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PHALAROPES

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Introduction

Phalaropes are shore birds that have largely abandoned the shore. Rather than wading at the boundary of water and land, as most shore birds do, red (*Phalaropus fulicaria*) and red-necked (*P. lobatus*) phalaropes spend up to 9 months of the year swimming on the open ocean. (Red phalaropes are commonly called gray phalaropes in Europe.) A third species, Wilson's phalarope (*P. tricolor*), does not have a marine life history (and thus will not be much considered here) but swims most of the year on saline lakes in the interior of North and South America, where its biology is similar to that of the marine phalaropes. During the breeding season, all three species frequent fresh-water wetlands. At around 20 cm long, phalaropes are among the smallest of oceanic birds. Phalaropes display un-waderlike adaptations for swimming, including lobed toes, legs that are flattened to reduce drag when paddling, and dense, waterproof feathers.

Those air-trapping feathers, combined with small body size, result in the corklike buoyancy of phalaropes, as a result of which it is almost comically difficult for the birds to dive. Restricted to surface waters, phalaropes are famous among birdwatchers and biologists for frenetic spinning in small circles. This behavior generates a miniature upwelling that brings prey from deep in the water column within reach. Once grasped, prey are rapidly moved up the beak into the mouth by a process that uses the surface tension of water.

The sex roles are reversed in phalaropes: larger, brightly colored females lay eggs for their mates, while smaller males with dull feathers perform all care of eggs and chicks. This unusual breeding system is further distinguished by polyandry: female phalaropes sometimes have multiple mates in a single season. Committed to an aquatic lifestyle, phalaropes do virtually everything but lay eggs on the water, nesting on land near pools or ponds. The marine phalaropes breed circumpolarly in the Arctic and sub-Arctic and migrate to pelagic wintering areas by flying out to sea. Some red-necked phalaropes also migrate overland by a series of short flights visiting every imaginable body of water, but especially saline lakes.

The population status of the two marine phalaropes is uncertain at best. The pelagic biology of these birds is poorly known, compared to other seabirds, and this hampers efforts to monitor populations and obtain data about their numbers. Breeding biology is better understood, but few breeding populations are being monitored. Large flocks at sea and on saline lakes imply that phalaropes are abundant, but human disturbance has reduced the breeding range of phalaropes. More disturbing, massive flocks have simply disappeared from former migratory staging sites, for example, the western Bay of Fundy on the north-eastern coast of Canada. We do not know whether this represents a real reduction in the population, or a shift to a new staging location caused by a change in the availability of plankton.

Phalaropes at Sea

Appearance

Phalaropes are small sandpipers, with the small heads, needle-shaped beaks, and elongate necks typical of the family Scolopacidae (**Figure 1**). As they paddle on the ocean surface, their long wader's legs are generally hidden from an observer. Their small size and shape make them unmistakable for any other kind of bird at sea, although they are easily mistaken for each other. Red and red-necked phalaropes are more similar to each other, and more closely related (see Systematics below), than either is to Wilson's phalarope. These degrees of relatedness show in appearance, structure, and behavior. When seen at sea in their white and gray nonbreeding plumage (**Figure 1B**) red and red-necked phalaropes are difficult to distinguish. Red-necked phalaropes are slightly smaller, and more lightly built, with an exceptionally fine needlelike black bill; red phalaropes are more heavily built, with a broader, deeper, more yellow bill. Either species is easily distinguished from Wilson's phalarope (which is the largest of the three species and lacks a dark eye patch and wing bars), which is only rarely seen in the marine environment, and never pelagically.

Female phalaropes are slightly larger than males and have brighter feathers during the breeding season (**Figure 1a**) a condition known as reverse sexual dimorphism (in most birds males are the larger and more colorful sex). These physical differences are accompanied in phalaropes by reversed sex roles (see 'Phalaropes on land' below). During most of the time they are at sea, however, males and females do not differ in their plumage and cannot be distinguished (**Figure 1b** and **c**). Some researchers have suggested that measures of body size can be used to discriminate between male and female phalaropes; however, the discriminant functions developed for this purpose will only reliably identify large females. Small females overlap males in body size and cannot be distinguished from them with a high degree of certainty on the basis of body size alone.

Aquatic Adaptations

All phalaropes have similar adaptations for an aquatic lifestyle that are not shared by the other sandpipers. The form of the adaptations tends to be less pronounced in Wilson's phalarope, which is less aquatic in its habits.

Phalaropes swim by paddling, and their toes are bordered by flaps or lobes of flesh (**Figure 2**). These toe lobes are flexible: when the foot is drawn forward through the water, the lobes fold flat behind the toe, reducing drag; on the backstroke the lobes flare out, boosting thrust. Phalarope legs are laterally flattened, another modification that reduces drag as they swing their legs through the water.

As befits birds that spend their time swimming, phalaropes have waterproof feathers, with particularly dense belly plumage. Immersion in salt water may present a constant challenge for them: red-necked phalaropes at saline lakes avidly seek freshwater sources in which to bathe and drink. It is unknown whether they seek out microhabitats with less saline water at sea for the same purpose.

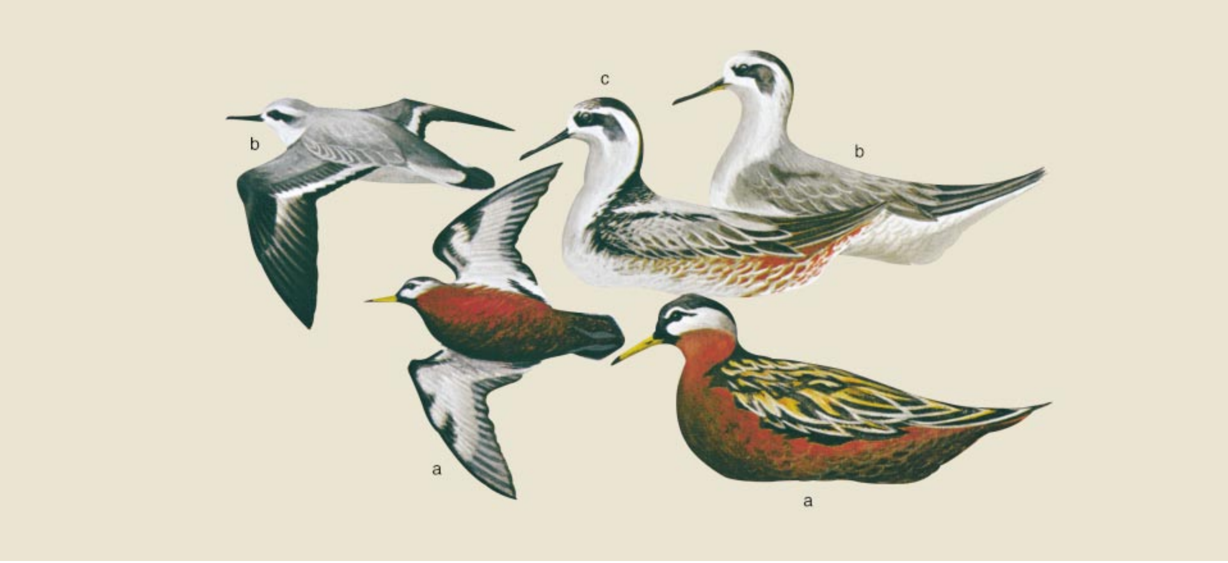

Figure 1 Examples of Phalaropes. Red phalarope (*Phalaropus fulicarius*). Other names: Grey Phalarope. (a) Adult female, breeding; (b) adult, non-breeding, both sexes; (c) adult, late summer/autumn. Length: 20 cm; wingspan: 37 cm; approximate body mass: 50 g. Range: Breeds throughout the Arctic and into the subarctic; migrates and winters throughout the North and South Atlantic Oceans, the North Pacific Ocean and the eastern South Pacific Ocean. Illustrations from Harrison P (1985) *Seabirds, an identification guide. Revised edition.* Boston, Massachusetts: Houghton Mifflin.

Figure 2 The lobed toes of phalaropes. These flaps of skin flare out to provide thrust when the bird is paddling through the water; they fold back around the toe on the upstroke to reduce resistance. Photo by author.

Retaining the hollow bones of more terrestrial birds, rather than the denser bones common in diving seabirds, phalaropes are very buoyant and ride lightly on the surface of the water. This buoyancy, combined with the air trapped in their dense belly feathers, makes diving very difficult for them. They dive shallowly and very seldom, generally only when pursued persistently by a predator at close range. When forced to dive, they quickly pop back to the surface.

Distribution

Phalaropes are pelagic during all but the short breeding season. Both red and red-necked phalaropes winter in or near the Humboldt Current, off the western coast of South America. Significant numbers of red phalaropes also winter off western Africa, and are found in the Pacific off the western United States from June through March. Red-necked phalaropes mix with reds off the western United States during migration, from July through early November. The Eurasian population of Red-necked phalaropes winters in the Arabian Sea, and from central Indonesia to western Melanesia.

Food and Feeding

Diet Phalaropes are planktivores, specializing on copepods, euphausiids, and amphipods. The marine phalaropes are size-selective; copepods taken apparently do not exceed 6 mm long by 3 mm wide. They also take almost anything else that is small and floats, including other crustaceans, insects, invertebrates (including hydrozoans, molluscs, polychaetes, and gastropods), small fish, and fish eggs. In addition, phalaropes regularly ingest nonnutritious materials, including small quantities of seeds, sand, feathers, and plastic particles.

Feeding behavior and mechanics Phalaropes are visual hunters. They typically swim in meandering, sinusoidal tracks, leaning forward and peering into the water. They peck at prey on, or just beneath, the water's surface, and where prey densities are high their peck rates may climb to 180 pecks per minute. They will occasionally seize a flying insect from the air or, rarely, catch aquatic organisms by rapidly swiping the bill sideways through the water in a motion known as scything. Unlike other planktivores, phalaropes are not filter feeders; they capture zooplankton one at a time, tweezering them out of the water between the tips of their beak.

When prey are successfully seized, red-necked phalaropes use the surface tension of water to move their tiny catch from the tip of their beaks to their mouths (**Figure 3**). They accomplish this by suspending a drop of water containing the prey between their upper and lower jaws. Since water molecules are attracted to one another, drops of water tend to assume shapes with the tightest packing of molecules, i.e., shapes with the least possible surface area. Work is required to pull enough molecules out of the center of the drop to make new surface area; the amount of work required in any particular instance of water temperature and salinity is a measure of the surface tension of water. Feeding red-necked phalaropes open their jaws; this action stretches the prey-containing drop, increasing its free surface area. Once the drop is stretched, the surface tension of the water drives the drop, and the prey it contains, to the back of the jaws, where the free surface area is minimized and the prey can be swallowed. This method of transporting prey, called 'surface tension feeding', can be completed in as little as 0.02 s. Wilson's phalaropes also use this method of prey transport; the feeding mechanics of red phalaropes have not been studied in detail.

When prey are below the surface, a bird may submerge its head and neck or (even more rarely) up-end, but a more typical response to prey deep in the water column is a conspicuous toplike spinning. All the phalaropes engage in this behavior; indeed, it is probably their best-known characteristic. Old accounts of their behavior attributed spinning variously to courtship behavior or stimulation of prey in cold water, but most authors suspected that spinning functioned to 'stir up' prey from the bottom of ponds and pools. This explanation was based on observations of birds on small ponds near breeding areas, and did not account for phalaropes spinning while at sea, when the bottom was hundreds of meters below.

Spinning does produce subsurface water flow that concentrates and lifts prey nearer the bird, but not by creating flow against the bottom. The whirling motion is produced by kicking harder and with higher frequency with the outer leg than with the inner leg. (Observations of captive phalaropes indicate that individuals are 'handed' — birds spin both clockwise and counterclockwise, but each individual only spins in one direction.) Birds spin around at about one complete rotation per second. This rapid cycling kicks water at the surface away from the axis of the bird's rotation. This deflection of surface water generates an upward-momentum jet of subsurface water; in other words, phalaropes make their own small upwellings in the center of the area they are circling by pushing surface water away so quickly that subsurface water must flow upward to replace it.

Birds watch this area of upwelling for rising prey in essentially the same way that a spinning ballerina keeps from falling over. They fix their gaze on one spot, holding their heads immobile until their rotating bodies force head movement, then they snap their heads one-quarter of a turn while still looking at the same spot. Birds can generate flows to as deep as 0.5 m, and each cycle of the spin is slightly off to the side of the previous one, so that birds slowly progress, and process water, along a track about one body length wide. As can be imagined by

Figure 3 Surface tension feeding in a red-necked phalarope. Phalaropes use this feeding mechanism to transport tiny prey to the mouth, where it can be swallowed. Jaw-spreading (also called mandibular spreading) stretches the drop; the surface tension of the water drives the drop to the back of the beak, where it will have the smallest possible free surface area. (Reproduced with permission from Rubega MA and Obst BS (1993) Surface tension feeding in phalaropes: discovery of a novel feeding mechanism. *Auk* 110: 169–178.)

anyone who has ever carried water in a bucket, lifting water is an energetically expensive proposition for a phalarope: about twice as expensive, per unit of water inspected, as simply swimming in a straight line to feed. Hence, they should only spin when absolutely necessary, and they generally select pelagic habitats in which spinning is unnecessary.

Habitat

The pelagic biology of phalaropes appears to revolve around food. Although the marine phalaropes spend the majority of their life cycle at sea, they do not breed in oceanic environments. Thus, unlike other marine birds such as petrels or penguins, their use of the ocean is not influenced by factors such as access to islands with nesting sites. This freedom to concentrate on prey shows in their relationship to physical structure in the ocean. Although they occasionally take small fish, phalaropes are fundamentally planktivores, and their habitats at sea are characterized by features of the ocean that concentrate and bring to the surface dense concentrations of zooplankton. They are commonly found at fronts, thermal gradients, convergences, upwellings, and slicks. Up to two million migratory birds have been estimated at a single upwelling near Mount Desert Rock off the Maine coast. Red-necked phalaropes in migration use a wide variety of aquatic habitats and are consistently associated within them with small-scale hydrographic features. At Mono Lake, in eastern California, red-necked and Wilson's phalaropes concentrate their feeding activities in areas where currents help to raise prey to the surface, and at drift lines where prey are concentrated.

When physical oceanography fails them, phalaropes make use of other marine organisms to locate and gain access to food. The few phalaropes found in the outer continental and slope domains of the South Atlantic Bight off the eastern coast of the United States are associated with mats of *Sargassum* seaweed, which are themselves the product of convergences. Red phalaropes associate with feeding whales and schools of fish that force plankton to the surface incidental to their feeding activities. The relationship of red phalaropes to whales is sufficiently dependable that whalers formerly used them as an indicator of the presence of whales. There are even reports of phalaropes picking parasites off the backs of whales. They are sometimes parasites themselves: red-necked phalaropes commonly dash in to seize prey that have been spun to the surface by the effort of another phalarope.

Phalaropes on Land

All oceanic birds must make landfall to breed and reproduce, and phalaropes are no exception. The marine phalaropes are essentially on land only during the brief breeding season; red-necked phalaropes also migrate over land to some extent, and are especially numerous on saline lakes (see 'Movements' below). In contrast, Wilson's phalaropes are almost entirely continental in their distribution, albeit more aquatic in their habits than most shore birds. What follows is a brief summary of the biology of phalaropes on land, and its bearing on their life at sea. Readers with an interest in the breeding biology of phalaropes will find more detail in works listed in the bibliography.

Appearance

Each species of phalarope has an extremely colorful, distinctive appearance during the breeding season, with striking patterns of black, gray, and red or rusty markings on the neck and face (**Figure 1a**). They are easily distinguished from one another and from other shore birds. All phalaropes exhibit reverse sexual dimorphism; females are more sharply and brightly colored than males when breeding. On average females are also larger.

Breeding Behavior

The breeding behavior of phalaropes is notable for the degree to which it is conducted on water. The nest may be on land, but most significant behavioral components of breeding are carried out on the waters of small pools and ponds. Breeding displays and fights over mates usually occur on the water, as do the resulting copulations. This is in contrast to most oceanic birds, which return to land in order to engage in these behaviors.

Phalaropes also differ from other oceanic birds in their unusual breeding system. First, in an arrangement that is rare for any bird, the roles of the sexes are reversed; females compete vigorously with one another for males, and provide no care for eggs or chicks, while males build the nest, brood the eggs, and care for the young when they hatch. Second, phalaropes, like most seabirds, are usually monogamous, but they differ in being polyandrous when the opportunity arises. When more males than females are present, females will breed with more than one male in a single season; female red phalaropes have laid second clutches of eggs within a few hundred meters of their first mate's nest. Whether monogamous or polyandrous, females normally leave a male after having laid the last of the

3–4 eggs in the clutch. Chicks hatch after about 20 days of incubation, can walk and swim a few hours later, and fledge within about 20 days. Although the male tends them, they feed themselves, and may become completely independent before they are able to fly.

Unlike many oceanic birds, phalaropes do not breed colonially, although pairs may breed in relatively close proximity when habitat is limited; the density of nests at any one site is highly variable from year to year. They show little tendency to return to any particular breeding site, or to the site where they were hatched. Red phalaropes will exploit the aggressive nature of colonial birds to ward off predators, by nesting in the colonies of other seabirds such as Arctic terns (*Sterna paradisaea*).

Distribution

The marine phalaropes breed in tundra habitats circumpolarly in Arctic and sub-Arctic, along coasts of the Arctic Ocean. The red-necked phalarope breeds farther south, and further into the interior of Eurasia, Alaska, and northern Canada than does the red phalarope. Red-necked phalaropes also breed in small numbers in the Aleutian Islands, Scotland, and Ireland. The nonpelagic Wilson's phalarope, in contrast, breeds only in the Nearctic, primarily in the interior of western North America.

Food and Feeding

Diet During the breeding season phalaropes essentially remain planktivores, eating small aquatic prey, especially the larvae of dipteran flies. However, on the breeding grounds their diet expands to contain adult dipteran flies (which they snap out of the air), mosquito larvae, dragonfly nymphs, water boatmen, backswimmers, caddisflies, beetles, bugs, ants, spiders, mites, snails, crustaceans, molluscs, and annelid worms. When food is limited they may eat seeds and other plant materials.

The diets of red-necked phalaropes at saline lakes consist almost entirely of brine flies, with third-instar larvae predominating, plus adult and larval dipterans. Brine shrimp are very abundant at saline lakes but are rarely taken by red-necked phalaropes. This lack of interest is the product of a nutrient limitation; captive birds are reluctant to eat brine shrimp, and those restricted to a brine shrimp diet lost about 5% of their body weight while eating three times their body weight over a 12-hour period. In contrast, Wilson's phalaropes do eat significant amounts of brine shrimp at saline lakes; their ability to extract nutrition from them has not been investigated in detail.

Movements

All phalaropes are migratory; they differ chiefly in the degree to which they move over land versus sea. Red phalaropes virtually always migrate pelagically; red-necked phalaropes migrate over both land and ocean; Wilson's phalaropes are thought to migrate southward over the Pacific after leaving North America, apparently without ever landing on the water, while the north-bound migration occurs almost entirely over land. In all three species the timing of movements is similar: nonbreeding birds of both sexes leave the breeding grounds first, followed consecutively by females, males, and juveniles.

The migration of red phalaropes is perhaps least well understood, since it is least easily observed. What is known about their migratory routes is inferred as much from information about where they are not seen as from sightings of them on the move. Nearctic breeders winter off western and southwestern Africa. Until recently large flocks occurred in the western Bay of Fundy during migration (see Conservation and Threats), but few have been seen farther south near the western Atlantic coasts. Thus, they presumably fly directly across the Atlantic to their destinations off the African coast after leaving the Bay of Fundy. Many red phalaropes winter in the Humboldt Current, off western South America, and large flocks are present during migration off the Pacific coast of North America. Sightings of red phalaropes in the central Pacific Ocean during the migratory period indicate that those breeding in the Siberian Arctic cross the Pacific to winter in the Humboldt current.

Red-necked phalaropes mix travel over land and sea to a much greater extent. Those breeding in Europe and western Siberia move through the Caspian Sea and overland via lakes across the former Soviet Union and Iran to arrive at their Arabian Sea wintering grounds through the Gulf of Oman. Birds that have bred in Fenno-Scandinavia move southeast through the gulfs of Bothnia and Finland. Breeding populations from eastern Siberia migrate overland and offshore of Japan to winter in the East Indies. Nearctic populations move south across Canada and the western United States, where tens of thousands stop at hypersaline lakes, along with smaller numbers at every conceivable body of water in their southward path; from these lakes they move out to sea and south to their wintering grounds at the northern edge of the Humboldt Current. Huge flocks estimated at 2 000 000 individuals occurred in the Bay of Fundy until recently (see Conservation and Threats), and these may include birds from

Table 1 The diversity of names for phalaropes

	Red phalarope	*Red-necked phalarope*	*Wilson's phalarope*
Other common names	Grey phalarope Red coot-footed tringa	Northern phalarope Hyperborean phalarope Cock coot-footed tringa	
Present scientific name	*Phalaropus fulicaria*	*Phalaropus lobatus*	*Phalaropus tricolor*
Previous scientific names	*Tringa fulicaria*	*Tringa tobata/lobata* *Lobipes lobatus*	*Steganopus tricolor* some authorities have resurrected this name for Wilson's phalarope
Synonymous scientific names	*Phalaropus glacialis*, *rufus*, *platyrhynchus*, *rufescens*, *griseus*, *cinereus*	*Lobipes hyperboreus*, *anguirostris*, *antarcticus*, *fuscus*, *ruficollis*, *tropicus*, *vulgaris*	*Steganopus wilsoni*, *incanus*, *frenatus*, *stenodactylus*

Greenland, Iceland, and the Nearctic. Where these birds winter is a mystery; they do not winter off western Africa with the red phalaropes with which they mingle in the Bay of Fundy, and only small flocks of red-necked phalaropes have been seen farther south in the western Atlantic in the winter. It has been suggested that they may fly to the Humboldt Current via routes crossing the Caribbean and Central America, but no more than a few red-necked phalaropes have been seen in these areas.

Systematics

The names and scientific classifications of phalaropes have histories nearly as colorful as the birds themselves (in South America, red-necked phalaropes are called 'pollito del mar,' roughly 'little chicken of the sea'). Both common and scientific names have changed repeatedly (**Table 1**). Each species was once considered to form a distinct genus, and was given a separate Latin first name (*Phalaropus*, *Lobipes*, and *Steganopus* for red, red-necked, and Wilson's phalarope, respectively). Subsequently, and for many years, the phalaropes have been placed in a single group in the family Scolopacidae (sandpipers), subfamily Phalaropodinae, genus *Phalaropus*.

The idea that all the phalaropes descended from a single common ancestor is sometimes disputed. Analyses of both their genetic material and skeletons showed that red and red-necked phalaropes are each other's closest relatives. Analyses of skeletal materials united the more distantly related Wilson's phalarope to the other two in a single group, but genetic analyses do not unambiguously support the idea that all three phalaropes belong to a single group. Both kinds of evidence indicate that phalaropes are either closely related to the Tringine or Scolopacine sandpipers. Thus, their scientific classification has recently depended on the authority consulted. For example, Sibley and Monroe's 1993 taxonomy of birds, based on DNA–DNA hybridization studies, put the phalaropes in the subfamily Tringinae, with red and red-necked phalaropes in the genus *Phalaropus*, and Wilson's phalarope returned to the genus *Steganopus*. The American Ornithologists' Union continues to classify them in a single genus *Phalaropus*, in the subfamily Phalaropidinae.

Conservation and Threats

Population Status

Phalarope populations are not thought to be threatened on a global scale, but their status is poorly known. Thus, significant population declines would be difficult to document with any degree of certainty. This lack of information arises from the peculiar life history of phalaropes; most seabirds are counted at their breeding colonies, while most shore birds are counted at migratory staging areas or wintering grounds because they do not nest in colonies. Phalaropes do not nest colonially, and in the nonbreeding season gather far out at sea, where it is difficult to find and count them.

Local declines of breeding birds have been documented; for instance, red-necked phalaropes no longer breed anywhere in Britain apart from in Scotland and Ireland (and there only irregularly) because of egg collecting in the nineteenth century. Breeding populations elsewhere are largely unstudied and, where they are monitored, information about population trends is equivocal. The population of male red-necked phalaropes at LaPerouse Bay, in Churchill, Manitoba declined by 94% between 1980 and 1993, but nesting densities have increased since 1981 near Prudhoe Bay, Alaska.

At sea, apparent declines are even more difficult to understand. The number of phalaropes staging for fall migration in the western Bay of Fundy declined from estimates of two million to almost nothing in the mid-1990s. This disappearance may represent a true population decline, or simply a shift of currents and prey, and thus of birds, to some as-yet undiscovered area of the Bay or the western Atlantic. Similar declines have been reported in the number of phalaropes seen off coastal Japan in spring. Limited evidence suggests that the numbers of birds passing through the Bay of Fundy during spring migration is unchanged.

Threats

Compared to many oceanic birds, phalaropes probably face relatively few threats. Their breeding populations are widely distributed and thus, unlike those of many colonially nesting seabirds breeding on islands, are resistant to depredations of introduced predators. Their predators on the breeding grounds include raptorial birds such as pomarine and parasitic jaegers, mammals such as arctic and red foxes and short-tailed weasels, and chick and egg predators such as glaucous gulls, sandhill cranes, and arctic ground squirrels. They are safe from most of these when at sea. However, they are not invulnerable even at sea: four red-necked phalaropes were once found in the stomach of a common dolphin taken off Baja California, Mexico. With the exception of minor subsistence hunting by indigenous northerners, phalaropes are not hunted by humans and as surface-swimming planktivores, are not incidentally taken in fishing nets, as so many seabirds are. They are potentially vulnerable to spilled oil, particularly since oil and food particles may be concentrated at the same convergence zone.

As for all oceanic organisms, human-caused disruption and destruction of marine environments is likely the most serious threat facing phalarope populations.

See also

Baleen Whales. Copepods. Plankton and Climate. Seabird Foraging Ecology. Seabird Migration. Seabird Population Dynamics. Seabirds and Fisheries Interactions. Seabirds as Indicators of Ocean Pollution. Upwelling Ecosystems.

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PHOSPHORUS CYCLE

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Introduction

The global phosphorus cycle has four major components: (i) tectonic uplift and exposure of phosphorus-bearing rocks to the forces of weathering; (ii) physical erosion and chemical weathering of rocks producing soils and providing dissolved and particulate phosphorus to rivers; (iii) riverine transport of phosphorus to lakes and the ocean; and (iv) sedimentation of phosphorus associated with organic and mineral matter and burial in sediments (**Figure 1**). The cycle begins anew with uplift of sediments into the weathering regime.

Phosphorus is an essential nutrient for all life forms. It is a key player in fundamental biochemical reactions involving genetic material (DNA, RNA) and energy transfer (adenosine triphosphate, ATP),