Assimilation Efficiency of Prey in the Hawaiian Monk Seal, *Monachus schauinslandi*

Gwen D. Goodman-Lowe, James R. Carpenter, and Shannon Atkinson

Gwen D. Goodman-Lowe. Dept. of Zoology, Hawaii Institute of Marine Biology, University of Hawaii, Box 1346, Kaneohe, HI 96744, (808) 236-7416, Fax (808) 236-7443, email: glowe@hawaii.edu

James R. Carpenter. Department of Animal Sciences, 1800 East-West Road, University of Hawaii, Honolulu, HI 96822

Shannon Atkinson. Hawaii Institute of Marine Biology, University of Hawaii, Box 1346, Kaneohe, HI 96744

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Abstract

Assimilation efficiency, digestive efficiency, metabolizable energy, and nitrogen retention in three captive adult male Hawaiian monk seals (*Monachus schauinslandi*) were measured using the indigestible marker, chromic oxide for four experimental diets: a control diet of herring (*Clupea harengus*), and three test diets consisting of flagtail (*Kuhlia sandvicensis*), squid (*Loligo* sp.), and lobster (*Panulirus marginatus*), each of which was used in combination with the herring diet. The addition of all three test prey to herring decreased the digestibility of gross energy by a mean of 3.58 $\pm$ 3.89%. Assimilation efficiency of gross energy for herring was 96.1 $\pm$ 4.0%, for flagtail was 73.8 $\pm$ 6.8%, and for squid was 94.1 $\pm$ 5.7%, but could not be determined for lobster. Digestive efficiency and metabolizable energy of the diets examined were high (4602.2 $\pm$ 247.1 kcal * d^{-1} and 4062.5 $\pm$ 178.4 kcal * d^{-1}, respectively) and were positively correlated with the amount of gross energy ingested. Nitrogen retention was highest for the flagtail/herring diet (33.2 $\pm$ 1.2 g * d^{-1}) followed by the squid/herring diet (11.5 $\pm$ 3.3 g * d^{-1}), lobster/herring diet (6.0 $\pm$ 0.0 g * d^{-1}), and herring (control) diet (-5.7 $\pm$ 1.6 g * d^{-1}). This study indicates that prey that are both higher in protein and lower in fat than herring provide greater metabolizable energy for productive functions in Hawaiian monk seals.

Introduction

The Hawaiian monk seal, *Monachus schauinslandi*, is considered one of the most endangered marine mammals found in US waters, with a population decline of approximately 5-6% occurring annually (Ragen 1993). One cause of this decline is the starvation of juvenile seals at French Frigate Shoals (FFS) (Gilmartin 1993), where the largest subpopulation of monk seals exists. Hence, obtaining information regarding the nutritive value of monk seals' prey and how those prey are assimilated is important to understanding this decrease in the FFS subpopulation.

Assimilation efficiency (AE) is defined as the proportion of ingested nutrients absorbed from the gastrointestinal tract and available for maintenance functions (e.g., respiration, circulation, and basal metabolic rate), growth, reproduction, and external work (e.g., swimming) (Hill and Wyse 1989). The AE of ingested prey can vary both inter- and intraspecifically within the consumer, and is a function of digestive tract morphology, rate of digestion, the age of the animal (Lawson et al. 1997), the nutritional state of the animal, and the biochemical make-up of the various prey ingested (Golley et al. 1965; Fadely et al. 1990).

As a prelude to determining the AE for the Hawaiian monk seal, its rate of digestion was determined (Goodman-Lowe et al. 1997) and the digestive tract morphology has been described (Goodman-Lowe et al. in review). In addition, differences in types and frequency of occurrence of natural prey of the Hawaiian monk seal were found during the years 1991-1994, among the main breeding islands of these seals, and among age/sex classes (Goodman-Lowe in press).

Relatively few studies have been conducted on the AE of marine mammals due to the difficulty in the logistics of the research. In the wild, it is impossible to obtain known weights of prey before the seals have ingested them, whereas in captivity, collection of fresh feces, which can only be obtained from confined animals, is often difficult. From the few studies conducted on AE in marine mammals (Parsons 1977; Ashwell-Erikson and Elsner 1981; Keiver et al. 1984; Ronald et al. 1984; Fadely et al. 1990; Fisher et al. 1992; Martensson et al. 1994; Lawson et al. 1997), it is apparent that the assimilation of prey is highly variable and dependent on both the seal species and their prey.

The purpose of this study was to determine if there are differences in AE, digestible energy (DE), metabolizable energy (ME), and nitrogen retention (NR) among three natural prey groups of Hawaiian monk seals to obtain a baseline understanding of the seals' digestive physiology. Understanding how these seals assimilate their prey will add to information already known about the diet of the monk seal, which will, in turn, help provide insight into the starvation of juvenile seals.

Materials and Methods

Animals and test diets

Three adult male Hawaiian monk seals currently held in captivity at the Waikiki Aquarium, Oahu, Hawaii, were used for this study, which was conducted from January-April, 1996. These seals were all older than 12 years, ranged in size from 163-193 kg, and have been in captivity for approximately 11-14 years. Daily observations and annual veterinary physical examinations determined that they were in good health. All experiments were conducted in accordance with US and Canadian Councils on Animal Care.

Prior to each experiment, the seals were trained to ingest the prey item to be tested. Quantities of the test diets to be administered to the seals were calculated from published energy values to total approximately 5000 kcal per day (Table 1). This daily energy level was the caloric content of the maintenance diet utilized by the Waikiki Aquarium. Test diets were based on studies that determined Hawaiian monk seals forage mainly on teleosts, followed by cephalopods and crustaceans (Goodman-Lowe in press).

The four different test diets were 1) herring only (control), 2) flagtail + herring, 3) squid + herring, and 4) lobster + herring (Table 1). The flagtail, *Kuhlia sandvicensis*, squid, *Loligo* sp., and Pacific spiny lobster, *Panulirus marginatus*, were used to represent the three major groups of naturally occurring Hawaiian monk seal prey (teleost, cephalopod, and crustacean, respectively). The percent that each prey contributed to the test diet itself varied considerably due to their availability, with squid being the most readily obtainable followed by flagtail and lobster (Table 1). Because monk seals in the wild often regurgitate indigestible items such as lobster chitin, and because the seals in this study could not be trained to ingest whole lobsters, only lobster tail flesh was used.

Assimilation efficiency by difference (Schneider and Flatt 1975), where a control diet is fed together with the test diet, was used in this study for two reasons: 1) it was extremely difficult to obtaining large enough quantities of the test prey required for training and 9 d trials for 3 seals, and 2) because monk seals forage on several types of prey (Goodman-Lowe in press) a monospecies diet is unnatural for assimilation efficiency experiments. Chromic oxide (Cr_2O_3) was used as an indigestible fecal marker, which allowed us to estimate the total quantity of feces produced by the seals based on previous studies (Goodman-Lowe et al. 1997). Gel capsules containing quantities of Cr_2O_3 averaging 0.17% wet weight of the total amount of test prey were placed in the opercular cavity of herring during each experiment. Seals were fed the daily allowance of the test diet in one feeding each day.

Experimental Design

Each experiment consisted of a 7 d pre-collection period to allow the marker and feed to equilibrate in the digestive tract, followed by a 40 h fecal collection period. This time period was chosen based on the rate of passage of approximately 39 h determined previously for the Hawaiian monk seal (Goodman-Lowe et al. 1997). Seals were allowed their normal access to water and haul-out area during the first 7 d, but were confined within a drained tank for the final 40 h collection period to facilitate the identification and collection of feces from each seal. Fecal samples were collected immediately upon defecation and were frozen for later analysis. During the collection period, the seals were observed continuously and were wetted every 15 min to help maintain their ability to thermoregulate.

To assess the proximate or nutrient composition of each test diet, two prey items were sampled during each day of the experiment resulting in a total of 18 prey sampled. These prey were pooled by species and analyzed in duplicate for dry matter, ash, crude protein and crude fat using standard methods of the Association of Official Analytical Chemists (1990). All diet and fecal samples were homogenized, dried at 50 ^{0}C in a mechanical convection oven, pulverized by mortar and pestle because of the high fat content, and ground through a 2 mm stainless steel screen in a Thomas Wiley Mill.

For each fecal sample collected, duplicate subsamples were analyzed for dry matter, ash, crude protein, crude fat and Cr_2O_3. Carbohydrate (CHO) was estimated by difference where:

[1] CHO (%) = 100% dry matter - (% crude protein + % crude fat + % ash).

Cr_2O_3 levels in the feces were determined by procedures outlined in Hill and Anderson (1958). Mean and standard deviations for these duplicate subsamples were expressed on a dry-matter basis.

Calculations and analysis

In order to formulate the combination test diets prior to experiments, gross energy (GE) was calculated for the prey based on published values (Pond et al. 1995) where:

[2] GE (kcal) = (% crude protein * 5.65) + (% crude fat * 9.40) + (% CHO * 4.15).

During the actual feeding trials, GE was determined in diet and fecal samples using a Parr Adiabatic Calorimeter. Total AE (%), which measures the overall amount of the feed digested by the animal, was calculated according to Schneider and Flatt (1975):

$$[3]\quad AE\ (\%) = 100 - \left(100 * \frac{\%\ \text{indicator in feed}}{\%\ \text{indicator in feces}}\right)$$

The AE of dry matter, crude protein and crude fat for the test diets was calculated according to Schneider and Flatt (1975) using the percent recovery of feces method:

$$[4]\quad AE\ (\%) = 100 - \left(\%\ \text{recovery of indicator} * \frac{\%\ \text{indicator in feed} * \%\ \text{nutrient in feces}}{\%\ \text{indicator in feces} * \%\ \text{nutrient in feed}}\right)$$

and where the % recovery of indicator, Cr_2O_3, was previously determined to be 72.2% (seal 1), 52.7% (seal 2), and 74.8% (seal 3) (Goodman-Lowe et al. 1997). The AE of dry matter, crude protein and crude fat for the prey calculated separately from the test diets, which all included herring (H), was calculated as follows:

$$[5]\quad AE(\%)\ \text{of test prey} = \frac{((\text{Total diet consumed} * \text{AE of diet}) - (\text{Total H consumed} * \text{AE of H}))}{\text{Total test prey consumed}}$$

To determine how the combination diets affected the digestibility of the control diet (H diet), the digestibilities of gross energy, dry matter, crude protein and crude fat were calculated relative to the digestibility of herring alone:

[6] Digestibility relative to H (%) = AE of H - AE of flagtail/herring, squid/herring, or lobster/herring

Apparent digestible nitrogen intake (ANI) was calculated as

$$[7]\quad ANI\ (g * d^{-1}) = \frac{\text{total crude protein consumed} * \text{AE of crude protein}}{6.25}$$

Urinary nitrogen loss and urinary energy loss were estimated using formulas based on data from Keiver, et al. (1984):

[8] Urinary nitrogen loss ($g * d^{-1}$) = 0.7371 * ANI + 3.364

[9] Urinary energy loss ($kcal * d^{-1}$) = 6.128 * ANI + 14.737

Apparent digestible energy (DE), which estimates the amount of energy digested by the seal, was calculated for each sample:

[10] DE ($kcal * g^{-1}$) = GE - fecal energy loss ($kcal * g^{-1}$)

Metabolizable energy (ME), which is an estimate of the dietary energy that is available for metabolism, was calculated for each sample:

[11] ME (kcal) = GE - (fecal energy loss + urinary energy loss + combustible gas loss)

and combustible gas loss is considered negligible in carnivores because they do not feed on gas producing plant material. Fecal nitrogen loss was calculated for each seal where:

$$[12]\ \text{Fecal nitrogen loss}\ (g * d^{-1}) = 100 - \left(\frac{\text{AE protein - quantity protein consumed}}{6.25}\right)$$

Nitrogen retention (NR) was calculated as

[13] NR ($g * d^{-1}$) = Total crude protein consumed - (UNL + FNL).

Comparisons were made using a Student's *t* test and analysis of variance (SAS, 1985); the level of significance was $p \leq 0.05$ for all analyses.

Results

Gross energy ($F = 23.04$, $p = 0.002$), dry matter ($F = 18.58$, $p = 0.008$), crude protein ($F = 81.80$, $p = 0.000$), crude fat ($F = 74.53$, $p = 0.001$), and ash ($F = 51.65$, $p = 0.001$) of herring fed to the seals all differed among the four test diets (Table 2). Because the mean and standard deviations for the four diets were based on two subsamples from 18 pooled organisms per test diet, the variances were quite low, and therefore, statistical significance in this case did not necessarily imply biological significance.

Squid, lobster and flagtail were all lower in gross energy, dry matter, and crude fat than herring ($F = 47.47$, $p = 0.000$; $F = 153.74$, $p = 0.000$; $F = 157.80$, $p = 0.000$, respectively), but were higher in % crude protein than herring ($F = 124.59$, $p = 0.000$; Table 2). Only flagtail was higher in ash than herring ($F = 7.59$, $p = 0.006$), whereas squid was higher in CHO than herring ($F = 128.01$; $p = 0.000$).

The defecation patterns and Cr_2O_3 concentrations within the feces of each seal varied considerably throughout the day and among the four different test diets. The Cr_2O_3 concentration in feces collected for the herring test diet ranged from 0.90 - 13.61 % (n = 11), for the squid/herring diet from 1.87 - 19.09 (n = 9), for the lobster/herring from 1.26 - 7.52 (n = 8), and for the flagtail/herring diet from 2.66 - 2.93 (n = 3).

Hawaiian monk seals assimilated similar amounts of gross energy when fed each of the test diets (Table 3), but assimilated more gross energy from herring and squid alone than flagtail alone ($F = 14.46$, $p = 0.005$). No difference occurred among the four test diets either in combination or separated from herring for the AE of dry matter. No difference occurred in the AE of crude protein among the combination diets; however, the assimilation of crude protein from squid alone was lower than that of either herring or flagtail alone ($F = 7.94$, $p = 0.021$). The digestibility of crude fat for the flagtail/herring diet was greater than for the squid/herring and lobster/herring diets ($F = 4.62$, $p = 0.037$); however, the digestibility of crude fat for flagtail/herring and flagtail alone was not greater than for herring alone. No correlation occurred among the daily intakes and AE of gross energy, dry matter or crude protein; however, there was a positive correlation between the daily intake and AE for crude fat ($r^2 = 0.781$).

The digestibility of gross energy (GE) relative to herring decreased by $8.0 \pm 4.7\%$ when flagtail was added to the herring diet, but increased by a mean of $1.37 \pm 3.4\%$ when squid and lobster were added to the diet (Fig. 1). The mean digestibility of dry matter was $14.5 \pm 2.0\%$ higher with the three combination test diets than with herring alone. The mean digestibility of crude protein was also greater with the three combination test diets by $5.1 \pm 2.7\%$, with squid having the least impact. Both squid and lobster had little influence over the mean digestibility of crude fat; however, these two test prey were both low in crude fat (Table 2). The addition of flagtail to the diet increased the digestibility of crude fat in herring by 6.0% (Fig. 1). None of the combination diets were significantly different from each other in how they affected the digestibility of gross energy, dry matter, crude protein, or crude fat.

The test diet with the greatest amount of GE intake was the squid/herring diet, followed by the flagtail/herring diet, the lobster/herring diet and the herring diet (Fig. 2). A consistent pattern of energy loss mirroring that of GE intake occurred among the urinary energy loss, digestible energy (DE) and metabolizable energy (ME) for all of the test diets. This pattern was slightly altered for fecal energy loss, which was greatest for the flagtail/herring diet, followed by the squid/herring diet, the lobster/herring diet and the herring diet. A significant difference occurred for fecal energy loss ($F = 4.89$, $p = 0.012$), DE ($F = 12.62$, $p = 0.000$), urinary energy loss ($F = 15.19$; $p = 0.001$) and ME ($F = 8.21$, $p = 0.008$) among the four test diets. The fecal energy loss for the flagtail/herring diet was greater than both the herring diet ($T = -3.41$, $p = 0.04$) and lobster/herring diet ($T = 5.04$, $p = 0.04$). The DE was greater for the squid/herring diet than the herring ($T = -4.79$, $p = 0.001$) and flagtail/herring ($T = -2.99$, $p = 0.02$) diets, and the lobster/herring diet was greater than the herring diet ($T = -5.05$, $p = 0.001$). The pattern was similar for urinary energy loss which where the squid/herring diet was greater than the herring ($T = 5.01$, $p = 0.04$) and flagtail/herring ($T = -5.64$, $p = 0.03$) diets, but differed in that the lobster/herring diet was greater for both

the flagtail/herring and herring diets (T = -3.70, p = 0.03). Only the ME of the squid/herring diet was higher than any other diet (herring diet: T = -4.66, p = 0.04).

A similar pattern occurred for the ANI and urinary nitrogen loss among the four test diets: squid/herring was the highest, followed by the lobster/herring, flagtail/herring, and herring diets (Fig. 3). Fecal nitrogen loss decreased in proportion to increases in ANI. No consistent pattern was seen for the ANI and NR, although NR was greater in all of the combination diets than it was for herring alone. ANI, fecal nitrogen loss, urinary nitrogen loss and NR among each of the four test diets differed significantly (F = 16.34, p = 0.001; F = 17.92, p = 0.001; F = 15.19, p = 0.001; F = 22.40, p = 0.000, respectively); however, in both the fecal nitrogen loss and NR, the flagtail/herring diet was not different from the lobster/herring diet.

Table 1. Quantities of test diets, herring only (H), flagtail + herring (F/H), squid +herring (S/H), lobster + herring (L/H), and totals (T) fed to Hawaiian monk seals.

Test Prey	Quantity Wet Weight (g)	Calculated Gross Energy Consumed (kcal/day)	Energy from Test Organism (%)
H	H: 2800	H: 4793.2	H: 100.0
	T: 2800	T: 4793.2	
F/H	F: 1400	F: 2168.3	F: 40.0
	H: 1700	H: 3255.5	
	T: 3100	T: 5423.8	
S/H	S: 3100	S: 3041.1	S: 54.4
	H: 1400	H: 2550.5	
	T: 4500	T: 5591.6	
L/H	L: 800	L: 992.1	L: 18.7
	H: 2400	H: 4322.2	
	T: 3200	T: 5314.3	

NOTE: all diet proportions were set to meet an approximate energy of 5000 kcal * day $^{-1}$.
Calculated GE (kcal* g $^{-1}$) = (% Protein x 5.65 kcal* g $^{-1}$+ % Fat x 9.4 kcal* g $^{-1}$+ % Carbohydrate x 4.15 kcal* g $^{-1}$), where % carbohydrate = 100- (% Protein + % Fat + % Ash).

Table 2. Proximate composition and total energy (expressed on dry matter basis) of herring, flagtail, squid, and lobster fed to Hawaiian monk seals.

Test Prey	Combination Diet No.	n	Gross Energy (kcal/g)	Dry Matter (%)	Crude Protein (%)	Crude Fat (%)	Ash (%)	Carbohydrate (%)
Herring	1	2	5.74 ± .02	27.86 ± .180	62.99 ± .50	26.98 ± .29	8.84 ± .10	1.20 ± .13
	2	2	6.18 ± .03	29.67 ± .003	57.63 ± .16	33.10 ± .43	7.18 ± .06	2.10 ± .52
	3	2	5.87 ± .03	28.54 ± .002	57.82 ± .20	32.42 ± .36	8.85 ± .09	0.93 ± .71
	4	2	5.84 ± .01	28.47 ± .004	60.31 ± 1.5	30.34 ± .37	7.76 ± .10	1.58 ± 1.1
pooled		8	5.90 ± .18[a]	28.61 ± .007[a]	59.69 ± 2.41[a]	30.71 ± 2.6[a]	8.03 ± .71[a]	1.45 ± .71[a]
Flagtail	2	2	5.39 ± .01[b]	26.72 ± .003[b]	68.16 ± .23[b]	20.01 ± .05[b]	10.28 ± .16[b]	1.55 ± .52[a]
Squid	3	2	4.84 ± .06[c]	19.13 ± .002[c]	76.07 ± .81[c]	3.89 ± .01[c]	8.10 ± .08[ac]	11.95 ± .87[c]
Lobster	4	2	4.76 ± .07[d]	23.80 ± .002[d]	89.17 ± .51[d]	0.61 ± .01[d]	7.45 ± .07[c]	2.77 ± .49[a]

NOTE: Values are given as the mean ± 1 standard deviation; n refers to the number of subsamples used to obtain the mean and standard deviation from a pool of 18 organisms per test diet.
Combination diet No: 1. herring only, 2. flagtail + herring, 3. squid + herring, 4. lobster + herring.
Values within columns with the same superscript are not significantly different at the $p \leq 0.05$ level.

Table 3. Daily intakes (DI) and assimilation efficiency (AE) of Hawaiian monk seals on four experimental diets, herring only (H), flagtail + herring (F/H), squid + herring (S/H), lobster + herring (L/H), and on test prey, flagtail only (F) squid only (S), and lobster only (L).

DIET	GROSS ENERGY		DRY MATTER		CRUDE PROTEIN		CRUDE FAT	
	DI (kcal)	AE (%)	DI (g)	AE (%)	DI (g)	AE (%)	DI (g)	AE (%)
H:	4475.58	96.09 ± 4.04[ax]	780.08	69.71 ± 21.25[ax]	491.37	89.82 ± 10.47[ax]	210.47	92.60 ± 3.33[abx]
F/H:	5133.09	88.09 ± 2.51[a]	878.50	80.50 ± 0.87[a]	545.65	96.27 ± 0.14[a]	241.80	97.47 ± 1.05[a]
F:	2016.29	73.76 ± 6.82[y]	374.08	83.70 ± 2.05[x]	254.97	81.69 ± 0.29[x]	74.85	96.59 ± 3.39[x]
S/H:	5212.41	94.01 ± 2.60[a]	992.60	80.30 ± 4.06[a]	682.15	91.37 ± 3.17[a]	152.61	90.35 ± 3.13[b]
S:	2866.14	94.05 ± 5.66[x]	593.03	66.87 ± 9.78[x]	451.12	67.17 ± 6.28[y]	23.07	-----
L/H:	4893.97	95.47 ± 0.89[a]	873.70	83.96 ± 2.65[a]	581.93	95.15 ± 1.49[a]	208.47	92.62 ± 1.18[b]
L:	906.11	-----	190.40	-----	169.78	-----	1.16	-----

Figure 1. The digestibility of gross energy, dry matter, crude protein and crude fat for the three test prey, flagtail (F), squid (S) and lobster (L), relative to herring in the Hawaiian monk seal. Digestibility relative to herring was calculated by subtracting the digestibility of the test prey from the digestibility of the herring only (control) diet for each of the proximate analyses. Error bars represent the mean ± 1 standard deviation.

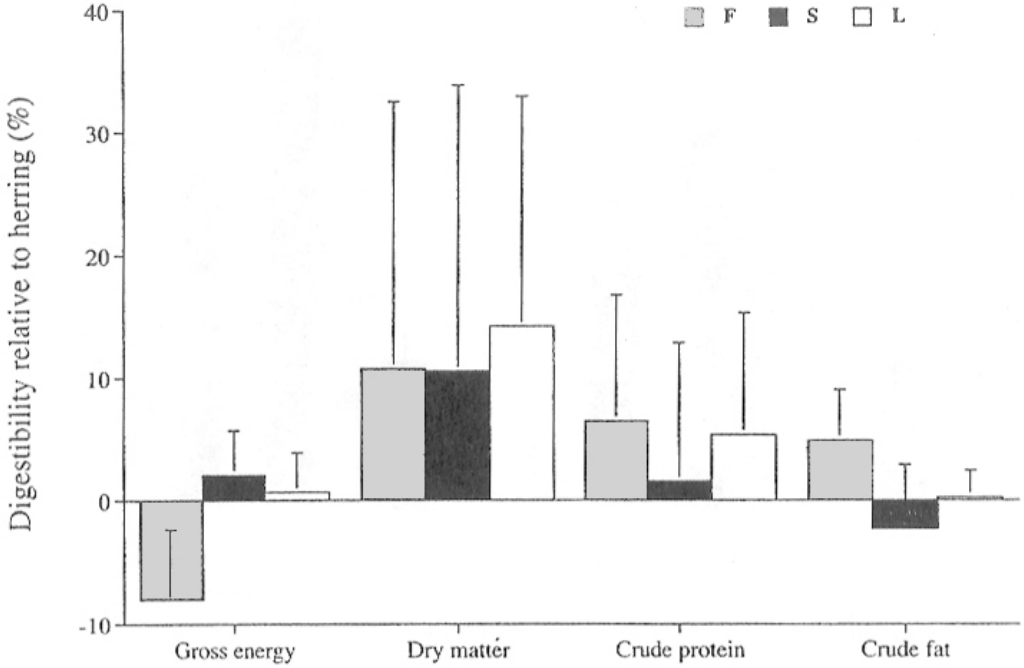


Figure 2. Daily gross energy intake, fecal energy loss, digestible energy, urinary energy loss, and calculated metabolizable energy for Hawaiian monk seals consuming each of the four test diets, herring only (H), flagtail + herring (F/H), squid + herring (S/H), and lobster + herring (S/H). Error bars represent the mean ± 1 standard deviation.

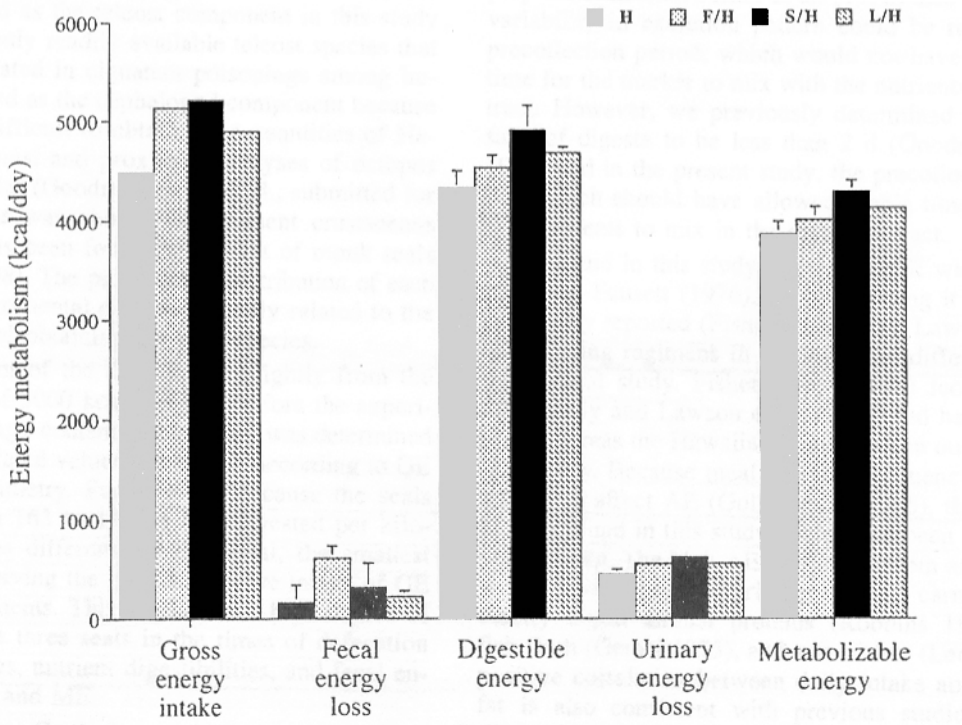
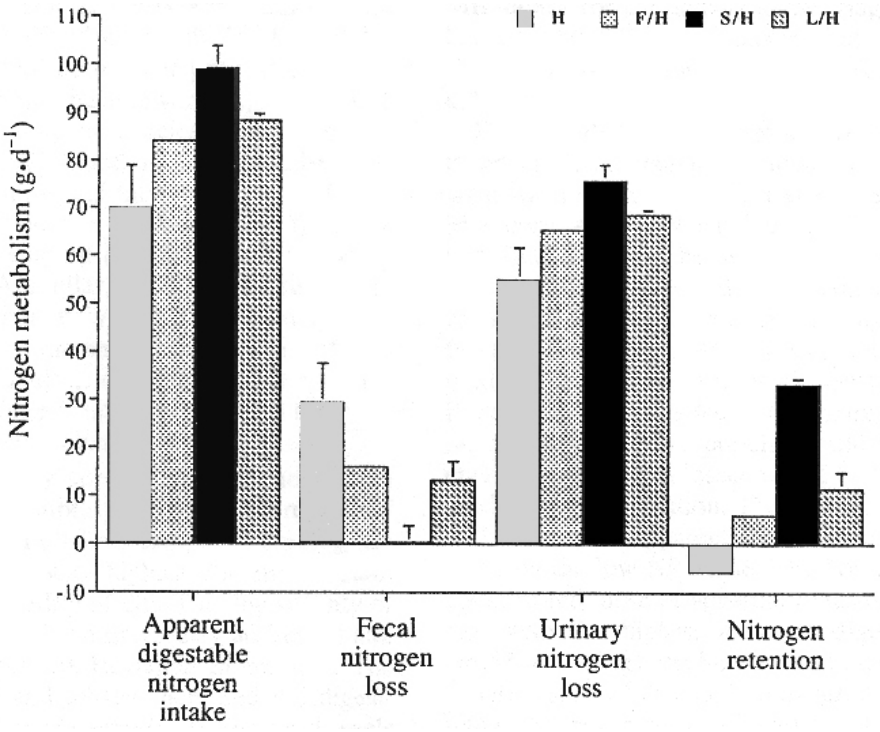


Figure 3. Total apparent digestible nitrogen intake, fecal nitrogen loss, urinary nitrogen loss, and calculated nitrogen retention for Hawaiian monk seals consuming each of the four test diets, herring only (H), flagtail + herring (F/H), squid + herring (S/H), and lobster + herring (L/H). Error bars represent the mean $\pm$ 1 standard deviation.



Discussion

Although herring is not a natural prey item of the Hawaiian monk seal, it was chosen as the control because the seals used in this study have been consuming herring daily since being placed in captivity, and herring is also a major dietary constituent of most captive marine mammals. Flagtail was selected to be the teleost component of this study because it was the only readily available teleost species that has not been implicated in ciguatera poisonings among humans. Squid were used as the cephalopod component because it was logistically difficult to obtain large quantities of Hawaiian octopus species and proximate analysis of both octopus and squid were similar (Goodman-Lowe et al. in review). Lobster was chosen to represent crustaceans because they have been previously found in the diet of monk seals (Goodman-Lowe in press). The percent that each test prey contributed to the experimental diet was directly related to the logistics of obtaining these prey.

The energy content of the diets varied slightly from the target energy level of 5000 kcal, because prior to the experiments, the energy content of each prey was based on calculated values rather than on GE determined by calorimetry. Furthermore, because the seal weights ranged from 163-193 kg, the GE ingested per kg body weight varied for each seal, with the smallest seal receiving the greatest relative intake of GE consistently over the course of the four experiments. This resulted in a high degree of variability within the times and quantities of defecation, the nutrient digestibilities, and the fecal energy loss, urinary energy loss, DE and ME among the three seals.

The defecation patterns, Cr_2O_3 concentrations, and nutrient excretion patterns varied within seal, day and diet, which is consistent with findings by Fisher et al. (1984), Goodman-Lowe et al. (1997) and Lawson et al. (1997). Inadequate mixing of the food with the Cr_2O_3 has been suggested as a possible reason for this variability (Fisher et al. 1992) and is the most likely explanation for the observed nutrient

excretion and Cr_2O_3 variability in the present study, because the Cr_2O_3 was placed in only a few of the test prey for each trial. Fisher et al. (1992) also reported that the variability in excretion patterns could be related to a short precollection period, which would not allow enough time for the marker to mix with the nutrients in the digestive tract. However, we previously determined the rate of passage of digesta to be less than two days (Goodman-Lowe et al. 1997) and in the present study, the precollection period was seven days, allowing ample time for mixing of the marker and nutrients in the digestive tract.

The AE of gross energy for squid in this study was similar to that found by Fausett (1976), but the AE of gross energy for herring was lower than values previously reported (Fisher et al. 1992; Lawson et al. 1997). The feeding regimes of these studies were quite different than in the present study. Fisher et al. (1992) fed walruses three times daily and Lawson et al. (1997) fed harp seals ad libitum, whereas in our study the Hawaiian monk seals were fed once per day. Because meal size and frequency of feeding are known to affect AE (Golley et al. 1965), the lower AE for herring found in this study could have been affected by the feeding regime. The high AE of crude protein and crude fat found is not surprising because carnivores can efficiently digest animal proteins (Robbins 1983), especially fish flesh (Geraci 1975), and animal fats (Leoschke 1959). A positive correlation between the daily intake and AE for crude fat is also consistent with previous studies conducted on pinnipeds (Fisher et al. 1992; Lawson et al. 1997).

The AE of gross energy for flagtail was less than that for either herring or squid even though previous studies have shown the energy digestibility of non-teleost diets fed to marine mammals to be lower than that of teleost diets (Keiver et al. 1984; Fausett 1976). However, neither Keiver et al. (1984) nor Fausett (1976) used low energy teleost prey to compare to the high energy herring diet. In the present study, the flagtail prey represented a low energy teleost prey with significantly less total gross energy and 25% less crude fat for comparison. The presence of indigestible items such as bones and teeth reduce the digestibility of protein (Davison et al. 1978), but, the digestibility of the both herring and flagtail by monk seals were higher than that of squid, which have fewer indigestible hard parts. Protein digestibility may be species-specific for the consumer, because Fisher et al. (1992) found no difference in protein digestibility between herring and clams among walruses. The crude fat AE for squid alone could not be determined from the present study because the amount of crude fat found in the squid was low ($3.89 \pm .01\%$). A similar problem occurred with determining the AEs for lobster separate from herring, where the problem was confounded by the small total amount of lobster (18.7%) used, thus making digestibility by difference difficult to determine. Consequently, we examined nutrient digestibility relative to herring alone.

Although the addition of the three test prey to herring all caused the digestibility of GE to decrease, the measurement of the digestibility of gross energy was based on the whole sample, including the ash content. The % ash intake was highest for the flagtail, whereas the GE digestibility for flagtail was the lowest. The digestibility of minerals in pinnipeds has not been previously addressed and could not be determined for the Hawaiian monk seal. The addition of flagtail, squid and lobster increased the digestibilities of dry matter and crude protein. In the wild, seals eat a highly diverse diet (Goodman-Lowe in press), which probably allows them to digest the nutrients of their prey more efficiently than if they ate large quantities of only one species.

The fecal energy loss for herring in this study was comparable to that found by Keiver et al. (1984) and Ronald et al. (1984). Although squid has a lower digestibility and therefore higher fecal energy loss due to its chitinous beaks (Keiver et al. 1984), in this study the flagtail had the highest fecal energy loss. This could be related to the size and indigestibility of its scales and bones.

The DE for herring was similar to that found by Lawson et al. (1997). DEs are affected by energy density (Maiorino et al. 1986; Martensson et al. 1994), where a higher energy density of food consumed results in higher DEs. This did not occur in the present study, which is similar to findings reported by Fisher et al. (1992); however, the energy densities of prey ingested by the Hawaiian monk seal were very

similar to each other and each combination diet contained herring. Furthermore, the lower DEs reported by Keiver et al (1984) and Martensson et al. (1994) occurred when the animals were fed crustaceans with the chitinous exoskeleton intact, whereas in this study, only lobster tail meat was used.

The urinary energy losses increased with increases in GE and were similar to values reported by Keiver et al. (1984) and Ronald et al. (1984). In addition, seals fed diets with higher apparent digestible nitrogen intakes (squid/herring and lobster/herring diets) had higher urinary energy losses, also similar to Keiver et al (1984). With the exception of the flagtail/herring diet, urinary energy losses were higher than fecal energy losses, which also corresponds to studies by Keiver et al. (1984).

Food that is higher in protein but lower in fat provides more metabolizable energy. In this study, all of the test prey were higher in protein and lower in fat than herring, and all provided significantly higher MEs than the herring diet alone. In addition, MEs for herring, flagtail/herring, squid/herring and lobster/herring fell within the range (77.94-86.16%) reported by others (Keiver et al. 1984; Ronald et al. 1984).

Seals fed diets with higher apparent digestible nitrogen intakes had correspondingly lower fecal nitrogen losses, contrary to that found by Keiver et al (1984), who found a positive correlation between apparent digestible nitrogen intake and fecal nitrogen loss. This may be related to the balance of amino acids within the test prey and their relative digestibilities. The urinary nitrogen losses positively corresponded to the apparent digestible nitrogen intakes for all of the test diets, which was similar to results of other pinniped studies (Keiver et al. 1984; Ronald et al. 1984). Because the test prey fed to the monk seals was low in both fat and carbohydrate, protein would be the main source of energy, resulting in high nitrogen losses due to the by-products of deamination. The herring diet provided the seals with the lowest apparent digestible nitrogen intake, resulting in the lowest NR. NR trends for the other test diets mirrored those of the apparent digestible nitrogen intakes, with the highest apparent digestible nitrogen intake test diet (squid/herring) resulting in the highest NR.

This study indicates the importance of examining assimilation efficiency of combination diets for those species of pinnipeds that consume a wide variety of prey, because the Hawaiian monk seal digests different prey and different combinations of prey with varying efficiency. Further studies should concentrate on determining the AEs and MEs of combinations of natural prey types, including teleosts, and should be conducted on juveniles and adults of sexes.

Acknowledgments

We thank the staff and volunteers at the Waikiki Aquarium for their help and support in the logistics of this study, along with C. Lowe, P. Ewanchuk, and A. Cheroske and the many people who volunteered their time to help in the collection process. We thank W. Gilmartin, D. Greenfield, R. Kinzie, and E. Reese and R. Niino-Dupont for reviewing this manuscript and R. Niino-DuPont for running the GE analyses. This project was funded by Waikoloa Marine Life Fund, and, in part, by the National Marine Fisheries Service, Honolulu and the Sea Grant College Program at the University of Hawaii (Institutional Grant No.NA36RG0507, Publication UNHI-SEAGRANT-JC-98-28). The views expressed herein are those of the authors and do not reflect the views of NOAA or any of its subagencies.

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