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Diet of the Hawaiian monk seal (*Monachus schauinslandi*) from the Northwestern Hawaiian islands during 1991 to 1994

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Abstract This study provides the first detailed description of the diet of the Hawaiian monk seal, *Monachus schauinslandi*. A total of 940 fecal and regurgitate samples were collected from the beaches of five islands in the Northwestern Hawaiian Islands (NWHI) between 1991 and 1994. Some samples were collected from known ages and sexes of seals. Prey were identified from all available hard parts and identified to the lowest possible taxa. Teleosts were the most represented prey (78.6%) followed by cephalopods (15.7%) and crustaceans (5.7%). Of the teleosts, 31 families were identified, 30 of which are prevalent reef-associated fishes. The most common families found were marine eels, Labridae, Holocentridae, Balistidae, and Scaridae. Of the cephalopods, 7 octopus species and 21 squid species were identified, representing coastal, benthic, and offshore-mesopelagic species. A significant difference was seen in both the teleost and cephalopod components of the diet of the Hawaiian monk seal among the years 1991 to 1994 among the islands in the NWHI chain, and among juvenile, subadult, adult female and adult male seals. Some overlap was seen between the diet of the Hawaiian monk seal and the commercial fisheries that currently exist in the NWHI. These findings indicate that Hawaiian monk seals are opportunistic predators that feed on a wide variety of available prey.

Introduction

The Hawaiian monk seal *Monachus schauinslandi* has been on the endangered species list since 1976, with a

present population estimated at 1300 individuals (NOAA 1995). This population has declined by $\approx 50\%$ since the late 1950s (Johnson et al. 1982), with a 5 to 6% decrease still occurring annually (Ragen 1993). The Hawaiian monk seal is found only in the Hawaiian Islands (Kenyon 1981), with established breeding colonies in the Northwestern Hawaiian Islands (NWHI). At the largest of these breeding islands, French Frigate Shoals (FFS), the population decline is mainly due to the starvation of juvenile seals (Gilmartin 1993), and this may be related to natural fluctuations in prey populations caused by environmental perturbations such as the influences of El Niño/Southern Oscillation (ENSO) events (Gilmartin 1993; Polovina and Mitchum 1994). In addition, commercial fisheries for both bottomfish and lobsters operate in the NWHI insular waters, resulting in some concern about competition between this endangered species and the fisheries.

Available information concerning the diet of the Hawaiian monk seal has previously been based on four studies (Kenyon and Rice 1959; Kenyon 1981; DeLong et al. 1984; R. T. Watson and G. A. Peiterson unpublished data). Each of these studies provided an overview of the diet, but were incomplete for a variety reasons, such as small sample sizes (Kenyon and Rice 1959), little description of methods used in obtaining diet information (Kenyon 1981; DeLong et al. 1984), and incomplete identification of prey (R.T. Watson and G.A. Peiterson unpublished data). Because complete data are not available on the diet of the Hawaiian monk seal, identifying the population decline from starvation at one island and/or competition with commercial fisheries is difficult to address.

Most pinniped scatological studies use fish otoliths to identify the teleost prey (e.g. Pitcher 1980; Prime and Hammond 1987; Antonelis et al. 1990), but otoliths are digested more rapidly than bones and scales (Murie and Lavigne 1986; Dellinger and Trillmich 1988; Harvey 1989), and are often completely digested (Chumbley et al. 1993); in addition, some seals remove the heads of fishes before ingesting them. Thus, the identification of all prey

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species using only otoliths is difficult. Recently, other hard structures such as fish scales, vertebrae, jaws, skull bones, teeth, and spines have been used in food-habit studies. In fact, teleost scales can be the most abundant hard part recovered from teleost-prey remains (Cottrell et al. 1996). The use of other hard structures in addition to otoliths has been shown to increase the positive identification of teleost prey (Olesiuk and Bigg 1985; Chumbley et al. 1993; Hanson 1993), in some cases by up to 20% (Cottrell 1993). Although the use of scales, spines and most bones still does not provide numbers or mass of teleosts consumed, it does afford a more complete picture of teleost-diet composition.

Scat sampling alone may underestimate the importance of prey in the diet of seals (Bigg and Fawcett 1985; Harvey 1989; Gales and Cheal 1992). For instance, some teleosts such as eels are extremely long and are often regurgitated instead of digested. Cephalopod beaks are irregular in shape and, consequently, some beaks do not pass through the digestive tract and are regurgitated instead (Bigg and Fawcett 1985). Augmenting the scat-sampling method with the recovery of regurgitated remains (spews) helps offset these underestimations.

This study provides a comprehensive examination of the diet of the Hawaiian monk seal using all recoverable prey remains present in the feces and spews from seals in the NWHI. The objectives of this study were to (1) identify all prey, (2) obtain size estimates for the more common cephalopod prey species, (3) examine temporal differences in diet among the years 1991 to 1994, (4) examine geographical differences in diet among the monk seals' five main breeding islands, and (5) examine ontogenetic differences in diet among juveniles, subadults, adult female and adult male seals. Because the Hawaiian monk seal is considered the most endangered pinniped in US waters, information concerning its diet composition is important for understanding its current population decline, as well as for future management of this species.

Materials and methods

Samples were collected by the National Marine Fisheries Service (NMFS), Honolulu Laboratory during 1991 to 1994 from the five principle Hawaiian breeding sites of *Monachus schauinslandi* in the North Western Hawaiian Islands: French Frigate Shoals (FFS), Laysan Island (LAY), Lisianski Island (LIS), Pearl and Hermes Reef (PHR) and Kure Atoll (KUR) (Fig. 1). Collection occurred mainly during spring and summer (April to August), and logistic constraints prohibited annual sampling on all islands. The samples were removed from haul-out areas (i.e. areas on beaches where seals rest), agitated in soapy water to break down the oily feces, and then passed through nested sieves of 0.09, 0.04, and 0.02 mm mesh-diam. The recovered hard parts were placed in 70% ethyl alcohol for later identification.

When possible, scats and spews were collected from seals of known age or sex by marking the haul-out site and collecting samples after the seal had left the area. Juvenile monk seals were defined as being younger than 2 yr-old, subadults as between 2 and 4 yr-old, and adults as >4 yr old. Most juveniles and subadults were not identified by sex, and consequently these samples included both females and males.

The data from the 4 years, 5 islands and 4 age/sex classes were analyzed for interaction effects using a multi-way chi-square analysis, Cochran-Mantel-Haenszel test (SAS 1985). The Cochran-Mantel-Haenszel option tests for a significant association within data after controlling for possible confounding effects of specified groups. Temporal, geographical, and ontogenetic differences in teleost, octopus and squid prey composition were determined using chi-square analyses (SAS Institute Inc. 1985).

Teleost prey

Scales, jawbones, vertebrae, spines and otoliths were identified to family level by comparison to reference collections developed by Ziegler and Goodman-Lowe (unpublished data). In many cases, species identification and number estimates were made; however, most of the identifications were based on the scales, which did not allow estimations to be made concerning number of prey items. Therefore, I reported only percent frequency of occurrence, defined as the number of samples in which a teleost prey was found nor-

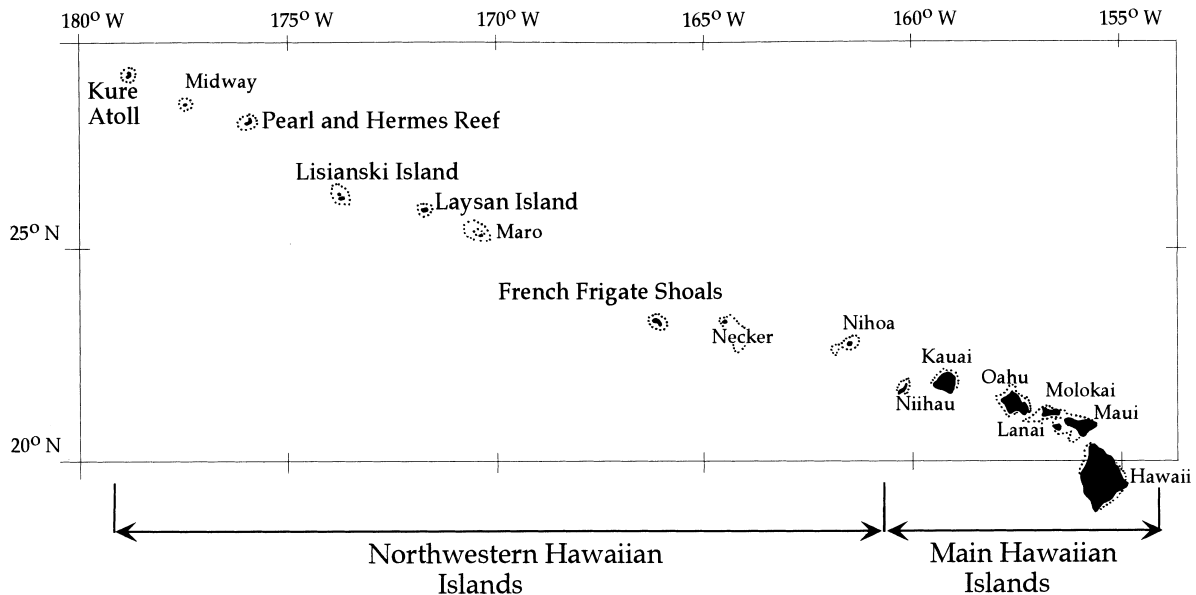


Fig. 1 The Hawaiian archipelago

malized to the number of samples examined. This method of quantifying the data allowed groups (i.e. years, islands, age/sexes) of disparate sample sizes to be compared.

Cephalopod prey

Identifications to the lowest possible taxon were based on upper and lower beak structure and morphometrics compared to reference collections at the National Marine Mammal Laboratory, Seattle, Washington, and at the Santa Barbara Museum of Natural History, Santa Barbara, California. The minimum number of cephalopods consumed was defined as the greater number of upper or lower beaks identified for each species found per sample.

Upper-beak hood length (UHL), upper-beak rostral length (URL), lower-beak hood length (LHL) and lower-beak rostral length (LRL) (Clarke 1986) were measured with vernier calipers to the nearest 0.1 mm. Squid wet weights were estimated from both URLs and LRLs by allometric equations of Wolff (1984) and from LRLs by allometric equations of Clarke (1986).

For two octopus species with relatively thick hoods, hood length was a better predictor of weight than was rostral length for both the upper and lower beaks. Wet weight was estimated for these two species by the following equations (Goodman-Lowe and Hochberg unpublished data): *Octopus cyanea*: $wt = 2.299 \ln(UHL) - 5.086$ $r^2 = 0.51$ ($n = 4$), $wt = 1.445 \ln(LHL) - 4.275$ $r^2 = 0.56$ ($n = 4$); *O. luteus*: $wt = 1.486 \ln(UHL) - 2.983$ $r^2 = 0.95$ ($n = 8$), $wt = 0.875 \ln(LHL) - 0.873$ $r^2 = 0.89$ ($n = 8$). Although the sample sizes used to obtain these formulas were low, they provided a rough estimate of wet weight.

Crustacean prey

Most crustacean parts were visible with a dissecting microscope, but were often fragmented; therefore, neither abundance nor size was estimated.

Results

Overall diet composition of *Monachus schauinslandi*

Of the 940 samples (891 scats and 49 spews) examined for diet composition, no hard structures were found in 78 (8.3%) (Table 1). Of the total number of prey recovered and identified in all samples, teleosts represented the largest component (78.6%), followed by cephalopods (15.7%) and crustaceans (5.7%).

Thirty-one families of teleosts were identified in the samples, representing a mixture of diurnally and nocturnally active species (Table 1). The five most common teleost prey were marine eels (22.0%), wrasses (Labridae) (20.6%), squirrelfishes and soldierfishes (Holocentridae) (14.4%), triggerfishes (Balistidae) (13.1%), and parrotfishes (Scaridae) (10.5%). The marine eel category, which included Muraenidae, Congridae and Ophichthidae, was identified as a general group by their vertebrae. All teleosts found were common, shallow-water reef fishes, except for the beardfish family, Polymixiidae (1.0%), which is recognized to consist of deep-water benthic fishes (Gosline and Brock 1976).

Unidentifiable teleost remains, which included scales damaged from digestion as well as miscellaneous bones, occurred in 40.4% of the samples. Otoliths occurred in only 85 (9.0%) of the samples. Of the identifiable oto-

Table 1 *Monachus schauinslandi*. Frequency of occurrence (FO) and percent frequency of occurrence (% FO) of teleost families identified by all remaining hard structures found in scat and spew samples ($n = 940$) from 1991 to 1994. FO defined as number of samples in which a teleost prey type was found, % FO as FO divided by total number of scat and spew samples examined

| Teleost prey type | FO | %FO |
|----------------------|-----|------|
| “Empty” samples | 78 | 8.3 |
| Diurnal | | |
| Labridae | 194 | 20.6 |
| Balistidae | 123 | 13.1 |
| Scaridae | 99 | 10.5 |
| Acanthuridae | 71 | 7.6 |
| Pomacentridae | 44 | 4.7 |
| Tetraodontidae | 41 | 4.4 |
| Kyphosidae | 32 | 3.4 |
| Monacanthidae | 29 | 3.1 |
| Synodontidae | 25 | 2.7 |
| Pomacanthidae | 17 | 1.7 |
| Cirrhitidae | 12 | 1.3 |
| Chaetodontidae | 10 | 1.1 |
| Diodontidae | 10 | 1.1 |
| Bothidae | 9 | 0.9 |
| Cheilodactylidae | 6 | 0.6 |
| Scorpaenidae | 5 | 0.5 |
| Ostraciidae | 1 | 0.1 |
| Nocturnal | | |
| Unidentified eels | 207 | 22.0 |
| Holocentridae | 135 | 14.4 |
| Muraenidae | 53 | 5.6 |
| Congridae | 52 | 5.5 |
| Priacanthidae | 40 | 4.3 |
| Kuhliidae | 14 | 1.5 |
| Apogonidae | 9 | 0.9 |
| Ophichthidae | 6 | 0.6 |
| Diurnal/nocturnal | | |
| Mullidae | 58 | 6.2 |
| Lutjanidae | 24 | 2.6 |
| Carangidae | 11 | 1.1 |
| Polymixiidae | 9 | 1.0 |
| Serranidae | 5 | 0.5 |
| Belonidae | 1 | 0.1 |
| Unidentified remains | 330 | 40.4 |

Table 2 *Monachus schauinslandi*. Frequency of occurrence (FO) and percent frequency of occurrence (% FO) of otoliths found in scat and spew samples ($n = 940$). FO defined as number of samples in which an otolith prey type was found and % FO as FO divided by total number of scat and spew samples examined Note: all otoliths in family Congridae were identified as *Ariosoma marginatum*

| Prey type | FO | %FO |
|---------------|-----|------|
| Congridae | 569 | 60.5 |
| Holocentridae | 20 | 2.1 |
| Labridae | 11 | 1.2 |
| Synodontidae | 7 | 0.7 |
| Kyphosidae | 4 | 0.4 |
| Scaridae | 3 | 0.3 |
| Mullidae | 2 | 0.2 |

liths, 92.4% belonged to the conger eel, *Ariostoma marginatum*, 33% of which occurred in one sample

(Table 2). The remaining 7.2% belonged to several families, and all were present at low percentages.

A total of 280 samples (32.5%) contained octopus remains, whereas only 55 samples (6.4%) contained squid remains. Among these remains, 383 upper and 304 lower octopus beaks, and 184 upper and 223 lower squid beaks were recovered. Since upper and lower beaks in a sample did not always belong to the same species, based on the above numbers it was determined that 468 octopus and 262 squid prey were consumed (Table 3).

Therefore, although the percentage frequency of occurrence (% FO) of octopi was almost six times greater than the %FO of squid (30.1% vs 5.2%), the actual number of octopi consumed was roughly 1.8 times greater than the number of squid consumed (468 vs 262).

Thirteen octopus species are known from the Hawaiian islands (Young et al. 1989), seven of which were identified in the diet of the Hawaiian monk seal. The largest species, *Octopus cyanea*, occurred most often in the samples (84.4%). One specimen of each of the pe-

Table 3 *Monachus schauinslandi*. Number of individual prey consumed (No.) and percent of total number of those individuals (%), frequency of occurrence (FO), percent frequency of occurrence (%FO), wet weight, and mantle length calculated from cephalopod prey remains found in diet of Hawaiian monk seal. FO defined as

number of samples in which a cephalopod prey type was found, % FO as FO divided by total number of scat and spew samples examined ($n = 940$). Total wet wt and mantle lengths are estimates based on beak measurements (*Unident.* unidentified species)

| | No. (%) | FO (% FO) | Wet wt (g) | | Mantle length, mm (range) |
|----------------------------------|------------|------------|------------|--------------|---------------------------|
| | | | total | (range) | |
| Samples without any prey remains | 78 | | | | |
| Samples with cephalopod remains | 290 (30.9) | | | | |
| Samples with octopus remains | 280 (29.8) | | | | |
| Samples with squid remains | 55 (5.9) | | | | |
| Order Octopoda | 468 (64.1) | 283 (30.1) | | | |
| Octopodidae | 466 (63.8) | 281 (29.9) | | | |
| <i>Octopus cyanea</i> | 245 (33.6) | 114 (12.1) | 378, 140.0 | (0.05–11.28) | |
| <i>Octopus</i> sp. A | 33 (4.5) | 27 (2.9) | | | |
| <i>Octopus luteus</i> | 80 (11.0) | 68 (7.2) | 45, 210.0 | (0.005–3.69) | |
| <i>Octopus ornatus</i> | 72 (9.9) | 49 (5.2) | | | |
| <i>Octopus hawaiiensis</i> | 36 (4.9) | 23 (2.4) | | | |
| Ocythoidae | 1 (0.1) | 1 (0.1) | | | |
| <i>Ocythoe tuberculata</i> | 1 (0.1) | 1 (0.1) | | | |
| Alloposidae | 1 (0.1) | 1 (0.1) | | | |
| <i>Haliphron atlanticus</i> | 1 (0.1) | 1 (0.1) | | | |
| Order Teuthoidea | 262 (35.9) | 49 (5.2) | | | |
| Enoploteuthidae | | | | | |
| <i>Pterygioteuthis</i> sp. | 185 (25.3) | 10 (1.1) | 800.0 | (1.9–10.0) | 30.5–405.4 |
| <i>Ancistrocheirus lesueurii</i> | 5 (0.7) | 1 (0.1) | 667.4 | (67.7–312.0) | 89.1–174.7 |
| <i>Abraliopsis</i> sp. A | 4 (0.5) | 3 (0.3) | 57.6 | (2.3–49.1) | 37.9–135.2 |
| Unident. Enoploteuthidae | 4 (0.5) | 4 (0.4) | | | |
| <i>Abralia trigonura</i> | 1 (0.1) | 1 (0.1) | | | |
| Histioteuthidae | | | | | |
| <i>Histioteuthis hoylei</i> | 13 (1.8) | 3 (0.3) | 1361.5 | (4.1–250.5) | 39.7–90.6 |
| <i>Histioteuthis corona</i> | 4 (0.5) | 1 (0.1) | 158.1 | (23.9–57.6) | |
| Cranchiidae | | | | | |
| <i>Taonis</i> sp. | 6 (0.8) | 2 (0.2) | | | |
| Unident. Cranchiidae | 3 (0.4) | 3 (0.3) | | | |
| <i>Galiteuthis</i> sp. | 2 (0.3) | 2 (0.2) | | | |
| Sepiolidae | | | | | |
| <i>Euprymna scolopes</i> | 7 (1.0) | 7 (0.7) | | | |
| Chiroteuthidae | | | | | |
| <i>Chiroteuthis</i> sp. | 6 (0.8) | 1 (0.1) | 134.6 | (12.7–31.0) | 94.6–106.8 |
| Octopoteuthidae | | | | | |
| <i>Octopoteuthis</i> sp. | 6 (0.8) | 1 (0.1) | 21.7 | (3.0–4.0) | 67.2–162.5 |
| Ommastrephidae | | | | | |
| <i>Nototodarus hawaiiensis</i> | 5 (0.7) | 5 (0.5) | 17.0 | (3.0–3.7) | 81.9–124.7 |
| <i>Eucleoteuthis luminosa</i> | 1 (0.1) | 1 (0.1) | 25.2 | | 167.2 |
| Unident. Ommastrephidae | 1 (0.1) | 1 (0.1) | | | |
| Oegopsidae | | | | | |
| Unident. Oegopsidae | 4 (0.5) | 1 (0.1) | | | |
| Onychoteuthidae | | | | | |
| <i>Onychoteuthis</i> sp. | 3 (0.4) | 1 (0.1) | | | |
| Lepidoteuthidae | | | | | |
| <i>Pholidoteuthis</i> sp. | 2 (0.3) | 1 (0.1) | | | |
| Total | 730 | | | | |

lagic species *Ocythoe tuberculata* and *Haliphron atlanticus* was also recovered. Nine families of the order Teuthoidea occurred in the diet of the Hawaiian monk seal, representing 12 identifiable and 7 unidentifiable species. Only *Pterygioteuthis* sp. (55.5%) occurred with a frequency of > 5%.

Of those species of cephalopods for which wet weight and mantle lengths were estimated, *Octopus cyanea* appeared to be the most important to the diet in terms of the total amount consumed (378.14 kg) (Table 3). This was followed by *O. luteus* (45.21 kg). The total wet weight for *O. cyanea* may be somewhat overestimated; the maximum known size of this species is 6 kg (Van Heukelem 1983), whereas the upper size limit based on UHL and LHL for this study was 11.28 kg. All mantle lengths calculated for known species of squid fell within the size ranges reported by Roper et al. (1984).

Crustacean remains found in the scat samples were not identifiable to species. Only two of the samples recovered could be positively identified as lobster – when the entire carapace was recovered from a spew sample. The rest of the crustacean remains were visible only with a dissecting microscope.

Interaction effects

Significant associations occurred between teleost prey and year after controlling for island and age ($\chi^2 = 111.67$, $p = 0.000$), between teleosts and island after controlling for year and age ($\chi^2 = 129.71$, $p = 0.000$), and between teleosts and age after controlling for year and island ($\chi^2 = 112.69$, $p = 0.000$). Therefore, no confounding effects of year, island and age for teleost diet were observed.

Significant associations occurred between octopus prey and year after controlling for island and age ($\chi^2 = 203.66$, $p = 0.000$), between octopi and island after controlling for year and age ($\chi^2 = 45.21$, $p = 0.000$), and between octopi and age after controlling for year and island ($\chi^2 = 45.713$, $p = 0.000$). Therefore, no confounding effects of year, island and age for octopus diet were observed.

Significant associations occurred between squid prey and year after controlling for island and age ($\chi^2 = 299.90$, $p = 0.000$), between squid and island after controlling for year and age ($\chi^2 = 66.97$, $p = 0.000$), and between squid and age after controlling for year and island ($\chi^2 = 61.55$, $p = 0.000$). Therefore, no confounding effects of year, island and age for squid diet were observed.

Temporal differences in diet composition

Although 31 families of teleosts were represented as hard-part remains in the Hawaiian monk seal scat and spew samples combined (Table 1), many families were rare and did not constitute a major portion of the diet. Therefore, families that occurred < 3% by percent fre-

quency of occurrence (%FO) were pooled as miscellaneous species in each category (diurnal sp., nocturnal sp. and diurnal/nocturnal sp.) (Fig. 2). The proportion of diurnal and nocturnal teleost families and octopus species found in the samples varied considerably over the 4 yr. In addition, no correlation between an increase or decrease in overall teleosts with either octopi or squid occurred among the 4 yr.

Significant differences were seen in the %FO of teleosts among the years 1991 to 1994 ($\chi^2 = 99.34$, $p < 0.01$, $df = 51$) (Fig. 2). The Balistidae gradually increased in the diet from 2.3% in 1991 to 16.5% in 1994, and the presence of marine eels increased dramatically from 11.6% in 1991 to 40% in 1994. Conversely, the Priacanthidae exhibited the opposite trend, with a high of 37.6% in 1991, decreasing to 2.1% in 1994. Polymixiidae was found only in samples from 1993 and 1994, both at 1.5%.

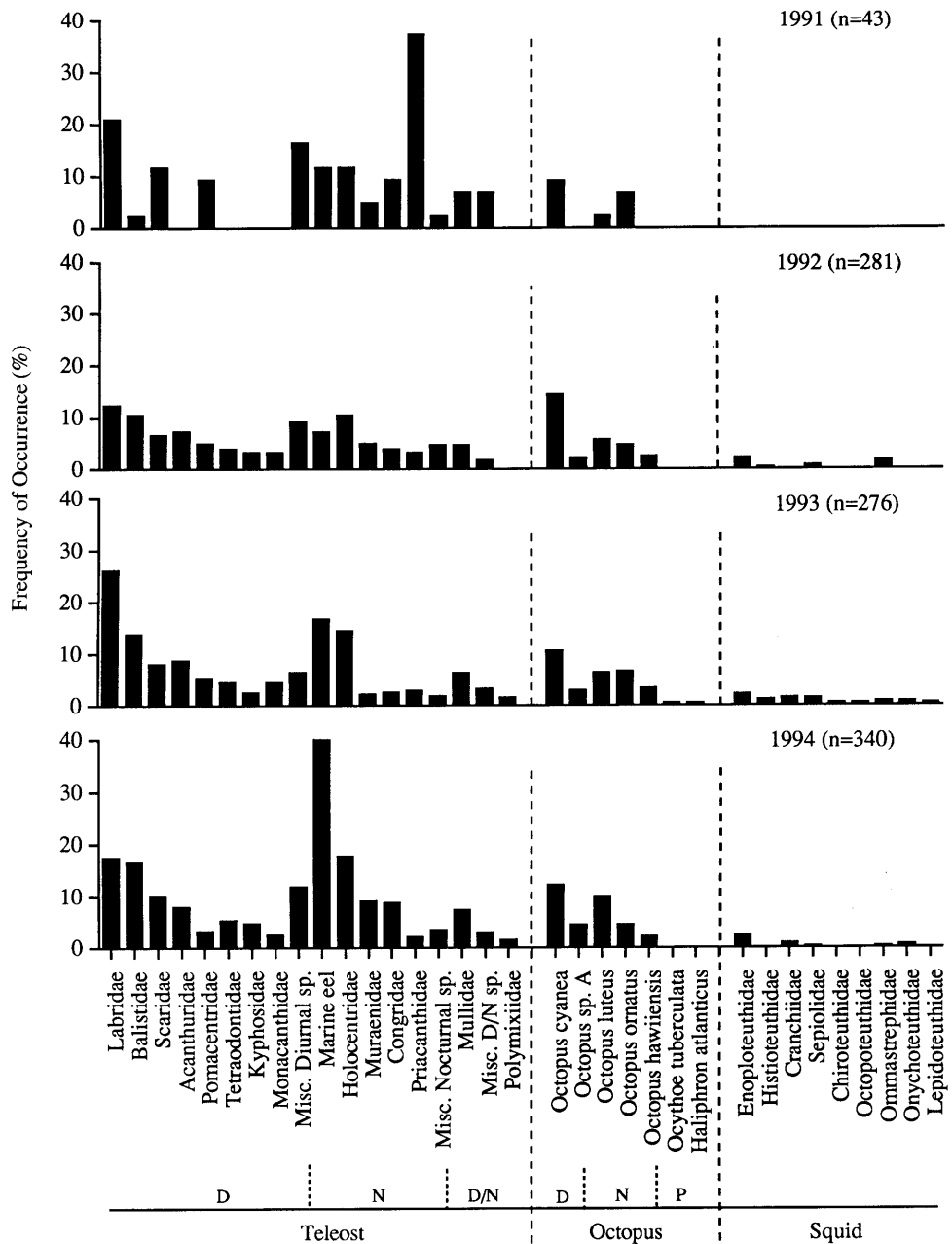
Although the %FO of octopi was not significant among the years 1991 to 1994 (Fig 2), significant differences in the numbers of octopi consumed by monk seals were found ($\chi^2 = 30.58$, $p < 0.01$, $df = 18$). Fewer numbers and species of octopi were seen in the samples in 1991 than in any other year, but at no time did an increase of any one octopus species occur from 1991 to 1994. *Octopus cyanea* was the most highly consumed octopus prey by number and %FO during all years examined. Neither *Octopus* sp. A nor *O. hawiiensis* occurred in the diet during 1991, and each of the pelagic octopods, *Ocythoe tuberculata* and *Haliphron atlanticus*, were found only in 1993. Overall, the greatest diversity of octopus species was consumed in 1993. The cephalopod component of the diet was not augmented by the consumption of squid during any one year. In fact, no squid appeared in the diet in 1991. Significant differences in %FO of squid diet were not seen among the years 1992 to 1994; however, a significant difference in number of squid occurred ($\chi^2 = 56.06$, $p < 0.01$, $df = 36$) (Fig. 2), even when *Pterygioteuthis* sp. was omitted from the analysis ($\chi^2 = 48.60$, $p < 0.05$, $df = 34$). Overall, the greatest number and diversity of squid species were in 1993.

Geographic differences in diet composition

The proportion of diurnal and nocturnal teleost families and octopus species recovered from the samples varied among the islands (Fig. 3). No correlation between an increase or decrease in overall teleosts with either octopus or squid diet-components occurred among the five islands.

Significant differences were seen in %FO of teleost diet among the islands FFS, LAY, LIS, PHR, and KUR ($\chi^2 = 240.62$, $p < 0.01$, $df = 68$). At FFS and LIS, the highest %FO was found in the Labridae (20.1 and 23.8%, respectively), followed by Balistidae (17.3 and 22.1%, respectively) (Fig. 3). At LAY and KUR, the highest %FO was found in the marine eels (32.1 and 42.3%, respectively), followed by Labridae (18.2 and

Fig. 2 *Monachus schauinslandi*. Frequency of occurrence of diurnal (D), nocturnal (N), and diurnal/nocturnal (D/N) teleost families; diurnal (D), nocturnal (N), and pelagic (P) octopus species; and squid families within seal diet during 1991 to 1994



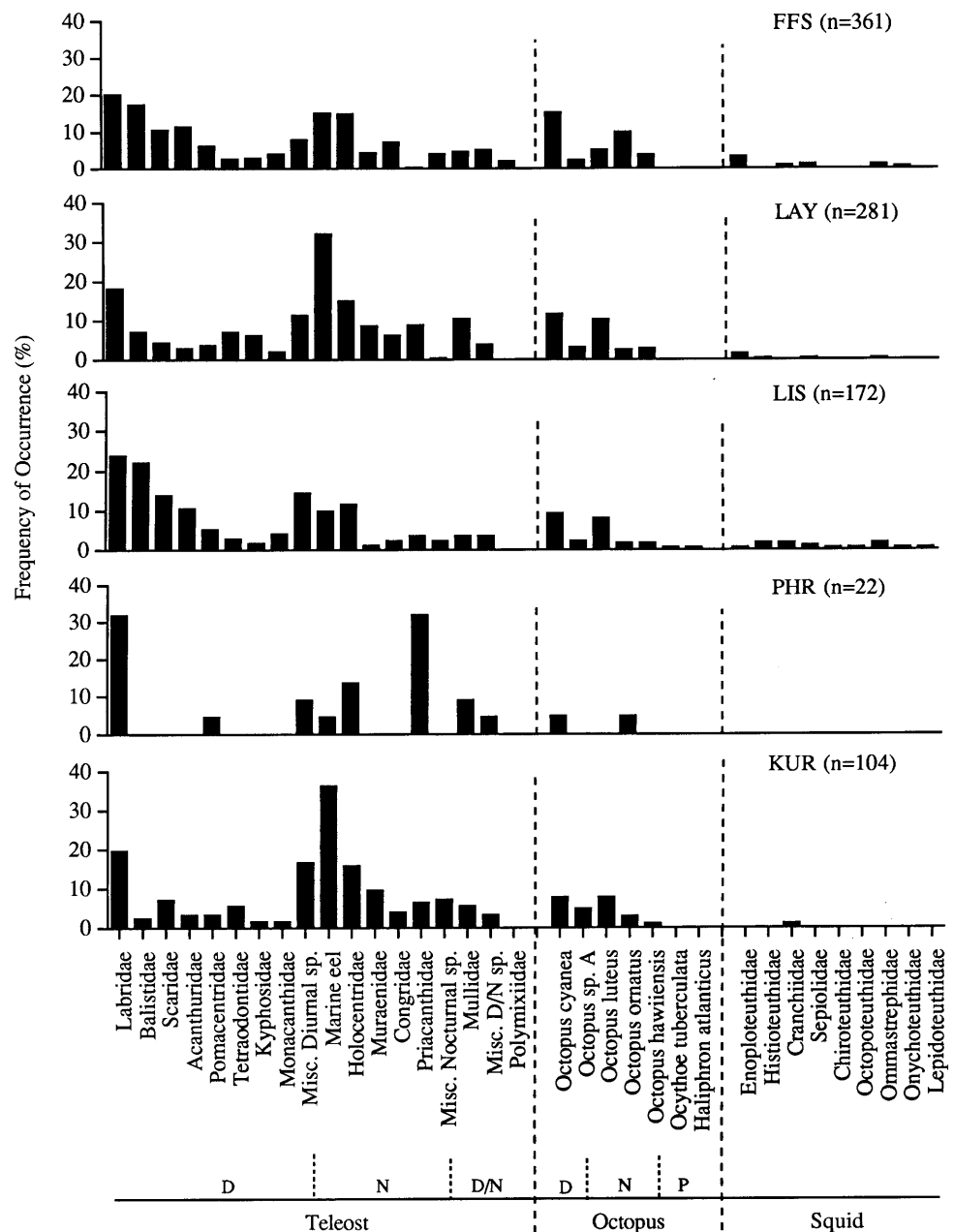
17.3%, respectively), and Holocentridae (15.0 and 15.3%, respectively). At PHR, the highest %FOs were found in the Labridae and Priacanthidae (31.8% each). Most occurrences of the teleost families changed little in number among the five islands examined; however, some interesting patterns were seen for a few teleost families. The Balistidae and Acanthuridae occurred in high percentages at both FFS and LIS and low percentages at LAY and KUR. The opposite was true for marine eels, which occurred in high percentages at LAY and KUR, but lower percentages at FFS and LIS (Fig. 3). Polymixiidae occurred at only FFS and KUR, at opposite ends of the NWHI archipelago.

Significant differences were not seen in %FO, but were seen in the number of octopi within the monk seal

diet among the islands FFS, LAY, LIS, PHR, and KUR ($\chi^2 = 37.57, p < 0.01, df = 28$) (Fig. 3). *Octopus cyanea* was the most highly consumed octopus prey at all the islands examined. *Octopus* sp. A occurred at the highest %FO at KUR, *O. luteus* at LAY, *O. ornatus* at FFS, and *O. hawaiiensis* at FFS. *Ocythoe tuberculata* and *Haliphron atlanticus* were both found only at LIS.

No difference in %FO of squid diet was seen among the five islands; however, a significant difference in the number of squid did occur ($\chi^2 = 242.16, p < 0.01, df = 72$), with PHR omitted because of low sample size ($\chi^2 = 67.99, p < 0.001, df = 36$), and with *Pterygioteuthis* sp. omitted because of the high numbers of this prey type found in the samples ($\chi^2 = 51.97, p < 0.025, df = 34$) (Fig. 3). Small numbers of various species occurred

Fig. 3 *Monachus schauinslandi*. Frequency of occurrence of diurnal (*D*), nocturnal (*N*), and diurnal/nocturnal (*D/N*) teleost families; diurnal (*D*), nocturnal (*N*), and pelagic (*P*) octopus species; and squid families within seal diet at French Frigate Shoals (*FFS*), Laysan Island (*LAY*), Lisianski Island (*LIS*), Pearl and Hermes Reef (*PHR*) and Kure Atoll (*KUR*) in Northwestern Hawaiian Islands



mainly at FFS and LIS; only six species occurred at LAY, none at PHR, and one at KUR. The greatest number of squid occurred in the diet of monk seals at FFS (74%), followed by LIS (19%), LAY (6%) and KUR (0.6%).

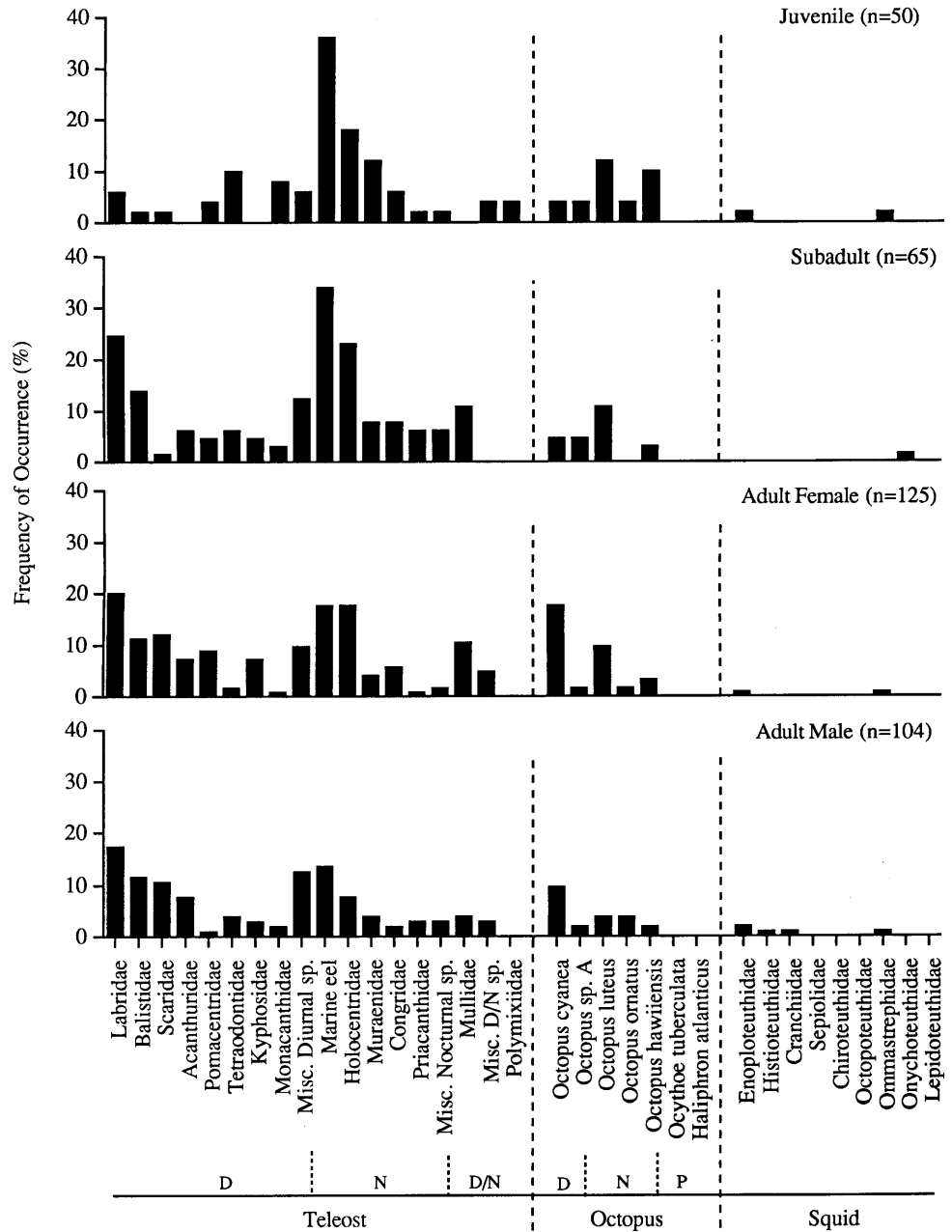
Ontogenetic differences in diet composition

An ontogenetic dietary shift occurred both in the proportion of diurnal and nocturnal teleost families and octopus species consumed (Fig. 4). Samples from juveniles contained 50 and 53% more nocturnal teleosts and octopi, respectively, than diurnal teleosts and octopi. Samples from subadults also contained more nocturnal

teleosts and octopi (10 and 11%, respectively) than diurnal samples. In comparison, samples from adult females contained 40% more diurnal teleosts and octopi than nocturnal samples, while those from adult males also contained more diurnal teleosts and octopi (53 and 30%, respectively) than nocturnal samples.

Significant differences in the %FO of the teleost diet occurred among juveniles, subadults, adult females and adult males ($\chi^2 = 99.34$, $p < 0.01$, $df = 51$) (Fig. 4). Among the diet of juvenile seals, the highest %FO of prey was unidentified marine eels (36%), followed by Holocentridae (18%) and Muraenidae (12%). Within the diet of subadult seals, the highest %FO of prey was again the marine eels (33.9%), but these were followed by Labridae (24.6%), and then Holocentridae (23.1%).

Fig. 4 *Monachus schauinslandi*. Frequency of occurrence of diurnal (*D*), nocturnal (*N*), and diurnal/nocturnal (*D/N*) teleost families; diurnal (*D*), nocturnal (*N*), and pelagic (*P*) octopus species; and squid families within seal diet of juvenile, subadult, adult female and adult male seals



Within the diet of adult females and adult males, the highest %FO of prey was the Labridae (20 and 17.3%, respectively), followed by Holocentridae (17.6 and 17.3%, respectively) and miscellaneous diurnal species (17.6 and 12.5%, respectively).

Some ontogenetic shifts in diet were apparent among the three age groups of seals examined, especially with respect to the Labridae, Balistidae and marine eels (Fig. 4). Juvenile seals had a noticeably low occurrence of Labridae in their diet (6%), whereas this family was one of the most highly consumed prey among the other age groups of seals (17.3 to 24.6%). The Balistidae were also a highly consumed prey (11.2 to 13.9%) among all age groups except juveniles (2%). The opposite trend was seen for marine eels, with both juvenile and subadult

seals foraging an average of 19.4% more on these species than were adult females and males. In addition, Mullidae were not seen at all in the juvenile diet, while the deep-water family, Polymixiidae ($n = 9$) was found solely in the diet of juveniles.

Differences were not seen in the %FO of the octopus component of the monk seal diet among juvenile, subadult, adult female and adult male seals, but numbers of octopi among the age/sex classes did differ significantly ($\chi^2 = 26.09, p < 0.05, df = 18$), with the fewest %FO of octopi occurring in the diet of subadults (Fig. 4). The %FO of *Octopus cyanea* was the highest in the diet of adult female and male seals, and increased with increasing age. The %FO of *O. luteus* was the highest in the diet of juveniles, followed by subadult and adult

seals. *O. hawaiiensis* also exhibited a high %FO in the diet of juvenile seals. The two pelagic octopods *Ocythoe tuberculata* and *Haliphron atlanticus* were both consumed by seals of unknown age or sex. Excluding samples collected from unknown seals, the greatest number of octopi was consumed by adult female monk seals (50%, $n = 125$), followed by adult males (25%, $n = 104$), juveniles (14%, $n = 50$), and subadults (10%, $n = 65$).

Relatively few samples from known seals contained squid remains (Fig. 4), therefore, no statistical tests were performed to examine ontogenetic differences in squid diet. Within the known samples, the greatest diversity and %FO of squid families was consumed by adult male seals, followed by juveniles, subadults and adult females.

Discussion

Overall diet composition

Both inshore, benthic and offshore teleosts and cephalopods were found in the diet of *Monachus schauinslandi*. Although monk seals may forage far offshore at times, the rate of passage of digesta of ≈ 39 h (Goodman-Lowe et al. 1997) allows ample time for beach haul-out between foraging bouts, and therefore it is assumed that the majority of teleosts and cephalopods preyed upon were represented in this study. Moreover, the commercial fisheries in the NWHI appear to be competing indirectly with the Hawaiian monk seal in that several families of teleosts found in the diet have also been reported as bycatch of the fisheries (R. Moffitt personal communication). However, the level of this indirect competition has yet to be determined.

Overall, the teleost and cephalopod prey consumed by Hawaiian monk seals represents a mixture of diurnally and nocturnally active species. This contrasts with studies by Kenyon and Rice (1959) and DeLong et al. (1984), who found that seals spent a majority of their time at sea during nighttime hours. Although it is possible that the seals are foraging on diurnal species at night when prey are resting, many of the diurnal species are cryptic at night, burying themselves in the sand (Labridae) or coral rubble (*Octopus cyanea*).

Hawaiian monk seals fed on a wide variety of teleost prey, but five teleost groups dominated the diet: Labridae, Scaridae, Balistidae, Holocentridae and marine eels (Muraenidae, Congridae and Ophichthidae). The occurrence of the labrids, scarids and balistids in the samples may be over-represented because both Labridae and Scaridae have scales that are extremely large relative to the size of the fish's body, Balistidae have scales that are exceptionally thick, and Scaridae have fused teeth. Therefore, these structures are less susceptible to degradation during digestion, leaving the scales and jaw bones easily identifiable. The eel families were also highly represented in the monk seal diet because of their characteristic vertebrae and the fact that many of the eel remains were found in the spew samples, where a large

part of the skeleton was found intact, thus aiding in identification. Regardless of these biases, diet remnants as described by scats and spews in this study show relative abundance patterns similar to fish censuses conducted at FFS and at Midway Island (DeMartini et al. 1996): species of Labridae were ranked as Nos. 1 and 2, respectively, Scaridae as Nos. 2 and 5, respectively, and Holocentridae as Nos. 10 and 43, respectively. Although the Balistidae and eels did not appear in the visual censuses conducted by DeMartini et al., balistids are common in these regions but tend to inhabit deeper areas outside the atolls where censusing did not occur, whereas Muraenidae, Congridae, and Ophichthidae are all mainly nocturnal species and only diurnal visual censuses were conducted (F. Parrish personal communication).

The majority of the otoliths found were large and robust and occurred in only 9% of the scat and spew samples collected, representing 7 of the 31 families of teleosts identified. Although many diet-composition studies utilize otoliths for prey identification, these data show that the sole use of otoliths for identifying prey of the Hawaiian monk seal would result in a severe underestimation of both numbers of prey species and frequencies of occurrence. Similar results were found for the Australian sea lion by Gales and Cheal (1992), who concluded that using only otoliths to identify teleost prey seriously underestimates the importance of some prey in the diet and also overestimates the importance of cephalopod prey.

Octopi play an important role in the diet of the Hawaiian monk seal in terms of number and mass. Wet weights of *Octopus cyanea* estimated from URLs were almost 5 kg larger than published values. Two explanations are possible: the size of this species may have been overestimated because the regression formulas were based on relatively few specimens or, alternatively, the published maximum size may be low because it was based on laboratory-reared individuals (Van Heukelem 1983).

Several squid species were recovered from the samples, but most occurred in low numbers. Cephalopod beaks have a slower rate of passage than other indigestible items because of their irregular shape (Bigg and Fawcett 1985), and the majority of squid beaks in this study were found in scat, rather than spew samples. Therefore, the small numbers of squid species found probably indicate that the monk seals are not preying heavily on these organisms rather than indicating a sampling bias due to seals foraging and defecating offshore.

The majority of the crustaceans found in the samples probably represented secondary prey items, since the seals consumed several teleost and octopus prey that are known to forage on small crustaceans. A small number of large crustacean remains found were identified as lobster parts, supporting the observation of seals foraging on lobsters in the wild (MacDonald 1982). However, this does not constitute conclusive evidence of

interactions between the commercial lobster fishery and Hawaiian monk seals. Methods such as serological protein and fatty acid analyses, which have been used to examine specific prey items in common and grey seals (Pierce et al. 1993) and harbor seals (Iverson et al. 1997) need to be developed specifically for Hawaiian lobster species so that the occurrence of lobsters in the diet can be accurately identified.

Temporal differences in diet composition

Temporal differences of both teleosts and cephalopods found in the diet of the Hawaiian monk seal occurred among the years 1991 to 1994. Because neither teleost nor cephalopod abundances have been studied in the NWHI, conclusions can not be drawn concerning these differences, but they may reflect natural fluctuations in these prey populations.

Fewer occurrences of teleost families, octopus and squid species were observed in the diet in 1991, which probably reflects the low number of samples collected during that year ($n = 43$). A higher percentage of Priacanthidae was consumed during 1991 than in any other year, whereas a higher percentage of marine eels was consumed in 1994. Annual fish censuses are not conducted in the NWHI, so there is little prey-occurrence data to explain these differences in diet composition. Nonetheless, one species of Priacanthidae that DeMartini et al. (1996) ranked as No. 9 at FFS between 1980 and 1983 had dropped to No. 78 by 1992. This decline is probably representative of a decreased carrying capacity in the NWHI during this time due to a large climatic event (Polovina et al. 1994). A greater number of octopi were found in the samples collected from 1993, possibly reflecting an increased abundance and availability of octopus during that year. A greater number of squid were also found in the 1993 samples; however, 11 of the 16 species of squid recovered, along with the two pelagic octopi species, were found in a single scat sample representing the foraging of one seal. Nevertheless, because pelagic cephalopod distributions are affected by ocean currents and water-mass distributions, these organisms may have occurred nearer to shore during 1993, thus affecting their availability as prey to Hawaiian monk seals.

Geographic differences in diet composition

Geographical differences occurred in both teleosts and cephalopods found in the diet of the Hawaiian monk seal among the five main breeding islands in the NWHI. Because the benthic topography of all of these islands is similar, it is unclear why differences in numbers of prey should exist, or why FFS in particular should have a declining population of seals due to starvation.

Although Hobson (1984) found differences in species assemblages between the southeastern-most and north-

western-most ends of the NWHI chain, this does not appear to be a likely explanation for the patterns of teleost prey found in the seals' diet during the present study, because the seals that had similar diets were not located on adjacent islands and, therefore, differences in teleost diet between the southern and northern ends of the NWHI chain were not apparent. The occurrence of *Octopus cyanea* in the diet of the Hawaiian monk seal, however, decreased from the southeastern to the northwestern end of the NWHI, even though it has an established distribution throughout the Indo-Pacific (Roper et al. 1984). All the islands have similar reef habitats; therefore, it is unknown why variations in the numbers of different octopus species should occur.

The Polymixiidae is considered a deep-water benthic family that does not vertically migrate, and it has been caught off FFS and KUR (R. Humphreys personal communication). Therefore, it would seem that seals at these islands are foraging on another teleost that is available, albeit in deep-water. The overall low % FO of this family does not seem to indicate a large-scale exploitation of another teleost in lieu of the absence of other, more preferred or abundant, teleost prey.

Small numbers of several species of squid occurred at both FFS and LIS, but at FFS they originated from 21 different samples, representing a minimum of 8 different seals; whereas most of the LIS species were recovered from one sample. The seals at FFS ate a greater number of octopi than at any other island. Although numbers of teleosts consumed at FFS are not available, it is possible that seals have fewer teleosts available to them and are therefore augmenting their diet with cephalopods. No pelagic cephalopods were consumed at KUR, even though 281 samples were collected there. The topography of all the NWHI is similar, with a reef system extending ≈ 17 km from shore; thus, the proximity to offshore pelagic waters is the same at all the islands. There may be suitable numbers of reef-associated prey at KUR, reducing the need for these seals to forage offshore.

Ontogenetic differences in diet composition

Ontogenetic shifts in the Hawaiian monk seal diet were observed for teleost families and octopus species. The Hawaiian monk seal is weaned at ≈ 5 to 6 wk, at which time the pup must learn how to feed on its own (Kenyon and Rice 1959). Hence, a significant ontogenetic difference in diet is not surprising. It is the juvenile seals at FFS that are most often found starving and emaciated; however, in this study only two samples were collected from juveniles at FFS. As a result, nothing can be concluded as to the reason for the starvation of juveniles at FFS, and future studies should concentrate on determining the diet of this age group in particular.

Noticeably lacking from the juvenile diet at all islands were the Labridae, even though this was found in high occurrences in the other age groups of seals and is one of the most abundant families found on the reef (DeMar-

tini et al. 1996). However, because labrids often bury in the sand at night and juvenile seals fed 38% more on nocturnal than on diurnal teleosts, labrids might not be as readily available. In addition, scales of the deep-water Polymixiidae were found exclusively in the diet of juveniles; this is consistent with the depth-of-dive data for juveniles collected by Schlexer (1984). The diets of both juveniles and subadults also had much higher occurrences of nocturnal octopi and eels than did adult females and males, and younger seals fed more often on smaller octopus species such as *Octopus luteus* and *O. hawiiensis*, whereas older seals fed more often on larger species such as *O. cyanea*. There are currently no observational or telemetry data available to confirm that juvenile seals forage more frequently at night than do adult seals: both deep and nocturnal foraging may help reduce the competition from larger adult seals that was observed by Rauzon and Kenyon (1982). Nighttime foraging by small, young seals slowly decreased with age, and a complete switch occurred in adult seals, which on average foraged 46.5% more diurnally than nocturnally. As the seals grow larger and more experienced, competition from older seals may decrease.

This study has shown that the Hawaiian monk seal has a broad and diverse diet, possibly because of foraging plasticity. In addition, it was found to shift its diet ontogenetically: as juveniles, feeding on small, slow-moving nocturnal species of teleosts and cephalopods; and as adults gradually shifting to larger diurnal or nocturnal prey. Because starvation of juveniles appears to be a major cause of population decline at FFS, studies concentrating on determining the abundances of teleost prey in the NWHI and the dietary needs of juvenile monk seals need to be conducted. Future studies should concentrate on nutritional aspects of the diet, along with the foraging patterns of the Hawaiian monk seal, to further our understanding of the decline of this endangered species.

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