

Northerly Distribution of White Sharks, *Carcharodon carcharias*, in the Eastern Pacific and Relation to ENSO Events

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Introduction

White sharks, *Carcharodon carcharias*, have been recorded throughout the North Pacific, from cold temperate coastal regions to tropical oceanic islands. Klimley (1985) reviewed white shark distribution in the eastern North Pacific. Captures were predominantly (90.8% of 109 records) from California waters, their frequency attenuating rapidly with increasing latitude. White shark captures (Bonham, 1942; LeMier, 1951), and attacks on humans (McCosker and Lea, 1996), inanimate objects (Collier et al., 1996), sea otters, *Enhydra lutris* (Ames and Morejohn, 1980), and small cetaceans (Long and Jones, 1996), as well as scavenging on gray whale, *Eschrichtius*

robustus, carcasses (Snow, 1976, 1980), demonstrated that this species occurs occasionally in Oregon and Washington waters. The primary literature contains only one record from British Columbia (Pike, 1962) and one from Alaska (Royce, 1963), although there are other records in the secondary and gray literature. Collier et al. (1996) reported an attack by a white shark on commercial fishing gear off the west coast of Vancouver Island, British Columbia, in the summer of 1961. Paust and Smith (1986) report a white shark from southeast Alaska captured during the summer of 1981. Karinen et al. (1985) list several records of white sharks from southeast Alaska, which they regarded as possibly associated with the 1983 El Niño. Mecklenburg et al. (2002) report that white sharks were found in commercial fishing nets off southeast Alaska during the summer of 1997, which they regard as during a strong El Niño event.

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White sharks are also found in the central and western North Pacific. Taylor (1985) reviewed historical and contemporary white shark records from Hawaii. Boustany et al. (2002) reported satellite

tracking of four white sharks from central California to the subtropical eastern Pacific, one of which traveled 3,800 km to the western coast of Kahoolawe, Hawaii. Compagno (1984) listed the Marshall Islands, the Philippines, China, the Koreans, and Bonin Island as localities from which white sharks have been recorded. Nakano and Nakaya (1987) and Nakaya (1994) reviewed white shark distribution in Japan and the western North Pacific. Additional Japanese records were documented by Yabe (1995) and Uchida et al. (1996) and four attacks were attributed to this species by Nakaya (1993, 1996). Although Fowler (1941) listed Kamchatka as part of the white shark's range, Soldatov and Lindberg (1930) advocated reexamination of this record and its validity was regarded as "doubtful" by Nakano and Nakaya (1987). Thus, white sharks are widespread in the North Pacific but appear to be rare at boreal latitudes.

The distribution and abundance of white sharks in northerly waters of the eastern Pacific is herein extended by 19 previously unpublished records from British Columbia and Alaska waters, drawn from newspaper archives, unpublished papers, and interviews with fisheries biologists and private citizens. Of a total of 29 records, species identification of 21 (72.4%) was confirmed on the basis of teeth, vertebral centra, and/or unambiguous photographs, with the remainder (8 cases or 27.6%) supported by curated physical evidence and/or the testimony of competent observers. These new records, combined with the 10 previously reported (Pike, 1962; Royce, 1963; Karinen et al., 1985; Paust and Smith, 1986; Collier et al., 1996; Mecklenburg et al., 2002), suggest that white sharks occur sporadically off British Columbia and Alaska irrespective of ENSO events.

ABSTRACT—Twenty-nine verified records of white sharks, *Carcharodon carcharias*, from British Columbia and Alaska waters (1961–2004) are presented. Record locations ranged from lat. 48°48'N to lat. 60°17'N, including the northernmost occurrence of a white shark and the first report of this species from the central Bering Sea. White sharks recorded from the study area were generally large, with 95% falling between 3.8 and 5.4 m in length. Mature white sharks of both sexes occur in British Columbia and Alaska waters, although they do not necessarily reproduce there. White sharks actively feed in the study area; their diet is similar to that reported for this species from Washington and northern California waters. Sea surface temperature

(SST) concurrent with white shark records from the study area ranged from 16°C to between 6.4°C and 5.0°C, extending the lower extreme of the range of SST from which this species has been previously reported. White shark strandings are rarely reported, yet 16 (55%) of the records in this study are of beached animals; strandings generally occurred later in the year and at lower latitudes than non-strandings. No significant correlation was found between white shark records in the study area and El Niño events and no records occurred during La Niña events. The data presented here indicate that white sharks are more abundant in the cold waters of British Columbia and Alaska than previous records suggest.

Among these records are the northernmost occurrence of a white shark and the first report of this species from the central Bering Sea. The latter case, combined with recent evidence of long-distance travel from satellite telemetry (Boustany et al., 2002) and mitochondrial DNA (Pardini et al., 2001), raises the possibility that white sharks may range across the Aleutian Archipelago and that the entire North Pacific may represent a single, interbreeding population.

Methods

Between 1986 and 2001, reports of white shark sightings, captures, and strandings in British Columbia and Alaska waters prompted the author to execute repeated searches through local newspaper archives and records of the Vancouver Aquarium as well as correspond with fisheries officers and commercial fishermen working in the region.

The following data were tabulated for each verified white shark record: record number, location description, latitude and longitude, date, length, sea surface temperature (SST), whether or not the record is of a stranding, basis for species identification, observers and biologists, source, and general remarks. Data initially based on newspaper reports were later verified by interviews with observers or attending biologists. Capture location given is the most precise local name in current usage, often initially from newspaper accounts and later verified by local observers or attending biologists. Latitude and longitude were either provided by the attending biologist or calculated from one or more atlases.

“Observer” identifies the individual who found, observed, or captured the shark initially and could verify at least some particulars about the specimen. “Biologist” identifies, where appropriate, the trained scientist who could verify the species identification and particulars about the specimen.

Basis for species identification is given, usually categorized as teeth, vertebrae, or unambiguous photographs; in six (20.7%) cases two or more were available. Tooth terminology follows Shimada (2002) and Welton and Farish (1993), while tooth measurements follow

Chandler.¹ Vertebral centra were identified following Kozuch and Fitzgerald (1989). To gain experience in distinguishing white shark centra from those of the basking shark, *Cetorhinus maximus*, the following specimens were examined at the Los Angeles County Museum of Natural History: *C. carcharias*: LACM 35875-1, LACM 42094-1, LACM 42133-1 and *C. maximus*: LACM 42128-1

Shark length is total length (TL) with the caudal fin in a “natural position”, given in meters as measured or estimated by observers and/or attending biologists. Only specimens 13 and 15 were measured, but the estimated length of specimens 16 and 26 can be tested against measurements of teeth examined by the author. Mollet et al. (1996) presented a 95% confidence band for a morphometric relationship between tooth enameloid height (as %TL) and TL (in m) in white sharks, basing their regression on upper anterior teeth. The ratio of enameloid height in second upper anterior teeth vs. that of second lower anterior teeth in six white sharks measuring 1.4–5.2 m TL is 1:0.845, while that of first and second upper lateral teeth vs. second upper anterior teeth ranges from 1:0.9474–1.0000 according to the author’s calculations. Extrapolating from the largest lower anterior tooth of specimen 15 and the upper first lateral tooth of specimen 26, gives an estimated enameloid height for the corresponding upper anterior tooth, which equals 0.7% TL (Mollet et al., 1996).

Sea surface temperature (SST) is the measured monthly mean from the nearest available government-operated oceanographic data recorder (National Environmental Satellite, Data, and Information Service (NESDIS) and Meteorology and Oceanography (METOC) Center for Gulf of Alaska; the Institute of Ocean Sciences, operated by Fisheries and Oceans Canada or Langara Lighthouse Station, maintained by Canada Coast Guard, for Queen Charlotte Islands and southeastern Alaska), from National Oceanic and Atmospheric Administration (NOAA) thermographic image data for

the Aleutian–Bering Sea region, or, in one case (record 2), as measured by shipboard thermographic recorder.

Remarks are any noteworthy information not fitting any of the other categories, as reported by observers and/or attending biologists, and may include shark stomach contents, mass, and sex. Stomach contents—if any—are reported to lowest identifiable taxon, based on reports by observers or attending biologists. Shark mass (kg) is based on estimates of observers or attending biologists, verified against predicted length-mass regressions given in Mollet and Cailliet (1996). Shark sex is given if determined, based on the presence or absence of claspers, and maturity state is noted, if determined by an attending biologist. Source lists any published account that can serve to verify the authenticity of a given white shark record.

Records of white sharks from British Columbia and Alaska were analyzed as percent occurrence by month and mean monthly SST. Investigation of whether ENSO events are correlated with white shark occurrence in British Columbia and Alaska waters required identification of El Niño and La Niña years. Consensus data identifying ENSO years, classified as “strong”, “normal”, or “weak”, between 1950–2004 are from Allan et al. (1996) and Null.² Statistical analysis consisted of two-sided χ^2 test of 2×2 contingency tables of observed vs. expected occurrences of white sharks in boreal waters of the eastern North Pacific if ENSO events had no effect (H_0), for which $\nu = 1$ and $P = 0.05$ (Campbell, 1974).

Results

Distribution records of 29 white sharks from cold waters of Alaska and British Columbia are summarized in Table 1 and mapped in Figure 1. Number of each record in Figure 1 refers to the corresponding record as listed in Table 1.

White shark records ranged from lat. 48°48'N (record 29) to lat. 60°17'N (record 1). Species identification is supported by teeth, vertebrae, and/or

¹Chandler, R. 1995. Cretaceous and Paleogene fossils of North Carolina: a field guide. North Carolina Fossil Club, Durham, 70 p.

²Null, J. 2004. El Niño and La Niña years: a consensus list. <http://ggweather.com/enso/years.htm>.

Table 1.—White shark records from British Columbia and Alaska waters, 1961–96. Record numbers correspond with those mapped in Figure 1.

No.	Location	Latitude/Longitude	Date	Shark TL(m)
1	Cordova, Gulf of Alaska, AK Remarks: Prey/Stomach contents - <i>Oncorhynchus nerka</i> , specimen at Oregon State University (OU 11040)	60°17'N, 145°35'W	27 May 1985	4
2	NW Bering Sea Remarks: Prey/Stomach contents - <i>Eumetopias jubatus</i>	59°56'N, 178°56'W	11 Aug. 1979	4+
3	Ocean Cape, Yakutat, AK Remarks: Prey/Stomach contents - 3 <i>Phoca vitulina richardii</i> , seals well macerated, decapitated	59°30'N, 139°50'W	Early Summer 1981	6
4	Yakutat Bay, AK Remarks: Attempts at independent verification unsuccessful	59°24'N, 140°00'W	Summer 1997	
5	Yakutat Bay, AK Remarks: Attempts at independent verification unsuccessful	59°24'N, 140°00'W	Summer 1997	
6	14 miles off Yakutat, AK Remarks: Bit piece from hooked halibut	59°24'N, 140°00'W	6 Sept. 2004	6
7	Yakutat, AK, ½ Mile E of mouth of Akwe River Remarks: Very decomposed, remains scavenged/scattered by bears	59°20'N, 139°26'W	Summer 2003	4.6
8	Sitka, AK Remarks: Shark did not linger, no photos available	59°00'N, 135°08'W	July 2004	2.4
9	Naknek, Bristol Bay, AK Remarks: Prey/Stomach contents - <i>Oncorhynchus</i> spp.	58°44'N, 157°30'W	Summer 1982	5+
10	Lynn Canal, AK Remarks: Shark chummed, killed, but lost	58°30'N, 135°09'W	Mar. 1984	
11	Cross Sound, AK Remarks: Collected by salmon trawler	58°06'N, 136°18'W	Summer 1983	4.3
12	Stephen's Passage, Hobart Bay, AK Remarks: Unconfirmed sightings (<i>Lamna ditropis</i> also seen)	57°30'N, 133°30'W	Aug.–Sept. 1983	
13	Picnic Cove, Goddard, AK Remarks: Prey/Stomach contents - 45 kg <i>Hippoglossus stenolepis</i> , Shark Mass = 900 kg (est.); Shark Girth = 2.6 m; liver produced 9.5 l of oil	56°51'N, 135°02'W	Late Oct. 1996	4
14	Craig, AK	55°28'N, 133°08'W	24 Oct. 1961	4.7
15	Dall Head, South tip of Gravina Island, AK Remarks: Shark Sex = M, sexually mature; Prey/Stomach contents - partial liver of <i>Phoca vitulina richardii</i> , 100's of lenses of <i>Oncorhynchus</i> spp.; shark girth = 2.45 m; teleost lenses ID by J.E. Fitch	55°12'N, 131°50'W	30 Sept. 1977	4.7
16	Cape Ball, Graham Island, QCI, BC Remarks: Shark Sex = F, probably sexually mature	53°42'N, 131°52'W	20 Oct. 1977	5.5
17	East Beach, near Cape Ball, Graham Island, QCI, BC	53°42'N, 131°52'W	Autumn 1988	±5
18	Cape Ball, Graham Island, QCI, BC	53°42'N, 131°52'W	Late Summer/ Early Autumn 1983	±4
19	Cape Ball, Graham Island, QCI, BC Remarks: 25 vertebrae, bits of cartilage (including left Meckel's cartilage), chondrocranium, teeth and patches of skin	53°42'N, 131°52'W	25 Oct. 2004	4.6
20	Long Inlet, Graham Island, QCI, BC Remarks: Prey/Stomach contents—probably <i>Phoca vitulina richardii</i> ; Shark Mass = 1,135 kg (est.)	53°12'N, 132°19'W	16 Dec. 1986	5
21	Long Inlet, Graham Island, QCI, BC	53°12'N, 132°19'W	16 Dec. 1987	5.2
22	Lawn Point, Graham Island, QCI, BC Remarks: Shark in advanced state of decomposition when found	53°25'N, 131°55'W	Late Sept. 1977	3–4
23	Near Queen Charlotte City, Graham Island, QCI, BC	53°16'N, 132°04'W	Late Summer/ Early Autumn 1987	±5
24	Skidegate Inlet, Graham Island, QCI, BC	53°12'N, 132°00'W	Autumn 1988	4–5
25	Un-named beach, Lyell Island, QCI, BC	52°41'N, 131°21'W	25 Nov. 1977	4.5
26	Un-named beach, Moresby Island, QCI, BC	52°31'N, 131°34'W	Oct. 1977	4.5
27	Creek Mouth, Island Bay, QCI, BC	52°21'N, 131°24'W	24 Oct. 1961	3.4
28	North side of Goose Island, Queen Charlotte Sound, BC Remarks: Vertebral samples examined by author	51°32'N, 128°17'W	4 Sept. 2004	5.6
29	Esperanza Inlet, Vancouver Island, BC Remarks: Shark attacked canvas float bag of commercial salmon fishing vessel	48°48'N, 127°07'W	17 Aug. 1961	4–6

¹Cook, S. F. 1987. Argus-Mariner Consulting Scientists, Corvallis, Oregon. Personal commun.

²Collier, R. S. 2004. Shark Research Committee, Van Nuys, California. Personal commun.

³Russell, C., and D. Courtney. 2004. National Marine Fisheries Service, Auke Bay Laboratory, Juneau, Alaska. Personal commun.

⁴Karinen, J., and D. Hanselman. 2004. National Marine Fisheries Service, Auke Bay Laboratory, Juneau, Alaska. Personal commun.

⁵Wing, B. L., and J. Karinen. 2004. National Marine Fisheries Service, Auke Bay Laboratory, Juneau, Alaska. Personal commun.

⁶Urias, D. 2002. Sitka, Alaska. Personal commun.

⁷Larson, R. 2001. United States Department of Agriculture, Forest Service, Subsistence Fisheries, Petersburg/Wrangell Ranger Districts, Petersburg, Alaska. Personal commun.

⁸Hewlett, S. (Editor). 1978. Great white sharks! Sea Pen (Vancouver Aquarium newsletter), 22(2): 5–6.

SST(°C)	Stranded (Y/N)	ID basis	Observers and biologists	Source
5.0–6.4	N	Tooth punctures on salmon carcass	J. Thomas, S. F. Cook	Cook ¹
9.5	N	Experienced observer	S. F. Cook	Cook ¹
8.9–10.8	N	Jaws, teeth	R. Maygard, B. Paust, R. Smith	Paust and Smith (1986)
15	N	Experienced observer	B. Johnson	Mecklenburg et. al. (2002)
15	N	Experienced observer	B. Johnson	Mecklenburg et. al. (2002)
16	N	Photo	J. Huppert	Collier ²
13	Y	Photos	C. Russell, D. Courtney	Russell and Courtney ³
16.0	N	Experienced observers	J. Karinen, D. Hanselman	Karinen and Hanselman ⁴
0–9.8	N	Anecdotal	S. F. Cook	Cook ¹
6	N	Anecdotal	R. Straty	Karinen et al. (1985), Wing and Karinen ⁵
13	N	Jaws, tail, photos	J. Karinen, R. Straty	Karinen et al. (1985), Wing and Karinen ⁵
13	N	Anecdotal	R. Straty	Karinen et al. (1985), Wing and Karinen ⁵
10	N	Teeth, photo	J. and F. Timmer, S. Sturm, D. Urias	Urias ⁶
9.6	Y	Teeth, photo	L. R. Hall, W. F. Royce	Royce (1963), Larson ⁷
11.4	Y	Teeth, photos	H. Ludwigsen, R. Larson, G. Freitag	Larson ⁷
10.8	Y	Teeth, photos	D. and A. Manson, G. Hewlett ⁹	Manson ⁹
11.3	Y	Photo	T. Husband, R. Sjolund	Sjolund ¹⁰
11.9	Y	Teeth		CBC News Radio, October 1990
12	Y	Teeth, photos	J. Davis, C. Tarver	Davis ¹¹
8.2	Y	Teeth	L. Vogstad, R. Sjolund, M. Saunders	Sjolund ¹⁰
8.2	Y	Teeth		Coad (1995), Saunders ¹²
11.9	Y	Teeth	K. Harley	Sjolund ¹⁰
11.8	Y	Teeth	W. Noddin, R. Sjolund	Sjolund ¹⁰
11.3	Y	Teeth		CBC News Radio, October 1990
7.6	Y	Teeth	B. Wilchere, K. S. Ketchen	Ketchen ¹³
10.8	Y	Teeth	K. S. Ketchen	Ketchen ¹³
9.6	Y	Teeth	K. R. Harley	Pike (1962)
16	Y	2.5 m of vertebrae	J. Watson, G. Ellis	Wallace ¹⁴
13.8	N	Tooth and several fragments	G. Trenholme, K. S. Ketchen	Collier et al. (1996)

⁹Manson, D., and A. Manson. 2002. West Vancouver, British Columbia, Canada. Personal commun.

¹⁰Sjolund, R. 2002. Fisheries and Oceans Canada, North Coast Area, Conservation and Protection. Queen Charlotte City, Queen Charlotte Islands, British Columbia, Canada. Personal commun.

¹¹Davis, J. 2004. Tiell, Queen Charlotte Islands, British Columbia, Canada. Personal commun.

¹²Saunders, M. 2002. Fisheries and Oceans Canada, Pacific Biological Station. Nanaimo, British Columbia, Canada. Personal commun.

¹³Ketchen, K. S. 2002. Nanaimo, British Columbia, Canada. Personal commun.

¹⁴Wallace, S. 2004. Fisheries and Oceans Canada, Pacific Biological Station. Nanaimo, British Columbia, Canada. Personal commun.

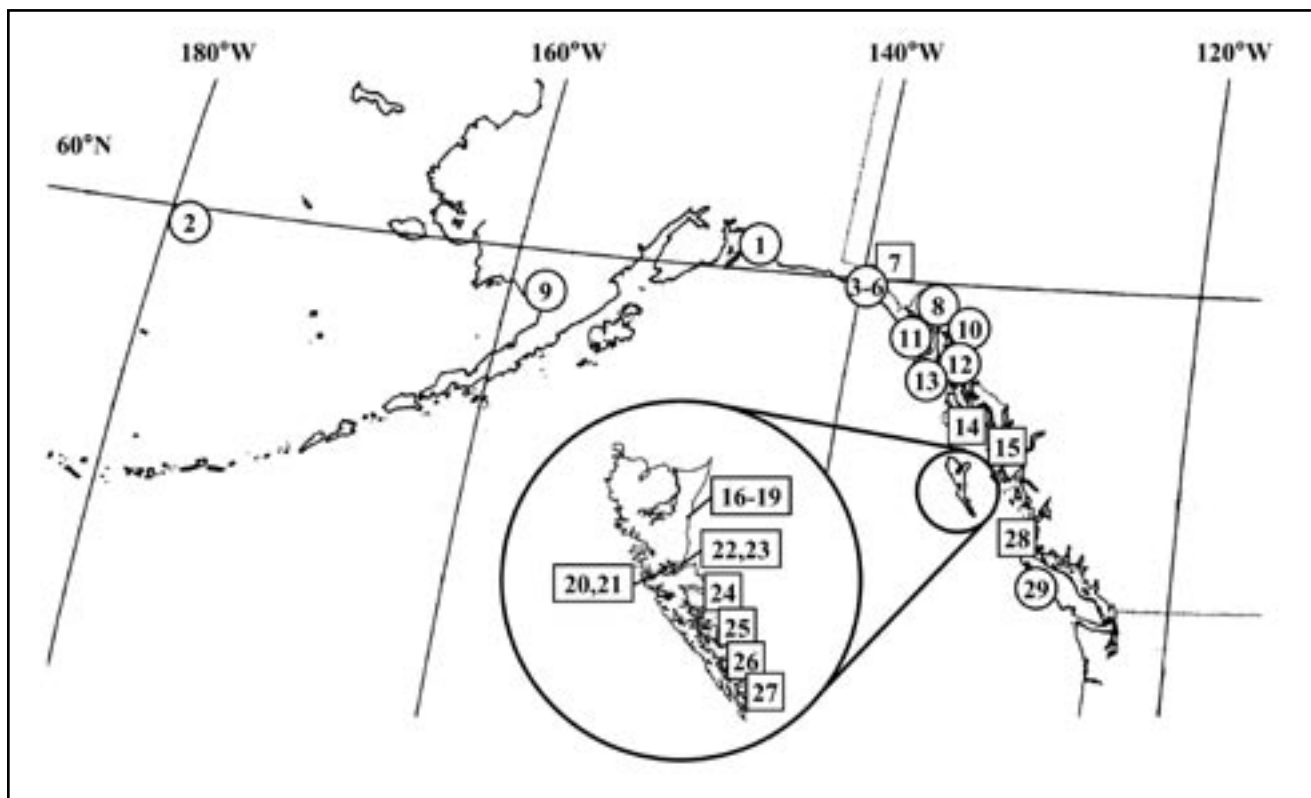


Figure 1.—Distribution of white sharks, *Carcharodon carcharias*, from British Columbia and Alaska, 1961–2004. Numbers correspond to records in Table 1. Squares represent strandings and circles show captures or observations by competent observers.

unambiguous photographs in 21 (72.4%) records. Representative photographic evidence supporting 10 (34.5%) records is presented in Figure 2.

Reported lengths of white sharks ranged from 2.4 to 6.2 m TL, with a mean of 4.6 m TL, a standard deviation of 0.8 m, and 95% confidence limits of ± 0.8 m. Only specimens 13 and 15 were measured, but the estimated length of specimens 16 and 26 was tested against the size of the teeth examined by the author. Extrapolating from the largest lower anterior tooth of specimen 15 gives an estimated enameloid height for the corresponding upper anterior tooth of 3.8 cm and an estimated TL between 3.8 and 5.4 m. Extrapolating from the first upper lateral tooth of specimen 26 gives an estimated TL between 3.9 and 5.2 m. White shark lengths calculated from tooth allometry thus agree well with estimates made by observers in the field.

Shark mass was not measured for any record but was estimated for specimens 13 and 20 as 900 kg and 1,135 kg, respectively. The calculated mass given for specimen 13, based on a linear length-girth-mass relationship, is 326 kg (58.7%) larger than the predicted mass of 574 kg based on length-mass regressions given in Mollet and Cailliet (1996). The estimated mass for specimen 20 given in Hauka³ compares well with the predicted mass of 1,310 kg based on Mollet and Cailliet (1996), being only 175 kg (15.4%) too low.

Shark sex was reported in only one record, specimen 15, which featured conspicuous claspers. Palpation revealed that the claspers were highly calcified; upon dissection, the epididymis was found to be highly convoluted and semen

was identified in the clasper grooves (Larson⁴). Ventral photos of specimen 16 (Fig. 2h) clearly show that it lacks claspers. The internal organs were not examined.

Stomach contents were reliably reported for only four records, numbers 3, 9, 13, and 15. Reported stomach content in specimen 20 (Hauka³) is regarded as dubious, based on interviews with the attending fisheries officer (Sjolund⁵). Predation was reported in two cases, records 2 and 6, and was reasonably inferred in one other, record 1. Diet of white sharks from the study area includes salmonids, such as the sockeye salmon,

⁴Larson, R. 2001. United States Department of Agriculture, Forest Service, Subsistence Fisheries, Petersburg/Wrangell Ranger Districts, Petersburg, Alaska. Personal commun.

⁵Sjolund, R. 2002. Fisheries and Oceans Canada, North Coast Area, Conservation and Protection. Queen Charlotte City, Queen Charlotte Islands, British Columbia, Canada. Personal commun.

³Hauka, D. 1988. Tide yields great white shark. The Province (Vancouver, B.C.), 6 Jan. 1988, p. 5.

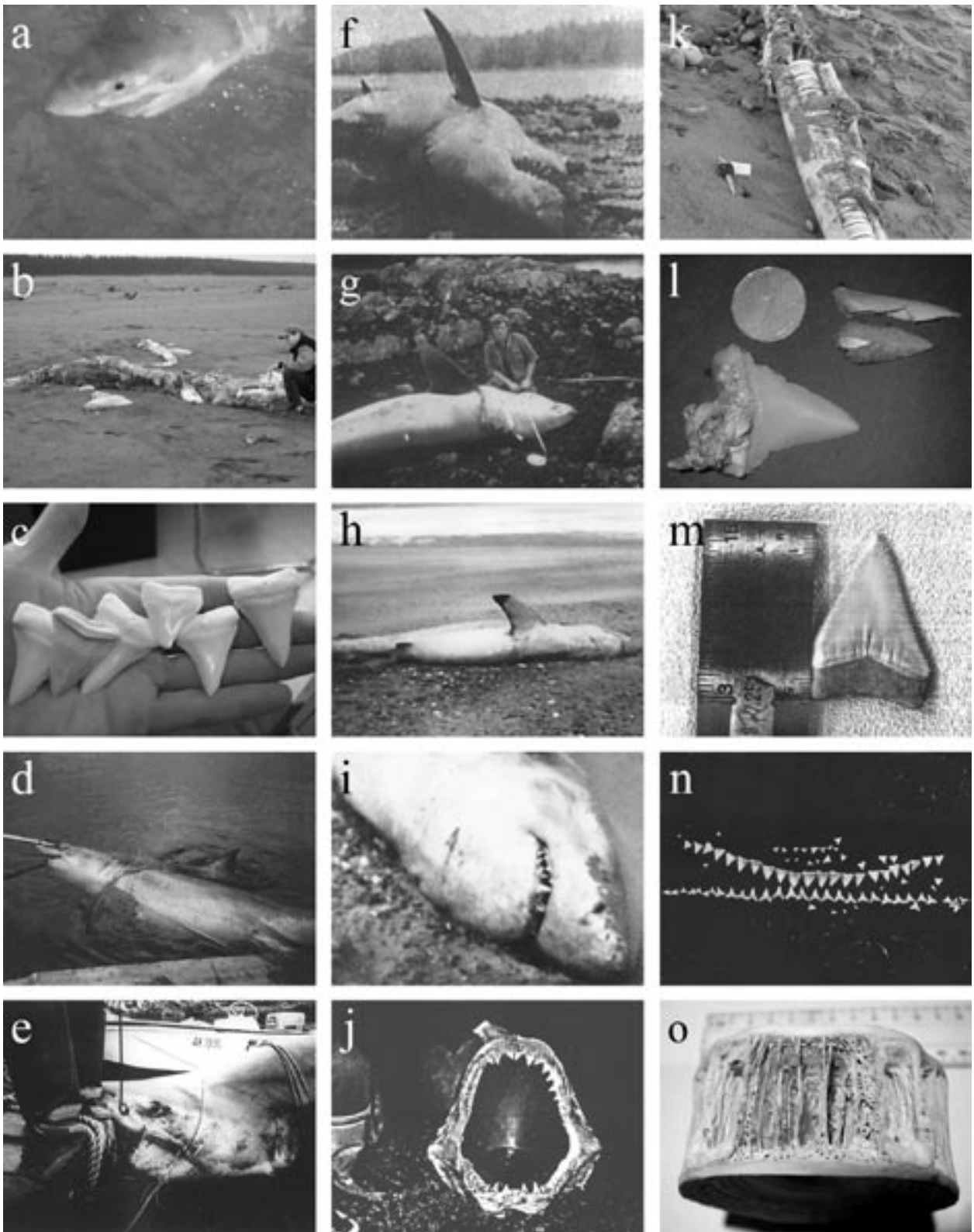


Figure 2.—White sharks from British Columbia and Alaska. Record numbers correspond with Table 1. a, record 6 (photo courtesy J. Huppert); b and c, record 7 (photos courtesy D. Courtney); d and e, record 13 (photo courtesy D. Urias); f, record 14 (photo courtesy Ruth Ann's Pub); g, record 15 (photo courtesy R. Larson); h and i, record 16 (photos courtesy D. and A. Manson); j, record 17 (photo courtesy R. Sjolund); k and l, record 19 (photos courtesy J. Davis); m and n, record 23 (photos courtesy R. Sjolund); o, record 28.

Oncorhynchus nerka; Pacific halibut, *Hippoglossus stenolepis*; and at least two species of pinniped, the Steller sea lion, *Eumetopias jubatus*, and the harbor seal, *Phoca vitulina richardii*.

White shark records from the study area occurred during March, and May through December; most occurred during the months of October (28%) and September (21%), while none occurred

during the months of January, February, or April.

Sea surface temperature (SST) at locations and times of white shark records from British Columbia and Alaska ranged from 16°C to at least 6.4°C and possibly to 5.0°C (which represents the lower value of the temperature category obtained from NOAA thermographic data). Mean temperature was 11.1°C, with a standard deviation of 3.0°C (Fig. 3).

Sixteen specimens (55.2% of records, numbers 7 and 14–28, inclusive) were reported stranded or beached between July and mid December, with 75% of these occurring in September and October. SST at stranding locations and times ranged from 5.7–16°C (mean 11.4°C, SD 4.0°C). Twelve of 16 (75%) strandings occurred between 52 and 54 degrees north latitude, while 12 of 13 (92%) of non-stranding records occurred at or north of latitude 56 degrees (Fig. 4).

El Niño events (1950–2004), with “strong” oscillations indicated in bold type face, occurred during the years: 1957–1958, 1965–1966, **1972–1973**, 1977–1978, **1982–1983**, 1987–1988, **1991–1992**, 1992–1993, 1994–1995, **1997–1998**, 2002–2003, and 2003–2004 (Allan et al. 1996; Null⁶). Yearly breakdown of white shark records in British Columbia and Alaska waters and occurrence of El Niño and La Niña events, differentiated into “strong”, “normal”, and “weak” intensities, is presented in Figure 5.

Statistical analysis of two-sided χ^2 test of 2 × 2 contingency tables of observed vs. expected occurrences of white sharks in boreal waters of the eastern North Pacific if El Niño events had no effect (H_{0n}) resulted in a value of 0.441 (Table 2). This value is insufficient to reject H_{0n} ($P=0.05$), which requires a χ^2 value of > 3.84 (Campbell, 1974). The same test was performed if “strong” El Niño events (H_{0s}) and La Niña (H_{0l}) events had no effect, resulting in values of 0.0019 and 5.4, respectively. The first value is insufficient to reject H_{0s} but the second

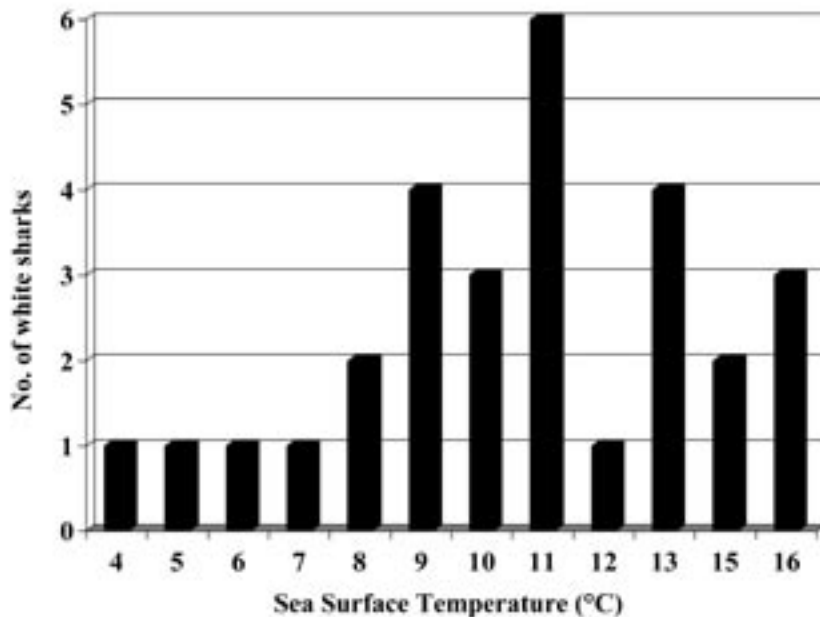


Figure 3.—Sea surface temperature vs. number of white shark records from British Columbia and Alaska (1961–2004).

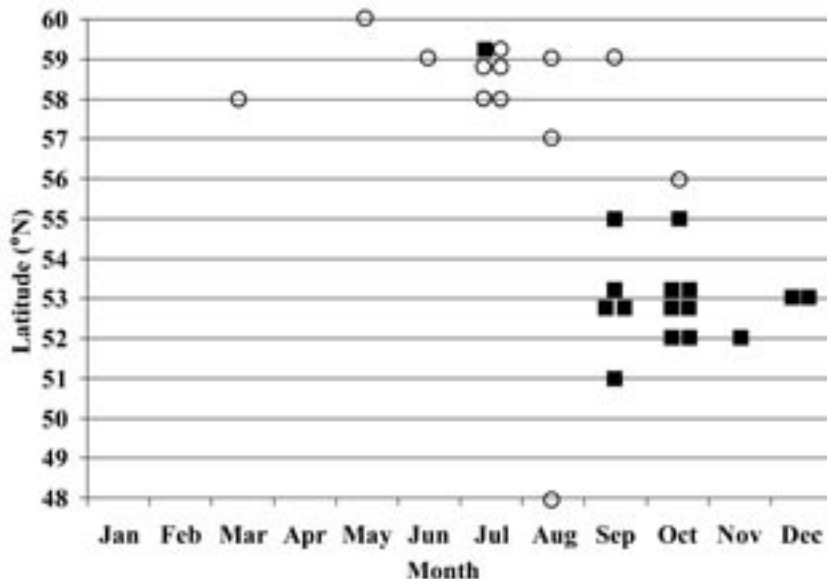


Figure 4.—Month of 16 white shark strandings (black squares) and 13 non-strandings (open circles) vs. latitude (1961–2004).

⁶Null, J. 2004. El Niño and La Niña years: a consensus list. <http://ggweather.com/enso/years.htm>.

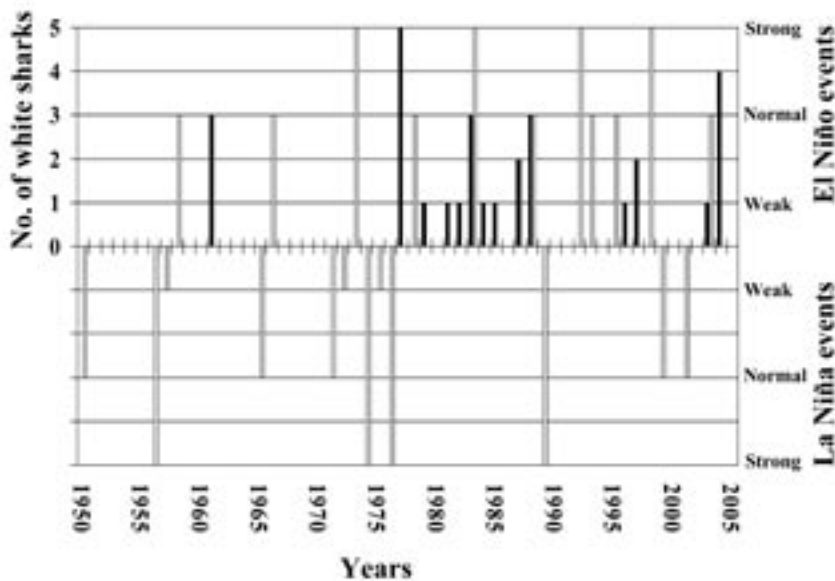


Figure 5.—Relationship between “strong”, “normal”, and “weak” ENSO events (1950–2004) and number of white shark records from British Columbia and Alaska. Years of ENSO events are indicated by white bars, where El Niño events are indicated by ascending bars, and La Niña events by descending bars. Dark bars represent the number of white shark records during the year indicated.

is sufficient to reject H_0 , both of which require a χ^2 value of > 3.84 .

Discussion

Distribution and Abundance

The 19 new records presented here indicate that white sharks are significantly more abundant in northerly waters of the eastern Pacific than previously reported. Record 1 provides circumstantial evidence for the northernmost record of a white shark (lat. $60^{\circ}17'N$). Record 2, in which the shark was seen by a competent observer, occurred only slightly south (lat. $59^{\circ}56'N$), and likewise extends the known northerly range of this species. Previously, the northernmost occurrence of a white shark in the eastern North Pacific was lat. $59^{\circ}30'N$, (Paust and Smith, 1986). For comparative purposes, the northernmost records of white sharks from other areas and their latitudes are: western North Pacific = Furubira, Hokkaido, Japan (lat. $43^{\circ}23'N$) (Nakano and Nakaya, 1987; Nakaya, 1994); western North Atlantic = Hare Bay, Newfoundland, Canada (lat. $51^{\circ}18'N$)

(Templeman, 1963); eastern North Atlantic = La Rochelle, Bay of Biscay, France (lat. $46^{\circ}10'N$) (Moreau, 1881); Mediterranean Sea = Santa Croce di Trieste, Adriatic Sea, Italy (lat. $45^{\circ}45'N$) (Brusina, 1888). Record 2 extends the northernmost range of the white shark north $26'$ (48 km), while record 1 extends it $47'$ (87 km) north. The southernmost record of a white shark is from Middle Bay, Campbell Island, New Zealand (lat. $52^{\circ}30'S$), verified on the basis of a tooth fragment removed from a diver (Francis⁷). This is latitudinally consistent with the northernmost records reported here. Thus the known latitudinal range of the white shark encompasses more than 115° , giving this species one of the broadest ranges of any elasmobranch.

Size

White sharks recorded from British Columbia and Alaska waters were generally large, with 95% falling between 3.8

⁷Francis, M. 2004. National Institute of Water and Atmospheric Research. Wellington, New Zealand. Personal commun.

Table 2.—Contingency values and results of two-sided χ^2 test of 2×2 contingency tables of observed vs. expected occurrences of white sharks in boreal waters of the eastern North Pacific if El Niño events had no effect (H_{0n}), if “strong” El Niño events had no effect (H_{0s}), and if La Niña events had no effect (H_{0l}).

El Niño	ENSO event years		Total
	El Niño	Not El Niño	
Observed:			
White Shark	4	10	14
No White Sharks	8	32	40
Total	12	42	54
Expected:			
White Shark	3.11	10.89	14
No White Sharks	8.89	31.11	40
Total	12	42	54
$\chi^2 = 0.441$, insufficient to reject H_{0n}			
Strong El Niño	Strong El Niño	Not strong El Niño	Total
Observed:			
White Shark	1	13	14
No White Sharks	3	37	40
Total	4	50	54
Expected:			
White Shark	1.04	12.96	14
No White Sharks	2.96	37.04	40
Total	4	50	54
$\chi^2 = 0.002$, insufficient to reject H_{0s}			
La Niña	La Niña	Not La Niña	Total
Observed:			
White Shark	0	14	14
No White Sharks	12	28	40
Total	12	42	54
Expected:			
White Shark	3.11	10.89	14
No White Sharks	8.89	31.11	40
Total	12	42	54
$\chi^2 = 5.40$, sufficient to reject H_{0l}			

and 5.4 m TL. Large body size confers significant advantages in thermoregulation, hydrodynamics, and energy storage (Baker, 1978; Cossins and Bowler, 1987; Webb, 1994) and may enable white sharks to exploit rich feeding resources at boreal latitudes (Nybakken, 1988).

Sex

From the highly calcified claspers and condition of the reproductive tract of the male white shark in record 15, it can be concluded that this animal was sexually mature. Francis (1996) concluded that most females of this species become sexually mature between 4.5 and 5 m TL. Based on the estimated size of the female specimen in record 16, it is likely that it was sexually mature. Therefore, sexually mature white sharks of both sexes occur in British Columbia and Alaska waters, although they do not necessarily reproduce there.

Diet

White shark diet from the study area is similar to that reported for this species from Washington and northern California waters (Bonham, 1942; LeMier, 1951; Klimley, 1985). This diet broadly overlaps that reported in killer whales, *Orcinus orca*, from the region (Felleman et al., 1991), raising the possibility of trophic competition (Heithaus, 2001), competitive displacement, or even predation (Pyle et al., 1999) by this mammalian apex predator. In any case, white sharks actively feed in British Columbia and Alaska waters.

Seasonality

Seasonal distribution of white sharks in British Columbia and Alaska waters is: 6.9% spring, 34.5% summer, 51.7% autumn, and 6.9% winter. This roughly normal distribution may reflect favored water temperature regimes of white sharks, that of its prey, or a paucity of observers in the study area during the coldest and stormiest seasons. Seventeen of 29 (58.6%) white shark records reported in this study occurred from August to October. A similar seasonal pattern of occurrence has been documented in sea turtle records from British Columbia and Alaska between 1960 and 2000 (Hodge and Wing, 2000; McAlpine et al., 2002). In his analysis of white shark records from southern California to southeast Alaska, Klimley (1985) found 54 of 108 (50.0%) records occurred during the same months. Thus, seasonal occurrence of white sharks in the northernmost part of their range in the eastern North Pacific is similar to that in warmer waters south of Point Conception.

Sea Surface Temperature

The known or suspected SST range of white sharks from cold waters of British Columbia and Alaska is 16°C to between 6.4°C and 5.0°C. The latter figure is consistent with ambient temperatures reported by Boustany et al. (2002) for white sharks at depth and extends the lower extreme of the range of SST (7–27°C) from which white sharks have been previously reported (Nakaya, 1994). SST for white shark records presented here is

roughly normally distributed, suggesting that those temperatures from which most records occurred (9.6°C–12.7°C) may represent favored temperature regime of white sharks or possibly their prey. Eurythermal tolerance of white sharks is probably due, in part, to their ability to thermoregulate (Carey et al., 1982; Goldman, 1997). Block et al. (1993) suggest the evolution of endothermy in fishes, including lamnids such as the white shark, was selected to permit niche expansion rather than increased aerobic capacity. This suggestion has been strongly criticized on physiological grounds (Brill et al., 1998; Katz, 2002). Heat retention in the lateral swimming musculature of white sharks may increase the rapidity and strength of muscle contraction and thus enhance their tailbeat frequency and swimming power (Tricas and McCosker, 1984). These benefits, combined with large size and efficient locomotion (Compagno, 1984), may have enabled white sharks to exploit the resources of cold waters of the eastern North Pacific.

White Shark Strandings

White shark strandings have previously been reported rarely in the primary literature. Three white shark strandings have been reported from the northern Mediterranean (Barrul, 1993; Fergusson, 1996; Munthe⁸), one from the eastern South Atlantic (Maxwell⁹), and five from the eastern North Pacific—two from British Columbia (Pike, 1962; Coad, 1995), one from Alaska (Royce, 1963) and two from California (Le Boeuf et al., 1982). Strandings in this study occurred over a narrower range of SST than non-strandings, but mean SST of strandings and non-strandings were not significantly different. White shark strandings are relatively common in the study area. In general, white shark strandings occurred later in the year and at lower latitudes than non-strandings (Fig. 4). This appar-

ent latitudinal difference may represent observer bias, as the Aleutian Islands and much of the Alaska coastline south of 59 degrees is not readily accessible to beachcombing (Hodge and Wing, 2000). Most (68.8%) white shark strandings occurred along the eastern shore of the Queen Charlotte Islands, but this may also represent a bias in human distribution, as the exposed western coasts of these islands are virtually uninhabited (Sjolund¹⁰). A similar bias of cetacean and teleost stranding records has been noted along the east coast of the islands of New Zealand and the United Kingdom, which can also be attributed to demography (McCann, 1964). Lack of biological data on stranded white sharks from the study area preclude detailed analysis of this phenomenon and frustrate attempts to identify causal factors.

Correlation With ENSO Events

No clear correlation exists between white shark records in the study area and ENSO events. Since onset of El Niño events typically occurs in December (Glantz, 1996), they cannot be causally related to white shark records from earlier in the same year. Therefore, the following records are considered unrelated to El Niño events: records 15, 16, 22, 25, and 26 in 1977; record 9 in 1982; record 23 in 1987. It is feasible to link some white shark records from British Columbia and Alaska to concurrent El Niño events (1982–1983: records 11, 12, 18; 1987–1988: records 17, 21, 24; 1997–1998: records 4, 5; 2002–2003: record 7; 2003–2004: records 8, 19, 28). But the lack of white shark records during other El Niño events suggests there may be no causal relationship between these events and the occurrence of white sharks in British Columbia and Alaska waters. Further, the correlation between “strong” El Niño events is weaker than for El Niños as a whole, contrary to what one would expect if there were a positive correlation between El Niño

⁸Munthe, A. 1928. The story of San Michele. [No publ. or city listed; unpagin.]

⁹Maxwell, C. 1991. The shark and the scuba diver. In T. Condon (Editor), Great white sharks—*Carcharodon carcharias*: a perspective, p. 16–17. Under Water, May 1991. Northway, (Natal), South Africa.

¹⁰Sjolund, R. 2002. Fisheries and Oceans Canada, North Coast Area, Conservation and Protection. Queen Charlotte City, Queen Charlotte Islands, British Columbia, Canada. Personal commun.

and occurrence of white sharks at boreal latitudes in the eastern North Pacific. Intriguingly, although El Niño events could not be statistically correlated with white shark records from British Columbia and Alaska waters, there appears to be a significant negative correlation between La Niña events and white shark records from the region. More records of white sharks from the study area are needed to resolve this apparent contradiction. Hodge and Wing (2000) noted a similar lack of correlation between warm-water years and sea turtle occurrence in Alaska waters between 1960 and 1988.

North Pacific Distribution

The new records presented here indicate that white sharks are more abundant in the cold waters of British Columbia and Alaska than previous records suggest. For each of the 19 new records reported here, there is at least one other report that could not be verified. Two of these anecdotal reports have, on investigation, proved to be hoaxes (Martin¹¹, Wing¹²), but it is likely that at least some of the remaining reports represent valid records. It is not yet clear whether the authenticated northerly records collected here represent a normal part of the white shark's range in the eastern North Pacific or extralimital strays dispersed from a more southerly (Californian) center of abundance. Unfortunately, the inherent logistical challenges (expansiveness of the area, inaccessibility of much of the coastline, and inclemency of weather, especially at high latitudes during winter months) render comprehensive monitoring or randomized sampling difficult, if not impossible, at present. Likewise, further work is needed to determine whether white sharks from the eastern North Pacific range across the Aleutian Archipelago to form a continuous population with those from Japan. It is feasible that white sharks from California, Alaska, Japan, and Hawaii form a single, interbreeding population, but this remains to be demonstrated.

¹¹Author. Unpubl. data.

¹²Wing, B. L. 2005. National Marine Fisheries Service, Auke Bay Laboratory, Juneau, Alaska. Personal commun.

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Table 1.—White shark records from British Columbia and Alaska waters, 1961–96. Record numbers correspond with those mapped in Figure 1.

No.	Location	Latitude/Longitude	Date	Shark TL(m)	SST(°C)	Stranded (Y/N)	ID basis	Observers and biologists	Source
1	Cordova, Gulf of Alaska, AK Remarks: Prey/Stomach contents - <i>Oncorhynchus nerka</i> , specimen at Oregon State University (OU 11040)	60°17'N, 145°35'W	27 May 1985	4	5.0–6.4	N	Tooth punctures on salmon carcass	J. Thomas, S. F. Cook	Cook ¹
2	NW Bering Sea Remarks: Prey/Stomach contents - <i>Eumetopias jubatus</i>	59°56'N, 178°56'W	11 Aug. 1979	4+	9.5	N	Experienced observer	S. F. Cook	Cook ¹
3	Ocean Cape, Yakutat, AK Remarks: Prey/Stomach contents - 3 <i>Phoca vitulina richardii</i> , seals well macerated, decapitated	59°30'N, 139°50'W	Early Summer 1981	6	8.9–10.8	N	Jaws, teeth	R. Maygard, B. Paust, R. Smith	Paust and Smith (1986)
4	Yakutat Bay, AK Remarks: Attempts at independent verification unsuccessful	59°24'N, 140°00'W	Summer 1997		15	N	Experienced observer	B. Johnson	Mecklenburg et. al. (2002)
5	Yakutat Bay, AK Remarks: Attempts at independent verification unsuccessful	59°24'N, 140°00'W	Summer 1997		15	N	Experienced observer	B. Johnson	Mecklenburg et. al. (2002)
6	14 miles off Yakutat, AK Remarks: Bit piece from hooked halibut	59°24'N, 140°00'W	6 Sept. 2004	6	16	N	Photo	J. Huppert	Collier ²
7	Yakutat, AK, ½ Mile E of mouth of Akwe River Remarks: Very decomposed, remains scavenged/scattered by bears	59°20'N, 139°26'W	Summer 2003	4.6	13	Y	Photos	C. Russell, D. Courtney	Russell and Courtney ³
8	Sitka, AK Remarks: Shark did not linger, no photos available	59°00'N, 135°08'W	July 2004	2.4	16.0	N	Experienced observers	J. Karinen, D. Hanselman	Karinen and Hanselman ⁴
9	Naknek, Bristol Bay, AK Remarks: Prey/Stomach contents - <i>Oncorhynchus</i> spp.	58°44'N, 157°30'W	Summer 1982	5+	0–9.8	N	Anecdotal	S. F. Cook	Cook ¹
10	Lynn Canal, AK Remarks: Shark chummed, killed, but lost	58°30'N, 135°09'W	Mar. 1984		6	N	Anecdotal	R. Straty	Karinen et al. (1985), Wing and Karinen ⁵
11	Cross Sound, AK Remarks: Collected by salmon trawler	58°06'N, 136°18'W	Summer 1983	4.3	13	N	Jaws, tail, photos	J. Karinen, R. Straty	Karinen et al. (1985), Wing and Karinen ⁵
12	Stephen's Passage, Hobart Bay, AK Remarks: Unconfirmed sightings (<i>Lamna ditropis</i> also seen)	57°30'N, 133°30'W	Aug.–Sept. 1983		13	N	Anecdotal	R. Straty	Karinen et al. (1985), Wing and Karinen ⁵
13	Picnic Cove, Goddard, AK Remarks: Prey/Stomach contents - 45 kg <i>Hippoglossus stenolepis</i> , Shark Mass = 900 kg (est.); Shark Girth = 2.6 m; liver produced 9.5 l of oil	56°51'N, 135°02'W	Late Oct. 1996	4	10	N	Teeth, photo	J. and F. Timmer, S. Sturm, D. Urias	Urias ⁶
14	Craig, AK	55°28'N, 133°08'W	24 Oct. 1961	4.7	9.6	Y	Teeth, photo	L. R. Hall, W. F. Royce	Royce (1963), Larson ⁷
15	Dall Head, South tip of Gravina Island, AK Remarks: Shark Sex = M, sexually mature; Prey/Stomach contents - partial liver of <i>Phoca vitulina richardii</i> , 100's of lenses of <i>Oncorhynchus</i> spp.; shark girth = 2.45 m; teleost lenses ID by J.E. Fitch	55°12'N, 131°50'W	30 Sept. 1977	4.7	11.4	Y	Teeth, photos	H. Ludwigsen, R. Larson, G. Freitag	Larson ⁷
16	Cape Ball, Graham Island, QCI, BC Remarks: Shark Sex = F, probably sexually mature	53°42'N, 131°52'W	20 Oct. 1977	5.5	10.8	Y	Teeth, photos	D. and A. Manson, G. Hewlett ⁸	Manson ⁹
17	East Beach, near Cape Ball, Graham Island, QCI, BC	53°42'N, 131°52'W	Autumn 1988	±5	11.3	Y	Photo	T. Husband, R. Sjolund	Sjolund ¹⁰
18	Cape Ball, Graham Island, QCI, BC	53°42'N, 131°52'W	Late Summer/ Early Autumn 1983	±4	11.9	Y	Teeth		CBC News Radio, October 1990
19	Cape Ball, Graham Island, QCI, BC Remarks: 25 vertebrae, bits of cartilage (including left Meckel's cartilage), chondrocranium, teeth and patches of skin	53°42'N, 131°52'W	25 Oct. 2004	4.6	12	Y	Teeth, photos	J. Davis, C. Tarver	Davis ¹¹
20	Long Inlet, Graham Island, QCI, BC Remarks: Prey/Stomach contents—probably <i>Phoca vitulina richardii</i> ; Shark Mass = 1,135 kg (est.)	53°12'N, 132°19'W	16 Dec. 1986	5	8.2	Y	Teeth	L. Vogstad, R. Sjolund, M. Saunders	Sjolund ¹⁰
21	Long Inlet, Graham Island, QCI, BC	53°12'N, 132°19'W	16 Dec. 1987	5.2	8.2	Y	Teeth		Coad (1995), Saunders ¹²
22	Lawn Point, Graham Island, QCI, BC Remarks: Shark in advanced state of decomposition when found	53°25'N, 131°55'W	Late Sept. 1977	3–4	11.9	Y	Teeth	K. Harley	Sjolund ¹⁰
23	Near Queen Charlotte City, Graham Island, QCI, BC	53°16'N, 132°04'W	Late Summer/ Early Autumn 1987	±5	11.8	Y	Teeth	W. Noddin, R. Sjolund	Sjolund ¹⁰
24	Skidegate Inlet, Graham Island, QCI, BC	53°12'N, 132°00'W	Autumn 1988	4–5	11.3	Y	Teeth		CBC News Radio, October 1990
25	Un-named beach, Lyell Island, QCI, BC	52°41'N, 131°21'W	25 Nov. 1977	4.5	7.6	Y	Teeth	B. Wilchere, K. S. Ketchen	Ketchen ¹³
26	Un-named beach, Moresby Island, QCI, BC	52°31'N, 131°34'W	Oct. 1977	4.5	10.8	Y	Teeth	K. S. Ketchen	Ketchen ¹³
27	Creek Mouth, Island Bay, QCI, BC	52°21'N, 131°24'W	24 Oct. 1961	3.4	9.6	Y	Teeth	K. R. Harley	Pike (1962)
28	North side of Goose Island, Queen Charlotte Sound, BC Remarks: Vertebral samples examined by author	51°32'N, 128°17'W	4 Sept. 2004	5.6	16	Y	2.5 m of vertebrae	J. Watson, G. Ellis	Wallace ¹⁴
29	Esperanza Inlet, Vancouver Island, BC Remarks: Shark attacked canvas float bag of commercial salmon fishing vessel	48°48'N, 127°07'W	17 Aug. 1961	4–6	13.8	N	Tooth and several fragments	G. Trenholme, K. S. Ketchen	Collier et al. (1996)

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