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Diet of Pacific sleeper shark, a potential Steller sea lion predator, in the north-east Pacific Ocean

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Pacific sleeper sharks *Somniosus pacificus* were captured near Steller sea lion *Eumetopias jubatus* rookeries during the period when Steller sea lion pups are most vulnerable to Pacific sleeper shark predation (first water entrance and weaning). Analysis of stomach contents revealed that teleosts were the dominant prey in August and cephalopods were the dominant prey in May ($n = 198$). Marine mammals were found in 15% of stomachs regardless of season, but no Steller sea lion tissues were detected. Molecular genetic analysis identified grey whale *Eschrichtius robustus* and harbour seal *Phoca vitulina* remains in some Pacific sleeper shark stomachs. Most mammals were cetacean and at least 70% of the cetaceans were probably scavenged. Although Pacific sleeper shark and Steller sea lion ranges overlapped, so predation could potentially occur, the diet study suggested that predation on Steller sea lions is unlikely, at least when pups first enter the water or during weaning. Harbour seals were infrequent prey and may have been consumed alive. Pacific sleeper sharks consume fast-swimming prey like Pacific salmon *Oncorhynchus* sp., most likely live animals rather than scavenged animals. Pacific sleeper sharks appeared to be opportunistic consumers of the available prey and carrion, feeding both on the bottom and in the water column, and their diet shifted to teleosts and cetacean carrion as the fish grew larger. © 2006 The Fisheries Society of the British Isles (No claim to original US government works)

Key words: diet; predation; sea lion; sleeper shark.

INTRODUCTION

The Pacific sleeper shark *Somniosus pacificus* Bigelow & Schroeder is a common shark of the North Pacific continental shelf and slope, ranging from Japan, along the Siberian coast to the Bering Sea, and across the northern Pacific

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Ocean to southern California, U.S.A. and Baja California, Mexico (Compagno, 1984). At high latitudes, the fish occur in littoral and even intertidal areas; in lower latitudes, they may never come to the surface and may range down to at least 2 000 m. The Pacific sleeper shark is a large shark that may reach total lengths (L_T) of >7 m (Compagno, 1984), although pre-caudal lengths (L_P) of >3 m are rare in Alaska.

The Pacific sleeper shark is a versatile predator capable of feeding on a wide spectrum of prey, including teleosts, other sharks, cephalopods, crustaceans and carrion (Compagno, 1984). Red squid *Berryteuthis magister* (Berry), chum salmon *Oncorhynchus keta* (Walbaum), walleye pollock *Theragra chalcogramma* (Pallas), giant grenadier *Albatrossia pectoralis* (Gilbert), popeye grenadier *Coryphaenoides cinereus* (Gilbert) and Kamchatka flounder *Atheresthes evermanni* Jordan & Starks were common prey by mass in the north-west Pacific Ocean (Orlov & Moiseev, 1999). Giant Pacific octopus *Octopus dofleini* (Wulker), Pacific salmon *Oncorhynchus* sp., walleye pollock and arrowtooth flounder *Atheresthes stomias* (Jordan & Gilbert) were common prey by mass in the Gulf of Alaska (Yang & Page, 1999). Despite moving lethargically, Pacific sleeper sharks consume large fast-swimming fishes like Pacific salmon (Gotshall & Jow, 1965; Orlov & Moiseev, 1999; Yang & Page, 1999) and albacore tuna *Thunnus alalunga* (Bonnaterre) (Ebert *et al.*, 1987). Portions of harbour seals *Phoca vitulina* (L.) have been found also occasionally in Pacific sleeper shark stomachs (Bright, 1959; Compagno, 1984; Orlov & Moiseev, 1999) and are a common prey of the Pacific sleeper sharks' Atlantic congener, the Greenland shark *Somniosus microcephalus* (Bloch & Schneider) (Bigelow & Schroeder, 1948; Fisk *et al.*, 2002).

The Pacific sleeper shark is considered a potential predator of the Steller sea lion *Eumetopias jubatus* (Schreber) because of habitat overlap between the two species (National Research Council, 2003). The potential predation of Steller sea lion by Pacific sleeper shark is a concern because the Steller sea lion population in Alaska from Prince William Sound westward declined by $>80\%$ since the 1960s (Loughlin *et al.*, 1992; Trites & Larkin, 1996). The extent of this decline led the U.S. National Marine Fisheries Service to list the Steller sea lion as threatened over its range under the U.S. Endangered Species Act (1973) in April 1990 and to declare the western stock as endangered in 1997. The predation hypothesis is one of several hypotheses for the Steller sea lion abundance decline; these hypotheses include nutritional stress (Trites & Donnelly, 2003), fisheries competition, environmental change, anthropogenic effects, disease and contaminants (National Research Council, 2003).

No previous Pacific sleeper shark diet studies for the North Pacific Ocean have documented predation of Steller sea lions (Ebert *et al.*, 1987; Orlov & Moiseev, 1999; Yang & Page, 1999). Only Yang & Page (1999) focused on areas nearby Steller sea lion rookeries and haulouts, but sample size was small (13 sharks) and sampling was relatively distant from rookeries and haulouts (a terrestrial site used for breeding, caring for young and for molting) (minimum distance of 14 km, average distance of 32 km). Thus, the possibility remained that predation occurred during vulnerable periods for Steller sea lion pups such as first water entrance and weaning. The objectives of the present study were to

describe the diet of Pacific sleeper sharks and to determine if they preyed on live Steller sea lions.

MATERIALS AND METHODS

Sampling locations and timing were chosen to maximize the chance of documenting predation, if it occurred. The study area was located in the northern Gulf of Alaska between Cape St Elias and Kodiak Island, an area inhabited by the endangered western stock of Steller sea lions. The four largest Steller sea lion rookeries in this area were selected: Marmot Island, Sugarloaf Island, Outer Pye Island (Outer Island) and Seal Rocks (Fig. 1). Standard International Pacific Halibut Commission (IPHC) longline surveys have found Pacific sleeper sharks near these rookeries. Survey timing was chosen to match when Steller sea lions pups were most vulnerable to predation: (1) when Steller sea lion pups first enter the water (July to August) and (2) when Steller sea lion pups often wean (April to May). The majority of the births on Sugarloaf and Marmot islands occur during June (Pitcher & Calkins, 1981). Sampling periods were 1–10 August 2001 and 12–18 May 2002.

Pacific sleeper sharks were captured with bottom longline gear. Standard IPHC survey gear was used so that study abundance estimates would be comparable to those in standard longline surveys in the north-east Pacific Ocean. Each skate (unit of gear) was 549 m long and contained 100 size 16/0 circle hooks attached to 61–122 cm long gangions spaced 5.5 m apart. Each hook was hand-baited with previously frozen #2 chum salmon *Oncorhynchus keta* (Walbaum). Each set consisted of six skates tied together. Five or six longline sets were completed nearby each rookery for each sampling period.

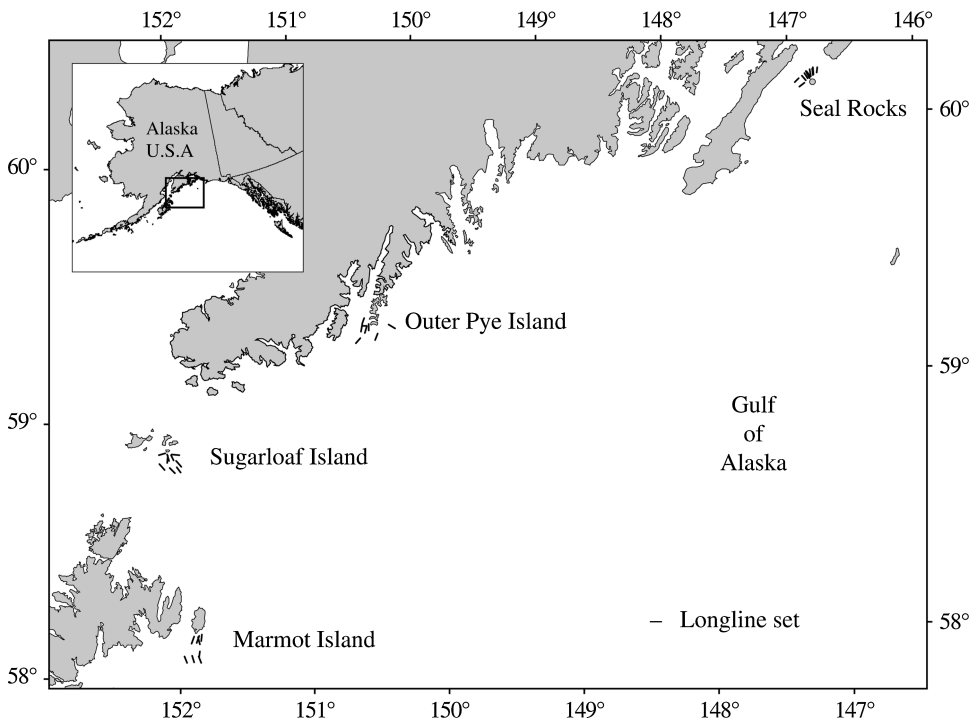


FIG. 1. Locations of longline sets (–) for Pacific sleeper sharks near Steller sea lion rookeries in the northern Gulf of Alaska during August 2001 and May 2002.

Three sets generally were completed per day depending on weather and travel times between stations. The chartered fishing vessel F/V *Norska* (21 m long) was used. Sampling began as close to shore as reasonable without disturbing Steller sea lions on the rookery (>1 km) and extended out up to 12 km. Sampled depths were 100–300 m. The gear was retrieved at a slow rate (*c.* 1 km h⁻¹) to minimize regurgitation of stomach contents. Captured Pacific sleeper sharks were brought on board and weighed. They were also sexed and L_P measured.

At the time of capture, the contents of each stomach were visually identified and marine mammal tissues were separated from the other stomach contents. Baits were separated also from other stomach contents and discarded. The stomach contents were frozen for storage. At the laboratory, each prey item was weighed and classified to the lowest taxonomic level. Tissues from small marine mammals were sampled for genetic analysis and stable isotope analysis and were identified to determine whether these tissues were those of Steller sea lions. A sub-set of tissues from large marine mammals also was sampled for genetic analysis. Diet composition was analysed using four indices (Cortes, 1997): the numerical index (%*N*), the wet mass index (%*M*), the per cent frequency of occurrence (%*O*) and the index of relative importance (%*R*). The %*R* incorporates the three previous indices: $R_j = (\%N_j + \%M_j) \cdot \%O_j$ and $\%R_j = 100 R_j (\sum R_j)^{-1}$, where *j* indicates the *j*th prey item and \sum indicates the sum over all values of R_j .

Marine mammal tissues found in Pacific sleeper shark stomachs were examined for haemorrhage to determine whether the tissue was consumed live (predation) or dead (scavenged). Haemorrhage is an evidence that the wounds were inflicted on a live animal and indicates predation. A gross examination was conducted while in the field. A 10 × 10 × 3 mm slice of tissue perpendicular to a surface exposed to digestion was fixed and stored in 10% neutral buffered formalin for histological examination. The superficial digested and deeper undigested regions were collected to compare predigestive autolytic changes in deeper tissue with those due to digestion at the tissue surface. In the laboratory, the samples were processed in a series of alcohol, xylene and paraffin baths, embedded in paraffin, and stained with haematoxylin and eosin for histological examination. The tissues were classified based on a set of diagnostic characteristics (Table I).

Tissues identified as those of small marine mammal organs were analysed by stable isotope analysis to determine whether the tissues were from Steller sea lions. Tissue samples, *c.* 1 cm², were repeatedly soaked and rinsed in deionized water to remove Pacific sleeper shark enzymatic acids, dried at 60° C for at least 48 h and pulverized for homogeneity in a microball mill (Wig-L-Bug). Stable carbon and nitrogen isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) were measured using a Thermo-Finnigan Delta Plus isotope ratio mass spectrometer. Replicability of standards and samples was $\leq 0.2\%$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Stable isotopes are expressed in δ notation as per mil (‰) by the following expression: $\delta X = 1000 [(R_{\text{sample}}/R_{\text{standard}}) - 1]$, where *X* is ¹³C or ¹⁵N and R_{sample} is the ratio of ¹³C:¹²C or ¹⁵N:¹⁴N for the sample. R_{standard} is the ratio of ¹³C:¹²C or ¹⁵N:¹⁴N of the corresponding standard, Pee Dee Belemnite and atmospheric air, respectively. Stable isotope values for the small marine mammal tissues found in Pacific sleeper shark stomachs were compared to reference collections of Steller sea lion tissues (Hirons, 2001; A. C. Hirons, unpubl. data) using MANOVA and Bonferroni *post hoc* tests at $\alpha = 0.05$.

Tissues identified as those of small marine mammal organs were analysed by genetic analysis to determine whether the tissues were from Steller sea lions. Total DNA was extracted by two methods: a silica-based method for fresh tissues and a modified version of Höss & Pääbo's (1993) silica-based method for ancient bone. The DNA yield was estimated by spectrophotometry. Target DNA was amplified *via* polymerase chain reaction (PCR) (Saiki *et al.*, 1988) and was sequenced by the direct dideoxy sequencing method of Sanger *et al.* (1977). Sequences were run on an ABI 3100 automated sequencer and were edited and aligned with the Sequencher™ multiple sequence editor programme. Edited and type sequences were compared using MacMatch computer software. Taxonomic identification was based on the highest levels of homology observed.

TABLE I. Classification of marine mammal tissues based on diagnostic characteristics from histological analysis. The tissues were found among stomach contents of Pacific sleeper sharks

Tissue classification	Diagnostic characteristics from histological analysis	Harbour seal	Cetacean	Unknown	Total
1. Predated	Red blood cells among tissues (extravasated blood), indicating that the animal was alive when consumed	0	0	0	0
2. Scavenged	Micro-organisms among tissue, indicative of opportunistic growth; adipocere (saponified fat), which is associated with coldwater immersion; either characteristic indicates that the tissue was dead when consumed	0	3	0	3
3. Probably scavenged	Digestive surface (red dye) is apparent and the tissue lacks nuclear detail throughout, including tissue adjacent to the digestive surface, indicating that the tissue was dead when consumed	0	4	2	6
4. Unknown	Tissue lacks nuclear detail, but no digestive surface is apparent	0	11	0	11
5. Unknown fresh	Tissue shows nuclear detail, indicating that the tissue was fresh when consumed	1	3	1	5
Total		1	21	3	25

Unknown, tissues were partially digested blubber with no solid tissue available for histological examination.

RESULTS

One hundred and sixteen Pacific sleeper sharks were caught on 21 sets of longline gear during August 2001; 99 were collected, 10 were tagged and released and seven were lost during capture. The Pacific sleeper shark catch per 100 hooks in August was highest at Seal Rocks (2.8), followed by Outer Pye Island (0.7), Marmot Island (0.3) and Sugarloaf Island (0.1). One hundred and twenty-four Pacific sleeper sharks were caught on 15 sets of longline gear during May 2002; 99 were collected, 24 were tagged and released and one was lost. The Pacific sleeper shark catch rate per 100 hooks in May was highest at Seal Rocks (2.5), followed by Outer Pye Island (1.6), Marmot Island (0.2) and Sugarloaf Island (0.1). Catch rates were lower at Marmot and Sugarloaf Islands because nearby habitat is relatively shallow (<200 m); Pacific sleeper shark catch rates at 100–200 m from standard longline surveys average one-fifth of catch rates at 200–300 m (D. L. Courtney, unpubl. data). Pacific sleeper shark L_P ranged from 106 to 226 cm in August 2001 and 116 to 240 cm in May 2002 (Fig. 2). Overall, males averaged 166 and females 170 cm L_P . Pacific sleeper shark masses during August and May ranged from 15 to 215 kg. The ratio of female to male sharks was 1.48:1 in August 2001 and 1.54:1 in May 2002.

DIET

One hundred and ninety-eight Pacific sleeper shark stomachs were analysed; 165 contained food and 33 were empty (Table II). Teleosts were more important than cephalopods in August 2001 (% R = 64 v. 32), while the opposite was true in May 2002 (35 v. 61). The principal seasonal distinctions for teleost and

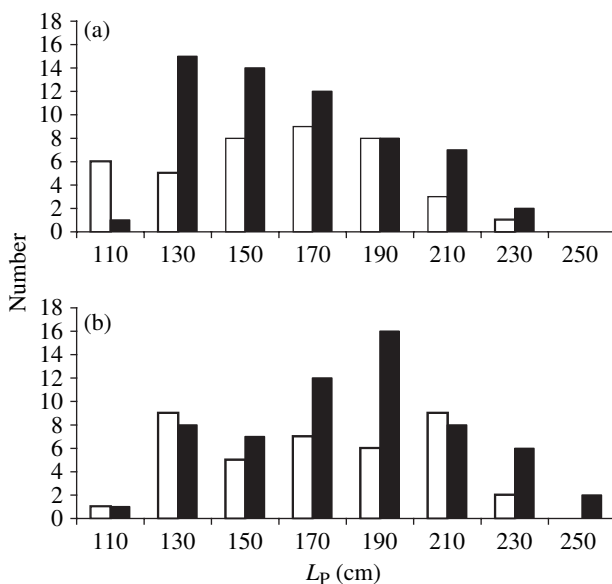


FIG. 2. Number of male (□) and female (■) Pacific sleeper sharks caught by 20 cm pre-caudal length intervals in (a) August 2001 and (b) May 2002.

TABLE II. Diet items of Pacific sleeper shark in the northern Gulf of Alaska during August 2001 and May 2002 expressed as per cent number (%*N*), per cent mass (%*M*), per cent frequency of occurrence in stomachs with food (%*O*) and per cent index of relative importance (%*R*). The %*R* for the higher taxonomic categories of Teleostei, Cephalopoda and Mammalia includes only these higher taxonomic categories

Prey items	% <i>N</i>		% <i>M</i>		% <i>O</i>		% <i>R</i>	
	August	May	August	May	August	May	August	May
Cephalopoda	58.3	80.6	11.7	25.2	57.3	68.4	31.5	61.2
Teuthoidea (squid)	31.5	55.8	1.0	<0.1	23.3	38.0	14.0	38.5
<i>Octopus dofleini</i> (giant Pacific octopus)	26.8	24.8	10.7	25.2	45.3	39.2	31.5	35.7
Decapoda (unidentified crab)	0.0	0.2	0.0	<0.1	0.0	1.3	0.0	<0.1
Chondrichthyes; <i>Squalus acanthias</i> (spiny dogfish)	0.3	0.0	0.1	0.0	1.2	0.0	<0.1	0.0
Teleostei	37.4	16.5	56.8	41.1	86.0	70.9	64.0	34.5
Unidentified teleosts	15.2	9.1	10.4	10.0	53.5	45.6	25.4	15.8
<i>Oncorhynchus</i> sp. (Pacific salmon)	4.3	1.0	8.8	4.4	14.0	5.1	3.4	0.5
Gadidae (gadid fish)	1.7	1.2	3.4	2.4	5.8	3.8	0.5	0.2
<i>Gadus macrocephalus</i> (Pacific cod)	1.7	0.5	11.5	2.9	5.8	2.5	1.4	0.2
<i>Theragra chalcogramma</i> (walleye pollock)	12.6	1.2	16.4	2.3	26.7	6.3	14.3	0.4
Pleuronectid (unknown flatfishes)	0.3	0.7	0.2	2.5	1.2	2.5	<0.1	0.1
<i>Atheresthes stomias</i> (arrowtooth flounder)	0.3	1.0	1.1	4.3	1.2	3.8	<0.1	0.4
<i>Hippoglossus stenolepis</i> (Pacific halibut)	0.7	1.2	3.9	9.7	2.3	6.3	0.2	1.3
<i>Sebastes</i> sp. (rockfish)	0.3	0.2	0.5	1.8	1.2	1.3	<0.1	<0.1
<i>Anoplopoma fimbria</i> (sablefish)	0.3	0.2	0.6	0.8	1.2	1.3	<0.1	<0.1
Mammalia	4.0	2.7	31.4	33.7	16.3	13.9	4.5	4.3
Cetacean	4.0	2.2	31.4	30.6	10.5	10.1	6.4	6.8
<i>Phoca vitulina</i> (harbour seal)	0.0	0.2	0.0	3.1	0.0	1.3	0.0	0.1
Unknown origin	0.7	0.2	<0.1	<0.1	2.3	1.3	<0.1	<0.1
Total prey mass (kg)	96.2	74.3						
Number of prey items	317	427						
Number of stomachs with food	86	79						
Number of empty stomachs	13	20						

cephalopod prey were the much higher incidence of walleye pollock and Pacific salmon in August (all indices) and higher incidence of squid in May (%*N* and %*O*). Identified Pacific salmon species also differed seasonally, with pink salmon *Oncorhynchus gorbuscha* (Walbaum) and chum salmon consumed in August and

chinook salmon *Oncorhynchus tshawytscha* (Walbaum) and sockeye salmon *Oncorhynchus nerka* (Walbaum) consumed in May. The Pacific salmon were adults. Giant Pacific octopus and Teuthoidea squid were the most important non-teleost prey. Squid was common prey (%*N* and %*O*) but of low mass (%*M*) because of the common presence of beaks with no flesh.

Mammalian tissue was an important diet item during both sampling periods. Marine mammal tissues comprised one-third of the mass of diet items (%*M c.* 33) and were found in one in every seventh Pacific sleeper shark stomach examined (%*O c.* 15). The mammalian tissue was composed of cetacean (31) and unidentified mammal (<0.1) tissues during August 2001 and cetacean (31), harbour seal (3) and unidentified mammal (<0.1) tissues during May 2002. The unidentified mammal tissues were composed of collagen, fat and muscle and were too small to identify. No Steller sea lion tissues were identified. The per cent mass of marine mammals dramatically increased with Pacific sleeper shark size as the per cent mass of teleosts and cephalopods decreased (Fig. 3).

IDENTITY OF MARINE MAMMAL DIET ITEMS

Marine mammal tissues were collected from 25 Pacific sleeper shark stomachs. The tissues were connective tissue and tissues from muscle, fat and internal

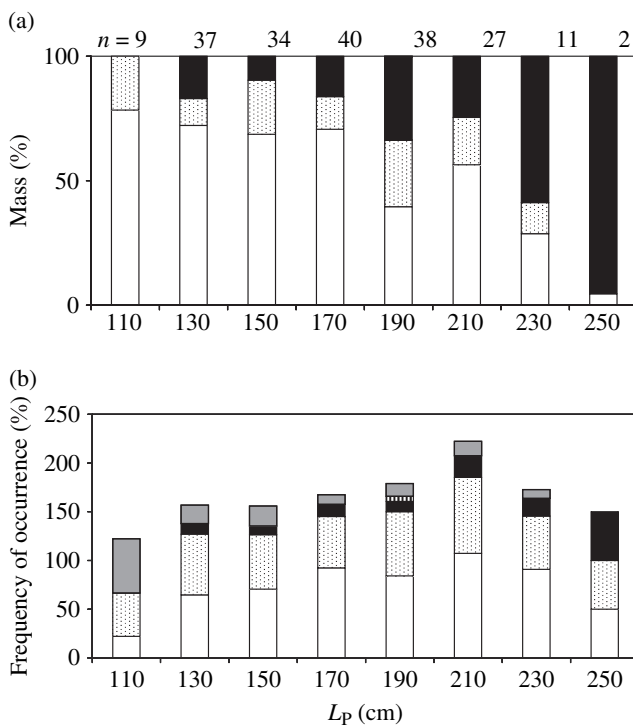


FIG. 3. Per cent (a) mass and (b) frequency of occurrence of prey of Pacific sleeper shark by 20 cm pre-caudal length intervals. Prey categories are teleost (□), cephalopod (▨), mammal (■), other (▩) and empty (■). n , sample size.

organs (stomach, spleen, pancreas and lung). No bones were found. Of these 25 sets of tissues, 20 were classified as tissues of cetacean, two as those of small marine mammal and three as unknown. The three unknowns were pieces of tissue that were too small to identify. The first tissue identified initially as that of a small marine mammal was composed of a mammalian oesophagus, simple stomach, trachea, spleen and pancreas. The proximal trachea including the epiglottis was 19 cm long with no bifurcation and extended to the midsection of the oesophagus. The most likely species was a seal (Phocidae) because this was of mammalian origin with a simple stomach and a long trachea without early bifurcation. Cetacean stomachs have multiple compartments, and sea lion tracheas bifurcate early. The second tissue initially identified as those of a small marine mammal was mostly a mammalian lung and mainstem bronchus. The diameter of the mainstem bronchi was large, *c.* 4 cm. The visceral pleura was thick and extended in a thick flap off the caudal edge of the lung. The anatomical features of a large bronchus and the pleural thickening at the caudal edge of the lung suggested a cetacean lung.

The two tissues initially identified as those of small marine mammals were examined also by stable isotope analysis. The stable isotope ratios of the pancreatic tissue were measured for the first sample ($\delta^{13}\text{C} = -18.5$ and $\delta^{15}\text{N} = 15.6$) and compared to reference values for Steller sea lion liver ($\delta^{13}\text{C} = -17.7$ and $\delta^{15}\text{N} = 16.8$), a similar metabolic tissue. The stable isotope ratios of the lung tissue were measured for the second sample ($\delta^{13}\text{C} = -19.8$ and $\delta^{15}\text{N} = 14.9$) and compared to reference values for Steller sea lion lung ($\delta^{13}\text{C} = -18.2$ and $\delta^{15}\text{N} = 16.0$). Isotope ratios for both samples are significantly different ($\alpha \leq 0.004$ and $\alpha \leq 0.0004$, respectively) and indicate that neither tissue is from Steller sea lions or from any other marine organism occupying the same trophic level (DeNiro & Epstein, 1978, 1981; Hirons, 2001).

Standard extraction methods for molecular genetic analysis recovered low quantity and low quality DNA from tissues, resulting in poor PCR and sequence analysis success. The specialized 'ancient DNA' extraction method was applied to two tissues with more success. Mitochondrial DNA from two individuals was successfully amplified and sequenced. One individual's DNA was amplified and sequenced for a 209 bp region. The other individual's DNA was amplified for a 650 bp region that was subsequently sequenced for 431 bp. The comparison of these two sequences to the homologous sequence from 47 (10 mysticete, 30 odontocete and seven pinniped) Pacific marine mammal species identified the former sample as a grey whale *Eschrichtius robustus* (Lilljeborg) and the latter as a harbour seal. The latter genetic identification confirmed the identification of a seal. Thus, of the 25 prey identified as marine mammals, 21 were cetacean, one was a harbour seal and three were unknown (Table I). No evidence of Steller sea lions as prey was found.

EVIDENCE FOR PREDATION OF MARINE MAMMALS

No blood was found among marine mammal tissues by gross examination, so no obvious evidence of predation was found. Fourteen tissues (categories 2, 3 and 5 in Table I) were examined by histological methods. The other 11 (category 4 in Table I) were partially digested blubber, with no solid tissue

available for histological examination. Three of the 14 marine mammal tissues showed clear evidence of being scavenged (Table I). Micro-organisms were found throughout two of the tissues, indicating that the tissues were putrefying before being consumed. The third tissue contained adipocere, which are fat cells containing saponified fat. Fat saponifies after lengthy coldwater immersion, indicating that the tissue was exposed to cold water for weeks to months before being consumed.

Six of the 14 marine mammal tissues were probably scavenged. Nuclear detail was absent throughout the tissue, implying that the change was due to autolysis occurring before consumption rather than before digestion. If the effect was due to the digestion of a freshly killed organism, then a differential effect would appear, with less nuclear detail seen near the surface exposed to digestion and preservation of nuclear detail in deeper tissues.

The remaining five of the 14 marine mammal tissues were indeterminate regarding predation *v.* scavenging. One tissue lacked nuclear detail, but the digestive surface was uncertain. The other four tissues showed nuclear detail, indicating that they were fresh at the time of consumption, but lacked extravasated blood in histological examination. Extravasated blood lies outside the circulatory system, occurs if blood vessels are damaged due to physical impact or cutting, and is evidence that a live animal was preyed upon bleeding. When lacking extravasated blood, it is unknown if the fresh tissues were predated or scavenged from recently dead animals.

DISCUSSION

DIET

Pacific sleeper shark diet is diverse as teleosts, cephalopods and marine mammals commonly occurred during both sampling periods. Previous studies also report diverse diets for Pacific sleeper sharks (Ebert *et al.*, 1987; Orlov & Moiseev, 1999; Yang & Page, 1999). This study found that Pacific cod *Gadus macrocephalus* Tilesius, walleye pollock, Pacific salmon and Pacific halibut *Hippoglossus stenolepis* Schmidt were the predominant teleost prey by per cent mass. Cephalopods, represented by Teuthoidea squid and giant Pacific octopus, were the most abundant prey by per cent number during both sampling periods. Squid tissues, however, other than beaks and eye lenses in the stomachs were found rarely. Their importance is overestimated in terms of %N and %O if beaks and eye lenses accumulate in the Pacific sleeper shark stomach. While Yang & Page (1999) identified a number of non-cephalopod invertebrates in the sharks' diet, this study determined that all but one non-cephalopod invertebrate prey item found in Pacific sleeper shark stomachs (a decapod crab) originated from the stomachs of their teleost prey.

Cetaceans were an important part of Pacific sleeper shark diet. Cetaceans also were common food of the Pacific sleeper sharks as reported in a study in Prince William Sound in August 2000 (seven of 33 stomachs) (L. B. Hulbert, unpubl. data). Previous researchers have noted occasional harbour seals in Pacific sleeper shark stomachs (Bright, 1959; Compagno, 1984; Orlov & Moiseev, 1999), as did this study, but not cetaceans. Yang & Page (1999) found no marine

mammal tissue in 13 Pacific sleeper sharks collected near Kodiak Island, Alaska. In contrast, the Pacific sleeper sharks' Atlantic congener, the Greenland shark, regularly consumes small cetaceans, possibly as carrion (Compagno, 1984). This study's findings indicate that cetaceans also can be regular food of Pacific sleeper sharks. Given that cetaceans comprised one-third of their diet by mass, they are probably energetically important, especially for larger Pacific sleeper sharks. Although marine mammals were common food, none of these tissues were identified as Steller sea lion. This suggests that Pacific sleeper sharks are unlikely to be a significant source of Steller sea lion mortality, especially because Pacific sleeper sharks were sampled when Steller sea lion pups are most vulnerable to predation (first water entrance and weaning).

The principal seasonal difference in diet was the relative importance of fishes and cephalopods. In August, teleosts were the most important prey group (%R) largely due to walleye pollock and pink and chum salmon. In May, cephalopods were the most important prey group (%R) due to both squid (%N, %O) and giant Pacific octopus (%M). No previous studies have reported seasonal differences in Pacific sleeper shark diet. Walleye pollock were less common prey in May possibly because they remained concentrated outside the study area after the winter spawning period. Pink and chum salmon were more common prey in August possibly because nearshore abundance increased during return to their natal streams. Pacific salmon were also common in a study in Prince William Sound in August 1999; 13 of 33 Pacific sleeper shark stomachs contained at least one pink, chum, coho or unidentified Pacific salmon; one stomach contained the remains of nine Pacific salmon and a total of 37 Pacific salmon were identified (L. B. Hulbert, unpubl. data).

SCAVENGING OR PREDATION OF MARINE MAMMAL TISSUE

Scavenging of cetacean tissue by Pacific sleeper sharks appears common. Seven of 10 cetacean tissues intact enough for histological examination were probably scavenged. The other three were fresh at the time of consumption, but whether the tissues were predated or scavenged is unknown. Eleven cetacean tissues not intact enough for histological examination were partially digested blubber. Circular- to oval-shaped lesions on Stejneger's beaked whale *Mesoplodon stejnegeri* (Gervais) were attributed to cookie cutter sharks *Isistius brasiliensis* (Quoy & Gaimard) (Walker & Hanson, 1999). Conceivably, the partially digested blubber in Pacific sleeper shark stomachs occurs by Pacific sleeper sharks taking bites from cetaceans without killing the prey.

Pacific sleeper sharks feed occasionally on harbour seals, possibly on live animals. Portions of harbour seals occasionally have been found in Pacific sleeper shark stomachs (Bright, 1959; Compagno, 1984; Orlov & Moiseev, 1999). Harbour seal was found in one of 198 Pacific sleeper shark stomachs (210 cm L_P) in this study and one of 33 stomachs in a study in Prince William Sound (L. B. Hulbert, unpubl. data); both tissues were fresh and thus may have been predated. Pacific sleeper sharks prey upon small, live marine mammals in other parts of the world. A sleeper shark *Somniosus cf. pacificus* Bigelow & Schroeder caught in Chilean waters with the genital zone and complete foetus of a female

southern right whale dolphin *Lissodelphis peronii* (Lacépède) in its stomach was presumed to have attacked a live dolphin (Crovetto *et al.*, 1992). Seals were presumed to be taken alive by Greenland sharks (Bigelow & Schroeder, 1948) because they were common prey (Bigelow & Schroeder, 1948; Fisk *et al.*, 2002). The conclusion that harbour seals are occasional prey of Pacific sleeper sharks may depend on the sampling design. Predation rates may be higher in areas of greater harbour seal and Pacific sleeper shark densities.

FORAGING BEHAVIOUR

Pacific sleeper sharks appear to feed on the bottom and in the water column. Yang & Page (1999) infer that Pacific sleeper sharks feed mainly on the bottom based on the prevalence of arrowtooth flounder and octopus in their samples and because benthic fishes and invertebrates are described as the predominant items in Pacific sleeper shark diet by other researchers (Phillips, 1953; Gotshall & Jow, 1965). Diet data from this study indicate that Pacific sleeper sharks feed in the water column as well. All five species of Pacific salmon appear in Pacific sleeper shark diet in this study, and maturing coho, sockeye, chum and pink salmon inhabit near surface waters, mostly shallower than 20 m (Ogura & Ishida, 1992, 1995). The Pacific salmon were probably consumed alive rather than scavenged because no Pacific salmon fishery operated nearby to provide a source of scavenged fishes and some were fresh Pacific salmon that were whole or cleanly bitten into two or three pieces that together formed a whole fish. Besides benthic species, Gotshall & Jow (1965) reported three chinook salmon in one of the two Pacific sleeper shark stomachs they examined. Pacific salmon were reported by Orlov & Moiseev (1999) and albacore tuna by Ebert *et al.* (1987). That the Pacific sleeper shark hunts in the water column is supported also by data from satellite-linked electronic tags that record depth and temperature (Hulbert *et al.*, 2006). The most striking behavioural feature of the tagged Pacific sleeper sharks is their extensive, nearly continuous vertical movements.

Pacific sleeper sharks are able to capture large fast-swimming species. Moss (1981) suggested that cryptic colouration in apparently lethargic fish may allow them to approach fast-swimming prey undetected. The Pacific sleeper shark's large buccal cavity appears to act as a vacuum that inhales prey; the Pacific sleeper shark may catch fast-swimming prey by lying in wait and ambushing them (Ebert, 1994). The sevengill shark *Notorhynchus cepedianus* (Péron) may catch fast-swimming prey by gliding, undetected with very little body movement (Ebert, 1991). Pacific sleeper sharks, by their slow and deliberate vertical oscillations through the water column (Hulbert *et al.*, 2006), also may employ this hunting strategy.

Energetically, it is beneficial for a large shark to consume one large prey item rather than numerous small items such as squid. A size-related shift in the diet to larger, more active prey has been observed for Pacific sleeper sharks in the north-west Pacific Ocean (a shift from cephalopods to teleosts; Orlov & Moiseev, 1999) and for other large sharks (Ebert, 1994). This study also found that teleosts and marine mammals, predominantly cetaceans, were more frequent food of larger Pacific sleeper sharks. Pacific sleeper shark length

ranged from 106 to 240 cm L_P in this study, similar to the that in a study in Prince William Sound, Alaska of 60 to 280 cm L_P ($n = 429$) (W. R. Bechtol, unpubl. data) and in the western Bering Sea and north-west Pacific Ocean of 66 to 300 cm L_T ($n = 274$) (Orlov & Moiseev, 1999). The similarity in fish sizes implies that the size range in this study is representative of Pacific sleeper sharks in the North Pacific Ocean. Pacific sleeper sharks appear to be opportunistic consumers of the available prey and carrion, feeding on the bottom and in the water column, and their diet shifts to teleosts and cetacean carrion as the fish grow larger.

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