

FEEDING ECOLOGY OF TWO SUBTROPICAL SEABIRD SPECIES AT FRENCH FRIGATE SHOALS, HAWAII

Michael P. Seki and Craig S. Harrison

ABSTRACT

Regurgitated food samples from black noddy, *Anous minutus*, and red-footed booby, *Sula sula*, were collected and analyzed from French Frigate Shoals, Hawaii. Eighteen families of fishes, three families of cephalopods, and miscellaneous crustaceans were found in 396 black noddy samples. The most common prey were identified as fishes belonging to the families Synodontidae, Mullidae, and Microdesmidae and as the cephalopod family Ommastrephidae. Twenty-two families of fishes, primarily the Exocoetidae, Carangidae, and Mullidae, along with ommastrephid squids were found in the 456 red-footed booby samples. Our results suggest that these two species of seabirds are apex, opportunistic predators. Seasonal analyses reflect the variation of prey availability over the course of a year and lend support to the notion that this variation is a controlling factor in the timing of the species' breeding. The relationship between the trophic ecology of the seabirds and a tropical fishery is discussed.

In recent years, interest involving the trophic relationships among seabirds has grown immensely. Much of the related research has been directed toward topics relevant to the management of commercial fisheries and the impact of such fisheries on seabird populations (Nettleship et al., 1984).

Seabirds are generally apex predators in marine ecosystems and, as such, are potential competitors with commercial fisheries. Overfishing (Furness, 1984; Springer et al., 1986) and natural climatic fluctuations such as an El Niño event (Schaefer, 1970; Idyll, 1973; MacCall, 1984; Gibbs et al., 1987) have historically altered the availability, quantity, or quality of seabird food supplies and, likewise, seabird populations of many world oceans. To make management decisions or simply predict the effect of such changes, it is important to know what effects fishing practices are likely to have on seabird populations and, conversely, whether seabirds do indeed compete with commercial fisheries. Idyll (1973) suggested that fishery-seabird competition is most severe when the target involves identical species in identical size classes. Basic to the examination of seabird-fisheries interactions is that we acquire an understanding of the food requirements of the involved species.

In the northwestern Hawaiian Islands (NWHI), fishery development proposals prompted an investigation into the feeding ecology of the 18 breeding species of seabirds. The results of the study are described in Harrison et al. (1983). Although the phenomenally large sample size of the study eclipsed any prior tropical or subtropical seabird trophic study, it was not without deficiencies. In an attempt to represent all seabird species from each island, sampling was still inadequate for anything other than superficial seasonal analyses. Diamond (1983) pointed out that, because the samples were taken from such a large geographical range, the species sampled cannot be said to constitute a community.

Our study was undertaken in an attempt to limit and control geographical and seasonal variables and to establish a baseline from which future sampling could be used to monitor seabird population trends and food availability.

METHODS

Food samples from black noddy, *Anous minutus*, and red-footed booby, *Sula sula*, were collected at French Frigate Shoals in the NWHI. The study site, located at the midpoint of the Hawaiian

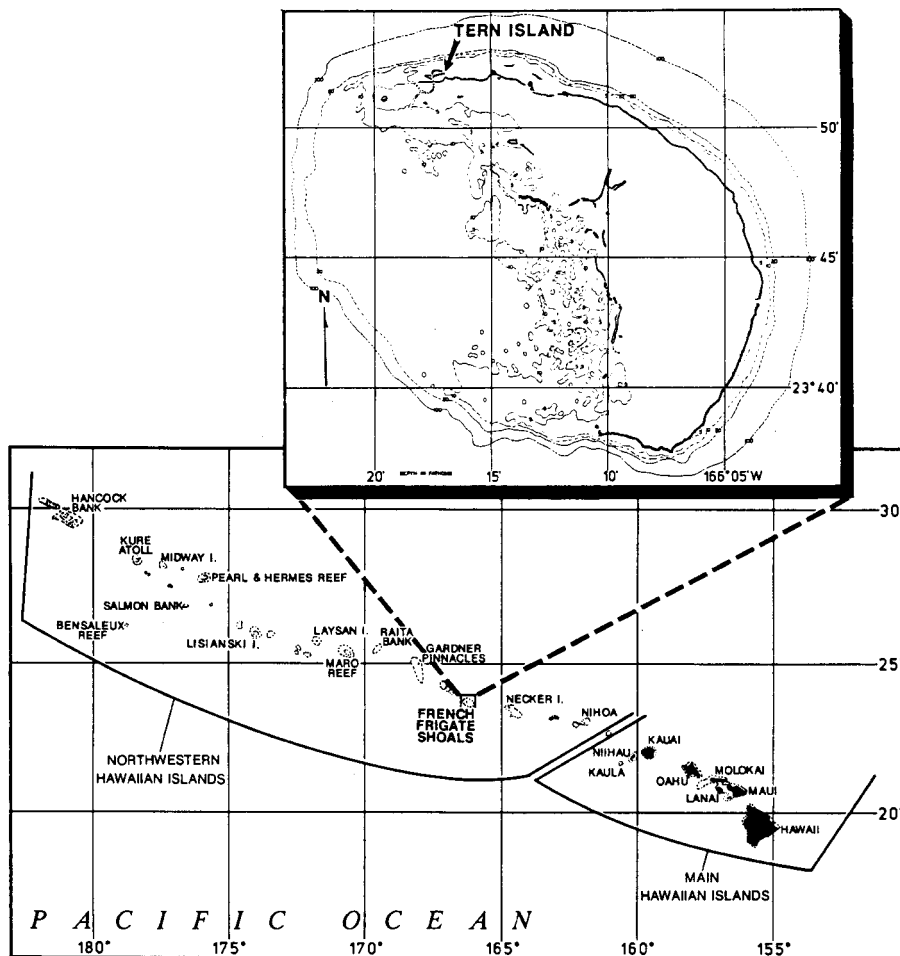


Figure 1. French Frigate Shoals and the Hawaiian Archipelago.

Archipelago at lat. $23^{\circ}45'N$ and long. $166^{\circ}10'W$, is a coral atoll consisting of 12 sandy islets and 1 volcanic pinnacle on a platformed crescent-shaped reef. The reef to a depth of 55 m covers about 648 km^2 and forms a 363 km^2 lagoon (Fig. 1). Sampling was conducted on Tern Island, the largest of the sandy islets located near the northwest tip of the crescent (Amerson, 1971; Uchida and Uchiyama, 1986).

French Frigate Shoals is influenced during most of the year by the North Pacific high with northeasterly trade winds predominating. Surface water temperatures range from 20° to $25^{\circ}C$ during the winter and from 25° to $27.5^{\circ}C$ during the summer (Seckel, 1962; Armstrong, 1983).

The decision to study the black noddy and the red-footed booby was based primarily upon their availability to be sampled throughout the year. Five stomach samples from each species were collected weekly between January 1981 and October 1982. Birds were generally captured alive by hand or with a long-handled, polypropylene fish net and induced to regurgitate. Each sample was then preserved in 10% formalin and returned to the laboratory for analysis. Most of the samples were taken from adult birds with sampling efforts concentrated between 1900 and 2300.

Laboratory procedures for examination of the samples were similar to those employed by Harrison et al. (1983). Sample contents were emptied into a fine mesh strainer, rinsed in running water, sorted into identifiable groups, and counted. In lieu of using water displacement to measure prey biomass, food items were blotted dry and wet weights were measured to the nearest 0.1 g. If more than one

Table 1. Number, frequency of occurrence, weight, and index of relative importance (IRI) of the prey items in 396 black nobby food samples at Tern Island, French Frigate Shoals

Prey species	Total no.	% No.	Freq. occur.	% Freq.	Total wt	% Wt	IRI
Crustacea							
Penaeidae	2	0.03	1	0.25	0.5	0.02	0.01
<i>Penaeus marginatus</i>	8	0.13	8	2.02	2.3	0.10	0.46
Brachyura (crab megalopa)	4	0.07	4	1.01	0.4	0.02	0.09
Stomatopoda	13	0.22	3	0.76	0.3	0.01	0.17
<i>Pseudosquilla</i> sp.	1	0.02	1	0.25	0.1	0.00	0.01
<i>Squilla</i> sp.	28	0.47	7	1.77	3.4	0.15	1.10
<i>Lysiosquilla</i> sp.	3	0.05	3	0.76	0.4	0.02	0.05
Cephalopoda							
Teuthoidea	42	0.70	29	7.32	11.0	0.49	8.71
Onychoteuthidae	3	0.05	3	0.76	9.1	0.41	0.35
Ommastrephidae	110	1.83	64	16.16	131.5	5.91	125.08
<i>Sthenoteuthis oualaniensis</i>	16	0.27	11	2.78	62.4	2.80	8.53
Cranchiidae	1	0.02	1	0.25	0.1	0.00	0.01
<i>Cranchia scabra</i>	1	0.02	1	0.25	0.4	0.02	0.01
Osteichthyes (unidentified fishes)	117	1.95	28	7.07	16.7	0.75	19.09
Leptocephali	64	1.07	41	10.35	21.2	0.95	20.91
Clupeidae							
<i>Spratelloides delicatulus</i>	144	2.40	22	5.56	70.2	3.16	30.91
Photichthyidae							
<i>Vinciguerria</i> sp.	13	0.22	1	0.25	6.9	0.31	0.13
Synodontidae	3,294	54.83	271	68.43	861.5	38.73	6,402.31
<i>Trachinocephalus myops</i>	107	1.78	33	8.33	36.7	1.65	28.57
<i>Synodus</i> sp.	23	0.38	7	1.77	3.4	0.15	0.94
Gonorhynchidae							
<i>Gonorhynchus gonorhynchus</i>	29	0.48	17	4.29	23.0	1.03	6.48
Hemiramphidae	1	0.02	1	0.25	0.1	0.00	0.01
<i>Oxyporhamphus micropterus</i>	3	0.05	3	0.76	7.7	0.35	0.30
Exocoetidae	63	1.05	37	9.34	36.7	1.65	25.22
<i>Parexoetus brachypterus</i>	2	0.03	2	0.51	1.7	0.08	0.06
<i>Exocoetus volitans</i>	5	0.08	5	1.26	5.4	0.24	0.40
Holocentridae	124	2.06	40	10.10	23.6	1.06	31.51
<i>Neoniphon</i> sp.	2	0.03	1	0.25	2.2	0.10	0.03
<i>Neoniphon sammara</i>	1	0.02	1	0.25	2.6	0.12	0.03
Macrorhamphosidae							
<i>Macrorhamphosus</i> sp.	2	0.03	2	0.51	0.6	0.03	0.03
Scorpaenidae	12	0.20	7	1.77	1.1	0.05	0.44
Dactylopteridae							
<i>Dactyloptena orientalis</i>	1	0.02	1	0.25	0.3	0.01	0.01
Echeneidae	2	0.03	2	0.51	0.2	0.01	0.02
Carangidae							
<i>Naucrates ductor</i>	3	0.05	3	0.76	1.4	0.06	0.08
<i>Decapterus</i> sp.	5	0.08	5	1.26	3.1	0.14	0.28
<i>Decapterus tabl</i>	1	0.02	1	0.25	1.8	0.08	0.03
Coryphaenidae							
<i>Coryphaena</i> sp.	3	0.05	3	0.76	1.8	0.08	0.10
<i>Coryphaena equiselis</i>	3	0.05	3	0.76	1.0	0.04	0.07
Mullidae	959	15.96	185	46.72	684.6	30.77	2,183.23
Pomacentridae	1	0.02	1	0.25	0.4	0.02	0.01
Cheilodactylidae							
<i>Cheilodactylus vittatus</i>	2	0.03	2	0.51	1.7	0.08	0.06
Sphyraenidae	5	0.08	4	1.01	1.5	0.07	0.15
<i>Sphyraena</i> sp.	1	0.02	1	0.25	0.4	0.02	0.01
Labridae	6	0.10	5	1.26	1.0	0.04	0.18
Blenniidae	12	0.20	9	2.27	2.9	0.13	0.75

Table 1. Continued

Prey species	Total no.	% No.	Freq. occur.	% Freq.	Total wt	% Wt	IRI
Microdesmidae							
<i>Ptereleotris heteroptera</i>	556	9.25	83	20.96	100.1	4.50	288.20
<i>Gunnelichthys curiosus</i>	2	0.03	2	0.51	0.2	0.01	0.02
Gempylidae	29	0.48	16	4.04	6.3	0.28	3.07
<i>Gempylus serpens</i>	145	2.41	60	15.15	65.4	2.94	81.05
Scombridae	14	0.23	7	1.77	2.1	0.09	0.57
Istiophoridae	2	0.03	2	0.51	0.3	0.01	0.02
Nomeidae	7	0.12	2	0.51	1.3	0.06	0.09
<i>Nomeus gronovii</i>	3	0.05	2	0.51	1.3	0.06	0.06
Pleuronectoidei (flatfishes)	3	0.05	3	0.76	0.6	0.03	0.06
Bothidae	3	0.05	2	0.51	1.1	0.05	0.05
Balistidae	1	0.02	1	0.25	0.2	0.01	0.01
Tetraodontidae							
<i>Lagocephalus lagocephalus</i>	1	0.02	1	0.25	0.4	0.02	0.01

item in the same taxon was present and could not be distinguished as a whole individual, the total weight and number of individuals were recorded. When possible, lengths of the prey were taken, including standard length (SL) for fishes, mantle length (ML) for cephalopods, carapace length for shrimps, carapace width for crabs, and total length for all others. No attempt was made to measure the lengths of any prey items that were well digested.

Prey items were identified to the lowest possible taxon by using the methods described in Harrison et al. (1983). When possible, fishes were identified by external anatomical characters and morphometrics. In many cases, however, the fishes were in an advanced stage of digestion and required clearing of the flesh and staining of the vertebrae with Alizarine S (Taylor, 1967). A combination of vertebral counts and morphological characters was then used for identification. Invertebrates were identified by undigested hard parts and external morphological features. In the case of cephalopods, this included beaks, pens, and luminous organs among other anatomical features; for crustaceans, exoskeletons and walking appendages were the primary identification characters.

To analyze the data, we employed the index of relative importance (IRI) developed by Pinkas et al. (1971) to assess the value of prey items. The IRI incorporates percentage by number (N), weight (W), and frequency of occurrence (F):

$$\text{IRI} = \%F(\%N + \%W).$$

Although this index has its shortcomings (Hyslop, 1980), it provides a basis for ranking the prey items that is representative of the three measures traditionally used in stomach content analyses. Because the objective of the study was to identify the major prey and their importance to the birds, we excluded the unidentifiable remains from the IRI analyses.

To examine effects due to seasonal variation in prey availability as reflected by any differences in diet, the data were separated by season [winter (December–February), spring (March–May), summer (June–August), and fall (September–November)] and then analyzed.

RESULTS

Black Noddy. — Three hundred and ninety six black noddy samples were collected and analyzed for this study. Regurgitated samples averaged 5.7 g and 15.2 prey items (Table 1). Overall, the diet was composed of fishes (IRI = 18,287.5), cephalopods (IRI = 316.1), and crustaceans (IRI = 7.94). The fishes, representing 18 families, occurred in 98.2% of the samples, comprised 90.0% of the total aggregate weight, and accounted for 96.1% of the total number of food items. Fish families with the highest IRI values were Synodontidae (IRI = 6,723.0), Mullidae (IRI = 2,183.2), and Microdesmidae (IRI = 296.15). To a lesser degree, Gempylidae and Holocentridae also were common forage items. Nearly all of the fishes taken as prey were juveniles or larvae; unfortunately, this meant that many of the specimens were not identifiable beyond the family level. The only synodontid that was

Table 2. Percent frequency of occurrence of prey families by season for the black noddy at Tern Island, French Frigate Shoals

Prey families	Winter (N = 98)	Spring (N = 121)	Summer (N = 111)	Fall (N = 66)
Penaeidae	6.12	1.65		1.52
Brachyura (crab megalopa)	2.04			3.03
Stomatopoda	7.14	1.65	3.60	1.52
Teuthoidea	11.22	7.44	6.31	3.03
Onychoteuthidae	1.02	0.83	0.90	
Ommastrephidae	20.41	11.57	18.92	27.27
Cranchiidae	2.04			
Unidentified fishes	10.20	4.96	6.31	7.58
Leptocephali	11.22	11.57	4.50	16.67
Clupeidae	1.02	1.65	15.32	3.03
Photichthyidae		0.83		
Synodontidae	92.86	70.25	42.34	75.76
Gonorrhynchidae	13.27	2.48	0.90	
Hemiramphidae		1.65		3.03
Exocoetidae	7.14	6.61	17.12	9.09
Holocentridae	5.10	3.31	9.01	34.85
Macrorhamphosidae	2.04			
Scorpaenidae	3.06	0.83	1.80	1.52
Dactylopteridae				1.52
Echeneidae			1.80	
Carangidae	3.06	3.31	1.80	
Coryphaenidae	1.02	0.83	2.70	1.52
Mullidae	20.41	59.50	61.26	37.88
Pomacentridae	1.02			
Cheilodactylidae		0.83	0.90	
Sphyracidae	1.02	3.31		
Labridae	4.08			1.52
Blenniidae	4.08	2.48	1.80	
Microdesmidae	44.90	4.96	9.01	37.88
Gempylidae	25.91	19.01	12.61	19.70
Scombridae		2.48	1.80	3.03
Istiophoridae			0.90	1.52
Nomeidae	2.04	1.65		
Pleuronectoidei	2.04	0.83		
Bothidae	2.04			
Balistidae				1.52
Tetraodontidae				1.52

identified to species was *Trachinocephalus myops*, and no mullids were identified beyond family, a problem also encountered during the Harrison et al. (1983) study. *Ptereleotris heteroptera* comprised nearly all of the microdesmids with the exception of two *Gunnelichthys curiosus*. The pelagic ommastrephid squids were the most important cephalopod, and stomatopods were the most important crustacean.

None of the previous studies effectively examined seasonal differences in diet composition. In this study, we found that the prey items that ranked high when all data were pooled remained high when the data were separated by season (Table 2), although the order of their ranking may have changed. With the assumption that the birds are high-level, opportunistic predators, we believe that this result reflects seasonal changes in prey availability. The frequency of occurrence of the highest ranked families was plotted against season and analyzed by years. We extracted the data for black noddies sampled at French Frigate Shoals in 1978–1980 from the Harrison et al. (1983) study for inclusion in this analysis (Fig. 2).

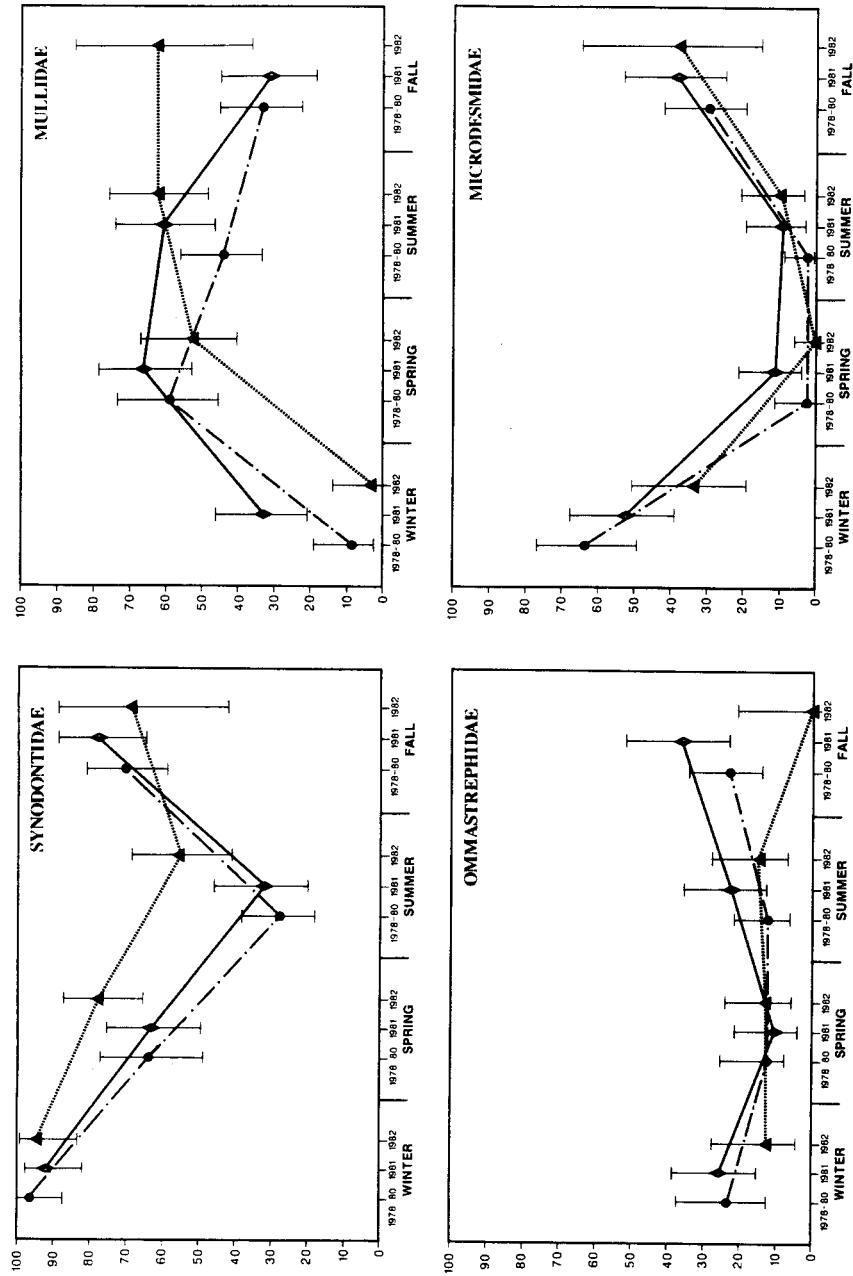


Figure 2. Seasonal frequencies of occurrence and the 95% confidence limits of major black noddy prey families at French Frigate Shoals. The 1978-1980 data are from Harrison et al. (1983).

Table 3. Number, frequency of occurrence, weight (in grams), and index of relative importance (IRI) of the prey items in 456 red-footed booby food samples at Tern Island, French Frigate Shoals

Prey species	Total no.	% No.	Freq. occur.	% Freq.	Total wt	% Wt	IRI
Cephalopoda	1	0.04	1	0.22	0.6	0.00	0.01
Teuthoidea	22	0.91	16	3.51	70.9	0.19	3.86
Ommastrephidae	704	29.10	214	46.93	4,597.9	12.21	1,938.68
<i>Ommastrephes</i> sp.	1	0.04	1	0.22	14.4	0.04	0.02
<i>Ommastrephes bartramii</i>	30	1.24	17	3.73	963.4	2.56	14.17
<i>Sthenoteuthis oualaniensis</i>	124	5.13	66	14.47	2,723.7	7.24	178.99
Osteichthyes (unidentified fishes)	9	0.37	7	1.54	28.3	0.08	0.69
Photichthyidae							
<i>Vinciguerria</i> sp.	1	0.04	1	0.22	0.9	0.00	0.01
Synodontidae	5	0.21	1	0.22	1.3	0.00	0.05
Gonorhynchidae							
<i>Gonorhynchus gonorhynchus</i>	13	0.54	5	1.10	16.0	0.04	0.64
Hemiramphidae	36	1.49	29	6.36	444.0	1.18	16.98
<i>Oxyporhamphus micropterus</i>	41	1.69	30	6.58	992.3	2.64	28.49
<i>Euleptorhamphus viridus</i>	26	1.07	20	4.39	871.6	2.32	14.88
<i>Hyporhamphus acutus pacificus</i>	1	0.04	1	0.22	2.8	0.01	0.01
Exocoetidae	480	19.84	276	60.53	12,181.3	32.36	3,159.67
<i>Parexocoetus brachypterus</i>	145	5.99	77	16.89	3,261.7	8.66	247.44
<i>Exocoetus</i> sp.	65	2.69	48	10.53	3,217.0	8.55	118.36
<i>Exocoetus voltans</i>	24	0.99	16	3.51	1,107.2	2.94	13.79
<i>Exocoetus monocirrhus</i>	2	0.08	2	0.44	143.1	0.38	0.20
<i>Cypselurus</i> sp.	10	0.41	9	1.97	955.1	2.54	5.81
<i>Cheilopogon</i> sp.	6	0.25	6	1.32	545.9	1.45	2.24
<i>Hirundichthys speculiger</i>	2	0.08	2	0.44	176.7	0.47	0.24
Holocentridae	2	0.08	2	0.44	2.3	0.01	0.04
Veliferidae							
<i>Metavelifer multispinosus</i>	3	0.12	3	0.66	17.6	0.05	0.11
Priacanthidae	2	0.08	2	0.44	6.2	0.02	0.04
<i>Priacanthus</i> sp.	27	1.12	7	1.54	209.1	0.56	2.59
<i>Priacanthus alalaua</i>	6	0.25	4	0.88	144.7	0.38	0.55
Carangidae	1	0.04	1	0.22	2.3	0.01	0.01
<i>Naucrates ductor</i>	2	0.08	2	0.44	2.2	0.01	0.04
<i>Decapterus</i> sp.	29	1.20	22	4.82	491.9	1.31	12.10
<i>Decapterus macarellus</i>	6	0.25	6	1.32	730.7	1.94	2.89
<i>Decapterus tabl</i>	18	0.74	9	1.97	268.3	0.71	2.86
<i>Decapterus macrosoma</i>	85	3.51	29	6.36	1,511.8	4.02	47.89
<i>Selar crumenophthalmus</i>	4	0.17	3	0.66	41.6	0.11	0.18
Coryphaenidae							
<i>Coryphaena</i> sp.	8	0.33	7	1.54	57.7	0.15	0.74
<i>Coryphaena hippurus</i>	3	0.12	2	0.44	70.8	0.19	0.14
<i>Coryphaena equiselis</i>	8	0.33	8	1.75	332.0	0.88	2.12
Emmelichthyidae	2	0.08	1	0.22	11.5	0.03	0.02
Mullidae	362	14.96	55	12.06	679.7	1.81	202.25
Kyphosidae							
<i>Kyphosus bigibbus</i>	2	0.08	2	0.44	7.7	0.02	0.04
Cheilodactylidae							
<i>Cheilodactylus vittatus</i>	1	0.04	1	0.22	0.9	0.00	0.01
Ammodytidae	3	0.12	1	0.22	0.6	0.00	0.03
Gempylidae							
<i>Gempylus serpens</i>	54	2.23	30	6.58	183.7	0.49	17.90
Scombridae	1	0.04	1	0.22	0.3	0.00	0.01
<i>Auxis thazard</i>	1	0.04	1	0.22	35.9	0.10	0.03
<i>Katsuwonus pelamis</i>	29	1.20	18	3.95	440.0	1.17	9.36
<i>Thunnus alalunga</i>	1	0.04	1	0.22	12.6	0.03	0.02
Istiophoridae	1	0.04	1	0.22	0.4	0.00	0.01

Table 3. Continued

Prey species	Total no.	% No.	Freq. occur.	% Freq.	Total wt	% Wt	IRI
Nomeidae	1	0.04	1	0.22	4.7	0.01	0.01
<i>Nomeus gronovii</i>	2	0.08	2	0.44	3.7	0.01	0.04
Monacanthidae	1	0.04	1	0.22	1.9	0.01	0.01
Tetraodontidae							
<i>Lagocephalus lagocephalus</i>	1	0.04	1	0.22	20.2	0.05	0.02
Molidae							
<i>Ranzania laevis</i>	5	0.21	3	0.66	36.8	0.10	0.20

Using the 1978–1980 data as the initial baseline, there is little difference in the 1981 data and definite trends in the occurrence of the major species in the diet through the course of a year. Winter and fall peaks of synodontid and microdesmid occurrences coincide with lower occurrence frequencies of mullids. Likewise, spring and summer frequencies of mullids in the diet seem correlated with lower frequencies of synodontids and microdesmids. It is likely that these trends also reflect relative abundance of the fishes in the epipelagic environment during these seasons. Samples taken in 1982, however, appear to deviate from the trends of prior years for some of the prey families. For example, the frequency of mullids in the diet increased in fall 1982 when compared to previous years, and ommastrephid squids were absent in the black noddy diets, whereas in previous years their occurrence peaked in the fall. Conversely, the occurrence of microdesmids showed little variation between any of the years.

We collected 386 prey items in sufficiently good condition to obtain reliable length measurements. These prey items ranged in length from 4 mm (brachyuran crab megalopa) to 74 mm (*Gempylus serpens*) ($\bar{x} = 32.45$ mm, $s = 11.49$). The smallest fishes among the diet components were three larval scorpaenids, 9 mm each. Among major prey families, Synodontidae (N = 118) were 21–53 mm SL ($\bar{x} = 40.1$, $s = 4.6$), Mullidae (N = 21) were 46–62 mm SL ($\bar{x} = 52.8$, $s = 3.9$), Microdesmidae (N = 120) were 18–34 mm SL ($\bar{x} = 27.8$, $s = 2.4$), and Ommastrephidae (N = 12) were 22–55 mm ML ($\bar{x} = 40.5$, $s = 8.7$).

Individual weights of prey items that were nearly intact were also recorded. The 390 measurements ($\bar{x} = 0.5$, $s = 0.7$) ranged from numerous items weighing 0.1 g to an ommastrephid squid, *Sthenoteuthis oualaniensis*, weighing 4.3 g. Both length and weight data collection involved only prey items with minimal digestion, and we did encounter a few cases in which some larger prey items had undergone more significant digestion and accurate measurements could not be obtained. These prey are not included in the above summaries, and any resultant bias should be considered.

Red-footed Booby.—We collected and analyzed 456 red-footed booby samples. Food samples averaged 83.0 g and 5.3 prey items (Table 3). Overall, fishes (IRI = 13,200.2) and cephalopods (IRI = 3,192.7) made up the entire composition of prey items identified in the samples. The fishes, representing 22 families, occurred in 93.4% of the samples, comprised 77.8% of the total aggregate weight, and represented 63.5% of the total number of food items. Fish families with the highest IRI values were Exocoetidae (IRI = 6,306.8), Carangidae (IRI = 207.0), and Mullidae (IRI = 202.2). Of the exocoetids identified to species, *Parexocoetus brachypterus* and *Exocoetus volitans* appear to be the most important. Although

Table 4. Percent frequency of occurrence of prey families by season for the red-footed booby at Tern Island, French Frigate Shoals

Prey families	Winter (N = 104)	Spring (N = 129)	Summer (N = 124)	Fall (N = 99)
Cephalopoda			0.81	
Teuthoidea	11.54	4.65	2.42	1.01
Ommastrephidae	45.19	46.51	66.13	47.47
Unidentified fishes	0.96	0.78	3.23	1.01
Photichthyidae				1.01
Synodontidae	0.96			
Gonorrhynchidae	4.81			
Hemiramphidae	31.73	13.95	4.03	16.16
Exocoetidae	65.38	85.27	62.10	73.74
Holocentridae			0.81	1.01
Veliferidae		1.55	0.81	
Priacanthidae			6.45	3.03
Carangidae	10.58	3.88	30.65	13.13
Coryphaenidae	4.81	3.10	3.23	3.03
Emmelichthyidae			0.81	
Mullidae	8.65	10.08	20.97	7.07
Kyphosidae	0.96	0.78		
Cheilodactylidae		0.78		
Ammodytidae		0.78		
Gempylidae	4.81	8.53	10.48	1.01
Scombridae			10.48	7.07
Istiophoridae			0.41	
Nomeidae			2.42	
Monacanthidae		0.78		
Tetraodontidae				1.01
Molidae		1.55	0.81	

many of the flyingfishes could not be identified beyond the family level, it is possible that many of the larger cypselurine flyingfishes were the bulk of the unidentified family members. Fishes of the genus *Decapterus* (especially *D. macrostoma*) comprised nearly all of the carangids, and as mentioned earlier, none of the mullids could be identified more specifically. Other fishes that contributed significantly to the red-footed booby diet included halfbeaks (Hemiramphidae), snake mackerels (Gempylidae), and tunas (Scombridae). The pelagic squid family Ommastrephidae (IRI = 2,978.7) accounted for all of the identified cephalopods, most of which were identified as *S. oualaniensis*.

We again found that the prey families that ranked high when all data were pooled, also ranked high when separated into seasons (Table 4). The frequency of occurrence of these prey families was then plotted against season and analyzed by years (Fig. 3). Unfortunately the red-footed booby samples for French Frigate Shoals in Harrison et al. (1983) were insufficient to compare to our current information. Although there are variations between years (especially between ommastrephids and exocoetids), abundances of mullids, carangids, and ommastrephids appear to peak during the summer, whereas exocoetids peak in the spring and are least abundant in the summer. At Aldabra Atoll, Diamond (1974) reported ommastrephids to be most abundant during the wet season (November–March) and exocoetids, although present throughout the year, to be most abundant during the dry season (April–October).

We obtained 245 measurements of prey items with a mean length of 86.4 mm SL ($s = 22.4$) and ranging from 11 mm ML (*S. oualaniensis*) to 304 mm SL

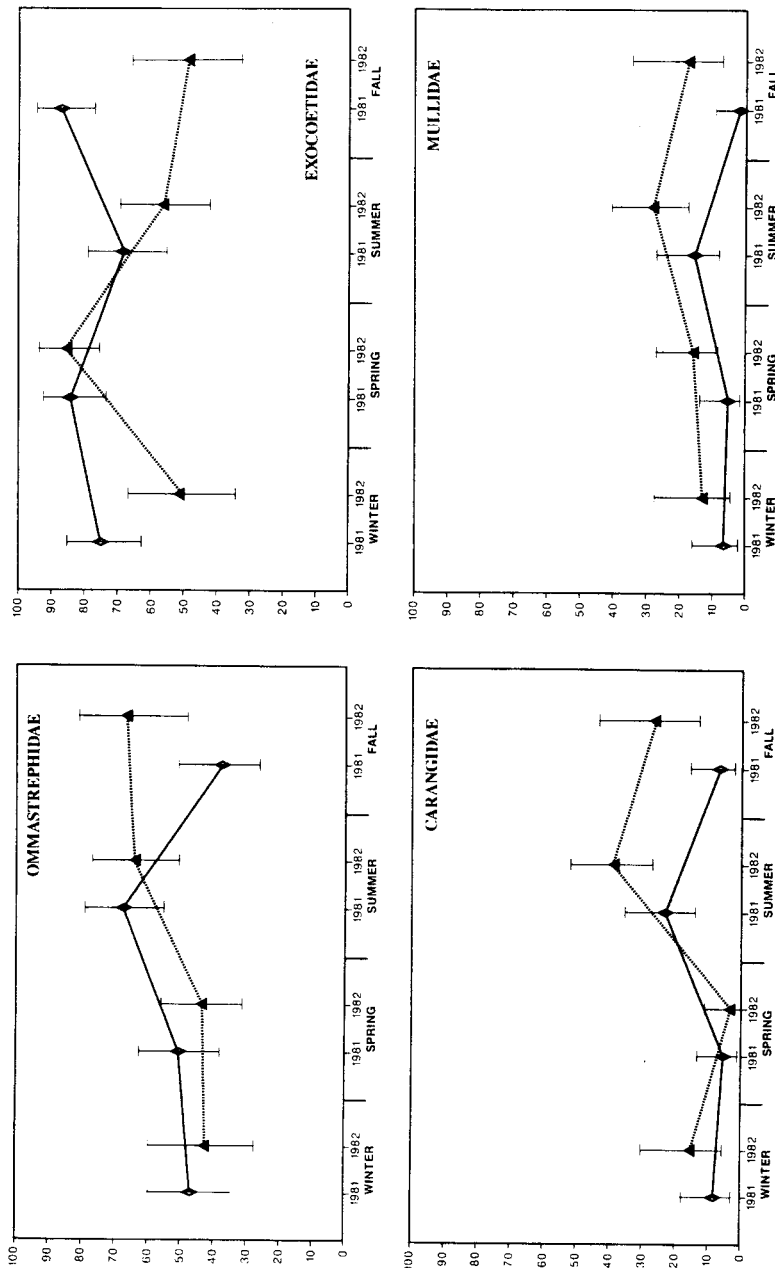


Figure 3. Seasonal frequencies of occurrence and the 95% confidence limits of major red-footed booby prey families at French Frigate Shoals.

(*Euleptorhamphus viridus*). The smallest fish collected was a juvenile flyingfish, *Cheilopogon* sp., at 35 mm SL. Among major prey families, Exocoetidae (N = 64) were 35–188 mm SL (\bar{x} = 134.8, s = 27.8), Mullidae (N = 23) were 38–102 mm SL (\bar{x} = 62.7, s = 18.3), and Ommastrephidae (N = 106) were 11–141 mm ML (\bar{x} = 86.4, s = 22.4).

A total of 261 prey items in condition good enough to obtain accurate weight data were collected. These prey ranged from a juvenile billfish weighing 0.4 g to a flyingfish, *Hirundichthys speculiger*, weighing 97.7 g (\bar{x} = 25.6 g, s = 18.6). Again, we emphasize that both length and weight data collection involved only prey items with minimal digestion. Larger and more digested prey were taken, but accurate measurements were not obtainable and, therefore, not summarized here.

DISCUSSION

Monitoring food habits can be extremely important in assessing the general health and stability of seabird populations (Fefer et al., 1984). Such assessments require the establishment of comprehensive baselines and must overcome a problem common among past seabird diet studies, that is, the inability to obtain samples year-round. This is a reflection of individual phenologies of seabird species, many of which spend much of the year entirely at sea. As mentioned earlier, black noddies and red-footed boobies were selected as our study species primarily because both reside at Tern Island throughout the year. In addition, the feeding ecology of these species could provide valuable insights into fisheries interactions. Our preliminary study indicated that both seabirds relied, at least in part, on fishes targeted for fisheries development (Harrison et al., 1983). Black noddies typically feed nearshore, often in association with jacks (*Caranx* sp.); red-footed boobies are deepwater feeders occasionally found in association with tuna schools.

Our description of the black noddy diet is consistent with prior studies in that fishes form a very high proportion of this species' diet composition (Stonehouse, 1962; Ashmole and Ashmole, 1967b; Diamond, 1983; Harrison et al., 1983). Ashmole and Ashmole (1967b) found 17 fish families accounting for 95% of the number of food items and occurring in 96% of the samples. The major families found in their study at Christmas Island were Exocoetidae (which ranked highest) followed by Scombridae and Blenniidae (ranking equally second). Diamond (1983) found Mullidae (*Upeneus* sp.) to be the most abundant prey item at Cousin Island. The most related study was that conducted by Harrison et al. (1983) in which pooled samples collected at seabird colonies throughout the NWHI showed the highest ranked prey for the black noddy to be mullids, followed by synodontids and clupeids. When considering only those samples collected from French Frigate Shoals, there was no difference from the current study in the highest ranked fish prey; synodontids were by far the highest, followed by mullids and microdesmids. In all of the studies, the only invertebrate found to be of importance to black noddies is the squid family Ommastrephidae (in particular, *Sthenoteuthis* [*Symplectoteuthis*] *oualaniensis*).

Similarly, our results of the red-footed booby diet further document the findings of previous studies conducted at Oahu, Hawaii (Ashmole and Ashmole, 1967a), at Christmas Island (Schreiber and Hensley, 1976), Aldabra Atoll (Diamond, 1974; 1983), and the NWHI (Harrison et al., 1983): The diet of red-footed boobies is composed predominantly of flyingfishes and ommastrephid squids. Ashmole and Ashmole (1967a) found that, in addition to these major prey, snake mackerels were important. Carangidae (primarily *Decapterus* sp.), Mullidae, Scomberesoc-

idae (*Cololabis saira*), and Scombridae were the other highly ranked fish prey families found in pooled samples collected at seabird colonies throughout the NWHI (Harrison et al., 1983). When only the samples collected from French Frigate Shoals were considered, there was no difference in the highest ranked prey families from the current study.

These results suggest that, as with other subtropical seabirds, black noddies and red-footed boobies are apex, opportunistic predators. They apparently will feed on almost anything of appropriate size that becomes available in the surface waters near roosting and breeding areas. Their opportunistic character is evidenced by prey diversity. The 34 prey families taken by black noddies and the 23 prey families taken by red-footed boobies represent very diverse diets when compared to seabird diets in temperate areas (Pearson, 1968) or in Peru where anchovies constituted 80–96% of the seabirds' food (Jordan, 1967). Although many prey families are represented by just a few specimens taken during a single season, these incidental prey are further indicators of an opportunistic predator (Diamond, 1983). These prey may be eaten only when common prey items are scarce, but their presence enables a species to survive during food shortages. Their importance should not be underestimated (Ashmole and Ashmole, 1967b).

Our seasonal analyses lend support to the notion that peak food availability created by natural distribution of prey species is the controlling factor in the timing of seabird breeding. Although most of the seabirds in the NWHI breed in the spring and summer months, black noddies have adapted to a breeding season that begins in the winter (Fefer et al., 1984). It has been proposed that black noddies are able to raise their young in the winter because they feed in association with winter-resident, inshore, predatory fishes; their phenology, however, may be attributed more to the apparent natural fall and winter abundance of synodontids and microdesmids. This is discussed more in detail below. The importance of the dartfish, *Ptereleotris heteroptera*, as a prey item is unique to black noddies among the NWHI seabirds (Harrison et al., 1983). Mullids reportedly spawn during spring-summer in Hawaii (Miller, 1974; Moffitt, 1979) and, hence, the lower occurrence of these juveniles in the fall. Corbin (1977) hypothesized that juvenile mullids have 1.5- to 2-month pelagic stages before settling into their adult benthic habitat. Red-footed boobies breed primarily in the spring-summer but are capable of egg laying throughout the year (Nelson, 1978). Likewise, occurrence frequencies of exocoetids and ommastrephid squids in the booby diet peak in the spring-summer but boobies exploit this resource year-round. The distribution and abundance of flyingfishes reportedly alter with seasonal shifts of sea-surface isotherms (Bruun, 1935; Parin, 1963; 1968; Shuntov, 1968). For subtropical exocoetid species, optimal surface temperatures are 21.5°–26°C (Parin, 1963). Harman and Young (1985) reported that early growth stages of ommastrephid squids were collected throughout the year in Hawaii indicating year-round spawning. Specifically, larval *S. oualaniensis* were found in greatest abundance in the fall. Seasonal prey availability, breeding phenology, and the trophic relationships of these seabirds are further influenced by their interactions with the local fisheries.

Perhaps the greatest concern involving seabirds is their interrelationships with various aspects of commercial fisheries. It has been well-documented that, in many parts of the world, there is significant competition between seabirds and fisheries (Crawford and Shelton, 1978; Furness, 1982; Safina and Burger, 1985). In the relatively pristine environment of the NWHI, commercial fisheries are still very much in their infancy, and considerable attention is directed towards seabirds and their role in the marine ecosystem as the interest in the exploitation of the resources continues to grow. Prior studies in the NWHI have recognized that

seabirds remove significant amounts of energy from the ecosystem. Fefer et al. (1984) reported that NWHI seabirds consume some 410,000 t of marine resources each year, and Polovina (1984) estimated that seabirds consume 42% of the annual production of small pelagic fishes and squid in an ecosystem model of the French Frigate Shoals. Nevertheless, it is difficult to assess what, if any, impact the NWHI seabirds have on commercial fisheries or vice versa, even when they remove such substantial amounts of energy. Tropical ecosystems are complicated by the migratory nature of tuna stocks and other predators on which the birds depend to drive prey to the surface. The juvenile forms of fishes and squid that comprise much of the food consumed by seabirds are below the trophic levels that would directly affect commercial fisheries.

The development of a fishery that exploits coastal pelagic species would have the most significant impact on the natural existence of the seabirds. Both black noddies and red-footed boobies have been identified as species that regularly occurred in flocks feeding in association with predatory fishes (King, 1970; Gould, 1971). A great majority (75.4%) of predatory fish schools found under flocking birds in Hawaii have been identified as skipjack tuna, *Katsuwonus pelamis* (Harrison and Seki, 1987); therefore, the relationship of the birds with this tuna species requires some discussion. The diet composition of Hawaiian skipjack tuna is similar to that of these seabirds (Yuen, 1959; Waldron and King, 1963). The fish families Carangidae (predominantly *Decapterus* sp.), Scombridae, and Mullidae and the squid family Ommastrephidae were the most common prey in both studies. There is obviously some overlap of components with the noddy diet, which includes mullids and ommastrephids among its major components, and with the booby diet, which includes all of these common prey. Although no seasonal analysis was conducted on the tuna feeding studies, skipjack tuna are in greatest abundance during their peak spawning season from May to September (Matsumoto et al., 1984). We can speculate that, if indeed the birds depend on predatory fishes to make the prey available, the major prey of both the fishes and birds should be similar during these months. It is, therefore, not surprising that carangids and mullids are taken most frequently during the spring and summer months by both noddies and boobies and that juvenile scombrids only occur in the bird diets during the summer and fall. Likewise, the overlapping occurrence frequencies of prey families are lowest during the winter months. Size ranges of the major prey taken were also similar between skipjack (Harrison and Seki, 1987) and the birds, which provides further evidence that prey of the seabirds are also probably the forage for tunas. Ashmole and Ashmole (1968) suggested that the lack of flyingfishes in the diets of tunas compared to seabirds is probably due to the ability of these fishes to escape submarine predators by flying and, thus, rendering them vulnerable to aerial predation. For black noddies that also feed in association with inshore resident jacks, there was no overlap in dietary components (Parrish et al., 1980), and it is doubtful that predatory fishes play a major role in the noddies' ability to exploit the large numbers of synodontids and microdesmids in the winter. Such a phenomenon is strictly attributed to a seasonal influx of prey in the ecosystem and the opportunistic predatory ability of the noddies.

In conclusion, although we have furthered our understanding of the trophic ecology of tropical and subtropical seabirds, our limited knowledge of the marine ecology and fisheries of the region prevent further insight into the role of seabirds in the ecosystem. Improvements in our ability to identify postlarval and juvenile fishes and squids will result in refinements in our analyses of dietary specialization. Such a task will not be easy because young stages of fishes and squids are very

difficult to sample with even state-of-the-art gear. It is ironic that pelagic seabirds have served as the most effective sampling gear for much of the small nektonic epipelagic fauna. Distributional data of juvenile organisms, such as the ommastrephid squid, *S. oualaniensis* (Young, 1975; Okutani and Tung, 1978), the dartfish, *P. heteroptera* (Randall and Hoese, 1985), and the morwong, *Cheilodactylus vittatus* (Randall, 1983), are based primarily on the collections of seabird food samples. Our results here support the proposition by Ashmole and Ashmole (1968) to use seabird food samples to study seasonal variation of epipelagic fauna of tropical oceanic areas.

We need to improve our knowledge of seabird foraging ranges and locations. This information would be most critical during the incubation and chick-rearing periods when food demands become more localized around nesting areas. Preliminary foraging distances have been inferred from incubation shifts and feeding frequencies of young (Harrison and Hida, 1980), but these estimations are extremely crude, and alternative methods of assessment should be sought. The use of radiotelemetry to identify feeding locations has been employed experimentally on the brown noddy, *Anous stolidus*, a congener of the black noddy (Harrison and Stoneburner, 1981). Use of this technology should be expanded in the future.

Finally, historical studies have failed to incorporate concurrent oceanographic data with diet. Occurrences of major ecological perturbations such as an El Niño Southern Oscillation (ENSO) event have been shown to have significant impacts on diets as well as breeding phenologies of birds in other areas (Schaefer, 1970; Idyll, 1973; MacCall, 1984; Gibbs et al., 1987). Our seasonal analyses of black noddy prey frequencies reveal considerable deviations in the fall 1982 from trends of prior years. Although we did not have concurrent time series of oceanographic and environmental data to examine any perturbations that may have influenced the changes in trends, we could not help but speculate as to the possibility that limited effects of the 1982–1983 ENSO may have had some impact even this far west in the Pacific. Whatever the reason for the variation in diet, breeding populations were not adversely affected as they were at Christmas Island during the same period (Schreiber and Schreiber, 1983; 1984; Gibbs et al., 1987). Obtaining oceanic physical information around the colonies and foraging areas would be most beneficial to the monitoring of seabird populations and to the understanding of the ecosystem dynamics.

ACKNOWLEDGMENTS

We thank the many individuals who committed their time and efforts to this research project. The U.S. Fish and Wildlife Service staff and volunteers who collected the food samples in the field include J. B. Andre, G. Fairaizl, S. Fairaizl, E. Flint, R. Ittner, R. P. Schulmeister, S. D. Schulmeister, E. A. Sheekey, and J. Young. D. T. Tagami provided programming assistance. G. W. Boehlert, S. I. Fefer, E. A. Schreiber, the late R. W. Schreiber, and D. A. Somerton kindly read and constructively criticized earlier drafts of the manuscript. R. S. Shomura, former Director of the National Marine Fisheries Service Honolulu Laboratory, was largely responsible for making this study possible.

LITERATURE CITED

- Amerson, A. B., Jr. 1971. The natural history of French Frigate Shoals, Northwestern Hawaiian Islands. Atoll Res. Bull. 150. 383 pp.
- Armstrong, R. W. 1983. Atlas of Hawaii, 2nd ed. University of Hawaii Press, Honolulu. 238 pp.
- Ashmole, M. J. and N. P. Ashmole. 1967a. Notes on the breeding season and food of the red-footed booby (*Sula sula*) on Oahu, Hawaii. Ardea 55: 265–267.
- and ———. 1968. The use of food samples from sea birds in the study of seasonal variation in the surface fauna of tropical oceanic areas. Pac. Sci. 22: 1–10.
- Ashmole, N. P. and M. J. Ashmole. 1967b. Comparative feeding ecology of sea birds of a tropical oceanic island. Peabody Mus. Nat. Hist., Yale Univ. Bull. 24. 131 pp.

- Bruun, A. F. 1935. Flying-fishes (Exocoetidae) of the Atlantic, systematic and biological studies. Dana Rep. 2, No. 6: 1-106.
- Corbin, J. S. 1977. Laboratory derived nitrogen and energy budgets for a juvenile goatfish, *Parupeneus porphyreus*, fed brine shrimp, *Artemia salina*, with a description of the pattern of growth in wild fish. M.S. Thesis, Univ. Hawaii, Honolulu. 194 pp.
- Crawford, R. J. M. and P. A. Shelton. 1978. Pelagic fish and seabird interrelationships off the coasts of south west and south Africa. Biol. Conserv. 14: 85-109.
- Diamond, A. W. 1974. The red-footed booby on Aldabra Atoll, Indian Ocean. Ardea 62: 196-218.
- . 1983. Feeding overlap in some tropical and temperate seabird communities. Pages 24-46 in R. W. Schreiber, ed. Tropical seabird biology, studies in avian biology 8. Allen Press, Inc., Lawrence, Kansas.
- Fefer, S. I., C. S. Harrison, M. B. Naughton and R. J. Shallenberger. 1984. Synopsis of results of recent seabird research conducted in the Northwestern Hawaiian Islands. Pages 9-76 in R. W. Grigg and K. Y. Tanoue, eds. Proceedings of the Second Symposium on Resource Investigations in the Northwestern Hawaiian Islands, Vol. 1. May 25-27, 1983, University of Hawaii, Honolulu, Hawaii. UNIH-SEAGRANT-MR-84-01.
- Furness, R. W. 1982. Competition between fisheries and seabird communities. Adv. Mar. Biol. 20: 225-307.
- . 1984. Seabird biomass and food consumption in the North Sea. Mar. Pollution Bull. 15(7): 244-248.
- Gibbs, H. L., S. C. Latta and J. P. Gibbs. 1987. Effects of the 1982-83 El Niño event on blue-footed and masked booby populations on Isla Daphne Major, Galapagos. Condor 89: 440-442.
- Gould, P. J. 1971. Interactions of seabirds over the open ocean. Ph.D. Thesis, Univ. Arizona, Tucson. 110 pp.
- Harman, R. F. and R. E. Young. 1985. The larvae of ommastrephid squids (Cephalopoda, Teuthoidea) from Hawaiian waters. Vie Milieu 35: 211-222.
- Harrison, C. S. and T. S. Hida. 1980. The status of seabird research in the Northwestern Hawaiian Islands. Pages 17-31 in R. W. Grigg and R. T. Pfund, eds. Proceedings of the Symposium on Status of Resource Investigations in the Northwestern Hawaiian Islands, April 24-25, 1980, University of Hawaii, Honolulu, Hawaii. UNIH-SEAGRANT-MR-80-04.
- and M. P. Seki. 1987. Trophic relationships among tropical seabirds at the Hawaiian Islands. Pages 305-326 in J. P. Croxall, ed. Seabirds: feeding ecology and role in marine ecosystems, Cambridge University Press, Cambridge.
- and D. L. Stoneburner. 1981. Radiotelemetry of the brown noddy in Hawaii. J. Wildl. Manage. 45: 1021-1025.
- , T. S. Hida and M. P. Seki. 1983. Hawaiian seabird feeding ecology. Wildl. Monogr. 85: 1-71.
- Hyslop, E. J. 1980. Stomach contents analysis—a review of methods and their application. J. Fish. Biol. 17: 411-429.
- Idyll, C. P. 1973. The anchovy crisis. Sci. Am. 228: 22-29.
- Jordan, R. 1967. The predation of guano birds on the Peruvian anchovy (*Engraulis ringens* Jenyns). Calif. Coop. Oceanic Fish. Invest. Rep. 11: 105-109.
- King, W. B. 1970. The trade wind zone oceanography pilot study. Part VII: observations of sea birds, March 1964 to June 1965. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 586. 136 pp.
- MacCall, A. D. 1984. Seabird-fishery trophic interactions in eastern Pacific boundary currents: California and Peru. Pages 136-148 in D. N. Nettleship, G. A. Sanger and P. F. Springer, eds. Marine birds: their feeding ecology and commercial fisheries relationships. Proceedings of the Pacific Seabird Group Symposium, Seattle, Washington, 6-8 January 1982. Ottawa: Can. Wildl. Serv. Spec. Publ.
- Matsumoto, W. M., R. A. Skillman and A. E. Dizon. 1984. Synopsis of biological data on skipjack tuna, *Katsuwonus pelamis*. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 451. 92 pp.
- Miller, J. M. 1974. Nearshore distribution of Hawaiian marine fish larvae: effects of water quality, turbidity and currents. Pages 217-231 in J. H. S. Blaxter, ed. The early life history of fish. Springer-Verlag, New York.
- Moffitt, R. B. 1979. Age, growth, and reproduction of the kumu, *Parupeneus porphyreus* Jenkins. M.S. Thesis. Univ. Hawaii, Honolulu. 42 pp.
- Nelson, J. B. 1978. The Sulidae: gannets and boobies. Oxford University Press, Oxford. 1012 pp.
- Nettleship, D. N., G. A. Sanger and P. F. Springer (eds.). 1984. Marine birds: their feeding ecology and commercial fisheries relationships. Proceedings of the Pacific Seabird Group Symposium, Seattle, Washington, 6-8 January 1982. Ottawa: Can. Wildl. Serv. Spec. Publ. 220 pp.
- Okutani, T. and I-H. Tung. 1978. Reviews of biology of commercially important squids in Japanese and adjacent waters. I. *Symplectoteuthis oualaniensis* (Lesson). Veliger 21: 87-94.
- Parin, N. V. 1963. The flying fishes (Exocoetidae) of the Northwest Pacific. [In Russ.] Academy of

- Sciences of the U.S.S.R. Institute of Oceanology, 1960. [Transl. by O. Ronen, IPST Cat. 618. Israel Prog. Sci. Transl., available U.S. Dep. Commer., Off. Tech. Serv., Wash., D.C.] 84 pp.
- . 1968. Ichthyofauna of the epipelagic zone. [In Russ.] Academy of Sciences of the U.S.S.R. Institute of Oceanology, Izdatel'stvo "Nauka," Moskva 1968. [Transl. by M. Raveh, edited by H. Mills, 1970, 206 pp.; Israel Prog. Sci. Transl., available U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, Va. 22151, as TT 69-59020.] 205 pp.
- Parrish, J., L. Taylor, M. DeCrosta, S. Feldkamp, L. Sanderson and C. Sorden. 1980. Trophic studies of shallow-water fish communities in the Northwestern Hawaiian Islands. Pages 175-188 in R. W. Grigg and R. T. Pfund, eds. Proceedings of the Symposium on Status of Resource Investigations in the Northwestern Hawaiian Islands, April 24-25, 1980. University of Hawaii, Honolulu, Hawaii. UNIHI-SEAGRANT-MR-80-04.
- Pearson, T. H. 1968. The feeding biology of sea-bird species breeding on the Farne Islands, Northumberland. *J. Anim. Ecol.* 37: 521-552.
- Pinkas, L., M. S. Oliphant and I. L. K. Iverson. 1971. Food habits of albacore, bluefin tuna, and bonito in California waters. Calif. Dep. Fish and Game, Fish Bull. 152, 105 pp.
- Polovina, J. J. 1984. Model of a coral reef ecosystem. I. The ECOPATH model and its application to French Frigate Shoals. *Coral Reefs* 3: 1-11.
- Randall, J. E. 1983. A review of the fishes of the subgenus *Goniistius*, genus *Cheilodactylus*, with description of a new species from Easter Island and Rapa. *Occas. Pap. Bernice P. Bishop Mus.* 25(7): 1-24.
- and D. F. Hoese. 1985. Revision of the Indo-Pacific dartfishes, genus *Ptereleotris* (Perciformes: Gobioidae). *Indo-Pac. Fishes* 7: 36 pp.
- Safina, C. and J. Burger. 1985. Common tern foraging: seasonal trends in prey fish densities and competition with bluefish. *Ecology* 66: 1457-1463.
- Schaefer, M. B. 1970. Men, birds and anchovies in the Peru Current—dynamic interactions. *Trans. Am. Fish. Soc.* 99: 461-467.
- Schreiber, R. W. and D. A. Hensley. 1976. The diets of *Sula dactylatra*, *Sula sula*, and *Fregata minor* on Christmas Island. *Pacific Ocean. Pac. Sci.* 30: 241-248.
- and E. A. Schreiber. 1983. Reproductive failure of marine birds on Christmas Island, fall 1982. *Tropical Ocean-Atmosphere Newsl.* 16: 10-12.
- and ———. 1984. Central Pacific seabirds and the El Niño southern oscillation: 1982 to 1983 perspectives. *Science* 225: 713-716.
- Seckel, G. R. 1962. Atlas of the oceanographic climate of the Hawaiian Islands region. U.S. Fish Wildl. Serv., Fish. Bull. 13: 371-421.
- Shuntov, V. P. 1968. Counts of flying fishes in the eastern Indian Ocean. *Probl. Ichthyol.* 8: 784-789.
- Springer, A. M., D. G. Roseneau, D. S. Lloyd, C. P. McRoy and E. C. Murphy. 1986. Seabird responses to fluctuating prey availability in the eastern Bering Sea. *Mar. Ecol. Prog. Ser.* 32: 1-12.
- Stonehouse, B. 1962. Ascension Island and the British ornithologists' union centenary expedition 1957-59. *Ibis* 103b: 107-123.
- Taylor, W. R. 1967. An enzyme method of clearing and staining small vertebrates. *Proc. U.S. Natl. Mus.* 122(3596): 1-17.
- Uchida, R. N. and J. H. Uchiyama (eds.). 1986. Fishery atlas of the Northwestern Hawaiian Islands. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 38: 142 pp.
- Waldron, K. D. and J. E. King. 1963. Food of skipjack in the central Pacific. Pages 1431-1457 in H. Rosa, Jr., ed. Proceedings of the world scientific meeting on the biology of tunas and related species, 2-14 July 1962. FAO Fish. Rep. 6(3).
- Young, R. E. 1975. A brief review of the biology of the oceanic squid, *Symplectoteuthis oualaniensis* (Lesson). *Comp. Biochem. Physiol.* 52B: 141-143.
- Yuen, H. S. H. 1959. Variability of skipjack response to live bait. U.S. Fish Wildl. Serv., Fish. Bull. 60: 147-160.

DATE ACCEPTED: May 19, 1988.

ADDRESSES: (M.P.S.) Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, Hawaii 96822-2396; (C.S.H.) 46-024 Puulena Street #614, Kaneohe, Hawaii 96744.