1	A review of the Pacific sleeper shark Somniosus pacificus: biology and fishery interactions
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34	
35	Abstract
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37	The Pacific sleeper shark Somniosus pacificus is a large-bodied and broad-ranging squaliform
38	shark that occupies diverse habitats throughout the Pacific Ocean. Despite its large size and
39	occurrence as bycatch in various commercial fisheries, little is known about even the most basic
40	aspects of its biology and ecology. Observed declines in certain parts of its range, coupled with
41	life history characteristics associated with low productivity, have led to conservation concerns
42	for this cryptic but charismatic species. Here, we provide a comprehensive review of the current
43	state of knowledge regarding the distribution, diet, life history, and other aspects of the Pacific
44	sleeper shark and present updated fisheries and survey data for the eastern North Pacific Ocean.
45	The most pressing research gaps identified during the course of this review concern habitat use at
46	different life stages and basic life history information. While work is currently in progress to
47	expand our base of knowledge for this species, we recommend a precautionary approach to
48	management until sufficient information becomes available to ensure its conservation.
49	
50	Keywords
51	elasmobranch, bycatch, North Pacific Ocean, ecology, life history, deep-sea
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56 Introduction

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58 The Pacific sleeper shark *Somniosus pacificus* ranges broadly throughout the Pacific Ocean, yet 59 it has been poorly studied. Deficiencies in our understanding are due in part to its lack of 60 commercial value, its occupancy in habitats that are difficult to sample with traditional survey 61 methods, and logistical challenges associated with safely landing, handling, and sampling such a 62 large-bodied animal. The lack of data makes it challenging to adequately monitor and assess the 63 stock status of this species. In general, the life history traits of elasmobranchs (e.g., slow growth, 64 late maturity, high longevity) make them susceptible to overfishing (Musick et al. 2000; 65 Simpfendorfer and Kyne 2009), and there is reason to believe that the Pacific sleeper shark may 66 be especially vulnerable (Ormseth and Spencer 2011). 67 The first objective of this review was to collate the limited information that is known 68 about the Pacific sleeper shark from the available published literature. The second objective was 69 to identify and prioritize the most pressing knowledge gaps. The final objective was to outline 70 potential directions of future research and describe the implications of that research for 71 ultimately improving management of the species. This is particularly important as the

72 International Union for Conservation of Nature and Natural Resources (IUCN) recently changed

73 its Red List designation of the Pacific sleeper shark from Data Deficient to Near Threatened due

to this species' high vulnerability and apparent population declines in portions of its range

75 (Rigby et al. 2021). Furthermore, a recent review of the stock structure of the Pacific sleeper

shark in Alaska waters highlighted potential conservation concerns, and the North Pacific

77 Fishery Management Council's Scientific and Statistical Committee (SSC) acknowledged these

concerns in recent stock assessment reviews for Alaska management areas (Matta et al. 2022;

79 SSC 2022).

Here, we summarize the existing body of literature on the Pacific sleeper shark. We also present new information from the waters of Alaska, British Columbia, and the US West Coast on survey and fishery distribution, catch, and size. Whenever possible, we describe publications and data that are specific to the Pacific sleeper shark. However, for some topics where studies are limited, we refer to publications on its congener, the Greenland shark *Somniosus microcephalus*, to make inferences regarding the biology of the Pacific sleeper shark. Compared to the Pacific sleeper shark, more information is available for the Greenland shark, with an explosion in 87 focused research studies in recent years. Literature was gathered from the Clarivate Web of

88 Science (www.webofscience.com) using the search terms "sleeper shark", "Greenland shark",

89 "Somniosus", and "Somniosidae", as well as from the citation sections of papers already in hand.

90 We conclude with suggestions for new research on the Pacific sleeper shark to better understand

- 91 how to more appropriately assess and manage this species.
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- 93

94 **Taxonomy and Population Dynamics**

95

96 Species description and systematics

97 The Pacific sleeper shark (Fig. 1), first described by Bigelow and Schroeder (1944), is a member 98 of the Order Squaliformes, a diverse taxonomic grouping that includes bramble 99 (Echinorhinidae), lantern (Etmopteridae), rough (Oxynotidae), kitefin (Dalatiidae), gulper 100 (Centrophoridae), sleeper (Somniosidae), and dogfish sharks (Squalidae). Sharks in Squaliformes 101 are characterized as having two dorsal fins (with or without fin spines), spiracles, no anal fin or 102 nictitating membrane, and five pairs of gill slits (Compagno 1984). The Pacific sleeper shark is a 103 large-bodied shark with gray to brown or black dorsal coloration and slightly lighter coloration 104 ventrally (Fig. 1a; Ebert 2003; Stevenson et al. 2007). This species, frequently described using 105 adjectives such as "flabby" and "sluggish" in the literature, possesses small eyes, mouth, and 106 teeth relative to its size (Fig. 1b), and a broad heterocercal tail (Ebert 2003).

107 Pacific sleeper sharks are members of the genus Somniosus (Family Somniosidae), found 108 throughout the world from shallow polar waters to abyssal depths at temperate and tropical 109 latitudes (Compagno 1984; Ebert 2003). Systematic classifications within this genus have varied 110 over time, largely due to the rarity of encounters in many regions and similarities in appearance 111 among Somniosus species. Studies on meristic and morphological characteristics have suggested 112 that Somniosus comprises five species in two subgenera: subgenus Somniosus containing three 113 large-bodied species (Greenland shark S. microcephalus, Pacific sleeper shark S. pacificus, and 114 southern sleeper shark Somniosus antarcticus), and subgenus Rhinoscymnus containing two 115 small-bodied species (frog shark Somniosus longus and little sleeper shark Somniosus rostratus) 116 (Yano et al. 2004). Recently, a small-bodied shark collected from waters off Taiwan was 117 proposed as a new species (the Taiwan sleeper shark, *Somniosus (Rhinoscymnus) cheni* sp. nov.) (Hsu et al. 2020). Besides adult size, the two subgenera also differ in the level of calcification of
their vertebral column, spiral valve and vertebral counts, tooth shape and the number of tooth
rows, and dermal denticle shape (Yano et al. 2004).

121 Yano et al. (2004) proposed that morphological features including dorsal fin height and 122 position, the number of spiral valves and vertebrae, and the distance from the tip of the snout to 123 the first gill slit, could generally be used to distinguish among the three putative large-bodied 124 Somniosus (Somniosus) species. Based on these findings, Yano et al. (2004) concluded that each 125 of the species is largely confined to specific geographical regions, with S. microcephalus 126 occupying the North Atlantic and Arctic oceans, S. pacificus occupying the North Pacific and 127 Arctic oceans, and S. antarcticus occupying the Southern Hemisphere, despite some degree of overlap in the morphological characteristics measured. Additionally, ongoing, directed research 128 129 suggests that the morphometric relationships identified in S. pacificus by Yano et al. (2004) are 130 inconsistent with data collected in situ during optimal field conditions, further clouding the 131 purported physical distinctions among the three species (Fuller et al. in prep.).

132 Genetic analyses have called into question the morphologically and geographically based 133 classifications of species within the Somniosus subgenus. Comparison of nuclear and 134 mitochondrial DNA markers has provided strong support for considering S. microcephalus and 135 S. pacificus as distinct but closely-related sister species (Murray et al. 2008; Santaquiteria et al. 136 2017; Walter et al. 2017). However, there is genetic evidence to support possible hybridization 137 between S. pacificus and S. microcephalus in the Canadian Arctic where their ranges may 138 overlap (Hussey et al. 2015; Walter et al. 2017). A specimen collected from the Mid-Atlantic 139 Ridge, near the Azores, had a genetic signature concordant with S. pacificus, and a S. 140 microcephalus-S. pacificus hybrid was detected in the Gulf of Mexico (Walter et al. 2017), 141 further complicating the simple distinction of species along geographical boundaries. Most 142 strikingly, multiple investigators have concluded that there isn't sufficient genetic variation in 143 mitochondrial or nuclear DNA to distinguish between S. pacificus and S. antarcticus, suggesting 144 that despite the morphometric differences noted by Yano et al. (2004), they comprise a single 145 species ranging throughout the Pacific Ocean, warranting revision of the taxon (Murray et al. 146 2008; Christensen 2022; Timm et al. 2022). There is also currently little evidence to support the 147 existence of subpopulations of S. pacificus. Using population genomics, Timm et al. (2022) 148 noted a high degree of similarity among individuals, suggesting persistent gene flow and a lack

- 149 of significant population genetic stock structure in either *S. pacificus* or *S. microcephalus*.
- 150 However, Swintek and Walter (2021) found subtle, but significant, population genetic structure
- 151 based on a suite of microsatellites for *S. microcephalus*. Such analyses may reveal similar
- 152 distinctions that are slight within *S. pacificus*, and it is worthy of further investigation.
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154 **Distribution and abundance**

155 The Pacific sleeper shark is broadly distributed over the continental shelves and slopes of the 156 Pacific Ocean. Its range in the North Pacific Ocean extends from Palau to Taiwan, Korea, Japan, 157 and Siberia, throughout the Bering Sea and Gulf of Alaska, and along the west coast of Canada 158 and the USA to Baja California, Mexico (Tanaka et al. 1982; Applegate et al. 1993; Orlov and 159 Moiseev 1999; Ebert 2003; Wang and Yang 2004; Grigorov and Orlov 2014; Kang et al. 2015; 160 Becerril-Garcia et al. 2020; Tribuzio et al. 2022; Claassens et al. 2023). Its distribution north of 161 the Arctic Circle (66°30' N) is uncertain, and due to a possible overlap in ranges between the two 162 regional species, it may be confused with the Greenland shark in the Canadian Arctic (Ebert 163 2003). One positively identified specimen washed up on the shore at Point Hope, Alaska, on the 164 Chukchi Sea (Benz et al. 2004), although it is possible that this individual drifted northward from 165 the Bering Sea (Love et al. 2005). The Pacific sleeper shark has also been reported in the Salish 166 Sea, the inland waters of Washington State, USA, and British Columbia, Canada, though it is 167 thought to be very rare in this area (Pietsch and Orr 2015).

168 In the Southern Hemisphere, Pacific sleeper sharks have been reported in both the Pacific 169 and Atlantic oceans (e.g., Francis et al. 1988; Crovetto et al. 1992; Cione 1998; de Astarloa et al. 170 1999; Brito 2004). Based on the species descriptions of Yano et al. (2004), these observations 171 had previously been considered likely misidentifications of S. antarcticus (Love et al. 2005; 172 Ebert et al. 2017). However, recent next-generation sequencing has provided a lack of support 173 for S. antarcticus as a separate species and suggests that identifications of S. pacificus in the South Pacific Ocean are legitimate (Christensen 2022; Timm et al. 2022). Broader genetic 174 175 sampling is needed to confirm whether the range of S. pacificus extends outside the Pacific 176 Ocean into regions such as the South Atlantic and Indian oceans (Timm et al. 2022). At tropical 177 low latitudes, Pacific sleeper sharks have been recorded by submersibles, drop cameras, and 178 remotely operated vehicles in deep (1,000-2,000 m) waters off Hawaii, Palau, the Solomon 179 Islands, and Revillagigedo Archipelago National Park, Mexico (Lee 2015; Becerril-Garcia et al.

2020; Claassens et al. 2023; see also observations from the Hawai'i Undersea Research
Laboratory: https://www.soest.hawaii.edu/HURL/).

182 Fisheries-independent surveys differ in their presumed efficacy at catching Pacific 183 sleeper sharks, and therefore it is difficult to accurately estimate population abundance for this 184 species. Catchability is composed of availability (i.e., sharks occur in the same area and depth as 185 the gear) and susceptibility to the gear. Based on available data, it is not possible to evaluate if 186 low levels of catch in fishery-independent surveys, which operate differently from commercial 187 fisheries, are due to Pacific sleeper sharks not being present in the survey area or differences in 188 susceptibility to survey trawl or longline gears. (In this paper, the word "longline" refers to 189 fishing gear that uses extended groundlines with hooks stretched across the seafloor, whereas 190 three-dimensional pots, either fished singularly or strung together on a line, are referred to as 191 "pots".) Further complicating matters is the fact that mature individuals are rarely encountered, 192 either due to occupation of unsurveyed habitats (i.e, not available to the gear) or to susceptibility 193 to the gear (i.e., selectivity). Therefore, a potentially large portion of the population is currently 194 unobserved. Indices of abundance based on trawl survey catches in Alaska waters are generally 195 not considered reliable because they are frequently extrapolated from a relatively small number 196 of hauls with catch (Tribuzio et al. 2022). In some years, particularly in the Bering Sea and 197 Aleutian Islands regions, no specimens are captured during the trawl surveys, despite occurring 198 in trawl fisheries (Tribuzio et al. 2022). Fishery-independent longline surveys, such as those 199 operated by the International Pacific Halibut Commission (IPHC) and the Alaska Department of 200 Fish and Game (ADFG), may therefore be better indicators of stock trends (Matta et al. 2022).

201 Despite the limitations associated with certain gear types, the available survey indices 202 from the waters off Alaska, British Columbia, and the US West Coast appear to indicate long-203 term variation in the abundance of Pacific sleeper sharks (Fig. 2; Tribuzio et al. 2022). While it is 204 important to note that none of the existing surveys were designed to explicitly target Pacific 205 sleeper sharks, it may be possible to infer trends in relative abundance over time. Consistently 206 across almost all areas and surveys, including the IPHC longline survey, which is considered to 207 be the most reliable survey index (Matta et al. 2022), catches were highest in the late 1990s and 208 early 2000s, and have since declined to lower levels (Fig. 2). These trends are reflected in 209 fisheries catches as well (Tribuzio et al. 2022). Mueter and Norcross (2002) noted a significant 210 increase in Pacific sleeper sharks between 1984 and 1996 in the waters off Chirikof and Kodiak

211 Islands, and similarly, a small survey of fishers in Aleut communities provides anecdotal 212 evidence for an increase in this and other shark species in the Bering Sea, eastern Aleutian 213 Islands, and western Gulf of Alaska in the late 1990s and early 2000s (Okey et al. 2007). 214 Subsequent surveys have indicated large reductions in abundance since the mid- to late 2000s to 215 current low levels (Fig. 2). A reduction in the spatial extent of fisheries catches and IPHC survey 216 catches has also been noted in Alaska waters, with fewer sharks observed in the Gulf of Alaska 217 and around the Aleutian Islands in recent years than in the late 1990s to mid-2000s (Matta et al. 218 2022). Similarly, the population off Taiwan, which was once large enough to support a fishery, 219 has since declined (Rigby et al. 2021). However, trawl surveys indicate that Pacific sleeper shark 220 abundance in Russian waters appears to have increased over the past 40 years (Rigby et al. 221 2021). Even though many survey indices represent imperfect estimates of abundance of Pacific 222 sleeper sharks due to issues with catchability and the short length of these time series relative to 223 the potential generation time, they can still identify trends in local stock abundance that may 224 inform stock status and conservation assessments. Technological advances, such as eDNA 225 assays, may help to improve estimates of relative abundance of Pacific sleeper sharks in the 226 future, particularly in environments that cannot be sampled using conventional means (Thomsen 227 et al. 2016).

228 Some older and anecdotal accounts of Pacific sleeper sharks have described them as 229 "common" (e.g., Compagno 1984). This may be due to occasions where multiple, and in some 230 cases, large numbers of sharks are caught in a set, such as reported both contemporarily and 231 historically by fishers operating in certain areas of Southeast Alaska and Prince William Sound 232 (K. R. Fuller, G. C. Dunne, and C. A. Tribuzio, personal communication). Scientific surveys 233 have also occasionally encountered localized large numbers of Pacific sleeper sharks with 234 relatively little fishing effort. For example, two recent charters targeting Pacific sleeper sharks 235 for a research study succeeded in catching 63 sharks in under seven days at inshore locations in 236 Southeast Alaska (K. R. Fuller and C. A. Tribuzio, unpublished data). Another instance occurred 237 in 2002, when the Resource Assessment and Conservation Engineering (National Oceanic and 238 Atmospheric Administration, NOAA) eastern Bering Sea bottom trawl survey of the continental 239 slope caught over 5,000 kg of immature Pacific sleeper sharks in a single tow (Hoff and Britt 240 2003). The temporal persistence of areas of high catch has been somewhat difficult to ascertain, 241 due to the lower effectiveness of trawl gear as a surveying tool for this species relative to

242 longline gear, changes in fishery dynamics (e.g., vessels switching from longline to pot gear, 243 which likely have different catchabilities), and because reporting requirements vary among 244 fisheries sectors and between state and federal waters. However, there is some indication that 245 Shelikof Trough, an extensive glacier-carved depression off Kodiak Island in the western Gulf of 246 Alaska, could represent a persistent "hotspot" of Pacific sleeper sharks. High catches of Pacific 247 sleeper sharks have been consistently reported here in IPHC surveys and NOAA longline 248 surveys for sablefish Anoplopoma fimbria (Courtney and Sigler 2007; Matta et al. 2022) as well 249 as in commercial fisheries (Fig. 3). Within the eastern Bering Sea, catches are high in some areas; however, this is more likely a function of fishing effort in the highly valuable walleve 250 251 pollock Gadus chalcogrammus fishery, with catch spread across the eastern Bering Sea shelf and 252 highest catches generally just north of Unimak Pass. In the western North Pacific Ocean, regular 253 areas of high Pacific sleeper shark abundance have been reported off Sakhalin Island, south of 254 the Kamchatka Peninsula, and between Cape Navarin and Karagin Island (Orlov and Baitalyuk 255 2014; Dyldin and Orlov 2018). Due to the spatiotemporally patchy nature of Pacific sleeper 256 shark catch, and given that this species is a large, slow-growing, and long-lived, high trophic 257 level predator, it is possible that any appearance of high abundance may be due to situations that 258 may cause sharks to aggregate, such as high concentrations of prey or habitats that support 259 biologically important functions, such as nursery areas.

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262 Biology and Ecology

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264 Size, age, and growth

265 Data on body size and age are highly important to understanding demographic rates and 266 assessing health of fish populations. Unfortunately, infrequent encounter rates, handling 267 difficulty, and low commercial value of Pacific sleeper sharks have limited the availability of age 268 and growth data to support stock assessments. Biological data collection in the eastern North 269 Pacific Ocean has mostly been opportunistic across a variety of platforms, including scientific 270 surveys and commercial fishing operations. Due to their size, accurate length and weight 271 measurements of Pacific sleeper sharks, especially of larger individuals, are difficult to obtain. 272 Weight data in particular are scarce, as Pacific sleeper sharks caught as by catch frequently are

not landed in commercial longline fisheries or are too large for at-sea observers to weigh, in
which case a reference table is used to estimate weight from length. The best available data
collected to date are presented here.

276 Shark body length can be measured in several different ways (FAO 2016), and the length 277 method presented for a given species isn't always uniform among studies. We are only aware of 278 a single study in which precaudal length (PCL), fork length (FL) and total length (TL, measured 279 with the upper caudal fin lobe in a natural position) were all measured from the same individual 280 Pacific sleeper sharks (Hulbert et al. 2006), although the data were not published in their 281 resulting manuscript. Hulbert et al. (2006) have kindly shared their unpublished length data with 282 us, permitting us to produce equations to allow conversions among length measurement types 283 reported in published literature (Fig. 4). Unless otherwise noted, lengths hereafter in this review 284 are presented as units of TL.

285 Large Pacific sleeper sharks are rare in the catch records, and much of the length data 286 available come from animals less than 220 cm TL (Fig. 5a). Due to the difficulty associated with 287 obtaining reliable measurements of large individuals, there is some debate on the accuracy of 288 maximum body size for Pacific sleeper shark. The largest confirmed Pacific sleeper shark landed 289 to date was a 465 cm TL female caught in October 2021 in the eastern Aleutian Islands that was 290 measured by a trained fisheries observer. The largest reliably measured Greenland shark was 510 291 cm TL (Campana et al. 2015, as cited in Nielsen 2017), with most individuals caught ranging 292 between 288 and 504 cm in length (MacNeil et al. 2012). Sleeper sharks estimated as exceeding 293 700 cm in length have been photographed in very deep water, and though these length records 294 are far less precise and difficult to confirm with certainty, they do appear to be significantly 295 larger than sharks encountered during normal fishing or survey operations (Isaacs and 296 Schwartzlose 1975; Compagno 1984; Clark et al. 1990; Stevenson et al. 2007). An individual 297 observed during a submersible dive in Suruga Bay, Japan, at a depth of about 1,200 m was 298 photographed next to an object of known size, and it was estimated to exceed 23 feet (700 cm) in 299 length (Clark et al. 1990). We compared the photograph of this shark to measurements made 300 from photographs of sharks caught during surveys and deemed their estimate reliable (our own 301 estimates of length for the Suruga Bay individual ranged from 21.7 to 23.5 feet, or 660-720 cm 302 TL).

303 Some authors have suggested that female sleeper sharks grow larger than males. Sexual 304 dimorphism in size has been noted in Greenland sharks (MacNeil et al. 2012; Nielsen 2017) and 305 Pacific sleeper sharks (Yano et al. 2007; Orlov and Baitalyuk 2014). Examination of data pooled 306 coast-wide from Alaska to Baja California indicates no significant difference between overall 307 length distributions of male and female Pacific sleeper sharks in the eastern North Pacific Ocean 308 (Fig. 5a; two-sample Kolmogorov-Smirnov test: D = 0.069, p = 0.0504, n = 1.562). However, as 309 noted earlier, large individuals are seldom encountered, and it is unknown whether female 310 Pacific sleeper sharks are capable of attaining larger maximum sizes than males in unobserved 311 parts of the ocean.

312 Size distributions of Pacific sleeper sharks appear to differ regionally. Along the west 313 coast of North America, sharks are on average smallest in the Bering Sea (mean = 150 cm TL) 314 and along the US West Coast (mean = 143 cm TL) (Fig. 6). Average size is greatest in the Gulf 315 of Alaska (mean = 210 cm TL), but a small number of relatively large (> 350 cm TL) individuals 316 have also been caught off British Columbia and the US West Coast (Fig. 6). However, the largest 317 individuals have been reported, both empirically and anecdotally, from the Aleutian Islands (Fig. 318 6), despite the number of small individuals also present and limited number of observations 319 where size was recorded (Tribuzio et al. 2022). Biological inferences are difficult to make due to 320 the mostly opportunistic nature of Pacific sleeper shark length data collections, and it is possible 321 that regional differences in fishing gear can at least partially explain these patterns. For example, 322 targeted surveys in the Southeast Alaska region found no individuals under 260 cm TL; one 323 proposed reason for this is the size of the hooks of the commercial Pacific halibut *Hippoglossus* 324 stenolepis gear that was used (K. R. Fuller and C. A. Tribuzio, unpublished data). However, 325 regional differences in size distributions have also been reported in the western North Pacific 326 Ocean, with Pacific sleeper sharks in the western Bering Sea generally being larger than those 327 caught off the Kuril Islands and Kamchatka Peninsula (Orlov and Moiseev 1999). Some regional 328 variation in size may be expected given the differences among the ecosystems of the eastern and 329 western North Pacific Ocean (Aydin et al. 2002, 2007). Spatial variation in size distribution has 330 similarly been observed in Greenland sharks, indicating potential shifts in habitat usage among 331 sharks at different life stages or by sex (Edwards et al. 2019). Indeed, segregation by sex and size 332 has been observed in many shark species (Bres 1993); the extent to which Pacific sleeper sharks 333 exhibit similar behavior is worthy of further investigation.

334 Length and weight data have been opportunistically collected in Alaska waters since the 335 1980s by fisheries observers aboard commercial vessels and during scientific survey operations 336 (n = 674). These fish were landed and measured to generate a dataset from which accurate 337 length-weight parameters could be estimated, presented here for comparison with relationships 338 previously published for this species. Sex was determined in most cases, but for some 339 individuals, sex was not recorded (n = 77). There were also two obvious transcription errors in 340 the dataset (a 40-cm shark weighing 27 kg and a 93-cm shark weighing 62 kg) that were omitted 341 from further analysis. Based on these data, there was no detectable difference between males and 342 females in the length-weight relationship (Fig. 7a). This contrasts with Orlov and Baitalyuk 343 (2014), who found large differences in the length-weight parameters between the sexes, though 344 their estimates were based on relatively few individuals. Our length-weight relationship for both 345 sexes combined is fairly similar to those previously published for Pacific sleeper sharks (Fig. 346 7b). The *b* parameter (exponent) in the exponential length-weight relationship is 3.043, 347 indicating slightly positive allometric growth.

348 The ages of elasmobranchs are most commonly estimated from counts of growth band 349 pairs visible in hard structures including vertebrae, spines, and caudal thorns (Natanson et al. 350 2019). Multiple researchers have attempted to use these structures to determine the age of Pacific 351 sleeper sharks with no success (Wischniowski 2009; Matta et al. 2017). This is due in part to 352 poor calcification of their hard structures, a phenomenon that has been noted in a variety of other 353 deepwater sharks (Cailliet 1990, 2015). Despite testing various preparation methods, no 354 discernable banding patterns have been detected, and Pacific sleeper sharks do not possess 355 alternate structures such as spines or thorns. Moreover, the presumed annual periodicity of 356 banding patterns visible in the vertebrae of other elasmobranch species has increasingly been 357 called into question. There is evidence that these patterns may form due to increases in size 358 (somatic growth) rather than as a function of time, or that they may be annual in juvenile stages 359 but cease forming following maturity or upon approaching maximum size (Passerotti et al. 2014; 360 Natanson et al. 2018; James 2020). Thus, even if banding patterns could be detected in the 361 skeletal structures of Pacific sleeper sharks, there would be no assurance that band-pair counts 362 would represent age. Lastly, even if age determination was possible for the Pacific sleeper shark, 363 low encounter rates and difficulty in handling large sharks preclude the ability to generate 364 traditional estimates of catch-at-age that could be used in stock assessments.

These limitations necessitate alternative methods of age determination to estimate growth rates and longevity of the Pacific sleeper shark. Such metrics are highly desirable as they can be used in conjunction with reproductive information to indirectly estimate natural mortality and intrinsic rates of population increase (Denney et al. 2002; Hamel and Cope 2022). These parameters are often the foundation in emerging methods to assess and protect marine resources for which data are limited or unavailable (e.g., Carruthers et al. 2014).

371 Age determination results based on alternative methods suggest slow growth and high 372 longevity of Greenland sharks. A recent study analyzed bomb-produced and naturally occurring radiocarbon (¹⁴C) in Greenland shark eye lenses to estimate age (Nielsen et al. 2016). Vertebrate 373 374 eye lenses are composed of fiber cells that are continually deposited in concentric layers around 375 a core area that is formed during pre-natal development and conserved throughout the life of the 376 animal (Quaeck-Davies et al. 2018). Bomb-produced radiocarbon can act as a time-specific 377 marker in hard or conserved tissues of marine organisms, allowing for accurate dating of 378 individuals alive during the 1950s and 1960s, a period of intensive atmospheric testing of 379 thermonuclear bombs (Kalish 1993). Based on radiocarbon analysis of eye lens cores, the 380 Greenland shark study proposed an age at maturity of 156 years and a longevity of 392 years by 381 restricting age probabilities with measures of fish length (Nielsen et al. 2016). Some authors 382 have raised doubts regarding the accuracy of these ages, and suggest that while the Greenland 383 shark could certainly be capable of a centenarian life span, the maximum age may be 384 overestimated due to the assumptions made regarding age-at-length coupled with the 385 interpretation of pre-bomb radiocarbon values (Alex 2016; Natanson et al. 2019). This 386 observation is supported by recent adjustments to some of the assumptions and additional ¹⁴C 387 measurements that have led to a revised lifespan of ~262 years (Olsen et al. 2022). However, 388 others suggest that metabolic theory and our limited knowledge of Greenland shark life history 389 characteristics indicate the estimated life span of 392 years may be too low (Augustine et al. 390 2017). In support of this observation, an early tag-recapture study reported extremely slow 391 growth, where an individual at liberty for 16 years grew only 8 cm (262 to 270 cm TL; Hansen 392 1963), and based on its length, the individual would have been immature.

In contrast to the recent findings for Greenland shark, a pilot study of radiocarbon in the cores of both eye lenses of a 3.1 m Pacific sleeper shark indicated that the growth rate, while still very slow compared to most fishes, is approximately two times faster than estimated for

396 Greenland sharks (Fig. 8). The limits placed on age-at-length by alignment of the measured 397 values to the bomb-produced radiocarbon rise period (late 1950s to early 1960s) — similar in manner to the minimum age set for a small Greenland shark individual (Nielsen et al. 2016) — 398 399 led to an age of no more than ~50 years, as opposed to an estimated 105 years based on the Greenland shark growth curve (Fig. 8). These radiocarbon values ($\Delta^{14}C = 9.4$ and -51.1%) are 400 401 considered diagnostic because it is very unlikely that measured radiocarbon levels of this 402 magnitude were present in the marine environment prior to these estimated formation years of ~1962-1965. In addition, it is likely that the lowest value ($\Delta^{14}C = -51.1\%$) was not much earlier 403 404 than the early to mid-1960s, indicating the age of this individual was not much less than 50 405 years, unless the signal is significantly phase-lagged, as is the case for porbeagle shark Lamna 406 nasus (Campana et al. 2002). It should be noted when the pilot study was initiated, eye lens core extraction methods were still being developed, which may explain the difference in Δ^{14} C values 407 408 and consequently the three-year difference in the estimated birth year for the same fish. A small 409 amount of material left on one of the cores could have increased its value (the rise period for 410 bomb-produced radiocarbon shows a rapid increase within just a few years following the bomb 411 testing period). Since the pilot study, core extraction methodology has been refined and a full 412 investigation into the plausible age range and growth of Pacific sleeper sharks using radiocarbon 413 analysis of eye lenses is underway (C. A. Tribuzio, personal communication).

414

415 **Reproduction**

416 Little is known about reproduction in Pacific sleeper sharks due to infrequent observations of 417 large sharks and difficulty in assessing reproductive status of large animals. Most of what is 418 currently understood is based on the Greenland shark, for which the number of observations is 419 somewhat greater, allowing directed assessments of maturity (Nielsen et al. 2020). Adult Pacific 420 sleeper sharks are rarely encountered in fisheries or during scientific surveys, and to date, no 421 pregnant female has ever been retained. The only reported case of a pregnant female being 422 landed occurred on a trawl vessel operating in waters off British Columbia in the mid-1990s. An 423 at-sea observer reported that between 8 and 12 live pups were actively birthed by the female 424 before she was released back into the water (C. Dykstra, IPHC, personal communication). 425 Unfortunately, no scientific data or photographs of this event were recorded, and it is unknown 426 whether the number of pups observed represented the full litter.

427 Sleeper sharks employ lecithotrophic viviparity (sometimes referred to as "ovoviviparity" 428 or "aplacental viviparity"), wherein embryos are nourished primarily by yolk and females give 429 birth to live young (Ebert et al. 2017; Carter and Soma 2020). Histotrophy (in which embryos are 430 fed by maternal uterine secretions) is believed to be minimal (Carter and Soma 2020). The 431 fecundity and gestation period of the Pacific sleeper shark are uncertain, with most inferences 432 drawn from related species. Litter sizes of the few observed pregnant females of any Somniosus 433 species have been somewhat variable but generally small. To date, a single pregnant 5-m female 434 Greenland shark has been observed that had 10 near-term embryos of similar size in its right 435 uterus (Koefoed 1957). A 134 cm TL pregnant female of the putative new species of small-436 bodied sleeper shark off Taiwan, Somniosus (Rhinoscymnus) cheni sp. nov., contained 33 mid-437 term embryos with a mean size of 14 cm TL (Hsu et al. 2020). There are several reports of 438 pregnant individuals of the little sleeper shark from the Mediterranean Sea, in which litters have 439 varied from 5 to 17 embryos per female (multiple sources in Capapé et al. 2020). Size at birth of 440 Pacific sleeper sharks is thought to be near 40 cm (Francis et al. 1988; Yano et al. 2007), though 441 there have been reports of larger free-swimming individuals bearing umbilical scars (Ebert et al. 442 1987). Mature female Greenland and Pacific sleeper sharks have been observed with high 443 numbers of yolked ovarian eggs (Gotshall and Jow 1965; Ebert et al. 1987; Nielsen et al. 2020), 444 leading some to speculate that litter sizes may be quite large (>200 pups). However, this seems 445 improbable due to the relatively large size at birth, oxygen limitations within the uterus during 446 gestation, and small litter sizes observed in other members of Somniosidae (Carter and Soma 447 2020). It may be more likely that the majority of these ovarian eggs constitute a reserve, or that 448 these eggs are resorbed by the mother (Augustine et al. 2022).

449 Estimates of the size at maturity of Pacific sleeper sharks are based on relatively few 450 observations. While male maturity state can be inferred from external examination of the 451 claspers, maturity state of females must be verified by internal examination of the reproductive 452 organs, which presents logistical challenges associated with dissecting large animals at sea. 453 Because verified mature or maturing individual Pacific sleeper sharks have not been captured in 454 sufficient numbers, the estimate of the size of maturity should be considered more of a general 455 approximation than a precise figure. Based on the smallest recorded mature female Pacific 456 sleeper shark (Gotshall and Jow 1965) and examination of 15 additional individuals captured off 457 California, Ebert et al. (1987) estimated that females mature at around 370 cm TL. However,

458 larger individuals that were believed to be immature have been observed (Bakes and Nichols 459 1995; Tribuzio et al. 2022), including a 428 cm TL female captured during a bottom trawl survey 460 in the Aleutian Islands in 2022 (J. R. Hoff, AFSC, personal communication). Maturity stage was 461 not recorded for the largest landed Pacific sleeper shark (465 cm TL) mentioned in the previous 462 section. Adult Greenland sharks have been more frequently encountered, and therefore, estimates 463 of length at maturity in that species are more refined. Based on the available data, there appears 464 to be sexual dimorphism in size at maturity of Greenland sharks, with males and females 465 attaining 50% maturity at 284 and 419 cm TL, respectively (Nielsen et al. 2020). As there is a 466 paucity of observations of mature Pacific sleeper sharks, more work is needed to determine 467 whether maturity in that species is similarly disparate among males and females.

468 The majority of Pacific sleeper sharks caught in the eastern Bering Sea and eastern North 469 Pacific Ocean are likely immature (Fig. 6), suggesting that adults primarily inhabit waters not 470 well-sampled by commercial fisheries or scientific surveys. Similarly, catches in Russian waters 471 are predominantly immature fish (Orlov 1999; Orlov and Baitalyuk 2014). Adult males seem to 472 be particularly rare (Ebert 2003); however, one of the authors of this review observed what 473 appeared to be a mature male from visual external examination of the claspers (Fig. 9) during a 474 fishery-independent longline survey in the Gulf of Alaska in 2019 (C. A. Tribuzio, unpublished 475 data). As has been observed in many other elasmobranch species, habitat use may vary by sex 476 and reproductive stage (Bres 1993). This appears to be the case for the Greenland shark, with 477 adult females occupying different waters than juveniles (Edwards et al. 2019). Of Pacific sleeper 478 sharks caught from Alaska to California, sex ratios are nearly even in the Bering Sea and are 479 approximately 58% female in the Gulf of Alaska (Fig. 5b). While the other regions have 480 relatively few observations, it is interesting to note that females have been caught nearly 2.6 481 times more often than males off British Columbia (Fig. 5b). Additional measurements may help 482 ascertain the degree to which the sex ratio varies across their range in the eastern North Pacific 483 Ocean.

484 Nothing is known of the mating or pupping habits of Pacific sleeper sharks, or whether 485 these aspects are seasonal in nature. Bjerken (1957) speculated that the reason so few pregnant 486 Greenland sharks have been detected is that they may move to deep waters during the gestation 487 period. An alternative hypothesis is that they may migrate through the deep scattering layer of 488 the open ocean, a region of the water column associated with a high abundance of marine

489 organisms (Campana et al. 2015). Female Greenland sharks that appeared to be gravid have also 490 been observed in relatively shallow waters of the St. Lawrence Estuary (Harvey-Clark et al. 491 2005; Gallant et al. 2016). Based on capture locations of pregnant females in the Mediterranean 492 Sea, Capapé et al. (2020) theorized that the little sleeper shark uses shallow coastal areas as 493 nursery grounds. Nursery habitat utilization has also been posited as an explanation for observed 494 large aggregations of juvenile Pacific sleeper sharks in Alaska waters. For example, there are 495 reports of large catches of small Pacific sleeper sharks in Prince William Sound around the late 496 1990s, suggesting that this area could represent a nursery area, though due to a lack of formal 497 reporting requirements, these catches are largely anecdotal (G. C. Dunne, personal 498 communication). Numerous anecdotal reports exist from local fishers (usually longlining) of 499 capturing many, even hundreds, of small Pacific sleeper sharks of similar size in glacial fjords in 500 Alaska (C. A. Tribuzio, personal communication), suggesting that they may function as 501 important habitats during the juvenile life stage. Another possible nursery area has been 502 identified in the southeastern Bering Sea near Unalaska Island, due the detection of a sibling pair 503 of small (96 cm and 111 cm) sharks 10 days apart and repeated captures of other immature 504 sharks in the vicinity (Matta et al. 2022; Timm et al. 2022). Repeated captures of juvenile 505 Greenland sharks have also been observed at specific sites in the eastern Canadian Arctic, with 506 smaller animals generally having longer residency times, suggesting that these areas may serve 507 as nursery or juvenile habitats (Hussey et al. 2015; Edwards et al. 2022a). The largest 508 aggregation of Pacific sleeper sharks on record occurred during a trawl survey along the upper 509 continental slope of the eastern Bering Sea (Hoff and Britt 2003). During the 2002 survey, 119 510 individuals were caught in a single tow at a depth of approximately 700 m at the northern end of 511 Zhemchug Canyon, a massive underwater canyon located about 300 km northwest of the Pribilof 512 Islands. These fish were all immature and ranged in length from 104 to 237 cm. Due to the fact 513 that all of the sharks captured were immature, there was some speculation that Zhemchug 514 Canyon could represent an important nursery or juvenile habitat for Pacific sleeper sharks. 515 However, even despite resampling in the same area in the years since, the 2002 occasion remains 516 the only time when more than a few individuals were caught at that location. Further work, such 517 as tagging studies, could help determine whether Pacific sleeper sharks utilize certain habitats 518 with fidelity.

519

520 Trophic ecology

521 The Pacific sleeper shark fulfills an ecologically important role as a top predator, occupying a 522 relatively high trophic position (Courtney and Foy 2012; Bizzarro et al. 2017). The species was 523 long characterized primarily as a benthic-oriented scavenger, and indeed, its keen sense of smell 524 (Yopak et al. 2019) likely allows it to detect food oases such as whale falls in the deep ocean 525 (Smith et al. 2002; Smith and Baco 2003). However, diet analysis and tagging studies have 526 indicated that Pacific sleeper sharks are opportunistic and, in addition to scavenging, are capable 527 of consuming live prey, such as salmon or other pelagic species, throughout the water column 528 (Orlov and Moiseev 1999; Hulbert et al. 2006; Sigler et al. 2006). Sleeper sharks are very slow-529 swimming compared to other fishes and are not believed to be capable of fast bursts of speed 530 (Watanabe et al. 2012; Shadwick et al. 2018; Fujiwara et al. 2021). Instead, it is believed that 531 sleeper sharks hunt using stealth, taking advantage of their slow movements and cryptic 532 coloration to ambush fast-swimming fish and sleeping seals (Ebert et al. 1987; Watanabe et al. 533 2012; Lydersen et al. 2016). The Pacific sleeper shark has teeth that differ in shape between the 534 upper and lower jaws, with the upper teeth being longer and lance-like and the lower teeth 535 having short oblique cusps and high narrow roots (Compagno 1984; Yano et al. 2004; Stevenson et al. 2007). This specialization of upper teeth for grabbing and lower teeth for tearing, along 536 537 with the ability to suction feed (Bizzarro et al. 2017; Grant et al. 2018), may afford Pacific 538 sleeper sharks greater flexibility in the types of prey they can consume.

539 The Pacific sleeper shark has a varied diet, consuming teleost fishes, cephalopods, 540 pinnipeds, cetaceans, crustaceans, and offal (Gotshall and Jow 1965; Ebert et al. 1987; Orlov and 541 Moiseev 1999; Yang and Page 1999; Schaufler et al. 2005; Sigler et al. 2006; Yano et al. 2007). 542 Most direct studies on the diet of Pacific sleeper sharks are based on only a few individuals. 543 Comparison across the patchwork of existing regional studies appears to suggest that the diet of 544 Pacific sleeper sharks is both spatially and temporally heterogeneous, perhaps owing to their 545 opportunistic nature (Sigler et al. 2006; Courtney and Foy 2012). One of the more 546 comprehensive studies noted a seasonal shift in the diet of sharks caught in the Gulf of Alaska 547 from teleosts to cephalopods, likely due to changes in relative prey availability, though marine 548 mammals remained important throughout the study period (Sigler et al. 2006). An ontogenetic 549 shift in the diet has also been noted, whereby smaller sharks generally consume prey of lower 550 trophic levels (e.g., cephalopods) and increasingly consume higher trophic level prey (e.g., fish

and marine mammals) as they grow (Sigler et al. 2006; Yano et al. 2007; Courtney and Foy

2012; Orlov and Baitalyuk 2014). Sex and depth may also contribute to differences in diet (Orlov
and Moiseev 1999; Orlov and Baitalyuk 2014).

554 Somewhat surprisingly, fast-swimming midwater and epipelagic fishes such as salmon 555 Oncorhynchus sp., mahi mahi Coryphaena hippurus, wahoo Acanthocybium solandri, and 556 albacore Thunnus alalunga have been found in the stomachs of Pacific sleeper sharks (Ebert et 557 al. 1987; Wang and Yang 2004; Sigler et al. 2006). While it is possible they could have been 558 consumed as carrion on the seafloor, some prey items in these stomach content studies were 559 fresh and intact, suggesting that they were captured through ambush attacks (Ebert et al. 1987; 560 Wang and Yang 2004; Sigler et al. 2006). In addition to pelagic species, groundfish species, 561 including rockfishes (Sebastidae), flatfishes (Pleuronectiformes), cods (Gadidae), eelpouts 562 (Zoarcidae), and sculpins (Cottidae) have also been reported in Pacific sleeper shark stomachs, 563 indicating that they feed throughout the water column (Gotshall and Jow 1965; Ebert et al. 1987; 564 Orlov and Moiseev 1999; Yang and Page 1999; Sigler et al. 2006; Gorbatenko et al. 2009).

565 Marine mammals are an important component of the Pacific sleeper shark diet, 566 particularly of larger sharks (Sigler et al. 2006; Yano et al. 2007). A 393 cm female caught in 567 very shallow water in Kachemak Bay, Cook Inlet, Alaska, was found to have at least three 568 harbor seals Phoca vitulina in its stomach (Bright 1959). Numerous bite marks attributed to 569 scavenging Pacific sleeper sharks have been observed on carcasses of gray whales *Eschrichtius* 570 robustus that were killed by killer whales Orcinus orca in shallow waters near Unimak Island; 571 annual killer whale predation events may attract the sharks to the area every spring (Barrett-572 Lennard et al. 2011). Pacific sleeper sharks of varying size (estimated 150-350 cm TL) have also 573 been photographed voraciously feeding on whale falls in deep water off California (Smith et al. 574 2002; Smith and Baco 2003). Consistent with these observations was the landing of 575 approximately 50 small individuals (all near a meter in length) that were caught together by a 576 bottom trawler off Carmel Canyon, south of Monterey Bay, California, of which the stomach 577 contents of some individuals contained bite-sized and -shaped pieces of red meat (A. H. 578 Andrews, personal observation at Moss Landing Marine Laboratories in the mid-1990s). The 579 presence of an intact fetus, along with adult female genital tissue, of southern right whale 580 dolphins Lissodelphis peronii, in the stomach of a 360 cm Pacific sleeper shark led Crovetto et 581 al. (1992) to conclude that the shark attacked a pregnant female. Fatty acid analysis has indicated 582 the relative importance of cetaceans, as well as fish, in the Pacific sleeper shark diet (Schaufler et 583 al. 2005). The Pacific sleeper shark has also been implicated as a predator of juvenile Steller sea 584 lions *Eumetopias jubatus* based on a small study that surgically implanted sea lions with 585 temperature-recording satellite tags (Horning and Mellish 2014). However, direct evidence of 586 Steller sea predation has never been established (Schaufler et al. 2005; Sigler et al. 2006), and 587 any predation that may occur is thought to be low (Loughlin and York 2000). Still, there is 588 opportunity for overlap between the two species in the winter months, when juvenile Steller sea 589 lions dive to deeper depths (Bishop et al. 2019). Modeling exercises suggest that sea lions, as 590 well as harbor seals (a known previtem), may alter their foraging behavior to avoid areas where 591 predation risk by Pacific sleeper sharks is greater (Frid et al. 2006, 2008, 2009).

592 In Alaska waters, the majority of Pacific sleeper shark mortality is due to fisheries 593 bycatch (Aydin et al. 2007). However, an offshore killer whale population has been documented 594 feeding on Pacific sleeper sharks (Ford et al. 2011). This killer whale ecotype may be specialist 595 consumers of Pacific sleeper sharks and other elasmobranchs, which may comprise an important 596 component of their diet (Ford et al. 2011). A necropsy on a recently dead 304 cm TL Pacific 597 sleeper shark that washed ashore at Sunshine Cove in March 2022 near Juneau, Alaska, provides 598 further evidence of predation by killer whales. Bruising and puncture marks consistent with the 599 size and shape of killer whale teeth were visible on the body, and the throat, tongue, liver, and 600 heart were ripped out (Fig. 10; Tribuzio et al. in prep). The removal of only the relatively 601 nutritionally dense organs could indicate selective feeding by the killer whales.

602

603 Behavior, habitat use, and movement

604 Sleeper sharks are often regarded as slow-moving and sluggish. The genus name Somniosus is 605 apropos for describing the behavior of these species upon capture. As Hansen (1963) noted, it is 606 often difficult to tell whether they are alive or dead, as most individuals move little on longlines 607 at the surface or once on deck. Whether their on-deck behavior represents that *in situ* has been 608 somewhat debated, as they are capable of catching fast-moving prey (see Trophic Ecology). 609 However, they have been noted to be among the slowest swimming of the fishes (Watanabe et al. 610 2012; Fujiwara et al. 2021) and likely rely on the power of ambush to capture prey. 611 Pacific sleeper sharks occupy a variety of habitats, ranging from very shallow water in

the intertidal zone to oceanic depths of at least 2,000 m (Bright 1959; Compagno 1984;

613 Stevenson et al. 2007). It is unknown whether or to what extent Pacific sleeper sharks utilize 614 habitats of the abyssal plain. While Pacific sleeper sharks can be found in shallow water at high 615 latitudes, they occur deeper in subtropical and tropical waters (Ebert 2003; Walter et al. 2017). 616 Different studies have reported conflicting results on the relationship between latitude and depth 617 for the Greenland shark. Yano et al. (2007) observed a negative relationship off western 618 Greenland, whereas Nielsen et al. (2014) did not detect any discernable trend over a wider 619 geographic and latitudinal range around Greenland. However, Campana et al. (2015) found that 620 Greenland sharks in the Arctic Ocean were in significantly shallower and colder waters than 621 those in the northwest Atlantic Ocean, suggesting that the latitude-depth relationship may be 622 more relevant at greater spatial scales. The majority of Greenland shark catches occur in waters 623 below 5°C (MacNeil et al. 2012), though archival tagging work in the northwest Atlantic Ocean 624 has demonstrated that they are capable of tolerating temperatures up to 17.2°C (Campana et al. 625 2015). In a study of tagged Pacific sleeper sharks in the Gulf of Alaska, ambient temperatures 626 ranged from 4.4 to 11.8°C but were mostly between 5.5 and 8.2°C (Hulbert et al. 2006).

627 Little is known about the life cycle of Pacific sleeper sharks, quite possibly due to a 628 mismatch between their distribution or catchability during certain life stages and fisheries and 629 survey data. Because mature individuals are encountered so rarely, it is possible they typically 630 occupy abyssal habitats that are inaccessible to standard fishing gear. Very large sleeper sharks, 631 putatively identified as S. pacificus based on geographic locations, have been observed near the 632 seafloor in deep water by submersibles and remote cameras (Isaacs and Schwartzlose 1975; 633 Clark et al. 1990). While juveniles typically are captured in the bottom waters of the continental 634 shelf and slope, they have also been caught in midwater trawls over very deep water (Ebert 635 2003). It is possible that Pacific sleeper sharks actively seek out certain habitats, such as 636 deepwater canyons and troughs, as refugia. There is some indication that, at least in Alaska 637 waters, they may also prefer relatively inshore habitats that are poorly sampled by federal bottom 638 trawl surveys. In particular, glacial fjords have also been identified as potentially important 639 nursery areas due to large catches of small sharks in these areas (see Reproduction). Glacial 640 fjords share many of the same conditions of deepwater offshore environments, thereby providing 641 refugia to cold-adapted organisms despite their proximity to shore (Häussermann et al. 2021; 642 Smith et al. 2022). Clearly, more work is needed to elucidate the distribution, preferred habitats, 643 life history, and behavior patterns of Pacific sleeper sharks across life stages.

644 A tagging study in the western Gulf of Alaska indicated that Pacific sleeper sharks are 645 capable of making long-distance horizontal movements of at least several hundred kilometers 646 over the course of a year, but in general they appear to stay relatively localized, with most 647 recoveries occurring within 100 km of tagging locations (Hulbert et al. 2006). Stable isotope 648 studies, which provide a long-term snapshot of diet, have found distinct differences between the 649 Bering Sea and Gulf of Alaska, suggesting that there is little exchange between the two regions 650 (Courtney and Foy 2012), in contrast with a recent genetics study that reported that Pacific 651 sleeper sharks are genetically homogenous throughout the Pacific Ocean, suggesting mixing 652 among regions (Timm et al. 2022). Hulbert et al. (2006) noted that tagged individuals made 653 "extensive, nearly continuous vertical movements", spending the majority of their time at depths 654 between 150 and 450 m, but frequently rising to depths shallower than 100 m, including one 655 individual that regularly rose to the surface (0-2 m) (Hulbert et al. 2006). However, despite these 656 frequent ascents, they spent relatively little time at the shallower depths, remaining below the 657 photic zone during the day and moving shallower at night, which the authors speculated may be 658 related to foraging (Hulbert et al. 2006). The high levels of alkyldiacylglycerols in the very large 659 liver (20-30% of body mass) of Pacific sleeper sharks may facilitate these regular vertical 660 migrations through buoyancy regulation (Phleger 1998). Additional tagging studies are currently 661 in progress to gain a better understanding of Pacific sleeper shark movements and behavior.

662 Movements and habitat preferences of the Greenland shark are more well-known. 663 Greenland sharks make large horizontal and vertical movements across a range of temperatures 664 (Fisk et al. 2012; Campana et al. 2015). Similar to the Pacific sleeper shark, Greenland sharks 665 have been observed making diel vertical migrations in certain areas including the Gulf of St. 666 Lawrence and the Canadian Arctic, residing in deeper, colder waters during the day and 667 shallower, warmer waters at night (Skomal and Benz 2004; Stokesbury et al. 2005; Gallant et al. 668 2016), though they do not appear to exhibit this behavior consistently through their range (Fisk et al. 2012; Campana et al. 2015). Greenland sharks have also been observed making excursions 669 670 into shallow waters, including nearshore and brackish habitats (Stokesbury et al. 2005; Gallant et 671 al. 2016). Hussey et al. (2018) found evidence of migration routes between Canada and 672 Greenland, including movements into deepwater fjords. Long-term acoustic telemetry has 673 revealed migrations of Greenland sharks between coastal and offshore locations in Baffin Bay, 674 Canada, with some individuals displaying site fidelity across multiple years (Edwards et al.

675 2022a, b). The inshore-offshore migrations observed in Baffin Bay appear to be related to

676 seasonal ice cycles, with sharks residing in coastal fjords during the summer and fall ice-free

677 period and in offshore waters during the period of ice formation and cover (Edwards et al.

678 2022b). Juveniles have longer occupancy times in the coastal fjords than sub-adults (Edwards et

al. 2022a), lending further support to these habitats as important refugia during more vulnerable

- 680 life stages.
- 681

682 Internal anatomy and physiology

683 Sleeper sharks possess anatomical and physiological features that make them well-suited to their 684 environment. Their slow swimming speeds likely allow them to conserve energy and reduce 685 metabolic demands, important attributes for an opportunistic predator (Fujiwara et al. 2021; 686 Smith et al. 2022). Furthermore, their large livers, composed primarily of diacylglyceryl ethers 687 and triacylglycerols, play a key role in energy storage and likely allow them to regulate 688 buoyancy during their extensive vertical migrations (Bakes and Nichols 1995; Phleger 1998). As 689 a result of these adaptations, the energy budgets of sleeper sharks are estimated to be relatively 690 low, despite having metabolic rates that are similar to those of other sharks when scaled for 691 temperature (Ste-Marie et al. 2020; Smith et al. 2022). For instance, field and captive 692 respirometry studies have demonstrated that an 84.5 kg Pacific sleeper shark would be expected 693 to burn 153 kcal/day under average swimming conditions and that the maintenance ration of an 694 average Greenland shark weighing 224 kg is only 61-193 g of fish or mammal tissue daily, 695 suggesting that these sharks require relatively little energy (Ste-Marie et al. 2020, 2022; Smith et 696 al. 2022).

697 The immune functioning of sleeper sharks is not well-studied. The Greenland shark 698 possesses Leydig's organ, a lymphomyeloid tissue found only in certain elasmobranchs. Based 699 on high lysozyme activity observed in Leydig's organ, the pancreas, and the spleen, the 700 Greenland shark may have a strong immune response to bacterial and viral infections (Fänge et 701 al. 1980). It has not been noted in the scientific literature whether Leydig's organ is also present 702 in Pacific sleeper sharks. There is no macroscopically visible epigonal organ in male or female 703 sleeper sharks (Yano et al. 2007). The epigonal organ, another lymphomyeloid tissue unique to 704 chondrichthyans, is associated with the gonads and is part of the immune system, possibly 705 involved with leukocyte production (Honma et al. 1984; Luer et al. 2004; Bircan-Yildirim et al.

2011). Whether the epigonal organ is greatly reduced or completely absent in sleeper sharks isunknown.

708 Examination of the structures of the brains of sleeper sharks reveal some differences 709 compared to other shark species. Unlike other large-bodied sharks, the cerebellum, the region 710 that controls motor function, is small and smooth in both Greenland and Pacific sleeper sharks, 711 suggesting lower activity levels in these species (Yopak et al. 2019). Additionally, the optic 712 tectum, a part of the brain responsible for visual processing, is reduced while the olfactory 713 regions are some of the largest of any shark species studied, indicating that sleeper sharks likely 714 rely far more on their sense of smell than their visual acuity (Ferrando et al. 2015; Yopak et al. 715 2019). Further supporting this hypothesis are their ability to detect carrion below the photic zone 716 in deep oceanic waters and their seeming indifference to corneal infections of parasitic copepods 717 (see Parasites).

718

719 Parasites

720 Individuals of the parasitic copepod species Ommatokoita elongata have long been observed 721 attached to the corneas of Greenland sharks (Berland 1961; Beck and Mansfield 1969). The 722 species was first documented on the eyes of Pacific sleeper sharks in Prince William Sound, 723 Alaska, with infections appearing to be quite common (Benz et al. 1998, 2002). Parasitic 724 copepod infections can cause lesions of the cornea, which likely lead to vision impairment or 725 even blindness (Borucinska et al. 1998; Benz et al. 2002). It is questionable to what degree this 726 adversely affects the sharks since they appear to rely more on their olfactory senses than their 727 visual acuity for detecting prey, and infected sharks appear to be otherwise healthy (Borucinska 728 et al. 1998; Benz et al. 2002). Greenland sharks in the St. Lawrence Estuary have been reported 729 to be largely copepod-free; it has been postulated that the sharks enter brackish waters in an 730 attempt to rid themselves of the copepods and other parasites (Harvey-Clark et al. 2005; Gallant 731 et al. 2016). The St. Lawrence Estuary sharks appear to be highly visual and display different 732 behaviors than Greenland sharks in the Arctic Ocean, where parasitic copepod infections are 733 endemic (Harvey-Clark et al. 2005).

Other parasites of sleeper sharks appear to be far rarer in occurrence and may vary geographically. Ho et al. (2003) observed the ectoparasitic copepod *Dinemoura ferox* on the heads or fins of four of 27 Pacific sleeper sharks caught off eastern Taiwan. Interestingly, while 737 Ho et al. (2003) also noted infections of *O. elongata* attached to the corneas of eight of the sharks 738 they examined, none of those same sharks had concurrent D. ferox infections. An unidentified 739 species of copepod, possibly D. ferox, was observed on the pelvic fin of a juvenile male Pacific 740 sleeper shark in 2022 on a survey out of Petersburg, Alaska (K. R. Fuller, personal 741 communication). The same parasite was found on a number of Pacific sleeper sharks near 742 Juneau, Alaska, indicating a fairly high rate of occurrence at a local level (K. R. Fuller, personal 743 communication). Wang and Yang (2004) observed D. ferox on the skin and monogeneans 744 (Polyopisthocotylea), a type of flatworm, on the gills of Pacific sleeper sharks caught off eastern 745 Taiwan, as well as apparent wounds caused by cookie-cutter sharks *Isistius* sp. Causey (1926) 746 noted flukes (Trematoda) on the gills of sleeper sharks in Excursion Inlet, Alaska. Tapeworms 747 (Cestoda) and nematodes (Nematoda) have been periodically reported from the stomachs of 748 Pacific sleeper sharks (Gotshall and Jow 1965; Wang and Yang 2004; Taggart et al. 2005). A sea 749 lamprey *Petromyzon marinus* was observed attached to a 3-m male Greenland shark in the St. 750 Lawrence Estuary, although this doesn't appear to be a common occurrence as this is the only 751 known report of a lamprey on a sleeper shark (Gallant et al. 2006). Finally, there is a single 752 record of the parasitic barnacle (Anelasma squalicola) inside the cloaca of a 275 cm TL female 753 Greenland shark collected from Tremblay Sound in the eastern Canadian Arctic (Ste-Marie et al. 754 2023).

755

756 Contaminants

757 Naturally occurring and anthropogenic toxins, such as heavy metals and persistent organic 758 pollutants (POPs), tend to be higher in long-lived, upper trophic level organisms due to the 759 process of bioaccumulation. Toxic contaminants including mercury, cadmium, lead, selenium, 760 and various POPs have been detected in the muscle, liver, pancreas, and other organs of 761 Greenland sharks, with loads varying among tissues (Strid et al. 2007; Corsolini et al. 2014). Dichlorodiphenyltrichloroethane (DDT), an insecticide that was widely used from the 1940s to 762 763 1970s, has been detected in liver and muscle tissue of Greenland sharks with concentrations 764 varying geographically, which could be due to differences in contamination levels or in feeding 765 ecology among regions (Fisk et al. 2002; Corsolini et al. 2014; Cotronei et al. 2018). 766 Polychlorinated biphenyls (PCBs), another group of organic chemicals that persist in the 767 environment despite widespread bans enacted in the mid-1970s, have also been found to vary

spatiotemporally in Greenland sharks (Lu et al. 2014). Similarly, endocrine-disrupting
compounds including bisphenol A vary regionally and among tissue types in Greenland sharks
(Ademollo et al. 2018).

771 We know of only one study that has examined contaminants (non-essential elements) in 772 Pacific sleeper sharks, and concentrations were generally higher than those in Greenland sharks, 773 likely due to geographic differences in levels of exposure or to differences in diet (McMeans et 774 al. 2007). In the studies to date, concentrations of various contaminants do not appear to be 775 related to shark size, with most observed differences attributed to diet variation (McMeans et al. 776 2007, 2015; Strid et al. 2010; Cotronei et al. 2018). It has been suggested that the high levels of 777 POPs in blood plasma of Greenland sharks off Norway may interfere with vitamin A and vitamin 778 E homeostasis, though more work is needed to confirm any adverse effects on physiological and 779 developmental processes (Molde et al. 2013).

780

781 Toxicity

782 The fresh flesh of sleeper sharks has long been believed to be toxic due to a case in which sled 783 dogs exhibited symptoms consistent with trimethylamine poisoning after consuming large 784 quantities of raw Greenland shark meat (Boje 1939; Anthoni et al. 1991; MacNeil et al. 2012). 785 These symptoms mimic acute alcohol intoxication, and have anecdotally been noted in dogs as 786 well as people (Jensen 1914; Clark 1915). Greenland sharks, like many other elasmobranchs, 787 possess high levels of trimethylamine oxide, which is converted to trimethylamine during 788 digestion (Anthoni et al. 1991). However, the amount of shark flesh that would be necessary to 789 induce an adverse response is likely larger than a person could reasonably consume in one sitting 790 (MacNeil et al. 2012; Nielsen 2017). Adequate preparation is also thought to reduce any 791 potential effects of trimethylamine toxicity (Jensen 1914; Clark 1915; Anthoni et al. 1991; Orlov 792 2017), though Wang and Yang (2004) write that Pacific sleeper shark meat is consumed fresh in 793 Taiwan as a substitute for whale shark Rhincodon typus, despite being "rather bland and 794 tasteless". Fermented Greenland shark, known as the national delicacy kæstur hákarl in Iceland, 795 is typically only eaten in small amounts due to its pungent taste. Microbes, such as Pseudomonas 796 aeruginosa, introduced by the fermentation process are hypothesized to detoxify trimethylamine 797 and trimethylamine oxide in hákarl (Osimani et al. 2019).

798

799	
800	Fishing Pressure and Management
801	
802	Catch and fishery interactions
803	While the Greenland shark has been fished for its liver oil and meat at times throughout history
804	(Jensen 1914; Compagno 1990; MacNeil et al. 2012; Davis et al. 2013), the Pacific sleeper shark
805	has, to the best of our knowledge, never been targeted on a commercial scale except for a
806	localized fishery in the waters off Hualien, Taiwan (Wang and Yang 2004). There are also a few
807	anecdotal reports of fishers in Southeast Alaska targeting Pacific sleeper sharks to sell the livers
808	during the brief shark liver fishery that also existed for the Pacific spiny dogfish Squalus suckleyi
809	in that region (C. A. Tribuzio, personal communication). However, no official records of this
810	activity exist.
811	There are relatively little reliable historic data available on incidental catches of Pacific
812	sleeper sharks, as any sharks caught are not typically retained. Increased interest in shark
813	conservation and awareness of their relative vulnerability has resulted in improved catch
814	reporting over the past two decades. Prior to 2003, shark catches in Alaska waters were reported
815	in aggregate, requiring estimation of species-specific removals, but since have much improved

thanks to the introduction of the NOAA Fisheries Catch Accounting System (Cahalan et al. 816 817 2015a, b). Similarly, improved species identification and reporting of shark catches were 818 initiated in 2001 in Canadian waters, which resulted in an increase in reporting of discards of 819 Pacific sleeper sharks (King et al. 2017). However, given the data-limited nature of the stock 820 assessment and lack of exploitable biomass estimates, exploitation rates cannot be determined 821 and are likely highly uncertain (Courtney et al. 2016).

822 Somniosus species are generally regarded as a nuisance when they are caught incidentally 823 in other target fisheries (Nielsen 2017; Orlov 2017). They frequently become entangled in 824 longlines and are cumbersome on deck when caught in bottom trawls, both requiring long 825 handling times to discard (Orlov 2017; Grant et al. 2018). An ongoing study aimed at developing 826 tools that can more accurately identify and size-grade large shark species from video taken on 827 vessels participating in an electronic monitoring program for fixed-gear fisheries in Alaska (i.e., 828 vessels carrying cameras in lieu of at-sea observers) found that out of 57 Pacific sleeper sharks 829 captured across 11 fishing vessels since 2015, 15 (26.3%) were entangled with the line in some

fashion, and six sharks (10.5%) required more than three minutes to extricate (K. R. Fuller,

unpublished data). Over 60% of these sharks were removed from the line by cutting one or more

832 gangions (K. R. Fuller, unpublished data). Greenland and Pacific sleeper sharks have also been

833 implicated in longline depredation of valuable target species, such as Greenland halibut

834 *Reinhardtius hippoglossoides* and Pacific halibut (Wright and Hulbert 2000; Grant et al. 2018;

Madigan et al. 2022). Research efforts on modifications of fishing gear have shown promise for
reducing bycatch of Greenland sharks in target fisheries (Munden 2013; Folkins 2019; Grant et
al. 2020).

Catches of Pacific sleeper sharks off British Columbia are variable year-to-year but are generally low (Fig. 11; Anderson et al. 2019). Bottom-trawl and longline fisheries for more valuable target groundfish species comprise the majority of the Pacific sleeper shark catch (Fig. 11). Estimates of discards in trawl fisheries prior to 1996 and in non-trawl fisheries prior to 2006 are considered less reliable, as this is when at-sea observer coverage was implemented in each sector, respectively. Nearly all of the catch of Pacific sleeper sharks in British Columbia waters is discarded.

845 In federal waters off Alaska, Pacific sleeper sharks are most frequently taken in the 846 commercial walleye pollock, Pacific halibut, mixed flatfish, and Pacific cod Gadus 847 macrocephalus fisheries (Fig. 12a). They are also caught incidentally in state recreational 848 fisheries for Pacific halibut and other bottomfish (Baumer et al. 2019; Tribuzio et al. 2022). 849 Increases in bycatch were observed from the early to late 1990s in the Prince William Sound 850 longline fishery (Wright and Hulbert 2000), which coincided with trends in abundance 851 throughout the Gulf of Alaska at that time (Mueter and Norcross 2002). Fishery catches of 852 Pacific sleeper sharks have decreased since the mid-2000s, with shifts in the proportion taken by 853 each target fishery (Fig. 12b). The exception to this trend is from federal fisheries operating 854 within the inside waters of the Gulf of Alaska (e.g., the Individual Fishing Quota Pacific halibut 855 fishery); however, this trend is more likely driven by changes to data collection procedures in 856 2013 that expanded observer coverage to inside waters. Very little (1% in the Gulf of Alaska and 857 10% in the Bering Sea, on average) of these incidental catches is retained due to low commercial 858 value (Tribuzio et al. 2022). Similarly, nearly all catches of Pacific sleeper sharks off the US 859 West Coast are discarded (Jannot et al. 2021). The survival rate of discarded Pacific sleeper 860 sharks is unknown, but likely varies according to fishing gear and behavior (Morgan and Burgess 861 2007; Braccini et al. 2012). Preliminary tagging data suggest that trawl-caught Pacific sleeper

sharks are all deceased when released (C. A. Tribuzio, unpublished data). The degree of stress

- associated with capture and handling, indicated by blood glucose and lactate levels, is variable in
- 864 Greenland sharks but has been found to be correlated with body size and depth of capture
- 865 (Barkley et al. 2016).

866 Catches of *Somniosus* species tend to occur in spatially clustered hotspots that may be 867 temporally variable (Menon 2004; Cosandey-Godin et al. 2015). In Alaska waters, fisheries 868 catches are broadly distributed but have been historically highest in Shelikof Strait and the heads 869 of submarine canyons along the continental slope of the Bering Sea, particularly Bering Canyon 870 north of Unimak Pass (Fig. 3). Menon (2004) demonstrated that bycatch of Pacific sleeper sharks 871 had a weak, positive relationship with depth and a negative relationship with abundance of 872 Pacific spiny dogfish. The spatial distribution of Pacific sleeper shark catch in Alaska waters has 873 reduced since the late 1990s and 2000s, mirroring patterns observed in fisheries-independent 874 indices (Matta et al. 2022).

875

876 Management and conservation

877 Management of the catch of Pacific sleeper sharks is limited to a few regions within their 878 distribution. In federal waters of Alaska, the overfishing status of Pacific sleeper sharks is 879 assessed and the catch is managed as part of multi-species shark stock complexes within each of 880 the two main management areas: the Bering Sea/Aleutian Islands and the Gulf of Alaska. 881 Harvest control rules for Alaska groundfish are set using a descending six-tier system 882 corresponding to the amount of data available for a given stock (NPFMC 2020). Little 883 information exists to support single-species stock assessments for Pacific sleeper shark or most 884 of the other component species within the shark stock complexes, placing them in the lowest 885 tiers, in which the status of the stock cannot be determined. For example, the Gulf of Alaska 886 Pacific spiny dogfish stock falls into Tier-5 of the North Pacific Fishery Management Council's 887 harvest control rule structure because their biomass estimate from trawl surveys is considered 888 reliable. Harvest limits of Tier-5 species are partially estimated based on fishery-independent 889 trawl survey biomass estimates (NPFMC 2020). In contrast, fishery-independent surveys are 890 inadequate to generate estimates of abundance for the remaining species of the shark complexes 891 (including Pacific sleeper sharks), due to either their distribution or catchability, and they are

892 therefore considered Tier-6, the most data-limited tier category. Harvest limits for these Tier-6 893 species are estimated based on historical catch. The current management strategy is to set the 894 maximum harvest limits for the shark complexes in each management area based on the 895 aggregate of the individual species' harvest limits or as a single harvest limit estimated for the 896 complex as a whole; thus, there is no species-specific management for any of the shark species in 897 Alaska waters. This approach assumes that maintaining historical catch levels is sustainable, will 898 not result in overfishing, and that all species within the complex are equally vulnerable. 899 Generally, shark catches in Alaska waters have stayed well under the maximum amount allowed 900 (Tribuzio et al. 2022). However, this method for setting harvest limits ignores any biological 901 information and is associated with a high risk of overfishing (Carruthers et al. 2014). 902 Furthermore, it is important to note that Pacific sleeper sharks appear to have declined in 903 abundance during the period when Tier-6 assessment methods have been used (Fig. 2). 904 Assessment methods applicable to data-limited stocks are currently being explored to better 905 manage Pacific sleeper sharks in Alaska (Tribuzio et al. 2022), including incorporating accessory 906 information into harvest specifications, demographic-based population models that incorporate 907 movement analysis, and plausible estimates of life history parameters (Tribuzio and Kruse 2011; 908 Free et al. 2017; Pantazi et al. 2020; Dureuil et al. 2021). As Pacific sleeper sharks have been 909 identified as among the most vulnerable to overfishing of all managed stocks in Alaska waters 910 due to their likely low productivity (Ormseth and Spencer 2011), such research into alternative 911 management methods is timely.

912Research into the use of electronic monitoring (EM) video data to improve Pacific913sleeper shark catch estimates in Alaska waters is ongoing (C. A. Tribuzio and K. R. Fuller,914personal communication). These projects aim to develop machine learning tools to identify and915size-grade Pacific sleeper sharks in recorded video, thereby making the video review process916more efficient while providing previously unavailable size data to refine estimates of total catch.917This information will be especially useful to improve catch estimates in longline fisheries, where918sharks are incidentally caught but not necessarily landed.

Pacific sleeper sharks do not appear to be formally assessed elsewhere, though biological
and demographic data are collected through various scientific survey and fisheries research
platforms in other parts of their range. In British Columbia, their conservation status has not been
assessed and is currently unknown. Additionally, no stock assessment process has been

923 completed and there is little known about their population, distribution, and abundance. When 924 possible, data on Pacific sleeper shark encounters are collected during fisheries-independent 925 surveys; however, individuals are not generally sampled or sexed. In 2011, the US West Coast 926 management region made a change requiring that the groundfish fishery monitor 100% of 927 discards, resulting in improved data (Jannot et al. 2021). Still, Pacific sleeper sharks do not 928 qualify as a managed species under any of the Pacific Fishery Management Council fishery 929 management plans.

930 Because they can be perceived as a nuisance due to their tendency towards longline 931 depredation and entanglement in fishing gear, directing fishing on Pacific sleeper sharks has 932 been proposed to reduce negative impacts on other groundfish fisheries (Orlov 2017). The 933 majority of the catch throughout its range is immature, and due to its likely life history attributes 934 of slow growth, long generation time, and low overall productivity, it is highly improbable that a 935 sustainable fishery for this species could be established (Smith et al. 1998; Simpfendorfer and 936 Kyne 2009; Tribuzio and Kruse 2011; Au et al. 2015; Matta et al. 2022). Furthermore, the IUCN 937 status of the Pacific sleeper shark recently changed from Data Deficient to Near Threatened in 938 large part due to possible population declines in portions of their range (Rigby et al. 2021), and 939 the North Pacific Fishery Management Council's Scientific and Statistical Committee noted 940 conservation concerns in its most recent review of the stock assessment (SSC 2022). Given these 941 concerns, a conservative management approach is warranted pending better understanding of this 942 species.

943

944 Future studies/conclusions

945 This review demonstrates that there are many areas in which our understanding of Pacific sleeper 946 shark biology and ecology could be improved, particularly regarding habitat use and life history. 947 These knowledge deficits should be the focus of future research for improving the assessment 948 and management of this potentially long-lived and vulnerable species. There are a number of 949 ongoing studies to fill research gaps, including longevity estimation, bioenergetics, movement, 950 reproduction, and advancing stock assessments of Pacific sleeper sharks in Alaska waters. Catch 951 estimates, a main factor in determining harvest limits in stock assessments in the Bering 952 Sea/Aleutian Islands and Gulf of Alaska federal management regions, have been much improved 953 over the past decade thanks to the teamwork of scientists and fishery managers. Advanced

954 computing methods such as machine learning are being used to process electronic monitoring 955 video data and to further improve estimates of catch, particularly in fisheries sectors that have 956 not been historically well-observed. Researchers are currently working towards refining 957 estimates of maturity and estimating movements from a blend of survey data, tag information, 958 and baited cameras. The pilot project described herein to determine estimates of age from eye 959 lens radiocarbon has been fully funded, with the objective of providing estimates of life history 960 parameters including growth and natural mortality that are critical for improving stock 961 assessment. Until more information becomes available, a precautionary approach to its 962 management is warranted throughout its range.

963 964

965 Author contributions

MM reviewed literature, analyzed data, and conceived of and drafted the original manuscript;
CT, LD, and AA compiled and analyzed data and contributed to the manuscript; KF and GD
edited the original draft and contributed additional text. All authors read, edited, and approved
the manuscript.

970

971 Data availability

972 Much of the data for this review are from published studies, referenced throughout the document. 973 Data from Alaska are from a variety of sources: fisheries data are available from the NOAA 974 Alaska Regional Office and the Department of Fisheries and Oceans, Canada (DFO); survey data 975 are from the NOAA Alaska Fisheries Science Center, the Alaska Department of Fish and Game, 976 and DFO; at-sea observer data are from the North Pacific Observer Program; opportunistic 977 reports are from fishers and other researchers. Size data from the US West Coast and British 978 Columbia are from the International Pacific Halibut Commission, DFO, and the At-Sea Hake 979 Observer Program (NOAA Northwest Fisheries Science Center). Non-confidential data and code 980 used to create figures (R Core Team 2021) are available at https://github.com/BethMatta-981 NOAA/sleeper-shark-review.

982

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Figures

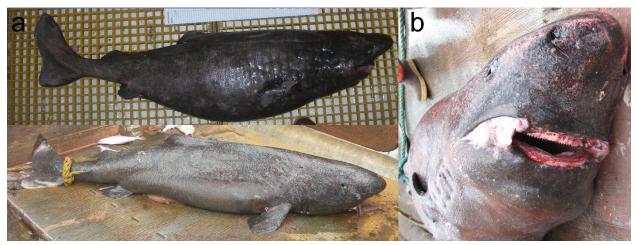


Fig. 1 The Pacific sleeper shark *Somniosus pacificus*. All individuals pictured are immature and under 200 cm total length. a) Two individuals showing variation in coloration. b) Pacific sleeper sharks have relatively small mouths and teeth.

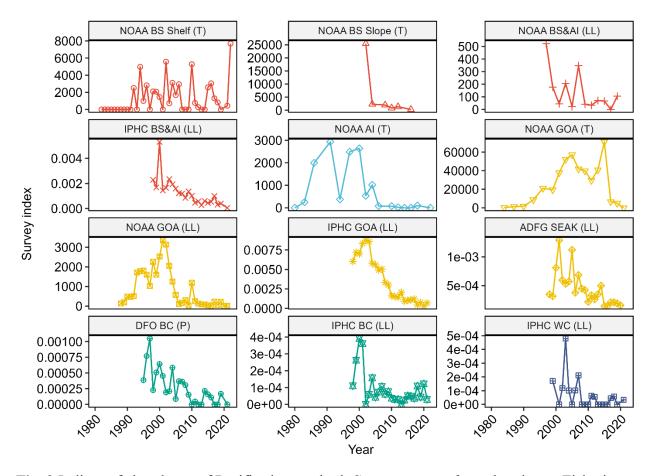
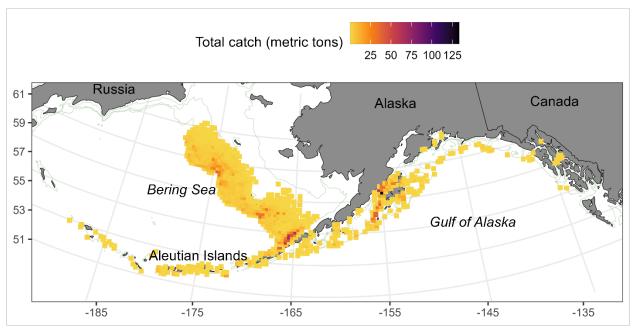
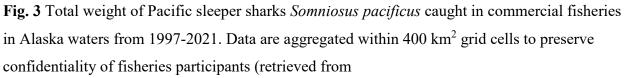


Fig. 2 Indices of abundance of Pacific sleeper shark *Somniosus pacificus* abundance. Fisheriesindependent trawl (T), longline (LL), and pot (P) surveys operated by federal and state agencies (NOAA: National Oceanic and Atmospheric Administration Fisheries; IPHC: International Pacific Halibut Commission; ADFG: Alaska Department of Fish and Game; DFO: Department of Fisheries and Oceans, Canada) within large management areas in the eastern North Pacific Ocean (color-coded by region; BS: Bering Sea; AI: Aleutian Islands; GOA: Gulf of Alaska; SEAK: Southeast Alaska; BC: British Columbia; WC: United States West Coast). Units of measurement differ across surveys (NOAA T: biomass; NOAA LL: relative population numbers; IPHC LL, ADFG LL, and DFO P: catch per unit effort)





https://www.fisheries.noaa.gov/resource/map/alaska-groundfish-fishery-observer-data-map on August 8, 2022)

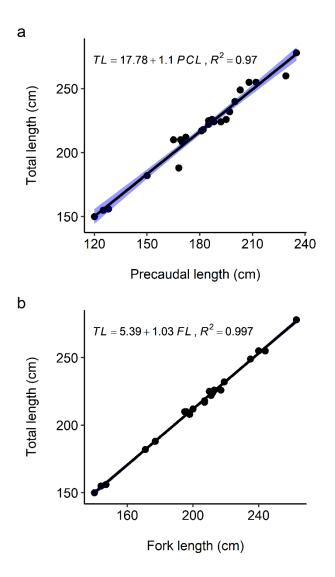


Fig. 4 Length-length relationships of Pacific sleeper sharks *Somniosus pacificus*. Linear regressions between total length (TL) and a) precaudal length (PCL, n=24) and b) fork length (FL, n=21). Blue shading indicates 95% confidence regions. Data collected by Hulbert et al. (2006)

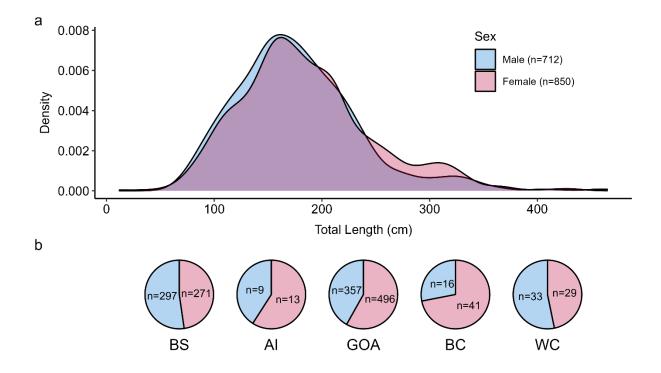


Fig. 5 Size and sex information for Pacific sleeper sharks *Somniosus pacificus* caught along the west coast of North America (Bering Sea to Baja California). a) Length distributions of landed and measured males and females. b) Sex ratios of lengthed Pacific sleeper sharks caught within management regions (BS: Bering Sea, AI: Aleutian Islands, GOA: Gulf of Alaska, BC: British Columbia, WC: US West Coast). Sample sizes indicated by *n*

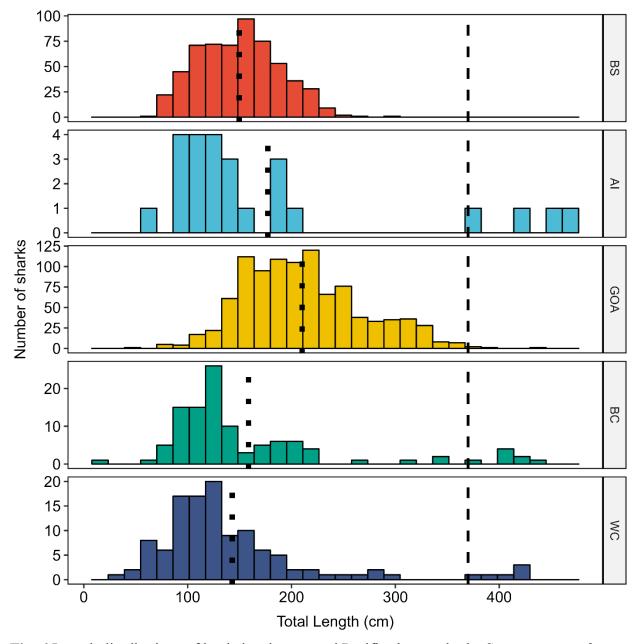


Fig. 6 Length distributions of landed and measured Pacific sleeper sharks *Somniosus pacificus* along the west coast of North America. Dotted lines indicate mean size in each region (BS: Bering Sea, n=584; AI: Aleutian Islands, n=25; GOA: Gulf of Alaska, n=982; BC: British Columbia, n=109; WC: US West Coast, n=117). Dashed line is the length at maturity of 370 cm total length estimated by Ebert et al. (1987)

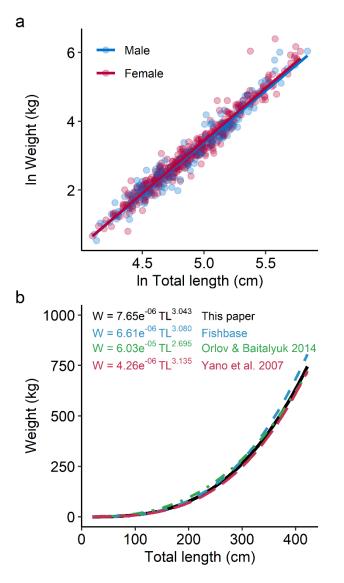


Fig. 7 Length-weight relationships of Pacific sleeper sharks *Somniosus pacificus*. a) Relationship between natural log-transformed length and weight for males (n=230) and females (n=367) collected from Alaska waters. An analysis of covariance determined no significant effect of sex on weight. b) Fitted length-weight relationship from the present paper (both sexes combined, back-transformed to original scale) in comparison with published relationships for Pacific sleeper sharks from Yano et al. (2007), Orlov and Baitalyuk (2014), and www.fishbase.se

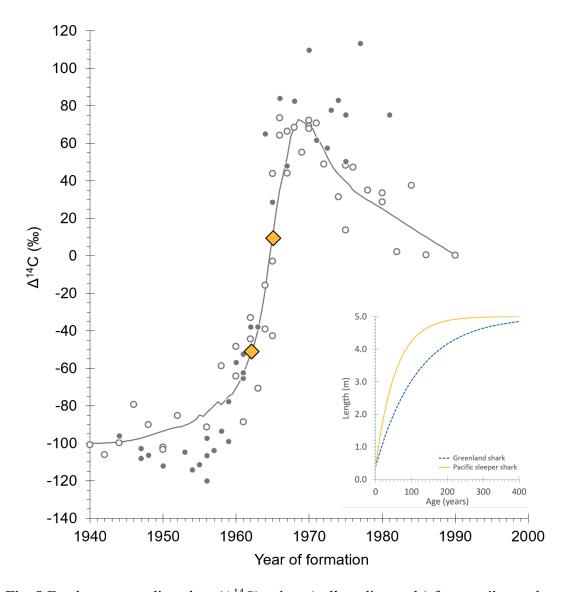


Fig. 8 Eye lens core radiocarbon (Δ^{14} C) values (yellow diamonds) from a pilot study on a 3.1 m Pacific sleeper shark *Somniosus pacificus* that are aligned with regional chronologies to estimate a birth year. The specimen was collected in 2011 and each eye lens core (formed during pre-natal development) provided a diagnostic radiocarbon value (Δ^{14} C = 9.4 and -51.1‰) that can be attributed to a formation date (birth year) between 1962 and 1965. Note that while the Δ^{14} C values from cores of the same individual differ, likely due to imprecision in the lens core extraction method, they still indicate a small range of potential birth years. Hence, this specimen was at most ~50 years of age and had a consequent growth rate (k) two times greater than Greenland shark *Somniosus microcephalus* (k ~0.018 *cf*. 0.009; see inset hypothetical growth curves). The bomb radiocarbon chronologies used as temporal references were from yelloweye

rockfish *Sebastes ruberrimus* (open circles) and Pacific halibut *Hippoglossus stenolepis* (solid circles) from the northeast Pacific Ocean (Kerr et al. 2004; Piner and Wischniowski 2004)

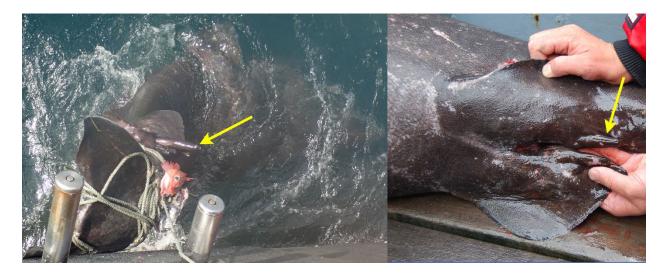


Fig. 9 Male Pacific sleeper sharks *Somniosus pacificus* thought to be mature (left) and immature (right) based on examination of the claspers (indicated by yellow arrows)



Fig. 10 A necropsy of a Pacific sleeper shark *Somniosus pacificus* that washed ashore after an apparent predation event by killer whales *Orcinus orca* off the coast of southeast Alaska in March 2022. Tooth marks are evident on the flank and the throat was ripped out, resulting in the removal of the heart, tongue, and liver. Images from Tribuzio et al. (in prep).

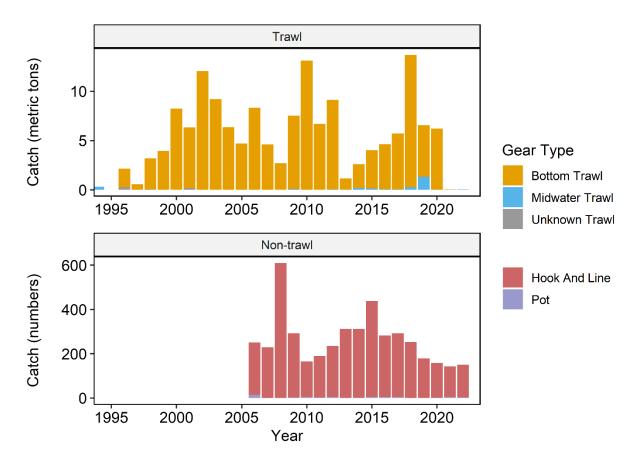


Fig. 11 Commercial catches (discards and landings) of Pacific sleeper sharks *Somniosus pacificus* in target groundfish fisheries in British Columbia waters. Catch in trawl fisheries is reported as total weight; catch in non-trawl fisheries is reported in numbers of sharks

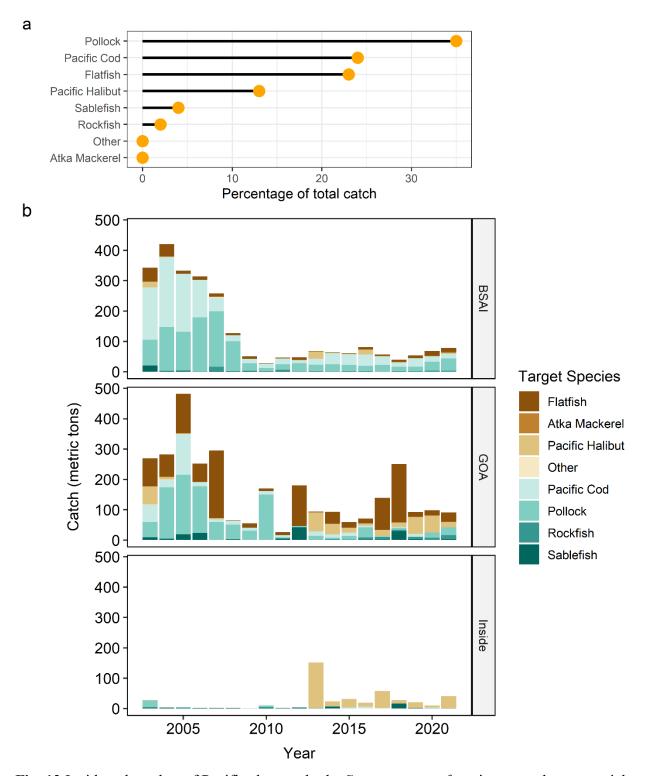


Fig. 12 Incidental catches of Pacific sleeper sharks *Somniosus pacificus* in targeted commercial fisheries in Alaska. a) Percentage of Pacific sleeper shark catch by weight in each target fishery (walleye pollock ("pollock") *Gadus chalcogrammus,* Pacific cod *Gadus macrocephalus,* mixed flatfish species Pleuronectidae, Pacific halibut *Hippoglossus stenolepis,* sablefish *Anoplopoma*

fimbria, mixed rockfish species Sebastidae, Atka mackerel *Pleurogrammus monopterygius*, and miscellaneous "other" groundfish species). b) Time series of sharks caught in target fisheries by area and management region (BSAI: Bering Sea/Aleutian Islands; GOA: Gulf of Alaska; Inside: waters 0-3 nautical miles from shore in Southeast Alaska and Prince William Sound) from 2003-2021. Note that the North Pacific Groundfish Observer Program restructured in 2013, resulting in increased coverage of inside waters. Data provided by the Alaska Regional Office Catch Accounting System