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HAWAIIAN SEABIRD FEEDING ECOLOGY

by

CRAIG S. HARRISON, THOMAS S. HIDA, AND MICHAEL P. SEKI

OCTOBER 1983 NO. 85

FRONTISPIECE. White tern carrying flyingfish (*Parexocoetus brachypterus*), French Frigate Shoals.

HAWAIIAN SEABIRD FEEDING ECOLOGY

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Abstract: The Northwestern Hawaiian Islands are the nesting grounds of about 10 million seabirds of 18 species. Fishery development proposals for this area led to a need for food habit studies of these birds to aid in their management. Food habits are diverse, with 56 families of fish, 8 families of squid, and 11 groups of crustaceans identified. Similar to other tropical seabird communities, this community feeds largely on flyingfishes and squids. In addition, however, this community consumes many *Decapterus* spp., juvenile goatfishes, juvenile lizardfishes, and mesopelagic fishes that rarely occur in the diets of tropical seabirds elsewhere. Albatrosses fed largely on squids and flyingfish eggs. They also ate many mysids, isopods, leptostracans, and shrimps that occur in very deep water. Pelecaniforms ate large flyingfishes and *Decapterus* spp., many of which were more than 25 cm in length. Squids, especially the surface-dwelling Ommastrephidae, were consumed frequently. Certain boobies ate Pacific sauries, anchovies, and juvenile goatfishes at some locations. The terns and shearwaters that usually feed in association with predatory fishes ate 2–8 cm prey, especially small ommastrephid squids and juvenile forms of flyingfishes, goatfishes, lizardfishes, and *Decapterus* spp. Small nocturnal-feeding procellariiforms ate many 1–3 cm mesopelagic organisms such as lanternfishes, hatchetfishes, bristlemouths, and squids. Small terns ate primarily juvenile flyingfishes, goatfishes, lizardfishes, dolphin-fishes, and a cow fish. In addition, the blue-gray noddy ate minute prey such as sea-striders and copepeds. Most birds feed most of their young during the spring and summer. Breeding in the Northwestern Hawaiian Islands is correlated with and may be controlled by the period of maximum availability of food. Breeding seasons for seabirds in tropical climates are generally less predictable compared to seabird communities in temperate or cold water regimes. The relative predictability of the breeding season for tropical seabirds in the Hawaiian Archipelago may be explained by the fact that most islands there are subtropical. Many seabirds in Hawaii breed at the northern extent of their range. Some seabird species breed largely during winter. Several of these species are adapted for nocturnal feeding. Other winter breeding species may be outcompeted for nesting sites during spring and summer by larger species that have similar nesting requirements. Poor weather conditions during winter may also encourage spring and summer breeding for some species. All seabirds were opportunistic and fed on a wide variety of shoaling fish and squid. They apparently took any organism of appropriate size that occurred in surface waters. Variation in diet for most species was more correlated with season than with location. Some resource partitioning among species was evident both in the composition and in the size of prey. Differences in diet may reflect differences among species in morphology, feeding technique, time of day that feeding occurs, seasonality of breeding, or feeding location. The most numerous species in this community are those that ate many squid. The population differences among species may be merely another expression of the proposition that pelagic feeding seabirds are more numerous than inshore feeding seabirds in tropical waters. Many fundamental questions concerning the biology of tropical and subtropical seabirds cannot be answered until better methods of measuring the availability of prey are developed. Our results will enable wildlife and fishery managers to more accurately predict the effects of various fisheries on marine birds.

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INTRODUCTION

No comprehensive work has been published on the diets of Hawaiian seabirds, and most of the information that does exist is fragmentary or anecdotal (e.g., Munro 1944, Berger 1972). Brown (1975) gave quantitative information on the diets of sooty terns and brown noddies breeding on Manana Island (Oahu), and Ashmole and Ashmole (1967*a*) presented limited information on the diet of the red-footed booby on Oahu (scientific names of birds are given in Appendix 1). Feeding habits of several species may be inferred from studies on Christmas Island (Pacific Ocean) by Ashmole and Ashmole (1967*b*) and Schreiber and Hensley (1976). Christmas Island is 2,000–3,000 km south of the Hawaiian Archipelago.

Fishery development proposals for spiny lobsters, carangids, snappers, and live bait for tuna fishing in the Northwestern Hawaiian Islands (NWHI) prompted the U.S. Fish and Wildlife Service and the National Marine Fisheries Service to investigate ecological relationships that could be altered by intensive harvest of various target species. Altered food webs could potentially affect seabirds, which are abundant in this area. The NWHI are the nesting grounds of an estimated 10 million seabirds of 18 species (Table 1). Many of their breeding islands have been protected since 1911. Because seabird population crashes were correlated with fishery development in Peru (Schaefer 1970, Idyll 1973), Southwest Africa (Crawford and Shelton 1978), and California (Ainley and Lewis 1974) it seemed imperative that the feeding ecology of Hawaiian seabirds be documented before fishery development. Few integrated studies of the diets of large, complex seabird communities have been published. The work on 18 species in the Barents Sea (Belopol'skii 1957), 11 species on Christmas Island (Ashmole and Ashmole 1967*b*, Schreiber and Hensley 1976), and 9 species in the North Sea (Pearson 1968) elucidated the interspecific feeding relationships of colonial nesting birds in those parts of the world. The present study was designed to provide an understanding of the trophic structure of the unique seabird community in the subtropical NWHI. Results should be useful to both community ecologists and resource managers. When feasible, ancillary food samples were collected in the main Hawaiian Islands. A preliminary report of this work has been published elsewhere (Harrison and Hida 1980).

Table 1. Maximum recent population estimate (individual birds), Northwestern Hawaiian Islands.[a]

	Nihoa	Necker	French Frigate Shoals	Gardner Pinnacles	Laysan	Lisianski	Pearl and Hermes Reef	Midway	Kure
Black-footed albatross	100	350	4,700	0	67,000	3,500	14,000	30,000	600
Laysan albatross	tr[b]	1,800	1,600	tr	550,000	8,000	45,000	500,000	2,400
Bonin petrel	0	0	750	0	40,000	1,000,000	1,000	10,000	2,500
Bulwer's petrel	250,000	200	500	tr	20,000	tr	tr	0	0
Wedge-tailed shearwater	25,000	4,500	13,000	tr	1,000,000	500,000	26,500	20,000	1,500
Christmas shearwater	800	0	tr	0	10,000	2,000	tr	100	tr
Sooty storm-petrel	tr	0	tr	0	2,500	0	7,500	0	0
Red-tailed tropicbird	500	200	450	100	4,000	4,500	200	3,000	2,000
Masked booby	350	500	1,200	800	2,000	1,200	600	20	100
Red-footed booby	3,500	1,400	750	tr	2,500	3,000	200	1,000	600
Brown booby	225	50	135	20	250	200	200	tr	100
Great frigatebird	10,000	2,000	1,400	250	8,000	2,500	900	200	500
Sooty tern	100,000	50,000	250,000	750	2,000,000	1,700,000	80,000	50,000	12,000
Gray-backed tern	10,000	7,500	1,750	4,000	40,000	15,000	1,900	50	100
Blue-gray noddy	2,500	2,500	tr	tr	0	0	0	0	0
Brown noddy	20,000	50,000	10,000	5,000	30,000	15,000	8,400	3,000	1,200
Black noddy	2,000	1,000	11,000	400	5,000	5,000	4,300	5,000	2,000
White tern	3,000	600	3,700	400	1,500	500	tr	6,000	tr

[a] Data from Amerson (1971), Clapp (1972), Woodward (1972), Ely and Clapp (1973), Amerson et al. (1974), Clapp and Wirtz (1975), Clapp et al. (1977), and Clapp and Kridler (1977). Estimates from Midway are our own.
[b] tr Indicates species is present in low but undetermined numbers.

The species studied were the black-footed albatross, Laysan albatross, Bonin petrel, Bulwer's petrel, wedge-tailed shearwater, Christmas shearwater, sooty storm-petrel, red-tailed tropicbird, masked booby, red-footed booby, brown booby, great frigatebird, sooty tern, gray-backed tern, blue-gray noddy, brown noddy, black noddy, and white tern. Both albatrosses nest primarily in the NWHI (Palmer 1962). Bonin petrels and sooty storm-petrels breed in the Volcano Islands in addition to islands in the study area (King 1967). Christmas shearwaters, gray-backed terns, and blue-gray noddies breed at various locations in the tropical Pacific (King 1967). Bulwer's petrels nest on islands in the warmer waters of the Atlantic and Pacific but not the Indian Ocean (Alexander 1954). Red-tailed tropicbirds (Fleet 1974) and wedge-tailed shearwaters (Alexander 1954) nest in the tropical Indo-Pacific but not the Atlantic Ocean. The boobies (Nelson 1978), great frigatebird (Nelson 1975), sooty tern, white tern, brown noddy, and black noddy (Alexander 1954) are widespread pantropic species.

Acknowledgments.—We thank the many experts who helped us with identifications and contributed significantly to the results of this cooperative study. William F. Smith-Vaniz, Academy of Sciences of Philadelphia, identified the *Decapterus* group; Izumi Nakamura, Kyoto University, identified billfish juveniles and larvae; Richard E. Young, Department of Oceanography, University of Hawaii, identified squids; Thomas E. Bowman, Austin B. Williams, and Isabel Perez Farfante, National Marine Fisheries Service Systematic Laboratory, Smithsonian Institution, identified crustaceans; Geoffrey Moser, National Marine Fisheries Service, La Jolla Laboratory, identified fish eggs. John E. Randall, Bernice P. Bishop Museum, and Bruce B. Collette, National Marine Fisheries Service Systematic Laboratory, U.S. National Museum of Natural

History, supplied reprints, identifications, and referrals; Lanna Cheng, Scripps Institution of Oceanography, identified *Halobates* species; Walter Matsumoto, National Marine Fisheries Service, Honolulu Laboratory, aided in the identification of larval and juvenile scombrids; John E. Fitch (deceased), California Department of Fish and Game, identified several myctophid otoliths; Frederick H. Berry, National Marine Fisheries Service, Miami Laboratory, helped identify *Seriola* spp.; Tadashi Kubota, Tokai University, furnished *Decapterus* specimens; A. Binion Amerson, Jr., identified ticks; the captain and crew of the research vessel *Townsend Cromwell* provided logistic support of field personnel during the sampling program; Sally H. Kuba wrote the computer programs used in this study; Bernie M. Ito photographed the fishes; Tamotsu Nakata drew figures.

Many biologists helped with collections of samples in the field to make this study possible. Eric P. Knudtson, Maura B. Naughton, and Audrey L. Newman suffered the deprivations of field camp living for months at a time during collecting periods on Laysan Island. John B. Andre, John V. Gravning, Ruth Ittner, Robert P. Schulmeister, and Susan D. Schulmeister collected while resident on Tern Island, French Frigate Shoals. The following also helped collect food samples: Stephen I. Apfelbaum, Gordon H. Black, Dylan A. Bulseco, Timothy A. Burr, G. Vernon Byrd, Roger B. Clapp, Richard A. Coleman, Mark Collins, Sheila Conant, Cynthia J. Cookinham, Elisabeth C. Cummings, Douglas J. Forsell, J. Brent Giezentanner, Gilbert S. Grant, Brian W. Johnson, Patricia A. Johnson, Ernest F. Kosaka, Catherine E. Ludwig, Gerald M. Ludwig, James P. Ludwig, L. A. Paloma, Ted N. Pettit, Mark J. Rauzon, Nelson K. Rice, Donald Richardson, Jennifer Richardson, Ralph S. Saito, Nelson Santos, Robert J. Shallenberger, Elizabeth A. Sheekey, Daniel L. Stoneburner, and Kawika H. Woodside.

Richard S. Shomura, Director, Honolulu Laboratory, National Marine Fisheries Service, was largely responsible for making this interagency cooperative study possible. Shirley Hernandez patiently typed the various drafts of this paper. David G. Ainley, Bruce B. Collette, A. W. Diamond, and R. W. Schreiber made valuable comments on earlier drafts of this manuscript.

THE NORTHWESTERN HAWAIIAN ISLANDS

The biologically isolated Hawaiian Archipelago is 4,000 km from the nearest continental land mass and stretches about 2,600 km from Hawaii to Kure Atoll (Fig. 1). Each small island between Nihoa and Kure is associated with a relatively large bank. Nihoa and Necker are remnant volcanic cones of 63 and 17 ha, respectively (Clapp et al. 1977, Clapp and Kridler 1977). French Frigate Shoals is a coral atoll consisting of 12 sandy islets and 1 volcanic pinnacle on a 360-km^2, crescent-shaped lagoon with a total land area of 45 ha (Amerson 1971). Gardner Pinnacles are 2 small volcanic rocks of approximately 1.2 ha (Clapp 1972). Laysan, 20% of which is an interior brackish lagoon (Ely and Clapp 1973), is a coral island of about 370 ha atop a massive submerged volcanic peak. Lisianski is a low sandy coral island of 182 ha at the northern end of a 170-km^2 bank (Clapp and Wirtz 1975). Pearl and Hermes Reef is an atoll comprised of 9 low, coral islands, 4 of which are non-vegetated sand bars. The land mass of 34 ha is scattered in a 370-km^2 lagoon (Amerson et al. 1974). Midway is a coral atoll consisting of 2 islands with a total land area of 550 ha, the largest in the NWHI (Gross et al. 1969). Kure is the northernmost coral atoll in the world, and consists of 2 islands with a land area of about 100 ha and a lagoon with an area of 46 km^2 (Gross et al. 1969, Woodward 1972). A more complete description of each island may be obtained by consulting the references cited above.

Northeastern trade winds predominate throughout most of the year. Surface water temperatures range from 20–25 C from

November–February and from 25–27.5 C from April–August (Fig. 1). The Hawaiian Islands are bathed by central North Pacific water that is seasonally displaced by the California current extension in spring and summer (Seckel 1962). Storms and associated high winds and swells are frequent from November–March.

METHODS

During the course of this study, we measured several morphological characters of each seabird species, including weight, bill width, and culmen length. Observations of breeding stage of each species by field personnel were recorded to determine the breeding chronologies of each species.

Field Collection of Food Samples

The 4,315 food samples that provide the basis for this paper were collected from 1978–81 on an irregular series of visits to various islands in the study area. Cruises in August–September 1978, May 1979, and June 1980 allowed visits to all islands between Nihoa and Kure (Fig. 1). Cruises in February–March 1978 included Laysan and Midway; May 1978 included French Frigate Shoals, Laysan, and Lisianski; July 1978 included French Frigate Shoals, Laysan, Lisianski, Pearl and Hermes Reef, and Midway; November 1980 included all islands except Lisianski and Kure; January–February 1981 included Laysan and Nihoa. Visits to Midway occurred during the following months: October and November 1978; January, February, August, September, October, November, and December 1979; January, March, and April 1980. Visits to Kure occurred in November 1979, March 1980, and October 1980. Biologists were stationed in a field camp on Laysan Island (Fig. 1) and collected food samples March–August 1979 and March–August 1980. Biologists manned a field station at Tern Island (French Frigate Shoals) and collected samples from July 1979 until December 1980. A biologist on Kure obtained samples March–April 1978 and March–April 1979. A 1-day visit to French Frigate Shoals occurred in January 1979. Visits to various islands offshore of the windward Oahu coast took place in July 1978, May 1979, November 1979, July 1980, and November 1980. It is the nature of work in a study area as remote as the NWHI that collecting visits were opportunistic and sampling design could not be entirely controlled by the investigators.

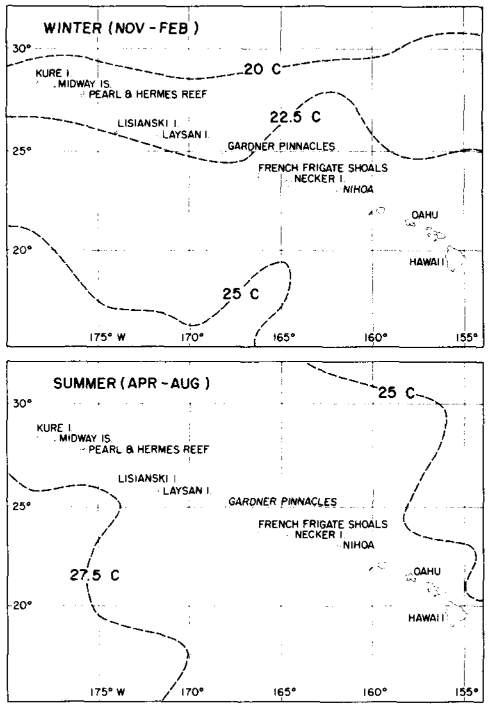

Fig. 1. The Hawaiian Archipelago with winter and summer surface isotherms from Armstrong (1973).

We intended to sample food habits of all species on each island during each 3-month season, but this proved impossible because of personnel limitations and the inherent inaccessibility of many islands. Nihoa, Necker, Laysan, Lisianski, and Pearl and Hermes Reef could be visited only on an expedition supported by a large vessel. Bad weather precluded landing on certain islands during scheduled cruises. Furthermore, many species occur only seasonally in the NWHI. For example, Laysan and black-footed albatrosses were present only November–July, sooty storm-petrels were present only January–May, and gray-backed terns were present only March–June. Several species have a limited distribution within the study area. Blue-gray noddies are found only on 4 islands (Table 1), and 2 of these (Gardner Pinnacles and La Perouse Pinnacle [French Frigate Shoals]) were inaccessible. Consequently, sampling of this species was limited to Nihoa and Necker Islands at times when vessel support was available and weather conditions permitted making the hazardous landings.

Finally, the presence of birds on an island did not insure that samples could be obtained. Laysan albatrosses present in July were mostly fledglings living off fat reserves, whereas those present in November were adults setting up breeding territories and establishing pair bonds (Fisher and Fisher 1969). In both cases, birds present on the islands appeared to contain no food during those months. Courting, nonfeeding adults of Bonin petrels, red-tailed tropicbirds, and great frigatebirds were also present. Few black noddy food samples were obtained from Midway or Kure because this species roosted high in ironwood trees (*Casuarina equisetifolia*), and live capture was rarely possible. Similar problems in food collection occurred with black noddies on Nihoa and Necker where roosting sites were faces of sheer cliffs.

We generally captured birds alive by hand or with a long-handled polypropylene fish net (Ashmole and Ashmole 1967*b*). Some populations on some islands were small (Table 1), and killing individuals for this study was undesirable (Tomback 1975).

We sampled adults, chicks, and immature birds. Upon capture, each bird was turned upside down. If the bird did not regurgitate immediately, it was squeezed or shaken. We quickly learned to determine when a bird in hand was likely to produce a food sample using weight, size, and distention as criteria. We found that food samples were most easily obtained during periods when parents were feeding young. Young of all species readily regurgitated when handled, and adults feeding young usually regurgitated when captured on the colony. The observation of a parent feeding a nestling was often used to indicate which bird to sample in order to economize effort in the field. Additionally, collections in the late afternoons and early evenings gave samples of better condition more readily than at other times of the day. Samples were taken at all hours of the day, but efforts were maximized from 1600–2100 hours. Samples that were too digested to be identifiable were often discarded in the field.

All pelecaniforms regurgitated readily if they contained food, and empty birds often regurgitated digestive juice. Terns readily regurgitated or dropped (white terns) samples for this study. The 7 procellariiforms presented the greatest sampling problems. Adult albatrosses rarely regurgitated, but chicks did immediately if recently fed. Christmas shearwaters and wedge-tailed shearwaters could be induced to regurgitate by holding the birds upside down and applying strong enough pressure to the abdomen to visibly stress the bird. Our initial samples from sooty storm-petrels, Bulwer's petrels, and Bonin petrels consisted only of oil or food so digested that only gross identification of prey items was possible. Attempts to induce Bonin petrels to regurgitate by use of emetics (e.g., Radke and Fryendall 1974, Tomback 1975) were unsuccessful. About 100 birds (wedge-tailed shearwaters, Bonin petrels, and Bulwer's petrels), many of which were empty, were sacrificed at the onset of the study to provide sample material.

Each sample was preserved in 10% formalin. Because isopropyl alcohol was not used as a preservative due to its less desirable quality of preserving fish for our identification techniques, we could not identify otoliths (Fitch and Brownell 1968). After failing to get many identifiable fish specimens from Bonin and Bulwer's petrels, a few samples were preserved in alcohol so that otolith identification could be made. Field data recorded include island, species, date, time, age of bird (adult, juvenile, nestling), sex of bird (if possible), and any additional comments that seemed pertinent.

Laboratory Procedures

The laboratory procedures used in processing the samples of seabird regurgitations were similar to those used by Ashmole and Ashmole (1967*b*), Reintjes and King (1953), and King and Ikehara (1956). The methods used by Schreiber and Hensley (1976) in their study of the diets of 3 pelecaniforms on Christmas Island differed from ours in that they analyzed only the fresh or slightly digested material. Additionally, they both weighed and measured the volume of individual prey items.

We poured each sample into a strainer, rinsed it with running water, and removed any objects not considered to be food items. Such objects included sand, twigs, leaves, flies, strands of monofilament line, plastic chips, pumice, and styrofoam pieces. These items were weighed for a subset of the albatross samples. The densities of such objects are extremely variable, and volumes would have been misleading.

We frequently found clusters of fish eggs attached to floating objects in samples taken from Laysan and black-footed albatrosses. We removed the clusters and treated the thousands of eggs as a single mass. Prey items were segregated into major groups and then identified to the lowest taxon possible.

We recorded the number of individuals of each taxon. In many instances we had to make a decision regarding what to count. For example, we encountered a large number of chitinous squid beaks that "resist attack by the digestive juices in the stomach for some time after other tissues have been digested" (Clarke 1977:92). We followed the method of Pinkas et al. (1971) and counted either upper or lower beaks, using the count with the highest number. Although the time it took the predator to accumulate all of the squid beaks is unknown, we believe it is important to show that many squids were consumed. Squid beaks have been enumerated differently by various investigators. Imber (1973) in his study of the food of gray-faced petrels counted the number of lower squid beaks. Ashmole and Ashmole (1967*b*) counted all squid beaks in a sample as 1 squid. Fish remains and invertebrate remains were enumerated as 1 whenever the actual number of individuals could not be determined. Frequently the posterior parts of a fish persisted although the head and otoliths were digested. Swallowing fish head first has been recorded by Imber (1973) and is an apparent adaptation to prevent a bird from being impaled by the spines and rays (Gochfeld 1975). Fish counts were based on the number of caudal peduncle-hypural fan sections that were present whenever heads were separated from tail sections or when there were fragments of fishes.

Volumes were determined by water displacement using a graduated cylinder. The smallest volume used in our analyses was 0.1 ml. This presented a problem with copepods and sea-striders because 0.1 ml is greater than their true volume. However, the volumes of most of the tiny prey items were measured in aggregate so that there was no gross distortion of volume.

Length measurements of prey items were made whenever possible. The lengths of most fishes were measured from the tip of the snout to the tip of the hypural fan (standard length). The lengths of marlins and needlefishes (scientific names of fishes are given in Appendix 2) were measured from the nostril to the tip of the hypural fan. The accuracy of the measurements were ranked as grade 1 for precise and grade 2 for slightly estimated. Grade 2 fish lengths were good measurements where only a small part of the fish was missing, i.e., the snout or hypural fan. Grade 3 fishes had a larger portion of the body missing and were rough estimates. Grade 4 fishes had most of the body missing and the length was estimated.

Mantle lengths were measured for the squids and total lengths for isopods. For

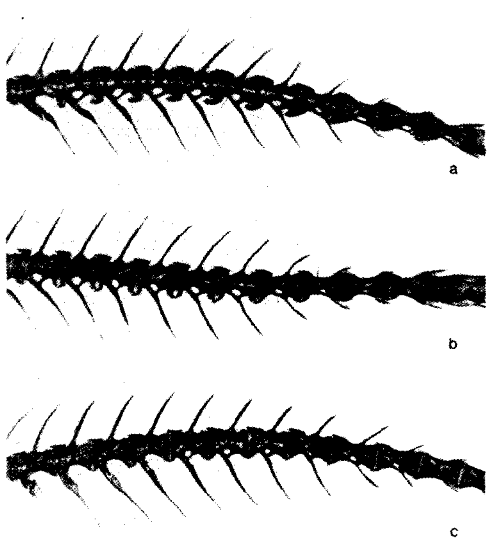

Fig. 2. Vertebral comparisons for *Decapterus macrosoma* (a), *D. tabl* (b), and *D.* sp. (c).

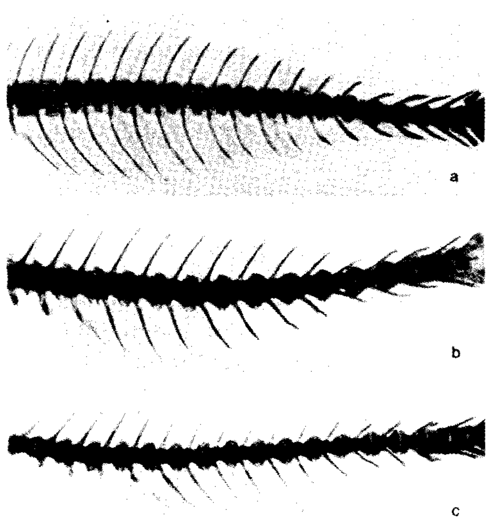

Fig. 3. Vertebral comparison of *Coryphaena equiselis* (a), *Seriola* sp. (b), and *Naucrates ductor* (c).

odd-shaped organisms such as medusae and wind-sailers, we measured the largest diameter.

The stage of digestion of prey items was graded as 1 for fresh, 2 for slightly digested, 3 for advanced state of digestion, and 4 for bone, squid beak, or exoskeleton remains. We assigned grade 5 to prey that was semidehydrated or dehydrated. The latter items were always dropped by white terns, which are well-known for carrying food to young lengthwise in the bill (Stonehouse 1962). In comparison to our method, Ashmole and Ashmole (1967*b*) recorded the fish and squid remains as grade 1 for those in good condition whose lengths could be measured accurately, grade 2 for those that were slightly broken or digested but fairly accurate measurements could be obtained, and grade 3 for items largely digested for which lengths were estimated.

The mean, minimum, maximum, and standard error for both length and volume have been presented for common items. We restricted those analyses to prey items in grades 1 and 2, but used all grades for frequency of occurrence and average percent volume.

We often found it necessary to assign a different grade for the length measurement than for the stage of digestion for a prey item. Very frequently a well-digested fish had its axial skeleton intact and a fairly accurate length measurement could be obtained. This was recorded as grade 3 for volume but grade 2 for length measurement because the length was reasonably accurate. We sometimes encountered fresh chunks of fish that appeared to have been chopped; these were graded 2 for volume but 4 for length. We considered parasitic isopods (crustacean ectoparasites) to be part of the host and processed them as such rather than as independent prey items. However, when an ectoparasite occurred alone, it was processed as a food item. Ashmole and Ashmole (1967*b*) treated the crustacean ectoparasites of fish as food items when they occurred in a sample, stating that some of the prey items in their samples may have come from the stomach of a larger prey item but was recorded as prey of the seabird. We agree that food consumed by a prey species may

Fig. 4. The cleithrums of 2 hatchetfishes.

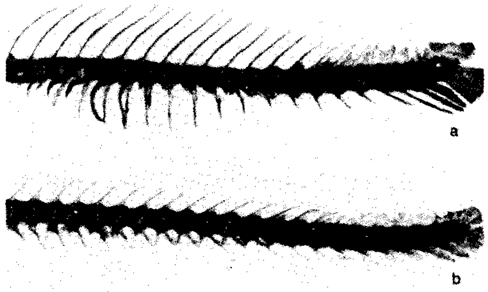

Fig. 5. Vertebral comparison of a flyingfish (a) and a halfbeak (b).

confound the results of any food study, but it was a minor problem here.

Prey Identification

A wide variety of prey items that included 78 fish species belonging to 56 families, 9 groups of crustaceans, and 7 squid families encountered in various stages of digestion made identification a challenge. Prey items ranged in size from tiny sea-striders and copepods measuring a few millimeters and displacing <0.1 ml to adult flyingfishes, juvenile tunas, and juvenile dolphin-fishes measuring >340 mm and displacing >300 ml. Very often the prey items were so well digested that only a few loose bones or squid beaks remained. A reference collection of fish axial skeletons was made during the course of the laboratory work to help identify the fishes. Many fishes could not be identified because key identifying characters were missing and the reference collection was inadequate.

Fish vertebrae were prepared by removing the flesh from either the whole fish or 1 side of the fish and subsequently staining it with Alizarin S, a water soluble bone stain. A weak concentration of stain was used when soaking overnight to bring out the finer configurations of the zygapophysis and other bony parts whereas a stronger concentration was used for quick staining to facilitate the counting of vertebrae, fin rays, and spines.

The vertebrae of 3 *Decapterus* spp. are compared in Fig. 2. The haemal post-zygapophysis is overlapped by the haemal pre-zygapophysis of the posterior vertebrae in *D. macrosoma*, and the high neural zygapophysis and presence of the first inferior vertebral foramina on the first caudal vertebra identifies *D. tabl* (R. L. Humphreys, pers. commun.). The other vertebra illustrated represents either *D. muroadsi* or *D. macarellus*. We lack *D. muroadsi* specimens that would aid recognition of vertebral differences between these 2 species.

The similar vertebrae of *Coryphaena equiselis*, amberjacks, and pilot fish can be distinguished (Fig. 3). In some cases, the presence of just a few pieces of flesh and a bone such as the cleithrum of the hatchetfishes could be adequate to identify the prey item to family or genus (Fig. 4). The shape of spines in the area of the caudal peduncle helped to distinguish flyingfishes from halfbeaks (Fig. 5). The young of a swordfish (*Xiphias gladius*) was identified using its unique spined scales. Potthoff and Richards (1970) used adult characteristics and features of the axial skeleton to aid in their identification of scombrids.

Squids were identified by use of their locking mechanisms, pens, and luminous organs. Squid beaks were not identified because there are no reliable keys for Hawaii (R. E. Young, pers. commun.). The identification of squids in the Hawaiian area is still incomplete, and it would take a major effort to collect specimens of all species and size ranges. Some researchers

(Imber 1973) have identified squid beaks using Clarke's (1962) key and illustrations.

Crustaceans pose less of a problem of identification because of their digestion-resistant exoskeleton (Reintjes and King 1953, Imber 1973). Identification to order usually presented very little problem, but further identification depended upon the condition of the prey item. Copepods were usually identifiable to genus or species because their exoskeletons remained fairly intact.

Numerous keys and guides were consulted to identify the prey items. The most useful were Wilson (1932), Rose (1933), Townsley (1953), Gosline and Brock (1960), Matsumoto (1963, 1967), Strasburg (1964), Nakamura and Kikawa (1966), Collette et al. (1969), Lindberg and Legeza (1969), Lindberg and Krasyukova (1971), Ovchinnikov (1971), Tinker (1978), and Tyler (1980).

Data Analysis

The data are presented as numerical abundance, volume, and frequency of occurrence. The use of these 3 kinds of data is widespread in food studies in the marine environment, and we agree that each measures a different yet important aspect of prey utilization (Reintjes and King 1953, Waldron and King 1963, Ashmole and Ashmole 1967*b*). Reintjes and King (1953) stated that each individual method has shortcomings but that a prey item that ranks high in number, volume, and frequency of occurrence is important at the time and place sampled.

Various combinations of these basic types of data have been used to achieve a single ranking of the importance of prey items because the repetition of each becomes cumbersome in a textual discussion. We adopted the ranking method used by Waldron and King (1963) and Ashmole and Ashmole (1967*b*) but modified their method of calculating volume. We ranked prey organisms separately in terms of number, volume, and frequency of occurrence. We then summed and arranged these 3 subrankings in a single sequence from lowest to highest to produce a final ranking for each prey taxon. This ranking method weights each method equally. Our method gives equal weight to each sample by summing the volumetric percentage of each item and dividing by the sample size to arrive at an average percentage volume. The aggregate total volume method (Ashmole and Ashmole 1967*b*) weights large-sample volumes more than small-sample volumes, and a 200-ml sample would have twice the weight of a 100-ml sample. We compared our ranking method for several seabird species with the one used by Pinkas et al. (1971) and found only minor differences in rank for highly ranked prey items.

The ranking of prey taxa gives a good idea of their relative importance in the diet without excessive attention to an illusory sense of precision, which can come, for example, from a strict comparison of numerical or volumetric data. Matthews et al. (1977) stated that the number of taxa from any 1 category of forage items should not be considered quantitatively because of the differences in taxonomic level to which the prey items were identified. The rankings for prey items by families or major groups show which are relatively the most important. The list of genera and species gives an idea of which species are important within the family or group. It must be noted that the categories of unidentified fishes and unidentified remains rank high because they are a composite of unidentified material presumably from many species, which by necessity have been pooled together. It is unlikely that for any seabird "unidentified fishes" refers to a single species.

We analyzed the data by grouping adjacent islands. The Midway Island group also included Kure Island and Pearl and Hermes Reef. The Laysan Island group included Lisianski Island. The French Frigate Shoals group also included Necker and Nihoa Islands. For each group, the data were analyzed using winter (Jan–Mar), spring (Apr–Jun), summer (Jul–Sep),

Table 2. Weights and bill measurements of Hawaiian seabirds from this study.

Species	Wt (g)[a]					Bill (cm)				
	N	$\bar{x}$	SE	Range	Months	*N*	Culmen length[b]	SE	Width[c]	SE
Black-footed albatross	84	2,820	64	2,025–3,800	Apr–Jun	10	10.40	0.12	3.25	0.04
Laysan albatross	87	2,410	31	1,900–3,075	Apr–Jun	10	11.10	0.12	3.26	0.04
Bonin petrel	168	176	1	150–220	Mar–Oct	10	2.61	0.03	1.11	0.02
Bulwer's petrel	191	99	1	78–130	Apr–Aug	10	2.04	0.04	0.74	0.01
Wedge-tailed shearwater	124	388	3	320–510	May–Aug	10	3.94	0.07	1.19	0.02
Christmas shearwater	99	356	3	280–415	Apr–Aug	10	3.23	0.04	1.01	0.02
Sooty storm-petrel	61	84	1	66–105	Apr–May	20	1.80	0.05	0.93	0.02
Red-tailed tropicbird	84	624	5	540–750	Apr–Aug	10	6.09	0.07	2.00	0.08
Masked booby	132	2,160	18	1,770–2,800	Apr–Aug	10	11.50	0.09	3.00	0.04
Red-footed booby	80	1,110	12	905–1,400	Apr–Aug	10	8.38	0.10	2.57	0.04
Brown booby	43	1,340	18	1,050–1,775	Jun–Sep	10	12.47	0.15	3.30	0.03
Great frigatebird	117	1,440	13	1,060–1,950	Apr–Aug	10	10.90	0.20	3.13	0.07
Sooty tern	94	198	3	153–320	Apr–Jul	10	4.68	0.08	0.99	0.02
Gray-backed tern	83	146	1	115–177	Apr–Aug	10	4.26	0.05	1.00	0.02
Brown noddy	99	205	2	153–275	Apr–Aug	10	4.62	0.05	1.11	0.02
Black noddy	86	108	1	85–133	Apr–Sep	10	4.76	0.08	0.90	0.02
White tern	109	111	1	92–139	May–Sep	20	4.34	0.04	0.79	0.02
Blue-gray noddy	52	53	1	46–65	Jun	30	2.55	0.02	0.81	0.02

[a] Weights from Laysan Island except some Bonin petrel weights were from Midway Islands and all blue-gray noddy weights were from Necker and Nihoa Islands.
[b] Length from tip to angle of gonys.
[c] Proximal end of gonys.

and fall (Oct–Dec). These groupings were necessary because we obtained insufficient samples to compare each month and each island.

Prey lengths for common prey items were compared using analysis of variance (ANOVA). Means and standard errors were calculated for weight, bill width, and culmen length of each seabird species.

RESULTS

Weights and bill measurements (Table 2) indicate that Hawaiian species are similar to those studied elsewhere. However, except for the red-tailed tropicbird, each species, for which a comparison can be made with Christmas Island (Ashmole and Ashmole 1967*b*:18, Schreiber and Hensley 1976:245), is heavier in the NWHI (Table 2). The significance of this difference bears further study.

Most seabirds in this community feed most of their young during spring and summer (Fig. 6). There are several exceptions, however. Four procellariiforms and the black noddy feed nestlings during winter.

Species Accounts

The species are treated in order of decreasing body weight, following Ashmole and Ashmole (1967*b*).

Black-footed Albatross.—We collected and analyzed 172 black-footed albatross samples from 1978–80. Most were from Laysan and Midway Islands, but we also collected at Kure and French Frigate Shoals. Samples were collected from February, when chicks hatch, until June, when young are abandoned by their parents. Obtaining food samples from adult birds proved to be difficult. Consequently 84% of the samples were taken from chicks, and the remainder were taken from adults. The samples averaged 96 ml and contained an average of 15 items. The samples generally were in poor condition, even when obtained from adult birds or chicks

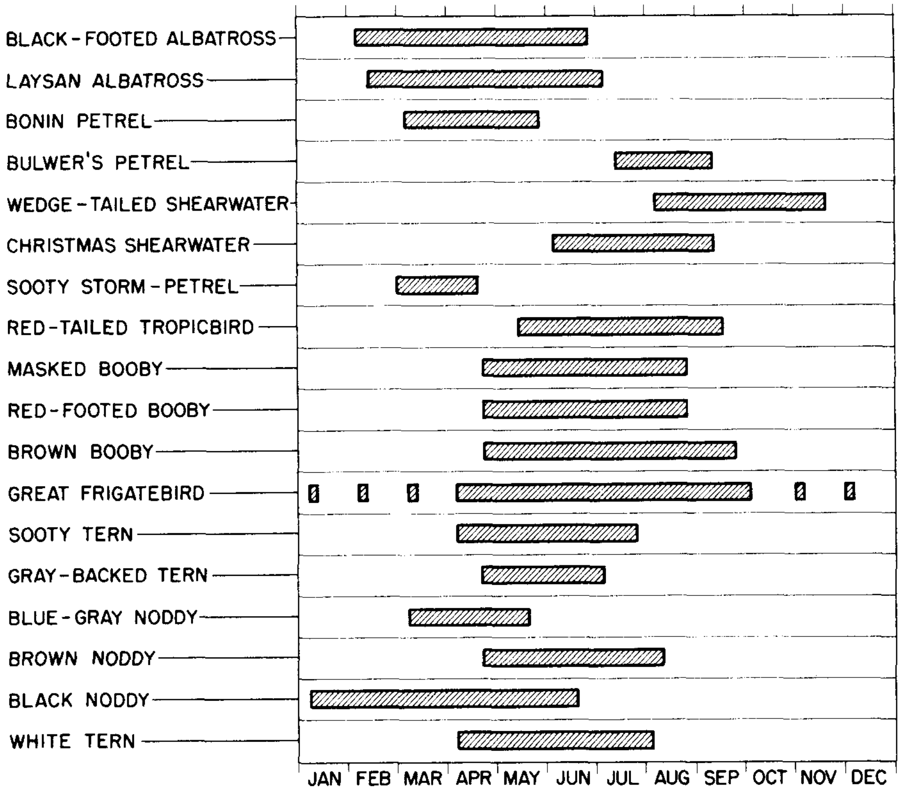

Fig. 6. Maximum feeding periods for dependent young of Hawaiian seabirds, representing about 80% of the feeding activity. Great frigatebirds feed dependent young throughout the year.

that had just been fed by an adult returning from sea. Consequently, identification of prey beyond family level was very difficult.

Prey consisted of 4 fish families, 3 squid families, an octopus, 8 crustacean groups, and a variety of other objects (Table 3). Samples also contained many floating objects, some of which provided a substrate for flyingfish ova (Table 4). About 10% of the volume of black-footed albatross samples was stomach oil, a common feature of procellariiformes (Imber 1976, Warham et al. 1976). Our laboratory analysis excluded the oil and found prey to be 50% fish, 32% squid, and 5% crustacean by volume. Common food items throughout the sampling period were squid, especially Ommastrephidae, and flyingfish ova. The high ranking of unidentified remains, unidentified crustaceans, and unidentified fishes gives an indication of the poor condition of samples (Table 3). However, it is probable that most important taxa are included in the species list. Squid rank particularly high due to the frequent occurrence of digestion-resistant beaks (as many as 66 in 1 sample). Although Imber (1973) identified squid from their beaks, we made no effort to identify ours because no suitable reference collection of beaks exists for the NWHI. Flyingfish ova were the most important prey item by volume (44%), and each egg mass was counted as a single prey item. The abundance in the diet of certain large crustaceans was unexpected, because they are believed to inhabit only very deep water. These include the mysids *Gnathophausia gigas* and *G. ingens*, the isopod *Anuropus branchiatus*, the leptostracan *Nebaliopsis typica*, and the shrimp *Notostomus japonicus*.

Table 3. Prey items identified to lowest taxon in 172 black-footed albatross samples. Prey items were ranked separately in terms of number, volume, and frequency of occurrence. These 3 subrankings were summed and arranged in a single sequence from lowest to highest to achieve the rank reported here for each prey taxon.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Carangidae	19			
Decapterus sp.		1	0.6	0.3
Exocoetidae	2			
Exocoetidae (ova)		139	80.2	44.2
Unidentified exocoetid		7	4.1	1.8
Gempylidae	19	1	0.6	0.3
Sternoptychidae	23.5	1	0.6	0.1
Unidentified fishes	6	24	13.4	3.0
SEABIRDS	13			
Puffinus sp.		1	0.6	0.1
P. pacificus		1	0.6	0.2
Pterodroma hypoleuca		1	0.6	0.1
MOLLUSCA				
Decapoda				
Ommastrephidae	4			
Symplectoteuthis oualaniensis		1	0.6	0.2
Hyaloteuthis pelagicus		1	0.6	<0.1
Unidentified ommastrephid		47	10.5	3.2
Cranchiidae	23.5	1	0.6	<0.1
Octopoteuthidae	19	1	0.6	0.3
Unidentified squid	1	2,182	91.9	28.1
Octopoda	17	2	0.6	0.2
CRUSTACEA				
Mysidacea	7			
Gnathophausia spp.		5	2.3	0.1
G. gigas		6	3.5	0.9
G. ingens		1	0.6	<0.1
Unidentified mysid		4	2.3	0.1
Euphausiacea	23.5	1	0.6	<0.1
Amphipoda	12			
Alicella sp.		1	0.6	0.4
Unidentified amphipod		2	1.2	0.1
Isopoda	10			
Anuropus sp.		1	0.6	0.1
A. branchiatus		3	1.7	0.8
Parasitic isopod		1	0.6	<0.1
Unidentified isopod		1	0.6	<0.1
Nebaliacea	23.5			
Nebaliopsis typica		1	0.6	<0.1
Copepoda	11			
Penella spp.		17	1.7	0.1
Shrimp	8.5			
Oplophoridae				
Notostomus spp.		2	1.2	<0.1
N. japonicus		2	1.2	0.1
Unidentified oplophorid		1	0.6	<0.1
Pasiphaeidae		3	1.7	0.1
Unidentified shrimp		5	2.9	0.3
Crab	14			
Brachyura		6	2.3	<0.1
Grapsidae				
Planes cyaneus		1	0.6	<0.1
Unidentified crustacean	5	39	22.1	1.2

Table 3. Continued.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
INSECTA				
Gerridae	15			
Halobates sericeus		5	1.2	<0.1
Caterpillar	23.5	1	0.6	<0.1
COELENTERATA				
Velellidae	16			
Velella velella		1	0.6	0.6
TUNICATA				
Pyrosomatidae	8.5	15	4.7	0.5
ALGAE				
Sargassum sp.	23.5	1	0.6	<0.1
UNIDENTIFIED REMAINS	3	51	29.7	11.1
UNIDENTIFIED MEAT		3	1.7	0.9

Measured lengths of intact prey ranged from a 4-mm sea-strider to a 300-mm amphipod, the latter probably being the largest known (Barnard and Bowman, pers. commun.). Most length measurements were ommastrephid squids ($\bar{x} = 74$ mm, Table 5). Some crustaceans were longer than the squids. *G. gigas* and *A. branchiatus* averaged 112 and 106 mm, respectively. Length data of prey of this species must be interpreted with some caution. They often feed in groups and have strong bills capable of ripping and tearing flesh. It is probable that many of the squid fragments occurring in the samples were not taken whole but were shredded from individuals much larger than those that we were able to measure or that an albatross could swallow whole. Squid arms of at least 200 mm were found next to albatross nests on Midway and Laysan Islands, apparently too large for the young to swallow. The mantles from such individuals were certainly much larger than 120 mm, the largest ommastrephid squid that we measured (Table 5). Flyingfish ova clusters averaged 86 ml and appeared to be relatively fresh, perhaps indicating a resistance to digestion. The largest egg mass displaced 301 ml and weighed 314 g. We estimated that it contained more than 156,000 ova. Most diameters of in-

Table 4. Weights and percent of sample by weight of indigestible items in 14 black-footed and 12 Laysan albatrosses.[a]

Species	Mean wt of indigestible items (g)	SE	Percent of sample by wt	SE
Black-footed albatross	9.9	1.7	12.2	2.6
Laysan albatross	10.6	3.2	14.7	5.2

[a] Both species contained squid beaks, squid lenses, plastic chips, styrofoam, pumice, and monofilament. The black-footed albatross also yielded rubber, sponges, and a paper wrapper. The Laysan albatross additionally yielded bird bones and a kukui nut (*Aleurites moluccana*).

dividual ova were 1.5–1.7 mm, but some were as large as 2.3 mm.

There were few differences in the major prey items consumed by this predator between either winter and spring or among any of the 3 island groups of the NWHI. During winter and spring, squid and egg masses of flyingfishes were the first and second ranked prey items in each island group. This order was reversed during spring in the French Frigate Shoals region, but the number of samples collected there was relatively low, and we attach no importance to this difference.

These results generally correspond to anecdotes concerning the feeding habits of this species, where it has been reported to feed on flyingfishes (Fisher 1945), shrimps (Anderson 1954), squids, gammarids, sea urchins (Cottam and Knappen 1939), fish eggs, sun fish, and algae (Miller 1940). The black-footed albatross is so renowned for its habit of following ships and feeding on refuse that Miller (1940) referred to it as the "feathered pig."

Laysan Albatross.—We collected 183 samples from Laysan albatrosses from 1978–80 with samples taken from Laysan, Midway, Kure, and French Frigate Shoals. Samples were collected February–July when chicks were being fed by parents. Food samples from adult birds were particularly difficult to obtain from this species, and more than 95% of our samples came from chicks. Sample volumes averaged 64 ml and contained a mean of 32 items. Samples generally were in an advanced state of digestion, which limited our ability to identify and measure prey items.

We identified 9 fish families, 6 squid families, a gastropod, 8 groups of crustaceans, an insect, a coelenterate, and a tunicate as prey (Table 6). Plastic particles, styrofoam, and pumice were regularly obtained from Laysan albatrosses, but we kept records of nonfood items from only a portion of our samples (Table 4). Kenyon and Kridler (1969) also found large amounts of indegistible matter, especially plastics, in stomachs of Laysan albatrosses. As with the black-footed albatross, about 10% by volume consisted of stomach oil that we ignored in the laboratory analysis. We found the prey to be 9% fish, 65% squid, 9% crustaceans, and 4% coelenter-

Table 5. Lengths and volumes of some prey items[a] of the black-footed albatross. Length and volume values are not necessarily for the same individuals.

Prey	Sample size		Minimum		Maximum		Mean		SE	
	Length	Vol	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)
FISHES										
Exocoetidae ova		48		1.4		301		86		10
MOLLUSCA										
Ommastrephidae	42		36		120		74		3	
CRUSTACEA										
Gnathophausia gigas	3		80		140		112		17	
Anuropus branchiatus	3		94		115		106		6	
TUNICATA										
Pyrosomatidae	5		29		72		48		7	

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods).

Table 6. Prey items identified to lowest taxon in 183 Laysan albatross samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Exocoetidae	4.5			
Cypselurus sp.		1	0.5	0.5
Exocoetidae (ova)		20	10.9	3.6
Unidentified exocoetid		6	2.7	0.1
Gempylidae	27	1	0.5	0.1
Gonostomatidae	23			
Vinciguerria spp.		6	0.5	<0.1
Hemiramphidae	19			
Euleptorhamphus viridis		1	0.5	0.1
Unidentified hemiramphid		2	1.1	<0.1
Molidae	13			
Ranzania laevis		12	2.2	0.9
Unidentified molid		2	1.1	0.7
Mullidae	28.5	2	0.5	<0.1
Myctophidae	20	5	2.7	<0.1
Scomberesocidae	12			
Cololabis saira		13	4.4	0.5
C. saira (ova)		3	1.6	<0.1
Sternoptychidae	31			
Argyropelecus sp.		1	0.5	<0.1
Unidentified fishes	8	24	12.6	2.1
MOLLUSCA				
Decapoda				
Ommastrephidae	2			
Symplectoteuthis spp.		4	1.1	0.5
S. oualaniensis		2	1.1	0.9
Unidentified ommastrephid		196	26.8	14.6
Lepidoteuthidae	18	2	1.1	0.9
Mastigoteuthidae	26			
Mastigoteuthis sp.		1	0.5	0.3
Enoploteuthidae	31			
Thelidioteuthis alessandrinii		1	0.5	<0.1
Onychoteuthidae	21	3	0.5	0.3
Histioteuthidae	25	1	0.5	0.4
Unidentified squids	1	3,224	82.5	46.6
Janthinidae	15			
Janthina sp. (ova)		5	2.7	1.8
Unidentified mollusk	22	3	1.1	0.1
CRUSTACEA				
Mysidacea	7			
Gnathophausia spp.		12	4.4	1.0
G. gigas		3	1.1	0.1
G. ingens		7	2.7	0.9
Unidentified mysid		4	2.2	0.3
Euphausiacea	17	1,415	0.5	0.1
Stomatopoda	31			
Pseudosquilla sp.		1	0.5	<0.1
Amphipoda	14			
Eurythenes gryllus		1	0.5	<0.1
Unidentified amphipod		8	3.8	0.6
Isopoda	10			
Anuropus sp.		1	0.5	0.1
A. branchiatus		12	6.0	1.2
Parasitic isopod		1	0.5	0.5
Unidentified isopod		3	1.6	<0.1
Nebaliacea	24			
Nebaliopsis typica		2	1.1	<0.1

Table 6. Continued.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
Shrimp	9			
Caridea		2	1.1	0.1
Oplophoridae		3	1.6	<0.1
Notostomus spp.		4	2.2	0.2
Acanthephyra sp.		1	0.5	<0.1
A. exima		1	0.5	0.3
Pasiphaeidae		2	1.1	<0.1
Unidentified shrimp		11	5.5	0.3
Crab	16			
Brachyura		3	1.6	0.1
Grapsidae				
Planes cyaneus		11	2.2	<0.1
Unidentified crustacean		56	27.9	2.8
TUNICATA				
Pyrosomatidae	11	25	4.4	0.6
INSECTA				
Gerridae	28.5			
Halobates sericeus		2	0.5	<0.1
COELENTERATA				
Velellidae	6			
Velella velella		668	9.8	4.0
UNIDENTIFIED REMAINS	3	67	32.2	10.8

ates by volume. Squids (especially Ommastrephidae), flyingfishes, wind-sailers, and mysids (*G. gigas* and *G. ingens*) were the highest ranking prey items (Table 6). The ranking of unidentified crustaceans, fishes, and other remains within the top 8 categories underscores the poor sample condition. Laysan albatrosses very frequently ate squid, which occurred in 93% of our samples. Flyingfishes (including ova), the next highest ranked prey, occurred in only 13% of our samples and accounted for only 4% of the volume of the prey (Table 6). By-the-wind sailors ranked below flyingfishes, occurring in <10% of the samples and accounting for 4% of the prey volume. Mysids of both *Gnathophausia* species and the isopod *Anuropus branchiatus* were not expected to be prey because they are believed to occur only in very deep water. Because Laysan albatrosses are surface feeders, these crustaceans must occur regularly in surface waters.

Table 7. Lengths and volumes of some prey items[a] of the Laysan albatross. Length and volume values are not necessarily for the same individuals.

Prey	Sample size		Minimum		Maximum		Mean		SE	
	Length	Vol	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)
FISHES										
Exocoetidae ova		6		3.4		195		44		30
MOLLUSCA										
Ommastrephidae	155		28		144		71		2	
Symplectoteuthis spp.	4		77		92		86			3
CRUSTACEA										
Anuropus branchiatus	7		49		840		187		109	
Planes cyaneus	11		8		17		10		1	
Amphipoda	7	2	12	0.2	58	0.7	28	0.4	6	0.3
TUNICATA										
Pyrosomatidae	15		21		80		39		5	

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods).

Only 229 prey items were sufficiently intact to measure, and they ranged from an 8-mm crab to a 150-mm mysid. Most measurements were of ommastrephid squids, which averaged 71 mm in length (Table 7). We were unable to obtain length or volume data from any fish prey. We did measure the volumes of flyingfish ova masses that averaged 44 ml. Prey length data from a species that is known to shred its prey before ingestion must be interpreted with caution. Squid arms on Laysan albatross colonies were found that must have come from much larger individuals than the largest squid (144 mm) that we were able to measure. Okutani and Ih-Hsiu (1978) stated that *Symplectoteuthis oualaniensis* (Ommastrephidae) attains lengths >460 mm. In addition, some of the large beaks that we found probably came from very large squids.

Our rankings of prey items of the Laysan albatross showed only minor variation among island groups or seasons. In all 3 regions, unidentified or ommastrephid squids were the highest ranked prey during both winter and spring. Wind-sailers ranked high in the Midway region during spring but not winter and in the Laysan region during winter but not spring. This prey item did not occur in the French Frigate Shoals region. Pacific sauries were consumed both as fish and as egg masses. They ranked high only during winter in the Midway region and did not occur during spring. They occurred sporadically in samples from other regions. Mysids were generally found January–June in each of the 3 regions but proved to be especially common in the diet of the Laysan albatross during this period in the French Frigate Shoals region and during spring at Midway.

Our results corroborate earlier qualitative reports that this species feeds on squids (Fisher 1904), shrimps, and fish roe (Anderson 1954). Kenyon and Kridler (1969) identified squid beaks from Octopodoteuthidae and Onychoteuthidae in addition to Ommastrephidae.

Masked Booby.—We obtained 305 samples from masked boobies from most of the islands within the Hawaiian Archipelago but predominantly from French Frigate Shoals, Laysan, and Kure. Samples were collected March–November. Samples were obtained easily from adults (76%), subadults (7%), and nestlings (16%). Pooling all samples collected 1978–80, the mean volume was 167 ml, and there was a mean 2.5 prey items/sample. Samples from masked boobies generally were in good condition. More than 97% of the fishes from these samples were identified to family and more than 65% to genus or species.

Fish constituted over 97% of the sample volumes with squid comprising the re-

Table 8. Prey items identified to lowest taxon in 305 masked booby samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Belonidae	11			
Platybelone argalus platyura		3	0.7	0.1
Ablennes hians		1	0.3	<0.1
Unidentified belonid		1	0.3	<0.1
Carangidae	2			
Decapterus spp.		126	25.6	22.7
D. macarellus		10	2.0	1.7
D. macrosoma		71	6.2	4.6
Cirrhitidae	18.5			
Cirrhitops fasciatus		1	0.3	<0.1
Coryphaenidae	5			
Coryphaena spp.		2	0.7	0.1
C. hippurus		3	1.0	0.7
C. equiselis		16	3.0	2.0
Echeneidae	17	2	0.3	0.1
Exocoetidae	1			
Parexocoetus brachypterus		21	2.3	1.0
Exocoetus volitans		45	6.2	3.7
Cypselurus spp.		89	26.2	22.7
C. speculiger		6	2.0	0.8
C. atrisignis		1	0.3	0.3
Unidentified exocoetid		202	43.9	29.5
Gempylidae	14			
Gempylus serpens		3	1.0	<0.1
Hemiramphidae	3.5			
Euleptorhamphus viridis		31	7.2	2.7
Unidentified hemiramphid		4	0.7	0.1
Istiophoridae	13			
Tetrapterus angustirostris		1	0.3	<0.1
Unidentified istiophorid		1	0.3	<0.1
Kyphosidae	9			
Kyphosus bigibbus		6	1.3	0.6
Mullidae	10	10	1.3	0.1
Nomeidae	12			
Psenes cyanophrys		3	0.7	0.1
Pomacentridae	15	1	0.3	0.3
Scomberesocidae	16			
Cololabis saira		2	0.3	0.1
Scombridae	7			
Auxis thazard		2	0.7	0.7
Katsuwonus pelamis		6	1.6	1.5
Unidentified fishes	6	18	5.9	0.8
MOLLUSCA				
Decapoda				
Ommastrephidae	3.5			
Symplectoteuthis spp.		6	1.3	0.2
S. oualaniensis		4	0.7	0.1
Hyaloteuthis pelagicus		2	0.3	<0.1
Unidentified ommastrephid		58	8.5	2.2
Unidentified squids	8	12	2.6	0.1
UNIDENTIFIED REMAINS	18.5	1	0.3	<0.1

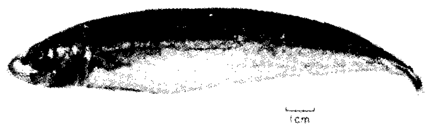

Fig. 7. *Decapterus* sp., a prey item.

mainder. Fifteen fish families and a single family of squid were identified. Flyingfishes ranked highest among the prey items, followed by jacks, halfbeaks, squids (Ommastrephidae), and dolphin-fishes (Table 8). Many of the flyingfishes were identified, including *Cypselurus speculiger*, *C. atrisignis*, *Parexocoetus brachypterus*, and *E. volitans*. All carangids were *Decapterus* spp. (Fig. 7), with many identified as *D. macrosoma* or *D. macarellus* (Fig. 2). All of the halfbeaks identified were *Euleptorhamphus viridis*. Some of the squids were identified as *S. oualaniensis* and *Hyaloteuthis pelagicus*. All of the dolphin-fishes were genus *Coryphaena* with the preponderance being *C. equiselis* rather than *C. hippurus*.

Length measurements were taken for 193 prey items and ranged from a 29-mm hawk fish to a 343-mm flyingfish. The mean for all measured prey was 161 mm. The fishes with the longest mean lengths were *E. viridis* (276 mm), *Cypselurus* spp. (231 mm), and *D. macarellus* (207 mm) (Table 9). The lengths of ommastrephid squids averaged 90 mm. The few displacement volumes of prey that we measured averaged 51 ml and ranged from 0.7 to 220 ml.

The families of prey items that ranked high when all data were combined (Table 8) remained high when the data were separated into seasons and island groups. Flyingfishes and carangids were the 2 highest ranking families, with flyingfishes ranking higher during the first 6 months of the year and carangids ranking higher during the second 6 months. Similarly halfbeaks ranked higher than dolphin-fishes during March–June, but dolphin-fishes were higher than halfbeaks July–November. Ommastrephid squids ranked

Table 9. Lengths and volumes of some prey items[a] of the masked booby. Length and volume values are not necessarily for the same individuals.

Prey	Sample size		Minimum		Maximum		Mean		SE	
	Length	Vol	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)
FISHES										
Decapterus macarellus	8	2	185	132	224	139	207	136	5	4
D. macrosoma	8		66		165		133		14	
Decapterus spp.	29	1	66	220	240	220	195	220	6	
Parexocoetus brachypterus	11	5	125	34	153	44	136	37	3	2
Exocoetus volitans	30	3	95	32	184	56	144	47	4	8
Cypselurus spp.	22	2	134	90	343	102	231	96	13	6
Euleptorhamphus viridis	9	1	169	53	301	53	267	53	14	
MOLLUSCA										
Ommastrephidae	35	4	46	8	1,280	18	90	12	3	2
Symplectoteuthis spp.	6	1	73	13	100	13	88	13	4	

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods).

higher throughout the year in the French Frigate Shoals region than elsewhere, and were common in the Laysan and Midway regions only during spring. Pacific sauries ranked third during winter in the Midway Island group. Large flyingfishes and *Decapterus* spp. dominated the diet of this booby throughout the seasons and areas studied, but some changes in order of ranking are evident.

The diet of this species in Hawaii is similar to that reported from Christmas Island (Pacific Ocean) (Schreiber and Hensley 1976) and Ascension Island (Stonehouse 1962, Dorward 1963*a*). However, the diet in Hawaii is unique in the importance of *Decapterus* spp.

Great Frigatebird.—We collected and analyzed 284 regurgitations from great frigatebirds, primarily from Midway, Laysan, and French Frigate Shoals. We obtained samples during all months except December and January when 1978–80 are combined. Adults (37%), subadults (17%), and nestlings (45%) were sampled. The samples averaged 104 ml and 4.5 prey items. More than 96% of the fishes were identified at least to family.

Sample volumes were 85% fish, 14% squid, and 1% juvenile sooty terns. Twenty-three fish families and a single squid family were identified. We found no crustaceans. The highest ranking prey were flyingfishes (Fig. 8). Most were too digested to permit identification but *Cypselurus* spp., *Exocoetus volitans*, and *Parexocoetus brachypterus* were the most common (Table 10) of those identified. The second ranked item was ommastrephid squids. Of the few that could be identified, all were *Symplectoteuthis*, including *S. oualaniensis* and *S. luminosa*. Ranking third was Carangidae, mostly *Decapterus*, especially *D. macrosoma*. *D. macarellus* was also identified but is presented in Table 10 as *D.* spp. until the vertebrae of this species can be distinguished from *D. muroadsi*. Other highly ranked prey items included unidentified squids, a filefish (*Pervagor spilosoma*), and halfbeaks. We found few sooty terns, but B. Flint (pers. commun.) observed hundreds taken during 1980–81 at Tern Island, French Frigate Shoals.

We obtained lengths from 248 prey items. They averaged 83 mm and ranged from a 12-mm cow fish to a 272-mm halfbeak. The flyingfishes *E. volitans* and *P. brachypterus* averaged 141 and 135 mm, respectively (Table 11). *Symplectoteuthis* spp. averaged 85 mm. The fact that great frigatebirds will take cow fish ($\bar{x}$ = 17 mm) and filefish ($\bar{x}$ = 60 mm) in addition to the much larger flyingfishes demonstrates wide flexibility in the size classes of prey that may be exploited (Table 11).

Sampling was adequate to allow comparison among seasons and among the 3 island groups in the NWHI. Flyingfishes ranked very high throughout the year in each island group, usually first or second. Ommastrephid squids also ranked high throughout the archipelago, but peaked during spring and were absent from the Midway region during summer. Carangids were not found in any of 43 samples collected in winter, occurred to a limited degree in spring, but ranked very high in summer and fall, especially at French Frigate Shoals. Dolphin-fishes were very important in the Midway region during summer but occurred rarely elsewhere. Halfbeaks ranked fairly high throughout the archipelago, apparently ranking highest February–June. Pacific sauries ranked high during winter in the Midway region, and filefish ranked high during summer in the Laysan region. Neither of these fishes occurred in other regions, nor in other seasons within the region where they were found. This demonstrates the ability of the great frigatebird to locally exploit whatever prey is available, which is usually flyingfishes and squids.

The reliance of this species on flyingfishes and squids has also been reported at Ascension Island (Stonehouse 1962), Aldabra Atoll (Diamond 1974*a*), and Christmas Island (Schreiber and Hensley 1976). Great frigatebirds in Hawaii consume more *Decapterus* spp. than other areas studied and may feed on fewer juvenile sooty terns (Beard 1939, Schreiber and Hensley 1976) than they do elsewhere.

Brown Booby.—We collected 244 regurgitations from brown boobies, primarily from Laysan and Kure, but including samples from Lisianski, Pearl and Hermes Reef, Oahu, and Nihoa. We combined samples collected 1978–80, including material from each month March–November. Samples were readily obtained from adults (22%), juveniles (8%), and nestlings (69%). Brown boobies often spontaneously regurgitate upon seeing a human intruder in their colony. The samples averaged 100 ml and 12 prey items. The condition of samples from this species were among the best in this study, resulting in greater than

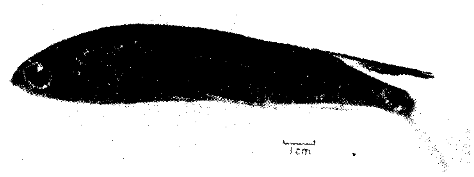

Fig. 8. Flyingfish, *Parexocoetus brachypterus*, a prey item.

98% of the fishes being identified to family or lower.

Fish made up 95% of the sample volumes, and virtually all of the remainder was squid. Eighteen fish families, a single squid family, and an isopod were identified. The highest ranking family was Carangidae. Most of the fishes from this family were *Decapterus*, especially *D. macrosoma*, but large numbers of amberjacks and fair numbers of pilot fish, *Selar crumenophthalmus*, and *Caranx* spp. were found (Table 12). Ranking next were flyingfishes and juvenile goatfishes. No attempt was made to further identify any of the goatfishes, but 7 species of flyingfishes were identified. Ranking highest were *E. volitans* and *P. brachypterus* with *Cypselurus* spp. following very closely. Halfbeaks (especially *E. viridis*) and ommastrephid squids (especially *Ommastrephes* spp. and *Symplectoteuthis* spp.) ranked next.

The generally good condition of the samples allowed length measurement of 463 prey items. These items had a mean of 94 mm and ranged from a 3-mm isopod to a 319-mm halfbeak. The mean lengths of some common prey items include *D. macrosoma* (158 mm), goatfishes (54 mm), *E. volitans* (128 mm), rudderfish (81 mm), and Ommastrephidae (81 mm) (Table 13). Brown boobies exploit prey over a fairly wide range of lengths. Few prey items were considered intact enough to warrant the measurement of displacement volumes. The volumes we obtained averaged 25 ml, ranging from a 2-ml squid to a 68-ml halfbeak (Table 13).

An analysis of seasonal and geographical differences in this diet suffers from the fact that it was not feasible to collect sam-

Table 10. Prey items identified to lowest taxon in 284 great frigatebird samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Atherinidae	20			
Pranesus insularum		8	0.4	0.1
Balistidae	26	1	0.4	<0.1
Bramidae	26			
Brama orcini		1	0.4	<0.1
Carangidae	3			
Decapterus spp.		40	7.0	3.3
D. macrosoma		74	8.1	5.1
D. tabl		11	1.4	0.6
Selar crumenophthalmus		1	0.4	<0.1
Coryphaenidae	8			
Coryphaena spp.		4	1.1	0.5
C. hippurus		4	1.4	0.8
C. equiselis		4	1.4	0.5
Dactylopteridae	26			
Dactyloptena orientalis		1	0.4	<0.1
Exocoetidae	1			
Parexocoetus brachypterus		15	1.1	0.9
Exocoetus volitans		35	7.4	4.4
Cypselurus spp.		51	13.7	11.7
C. speculiger		1	0.4	0.2
C. simus		1	0.4	0.4
C. spilopterus		1	0.4	0.4
Unidentified exocoetid		346	61.6	42.5
Gempylidae	21			
Gempylus serpens		2	0.7	<0.1
Hemiramphidae	5			
Euleptorhamphus viridis		33	6.7	3.1
Oxyporhamphus micropterus		1	0.4	0.1
Unidentified hemiramphid		15	3.9	1.3
Istiophoridae	18			
Tetrapterus angustirostris		2	0.7	0.2
Kyphosidae	17			
Kyphosus bigibbus		4	0.7	0.2
Macrouridae	23	1	0.4	0.1
Molidae	16			
Ranzania laevis		2	0.4	0.2
Masturus lanceolatus		5	0.4	0.1
Monacanthidae	5			
Pervagor spilosoma		81	2.5	1.5
Unidentified monacanthid		20	1.1	0.3
Mullidae	9	49	2.8	0.6
Nomeidae	26	1	0.4	<0.1
Ostraciontidae	12			
Lactoria fornasini		85	1.4	0.5
Polymixiidae	22			
Polymixia japonica		1	0.4	0.4
Priacanthidae	19			
Priacanthus cruentatus		1	0.4	<0.1
Unidentified priacanthid		1	0.4	<0.1
Scomberesocidae	10.5			
Cololabis saira		15	1.4	1.3
Scombridae	10.5			
Auxis spp.		3	0.4	0.4
Katsuwonus pelamis		5	1.8	0.6
Thunnus alalunga		1	0.4	0.1
Unidentified scombrid		1	0.4	0.1
Tetraodontidae	13			
Lagocephalus lagocephalus		3	1.1	0.6
Unidentified tetraodontid		1	0.4	0.1
Xiphiidae	26			
Xiphias gladius		1	0.4	0.1
Unidentified fishes	7	32	11.3	1.9
SEABIRDS				
Sterna fuscata	15	2	0.7	0.7
MOLLUSCA				
Decapoda				
Ommastrephidae	2			
Symplectoteuthis spp.		14	3.2	0.9
S. oualaniensis		4	1.4	0.3
S. luminosa		2	0.4	0.1
Unidentified ommastrephid		209	23.6	10.7
Unidentified squids	5	73	11.6	1.6
UNIDENTIFIED REMAINS	14	3	1.1	0.2
UNIDENTIFIED MEAT		1	0.4	0.4

ples from many locations when we desired. Carangids were the highest ranked prey family overall, and this ranking is generally consistent at each island group and season. However, carangids ranked low during winter in the Midway Island group (perhaps due to a small sample size) and ranked fourth during spring in the Laysan Island group, where they made up 8% of the volume of prey consumed. During summer at Laysan, carangids ranked highest, comprising 42% of the volume of prey taken. Goatfishes ranked very high in the Laysan group during both seasons (spring and summer) during which adequate samples were collected. Nevertheless, in the Midway Island group, goatfishes were most important during spring but were absent in the 64 samples collected during the other 3 seasons. Flyingfishes ranked uniformly high in the Laysan group throughout the seasons sampled. In contrast, this family varied in ranking and

Table 11. Lengths and volumes of some prey items[a] of the great frigatebird. Length and volume values are not necessarily for the same individuals.

Prey	Sample size		Minimum		Maximum		Mean		SE	
	Length	Vol	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)
FISHES										
Decapterus macrosoma	3		147		160		153		4	
Pervagor spilosoma	22		42		71		60		1	
Parexocoetus brachypterus	11		129		141		135		1	
Exocoetus volitans	20	1	107	54	165	54	141	54	4	
Lactoria fornasini	42		12		22		17		<0.5	
MOLLUSCA										
Ommastrephidae	103	1	42	25	118	25	78	25	2	
Symplectoteuthis spp.	9		64		105		85		5	

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods).

percentage total volume in the Midway group, being first during winter (36%) and summer (53%) but fourth during spring (13%) and fall (10%). Ommastrephid squids ranked high only during spring and summer. Needlefishes (fall) and rudderfish (winter) ranked high at Midway. This analysis demonstrates that overall patterns are relatively constant, but some subtle changes in diet take place.

The diet of brown boobies in Hawaii is distinguished from diets elsewhere in the prevalence of *Decapterus* spp. and goatfishes. The brown booby apparently changes its diet greatly with location. Murphy (1936:859) mentioned the consumption of flatfishes, parrot fishes, and large prawns. Serventy (1952) listed *Rastrelliger kanagurta, Trachurus,* and *Chorinemus lysan* as prey in the Sahul Shelf, Australia. Dorward (1963*a*) stated it fed on blennies at Ascension Island. However, most authors have found flyingfishes to be an important component of the diet.

Red-footed Booby.—We collected and analyzed 369 samples from red-footed boobies from 1978–80. Most were taken from Midway, Laysan, and French Frigate Shoals, but some were collected on each island in the study area with the exception of Pearl and Hermes Reef. Samples came from all months except December and included adults (79%), subadults (1%), and nestlings (20%). They averaged 73 ml and 5.8 prey items. The condition of the samples was reasonably good, and more than 97% of the fishes were identified at least to family.

Fish accounted for more than 72% of the sample volumes with squid representing most of the remaining 27%. Twenty-seven fish families, 1 squid family, a copepod, and an insect were found. Pooling all years, areas, and seasons, flyingfishes ranked highest among the prey. Most of these fishes could not be identified further, but of those identified, *E. volitans, P. brachypterus,* and *Cypselurus* spp. were common (Table 14). Ommastrephid squids ranked second and included *Ommastrephes* spp., *Hyaloteuthis pelagicus, S. oualaniensis,* and *S. luminosa.* Carangidae ranked third and consisted mostly of *Decapterus* spp., especially *D. macrosoma* and *D. tabl.* Unidentified squids ranked fourth, followed by juvenile goatfishes and Pacific sauries (Table 14).

We obtained 550 measurements of prey items with a mean length of 88 mm and ranging from a 32-mm balloon fish to a 282-mm halfbeak. These data show that red-footed boobies take prey with mean lengths 50–150 mm, including *Decapterus* spp. (149 mm), *E. volitans* (126 mm), and *S. oualaniensis* (82 mm) (Table 15). The red-footed booby had fairly wide flexibility in the size of prey it consumed. We had only 41 prey items in good enough condition to be measured volumetrically.

Table 12. Prey items identified to lowest taxon in 244 brown booby samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Ammodytidae	13			
Bleekeria gillii		20	1.2	0.3
Atherinidae	15			
Pranesus insularum		12	0.4	0.3
Belonidae	6			
Platybelone argalus platyura		50	8.2	4.4
Ablennes hians		4	1.6	0.1
Blenniidae	14	5	0.4	0.4
Carangidae	1			
Decapterus spp.		145	23.8	13.8
D. macarellus		8	1.6	0.5
D. macrosoma		99	11.9	7.2
D. tabl		16	4.5	1.3
Selar crumenophthalmus		5	0.8	0.5
Naucrates ductor		14	0.2	0.2
Seriola spp.		53	8.2	3.5
Caranx spp.		9	0.8	0.1
Unidentified carangid		13	2.0	0.1
Coryphaenidae	12			
Coryphaena spp.		2	0.4	0.2
C. hippurus		3	0.8	<0.1
C. equiselis		8	1.6	0.5
Echeneidae	18.5			
Remoropsis brachypterus		2	0.8	0.1
Unidentified echeneid		1	0.4	<0.1
Exocoetidae	2.5			
Parexocoetus brachypterus		22	2.9	1.9
Exocoetus sp.		1	0.4	0.4
E. volitans		56	9.4	4.9
Prognichthys gilberti		8	0.8	0.5
Cypselurus spp.		24	7.0	5.4
C. speculiger		4	1.2	0.4
C. spilonotopterus		1	0.4	0.4
C. atrisignis		5	0.8	0.4
Unidentified exocoetid		104	24.2	11.5
Gempylidae	17			
Gempylus serpens		3	1.2	<0.1
Unidentified gempylid		1	0.4	0.1
Hemiramphidae	4			
Euleptorhamphus viridis		53	13.1	7.5
Hyporhamphus acutus pacificus		2	0.4	0.1
Oxyporhamphus micropterus		1	0.4	0.2
Unidentified hemiramphid		35	4.5	1.9
Kyphosidae	7			
Kyphosus bigibbus		68	9.0	3.6
Labridae	16			
Hemipteronotus leclusei		4	0.4	0.4
Mullidae	2.5	1,852	30.0	15.3
Nomeidae	11			
Nomeus gronovii		3	1.2	0.1
Psenes cyanophrys		11	2.0	0.6
Unidentified nomeid		9	1.6	0.1
Priacanthidae	20			
Priacanthus sp.		1	0.4	0.1
Unidentified priacanthid		2	0.4	0.1
Scomberesocidae	18.5			
Cololabis saira		4	0.4	0.3
Scombridae	10			
Scomber japonicus		2	0.8	0.7
Katsuwonus pelamis		8	2.9	1.4
Acanthocybium solandri		3	0.8	0.4
Unidentified scombrid		1	0.4	0.1
Sphyraenidae	21			
Sphyraena helleri		1	0.4	0.2
Unidentified fishes	8	46	17.6	2.3
MOLLUSCA				
Decapoda				
Ommastrephidae	5			
Ommastrephes spp.		3	0.8	0.3
Symplectoteuthis spp.		2	0.8	0.1
S. oualaniensis		1	0.4	0.1
S. luminosa		1	0.4	0.1
Unidentified ommastrephid		61	12.7	3.7
Unidentified squids	9	35	6.1	0.5
CRUSTACEA				
Isopoda	22	1	0.4	0.1

These items ranged from 0.6 to 129 ml, averaging 26 ml.

Sampling was generally adequate to compare the most common prey items for all seasons in all of the island groups of the NWHI. Flyingfishes ranked first or second in almost all seasons for all regions. Ommastrephid squids also ranked high in each season and area sampled, but were apparently most important in the French Frigate Shoals region. Carangids ranked highest during summer but were present in the species lists for most areas throughout the year. Goatfishes were present at low levels throughout the year but ranked highest in the diet of the red-footed booby during spring. Several fishes were common only during a single season. At Midway, Pacific sauries ranked second in winter and anchovies ranked third in fall. Neither occurred elsewhere during any season, nor was found in the diet of this booby during other seasons at Midway. Skipjack tunas ranked high only in fall at Midway and French Frigate Shoals. Snake

Table 13. Lengths and volumes of some prey items[a] of the brown booby. Length and volume values are not necessarily for the same individuals.

Prey	Sample size		Minimum		Maximum		Mean		SE	
	Length	Vol	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)
FISHES										
Seriola spp.	27	5	49	6	165	41	100	31	6	6
Decapterus spp.	19	3	63	4	215	24	146.3	11	12	6
D. macrosoma	12	1	110	67	200	67	158	67	7	
Mullidae	164	2	37	2	83	2	54	2	<0.5	0
Exocoetidae	11		31		219		115		17	
Parexocoetus brachypterus	15	1	129	27	146	27	137	27	1	
Exocoetus volitans	32		107		179		128		3	
Cypselurus spp.	11		117		234		166		12	
Euleptorhamphus viridis	9		191		319		281		13	
Kyphosus bigibbus	24	1	41	9	170	9	72	9	6	
Psenes cyanophrys	8		51		128		81		10	
Cololabis saira	3		218		233		223		5	
Platybelone argalus platyura	5		205		248		231		8	
MOLLUSCA										
Ommastrephidae	48	6	41	2	129	50	81	37	4	7

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods).

mackerels ranked fourth at Laysan during winter. These changes in relative abundance of dietary components implies some differences of availability within a fairly constant framework.

Our results correspond generally with previous studies that indicate the prevalence of flyingfishes and ommastrephid squids in the diet of this species at Oahu, Hawaii (Ashmole and Ashmole 1967*a*), South America (Murphy 1936:869), Aldabra Atoll (Diamond 1974*b*), and Christmas Island (Pacific) (Schreiber and Hensley 1976). The diet of Hawaiian birds is unique because carangids, goatfishes, and Pacific sauries are common components.

Red-tailed Tropicbird.—We collected and analyzed 270 samples from red-tailed tropicbirds. Most were taken from French Frigate Shoals, Laysan, and Midway, with others coming from Lisianski, Nihoa, and Kure. By pooling all samples together from 1978–80, samples representing each month except January were collected. Samples were taken from adults (28%), subadults (12%), and chicks (60%). They contained an average of 57 ml and 4 prey items. The condition of the samples was fairly good, allowing for identification to family of more than 90% of the fishes.

The prey of this species consisted of 24 fish families, 2 squid families, stomatopods, and shrimps (Table 16). Prey items were 82% fish and 18% squid by volume, and a few crustaceans. Flyingfishes were the most prominent prey. Seventy-eight percent of these could not be identified further, but *E. volitans* and *Cypselurus* spp. were common among those identified. Ommastrephid squids ranked second and were primarily *S. oualaniensis*, *Ommastrephes* spp., and *Hyaloteuthis pelagicus*. The third ranked prey were the carangids, mostly *Decapterus macrosoma*. Ranking fourth and fifth were unidentified squids and dolphin-fishes, respectively (Fig. 9). The latter were *Coryphaena* and included more *C. equiselis* than *C. hippurus*. Other common prey items were truncated sunfish and balloonfish.

We obtained 169 prey items that were in good enough condition to measure. Their mean length was 101 mm and ranged from a 10-mm stomatopod to a 237-mm balloonfish. *Decapterus* spp. had a mean length of 168 mm and squids ranged 70–90 mm (Table 17). One flyingfish was only 13 mm.

The distribution of our sampling effort limits comparisons we can make among island groups and among seasons because most samples were collected during spring

Table 14. Prey items identified to lowest taxon in 360 red-footed booby samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Ammodytidae	12			
Bleekeria gillii		59	3.3	0.3
Belonidae	24			
Ablennes hians		1	0.3	0.2
Carangidae	3			
Decapterus spp.		124	13.9	6.5
D. macarellus		1	0.3	0.3
D. macrosoma		67	5.0	2.6
D. tabl		32	2.2	0.8
Seriola sp.		1	0.3	0.1
Unidentified carangid		6	0.8	0.1
Cheilodactylidae	30			
Cheilodactylus vittatus		1	0.3	<0.1
Coryphaenidae	14.5			
Coryphaena spp.		2	0.6	<0.1
C. hippurus		3	0.8	0.1
C. equiselis		3	0.6	<0.1
Diodontidae	30	1	0.3	<0.1
Engraulidae	10			
Stolephorus buccaneeri		131	2.8	0.7
Exocoetidae	1			
Parexocoetus brachypterus		22	3.3	2.3
Exocoetus volitans		59	9.4	4.7
Cypselurus spp.		48	10.0	7.1
C. speculiger		7	1.7	1.1
C. atrisignis		1	0.3	0.1
C. spilopterus		4	1.1	0.7
Unidentified exocoetid		319	50.3	29.4
Gempylidae	11			
Gempylus serpens		32	5.8	0.5
Unidentified gempylid		1	0.3	<0.1
Gonorhynchidae	18			
Gonorhynchus gonorhynchus		7	0.6	0.1
Gonostomatidae	16			
Vinciguerria spp.		2	0.3	<0.1
V. nimbaria		33	0.3	0.1
Hemiramphidae	9			
Euleptorhamphus viridis		11	3.1	1.1
Oxyporhamphus micropterus		10	1.7	0.8
Unidentified hemiramphid		2	0.6	0.2
Holocentridae	22.5			
Sargocentron sp.		1	0.3	<0.1
Unidentified holocentrid		1	0.3	<0.1
Istiophoridae	22.5	2	0.6	<0.1
Kyphosidae	25.5			
Kyphosus bigibbus		2	0.3	<0.1
Macrorhamphosidae	30			
Macrorhamphosus gracilis		1	0.3	<0.1
Molidae	13			
Ranzania laevis		18	3.1	1.7
Masturus lanceolatus		2	0.3	0.1
Monacanthidae	19	4	0.6	0.1
Mullidae	6	156	8.9	1.6
Myctophidae	30	1	0.3	<0.1

Table 14. Continued.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
Nomeidae	14.5			
Psenes cyanophrys		4	0.3	0.1
Unidentified nomeid		10	1.1	0.1
Priacanthidae	20	2	0.6	0.1
Scomberesocidae	5			
Cololabis saira		59	6.4	4.3
Scombridae	8			
Katsuwonus pelamis		19	4.4	2.5
Thunnus sp.		1	0.3	0.3
Unidentified scombrid		3	0.8	0.3
Sphyraenidae	30	1	0.3	<0.1
Synodontidae	21	3	0.8	<0.1
Tetraodontidae	30			
Lagocephalus lagocephalus		1	0.3	<0.1
Unidentified fishes	7	39	10.6	1.4
MOLLUSCA				
Decapoda				
Ommastrephidae	2			
Ommastrephes spp.		9	0.8	0.3
Symplectoteuthis spp.		41	8.3	1.9
S. oualaniensis		57	7.2	3.2
S. luminosa		11	0.8	0.5
Hyaloteuthis pelagicus		16	1.9	0.3
Unidentified ommastrephid		508	37.5	19.0
Unidentified squids	4	130	14.2	2.0
CRUSTACEA				
Copepoda	25.5			
Pennellidae				
Penella spp.		2	0.3	<0.1
INSECTA	30	1	0.3	<0.1
UNIDENTIFIED REMAINS	17	3	0.8	0.2

or summer. Flyingfishes ranked highest at most locations for all seasons in which sampling was possible. Ommastrephid squids also ranked high throughout the year but were apparently more so during spring than during summer. *Decapterus* spp. were common during summer but not during winter or spring. Dolphin-fishes were sporadically common throughout the sampling period at various locations. Two fishes were taken only seasonally. Pacific sauries ranked high during winter in the Midway region but did not occur elsewhere. Truncated sun fish occurred only during summer and did not rank high anywhere except French Frigate Shoals. Red-tailed tropicbirds fed heavily on 130–

Table 15. Lengths and volumes of some prey items[a] of the red-footed booby. Length and volume values are not necessarily for the same individuals.

Prey	Sample size		Minimum		Maximum		Mean		SE	
	Length	Vol	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)
FISHES										
Decapterus tabl	8		62		177		97		16	
Decapterus spp.	9		83		214		149		13	
D. macrosoma	4		147		173		163		5	
Stolephorus buccaneeri	45		57		83		69		1	
Oxyporhamphus micropterus	8	5	111	12	180	38	141	25	8	5
Parexocoetus brachypterus	10	3	113	19	142	33	131	27	3	4
Exocoetus volitans	36	3	76	16	208	26	126	21	5	3
Mullidae	3		54		60		58		2	
MOLLUSCA										
Ommastrephidae	256	17	40	6	208	43	78	24	1	2
Symplectoteuthis spp.	32	1	38	13	117	13	70	13	3	
S. oualaniensis	45	3	54	12	131	26	82	21	2	5
Hyaloteuthis pelagicus	14		49		110		60		4	

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods).

160 mm flyingfishes and *Decapterus* spp. and 70–90 mm ommastrephid squids.

Flyingfishes (especially *Cypselurus* spp. and *E. volitans*) and squids are known to occur in the diet of this species at Christmas Island (Indian) (Gibson-Hill 1947), Kure (Fleet 1974), Christmas Island (Pacific) (Ashmole and Ashmole 1967*b*), and Aldabra Atoll (Diamond 1975). The diet of this species in Hawaii is unique in the prevalence of carangids, dolphin-fishes, and sun fish.

Wedge-tailed Shearwater.—During 1978–80, we collected 233 samples from wedge-tailed shearwaters. Collections were possible only May–November. This species does not visit its colonies between breeding seasons, and courting adults that come to shore in early spring apparently live off fat reserves and have empty stomachs. Most of our samples were taken from Oahu, Laysan, and Midway, but some were taken from each island in our study area except Necker and Lisianski. Many of the samples were in fairly advanced states of digestion. For this reason 80% of the samples were taken from adults and 20% from dependent young because adults had less-digested samples. Samples displaced an average 16 ml and contained 8.4 prey items. More than 96% of the fishes could be identified to family, and 51% could be identified to genus or species.

We found 21 fish families, a squid family, an octopus, a stomatopod, an isopod, a crab, an insect, and a coelenterate (Table 18). By volume, the prey constituted 66% fish, 28% squid, and 1% crustaceans. As with all procellariiformes, stomach oil was regurgitated, but we ignored this component in our laboratory analysis. Pooling all months, years, and locations, the highest ranked prey was goatfishes (Fig. 10). No attempt was made to further identify this family because samples were comprised of juveniles, many of which were very well-digested. The second ranked prey item was Carangidae, including *Decapterus macrosoma*, *D. tabl*, and probably *D. macarellus* and *D. muroadsi*. The third and fourth ranked prey items were Ommastrephidae (including *S. oualaniensis*) and unidentified squids. It is likely that most of the unidentified squids were ommastrephids. Other common prey items included filefish, flyingfishes, and gobies.

The lengths of the 212 prey items that were in good enough condition for reliable measurement averaged 57 mm, rang-

Table 16. Prey items identified to lowest taxon in 270 red-tailed tropicbird samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Ammodytidae	29			
Bleekeria gillii		1	0.4	0.1
Belonidae	19			
Ablennes hians		1	0.4	0.1
Unidentified belonid		1	0.4	0.2
Carangidae	3			
Decapterus spp.		53	15.9	9.5
D. macrosoma		29	4.8	3.6
D. tabl		1	0.4	0.1
Naucrates ductor		1	0.4	0.4
Coryphaenidae	5			
Coryphaena spp.		13	4.8	2.9
C. hippurus		9	3.3	2.4
C. equiselis		18	6.7	3.9
Diodontidae	14			
Diodon spp.		3	1.1	0.3
D. hystrix		1	0.4	0.1
Unidentified diodontid		2	0.7	0.2
Echeneidae	21			
Remoropsis brachypterus		1	0.4	0.1
Unidentified echeneid		1	0.4	0.1
Exocoetidae	1			
Parexocoetus brachypterus		3	0.7	0.5
Exocoetus volitans		22	7.4	3.2
Cypselurus spp.		20	5.9	3.4
C. speculiger		1	0.4	0.3
C. spilopterus		1	0.4	0.4
Unidentified exocoetid		167	39.6	24.1
Gempylidae	13			
Gempylus serpens		8	3.0	0.3
Unidentified gempylid		1	0.4	<0.1
Hemiramphidae	11			
Euleptorhamphus viridis		10	2.6	1.6
Unidentified hemiramphid		5	1.5	0.4
Istiophoridae	22	1	0.4	0.4
Kyphosidae	15.5			
Kyphosus bigibbus		4	1.1	0.6
Molidae	7			
Ranzania laevis		23	5.2	4.3
Masturus lanceolatus		2	0.7	0.5
Monacanthidae	23	2	0.4	0.1
Mullidae	17	5	1.5	0.3
Myctophidae	29	1	0.4	<0.1
Nomeidae	15.5			
Cubiceps pauciradiatus		1	0.4	0.1
Unidentified nomeid		4	1.5	0.2
Pomacentridae	25.5	1	0.4	0.1
Priacanthidae	29			
Priacanthus sp.		1	0.4	<0.1
Scomberesocidae	9			
Cololabis saira		18	4.1	4.1
Scombridae	16			
Auxis spp.		2	0.7	0.5
Katsuwonus pelamis		7	2.6	2.2
Unidentified scombrid		3	1.1	0.7
Synodontidae	20	11	0.4	0.1
Tetraodontidae	8			
Lagocephalus lagocephalus		13	4.8	3.2
Unidentified tetraodontid		4	1.1	0.6
Xiphiidae	12			
Xiphias gladius		7	2.6	1.5
Tetrodontoidei (puffer)	25.5	1	0.4	0.1
Unidentified fishes	6	50	16.7	4.0
MOLLUSCA				
Decapoda				
Ommastrephidae	2			
Ommastrephes sp.		1	0.4	<0.1
Symplectoteuthis spp.		20	6.3	2.2
S. oualaniensis		16	4.8	2.4
Hyaloteuthis pelagicus		1	0.4	0.1
Unidentified ommastrephid		139	24.4	10.1
Onychoteuthidae	18			
Onychoteuthis spp.		2	0.4	0.4
Unidentified onychoteuthid		1	0.4	<0.1
Unidentified squids	4	354	17.4	2.6
CRUSTACEA				
Stomatopoda	24			
Lysiosquilla spp.		2	0.4	<0.1
Unidentified stomatopod		1	0.4	<0.1
Shrimp	29	1	0.4	<0.1
UNIDENTIFIED REMAINS	29	1	0.4	<0.1

ing from a 4-mm sea-strider to a 145-mm *D. macrosoma* (Table 19). Juvenile goatfishes had a mean length of 54 mm, and ommastrephid squids had a mean length of 63 mm. Unfortunately, we only had a few *Decapterus* spp. measurements, but those we had were in the 80–100 mm range.

Our inability to collect samples from several places in the archipelago during some seasons precludes a detailed analysis of changes in diet with season and island group. It is apparent that goatfishes ranked highest during spring and continued to rank high in the Laysan region but not Midway during summer. Ommastrephid squids ranked high in the Midway region throughout the 3 seasons sampled and ranked first at Oahu during fall. These

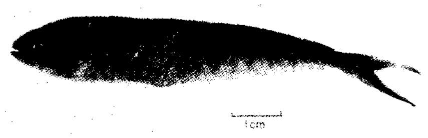

Fig. 9. Dolphin-fish, a prey item.

Fig. 10. Goatfish, a prey item.

squids also ranked high in the Laysan region during spring but less so during summer. Carangids ranked higher in the Laysan Island group than Midway, especially during summer when they constituted 60% by volume at Laysan, but they did not occur in any of the 12 samples from Midway. Lanternfishes ranked high only during spring at Midway, and filefishes were important only in the Laysan Island group. Wedge-tailed shearwaters fed heavily on ommastrephid squids during fall but supplemented this food source with prey items that were not taken during spring or summer. These included anchovies, crabs, and stomatopods in the Midway region and gobies in the Oahu region, neither of which were taken anywhere during spring or summer. This species fed heavily on goatfishes, *Decapterus* spp., and ommastrephid squids in the 50–100 mm size class and took other prey items when available. Fragmentary information from the Indian Ocean (Bailey and Bourne 1963) indicates that squids are consumed by this species elsewhere.

Christmas Shearwater.—During 1978–80 we collected and analyzed 182 samples from Christmas shearwaters. Most came from Laysan, but some were collected on each island in the Hawaiian Archipelago with the exceptions of Necker and Oahu. Because this species does not make landfall when it is not breeding, our sampling was restricted to March–September. Although a few samples were taken from nestlings (4%), most (96%) were taken from adults. The samples had a mean volume of 15 ml and contained a mean of 5.4 prey items. This is half the number of prey items per sample found by Ashmole and Ashmole (1967*b*). Despite the fairly digested condition of many of the sam-

Table 17. Lengths and volumes of some prey items[a] of the red-tailed tropicbird. Length and volume values are not necessarily for the same individuals.

Prey	Sample size		Minimum		Maximum		Mean		SE	
	Length	Vol	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)
FISHES										
Decapterus spp.	6		140		216		168		13	
D. macrosoma	5	1	131	65	181	65	153	65	8	
Coryphaena hippurus	3	2	111	12	189	78	148	45	23	33
C. equiselis	4		134		183		163		11	
Exocoetidae	11		13		201		133		14	
Exocoetus volitans	16	2	124	36	159	46	140	41	3	5
Ranzania laevis	5	1	123	34	140	34	130	34	4	
MOLLUSCA										
Ommastrephidae	58		23		128		82		3	
Symplectoteuthis spp.	10		52		120		80		6	
S. oualaniensis	14	1	60	32	113	32	90	32	4	

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods).

Table 18. Prey items identified to lowest taxon in 233 wedge-tailed shearwater samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Ammodytidae	30.5			
Bleekeria gillii		1	0.4	<0.1
Carangidae	2			
Decapterus spp.		64	13.3	8.5
D. macrosoma		55	14.6	11.5
D. tabl		19	6.4	4.7
Selar crumenophthalmus		4	0.9	0.2
Seriola sp.		1	0.4	0.2
Unidentified carangid		2	0.9	0.1
Clupeidae	15			
Sardinella marquesensis		7	0.9	0.5
Coryphaenidae	17			
Coryphaena sp.		1	0.4	<0.1
C. equiselis		3	1.3	0.2
Dactylopteridae	30.5			
Dactyloptena orientalis		1	0.4	<0.1
Engraulidae	14			
Stolephorus buccaneeri		8	0.9	0.8
Exocoetidae	8.5			
Parexocoetus brachypterus		1	0.4	0.4
Unidentified exocoetid		22	7.7	3.4
Fistulariidae	30.5	1	0.4	<0.1
Gempylidae	19.5			
Gempylus serpens		4	1.3	0.1
Gobiidae	7			
Ptereleotris heteropterus		517	2.6	1.4
Gonostomatidae	13			
Vinciguerria spp.		38	0.9	0.4
Holocentridae	17	6	2.1	0.1
Kyphosidae	30.5			
Kyphosus bigibbus		1	0.4	<0.1
Monacanthidae	6			
Pervagor spilosoma		13	0.9	0.7
Unidentified monocanthid		33	6.9	3.0
Mullidae	1	521	31.8	17.6
Myctophidae	8.5	28	4.7	3.8
Nomeidae	10			
Psenes sp.		1	0.4	0.1
Unidentified nomeid		24	3.9	1.5
Priacanthidae	27	1	0.4	0.4
Scombridae	17			
Katsuwonus pelamis		4	1.7	0.2
Synodontidae	22	4	0.9	0.1
Tetraodontidae	25.5	2	0.9	0.1
Leptocephalus larvae	30.5	1	0.4	<0.1
Unidentified fishes	5	53	15.0	5.8
MOLLUSCA				
Decapoda				
Ommastrephidae	3			
Symplectoteuthis spp.		21	6.4	4.0
S. oualaniensis		9	3.0	2.5
Hyaloteuthis pelagicus		1	0.4	0.3
Unidentified ommastrephid		138	25.8	15.0
Unidentified squids	4	281	21.5	6.4
Octopoda	24	2	0.4	0.4
CRUSTACEA				
Stomatopoda	23			
Lysiosquilla spp.		5	0.4	0.2
Parasitic isopod	25.5	2	0.9	0.1
Crab	19.5			
Brachyura		1	0.4	<0.1
Crab megalopa		19	0.4	0.2
Unidentified crustacean	12	24	1.3	0.6
INSECTA				
Gerridae	21			
Halobates sericeus		3	1.3	0.1
COELENTERATA				
Scyphozoa	30.5	1	0.4	<0.1
UNIDENTIFIED REMAINS	11	15	6.4	3.2

ples, 95% of the fishes could be identified at least to family.

Prey items came from 17 fish families, 2 squid families, and a crustacean. Ignoring the stomach oil component of the samples, we found the prey to be 50% fish and 48% squid by volume. The highest ranking prey item was Ommastrephidae (Table 20), including *S. oualaniensis* and *H. pelagicus*. Ranking next were goatfishes. Flyingfishes ranked third and although few were identified, *E. volitans* was present. The fourth ranking family was Carangidae, consisting entirely of the genus *Decapterus*, and included *D. macrosoma*. Other common prey families included squirrelfishes and rudderfish (Table 20).

We obtained 198 measureable prey items. The mean prey length was 65 mm, ranging from a 25-mm squid to a 134-mm *D. macrosoma*. Most measurements were squids, with a mean length of 62 mm for Ommastrephidae (Table 21). Average lengths for commonly consumed fishes ranged from 53 mm (goatfishes) to 126 mm (*Decapterus* spp.).

Table 19. Lengths and volumes of some prey items[a] of the wedge-tailed shearwater. Length and volume values are not necessarily for the same individuals.

Prey	Sample size		Minimum		Maximum		Mean		SE	
	Length	Vol	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)
FISHES										
Mullidae	41		48		64		54		1	
Ptereleotris heteropterus	30	20	22	0.2	30	0.2	28	0.2	<0.5	0
Myctophidae	14		14		80		71		5	
MOLLUSCA										
Ommastrephidae	69		29		115		63		3	
Symplectoteuthis spp.	21		39		112		67		4	
S. oualaniensis	9		57		100		85		5	

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods).

Sampling was adequate to discuss seasonal changes only for the Laysan region. It is apparent that Ommastrephidae was the highest ranked prey item in the diet of the Christmas shearwater in virtually all island groups and seasons sampled. Goatfishes ranked high during winter, spring, and summer on Laysan. They comprised much more of the prey volume during spring (30%) than summer (6%). In contrast, flyingfishes were ranked highest there during summer, climbing from 1% by volume in spring to 21% in summer. The limited sampling in the Midway and French Frigate Shoals regions indicated flyingfishes were eaten whenever samples were obtained. Carangids were not present in the Midway samples, but this may have been due to insufficient sampling. In the Laysan region, where sampling was sufficient, carangids were more important by volume in summer (25%) than spring (5%). Lizardfishes ranked second in the Laysan area during winter, and rudderfish ranked first during summer in the Midway region. Christmas shearwaters exploited many food sources but fed most heavily on ommastrephid squids, goatfishes, flyingfishes, and *Decapterus* spp. in the 50–100 mm range.

Hawaiian birds consumed less squid (48% vs. 71%, by volume) than shearwaters on Christmas Island (Ashmole and Ashmole 1967*b*). In addition, Hawaiian birds ate many goatfishes and carangids whereas Christmas Island birds consumed many tunas and bristlemouths. Birds at both locations commonly took flyingfishes.

Brown Noddy.—We collected and analyzed 354 samples from brown noddies, most coming from Pearl and Hermes Reef, Lisianski, Laysan, and French Frigate Shoals. Some samples were obtained from each island in the archipelago. Samples were collected March–November with many more (84%) coming from adults than subadults (5%) or nestlings (11%). Pooling all samples collected 1978–80, the mean volume was 14 ml and contained an average 7.7 prey items/sample. Sample condition was relatively good, enabling 97% of the fishes to be identified to family.

The sample volumes contained 66% fish and 33% squid. Thirty-three fish families, 2 squid families, 2 crustacean groups, and a marine insect were found (Table 22). The highest ranking prey was juvenile goatfishes. Ommastrephid squids ranked next and included *S. oualaniensis*, *S. luminosa*, and *Ommastrephes* spp. Juvenile lizardfishes ranked third. Carangids, most of which were *Decapterus* spp., ranked fourth. Other common prey families were flyingfishes (especially *E. volitans*) and snake mackerels.

We found 460 measureable prey items. They averaged 48 mm and ranged from a 3-mm sea-strider to a 185-mm *Decapterus* sp. Goatfishes and ommastrephid squids had mean lengths of 58 and 53 mm,

Table 20. Prey items identified to lowest taxon in 182 Christmas shearwater samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Ammodytidae	14			
Bleekeria gillii		10	3.8	0.4
Carangidae	4			
Decapterus spp.		57	15.4	10.6
D. macrosoma		6	2.7	1.8
Unidentified carangid		2	0.5	0.5
Coryphaenidae	19			
Coryphaena hippurus		1	0.5	<0.1
C. equiselis		1	0.5	0.1
Dactylopteridae	22			
Dactyloptena orientalis		2	1.1	<0.1
Exocoetidae	3			
Exocoetus volitans		1	0.5	0.2
Unidentified exocoetid		81	26.4	9.6
Gempylidae	12			
Gempylus serpens		8	4.4	0.9
Gonorhynchidae	16			
Conorhynchus gonorhynchus		5	2.7	0.2
Gonostomatidae	11			
Vinciguerria spp.		39	2.2	1.4
Hemiramphidae	20			
Oxyporhamphus micropterus		1	0.5	0.5
Holocentridae	7	25	7.1	2.3
Istiophoridae	24	1	0.5	0.1
Macrorhamphosidae	15			
Macrorhamphosus gracilis		5	1.6	0.5
Monacanthidae	21	2	0.5	0.2
Mullidae	2	256	35.2	14.2
Nomeidae	8	22	4.4	2.4
Scombridae	13			
Katsuwonus pelamis		6	2.7	0.8
Sternoptychidae	17	3	1.1	0.2
Synodontidae	9	28	4.9	0.7
Unidentified fishes	6	31	14.8	2.3
MOLLUSCA				
Decapoda				
Ommastrephidae	1			
Symplectoteuthis spp.		42	12.6	7.0
S. oualaniensis		7	3.3	1.5
Hyaloteuthis pelagicus		12	3.8	2.0
Unidentified ommastrephid		260	47.8	31.7
Onychoteuthidae	18	2	0.5	0.5
Unidentified squids	5	58	20.3	5.3
CRUSTACEA				
Crustacean larvae	23	4	0.5	<0.1
UNIDENTIFIED REMAINS	*10*	*10*	*4.4*	*1.7*

respectively. Juvenile lizardfishes averaged 40 mm (Table 23). Most prey taken by brown noddies was 20–80 mm.

Although sampling was somewhat inadequate during fall and winter, some interesting patterns emerge from a comparison of the 4 island groups and 4 seasons. Goatfishes ranked highest throughout the Hawaiian Archipelago in spring, but declined in summer, especially in the 2 northern island groups. They remained fairly common during fall and winter but much less so compared to spring and summer. Ommastrephid squids ranked higher than goatfishes during fall and winter, ranking first in both areas sampled. They ranked second in most island groups during spring and summer and were consequently a very common prey item throughout the year. Lizardfishes ranked highest of the fish prey during winter. They also ranked high during spring but declined considerably during summer when other prey resources were eaten. During summer and fall, goatfishes occurred in only 1 of 36 samples at Midway. *Decapterus* spp. did not occur in any of 15 fall or 40 winter samples, yet ranked high during spring and very high during summer, especially in the Laysan Island group. Flyingfishes were highly ranked only in summer, especially in the Midway Island group where many *E. volitans* were taken. A few flyingfishes were taken during winter and spring. Many were taken on Midway during October. Dorward and Ashmole (1963:453) found that brown noddies took few *E. volitans* on Ascension Island, even though other seabirds obtained it. Snake mackerels were regularly taken in all island groups during all seasons, whereas squirrelfishes were most important only during summer at the northern end of the archipelago. Anchovies occurred only during fall at Midway, ranking second there. These results display intriguing changes in diet with season, presumably due to changes in prey availability in surface waters.

The diet of the brown noddy is different in Hawaii than at other locations. We found many goatfishes, ommastrephid squids, flyingfishes, and carangids as did Brown (1975) at Oahu. Dorward and Ashmole (1963) found blennies, halfbeaks, flyingfishes, and squirrelfishes but few

Table 21. Lengths and volumes of some prey items[a] of the Christmas shearwater. Length and volume values are not necessarily for the same individuals.

Prey	Sample size		Minimum		Maximum		Mean		SE	
	Length	Vol	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)
FISHES										
Decapterus spp.	4		120		131		126		3	
Mullidae	7		51		57		53		1	
Exocoetidae	15		38		125		80		6	
MOLLUSCA										
Ommastrephidae	109		25		107		62		2	
Symplectoteuthis spp.	39	4	30	1	99	17	61	7	3	4
S. oualaniensis	7	1	74	12	94	12	84	11	3	
Hyaloteuthis pelagicus	10		53		64		58		1	

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods).

squids at Ascension Island. At Christmas Island (Pacific), most fishes were flyingfishes, tunas, and snake mackerels (Ashmole and Ashmole 1967*b*).

Sooty Tern.—We collected 356 samples from sooty terns, obtaining some from each island group in the Hawaiian Archipelago. Most came from Laysan, Lisianski, and French Frigate Shoals. Because this species does not make landfall when not breeding, collecting was restricted to March–September. We took samples from adults (68%), subadults (8%), and nestlings (24%). Pooling all samples from 1978–80, the mean sample volume was 10.4 ml, and a sample contained an average 4.5 prey items. Sample condition was reasonably good with 97% of the fishes identified to family.

Sample volumes were 46% fish and 53% squid, a separation almost identical to that reported by Brown (1975). Twenty-six fish families, 1 squid family, 1 shrimp, and 2 coelenterate groups were identified (Table 24). Squids were clearly the highest ranked prey items, with ommastrephid squids ranking first and the unidentified ones ranking third. Most of those identified were *Symplectoteuthis* spp., including *S. oualaniensis*. *Ommastrephes* spp. and *H. pelagicus* were also present. Goatfishes ranked highest among fish families. Next were flyingfishes, especially *Cypselurus* spp. and *E. volitans*. Other highly ranked prey included snake mackerels, carangids (especially *Decapterus* spp.), nomeids, and squirrelfishes.

Reliable length measurements were taken of 326 prey items. They ranged from a 1-mm gastropod to a 120-mm needlefish and averaged 48 mm. All of the common prey items for which adequate measurements were available were 20–70 mm (Table 25). The smallest of the highly ranked prey, the squirrelfishes, averaged 25 mm whereas the largest, *Exocoetus volitans*, averaged 71 mm. A few of the prey items were in good enough condition for reliable volumetric measurements. Ommastrephid squids and *E. volitans* had average volumes of 5 and 6 ml, respectively (Table 25).

Although we could not obtain samples from sooty terns during fall, some interesting patterns of seasonal and geographical variation in diet are evident. Squids were commonly eaten in all island groups, ranking either first or second in winter, spring, and summer. If the unidentified squids, which are probably Ommastrephidae, were to be added to those that were definitely from this family, the importance of ommastrephid squids in the diet would be further underscored. Goatfishes were most prominent during spring and were also commonly eaten during winter and summer. Flyingfishes were eaten seasonally. They did not occur in any of the 33 samples collected during winter, occurred in only a few of the sam-

Table 22. Prey items identified to lowest taxon in 354 brown noddy samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Ammodytidae	19			
Bleekeria gillii		10	2.0	0.2
Blenniidae	15.5	20	2.8	0.1
Bothidae	39	1	0.3	<0.1
Bramidae	39			
Pteraclis velifer		1	0.3	<0.1
Carangidae	4			
Decapterus spp.		68	11.6	6.5
D. macrosoma		24	2.5	1.8
D. tabl		11	2.0	0.9
Selar crumenophthalmus		7	1.4	0.8
Naucrates ductor		1	0.3	<0.1
Seriola sp.		1	0.3	<0.1
Unidentified carangid		6	0.8	<0.1
Chaetodontidae	39	1	0.3	<0.1
Cheilodactylidae	26.5			
Cheilodactylus vittatus		4	0.8	0.1
Cirrhitidae	29.5			
Cirrhitops fasciatus		5	0.3	0.2
Clupeidae	11			
Spratelloides delicatulus		67	0.8	0.8
Coryphaenidae	28			
Coryphaena equiselis		2	0.6	0.3
Engraulidae	17			
Stolephorus buccaneeri		9	0.8	0.6
Exocoetidae	5			
Parexocoetus brachypterus		2	0.6	0.6
Exocoetus volitans		10	2.8	2.3
Cypselurus spp.		5	1.4	0.6
Unidentified exocoetid		59	12.4	5.4
Fistulariidae	35	2	0.3	<0.1
Gempylidae	6			
Gempylus serpens		83	12.1	2.5
Unidentified gempylid		2	0.6	0.2
Gobiidae	32			
Ptereleotris heteropterus		6	0.6	<0.1
Gonorhynchidae	13			
Gonorhynchus gonorhynchus		16	2.8	0.4
Gonostomatidae	20.5			
Vinciguerria spp.		30	0.6	0.3
Hemiramphidae	39	1	0.3	<0.1
Holocentridae	8			
Neoniphon sammara		6	0.3	0.3
Sargocentron spp.		21	2.3	0.6
Unidentified holocentrid		81	5.6	1.0
Istiophoridae	33			
Makaira nigricans		2	0.6	<0.1
Unidentified istiophorid		1	0.3	<0.1
Kyphosidae	39			
Kyphosus bigibbus		1	0.3	<0.1
Macrorhamphosidae	18			
Macrorhamphosus gracilis		10	2.3	0.2
Molidae	23			
Ranzania laevis		3	0.8	0.6
Monacanthidae	14			
Pervagor spilosoma		3	0.3	0.3
Unidentified monacanthid		10	1.1	0.7
Mullidae	1	945	48.0	28.3

Table 22. Continued.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
Myctophidae	24	4	0.6	0.4
Nomeidae	20.5	13	0.8	0.3
Pomacentridae	31	4	0.8	<0.1
Scomberesocidae	39			
Cololabis saira		1	0.3	<0.1
Scombridae	12			
Katsuwonus pelamis		6	1.7	0.3
Thunnus alalunga		1	0.3	<0.1
Unidentified scombrid		8	1.4	0.1
Sphyraenidae	15.5			
Sphyraena helleri		1	0.3	0.3
Unidentified sphyraenid		6	1.7	0.1
Synodontidae	3	682	23.7	5.9
Tetraodontidae	26.5			
Lagocephalus lagocephalus		2	0.3	0.1
Unidentified tetraodontid		2	0.6	<0.1
Leptocephalus larvae	10	17	3.1	0.5
Unidentified fishes	9	50	12.7	1.6
MOLLUSCA				
Decapoda				
Ommastrephidae	2			
Ommastrephes spp.		4	0.6	0.3
Symplectoteuthis spp.		51	9.0	4.9
S. oualaniensis		6	1.7	1.1
S. luminosa		3	0.3	0.1
Unidentified ommastrephid		228	33.6	21.6
Onychoteuthidae	34			
Onychoteuthis sp.		1	0.3	0.1
Unidentified squids	7	58	14.1	4.8
CRUSTACEA				
Euphausiacea	25	28	0.3	0.1
Stomatopoda	29.5			
Lysiosquilla sp.		1	0.3	<0.1
Odontodactylus spp.		2	0.3	<0.1
O. brevirostris		1	0.3	<0.1
INSECTA				
Gerridae	39			
Halobates sericeus		1	0.3	<0.1
UNIDENTIFIED REMAINS	22	4	1.1	0.3

ples from spring, yet ranked first or second for 3 island groups during summer. The 8 samples collected on Oahu in summer contained no flyingfishes, but Brown (1975) found them to be common in the diet there during July and August. Snake mackerels were a common component of the diet at all island groups and seasons sampled. *Decapterus* spp. did not occur

Table 23. Lengths and volumes of some prey items[a] of the brown noddy. Length and volume values are not necessarily for the same individuals.

Prey	Sample size		Minimum		Maximum		Mean		SE	
	Length	Vol	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)
FISHES										
Holocentridae	25	14	15	0.1	38	0.4	24	0.2	1	0
Decapterus spp.	7		21		185		93		21	
Mullidae	95	2	40	2	108	2	58	2	2	0
Monacanthidae	7		31		60		45		4	
Blenniidae	16		20		27		24		1	
Spratelloides delicatulus	37		21		47		39		1	
Synodontidae	84	6	24	0.2	55	0.4	40	0.3	1	0
MOLLUSCA										
Ommastrephidae	89	3	19	2	96	28	53	13	2	8
Symplectoteuthis spp.	30	9	27	1	72	10	47	4	2	1

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods).

in any of the 33 samples taken during winter but were ranked fairly high during spring and summer. Squirrelfishes ranked highest during summer at the northern end of the Hawaiian Archipelago, and 75 of the 76 individuals found in this study were collected July–September. Striped hawkfish, skipjack tuna, bristlemouths, and nomeids ranked fairly high at certain areas and seasons. Sooty terns ate ommastrephid squids throughout the year and supplemented this with seasonally available fishes from several families in the 20–70 mm size range.

Sooty terns fed heavily on ommastrephid squids and flyingfishes at Ascension Island (Ashmole 1963*b*), Christmas Island (Pacific) (Ashmole and Ashmole 1967*b*), and Oahu (Brown 1975). Squid and fish species changed with location. Goatfishes and *Decapterus* spp. were common in the diet in Hawaii but unreported elsewhere.

Bonin Petrel.—During 1979–80, we collected 144 samples from Bonin petrels. A single sample was obtained in December and the remainder March–June. All but 2 were from adults (99%) and, except for 5 samples from Midway, all came from Laysan or Lisianski. Although Bonin petrels will make landfall during almost any month, we had extreme difficulty collecting samples during months when adults were not feeding their young. Most birds handled June–January would not regurgitate, and stomachs from sacrificed birds were empty during those months. Samples were well-digested. Nevertheless, more than 74% of the individual fishes could be identified at least to family. Sample volumes averaged 5.9 ml and contained on an average 4.5 prey items.

We found 12 fish families, 3 squid families, 7 crustacean groups, 1 insect, and a tunicate in the diet of this species (Table 26). By volume, the prey consisted of 47% fish, 21% squid, 7% crustaceans, and 24% unidentified remains. The highest ranking prey categories were unidentified squids, unidentified fishes, and unidentified remains. These categories are not very useful because each may be an aggregate of many taxa. Midwater lanternfishes and hatchetfishes ranked as the most important identifiable families. Two of the lanternfishes were identified by John E. Fitch using otoliths to be *Hygophum* sp. and *Myctophum* sp., and 2 of the hatchetfishes were *Argyropelecus* spp. Juvenile goatfishes and sea-striders were also high ranking components of the diet. The most common squid family was Ommastrephidae.

We obtained only 57 reliable prey lengths, which averaged 28 mm and ranged from a 3-mm sea-strider to a 112-mm conger eel. Our best measurements

Table 24. Prey items identified to lowest taxon in 356 sooty tern samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Ammodytidae	14			
Bleekeria gillii		18	3.1	0.7
Atherinidae	28			
Pranesus insularum		1	0.3	<0.1
Belonidae	27			
Ablennes hians		1	0.3	<0.1
Blenniidae	18	10	0.8	0.1
Bramidae	23			
Pteraclis velifer		1	0.3	0.1
Carangidae	5.5			
Decapterus spp.		21	4.8	2.7
D. macrosoma		9	2.2	1.8
D. tabl		26	4.2	2.0
Naucrates ductor		2	0.6	0.2
Unidentified carangid		1	0.3	<0.1
Cheilodactylidae	21			
Cheilodactylus vittatus		2	0.6	0.2
Cirrhitidae	16	7	1.4	0.2
Clupeidae	17			
Spratelloides delicatulus		27	0.3	0.3
Coryphaenidae	28			
Coryphaena hippurus		1	0.3	<0.1
Dactylopteridae	28			
Dactyloptena orientalis		1	0.3	<0.1
Echeneidae	28	1	0.3	<0.1
Exocoetidae	4			
Exocoetus volitans		21	2.8	2.2
Cypselurus spp.		41	2.5	1.0
Unidentified exocoetid		124	14.3	5.3
Gempylidae	5.5			
Gempylus serpens		73	12.6	2.9
Unidentified gempylid		2	0.6	<0.1
Gonostomatidae	13			
Vinciguerria spp.		18	0.8	0.1
V. nimbaria		20	0.3	0.3
Hemiramphidae	20			
Oxyporhamphus micropterus		3	0.8	0.1
Holocentridae	8			
Sargocentron spp.		17	1.7	0.6
Unidentified holocentrid		59	3.9	0.9
Macrorhamphosidae	28			
Macrorhamphosus gracilis		1	0.3	<0.1
Molidae	15			
Ranzania laevis		11	2.2	1.0
Monacanthidae	11			
Pervagor spilosoma		2	0.3	0.1
Cantherhines spp.		9	1.7	0.8
C. verecundus		1	0.3	0.3
Unidentified monacanthid		9	1.7	0.6
Mullidae	2	317	31.7	14.0
Myctophidae	28	1	0.3	<0.1
Nomeidae	7			
Nomeus gronovii		1	0.3	0.2
Unidentified nomeid		49	7.3	2.8
Pomacentridae	28	1	0.3	<0.1
Scombridae	10			
Katsuwonus pelamis		28	5.3	1.6
Thunnus sp.		1	0.3	0.1
Unidentified scombrid		7	2.0	0.7
Synodontidae	12	27	3.7	0.5
Xiphiidae	22			
Xiphias gladius		2	0.6	0.1
Unidentified fishes	9	38	9.3	1.5
MOLLUSCA				
Decapoda				
Ommastrephidae	1			
Ommastrephes sp.		1	0.3	0.3
Symplectoteuthis spp.		80	13.8	8.4
S. oualaniensis		19	3.9	2.8
Hyaloteuthis pelagicus		7	1.7	0.6
Unidentified ommastrephid		294	39.6	28.6
Unidentified squids	3	113	24.4	12.7
CRUSTACEA				
Shrimp	28	1	0.3	<0.1
COELENTERATA	19			
Vellellidae				
Velella velella		4	0.6	0.1
Scyphozoa		2	0.3	<0.1

were goatfishes ($\bar{x} = 51.3$ mm) and ommastrephid squids ($\bar{x} = 46$ mm) (Table 27).

We did not collect enough samples to draw many conclusions concerning variations in diet by area or season. Squids were the highest ranked prey during both winter and spring in the Laysan Island group, and they were followed in each season by lanternfishes. Hatchetfishes were present during winter and spring in the Laysan group but only during spring at Midway. Goatfishes and sea-striders occurred only during spring in the Laysan Island group.

There have been no previous studies of the diet of the Bonin petrel. Phoenix petrels at Christmas Island fed on 78% squid (primarily Ommastrephidae), 14% fish (primarily snake mackerels), and 8% invertebrates (sea-striders) (Ashmole and Ashmole 1967*b*). Gray-faced petrels fed

Table 25. Lengths and volumes of some prey items[a] of the sooty tern. Length and volume values are not necessarily for the same individuals.

Prey	Sample size		Minimum		Maximum		Mean		SE	
	Length	Vol	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)
FISHES										
Holocentridae	17	4	16	0.1	39	0.4	25	0.3	2	0
Mullidae	35		38		61		53		1	
Spratelloides delicatulus	11		22		45		31		2	
Exocoetus volitans	10	5	32	2	114	19	71	6	8	3
Nomeidae	10		14		78		51		8	
Cantherhines spp.	6	3	34	2	57	5	43	4	4	1
MOLLUSCA										
Ommastrephidae	94	11	18	1	104	18	51		2	2
Symplectoteuthis spp.	44		24		79		46		2	

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods).

on 58% squid, 28% fish (lanternfishes and bristlemouths), and 12% crustaceans in New Zealand (Imber 1973). The Bonin petrel is unique among *Pterodroma* in its heavy reliance on fish instead of squid.

Gray-backed Tern.—We collected and analyzed 272 regurgitations from gray-backed terns in 1978–80, including each month March–August. Most were collected on Laysan, Lisianski, and Pearl and Hermes Reef, but others were obtained on Nihoa, Necker, and French Frigate Shoals. We collected half of the samples from adult birds and half from dependent young. Samples averaged 4 ml and 8.8 prey items. The sample condition was generally very good, and 96% of the fishes could be identified at least to family.

We found the volume of the prey to be 92% fish, 4% squid, and 3% crustaceans. The diet proved to be complex, consisting of 41 families of fish (the highest for any species in this study), 3 mollusk families, 5 groups of crustaceans, 3 insects, and a coelenterate (Table 28). The highest-ranked prey item was a cowfish, which occurred in two-thirds of the samples and accounted for 42% of the sample volume. The next ranked family was flyingfishes. Most of the 167 specimens we obtained could not be identified further, but 17 were identified as *Cypselurus* spp. Goatfishes ranked third. Dolphin-fishes ranked fourth and consisted of both *Coryphaena hippurus* and *C. equiselis*. Round herrings, crabs, and man-o-war fish (Fig. 11) also ranked high in the diet.

We obtained 1,092 reliable prey lengths. The smallest was a 3-mm sea-strider and the largest a 138-mm blue marlin, with an average of 20 mm. The cowfish had a mean length of 15 mm and ranged as large as 25 mm (Table 29). Except for the crab megalopa and insects, most common prey items had average lengths 15–40 mm, including flyingfishes (*Cypselurus* spp., 38 mm), dolphin-fish (*C. hippurus*, 32 mm), and goatfishes (41 mm).

We collected enough samples to make some geographical and seasonal comparisons, although our analysis suffers from the fact that we could not collect samples during fall. Cowfish ranked first in all areas and seasons except during summer in the Midway Island group. Flyingfishes consistently ranked second or third during the 3 seasons for which we have samples but ranked lowest during spring at Midway. Goatfishes occurred seasonally. Only 1 occured in the 24 samples collected during winter, yet they ranked within the top 3 families during spring and summer in both the Laysan and French Frigate Shoals regions. At Midway, they did not occur in any of 24 samples collected during summer. Dolphin-fishes generally ranked high

Table 26. Prey items identified to lowest taxon in 144 Bonin petrel samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Blenniidae	26	1	0.7	<0.1
Carangidae	26	1	0.7	<0.1
Congridae	16.5	3	2.1	0.5
Exocoetidae	21	2	1.4	0.1
Gempylidae	14			
Gempylus serpens		4	2.8	0.3
Unidentified gempylid		1	0.7	0.2
Gonostomatidae	10			
Vinciguerria spp.		21	6.3	1.2
V. nimbaria		4	1.4	0.4
Holocentridae	26	1	0.7	<0.1
Monacanthidae	20	2	0.7	0.6
Mullidae	7.5	36	7.6	2.4
Myctophidae	4			
Hygophum sp.		1	0.7	<0.1
Myctophum sp.		1	0.7	<0.1
Unidentified myctophid		76	33.3	14.1
Sternoptychidae	5			
Argyropelecus spp.		2	1.4	0.1
Unidentified sternoptychid		56	24.3	6.6
Synodontidae	13	40	2.1	1.3
Pleuronectoidei (flatfish)	26	1	0.7	<0.1
Unidentified fishes	2	87	47.2	19.9
MOLLUSCA				
Decapoda				
Ommastrephidae	11.5	11	4.0	2.0
Enoploteuthidae	26			
Pterygioteuthis microlampas		1	0.7	<0.1
Histioteuthidae	22	1	0.7	0.4
Unidentified squid	1	113	61.1	18.5
CRUSTACEA				
Mysidacea	15			
Gnathophausia spp.		2	1.4	0.2
Unidentified mysid		1	0.7	0.5
Euphausiacea	26	1	0.7	<0.1
Amphipoda	11.5			
Oxycephalidae		1	0.7	<0.1
Unidentified amphipod		12	6.9	1.1
Isopoda	19			
Anuropus sp.		1	0.7	0.3
Parasitic isopod		2	1.4	<0.1
Copepoda	18			
Calanoid copepod		1	0.7	<0.1
Parasitic copepod		2	1.4	0.1
Unidentified copepod		1	0.7	0.1
Shrimp	9	40	6.3	1.6
Crab	16.5			
Crab megalopa		4	1.4	0.3
Galatheidae		1	0.7	<0.1
Unidentified crustacean	6	27	13.9	2.6
INSECTA				
Gerridae	7.5			
Halobates sericeus		84	16.7	0.5
TUNICATA				
Pyrosomatidae	26	1	0.7	<0.1
UNIDENTIFIED REMAINS	3	69	50.7	23.5

only during spring and summer in the Laysan and Midway Island groups. Round herrings ranked high during summer at Midway. They occurred only in small numbers elsewhere and were found in but 1 of 161 samples collected in the Laysan Island group. Man-o-war fish did not occur during winter, ranked second during summer at Midway, and yet did not occur at Laysan during that season. Crabs occurred in small numbers in most areas and seasons sampled, but ranked highest during spring at Midway. Striped hawkfish, bristlemouths, and flying gurnards ranked high at certain locations during a single season. We conclude that gray-backed terns fed heavily at all times on cow fish. There are no previous studies of the diet of this species, but Munro (1944:61) found it fed on 100-mm squid and Clapp (1976) reported it fed on lizards.

White Tern (Fairy Tern).—We collected 241 samples from white terns, most coming from Midway, Laysan, and French Frigate Shoals, with others collected on Lisianski and Kure Islands. Samples were collected during 1978–80 and represent each month except December. We obtained samples from adults (43%), nestlings (24%), and from dropped items beneath roosts or nests (33%). Sample volumes averaged 3.8 ml and contained a mean of 2.6 prey items. Sample condition was excellent, and 98% of the fishes obtained were identified to family.

By volume, the samples consisted of 88% fish, 12% squid, and 0.4% crustaceans. We identified 33 fish families, 1 squid family, and shrimp (Table 30). Goatfishes ranked highest, followed by flyingfishes. *E. volitans* accounted for two-thirds of those flyingfishes that could be identified to genus, and much of the rest were *Cypselurus* spp. Ommastrephid squids ranked third and consisted of *S. oualaniensis* and *H. pelagicus*. The fourth ranking family was the dolphin-fishes, which was represented by nearly equal numbers of *Coryphaena hippurus* and *C. equiselis*. Other common prey included needlefish, halfbeaks, and silversides.

We obtained 319 length measurements and 142 volume measurements for various

Table 27. Lengths and volumes of some prey items[a] of the Bonin petrel. Length and volume values are not necessarily for the same individuals.

Prey	Sample size		Minimum		Maximum		Mean		SE	
	Length	Vol	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)
FISHES										
Mullidae	9		46		56		51		1	
SQUID										
Ommastrephidae	6		20		72		46		7	
CRUSTACEA										
Anuropus sp.	1	1	54	5	54	5	54	5		
Amphipoda	3		11		40		23		9	
Crab megalopa	3		7		7		7		0	
INSECTA										
Halobates sericeus	18	2	3	0.1	4	0.1	4	<0.1		0

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods).

prey items. Lengths averaged 46 mm and ranged from a 12-mm snake mackerel to a 200-mm needlefish. Most of the important prey items averaged 30–80 mm, including goatfishes (35 mm), ommastrephid squids (50 mm), and *Cypselurus* spp. (80 mm) (Table 31). We included all samples for this analysis, even some dropped fishes collected under roosting young that may have been too long for them to swallow. However, it seems unlikely that a tern would take a fish that would be too long for adult consumption. Some nestlings were seen perched with a fish tail protruding from the bill, indicating that some long fishes were consumed by the young.

Our sampling was throughout the year only in the Midway Island group and was generally restricted to spring and summer for the Laysan and French Frigate Shoals groups. Our results concerning seasonal and geographical patterns are difficult to interpret because the diet of this species is particularly varied. Flyingfishes were not found in any of 16 samples taken during winter. One flyingfish was found in 17 samples collected during spring at Midway, yet this family ranked second highest at both Laysan and French Frigate Shoals in that season. Flyingfishes were most common during summer, ranking first or second in each of the 3 island groups. Goatfishes ranked first during spring at each island group. During summer they were not present in any of 50 samples taken at Midway, yet they ranked first in the Laysan Island group. The ranking of ommastrephid squids shows no pattern, but they commonly occurred in all island groups and seasons. Dolphin-fishes did not occur anywhere during winter, nor at Midway or French Frigate Shoals during spring. However, this family ranked high during both spring and summer at Laysan. The young of the striped hawkfish ranked high, especially at Midway, during winter and spring but did not occur during summer or fall. Silversides ranked high during summer at Midway, but were never common elsewhere. Lanternfishes only occurred at the Midway Island group, where they ranked first during spring. Anchovies occurred only at Midway during fall, where they ranked first. Snake mackerels, lizardfishes, bristlemouths, halfbeaks, and needlefishes ranked within the top 5 prey during certain seasons at certain island groups. These findings indicate that white terns prey opportunistically on most any species of appropriate size that is available in surface waters, especially those between 30–80 mm.

The white tern has a diversified diet wherever it has been studied. It fed on at least 16 fishes at Ascension Island, principally cutlass fishes, blennies, and flyingfishes (Stonehouse 1962, Dorward 1963*b*).

Table 28. Prey items identified to lowest taxon in 272 gray-backed tern samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Ammodytidae	52.5			
Bleekeria gillii		1	0.4	<0.1
Atherinidae	52.5			
Pranesus insularum		1	0.4	<0.1
Balistidae	13			
Xanthichthys mento		11	2.6	1.4
Unidentified balistid		15	2.6	0.3
Belonidae	42.5			
Ablennes hians		1	0.4	<0.1
Unidentified belonid		1	0.4	<0.1
Blenniidae	34	3	1.1	0.2
Bramidae	42.5			
Brama orcini		1	0.4	<0.1
Pteraclis velifer		1	0.4	0.1
Carangidae	9			
Decapterus spp.		19	2.6	0.3
D. macrosoma		1	0.4	0.1
Naucrates ductor		10	3.3	0.3
Seriola spp.		10	1.5	0.3
Carangoides ferdau		1	0.4	0.1
Unidentified carangid		9	2.9	0.8
Chaunacidae	16	75	3.3	1.0
Cheilodactylidae	14.5			
Cheilodactylus vittatus		22	4.8	1.4
Clupeidae	5			
Spratelloides delicatulus		182	6.6	5.4
Congridae	48	1	0.4	0.1
Coryphaenidae	4			
Coryphaena spp.		19	5.1	0.7
C. hippurus		76	11.4	2.3
C. equiselis		57	4.0	0.8
Dactylopteridae	28			
Dactyloptena orientalis		7	1.1	0.4
Diodontidae	18.5			
Diodon spp.		5	1.8	0.3
Unidentified diodontid		9	2.6	0.4
Echeneidae	46.5			
Rhombochirus osteochir		2	0.7	<0.1
Exocoetidae	2			
Parexocoetus brachypterus		1	0.4	0.3
Exocoetus monocirrhus		1	0.4	0.2
Prognichthys gilberti		4	1.5	0.4
Cypselurus spp.		17	4.8	1.4
Unidentified exocoetid		143	26.8	7.1
Gempylidae	22			
Gempylus serpens		9	2.6	0.8
Gonorhynchidae	52.5			
Gonorhynchus gonorhynchus		1	0.4	<0.1
Gonostomatidae	21			
Vinciguerria nimbaria		20	1.5	1.1
Hemiramphidae	53			
Oxyporhamphus micropterus		1	0.4	<0.1
Holocentridae	30	8	1.1	0.2
Istiophoridae	17			
Istiophorus platypterus		3	0.7	0.2
Tetrapterus angustirostris		1	0.4	0.1
Makaira nigricans		3	1.1	0.4
Unidentified istiophorid		6	2.2	0.3
Kyphosidae	29			
Kyphosus bigibbus		5	1.5	0.4
Macrorhamphosidae	18.5			
Macrorhamphosus gracilis		17	4.0	0.7
Macrouridae	52.5	1	0.4	<0.1
Monacanthidae	23			
Pervagor spilosoma		3	0.7	0.4
Alutera scripta		5	0.7	0.2
Unidentified monacanthid		2	0.7	0.1
Mugilidae	27	7	1.5	0.3
Mullidae	3	173	16.9	7.4
Myctophidae	20	11	2.9	0.9
Nomeidae	8			
Nomeus gronovii		48	6.3	2.3
Psenes cyanophrys		2	0.7	0.1
Unidentified nomeid		65	4.0	1.0
Ostraciontidae	1			
Lactoria fornasini		708	66.5	41.8
Pegasidae	10			
Pegasus papilio		48	8.8	2.3
Pomacentridae	31	7	1.5	0.1
Priacanthidae	39	2	0.7	0.4
Scombridae	45			
Katsuwonus pelamis		2	0.4	<0.1
Unidentified tuna		1	0.4	<0.1
Serranidae	49			
Odontanthias elizabethae		2	0.4	<0.1
Soleidae	42.5			
Aseraggodes kobensis		1	0.4	<0.1
Unidentified soleid		1	0.4	0.1
Sphyraenidae	46.5	2	0.7	<0.1
Sternoptychidae	26			
Sternoptyx diaphana		1	0.4	0.4
Unidentified sternoptychid		4	1.5	0.3
Synodontidae	32	5	1.8	0.1
Tetraodontidae	36.5			
Lagocephalus lagocephalus		1	0.4	0.1
Unidentified tetraodontid		3	0.7	<0.1
Xiphiidae	24			
Xiphias gladius		7	2.6	0.5
Unidentified fishes	6.5	83	19.1	2.5
MOLLUSCA				
Decapoda				
Ommastrephidae	14.5			
Symplectoteuthis spp.		2	0.7	0.1
Unidentified ommastrephid		15	4.4	2.0
Unidentified squids	11	29	7.0	1.7
Janthinidae	40			
Janthina spp.		2	0.4	0.1

Table 28. Continued.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
J. pallida		2	0.4	<0.1
J. prolongata		1	0.4	<0.1
Cavolinidae	53			
Cavolinia tridentata		1	0.4	<0.1
CRUSTACEA				
Euphausiacea	36.5	14	0.4	0.1
Isopoda	35			
Parasitic isopod		3	1.1	<0.1
Unidentified isopod		3	0.7	<0.1
Copepoda	53			
Pontellidae				
Pontella atlantica		1	0.4	<0.1
Shrimp	33	5	1.5	0.1
Crab	6.5			
Brachyura		6	2.2	0.4
Unidentified megalopa		167	6.3	2.2
Portunidae				
Planes cyaneus		6	1.1	0.4
Portunid megalopa		1	0.4	<0.1
INSECTA				
Gerridae	12			
Halobates sericeus		135	9.9	0.6
Lepidoptera (moth)		2	0.7	<0.1
Orthoptera (grasshopper)				
Euconocephalus nasutus		1	0.4	0.1
COELENTERATA				
Velellidae	25			
Velella velella		11	1.8	0.2
UNIDENTIFIED REMAINS	42.5	2	0.7	0.1

Dorward also found that it ate hatchetfishes and lanternfishes. On Christmas Island (Pacific), white terns fed about half on ommastrephid squids and half on fishes by volume (Ashmole and Ashmole 1967*b*). A wide variety of fishes was consumed there, among which the most important were blennies, flyingfishes, halfbeaks, lanternfishes, and bristlemouths. In Hawaii, white terns have been reported to feed on halfbeaks (Fisher 1903:785), anchovies, and silversides (Anderson 1954). All workers have found the condition of prey taken from this species to be excellent due to its habit of bringing fishes to young crosswise in the bill, and such specimens have been used to identify new fish species (Tyler and Paxton 1979).

Fig. 11. Man-o-war fish, a prey item.

Black Noddy.—During 1978–80 we collected 494 samples (the largest sample size in this study) from black noddies, most coming from Laysan, Lisianski, and French Frigate Shoals. Other samples were collected on Kure, Midway, and Pearl and Hermes Reef. Collections included samples from all 12 months. We collected samples from both adults (79%) and dependent young (21%). The samples averaged 5 ml and 12.6 prey items. We identified 94% of the fishes to family or better.

By volume, the prey was 92% fish, 7% squid, and 1% crustaceans. We were able to identify 36 fish families, 2 squid families, 3 groups of crustaceans, and an insect (Table 32). The highest ranked prey family was goatfishes, followed by lizardfishes. Round herrings (Fig. 12) ranked third. Next were flyingfishes, of which the most common of the 5 species identified was *E. volitans* (Table 32). Other common prey items included gobies, ommastrephid squids, and snake mackerels.

We had 1,038 prey items for which we could make reliable length measurements. These items averaged 34 mm and ranged from a 5-mm crab megalopa to a 167-mm leptocephalus larvae. The highest ranked taxa had mean lengths in the 20–50 mm range and included ommastrephid squids (32 mm), lizardfishes (38 mm), and goatfishes (45 mm) (Table 33). We made 142 reliable volumetric measurements.

Although sampling was inadequate for some areas and seasons, several generalizations can be made regarding geographical and seasonal changes in diet. Goatfishes ranked first or second in each season in the Laysan Island group. At French

Table 29. Lengths and volumes of some prey items[a] of the gray-backed tern. Length and volume values are not necessarily for the same individuals.

Prey	Sample size		Minimum		Maximum		Mean		SE	
	Length	Vol	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)
FISHES										
Seriola spp.	10	3	18	0.3	32	0.7	23	0.5	1	<0.5
Mullidae	14	3	28	0.7	65	2.1	41	1.3	3	<0.5
Balistidae	10	3	6	0.2	23	0.5	16	0.4	2	<0.5
Xanthichthys mento	11	8	15	0.4	34	2.3	24	1.1	2	<0.5
Chaunacidae	34		6		13		9		<0.5	
Coryphaena hippurus	35	5	14	0.3	57	1.5	32	0.7	2	<0.5
C. equiselis	43	33	15	0.1	48	1	24	0.2	1	0
Spratelloides delicatulus	67	70	18	0.1	51	1.7	38	0.7	1	0
Exocoetidae	28	14	13	0.1	42	0.9	26	0.4	2	0
Cypselurus spp.	11	5	29	0.4	63	0.7	38	0.6	3	0
Nomeidae	23	3	10	0.1	42	0.3	22	0.2	2	0
Nomeus gronovii	21	19	18	0.1	48	1.5	29	0.4	2	<0.5
Lactoria fornasini	535	123	7	0.1	25	1.5	15	0.5	<0.5	0
Pegasus papilio	44	2	8	0.1	24	0.1	16	0.1	<0.5	0
CRUSTACEA										
Crab megalopa	14	7	5	0.1	15	0.2	9	0.1	1	0
INSECTA										
Halobates sericeus	34	22	3	0.1	4	0.1	4	0.1	<0.5	0

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods).

Frigate Shoals, they ranked third in all seasons except spring, when they ranked first. In the Midway Island group, goatfishes occurred only during spring and were absent from all 28 samples taken in the remainder of the year. Lizardfishes ranked high during each season in the Laysan and French Frigate Shoals regions, either first or second. They also ranked second during fall and winter in the Midway Island group, and their apparent absence during spring and summer there may be an artifact of inadequate sampling. Round herrings were not found in any of the 76 samples collected during winter, yet ranked third and fourth during spring and summer at Laysan and French Frigate Shoals. Flyingfishes were very common during summer, ranking first at French Frigate Shoals. Bristlemouths were commonly eaten during winter at Midway and Laysan while during the same season at French Frigate Shoals gobies ranked very high. Ommastrephid squids ranked third or fourth at several locations during fall, winter, and spring. Our data indicate that black noddies fed most heavily on goatfishes and lizardfishes throughout the Hawaiian Archipelago throughout the year. Other prey in the 20–50 mm size range were also taken.

The diet of black noddies in Hawaii is unique because of the common occurrence of goatfishes, lizardfishes, and round herrings. At Ascension (Stonehouse 1962) and Christmas Island (Ashmole and Ashmole 1967*b*), black noddies fed on flyingfishes, halfbeaks, blennies, and an anchovy (*Engraulis* sp). This bird has been reported feeding on *Stolephorus delicatulus* (we believe this could be *Stolephorus buccaneeri* or *Spratellodes delicatulus*) in the Marshall Islands (Marshall 1951).

Bulwer's Petrel.—During 1978–80 we could collect only 100 samples from Bulwer's petrels. Samples were taken during the breeding season, May–September, because this species rarely comes to land in other months. Most samples were collected on Laysan, but 2 were obtained on Nihoa. Sample condition was generally poor,

Table 30. Prey items identified to lowest taxon in 241 white tern samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Atherinidae	7.5			
Pranesus insularum		16	3.3	3.2
Belonidae	6			
Ablennes hians		17	5.4	3.9
Unidentified belonid		1	0.4	<0.1
Blenniidae	15			
Plagiotremus goslinei		3	0.8	0.5
Unidentified blenniid		9	1.7	1.1
Bramidae	30.5			
Pteraclis velifer		1	0.4	0.4
Canthigasteridae	33.5			
Canthigaster sp.		1	0.4	0.2
Carangidae	7.5			
Decapterus sp.		1	0.4	0.4
D. macrosoma		3	0.4	0.1
Naucrates ductor		6	1.7	0.7
Seriola sp.		1	0.4	0.4
Caranx spp.		2	0.8	0.8
Unidentified carangid		1	0.4	0.4
Chaetodontidae	35			
Chaetodon sp.		1	0.4	0.1
Cheilodactylidae	11.5			
Cheilodactylus vittatus		8	3.3	2.9
Clupeidae	15			
Spratelloides delicatulus		13	2.1	1.6
Coryphaenidae	5			
Coryphaena spp.		3	0.8	0.4
C. hippurus		8	2.1	1.7
C. equiselis		9	3.7	2.2
Diodontidae	25.5			
Diodon sp.		1	0.4	0.4
Unidentified diodontid		1	0.4	0.1
Echeneidae	19			
Rhombochirus osteochir		6	2.1	0.7
Remora sp.		1	0.4	<0.1
Unidentified echeneid		2	0.8	<0.1
Engraulidae	21			
Stolephorus buccaneeri		13	0.8	0.8
Exocoetidae	2			
Parexocoetus brachypterus		2	0.8	0.2
Exocoetus volitans		66	8.7	6.8
E. monocirrhus		2	0.8	0.8
Prognichthys gilberti		2	0.8	0.7
Cypselurus spp.		17	7.1	6.0
C. speculiger		2	0.8	0.8
C. atrisignis		1	0.4	0.4
Unidentified exocoetid		44	12.9	6.6
Gempylidae	13			
Gempylus serpens		11	2.9	1.3
Unidentified gempylid		3	0.4	0.1
Gonorhynchidae	25.5			
Gonorhynchus gonorhynchus		2	0.8	0.5
Hemiramphidae	6			
Euleptorhamphus viridis		4	1.2	1.2
Hyporhamphus acutus pacificus		9	2.5	1.6
Oxyporhamphus micropterus		7	2.5	1.5
Unidentified hemiramphid		3	0.8	0.2
Holocentridae	17			
Myripristis chryseres		1	0.4	0.4
Unidentified holocentrid		11	1.7	1.4
Hoplichthyidae	30.5			
Hoplichthys sp.		1	0.4	0.4
Istiophoridae	11.5			
Istiophorus platypterus		8	2.9	2.8
Makaira nigricans		1	0.4	<0.1
Macrorhamphosidae	24			
Macrorhamphosus gracilis		3	1.2	0.9
Monacanthidae	30.5			
Cantherhines sp.		1	0.4	0.4
Mugilidae	20	5	1.7	1.3
Mullidae	1	185	29.5	19.5
Myctophidae	15			
Benthosema fibulatum		1	0.4	0.4
Unidentified myctophid		6	2.5	2.5
Nomeidae	23			
Nomeus gronovii		3	1.2	0.9
Unidentified nomeid		1	0.4	0.2
Pomacentridae	22			
Chromis vanderbilti		1	0.4	0.1
C. struhsakeri		1	0.4	0.4
Unidentified pomacentrid		3	1.2	0.5
Scombridae	27			
Katsuwonus pelamis		1	0.4	0.2
Unidentified tuna		1	0.4	0.1
Serranidae	33.5			
Grammatonotus laysanus		1	0.4	0.2
Soleidae	36.5	1	0.4	0.1
Synodontidae	9			
Synodus sp.		1	0.4	0.4
Unidentified synodontid		21	3.7	1.0
Tetraodontidae	30.5	1	0.4	0.4
Xiphiidae	36.5			
Xiphias gladius		1	0.4	0.1
Unidentified fishes	10	13	5.0	1.5
MOLLUSCA				
Decapoda				
Ommastrephidae	3			
Symplectoteuthis spp.		5	1.7	1.7
S. oualaniensis		1	0.4	0.4
Hyaloteuthis pelagicus		2	0.4	0.4
Unidentified ommastrephid		32	9.5	7.9
Unidentified squids	18	8	3.3	1.2
CRUSTACEA				
Shrimp	28			
Penaeidae				
Gennadus sp.		1	0.4	0.1
Unidentified penaeid		1	0.4	0.1

Table 31. Lengths and volumes of some prey items[a] of the white tern. Length and volume values are not necessarily for the same individuals.

Prey	Sample size Length	Sample size Vol	Minimum Length (mm)	Minimum Vol (ml)	Maximum Length (mm)	Maximum Vol (ml)	Mean Length (mm)	Mean Vol (ml)	SE Length (mm)	SE Vol (ml)
FISHES										
Mullidae	89	38	15	0.1	65	4	35	1.2	1	<0.5
Pranesus insularum	9	7	22	0.1	63	3	45	1.1	5	<0.5
Ablennes hians	4	6	98	0.8	200	11	141	5.3	21	2
Spratelloides delicatulus	9	2	18	0.1	51	1	29	0.8	4	1
Exocoetidae	11		17		104		38		8	
Exocoetus volitans	39	19	15	0.1	107	9	42	0.8	5	1
Cypselurus spp.	13	2	22	0.2	114	0.8	80	0.5	9	<0.5
MOLLUSCA										
Ommastrephidae	24	10	14	0.2	99	16	50	7.5	6	2

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods).

with many regurgitations being rejected in the field because they were only oil or because the prey items were digested beyond recognition. We also experienced difficulty in getting this species to regurgitate. Most samples (78%) were taken from adult birds, but 22% came from nestlings. The relatively poor condition is reflected in the fact that by volume 5% of the samples were unidentified remains, 20% were unidentified squids, and 30% were unidentified fishes. However, 67% of the individual fishes collected were identified to family or better. It is likely that some of the unidentified fishes were midwater species for which we lacked a reference collection of skeletal material. Food samples from this bird yielded an average volume of 3 ml and contained an average of 3.9 prey items.

We found 7 fish families, 1 squid family, a gastropod, an annelid, 4 groups of crustaceans, and an insect (Table 34). By volume, ignoring stomach oil and unidentified remains, the prey was 71% fish, 22% squid, 4% crustaceans, and 3% sea-striders. The 2 highest ranked categories were unidentified fishes and squids. These categories are artificially high because they pool unidentified material from numerous families and species. The highest ranked family was lanternfishes, and 5 genera were identified (Table 34). The next highest item was the hatchetfishes, where *Argyropelecus* spp. was common. Other common prey included sea-striders and flyingfish ova. We found small plastic particles in some of the samples which, as in the albatrosses, could have been ingested while feeding on fish eggs that were attached to these floating particles.

We had measurements of only 30 prey lengths. These averaged 23 mm and ranged from a 3-mm sea-strider to a 130-mm flyingfish. Five ommastrephid squids had a mean length of 57 mm (range 38–68 mm).

The distribution of sampling made it impossible to draw conclusions for any area except Laysan Island. There, 16 samples were collected during spring and 82 during summer. Bulwer's petrels fed more on squids during spring (61% by volume) than summer (13%). During summer, lanternfishes (20%) and hatchetfishes (19%) were common prey. The samples contained no midwater fishes during spring. Sea-striders ranked high during both seasons. Bulwer's petrels fed primarily on squids and mesopelagic fishes, most of which were <100 mm in length. There are no previous published accounts of the diet of this species, but *B. fallax* eats 20-mm squid (Bailey and Bourne 1963).

Sooty Storm-petrel.—During 1979–81, 8 samples from sooty storm-petrels were collected January–May at Laysan, and 2 were collected during February 1981 at

Table 32. Prey items identified to lowest taxon in 494 black noddy samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Ammodytidae	29			
Bleekeria gillii		5	0.4	0.2
Atherinidae	14.5			
Pranesus insularum		27	2.0	1.8
Balistidae	45.5	1	0.2	<0.1
Belonidae	28			
Platybelone argalus platyura		2	0.4	0.2
Ablennes hians		2	0.4	<0.1
Blenniidae	25	11	1.0	0.2
Bothidae	38	3	0.4	<0.1
Carangidae	12			
Decapterus spp.		22	1.4	0.3
D. macrosoma		7	0.8	0.4
D. tabl		2	0.4	0.1
Naucrates ductor		8	1.2	0.3
Unidentified carangid		12	1.4	0.3
Cheilodactylidae	16			
Cheilodactylus vittatus		23	3.0	0.8
Cirrhitidae	34	4	0.6	<0.1
Clupeidae	3			
Spratelloides delicatulus		560	11.9	10.2
Coryphaenidae	19			
Coryphaena spp.		6	1.2	0.4
C. hippurus		2	0.4	0.1
C. equiselis		11	1.8	0.3
Dactylopteridae	41			
Dactyloptena orientalis		1	0.2	0.1
Echeneidae	39.5			
Remora remora		1	0.2	<0.1
Rhombochirus osteochir		1	0.2	<0.1
Engraulidae	26			
Stolephorus buccaneeri		25	1.0	0.1
Exocoetidae	4.5			
Parexocoetus brachypterus		4	0.2	0.1
Exocoetus volitans		31	2.2	1.2
Prognichthys gilberti		1	0.2	0.1
Cypselurus spp.		7	1.4	0.5
C. atrisignis		1	0.2	<0.1
Unidentified exocoetid		286	18.2	6.3
Gempylidae	8			
Gempylus serpens		104	13.4	2.1
Unidentified gempylid		2	0.4	0.1
Gobiidae	6			
Ptereleotris heteropterus		435	11.7	2.8
Gonorhynchidae	10			
Gonorhynchus gonorhynchus		85	6.5	1.8
Hemiramphidae	23			
Euleptorhamphus viridis		2	0.4	<0.1
Oxyporhamphus micropterus		4	0.4	0.2
Unidentified hemiramphid		4	0.6	<0.1
Holocentridae	9			
Sargocentron sp.		1	0.2	<0.1
Unidentified holocentrid		112	9.1	1.4

Table 32. Continued.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
Istiophoridae	30			
Makaira nigricans		3	0.4	<0.1
Unidentified istiophorid		2	0.4	0.1
Kyphosidae	32			
Kyphosus bigibbus		4	0.2	0.2
Macrorhamphosidae	20			
Macrorhamphosus gracilis		13	2.6	0.6
Molidae	24			
Ranzania laevis		9	1.2	0.4
Monacanthidae	37			
Pervagor spilosoma		2	0.2	0.2
Mugilidae	45.5	1	0.2	<0.1
Mullidae	1	1,204	49.8	31.2
Myctophidae	33	6	0.2	0.1
Nomeidae	17.5			
Nomeus gronovii		9	1.6	0.5
Psenes cyanophrys		4	0.4	0.1
Unidentified nomeid		7	0.8	0.2
Pomacentridae	31			
Chromis sp.		1	0.2	<0.1
Unidentified pomacentrid		5	1.0	<0.1
Scomberesocidae	39.5			
Cololabis saira		2	0.4	<0.1
Scombridae	13			
Katsuwonus pelamis		9	1.0	0.1
Thunnus alalunga		5	0.4	0.1
Unidentified tuna		20	2.4	<0.1
Unidentified scombrid		15	1.8	0.1
Scombrid larvae		6	0.4	<0.1
Tuna larvae		18	0.8	0.1
Sphyraenidae	35.5	2	0.4	0.1
Sternoptychidae	42	2	0.2	<0.1
Synodontidae	2	2,365	45.3	20.7
Tetraodontidae	45.5			
Lagocephalus lagocephalus		1	0.2	<0.1
Unidentified fishes	4.5	340	22.3	4.3
Leptocephalus larvae	14.5	36	4.3	0.4
Anguilliformes	45.5	1	0.2	<0.1
Pleuronectoidei (flatfish)	45.5	1	0.2	<0.1
MOLLUSCA				
Decapoda				
Ommastrephidae	7			
Symplectoteuthis spp.		10	1.8	0.8
S. oualaniensis		1	0.2	0.2
Unidentified ommastrephid		93	11.1	3.9
Onychoteuthidae	35.5			
Onykia spp.		2	0.4	0.1
Unidentified squids	11	69	10.3	1.8
CRUSTACEA				
Stomatopoda	22			
Pseudosquilla sp.		1	0.2	<0.1
Squilla spp.		12	1.8	0.1
Lysiosquilla spp.		2	0.2	0.1
Coronida sp.		1	0.2	<0.1
Unidentified stomatopod		3	0.6	<0.1
Shrimp	17.5			

Table 32. Continued.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
Penaeidae				
Penaeus marginatus		15	0.6	<0.1
Unidentified penaeid		4	0.4	<0.1
Aristaeidae		1	0.2	<0.1
Caridea		31	0.2	0.1
Unidentified shrimps		20	2.8	0.1
Crab megalopa	21	34	1.4	0.2
INSECTA				
Caterpillar	45.5	1	0.2	<0.1
UNIDENTIFIED REMAINS	27	4	0.8	0.2

Nihoa. This species breeds only in inaccessible islands during winter and spring, making sampling difficult. We also had difficulties inducing birds to regurgitate, and many of the samples that we did collect were entirely stomach oil. All samples came from adults. The advanced state of digestion of the samples made identification difficult, but aside from unidentified remains and stomach oil, we found 23% fish, 29% squid, 12% coelenterates, and 5% crustaceans by volume (Table 35). We could not identify any squid family and identified only 1 fish family, the hatchetfishes. Wind-sailers and sea-striders ranked high among prey items. These data give an indication of the types of prey eaten by this species, but the unlikely result that the common seabird tick accounted for 10% of the volume emphasizes the fact that conclusions must be limited. Small plastic particles occurred in samples from this species.

The length measurements of only 7 prey items were taken that averaged 11 mm and ranged from a 2-mm tick to a 27-mm wind-sailer. We do not have enough information to draw any conclusions concerning geographical or seasonal changes in the diet of sooty storm-petrels.

Blue-gray Noddy.—We collected 111 samples from blue-gray noddies from 1978–81. Because of the limited distribution of this species, all samples were collected on Nihoa (46%) and Necker (54%). We could obtain samples only during February, May, June, and August. Except for 4 samples, all were taken from adult birds (96%). The samples had a mean volume of 1.8 ml and averaged 55 prey items. Even eliminating the large numbers of sea-striders, the blue-gray noddy had an average of 31 prey items/sample, by far the largest number for any of the 18 seabirds in this study. The condition of the samples was relatively good, yet only 46% of the fishes could be identified to family because of their extremely small size.

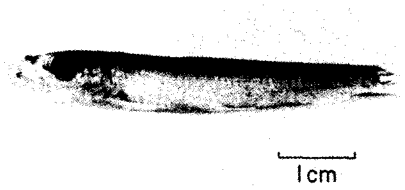

Fig. 12. Round herring, a prey item.

By volume, our samples were 61% fish, 1.5% squid, 18% crustacean, and 19% insect. We could identify 28 fish families, 1 squid family, 8 groups of crustaceans, 2 coelenterates, and a marine insect (Table 36). The highest ranking prey item was sea-striders, which occurred in 81% of the stomachs sampled and accounted for 19% of the prey volume. Unidentified fishes ranked second. These accounted for 16% of the prey volume and were therefore a substantial component of the diet, but probably included many families and species. Lizardfishes ranked third. Flyingfishes and goatfishes also were common. Copepods, almost exclusively *Pontella atlantica*, ranked seventh. This species was reported by Wilson (1950) in the Hawaiian Archipelago and is associated with surface waters around islands. Stomatopods also were common and included 5 genera, especially *Pseudosquilla* and *Coronida*.

Blue-gray noddies ate the smallest fishes and invertebrates of all seabirds in this study. We measured 635 prey items. They averaged 10 mm, ranging from a 2-mm sea-strider to a 50-mm halfbeak. The most

Table 33. Lengths and volumes of some prey items[a] of the black noddy. Length and volume values are not necessarily for the same individuals.

Prey	Sample size		Minimum		Maximum		Mean		SE	
	Length	Vol	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)
FISHES										
Holocentridae	44		9		56		19		2	
Mullidae	95	7	20	0.3	61	3	45	1.5	1	<0.5
Pranesus insularum	11		32		86		64		4	
Spratelloides delicatulus	130	20	29	0.2	61	3	45	1.5	1	<0.5
Exocoetidae	32		18		52		33		2	
Exocoetus volitans	23		32		67		48		2	
Ptereleotris heteropterus	161	54	13	0.1	35	0.3	27	0.2	<0.5	0
Synodontidae	266	21	25	0.1	65	1	38	0.4	<0.5	0
MOLLUSCA										
Ommastrephidae	48		11		67		32		1	
CRUSTACEA										
Stomatopod larvae	9		11		40		23		4	
Caridean shrimp	22		9		9		9		0	
Squilla spp.	10	4	12	0.1	41	0.2	35	0.1	3	0

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods).

common fishes had average lengths 10–30 mm, including flyingfishes (16 mm), goatfishes (18 mm), and lizardfishes (32 mm). The crustaceans and insects were smaller: *Pseudosquilla* spp. (9 mm), *Pontella atlantica* (5 mm), and sea-striders (3 mm). These lengths and displacement volume data, where many common prey items had mean volumes <0.1 ml, give a good indication of the minute prey on which blue-gray noddies fed (Table 37).

We cannot make any geographical comparisons, but we can draw some tentative conclusions concerning seasonality in the diet of the blue-gray noddy. Comparing winter with spring, the only similarities are the high rankings of unidentified fishes and lizardfishes. During winter, blue-gray noddies fed on shrimp, flounder larvae, and squids. During spring sea-striders, flyingfishes, and goatfishes ranked high. Few samples were collected during winter, but it is probable that this species fed most heavily on lizardfishes, supplementing this with various other items. The small prey size and reliance on crustaceans and insects is consistent with the findings of Ashmole and Ashmole (1967*b*). At Christmas Island, they fed on fish (75%), squid (10%), and other invertebrates (16%) (Ashmole and Ashmole 1967*b*). Snake mackerels ranked highest among the fishes, followed by flyingfishes, tunas, and blennies. Sea-striders (*H. micans*) and copepods (*Pontella* sp.) also were common. These findings are similar to ours, but Hawaiian birds also fed on lizardfishes and goatfishes.

Prey Length Comparisons

Prey length comparisons, using all prey from all taxa of grades 1 and 2, indicate that larger predators take larger prey (Fig. 13). It is useful to compare the same prey taken by seabirds with similar diets during the spring–summer chick feeding period (Fig. 6). Masked boobies took larger flyingfishes than the other 4 pelecaniforms (ANOVA, $P < 0.001$), which had no statistical differences among them. Pooling all *Decapterus* spp., the smallest 4 species again had no differences among them, but the masked booby fed on larger fishes (ANOVA, $P < 0.01$). Masked and brown boobies had no significant difference between them for ommastrephid squids, nor were there differences among

Table 34. Prey items identified to lowest taxon in 100 Bulwer's petrel samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Carangidae	13			
Decapterus macrosoma		1	1.0	0.4
Exocoetidae	7			
Exocoetus volitans		1	1.0	0.6
Exocoetidae (ova)		6	6.0	3.2
Unidentified exocoetid		2	1.0	0.2
Gonostomatidae	11			
Vinciguerria sp.		1	1.0	0.1
V. nimbaria		2	1.0	<0.1
Diplophos sp.		1	1.0	0.4
Myctophidae	3			
Hygophum spp.		2	2.0	0.4
Myctophum sp.		1	1.0	0.6
Lampanyctus spp.		2	2.0	1.2
Diaphus spp.		3	1.0	0.4
Symbolophorus sp.		1	1.0	0.3
Unidentified myctophid		49	36.0	13.4
Nomeidae	19.5	1	1.0	<0.1
Opisthoproctidae	19.5			
Opisthoproctus sp.		1	1.0	<0.1
Sternoptychidae	4			
Argyropelecus spp.		24	17.0	5.2
Unidentified sternoptychid		41	25.0	10.5
Pleuronectoidei (flatfish)	16.5	1	1.0	0.1
Unidentified fishes	1	67	48.0	29.5
MOLLUSCA				
Decapoda				
Ommastrephidae	10	6	3.0	0.9
Unidentified squids	2	90	46.0	19.8
Gastropoda	16.5	1	1.0	0.1
ANNELLIDA				
Polychaeta	16.5	1	1.0	0.1
CRUSTACEA				
Amphipoda	8	16	5.0	1.5
Copepoda	12	7	1.0	0.1
Shrimp	16.5	1	1.0	0.1
Crab megalopa	14	1	1.0	0.3
Unidentified crustacean	9	8	5.0	1.9
INSECTA				
Gerridae	6			
Halobates sericeus		55	12.0	2.6
UNIDENTIFIED REMAINS	5	13	13.0	5.2

red-tailed tropicbirds, red-footed boobies, or great frigatebirds. The former 2 species took larger squids than the latter 3 (ANOVA, $P < 0.05$).

There were no significant differences among goatfishes eaten by wedge-tailed shearwaters, Christmas shearwaters, sooty terns, or brown noddies. Black noddies took smaller goatfishes than these 4 species, and white terns ate smaller ones than black noddies (ANOVA, $P < 0.001$). Both shearwaters took larger squids than brown noddies, sooty terns, or white terns, all of which took larger squids than black noddies (ANOVA, $P < 0.001$). Lizardfishes eaten by brown noddies were larger than those taken by black noddies (ANOVA, $P < 0.05$). Flyingfish were taken in successively decreasing lengths by Christmas shearwaters, sooty terns and brown noddies, white terns, and black noddies (ANOVA, $P < 0.05$). Gray-backed terns ate larger prey than blue-gray noddies, including goatfishes (ANOVA, $P < 0.01$), flyingfishes ($P < 0.001$), and crab megalopae ($P < 0.001$).

Table 35. Prey items identified to lowest taxon in 10 sooty storm-petrel samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Sternoptychidae	8	1	10.0	10.0
Unidentified fishes	3	5	40.0	13.0
MOLLUSCA				
Unidentified squids	1	7	60.0	28.8
CRUSTACEA				
Euphausiacea	13	1	10.0	0.1
Amphipoda	10	1	10.0	1.3
Isopoda	9	1	10.0	1.7
Shrimp	6	4	20.0	1.5
Unidentified crustacean	11	1	10.0	0.4
INSECTA				
Gerridae	5			
Halobates sericeus		8	30.0	1.1
Caterpillar	12	1	10.0	0.3
TICKS				
Argasidae	7			
Ornithodorus capensis		2	10.0	10.0
COELENTERATA				
Velellidae	2			
Velella velella		9	40.0	11.9
UNIDENTIFIED REMAINS	4	3	30.0	10.1

DISCUSSION

It is evident from the preceding species accounts that the diets of seabirds in the

Table 36. Prey items identified to lowest taxon in 111 blue-gray noddy samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Balistidae	40	2	0.9	<0.1
Belonidae	35			
Ablennes hians		2	0.9	0.1
Blenniidae	18	11	7.2	0.4
Bothidae	13			
Bothidae larvae		6	0.9	0.4
Unidentified bothid		13	5.4	0.9
Carangidae	28			
Naucrates ductor		1	0.9	<0.1
Seriola spp.		3	1.8	0.1
Coryphaenidae	33			
Coryphaena sp.		1	0.9	<0.1
C. hippurus		1	0.9	0.1
Dactylopteridae	21.5			
Dactyloptena orientalis		11	5.4	0.3
Diodontidae	27			
Diodon spp.		6	1.8	0.2
Unidentified diodontid		4	0.9	<0.1
Echeneidae	33			
Rhombochirus osteochir		1	0.9	0.1
Remora sp.		1	0.9	<0.1
Eleotridae	42.5			
Asterropteryx sp.		1	0.9	<0.1
Exocoetidae	4			
Cypselurus sp.		1	0.9	0.2
Unidentified exocoetid		314	45.0	10.7
Gempylidae	11			
Gempylus serpens		13	8.1	1.5
Unidentified gempylid		2	0.9	<0.1
Gobiidae	21.5			
Ptereleotris heteropterus		3	2.7	0.2
Unidentified gobiid		4	2.7	0.2
Gonorhynchidae	33			
Gonorhynchus gonorhynchus		2	1.8	0.1
Hemiramphidae	25			
Euleptorhamphus viridis		2	1.8	0.2
Hyporhamphus acutus pacificus		1	0.9	0.1
Unidentified hemiramphid		4	1.8	0.1
Holocentridae	24	5	4.5	0.5
Istiophoridae	20			
Makaira nigricans		3	2.7	0.4
Istiophorus spp.		2	0.9	0.1
Unidentified istiophorid		1	0.9	0.3
Macrorhamphosidae	37.5			
Macrorhamphosus gracilis		1	0.9	0.1
Mullidae	5	288	42.3	10.4
Nomeidae	29.5			
Nomeus gronovii		2	1.8	0.1
Unidentified nomeid		1	0.9	<0.1
Ostraciontidae	26			
Lactoria fornasini		7	2.7	0.3
Unidentified ostraciontid		1	0.9	<0.1
Pomacentridae	31	2	1.8	0.3
Scomberesocidae	42.5	1	0.9	<0.1
Scombridae	15	11	7.2	0.6
Soleidae	42.5	1	0.9	<0.1
Sphyraenidae	37.5	1	0.9	0.1
Synodontidae	3			
Trachinocephalus myops		1	0.9	<0.1
Unidentified synodontid		319	58.6	14.6
Xiphiidae	14			
Xiphias gladius		11	8.1	0.6
Leptocephalus larvae	29.5	3	2.7	0.1
Unidentified fishes	2	1,259	78.4	16.1
MOLLUSCA				
Decapoda				
Ommastrephidae	37.5	1	0.9	0.1
Unidentified squids	10	34	16.2	1.4
CRUSTACEA				
Crustacean larvae	37.5	1	0.9	0.1
Mysidacea	12			
Siriella spp.		14	3.6	0.2
Unidentified mysid		16	7.2	0.3
Euphausiacea	17	23	7.2	0.3
Stomatopoda	7			
Pseudosquilla spp.		105	12.6	1.6
Squilla spp.		4	3.6	0.3
Lysiosquilla spp.		15	6.3	0.6
Coronida spp.		75	15.3	2.0
Odontodactylus spp.		20	8.1	0.6
Unidentified stomatopod		9	4.5	0.4
Amphipoda	19	25	3.6	0.4
Isopoda	23			
Parasitic isopod		4	3.6	0.2
Unidentified isopod		2	1.8	0.2
Copepoda	6			
Pontellidae		1	0.9	0.1
Pontella spp.		4	2.7	0.3
P. atlantica		319	20.7	2.4
Calanoid copepod		14	2.7	0.3
Unidentified copepod		11	2.7	0.3
Shrimp	8			
Sergestidae		22	0.9	0.2
Lucifer spp.		13	4.5	0.2
Unidentified shrimps		88	42.3	3.2
Crab megalopa	9	247	28.8	3.7
INSECTA				
Gerridae	1			
Halobates sericeus[a]		2,652	81.1	18.8
COELENTERATA	16			
Velellidae				
Velella velella		5	3.6	0.3
Scyphozoa		11	2.7	0.2
UNIDENTIFIED REMAINS	42.5	1	0.9	<0.1

[a] A single *H. micans* is included.

Hawaiian Archipelago are complex. We found 56 families, 86 genera, and 74 species of fish, and 8 families, 8 genera, and 5 species of squid. We also found an

Table 37. Lengths and volumes of some prey items[a] of the blue-gray noddy. Length and volume values are not necessarily for the same individuals.

Prey	Sample size		Minimum		Maximum		Mean		SE	
	Length	Vol	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)
FISHES										
Blenniidae	10	6	10	<0.1	13	<0.1	12	<0.1	<0.5	0
Exocoetidae	43	8	9	<0.1	39	<0.1	16	<0.1	1	0
Mullidae	24	3	9	<0.1	32	<0.1	18	<0.1	1	0
Synodontidae	36	9	20	<0.1	43	0.4	32	0.2	1	0.1
CRUSTACEA										
Pseudosquilla spp.	34	22	6	<0.1	12	<0.1	9	<0.1	<0.5	0
Coronida spp.	24	14	6	<0.1	12	<0.1	10	<0.1	<0.5	0
Pontella atlantica	29	26	3	<0.1	6	<0.1	5	<0.1	<0.5	0
Shrimps	29	13	6	<0.1	25	<0.1	14	<0.1	1	0
Crab megalopa	46	28	2	<0.1	7	0.3	5	<0.1	0	0
INSECTA										
Halobates sericeus	195	194	2	<0.1	5	<0.1	3	<0.1	0	0

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods).

octopod, 2 gastropod families, an annelid, 11 groups of crustaceans, 2 coelenterates, a tunicate, 3 seabirds, and an alga in the diets (Appendix 3). Plastic particles were found in the stomachs of 4 species, indicating that this potential problem (Baltz and Morejohn 1976, Ohlendorf et al. 1978) is not restricted to northern waters. Nevertheless, it is also evident that relatively few of these prey items comprise most of the food consumed by this seabird community in terms of number, volume, or frequency of occurrence. It is possible that some of the prey items that occur infrequently are necessary to survival in the absence of other food (Ashmole and Ashmole 1967*b*).

For ease of discussion, we have grouped the 18 species into 5 guilds. These are the albatrosses, pelecaniforms, terns and shearwaters associated with predatory fishes, small nocturnal procellariiforms, and neuston feeding terns. These categories are somewhat artificial, and it might be argued that a species could more conveniently be placed in another group. However, we believe this characterization highlights some of the more important similarities and differences among the diets of the seabirds within the tropical and subtropical Hawaiian Archipelago. Each species requires a food source near the surface of the water, and diversification of foraging patterns in such a structurally simple habitat is limited compared to colder waters. We recognize that many differences in prey consumption may be a result of relative rather than absolute prey abundance, but absolute prey abundance data are unavailable. Without such data, it is difficult to assess the "importance" of a prey item. We believe that any prey that ranks high during any season (especially when nestlings are fed) to be important. We acknowledge the probability that some prey rank high simply because they are seasonally abundant. We have no other objective criterion to judge the importance of forage items.

Albatrosses

Albatrosses generally feed well offshore by surface seizing (Ashmole 1971) (Fig. 14). Black-footed and Laysan albatrosses have similar nesting requirements with the exception that black-footed albatrosses nest closer to beaches. Therefore we wished to distinguish between their feeding habits to see if or how they partition food resources. Both species are very dependent on squid (Tables 3 and 6), like other al-

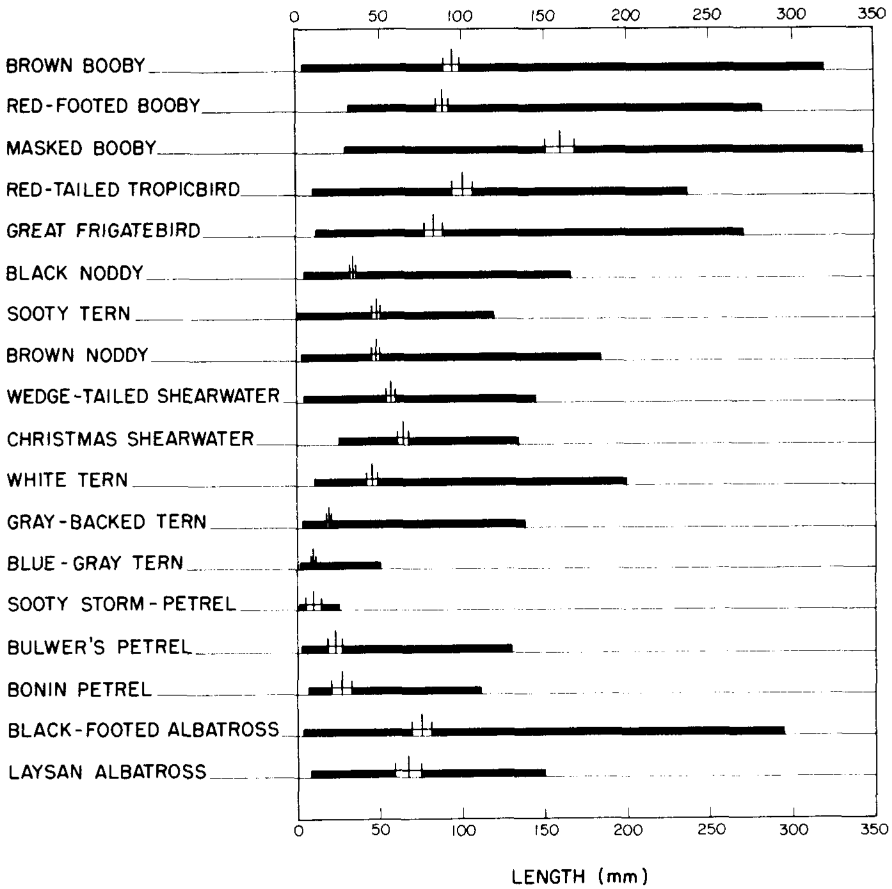

Fig. 13. Comparison of measurable prey lengths for Hawaiian seabirds. Depicted are mean ($\bar{x}$), 95% confidence interval around mean (CI), and range.

batross species (Harris 1973, Imber and Russ 1975). However, Laysan albatrosses consumed by volume far more squid (65%) than black-footed albatrosses (32%). Although it is possible that these birds fed on different species of squid, we could identify to family only 2% of those found in black-footed albatross samples and 6% of those found in the Laysan albatross samples and therefore cannot draw any conclusions. Certainly, ommastrephid squids were commonly eaten by both. A reliable method of identifying the beaks of the species in Hawaii is necessary to determine which squids are most frequently consumed. Fishes were consumed far more by black-footed albatrosses (50% by volume) than Laysan albatrosses (9%). Most of this difference came from the large amount of flyingfish ova in the black-footed albatross diet (44%) compared to that of the Laysan albatross (4%). A comparison of optical density units (D) of rhodopsin in the eyes of these species indicated that Laysan albatrosses are much better adapted for nocturnal vision than are black-footed albatrosses, the former having 16 D/gram and the latter 4 D/gram (A. J. Sillman, pers. commun.). By comparison, pigeons had very little rhodopsin, barn owls had 20 D/gram, and great horned owls had 46 D/gram. An ad-

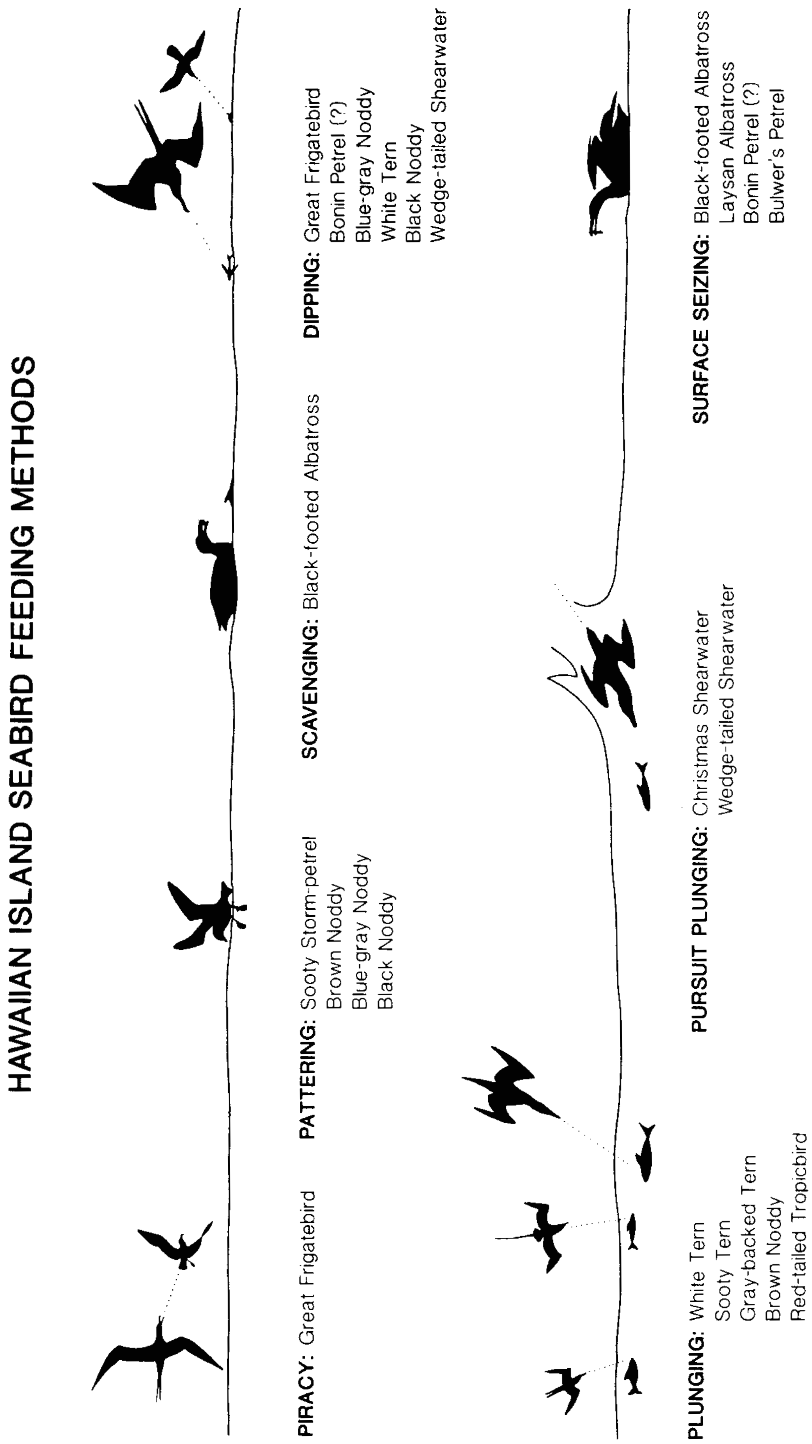

Fig. 14. Seabird feeding methods following Ashmole (1971) and Gould (1971). Used by permission. Drawn by Jon Ahlquist.

aptation for nocturnal feeding explains why Laysan albatrosses took more squid, inasmuch as squid migrate vertically and are more likely to be on the surface during darkness (Clarke 1966). Black-footed albatrosses, by exploiting prey that is more likely to be obtained during daylight hours, ate more flyingfish ova and offal from ships (Miller 1940, Palmer 1962) or dead birds (Table 3). Many of the prey items taken by both species are capable of bioluminescence, which may be important to any predator that feeds at night on vertically migrating prey (Imber 1973). Such items include lanternfishes and hatchetfishes, squids (Onychoteuthidae, Histioteuthidae, Octopodoteuthidae, and Cranchiidae), mysids (*Gnathophausia* spp.), and tunicates (*Pyrosoma* spp.) (Imber 1973). Most importantly, the form of *S. oualaniensis* that occurs in Hawaii has photophores (Young 1975).

There is considerable overlap in the diets of these birds, as evidenced by a comparison of the prey items each consumed, but the proportions of the major items are very different (Tables 2, 6). Feeding at different times of the day may account for much of this difference. Both species feed their young at the same time of the year (Fig. 6), and we detected few differences among seasons in prey consumption in either species. However, Laysan albatrosses exploited Pacific sauries during winter and wind-sailers during spring.

Black-footed albatrosses are heavier and in hand appear to be the stronger, although their bills are shorter than those of Laysan albatrosses (Table 2). The lack of reliable prey measurements and the fact that much of the prey of albatrosses may be shredded before ingestion makes attempts to discuss differences in prey lengths speculative. Laysan albatrosses are much more numerous, outnumbering black-footed albatrosses about 10 to 1 (Table 1).

Pelecaniformes

The 5 species of this order within the study area form a convenient ecological unit for discussion apart from any taxonomic considerations. Each species occurs throughout most of the study area (Table 1), but populations of brown boobies are relatively small. The boobies and tropicbird plunge (Fig. 14) to depths of several meters (Ashmole 1971). Great frigatebirds are limited to snatching prey from surface waters, probably no more than 15 cm in depth, because of a structural inability to take off from the water if they land (R. W. Schreiber, pers. commun.). At sea, frigatebirds often associate with fairly large flocks of other species (Gould 1971). Masked and red-footed boobies are moderately social at sea, feeding in association with small groups of birds. Brown boobies and red-tailed tropicbirds feed in a solitary fashion (Gould 1971). Only brown boobies are thought to feed inshore, the others foraging far at sea (King 1970, Diamond 1978). All species breed in Hawaii during spring and summer, and most dependent young are fed April–September (Fig. 6).

One way in which this guild partitions available prey is in the proportion of fish and squid taken, an observation made on Christmas Island (Pacific) for several of these species by Schreiber and Hensley (1976:247). Red-footed boobies took 27% of their prey volume as squid, the most for any in this group. Red-tailed tropicbirds (18%) and great frigatebirds (14%) took moderate amounts whereas masked boobies (3%) and brown boobies (5%) consumed relatively small amounts. Except for 3 Onychoteuthidae, all identified squids from these species were from the surface-dwelling Ommastrephidae. Flyingfishes were commonly consumed by all species, ranking first for each except for brown boobies, in which they tied for second. Flyingfishes were especially common in the diet of great frigatebirds, accounting for more than 60% of the prey volume (Table 10), a predictable result considering the inability of this species to dive to exploit other fishes. Flyingfishes ranged in percent volume from 58% for masked boobies to 26% for brown boobies. Eight flyingfishes were identified from stomachs of this group (Appendix 3) with *E. voli-*

tans and *Cypselurus* spp. the most frequently identified. Had we been able to identify more of the flyingfishes we may have learned if there were species preferences among the different birds. Carangids, chiefly adult *Decapterus* spp., also were commonly eaten and ranked second or third for each species except brown boobies, where they ranked first. Halfbeaks (especially *Euleptorhamphus viridis*) occurred in the diets of all pelecaniforms but ranked highest in masked and brown boobies. Goatfishes were preyed on by each bird in this guild but ranked high only in the diet of brown boobies (tied for second) and red-footed boobies (fifth). We found little geographical variation in diet, but the ranking of some major prey items changed with season. Flyingfishes and ommastrephid squids generally were taken in substantial quantities throughout the year by each species, but *Decapterus* spp. ranked highest during summer and ranked higher during fall than during spring. Goatfishes ranked highest during spring. Pacific sauries were taken only at Midway during winter where they were commonly eaten by each species except the brown booby. Several birds, at certain seasons and locations, exploited prey species that were not taken by the others. Great frigatebirds took juvenile sooty terns during spring and summer. They ate filefish only in the Laysan Island group during summer. Red-footed boobies took anchovies only on Midway during winter. Red-tailed tropicbirds ate many truncated sun fish on French Frigate Shoals during summer.

Selection of different prey lengths is often considered to be a means of partitioning food resources in the marine environment. Pelecaniforms that weigh more or have longer bill lengths generally take larger prey (Fig. 13). Masked boobies took larger prey than the other 4 species during the spring–summer chick feeding period (Fig. 6) when local food resources probably are most strained. Ommastrephid squids and flyingfishes are likely to be more abundant during spring–summer than fall–winter (Waldron 1964, Akimushkin 1965, Parin 1968, Shuntov 1968, Okutani and Ih-Hsiu 1978). Resource partitioning among the 4 smaller species may occur to some extent by feeding area, e.g., brown boobies feed closer to shore than the others. Feeding methods are also a factor, and the structural differences and behavior may come into play primarily during food shortages when competition would be intensified. Red-tailed tropicbirds, which weigh much less than the other species considered here (Table 2), take prey as large as the other birds. This species has been reported to so seriously misjudge prey length that it can harm itself (Clancy 1974).

The Hawaiian Island pelecaniform community eats organisms similar to those eaten by communities at Christmas Island (Pacific) (Ashmole and Ashmole 1967*b*, Schreiber and Hensley 1976), Ascension Island (Stonehouse 1962, Dorward 1963*a*), and Aldabra Atoll (Diamond 1974*a,b*, 1975). Percentages of flyingfishes and squids consumed by each species are similar at Aldabra Atoll and Hawaii. At Christmas Island, however, red-tailed tropicbirds and great frigatebirds ate much larger percentages of squid than in the former locations. The most striking difference was the prevalence of *Decapterus* spp. and goatfishes in the diets of Hawaiian birds. These fishes are rarely eaten elsewhere, and their prevalence here underscores the influence that local availability of surface schooling fishes have on the diets of seabirds in a given location.

Terns and Shearwaters Associated with Predatory Fishes

These 6 species are of fairly similar size, ranging from wedge-tailed shearwaters (388 g) to black noddies (108 g) (Table 2). Other species are the Christmas shearwater, brown noddy, sooty tern, and white tern. Each species fed on similar prey items of similar size and reportedly feeds largely in association with predatory fishes, especially tunas (Ashmole and Ashmole 1967*b*:97). Murphy and Ikehara

(1955:2) found birds so frequently associated with tuna schools in the Central Pacific that they were "virtually inseparable in our observations." At sea these species occur in flocks, with 5 of them associated with other birds between 67% (white tern) and 97% (black noddy) of the time (King 1970). Gould (1971) reported that Christmas shearwaters occurred in flocks in about half of his sightings. These species generally breed throughout the Hawaiian Archipelago, but Christmas shearwaters are restricted in distribution and sooty terns and wedge-tailed shearwaters are especially abundant (Table 1). All species feed most heavily on resources near the islands when young are being fed. This occurs during spring–summer for most species, but wedge-tailed shearwaters feed young during fall and black noddies feed young during winter at some locations (Fig. 13).

This guild feeds using a variety of techniques (Fig. 14). Shearwaters can pursue prey under water whereas terns plunge dive. Sooty terns will plunge dive only to the surface and cause a splash (Gould 1974: 8), yet this species can rarely submerge because it lacks a substantial uropygial gland (Johnston 1979) and cannot get wet without becoming waterlogged. Black noddies feed by pattering on the surface. This guild partitions prey resources in part by selecting different feeding areas. Most of these 6 species feed well offshore, but both black noddies and white terns can feed inshore (Diamond 1978). One of us (CSH) observed black noddies feeding within a few meters of shore at several of the NWHI, often in association with jacks *Caranx* spp. Sooty terns and wedge-tailed shearwaters can feed at night under full moon conditions (Bruyns and Voous 1965, Gould 1967). Christmas shearwaters have a rhodopsin density of 3 D/g, which is not particularly adapted for nocturnal behavior (A. J. Sillman, pers. commun.).

As with pelecaniforms, this guild partitions prey resources by consuming different proportions of fish and squid. The inshore feeding black noddy (92%) and white tern (88%) had diets that were largely fish by volume, with most of the remainder squid. Brown noddies and wedge-tailed shearwaters fed on 66% fish and 33% squid. Christmas shearwaters and sooty terns took half or more of their prey as squid. Except for 4 Onychoteuthidae, all identified squids were Ommastrephidae. These were primarily *S. oualaniensis* but also *H. pelagicus* and *Ommastrephes* spp.

Juvenile goatfishes were consistently the highest ranked prey item in the diets of this guild, ranking first of all prey for 4 species and first among fishes for each. Flyingfishes ranked high but not nearly as high as with the pelecaniforms. Flyingfishes did not rank first in any diet but did rank from second to fifth for each species except wedge-tailed shearwaters. Most identified flyingfishes were *E. volitans* or *Cypselurus* spp. *Decapterus* spp. were relatively common for several birds and ranked second for wedge-tailed shearwaters and fourth or fifth for 3 other species. *Decapterus* spp. was less frequently consumed by the small, inshore feeding white tern and black noddy. Lizardfishes occurred in the diets of each bird but ranked high only in black noddies (second) and brown noddies (third).

We generally found more variation in the diet with season than with location, and some prey items were exploited exclusively in 1 area during 1 season. Ommastrephid squids were taken regularly throughout the archipelago all year by the species that feed on squid. Lizardfishes and flyingfishes were also taken throughout the year, but flyingfishes ranked highest during summer. Goatfishes, the highest ranked family of this guild, were far more prevalent during spring than other seasons but also were common in summer. *Decapterus* spp. were eaten most frequently during summer but also ranked high during spring. Most of the round herrings were taken during spring and summer by terns and noddies, but black noddies ate many at Midway during fall. A filefish (*Pervagor spilosoma*) ranked high in the diet of wedge-tailed shearwaters on Laysan during summer, and lanternfishes were commonly eaten by white terns during spring on Midway.

Prey lengths were fairly similar, but shearwaters generally took larger prey than terns, and black noddies took the smallest prey (Fig. 13). Some stratification or partitioning by prey length clearly takes place, but for several of the most commonly eaten taxa, birds of similar size fed on prey of the same size.

Our results are similar to those at Christmas Island (Ashmole and Ashmole 1967*b*), Ascension Island (Stonehouse 1962, Dorward 1963*b*, Dorward and Ashmole 1963), and Hawaii (Brown 1975). There, ommastrephid squids, flyingfishes, halfbeaks, and tunas are commonly eaten. Hawaiian seabirds generally consumed a smaller proportion of squid than those at Christmas Island. For example, Hawaiian Christmas shearwaters fed on 48% squid compared to 71% on Christmas Island, and white terns fed on 12% squid compared to 50%. In addition, Hawaiian birds ate fewer flyingfishes (although flyingfishes ranked high with several species, especially the white tern) but fed instead on juvenile goatfishes, juvenile lizardfishes, and *Decapterus* spp. Both Christmas Island and Ascension Island birds ate many blennies, which were rarely consumed in Hawaii. Birds at Ascension Island fed on the squid *H. pelagicus*, but those at Christmas Island and the Hawaiian Archipelago fed on *S. oualaniensis*. Size ranges of prey were similar in all areas for which information is available. We conclude that this group of birds is opportunistic in their feeding habits and secures any prey of appropriate size that is available in the surface waters near breeding colonies. Prey for this guild becomes available primarily when it is driven to the surface by predatory fishes, and in the resulting feeding flocks partitioning of prey probably results from differences in feeding technique and morphology. The close association of these birds with tuna schools, especially for foraging, has been reported frequently (Murphy and Ikehara 1955, Ashmole and Ashmole 1967*b*, Gould 1971).

Small Nocturnal Procellariiforms

We consider here the 3 smallest procellariiforms in this seabird community: Bonin petrels, Bulwer's petrels, and sooty storm-petrels. Apparently each feeds extensively at night. Populations of each species occur at several locations in the Hawaiian Archipelago but do not necessarily overlap (Table 1). Sooty storm-petrels and Bonin petrels breed during winter and fledge young in spring, whereas Bulwer's petrels breed during summer (Fig. 6). Bonin petrels are thought to feed by dipping or surface seizing (Fig. 14), but we could not locate definitive observations. Bulwer's petrels feed sitting on the water with wings spread and heads dipped below the surface (Gould 1971:56), and all storm-petrels are strictly surface feeders that feed principally by pattering (Ashmole 1971). Each species feeds offshore in a solitary fashion, occasionally in association with other birds. All have been reported feeding at night (Ashmole 1971, Gould 1971, Crossin 1974). The Bonin petrel has 11 D/g of rhodopsin, which implies some adaptation for nocturnal behavior (A. J. Sillman, pers. commun.).

We acknowledged the difficulties presented by the advanced state of digestion of samples collected from these birds in the species accounts. Bonin and Bulwer's petrels took substantially more fish than squid, whereas sooty storm-petrels took these prey in roughly equal volumes. Most identified fishes from Bonin and Bulwer's petrels were lanternfishes and hatchetfishes, but they also took numerous bristlemouths. These fishes inhabit midwater during daylight, possess photophores, and normally occur on the surface of the ocean only at night or in reduced light conditions (Clarke 1973, Imber 1973). The single fish identified from a sooty storm-petrel was a hatchetfish. Each bird took numerous sea-striders and various crustaceans. Bonin petrels consumed several goatfishes. Flyingfishes were rarely taken, although Bulwer's petrels took enough egg masses from this family for it to rank seventh in its diet. Most of the identified squids were Ommastrephidae, but individual Enoploteuthidae and Histioteuthidae were identified. These families consist largely of individuals with photophores in Hawaii (Imber 1973, Young 1975).

We do not have enough information to draw conclusions concerning seasonal variations in diets among these species or to discuss prey size in detail. Bulwer's and Bonin petrels apparently take somewhat larger prey than sooty storm-petrels. Bonin and Bulwer's petrels breed at sufficiently staggered seasons that competition for prey in the vicinity of the breeding islands probably is avoided (Fig. 6). Bonin petrels ate relatively more fish than squid compared to other *Pterodroma* spp. (Ashmole and Ashmole 1967*b*, Imber 1973) but were similar in feeding on mesopelagic fishes and sea-striders. The taking of hatchetfishes, sea-striders, and by-the-wind sailors by sooty storm-petrels is consistent with studies indicating that storm-petrels feed on surface organisms (Crossin 1974). Our conclusion that these species feed to a large extent at night does not preclude the probability that daylight feeding also occurs. Lanternfish occur on the surface of the sea during daylight hours when chased there by yellowfin or skipjack tunas (Alverson 1961). Fresh lanternfish were taken by one of us (CSH) from a white tern chick that had just been fed by a marked adult at 1000 and 1100 hours on Midway Island. The heavy reliance by Bonin and Bulwer's petrels on midwater fishes makes it probable that nocturnal feeding accounts for much of their diets.

Neuston Feeding Terns

We treat gray-backed terns and blue-gray noddies as a guild because their unique feeding habits do not conveniently fit elsewhere and because they have some similarities in their diets. Both are thought to feed inshore (Diamond 1978), and both took small prey (Fig. 13). Gould (1971) stated that gray-backed terns are gregarious and feed by plunging in flocks with other species, but his data are limited (29 sightings). The lack of sightings at sea may be due to the fact that from a distance gray-backed terns can be mistaken for the more numerous sooty terns. Blue-gray noddies feed by dipping and pattering at the surface (Fig. 14) and seemingly are not dependent on schools of predatory fishes to drive prey to the surface. Gray-backed terns breed at most of the islands in the Hawaiian Archipelago, but blue-gray noddies are restricted to the southern portion (Table 1). Blue-gray noddies feed most of their young during late winter and spring whereas gray-backed terns feed most chicks during spring and early summer (Fig. 6).

Neither of these species ate much squid, gray-backed terns taking 4% by volume and blue-gray noddies 1.5%. The tern ate 92% fish whereas the noddy took only 61%, eating instead crustaceans (copepods and stomatopods) (18%) and sea-striders (18%). Blue-gray noddies are the most important avian predator on sea-striders in the NWHI (Cheng and Harrison 1983). Gray-backed terns ate many cow fish (42%), a prey item rarely taken by other birds. Blue-gray noddies also took some cowfish, and gray-backed terns also ate sea-striders. Both birds ate juvenile flyingfishes and goatfishes. Gray-backed terns also ate many dolphin-fishes and round herrings, whereas blue-gray noddies supplemented their diet with larval lizardfishes. Hence, these species fed on many taxa common to those taken by other seabirds in this community. The reliance of gray-backed terns on cow fish and blue-gray noddies on minute prey such as sea-striders, copepods, and stomatopods is unique.

We have no information on the absolute abundance of prey species. However, goatfishes ranked highest for both species during spring. Sea-striders were consumed more frequently during spring than winter, and dolphin-fishes were eaten primarily during spring and summer. Gray-backed terns are larger than blue-gray noddies (Table 2) and took larger prey.

The diet of blue-gray noddies at Christmas Island (Pacific) is very similar (Ashmole and Ashmole 1967*b*). There, as in Hawaii, they fed largely on sea-striders and crustaceans, in sharp contrast to other species. At both locations flyingfishes ranked high and prey was minute, with fish having mean volumes of about 0.1 ml. Hawaiian birds fed heavily on lizardfishes and goatfishes, which were absent in the diet at Christmas Island. Christmas Island birds fed largely on snake mackerels, tunas, and blennies, which were present but did not rank very high in the diet of Hawaiian birds. Blue-gray noddies occupy the same trophic level and have similar diets in each location. Differences in their diets probably result primarily from differences in prey species in waters adjacent to study islands.

Timing of Breeding Season and Food Availability

It is well understood that breeding season for marine birds is related to the food supply in temperate and cold waters (Belopol'skii 1957, Pearson 1968, Bedard 1969, Croxall and Prince 1980). Breeding seasons in tropical waters are less predictable (Harris 1969, Schreiber and Ashmole 1970), in part because birds in moderate climates do not face the ecological imperatives encountered in cold water regions. The modal breeding season of Hawaiian seabirds is predictable (Fig. 6) even though (1) year to year variations may change egg-laying dates by many weeks, (2) breeding of terns and pelecaniforms is generally protracted, and (3) a few individual birds of most species may be found in any stage of the breeding cycle for much of the year (Richardson 1957).

Why is the breeding season of the Hawaiian seabird community more predictable than that of others comprising similar species? One consideration in determining why this community displays the spring–summer breeding season found in more northern marine bird communities is its location. Much of the Hawaiian Archipelago is subtropical and is at the northern extent of the breeding ranges for many of its tropical bird species; Kure is the northernmost coral atoll on earth (Woodward 1972). Peak food availability often has been suggested as a controlling factor in the timing of seabird breeding. Pearson (1968:527) found the breeding of the seabirds in Scotland to coincide "with the period of greatest abundance of the Ammodytidae and Clupeidae in the area." Harris (1969:151) found in the Galapagos that unpredictable food shortages were closely related to breeding success for the Audubon shearwater and concluded that food supply is "the proximate factor controlling breeding." The chick feeding interval is generally much less than the incubation shift with tropical marine birds (Diamond 1978:218, Harrison and Hida 1980:27). This phenomenon implies that during the chick feeding period (Fig. 14) the local waters near the breeding islands must provide most of this food. Ashmole (1963*a*:464) stated that high latitudes have an enormous flush of food in spring, but in "tropical oceans seasonal fluctuations in food abundance are generally much less extreme." It was beyond the scope of our investigation to measure seasonal or annual levels of major prey resources, but we recognize that such information would be useful in interpreting these data.

Juvenile goatfishes were the most commonly eaten prey item for the guild that associates with tunas. Goatfishes spawn during spring–summer in Hawaii (Miller 1974), and juvenile goatfishes are not abundant during fall and winter. Akimushkin (1965:184) stated that squids generally migrate with season, especially shoreward to deposit eggs. The biology of ommastrephid squids in Hawaii is insufficiently known to be sure whether they have predictable breeding seasons or migrations (R. E. Young, pers. commun.). The distribution of flyingfishes indicates that they vary in abundance with water temperature (Parin 1963, 1968; Shuntov 1968). Shuntov (1968:784) found that "flyingfishes were found singly when surface water temperature was 19–20 C, were practically a common occurrence at 23–25 C, and were very sharply increased in numbers in areas where the water was above 25 C." The surface isotherms for the Hawaiian Archipelago (Fig. 1) indicate that flyingfishes are far more common during spring–summer than winter. *Decapterus* spp. spawn during spring–summer (Yamaguchi 1953) as do dolphinfishes (Mito 1960). Consequently, juveniles of these fishes would not be abundant during fall and winter. Adult *Decapterus* spp. are resident but may become more available during summer when chased to the surface by migratory tunas, which are usually far more numerous during spring–summer than winter (Waldron 1964). The presence of tunas or other predatory fishes is apparently essential to enable many species to obtain prey (Ashmole and Ashmole 1967*b*:97). The biology of sea-striders is insufficiently known to determine if or when they have a breeding season (Cheng 1973, 1974), but they are known to be most abundant in 24–28 C water (Cheng and Shulenberger 1980). Winter temperatures in the Hawaiian Archipelago (Fig. 1) are at or below the lower end of this range.

The majority of young of most bird species are fed during spring–summer (Fig. 6), and the increased availability of food resources during this time is the best explanation for the observed breeding season. We do not contend that prey is altogether unavailable in winter; indeed we found some flyingfishes, ommastrephid squids, and lizardfishes throughout the year. However, the surge in available prey during spring–summer because of spawning activities (e.g., goatfishes, *Decapterus* spp.) and tuna migration is a controlling factor for the regular spring–summer breeding seasons. Tropical birds that feed by daylight have less time each day to search for food than their northern counterparts and need the relative certainty of encountering prey near the breeding colonies during spring–summer to reproduce. Several bird species are migratory, abandoning breeding colonies during winter months to forage elsewhere, an adaptation argued by Diamond (1978:222) to be "rewarded by greater population size with its attendant diminution of the risk of extinction."

Five of the 18 species in this community feed their young during winter (Fig. 14). Laysan albatrosses, Bonin petrels, and sooty storm-petrels all feed nocturnally and thereby exploit different prey than summer breeders that feed by day. The ability to breed during winter is enhanced by decreased day length because this allows more time to forage. Black-footed albatrosses exploit a unique resource, flyingfish eggs, that may be available only in winter–spring. In addition, both albatrosses fly much further from the nesting site than other species, especially during incubation (Harrison and Hida 1980) and may be less dependent on local food resources because they can forage over a larger area. It is likely that Bonin petrels and sooty storm-petrels are forced to breed during winter because of competition for nest sites by the larger wedge-tailed shearwaters and Bulwer's petrels. Wedge-tailed shearwaters arriving on Laysan in spring kill juvenile Bonin petrels and sooty storm-petrels and cast them from their burrows (M. B. Naughton, pers. commun.). Black noddies have the least predictable breeding season of any Hawaiian seabird. They feed in association with inshore predatory fishes (*Caranx* spp.) that drive prey to the surface, enabling young to be raised during winter because these fishes are resident.

An alternative hypothesis is that breeding during winter months is inefficient because of weather. Winter temperatures are much cooler than summer, and storms are frequent in the Hawaiian Archipelago. Black noddy colonies at French Frigate Shoals have been decimated in winter by high winds blowing nests from heliotrope shrubs (*Tournefortia argentea*) and hundreds of black-footed albatross chicks have been drowned by storm tides (R. P. Schulmeister, pers. commun.). This is another relevant factor that explains why this seabird community breeds during spring–summer, but we believe that food availability is much more important. The fact that even small species such as sooty storm-petrels and black noddies can fledge young in a winter breeding cycle is evidence against weather being a limiting factor.

Opportunistic Feeding and Diet Diversity

Seabirds in Hawaii feed on a wide variety of shoaling fish and squid and apparently take anything of appropriate size that occurs in surface waters. This diversity is reflected in the fact that no bird ate any 1 prey species to an extent that it comprised half or more of the volume of the diet. Our analysis is confounded by prey material that could not be identified to species, but even the highest ranking prey family for many birds was relatively low by volume: brown booby (15%), wedge-tailed shearwater (18%), white tern (20%), brown noddy (28%), and black noddy (31%). Diets that contain 20–40 prey families are very diverse compared to those in northern latitudes (Pearson 1968). The most specialized diets were those of gray-backed terns (42% cowfish) and black-footed albatrosses (44% flyingfish eggs), but the latter included more than 1 species. Percentage volumes are higher for unidentified flyingfishes and unidentified squids for Laysan albatrosses and some pelecaniforms, but these categories include many prey species and it is unlikely that any one accounts for as much as half of the prey. In contrast, seabirds in Peru feed 80–96% on a single fish (Jordan 1959, 1967).

The opportunistic character of these feeding strategies is evidenced by the many prey items that were taken only during 1 season or at 1 location. Many prey taxa were taken only seasonally, probably reflecting seasonal occurrence in surface waters. We are limited by an inability to distinguish between relative and absolute prey abundance. Much of the variation in diet occurs in the relative proportions of several common prey families.

The most numerous birds in this community are those that eat many squid (compare Laysan and black-footed albatrosses; red-footed, masked, and brown boobies; sooty and gray-backed terns; brown and black noddies). These population differences may be merely another expression of the proposition that pelagic feeders are more numerous than inshore feeders (Diamond 1978). Without data on the availability of prey, we cannot know whether food directly controls population size. Inshore feeding species seem to have more diverse diets than offshore feeding ones. It is tempting to attribute this difference to enhanced competition in inshore feeding areas, but inshore fauna is much more diverse than pelagic fauna.

Differences in feeding zones and feeding locations are used to explain differences in diets, often without convincing evidence (Ashmole and Ashmole 1967*b*, Pearson 1968) and are based on inferences from incubation shifts, chick feeding frequencies, or scattered observations at sea in the vicinity of the colony without means to distinguish breeding from nonbreeding birds. Ashmole and Ashmole (1967*b*:63) analyzed feeding zonation using percentages of fish that belonged to pelagic and reef-originating families. This analysis is useful but is limited by the fact that epipelagic species such as flyingfishes and halfbeaks regularly occur in shallow water in the NWHI. As Diamond (1974*b*:208) pointed out, the pelagic-feeding red-footed booby on Aladabra Atoll could feed over water 500 m deep at 1 km from the reef, a situation common in the Hawaiian Archipelago. Future investigators must locate feeding areas of tropical seabirds to determine the importance of feeding zones and to protect them from marine development. Radiotelemetry (Harrison and Stoneburner 1981) is a useful technique in this endeavor. The notion that most tropical birds feed far offshore must be challenged if we are to further our understanding of the forces that shape their feeding and breeding ecology.

CONCLUSIONS

1. Seabirds in Hawaii are opportunistic and feed on any prey of appropriate size that occurs in surface waters.
2. Similar to other tropical communities,

Hawaiian seabirds consume many flyingfishes and ommastrephid squids. This community is distinguished by the occurrence in the diets of many juvenile goatfishes, juvenile lizardfishes, *Decapterus* spp., and mesopelagic fishes.

3. Compared to Christmas Island, seabirds in Hawaii consume more fish than squid.
4. Variation in diets is more correlated with season than with location. However, during certain months at Midway, prey species such as Pacific sauries and round herrings are taken that do not occur elsewhere.
5. The time of year during which most young are fed (spring–summer) is correlated with the maximum availability of prey.
6. Larger predators took larger prey than smaller predators, but during spring–summer, similar-sized birds had few significant differences among lengths of common prey items.
7. Diets provide circumstantial evidence that Laysan albatrosses, Bonin petrels, Bulwer's petrels, and sooty storm-petrels feed at night.
8. Many fundamental questions concerning the biology of tropical and subtropical seabirds cannot be answered until better methods of measuring the availability of prey are developed.

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APPENDIXES

Appendix 1. Common and scientific names of birds.

Common name	Scientific name
Barn owl	*Tyto alba*
Black-footed albatross	*Diomedea nigripes*
Black noddy	*Anous minutus (tenuirostris)*
Blue-gray noddy	*Procelsterna cerulea*
Bonin petrel	*Pterodroma hypoleuca*
Brown booby	*Sula leucogaster*
Brown noddy	*Anous stolidus*
Bulwer's petrel	*Bulweria bulwerii*
Christmas shearwater	*Puffinus nativitatis*
Gray-backed tern	*Sterna lunata*
Gray-faced petrel	*Pterodroma macroptera gouldi*
Great frigatebird	*Fregata minor*
Great horned owl	*Bubo virginianus*
Laysan albatross	*Diomedea immutabilis*
Masked booby	*Sula dactylatra*
Phoenix petrel	*Pterodroma alba*
Red-footed booby	*Sula sula*
Red-tailed tropicbird	*Phaethon rubricauda*
Rock dove	*Columbia livia*
Sooty storm-petrel	*Oceanodroma tristrami*
Sooty tern	*Sterna fuscata*
Wedge-tailed shearwater	*Puffinus pacificus*
White tern (fairy tern)	*Gygis alba*

Appendix 2. Common and scientific names for frequently consumed prey.

Common name	Scientific name
Amberjack	*Seriola* spp.
Anchovy	*Stolephorus buccaneeri*
Balloon fish	*Lagocephalus lagocephalus*
Blenny	Blenniidae
Bristlemouth	*Gonorhynchus gonorhynchus*
Cowfish	*Lactoria fornasini*
Dolphin-fish	*Coryphaena* spp.
Filefish	Monacanthidae
Flying fish	Exocoetidae
Flying gurnard	*Dactyloptena orientalis*
Goatfish	Mullidae
Goby	*Ptereleotris heteropterus*
Halfbeak	Hemiramphidae
Hatchetfish	Sternoptychidae
Lanternfish	Myctophidae
Lizardfish	Synodontidae
Man-o-war fish	*Nomeus gronovii*
Marlin	Istiophoridae
Mantis shrimp	Stomatopoda
Needlefish	Belonidae
Pacific saury	*Cololabis saira*
Pilot fish	*Naucrates ductor*
Round herring	*Spratelloides delicatulus*
Rudderfish	*Kyphosus bigibbus*
Sea-strider	*Halobates sericeus*
Silverside	*Pranesus insularum*
Skipjack tuna	*Katsuwonus pelamis*
Snake mackerel	*Gempylus serpens*
Squirrelfish	Holocentridae
Striped hawkfish	*Cheilodactylus vittatus*
Truncated sun fish	*Ranzania laevis*
By-the-wind sailor	*Velella velella*

Appendix 3. List of occurrence of prey items by bird species: white tern (WHTE), black noddy (BLNO), brown noddy (BRNO), blue-gray noddy (BGNO), gray-backed tern (GBTE), sooty tern (SOTE), great frigatebird (GRFR), brown booby (BRBO), red-footed booby (RFBO), masked booby (MABO), red-tailed tropicbird (RTTB), sooty storm-petrel (SSPE), Bulwer's petrel (BUPE), Bonin petrel (BOPE), Christmas shearwater (CHSH), wedge-tailed shearwater (WTSH), Laysan albatross (LAAL), and black-footed albatross (BFAL). A plus (+) designates occurrence and an asterisk (*) designates an item especially important in dietary ranking.

	WHTE	BLNO	BRNO	BGNO	GBTE	SOTE	GRFR	BRBO	RFBO	MABO	RTTB	SSPE	BUPE	BOPE	CHSH	WTSH	LAAL	BFAL
FISHES																		
Ammodytidae																		
Bleekeria gillii		+	+		+	+		+	+		+				+	+		
Atherinidae																		
Pranesus insularum	*	+			+	+	+	+										
Balistidae		+		+	+		+											
Xanthichthys mento					+													
Belonidae	+				+					+	+							
Platybelone argulus platyura		+						+		+								
Ablennes hians	*	+		+	+	+		+	+	+	+							
Blenniidae	+	+	+	+	+	+		+						+				
Plagiotremus goslinei	+																	
Bothidae		+	+	+														
Bothid larvae				+														
Bramidae																		
Brama orcini					+		+											
Pteraclis velifer	+		+		+	+												
Canthigasteridae																		
Canthigaster sp.	+																	
Carangidae	+	+	+		+	+		+	+					+	+	+		
Decapterus spp.	+	+	*		+	+	*	*	*	*	*				*	*		+
D. macarellus								+	+	+								
D. macrosoma	+	+	+		+	+	*	*	+	*	+		+		+	*		
D. tabl		+	+			+	+	+	+		+					+		
Selar crumenophthalmus			+				+	+								+		
Naucrates ductor	+	+	+	+	+	+		+			+							
Seriola spp.	+		+	+	+			+	+							+		
Caranx spp.	+							+										
Carangoides ferdau					+													
Chaetodontidae			+															
Chaetodon sp.	+																	
Chaunacidae					+													
Cheilodactylidae																		
Cheilodactylus vittatus	+	+	+		+	+			+									
Cirrhitidae		+				+												
Cirrhitops fasciatus			+							+								
Clupeidae																		
Spratelloides delicatulus	+	*	+		*	+												
Sardinella marquesensis																+		
Congridae					+									+				
Coryphaenidae																		
Coryphaena spp.	+	+		+	+		+	+	+	+	+					+		
C. hippurus	+	+		+	*	+	+	+	+	+	+				+			
C. equiselis	*	+	+		+		+	+	+	+	+				+	+		
Dactylopteridae																		
Dactyloptena orientalis		+		+	+	+	+								+	+		
Diodontidae	+			+	+				+		+							
Diodon spp.	+			+	+						+							
D. hystrix											+							
Echeneidae	+					+		+		+	+							
Remora spp.	+			+														
R. remora		+																
Remoropsis brachypterus								+			+							
Rhombochirus osteochir	+	+		+	+													
Eleotridae																		
Asterropteryx sp.				+														
Engraulidae																		
Stolephorus buccaneeri	+	+	+						+							+		

Appendix 3. Continued.

	WHITE	BLNO	BRNO	BGNO	CBTE	SOTE	GRFR	BRBO	RFBO	MABO	RTTB	SSPE	BUPE	BOPE	CHSH	WTSH	LAAL	BFAL
Exocoetidae	*	*	*	*	*	*	*	*	*	*	*		+	+	*	*	+	+
Exocoetus sp.								+										
E. volitans	+	+	+			+	*	*	*	*	*		+		+			
E. monocirrhus	+				+			+										
Prognichthys gilberti	+	+			+			+										
Cypselurus spp.	*	+	+	+	+	+	*	+	*	*	+						+	
C. speculiger	+						+	+	+	+	+							
C. simus							+											
C. spilonotopterus								+										
C. atrisignis	+	+						+	+	+								
C. spilopterus							+		+		+							
Exocoetidae ova													+				*	*
Fistulariidae			+													+		
Gempylidae	+	+	+	+		+		+	+		+			+			+	+
Gempylus serpens	+	*	*	+	+	*	+	+	+	+	+			+	+	+		
Gobiidae		+		+														
Ptereleotris heteropterus		*	+	+												+		
Gonorhynchidae																		
Gonorhynchus gonorhynchus	+	+	+	+	+				+						+			
Gonostomatidae																		
Vinciguerria spp.			+			+			+				+	+	+	+	+	
V. nimbaria					+	+			+				+	+				
Diplophos sp.													+					
Hemiramphidae	+	+	+	+			+	+	+	+	+						+	
Euleptorhamphus viridis	+	+		+			+	*	+	*	+						+	
Hyporhamphus acutus pacificus	+			+				+										
Oxyporhamphus micropterus	+	+			+	+	+	+	+						+			
Holocentridae	+	+	+	+	+	+			+					+	*	+		
Neoniphon sammara			+															
Sargocentron spp.		+	+			+			+									
Holocentrid larvae		+																
Myripristis chryseres	+																	
Hoplichthydae																		
Hoplichthys sp.	+																	
Istiophoridae		+	+	+	+				+	+	+				+			
Istiophorus platypterus	+				+													
Tetrapterus angustirostris					+		+			+								
Makaira nigricans	+	+	+	+	+													
Istiophorus spp.				+														
Kyphosidae																		
Kyphosus bigibbus		+	+		+		+	*	+	+	+					+		
Labridae																		
Hemipteronotus leclusei								+										
Macrorhamphosidae																		
Macrorhamphosus gracilis	+	+	+	+	+	+			+						+			
Macrouridae					+		+											
Molidae																	+	
Ranzania laevis		+	+			+	+		+		*						+	
Masturus lanceolatus							+		+		+							
Monacanthidae			+		+	+	+		+		+			+	+	*		
Pervagor spilosoma		+	+		+	+	+									+		
Alutera scripta					+													
Cantherhines spp.	+					+												
C. verecundus						+												
Mugilidae	+	+			+													
Mullidae	*	*	*	*	*	*	+	*	*	+	+			*	*	*	+	
Myctophidae	+	+	+		+	+			+		+		*	*		+	+	
Benthosema fibulatum	+																	
Hygophum spp.													+	+				
Myctophum spp.													+	+				
Lampanyctus spp.													+					
Diaphus spp.													+					
Symbolophorus sp.													+					

Appendix 3. Continued.

	WHTE	BLNO	BRNO	BGNO	GBTE	SOTE	GRFR	BRBO	RFBO	MABO	RTTB	SSPE	BUPE	BOPE	CHSH	WTSH	LAAL	BFAL
Nomeidae	+	+	+	+	+	*	+	+	+		+		+		+	+		
Nomeus gronovii	+	+		+	+	+		+										
Psenes sp.																+		
P. cyanophrys		+			+			+	+	+								
Cubiceps pauciradiatus											+							
Opisthoproctidae																		
Opisthoproctus sp.													+					
Ostraciontidae				+														
Lactoria fornasini				+	*		+											
Pegasidae																		
Pegasus papilio					*													
Polymixiidae																		
Polymixia japonica							+											
Pomacentridae	+	+	+	+	+	+				+	+							
Chromis sp.		+																
C. vanderbilti	+																	
C. struhsakeri	+																	
Priacanthidae					+		+	+	+							+		
Priacanthus spp.								+			+							
P. cruentatus							+											
Scomberesocidae				+														
Cololabis saira		+	+				+	+	*	+	+						+	
C. saira (ova)																	+	
Scombridae		+	+	+		+	+	+	+		+							
Scomber japonicus								+										
Auxis spp.							+				+							
A. thazard										+								
Katsuwonus pelamis	+	+	+		+	+	+	+	+	+	+				+	+		
Thunnus spp.						+			+									
T. alalunga		+	+				+											
Acanthocybium solandri								+										
Unidentified tuna	+	+			+													
Scombrid larvae		+																
Tuna larvae		+		+														
Serranidae																		
Grammatonotus laysanus	+																	
Odontanthias elizabethae					+													
Soleidae	+			+	+													
Aseraggodes kobensis					+													
Sphyraenidae		+	+	+	+				+									
Sphyraena helleri			+					+										
Sternoptychidae		+			+							+	*	*	+			+
Sternoptyx diaphana					+													
Argyropelecus sp.													*	+			+	
Synodontidae	+	*	*	*	+	+			+		+			+	+	+		
Synodus sp.	+																	
Trachinocephalus myops				+														
Tetraodontidae	+		+		+		+				+					+		
Lagocephalus lagocephalus		+	+		+		+		+		+							
Xiphiidae																		
Xiphias gladius	+			+	+	+	+				+							
Unidentified fishes	*	*	+	*	*	*	*	+	+	+	*	*	*	*	*	*	*	*
Unidentified fish larvae	+	+		*	+													
Unidentified fish juvenile		+		+														
Leptocephalus larvae		+	+	+												+		
Anguilliformes		+																
Pleuronectoidei (flatfish)		+											+	+				
Tetrodontoidei (puffer)											+							
MOLLUSCA																		
Decapoda (squid)	+	+	*	+	+	*	*	+	*	+	*	*	*	*	*	*	*	*
Ommastrephidae	*	*	*	+	+	*	+	*	*	*	*		+	+	*	*	*	*
Ommastrephes spp.			+			+		+	+		+							

Appendix 3. Continued.

	WHTE	BLNO	BRNO	BGNO	GBTE	SOTE	GRFR	BRBO	RFBO	MABO	RTTB	SSPE	BUPE	BOPE	CHSH	WTSH	LAAL	BFAL
Symplectoteuthis spp.	+	+	*		+	*	+	+	+	+	+				*	+	+	
S. oualanienis	+	+	+			+	+	+	+	+	+				+	+	+	+
S. luminosa			+				+	+	+									
Hyaloteuthis pelagicus	+					+			+	+	+				+	+		+
Cranchiidae																		+
Lepidoteuthidae																	+	
Mastigoteuthidae																		
Mastigoteuthis sp.																	+	
Enoploteuthidae																		
Thelidioteuthis alessandrinii																	+	
Pterygioteuthis microlampas														+				
Onychoteuthidae											+				+		+	
Onychoteuthis spp.			+								+							
Onykia spp.		+																
Histioteuthidae														+			+	
Octopoteuthidae																		+
Octopoda																+		+
Gastropoda													+					
Janthinidae																		
Janthina spp.					+													
J. pallida					+													
J. pallida (egg masses)																	+	
J. prolongata					+													
Cavolinidae																		
Cavolinia tridentata					+													
ANNELLIDA																		
Polychaeta													+					
ARTHROPODA																		
Crustacea (unidentified)												+	+	*		+	*	*
Crustacean larvae				+									+		+	+		
Mysidacea				+										+			+	+
Lophogastridae																		
Gnathophausia spp.														+			+	+
G. gigas																	+	+
G. ingens																	+	+
Mysidae																		
Siriella spp.				+														
Euphausiacea			+	+	+							+		+			+	+
Stomatopoda		+		+							+							
Stomatopod larvae		+		+														
Squillidae																		
Pseudosquilla spp.		+		+													+	
Squilla spp.		+		+														
Lysiosquilla spp.		+	+	+							+					+		
Coronida spp.		+		+														
Odontodactylus spp.			+	+														
O. brevirostris			+															
Amphipoda				+								+	+	+			+	+
Oxycephalidae														+				
Eurythenes gryllus																	+	
Alicella sp.																		+
Isopoda				+	+			+				+					+	+
Cymothoidae																		
Anuropus spp.														+			+	+
A. branchiatus																	+	+
Parasitic Isopoda				+	+									+		+	+	+
Nebaliacea																		
Nebaliidae																		
Nebaliopsis typica																	+	+
Copepoda				+									+	+				
Pennellidae																		
Penella spp.									+									+

Appendix 3. Continued.

	WHTE	BLNO	BRNO	BCNO	GBTE	SOTE	GRFR	BRBO	RFBO	MABO	RTTB	SSPE	BUPE	BOPE	CHSH	WTSH	LAAL	BFAL
Pontellidae				+														
Pontella spp.				+														
P. atlantica				*	+													
Calanoid copepod				+										+				
Parasitic copepod														+				
Decapoda																		
Shrimp		+		+	+	+					+	+	+	+			+	+
Penaeidea	+	+																
Penaeus marginatus		+																
Gennadus sp.	+																	
Aristaeinae		+																
Caridea		+															+	
Oplophoridae																	+	+
Notostomus spp.																	+	+
N. japonicus																		+
Acanthephyra sp.																	+	
A. eximia																	+	
Sergestidae				+														
Lucifer spp.				+														
Pasiphaeidae																	+	+
Crab (Brachyura)					+											+	+	+
Crab megalopa		+		*	*								+	+		+		
Portunidae					+													
Galatheidae														+				
Grapsidae																		
Planes cyaneus					+												+	+
Insecta									+									
Gerridae																		
Halobates sericeus			+	*	+							+	*	*		+	+	+
H. micans				+														
Lepidoptera (moth)					+													
Caterpillar		+										+						+
Orthoptera (grasshopper)																		
Euconocephalus nasutus					+													
Argasidae (tick)																		
Ornithodorus capensis												+						
COLENTERATA																	+	
Velellidae																		
Velella velella				+	+	+						*					*	+
Scyphozoa				+		+										+		
TUNICATA																		
Pyrosomatidae														+			+	+
BIRDS																		
Procellariiformes																		
Puffinus sp.																		+
P. pacifucus																		+
Pterodroma hypoleuca																		+
Laridae																		
Sterna fuscata							+											
ALGAE																		
Fucaceae																		
Sargassum sp.																		+
UNIDENTIFIED REMAINS		+	+	+	+		+		+	+	+	+	*	*	+	+	*	*
UNIDENTIFIED MEAT							+											+