 avocets occurred between 1994 and 1999 (Table 2). Except for records of no more than four individuals in 1969, 1975, and 1978, avocets first appeared on the Centerville CBC in 1994, when 39 were in the Eel River lowlands. In 1995 none were reported; in 1996, when inclement weather compromised survey efforts, eight were at HBNWR adjacent to South Bay. From 1997 to 1999, 98 to 99% of avocets occurred on HBNWR; no more than four were reported in the Eel River lowlands.

Avocets occurred on all 16 Arcata CBCs (Table 2). Total numbers varied greatly (mean 763 ± 379); high numbers reported from 1993 to 1995 almost

Table 2 Averages and Ranges of American Avocet Numbers on the Centerville and Arcata Christmas Bird Counts by Five-Year Periods

5-Year Interval	Centerville CBC	Arcata CBC
1955–1959	0[a]	—
1960–1964	0	—
1965–1969	0.2 (0–1)	—
1970–1974	0	—
1975–1979	1 (0–4)	—
1980–1984	0	839[a]
1985–1989	0	590 (500–800)
1990–1994	8 (0–39)	825 (564–1806)
1995–1999	65 (0–165)	665 (382–1176)

[a]One estimate only; CBC began the last year of this interval.

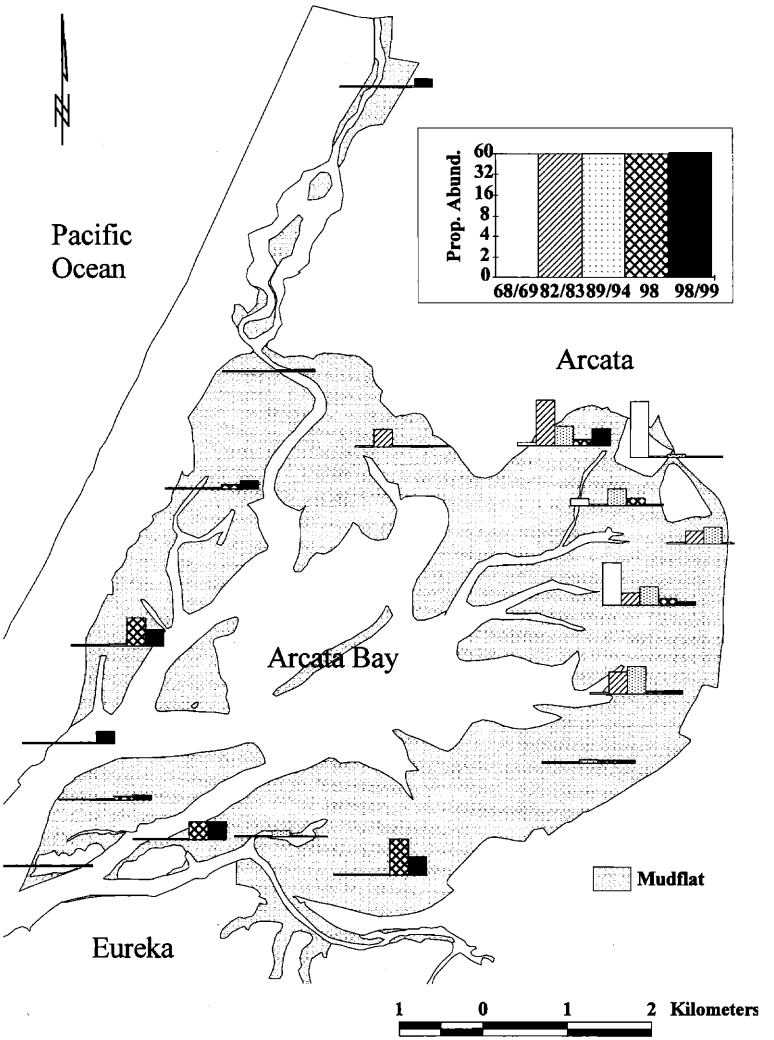

Figure 2. A 30-year history of changes in the proportional abundance of American Avocets around Arcata Bay, California, based on field notes, graduate theses, shorebird surveys, and recent research. Data are from shore-based surveys and do not include the center of Arcata Bay.

certainly represent summed counts from different observers. A decline in avocet observations in Arcata Bay paralleled the increase in South Bay.

Over the past three decades, the spatial distribution of avocets in intertidal habitats of Humboldt Bay has changed (Figure 2). During the late 1960s (Gerstenberg 1972) and mid-1980s (Evans 1988), avocets used the north and east parts of Arcata Bay nearly exclusively. During the early 1990s, baywide surveys revealed a similar pattern, but a few avocets (6.1%) occurred on the south and west shores of Arcata Bay; only six occurred outside Arcata Bay in the southwest corner of South Bay (1992 and 1993). During January and February 1998, avocet use of the north and east sectors of Arcata Bay declined, whereas use of south and west areas increased sharply. From November 1998 to January 1999, avocets were more evenly distributed around Arcata Bay than they were 10–30 years earlier. On numerous occasions during January and February 1998, S. Manion and Mathis observed 5–32 avocets feeding at low tide in flooded pastures north and west of Arcata Bay. On 16 February 2000, Colwell observed 15 avocets feeding in flooded fields of HBNWR.

Avocet densities during winter 1999 and 2000. From the total number of birds in each grid cell, we determined that avocets were concentrated (Table 1) along channels and on intertidal flats of Arcata Bay and in the southeast corner of South Bay (Figure 3).

DISCUSSION

The number of nonbreeding avocets at Humboldt Bay clearly has varied greatly over the past 50 years. Although Grinnell and Miller (1944) listed no coastal records for the avocet north of Marin County (Novato), they omitted two specimens collected at Humboldt Bay 17 and 18 August 1935 (Humboldt State University; Davis 1939). From 1945 through 1958, 17 avocets occurred on Humboldt Bay on six occasions. Beginning in 1959, their numbers increased steadily from 75 (1959) to 800–1400 (1980s–90s). A similar increase occurred in the Point Reyes region, another important wintering area on California's north coast (G. W. Page pers. comm., Shuford et al. 1989). More recently, the number of avocets wintering at Humboldt Bay appears to have declined by 50% to approximately 500.

Virtually all early records of avocets were concentrated in the northeast quarter of Arcata Bay. Nelson (1989) surveyed waterbirds in South Bay from July 1987 to June 1988 and listed avocets as seen irregularly, with numbers insufficient to warrant analysis. CBC data corroborate the early differences between Arcata Bay and South Bay. Beginning in the 1990s, avocets expanded to the south and west shores of Arcata Bay. CBC data show that in 1994 a small number of avocets began to feed on intertidal flats in the southeast corner of South Bay; at high tide they roosted in freshwater habitats of HBNWR. Most recently, during the winters of 1998 and 2000, avocets fed in flooded pastures adjacent to Arcata Bay, which had rarely been observed previously (Harris unpubl. data).

Establishment and growth of the Humboldt Bay population. At least two explanations, not mutually exclusive, exist for the establishment and increase in numbers of avocets at Humboldt Bay: (1) the avocet's breeding

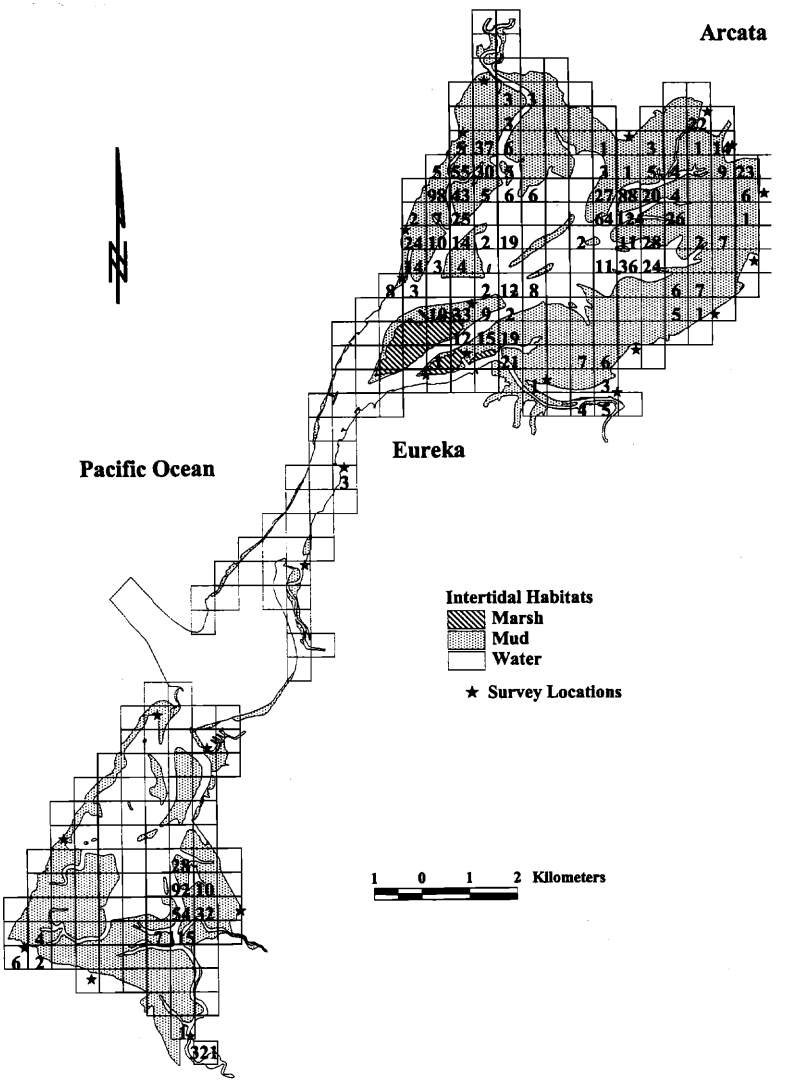

Figure 3. Low-tide distribution of wintering American Avocets in intertidal habitats of Humboldt Bay during winter mapping surveys (see Table 1). Numbers represent the total number of avocets observed in each grid cell (500 × 500 m).

population has increased in the region supplying winter visitors to Humboldt Bay; (2) nonbreeding habitat has changed, allowing avocets to expand their range into formerly unoccupied areas. On the basis of the Breeding Bird Survey, Robbins et al. (1986) reported that from 1965 to 1979 the population of the American Avocets increased significantly. This increase coincided with the major period of growth in the Humboldt Bay avocet population. Breeding Bird Survey data for 1966 to 1996 suggest that the population increased at >0.25% per year in Oregon, California, and Nevada, all breeding locales for color-marked birds observed at Humboldt Bay (Robinson and Oring 1996, Plissner et al. 1999).

Evaluating the habitat hypothesis is difficult. Specimens show that nonbreeding avocets visited Humboldt Bay occasionally earlier in the 20th century (and probably before that). In the late 1950s local numbers began to increase. Evans and Harris (1994) speculated that construction of sewage-oxidation ponds in the northeast corner of Arcata Bay in 1957 offered important habitat that was previously unavailable. Their habitat-limitation argument was based on spatial and temporal coincidence and seems plausible—numbers increased dramatically after the ponds' construction, and avocets occurred only in their vicinity. From 1980s data, Evans and Harris (1994) described an "avocet home range" (868 ha) in the north-east corner of Arcata Bay where avocets occurred predictably; they recorded only 30 observations of avocets outside this home range during 1142 hours observation.

The habitat-limitation hypothesis posits that, prior to the construction of oxidation ponds, Humboldt Bay lacked one or more habitat requirements (e.g., food, water, sanctuary from predators) necessary to support wintering avocets (Evans and Harris 1994). Evans (1988) reported that avocets used these oxidation ponds to feed on cladocerans (*Daphnia magna*), especially during October and November; most other times, however, avocets fed on nearby intertidal flats exposed during low tide. In addition to food, oxidation ponds may provide an important source of fresh water for avocets occupying saltwater habitats (Evans and Harris 1994). Evans and Harris (1994) discounted the importance of fresh water because avocets breed in hypersaline environments and have a well-developed salt gland (Mahoney and Jehl 1985). In hypersaline habitats, however, avocets concentrate in areas of fresh water (L. W. Oring pers. comm.). This suggests that although avocets possess the physiological adaptation to tolerate these habitats, they pay an energetic cost in doing so, possibly influencing their distribution.

Avocet distributions within Humboldt Bay and along the Pacific coast. An extension of the habitat-limitation hypothesis posits that the absence of avocets from some areas of Humboldt Bay stemmed from an absence of essential habitat requirements. A partial explanation for the patchy distribution of avocets within the bay (Figure 3) may be related to the distribution of intertidal sediment types—avocets occurred in areas characterized by fine (silty-clay) sediments and were absent from areas with coarse (sandy) sediments (Thompson 1971). Danufsky (2000) found support for this hypothesis in an inverse relationship between avocet occurrence and substrate particle size. The aggregated baywide distribution of avocets probably stems from a relationship between substrate composition, prey availability,

and the manner in which avocets feed. At Humboldt Bay, most avocets feed with a single scything maneuver (Evans and Harris 1994), a tactile foraging method of sweeping the bill through the upper film of sediment (Hamilton 1975). Sediment type influences habitat use by avocets. For example, Quammen (1982) experimentally manipulated substrates at Newport Bay, California, and found that avocets moved more quickly through and scythed less (pecked more) where sand was added to a mud substrate. We hypothesize that avocet distributions are related to their scything for prey in fine substrates, which vary in their distribution in Humboldt Bay.

If substrate particle size influences distributions of foraging avocets, then historical changes in avocet distribution in Humboldt Bay suggest that this habitat characteristic changed abruptly in the 1990s. In the mid-1990s, avocets began using areas of the bay that they rarely used during the period of population expansion (1960–1995). We speculate that wet years (1995–1999), coupled with logging of Humboldt Bay's watershed, increased the amount of fine sediments in the bay, altering avocet foraging habitat. Interestingly, the February 1998 observations of avocets feeding in flooded pastures adjacent to Arcata Bay coincided with the strongest (wettest) El Niño on record.

Furthermore, we speculate that, in part, the northern limit of the avocet's winter range on the Pacific coast also may be related to the preference for feeding in fine sediments (Robinson et al. 1997). Specifically, the broad flats and fine sediments of Humboldt Bay are uncommon at bays along the Oregon and Washington coast. At least 17 major estuaries occur on the Oregon coast; Washington has five such estuaries. Fifteen of the estuaries in Oregon (e.g., Nestucca, Nehalem, and Rogue) are steep-banked with sandy substrates. Grays Harbor and Willapa Bay, Washington, and perhaps Coos Bay and Tillamook Bay, Oregon, offer broad intertidal flats and fine substrates of the type apparently favored by avocets. During migration, avocets occur occasionally on the Oregon–Washington coast. Paulson (1993) reported two avocets at Coos Bay on 12 December 1980, but they were not observed after that date. In summary, the combination of Humboldt Bay's fine sediments, abundant prey (e.g., crustaceans, oligochaetes, polychaetes) linked to these substrates (Robinson et al. 1997), and moderate climate provide conditions sufficient to support avocets. These conditions are generally absent farther north on the Pacific coast.

CONSERVATION IMPLICATIONS

During January and February 1998 and February 2000, avocets fed in flooded pastures adjacent to Humboldt Bay. In this area, avocets had been observed in pastures rarely—Gerstenberg (1972) reported two in pastures during September 1969. Pastures commonly flood each winter following heavy rain. These observations strongly suggest that during winter 1998 food availability in intertidal habitats was reduced because of habitat changes.

In 1997–1998, winter use of flooded pastures coincided with two noteworthy environmental events. First, on 7 November 1997, an oil spill (~5000 gallons Bunker C fuel) occurred in Humboldt Bay, and oil contaminated intertidal flats throughout the west and southwest portions of Arcata Bay, the main channel, and limited areas of

South Bay. As yet, the effect of this oil on avocets remains undetermined, but oil may have killed some proportion of the avocets' invertebrate prey, forcing the birds to feed in pastures. Second, the record rainfall generated by El Niño of winter 1998–1999, coupled with soil exposed by timber harvesting, may have increased the amount of sediments deposited on flats during winter storms. We speculate that during winter 1998 these factors reduced invertebrate populations and habitat, forcing avocets to seek food in alternative foraging habitats.

The hypothesis that avocets and their prey were influenced by heavy sedimentation in the bay is bolstered by similar observations for another bay-dependent species with a very different feeding ecology, the Black Brant (*Branta bernicla nigricans*). During winter, and more so during spring migration, thousands of Brant stage at Humboldt Bay where they feed nearly exclusively on eelgrass. During winter and spring 1998, Brant fed extensively in pastures adjacent to Arcata Bay and South Bay. This pattern was observed only once before, during winter 1953, another El Niño year. During winter 1998–1999, K. Kovacs (pers. comm) and Mathis commented independently on the poor quality of eelgrass and its covering by sediment.

Historical accounts of avocets and recent studies seeking to estimate their population and distribution within Humboldt Bay establish the foundation for long-term monitoring of avocets. Moreover, features of the American Avocet make it an ideal subject for monitoring changes in population size, distribution, and habitat use at Humboldt Bay and elsewhere. Its conspicuous pied plumage, large size, and loose flocking tendencies make it easy to identify, observe, and count. Its use of fine sediment in intertidal habitats and dependence on prey taken from surface sediments render it a strong candidate as an indicator species for habitat change, which may influence other coastal waterbirds. We urge researchers at other locations to monitor avocets and expand our understanding of the relationships between avocet population size, distribution, and changes in the habitats in which they forage.

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