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Trans-Pacific Consumption of Cephalopods by North Pacific Killer Whales (*Orcinus orca*)

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Abstract

Cephalopods are an important component of many cetacean diets. Although some odontocete species in the subfamily, which includes killer whales, primarily consume squid (e.g., pilot whales, beaked whales), killer whales, for the most part, are thought to specialize. In the North Pacific Ocean, three *ecotypes* have been identified based on dietary specialization. These ecotypes include *residents*, which have been documented to be piscivorous, feeding primarily on salmonids; *offshores*, which are also piscivorous but feed primarily on sharks and other fish species; and *transients*, which feed primarily on marine mammals. Based on the occurrence of cephalopods in the stomach contents of two confirmed transient ecotype killer whales from the west coast of the United States, and two others that are likely closely related to the transient ecotype from across the North Pacific Ocean, we suggest that cephalopods may represent an underappreciated component of the diet of transient killer whales or closely related ecotypes throughout the North Pacific Ocean. Only cephalopods that are known to occur at relatively deep depths were present in the stomach of a killer whale from Hawai'i. The stomach of a killer whale collected in the Sea of Okhotsk not only contained marine mammal and fish parts, but also squid known to only occur at deep depths. Of the two whales from the west coast of the United States that were genetically identified as transients, one contained only squid and the other contained squid and marine mammal parts. If squid were to comprise a substantial portion of the diet in these west coast United States transient killer whales, instead of primarily marine mammals as currently thought, this could account for a mismatch between expected and observed stable isotope values of transient killer whales previously sampled in the eastern North Pacific.

Key Words: killer whale, *Orcinus orca*, diet, cephalopods, fish, marine mammals

Introduction

Cephalopods are an important component of many cetacean diets (Clarke, 1996; Santos et al., 2001), with some cetacean species foraging almost exclusively on squid (e.g., beaked whales: Walker & Hanson, 1999; sperm whales [*Physeter macrocephalus*]: Clarke, 1980). The odontocete subfamily Globcephalinae is comprised of nine species (Vilstrup et al., 2011), several of which have diets that are comprised of some, if not primarily, squid (i.e., pilot whales [*Globicephala macrorhynchus* and *G. melas*): Bernard & Reilly, 1999; Risso's dolphin [*Grampus griseus*]: Clarke & Young, 1998; melon-headed whales [*Peponocephala electra*]: Clarke & Young, 1998; pygmy killer whales [*Feresa attenuata*]: Zerbini & Oliveira Santos, 1997). This subfamily also includes killer whales (*Orcinus orca*), which, worldwide, have diets that include a diverse array of species (see Hoyt, 1981). Although there are numerous records of killer whales feeding on marine mammals and fish (see Hoyt, 1981), this species has also been documented to feed on cephalopods (Scheffer & Slipp, 1948; Tomilin, 1957; Nishiwaki & Handa, 1958; Rice, 1968; Jonsgard & Lyshoel, 1970; Shevchenko, 1975; Christensen, 1978; Santos & Haimovici, 2001). However, despite the appearance that killer whales have diverse diets which suggests they may be generalist predators, several studies have documented dietary specializations (Ford et al., 1998; Pitman & Ensor, 2003; Burdin et al., 2004; Foote et al., 2009; Pitman et al., 2011; Filatova et al., 2014). These dietary specializations (associated with variations in external morphology, movements, social behavior, and genetics) maintain social, and thus reproductive, isolation between groups and, therefore, represent unique ecotypes (de Bruyn et al., 2013) throughout the world. In the North Pacific Ocean, there are currently three recognized ecotypes with dietary specializations. Resident killer whales are reported to be piscivorous, feeding mostly on several species of salmon (Ford et al., 1998; Saulitus et al., 2000; Hanson et al., 2010), whereas offshore killer whales, for which diet data are limited, are also thought to be piscivorous, primarily consuming fish and sharks (Dahlheim et al., 2008). In contrast, transient killer whales in this region have been documented to predate primarily on marine mammals (Jefferson et al., 1991; Baird & Dill, 1996; Ford et al., 1998). Diet assessment for these three ecotypes has come from both stomach contents analysis and behavioral observations. For transient killer whales, there has been a relatively large number of observational data on feeding events but relatively few opportunities to examine stomach contents. In general, observational data for this ecotype has documented the consumption of numerous species of marine mammals and sea birds (Jefferson et al., 1991; Baird & Dill, 1996; Ford et al., 1998; Dahlheim & White, 2010). Historically, squid have been documented in the stomach contents of only one known transient ecotype killer whale in the North Pacific (Ford et al., 1998), although this was thought to be secondary prey. Although squid have been documented in the stomach contents of killer whales in the North Pacific, this was in only two other cases, and the ecotypes of these whales were unknown (Nishiwaki & Handa, 1958; Rice, 1968). Herein, we present stomach content data from (1) two confirmed transient ecotype killer whales from the west coast of the United States, (2) a killer whale from Hawai'i that is closely related to the transient ecotype, and (3) a killer whale from the Sea of Okhotsk that is likely to be a transient ecotype, all of which contained numerous cephalopod hard parts, suggesting that squid may be potentially a more important prey species to these ecotypes than previously indicated.

Methods

Killer Whale Specimens

Stomach contents were obtained opportunistically for three killer whales that stranded on the west coast of the United States and in Hawai'i, and one whale that was taken in the coastal waters of the Sea of Okhotsk in a local shore-based whaling operation in Japan (Table 1). The stomach contents of the whale from the Sea of Okhotsk were collected by a Japanese fisheries observer and sent to WAW (the author) for analysis.

Genetic samples were available from the killer whales from the west coast of the United States and Hawai'i to assess ecotype. The mtDNA control region sequence reported for both of the west coast United States killer whales were identified as Gulf of Alaska transient killer whale (GAT; Hoelzel et al., 1998; P. Morin, pers. comm., 9 September 2013) and, thus, can be classified as the west coast United States transient ecotype. Genetic data collected from eastern tropical Pacific (ETP) killer whales (including Hawai'i) have a nuclear genetic pattern that is different from the rest of the North Pacific killer whales, which indicates that they are currently likely a genetically distinct group separate from the transients, residents, and offshores (Morin et al., in prep.; Parsons, pers. comm., 9 September 2013). The Hawai'i killer whale in our sample had a unique mitogenome haplotype that clustered closest to ETP killer whales and is within the phylogenetic clade that contains all the transients and some ETP killer whales (Morin et al., in prep.) such that we have classified this as an ETP pelagic ecotype. For the Sea of Okhotsk whale, no tissue samples for genetics were collected. However, circumstantial evidence (the presence of marine mammal parts) suggests that it is likely that this whale was closely related to the transient ecotype. First, recent analysis of killer whale genetic samples collected in the Sea of Okhotsk indicates the occurrence of both transient and resident ecotypes, similar to the structure further to the east in Alaska and along the west coast of North America (Parsons et al., 2013; Filatova et al., 2014). In addition, several killer whales that were entrapped in the ice in this region and which had both squid and marine mammal parts in their stomachs genetically fell within the transient clade in the North Pacific, closest to eastern North Pacific transient killer whales (Yamada et al., 2007). Thus, we feel it is likely that this specimen

Table 1. North Pacific killer whale (*Orcinus orca*) specimens recovered with prey remains in their stomachs

Specimen #	Date	Location	Sex	Length (m)	Regional ecotype
AB-88-15	18 Sept 1988	Abashiri, Hokkaido, Japan (Sea of Okhotsk)	F	6.5	Western North Pacific transient[a]
NMFS-00-04-14-SA	6 April 2004	Lanai, Hawai'i	F	5.8	Eastern Tropical Pacific pelagic
OIMB-079	3 May 2004	Bandon, Oregon	F	6.5	West coast U.S. transient
CRC-1050	17 June 2010	Cape Ozette, Washington	F	6.1	West coast U.S. transient

[a] Suspected regional ecotype based on the presence of marine mammal parts in the stomach

was part of the western North Pacific transient ecotype.

Field Collection and Laboratory Analyses

Due to the large stomach size of *Orcinus*, the stomachs were opened and examined in the field and all prey remains carefully removed. With the exception of the prey remains from the stomach sample from the Sea of Okhotsk, which were initially preserved in 70% isopropyl alcohol, all the prey remains were subsequently frozen prior to laboratory analysis. Prey identification, enumeration, and diagnostic prey item measurements were conducted in the laboratory. Wherever possible, diagnostic fish bones or intact or partially intact fish, cephalopods, and crustaceans were also used to supplement or confirm identifications. All remains were identified using reference material housed at the food habits laboratory of the National Marine Mammal Laboratory (NMML) in Seattle, Washington. The minimum number of individual prey ingested was determined by the greater number of left or right otoliths or upper or lower cephalopod beaks. Diagnostic measurements of otoliths and cephalopod beaks were made to the nearest 0.1 mm using an ocular micrometer or Vernier calipers. Regression equations used to derive prey size and weight estimates were obtained from the following sources: Frost & Lowry (1981), Walker et al. (2002) (fishes), Wolff (1982), Robinson & Hartwick (1983), Clarke (1986), Walker (1996), and Walker et al. (2002) (cephalopods). Published regressions were unavailable for four cephalopod species: *Gonatus berryi*, *Eogonatus tinro*, *Chiroteuthis picteti,* and *Onychoteuthis borealijaponica*. For these, we used as yet unpublished regressions developed at NMML. Because evidence indicates they were ingested only in part, weight estimates for marine mammal remains were not attempted. As a result, they are excluded from the estimated contribution by mass calculations. A voucher series of beaks and otoliths representative of each prey taxon identified have been incorporated into the NMML reference collection. The remainder of the samples was placed in storage at the NMML facility.

Results

Prey remains totaling 77, 20, and 140 parts, respectively, were recovered from the Sea of Okhotsk, Hawai'i, and west coast United States killer whales (Tables 2-4). By number, cephalopods comprised the majority of prey ingested in all three regions in that they made up 89.6% of the prey found in the Sea of Okhotsk specimen, 90.0% of the prey found in the whale stranded in Hawai'i, and 99.3% of the prey found in the west coast United States killer whales. Eleven cephalopod families were represented across samples, including three, seven, and eight families in the Sea of Okhotsk, Hawai'i, and west coast United States samples, respectively. A total of 24 species were documented: seven in the Sea of Okhotsk sample, nine in Hawai'i, and 14 in the west coast United States stomach samples (Tables 2-4). Fish were found only in the sample from the Sea of Okhotsk. Only three fish species, from the families Moridae and Gadidae, were ingested, and they represented only 9.1% by number and 8.1% by mass. A mesopelagic crustacean, *Pasiphaea* sp., was found in the stomach of the Hawai'i specimen at 10.0% by number but only 1.0% by mass. Partial mammal remains were found in two stomachs—the Sea of Okhotsk and the Oregon whale stomachs. This included chunks of Dall's porpoise (*Phocoenoides dalli*) blubber in the Sea of Okhotsk whale and vibrissae, hair, and claws from an elephant seal (*Mirounga*) in the Oregon whale.

Squid of the family Gonatidae dominated the Sea of Okhotsk and west coast United States samples, whereas the Histioteuthidae were the most prevalent in the Hawai'i sample. Gonatid squid also represented the majority (85.7%) of the beaks in the Sea of Okhotsk animal with two species (*Berryteuthis magister* and *G. berryi*) accounting for 74.0% of the contents. These two species also accounted for 79.8% by total mass. In the stomach from Hawai'i, 80.0% of the beaks were from three predominantly mesopelagic squid families (Histioteuthidae, Chiroteuthidae, and Cranchiidae), with three species (*Stigmatoteuthis hoylei*, *Chiroteuthis picteti*, and *Taonius belone*) contributing by number the majority of beaks (70.0%) to the sample. While *S. hoylei* contributed 54.0% by mass, the other two nominally abundant species (*C. picteti* and *T. belone*) contributed only 3.9% and 3.7% by mass, respectively. However, the relatively larger ommastrephid squid (*S. oualaniensis*), while only occurring with 5.0% frequency, was estimated to contribute 20.7% by mass. Of the west coast United States samples, 93.6% of the prey by number was contributed by three families (Gonatidae, Onychoteuthidae, and Ommastrephidae), with five species (*Onychoteuthis borealijaponica, Gonatopsis borealis*, *Gonatus onyx*, *Gonatus middendorffii*, and *Dosidicus gigas*) accounting for 85.7%. However, 92.4% of the mass was contributed by only three species. In particular, *D. gigas*, the relatively larger jumbo squid, contributed the most mass at 52.4%, whereas *O. borealijaponica* and *G. borealis* contributed 27.4% and 12.9% of the mass, respectively.

Table 2. Prey items in the stomach of the Sea of Okhotsk killer whale AB-88-15

Prey species	No.	% frequency	Estimated mean prey length (mm)*	Estimated prey length range (mm)	Estimated mean weight (g)	Estimated total mass (g)	% contribution by mass
CEPHALOPOD FAMILY	69	89.6	--	--	--	34,959.9	93.1
Gonatidae	66	85.7	--	--	--	29,393.9	78.3
Berryteuthis magister	41	53.2	246	236 - 314	497.7	20,405.7	54.3
Gonatus madokai	3	3.9	244	192 - 295	292.7	878.1	2.3
Gonatus berryi	16	20.8	229	201 - 360	327.7	5,243.2	14.0
Eogonatus tinro	6	7.8	127	99 - 165	76.0	456	1.2
Gonatopsis sp. A	1	1.3	417	417	2,410.9	2,410.9	6.4
Cranchiidae							
Galiteuthis phyllura	2	2.6	513	??	83	166	0.4
Octopodidae							
Enteroctopus dofleini	1	1.3	240	240	5,400.0	5,400.0	14.4
FISHES	7	9.1	--	--	--	2,594.7	6.9
Gadidae	4	5.19	--	--	--	1,495.8	4.0
Eleginus gracilis	1	1.3	244	--	98.4	98.4	0.3
Theragra chalcogramma	3	3.9	441	410 - 516	465.8	1,397.4	3.7
Moridae							
Laemonema longipes	3	3.9	323	315 - 330	366.3	1,098.9	2.9
MAMMAL FAMILY	1	1.3	--	--	--	--	--
Phocoenidae							
Phocoenoides dalli	1	1.3	--	--	--	--	--
Totals	77	100	--	--	--	37,554.6	100.0

* All cephalopod prey lengths are dorsal mantle length (DML). All fish prey lengths are standard length (SL).

Table 3. Prey items in the stomach of Hawai'i killer whale NMFS-00-04-14-SA

Prey species	No.	% frequency	Estimated mean prey length (mm)*	Estimated prey length range (mm)	Estimated mean weight (g)	Estimated total mass (g)	% contribution by mass
CEPHALOPOD FAMILY	20	90.0	--	--	--	3,730.5	99.0
Gonatidae							
Gonatus californiensis	1	5.0	210	210	191.7	191.7	5.1
Ommastrephidae							
Sthenoteuthis oualaniensis	1	5.0	262	262	780	780	20.7
Octopoteuthidae							
Octopoteuthis neilsoni	1	5.0	131	131	127.8	127.8	3.4
Histioteuthidae	11	55.0	--	--	--	2,245.2	59.6
Stigmatoteuthis hoylei	10	50.0	116	71 - 161	203.4	2,034.0	54.0
Histioteuthis corona	1	5.0	114	114	211.2	211.2	5.6
Mastigoteuthidae							
Mastigoteuthis dentata	1	5.0	117	117	69.4	69.4	1.8
Chiroteuthidae							
Chiroteuthis picteti	2	10.0	104	104 - 134	73.5	147.0	3.9
Cranchiidae	3	15.0	--	--	--	169.4	4.5
Taonius belone	2	10.0	267	265 - 268	69.4	138.8	3.7
Leachia dislocata	1	5.0	114	114	30.6	30.6	0.8
CRUSTACEAN FAMILY	2	10.0	--	--	--	--	--
Pasiphaeidae							
Pasiphaea sp.	2	10.0	53	52 - 54	19.5	39.0	1.0
Totals	22	100.0	--	--	--	3,769.5	100.0

* All cephalopod prey lengths are dorsal mantle lengths (DML). Shrimp prey lengths are carapace length.

Table 4. Prey items in the stomachs of west coast United States transient killer whales OIMB-079 and CRC–1050 combined

Prey species	No.	% frequency	Estimated mean prey length (mm)*	Estimated prey length range (mm)	Estimated mean weight (g)	Estimated total mass (g)	% contribution by mass
CEPHALOPOD FAMILY	139	99.3	--	--	--	28,662.1	100.0
Enoploteuthidae							
Abraliopsis felis	2	1.4	38	37 - 39	4.3	8.6	< 0.1
Octopoteuthidae							
Octopoteuthis deletron	1	0.7	--	--	--	--	< 0.1
Onychoteuthidae							
Onychoteuthis borealijaponica	22	15.7	247	213 - 315	357.6	7,867.2	27.4
Gonatidae	96	68.6	--	--	--	4,812.1	16.8
Berryteuthis anonychus	2	1.4	102	102	29.9	59.8	0.2
Gonatopsis borealis	48	34.3	126	56 - 277	76.9	3,691.2	12.9
Gonatus onyx	21	15.0	55	44 - 56	6.3	132.3	0.5
Gonatus berryi	1	0.7	44	44	4.8	4.8	< 0.1
Gonatus californiensis	2	1.4	224	224	390.0	780	2.7
Gonatus middendorffii	16	11.4	57.6	39 - 101	9.0	144	0.5
Gonatus sp.	6	4.3	--	--	--	--	< 0.1
Histioteuthidae							
Stigmatoteuthis dofleini	1	0.7	163	163	954.3	954.3	3.3
Ommastrephidae							
Dosidicus gigas	13	9.3	360	344 - 427	1,148.7	14,933.1	52.1
Cranchiidae							
Taonius borealis	2	1.4	232.5	206 - 259	43.4	86.8	0.3
Ocythoididae							
Ocythoe tuberculata	2	1.4	--	--	--	--	< 0.1
MAMMAL FAMILY	1	0.7	--	--	--	--	--
Phocidae							
Mirounga angustirostris	1	0.7	--	--	--	--	--
Total	140	100.0	--	--	--	--	--

* All cephalopod prey length measurements are dorsal mantle length (DML).

Discussion

Our results suggest that squid comprise a potentially substantial part of the diet of transient killer whales or those ecotypes that may be closely related to transient killer whales throughout the North Pacific Ocean. These observations are perhaps not surprising given that cephalopods have been documented to comprise a substantial portion of the killer whale diet in the northwestern Pacific Ocean and the Sea of Okhotsk (Nishiwaki & Handa, 1958; Yamada et al., 2007). Squid have also been documented to form an important dietary component of killer whales in the South Atlantic (Santos et al., 2001). This study provided (1) the first species level identification of fish, mesopelagic squid, and marine mammal remains in a likely transient ecotype killer whale in the southern Sea of Okhotsk; (2) species-level identification of mesopelagic squid as a prominent dietary component of killer whales from the ETP (i.e., Hawai'i), and (3) documentation of squid as a substantial dietary component of transient killer whales from the west coast of the United States that had been previously thought to predate almost exclusively on marine mammals.

There is one potential bias associated with our stomach content analyses that deserves consideration. Because killer whales do consume large prey, such as other marine mammals, fish, or squid, there is potential for the secondary introduction of prey hard parts. There is the possibility that beaks, bones, and otoliths could be introduced as the prey of larger prey that were consumed and thus be mistaken as primary food items of the predator. We feel that this secondary introduction has a minimal effect in our samples. Our rationale is as follows: Secondary introduction of prey remains from marine mammals is very unlikely in that in the two cases for which marine mammals were found in the stomach contents, neither animal was consumed intact. The Dall's porpoise remains in the killer whale from the Sea of Okhotsk consisted of only freshly consumed chunks of skin and blubber. No muscle tissue, bones, or other internal parts were present. Likewise, the elephant seal remains found in the whale from Oregon consisted of only blubber, hide, and vibrissae with no muscle, bones, or other internal parts present. Secondary introduction from primary fish prey or large squid in the specimen from the Sea of Okhotsk is also unlikely in that almost all the prey in this sample were near parity in size and all were recovered in a partially intact or nearly intact state. Secondary introduction is a potential factor in the west coast United States samples in which the jumbo squid (*D. gigas*) is a major prey species. This *D. gigas* is well-documented to prey on a wide variety of smaller fish and squid (Field et al., 2007) and may have secondarily introduced beaks from small squid species such as *Abraliopsis felis* and *Berryteuthis anonychus* as well as some of the smaller juvenile Gonatids. However, we believe the number of beaks would be small and would not appreciably change the overall picture.

Although squid have been documented to commonly occur in the diet of killer whales off the coast of Japan (Nishiwaki & Handa, 1958; Yamada et al., 2007), it was unclear from Nishiwaki & Handa's (1958) results if fish and squid co-occurred in these stomachs. Yamada et al. (2007) found pinniped and squid remains in the stomachs of all the adult whales. In our study, not only were squid and fish present in the same stomach, there were also marine mammal parts (porpoise), indicating it was likely a transient or closely related killer whale ecotype. The killer whales reported on by Yamada et al. (2007) were most closely related to eastern North Pacific transients based on genetic analyses. Analyses of biopsies from killer whales from the western and central North Pacific Ocean indicate that transient ecotype killer whales in this area appear to be part of a transient community in the Sea of Okhotsk/Kamchatka region of the western North Pacific Ocean (Parsons et al., 2013). The similarity of stomach contents (squid and marine mammals) between our specimen and those closely related to the transient ecotype (Yamada et al., 2007), as well as the prominence of squid reported in the stomachs of other killer whales in this region (see Nishiwaki & Handa, 1958), suggest that squid may play a prominent role in the diet of transient ecotype killer whales in this region. However, the presence of fish in a killer whale stomach which also has marine mammal parts is very different than what had been previously reported for transient ecotype killer whales in the northeast Pacific (Ford et al., 1998). The squid consumed by the Sea of Okhotsk whale were generally similar in composition to the whales examined by Yamada et al. (2007) with the notable exception of the presence and large dietary contribution of neon flying squid (*Ommastrephes bartrami*), which indicates that those whales fed on these squid previously in the North Pacific oceanic pelagic region where these squid are known to occur. However, the squid in the Sea of Okhotsk whale were very similar to those reported from Baird's beaked whales from the Sea of Okhotsk (Walker et al., 2002). The Sea of Okhotsk killer whale consumed seven of the 11 cephalopod species and two of the five fish species found in Baird's beaked whales. The presence of several mesopelagic cephalopods and a benthic fish species suggest that killer whales in this area may make relatively deep dives. They appear to eat longfin codling (*Laemonema longipes*), which are slightly smaller than those Baird's beaked whales eat, but consume larger *B. magister* than Baird's beaked whales. This killer whale also had consumed many of the same prey species consumed by Dall's porpoise in this region (Walker, 1996), but the whale's prey were represented by much larger size classes.

Very little is known about killer whales near Hawai'i or in the ETP. They are rarely encountered (Barlow et al., 2004; Baird et al., 2006, 2013) such that there is limited observational data on their foraging habits (see Baird et al., 2006). Similarly, strandings are rare with only one other killer whale stranded in Hawai'i (with an empty stomach) such that our specimen represents the only record of stomach contents for this species in this region. The closest report for an observation of cephalopod consumption by killer whales in this region was a report of "feeding on octopus" off Lanai (Shimote, 2001; Roberts & Meadows, 2004). Additional circumstantial evidence of feeding on squid was from a killer whale recently tagged with a satellite-linked transmitter that reported depth. It had one dive to over 400 m during its 5.6 d record, indicating that killer whales in this area do dive deep enough to predate on mesopelagic squid species (R. W. Baird, pers. comm., 18 November 2013). Several of the prey species recovered from the Hawai'i killer whale are similar to those found in the pygmy sperm whale (*Kogia breviceps*) (West et al., 2009). The mesopelagic crustacean *Pasiphaea tarda* was found in small numbers in both *Kogia* and the killer whale stomach. However, squid were the most prominent in both whale species, and in particular, the Histioteuthid, *Stigmatoteuthis hoylei*, which had the greatest contribution by mass in both *Kogia* and in the Hawai'i killer whale. Some of the prey species present in this sample are found deep in the water column, particularly *Taonius belone* (400 to 800 m; Young, 2011), suggesting that these ETP pelagic killer whales may dive to much deeper depths than transient killer whales that typically occupy the relatively shallow continental shelf of the west coast of North America (Hanson, unpub. data). Besides the mesopelagic squid found in the Sea of Okhotsk and Hawai'i whales, mesopelagic squid have also been documented as the prey of killer whales in the South Atlantic Ocean (Santos et al., 2001).

Until recently, transient killer whales on the west coast of the United States and British Columbia were previously thought to feed exclusively on marine mammals and seabirds (Jefferson et al., 1991; Baird & Dill, 1996; Ford et al., 1998). However, these conclusions have been based primarily on observational data which may be biased because larger or surface associated prey items may be disproportionately handled at the surface during the predation process or result in prolonged feeding episodes due to sharing with conspecifics. Stomach content data from this region has been scarce. The only transient killer whale that had stranded with stomach contents in this region prior to this study contained a single squid beak, although this was dismissed as secondary prey item of an elephant seal that was present (Ford et al., 1998). However, very recent killer whale stomach content data from this region (Ford et al., 2013), and foraging observations in the Aleutian Islands (Wade et al., 2013) included squid. Rice (1968) reported the presence of a squid in the stomach of a killer whale collected off central California, and while the ecotype was not known, it is likely a transient killer whale based on the other marine mammal parts in its stomach. Conversely, if squid have been a common component of the transient killer whale diet, this may explain an observed disparity in a diet assessment of transients using stable isotopes. Newsome et al. (2009) noted that the observed isotopic levels for west coast United States transient killer whales were higher than expected (assuming a diet composed exclusively of marine mammals), and they suggested that California transient killer whales consumed lower trophic prey than Alaska transients. Miller et al. (2013) documented that the stable isotope values of jumbo squid collected in the Northern California Current were much lower (mean = 12.9 $\delta^{15}N$ and -17 $\delta^{13}C$) than other likely killer whale prey such as California sea lion (*Zalophus californianus*): 18.5 $\delta^{15}N$ and -13.8 $\delta^{13}C$; harbor seal (*Phoca vitulina*): 18.6 $\delta^{15}N$ and -12.4 $\delta^{13}C$; harbor porpoise (*Phocoena phocoena*): 15.7 $\delta^{15}N$ and -13.4 $\delta^{13}C$; and gray whale (*Eschrichtius robustus*): 14.2 $\delta^{15}N$ and -13.1 $\delta^{13}C$ (Newsome et al., 2009). Similarly, several other species of squid that were documented as prey in the Sea of Okhotsk whale also had much lower stable isotope values (Takai et al., 2000). Given that many of the killer whale specimens in the Newsome et al. (2009) analysis were collected several decades ago, we think it is probable that squid predation by transient ecotype killer whales has been occurring for an extended time period. These data, taken together with the results of our study and another recent study (see Ford et al., 2013), suggest predation on squid by west coast United States transient killer whales may not be an uncommon occurrence. In addition, documentation of squid consumption by killer whales in Alaska (Wade et al., 2013) indicates that this dietary component is widespread such that the role of squid in the diet of North Pacific killer whales has been underappreciated. Although our sample size is small, these results suggest that squid contribute substantially to the diets of North Pacific transient killer whales and those killer whales that are thought to be closely related to the transient ecotype that occur in the Eastern Tropical Pacific Ocean.

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