Seabirds of Hawaii

Natural History and Conservation

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To Mom and Dad

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7 FEEDING ECOLOGY

The forage fish frantically try to elude the large billfish, skipjack, and yellowfin tunas. Gathering in thronging legions to feed on countless tiny plants and animals that are seasonally available, the balls of small goatfish and mackerel scad wheel and dart in the currents. They are easy pickings for the vast undersea convoys of migratory fish that venture north into Hawaiian waters during spring and summer to devour them. Silvery bodies erupt from the surface in wave after wave, then strike the water like the burst of a sudden squall. Here and there the water boils where pursuers slash through the school. Like exocet missiles, flyingfish and halfbeaks propel themselves on outstretched pectoral fins in all directions, skimming just above the surface. But escape is not so easy. The air is filled with fluttering wings and querulous cries as interlopers enter the piscine world. Plunging from above, snatching up bait fish by the thousands, seabirds converge to join in the carnage. Natural history writers long ago remarked on similar phenomena. Thomas Pennant's *Arctic Zoology* in 1785 described seabirds "watching the motions of the flying fish, which they catch when these miserable beings spring out of their element to shun the jaws of Coryphenes (dolphinfish)."

Seabirds are genuine marine creatures. They spend most of their lives at sea, earning a living from the ocean's resources. In many ways Hawaiian seabirds are truly "flying fish" because their feeding ecology is remarkably similar to that of all organisms that inhabit the epipelagic or surface waters of the sea. Food supplies, like the availability of breeding grounds, can place upper limits on seabird populations. Competition within the Hawaiian seabird community has resulted in a partitioning of food resources, and a comparison of seabird diets indicates that each species has developed its own individual food spectrum.

Although some overlap is inevitable in such a simple ecosystem, diets differ by prey species, proportions of common prey items, and size of prey. Of course, each diet is strongly influenced by where, when, and how the species feeds. Tropical seabirds are extremely opportunistic and consequently their diets are far more diverse than those of their counterparts in temperate- and cold-water ecosystems. The quantities of marine organisms consumed by Hawaiian seabirds each year greatly exceed the tonnage landed by Hawaiian fishermen.

Diets and Feeding Behavior

The twenty-two seabirds that breed in Hawaii feed on a wide variety of shoaling fishes, squid, and crustaceans, apparently taking anything they can find in surface waters which they can swallow. Their diets are complex. In a study of the species that breed in the Northwestern Hawaiian Islands, Thomas S. Hida and Michael P. Seki of the National Marine Fisheries Service's Honolulu Laboratory identified eighty-six genera of fish, eight families of squid, and eleven groups of crustaceans. Because we obtained the food samples by inducing birds to regurgitate their stomach contents, samples were usually partially digested and it was impossible to identify the species of many of the half-digested fishes and squid. Hawaiian seabirds probably eat several hundred species of marine organisms.

The diversity in selection of food is underscored by the fact that no single prey species accounts for as much as half of the diet of any seabird. Juvenile goatfishes, the most commonly eaten prey of many birds, do not make up a high proportion of any diet. They account for one-seventh of the diet of brown boobies, one-sixth for wedge-tailed shearwaters, one-fifth for white terns, and between one-fourth and one-third for brown and black noddies. No doubt these fractions would drop considerably if it had been possible to identify which of the ten species of Hawaiian goatfishes were found in the food samples. The most specialized diets are those of gray-backed terns (40 percent five-horned cowfish) and black-footed albatrosses (40 percent flyingfish eggs, but the flyingfish eggs represent at least two species). Many Hawaiian seabird diets include between twenty and forty families of prey species, in sharp contrast with the diets of seabirds in Alaska, Antarctica, and Scotland, which typically include only a handful of fishes or a single crustacean. Diet diversity in Hawaii is probably related to the patchy distribution of prey in tropical waters.

The opportunism of Hawaiian seabirds' feeding strategies is strikingly seen among blue-gray noddies. These small seabirds eat some of the largest fishes, occasionally even dolphinfishes and blue marlins. Naturally they eat the smallest larval forms of such giant fishes, but the parentage of fish fry is of no concern to a hungry noddy when it patters along the sea surface in search of anything it can grasp with its beak. Many prey organisms are taken only during certain months or only offshore certain islands, probably a reflection of seasonal occur-

rence. Because state-of-the-art oceanographic techniques do not permit the measurement of absolute abundance of marine creatures in the water column, biologists can only infer that prey that is eaten exclusively during certain months is locally or seasonally abundant in surface waters. Much of the variation in diets among seabirds results from the proportions of several common organisms that account for most of the food consumed by the Hawaiian seabird community. Flyingfishes, flying squid, mackerel scads, juvenile goatfishes, juvenile Forster's lizardfish, and several midwater fishes provide the bulk of the Hawaiian seabirds' food. Birds readily supplement this diet whenever other prey is available. While flyingfishes and flying squid are common in the diets of tropical seabirds throughout the world, tropical seabirds elsewhere rarely eat goatfishes, lizardfishes, mackerel scads, or midwater fishes.

Hawaiian seabirds have developed the strategy of consuming a mixed portfolio of prey species because it is impossible to rely on the availability of any particular fish or squid. William Beebe's observations of a lava flow in the Galápagos reveal the opportunism of seabirds in tropical waters:

> As molten lava reached 3000°, the ocean under the cliffs was literally boiling. A sea lion flung itself in agony from the scalding immersion, five times leaping all clear, and then seen no more. Shearwaters and frigatebirds stooped through the vapor to snatch at fish floating in the gigantic cauldron, and we saw dead petrels and shearwaters that had ventured once too often to this tempting feast.

Over the millennia, the individual birds that diversified their approaches to foraging are those that survived periodic food shortages in the unpredictable Hawaiian marine environment. The birds that eat anything are the survivors of the natural selection process. Birds that have been too finicky have joined the dinosaurs.

Hawaiian seabirds can be divided into five feeding guilds, or groups of species with closely related feeding requirements. The concept of a feeding guild groups species in accordance with ecological requirements rather than taxonomy, although taxonomy does have an important influence on the feeding habits of Hawaiian seabirds. The guilds consist of (1) albatrosses, (2) Pelecaniformes, (3) tuna birds, (4) nocturnal petrels, and (5) neuston-feeding terns. Birds within each guild have similar feeding strategies and similar diets, and eat prey of similar sizes. Because Hawaiian seabirds feed so opportunistically, their feeding habits are difficult to categorize. A focus on feeding guilds emphasizes the most common prey taken and the most common feeding methods used by each species.

Albatrosses

Each of the three North Pacific albatrosses feeds by sitting on the surface of the water and seizing prey (Figure 11), often in flocks with other albatrosses but

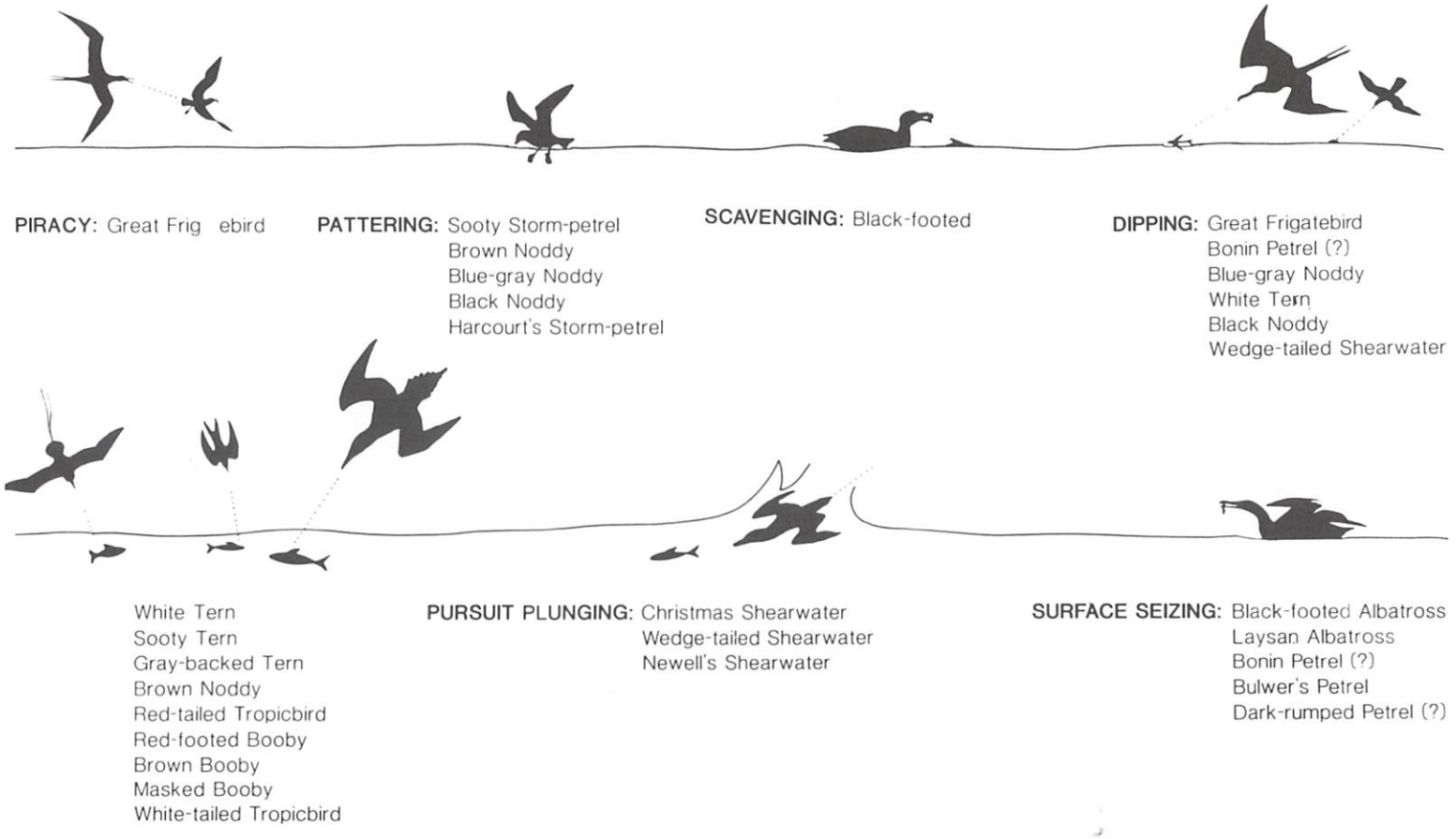


Figure 11. Feeding methods of Hawaiian seabirds

rarely with other types of seabirds. Albatrosses use their powerful bills to tear and shred large prey. Black-footed and Laysan albatrosses eat primarily squid, flyingfish eggs, and deep-water crustaceans (Figure 12). The diet of short-tailed albatrosses is less well known, but includes squid, fish, and shrimp. All Hawaiian albatrosses scavenge naturally occurring carrion or refuse from ships, but black-foots have developed this behavior into a fine art. They are not always fastidious in their selection of floating refuse. Stomachs contain such late-twentieth-century flotsam as plastic chips, rubber, styrofoam, sponges, nylon fishing line, and paper wrappers.

Eight squid families are eaten by albatrosses. Surface-dwelling flying squid are by far the most common, but most squid recovered are too well digested to be identified. When biologists develop better techniques to identify semi-digested squid, it will be possible to learn whether Laysan as and black-footed albatrosses consume different species. The proportions of fish and squid consumed by the two albatrosses are quite different. Laysans eat twice as much squid as black-foots, which eat eleven times as many flyingfish eggs as Laysans. Such differences probably result from their feeding times: Laysans tend to feed at night and black-foots during daylight hours. Both species forage in the waters north of the Northwestern Hawaiian Islands, much farther offshore than other Hawaiian seabirds. Their cool-water feeding locations imply that Hawaiian albatrosses are actually temperate species that have a somewhat tenuous relationship with the tropical marine environment.

Waved albatrosses in the Galápagos are the only other tropical albatrosses. Like Hawaiian birds, waved albatrosses eat primarily squid, fish, and deep-water crustaceans. However, they eat different squid families and do not eat flyingfish eggs. Albatrosses' feeding strategies in Hawaii and the Galápagos are similar, so dietary differences are probably due to local differences in prey species.

Pelecaniformes

The birds that make up the guild of Pelecaniformes—three boobies, two tropicbirds, and the great frigatebird—form a convenient ecological unit apart from their close taxonomic relationship. Boobies and tropicbirds plunge-dive to pursue underwater fish and squid (Figure 11) to depths of several meters. Great frigatebirds are restricted to snatching prey no more than a beak's length beneath the ocean's surface because of their structural inability to take flight from the water if they land. At sea, pelecaniforms rarely associate with one another, but frigatebirds and masked and red-footed boobies sometimes feed in flocks with sooty terns and wedge-tailed shearwaters, especially off the coasts of Central America. Brown boobies and tropicbirds are strictly solitary feeders. Most of these birds feed in deep water, but brown boobies forage inshore, often just beyond the shoreline. Red-footed boobies are especially pelagic and are found 100 to 150 kilometers from their breeding colonies.

These birds consume much larger prey than other Hawaiian seabirds. Adult

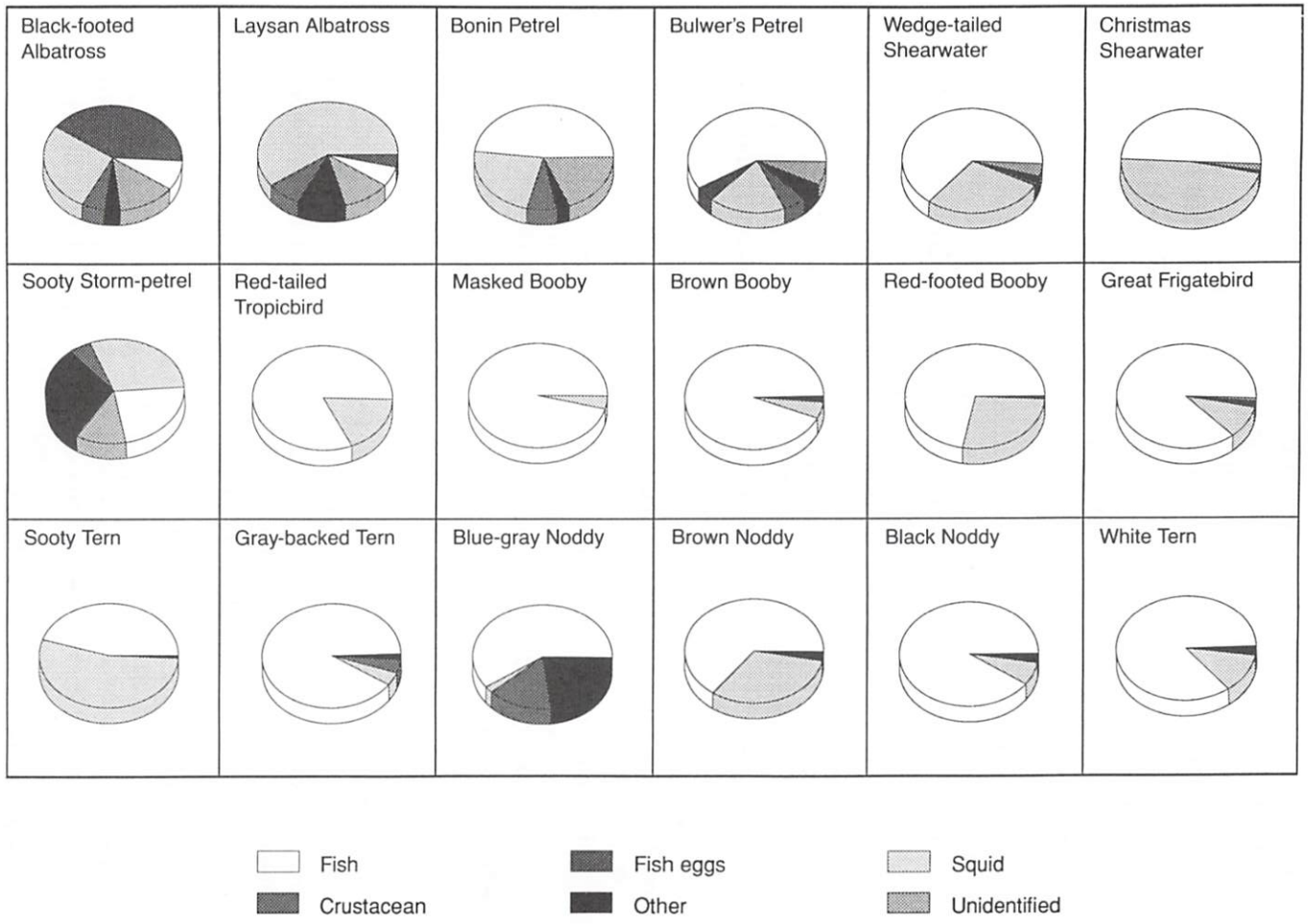
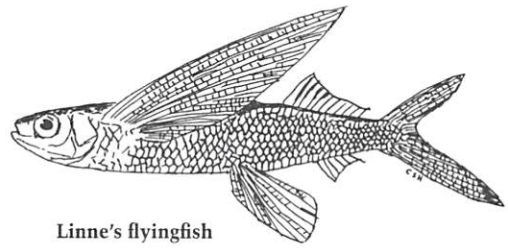


Figure 12. Diets of Hawaiian seabirds



Linne's flyingfish

flyingfishes (especially Linne's flyingfish and *Cypselurus* spp.) are the most common prey, but adult mackerel scad, adult halfbeaks, and juvenile flying squid also account for a substantial portion of their diets (Figures 12 and 13). The proportions and sizes of the major prey items differ substantially among the pelecaniforms. Masked boobies take the largest, including commercially valuable fish longer than twenty centimeters. Other birds eat prey between eight and fifteen centimeters, although brown boobies eat many juvenile goatfishes that are much smaller. Red-footed boobies eat much more squid than brown boobies do—an important difference between all pelagic and nearshore feeding species. As might be predicted by their surface feeding habits, flyingfishes are especially common in the diet of great frigatebirds. Some prey species are taken seasonally or exclusively at a single atoll. Red-footed boobies and red-tailed tropicbirds eat large amounts of Pacific sauries at Midway and Kure during winter, when sauries move south with the cool North Pacific water masses. Red-tailed tropicbirds take many truncated sunfish, an open-ocean fish that is rarely taken by other seabirds, during summer at French Frigate Shoals.

The diets of Hawaiian pelecaniforms are broadly similar to the diets of boobies, tropicbirds, and frigatebirds at Ascension, Christmas, the Seychelles, Rose Atoll, and the Galápagos, where flyingfishes and flying squid are also common components of the diet. Brown boobies everywhere eat a wide variety of inshore and reef fishes. The diets of Hawaiian pelecaniforms are distinguished by the prominence of juvenile goatfishes and adult mackerel scad, which are seldom eaten elsewhere.

Tuna Birds

Tuna birds form a large and complex foraging guild in Hawaii. It comprises seven species, including some of the world's most common tropical seabirds: sooty terns, wedge-tailed shearwaters, Christmas shearwaters, Newell's shearwaters, brown noddies, black noddies, and white terns. Tuna birds forage in large flocks over feeding schools of tunas, dolphinfish, porpoises, whales, and other large predators that drive smaller prey organisms to the surface, thus making them available to seabirds. Most feeding flocks in Hawaiian waters are associated with schools of skipjack tunas. David Au and Robert Pitman have learned that flocks in the eastern tropical Pacific feed with groups of yellowfin

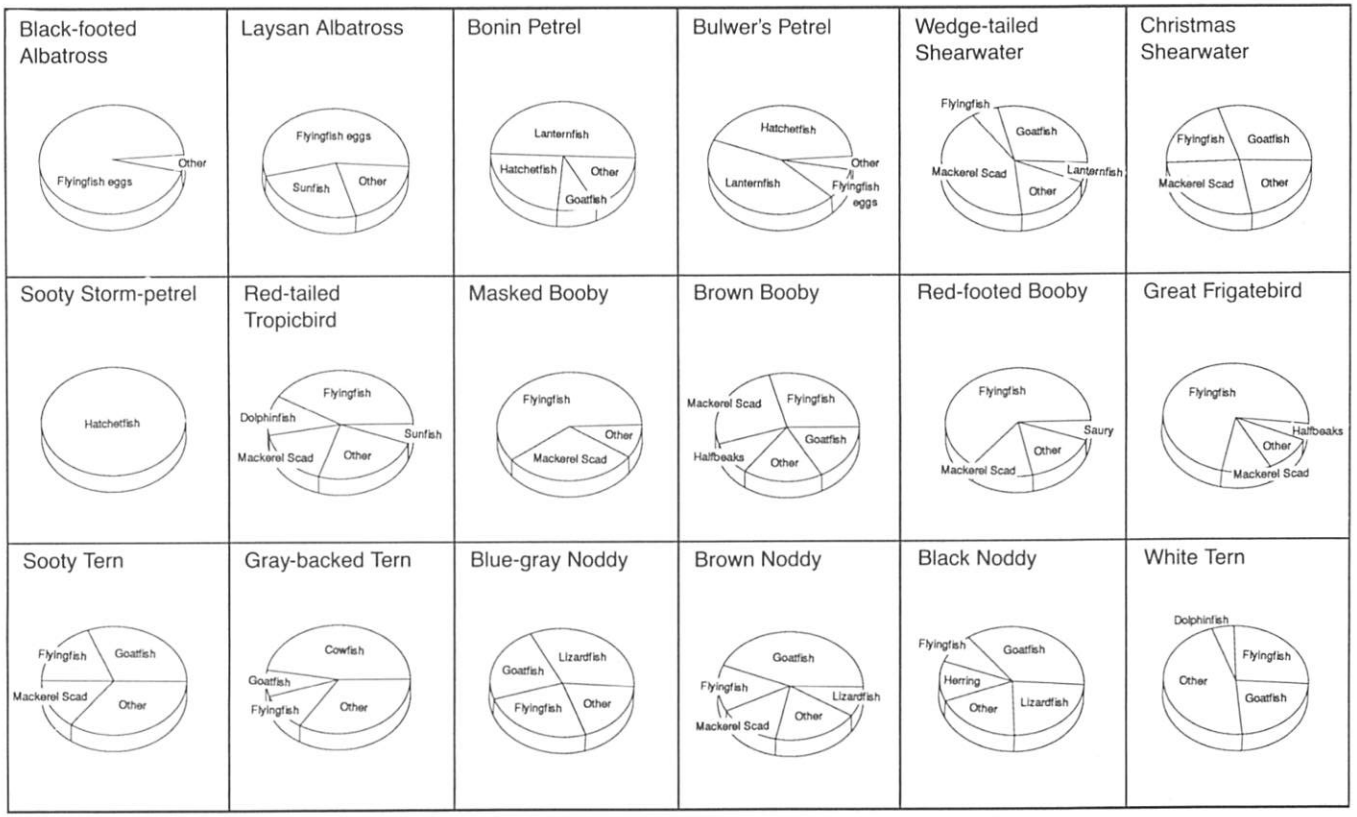


Figure 13. Proportions of fishes consumed by Hawaiian seabirds

tunas combined with spotted and spinner dolphins. Tuna birds rarely feed in the absence of fish or mammal schools and may depend on them to survive. Within a feeding flock, tuna birds use a wide variety of feeding methods to secure their prey, both on and beneath the water's surface (Figure 11). For centuries, probably as far back as the earliest Polynesian immigrants, Hawaiian fishermen have used the distinctive feeding patterns of seabirds as clues to the identity of schools of fish. When seabirds are active low over the water, they usually are feeding over skipjacks. If the flock alternates between low and high altitudes, they are probably following the deeper-foraging yellowfins. Wedge-tailed shearwaters and brown noddies fly near the surface of the water, while white and sooty terns fly much higher. As periods between surfacing fish schools become longer, the flock disperses and sooty terns fly higher and higher to act as the eyes of the flock. From distances up to eight kilometers, fishermen recognize the flash of white when sooties bank en masse from horizontal flight to make swooping dives on surfacing fish.

Tuna birds differ in their capabilities to exploit food far offshore. Sooty terns and shearwaters can forage farthest offshore, their range eclipsing that of the brown noddies. Black noddies and white terns usually feed inshore, yet some white terns are regularly seen far out at sea. All species feed on similar prey items of similar size, which are substantially smaller than prey taken by pelecaniforms. Juvenile forms of goatfishes, flying squid, mackerel scad, and flyingfishes are the primary prey consumed (Figures 12 and 13). Black noddies and to a lesser extent white terns forage with jacks and nearshore little tunas. Feeding flocks are sometimes seen hovering over jacks within a few meters of the shoreline. Inshore-feeding white terns and black noddies eat more herrings and juvenile Forster's lizardfish and somewhat fewer mackerel scads and flying squid than the others in this guild. The five remaining birds feed offshore and consume between one-third and one-half flying squid. Tuna birds select prey between three and eight centimeters long. Like all Hawaiian seabirds, they are opportunistic, and their diets change with the local availability of prey. Squirrelfish are a substantial component of sooty tern diets only during summer in the northern portion of the archipelago, but rarely are eaten elsewhere. White terns and brown noddies eat anchovies only during fall at Midway. Wedge-tailed shearwaters feed largely on gobies during fall at Manana Island, Oahu.

Given the close relationship between tuna birds and predatory fishes, it is no surprise that the birds and fishes have similar diets. There is a considerable degree of overlap among the diets of sooty terns, wedge-tailed shearwaters, skipjack tunas, and dolphinfish, both in the types and the sizes of prey taken. There is less overlap between those of tuna birds and yellowfin tuna, probably because yellowfins usually forage well below the surface. In contrast to tropical seabirds at Ascension, Christmas, and the Seychelles, tuna birds in Hawaii feed on larger proportions of fish than squid. Hawaiian birds also consume fewer flyingfishes than birds elsewhere, substituting goatfishes and mackerel scad.

Nocturnal Petrels

Bonin petrels, dark-rumped petrels, Bulwer's petrels, Harcourt's storm-petrels, and sooty storm-petrels seem to feed extensively at night. Because of their nocturnal habits and the consequent difficulties of observing them, their feeding techniques are only partially known. The three true petrels probably forage by sitting on the water and seizing prey from the surface, but Bonin petrels may also feed by dipping (Figure 11). All storm-petrels feed by pattering on the surface and do not submerge their bodies. Nocturnal petrels feed offshore, usually alone but occasionally in the company of other seabirds. They feed largely on squid, hatchetfishes, and lanternfishes (Figures 12 and 13). Most of their prey possess photophores, tiny light-emitting organs that can act as beacons to hungry birds, and rise to surface waters only at night or twilight. Food samples from nocturnal petrels are often so well digested that precise identification is impossible.

Differences in the locations of their colonies and in their breeding seasons minimize competition for food among nocturnal petrels. Bulwer's petrels, dark-rumped petrels, and Harcourt's storm-petrels breed during summer, Bonin petrels and sooty storm-petrels in winter. Dark-rumps and Harcourt's are restricted to the main islands, where the other species are rare. True petrels generally take larger prey than storm-petrels and take a higher proportion of fish than squid. The food habits of this guild are poorly known at other tropical locations, but Hawaiian petrels seem to eat higher proportions of fish than petrels elsewhere.

Neuston-Feeding Terns

The feeding habits of gray-backed terns and blue-gray noddies are unlike those of any other Hawaiian seabirds. Their diets are somewhat similar and consist of small prey obtained close to the islands. Blue-gray noddies feed in pure flocks, dipping and pattering at the surface. Unlike other Hawaiian terns, they do not depend on schools of predatory fishes to drive prey to the surface. Gray-backed terns are sometimes observed feeding at sea but probably do not feed with fish schools. They feed by plunging and occasionally associate with other terns and shearwaters.

The diets of blue-gray noddies and gray-backed terns are remarkable for the absence of squid (Figure 12). The most common prey organisms include sea striders (a marine insect), crustaceans, and juvenile forms of five-horned cowfish, flyingfishes, goatfishes, and Forster's lizardfish. Their diets vary widely in the proportions of several key organisms. Gray-backed terns eat many more cowfish, while blue-gray noddies consume more sea striders and lizardfishes. Competition is avoided to some degree by differences in breeding season: blue-grays feed most of their young two months earlier in spring than gray-backs. Furthermore, their breeding ranges overlap only on Nihoa and Necker. The food habits of blue-grays have been studied on Christmas Island, where diets are

Sea strider (*Halobates sericeus*)

somewhat similar in the importance of sea striders and minute crustaceans. However, the families of fish consumed on Christmas are quite different from those eaten in Hawaii.

Hawaiian seabird diets change with both season and island, but most variation is associated with season. In the large number and variability of their prey these birds contrast sharply with seabird communities in cold-water ecosystems. Eighty percent or more of the food of the huge seabird community off Peru consists of a single fish, the Peruvian anchovy. Many Antarctic penguin colonies have a similar dependence on krill. Seabird colonies off the coasts of Namibia and South Africa depend on but three fishes: pilchard, anchovies, and horse mackerel. Seabirds in Alaska and Scotland have relatively simple diets and gear their summer breeding strategies to take advantage of the superabundance of a few species of fish and crustaceans.

Avoidance of Competition

The simplicity of the tropical marine environment results in a great deal of overlap among the diets of the twenty-two Hawaiian seabirds. Flyingfishes, flying squid, and mackerel scad figure in virtually every diet. Yet some birds specialize in prey that others ignore. Blue-gray noddies eat large numbers of sea striders, a minute insect with an indigestible exoskeleton and fairly high levels of cadmium. Gray-backed terns eat large quantities of juvenile five-horned cowfish, a peculiar spined fish that may exude poison from its skin. Each diet has unique aspects that distinguish it from those of other birds in the community. Hawaiian seabirds have developed unique niches over the millennia by employing several mechanisms to avoid competition with one another. Some means may be important only during times of food stress, when competition among the birds could become acute. During most summers, food is probably abundant, and dietary overlap increases when birds take advantage of common prey. As most species feed their chicks in spring and summer, these are probably the seasons when demand for food is at its height, with resultant depletion of prey in the waters surrounding the colonies. Adults must obtain food both for growing chicks and for themselves. They are more constrained with regard to distant feeding locations now than at any other time of the breeding cycle because growing chicks must be fed frequently.

One means for a bird to avoid competition is to feed at a different time of day

than other species. Several species have developed eye modifications that enhance nocturnal vision and feed at night. They thus can exploit a completely different class of prey than daytime feeders. Hatchetfishes, lanternfishes, bristlemouths, many species of squid, and some crustaceans migrate vertically in the water column, remaining deep beneath the surface during daylight hours but rising to the surface at night. Many of these creatures possess photophores. By feeding at night, nocturnal petrels and Laysan albatrosses have the advantage of taking different prey than most other birds. The eyes of Bonins and Laysans have high levels of rhodopsin, which enhances nocturnal vision. Black-footed albatrosses lack such an adaptation. This difference in the ability to feed at night can explain the Laysans' greater dependence on squid, which are more available to birds at night, and the reliance of black-foots on flyingfish eggs and flotsam, which are taken in daylight.

Another important means of minimizing competition is to specialize in prey of a certain size. Such specializations result from variations in the size, shape, and attendant musculature of bills. While it seems natural that masked boobies would eat larger flyingfish than noddies of one-sixteenth their weight, subtle differences in prey size may be found among birds of similar sizes. Among tuna birds, the somewhat larger shearwaters take larger flyingfishes and flying squid than terns. Among the boobies, the heavier masked boobies take considerably larger fish than red-foots or browns. The larger brown noddies take longer fishes than black noddies; the larger gray-backed terns consume bigger prey than blue-gray noddies. Even when several species appear to be feeding on the same resource, they often select prey of different sizes.

Feeding area is yet another mechanism by which birds reduce competition for food. Although precise feeding locations of breeding Hawaiian seabirds are unknown and probably will remain so until there are further improvements in marine radiotelemetry, several generalizations can be made. Albatrosses feed far offshore, probably hundreds if not thousands of kilometers north in the cooler and more productive waters of the Kuroshio. By traversing such distances, they take food that is unavailable to other species. Brown boobies feed close to shore and consequently take more prey that is associated with coral reefs than red-footed boobies, which feed fairly far offshore. Among tuna birds, black noddies and white terns feed much closer to shore than brown noddies, wedge-tailed shearwaters, and sooty terns, even though each species seeks out schools of shoaling predatory fishes. Offshore-feeding tuna birds sometimes bypass feeding opportunities in nearshore waters when they commute to distant feeding grounds.

Differences in feeding behavior further divide up food resources. Some species have evolved means to catch prey that is unavailable to others. Seven Hawaiian seabirds depend heavily on fish schools to obtain prey; fifteen do not. Among tuna bird flocks, sooty terns feed by plunging to the surface, taking prey at the interface of air and water. They cannot get wet without becoming dangerously waterlogged. Because they are faster and more agile than other tuna

birds, they are usually the first to arrive at a shoaling fish school and feed before the rest of the flock arrives.

Shearwaters, in contrast, dive into the water and can swim below the surface, paddling and using vigorous wingbeats to pursue prey. They take squid and fishes in water too deep for sooty terns. Pelecaniforms also feed at different depths. White-tailed tropicbirds hover ten to fifteen meters above the ocean surface, then tuck their wings close to their bodies and plunge to depths of three meters or so. Masked boobies dive even deeper. Great frigatebirds, like sooty terns, do not enter the water but are confined to plucking prey from the surface. Some frigates use their superior speed and agility to steal food. A frigate will harass a tropicbird, booby, or shearwater until the pestered bird disgorges its last meal, which the frigatebird immediately swallows. Although frigates are renowned as man-o'-war birds because of such aerial piracy, theft accounts for only a small proportion of their diet.

All feeding in the tropics, in contrast to cooler zones, is restricted to the first few meters of the sea surface. No tropical seabird forages to the depths that cormorants, penguins, and murres do. One likely explanation is that sharks and other predatory fishes pose too great a threat to diving seabirds in the clear tropical waters; no deep-diving species could survive in tropical waters.

Choice of breeding season, as we saw in chapter 6, is a means of avoiding competition for prey. Several species with similar diets breed at different times of the year, thus minimizing competition for food during the critical chick-rearing period. Two nocturnal petrels have diametrically opposed breeding seasons. Bulwer's petrels breed during summer, laying in May and June. When adult Bonin petrels arrive to concentrate their foraging activities near the colonies in winter, Bulwer's petrels have already migrated far out to sea. Though wedge-tailed and Christmas shearwaters have similar diets, their chick-feeding activities overlap only slightly. Christmas shearwater chicks are fed from June to mid-September, whereas wedge-tailed young are fed from mid-August to November. The shearwaters do not compete for food during most of the critical chick-rearing season, a strategy also employed by blue-gray noddies and gray-backed terns.

Consumption Rates: The Impact of Birds on the Marine Ecosystem

It is difficult if not impossible to measure directly the amount of food that seabirds consume. Instead, biologists must use mathematical models to estimate the energy that Hawaiian seabirds need for various aspects of their life cycles. Such a model has been devised. In simplistic terms, estimates of the amount of food that each seabird needs for daily existence were multiplied by the total number of birds on each island, including breeding and nonbreeding birds. The estimates were adjusted downward for the portions of the year during

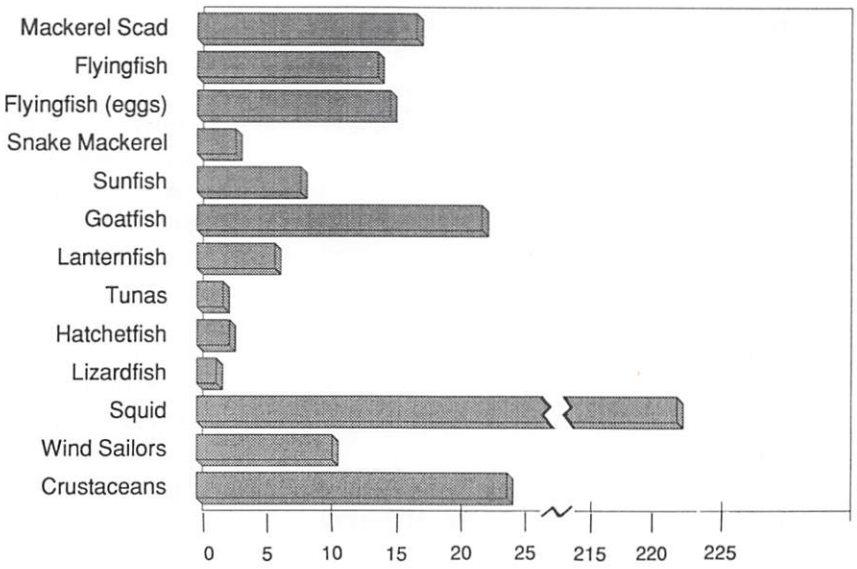


Figure 14. Estimated annual consumption of marine resources by Hawaiian seabirds (metric tons × 1,000)

which migratory birds are absent from the islands and upward for the additional food required by reproductive activities. Bomb calorimetry has been used to determine the amount of energy contained in seabirds' food sources. From this model, energy requirements were translated into an estimate of the food requirements of the Hawaiian seabird community (Figure 14).

Hawaiian seabirds consume over 400,000 metric tons of fish, squid, crustacea, and other food sources each year. By far the greater part of the consumption takes place in the Northwestern Hawaiian Islands, where 14 million of Hawaii's 15 million seabirds are found. Squid, especially flying squid, is the largest component of the community's diet and accounts for well over half of its annual consumption of prey. Fish constitutes about one-quarter of all food consumed, the bulk consisting of flyingfishes, goatfishes, and mackerel scad.

Albatrosses and tuna birds account for almost all of the prey consumed. Albatrosses eat almost two-thirds, a reflection of both their substantial populations and their relatively large size. Tuna birds take almost 30 percent of the annual consumption. Five of the twenty-two species account for 94 percent of the prey consumed: Laysan albatrosses, black-footed albatrosses, Bonin petrels, wedge-tailed shearwaters, and sooty terns. The neuston-feeding terns take trivial amounts of the resources consumed by the community, and the pelecaniforms take only about 2 percent.

A comparison of the estimates of prey consumed by Hawaiian seabirds with the present and projected fishery landings in Hawaii is interesting. Fisheries are fairly well established in the main islands, but the waters of the Northwestern

Hawaiian Islands remain relatively unexploited. Although fish landings fluctuate over the years, the 6,000 metric tons that were reported as landed by Hawaiian fishermen in 1978 represent a fairly typical annual haul. Even if fishermen report only about half of their catches, Hawaiian seabirds consume well over thirty times the annual human catch in Hawaii. The most optimistic estimate for future fishery landings in Hawaii is about 50,000 metric tons, about one-eighth of the amount taken by seabirds. Of course few of the juvenile forms of fish and squid that make up much of the diet of Hawaiian seabirds would survive to attain commercially valuable sizes. Two-thirds of the annual consumption is accounted for by squid, which are not exploited commercially in Hawaii.

An ecosystem model for French Frigate Shoals indicates that seabirds consume over two-fifths of the annual production of small surface pelagic fishes and squid. Such estimates are complicated by the imprecision of estimates of nonbreeding seabird populations, and more accurate information might change the results of the model substantially. Estimates of the effects of seabirds on marine ecosystems in cool-water systems in Oregon, Scotland, Peru, and Namibia indicate that birds take about one-fifth of the annual fish production. Seabirds are an important component of the marine ecosystem in Hawaii.