# 13

## Trophic relationships among tropical seabirds at the Hawaiian Islands

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### Introduction

Seabird communities in tropical and subtropical waters are often composed of large numbers of species that have complex trophic relationships. For example, 17 species breed on Laysan Island, Hawaii (Ely & Clapp, 1973) and 18 species breed on Christmas Island (Pacific) (Schreiber & Ashmole, 1970); trophic relationships are probably more complex than those in cold-water communities because of the larger number of food species available.

An important characteristic of tropical and subtropical zones is a relative lack of seasonal change in surface waters. Ryther (1963) and Ashmole (1971) defined these zones to include all areas where sea surface temperatures remain above 23°C all year. More precise definitions are probably impossible. A permanent thermocline is usually present which limits vertical enrichment of the euphotic zone throughout the year. Nutrient depletion in tropical oceans results in low primary productivity. This phenomenon is more pronounced in oceanic areas than near continents because land-based nutrients in neritic zones can increase productivity (Raymont, 1966).

Seabirds have adapted to life in tropical waters in various ways. Whereas cold-water species of a genus frequently have multi-egg clutches, tropical species often lay a single egg, presumably because the relatively impoverished food supplies allow fewer young to be raised successfully (Lack, 1967). Cold-water species tend to breed at predictable times each year to maximize the advantages of a seasonal abundance of food and to minimize the effects of cold weather and storms on vulnerable young. In contrast, tropical species often have ill-defined breeding seasons because they do not face severe winter weather and have fewer predictable feeding opportunities. Non-seasonal breeding occurs with many tropical species and at various locations (Nelson, 1979). Tropical seabirds have adopted foraging strategies that minimize contact with predatory fish such as tunas, sharks, and billfish that eat birds. They plunge rather than dive (Ainley, 1977), which restricts feeding to surface waters, and prey largely on epipelagic fauna (Harrison & Hida, 1980). Tropical oceanic areas do not have seasonal abundances of food that would attract vast numbers of migratory birds. Most migrant seabird species avoid tropical and subtropical areas and fly through them quickly to spend their non-breeding period in polar or subpolar areas (Ainley & Boekelheide, 1984). For example, Sooty and Short-tailed Shearwaters *Puffinus griseus* and *P. tenuirostris*, from the southern hemisphere migrate to Alaska to forage during their non-breeding season (Harrison, 1982), but few stop to feed in the tropical Pacific (King, 1970). These shearwaters are important consumers on migration in the colder water systems of California (see Chapter 12) and Oregon (Wiens & Scott, 1975).

From 1977 to 1983 we studied the ecology of Hawaiian seabirds to discover how they might be influenced by the growing fishery. Research on the biology of important commercial fishes has also helped to clarify the role of Hawaiian seabirds in the marine ecosystem. In this chapter we review the trophic relationships among Hawaiian seabirds and compare these with other tropical and subtropical seabird communities, discuss fishery interactions, and suggest directions for future research.

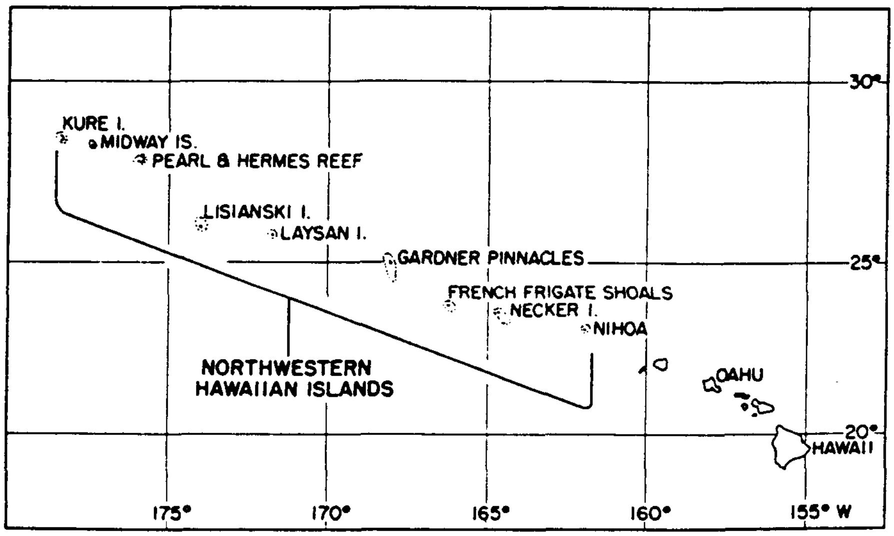
## The Hawaiian Archipelago

We concentrated our work in the Northwestern Hawaiian Islands (NWHI) where 18 seabird species (two albatrosses, two shearwaters, one storm petrel, two petrels, three boobies, one frigatebird, one tropicbird, and six terns) breed. The NWHI are subtropical, extending from latitude 23° N to 28° N and longitude 162° W to 178° W in the North Pacific (Fig. 13.1). This location has several important influences on the seabird community. Many species are at or near the northern limit of their breeding range. The depth of the mixed layer is much shallower than in the main Hawaiian Islands (Hirota *et al.*, 1980), and the NWHI are often in the path of North Pacific winter storms. Apparently the food supply is seasonal. Fish larvae are much more abundant during summer than winter (Hirota *et al.*, 1980). Like the situation around Tahiti (Rougerie & Chabanne, 1983), the migratory tunas are much more abundant in Hawaii during summer (Waldron, 1964). These factors are presumably responsible for the tendency for seabirds to breed during summer, although albatrosses and petrels are important exceptions (Harrison, Hida & Seki, 1983).

## Resource partitioning

The diets of Hawaiian seabirds are very complex. Representatives of 56 families, 86 genera, and 74 species of fish were found in the diets of the 18 species that breed in the NWHI (Harrison *et al.*, 1983). Numerous squid families and various groups of crustaceans were also represented in their diets. As previously, we group the seabirds of the NWHI into five guilds based on similarities in composition of diet, size of prey taken, and feeding strategies. These guilds are the albatrosses, pelecaniforms, terns and shearwaters that associate with predatory fishes, nocturnal petrels, and neuston-feeding terns. We acknowledge that tropical seabirds do not fit neatly into these categories and there are some difficulties with the characterization. For example, boobies and frigatebirds occasionally feed in association with tunas; however, they occur only with about 1% of the tuna schools sighted in Hawaiian waters (National Marine Fisheries Service (NMFS), unpublished data). Sooty Terns *Sterna fuscata* and Wedge-tailed Shearwaters *Puffinus pacificus* occasionally feed at night (Gould, 1967). Our information suggests that these feeding strategies do not

Fig. 13.1. The Hawaiian Archipelago.



represent modal feeding behaviour in Hawaiian waters, and we have ignored such details in our analysis.

*Albatrosses*

Black-footed and Laysan Albatrosses *Diomedea nigripes* and *D. immutabilis*, eat primarily squid, flyingfish eggs, and deep-water crustaceans (Table 13.1). Many of the crustaceans and squid that were consumed possess photophores and may be bioluminescent at night. At least eight squid families were identified, but Ommastrephidae was the most common. When adequate keys are developed to identify squid beaks in Hawaii, it will be interesting to determine the differences and similarities between these birds with respect to squid predation. The proportions of prey consumed by each congener was very different. By volume, Laysan Albatrosses consumed twice as much squid, and Black-footed Albatrosses ate 11 times more flyingfish eggs. The differences in diets may result from the apparent tendencies of Laysan Albatrosses to feed at night and of Black-footed Albatrosses to feed during the day. Both species forage in the cool waters north of the NWHI, much farther from the islands than other seabirds in this community. Their feeding locations suggest a tenuous relationship with the tropical marine environment.

The albatross guild in Hawaii can be compared with the Waved Albatross *D. irrorata* in the Galapagos Islands, the only other tropical albatross. Like Hawaiian birds, Waved Albatrosses eat primarily squid, fish, and deep-water crustaceans (Harris, 1973). The squid families consumed in Hawaii, however, were different from those consumed in the Galapagos, where mostly representatives of Histioteuthidae and Octopoteuthidae are eaten. These squid families are rarely taken by Hawaiian birds, who feed predominantly on ommastrephid squid. The differences in the composition of squid in the diets may be attributed to the availability of the representative squid families to the birds at the different localities. Galapagos birds consume flyingfish and mackerel scad *Decapterus* spp., but no flyingfish eggs. The guild in Hawaii is therefore broadly similar to the only other tropical albatross, but there are some notable differences.

*Pelecaniformes*

The Red-footed Booby *Sula sula*, Brown Booby *S. leucogaster*, Masked Booby *S. dactylatra*, Great Frigatebird *Fregata minor*, and Red-tailed Tropicbird *Phaethon rubricauda*, comprise this guild. Adult flyingfish (especially *Exocoetus volitans* and *Cypselurus* spp.) were the most commonly taken prey, but adult mackerel scad and juvenile ommastrephid squid were also very important components of the diet (Table 13.1). Members of this guild have diets with different percentage compositions of major prey items and consume prey of different sizes. Masked Boobies took the largest prey: the mean prey length was almost twice that of the other species. Masked Boobies frequently took fish larger than 20 cm. The other birds consumed prey primarily in the 8–15 cm range, although Brown Boobies took many 5 cm juvenile goatfish (Mullidae). Red-footed Boobies, an offshore species, ate much more squid than Brown Boobies, an inshore species. Flyingfish were especially common (> 60% by volume) in the diet of Great Frigatebirds. Frigatebirds have a structural inability to take flight from the ocean's surface and therefore do not enter the water. Certain prey were taken exclusively by a single species at one location when presumably such prey was abundant. For example, virtually all Pacific Saury *Cololabis saira* were taken by Red-footed Boobies during the winter months at the northern end of the archipelago.

Table 13.1. *Average percent volumes for major prey (families or groups that constitute 2% or more of the volume of a guild) items of Northwestern Hawaiian Islands birds*

| Prey | Albatrosses | Pelecaniforms | Terns and shearwaters associated with predatory fishes | Nocturnal petrels | Neuston-feeding terns |
|---|---|---|---|---|---|
| Carangidae | 17.8 | 9.8 | — | — | — |
| Clupeidae | — | — | 2.2 | — | 2.7 |
| Coryphaenidae | — | 2.9 | — | — | 2.0 |
| Exocoetidae | 25.1 | 44.3 | 10.2 | — | 10.2 |
| Hemiramphidae | — | 4.2 | — | — | — |
| Mullidae | — | 3.6 | 20.8 | — | 8.9 |
| Myctophidae | — | — | — | 10.2 | — |
| Ostraciontidae | — | — | — | — | 21.1 |
| Scombridae | — | 2.5 | — | — | — |
| Sternoptychidae | — | — | — | 10.8 | — |
| Synodontidae | — | — | 4.9 | — | 7.4 |
| Other fishes | 4.2 | 8.8 | 19.1 | 24.4 | 24.1 |
| Squid | 48.2 | 13.2 | 30.2 | 23.5 | 2.7 |
| Crustaceans | 6.6 | — | — | 5.6 | 10.6 |
| Marine insects | — | — | — | — | 9.7 |
| Unidentified remains | 11.0 | — | — | — | 12.9 |

This guild may be compared with seabird communities at Ascension Island (Stonehouse, 1962; Dorward, 1963), Christmas Island (Ashmole & Ashmole, 1967; Schreiber & Hensley, 1976), the Seychelles Islands (Diamond, 1974, 1984), Rose Atoll (Harrison, Hida & Seki, 1984), and the Galapagos Islands (Harris, 1969). It consumes primarily flyingfish and ommastrephid squid throughout its range, but inshore feeding Brown Boobies have much greater diet diversity (Diamond, 1984). In Hawaii, this guild is distinguished by the prominence of juvenile goatfish and adult mackerel scad in the diet.

*Terns and shearwaters associated with predatory fish*

This guild includes many of the most common tropical seabirds: the Sooty Tern, Brown Noddy *Anous stolidus*, Black Noddy *A. tenuirostris*, White Tern *Gygis alba*, Wedge-tailed Shearwater, and Christmas Shearwater *Puffinus nativitatis*. These species feed largely in association with predatory fishes, especially tunas (Murphy & Ikehara, 1955; Waldron, 1964; Ashmole & Ashmole, 1967; Erdman, 1967). Recent observations in the eastern tropical Pacific indicate little feeding in the absence of fish schools (R.L. Pitman, personal communication).

Juvenile forms of goatfish, ommastrephid squid (especially *Symplectoteuthis* spp.), mackerel scad, and flyingfish were the main prey consumed by this guild (Table 13.1). Black Noddies and to a lesser extent White Terns feed inshore in association with the jacks *Caranx* spp. and nearshore tunas (e.g. *Euthynnus affinis*). Consequently, inshore-feeding terns eat more herrings Clupeidae and juvenile lizardfish Synodontidae and somewhat fewer mackerel scads and squid than the remaining birds in this guild. The offshore-feeding Sooty Terns, Brown Noddies, Wedge-tailed Shearwaters, and Christmas Shearwaters associate with Skipjack Tuna *Katsuwonus pelamis*, Yellowfin Tuna *Thunnus albacares*, and Dolphinfish *Coryphaena hippurus* (Table 13.4). Squid account for 30–50% of the dietary volumes of the offshore birds. The mean prey length of shearwaters, the heaviest species in this guild, is almost twice that of the lightest tern. For many of the common prey taxa, all species in the guild took similar size classes, usually 3–8 cm. This guild takes prey much smaller than that consumed by pelecaniforms. Feeding techniques account for some resource partitioning. Shearwaters can pursue prey underwater, whereas terns feed at the surface and rarely wet their feathers. Feeding locations may account for many of the differences among the diets of these species, but detailed information does not exist. Seasonal variation was apparent in the diet of each species in this guild.

The Hawaiian guild consumes higher proportions of fish than squid compared with guilds of Ascension Island, Christmas Island (Ashmole & Ashmole, 1967), and the Seychelles (Diamond, 1984). Hawaiian birds generally eat fewer flyingfish, substituting goatfish and mackerel scad. The Seychelles are the only other location where the latter two families are important components of the diet.

### *Nocturnal petrels*

The Bonin Petrel *Pterodroma hypoleuca*, Bulwer's Petrel *Bulweria bulwerii*, and Sooty Storm Petrel *Oceanodroma tristrami*, apparently feed extensively at night. Each species feeds offshore in surface waters, usually alone but occasionally in association with other birds. This guild feeds primarily on squid, hatchetfish Sternoptychidae and lanternfish Myctophidae (Table 13.1). Most of their prey possess photophores and occur in surface waters only under reduced light conditions (Harrison *et al.*, 1983). Food samples from this guild are usually in very poor condition, making identification to genus or species difficult. Timing of breeding may be an important means to avoid competition for prey resources. Bulwer's Petrels breed during summer whereas Bonin Petrels and Sooty Storm Petrels breed during winter. Bulwer's and Bonin Petrels take larger prey than the storm petrels. They also consume more fish than squid, whereas the storm petrels take fish and squid in equal volumes. Improved identification technique for midwater fish may enable a better understanding of resource partitioning among the species in this guild.

Few comparisons with other tropical areas are possible because little work on these or similar species is published. Great-winged Petrel *Pterodroma macroptera* in New Zealand consumed similar midwater fish but different families of squid (Imber, 1973). Phoenix Petrels *P. alba* at Christmas Island ate 78% squid and 14% fish (Ashmole & Ashmole, 1967). Bonin Petrels are unusual among *Pterodroma* because they eat primarily fish rather than squid.

### *Neuston-feeding terns*

The Gray-backed Tern *Sterna lunata* and Blue-gray Noddy *Procelsterna cerulea* have somewhat similar diets and, unlike other terns in Hawaii, rarely feed in association with predatory fishes. They feed inshore and take small prey during the breeding season. Their diets are remarkable because of the very small proportion of squid (Table 13.1). Their primary preys were marine insects (*Halobates sericeus*), crustaceans, and juvenile forms of Cowfish *Lactoria fornasini*, flyingfish, goatfish, and lizardfish. Their diets differed widely in the proportions of several taxa. Gray-backed Terns feed far more on Cowfish, whereas Blue-gray Noddies feed far more on marine insects (Cheng & Harrison, 1983) and lizardfish. Some competition is avoided because of slightly different breeding seasons: Blue-gray Noddies feed most of their young in March–May and Gray-backed Terns feed their young in May–July. In addition, Gray-backed Terns feed throughout the NWHI, but Blue-gray Noddies are restricted to the southern islands because of an absence of suitable breeding habitat elsewhere. Gray-backed Terns are larger birds and take somewhat larger prey than the noddies.

Neuston-feeding terns are little studied elsewhere. Blue-gray Noddies on Christmas Island have similar diets to Hawaiian birds in regard to the consumption of *Halobates* and minute crustaceans. However, Hawaiian birds ate goatfish and lizardfish and Christmas Island birds ate tunas, blennies, and snake mackerels (Ashmole & Ashmole, 1967).

## Consumption of major prey items

It is very difficult to measure directly the amount of food that seabirds consume (Furness, 1982). Consequently, we have developed a model to estimate the energy and food requirements of the NWHI seabird community.

Table 13.2. *Recent population estimate of seabird breeding pairs in the Hawaiia*

| | Main Hawaiian Islands | Kaula | Nihoa | Necker | French Frigate Shoals | Gardner Pinnacles |
|---|---|---|---|---|---|---|
| *Diomedea nigripes* | 0 | 25–50 | 40–60 | 200–250 | 2000–2250 | 0 |
| *D. immutabilis* | 10 | 30–70 | 1–5 | 800–900 | 900–1000 | 10–15 |
| *Pterodroma phaeopygia* | 400–600 | 0 | 0 | 0 | 0 | 0 |
| *Pt. hypoleuca* | 0 | 0 | 0 | 0 | 30–50 | 0 |
| *Bulweria bulwerii* | 500–1000 | 20–50 | 75000–100000 | 250–500 | 200–500 | 10–15 |
| *Puffinus pacificus* | 40000–60000 | 1500–2500 | 30000–40000 | 1500–2500 | 1500–1750 | 50–100 |
| *P. nativitatis* | 40–60 | 75–125 | 200–250 | 0 | 15–20 | 0 |
| *P. puffinus newelli* | 4000–6000 | 0 | 0 | 0 | 0 | 0 |
| *Oceanodroma castro* | + | 0 | 0 | 0 | 0 | 0 |
| *O. tristami* | 0 | 0 | 2000–3000 | + | + | 0 |
| *Phaethon rubricauda* | 200–400 | 250–400 | 250–300 | 100–150 | 550–600 | 20–23 |
| *P. lepturus* | 500–3000 | 0 | 0 | 0 | 0 | 0 |
| *Sula dactylatra* | 3–4 | 200–400 | 250–300 | 250–300 | 500–600 | 125–150 |
| *S. leucogaster* | 75–100 | 300–500 | 150–200 | 20–25 | 40–60 | 5–10 |
| *S. sula* | 900–1200 | 250–350 | 1500–2000 | 650–750 | 550–600 | 0 |
| *Fregata minor* | 5–10 | 250–350 | 3500–4500 | 700–900 | 350–375 | 0 |
| *Sterna lunata* | 10 | 500–600 | 9000–12000 | 3500–4500 | 750–1000 | 1500–2500 |
| *S. fuscata* | 60000–90000 | 35000–50000 | 10000–25000 | 12500–25000 | 60000–78000 | 250–500 |
| *Procelsterna cerulea* | 0 | ? | 2000–2500 | 1000–1500 | + | + |
| *Anous stolidus* | 15000–20000 | 15000–25000 | 25000–35000 | 10000–15000 | 5000–7500 | 1000–1500 |
| *A. tenuirostris* | 300–800 | 20–30 | 1000–5000 | 300–500 | 750–850 | 200–300 |
| *Gygis alba* | 50–100 | 30–40 | 1000–5000 | 100–300 | 500–750 | 150–250 |

The model was largely developed by Pettit, Whittow & Ellis (1984) and was expanded to encompass the entire NWHI seabird community. Estimates will be refined in the future as improved date become available.

*Model methods and input*

The model includes a component for adult maintenance energy. An estimate of the energy required for daily existence for each of the 18 species in the NWHI community was multiplied by the total number of days each year that each species is associated with the breeding islands. This amount was then multiplied by the total number of birds on each island. The estimate of daily existence energy includes the energy for foraging based upon gliding flight. It is particularly difficult to estimate the costs of foraging flight, yet we recognize it to be an extremely important component of the model (Furness, 1982). More than 5 million seabirds breed in Hawaii. The populations of each species and island are presented in Table 13.2. Non-breeding populations are included in this model and have been estimated as a percentage of the known breeding population, ranging from 31% to 70% (Fefer *et al.*, 1984). Tropical seabirds moult throughout the year, and this model assumed that daily existence energy requirements reflect the daily cost of moulting.

*Archipelago (from Harrison et al., 1984, where full references are given)*

| Laysan | Lisianski | Pearl & Hermes Reef | Midway | Kure | |
|---|---|---|---|---|---|
| 14000–21000 | 2800–3800 | 8000–11000 | 6500–7500 | 700–1300 | *Diomedea nigripes* |
| 105000–132000 | 23000–30000 | 9000–12000 | 150000–200000 | 3000–4000 | *D. immutabilis* |
| 0 | 0 | 0 | 0 | 0 | *Pterodroma phaeophgia* |
| 50000–75000 | 150000–250000 | 400–600 | 2500–5000 | 400–600 | *Pt. hypoleuca* |
| 1000–2000 | 50–100 | < 10 | 0 | 0 | *Bulweria bulwerii* |
| 125000–175000 | 10000–30000 | 5000–10000 | 500–1000 | 900–1100 | *Puffinus pacificus* |
| 1500–2000 | 400–600 | < 10 | 25–50 | 20–30 | *P. nativitatis* |
| 0 | 0 | 0 | 0 | 0 | *P. puffinus newelli* |
| 0 | 0 | 0 | 0 | 0 | *Oceanodroma castro* |
| 500–2500 | ? | 300–500 | 0 | ? | *O. tristrami* |
| 1500–2500 | 900–1300 | 10–60 | 4000–5000 | 1000–1300 | *Phaethon rubricauda* |
| 0 | 0 | 0 | 1 | 0 | *P. lepturus* |
| 400–425 | 300–350 | 140–160 | 5–10 | 65–75 | *Sula dactylatra* |
| 34 | 15–25 | 50–60 | 0 | 50–60 | *S. leucogaster* |
| 700–800 | 350–450 | 40–60 | 450–500 | 400–450 | *S. sula* |
| 2000–2500 | 750–850 | 300–400 | 60–75 | 200–250 | *Fregata minor* |
| 5000–10000 | 15000–20000 | 650–750 | 100–200 | 30–50 | *Sterna lunata* |
| 375000–500000 | 400000–600000 | 35000–45000 | 30000–45000 | 8000–12000 | *S. fuscata* |
| 0 | 0 | 0 | 0 | 0 | *Procelsterna cerulea* |
| 10000–15000 | 7500–15000 | 1700–2000 | 500–1000 | 700–800 | *Anous stolidus* |
| 1500–2500 | 500–1000 | 75–125 | 2000–6000 | 0 | *A. tenuirostris* |
| 1000–2000 | 50–100 | 10–20 | 5000–7500 | 5–10 | *Gygis alba* |

Added to the adult maintenance energy in the model is a component that estimates the costs of producing an egg. This was determined using bomb calorimetry and estimations of the efficiency of egg production. We assumed that birds laid a single egg and that each breeding pair produced one egg per year. The cost of producing an egg was then multiplied by an estimate of the number of eggs laid each year for each species. The amount of energy expended in raising a chick was estimated using growth equations and chick weight data. This amount was then multiplied by the number of chicks raised, using the highest observed reproductive success for that species in the NWHI (Pettit *et al.*, 1984).

The food requirement for each species was determined by use of volumetric estimates of the percentage of the diet for each prey species for each seabird (Harrison *et al.*, 1983). These estimates were converted into estimates of food consumption by using bomb calorimetric data for common prey items. The estimates of food consumed were calculated individually for each species and later pooled into feeding guilds.

### *Model results and discussion*

Seabirds in the NWHI consume 410 000 tonnes of fish, squid, crustaceans, and other food sources each year (Table 13.3). Squid is the largest component, comprising over 54% of the total consumption. Fish accounts for 35% of the prey consumption of this community, the most important families being Exocoetidae (7%), Mullidae (5%), and Carangidae (primarily mackerel scad) (4%). Most of the squid were Ommastrephidae, especially *Symplectoteuthis oualaniensis*, but the large amount of unidentified squid in the albatross diets (Harrison *et al.*, 1983) makes this conclusion tentative.

Two feeding guilds account for almost all of the prey consumed. Albatrosses take 264 000 tonnes (64%) and birds that feed in association with predatory fishes consume 117 000 tonnes (29%). For individual species, Laysan Albatrosses account for 60% of the consumption. Laysan Albatrosses, Black-footed Albatrosses, Bonin Petrels, Wedge-tailed Shearwaters, and Sooty Terns together account for 94% of the prey consumed. Each of these birds consumes a large proportion of squid. The impact of neuston-feeding terns on the marine ecosystem is trivial, as biological intuition might suggest, but the minor role of pelecaniforms (2%) is unexpected.

It is interesting to compare the estimates of prey consumed by the NWHI seabird community with the present and projected fishery landings in the Hawaiian Archipelago. Although fish landings fluctuate each year and may be under-reported by as much as a factor of two. 6100 tonnes were reported as landed in 1978. The most optimistic estimates for increased fishery landings are 34 000–53 000 tonnes (Swerdloff, 1980). Hawaiian seabirds take 67 times the current reported landings of commercial fish in Hawaii, and more than seven times the highest projected fishery yields. Clearly seabirds are a very important component of the marine ecosystem in Hawaii, as they take more than a trivial quantity of the production of lower trophic levels. For example, an ecosystem model applied at French Frigate Shoals estimates that seabirds consume 42% of the annual production of small surface pelagic fishes and squid (Polovina, 1984). Several potential errors complicate this estimate of total food consumption. The largest is the population estimate of non-breeding seabirds. This population is very difficult to estimate accurately (Fefer *et al.*, 1984) and accounts for almost two-thirds of the consumption estimated by this model. In addition, there is considerable imprecision in the breeding

Table 13.3. *Annual consumption (thousand tonnes) of major prey (families or groups that constitute 2% or more of the volume of the diet of a guild)*

| Prey | Albatrosses | Pelecaniforms | Terns and shearwaters associated with predatory fishes | Nocturnal petrels | Neuston feeding terns | Total |
|---|---|---|---|---|---|---|
| Carangidae | — | 1.1 | 15.6 | — | — | 16.7 |
| Clupeidae | — | — | 0.2 | — | 0.1 | 0.3 |
| Coryphaenidae | — | 0.2 | 0.1 | — | 0.1 | 0.4 |
| Exocoetidae | 14.8 | 5.1 | 8.9 | 0.1 | 0.1 | 29.0 |
| Hemiramphidae | — | 0.4 | 0.1 | — | — | 0.5 |
| Mullidae | — | 0.1 | 20.2 | 0.6 | 0.1 | 21.0 |
| Myctophidae | — | — | 1.6 | 4.5 | — | 6.1 |
| Ostraciontidae | — | — | — | — | 0.5 | 0.5 |
| Scombridae | — | 0.2 | — | — | — | 0.2 |
| Sternoptychidae | — | — | — | 2.6 | — | 2.6 |
| Synodontidae | — | — | 0.8 | 0.3 | — | 1.1 |
| Other fishes | 6.8 | 0.8 | 16.0 | 0.9 | 0.2 | 24.7 |
| Squid | 167 | 1.3 | 51.4 | 3.4 | 0.1 | 223.2 |
| Crustaceans | 22.2 | — | 0.4 | 1.2 | 0.1 | 23.9 |
| Unidentified remains | 28.6 | — | 1.1 | 3.7 | — | 33.4 |
| Other | 25 | 0.1 | 1.0 | 0.3 | — | 26.4 |
| Total | 264.4 | 9.3 | 117.4 | 17.6 | 1.3 | 410.0 |

population estimates. Many species are very difficult to census. Nesting in the NWHI is often protracted over several months, and the colonies are remote and difficult to visit. We have inadequate knowledge of the budgets of adult foraging activites and do not know their feeding locations. Most estimates of feeding distances from colonies are speculation (Harrison & Stoneburner, 1981). It is important to learn the extent of foraging so that an area can be defined to estimate fish production.

These estimates of the amounts of food taken by seabirds are the first for a subtropical or tropical community. Seabirds play as important a role in tropical waters as they do in temperate areas. Wiens & Scott (1975) estimated that seabirds consume as much as 22% of the annual production of pelagic fish in Oregon. Schaefer (1970) estimated that seabirds in Peru consume 2.8 million tonnes of anchovies each year (one-third of the commercial catch) and account for 20% of the fish mortality (Furness & Cooper, 1982). Seabirds at one colony in Shetland, Scotland, consume about 29% of the fish production within a 45 km radius of the colony. Seabirds in the Benguela region take about 30% of the mean annual catch in the adjacent fishing grounds and about 17% of the annual fish production (Furness & Cooper, 1982). Primary productivity in Hawaii is about 36 g C $m^{-2}$ (Hirota *et al.*, 1980), or 12–36% of the productivity of continental shelf or upwelling areas (Ryther, 1963). To the extent that fish production can be correlated with primary productivity, Hawaiian seabirds may consume a greater percentage than those in other areas.

### Fishery interactions

Do seabirds in Hawaii compete with commercial fishermen? Because much of the NWHI remains unexploited, it is difficult to compare this community with areas that have established fisheries. Tropical ecosystems are complicated by the migratory nature of tuna stocks and other prey, including squid. It is difficult to define a discrete ecosystem, and annual fish production estimates could be misleading. The juvenile forms of fish and squid that comprise much of the food consumed by seabirds are below the trophic levels that would directly affect commercial fisheries. Prey of the seabirds may also be forage for commercial fish. Commercial fisheries for large species might result in increased forage for seabirds, as has occurred in the North Sea (Furness, 1982). Fishery–seabird competition is most severe when humans and birds compete for identical species in identical size classes (Idyll, 1973). The situation in tropical waters is greatly complicated by the dependency of many birds on tunas to drive their prey to the surface.

*Bird flocks and predatory fish*

The occurrence of terns and shearwaters in flocks provides invaluable assistance to tuna fishermen. Gould (1971) estimated that a trained observer could see and recognize a large feeding flock at a distance of at least 8 km and stated that some fishermen use the distinctive feeding patterns of birds as clues to determine the species of tuna feeding below the flock. If the flocking birds remain active low over the water. they are believed to be feeding over surface-feeding Skipjack Tuna. If the flock activity alternates between low and high altitudes. the fish beneath are presumed to be the deeper-foraging Yellowfin Tuna.

Between 1953 and 1969. the Southwest Fisheries Center Honolulu Laboratory. NMFS. NOAA (formally Pacific Oceanic Fishery Investigations (POFI) and the Bureau of Commercial Fisheries (BCF)) conducted tuna pole-and-line research cruises around the Hawaiian Islands aboard the research vessel *Charles H. Gilbert*. On these cruises. observations of bird flocks and fish schools were recorded using the scouting method (described and evaluated by Royce & Otsu (1955)) by which an experienced fisherman logs all observations of bird flock (as well as solitary individuals) and fish schools. During the *Gilbert* cruises (with at least 30 flock observations) 2138 bird flocks were investigated and 681 (32%) of the fish schools under these flocks were identified (Table 13.4). Tunas constituted 88% of the identified schools. and 86% of these tuna schools were composed of Skipjack Tuna. Because actual fishing verified the composition of schools. the high proportion of unidentified schools (68%) is not unusual. On these pole-and-line cruises. live baitfish were chummed to attract and hold the school close to the vessel. Often. fish will not respond to chumming. Royce

Table 13.4. *Number and percent of fish species associated with 681 bird flocks investigated on pole-and-line cruises in the Hawaiian Islands. 1953–69. Unidentified schools were excluded from this analysis*

| Species | Vernacular name | Number of schools | Percentage of schools |
|---|---|---|---|
| *Fish* | | | |
| *Katsuwonus pelamis* | Skipjack Tuna | 514 | 75.4 |
| *Thunnus albacares* | Yellowfin Tuna | 25 | 3.7 |
| *Euthynnus affinis* | Kawakawa | 25 | 3.7 |
| | Mixed tunas | 37 | 5.4 |
| *Coryphaena hippurus* | Dolphinfish | 68 | 10.0 |
| Mammals | | | |
| Delphinidae | Porpoises | 12 | 1.8 |

& Otsu (1955) and Yuen (1959) reported that fish were caught from only 43 and 47% of the schools chummed, respectively. The high rate of occurrence of Skipjack Tuna under flocks is not surprising. Murphy & Ikehara (1955) found Skipjack Tuna not only the most commonly sighted tuna species in Hawaiian waters, but also the single dominant species in oceanic areas. John J. Naughton (unpublished data) investigated bird flock–fish school interactions in the oceanic waters of the central Pacific and found 73% of identified fish schools to be Skipjack Tuna. Yellowfin Tuna accounted for only 15% of the schools. Naughton suggested that barring various degrees of difficulty in identifying different species, Skipjack Tuna would make up an equally high percentage of the unidentified schools.

Bird flock–fish school interaction is particularly important in Hawaiian commercial fisheries, especially in the Skipjack Tuna pole-and-line fishery. Thus tuna species contribute more than 80%, and Skipjack Tuna more than 65%, of the total catch of ten top-ranked species, which together comprise over 92% of the commercial landing reported to the State of Hawaii (Table 13.5).

Most of the major fisheries in Hawaii have been concentrated in the main Hawaiian Islands. There is, however, increasing interest in extending the various fisheries into the NWHI, where the Hawaiian Islands National Wildlife Refuge protects the breeding grounds of about 5.4 million seabirds

Table 13.5. *Commercial fish landings of the top 10 species for the State of Hawaii, 1961–79*

| | Vernacular name | Total landings (MT) | 19-year average (MT) |
|---|---|---|---|
| *Katsuwonus pelamis* | Skipjack Tuna | 77394.6 | 4073.4 |
| *Thunnus albacares* | Yellowfin Tuna | 8257.9 | 434.6 |
| *T. obesus* | Bigeye Tuna | 5322.7 | 280.1 |
| *Selar crumenophthalmus* | Bigeye Scad | 5251.7[a] | 208.2[a] |
| *Decapterus macarellus* | Mackerel Scad | 2322.7 | 122.2 |
| *Tetrapterus audax* | Striped Marlin | 2272.4 | 119.6 |
| *Makaira nigricans* | Blue Marlin | 1592.8 | 83.8 |
| *Pristipomoides filamentosus* | Pink Snapper | 1001.0 | 68.2 |
| *Coryphaena hippurus* | Dolphinfish | 960.6 | 50.6 |
| *Caranx* sp.[b] | Jacks | 678.2 | 35.7 |

[a] Includes the landings for juvenile *Selar crumenophthalmus*. [b] Includes the catches of 11 species of the deep-bodied carangids although *Caranx ignobilis* comprises most of the catch

(Harrison *et al.*, 1983). At present, the fisheries development in the NWHI concerns predominantly benthic stocks, such as lobsters, shrimps and bottom fishes. Although surface trollers have fished for Albacore *Thunnus alalunga*, in waters north of Midway, little effort has focused on other pelagic species. It seems likely that efforts to exploit other pelagic stocks will extend to the waters of the NWHI.

### *Tern–shearwater feeding guild*

Sooty Terns and Wedge-tailed Shearwaters are the most abundant of the 18 species that breed in the NWHI (Harrison *et al.*, 1983). Sooty Terns are by far the most numerous, comprising 48% of the total population; Wedge-tailed Shearwaters comprise 17%. Among the many species of tropical seabirds, terns and shearwaters are also the most frequently associated with schools of tuna and other commercially valuable fishes (King, 1967). Sooty Terns were found 75% of the time and shearwaters 38% within bird flocks on the *Gilbert* pole-and-line cruises. Naughton (NMFS, unpublished data) found that the species composition of bird flocks is most diverse close to islands and that a substantial reduction in the number of species occurs with distance from land.

Because of the strong relationship between the feeding activities of birds and tunas, it is important to determine how much of a dietary overlap exists. Ashmole & Ashmole (1967) examined the food of Yellowfin Tuna captured in surface waters near Christmas Island. They found major differences between the diets of the fish and birds: fish consumed fewer squid and a wider variety of invertebrates. The fish consumed by the tunas also differed significantly from those eaten by birds. They concluded, however, that a large proportion of the items taken by the birds are made available at the surface only by the feeding activities of the tunas. They attributed the difference in the diets mainly to the types of tuna prey that do not come to the surface even when pursued, whereas other organisms such as flyingfish are subject to predation by the birds while escaping the tunas.

Waldron & King (1963) examined 707 stomach samples from Skipjack Tuna in Hawaiian waters, including the Line and Phoenix Islands, and found material representing 11 invertebrate orders and 42 fish families. Fish occurred in 67% of the stomachs and, based on their frequency of occurrence, the highest ranking families were Gempylidae, Scombridae, Mullidae, Chaetodontidae, and Holocentridae in order of importance. Carangids (especially mackerel scad) were important only in the Skipjack Tuna sampled in Hawaii. Crustaceans and squid occurred in 36% and

35% of the stomachs, respectively. Most of the identified squid were ommastrephids. By volume, fish composed 75%, squid 20%, and crustaceans 4% of the Skipjack Tuna food. Scombridae, Carangidae, Mullidae, Nomeidae, and Molidae were the most important fish families. Yuen (1959) found similar results in his study of 573 Hawaiian Skipjack Tuna stomachs. Members of Carangidae (primarily mackerel scad) were by far the most important item in terms of both volume and frequency of occurrence. As in Waldron & King's study, Yuen found nomeids, molids, and scombrids among the highest-ranked fish families. Squid, stomatopods, and decapod crustaceans were also significant contributors to the diet.

By contrast, our study demonstrated that for Sooty Terns, squid (mostly ommastrephids) were the highest-ranked prey items, constituting 53% of the sample volumes (Harrison *et al.*, 1983). Fish accounted for 46% of the volumes; Mullidae, Exocoetidae, Gempylidae, Carangidae (mostly mackerel scad), Nomeidae, and Holocentridae were the highest ranked. Wedge-tailed Shearwaters ate 66% fish, 28% squid, and 1% crustaceans, by volume. Prey items ranked high were the fish species in Mullidae and carangidae (again, mostly mackerel scad) and the squids in Ommastrephidae. Other common prey fish were the monacanthids and exocoetids.

Based on these fish and bird feeding studies, there appears to be a considerable degree of overlap in the diet of Sooty Terns, Wedge-tailed Shearwaters, and Skipjack Tuna. Among the highest-ranking prey items, squid (Ommastrephidae), goatfish (Mullidae), and mackerel scad were very important in all the diets. Other fish belonging to Nomeidae, Gempylidae, and Holocentridae were also commonly taken by both birds and tunas. The higher degree of overlap between Skipjack Tuna and the birds as compared with Yellowfin Tuna and the birds is not surprising. Skipjack Tuna and seabirds are generally surface feeders, and most fish schools found beneath feeding bird flocks are Skipjack Tuna (Table 13.4). Yellowfin Tuna tend to forage at greater depth.

Skipjack Tuna and the seabirds also appear to prey upon organisms of similar sizes. Based on the various Skipjack Tuna feeding studies in the Pacific (Alverson 1963; Waldron & King, 1963; Nakamura, 1965), Blackburn & Laurs (1972) found that the prey of Skipjack Tuna fell mainly in the 10–100 mm size range. In comparison, Harrison *et al.* (1983) found the standard length of Sooty Tern prey items ($n = 326$) to range from 1 to 120mm (mean 48 mm s.d. 19). All of the common prey items, however, were 20–70 mm long. The prey of Wedge-tailed Shearwaters ($n = 212$) ranged from 4 to 145 mm in standard length (mean 57 mm s.d. 25).

To a lesser degree, seabirds also feed in association with schools of Dolphinfish. Unlike Skipjack Tuna, which traverse the water column vertically, Dolphinfish normally remain in the surface waters. This behavior is reflected in the composition of Dolphinfish forage items. In the Pacific, flyingfish and other surface-dwelling species were the dominant prey taken (Tester & Nakamura, 1957; Kojima, 1961; Rothschild, 1964). The size composition of the principal Dolphinfish food organisms is also similar to that taken by the Sooty Terns and Wedge-tailed Shearwaters. Kojima (1961) reported that although the size range of prey was wide, from about 1 to 34 cm, most of the prey were between 2–4 and 10–15 cm.

## Future research needs and conclusions

Unlike subpolar and temperate communities, tropical seabird communities have rarely been studied. Research on seabirds is usually restricted to those ecosystems that are faced with major developments such as offshore oil and gas activities or large commercial fisheries. Our recent studies in Hawaii complement the work by Ashmole & Ashmole (1967) at Christmas Island and represent a refinement of many of their ideas concerning diets and trophic relationships among tropical seabirds. However, much work remains for a better understanding of the role of seabirds in tropical and subtropical ecosystems.

Our model that estimates the consumption of prey by the NWHI seabird community would be improved with more precise input parameters. Better population estimates, especially for non-breeding birds, would refine our estimates of prey consumption. In addition, estimates of consumption rates of seabirds could be improved by studies utilizing captive birds in zoos, marine parks, or oceanaria. Most of our current estimates are largely based on theoretical considerations rather than direct measurements.

A major challenge in the study of seabirds in all ecosystems is to improve our understanding of foraging ranges and locations. Speculations concerning foraging locations are too often accepted as fact despite a virtual absence of data. Tropical seabirds range widely in warm waters and, like polar and subpolar species, live many years before breeding. Birds observed feeding at sea are not necessarily breeding birds, nor should they be assumed to be associated with the nearest colony. How far away from colonies birds feed may be inferred from incubation bouts and chicks' feeding frequencies (Harrison & Hida, 1980). However, such indices are very imprecise, and developments in radiotelemetry are necessary to determine feeding locations. In tropical waters, such technological progress would also be of great interest to fishery managers and fishermen. The movements of birds such as Sooty Terns could be used to locate tuna schools efficiently.

Our understanding of the role of marine birds in tropical ecosystems is most limited by our understanding of tropical marine ecology and fisheries. Improvements in our ability to identify juvenile and larval fish and squid in tropical waters will result in refinements in our analysis of dietary specialization among tropical species. In our work in Hawaii (Harrison *et al.*, 1983), we encountered many unidentifiable flyingfish, goatfish, lizardfish and squid, representing many species. For example, 10 goatfish and 9 flyingfish occur in Hawaiian waters (Tinker, 1978). Although there is undoubtedy some theoretical interest in examining feeding overlap using Morisita's Overlap Index (Diamond, 1984), dietary differences among tropical seabird species are masked by our inability consistently to identify prey beyond the family level. Conclusions based on such analyses repeat the unremarkable proposition that tropical seabirds eat much flyingfish and squid. This is roughly equivalent to concluding that Serengeti herbivores have similar diets because they eat various grasses. Because identification of prey is particularly difficult in tropical ecosystems, it is especially important to utilize a multidisciplinary approach to research and to include fishery biologists. Too often dietary studies of seabirds utilize untrained laboratory personnel whose opinions on the identity of half-digested prey are suspect. Improved estimates of available prey must be developed by fishery biologists if projections concerning the impacts of tropical fisheries on seabird communities are to be improved. This is a prerequisite if marine birds are to be used to monitor changes with time in epipelagic marine fauna (Ashmole & Ashmole, 1968). The remarkable Pacific-wide changes during the 1982–83 El Niño event underscore the interest in such studies.

The interaction between seabirds and predatory fish needs careful study. Only about half of the feeding bird flocks observed during the *Gilbert* cruises were confirmed to be associated with predatory fish. Are some seabirds strictly dependent on fish and marine mammals to drive prey to the surface, or are they merely opportunistic? Additional comparisons between the diets of seabirds and predatory fish are needed to clarify differences and similarities in size classes of prey species.

Lastly, the role of tropical seabird colonies in nutrient cycling deserves careful study. The consumption of prey is not a one-way transfer of energy. As much as 30% of the energy ingested by birds is voided as waste (Wiens & Scott, 1975). Birds enrich the waters surrounding their colonies with calories and nutrients (Hutchinson, 1950: 373; Tuck, 1960; Lindeboom, 1984). Ashmole & Ashmole (1967) hypothesized that seabird guano is an important source of nutrients for coral reef communities adjacent to bird colonies. This notion has recently been rejected in certain Canadian waters (Bédard, Therriault & Bérubé, 1980). Careful nearshore measurements of nutrients and estimates on quantities of guano from NWHI seabird colonies should render a realistic assessment of nutrient cycling as it pertains to tropical seabirds.

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