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Dietary specialization on elasmobranchs and seasonal foraging patterns of offshore killer whales *Orcinus orca* in the northeastern Pacific

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ABSTRACT: Dietary specialization allows species with overlapping ranges and similar trophic levels to coexist by reducing competition. Offshore killer whales are sympatric with other populations of *Orcinus orca* in the northeastern Pacific, but their feeding preferences are poorly known. Using genetic, drone videography, photographic, and observational evidence collected during 84 predation events, we found that elasmobranchs comprised almost 90% of all prey sampled, revealing that the offshore killer whale ecotype has a specialized diet. Sharks are energetically profitable prey because they are predictably available, large-bodied, and have a large, lipid-rich liver. In addition to previously documented prey, we identified 4 new species: salmon shark, Pacific electric ray, albacore tuna, and broadnose sevengill shark. Targeted species differed depending on the time of year and region, matching the known seasonal availability and migratory behaviour of sharks. Pacific sleeper sharks (45.2% of identified prey) and salmon sharks (6.0%) were primarily taken in Alaska, USA, and northern British Columbia (BC), Canada, in spring and early summer, whereas blue sharks (17.9%) and Pacific spiny dogfish (16.7%) were typically caught in southerly locations along the continental shelf edge off BC in late summer and fall. Blue, broadnose sevengill, and shortfin mako sharks were hunted off California, USA, in winter. Teleosts comprised only 10.7% of predation events. We conclude that in addition to fish-eating and marine mammal-eating ecotypes, offshore killer whales represent another example of pronounced, likely culturally transmitted, dietary specialization among the killer whales of the northeastern Pacific.

KEY WORDS: Offshore killer whale · *Orcinus orca* · Foraging specialization · Elasmobranch · Diet composition · Predation · Shark

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1. INTRODUCTION

Dietary specialization is thought to reduce competition between sympatric species or populations that occupy similar trophic levels (Miller 1967, Futuyma 2001). Specialists tend to be more efficient foragers than generalists when the selected resources are energetically profitable and occur predictably (Krebs et al. 1977, Futuyma & Moreno 1988). If natural selection favours divergent traits that enable foraging specializations, then assortative mating, social and reproductive isolation, and eventually speciation, may result (Dieckmann & Doebeli 1999, Schluter 2001). For instance, as a species, the killer whale *Orcinus orca* is a globally distributed apex predator that exploits a diverse array of prey (Ford 2002, Ford & Ellis 2014). At the population scale, however, distinct dietary specializations have arisen through natural selection and are likely maintained through cultural traditions (Foote 2012, Riesch et al. 2012, Filatova

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2024). These specialist populations, also known as ecotypes, do not interbreed even where they occur sympatrically and may even constitute separate species (Morin et al. 2010, 2024, Riesch et al. 2012).

Three sympatric killer whale ecotypes are found in the northeastern Pacific Ocean (Ford et al. 2000). The least encountered of these, first described in the 1980s and known as offshore killer whales (OKW), is genetically distinct but is more closely related to the fish-eating residents than to the mammal-eating Bigg's (formerly known as transient) killer whales (Hoelzel et al. 1998, 2002, Barrett-Lennard 2000, Riesch et al. 2012). The OKW population appears to be small, as it was last estimated to have an abundance of about 300 individuals (Ford et al. 2014) and is listed as threatened under Canada's Species at Risk Act (Government of Canada 2002). The OKW range extends along continental shelf and slope waters from the eastern Aleutian Islands, Alaska, to southern California (Dahlheim et al. 2008, Ford et al. 2011, 2014, Schorr et al. 2022). Within this vast latitudinal range, groups of OKW undertake long distance movements; individuals have been photographically matched between locations in Alaska and California that were over 2000–4000 km apart, within the same study year (Dahlheim et al. 2008). Satellite tags likewise showed that OKW travel large distances over fairly short time periods (e.g. >3800 km in 75 d), sometimes moving ⩾100 km d^{-1} (Schorr et al. 2022). Furthermore, individuals biopsied in Alaska had contaminant ratios indicating that they had fed in Californian waters for at least part of the year (Krahn et al. 2007).

The narrow niches occupied by specialist feeders render them particularly vulnerable to environmental change (Futuyma 2001, Whitehead & Ford 2018), thus ascertaining dietary composition has important conservation implications. However, the feeding ecology of marine animals that hunt underwater across large areas, far from shore, is difficult to study. As a result, the diet of OKW has remained poorly known, with previous studies characterizing it as entirely piscivorous (e.g. Krahn et al. 2007, Ford et al. 2011) or relatively generalist (Schorr et al. 2022). Early observations of OKW determined that they forage in large, widely dispersed groups in a manner comparable to that of piscivorous resident killer whales (Ford et al. 2000, 2011, 2014, Dahlheim et al. 2008). Like residents, but unlike Bigg's killer whales, OKW can be highly vocal while foraging and produce intense echolocation clicks (Ford et al. 2000, Dahlheim et al. 2008, Ford & Ellis 2014), which further suggests piscivory, because marine mammal prey would be alerted by such vocalizations (Deecke et al. 2005).

Stable isotope ratios, fatty acid profiles, and persistent organic pollutant patterns obtained from blubber biopsies indicate that OKW consume a prey assemblage that is composed of fish and that their diet diverges significantly from both the resident and Bigg's ecotypes (Herman et al. 2005, Krahn et al. 2007). OKW blubber also contains levels of bioaccumulating contaminants notably higher than those of residents, despite both being piscivorous (Herman et al. 2005, Krahn et al. 2007). Chemical tracer analyses have suggested a diet that includes long-lived, intermediate to high-trophic level fish species containing large amounts of omega-3 fatty acids, such as tuna and sharks (Herman et al. 2005, Krahn et al. 2007). However, given how rarely OKW are encountered, gaining a more detailed understanding of their diet has required many years of field effort. The first prey species attributed to the OKW ecotype were identified from tissue samples collected at the surface during feeding events (Ford et al. 2011, 2014, Ford & Ellis 2014) and from the stomach contents of 2 individuals harpooned in 1955 and 1964 (Rice 1968, Pike & MacAskie 1969, Morin et al. 2006). Collectively, these studies indicated that the Pacific sleeper shark *Somniosus pacificus* was an important prey species (Ford et al. 2011, Matkin et al. 2018), and to a lesser extent, the Pacific spiny dogfish *Squalus suckleyi* (hereafter referred to as dogfish) and blue shark *Prionace glauca* (Ford et al. 2014). Teleost fishes, including Chinook salmon *Oncorhynchus tshawytscha*, Pacific halibut *Hippoglossus stenolepis*, and opah *Lampris guttatus* have only been occasionally detected in the diet of OKW (Rice 1968, Pike & MacAskie 1969, Heise et al. 2003, Jones 2006, Morin et al. 2006, Dahlheim et al. 2008, Ford et al. 2011, 2014).

Extreme apical tooth wear found in all but the youngest age classes also suggested that OKW habitually prey on sharks (Ford et al. 2011). In adult OKW, teeth are often worn to the gumline, damage attributed to abrasion caused by the dermal denticles present in shark skin (Dahlheim et al. 2008, Ford et al. 2011, Raverty et al. 2020). Similar tooth wear is evident in other populations of killer whales known to prey on elasmobranchs, including a South African 'flat-toothed' morphotype described from 3 stranded individuals, one of which had over 2500 shark vertebrae in its stomach (Best et al. 2010, 2014). However, tooth wear is not apparent in a New Zealand killer whale population of elasmobranch specialists, a difference explained by the high proportion (>90%) of stingrays *Dasyatis* sp. and eagle rays *Myliobatis tenuicaudatus* in their diet (Visser 2005); unlike sharks, these species possess few to no abrasive dermal denticles (Meyer & Seegers 2012).

Here, we combine previous records of the diet of northeastern Pacific OKW (n = 12 encounters; 2008–2015) with new information (n = 18 encounters; 2004–2023) obtained from genetic analysis of prey and fecal samples, photographs, boat-based observations, and drone videography of feeding behaviours (see Table 1). These data were collected across the continental shelf waters of Alaska (AK), British Columbia (BC) and California (CA). Our aim was to determine the relative contribution of elasmobranchs to OKW diet and to assess whether this ecotype is a specialist forager like its sympatric resident and Bigg's counterparts. We examine OKW predation on various shark species, identify 4 new prey species, describe prey-specific hunting tactics, and outline the bathymetric habitat characteristics associated with foraging. Using these data, we evaluate OKW prey preferences and relate seasonal habitat use to prey distributions and migratory behaviour. Insights into the dietary breadth of a potentially stenophagous forager, such as the OKW, may indicate how vulnerable this population is to changes in the abundance or availability of its preferred prey.

2. MATERIALS AND METHODS

2.1. Field methodology

Predation events were sampled during opportunistic encounters with OKW from 2004–2023 off AK, BC, and CA. These results are presented alongside existing dietary information collected between 1955 and 2015 (Rice 1968, Pike & MacAskie 1969, Morin et al. 2006, Ford et al. 2011, 2014, Matkin et al. 2018; Table 1). The field methods used in this study are described in detail by Ford et al. (2011). We define an 'encounter' as the detection and photographic identification of an individual or group of OKW at one location on a given date, while a 'predation event' refers to the pursuit, capture and consumption of a single prey item by an individual or group of OKW during an encounter. Thus, one encounter may contain multiple predation events. When OKW were located, observers in small research vessels approached obliquely from the left side and photographed markings on their dorsal fins and saddle patches to identify as many individuals as possible, following the method developed by Bigg (1982). OKW were distinguished from other northeastern Pacific ecotypes through multiple means, including expert recognition of distinguishing acoustic, behavioural, and morphological characteristics in the field and photo-identification matches with individuals that were genetically assigned to this population or with close associates of such individuals.

While obtaining photo-identifications, observers also looked for behaviours indicative of foraging, including rapid changes in swimming direction and speed, high arching dives followed by long submersion times, and circling behaviour. A hydrophone deployed over the side of the small vessel was helpful in locating OKW and providing evidence of foraging behaviour (i.e. presence of frequent echolocation click trains with rapid inter-click intervals). Locations of suspected predation events were carefully approached once the whales had moved on, and the area was visually scanned for prey remains, including tissue fragments, fish scales, and oil slicks. The presence of seabirds was often an additional indicator that predation had occurred, and elasmobranch liver fragments were frequently found on the surface at locations where birds had congregated. Fecal plumes and particulates were opportunistically spotted at the water's surface in the wake of OKW, while we followed them to collect photo-identification images or search for prey remains. Prey fragments and whale fecal samples were collected using a fine-meshed dip net attached to a pole, or in the case of some fecal samples, a plastic bucket. Whenever possible, a different net head was used for each sample, and nets were rinsed with seawater and brushed with a bleach solution between encounters to minimize genetic cross-contamination. Samples were preserved in 95% ethanol or by freezing (−20°C), and the GPS coordinates of the collection site were recorded. To further minimize possible contamination, we also subsampled tissue from the interior of larger prey samples using a sterile scalpel prior to running the genetic analysis for species identification. When prey samples could not be collected, prey species were identified visually or by examining photographs or drone video footage. Maps of prey sampling locations were produced using R version 4.3.1 software (R Core Team 2021) and are displayed using the Albers Equal Area projection (EPSG:3005). Seafloor depths at sample collection locations were obtained from the ETOPO 2022 database hosted by NOAA (NOAA National Centers for Environmental Information 2022) using the 'marmap' R package (Pante et al. 2023) and were plotted at a grid resolution of 0.5 arc-minutes.

2.2. Genetic analysis for prey species identification

Extractions and subsampling were performed in an ultraviolet (UV) polymerase chain reaction (PCR) hood, and the equipment and work surface were ster-

Table 1. Collection date, location, species, and minimum number of prey consumed by offshore killer whales, identified either by examination of stomach contents, photographs, visual observation or video of predation events, or the genetic/morphological analysis of prey samples (fish scales or tissue fragments) or scats collected in the vicinity of foraging whales. Minimum numbers of prey per species were determined for each encounter using haplotype analysis (where possible), combined with assessments of the time elapsed and distance between subsequent sample collection points (samples separated by >1 km or >20 min were considered distinct kills). If the minimum number of individual prey differed from the total number of samples collected during an encounter, the number collected is indicated inside parentheses next to the minimum number. Sources are indicated for information obtained from previous publications; if no source is given, the entry represents new data from the present study. WCVI: west coast of Vancouver Island; na: not applicable

Date	Location	Prey species	Minimum no. (no. of samples)	ID method	Source (if previously publ.)
19 May 1955	Off SW Vancouver Island, BC	Pacific halibut	na	Stomach contents	Pike & MacAskie (1969) (see Ford et al. 2011)
09 Jan 1964	Southern California	Opah	2	Stomach contents	Rice (1968), Morin et al. (2006) (see Ford et al. 2011)
		Carcharhinidae sp.	2		
11 Mar 1996	Johnstone Strait, BC	Pacific sleeper shark	1	Tissue (DNA)	Ford et al. (2014)
23 Jun 2000	Haida Gwaii, BC	Pacific halibut?	1	Photo	Jones (2006)
19 Mar 2004	Johnstone Strait, BC	Pacific sleeper shark	1	Tissue (DNA)	
30 May 2008	Dixon Entrance, BC	Pacific sleeper shark	11 (13)	Tissue (DNA)	Ford et al. (2011)
13 Jun 2009	Prince William Sound, AK	Pacific sleeper shark	7	Tissue (DNA)	Ford et al. (2011)
22 Aug 2010	La Perouse Bank, WCVI, BC	Chinook salmon	1	Scales	Ford et al. (2014)
		Blue shark	1	Photo	Ford et al. (2014)
30 Mar 2011	Johnstone Strait, BC	Pacific sleeper shark	1	Tissue (DNA)	Ford et al. (2014)
08 Aug 2011	Hecate Strait, BC	Chinook salmon	1	Scales	Ford et al. (2014)
		Opah	1	Tissue (DNA)	
18 Aug 2011	Off SW Vancouver Island, BC	Blue shark	1 (3)	Tissue (DNA)	Ford et al. (2014)
05 Sep 2011	Off SW Vancouver Island, BC	Pacific spiny dogfish	1	Tissue (DNA)	Ford et al. (2014)
29 Jun 2012	Resurrection Bay, AK	Pacific sleeper shark	4 (5)	Tissue (DNA)	Ford et al. (2014)
07 Sep 2012	Barkley Canyon, WCVI, BC	Pacific spiny dogfish	7	Tissue (DNA)	Ford et al. (2014)
03 Mar 2013	Hecate Strait, BC	Chinook salmon	1	Scales & tissue (DNA)	Ford et al. (2014)
20 May 2013	Kachemak Bay, AK	Pacific sleeper shark	1	Visual	Matkin et al. (2018)
01 Sep 2014	Off SW Vancouver Island, BC	Pacific spiny dogfish	1	Tissue (DNA)	
04 Sep 2014	Dixon Entrance, BC	Blue shark	1	Tissue (DNA)	
23 Jun 2015	Prince William Sound, AK	Salmon shark	3	Tissue (DNA)	Matkin et al. (2018)
06 Oct 2015	Off SW Vancouver Island, BC	Pacific spiny dogfish	3	Tissue (DNA)	
05 Jul 2016	Hecate Strait, BC	Pacific halibut	2	Tissue (DNA)	
13 Dec 2016	Santa Cruz, CA	Broadnose sevengill shark	1	Drone video	S. Moore (pers. comm.)
21 May 2017	Resurrection Bay, AK	Pacific sleeper shark	2	Tissue (DNA)	
05 Jun 2018	Kenai Fjords, AK	Salmon shark	2	Tissue (DNA) & photo	
		Pacific sleeper shark	na	Fecal (DNA)	
10 Jun 2018	Kenai Fjords, AK	Pacific sleeper shark	1 (2)	Tissue (DNA)	
17 Apr 2020	Seward, AK	Pacific sleeper shark	1	Tissue (DNA)	
06 Aug 2021	Off SW Vancouver Island, BC	Pacific spiny dogfish	1	Tissue (DNA)	
		Blue shark	1	Tissue (DNA)	
12 Sep 2022	Off SW Vancouver Island, BC	Pacific electric ray	1	Tissue (DNA)	
13 Sep 2022	Off SW Vancouver Island, BC	Pacific electric ray	1	Tissue (DNA)	
		Albacore tuna	3	Tissue (DNA)	
		Blue shark	3	Tissue (DNA)	
14 Sep 2022	Off SW Vancouver Island, BC	Blue shark	1	Tissue (DNA)	
21 Aug 2023	Off SW Vancouver Island, BC	Pacific spiny dogfish	1	Tissue (DNA)	
		Blue shark	3	Tissue (DNA)	
24 Aug 2023	Off SW Vancouver Island, BC	Pacific sleeper shark	9	Tissue (DNA)	
6 Oct 2023	Off SW Vancouver Island, BC	Pacific sleeper shark	na	Fecal (DNA)	
		Blue shark	na	Fecal (DNA)	
29 Dec 2023	San Miguel Island, CA	Blue shark	4	Drone video	E. Parnes-Katz (pers. comm.)
		Shortfin mako shark[a]	1	Drone video	E. Parnes-Katz (pers. comm.)

[a] Unsuccessful predation attempt (chase but no capture or consumption)

ilized using bleach and UV light prior to use. DNA was extracted from the fecal samples using the DNeasy PowerSoil HTP 96 kit (Qiagen), following the manufacturer's protocols. Approximately 450 µl of resuspended scat was added to the garnet bead plate and prior to processing, excess ethanol was decanted off following centrifugation at 1377 × *g* for 3 min. A Proteinase K step was added post-homogenization and centrifugation steps, whereby 20 µl of Proteinase K (20 mg ml^{-1}) was added to the supernatant, vortexed and incubated at 60°C for 10 min prior to the addition of solution C2. Samples were eluted with 100 µl of 10 mM Tris (solution C6). Prey tissue samples were subsampled and excess ethanol blotted off prior to extraction using the DNeasy Blood and Tissue kit 96 (Qiagen), following the manufacturer's instructions and eluted in 100 µl of AE Buffer.

Three amplicon types for the characterization of different taxonomic groups of prey were applied to the extracted DNA samples to identify them to the species level. The amplicons used were a ~270 bp segment of the chordate (16SChord) and ~250 bp of the cephalopod 16S rRNA gene (16SCeph) (Deagle et al. 2009), and a ~260 bp segment of the cytochrome oxidase I (COI) gene, amplified with primers designed primarily for the amplification of salmonids (Thomas et al. 2017). As this COI primer set amplifies non-salmonid fish less efficiently due to sequence mismatches, it is used to validate and confirm salmon species detections and can only be used for non-salmonids to enhance the 16S identification when there is sufficient amplification. The 16SChord/16SCeph amplicons were multiplexed in one PCR reaction, and the COI was performed in a separate reaction. All PCR amplifications were performed in 20 µl volumes using the Multiplex PCR Kit (Qiagen). Reactions contained 10 µl (2X) master mix, 0.25 µM of each primer, and 2 µl template DNA. Thermal cycling conditions were as follows: 95°C for 15 min followed by 34 cycles of 94°C for 30 s, 57°C for 90 s and 72°C for 60 s, and a final extension at 72°C for 600 s. Along with extraction and PCR blanks, a positive control for each amplicon was added to the amplification tray. These consisted of ~1.0E+5 copies, synthesized gblocks Gene Fragments (IDT DNA) designed to unique sequences that were encompassed within the matching amplicon primers.

Amplified 16SChord/16SCeph and COI amplicon samples were barcoded with unique, matching 10 bp forward and reverse tags with an edit distance of 5. The 16SChord/16SCeph and COI amplified samples were pooled by amplicon into single libraries. These were cleaned and concentrated using DNA Clean and Concentrate-5 columns (Zymo) prior to library preparation and indexing using the KAPA Low Throughput Library Preparation kit (KAPA) for Illumina platforms as per the manufacturer's instructions. The quantity of the indexed library pools was assessed using dsDNA High Sensitivity kit (Qubit) and quality and size assessed using the DNA 1000 Bioanalyzer chip (Agilent). Finally, the pools were combined into a single library of 66 to 33% ratio and processed on a 301 bp single end MiSeq V2 chip (Illumina) with a 5% phiX spike in. The data were de-multiplexed by library pool (index) on the sequencer and produced as fastq files.

2.3. Bioinformatics for prey species identification

The bioinformatics pipeline for this analysis is available on GitHub (Sutherland 2022). Raw sequence files were evaluated with FastQC (Andrews 2010) and aggregated to view using MultiQC (Ewels et al. 2016). Single-end data (16S and COI) were assigned to individuals using *ngsfilter* (Boyer et al. 2016) based on the individual identifying barcode present on both sides of the read for single-end data. A fasta file with a single record obtained for each unique amplicon including the number of reads assigned per sample in the header was generated using *obiuniq* (Boyer et al. 2016). Amplicons with low read counts (⩽10 reads per amplicon summed across all samples for each experiment), or too short of read lengths (<55 bp for 16SChord, 16SCeph or COI) were removed. Amplicons that are slight derivations of an original amplicon and therefore likely sequencing errors (i.e. internal sequences) were removed using *obigrep* and *obiclean*, while singletons (no head sequence or internals) or head sequences were retained (Boyer et al. 2016). Data were then exported into tabular format using *obitab*.

The filtered amplicon fasta file was then used as an input for *blastn* (Altschul et al. 1997) using default parameters against the nt database (NCBI) to retrieve the top 10 alignments per query. The *blastn* output and the filtered fasta file were imported into MEGAN for taxonomic annotation of amplicons (Huson et al. 2016). The lowest common ancestor (LCA) algorithm (Huson et al. 2007) was implemented using the following parameters for all amplicons: min. score = 100; max. expected = 1.0E−8; min. % identity = 97; top % = 10; min. support % = 0 (off); and min. support = 1. Huson et al. (2007) suggest a min. score of 35−100 for 100−800 bp reads, respectively, and between 10 and 20% for top-percent. Taxonomy annotation was exported as a text file using the option 'readName_to_taxonName' within MEGAN. Amplicon annotation was merged with per sample amplicon counts in R (R Core Team 2021) using custom scripts. Human reads, either due to contamination or sourced from the environment, were removed from the datasets. Data were made proportional by dividing read counts per species against the total reads (not including human). For the read count output, any individual sample-taxon combination with less than 10 reads was transformed to 0.

2.4. Haplotype analysis

To determine whether prey tissues collected during each OKW encounter came from multiple individuals of the same species, or could represent repeat sampling of the same fish, we conducted haplotype sequencing of the mitochondrial DNA (mtDNA) control region (CR) using methods similar to those described by Ford et al. (2011). The CR was amplified from genomic DNA by PCR using taxon-specific primers. Primers flanking the CR were designed with binding sites in the tRNA-proline and tRNA-phenylalanine genes using Primer3 in Geneious Prime 2025.0.2 (www.geneious.com). Alternative binding sites in the tRNA-threonine and 12S rRNA genes were selected for rays and *Lampris*, respectively. Primer sequences are provided in Table S1 in the Supplement; www.int-res.com/articles/suppl/m763p171_supp.pdf. Reactions were performed in 20 µl volumes with 1× PCR Buffer (Qiagen), 83.6 µM deoxynucleotide triphosphate (dNTPs), 0.50 pmol forward primer, 0.50 pmol reverse primer, 2 µl genomic DNA (approx. 10 ng), and 0.0278 Units HotStarTaq DNA Polymerase (Qiagen). The thermal profile applied in TADVANCED Thermal Cyclers (Biometra Gmb) consisted of a 15 min denaturation at 95°C followed by 35–40 cycles of 95°C for 30 s, 58°C for 30 s, and 68°C for 90 s, and a 16°C hold. A longer extension time of 2.5 min was applied for amplicons exceeding 2000 bases. Amplicons were assessed for size on 1% agarose gels with SYBR Safe and the Azure c150 Imaging System.

In preparation for Sanger sequencing, CR amplicon concentration was determined with the Qubit dsDNA BR Assay Kit (Invitrogen) and treated with ExoSAP-IT PCR Product Cleanup (Applied Biosystems) to remove unincorporated primers and nucleotides. A total of 1 to 3 µl was then used as template for sequencing with the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems). Reactions were performed in duplicate with both forward and reverse primers. Lastly, the BigDye XTerminator Purification Kit (Applied Biosystems) was used to prepare sequencing reactions prior to capillary electrophoresis on the 3730xl DNA Analyzer (Applied Biosystems).

Raw sequencing outputs were manually edited and assembled into contigs in Geneious Prime 2025.0.2 using the default parameters. Consensus sequences were subsequently aligned and trimmed to produce identical 5′ and 3′ ends for comparison of the prey CR by species. For amplicons exceeding 1100 bases, forward and reverse reads were aligned independently. Highly similar published sequences were sought out with a Megablast (Morgulis et al. 2008) search of the NCBI core_nt database. To visualize the number of individual prey consumed in each OKW encounter, haplotype networks of the CR sequences were produced with the integer neighbour-joining (IntNJ) algorithm in PopART 1.7 (Leigh & Bryant 2015). A network reticulation tolerance (α) of 0.1 to 0.5 was applied so as not to produce overcomplicated networks. Nucleotide deletions at insertion–deletion positions identified in conspecific CR sequence alignments were replaced with mismatched nucleotides to ensure sequences differing in one or more indels would be recognized by the haplotype network algorithm (Joly et al. 2007).

3. RESULTS

Between 2004 and 2023, foraging activity or defecation was observed during 30 encounters with OKW, comprising a minimum (based on field observations and prey haplotypes) of 84 predation events and 1 predation attempt (Table 1). This includes both newly analysed (n = 44) and previously published (n = 40) predation events. Prey fragments were collected from 77 of these predation events, including tissue fragments from 75 events and fish scales from 3 events. The large size of collected prey tissues relative to possible residue from other sources of DNA found on collection nets (from either eDNA in seawater or from prior sampling events) meant that DNA from the prey sample overwhelmed any trace contamination. For all newly analyzed prey tissues (n = 42), >74% of reads (16SChord amplicon) were attributed to a single, top-ranked prey species, and for 90% of these tissues (n = 38), >90% of reads were attributed to the top-ranked species. In addition, the species identifications made using the 16SChord amplicon were verified using a second amplicon (COI). This allowed us to exclude possible contaminating DNA in our assignment of species to each prey sample.

In 2 cases, prey species were identified from photographs of whales handling and consuming prey at the surface (e.g. Fig. 1), and in one case the species was identified visually by an experienced observer (Table 1). Five predation events and the unsuccessful predation attempt were recorded using drones (e.g. Fig. 2) during 2 encounters in CA that were shared with us by the videographers (E. Parnes-Katz & S. Moore pers. comm.). Prey species in the drone videos were identified by observers in the field and verified by shark experts (R. McPhie, T. Chapple & J. Schulte pers. comm.). In addition, we collected 7 OKW fecal samples, but only 2 yielded genetic results beyond *Orcinus orca* DNA (Table 1). We did not include results from stomach contents (n = 2 encounters, 1955 and 1964), fecal samples (n = 2, 2018 and 2023), and a single tissue sample (1996) in the quantitative summaries, figures or maps because the locations or number of predation events were not known. We also discounted the photograph of a possible Pacific halibut described by Jones (2006), because the species identification was deemed uncertain. Prey samples were collected between March and October and spanned ~48–60° N, from Prince William Sound, AK, to the southwest coast of Vancouver Island, BC (Fig. 3A,B). The only observations of foraging OKW south of 48° N and during the winter months came from the 2 encounters recorded using drones in CA during December of 2016 (S. Moore pers. comm.) and 2023 (E. Parnes-Katz pers. comm.) (Fig. 3C).

The predation events documented between 2004 and 2023 (n = 84) indicated that the majority (89.3%) of prey consumed by OKW were elasmobranchs (Table 1). Prey species identified in both the current and earlier studies included Pacific sleeper shark (n = 38, 45.2%), blue shark (n = 15, 17.9%), and dogfish (n = 14, 16.7%). Our study also revealed that OKW consume salmon sharks *Lamna ditropis*. Evidence for salmon shark predation (n = 5, 6.0%) included tissue from 3 sharks collected in Prince William Sound, AK (23 June 2015), as well as tissue from 2 additional sharks in combination with photographic evidence (Fig. 1) collected in the Kenai Fjords area of AK (5 June 2018) (Fig. 3A). In addition, we discovered that OKW prey on Pacific electric rays *Tetronarce californica* from 2 tissue samples (2.4%) collected off the west coast of Vancouver Island, BC, in September 2022 (Fig. 3B). The first record of OKW consuming a broadnose sevengill shark *Notorynchus cepedianus* came from drone footage (Fig. 2) taken in Monterey Bay, CA (S. Moore pers. comm.). Genetic results from the 2 fecal samples indicated that individual OKW can prey on different shark species within a short interval. For instance, one fecal sample contained Pacific sleeper shark DNA, but came from a group of OKW that were actively feeding on a salmon shark when the feces were collected (Table 1). Likewise, the other fecal sample contained a mixture of Pacific sleeper and blue shark DNA (Table 1), suggesting that these 2 species were eaten in quick succession.

In addition to elasmobranchs, OKW are known to prey on teleost fishes

Fig. 1. Photographs of offshore killer whales *Orcinus orca* consuming a salmon shark *Lamna ditropis* in the Kenai Fjords area, Alaska, on 5 June 2018. The distinctive caudal fin shape and white underbelly of the salmon shark are visible in the photographs, and the species was confirmed by genetic analysis of tissue fragments collected following the kill (photographs by Dan Olsen)

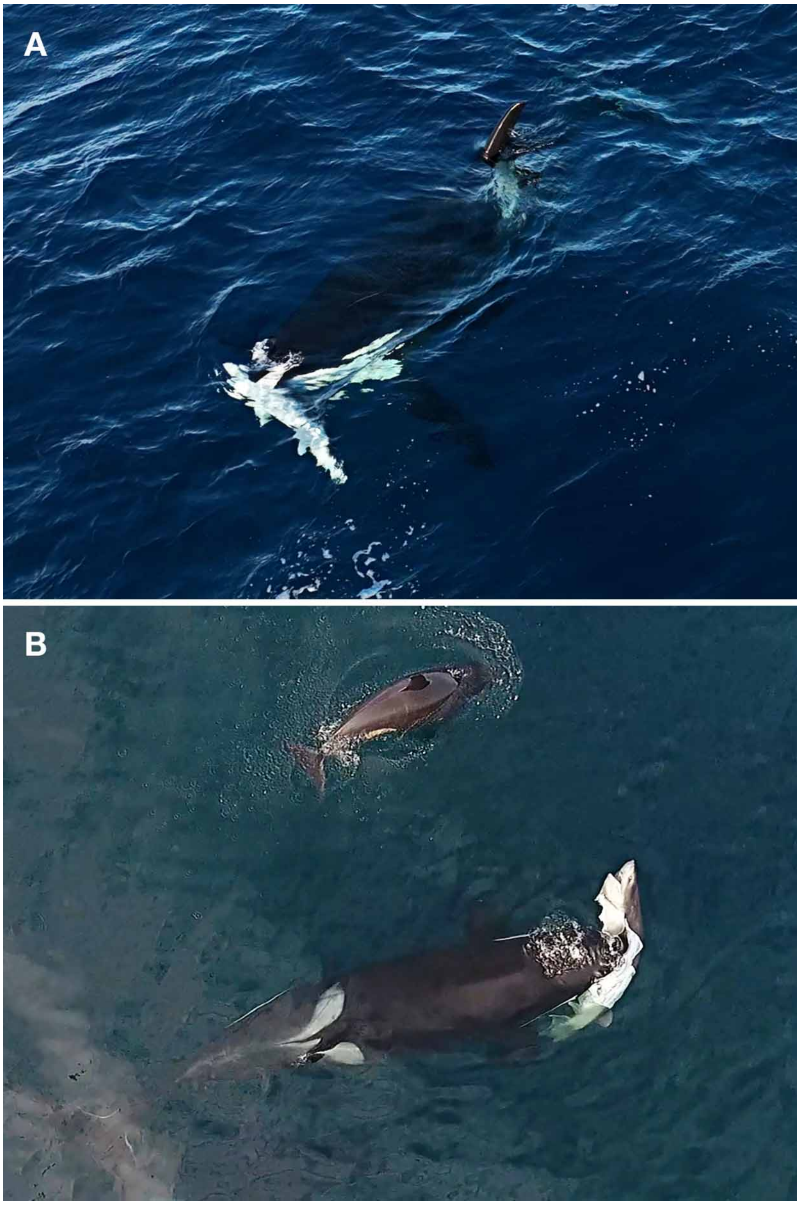

Fig. 2. Still photographs from drone videography of offshore killer whales *Orcinus orca* preying on (A) a blue shark *Prionace glauca*, filmed off San Miguel Island, California, on 29 December 2023 (videography and photographs by Eli Parnes-Katz, killer whale encounter information courtesy of Ryan Lawler) and (B) a broadnose sevengill shark *Notorynchus cepedianus*, filmed in Monterey Bay, California, on 13 December 2016 (videography and photographs by Slater Moore)

(Table 1) such as Chinook salmon (Ford et al. 2014) and Pacific halibut (Pike & MacAskie 1969, Ford et al. 2011). Complementing these findings, we obtained 2 additional halibut samples (5 July 2016) and the first record of OKW catching an opah in Canadian waters (8 August 2011) from predation events in Hecate Strait, BC (Fig. 3B). Prior evidence of OKW eating opah comes from the stomach contents of an individual harpooned off southern CA in 1964 (Rice 1968; Table 1). We also provide the first documentation of OKW hunting albacore tuna *Thunnus alalunga*, which occurred in conjunction with blue shark and electric ray predation in September 2022 along the continental shelf edge west of Vancouver Island, BC (Table 1, Figs. 3A & 4). Taken together, teleost fishes made up 10.7% (n = 9) of all documented OKW prey (Table 1).

We used haplotype sequencing of the mitochondrial DNA CR to determine whether prey samples of the same species collected during a single OKW encounter represented unique individuals (i.e. had different haplotypes) or were possible repeat sampling of the same fish (i.e. shared a haplotype) (see Table 2, Fig. 5; Figs. S1–S6 in the Supplement). If prey samples from a single species within an encounter shared a haplotype but were collected at locations separated by >1 km, or if >20 min had elapsed between sampling events (see Table 2), we designated these as unique predation events based on the previous approach by Ford et al. (2011). For 2 encounters (231 and 242, Table 2), precise sampling times and locations were unavailable, so we relied solely on haplotypes to determine the minimum number of fish caught. Where haplotype results, combined with sampling times and locations, led us to conclude that the minimum number prey caught by OKW differed from the number of samples collected per species (n = 4 encounters), we have indicated this in Table 1. Most of the prey samples collected during a single encounter represented a series of unique individuals (Table 2) rather than repetitive sampling of the same fish. Notably, the 9 sleeper shark tissues collected on 24 August 2023 (encounter 434) all had distinct haplotypes (Fig. 5) and thus came from different sharks. These sharks were often captured in quick succession (range = 7–50 min between captures) within a small area (distance between captures = 0.54–1.47 km, Table 2), similar to the haplotype results for the sleeper sharks sampled in May 2008 (n = 11) and June 2009 (n = 7, Table 1) that

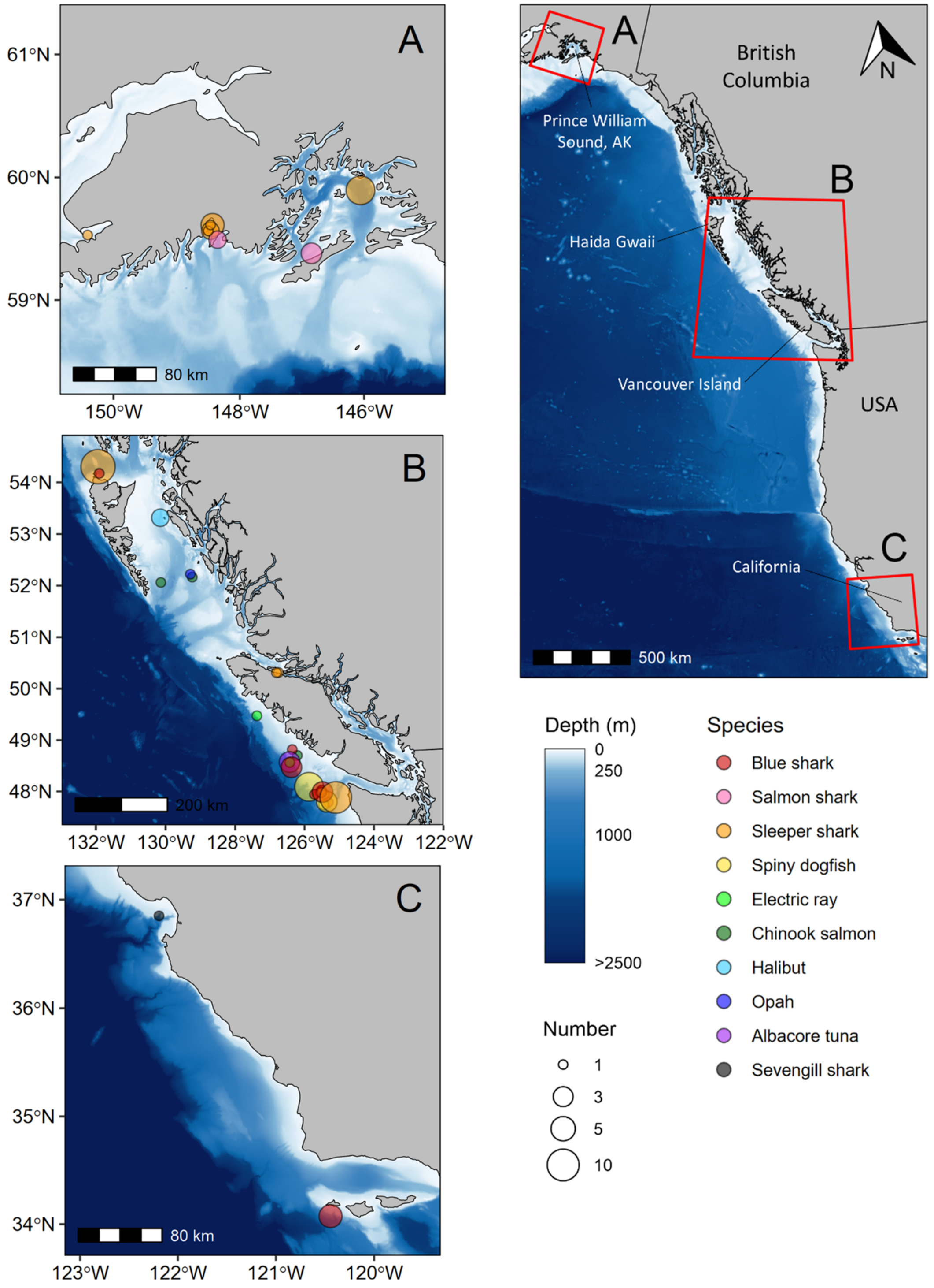

Fig. 3. Locations, species (point colour), and minimum numbers (point size; based on field observations and haplotype analysis) of prey consumed by offshore killer whales since 2004 (n = 84; see Table 1) encountered in (A) Kenai Fjords and Prince William Sound, Alaska, (B) coastal British Columbia, and (C) California. In cases where >1 prey item was consumed per encounter, the GPS coordinates of the first predation event were used to indicate the location for that event plus all subsequent events involving the same prey species during the encounter. Only tissue and fish scale samples collected immediately following kills were included; fecal samples are not shown, since there was no way to determine the location where the prey were originally consumed by killer whales. Blue shading: water depth (m), obtained from the NOAA ETOPO 2022 15 Arc-Second Global Relief Model, extracted at a grid resolution of 0.5 min (NOAA National Centers for Environmental Information 2022). Maps displayed using the Albers Equal Area projection

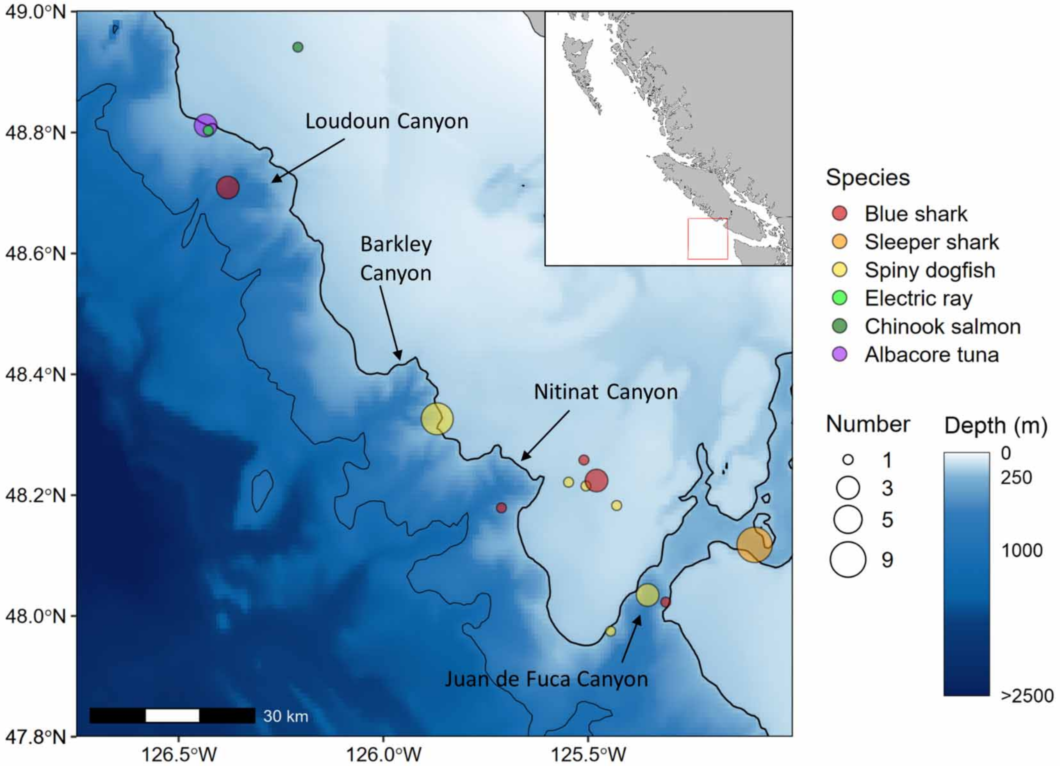

Fig. 4. Locations, species (point colour), and minimum numbers (point size; based on haplotype analysis) of prey consumed by offshore killer whales near the continental shelf edge off the west coast of Vancouver Island since 2004 (see Fig. 3B), with prominent submarine canyons indicated by name. In cases where >1 prey item was consumed per encounter, the GPS coordinates of the first predation event were used to indicate the location for that event plus all subsequent events involving the same prey species during the encounter. Only tissue and fish scale samples collected immediately following kills were included; fecal samples are not shown, since there was no way to determine the location where the prey were actually consumed. Blue shading: water depth (m), obtained from the NOAA ETOPO 2022 15 Arc-Second Global Relief Model, extracted at a grid resolution of 0.5 min (NOAA National Centers for Environmental Information 2022). Thick black line: 200 m bathymetric contour (continental shelf edge); thinner black line: 1000 m bathymetric contour (continental slope). Map displayed using the Albers Equal Area projection

are described by Ford et al. (2011). In order to consider the haplotypes of samples that were previously analysed by Ford et al. (2011, 2014), it was necessary to evaluate a shorter CR sequence for both sleeper shark and dogfish (Table 2, Figs. S2 & S3 in the Supplement). Haplotype analysis was unsuccessful for tissues from Pacific electric ray, opah, Chinook salmon, 1 blue shark (4 September 2014) and 4 dogfish (1 September 2014 and 6 October 2015, see Table 1). All of the samples for which haplotype analysis failed were treated as unique individuals, as they were either the only sample of that prey species to be collected during the encounter, or in the case of the 3 dogfish samples collected on 6 October 2015, were separated by >20 min.

OKW in our study targeted prey found both closer to the surface and at depth, and the hunting strategies we saw differed accordingly. For instance, OKW observed in both this study and by Ford et al. (2011) seemed to locate, subdue and process sleeper sharks at depth (indicated by long dive times). While sleeper shark predation was sometimes undertaken by single whales, it often involved small groups (2–4 whales, sometimes as many as 8) undertaking long, steep dives (⩾5–10 min) in turn at the same location before fragments of liver tissue eventually rose to the surface. Some of these pieces of liver were revisited and consumed by the whales, but many were left behind for seabirds and other scavengers. OKW were very vocal during sleeper shark predation events and echolocation was also prevalent. In one encounter (30 May 2008), the melons of several whales appeared abraded and were lighter in colour than the surrounding skin, implying that individuals had been ramming sleeper sharks with their heads or lifting the carcasses to prevent them from sinking. In contrast, smaller blue sharks and dogfish were caught at much shallower depths (indicated by shorter dive times), and whales often moved substantial horizontal distances while searching for and pursuing these species. Foraging on smaller sharks also involved surface-active

Table 2. Details of predation and defecation events by offshore killer whales for which haplotype sequencing analysis of the prey's mitochondrial DNA control region was successfully run. (—) First predation event observed on this date, thus distance and time from a previous event cannot be calculated; NR: no record available. Haplotype names begin with 2 letters denoting genus and species, followed by a number (e.g. SP01 for *Somniosus pacificus*, haplotype 1); GenBank accession numbers are provided for each nucleotide sequence. Note that for Encounter 409, 2 samples of tissue were collected at the same time and location

Date	Prey species	Encounter	Local time (h)	Latitude (°N)	Longitude (°W)	Previous predation event		Haplotype	GenBank acc. no.
						Distance (km)	Time (min)		
19 Mar 2004	Sleeper shark	162	15:25	50.5617	126.8033	—	—	SP01	PQ602707
30 Mar 2011	Sleeper shark	228	14:59	50.5583	126.8633	—	—	SP06[a]	PQ683627
29 Jun 2012	Sleeper shark	242	NR	60.0667	149.3533	—	—	SP08[a]	PQ683635
			NR	NR	NR	>0.2	Unknown	SP08[a]	PQ683636
			NR	NR	NR	>0.2	Unknown	SP03/SP07[a]	PQ683637
			NR	NR	NR	>0.2	Unknown	SP05[a]	PQ683638
			NR	NR	NR	>0.2	Unknown	SP09[a]	PQ683639
21 May 2017	Sleeper shark	404	12:30	60.0133	149.3567	—	—	SP08	PQ602712
			13:40	59.9867	149.3500	2.98	70	SP06	PQ602713
05 Jun 2018	Sleeper shark (fecal)	407	14:39	59.9617	149.1900	—	—	SP10[a]	PQ602710
10 Jun 2018	Sleeper shark	409	14:11	60.0057	149.3918	—	—	SP10	PQ602708
						0	0	SP10	PQ602709
17 Apr 2020	Sleeper shark	414	11:25	60.0617	149.3883	—	—	SP11	PQ602711
24 Aug 2023	Sleeper shark	434	14:01	48.1167	125.0874	—	—	SP02	PQ602714
			14:17	48.1207	125.0771	0.88	16	SP03	PQ602715
			14:35	48.1125	125.0761	0.91	18	SP04	PQ602716
			14:42	48.1109	125.0843	0.63	7	SP05	PQ602717
			15:01	48.1156	125.0862	0.54	19	SP06	PQ602718
			15:51	48.1122	125.0693	1.31	50	SP07	PQ602719
			16:11	48.1213	125.0836	1.47	20	SP01	PQ602720
			16:24	48.1141	125.0881	0.87	13	SP08	PQ602721
			16:46	48.1206	125.0938	0.84	22	SP09	PQ602722
18 Aug 2011	Blue shark	231	14:19	48.0234	125.3072	—	—	PG03	PQ683624
			NR	NR	NR	~0.60	<7	PG03	PQ683625
			14:26	NR	NR	~0.30	<7	PG03	PQ683626
06 Aug 2021	Blue shark	416	19:15	48.2598	125.5055	—	—	PG01	PQ602699
13 Sep 2022	Blue shark	425	17:48	48.7111	126.3874	—	—	PG02	PQ602700
			18:29	48.6472	126.3224	8.56	41	PG03	PQ602701
			19:15	48.6043	126.2859	5.47	46	PG04	PQ602702
14 Sep 2022	Blue shark	426	10:45	48.1813	125.7039	—	—	PG05	PQ602703
21 Aug 2023	Blue shark	433	14:52	48.2256	125.4748	—	—	PG06	PQ602704
			15:10	48.2254	125.4585	1.21	18	PG01	PQ602705
			15:49	48.1949	125.4158	4.64	39	PG05	PQ602706
5 Sep 2011	Spiny dogfish	233	06:51	48.1840	125.4257	—	—	SA02	PQ683623
7 Sep 2012	Spiny dogfish	239	14:19	48.3290	125.8671	—	—	SA02	PQ683628
			14:58	48.3501	125.8618	2.38	39	SA03	PQ683629
			15:17	48.3622	125.8535	1.48	19	SA04	PQ683630
			16:38	48.3588	125.8455	0.70	81	SA05	PQ683631
			16:46	48.3537	125.8485	0.61	8	SA06	PQ683632
			16:59	48.3423	125.8520	1.29	13	SA06	PQ683633
			17:13	48.3360	125.8492	0.73	14	SA07	PQ683634
06 Aug 2021	Spiny dogfish	416	17:09	48.2232	125.5437	—	—	SA01[a]	PQ602723
21 Aug 2023	Spiny dogfish	433	14:06	48.2168	125.5010	—	—	SA01[a]	PQ602724
23 Jun 2015	Salmon shark	386	16:38	60.1017	147.5650	—	—	LD01	PQ602727
			NR	60.0883	147.6167	3.23	Unknown	LD02	PQ602728
			17:57	60.0650	147.6533	3.29	Unknown	LD03	PQ602729
05 Jun 2018	Salmon shark	407	14:47	59.9597	149.1892	—	—	LD04	PQ602725
			15:11	59.9520	149.1950	0.92	24	LD04	PQ602726
13 Sep 2022	Albacore tuna	425	15:38	48.8135	126.4435	—	—	TA01	PQ602730
			16:12	48.7923	126.4363	2.42	34	TA02	PQ602731
			17:35	48.7166	126.3963	8.91	83	TA03	PQ602732
05 Jul 2016	Pacific halibut	400	NR	53.4883	130.7433	—	—	HS01	PQ602733
			NR	53.4800	130.7400	0.95	Unknown	HS02	PQ602734

[a] Sample for which a short nucleotide sequence was considered

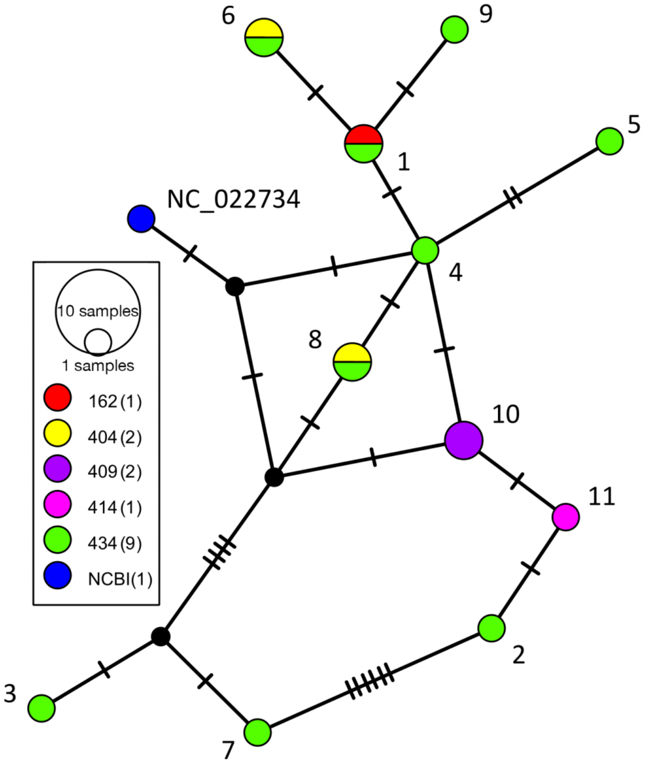

Fig. 5. Integer neighbour joining haplotype network (α = 0.1) of the mitochondrial DNA control region long sequence (1013 nucleotides) for 15 Pacific sleeper shark *Somniosus pacificus* tissues recovered from offshore killer whale (OKW) predation events. Colours used to distinguish separate OKW encounters (black circles: inferred or unsampled sequences); number of tissues collected during each encounter shown in the legend in brackets, next to each encounter number. Numbered circles: distinct haplotypes (SP01–SP11) with diameters proportional to the number of tissue samples with that haplotype. Hashmarks on the lines connecting haplotypes: number of nucleotide differences between them. One NCBI Genbank Reference Sequence (dark blue) from *S. pacificus* is indicated by accession number (NC_022734). Haplotype networks for Pacific sleeper shark tissues with short control region (CR) sequences (Fig. S2), as well as networks for the other OKW prey species examined in this study (Figs. S1, S3–S6), are given in the Supplement

behaviours, such as tossing prey in the air. These predation events more closely resembled resident killer whale salmon foraging, in that sharks were often pursued individually and were typically brought to the surface to be consumed and possibly shared.

We observed a seasonal pattern in both the prey taken and the regions in which OKW foraged. Sleeper and salmon sharks were largely consumed from March to June at latitudes >54°N (Fig. 6) in the coastal waters of AK and northern BC (75% of encounters involving either species; Table 2, Fig. 3A,B). However, 3 sleeper sharks were also taken at lower latitudes in Johnstone Strait off northeastern Vancouver Island, BC, in March 1996 (Table 1, not illustrated), 2004 and 2011 (Table 1, Fig. 3B), and 9 were captured along the continental shelf edge west of Vancouver Island during a single encounter in August 2023 (Table 1, Figs. 4 & 5). Conversely, blue sharks and dogfish were mainly taken between August and October at latitudes ≤49° N (Fig. 6) in open water along the continental shelf edge off Vancouver Island (83% of encounters; Table 2, Figs. 3B & 4). With the exception of albacore tuna and 1 Chinook, teleost fishes were caught at intermediate latitudes (52–54° N) in Hecate Strait between these 2 regions (Fig. 3B) in either March, July or August (60% of encounters; Table 2, Fig. 6). Finally, the only recorded winter predation events occurred farther south in coastal CA (34–37° N, Fig. 3C) during December of 2016 and 2023 (Table 1, Fig. 6). These events involved OKW killing a broadnose sevengill shark and 4 blue sharks (Fig. 2), as well as the unsuccessful pursuit of a shortfin mako shark *Isurus oxyrinchus*.

Most OKW predation events occurred in habitats with seafloor depths of around 200 m (median = 206 m, range = 57–496 m; see Fig. 7), regardless of where they were observed along the latitudinal gradient. The exception was blue shark predation, which occurred in habitats with greater maximum depths (median = 338 m, range = 133–644 m; Fig. 7). The ocean depth where the single broadnose sevengill shark was captured was not calculated, because the location for this event was approximate (Fig. 3C). Predation events frequently occurred in proximity to steep-sided bathymetric features, including the continental shelf break and continental slope, the edges of coastal banks, and the heads of submarine canyons (Figs. 3B,C & 4).

4. DISCUSSION

4.1. Evidence supporting elasmobranch specialization

Our study confirms that OKW are piscivores and offers compelling evidence that they specialize on elasmobranch prey when foraging in continental shelf waters. These results support earlier studies suggesting that OKW are piscivorous (Herman et al. 2005, Krahn et al. 2007, Ford et al. 2011, 2014, Matkin et al. 2018) but refute a previous suggestion that they are relative ecological generalists (Schorr et al. 2022). Genetic identification of prey fragments, along with photographs, observations, and aerial video of foraging behaviour, indicated that elasmobranchs made up

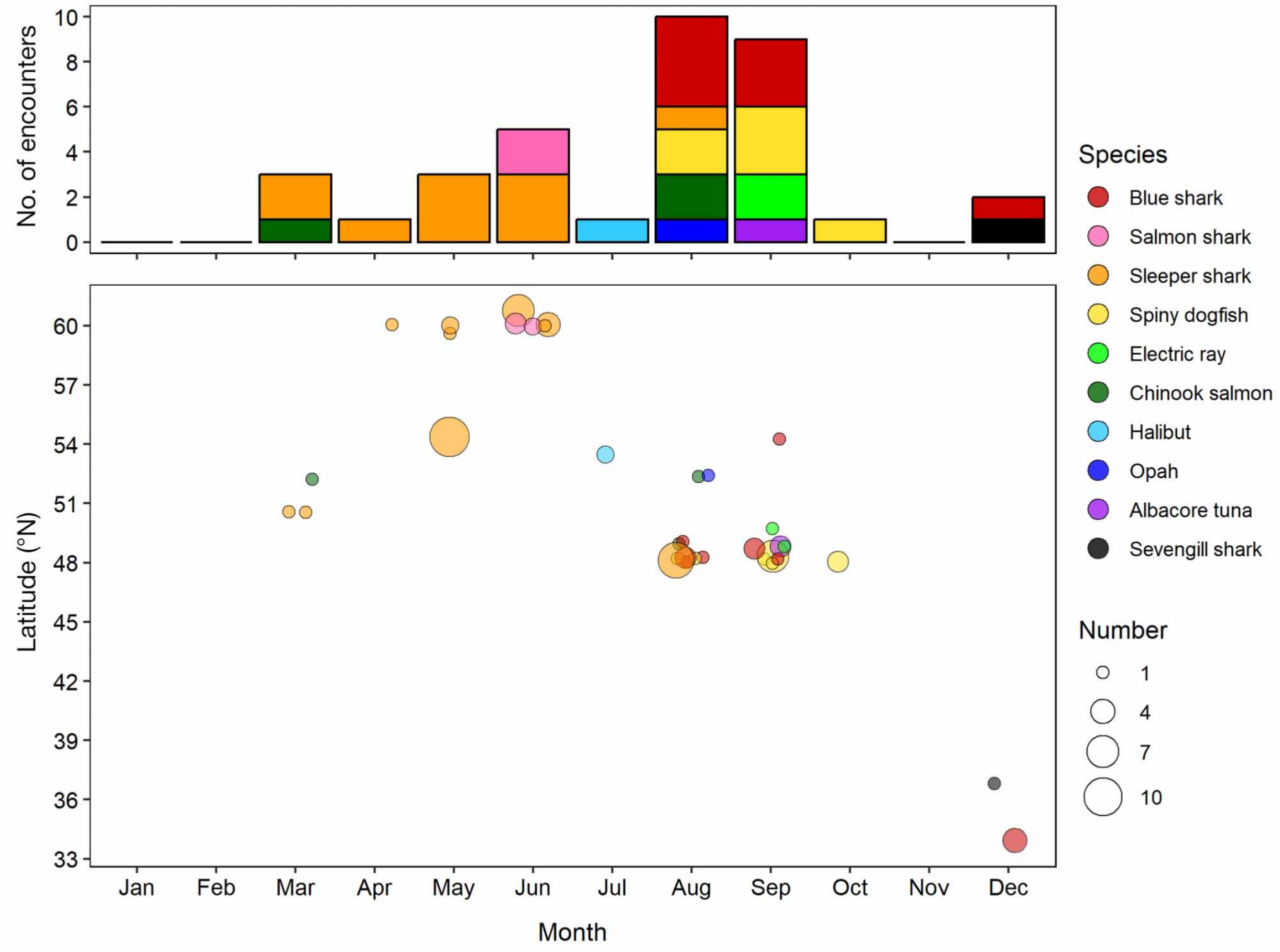

Fig. 6. Top panel: offshore killer whale (OKW) prey species identified by month, summarised by number of encounters (a single encounter may appear multiple times in a month if multiple prey species were taken). Bottom panel: OKW prey species by month and latitude of the first capture location within each encounter; minimum number of predation events per encounter (as determined by field observations and haplotypes) is indicated by the point size. Points have been horizontally jittered to improve readability. Encounters (n = 30) were recorded in the continental shelf waters off Alaska, British Columbia, and California between 2004 and 2023. Elasmobranch species represent the vast majority (89.3%) of identified prey consumed by OKW during the study period, with teleost fishes making up the remainder (10.7%). No predation events observed in January, February or November

89.3% of the sampled OKW diet, and prey DNA in 2 fecal samples (Table 1) further confirmed consumption of elasmobranchs. Although thresholds defining diets as 'specialized' are acknowledged to be somewhat arbitrary (Carneiro et al. 2017), OKW predation on elasmobranchs qualifies as such under metrics developed for marine birds, which characterize specialist diets as being >50–70% composed of one particular prey item or class of prey (Golet et al. 2000, Votier et al. 2004).

Specialists are predicted to maintain their dietary selectivity across broad geographic distributions that are subject to varying environmental conditions (Vorel et al. 2015), which appears to be true for OKW. Six species of elasmobranchs made up the bulk of the observed diet of OKW in both coastal and offshore waters from AK to CA. Notably, teleost fishes were consumed infrequently (10.7%) and may be taken when elasmobranchs are less available. Most predation on halibut, Chinook salmon and opah occurred in Hecate Strait, BC, in July and August, which represents an intermediate location and time period between the early summer, northern (AK and northern BC) foraging observations on sleeper and salmon sharks and later, more southerly summer and fall foraging observations on sleeper sharks, blue sharks and dogfish (off Vancouver Island, BC). In over 3 decades of study, there are no reports of OKW preying on marine mammals, and these species are not known to react fearfully or avoid this killer whale ecotype (Dahlheim et al. 2008, Ford et al. 2014). Thus, we suggest that elasmobranch specialization in OKW, in

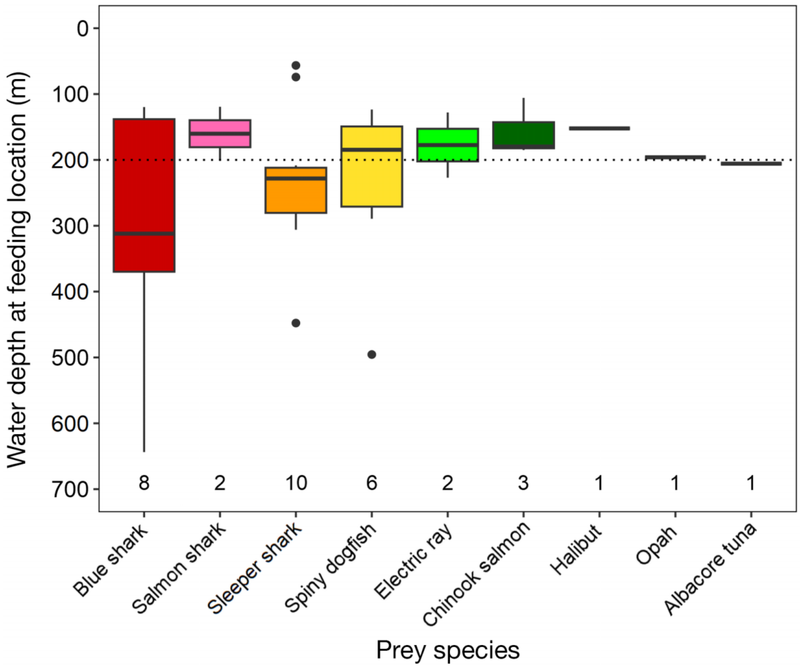

Fig. 7. Boxplots showing water depths (m) at the locations of predation events by offshore killer whales (OKW) (2004–2023), grouped by prey species. The broadnose sevengill shark observation made via drone videography is not included because only an approximate location was available for this predation event. Boxes: interquartile range (IQR); horizontal black bars: medians; whiskers: minimum and maximum values no more than 1.5 × IQR from either the lower or upper box extents; black dots: outliers beyond these calculated minima or maxima. Dotted horizontal line: 200 m seafloor depth around which most predation events are centred. Only one location per species per encounter is used (i.e. if the same group of OKW preyed upon multiple individuals of the same prey species during the same day, only the depth at the location of the first of these predation events was included). Numbers above the *x*-axis: number of encounters (n) recorded per prey species. Water depths obtained from the NOAA ETOPO 2022 15 Arc-Second Global Relief Model, extracted at a grid resolution of 0.5 min (NOAA National Centers for Environmental Information 2022). These values represent the seafloor depths at the locations where prey fragments were collected (at the surface); they do not indicate the dive depths at which OKW captured their prey

conjunction with the foraging specializations of resident and Bigg's killer whales, reduces niche overlap among these sympatric ecotypes and may be perpetuated through cultural transmission of learned behaviours (Whitehead 2007, Whitehead & Ford 2018). Globally, many other killer whale populations prey on elasmobranchs (Table 3), either as specialists or as a component of a more generalist diet, suggesting such species represent a valuable prey resource.

4.2. Newly reported prey species for OKW

We report the first evidence of OKW consuming rays. The Pacific electric ray, which we identified genetically from 2 tissue samples, is mentioned in a 1958 account from southern CA, where 3 killer whales of an unknown ecotype were seen ripping apart and eating a large individual (Norris & Prescott 1961). This species, which grows to >1.4 m, occurs from southern CA to northern BC (Hart 1973) in depths of 60–200 m (Love 2011), well within the known maximum (480 m) diving abilities of OKW (Schorr et al. 2022). Electric rays have been caught inshore of the continental slope along Vancouver Island, BC, in both summer and winter fisheries (McFarlane et al. 2010), in the same region where we observed OKW capturing them. Preying on electric rays likely requires adept handling, as they can deliver a shock of 45 V at instantaneous pulse rates of ⩽308 electric organ discharges (EODs) s^{-1} (Lowe et al. 1994). Globally, other killer whale populations use diverse hunting strategies to capture rays (Visser 1999, Alava & Merlen 2009, Higuera-Rivas et al. 2023), many of which have venomous spines (Duignan et al. 2000) and would need similarly careful handling.

We also present the first evidence of albacore tuna being preyed on by OKW. Other killer whale populations hunt Atlantic bluefin tuna *Thunnus thynnus* in the Strait of Gibraltar (Guinet et al. 2007, García-Tiscar 2009, Rudd et al. 2024) and the northwestern Atlantic (A. Ogilvie pers. comm.). Tuna are also depredated from fisheries by killer whales in the Strait of Gibraltar (Esteban et al. 2016), South Africa (Best et al. 2010), and Brazil (Secchi & Vaske 1998, Dalla Rosa & Secchi 2007). Strait of Gibraltar killer whales (Guinet et al. 2007) use an endurance-exhaustion tactic to catch free-swimming tuna. We do not know if a similar tactic is employed by OKW, but we did observe high-speed, nose-first surface strikes during tuna hunts, which resembled strategies used by Bigg's killer whales to subdue marine mammals. Albacore tuna can swim at speeds >80 km h^{-1} for short time periods (Love 2011), suggesting that OKW may prey on them using surprise as a foraging tactic. Off BC, albacore are surface-oriented (⩽25 m) (Childers et al. 2011, Love 2011) and most abundant in upwelling zones (Laurs et al. 1984),

Table 3. Elasmobranch species identified in the diets of killer whales globally (does not include prey taken by individuals definitively identified as offshore killer whales). Prey that could not be identified to the species level are indicated by their Genus or Family name. Note that pers. comm. and unpubl. data cited in other sources were not included, as the information could not be verified

Region	Common name	Scientific name	Source
North Atlantic	Greenland shark	*Somniosus microcephalus*	Remili et al. (2023)
	Blue shark[a]	*Prionace glauca*	Mucientes & Gonzáles-Pestana (2020)
North Pacific	Big skate	*Raja binoculata*	Van Cise et al. (2024)
California & Mexico (Pacific)	White shark	*Carcharodon carcharias*	Jorgensen et al. (2019), Pyle et al. (1999)
	Bull shark	*Carcharhinus leucas*	Ayres et al. (2024)
	Prickly shark	*Echinorhinus cookei*	Lara-Lizardi et al. (2025)
	Whale shark	*Rhinocodon typus*	O'Sullivan & Mitchell (2000), Ortega-Ortiz et al. (2023), Pancaldi et al. (2024)
	Munk's devil ray	*Mobula munkiana*	Higuera-Rivas et al. (2023)
	Cownose ray	*Rhinoptera steindachneri*	Higuera-Rivas et al. (2023)
	Pelagic sting ray	*Pteroplatytrygon violacea*	Higuera-Rivas et al. (2023)
	Manta ray	*Mobula* sp.	Guerrero-Ruiz et al. (2007)
	Pacific electric ray	*Tetronarce californica*	Norris & Prescott (1961)
	Basking shark[a]	*Cetorhinus maximus*	Brown & Norris (1956)
South America (Pacific)	Requiem shark	Family Carcharhinidae	Fertl et al. (1996), Merlen (1999)
	Hammerhead shark	*Sphyrna* sp.	Merlen (1999), Sonnino Sorisio et al. (2006)
	Galápagos shark	*Carcharhinus galapagensis*	Fertl et al. (1996)
	Giant manta ray	*Mobula birostris*	Merlen (1999), Alava & Merlen (2009)
	Sting ray	*Dasyatis* sp.	Merlen (1999)
	Eagle ray	*Myliobatis* sp.	Castello (1977), de Roy (1993), Dalla Rosa et al. (1994) in Fertl et al. (1996)
South America (Atlantic)	Broadnose sevengill shark	*Notorynchus cepedianus*	Reyes & García-Borboroglu (2004)
	Blue shark[a]	*Prionace glauca*	Passadore et al. (2015)
	Shortfin mako shark[a]	*Isurus oxyrinchus*	Passadore et al. (2015)
South Africa	White shark	*Carcharodon carcharias*	Best et al. (2010), Towner et al. (2022, 2023, 2024)
	Blue shark	*Prionace glauca*	Best et al. (2014)
	Broadnose sevengill shark	*Notorynchus cepedianus*	Engelbrecht et al. (2019)
	Shortfin mako shark[a]	*Isurus oxyrinchus*	Williams et al. (2009)
Indian Ocean	Portuguese dogfish	*Centroscymnus coelolepi*	Terrapon et al. (2021)
	Tiger shark	*Galeocerdo cuvier*	Terrapon et al. (2024)
	Requiem shark	Family Carcharhinidae	Terrapon et al. (2021)
	Mobulid ray	*Mobula* sp.	Terrapon et al. (2021)
	Giant manta ray	*Mobula birostris*	Terrapon et al. (2024)
	Sicklefin devil ray	*Mobula tarapacana*	Terrapon et al. (2024)
Papua New Guinea	Scalloped hammerhead shark	*Sphyrna lewini*	Visser & Bonoccorso (2003)
	Hammerhead shark	*Sphyrna* sp.	Skinner (1994) in Fertl et al. (1996)
	Grey reef shark	*Carcharhinus amblyrhynchos*	Visser & Bonoccorso (2003)
	Giant manta ray	*Mobula birostris*	Visser & Bonoccorso (2003)
	Blue-spotted ray	*Dasyatis kuhlii*	Visser & Bonoccorso (2003)
New Zealand	Eagle ray or sting ray	*Myliobatis tenuicaudatus* or *Dasyatis* sp.	Visser (1999)
	Electric ray	*Torpedo fairchildii*	Visser & Bonoccorso (2003)
	Basking shark	*Cetorhinus maximus*	Fertl et al. (1996)
	Shortfin mako shark	*Isurus oxyrinchus*	Visser et al. (2000)
	Common thresher shark	*Alopias vulpinus*	Visser (2005)
	Smooth hammerhead shark	*Sphyrna zygaena*	Visser (2005)
	School shark[a]	*Galeorhinus galeus*	Visser (2000)

[a] Species were fisheries depredations rather than hunted naturally

such as the shelf edge where we observed OKW preying on tuna (Table 1; Figs. 3B & 4). Our observations (September 2022) coincided with the albacore migration; fish arrive on the North American coast from the central Pacific Ocean in the early summer, move northward, and reach Vancouver Island by August and September (Beamish et al. 2005, Childers et al. 2011, Love 2011). Albacore usually depart the coast in late fall to overwinter in the open Pacific (Childers et al. 2011). No tuna depredation by OKW was noted, although both commercial and sport tuna fishers were present when the albacore foraging events occurred.

The planktivorous 12–15 m basking shark *Cetorhinus maximus* has vestigial teeth (Harrison Matthews & Parker 1950, Wallace & Gisborne 2006), swims slowly, and has a liver comprising 20–30% of its mass (Alexander 1990, Phelger 1998) — traits that make it a potentially high-value, low-risk prey. Although basking sharks once occurred throughout the northeastern Pacific and may have been important prey species for OKW in the past, they were largely eradicated from BC by the 1970s (Wallace & Gisborne 2006) and have been rare in CA since the 1990s (McInturf et al. 2022). However, Brown & Norris (1956) observed 7 killer whales of an unknown ecotype feeding on 2 basking sharks discarded as by-catch off CA (Table 3). Although basking shark sightings in the northeastern Pacific continue to be rare and there have been no observations of OKW preying on them, if the population recovers, they might provide an important prey resource for OKW in the future.

4.3. Hunting tactics, prey sharing and possible surface sampling bias

We describe and contrast the hunting tactics of OKW foraging on larger, more benthically distributed sleeper sharks, to the tactics used on smaller species such as dogfish and blue sharks that are found at shallower depths. Globally, a variety of strategies are used by killer whales to hunt sharks and rays. Tail strikes are used by OKW (Dahlheim et al. 2008) as well as killer whales in New Zealand (Visser 2005), Patagonia (Reyes & García-Borboroglu 2004), and the Gulf of California (Ayres et al. 2024, Lara-Lizardi et al. 2025), to help incapacitate sharks, a large and potentially dangerous prey. Killer whales also ram elasmobranchs at high speed (Ortega-Ortiz et al. 2023, Pancaldi et al. 2024, Reilly 2024) or breach on top of them (Terrapon et al. 2024), much as Bigg's killer whales do to subdue pinnipeds and porpoises. Killer whales hunting whale sharks in the Gulf of California attacked the ventral and pelvic areas to exsanguinate prey and provide access to the lipid-rich liver (Pancaldi et al. 2024). Killer whales may also flip or roll sharks over (Pyle et al. 1999, Visser & Bonoccorso 2003, Towner et al. 2023, Pancaldi et al. 2024), suggesting they subdue these prey species by inducing tonic immobility (Páez et al. 2023).

Describing the tactics of a predator that hunts underwater and often at substantial depths is difficult. Thus, in most cases, surface observations are used to infer hunting behaviour in killer whales. Underwater and aerial drone videography can augment these observations, providing a clearer view of prey pursuit and handling (Wright et al. 2016, Higuera-Rivas et al. 2023, Towner et al. 2023, Pancaldi et al. 2024, Reilly 2024, Lara-Lizardi et al. 2025). Although sampling prey tissues at the surface may miss some predation events occurring at depth, this bias is likely minimal. Our sampling technique detected both prey species that occur closer to the surface (e.g. blue sharks, albacore tuna, and Chinook salmon) as well as deep water, more benthically oriented species (e.g. sleeper sharks and halibut). Notably, prey found in stomach contents (opah, halibut and shark) were also present in the assemblage we identified using prey fragment sampling. Tagging data indicate that resident killer whales typically return to the surface to process their prey immediately after capture, rather than consuming salmon at depth (Wright et al. 2017). This is probably driven by the need to replenish oxygen stores and offload carbon dioxide after energetically costly underwater chases; OKW may do the same, particularly when prey are caught individually rather than cooperatively. Furthermore, lipid-rich shark liver is highly buoyant, meaning OKW do not need to bring shark prey to the surface for a tissue sample to be collected. We often collected pieces of sleeper shark liver floating at the surface without seeing the prey itself. Lastly, like other killer whale ecotypes (Baird & Dill 1996, Wright et al. 2016), OKW are likely to surface with their prey and engage in prey sharing, as was first proposed by Ford et al. (2011) and confirmed in drone video footage from CA in 2016 and 2023 (Table 1, Fig. 2). In this footage, blue and broadnose sevengill sharks being consumed by OKW at the surface were passed between multiple individuals, with large pieces of tissue being dropped and picked up by other group members. Sharing of shark prey is probably a form of mutualism, given that cooperation may be needed to take such large and potentially dangerous species, but it may also be a form of kin selection, as it is in resident killer whales (Wright et al. 2016). Further, sharing may help young animals learn specialized hunting and prey handling skills and assist older whales with extreme tooth wear that can no longer effectively grasp and tear prey (Ford et al. 2011).

4.4. Prey profitability and selective consumption of elasmobranch liver tissue

Many carnivores select prey species or tissue types based on macronutrient (i.e. lipid and protein) composition and caloric content (Gende et al. 2001, Kohl et al. 2015). More specifically, killer whales are known to select either prey species or tissues that are high in lipids (Jefferson et al. 1991, Whitehead & Reeves 2005, Ford & Ellis 2006, Jourdain et al. 2020). Likewise, OKW are probably targeting elasmobranchs specifically for their large, oily, energy-rich livers. Many sharks, especially the larger-bodied, deep-sea species, have large liver-to-body-size ratios because the lipid-filled liver provides neutral buoyancy (Bone & Roberts 1969, Alexander 1990, Phelger 1998, Lingham-Soliar 2005, Gleiss et al. 2017). The liver also provides elasmobranchs with an energy reserve (Craik 1978) more calorically dense than whale blubber (Bone & Roberts 1969, Del Raye et al. 2013, Pethybridge et al. 2014). For example, blue shark (Jayasinghe et al. 2003a), salmon shark (Jayasinghe et al. 2003b), and dogfish (Kang et al. 1998) livers can contain ⩾50% oil by mass, all species that were consumed by OKW (Table 1). Female sharks can have larger relative liver volumes and oil content than males of the same species (Jayasinghe et al. 2003a,b), and lipid quantity and composition of shark livers fluctuates with ontogeny, diet, season, migration, and other factors (Wetherbee & Nicols 2000, Jayasinghe et al. 2003a,b), all of which might affect OKW prey preferences. Furthermore, oily livers likely have acoustic scattering properties that differ from the surrounding muscle, possibly allowing OKW to assess a shark's relative liver size using echolocation and thereby select larger sharks.

Worldwide, killer whales that eat sharks frequently consume the liver but discard most other portions of the carcass (Pyle et al. 1999, Reyes & García-Borboroglu 2004, Engelbrecht et al. 2019, Mucientes & González-Pestana 2020, Towner et al. 2022, 2023, 2024, Reeves et al. 2025). In the drone video footage of OKW carrying a broadnose sevengill shark carcass off CA, the whales appeared to have eviscerated the shark and removed its liver. Likewise, a sleeper shark carcass recovered near Juneau, AK, that bore evidence of killer whale tooth marks similarly had its liver, throat, tongue and heart removed (Matta et al. 2024). In our sampling of OKW shark predation events, liver fragments were the most frequently recovered tissue type, and whales appeared to preferentially remove this organ during prey processing. The skin and muscle tissue of sleeper sharks *Somniosus* spp. is toxic to some mammals and birds, particularly when freshly killed (McAllister 1968, Anthoni et al. 1991, Coad 1995), explaining why OKW might discard the non-liver portions of this and possibly other elasmobranchs. Furthermore, the lower density of shark liver (Bone & Roberts 1969) means it floats more readily than other tissues (Towner et al. 2023), making it easier for an air-breathing predator to process, share, and consume at the surface. However, this property also means that liver tissue is more likely to be collected by researchers observing predation events, which represents a potential bias in the dietary importance assigned to this organ. Interestingly, discarded shark carcasses may release necromones, which are compounds that induce flight responses when detected by other elasmobranchs (Stroud et al. 2014, Gervais & Brown 2021). These chemical signals could explain why sharks tend to desert an area for periods of up to several months following killer whale predation events (Pyle et al. 1999, Engelbrecht et al. 2019, Jorgensen et al. 2019, Towner et al. 2023, Ayres et al. 2024), a response that may help account for the extensive movements that OKW seem to make in search of prey.

4.5. Seasonal and regional patterns of shark predation

Photo-identification and satellite tagging studies suggest that OKW typically occur in AK and BC in spring and summer and then move southward to CA by winter (Ford et al. 2000, 2014, Dahlheim et al. 2008, Schorr et al. 2022). Furthermore, Schorr et al. (2022) reported that tagged OKW used shallower continental shelf habitats at higher latitudes in AK, BC, and Washington (WA), but deeper continental slope waters at more southerly latitudes off Oregon (OR) and CA. Our observations align with this seasonal distribution: prey samples from AK were collected between April and June, most BC samples between July and October, and drone videography of predation events in coastal CA were recorded in December. This latitudinal pattern was accompanied by a seasonal shift in the prey species taken: OKW captured sleeper and salmon sharks in shallower coastal waters at high latitudes in the spring and early summer, but preyed on blue sharks, dogfish, and albacore tuna (in addition to sleeper sharks) at lower latitudes along the continental shelf edge off BC in late summer and early autumn. Winter observations off CA in December included predation on blue sharks and a broadnose sevengill shark, as well as a chase of a shortfin mako shark. Although these distributional shifts may in part be artifacts of the limited number of OKW encounters and a seasonal effort bias in northerly regions, our directed research efforts were relatively consistent from June to September in AK and along the continental shelf break west of Vancouver Island, BC, suggesting our observations reflect a true seasonal shift in OKW distribution and foraging behaviour.

The wide latitudinal range occupied by OKW in the northeastern Pacific may reflect the seasonal distributions of their elasmobranch prey. For example, salmon sharks segregate by sex and size across the North Pacific, with larger female salmon sharks aggregating on the continental shelf in the Gulf of Alaska (GOA) in summer and early autumn (June–September) to feed on salmonids returning to spawn (Nagasawa 1998, Wright & Hulbert 2000, Hulbert et al. 2005, Weng et al. 2005, 2008, Goldman & Musick 2008, Carlisle et al. 2011, Coffey et al. 2017). The 5 salmon shark predation samples we collected in June were within or adjacent to Prince William Sound, a region in the GOA known for high summer densities of salmon sharks (Carlisle et al. 2011). During summer, salmon sharks in the GOA occur above the thermocline (<60–100 m) (Wright & Hulbert 2000, Hulbert et al. 2005, Carlisle et al. 2011, Coffey et al. 2017), where they may be easier for OKW to capture. Once salmon enter spawning streams, many salmon sharks undertake southerly migrations offshore or along the North American coast, where they use progressively deeper water to feed (Hulbert et al. 2005, Weng et al. 2005, 2008, Block et al. 2011, Carlisle et al. 2011, Coffey et al. 2017, Garcia et al. 2021); this could mean that they become less available as prey for OKW. During late summer and early fall, most OKW predation events had shifted southward along the continental shelf edge off BC, where the whales fed on sleeper sharks, dogfish, blue sharks, and albacore tuna. Although this switch to more pelagic foraging may reflect the movement of salmon sharks to deeper offshore or waters, we had very little research effort south of Vancouver Island or west of the continental slope, where salmon sharks overwinter. During spring, female salmon sharks move to the northern California Current system, possibly attracted by early salmon runs (Weng et al. 2008). Thus, despite our salmon shark predation observations being restricted to summer in AK, this species may be important prey to OKW in other regions and throughout the year.

Pacific sleeper sharks were also frequently taken by OKW in the Gulf of Alaska and BC during spring and early summer (March–June). Most were captured at >54° N, although 3 were also taken in Johnstone Strait off northeastern Vancouver Island, BC, and 9 were taken during a single encounter in Juan de Fuca Canyon, BC. Sleeper sharks were the most commonly recorded OKW prey (n = 38, 45.2%), likely because their large size (typically 2.5–3 m; Orlov & Moiseev 1998, Sigler et al. 2006), slow swimming speed (Fujiwara et al. 2021), and large livers make them energetically profitable (Ford et al. 2011). Additionally, sleeper sharks represent a predictable prey resource because they are generally nonmigratory (Wright & Hulbert 2000, Hulbert et al. 2006, Orlov & Baitalyuk 2014), occurring year-round in continental shelf and slope waters throughout the range of OKW (Compagno 1984, Courtney & Sigler 2007, Love 2011, Matta et al. 2024). Fisheries-independent by-catch indices, however, suggest sleeper shark abundance in the GOA and BC was higher in the 1990s and early 2000s but has declined greatly since then (Matta et al. 2024). At high latitudes, sleeper sharks occur close to shore (Sigler et al. 2006), which coincides with the coastal habitats and relatively shallow water depths (~50–300 m), where we detected most sleeper shark predation events in AK and northern BC. The exception was 7 sharks taken by OKW in Prince William Sound, AK in 2009 at a location ~450 m in depth. Pacific sleeper sharks tagged in the northern GOA (an area that overlapped with our observations of sleeper shark predation), spent 61% of their time between 150 and 450 m and made regular forays to <100 m, especially at night (Hulbert et al. 2006). Conversely, in more southerly latitudes, sleeper sharks occur deeper (up to 2000 m) and seldom approach the surface (Compagno 1984, Ebert et al. 1987, Sigler et al. 2006). Thus, the northerly bias in observed sleeper shark predation events may result because this species is less accessible to OKW in the south. Average length of sleeper sharks is also greatest in the GOA (Matta et al. 2024), which may make it more energetically profitable for OKW to target them in this area.

Blue sharks, the most abundant shark in the north Pacific, occur as far north as the Gulf of Alaska, but are found in greatest densities between 20 and 50° N (Kleiber et al. 2009, Love 2011, King et al. 2015). Predation on blue sharks by OKW reflects this distribution; only 1 of the 15 blue sharks was taken north of 50° N. After sleeper sharks, blue sharks were the second-most commonly identified prey (n = 15, 17.9%). Like salmon sharks, blue sharks undertake seasonal north–south migrations. During summer, tagged immature female blue sharks made extensive use of habitat off southwestern Vancouver Island, BC, and WA (Maxwell et al. 2019), the same season and area where the majority of blue shark OKW predation samples were collected. This region also corresponds spatially with peak annual blue shark by-catch in recent Canadian Pacific fisheries (COSEWIC 2016) and had the highest historic fisheries CPUE for blue sharks in the North Pacific, with blue sharks being most common from June–September between 40 and 50°N (Strasburg 1958). Like salmon sharks, blue sharks segregate by sex and size, with those in Canadian Pacific waters being mostly subadult females (Nakano 1994, McKinnell & Seki 1998, COSEWIC 2006, 2016, Maxwell et al. 2019). Thus, specializing on sharks in the northeastern Pacific may be especially advantageous for OKW, since female sharks are most common in the region, and typically have higher oil content than males (Jayasinghe et al. 2003a).

The highest CPUEs and model-predicted spatial occurrence for blue sharks in Canadian waters are found along the continental shelf edge and slope from northern Haida Gwaii to the west coast of Vancouver Island, as well as within Hecate Strait (COSEWIC 2006, 2016, Proudfoot et al. 2024). Blue shark predation by OKW was observed along this shelf edge, but only a single kill was observed north of Vancouver Island (Fig. 3B). This gap may be due to both lower blue shark densities in northerly areas, as well as our limited research effort in these remote locations. In fall, blue sharks move to the coastal waters of southern CA and Baja on their way to presumed winter breeding grounds (Maxwell et al. 2019). The southward movement of OKW into Californian waters in fall and winter may in part reflect this seasonal shift, with 4 blue shark predation events being observed in CA in December. Blue sharks generally use the upper 350 m of the water column (COSEWIC 2006, Love 2011) and spend over half of their time above 50 m (Sciarotta & Nelson 1977, Weng et al. 2005, Stevens et al. 2010), well within the diving abilities of OKW (Schorr et al. 2022). As with sleeper sharks, blue sharks spend more time near the surface in the northernmost part of their range and are distributed more deeply in tropical regions (Strasburg 1958, Vedor et al. 2021). Thus, blue sharks may be more easily hunted by OKW off BC than they are farther south.

Pacific spiny dogfish are widely distributed across the shelf and upper continental slope waters of the northeastern Pacific but are most abundant between southeast AK and northern OR (Ketchen 1986, McFarlane & King 2003, Love 2011). This species was the third-most commonly recorded prey of OKW (n =14, 16.7%). Dogfish predation occurred between August and October along the shelf edge west of Juan de Fuca Strait, BC (~48° N), which corresponds spatially with the highest CPUE and model-predicted biomass of dogfish from fisheries surveys (Brodeur et al. 2009, McFarlane et al. 2010). Historically, this region was an important commercial fishing ground for dogfish (Alverson & Stansby 1963, Ketchen 1986). Dogfish caught in summer trawl surveys were most prevalent at shallow depths (<200 m) (Brodeur et al. 2009), well within the diving range of OKW (Schorr et al. 2022). Dogfish stocks in inner coastal waters, such as the Salish Sea, appear to be largely non-migratory (McFarlane & Beamish 1986, McFarlane & King 2003), suggesting that some aggregations may represent a predictable, year-round prey resource for OKW. A portion of the offshore dogfish stock, however, undertakes seasonal north–south movements along the North American coast (Holland 1957, Ketchen 1986, McFarlane & King 2003). As with salmon and blue sharks, north–south migration of dogfish may influence the seasonal movements of OKW. Although dogfish predation by OKW was not detected in the Gulf of Alaska, the species occurs there in nearshore waters, albeit at lower densities than in BC (Tribuzio et al. 2008, Gasper & Kruse 2013). OKW may also prey on dogfish east of Haida Gwaii in Hecate Strait (i.e. Dogfish Bank), where high probabilities of dogfish were predicted by a recent fisheries model (Thompson et al. 2023). At the turn of the 20th century and in the 1940s, Hecate Strait supported major fishing grounds for a dogfish liver oil industry (Alverson & Stansby 1963, Ketchen 1986). While there have been acoustic detections of OKW in this region in April, June and August (Ford et al. 2014), dogfish predation has not yet been observed there (likely due to limited research effort).

4.6. Association between shark predation events and bathymetric features

Most OKW prey samples were collected from habitats with bottom depths of around 200 m. Our observations in both AK and BC suggest that during the summer, foraging OKW often follow the 100–200 m bathymetric contours. For example, OKWs feeding on Pacific sleeper sharks in Dixon Entrance, BC, caught 11 individuals (Table 1) along the edge of Learmonth Bank, a feature that drops off sharply beginning at around 100–200 m (Ford et al. 2011). Off the west coast of Vancouver Island, BC, the 100–200 depth range demarcates the continental shelf edge and was a common foraging location for OKW (Fig. 4). This association between OKW and the shelf edge was also recognized during photo-identification (Ford et al. 2014) and satellite tagging (Schorr et al. 2022) analyses. The abrupt topography of the shelf edge amplifies currents and generates strong seasonal (April–October) upwelling (McFarlane & Robinson 1997, Genin 2004). The associated primary production attracts aggregations of zooplankton, forage fish, and predators, including sharks (Simard & Mackas 1989, Genin 2004, Evans et al. in press), making this region a reliable feeding ground for OKW. The continental shelf edge and slope of BC are predicted to support high densities of blue sharks and sleeper sharks (Proudfoot et al. 2024), and tagged blue sharks show movement and habitat use patterns that are broadly linked to related oceanographic features such as upwelling zones and thermal fronts (Vedor et al. 2021).

Seamounts also drive upwelling that aggregates marine life (Morato et al. 2010), and although these features are under-represented in our study, they may be important foraging areas for OKW. In the western and central Pacific, longline by-catch of blue shark and opah increased with proximity to seamounts, as did the probability of catching other shark and tuna species, suggesting that seamounts serve as resting, foraging, breeding, or nursery areas for many migratory pelagic fish (Morato et al. 2010). In the Gulf of Alaska, hydrophone detections of vocalizing OKW were most frequent at stations positioned on seamounts, compared to those on the shelf or slope (Rice et al. 2023). These detections occurred from October to December, when OKW may be moving away from continental shelf feeding grounds to follow migrating shark populations. Likewise, in the fall and winter, OKW vocalizations were detected at seamounts west of the continental shelf edge in BC (Dellwood, Bowie, and Explorer Seamounts and Paul Revere Ridge; Cetacean Research Program, Fisheries and Oceans Canada unpubl. data).

Blue sharks were the only prey species not taken by OKW in habitats of ~200 m but were instead captured in locations with a median seafloor depth of 338 m. This difference probably arose because OKW often captured blue sharks at the heads of submarine canyons along the shelf edge off southwestern Vancouver Island, BC (Fig. 4), where densities of this species are predicted to be high (Proudfoot et al. 2024). Dogfish were also caught by killer whales near these canyons but were more frequently taken inside of the shelf edge in shallower water. Like the shelf edge, upwelling at canyon heads supports concentrations of zooplankton, aggregations of forage fish, and higher level predators (Allen et al. 2001, Genin 2004), and these features may serve as rich foraging areas for OKW. The broadnose sevengill shark consumed in CA was similarly caught near the head of the Monterey Canyon. Likewise, Moresby Trough in Hecate Strait, BC, was identified as a potentially important foraging area because of the high number of OKW encounters relative to research effort (Ford et al. 2014) and the prediction that high densities of blue, salmon, and sleeper sharks occur in the canyons of southern Hecate Strait (Williams et al. 2010, Proudfoot et al. 2024). Despite this, elasmobranch predation has not yet been observed in the region, likely due to limited observational effort.

5. CONCLUSIONS

Killer whale populations are known for their pronounced culturally transmitted dietary specializations (Ford & Ellis 2014). Offshore killer whales, which prey primarily on elasmobranchs, represent another example of this, exhibiting a level of dietary specialization comparable to that of the Resident and Bigg's killer whale ecotypes of the northeastern Pacific (Ford et al. 1998, Ford & Ellis 2006). Furthermore, our results suggest that OKW, which are known to range from CA to AK, undergo predictable seasonal movements, tracking the availability and migration patterns of their preferred prey. Elasmobranchs, with their widespread distributions, large body mass, and lipid-rich livers, represent an energetically profitable food source. Globally, many shark species are in steep decline (Pacoureau et al. 2021) because life history traits such as slow growth, late maturation, and low fecundity make them susceptible to overfishing (Musick et al. 2000, Nakano & Stevens 2008). As specialist predators, OKW are predicted to be vulnerable to changes in the distribution and abundance of their prey (e.g. Ford et al. 2010). The historic near-extirpation of basking sharks in BC (Wallace & Gisborne 2006), which were likely an important prey species, the reduction of dogfish biomass by intense commercial liver-oil fisheries (Alverson & Stansby 1963, Ketchen 1986), and recent sleeper shark declines in Alaskan waters

(Matta et al. 2024) have all likely affected prey availability for OKW. Addressing such conservation issues into the future will require further insight into how seasonal shifts in OKW diet, as identified in this study, influence OKW movement, distribution and habitat use, particularly during the data-limited winter months and in under-sampled regions. Emerging techniques such as quantitative fatty acid signature analysis of blubber (as in Remili et al. 2023) might provide a more detailed, longer-term understanding of the dietary breadth of OKW that would complement the prey sampling results reported here. Finally, the impact that OKW have as wide-ranging, specialized apex predators on the tropho-dynamics of ecologically and commercially important fish populations may be under-appreciated and requires further study.

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