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THE MIGRATION OF SHOREBIRDS IN THE BAY OF FUNDY

PETER W. HICKLIN[1]

ABSTRACT.—Large populations of 34 species of shorebirds migrate in late summer and fall to the wide muddy intertidal areas of the upper Bay of Fundy in preparation for the transoceanic flight to South American wintering grounds. Southward migration through Fundy extends from 1 July to 11 November, although the main passage usually occurs between 20 July and 20 September. Shorebirds are most numerous during August. The average length of stay for the Semipalmated Sandpiper (*Calidris pusilla*) is 15 days. Estimates of total numbers for the migratory period of the nine most common species range between 800,000 and 1,400,000 birds. The Semipalmated Sandpiper constitutes 95% of all shorebirds recorded. The populations of Semipalmated Sandpipers stopping in the Bay of Fundy during southward migration each year represent 42–74% of the world population of this species. The Black-bellied Plover (*Pluvialis squatarola*) is the only species that migrates via the Bay of Fundy in spring in numbers comparable to those recorded in late summer and fall. *Received 16 Oct. 1986, accepted 30 Apr. 1987.*

In late summer and autumn each year, shorebirds migrate from arctic and subarctic breeding grounds to coastal staging areas in southeastern Canada and northeastern United States, where they deposit stores of fat in preparation for a nonstop flight over the Atlantic Ocean to Central and South American wintering areas (McNeil and Burton 1977, Williams et al. 1977, Morrison 1984). McNeil and Cadieux (1972:590) showed that seven shorebird species accumulated sufficient fat reserves on the Magdalen Islands in the Gulf of St. Lawrence to depart "south from Nova Scotia and the New England states on fall migration to the Lesser Antilles and northern South America." These investigators were likely unaware at that time that the Bay of Fundy proper (shared by New Brunswick and Nova Scotia) may have been the main stopover site of these birds prior to an overseas migration to South America. Large-scale movements of migratory shorebirds to the Bay of Fundy in autumn were clearly established by Richardson's (1979) radar studies in the Maritime Provinces. These studies also revealed that shorebirds left the Bay of Fundy in a southeasterly direction over the Atlantic Ocean, reaffirming McNeil and Cadieux's (1972) conclusion that the birds flew nonstop over the ocean to their wintering grounds in South America. Williams et al. (1977:257) substantiated the extensive use of an overseas migratory route by simultaneous observations of shorebird flocks from radar installations along

[1] Canadian Wildlife Service, P.O. Box 1590, Sackville, New Brunswick E0A 3C0, Canada.

the North American coast, on Bermuda, in the Caribbean, and ships at sea, during the autumn migration. By correcting for the effects of the strong easterly trade winds in the vicinity of the Sargasso Sea, they concluded that "birds could accomplish the crossing of the ocean by maintaining a constant southeast flight direction from the time they left the North American coast until they reached South America."

The return journey to the northern breeding grounds does not include a similar overseas route northward to the Bay of Fundy from the wintering area. McNeil and Burton (1977:167) indicated that most North American shorebird species departing northward from northeastern Venezuela in spring have insufficient energy reserves to fly much farther than across the Caribbean Sea, and that the spring migrants must reach their northern breeding grounds "by flying either along the Atlantic or through the Mississippi flyway." Based on morphometric studies and published accounts of shorebird numbers in spring, Harrington and Morrison (1979:96) concluded that "Semipalmated Sandpipers in eastern Canadian arctic regions apparently migrate north by an Atlantic route on the United States seaboard, probably turning cross-country in the northeastern United States and southeastern Canada." I show in this paper that there is actually very little movement of migrant shorebirds in the Bay of Fundy in spring except for Black-bellied Plovers (scientific names in Table 1). The cross-country turning point alluded to by Harrington and Morrison (1979) appears to be primarily in Delaware Bay, New Jersey, where over one million shorebirds gather in spring, including about 250,000 Semipalmated Sandpipers, to feed on the eggs of horseshoe crabs (Myers 1986). This elliptical migratory pattern, with the southward passage in autumn lying eastward of the northward route in spring, would explain why few shorebirds are recorded in the Bay of Fundy in spring, but attain large numbers in late summer and autumn. The most recent and detailed summary maps of the presumed spring and fall migratory routes of North American shorebirds can be found in Morrison (1984) and Myers et al. (1987).

Although it has long been known that the upper reaches of the Bay of Fundy harbor many shorebirds during autumn migration (Tufts 1917), published accounts regarding their numbers and the timing of migration are qualitative (Tufts 1973, Squires 1976). Morrison and Harrington (1979) presented data on maximum counts of three shorebird species present at key areas between James Bay and northern South America during southward migration in 1976. The numbers shown included nearly 318,000 shorebirds (mainly Semipalmated Sandpipers) in the Bay of Fundy, or 72.4% of the total (calculated from Table 1, Morrison and Harrington 1979), data that strongly emphasize the importance of the Bay of Fundy

TABLE 1
SPECIES OF MIGRANT SHOREBIRDS IN THE BAY OF FUNDY

Species	Relative abundance	Principal habitat
Semipalmated Plover (*Charadrius semipalmatus*)	B; U (Sp), A (Au)[a]	Mud and sand flats, salt marshes
Piping Plover (*C. melodus*)	B; R (Sp, Au)	Sand dunes and beaches
Killdeer (*C. vociferus*)	B; C (Sp, Au)	Open fields, salt marshes
Lesser Golden-Plover (*Pluvialis dominica*)	R (Sp), C–A (Au)	Mown hayfields and pastures
Black-bellied Plover (*P. squatarola*)	A–VA (Sp, Au)	Mud and sand flats, beaches, salt marshes
Ruddy Turnstone (*Arenaria interpres*)	R (Sp), C (Au)	Rocky and sandy beaches
Common Snipe (*Capella gallinago*)	B; C–A (Sp, Au)	Salt and freshwater marshes, pastures, mown hayfields
Whimbrel (*Numenius phaeopus*)	R (Sp), U–C (Au)	Beaches, blueberry fields
Spotted Sandpiper (*Actitis macularia*)	B; C (Sp, Au)	Beaches, salt and freshwater marshes
Upland Sandpiper (*Bartramia longicauda*)	U (Sp, Au)	Upland pastures and fields
Solitary Sandpiper (*Tringa solitaria*)	R (Sp, Au)	Freshwater ponds
Greater Yellowlegs (*T. melanoleuca*)	U (Sp), A (Au)	Salt marshes, mudflats, occasionally beaches
Lesser Yellowlegs (*T. flavipes*)	U (Sp), A (Au)	Salt marshes, mudflats, occasionally beaches
Willet (*Catoptrophorus semipalmatus*)	B; U (Sp, Au)	Salt marshes, occasionally mudflats
Red Knot (*Calidris canuta*)	R (Sp), C–A (Au)	Salt marshes and mudflats
Purple Sandpiper (*C. maritima*)	O; R (Sp, Au)	Rocky intertidal
Pectoral Sandpiper (*C. melanotus*)	R (Sp), U–C (Au)	Salt marshes
White-rumped Sandpiper (*C. fuscicollis*)	R (Sp), C–A (Au)	Beaches, mudflats, and salt marshes
Baird's Sandpiper (*C. bairdii*)	R (Sp), U (Au)	Beaches, mudflats, probably salt marshes
Least Sandpiper (*C. minutilla*)	U–A (Sp), A (Au)	Beaches, mudflats, salt marshes

TABLE 1
CONTINUED

Species	Relative abundance	Principal habitat
Curlew Sandpiper (*C. ferruginea*)	R (Sp, Au)	Beaches and mudflats
Dunlin (*C. alpina*)	R (Sp), C–VA (Au)	Beaches and mudflats
Semipalmated Sandpiper (*C. pusilla*)	C–A (Sp), VA (Au)	Beaches, mudflats, and salt marshes
Western Sandpiper (*C. mauri*)	R (Sp, Au)	Beaches, mudflats, and salt marshes
Sanderling (*C. alba*)	R (Sp), A (Au)	Beaches and mudflats, probably salt marshes
Short-billed Dowitcher (*Limnodromus griseus*)	R (Sp), A (Au)	Beaches, mudflats, and salt marshes
Long-billed Curlew (*L. scolopaceus*)	R (Sp, Au)	Salt marshes, probably mudflats
Stilt Sandpiper (*C. himantopus*)	R (Sp, Au)	Beaches and salt marshes
Marbled Godwit (*Limosa fedoa*)	R (Sp, Au)	Beaches and salt marshes
Hudsonian Godwit (*L. haemastica*)	R (Sp), U–C (Au)	Beaches, mudflats, and salt marshes
American Avocet (*Recurvirostra americana*)	R (Sp, Au)	Salt marshes
Red Phalarope (*Phalaropus fulicaria*)	C–A (Sp), VA (Au)	Pelagic
Wilson's Phalarope (*P. tricolor*)	R–U (Sp, Au)	Freshwater marshes
Red-necked Phalarope (*P. lobatus*)	A (Sp), VA (Au)	Pelagic

[a] B = breeding, O = overwintering, Sp = Spring, Au = Autumn, R (rare) = 5 individuals and not seen every year, U (uncommon) = 10 and seen every year, C (common) = 10–100, A (abundant) = 100–1000; VA (very abundant) = >1000.

as a shorebird staging area along the eastern seaboard during southward migration.

Population estimates based on annual maximum counts, however, presumably represent only a portion of the total number of migrants which pass through a staging area such as the Bay of Fundy over a 6- to 8-week migratory period. No attempt has been made previously to describe the timing of migration of the most numerous species and to estimate the total populations of shorebirds migrating through the Bay of Fundy during the late summer and fall.

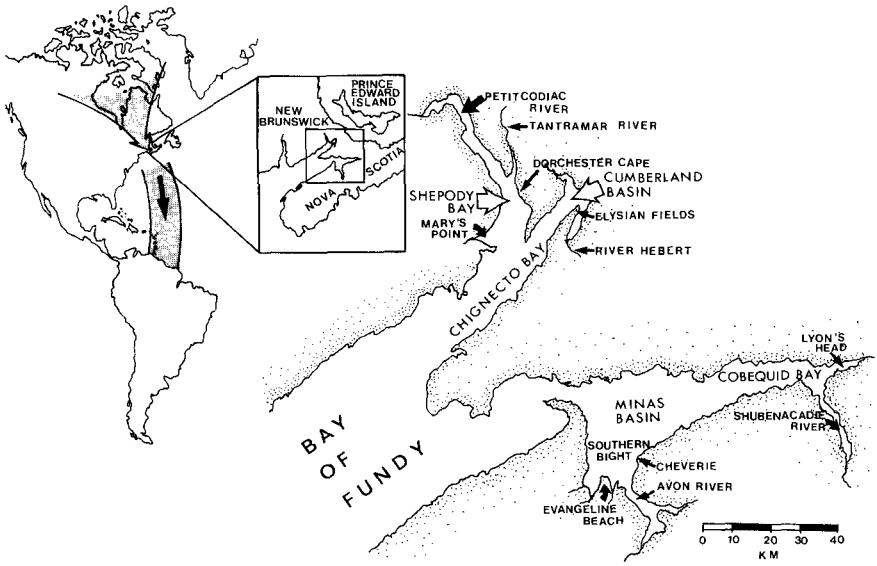


FIG. 1. The Bay of Fundy and its location along the autumn shorebird migratory flyway over the Atlantic Ocean to overwintering grounds in South America.

Thirty-four species of migrant shorebirds have been recorded in the Bay of Fundy during southward migration (Table 1). In this paper, I present information regarding the abundance, distribution, and migratory timing of the nine most common species that migrate annually to the Bay of Fundy and, typically, forage on intertidal mud and sand flats at low tide and roost on open beaches during high tide periods. These are the Black-bellied Plover, Semipalmated Plover, Short-billed Dowitcher, Red Knot, Sanderling, Least Sandpiper, Semipalmated Sandpiper, and White-rumped Sandpiper. I also included the Hudsonian Godwit which, although uncommon in the Bay of Fundy, was easily identifiable. Excluded are several other species that occupy principally fresh and salt water marshes, are rare, or occupy specialized habitats inland. Phalaropes, although numerous in autumn at the mouth of the Bay of Fundy, are not included here as these were the focus of a separate study (R. G. B. Brown, pers. comm.).

THE BAY OF FUNDY

The Bay of Fundy forms a natural boundary between the provinces of New Brunswick and Nova Scotia. The upper reaches of the bay bifurcate into two main embayments: (1) the Minas Basin and Cobequid Bay cutting eastward into Nova Scotia, and (2) Chignecto Bay pointing north into New Brunswick. Chignecto Bay further divides into Shepody Bay to the north and Cumberland Basin to the northeast (Fig. 1).

Some of the highest tidal amplitudes anywhere in the world have been measured in these areas. Tidal maxima of 17 m occur in Cobequid Bay. At mean low water, about 5000 ha of salt marsh and 35,000 ha of mud and sand flats are exposed (Pearce and Smith 1974).

The muddy intertidal zone supports a high-density, low-diversity assemblage of largely deposit-feeding invertebrates of which the burrowing amphipod *Corophium volutator* is a dominant component both numerically and by biomass (Yeo and Risk 1979, Hicklin et al. 1980). This amphipod, and to a lesser extent marine polychaetes, and the bivalve *Macoma balthica,* constitute the main prey of migrant shorebirds during autumn migration (Hicklin and Smith 1979, 1984; Gratto et al. 1984; Peer et al. 1986).

METHODS

The numbers of birds encountered at roost sites in Fundy are very large. Because of this and the wide distances between roosting areas and the relatively rapid passage of birds, I was unable to rely on a single comprehensive method of estimating total numbers stopping in the bay each year over a study period of eight years. The methods I describe here served to provide data on estimates of (1) total populations; (2) numbers of adults from air and ground surveys, respectively, conducted in 1976; (3) numbers of adults and immatures at the peak of the migratory period averaged over all survey years; and (4) ranges in population size of each species, and all species combined, using a turnover rate of 15 days as determined from color-marking studies (see below).

The count data for these estimates were obtained from aerial surveys in 1976 and from ground counts conducted by myself and volunteer observers between 1975 and 1983. In 1981, I banded and color marked Semipalmated Sandpipers to obtain some measure of turnover rate that could be applied to the ground-count data and thus account for birds which presumably had arrived and departed between censuses.

The analysis and interpretation of the data has required four important assumptions: (1) aerial and ground estimates by the same or different observers were comparable and provided a reasonably accurate reflection of absolute numbers, (2) movements of birds between roosts were minimal, (3) the rate of turnover was the same between years and roosting sites, and (4) the same rate of turnover was applicable to all species. There is some evidence to support assumptions 1 and 2, and this is presented in the appropriate sections that follow. I have no evidence to support or deny assumptions 3 and 4: data on turnover rate were obtained for one species only (Semipalmated Sandpiper, by far the most numerous), at a single site (Dorchester Cape), and for one year only. I treat the different survey methods and calculations of population size separately below.

Aerial surveys.—Between 19 July and 14 September 1976, I made 10 aerial surveys of the shorelines of Minas Basin, Cobequid Bay, and Chignecto Bay during high tide periods to locate shorebird roosting sites and to estimate the numbers of birds present. Surveys were conducted using a Cessna 172 high-wing airplane flying 25–50 m above the coastline at an average speed of 150 km/h. Most shorebird roosts encountered could be seen and numbers estimated before, or as, the birds flushed. I regularly ground-checked roosts in the Southern Bight, Minas Basin, the day before and the day following an aerial survey. Ground observers were also present at selected locations during each flight so that species identifications and counts could be compared. All counts were undertaken while birds were roosting.

Ground censuses: large roosts.—Ground censuses were undertaken regularly at three main roosting areas: (1) Evangeline Beach in the Southern Bight, Minas Basin, (2) Dorchester Cape, and (3) Mary's Point in Shepody Bay (Fig. 1). Counts of shorebirds on Evangeline Beach were made almost daily during high-tide periods from spring to late fall, 1975 and 1976 (Elliot 1977, Hicklin 1981). Additional counts of Semipalmated Plovers at Evangeline Beach were made in 1980 (Peach 1981). Similarly, volunteer observers censused shorebirds

daily in July, August, and September at Dorchester Cape and Mary's Point in 1976–1983 and 1976–1981, respectively. Less regular counts were made from April to June and October to November at all three locations.

Throughout the surveys, immature birds were identified by plumage whenever possible. However, separating the numbers of immatures from those of adults, especially for the numerous calidrine sandpipers, was often difficult and unreliable. I determined the ratio of adults to birds-of-the-year by comparing secondary peaks (identified as comprising mainly immature birds) with the earlier adult peaks at Evangeline Beach, Dorchester Cape, and Mary's Point, for each year between 1976 and 1983.

The same four observers, including myself, were responsible for taking counts at those three sites throughout all the years of this study. Two methods of counting were used, most often by two observers together or, on occasion, independently on the same day. One method involved doing a "head count" at a roost early the migration period (18–25 July) until the day it contained about 1000 birds. Once this figure was reached, numbers increased rapidly and it became impossible to take exact counts from that time on. The observer would then count a portion of a flock, 500 or 1000 birds, and multiply this number by an appropriate order of magnitude which represented the entire roost. For example, I would count X birds in a portion of a roost then estimate that there were twice, three times . . . or 10-times as many birds in the remainder of the flock. A second method relied on data on the densities of roosting sandpipers obtained from overhead photographs of a large roost taken at Dorchester Cape in 1977. The photos were taken with a 600-mm Novaflex telephoto lens from the roof of a summer cottage. The pictures were enlarged and the birds inside three 10.5-m^2 sections of the roost, measured in the field and marked on the photographs, were counted. The densities inside the squares were 55, 65, and 68 birds/m^2. A rectangle representing 31.5 m^2 of the same roost contained 1986 birds for a density of 63 shorebirds/m^2. As the roosts in Fundy typically take on a square or rectangular shape, not unlike a large feathered carpet on the beach, an observer in the field could note markers along the edges of a roost (e.g., large stones, driftwood, seaweed) and, once the birds left the site to feed, measure by pacing the distances between the markers. The calculated area of the roost in m^2 was then multiplied by 60 to provide an estimate of the numbers of roosting birds. Often, the results obtained by the two observers on the same day using both methods were similar (e.g., $\pm$ 10,000 birds for roosts estimated at around 100,000). The two estimates were averaged except for occasions when only one estimate was available. These means of estimating numbers applied principally to flocks of Semipalmated Sandpipers, with Least Sandpipers and Semipalmated Plovers often mixed in. The large shorebirds such as Black-bellied Plover, dowitcher, knot, and Hudsonian Godwit were much less numerous and could often be counted individually.

Miscellaneous sites.—Outside of the three main roosting areas, I counted birds at irregular intervals in small bays, creeks, and salt marshes (hereafter referred to as miscellaneous sites) in the upper Bay of Fundy between 1975 and 1983. I also extracted data for the Bay of Fundy (mainly southwestern New Brunswick and Minas Basin) for miscellaneous sites from the results of the Maritimes Shorebird Survey Scheme (MSSS, ground surveys conducted by volunteers in 1974–1981), organized and coordinated by the Canadian Wildlife Service (see Morrison and Campbell 1983 for an example of the annual report series produced between 1976 and 1983). Because of the relatively small numbers of birds in those areas, they could be counted accurately.

Banding: estimating length of stay.—I present some results of the color-marking procedures here as they are relevant to the section that immediately follows. More detail on the derivation of turnover rate is also given in the Results section. In 1981, I determined the length of stay of Semipalmated Sandpipers based on observations of 1216 color-marked birds. I

attempted to catch birds daily at Dorchester Cape using mist nets at high tide, in daytime, between 20 July and 26 August. Sandpipers were captured on 29 banding days for an average daily catch of 43 ± 33 birds. Each bird was color-marked with a nontoxic fluorescent spray paint in a manner which identified the 5-day period in which a bird was initially captured. Each day, prior to banding, the numbers and color combinations of marked sandpipers in the roost were recorded. Fourteen percent of the 702 marked sandpipers subsequently seen following capture were also found at Mary's Point, Hopewell Cape, and Minudie (see Fig. 1). These areas were checked regularly, though not on a daily basis, and data from marked birds seen at these sites are included in turnover rate calculations. As I could not recognize individual birds to calculate an average length of stay (a more desirable method), I chose the median date between the day the largest proportion of birds marked on 20–30 July was recorded (30 July) the day when the lowest proportion of that sample was present (9 August) as an average date of departure (see Fig. 4B). The period between the first day of capture (also the first day the migrants arrived at the site) and the median date, gave an average length of stay of 15 days. Admittedly, this is a crude means of estimating length of stay, but under the conditions where many tens of thousands of birds roost in tightly packed flocks and feed over very wide intertidal areas (about 15 km^2 at Dorchester Cape alone), encountering a large sample of the same individuals over many days is extremely difficult. (In 1982 we placed numbered leg flags on 1795 sandpipers but failed to find a sufficient number of individuals, from which the numbers on the leg flags could be read, to obtain any meaningful data.) I therefore used this value of 15 days, as determined from the 1981 sample, as the turnover time.

In the Species Accounts that follow I use the terms "peak number" to signify the single highest count recorded at any one location in a particular year and "maximum number" to signify those counts that represent 50% or more of the peak number for each location and year.

Calculations of population size.—(a) Aerial surveys.—I totalled the numbers of all species groups for each flight. The numbers of birds were recorded from the air as "peeps" (Semipalmated Sandpiper, Least Sandpiper, Sanderling, Semipalmated Plover, and Spotted Sandpiper. Medium-sized shorebirds (Black-bellied Plover, Short-billed Dowitcher, Ruddy Turnstone, and knot) and large shorebirds (Hudsonian Godwit, yellowlegs, and Willet). I summed these totals for all species groups combined to give an overall estimate of all the birds encountered from the air for the period 19 July–14 September. The primary objective of the aerial surveys was to determine the relative abundance and distribution of shorebirds over the entire upper Bay of Fundy shoreline, many parts of which were otherwise inaccessible by any other means. Although the population estimate obtained from aerial surveys is less accurate than those based on ground surveys, I nonetheless include it here since this technique provides the most complete coverage and some means of comparison with the ground census results.

(b) Ground surveys.—In 1976, volunteers and I were able to survey a large number of roost sites in the bay than in any subsequent year. Some previously unknown roosting areas, identified from the air that year, were ground-censused one or two days following a flight. Because of their relative inaccessibility, some of these sites were occasionally surveyed after 1976 but not in all years. For these reasons, I treat the 1976 estimates separately. Moreover, the ground census data in 1976 are presented independently of the aerial surveys.

Using the ground census data, I extracted and summed the highest single-day counts for each species in 1976 to obtain an estimate of the total number of adults (peak numbers of adults were always much larger than those of immature birds for all species) in the Bay of Fundy at the height of the migratory period.

The adult peak numbers described above provide estimates for one year only. Unfortu-

TABLE 2

NUMBERS OF ARRIVALS AND DEPARTURES OF ADULT SEMIPALMATED SANDPIPERS AT EVANGELINE BEACH 1976 AND CALCULATION OF THE RATIO, ESTIMATE/PEAK NUMBER[a]

Peak numbers per 5-day period		Arrivals and departures based on a 15-day stopover		
Period	Numbers at roost site	Arrive	Stay	Depart
30 June–4 July	521	521	0	0
5–9 July	252	0	252	269
10–14 July	10,000	9748	252	0
15–19 July	10,000	0	9748	252
20–24 July	20,000	10,252	9478	0
25–29 July	30,000	19,748	10,252	9748
30 July–3 August	40,000	10,000	19,748 + 10,252	0
4–8 August	40,000	10,252	10,000 + 19,748	10,252
9–13 August	12,000	0	10,252 + (10,000 − 8252[b])	19,748 + 8252[b]
14–18 August	6000	0	(10,252 − 4252)	1748 + 4252
19–23 August	6000	6000	0	6000
24–28 August	6000	0	6000	0
29 August–2 September	0	0	6000	0
3–7 September	0	0	0	6000
Totals		66,521		66,521

[a] Calculation: Peak number for season = 40,000. Ratio: $\frac{\text{Estimate}}{\text{Peak number}} = \frac{66,521}{40,000} = 1.66$.

[b] The highest counts between 4–8 August and 9–13 August dropped by 28,000; therefore, of the 10,000 that arrived on 30 July–3 August, 8252 were eliminated to account for the large decline.

nately, simultaneous large-scale ground and air surveys, as were done in 1976, were not undertaken in subsequent years. I therefore computed average peak numbers (=average of highest single day counts) for each species at each of the major roosting areas, using ground census data only, for all survey years (Evangeline Beach: 1975, 1976; Mary's Point: 1976–1981; Dorchester Cape: 1976, 1979–1983). I summed the averages for all sites by species to give a general estimate of total population of adults which incorporated any variations in peak numbers between years. I computed averages rather than presenting only maximum numbers because of errors likely to be inherent in estimating such large numbers where absolute numbers are unobtainable.

I also calculated the average peak numbers of shorebirds at miscellaneous sites surveyed between 1974 and 1981. I added these to the average peak numbers computed from the data for the three main roosting sites and thus obtained totals for each species which included all censused roosting sites in the Upper Bay of Fundy over all years. In effect, these data provide information on the number of adults of each species that could be expected in the Bay of Fundy in an average year during the peak of the migratory period.

I calculated the ratio of adults to birds-of-the-year by comparing secondary peaks (iden-

TABLE 3

POPULATION ESTIMATES OF SEMIPALMATED SANDPIPERS AT THREE MAJOR ROOST SITES BETWEEN 1975 AND 1981 BASED ON 15-DAY TURNOVER RATE (SEE TABLE 2 FOR SAMPLE CALCULATION)

Location and year	Peak number	Population estimate	Estimate/ peak number
Evangeline Beach 1975	22,000	44,000	2.00
Evangeline Beach 1976	40,000	66,521	1.66
Dorchester Cape 1976	72,000	145,200	2.02
Dorchester Cape 1979	120,000	257,394	2.14
Dorchester Cape 1980	100,000	143,200	1.43
Dorchester Cape 1981	125,000	190,405	1.52
Dorchester Cape 1982	90,000	165,500	1.84
Mary's Point 1976	150,000	218,766	1.46
Mary's Point 1977	350,000	473,000	1.35
Mary's Point 1978	100,000	168,300	1.68
Mary's Point 1979	100,000	183,535	1.84
Mary's Point 1980	150,000	239,400	1.60
Mary's Point 1981	120,000	147,500	1.23

tified from ground surveys as comprising mainly immatures) with the earlier adult peaks, for each year, at Evangeline Beach, Dorchester Cape, and Mary's Point. The ratios, expressed as percentages, were averaged for each species over the years surveyed and the results multiplied by the average total number of adults (methods described above) to provide an estimate of the average number of immatures. Adding the estimates for adults and immatures resulted in an estimate of average peak numbers for both age groups for each species censused.

In separate calculations using the data for Semipalmated Sandpipers obtained from the three main roost sites, I broke down the survey data for each roost by year into identical 5-day periods. Each 5-day period between 10 July and 17 September included, on average, 36 ± 6 counts (range: 28–40, N = 13) with fewer counts in spring (1 May–29 June: 11 ± 3, range: 4–17, N = 12) and late fall (18 September–21 November: 11 ± 4; range: 4–15, N = 13). I used the highest number of birds recorded in each of these periods as the total number of birds in that roost for that segment of time. To these data I applied a 15-day rate of turnover. In other words, on day 15 of migration a roost would have consisted of early arrivals (peak number for days 1–5) plus those birds that arrived in the second (days 6–10) and third periods (days 11–15). On day 16 of migration I subtracted the number of the earliest flock (i.e., peak number for days 1–5) from the total, assuming that those birds had deposited sufficient fat for the completion of their migration and had left the area. If the numbers of birds in the subsequent period (days 16–20) had increased, I assumed that the difference consisted of new arrivals. If it decreased, I eliminated the difference as outgoing migrants, assuming that these birds arrived with fat reserves accumulated elsewhere (e.g., Gulf of St. Lawrence) (see McNeil and Cadieux 1972) and left early (i.e., they stayed in the area for less than 15 days). I then summed the total number of birds which had entered and left the area throughout the migratory period for each roost. I then compared each new total with the peak number in each roost, by year, to obtain a ratio of total to peak number. A sample calculation is shown in Table 2. Using this procedure, I obtained population estimates ranging between 1.23 and 2.14 times the single-day peak number observed each year (Table 3). For convenience, I rounded off this range to 1.25 to 2.00 times the peak number. I

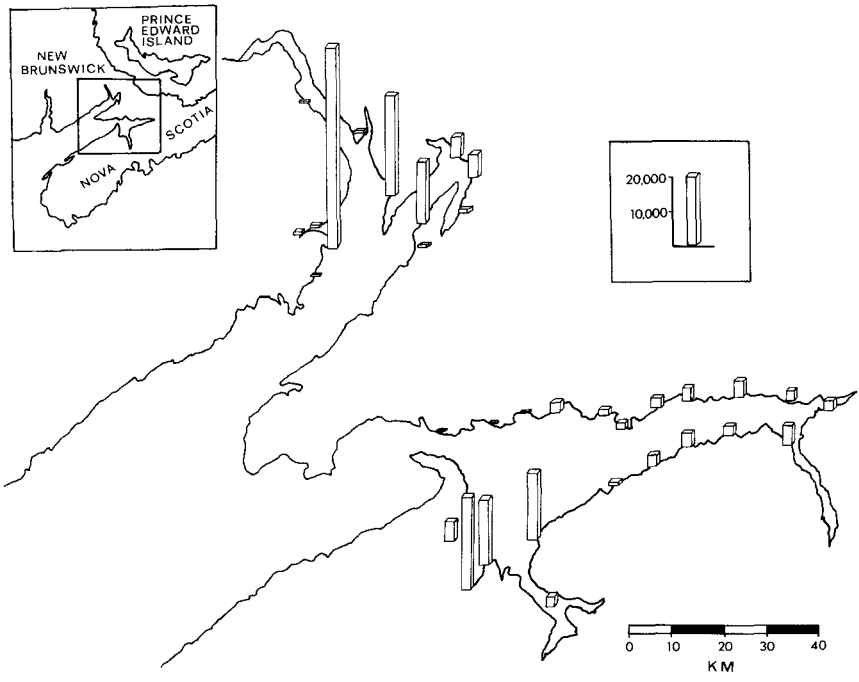


FIG. 2. Average number of shorebirds per roost based on 10 aerial surveys 19 July–12 September 1976.

therefore estimated the population of a species migrating through the upper Bay of Fundy by adding up the average peak numbers of adults and immatures for each roost site (plus miscellaneous sites) and multiplied this total by 1.25 and 2.00 to account for turnover resulting in a range within which population numbers should fall in any given year.

RESULTS

Distribution and abundance.—A total of 1,550,000 shorebirds was recorded over the 10 aerial surveys in 1976. Thirty-four roost sites were identified; the average number of shorebirds per roost throughout the July–September survey period ranged from 10 to nearly 58,000 birds for an overall average of 7000 birds per roost. The six largest roosts with 20,000 or more birds were in Shepody Bay, Cumberland Basin, and the Southern Bight, Minas Basin (Fig. 2). Numbers averaged 2600 birds per roost in other parts of Minas Basin and in Cobequid Bay. Tidal rivers such as the Petitcodiac River (Shepody Bay), River Hebert, Tantramar River (Cumberland Basin), Avon River (Southern Bight), and the Shubenacadie River (Cobequid Bay) contained comparatively low numbers (Fig. 2).

TABLE 4
PEAK NUMBERS OF SHOREBIRDS RECORDED IN 1976 FROM GROUND OBSERVATIONS

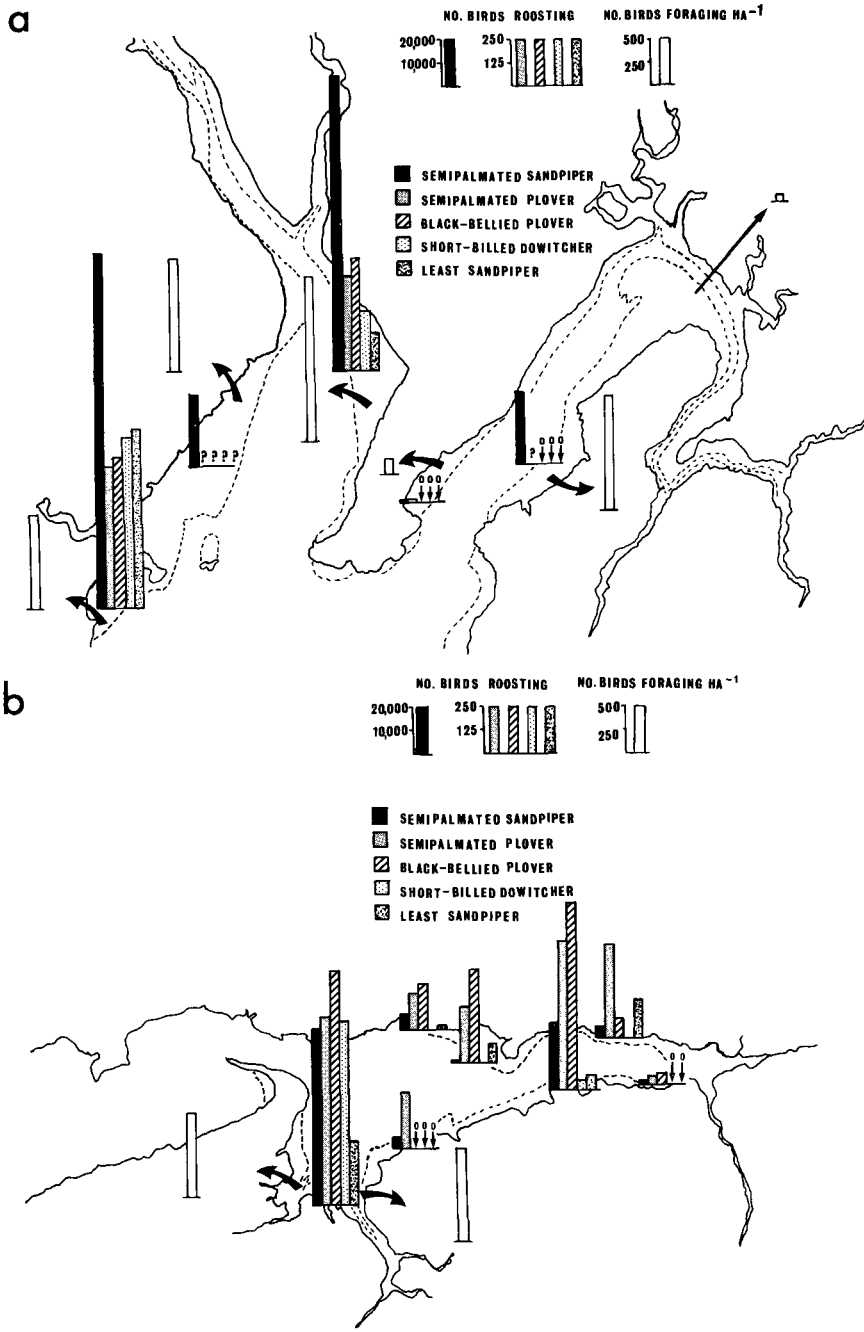
Species	Evangeline Beach	Dorchester Cape	Mary's Point	Miscellaneous sites	Total
Black-bellied Plover	1113	345	600	1701	3759
Semipalmated Plover	122	230	600	7543	8495
Short-billed Dowitcher	886	150	900	2299	4235
Red Knot	9	75	150	132	366
Sanderling	4	100	750	1114	1968
Least Sandpiper	37	50	1000	7518	8605
Semipalmated Sandpiper	40,000	72,000	150,000	274,884	536,864
All species					564,312

The maximum number of shorebirds recorded in one day in the upper reaches of the bay was 566,000 birds on 29 July 1976. Summation of peak numbers obtained by ground observers the same year was 564,312 (Table 4). This is a surprisingly close correspondence with the estimates made from the air. The three largest roost sites (Evangeline Beach, Dorchester Cape, and Mary's Point) accounted for 48.8% and 46.4% of those totals, respectively. The Semipalmated Sandpiper was by far the most numerous species and made up 95.1% of the total number of shorebirds recorded on ground surveys. If a 15-day turnover rate is applied (see below) to the ground survey data, then the total population migrating in Fundy in 1976 is estimated at 705,400 to 1,128,600 birds.

Ground observations made in 1976–1983 showed that the Semipalmated Sandpiper was more abundant at roost sites in Chignecto Bay than in Minas Basin and Cobequid Bay (Fig. 3A, B). Numbers of Semipalmated Plovers, Black-bellied Plovers, and Short-billed Dowitchers were high in the Southern Bight, and the two plover species were more widespread and collectively more numerous in Minas Basin and Cobequid Bay than elsewhere (Fig. 3A, B).

Some areas that had been identified as important sites based on results obtained from aerial surveys in 1976 were subsequently shown to be less important following repeated ground surveys in later years. Examples include the Elysian Fields in the Cumberland Basin and Cheverie and Lyon's Head in Cobequid Bay. Some sites such as Mary's Point, Dorchester Cape, and Evangeline Beach, however, may be termed "traditional" roosting areas because they are used by large numbers each year.

Turnover rate: Semipalmated Sandpipers. —Less than 1% of adult Semi-


a
NO. BIRDS ROOSTING
NO. BIRDS FORAGING HA⁻¹
20,000
10,000
250
125
500
250
SEMIPALMATED SANDPIPER
SEMIPALMATED PLOVER
BLACK-BELLIED PLOVER
SHORT-BILLED DOWITCHER
LEAST SANDPIPER
b
NO. BIRDS ROOSTING
NO. BIRDS FORAGING HA⁻¹
20,000
10,000
250
125
500
250
SEMIPALMATED SANDPIPER
SEMIPALMATED PLOVER
BLACK-BELLIED PLOVER
SHORT-BILLED DOWITCHER
LEAST SANDPIPER

palmated Sandpipers color marked early in migration, 20–25 July, were seen as late as 23 August, a duration of 31 ± 3 days. The largest proportions of sandpipers marked 20–25 July and 26–30 July were recorded in the area on 30 July (13.0% and 7.9%, respectively) (Fig. 4B). Sightings of marked birds decreased quickly from 30 July onwards, indicating a rapid movement out of the area between 31 July and 9 August (Fig. 4B). Similarly, daily estimates of the numbers of sandpipers at the roost site declined after 30 July (Fig. 4A). The highest proportion of birds weighing more than 40.0 grams occurred 30 July–4 August, and there was a substantial and sudden decrease in mean fresh weights between 1 and 2 August (P. W. Hicklin, unpubl. data) which further supports these departure dates. The color-marking data indicated that there were five separate and recognizable departure periods from the Dorchester Cape site between 31 July and 20 August (Hicklin, unpubl. data). Unfortunately, I could only determine the arrival dates of those birds which left the site between 30 July–9 August (the first birds were seen on 20 July and numbers increased rapidly until 30 July, so birds arrived in that 10-day period) and not of later-arriving sandpipers. Hence, only those data are presented here. The results obtained from the color-marked sample of birds captured 20–30 July showed that a major flight out of the area began around 31 July–1 August and continued daily until 9 August.

I assume that birds that might have initially arrived with some fat reserves stayed at least 10 days, and that lean arrivals may have stayed for as long as 20 days. I therefore chose the median date of 4 August as an average date of departure for birds which first arrived as early as 20 July, regardless of the numbers present or weight. The relatively low percentages of marked birds we found in roosts were not due to any biased mortality of birds which were captured, banded, and color marked. Predation is not a factor of any significance in the Bay of Fundy during shorebird migration, and dead marked birds or their remains were never found. Rather, the difficulty of finding a few marked birds amongst large assemblages of roosting sandpipers, as are found in Fundy, is the primary reason for the relatively low percentages from which turnover was derived.

Although this estimated length of stay applied to the Semipalmated

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FIG. 3. Maximum numbers of Semipalmated Sandpipers, Semipalmated Plovers, Black-bellied Plovers, Short-billed Dowitchers, and Least Sandpipers at roosting sites and densities on foraging areas (numbers counted inside 1-ha plots on mudflats) in (a) Chignecto Bay and (b) Minas Basin and Cobequid Bay 1976–1982. Open bars (feeding densities) refer to all species combined.

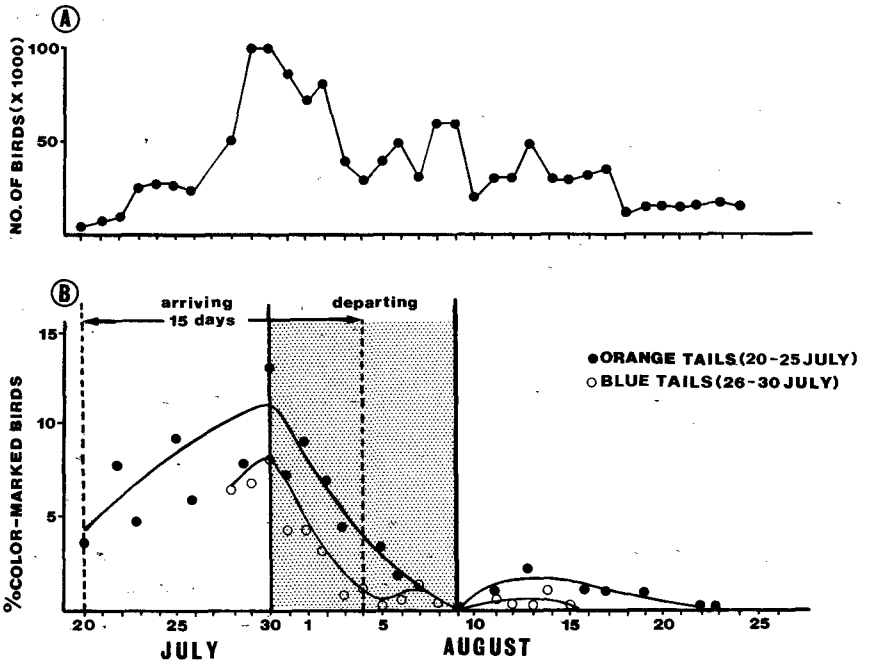

FIG. 4. A. Numbers of Semipalmated Sandpipers roosting at Dorchester Cape, 20 July–26 August, 1981. B. Daily sightings of color-marked Semipalmated Sandpipers at Dorchester Cape expressed as the percent of the total numbers of each color marked at the time of observation.

Sandpiper, I also used it to calculate the total numbers of eight other species passing through Fundy (see below). So far, it is the only means available to provide a broad estimate of numbers of these other species until further research is done. In any case, as 95% of all the birds in Fundy during autumn migration are Semipalmated Sandpipers, fluctuations in total numbers would be reflected mainly by changes in numbers of that species.

SPECIES ACCOUNTS

Black-bellied Plover.—This plover was the only species that occurred in large numbers during spring migration. The largest spring roost, at Dorchester Cape on 4 June 1983, contained 1387 birds. On average, the spring migration of Black-bellied Plovers extended from 26 April to 24 June, with peak numbers between years recorded 31 May–4 June (Fig. 5).

Southward migration in late summer began 25–29 July, and peak numbers were reached, on average, from 24 to 28 August (Fig. 5). The largest

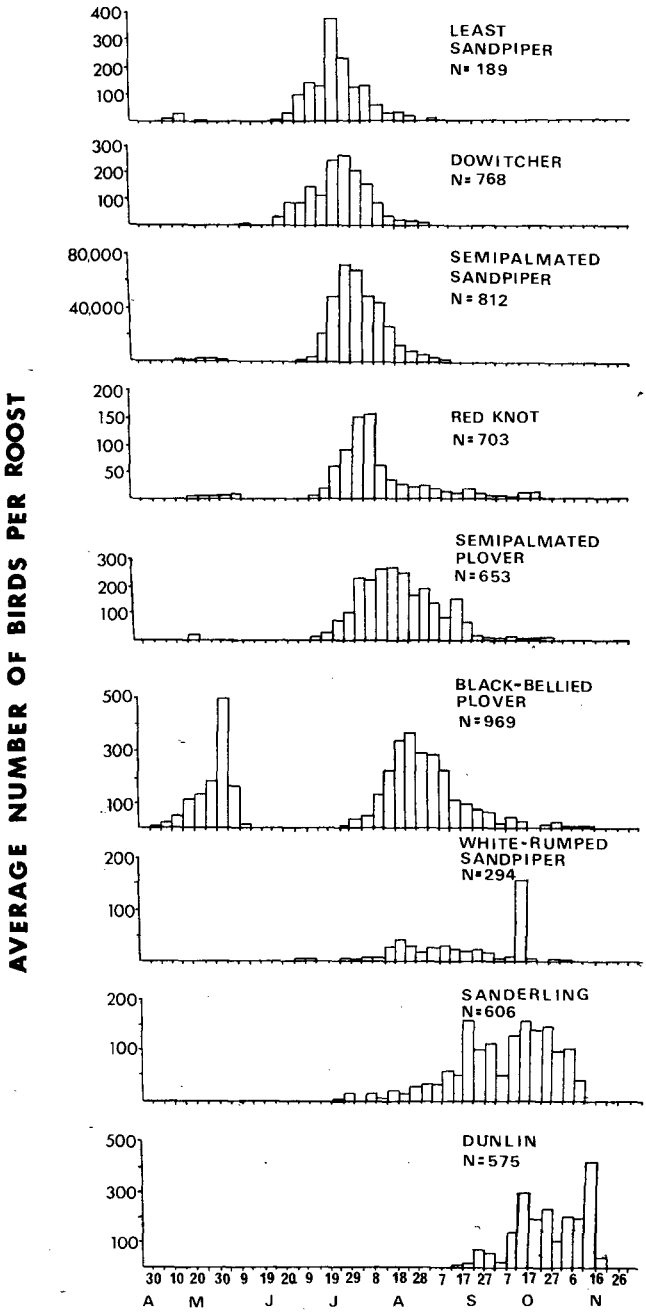

FIG. 5. Average number of shorebirds per 5-day period at Evangeline Beach, Dorchester Cape, and Mary's Point combined 1975–1983. N refers to the total number of counts for each species over all years.

roosting flock seen in late summer was of 1440 birds at Evangeline Beach on 27 August 1975.

Immatures were not seen at roost sites before 10 September. Elliot (1977) saw the first immatures at Evangeline Beach on 18 September 1975; peak numbers (300) were attained on 7 October, and the last immature bird was seen there on 11 November 1979 and at St. Andrews, New Brunswick, on the same date in 1985 (pers. obs.). On average, the peak numbers of immatures represented 20.6 ± 9.0% [SD] (N = 11) of the adult peaks. For all sites surveyed, average peak numbers of both age groups totalled 5050 birds (Table 5). Accounting for turnover, I estimate the total number of Black-bellied Plovers passing through the Bay each fall to be from 6300 to 10,000 birds (Table 5).

Semipalmated Plover.—This plover was uncommon in spring; 103 birds seen at Dorchester Cape on 23 May 1983, was the largest number recorded. In late summer and fall, Semipalmated Plovers were seen between 30 June and 6 November. Migration generally began around 15–19 July, and maximum numbers were reached on 19–23 August (Fig. 5). For all years combined, however, there was no well-defined peak, with large numbers recorded throughout the period 30 July–27 September (Fig. 5). Sites near the mouth of the Saint John River (Quaco Bay, Manawagonish Marsh, Saint's Rest Marsh and Maces Bay), Passamaquoddy Bay (Kent Island, St. Andrews), Grand Manan, and Minas Basin (Highland Village, Economy) contained large assemblages of Semipalmated Plovers, many more than were found at the three main roosting areas (Table 5, see also Appendix 1).

Although immatures were seen as early as 11 August, they did not contribute significantly to total numbers until the first week in September. The August immatures probably represented birds hatched from the southernmost part of the breeding range, in the maritimes, the Gulf of St. Lawrence, and Newfoundland (Godfrey 1966). At Mary's Point, the earliest peak of immatures occurred on 9 September 1981, and the latest at Evangeline Beach on 19 September 1975. Immature peaks averaged 19% of adult peaks at these sites. Assuming a 15-day turnover period, the population of Semipalmated Plovers passing through the Bay of Fundy is estimated to be from 13,600 to 22,000 birds (Table 5).

Short-billed Dowitcher.—Few dowitchers were recorded in spring. A flock of 100 was seen on 16 June 1979 at Mary's Point, that probably included nonbreeding birds or failed breeders. Typically, spring (between 8 May and 12 June) sightings of dowitchers consisted of flocks with fewer than five birds. In late summer and fall, dowitchers were seen 30 June–30 September. This species was the earliest southbound migrant to arrive in Fundy in substantial numbers, beginning 30 June–4 July, and peak

TABLE 5

POPULATION ESTIMATES OF SHOREBIRDS IN THE BAY OF FUNDY DURING LATE SUMMER AND FALL BASED ON MEANS OF PEAK NUMBERS 1974–1983,[a] INCLUSIVE

	Black-bellied Plover	Semi-palmated Plover	Red Knot	Sanderling	Semipalmated Sandpiper	Least Sandpiper	White-rumped Sandpiper	Dunlin	Dowitcher	Totals
Adults										
Evangeline	1278	735	0	0	31,000	346[b]	136[b]	0	968	
Dorchester Cape	484	407	300	239	118,000	346	136	1216	407	
Mary's Point	725	525	408	458	161,667	346	136	375	550	
Miscellaneous[c]	1701	7543	132	1114	273,220	7518	903	170	2299	
Total Adults	4188	9200	840	1811	583,887	8556	1311	1761	4224	598,666
% immatures	20.6	19.0	?	?	12.6	12.6[d]	?	?	24.8	
Total adults and immatures	5050	10,948	840+	1811+	657,457	9634	1311+	1761+	5271	694,093
Population estimate	6312–10,100	13,685–21,896	1050–1680	2264–3622	821,821–1,314,914	12,042–19,268	1639–2622	2201–3522	6589–10,542	867,603–1,388,166

[a] Mary's Point = 1976–1981; Dorchester Cape = 1976–1983; Miscellaneous = 1974–1981.

[b] Although the numbers of these species were not regularly identified and counted at Evangeline Beach and Dorchester Cape, the few counts available suggest that the numbers there were similar to those seen at Mary's Point.

[c] See Appendix 1.

[d] See text.

numbers were attained one month later in the period 30 July–3 August (Fig. 5). The largest single flock of 1100 birds was seen at Dorchester Cape on 27 July 1979. Comparatively few dowitchers were seen at roost sites when Semipalmated and Black-bellied plovers became abundant in late August.

No effort was made to distinguish age classes. Elliot (1977) noted that paler birds were seen after 15 August and were probably immatures. I therefore used the numbers of dowitchers seen after 15 August at the three main roost sites to estimate the proportions of immatures to adults. These amounted to 24.8% ± 9.9% (N = 14) of the adult peaks.

Outside the three main roosts, the birds were most numerous in southwestern New Brunswick (Appendix 1). Summation of counts from all areas provided an estimate of 4224 adult dowitchers at the peak of the migratory period. Including immatures and correcting for turnover, the estimated number of dowitchers passing through the Bay of Fundy is 6500 to 11,000 birds (Table 5).

Red Knot.—Knots were rarely seen in spring. Two were identified at Mary's Point on 2 June 1979, and the largest spring flock consisted of 39 birds at Dorchester Cape on 12 June 1983.

Postbreeders first appeared at these two main roost sites around 14–24 July and reached peak numbers 9–13 August (Fig. 5). In 1975 and 1976, Red Knots were seen only occasionally at Evangeline Beach, and the largest flock there consisted of 20 birds.

As peak numbers of knots recorded between 14 July and 15 August probably represented adult birds, I estimated population numbers of that age group only. The numbers of knots seen at sites other than the three main roosting areas were relatively low (Appendix 1). Based on these data, the population of adult Red Knots in Fundy is estimated to be from 1000 to 1700 birds (Table 5).

Sanderling.–Sanderlings began their migration to the Bay of Fundy in mid-July. The time of arrival of larger flocks varied among years. Maximum numbers were recorded from 13 August to 6 November, but the main movement occurred between 17 September and 6 November (Fig. 5).

In July, some of the early arrivals were in breeding plumage and may have been failed breeders or nonbreeders. From August on, all Sanderlings seen were in basic plumage, making distinction between adults and immatures very difficult. In other species where age classes could be distinguished, adults always constituted the first and largest peaks in numbers. I have therefore used early peak numbers to estimate the populations of adults only. For all sites combined (see Appendix 1), the numbers of adult Sanderlings migrating to the Bay of Fundy is estimated as 2000–3700 birds (Table 5).

Least Sandpiper.—Least Sandpipers roosted with the more numerous Semipalmated Sandpipers, and the two species were often difficult to separate. A greater effort to distinguish and count Least Sandpipers was made at Mary's Point during 1976–1981. Very few birds were seen there in spring. Maximum numbers of adult Least Sandpipers were recorded on 10 July through 13 August; maximum numbers of immatures occurred from 19 August to 17 September. On average, peak numbers of adults were reached on 25–29 July (Fig. 5).

Except for 1976 and 1979, almost twice as many immatures as adults were seen at Mary's Point. Counts of birds at other roosting or feeding areas totaled approximately 7500 birds, with large numbers concentrated in salt marshes (Appendix 1).

More effort was made to distinguish Least Sandpipers from Semipalmated Sandpipers at Mary's Point than at the other main roosting areas. Assuming that the proportions of Least to Semipalmated Sandpipers were similar at all three sites, I have therefore substituted the same average numbers as at Mary's Point for Evangeline Beach and Dorchester Cape. The number of adult Least Sandpipers in all of the Bay of Fundy is estimated at 8600 birds (Table 4). Assuming that the relative numbers of immature Least Sandpipers are similar to those of the Semipalmated Sandpiper (12.6%; see below), I estimate the population, including both age classes, as 12,000–19,000 sandpipers (Table 5).

Semipalmated Sandpiper.—The Semipalmated Sandpiper is by far the most numerous shorebird during migration in Fundy. In spring, the numbers recorded at Evangeline Beach, Dorchester Cape, and Mary's Point ranged from 428 to 10,000 birds between 21 May and 9 June. Maximum numbers at these three sites occurred in the period 20 July–23 August, and the largest roost seen was a single flock at Mary's Point containing about 350,000 sandpipers on 10 August 1977. For all years combined, peak numbers at those three sites occurred 30 July–7 August and averaged 70,000 birds per roost (Fig. 5).

The first juveniles were difficult to detect because of the large numbers of adults present. In the course of banding operations, the first immatures were captured on 14 and 19 August at Dorchester Cape in 1981 and 1982, respectively. After 23 August, the numbers of immatures captured exceeded those of adults, and from 25 August to 12 September (last banding day) nearly all the sandpipers captured were immatures. To obtain a measure of the numbers of immatures in relation to those of adults, I compared the peak numbers of sandpipers seen after 25 August with peak numbers before that date. On average, the secondary peaks amounted to $12.6 \pm 6.6\%$ ($N = 13$) of adult numbers.

Outside of the three main roosting areas, peak numbers of Semipal-

mated Sandpipers totalled about 275,000 (Appendix 1). For all sites combined, average peak numbers reached a total of nearly 584,000 sandpipers. By adding immatures and correcting for turnover, the estimated population of Semipalmated Sandpipers in the Bay of Fundy during southward migration is estimated as 800,000–1,300,000 (Table 5), which corresponds closely to the figures obtained from the air and ground surveys in 1976 (see above).

White-rumped Sandpiper.—This species was not abundant at any of the sites surveyed. At the three main roost sites, fewer than 10 were recorded in late June and early July. At Mary's Point, where the most detailed observations were made, they were not seen regularly until the middle of August. Four counts made between 13 and 17 October in 1976 and 1978 were unusually high and may reflect the passage of larger numbers of immatures during that short period in those years (Fig. 5). Similarly, White-rumped Sandpipers were scarce at other sites, except for a large flock of 600 seen at Manawagonish Marsh in 1974 (Appendix 1). If we assume that adults occurred at Evangeline Beach and Dorchester Cape in numbers similar to those counted at Mary's Point, then on average, their total numbers in the Bay of Fundy in late summer and fall lie in the range of 1600 to 3000 birds (Table 5).

Dunlin.—Dunlins are the latest migrant to pass through the bay in fall. The main passage of Dunlins occurs throughout October and early November (Fig. 5). I have no records of Dunlins from Evangeline Beach, and Tufts (1973) did not mention any notable concentrations for the area. Most birds were seen at Mary's Point and Dorchester Cape (Table 5) (Appendix 1). Based on those data, the total numbers of Dunlins migrating through Fundy is estimated as 2000 to 3500 birds (Table 5).

Hudsonian Godwit.—This large shorebird is seen each year at the main roost sites, although never in large numbers. In 1975–1983, 141 sightings of Hudsonian Godwit were recorded in Chignecto Bay for an average of 8 birds per sighting (Fig. 6). The largest single flock (80) was recorded along the Tantramar River at the head of Cumberland Basin on 29 July, 1978 (A. J. Erskine, pers. comm.). They are most commonly seen from mid-July to the latter part of August. The total number of godwits passing through Fundy in most years is probably about 100 birds.

DISCUSSION

I used three different methods: (1) aerial and (2) ground surveys in 1976 and (3) summation of the average peak numbers of adults between 1974 and 1983 to estimate the total number of adult shorebirds at the peak of the migratory period. Considering the sizes of bird flocks and the numbers of years and observers involved, there is close agreement among the three

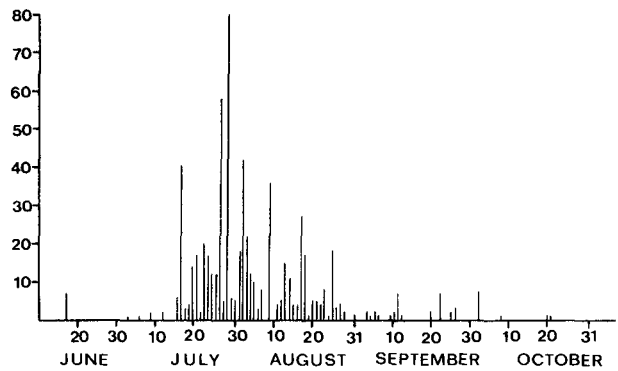

FIG. 6. Numbers of Hudsonian Godwits seen in the Bay of Fundy between 1975–1983, inclusive. Where counts were made on the same date, but in different years, the largest number was used.

estimates, which were 566,000, 564,000 and 599,000, respectively (Table 6). By adding the estimated numbers of immature birds, the total reaches slightly more than 694,000 plovers and sandpipers (Table 6).

These numbers refer only to those flocks of shorebirds recorded each year at the height of migration, and only at the sites most accessible to observers. This figure should therefore serve as a minimum estimate for the whole population throughout the migratory period. Correcting for turnover places the total population of shorebirds using the intertidal area of the Bay of Fundy somewhere in the range of 800,000 to 1,400,000 birds, 95% of which are Semipalmated Sandpipers.

The wide range reflects variations in peak numbers of Semipalmated Sandpipers between years and between roost sites. Richardson (1979) has shown, with the aid of radar, that although large flocks of shorebirds stopped in Fundy during southward migration, many flocks passed over central new Brunswick and continued in a southeasterly direction over the ocean. This suggests that many shorebirds are able to accumulate sufficient fat reserves at staging areas north of Fundy to continue directly over the Atlantic Ocean, presumably to the wintering grounds. The numbers that do so, however, may vary depending on the quality and quantity of available food resources at staging areas, which may fluctuate between years. Brousseau (1981) showed that approximately 80,000 sandpipers congregate in the St. Lawrence River, and large flocks also gather on the Magdalen Islands in the Gulf of St. Lawrence (McNeil and Cadieux 1972). McNeil and Cadieux (1972) reported that although large numbers of the Semipalmated Sandpipers on the Magdalen Islands had sufficient lipid reserves to fly a distance of 3200 km, many others departed with low fat

TABLE 6
COMPARISON OF POPULATION ESTIMATES FOR NINE SPECIES OF SHOREBIRDS STOPPING IN THE BAY OF FUNDY IN AUTUMN

Method	Single-day peak numbers (adults)	Peak numbers adults + immatures	Total population estimate[a]
1976 aerial survey	566,000		1,554,143[b]
1976 ground survey	564,312		705,390–1,129,000
Summation of average peak numbers of adults (1974–1983)	598,666		748,333–1,197,000
Summation of average peak numbers of adults and immatures (1974–1983)		694,093	867,603–1,388,166

[a] Range refers to 1.25 to 2 times as many birds as single-day peak count to account for turnover (see Methods).
[b] Summation of results from 10 aerial surveys over 8-week period (19 July–12 September 1976).

levels which would have had to be replenished elsewhere before undertaking a transoceanic flight to South America. Hence, in some years, more birds may fly from the St. Lawrence River or the Magdalen Islands to the Bay of Fundy before continuing to the wintering areas if food resources at the more northern staging areas were reduced.

That possibility is supported by banding and color-marking information. Semipalmated Sandpipers color marked in James Bay (Morrison and Gratto 1979), the Magdalen Islands (McNeil and Burton 1977), the St. Lawrence River (P. Dupuis, pers. comm.), and the coast of Maine (T. May, pers. comm.) were seen in the Bay of Fundy the same year they were color marked. The sandpipers that were marked in southeastern Maine flew north to feeding grounds in Chignecto Bay in the upper Bay of Fundy. The "funneling" of sandpipers to the Bay of Fundy from other staging sites contributes to its importance as a major foraging area for migrant shorebirds during the southward migration.

Spaans (1979) indicated that shorebirds in Suriname arrived "one to two weeks" after they were first seen in the Bay of Fundy. If this statement specifically means a period of 7 to 14 days, it suggests a faster turnover rate than the 10 to 20 days I have used here. However, those birds that arrived in the Bay of Fundy, and might have stopped previously along the Saint Lawrence River in Quebec or on the Magdalen Islands in the Gulf of St. Lawrence, would be expected to use the Bay of Fundy for a shorter period to "top off" their fat reserves prior to a long-distance flight. Sandpipers which might have flown to the Bay of Fundy directly from the Arctic breeding grounds presumably would arrive leaner and have to

stay longer. As I am unable to distinguish between these groups, a length of 15 days appeared most reasonable, as it would accommodate all weight classes at arrival. Hence, my estimates based on a 15-day turnover rate must be regarded as conservative until further research can determine the length of stay of specific individual birds of known arrival-departure dates and weights.

Recently, Morrison (1983) and Morrison et al. (1985) estimated the wintering population "of small shorebirds (mainly Semipalmated Sandpipers)" along the northern coast of South America at 1.9 million birds. Of those, 70% were seen in Suriname, 20% in French Guiana, and 0.5% in Guyana. These areas are most likely the wintering areas of those birds seen each autumn in the Bay of Fundy. On 6 June 1978, Boates (1980) collected a Semipalmated Sandpiper in the Southern Bight, Minas Basin, that had been banded near Paramaribo, Suriname, on 13 May 1976. In August of the same year, I saw 4 color-banded Semipalmated Sandpipers in Shepody Bay which had also been banded by Spaans in Suriname during 1976 and 1977 (A. Spaans, pers. comm.). On 11 August 1981, I recovered a band near Cumberland Basin from the leg of a Suriname-banded Semipalmated Sandpiper killed by a domestic cat on that date. Two Semipalmated Sandpipers banded in 1981 at Dorchester Cape were subsequently recovered in Guyana. One of these was found there the same month it was banded in the Bay of Fundy. Morrison (1984) reported that of 40,000 Semipalmated Sandpipers banded in James Bay between 1974 and 1982, 60 of 66 band recoveries from Guyana, Suriname, and French Guiana occurred in Guyana even though only a small proportion of over-wintering birds are found there. He attributed the high rate of band recoveries in Guyana to the greater accessibility of the coastline to people plus the practice of hunting shorebirds for food in that country during the birds' migration to Suriname and French Guiana. This may explain why the recoveries of the two sandpipers banded in the Bay of Fundy were in Guyana and not in Suriname as Morrison's (1984) survey data, and the banding observations noted above, would suggest.

Of the 1.9 million sandpipers estimated to winter in those three countries, my estimates for the Bay of Fundy (Table 5) represent 42–74% of that total.

Lack of information on the size of North American populations of shorebirds makes it difficult to assess quantitatively the relative importance of the Bay of Fundy to these populations in a continental context. For example, the number of Black-bellied Plovers may reach 10,000 in the Bay of Fundy during fall migration. This represents nearly 50% of the total number estimated for all of Britain (Moser 1987), equivalent to 20% of the European population (Cramp and Simmons 1983), but this may

be proportionally less significant with regard to the New World population. Spaans (1978) estimated that between 2500 and 50,000 Black-bellied Plovers occur throughout the year in Suriname. He also estimated numbers of Short-billed Dowitchers along the Suriname coast at 100,000 or more. Therefore, the numbers of dowitchers in the Bay of Fundy would represent 8.5% of the Suriname estimate at most. Similar comparisons for Semipalmated Plover and Least Sandpiper in the Bay of Fundy amount to 44% and 18%, respectively, of the population estimates made by Spaans (1978) for the Suriname coast. For Red Knot, the maximum of 1700 birds estimated in the Bay of Fundy amounts to about 1.0% of the nearly 150,000 Morrison (1984) estimated as the total New World population.

Except for the Black-bellied Plover, the spring migration of shorebirds in the Bay of Fundy is not significant. The few Semipalmated Sandpipers, Semipalmated Plovers, and dowitchers seen in spring probably represent birds that have strayed from a more commonly used inland route. Dunne et al. (1982) showed that in late May very large numbers of Semipalmated Sandpipers (nearly 175,000 on 21 May 1982) congregate in Delaware Bay, and as many as 25,000 have been seen in Cape Cod on 30 May (Hill 1965) and 35,000 on 1 June, 1957 (Bailey 1968 in Harrington and Morrison 1979). As only a small proportion of these numbers reaches the Bay of Fundy in late May and early June, the large flocks in Delaware Bay probably fly west-northwest towards the breeding grounds, thus bypassing the Bay of Fundy altogether. Dunne et al. (1982) did not report Black-bellied Plovers in Delaware Bay in spring as one of the "principal" migratory species, although Bailey (1955) mentioned peaks of 2000 to 2500 in Massachusetts. As single flocks of nearly 1400 Black-bellied Plover have been recorded in the Bay of Fundy in late May and early June, part of the population appears to follow a coastal route northwards to the Maritime Provinces.

During April and May, the densities of invertebrates in mud and sandflats in the Bay of Fundy are very low owing to severe ice-scouring throughout the winter months (Hicklin et al. 1980, Gordon and Desplanque 1983, Gordon et al. 1985). The resulting lack of food in spring may be partly responsible for the low use of the area by migrant shorebirds at this time. Consequently, Black-bellied Plovers in the Southern Bight during May and June foraged on the more elevated salt marshes where they preyed on the larvae of soldier and horse flies (Order Diptera). Conversely, in late summer and fall when food was more abundant, they confined their foraging activities to mudflats and primarily consumed polychaetes (Hicklin and Smith 1979).

The main passage of the seven major species examined in this paper occured during a five-week period beginning the last week of July. The

Sanderling and Dunlin are high arctic breeders that undergo a partial molt on the breeding grounds and leave the breeding areas much later.

The migration of shorebirds in the Bay of Fundy in late July and August coincides with the period of maximum invertebrate production, notably the 5 mm long amphipod *Corophium volutator* (Peer et al. 1986), which is a main prey of Semipalmated Sandpiper, Least Sandpipers, Short-billed Dowitchers, and Semipalmated Plovers (Hicklin and Smith 1979, 1984). An abundance of food in the Bay of Fundy at this time is probably the main factor for the strategic importance of this area to migratory shorebirds along the eastern seaboard, notably the very large population of Semipalmated Sandpipers. Throughout the migratory period, foraging sandpipers concentrate on mudflats where *Corophium* is most abundant (Hicklin and Smith 1984). Boates (1980) has shown that Semipalmated Sandpipers ingest between 9600–26,100 *Corophium*/bird/day, depending on tide height and the amount of time the flats are exposed in daytime. During the period that shorebirds are present in the bay, *Corophium* production from July to September is between 3.8 and 5.2 g dry weight/m^2 of mudflat at Pecks Cove, Cumberland Basin (Peer et al. 1986), a site of relatively low shorebird abundance (Hicklin, unpubl. data) to 22.0 g dry weight m^2 at Avonport Beach, Minas Basin (Gratto 1979), a major foraging area used by Semipalmated Sandpipers (Hicklin and Smith 1984).

The high biomass of food present each year during July and August would allow birds to put on the necessary fat stores to complete their migration to South America by an overseas route. In extreme cases, some sandpipers in Fundy attain weights in excess of 50 grams, which can impede the birds' ability to fly (Hicklin, unpubl. data), and represents 51% of body mass above fat-free weight (24.5 $\pm$ 2.3 grams, both sexes combined), presumably in the form of fat (Hicklin, unpubl. data). On average, 10 days following the onset of migration into the bay, 30% of the roost at Dorchester Cape consists of sandpipers weighing over 40.1 grams ($\bar{x}$ = 43.2 grams) for an average fat content of 17.3 grams (N = 31) or 40% of the fresh weight (Hicklin, unpubl. data). By using the methods in McNeil and Cadieux (1972) to calculate flight ranges, one can predict that these birds would have a flight range capability of 4400 km, or sufficient energy stores to fly directly from the Bay of Fundy to the northern coast of South America, a distance of about 4300 km.

The combination of wide intertidal flats and an abundant food supply in late summer in the Bay of Fundy allows for the large populations of birds described in this paper to stop in the bay and deposit fat stores prior to the long flight to their wintering areas. These attributes of the Bay of Fundy make it one of the more significant shorebird stopover areas during autumn migration along the eastern seaboard of North America.

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APPENDIX 1

AVERAGE PEAK NUMBERS OF SHOREBIRDS AT MISCELLANEOUS SITES IN THE BAY OF FUNDY

Sites	Species								
	Black-bellied Plover	Semi-palmated Plover	Red Knot	Sanderling	Semi-palmated Sandpiper	Least Sandpiper	White-rumped Sandpiper	Dunlin	Dowitcher
Cheverie (2)[a]	500	173	0	36	4950	0	3	35	0
Moose Brook (2)	25	76	0	0	2813	5	1	0	0
Noel Bay (5)	57	1876	0	3	4450	16	19	3	8
Noel Shore (4)	82	11	0	0	5500	0	0	1	3
Noel Point (4)	44	85	3	1	1238	0	1	43	5
Sterling Brook (3)	65	42	0	0	2300	25	0	0	1
Shubenacadie (2)	13	20	0	0	600	75	0	0	2
Highland Village (3)	93	400	0	15	4500	125	0	6	1
Economy (3)	200	200	1	150	1333	50	35	17	1
Five Islands (1)	0	0	0	0	0	0	0	0	0
Minudie (6)	—	—	—	—	30,000	—	—	—	—
Hopewell (3)	—	—	—	—	60,000	—	—	—	—
John Lusby (2)	5	225	0	0	100,000	200	1	0	100
Missaquash (1)	0	0	0	0	1	1	0	0	100
Tantramar River (1)	0	35	0	0	2900	100	0	0	50
Waterside (7)	4	46	5	73	196	34	4	3	21
Quaco Bay (5)	29	731	0	527	1067	554	2	0	32
Manawagonish Marsh (1)	70	303	0	0	8984	3150	600	1	951
Dipper and Chance Harbours (2)	13	43	1	28	168	99	6	5	1
Maces Bay (3)	107	1340	0	118	3690	1763	82	2	184
Courtenay Bay (2)	39	188	0	5	6500	7	0	8	230
Kent Island (3)	77	423	2	30	2983	417	74	1	370
St. Andrews (1)	10	300	1	0	10	2	5	0	0
Grand Manan (6)	185	344	29	60	3526	275	23	35	108

APPENDIX 1
CONTINUED

Sites	Species								
	Black-bellied Plover	Semi-palmated Plover	Red Knot	Sanderling	Semi-palmated Sandpiper	Least Sandpiper	White-rumped Sandpiper	Dunlin	Dowitcher
Point Lepreau (1)	16	580	0	11	1005	250	45	0	72
Saints Rest Marsh (1)	3	1000	20	10	20,000	300	2	0	150
Portapique River (3)	1	25	0	0	125	2	0	0	0
Bass River (3)	0	8	0	0	60	5	0	0	0
Little Dyke (3)	6	545	10	30	3488	23	0	10	4
Lyon's Head (1)	30	150	43	10	2000	15	0	0	4
Black Rock (3)	27	63	17	6	500	25	0	0	1
Total	1701	7543	132	1114	274,887	7518	903	170	2299

[a] Numbers in parentheses refer to number of years counts were made.