

MULTIDECADAL COMPARISON OF RED-FOOTED BOOBY *SULA SULA* DIET AT ULUPA‘U CRATER, O‘AHU, HAWAI‘I

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ABSTRACT

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We describe the diet of Red-footed Boobies *Sula sula* nesting at Ulupa‘u Crater, O‘ahu, Hawai‘i based on 106 regurgitations collected during 2014 and 2015. We also compare our results to a diet study at this colony five decades earlier. Both studies indicate that flying squid (Ommastrephidae) and flyingfish (Exocoetidae) are important prey for this population while provisioning chicks. In particular, Purpleback Flying Squid *Sthenoteuthis oualaniensis* occurred in the majority (> 70%) of the recent regurgitation samples, and their size (mantle length < 11 cm) indicates that they were mostly juveniles. Moreover, the size distribution of the squid prey varied by year, indicating inter-annual variability in the phenology of spawning and larval development. This study highlights the reliance of Red-footed Boobies on juveniles of this poorly-studied squid and underscores their value as biological samplers of epipelagic fish and squid within their foraging ranges.

Key words: Red-footed Booby, *Sula sula*, regurgitation, diet, Hawai‘i, Purpleback Flying Squid, *Sthenoteuthis oualaniensis*

INTRODUCTION

Philip and Myrtle Ashmole (1968), on the basis of their work at Christmas Island (Pacific Ocean), argued that the identification and quantification of food items from seabird regurgitations provides information on the seasonal availability, population size classes, and reproductive cycles of epipelagic fish and squid from tropical oceans, with particular focus on three families: flyingfish (Exocoetidae), juvenile tunas (Scombridae), and flying squid (Ommastrephidae). More specifically, their early comparative studies of tropical seabird foraging ecology highlighted the feasibility of using seabirds as samplers for studying the prevalence of epipelagic fish and squid (Ashmole & Ashmole 1967, 1968). The Ashmole’s pioneering work provided a baseline that facilitated our study at the same colony, over five decades later. We were further inspired by the work of Harrison *et al.* (1983) and Spear *et al.* (2007), who also studied seabird diet in the central Pacific.

As part of a study of the movements and diet of Red-footed Boobies *Sula sula* (RFBO) provisioning chicks, we analyzed 106 regurgitations collected opportunistically during June–July 2014/15 (Adams *et al.* 2020, Donahue *et al.* in press). Studying such samples is common in banding and tagging studies of boobies because they readily regurgitate upon being handled (Ashmole & Ashmole 1967, Harrison *et al.* 1983, Lerma *et al.* 2020). Before our study, the only RFBO diet observations previously available from this colony were notes from five visits during a two-month period (01 April–05 June 1963), when the Ashmoles opportunistically collected 12 regurgitations (Ashmole & Ashmole 1967). Herein, we compared the size and composition of prey in our contemporary (2014/15) RFBO regurgitations with the Ashmole (1963) observations.

METHODS

Study site

The study colony (21.4584°N, 157.7234°W) is located on the eastern crest of Ulupa‘u Crater, within the US Marine Corps Base Hawai‘i (MCBH), on the island of O‘ahu, Main Hawaiian Islands (MHI). The size of the colony has ranged from a maximum of 2 380 in 1969 to a minimum of 337 in 2008 (Russell & VanderWerf 2010). During the study years, the minimum RFBO breeding population estimate was 700 individuals (T. Russell pers. comm. 2015).

Diet quantification

For comparison of our samples with those of Ashmole & Ashmole (1967), we followed the same methods by: (i) quantifying diet composition using relative number, calculated as the proportion of all prey items belonging to a specific species; (ii) aggregating the species data into families; (iii) quantifying the frequency of occurrence (FO), calculated as the proportion of samples that contained a particular prey family; and (iii) measuring the length of complete prey in order to group them into size categories (2-cm fish standard lengths (SL), 4-cm squid dorsal mantle lengths (ML)). Our methods differed from those of the Ashmoles in two key ways: (i) we used morphological and genetic methods for species identification, which allowed us to identify all prey items; and (ii) we only measured complete prey items and did not estimate the size of partially-digested prey (Ashmole & Ashmole 1967).

Interannual diet comparison

We compared the historical and contemporary diet data in two ways: (i) we used pair-wise Spearman rank correlations to compare the relative importance (% of diet by number) of prey families from the three years; and (ii) used pair-wise Fisher Exact tests on size composition of prey from each year. We performed all tests with the R statistics package version 3.5.2 using “Rcmdr” package in R, version 2.6.0 (R Core Team 2018). Throughout this paper, variability is expressed as mean \pm standard deviation.

Oceanographic conditions

To assess the degree to which interannual diet differences might be related to ocean climate, we consulted the bi-monthly Multivariate El Niño Index (MEI) values between April–May and July–August for all study years. The MEI quantifies ocean-atmosphere conditions along the Tropical Pacific (~10°N to 10°S) by integrating six cross-correlated variables: sea-level pressure, zonal and meridional sea surface, wind speed (WSP), sea surface temperature (SST), air temperature, and total cloudiness fraction within the sky. “Average” MEI values typically range from slightly positive (+0.5) to slightly negative (-0.5) deviations from the long-term mean. In the El Niño–Southern Oscillation (ENSO) continuum, El Niño is characterized by positive anomalies ($\geq +0.5$) and La Niña by negative anomalies (< -0.5 ; Wolter & Timlin 2011).

Ethics statement

Jason Omick and Jason Misaki (Department of Land and Natural Resources, Division of Forestry and Wildlife; DLNR-DOFAW), kindly facilitated access and permitting in Hawai'i. Field work, bird capture, banding, and sampling in Hawai'i were authorized under US Geological Survey Federal Bird Banding and Auxiliary Marking Authority Master Bander Permit #23843, US Fish and

Wildlife Service and Hawai'i DLNR-DOFAW, Protected Wildlife Permits #WL12-4 and #WL17-10.

RESULTS

Historical diet

The 12 regurgitations collected during a two-month period (01 April–05 June) in 1963 contained 108 complete prey items, with a mean of nine items per sample (range = 1–33). Twenty unidentified prey items contributed 17.8% of numerical diet composition. The remaining 88 identified prey items, belonging to four families (one squid and three fish), contributed 82.2% of numerical diet composition (Table 1).

All cephalopods identified were flying squids (family Ommastrephidae) and were deemed most likely to be Purpleback Flying Squids *Symplectoteuthis* spp. (reclassified as *Sthenoteuthis oualaniensis*). These were the most common and abundant prey item: they were present in nine of the 12 samples (FO = 75.0% \pm 13.1) and contributed 35.6% of the diet (Fig. 1). Among the fish prey, snake mackerels (Gempylidae) were the most abundant species (29.7%) but had low frequency of occurrence (FO = 41.7% \pm 14.1%, five of 12 samples). Conversely, flyingfishes (Exocoetidae) had the highest frequency of occurrence (FO = 58.3%, seven of 12 samples) but lower abundance (13.9%; Table 1). Moreover, the ingested prey items ranged widely in size: 4–10 cm ML for squid and up to 20 cm SL for fish (Table 2).

Contemporary diet

For the recent study, we opportunistically collected 106 regurgitations during June–July in 2014 (51 samples) and 2015 (55 samples). The mean number of prey items per sample was 8.1 \pm 5.7 (range = 1–24) in 2014 and 10.6 \pm 8.4 (range = 1–34) in 2015. We genetically identified and measured 237 complete prey items and identified 32 species (29 fish and three squid; Donahue *et al.* in press) belonging to two squid families and nine fish families (Table 1).

TABLE 1

Diet composition by percent number of prey in Red-footed Booby *Sula sula* regurgitations collected during 1963, 2014, and 2015

| Prey Families | 1963 | 2014 | 2015 |
|--------------------------------|------|------|------|
| Acanthuridae (Tangs) | 0.0 | 0.5 | 0.0 |
| Carangidae (Jacks) | 0.0 | 1.4 | 4.4 |
| Coryphaenidae (Dolphinfishes) | 3.0 | 0.0 | 0.0 |
| Exocoetidae (Flyingfishes) | 13.9 | 21.8 | 19.7 |
| Gempylidae (Snake Mackerels) | 29.7 | 3.2 | 0.5 |
| Hemiramphidae (Halfbeaks) | 0.0 | 1.8 | 3.8 |
| Molidae (Sunfishes) | 0.0 | 0.5 | 0.0 |
| Mullidae (Goatfishes) | 0.0 | 10.6 | 6.0 |
| Nomeidae (Driftfishes) | 0.0 | 0.5 | 3.8 |
| Ommastrephidae (Flying Squid) | 35.6 | 56.9 | 60.7 |
| Onychoteuthidae (Hooked Squid) | 0.0 | 0.5 | 0.0 |
| Scombridae (Tunas & Mackerels) | 0.0 | 2.3 | 1.1 |
| Unidentified Fish | 17.8 | 0.0 | 0.0 |
| Fish Total | 64.4 | 42.6 | 39.3 |
| Squid Total | 35.6 | 57.4 | 60.7 |

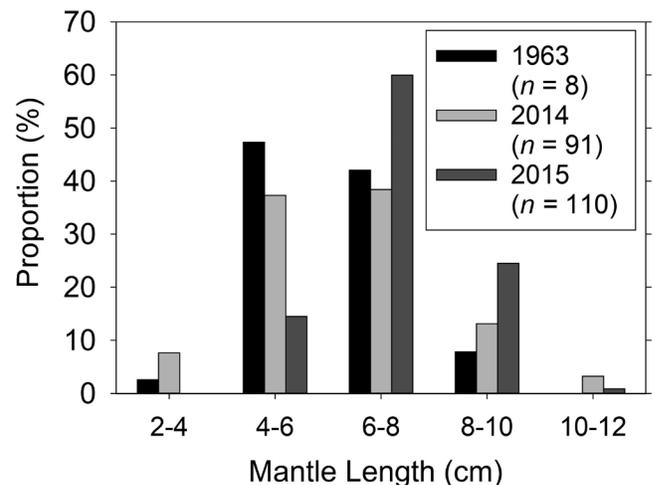


Fig. 1. Frequency distribution of squid mantle lengths consumed by Red-footed Boobies *Sula sula* during this study (2014, 2015) compared with data from 1963 (Ashmole & Ashmole 1967). Yearly sample sizes (number of individual squid measured) are indicated.

At the family level, flying squid and flyingfishes were the most prevalent in the diet during 2014 (56.9% and 21.8%, respectively) and 2015 (60.7% and 19.7%, respectively; Table 1). At the species level, Purpleback Flying Squids contributed the majority (98.7%) of the identified squid and were the most important species in the diet during both sampling years. We identified the remaining squid specimens as Neon Flying Squid *Ommastrephes bartramii* (one from each year) and *Onykia* spp. (family Onychoteuthidae). The prey items ranged widely in size, 2–12 cm ML for squid and up to 21 cm SL for fish (Table 2), underscoring the wide range of prey sizes ingested by RFBO.

Interannual diet comparison

Overall, the diet composition during recent years was significantly correlated (Spearman rank, $r_s = 0.838$, $n = 13$ families, $P = 0.004$), underscoring the importance of flying squid and flyingfish. Conversely, diet composition in 1963 was not significantly correlated to the data from 2014 (Spearman rank, $r_s = 0.257$, $n = 13$ families, $P = 0.395$) or from 2015 (Spearman rank, $r_s = 0.174$, $n = 13$ families, $P = 0.569$).

Although flying squid were the numerically dominant prey, we documented some year-to-year variability in their importance. Whereas the FO of squid in 2014 ($72.5\% \pm 6.3\%$) and 2015 ($74.6\% \pm 5.9\%$) was similar to the FO in 1963 ($75.0\% \pm 13.1\%$), squid were more abundant in the recent years (2014 and 2015) than in 1963. Overall, squid accounted for over one-third of the prey items in the previous study, and over half of the prey items in our study. Squid were most prevalent in 2015, when they accounted for > 60% of prey items (Table 1).

The size of prey items varied interannually. When we compared the squid prey using three pair-wise Fisher Exact Tests, their ML were statistically different only when we compared 2015 to 2014 ($df = 4$, $P < 0.001$) and 2015 to 1963 ($df = 4$, $P < 0.001$). The 2015 size distribution ranged 4–12 cm, with most individuals (60.0%, 66 of 110) being medium-sized (6–8 cm; Table 2, Fig. 1). In comparison, the 2014 size distribution involved a greater range (2–12 cm), with most individuals (38.5%, 35 of 91) being 6–8 cm. In 1963, squid ranged 2–10 cm, with most individuals (47.4%, 18 of 38) being 4–6 cm. However, squid size distributions in 1963 and 2014 were

not significantly different ($df = 4$, $P = 0.571$). When we compared the fish prey using three pair-wise Fisher Exact Tests, their standard lengths were statistically different in every case: 2014 vs. 2015 ($df = 4$, $P = 0.013$), 1963 vs. 2014 ($df = 4$, $P = 0.004$), and 1963 vs. 2015 ($df = 5$, $P < 0.001$).

Oceanographic conditions

Comparing the MEI values between April–May and July–August for the three study years, 1963 was an average year (median = 0.130, range = -0.473 to +0.590), 2014 was a transition from average to positive ENSO (median = 0.497, range = -0.144 to +0.734), and 2015 was a warm-water year with a consistently positive ENSO (median = 0.662, range = +0.404 to +0.805) (Figure 2).

DISCUSSION

Consistent with diet studies from other breeding sites in the central Pacific (Harrison & Seki 1983, Harrison *et al.* 1990, Lewis *et al.* 2005, Young *et al.* 2010), we found that flying squid and flyingfish are important prey for RFBO rearing chicks at the Ulupa'u Crater colony. They are also important prey elsewhere among the Hawaiian Islands (Harrison *et al.* 1983), as well as generally at sea in the region (Spear *et al.* 2007). In particular, Purpleback Flying Squid were consistently present in > 75% of the diet samples spanning 50 years, underscoring the ecological importance of this poorly-studied species in our study area.

Evidence of inter-annual variation in the size of the squid and fish in the diet of RFBO indicates that they consume a wide range of prey sizes, with the range in accord with their body/bill size (*cf.* Ashmole & Ashmole 1967, Harrison *et al.* 1983, Spear *et al.* 2007), and that they probably shift their diet in response to inter-specific competition and take advantage of opportunistically available prey, including epipelagic (e.g., Hemiramphidae, Exocoetidae), pelagic (Scombridae, Carangidae), and reef-

TABLE 2
Size distribution of fish and squid in Red-footed Booby *Sula sula* regurgitations collected during 1963, 2014, and 2015

| Fish Standard Length intervals (cm) | | | | | | | |
|-------------------------------------|-----|-----|------|-------|-------|-------|-------|
| Year | 0–4 | 4–8 | 8–12 | 12–16 | 16–20 | 20–22 | Total |
| 1963 | 3 | 20 | 34 | 6 | 6 | 0 | 69 |
| 2014 | 0 | 6 | 2 | 7 | 2 | 0 | 17 |
| 2015 | 0 | 15 | 0 | 3 | 0 | 1 | 19 |
| Squid Mantle Length intervals (cm) | | | | | | | |
| Year | 2–4 | 4–6 | 6–8 | 8–10 | 10–12 | Total | |
| 1963 | 1 | 18 | 16 | 3 | 0 | 38 | |
| 2014 | 7 | 34 | 35 | 12 | 3 | 91 | |
| 2015 | 0 | 16 | 66 | 27 | 1 | 110 | |

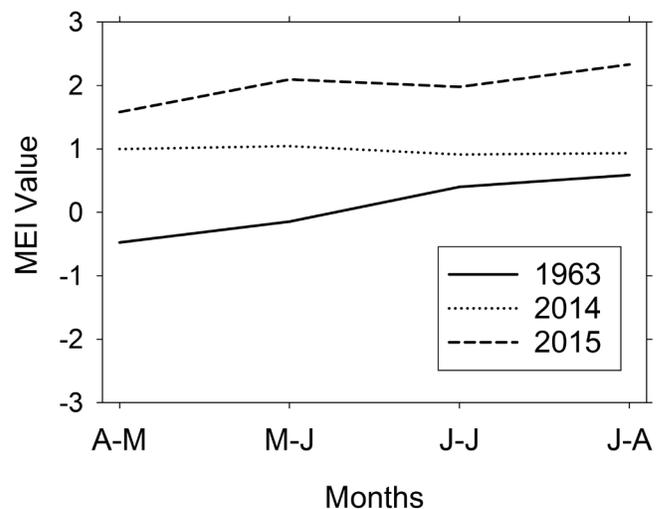


Fig. 2. Multivariate El Niño Southern Oscillation Index (MEI) values spanning diet sampling in three study years: April–May (A-M), May–June (M-J), June–July (J-J), and July–August (J-A). MEI values above and below zero are indicative of the warm-phase and the cold-phase of the El Niño Southern Oscillation.

associated (e.g., Acanthuridae, Mullidae) species. However, despite the inter-annual variability in squid size in RFBO diets, these results highlight the importance of juvenile (< 11 cm ML) Purpleback Flying Squid for RFBO nesting on O'ahu (Young & Hirota 1998). Observations indicating that juvenile Ommastrephid squid (< 10 cm ML) do not engage in diel vertical migration (R. Pitman pers. comm. 2018) provide evidence that they remain in surface waters throughout the day and are thus more available to foraging seabirds. Moreover, these prey are also forced closer to the surface and into the air by tuna, supporting evidence of RFBO associations with skipjack tuna (*Katsuwonus pelamis*) (Spear *et al.* 2007).

Because Purpleback Flying Squid spawn off eastern O'ahu during March (Young & Hirota 1998), environmental variability in ocean conditions may influence their phenology and size-distribution during the RFBO chick-provisioning season. Specifically, because regurgitations were collected from April to June in 1963, the Ashmoles likely sampled when smaller (younger) squids were available to RFBO. Nevertheless, we documented a significant difference in squid size distributions from the RFBO regurgitations collected during June–July of 2014 and 2015. Together, these results indicate that seasonality (April–June vs. June–July) and inter-annual variability (2014 vs. 2015) in ocean conditions influenced the size of the juvenile squids taken by RFBO, with larger juveniles present during summer, particularly during warmer water years (2015) associated with the positive phase of ENSO. Our results raise the possibility that Purpleback Flying Squid are more abundant and larger during the warm phase of ENSO. Nevertheless, long-term studies are needed to confirm if (i) the phenology and abundance of flying squid change in response to changing oceanographic conditions, and (ii) if there is an increase in the abundance or availability of flying squid to central-place foraging RFBO nesting on O'ahu in future years. More information is also needed on the species composition of seabird foraging flocks, including whether it changes with ocean conditions and breeding population size, given the strong influence of competition in the size selection of prey by central Pacific seabirds (Spear *et al.* 2007).

Ecosystem modelling and fisheries catches have documented increasing squid populations, attributed to the fishing down of marine food-webs and the warming of tropical oceans (Baum & Worm 2009, Doubleday *et al.* 2014). Yet, without larval surveys and fisheries-dependent catch-per-unit-of-effort data, marine predator diets provide an important tool to study the spawning and prevalence of these important prey species (e.g., Chérel & Weimerskirch, 1995), echoing the arguments of Ashmole & Ashmole (1967, 1968) and confirmed in this study. In anticipation of the potential future development of a jigging fishery for the Purpleback Flying Squid around the Hawaiian Islands, this information would be needed to develop an ecosystem-based management approach, including an understanding of the environmental drivers, population dynamics, and consumption by marine predators (Rodhouse *et al.* 2014, Suzuki *et al.* 1986).

Despite the opportunistic nature of the respective studies and the methodological changes over time, we were able to compare RFBO diet from the same location over a five-decade interval. It is our hope that standardized monitoring efforts will continue to track this colony and changes in the surrounding ocean over time. To this end, we provide some suggestions for using RFBO

diet samples to monitor changing epipelagic food webs, with an emphasis on epipelagic squid populations:

- 1) Sample RFBO diet through their breeding season, spanning from late winter (February) and late summer (August), to account for potential temporal shifts in prey spawning seasons and development over time;
- 2) Sample RFBO diet during several years, spanning a variety of oceanographic conditions (ENSO, Pacific Decadal Oscillation), in each decade;
- 3) Consider inter-annual and longer-term changes in the composition of seabird fauna and tuna distributions and catches around the MHI, which can influence RFBO prey accessibility;
- 4) Develop rarefaction curves and diversity indices to characterize seasonal, inter-annual, and inter-decadal changes in diet species richness;
- 5) Employ standardized morphological and genetic identification methods, and develop multiple metrics of species-specific prey importance, including the FO and relative mass (RM);
- 6) Measure the size (including mass) of the consumed juvenile squid to develop a condition index;
- 7) Collect and preserve tissue samples from the prey (muscle) and RFBOs (blood, feathers) for stable isotopic analysis, to augment diet characterization.

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