

Fatty acid composition of sleeper shark (*Somniosus pacificus*) liver and muscle reveals nutritional dependence on planktivores

L. Schaufler, R. Heintz, M. Sigler, and L. Hulbert

NOAA Auke Bay Laboratory
11305 Glacier Hwy
Juneau AK 99801
Lawrence.Schaufler@noaa.gov

Abstract:

Sleeper sharks (*Somniosus pacificus*) are large elasmobranchs found in the temperate and boreal portions of the north Pacific. At high latitudes they are frequently observed near the surface and in littoral areas. They are known to consume fast swimming prey such as salmon and have been identified as potential predators of pinnipeds, many of which have rapidly declining populations in the north Pacific. The objective of this study was to identify energy sources consumed by sleeper sharks by examining their fatty acid compositions. We sampled the triacylglycerols (TAG) from the liver and muscle of 15 sleeper sharks and compared the compositions to those of potential prey, as identified by stomach contents. TAG comprised approximately 73% and 78% of the muscle and liver lipids, respectively. Monounsaturated and saturated fatty acids dominated the muscle TAG, accounting for more than 86% of all fatty acids examined. Similarly, saturated and monounsaturated fatty acids accounted for 95% of the liver TAG, of which 85% was saturated. Both tissues contained high concentrations of C22:1n11 and C20:1n11, fatty acids derived from the alcohols of calanoid copepods. Comparisons of the shark fatty acid compositions with those of prey suggest cetacean blubber, Pacific herring, yellowfin sole, and walleye pollock are important energy sources. These results are consistent with other reports describing stomach contents and suggest that sleeper sharks are not significant predators of pinnipeds.

Introduction:

The frequency of marine mammal predation by sleeper sharks is not known but is of interest as a result of the opposing directions of marine mammal and sleeper shark population trends in the northern Gulf of Alaska. Populations of the Pacific sleeper shark *Somniosus pacificus* have been increasing in the North Pacific since the late 1980's while populations of pinnipeds have generally been declining. The loss of more than 80% of the Steller sea lion population in the Aleutian Islands and northern Gulf of Alaska prompted U.S. fishery managers to examine the evidence for Pacific sleeper shark predation on pinnipeds. Direct evidence for pinniped predation by sleeper sharks is scant (Hulbert et al., 2002), however adults are apparently capable of consuming pinnipeds as demonstrated by the presence of marine mammal tissues in their stomachs, as well as by their large size and geographic distribution. Adult sleeper sharks can reach a total length in excess of 7 m and their distribution coincides with that of pinniped rookeries, particularly those of Steller sea lions. Moreover, sleeper sharks have been known to consume fast swimming prey such as salmon (Yang and Page, 1999). The limited information available prompted fishery managers in the US to study sleeper shark diets in greater detail (DeMaster and Atkinson, 2001).

The large size of sleeper sharks makes them difficult to sample, limiting attempts to understand the importance of pinnipeds to their diet through stomach content analysis. For example, knowledge of sleeper shark diets in the northern Gulf of Alaska is derived from the analysis of a total of 211 animals in two reports. The first of these reports (Yang and Page, 1999) indicated that at least 67% of the stomach content mass collected from 11 Pacific sleeper sharks was comprised of arrowtooth flounder (*Artheresthes stomias*). The second report (Sigler et al., 2005), found arrowtooth flounder to contribute less than 4% of the total mass of stomach contents in 200 sharks. In contrast, it reported that cetacean blubber and gadids each comprised more than 30% of the stomach content mass. Consequently, the importance of marine mammals in the diets of Pacific sleeper sharks is equivocal.

Examining the energetic contributions of different prey to diets can lead researchers to a better understanding of the importance of various prey types to sleeper sharks. Stomach content analysis is biased by different rates at which hard parts are

retained in the guts of predators. The fatty acid compositions of sleeper shark tissues provide a complementary picture of sleeper shark diets, because prey lipids are absorbed in proportion to their rate of consumption. In addition, stomach content analysis serves more as a single snapshot of the diet, while the fatty acid composition integrates diet components over a significantly longer period. Lipids are a primary energy source for animals, and understanding the sources of lipid in the diet of predators provides a basis for identifying the relative energetic importance of different prey to a predator.

The objective of this report is to describe the diets of Pacific sleeper sharks by comparing their fatty acid compositions to that of potential prey. In addition we assess the nutritional value of prey found in sleeper shark diets to determine their primary sources of energy. These data are complementary to those reported by Sigler et al. (2005) and are ultimately aimed at understanding the potential role of sleeper sharks as predators of marine mammals such as Steller sea lions. Consequently, sharks were collected from areas near Steller sea lion rookeries at a time when juvenile sea lions should be vulnerable to predation.

Materials & Methods:

Sample Collection & Preparation:

Pacific sleeper sharks were collected for analysis using longline gear in the northern Gulf of Alaska near Kodiak Island, in the vicinities of three Steller sea lion rookeries: Seal Rocks, Outer (Pye) Island, and Marmot Island (Figure 1). Stomach contents were examined for 99 sharks and reported in Sigler et al. (2005), where detailed sampling procedures are described. All sharks were sexed, measured (by pre-caudal length), and weighed before stomach contents were removed and identified. Liver and muscle were sampled from 27 of these sharks and immediately frozen for laboratory analysis. In addition, blubber samples recovered from the stomachs of 6 sharks were retained for fatty acid analysis. The specific identities of these blubbers were unknown, hence they are referred to as blubbers 1 through 6.

Energy Contribution to Sleeper Sharks Diets:

We combined the data describing the composition of the diets (Sigler et al., 2005) with data describing the lipid and energy content of prey (Vollenweider, 2005) to identify the most important energy and lipid sources to Pacific sleeper sharks. We estimated the relative contributions of energy and lipid to sleeper shark diets using the total mass of prey recovered from the shark stomachs with the following equation:

$$R_i = \left(M_i V_i / \sum M_i V_i \right) \times 100 \quad (1)$$

Where R_i is the relative value of the i^{th} prey type expressed as a percentage; M_i is the total mass of the i^{th} prey type observed in the stomach contents of 99 sleeper sharks; and V_i is the nutritional value, either in kJ/g tissue or mg lipid/g tissue. Proxy data were used when no data were available to describe prey, such as unidentified blubber or unidentifiable fish remains. We assumed a blubber lipid content of 75% based on values for pilot whale blubber certified by the U.S. National Institute for Standards and Technology (NIST). Assuming the remainder of the mass was water, this yielded a mass-specific energy content of 27 kJ/g. For fish, we used the mean of the identifiable species weighted by their proportion of the total mass.

Lipid Extraction:

Tissues were homogenized and lipid content was extracted using a Dionex Accelerated Solvent Extractor (ASE), employing a modified Folch method (Christie, 2003). Wet sample homogenate was combined with Hydromatrix drying agent and loaded into ASE extraction cells with sand as a masticating agent. 2:1 (v/v) chloroform/methanol with 0.01% butylated hydroxytoluene (BHT) was used as the solvent at 1200 PSI and 120 °C, with two extraction cycles. Filtrates were evaporated to a volume less than 1 ml using a Yamato RE540 roto-evaporator, following liquid-liquid extraction as described by Christie (2003). Lipid extracts were diluted to 1.000 ml with chloroform, and lipid content was determined gravimetrically using 0.500 ml of the extract evaporated to dryness. Quality assurance samples were included with each sample batch, including a replicate sample, method blank containing no tissue, and an

in-house herring reference sample previously characterized for proximate composition. Shark lipids were fractionated into lipid classes by high pressure liquid chromatography (HPLC) and the triacylglycerol (TAG) fraction retained for fatty acid analysis.

Fatty Acid Analysis:

Fatty acids of whole lipid from the blubbers and shark TAG were transesterified to fatty acid methyl esters (FAMES) using Hilditch reagent, as described in Christie (2003) except that hexane was used as a solvent instead of toluene. C19:0 and C23:0 fatty acids were added as an internal standard and a surrogate standard for recovery calculations, respectively, prior to transesterification. Purified FAMES in hexane were evaporated under nitrogen to a final volume of approximately 1 ml, and a FAME internal standard (C21:0) was added before injection into an HP 6890 gas chromatograph (GC) with an HP 5973 mass-selective detector (MSD). FAMES were resolved using a Supelco (Bellefonte, PA) (30 m x 0.25 mm) Omegawax-250 fused silica capillary column with a temperature gradient elution program. The Supelco FAME-37 mixture of purified FAMES was used to construct 5-point calibration curves to quantify FAME concentrations. Blank, duplicate sample, and in-house reference sample spectra were used for quality assurance (QA) evaluations. The fatty acids identified are listed in Table 1.

Statistical Analyses:

We compared the fatty acid compositions of the shark tissues with that of their potential prey by examining the distances between sharks and potential prey using multivariate analysis. Distances between the tissues and potential prey ($D_{u-U}^{\frac{1}{2}}$) were calculated as:

$$D_{u-U} = \left[\sum_{j < n} \sum_{i < j} \left(\text{Ln} \left(\frac{u_i}{u_j} \right) - \text{Ln} \left(\frac{U_i}{U_j} \right) \right)^2 \right]^{\frac{1}{2}} \quad (2)$$

Where \mathbf{u} is a vector of n fatty acids describing a sample such that $\sum_{i=1}^n u_i = 1.0$ and all

$u_i > 0$. \mathbf{U} is a similarly composed vector describing the sample to be compared. The distances between each of the tissues and potential prey were plotted using the average linkage-distance clustering algorithm. This approach maintained the structure of the dataset, while revealing which prey had compositions most similar to that of the sleeper shark tissues.

Fatty acid compositions of potential prey were obtained from a variety of sources. We relied on our unpublished values for northern fur seals and chum salmon fry. Literature values were used for remaining prey items. Harbor seal data used were from Iverson et al. (1997), salmon shark data from Jayasinghe et al. (2003), and killer whale data from Worthy and Abend (1998). Data for all the remaining prey were taken from Iverson et al. (2002). Use of different reports required that only fatty acids that were common to all the data sets could be used. Consequently, the distance measures were based on the compositions¹ of: C14:0, C15:0, C16:0, C17:0, C18:0, C18:1n9, C18:1n7, C18:2n6, C18:3n3, C20:1n11, C20:1n9, C20:4n6, C20:5n3, C22:1n11, C22:1n9, C22:5n3, C22:6n3, and C24:1n9. These fatty acids accounted for more than 90% of the reported mass in all of the tissues and prey examined. Reported concentrations were renormalized to conform with the requirements of the distance equation (2).

Results:

Nutritional Value of Shark Prey:

Cetacean blubber was the most important source of energy and lipid to sleeper shark diets. A total of 92 kg of prey were recovered from 99 sleeper shark stomachs (Sigler et al., 2005). Prey items included six fish species, octopus, unidentified teuthoid squids, and cetacean blubber. Cetacean blubber and gadids (Pacific cod and walleye pollock) accounted for more than 60% of mass recovered (Figure 2). Use of the contribution measure (equation 1) revealed that more than 75% of the energy ingested by these sharks was derived from cetacean blubber (Figure 3). Gadids represented the most important source of non-mammalian energy, accounting for more than 9%, and

¹ We employ the following nomenclature for fatty acids: CX:YnZ where X is the number of carbons in the chain, Y the number of double bonds and Z the location of the first double bond counting from the methyl end. Note that fatty acids can be assigned to families based on the position of the first double bond, so we often refer to n3 or n11 families of fatty acids.

squid accounted for less than 1%. The large contribution of cetacean tissues to energy intake resulted from their high lipid contents. More than 90% of the lipid ingested by the sleeper sharks was derived from cetacean tissue (Figure 4). Gadids accounted for less than 4% of the ingested lipid and all other species combined accounted for less than 5%.

Relation between the fatty acid compositions of shark tissues and prey:

The fatty acid compositions of the shark livers and muscles are given in Table 1. Livers and muscles were distinct in composition with livers having relatively high concentrations of monounsaturated fatty acids and the muscles having higher concentrations of polyunsaturated fatty acids, particularly C20:5n3 and C22:6n3. In addition, both tissues had high levels of C20:1n11 and C22:1n11 fatty acids, which comprised approximately 15% of the total mass. Table 2 shows the fatty acid composition used in the distance measure calculations for the unidentified blubber samples acquired from the shark stomachs. There were apparently two types of blubbers recovered from the shark stomachs. Blubbers 4 and 5 were distinct from the rest as indicated by their relatively high concentrations of C20:1n11 and C22:1n11 and low concentrations of n3 polyunsaturates.

Comparison of the distances between fatty acid compositions revealed a high degree of similarity (i.e. small distance) between the shark tissues and blubbers 4 and 5. Inspection of the dendrogram shown in Figure 5 reveals a distinct separation between the shark liver and muscle compositions, however these tissues are more similar to each other than to any other group. The next closest cluster comprises three samples, blubbers 4 and 5 and the muscle from shark specimen #89, whose stomach contained only octopus and salmon. The next closest cluster contains walleye pollock, herring, squid, and capelin, which are all zooplanktivores. The next two clusters include eulachon and the remaining marine mammal samples. The distances depicted in Figure 5 are the mean distances between clusters as estimated by the distance equation (2).

Discussion:

Diet data collected in August 2001 from the northern Gulf of Alaska indicate that Pacific sleeper sharks have highly variable diets, but derive most of their energy from cetacean blubber. While only 12% of the stomachs examined contained cetacean tissues, the blubber accounted for more than 75% of the energy ingested by the sleeper sharks. Moreover, the average mass of the blubber pieces recovered was more than 2 kg, indicating that when sleeper sharks encounter a source of blubber they can ingest large amounts. This is important to the sharks, because each piece of blubber provides nearly ten times the amount of energy in a similarly sized walleye pollock.

The relatively large amounts of fat ingested by sharks when they consume blubber accounts for the importance of cetacean blubber in the fatty acid analyses. Twenty prey items were identified in the four closest clusters to the shark tissues and marine mammal blubber comprised 14 of these. However, it is important to note that the sharks were more similar to blubber samples 4 and 5 than they were to the remaining blubber tissues. In addition, blubbers 4 and 5, along with one of the shark muscle samples, comprised the first cluster of samples that was not completely made of shark tissues.

Examination of the species compositions of the clusters reveals the reliability of the multivariate method for separating groups. Fish species appear in three main clusters, which are exclusive of those comprising the unknown blubbers, phocid, and otariid seals. Killer whales and salmon sharks appear as distinct, independent clusters. In addition, the clusters that are closest together are those describing the salmon sharks, which represent mean values for males and females and are therefore less variable than individual measurements. The sleeper shark individuals are the clusters that have the next greatest similarity. Also, note that while the killer whales are most similar to each other than any other species, they are relatively distant on the overall scale. This is because one killer whale sample represents the mean for mammal-eating transients while the other is the average composition of fish-eating resident whales. Thus the distance measure and clustering algorithm consistently associates conspecific compositions first. Consequently, it appears that the fatty acid compositions of blubbers 4 and 5 are difficult to distinguish from those of the shark tissues.

The cluster involving fish nearest the shark tissues includes capelin, herring, pollock, and the commander squid (*Berryteuthis magister*). Each of these are typical forage species for the northern Gulf of Alaska and form the link between mesozooplankton and piscivores. Consequently, they share a dependence on calanoid copepods, causing them to have high levels of C22:1n11 and C20:1n11, fatty acids derived from the waxes of Pacific calanoids (Saito et al., 2000). The proximity of these zooplanktivores to blubbers 4 and 5 and the shark tissues indicates that species in these clusters must forage at a trophic level near that of the copepod energy source. Moreover, the relative distance between these zooplanktivores and the piscivorous pinnipeds suggests that the blubbers associated with the seal cluster are from piscivorous cetaceans. Thus it appears that the sleeper sharks derive important amounts of energy from filter-feeding baleen whales rather than piscivorous whales, explaining the presence of gray whale blubber among the stomach contents described by Sigler et al. (2005).

There are little data describing the fatty acid compositions of cetaceans in the northern Gulf of Alaska. However, reports of fin whale blubber fatty acids from the Atlantic indicate high concentrations of C22:1n11 and C20:1n9 (reviewed in Ackman, 1989), which are fatty acids associated with the waxes of Atlantic calanoids (Henderson and Tocher, 1987). Similarly, the combined concentrations of C22:1n11 and C20:1n9 can account for more than 20% of the fatty acids in Atlantic minke whale blubbers (Moller et al., 2003). Descriptions of some odontocetes, including bottlenose dolphins, harbor porpoise, beluga and sperm whales suggest low concentrations of these fatty acids and high concentrations of C16:1n7 (reviewed by Ackman, 1989), consistent with harbor seals (Iverson et al., 1997) and sea lions (Beck et al., 2005) from the northern Gulf of Alaska.

The dependence of Pacific sleeper sharks on baleen whale blubber as an energy source is consistent with the relative abundance of baleen whales in the northern Gulf of Alaska. Stock assessments of whales in the region suggest that the biomass of fin whales alone is more than an order of magnitude higher than that of the combined biomasses of all the toothed whales (NOAA, 2005). The most abundant of the toothed whales in the region are Dall's and harbor porpoises. It is important to note that Sigler et

al. (2005) found that the blubbers found in sleeper shark stomachs had been scavenged, indicating that carcasses of deceased whales are central to the energy budgets of sleeper sharks. While the probability of encountering a porpoise carcass is higher on the basis of the number of individuals in the northern Gulf of Alaska, a single fin whale carcass is likely to feed many sharks.

The fatty acid analysis described demonstrates the similarity of Pacific sleeper sharks to those individuals that forage low on the food chain, particularly those that acquire lipid reserves ultimately produced by calanoid copepods. Apparently these large sharks effectively scavenge copepod-based energy after it has been concentrated in the carcasses of baleen whales. While examination of sleeper shark stomach contents reveals a large variety of prey types, it appears that these non-cetacean prey items represent “snacks” consumed between feasts on whale carcasses.

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Table 1. Average fatty acid compositions (% of total TAG fatty acids) of sleeper shark liver (n=15) and muscle (n=13) tissues collected in the northern Gulf of Alaska in August 2001. Trace denotes < 0.01%.

Fatty Acid	Liver	Muscle
14:0	1.76 +/- 0.16	1.79 +/- 0.19
14:1n5	Trace	0.04 +/- 0.01
15:0	0.16 +/- 0.02	0.26 +/- 0.06
16:0	11.18 +/- 0.37	12.81 +/- 0.46
16:1n7	6.71 +/- 0.37	5.45 +/- 0.24
17:0	0.10 +/- 0.01	0.16 +/- 0.02
17:1n7	0.32 +/- 0.03	0.31 +/- 0.03
18:0	2.85 +/- 0.17	2.27 +/- 0.24
18:1n11	Trace	0.25 +/- 0.04
18:1n9	30.67 +/- 0.50	24.34 +/- 0.37
18:1n7	6.43 +/- 0.15	5.45 +/- 0.13
18:2n6	1.06 +/- 0.14	1.40 +/- 0.23
18:3n6	0.07 +/- 0.01	0.12 +/- 0.01
18:3n3	0.37 +/- 0.03	0.38 +/- 0.03
20:0	0.12 +/- 0.02	0.12 +/- 0.02
20:1n11	9.04 +/- 0.34	8.95 +/- 0.28
20:1n9	5.89 +/- 0.26	5.79 +/- 0.30
20:2n6	0.39 +/- 0.03	0.54 +/- 0.06
20:3n6	0.11 +/- 0.01	0.14 +/- 0.01
20:4n6	0.70 +/- 0.03	1.37 +/- 0.08
20:3n3	0.16 +/- 0.01	0.20 +/- 0.02
20:5n3	3.00 +/- 0.16	6.98 +/- 0.17
22:0	0.03 +/- 0.003	0.02 +/- 0.01
22:1n11	7.66 +/- 0.37	6.58 +/- 0.33
22:1n9	1.69 +/- 0.10	1.38 +/- 0.08
22:2n6	0.06 +/- 0.01	0.04 +/- 0.01
22:5n3	2.61 +/- 0.12	2.23 +/- 0.14
24:0	Trace	Trace
22:6n3	5.06 +/- 0.26	9.64 +/- 0.35
24:1n9	1.77 +/- 0.12	0.98 +/- 0.05
Saturates	16.21 +/- 0.62	17.44 +/- 0.98
Monounsats	70.20 +/- 0.70	59.51 +/- 0.85
PUFAs	13.59 +/- 0.39	23.05 +/- 0.52
w3	11.20 +/- 0.37	19.43 +/- 0.56
w6	2.39 +/- 0.13	3.62 +/- 0.15
w3/w6	4.85 +/- 0.29	5.49 +/- 0.27

Table 2. Fatty acid compositions (% of total fatty acids) of blubbers collected from the stomachs of sleeper sharks in the northern Gulf of Alaska in August 2001.

Fatty Acid	Blubber1	Blubber2	Blubber3	Blubber4	Blubber5	Blubber6
14:0	3.89	2.74	5.62	4.79	5.28	7.92
15:0	0.40	0.30	0.54	0.54	0.42	0.65
16:0	8.63	7.12	16.30	8.61	7.86	17.12
16:1n7	13.26	13.02	13.38	5.60	5.66	17.23
17:0	0.49	0.22	0.57	0.46	0.43	0.51
18:0	6.11	6.42	4.91	3.79	4.43	4.04
18:1n9	22.43	19.98	15.33	22.72	25.19	17.12
18:1n7	8.83	9.39	5.60	3.08	4.88	6.99
18:2n6	1.29	0.68	0.62	1.82	1.29	0.73
18:3n3	0.17	0.22	0.21	0.92	0.63	0.19
20:1n11	1.71	3.42	4.16	15.93	10.79	2.26
20:1n9	2.82	2.75	4.92	3.78	6.09	2.85
20:4n6	3.96	3.56	1.26	0.59	0.64	1.24
20:5n3	9.69	3.13	10.09	2.96	2.15	9.33
22:1n11	0.49	0.94	2.34	13.40	9.36	2.00
22:1n9	1.02	0.91	0.63	2.77	2.28	0.47
22:5n3	10.47	8.75	7.62	3.35	8.14	5.44
22:6n3	3.62	16.13	5.54	3.86	3.79	3.66
24:1n9	0.73	0.32	0.36	1.03	0.69	0.25

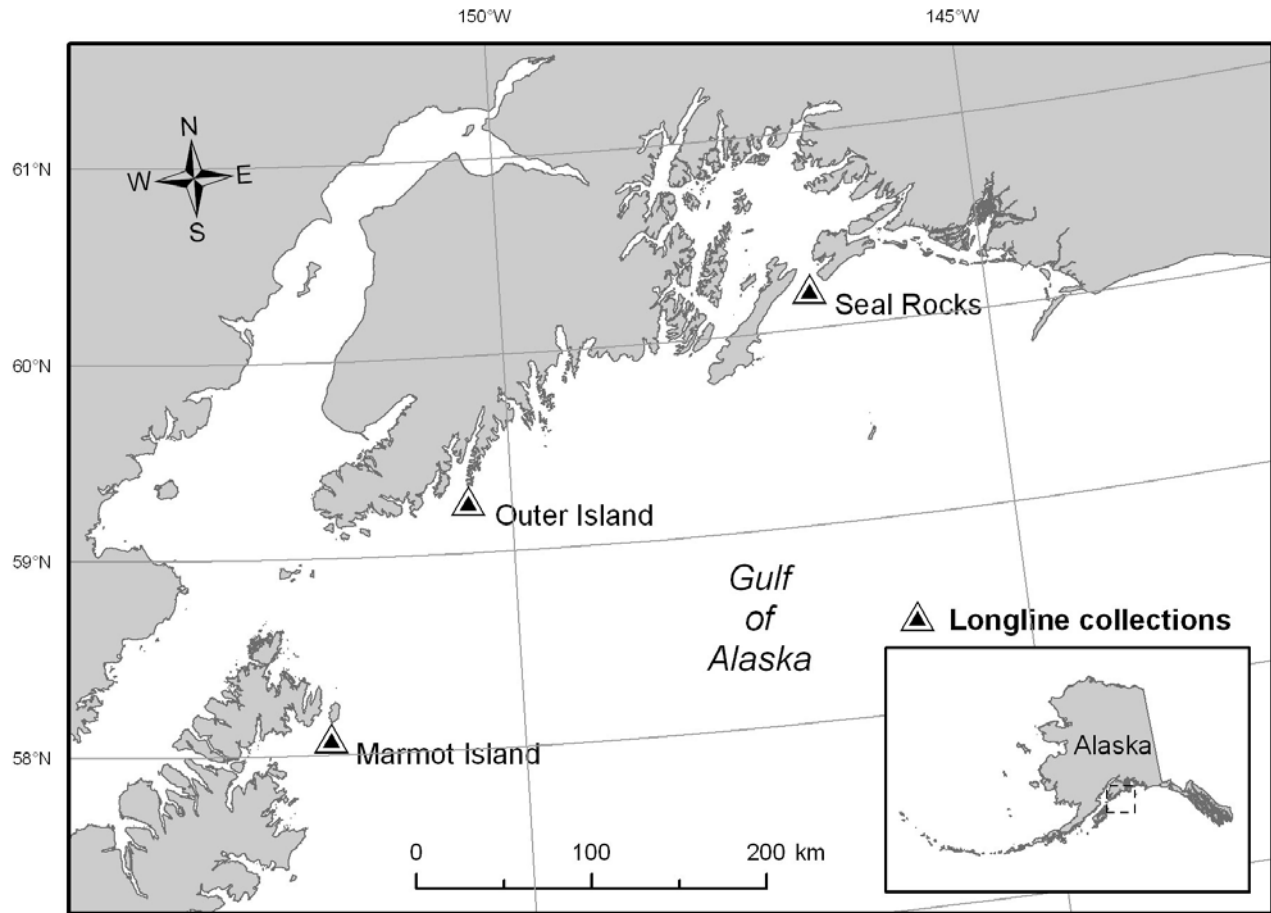


Figure 1. Longline collection locations for Pacific sleeper sharks in the Gulf of Alaska in August 2001.

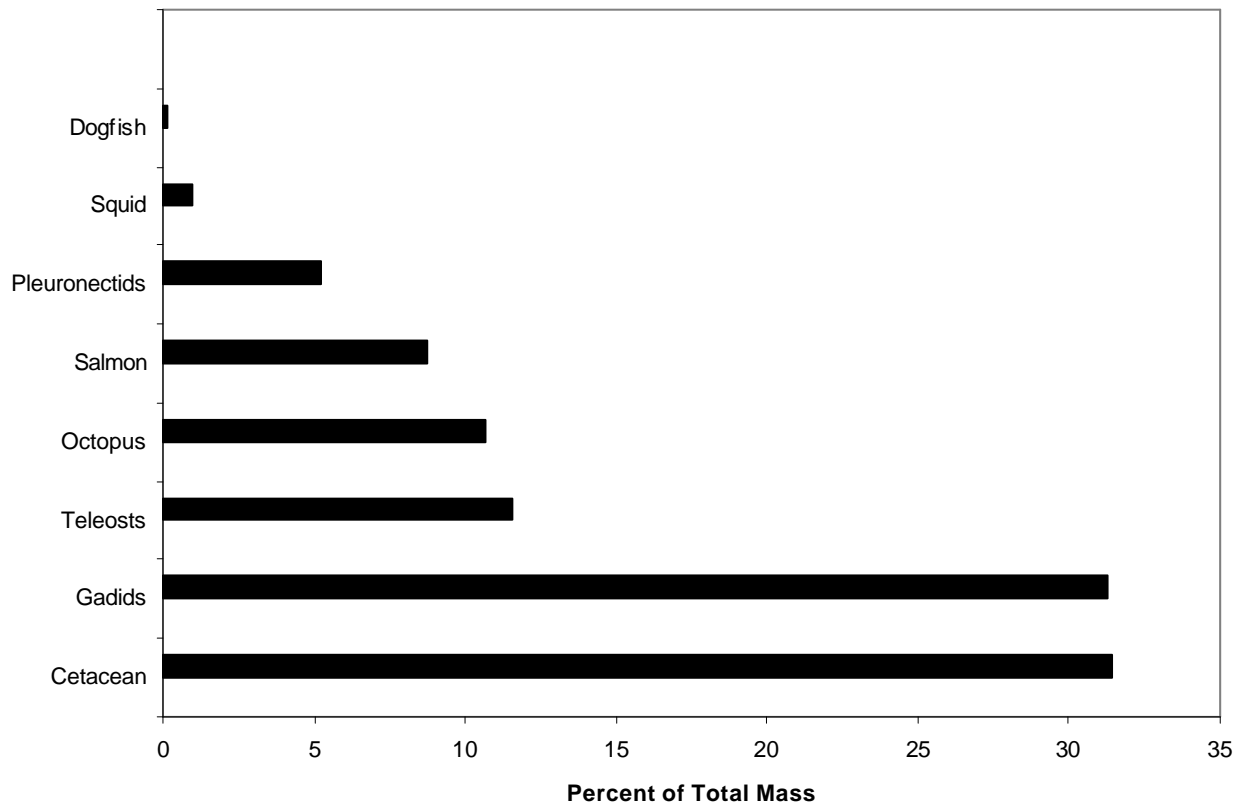


Figure 2. Composition of sleeper shark diets expressed as the percent of total mass observed. (Data from Sigler et. al., 2005)

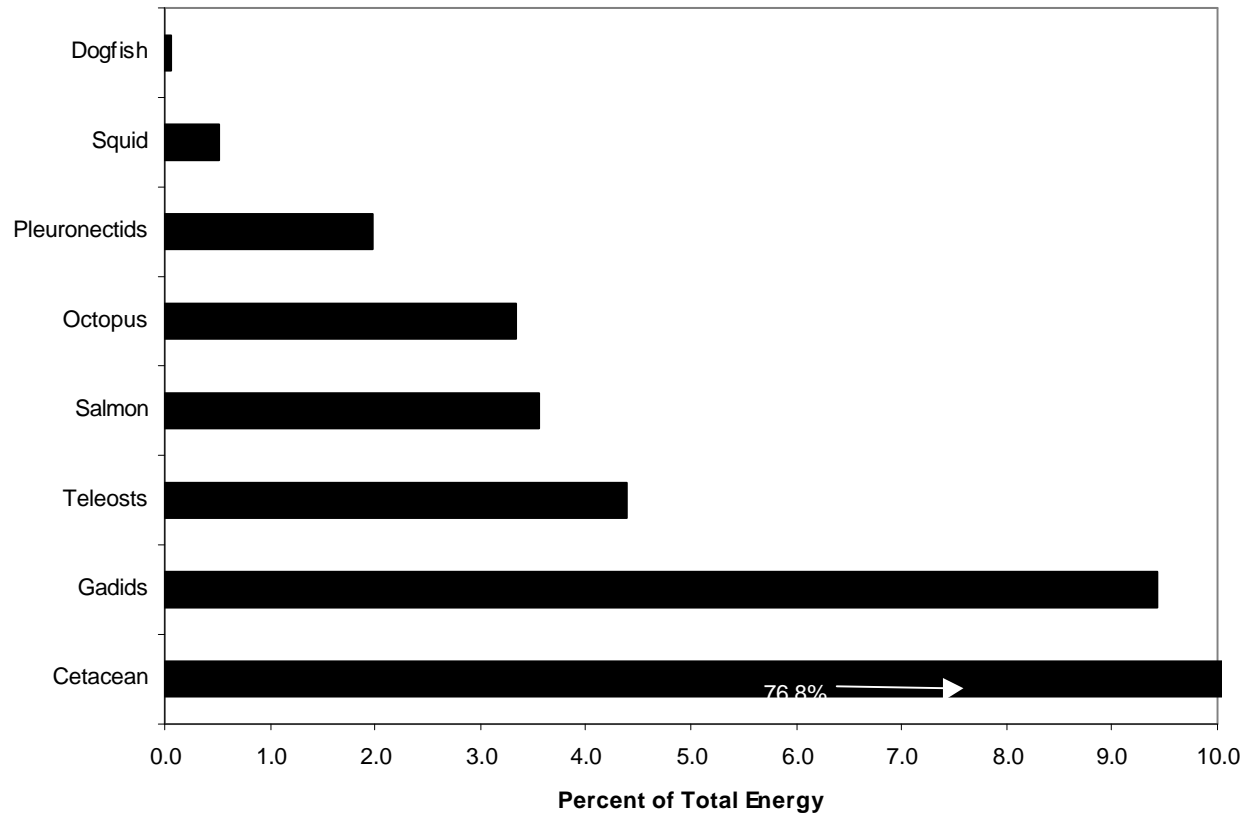


Figure 3. Energy contributions of different prey types to sleeper shark diets. Note the value for cetacean blubber (76.8%) exceeds the scale depicted in the figure.

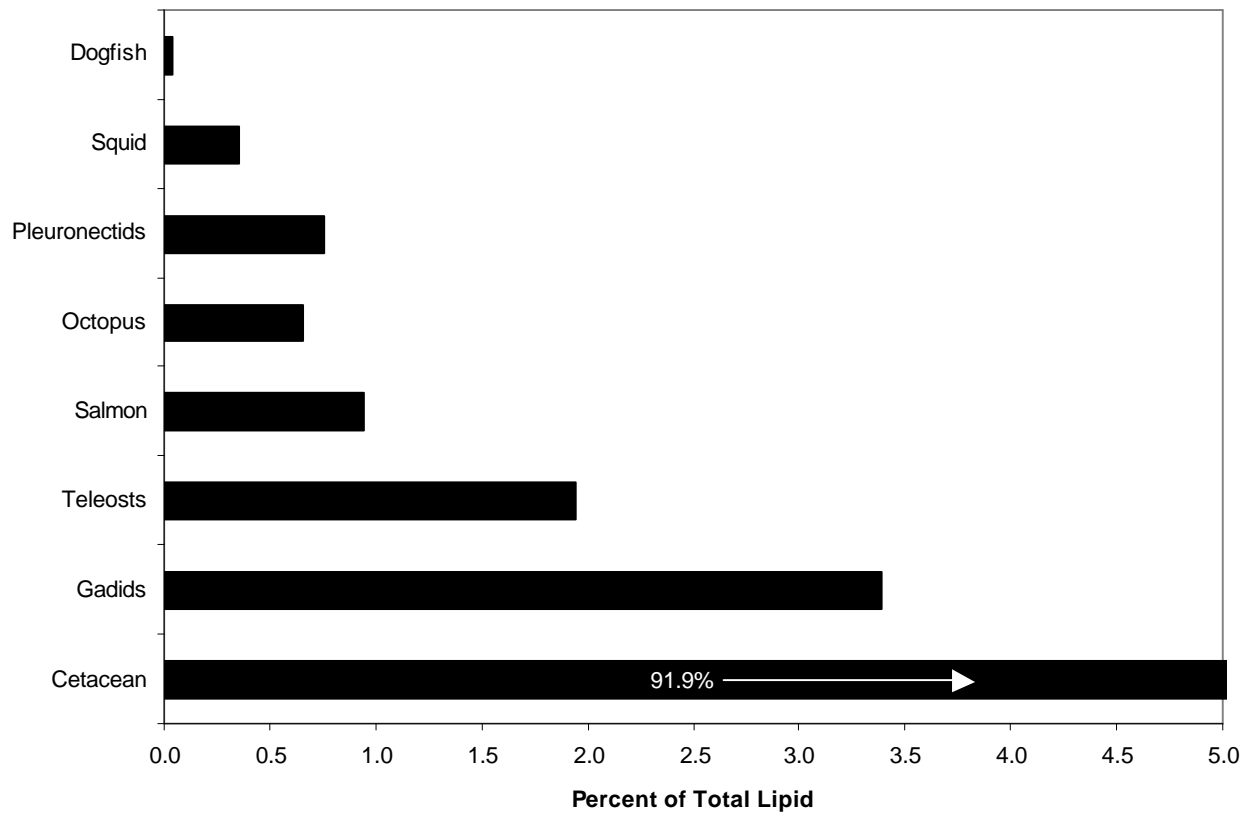


Figure 4. Contributions of different prey types to the lipid content of sleeper shark diets. Note that value for cetacean blubber (91.9%) exceeds the scale depicted in the figure.

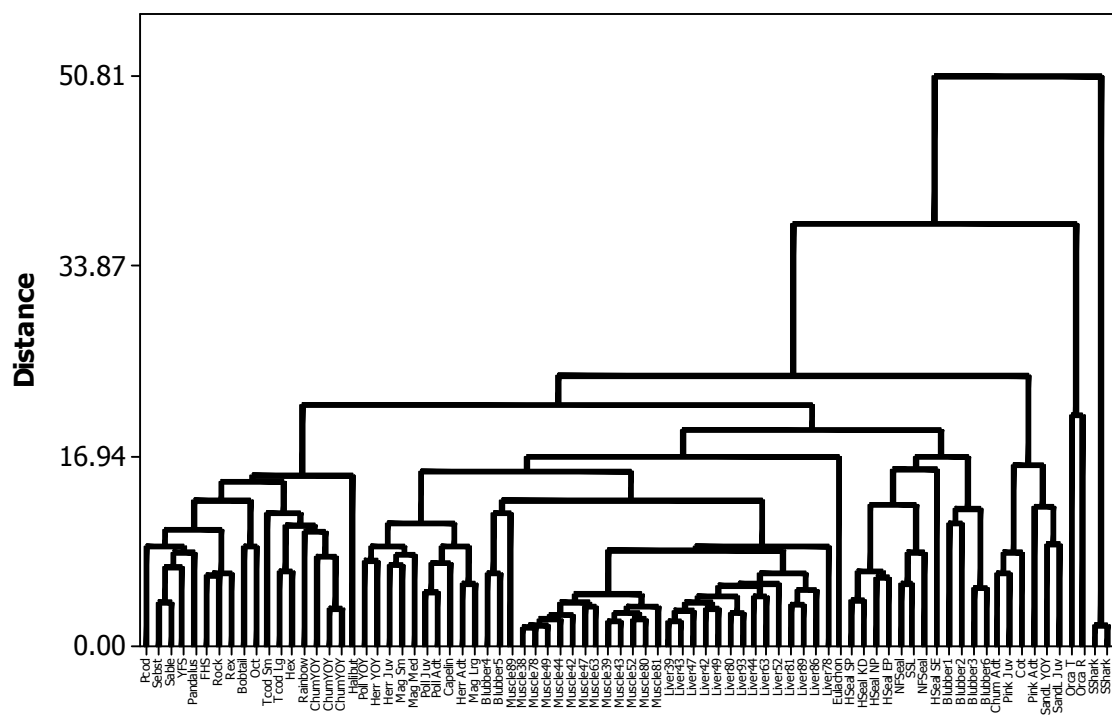


Figure 5. Dendrogram depicting distance relationships between the fatty acid compositions of sleeper shark triacylglycerols (TAG) and the whole lipid of potential prey. Clusters are based on the average distance to the nearest neighboring cluster, with distances calculated as described using equation 2. Abbreviations: Blubber# = sampled sleeper shark stomach content blubber (specimen #); Bobtail = bobtail squid; Chum (Adt, YOY) = chum salmon (adult, young-of-the-year); Cot = *Cottidae* (sculpin); Eulachon = eulachon; FHS = Flat head sole; Halibut = Pacific halibut; Herr Juv = Pacific herring (juvenile); Herr YOY = Pacific herring (young-of-the-year); Hex = *Hexagrammidae*; Hseal (EP, KD, NP, SE, SP) = harbor seal (eastern Prince William Sound (PWS), Kodiak, northern PWS, southeast Alaska, southern PWS); Liver# = sampled sleeper shark (specimen #); Mag (Lrg, Med, Sm) = commander squid (large, medium, small); Muscle# = sampled sleeper shark (specimen #); NFSeal = northern fur seal; Oct = giant Pacific octopus; Orca (R,T) = orca (resident, transient); Pandalus = *pandalus* (shrimp) species; Pcod = Pacific cod; Pink (Adt, Juv) = pink salmon (adult, juvenile); Poll (Adt, Juv) = walleye pollock (adult, juvenile); Rainbow = rainbow smelt; Rex = rex sole; Rock = rock sole; Sable = sablefish; SandL (Juv, YOY) = Pacific sand lance (juvenile, young-of-the-year); Sebst = *Sebastes* (rockfish) species; SShark = salmon shark; SSL = Steller sea lion; Tcod (Lg, Sm) = Pacific tomcod (large, small); YFS = yellow fin sole.