DISTRIBUTION, ABUNDANCE, AND IMPLICATIONS FOR CONSERVATION OF WINTER WATERBIRDS ON TOMALES BAY, CALIFORNIA

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Tomales Bay, on the Marin County coast, is one of California's largest and least disturbed estuaries, yet little has been published on the status of its waterbirds or their vulnerability to environmental threats. Shuford et al. (1989) reported the results of waterbird censuses of up to 10 consecutive years in the adjacent Point Reyes area between 1965 and 1982 but provided limited information on waterbird use of Tomales Bay. Other anecdotal accounts and aerial survey work over the last 30 years suggest that Tomales Bay supports unusually high abundances of some waterbird species (Moffitt 1943, Grinnell and Miller 1944, Calif. Dept. Fish and Game unpubl. data, U.S. Fish and Wildlife Service unpubl. data, National Audubon Society Christmas Bird Counts) and is worthy of protection (National Oceanic and Atmospheric Administration 1987, Neubacher et al. 1995).

In this paper, we present results from seven winters of baywide waterbird censuses on Tomales Bay, compare results with other studies to provide a historical and geographical perspective on the importance of Tomales Bay to waterbirds, evaluate species distributions within the bay with regard to possible habitat relationships and the importance of particular habitat areas, and, on the basis of these evaluations, identify needs for conservation of winter waterbird populations on Tomales Bay. We address these objectives with regard to all waterbird species associated with Tomales Bay and immediately adjacent ponds and marshes, with the exception of sandpipers (Scolopacidae), plovers (Charadriidae), and large and medium-sized gulls (Laridae; Table 1). Most gulls were excluded from the study because of difficulties in counting large numbers of moving birds and identifying species. Sandpipers, plovers, and gulls were also difficult or impossible to observe from survey boats because these species often concentrated on exposed tidal flats or in alternative habitats away from the bay. Abundances of winter shorebirds and gulls on Tomales Bay have been reported elsewhere (Kelly 1993, Kelly et al. 1996).

STUDY AREA

The long straight expanse of Tomales Bay floods the lower 20 km of the fault- generated Olema Valley on the central California coast, about 45 km northwest of San Francisco (Figure 1; Galloway 1977). The bay differs from other, generally shallower, Pacific coast estuaries and lagoons in having a much greater area of open water at low tide and therefore more waterbird habitat through the tidal cycle. Approximately 91% of the bay's 28.5-km^2 area is subtidal. With hills surrounding the narrow (1–2 km) bay, and little fetch when winds blow from directions other than northwest, surface waters remain relatively calm during winter. Tomales Bay contains 37 eelgrass (*Zostera marina*) beds covering a total area of 392 hectares, predominantly in the

Table 1 Mean Densities and Abundances of Winter Waterbirds on Tomales Bay, 1989–90 to 1995–96[a]

Species	Density (birds/km^2)				Baywide abundance	
	South of Tomasini Pt.	Tomasini Pt. to Pelican Pt.	Pelican Pt. to Tom's Pt.	Tom's Pt. to Sand Pt.	Mean	Range
Red-throated Loon, *Gavia stellata*	0.55 (0.11)	7.96 (1.02)	1.60 (0.30)	1.50 (0.29)	123.68 (14.11)	28–284
Pacific Loon, *G. pacifica*	0.25 (0.08)	5.22 (1.29)	0.76 (0.16)	0.86 (0.28)	78.20 (18.56)	7–365
Common Loon, *G. immer*	0.71 (0.10)	8.77 (0.98)	6.99 (0.66)	6.15 (0.40)	186.73 (14.73)	57–390
Unidentified loon	0.14 (0.05)	1.29 (0.68)	0.77 (0.22)	0.78 (0.32)	25.43 (11.22)	0–226
Pied-billed Grebe, *Podilymbus podiceps*	0.18 (0.06)	0.13 (0.03)	0.49 (0.28)	0.01 (0.01)	5.95 (2.17)	0–46
Horned Grebe, *Podiceps auritus*	1.73 (0.34)	28.55 (4.59)	18.73 (2.11)	13.91 (1.87)	557.21 (65.67)	175–1287
Red-necked Grebe, *P. grisegena*	0.01 (0.01)	0.13 (0.06)	1.60 (0.29)	1.97 (0.40)	19.14 (2.81)	3–61
Eared Grebe, *P. nigricollis*	0.43 (0.12)	10.20 (1.39)	14.24 (2.21)	3.35 (0.64)	242.31 (27.30)	16–467
Eared/Horned Grebe	0.33 (0.13)	4.48 (2.01)	3.04 (1.37)	3.01 (0.98)	91.24 (29.06)	0–512
Western Grebe, *Aechmophorus occidentalis*	9.37 (1.57)	30.00 (3.82)	4.82 (0.85)	0.45 (0.10)	478.75 (56.22)	90–958
Clark's Grebe, *A. clarkii*	2.54 (0.60)	5.67 (1.05)	0.57 (0.18)	0.14 (0.05)	92.44 (14.51)	1–293
Western/Clark's Grebe	4.79 (1.94)	0.32 (0.26)	2.12 (0.68)	0.12 (0.07)	43.81 (12.93)	0–195
White Pelican, *Pelecanus erythrorhynchos*	0.00 (0.00)	0.00 (0.00)	0.59 (0.31)	0.00 (0.00)	3.95 (2.06)	0–30
Brown Pelican, *P. occidentalis*	0.33 (0.14)	0.66 (0.18)	0.56 (0.27)	0.37 (0.15)	15.43 (3.93)	0–56
Double-crested Cormorant, *Phalacrocorax auritus*	15.64 (4.42)	26.33 (3.84)	16.80 (3.14)	3.82 (1.04)	553.73 (51.42)	261–1105
Brandt's Cormorant, *P. penicillatus*	0.55 (0.54)	6.02 (1.38)	7.40 (5.10)	3.61 (1.00)	143.46 (35.04)	26–750
Pelagic Cormorant, *P. pelagicus*	0.05 (0.05)	0.14 (0.04)	0.72 (0.11)	1.72 (0.60)	12.77 (2.45)	1–52
Unidentified cormorant	0.04 (0.03)	0.39 (0.28)	0.68 (0.49)	0.44 (0.28)	11.33 (5.70)	0–107
Great Blue Heron, *Ardea herodias*	0.20 (0.04)	0.21 (0.04)	0.74 (0.19)	0.40 (0.13)	10.10 (1.36)	1–25
Great Egret, *A. alba*	0.64 (0.14)	0.09 (0.02)	0.46 (0.10)	0.10 (0.04)	7.95 (1.08)	0–18
Snowy Egret, *Egretta thula*	0.07 (0.02)	0.05 (0.02)	0.29 (0.08)	0.18 (0.10)	3.52 (0.77)	0–11
Black-crowned Night-Heron, *Nycticorax nycticorax*	0.00 (0.00)	0.28 (0.08)	0.00 (0.00)	0.00 (0.00)	3.71 (1.10)	0–14
Black Brant, *Branta bernicla nigricans*	0.21 (0.14)	5.52 (1.90)	129.19 (21.94)	78.44 (29.23)	1194.30 (138.79)[b]	12–2711
Green-winged Teal, *Anas crecca*	2.86 (0.85)	0.34 (0.19)	0.12 (0.07)	1.08 (0.92)	23.95 (5.36)	0–70
Mallard, *A. platyrhynchos*	0.32 (0.12)	0.55 (0.17)	0.09 (0.05)	0.07 (0.07)	9.71 (2.12)	0–35
Northern Pintail, *A. acuta*	19.58 (6.12)	0.41 (0.33)	1.93 (0.97)	5.26 (4.66)	139.43 (41.69)	0–641
Cinnamon Teal, *A. cyanoptera*	0.02 (0.02)	0.05 (0.02)	0.00 (0.00)	0.00 (0.00)	0.81 (0.38)	0–6
Northern Shoveler, *A. clypeata*	0.64 (0.60)	0.40 (0.35)	0.07 (0.04)	1.18 (1.18)	13.10 (9.23)	0–186

Gadwall, *A. strepera*	6.23 (1.48)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	32.95 (7.80)	0–122
Eurasian Wigeon, *A. penelope*	0.05 (0.02)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.24 (0.12)	0–2
American Wigeon, *A. americana*	13.62 (3.48)	3.55 (1.23)	13.22 (4.23)	1.19 (0.66)	209.86 (42.034)	0–657
Canvasback, *Aythya valisineria*	0.24 (0.15)	0.94 (0.30)	1.89 (1.23)	0.07 (0.07)	26.33 (8.65)	0–146
Redhead, *A. americana*	0.03 (0.02)	0.00 (0.00)	0.54 (0.16)	0.11 (0.10)	4.10 (1.19)	0–17
Ring-necked Duck, *A. collaris*	0.34 (0.15)	0.09 (0.05)	0.00 (0.00)	0.00 (0.00)	3.00 (1.01)	0–12
Greater Scaup, *A. marila*	71.36 (11.93)	122.09 (29.80)	33.86 (9.83)	8.43 (4.87)	2239.7 (420.05)	2–8028
Lesser Scaup, *A. affinis*	9.99 (4.12)	0.71 (0.64)	0.11 (0.08)	0.18 (0.14)	63.41 (28.25)	0–532
Unidentified scaup	22.97 (7.10)	41.15 (16.75)	17.03 (5.17)	7.86 (1.98)	803.43 (247.35)	12–4878
Harlequin Duck, *Histrionicus histrionicus*	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	0.05 (0.05)	0–1
Oldsquaw, *Clangula hyemalis*	0.00 (0.00)	0.02 (0.01)	0.04 (0.02)	0.00 (0.00)	0.48 (0.18)	0–3
Black Scoter, *Melanitta nigra*	0.49 (0.15)	4.77 (0.66)	0.43 (0.16)	0.78 (0.46)	71.10 (8.46)	16–180
Surf Scoter, *M. perspicillata*	26.76 (5.32)	296.97 (35.43)	276.31 (16.79)	255.84 (35.88)	6810.30 (432.07)	3862–11112
White-winged Scoter, *M. fusca*	0.12 (0.07)	4.17 (3.84)	2.21 (0.30)	3.18 (0.82)	30.37 (3.59)	4–67
Unidentified scoter	0.37 (0.32)	0.00 (0.00)	0.04 (0.04)	2.44 (2.26)	10.62 (8.09)	0–169
Common Goldeneye, *Bucephala clangula*	0.47 (0.11)	2.89 (0.50)	5.12 (0.75)	6.36 (1.29)	96.24 (12.66)	9–185
Barrow's Goldeneye, *B. islandica*	0.00 (0.00)	0.05 (0.04)	0.07 (0.04)	0.00 (0.00)	1.14 (0.60)	0–12
Bufflehead, *B. albeola*	158.17 (10.98)	97.01 (7.33)	405.23 (30.99)	215.82 (20.03)	5524.80 (323.81)	2964–8361
Hooded Merganser, *Lophodytes cucullatus*	0.01 (0.01)	0.00 (0.00)	0.02 (0.02)	0.00 (0.00)	0.19 (0.15)	0–3
Common Merganser, *Mergus merganser*	0.02 (0.02)	0.05 (0.03)	0.14 (0.08)	0.11 (0.06)	2.05 (0.82)	0–13
Red-breasted Merganser, *Mergus serrator*	0.88 (0.18)	3.08 (0.50)	2.99 (0.39)	9.93 (1.12)	99.10 (9.13)	45–210
Ruddy Duck, *Oxyura jamaicensis*	131.51 (17.93)	4.32 (0.91)	83.85(13.57)	4.17 (1.54)	1317.00 (128.83)	375–2494
American Coot, *Fulica americana*	8.70 (1.15)	7.24 (0.86)	31.86 (5.77)	14.67 (4.32)	401.67 (44.03)	62–862
Red Phalarope, *Phalaropus fulicaria*	0.05 (0.05)	4.95 (4.90)	0.32 (0.32)	0.11 (0.11)	68.05 (67.40)	0–1416
Bonaparte's Gull, *Larus philadelphia*	0.05 (0.04)	0.16 (0.05)	0.00 (0.00)	0.00 (0.00)	2.29 (0.79)	0–11
Forster's Tern, *Sterna forsteri*	1.00 (0.33)	1.36 (0.53)	0.45 (0.17)	1.63 (1.16)	31.76 (9.41)	0–176
Common Murre, *Uria aalge*	0.00 (0.00)	0.01 (0.00)	0.01 (0.01)	0.03 (0.02)	0.29 (0.12)	0–2
Cassin's Auklet, *Ptychoramphus aleuticus*	0.00 (0.00)	0.01 (0.00)	0.00 (0.00)	0.00 (0.00)	0.05 (0.05)	0–1
Rhinoceros Auklet, *Cerorhinca monocerata*	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	0.05 (0.05)	0–1
Waterbird total	515.60 (34.58)	739.76 (55.44)	1091.10 (48.60)	653.10 (48.27)	21,943.00 (646.86)	14,832–25,553

[a]Figures in parentheses are standard errors.

[b]Mean abundance of Black Brant in December/January (n = 15), prior to February arrivals of migrants, was 1,047.4, SE 155.70, range 12–1781.

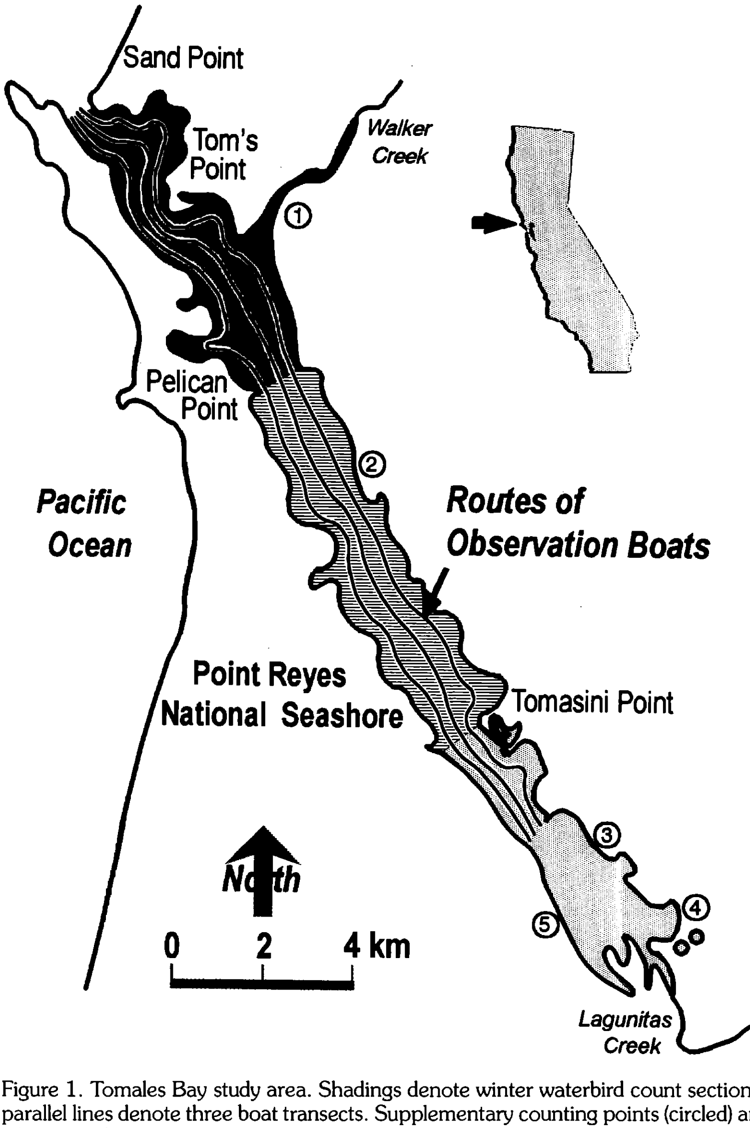

Figure 1. Tomales Bay study area. Shadings denote winter waterbird count sections; parallel lines denote three boat transects. Supplementary counting points (circled) are (1) Walker Creek, (2) Livermore Marsh, (3) Millerton Gulch to Bivalve, (4) Bivalve, and (5) Inverness.

northern half of the bay from Pelican Point northward to Tom's Point (Figure 1, Spratt 1989). Water depths in the bay average about 3 m below mean lower low water (MLLW) and vary from intertidal shoals along the east shore to areas up to 20 m deep in the main channel along the west shore. In general, sediments grade from primarily fine to coarse sand in the northern reaches of the bay to muddier substrates in southern portions (Daetwyler 1966).

The two primary points of freshwater inflow, and the largest tidal flats and marshes, are at Lagunitas Creek at the south end of the bay and Walker Creek near the north end (Figure 1). Numerous smaller perennial and ephemeral streams enter the bay along its perimeter, each associated with a small, generally insular delta marsh. Rainfall is highly seasonal, with 95% of annual rain falling from October through April and 55% from December through February, based on 42-year averages at Cypress Grove Preserve. Spatial and temporal variations in the bay's salinity are influenced by variably high levels of freshwater inflow during winter, low flows in summer, and constraints on tidal exchange with the ocean imposed by the linear shape of the bay and the narrow mouth at its northwest end. Therefore salinities in the southern reaches of the bay are highly variable, ranging from nearly fresh after heavy winter runoff to slightly hypersaline in summer, whereas regular tidal mixing at the north end of the bay maintains salinities that consistently reflect those of the outer coastal waters (Hollibaugh et al. 1988). The difference between mean high and mean low tides is about 1.1 m, with an average annual maximum tide swing of about 2.5 m, based on National Oceanic and Atmospheric Administration predictions. Tidal currents are strongest along the west shore within about 6 km of the northwest end but are generally gentle.

METHODS

We conducted 21 (mean 3/yr, minimum 1, maximum 4) baywide counts of waterbirds on Tomales Bay over the seven winters from 1989–90 to 1995–96. Each year, consecutive counts were made at 2- to 3-week intervals from mid-December to late February each year. Each baywide survey encompassed simultaneous counts conducted from three 17- to 21-ft (5.3- to 6.6-m) Boston Whalers or similar boats. The boats traveled in formation, following parallel 18-km transects from Millerton Point near the south end of the bay north to the Sand Point Buoy (Figure 1). Boats following the east-shore and west-shore transects each carried one team of observers. The midbay boat carried two (port and starboard) teams. Each team consisted of two competent waterbird observers, using binoculars, and one data recorder. Observers on the east-shore boat counted all waterbirds in a transect bounded by the path of their boat and the east shore. Similarly, observers on the west-shore boat counted all waterbirds in a transect bounded by their boat and the west shore. Observers on the midbay boat counted all waterbirds between the other two boats. Drivers of the east- and west-shore boats continually adjusted their positions visually to maintain roughly equal distances between boats and transect boundaries. Therefore, shoreline transects each represented approximately a fourth of the areal extent of the bay and the midbay transect covered approximately half of the bay's extent.

We maintained continual radio communication among observation boats to facilitate adjustments of interboat and boat-to-shore distances and to clarify counts of confusing birds or flocks along the transect borders.

Observers on each boat counted only those birds that passed southward through an imaginary vertical plane defined by the bows of the three boats. The boats traveled at velocities of about 4 knots, but occasionally we stopped to count dense aggregations of birds. Birds flushing ahead of the moving boats were not counted until they eventually passed southward through the observation plane. Birds passing northward over or around the boats were subtracted from the counts, but this seldom occurred as long as boats maintained a constant velocity.

Counts were generally conducted during rising neap tides, with at least a 4.5-ft tide height (MLLW) when the boats arrived at the shallow Walker Creek Delta/Tom's Point area, about two hours after starting each count. We began the counts between 0930 and 1000 to avoid early morning fog and rough afternoon seas, and each count was completed in about 3.5 hours. Conditions during counts were generally calm (Beaufort scale 0–2). In areas that could not be reached by boats, we conducted supplementary counts immediately prior to the boat counts, using telescopes from shore (Figure 1).

During each count, we partitioned the raw transect data into four sections: (1) south of Tomasini Point; (2) Tomasini Point to Pelican Point; (3) Pelican Point to Tom's Point; (4) Tom's Point to Sand Point (Figure 1). The sections correspond to intervals distinguished by estuarine conditions that might influence the composition, distribution, or availability of food for waterbirds. Such conditions include differences in water turbidity and color (pers. obs.), eelgrass distribution (Spratt 1989), substrate texture (Daetwyler 1966), water temperature, freshwater inflow, and ocean-water exchange (Hollibaugh et al. 1988). Therefore, data from each count were partitioned into 12 subsets, delineated by three transects each divided into four sections. Supplemental shore-based data were pooled with the appropriate section and transect counts. We recorded all waterbirds in the shallows at the extreme south end of the bay (south of Millerton Point) as occurring in either east-shore or west-shore transects.

We identified waterbirds to species whenever possible. Undifferentiated loons, Horned/Eared grebes, Western/Clark's grebes, cormorants, scaup, and scoters were allocated to species in proportion to the number of identified birds of those species, within each transect section on each count day, if the number of identified individuals exceeded the number of undifferentiated individuals and the number of identified individuals was greater than 50 for grebes or 100 for cormorants, scaup, or scoters. Generally, only very small numbers of birds were undifferentiated in the field.

To facilitate comparisons among count areas of different sizes, we transformed species abundances within each count area (section within transect) into densities (birds/km^2). We modeled differences in waterbird densities using a mixed-model analysis of covariance (ANCOVA), designating section and transect as fixed effects and year (winter season) as a random effect. Species that commonly exploit freshwater habitats in winter (43% of species analyzed) could exhibit intraseasonal fluctuations as a result of variable rainfall patterns and corresponding changes in the availability of freshwater wetlands in this region (Shuford et al. 1989). Furthermore, late migrants of some species could arrive during the winter census period. Therefore, we used days (since 1 December within each winter) as a covariate to control for possible differences related to the intraseasonal timing of counts. Species densities were log-transformed prior to analysis to improve the normality of the data. For species with significant section or transect effects on densities, we used the Tukey procedure for multiple pairwise comparisons to determine which section or transect means differed from others (Dixon 1992). We also conducted pairwise comparisons of proportional species diversity, based on the Shannon index (Magurran 1988), and species richness, but because sections and transects varied in extent, we limited our interpretation of differences to those that were not confounded by possible species–area effects. Finally, we looked for possible temporal trends by examining partial regression coefficients of baywide abundances on year and days.

RESULTS

We observed 51 species of waterbirds during our surveys on Tomales Bay. The total number of waterbirds averaged 21,943 individuals per count [standard error (SE) 647, min. 14,842, max. 25,553]. Mean waterbird density on Tomales Bay was 770 birds/km^2 (SE 22.7). Variability in total numbers of waterbirds was primarily a function of the numbers of the Surf Scoter, Bufflehead, Greater Scaup, Ruddy Duck, and Black Brant (Figure 2, Table 1). Waterfowl (Anatidae) accounted for 51.0% of the species and 85.3% of the total individuals observed; the Surf Scoter, Bufflehead, and Greater Scaup together accounted for 70.0% of the total waterbirds. Surface-feeding ducks, such as the Northern Pintail and Mallard, typically occurred in only low numbers.

All waterbird species for which our data were adequate for parametric analysis selected habitats within Tomales Bay nonrandomly with respect to the transects or sections used in this study ($P < 0.05$; Table 2). Area counts were generally not biased by the effects of observation boats on movements of waterbirds because birds rarely flushed across count-area boundaries. Results for the Greater Scaup and Black Scoter included a slight transect bias because they occasionally flushed from east-shore to midbay waters before they were counted, but they did not flush cross section boundaries. In general, waterbird densities were highest along the east shore and between Pelican Point and Tom's Point (Figure 2, Table 2). However, several species preferred other areas (Figure 2, Tables 1 and 2). For example, Pacific and Red-throated loons and Western Grebes occurred in significantly greater densities in the midbay transect and in the section from Tomasini Point to Pelican Point. Horned and Eared grebes concentrated in the middle two sections of the bay. Red-necked Grebes occurred almost exclusively north of Pelican Point, especially in the deep channel near the west shore (Table 1 and pers. obs.). Black Brant concentrated in the northern third of the bay, with highest densities between Pelican Point and Tom's Point (Figure 2, Table 2). In contrast, Greater Scaup concentrated south of Pelican Point, especially along the east shore north of Tomasini Point. Black Scoters also concentrated along the east shore north of Tomasini Point (Table 1 and pers. obs.).

Because species diversity and richness varied positively with section size, we could not determine if section differences were independent of possible species–area effects. We also found no significant differences in propor-

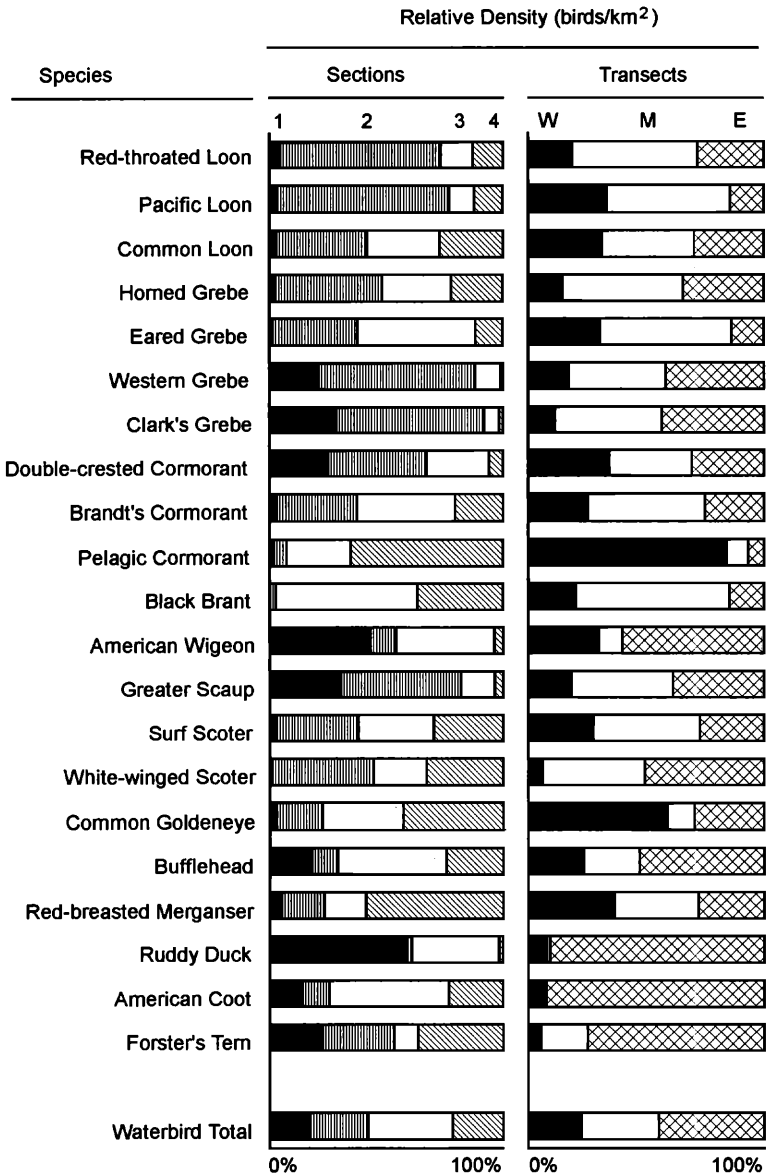

Figure 2. Relative waterbird densities by section and transect (Figure 1) and mean baywide abundances (standard errors) of waterbirds on Tomales Bay. Sections: 1, south of Tomasini Point; 2, Tomasini Point to Pelican Point; 3, Pelican Point to Tom's Point; 4, Tom's Point to Sand Point. Transects: W, west shore; M, midbay; E, east shore. Differences among section and transect densities are analyzed in Table 2.

Table 2 Effects of Section, Transect, and Year on Waterbird Densities in Tomales Bay[a]

		Section				Transect		
Species	ANCOVA[b]	1	2	3	4	E. shore	Midbay	W. shore
Red-throated Loon	S^{**}, T	A	**C**	B	B	A	**B**	A
Pacific Loon	S^{**}, T^{*}, ST^{**}	A	**B**	A	A	A	**B**	A
Common Loon	S^{**}, ST^{**}	A	**B**	**B**	**B**			
Horned Grebe	S^{**}, T^{*}, ST^{**}, TY	A	**C**	**B, C**	B	**B**	**B**	A
Eared Grebe	S^{**}, T^{**}, Y^{*}, ST^{**}, SY^{*}	A	**C**	**C**	B	A	**C**	B
Western Grebe	S^{**}, T^{**}, Y^{**}, ST^{**}	C	**D**	B	A	**B**	**B**	A
Clark's Grebe	S^{**}, T^{*}, Y, ST^{**}, SY^{*}	**B**	**B**	A	A	**B**	**B**	A
Double-crested Cormorant	S^{**}, T^{**}, ST^{**}	B	**C**	**B, C**	A	A	A	A
Brandt's Cormorant	S^{**}, T^{**}, ST^{**}	A	**B**	**B**	**B**	A	A	A
Pelagic Cormorant	S^{**}, T^{**}, ST^{**}	A	B	**C**	**C**	A	A	**B**
Black Brant	S^{**}, T^{*}, ST^{**}, SY^{*}	A	B	**D**	C	A	**B**	**A, B**
American Wigeon	S^{**}, T^{**}, ST^{**}	**B**	**A, B**	**B**	A	**B**	A	A
Greater Scaup	S^{**}, T^{*}, Y, ST^{**}	**B, C**	**C**	A, B	A	A	A	A
Surf Scoter	S^{**}, ST^{**}	A	**B**	**B**	**B**			
White-winged Scoter	S^{**}, T^{**}, ST^{**}, TY	A	B	**C**	**C**	**B**	**B**	A
Common Goldeneye	S^{**}, T^{*}, Y^{*}, ST^{**}	A	B	**B, C**	**C**	**B**	A	**B**
Bufflehead	S^{**}, T^{**}, Y^{*}, ST^{**}	B	A	**C**	B	**B**	A	A
Red-breasted Merganser	S^{**}, ST^{**}, TY	A	B	B	**C**			
Ruddy Duck	S^{**}, T^{**}, ST^{**}	**C**	B	**C**	A	**C**	A	B
American Coot	S^{**}, T^{**}, ST^{**}, TY^{*}	A	A	**B**	A	**C**	A	B
Forster's Tern	S, T^{*}, TY^{**}	A	A	A	A	**B**	**B**	A
Waterbird Total	S^{**}, T^{**}, ST^{**}	A	B	**C**	A, B	**C**	B	A

[a]Each significant main effect for section or transect is followed with multiple pairwise comparisons: means with the same letter are not significantly different (Tukey procedure, experimentwise $P > 0.05$). Significant differences among means are ranked: A < B < C < D. Section and transect preferences, suggested by significantly highest means and means that do not differ from significantly highest means, are in boldface. See Figure 1 for section and transect locations.

[b]Mixed-model analysis of covariance. Covariate, days since 1 December within year (winter season); letter indicates F ratio significant at $P < 0.05$, $^{*}P < 0.01$, $^{**}P < 0.001$.

tional species diversity among transects ($P > 0.10$). However, species richness was significantly greater along the east shore (mean 31.0, SE 0.94, $n = 21$) than in either the midbay (mean 24.4, SE 0.82, $n = 21$) or west-shore (mean 24.4, SE 0.62, $n = 21$) transects—in spite of the larger area represented by the midbay transect (experimentwise $P < 0.01$).

We found significant seven-year population trends ($P < 0.05$) reflecting annual increases for the Common Loon (mean annual increase, $b = 15.8$), Eared Grebe (b = 38.3), Western Grebe (b = 93.6), Black Brant (December/January only, to exclude northward migrants: b = 231.6), Common Goldeneye (b = 15.6), Red-breasted Merganser (b = 17.0), and American Coot (b = 65.0). Partial regression coefficients revealed slight but significant ($P < 0.05$) 7-year declines for the White Pelican (b = −2.1) and White-winged Scoter (b = −3.9) and a large annual decrease for the Surf Scoter (b = −515.9). However, the significant regression for Surf Scoter resulted from relatively high numbers in 1989–90 (mean 10,470; SE 347.6, n = 2); thereafter, abundances remained at significantly lower levels (mean 6315; SE 1601, n = 19; t = 8.1, $P < 0.001$) with no annual trend ($P > 0.05$). Similarly, the dramatic trend in wintering Black Brant resulted primarily from an early increase, from 1989–90 (mean 17.5, SE 5.5, n = 2) to 1991–92 (mean 1342; SE 356.5, n = 2); December/January abundances apparently stabilized at this level for the remainder of the study (mean 1275; SE 120.0, n = 12).

Regularly occurring species with the greatest variation from year to year were the Pacific Loon [coefficient of variation (CV) 0.83], Pied-billed Grebe (CV 1.02), White Pelican (CV 1.67), Brown Pelican (CV 0.88), Bonaparte's Gull (CV 0.90), and Forster's Tern (CV 0.97). In contrast, we observed relatively stable annual abundances of the Red-throated Loon (CV 0.37), Double-crested Cormorant (CV 0.30), Bufflehead (CV 0.25), and Ruddy Duck (CV 0.36). We found significant intraseasonal trends in the abundances of only a few species. The White Pelican, Bonaparte's Gull, Bufflehead, and American Wigeon declined significantly as winter progressed, while the Eared Grebe and White-winged Scoter increased significantly ($P < 0.05$).

DISCUSSION

Tomales Bay Populations

The number of waterbird species we observed on Tomales Bay was similar to that normally occurring in other wetlands along the outer Marin and Sonoma County coast (Shuford et al. 1989). Densities of many species were also similar to those reported for other estuaries in the Point Reyes area, but waterbird *abundances* were dramatically higher, presumably because of the greater extent of Tomales Bay in comparison to other sites (cf. Page et al. 1983, Shuford et al. 1989). In addition to the high waterbird numbers documented by our study, Tomales Bay also supports 11,000 to 18,000 wintering shorebirds (Kelly 1993) and tens of thousands of wintering gulls (Kelly et al. 1996 and unpubl. data).

Tomales Bay is probably of statewide significance for some waterbird species. Population estimates derived from the aerial Midwinter Waterfowl Survey during the same period (U.S. Fish and Wildlife Service, unpubl. data) are not directly comparable with the data we collected from boats on Tomales Bay. Waterbird abundances recorded from boats are based on relatively thorough observation, frequently using actual counts rather than estimates, and are probably closer to the actual numbers of birds than abundances recorded from aerial surveys (Conant et al. 1988). Comparisons of our January boat count data with January U. S. Fish and Wildlife Service (USFWS) aerial surveys of Tomales Bay, available only for 1990, 1991, and 1993, suggest that aerial counts underestimated numbers of Bufflehead, scoters, and Black Brant by 49.5%, 41.5%, and 17.4%, respectively (see also Conant et al. 1988). Using these differences to adjust comparisons with statewide results from 1989–90 to 1995–96 reported by the USFWS Midwinter Waterfowl Survey, we estimate that winter populations of the Bufflehead, scoters, and Black Brant (December/January only) on Tomales Bay represent 12.3%, 6.4%, and 30.8%, respectively, of statewide populations. We emphasize that these estimates are rough approximations at best and should be interpreted cautiously. In general, our data suggest that Tomales Bay supports numbers of Bufflehead, scoters, and Black Brant comparable to totals for all estuaries and lagoons in Mendocino, Humboldt, and Del Norte counties combined. Tomales Bay may be the single most important estuary, with the exception of San Francisco Bay, south of the Columbia River for wintering Bufflehead (cf. USFWS Midwinter Waterfowl Survey unpubl. data; Monroe 1973, Barnhart et al. 1992). On the basis of aerial surveys conducted from 1968 to 1970 by the California Department of Fish and Game and the Point Reyes Bird Observatory, Smail (1972) reported high counts of scoters (5788), Bufflehead (7502), and scaup (1437) and overall waterfowl abundances (mean 6786, max. 19,997), providing some evidence that waterbird numbers on Tomales Bay were similar to those observed in our study. In a statewide study of seabird abundances, Briggs et al. (1987) identified Tomales Bay as an important area of concentration for the Red-throated, Pacific, and Common loons, Eared and Horned grebes, and scoters.

Audubon Christmas Bird Count (CBC) results for Tomales Bay prior to 1989 provide rough estimates at best for waterbird species, because of the near impossibility of estimating baywide abundances from the single observation boat used on those counts. However, species with restricted distributions in the bay may be monitored more accurately by CBC data. For example, comparisons of our results with CBC data suggest that the number of American Coots has declined by an order of magnitude since the 1970s, a pattern that is also evident elsewhere in the Point Reyes area (Shuford et al. 1989). The median number of Redheads recorded on the Point Reyes CBC from 1970 to 1981, primarily from near the mouth of Walker Creek on Tomales Bay, was 376 (min. 1, max. 784) but has since dwindled to 9 (min. 0, max. 15). Since 1989, CBC data for Tomales Bay have been derived from December counts conducted for this study.

We have assumed, except where noted otherwise, that our data represent "wintering" populations only, but abundances of some species may have swelled or declined because of arrivals or departures of late migrants or birds with intraseasonal local or regional movements. The significant intraseasonal declines we detected in the Bufflehead and American Wigeon may have resulted from emigration associated with midwinter increases in rainfall and corresponding increases in the availability of seasonal and interior wetlands (Shuford et al. 1989). In contrast, significant intraseasonal increases in Eared Grebes conformed to patterns reported in San Francisco Bay salt ponds (Swarth et al. 1982) and other wetlands in the Point Reyes area (Shuford et al. 1989), possibly resulting from a protracted fall migration (Jehl 1988).

In general, the east shore of the Tomales Bay, with shallow shoals and mudflats, headlands and protected coves, supports greater abundances and more species of waterbirds than either the midbay or west shore. Nevertheless, preferred habitats of various species occur throughout the bay (Figure 2, Table 2). Waterbird distributions on Tomales Bay are associated with strong winter salinity and temperature gradients, differences in water circulation, turbidity, and exchange rates with nearshore coastal waters (Hollibaugh et al. 1988), distribution of eelgrass beds (Spratt 1989), and a wide range of bottom substrates (Daetwyler 1966). The most diverse and abundant concentrations of waterbirds in the bay occur between Pelican Point and Tom's Point, where eelgrass beds are the most concentrated and estuarine circulation is enriched by the tidal delivery of nutrients and plankton from the outer ocean, as well as by the inflow of freshwater and nutrients from Walker Creek, i.e., where habitat diversity and nutrient supplies are greatest (Figure 1; Hollibaugh et al. 1988, Smith and Hollibaugh 1997). The quality and extent of inflow from Walker Creek depends on management of a 189-km^2 watershed, which is dominated by agricultural grasslands, coastal scrub, mixed evergreen forest, and oak woodland, and on managed water releases from the Soulajule Reservoir (Storm 1972, Madrone Associates 1976).

Conservation Implications

The importance of wintering areas in the dynamics of waterbird populations is suggested by the potentially crucial role these areas play in courtship or pairing and deposition of fat stores used later as energy for reproduction (Heitmeyer and Fredrickson 1981, James 1989, Baldassarre and Bolen 1994). Winter habitat quality has been linked to annual survival, recruitment, and reproductive success of waterfowl (Raveling 1979, Haramis et al. 1986, Raveling and Heitmeyer 1989, Baldassarre and Bolen 1994).

Eelgrass, the most abundant large marine plant in Tomales Bay (Hardwick 1973), provides crucial winter food for Black Brant, surface-feeding ducks, and other waterfowl (Yocum and Keller 1961, Baldassarre and Bolen 1994). Our results show a recent increase in the use of Tomales Bay by wintering Black Brant, with abundances well above winter averages of approximately 200 birds in the 1980s (Calif. Dept. Fish and Game unpubl. data). Eelgrass also supports a rich estuarine fauna that provides additional food for waterbirds (Day et al. 1989). Although the distribution of eelgrass in Tomales Bay has been relatively stable (Spratt 1989, Moore and Mello 1995), it is sensitive to changes in salinity, turbidity, and temperature (Day et al. 1989, Baldassarre and Bolen 1994) and thus potentially vulnerable to reductions in the quality or quantity of fresh water supplied by Walker Creek.

In Tomales Bay, eelgrass provides winter spawning habitat for approximately 5500 tons (20-year average) of Pacific Herring (*Clupea harengus pallasi*; Moore and Mello 1995). From December through March, scoters, Bufflehead, scaup, Black Brant, goldeneyes, American Coots, and other species of waterbirds heavily exploit the roe of Pacific Herring (Hardwick 1973, Bayer 1980, Briggs et al. 1987, Haegele 1993), while adult herring are consumed by loons, large grebes, and cormorants (Palmer 1962). High rates of kleptoparasitism by gulls can limit the foraging activities of waterbirds feeding on recently deposited herring eggs (Bayer 1980). Such disturbance is probably enhanced by the daily arrival at Walker Creek delta of several thousand gulls from a local landfill near Cotati, Sonoma County (Kelly et al. 1996).

If some waterbirds depend on herring (or herring roe) in winter, overharvest by the commercial herring fishery could limit their populations. Because annual harvest quotas are based on estimates of spawning biomass from the previous year, which fluctuate considerably, the fishery can over- or underestimate the proportion of herring being harvested (Suer 1987, Moore and Mello 1995). Well-informed ecosystem management will require focused research on the link between Pacific herring and waterbirds, accurate forecasts of spawning biomass, and cautious harvest quotas to guide the commercial herring fishery.

Interestingly, scoters occur in large numbers south as well as north of Pelican Point, rather than concentrating over the dense eelgrass areas (available to spawning herring) to the north. Also, Greater Scaup concentrate in the southern portion of the bay. However, herring normally spawn as far south as Tomasini Point, suggesting that the herring's habit of spawning in eelgrass is influenced by a preference for reduced salinities that could cause them to shift southward when the flow of fresh water into the bay is reduced (Moore and Mello 1995). Alternatively, the spatial responses of waterbirds to irregular herring runs may not be adequately sampled by our counts. Scoters and scaup also feed on molluscs and other invertebrates (Bellrose 1976), suggesting that bottom sediments at the southern end of the bay (Daetwyler 1966) provide important foraging substrates for these species. Black Scoters, near the southern end of their Pacific winter range, are uncommon to rare elsewhere along the California coast (Grinnell and Miller 1944, McCaskie et al. 1979, Garrett and Dunn 1981). Our study indicates that annual concentrations of approximately 70 (max. 180) Black Scoters are regular along the east shore just north of Tomasini Point, reflecting similar concentrations, of approximately 60 birds, observed just below Highway One in this area each winter since 1961 (R. Stallcup pers. comm.) The cobbles and gravelly and shelly shoals that dominate the bottom substrates in this area (Daetwyler 1966) are consistent with preferred foraging substrates reported elsewhere for this species (Bordage and Savard 1995).

During winter, salinities, turbidity, sedimentation, and water exchange between the bay and the outer ocean vary greatly with the extent of freshwater runoff, especially near Lagunitas Creek (Hollibaugh et al. 1988). Because of the linear configuration of the bay, the availability of prey species may be especially sensitive to anthropogenic and other terrogenous influences. For example, the long water-residence times of up to four months in the southern part of the bay during drought or summer (Hollibaugh et al. 1988) imply that the bay may retain contaminants for long periods of time, potentially allowing toxic materials derived from watershed runoff to enter food webs or become trapped in bay sediments. Most diving ducks depend on benthic prey, which are in turn vulnerable to sediment contamination from the watershed (Cain 1988). Common Loons and other fish-eating birds avoid highly turbid water, presumably because it interferes with prey detection (Pehrsson 1984, Haney 1990). Extended water-residence times between periods of peak winter runoff interact with watershed erosion, leading to extended periods of high turbidity. Thus some waterbirds that concentrate in the shallow southern end of the bay or near the mouth of Walker Creek could be limited by high turbidity generated by development or other activities in the watershed. Rafts of Western and Clark's grebes usually concentrate over deeper areas (pers. obs.), possibly to avoid turbid runoff by foraging in pockets of clearer saline water near the bottom (Pehrsson 1984), although they may also reflect concentrations of prey fishes.

In a substantial portion of the bay, commercial aquaculture of oysters (*Crassostrea gigas*) and bay mussels (*Mytilus edulis*) has introduced various racks, floats, and bags that alter waterbird habitat on the surface and in the water column and may alter the structure of bottom substrates where diving ducks feed (Kelly et al. 1996). To our knowledge, scientific information on the effects of such structures on waterbird habitat does not exist.

In winter, waterbirds occupy open habitats where they generally rely on flight as a response to disturbance by predators or humans. Even diving birds such as loons and small grebes frequently rely on flight to escape disturbance by approaching boats, although large grebes escape by diving. Flight is energetically expensive in birds, with costs as high as 15 times the basal metabolic rate (King 1974). Optimal-foraging theory (Krebs et al. 1983) provides a framework for understanding disturbance, by predicting that birds must compensate for increased levels of disturbance, either by increasing their rate of food intake or flying to other, less profitable but less disturbed areas to feed. Many wintering waterbirds must also accumulate fat and protein reserves to override periods of low food availability and to prepare for spring migration (Davidson and Rothwell 1993, Baldassarre and Bolen 1994). If feeding opportunities are already restricted, or waterbirds are close to their energy threshold, direct disturbance by humans could have considerable energetic effects on individual birds, leading to abandonment of an area or starvation (Davidson and Rothwell 1993).

We observed dramatic increases in sport fishing, kayaking, and other recreational boating on Tomales Bay during the course of this study, especially where waterbirds concentrate in the northern third of the bay. Each boat is associated with a radius of disturbance determined by its speed of movement and the sensitivity of bird species. Fast-moving power boats, motorized personal watercraft ("jet skis"), and aggregations of boats such as occur around popular fishing spots create larger zones of disturbance (Burger 1981; pers. obs.). A few boats distributed across an eelgrass bed can prevent most waterbirds from using the area. Sea kayaks, unlike other recreational boats, tend to travel in loose groups that displace waterbirds from marsh edges, shallow coves, and sand bars. Low-flying aircraft occasionally track the linear shape of the bay, resulting in a wider band of disturbance than observed around boats (R. Stallcup pers. comm.).

Estuarine waterfowl may be seriously affected by even occasional disturbance during key parts of the feeding cycle. American Wigeon feeding in eelgrass beds return to feed if disturbed early in the (tidal) feeding cycle but abandon the site altogether, until the next tidal cycle, if disturbed after the eelgrass is exposed by the tide (Fox et al. 1993). Black Brant, which also feed on eelgrass in Tomales Bay, show similar avoidance responses to increased presence of humans (Stock 1993). In Tomales Bay, hunting disturbance is concentrated near the mouths of Lagunitas and Walker creeks; because these are the only two large areas of coastal marsh habitat, similar areas are not available for refuge elsewhere on the bay. We did not measure flight distances, return rates, or other behaviors of birds that flushed occasionally in response to the movement of our observation boats.

The array of potential conflicts between human activities and wintering waterbirds on Tomales Bay implies the likelihood of cumulative or synergistic effects. Long-term protection of waterbird populations on Tomales Bay may depend on broad-based planning, in which diverse agencies cooperatively consider overall management effects on abundances and distributions of waterbirds. We recommend that management efforts focus on controlling boat traffic and other forms of direct human disturbance, protecting eelgrass beds, assessing the effects of herring harvest and aquaculture on waterbirds, and monitoring human land use and other processes in the watershed that may affect the quality of waterbird habitats in the estuary.

SUMMARY

We analyzed patterns of abundance and distribution of wintering waterbirds in Tomales Bay, California, on the basis of 21 baywide winter surveys over 7 years from 1989–90 to 1995–96. Total waterbird abundances averaged 21,943 (min. 14,842, max. 25,553), excluding shorebirds and gulls. Mean waterbird density was 770 birds/km^2 with the greatest concentrations along the east shore and between Pelican and Tom's points. The Surf Scoter, Bufflehead, and Greater Scaup together accounted for 70% of the total waterbirds. Aerial count data from the U. S. Fish and Wildlife Service Midwinter Waterfowl Survey underestimated the numbers of waterbirds in comparison to our counts made from boats. Such differences adjusted for, our abundance estimates for scoters and Bufflehead appear similar to other abundances reported in the 1960s and 1970s. Compared to other coastal wetlands in California, Tomales Bay provides particularly important winter habitat for the Red-throated and Common loon, Eared and Horned grebe, Black Brant, Surf and Black scoter. Except for San Francisco Bay, Tomales Bay may provide the most important winter habitat for the Bufflehead on the Pacific coast south of the Columbia River. Waterbird distributions on Tomales Bay are associated with a dynamic array of habitat conditions. Increasing human activities in Tomales Bay and its watershed interact with these processes and conditions and suggest several concerns for conservation of winter waterbirds. Protection of waterbird populations will require particular attention to the control of human disturbance, protection of eelgrass beds, the possible effects of the herring fishery and aquaculture, and management of processes in the watershed.

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