Aquatic Mammals 2020, *46*(2), 191-199, DOI 10.1578/AM.46.2.2020.191

Short Note
Harbor Porpoises (*Phocoena phocoena vomerina*) Catching and Handling Large Fish on the U.S. West Coast

Cindy R. Elliser,[1] Sanne Hessing,[2] Katrina H. MacIver,[1]
Marc A. Webber,[3] and William Keener[3]

[1]*Pacific Mammal Research, 1513 A Avenue, Anacortes, WA 98221, USA*
E-mail: cindy.elliser@pacmam.org
[2]*CetaScience, Hazenakker 18, 3994 EJ, Houten, The Netherlands*
[3]*The Marine Mammal Center, 2000 Bunker Road, Sausalito, CA 94965, USA*

This short note documents instances of prey handling and consumption of large fish species along the West Coast of the United States (U.S.), including the Salish Sea (inland waters of Washington State and Canada); San Francisco Bay, California; and Cook Inlet, Alaska, which have not previously been documented as prey for harbor porpoises (*Phocoena phocoena vomerina*) in this region (Figure 1; Table 1). The sightings in the Salish Sea occurred in Burrows Bay off Fidalgo Island, Washington, during an ongoing photo-identification (photo-ID) and behavioral study of harbor porpoises by Pacific Mammal Research (Elliser et al., 2018). The sightings in San Francisco Bay occurred during an

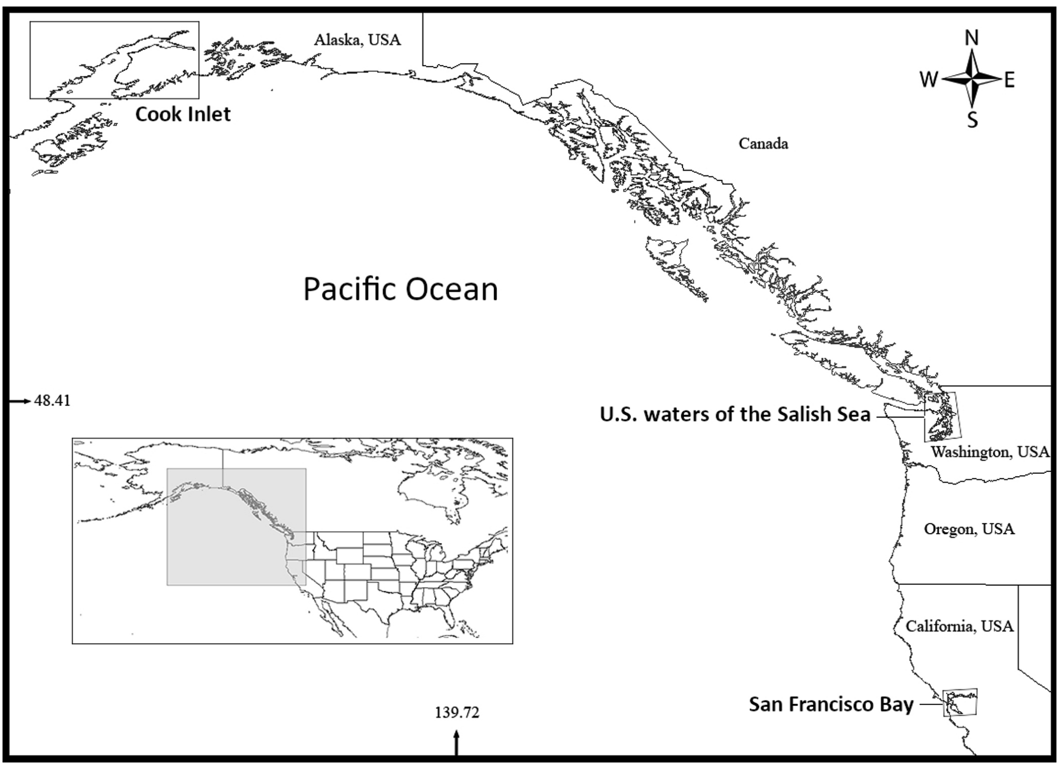

Figure 1. Map indicating the three areas where observations occurred along the U.S. West Coast: Cook Inlet, Alaska; Salish Sea, Washington; and San Francisco Bay, California

ongoing photo-ID and behavioral study of harbor porpoises by The Marine Mammal Center (Stern et al., 2017). The Cook Inlet observation occurred during a necropsy of a harbor porpoise that was entangled in a gillnet fishery.

The sightings and photographs in Burrows Bay were taken from a land-based observation point by S. Hessing on 7 August 2017 (Figure 2), 12 August 2017 (Figure 3), and 25 July 2019 (Figure 4). In all instances, the harbor porpoise appeared to be swimming in a circle at the same spot, diving and coming out of the water head first. The porpoise clearly accelerated, and the fish catch was observable not far below the surface. The porpoise then immediately appeared at the surface with the fish, accompanied by a lot of splashing. In the 7 August 2017 observation, the porpoise came to the surface with the head of the fish in its mouth, grabbing the fish near the gill area and carrying it sideways (Figure 2). Like most odontocetes,

Table 1. Summary of large fish captures by harbor porpoises (*Phocoena phocoena vomerina*) on the U.S. West Coast

Location	Date	Porpoise	Fish	Behaviors observed	Figure
Salish Sea, WA	7 Aug. 2017	Free swimming	Salmonid (*Oncorhynchus* sp.)	Capture; fish carried sideways	2
Salish Sea, WA	12 Aug. 2017	Free swimming	Salmonid (*Oncorhynchus* sp.)	Capture; fish thrown into air	3
Salish Sea, WA	25 July 2019	Free swimming	Coho salmon (*Oncorhynchus kisutch*)	Capture; fish carried sideways	4
San Francisco Bay, CA	17 Nov. 2017	Free swimming	American shad (*Alosa sapidissima*)	Capture; fish carried sideways	5
San Francisco Bay, CA	19 Oct. 2016	Free swimming	American shad (*Alosa sapidissima*)	Fish carried sideways	6
Cook Inlet, AK	8 Aug. 2014	Dead, bycatch	Pink salmon (*Oncorhynchus gorbuscha*)	Consumption; regurgitation	7

Figure 2a-d. Harbor porpoise (*Phocoena phocoena vomerina*) capturing and carrying a large fish (likely a salmonid) at the surface in Burrows Bay, Fidalgo Island, Washington, on 7 August 2017 (Photographs by Sanne Hessing)

Figure 3a-c. Harbor porpoise capturing, carrying, and throwing a large fish (likely a salmonid) at the surface in Burrows Bay, Fidalgo Island, Washington, on 12 August 2017 (Photographs by Sanne Hessing)

Figure 4a-c. Harbor porpoise capturing and carrying a large fish (likely a coho salmon) at the surface in Burrows Bay, Fidalgo Island, Washington, on 25 July 2019 (Photographs by Sanne Hessing) harbor porpoises usually ingest their prey head first (Kastelein et al., 1997) but may take time (milliseconds to seconds) to manipulate the prey into the head-first orientation (Kastelein et al., 1997; DeRuiter et al., 2009; Miller, 2010). Alternatively, Smith & Gaskin (1974) proposed that harbor porpoises in the Bay of Fundy, Canada, may capture larger fish from behind, biting them at the gills and not ingesting the head. During the 12 August 2017 observation, the porpoise appeared to be throwing the fish into the air (Figure 3). During the 25 July 2019 observation, the harbor porpoise surfaced with the fish in its mouth multiple times, sometimes losing the fish (Figure 4). In all three cases, it was unclear whether the harbor porpoise attempted to, or was successful in, consuming the fish.

Due to the relative size of the fish, the shape of the expanded tail, and the heavy tail stock (Figure 2) of the 7 August 2017 observation, it appears to be a species of salmonid (W. Walker, pers. comm., 21 February 2019). Photographs from the 12 August 2017 observation do not show enough of the fish to allow a more concrete identification of species; however, from the reports of S. Hessing and the tail stock visible in the photographs (Figure 3), we believe it is a similar size and likely the same species as seen on 7 August 2017. For the 25 July 2019 observation, more of the body was visible (Figure 4); thus, we could determine that it was most likely a coho salmon (*Oncorhynchus kisutch*; W. Walker, pers. comm., 26 July 2019).

The sightings and photographs in San Francisco Bay were taken by W. Keener on 17 November 2017 (Figure 5) and by M. Webber on 19 October 2016 (Figure 6) from the Golden Gate Bridge. The 2017 photographs show a harbor porpoise capturing a large fish, identified as an American shad (*Alosa sapidissima*; J. Ervin, pers. comm., 13 July 2019). The chase and capture took approximately 30 s. The sequence of events here was very similar to that seen for the harbor porpoise pursuing the salmon in Burrows Bay. The porpoise is clearly accelerating after the fish, turning tightly at the surface as the chase continues (Figure 5). After the fish is caught, the porpoise surfaced multiple times (Figure 5; supplemental video; the supplemental video is available on the *Aquatic Mammals* website: https://www.aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=10&Itemid=147), carrying the fish cross-wise in its mouth as did the harbor porpoise carrying the salmon in Burrows Bay. Similar behavior by a harbor porpoise carrying a large American shad (J. Ervin, pers. comm., 13 July

Figure 5a-d. Harbor porpoise capturing and carrying an American shad (*Alosa sapidissima*) at the surface in San Francisco Bay, California, on 17 November 2017 (Photographs by William Keener)

2019) at the surface was observed during the 2016 event (Figure 6). In this case, it is likely that the female handling the fish was lactating as she was accompanied by a calf. In both cases, it was unclear whether the harbor porpoise attempted to consume the fish.

Globally, harbor porpoises have a non-specialized diet consisting of many different species, including fish and invertebrates (e.g., Recchia & Read, 1989; Gearin et al., 1994; Santos & Pierce, 2003; Víkingsson et al., 2003; Sveegaard et al., 2012; Leopold, 2015; Andreasen et al., 2017). Along the U.S. West Coast (including California, Oregon, Washington, and Alaska) and the Salish Sea, harbor porpoises are known to feed on a variety of fish and squid; however, to our knowledge, salmonid species and American shad have not previously been documented as prey in this region or for this subspecies (Salish Sea: Walker et al., 1998; Nichol et al., 2013; California: Jones, 1981; Dorfman, 1990; Toperoff, 2002; Oliaro, 2013). It is important to note that these studies were based on stomach contents of stranded or bycaught harbor porpoises; therefore, they may not be fully representative samples of a typical harbor porpoise diet. Although salmonid species have not been documented in the diet of harbor porpoises along the U.S. West Coast and the Salish Sea, they have been reported in the diets of other harbor porpoise populations in the Atlantic (Gulf of St. Lawrence: Fontaine et al., 1994; Scandinavia: Aarefjord et al., 1996; West Greenland: Heide-Jørgensen et al., 2011; Baltic Sea: Andreasen et al., 2017). However, we present a case of a Pacific harbor porpoise that fed on large salmonids in Cook Inlet, near the Kenai River in Alaska, which has not previously been published. On 8 August 2014, a healthy, lactating female harbor porpoise drowned in drift net gear (self-reported by the commercial fishermen), and M. Webber assisted in the necropsy. This female had multiple salmonids partially digested in her stomach (496 g; National Oceanic and Atmospheric Administration National Marine Fisheries Service [NOAA NMFS] Alaska Stranding Network, pers. comm., 15 August 2014) as well as in her throat and mouth as a result of apparent regurgitation (Figure 7). No detailed examination of the prey remains was completed, so the exact species cannot be confirmed; however, by early August, the salmon fisheries in that area switch over to pink salmon (*Oncorhynchus gorbuscha*) from sockeye salmon (*Oncorhynchus nerka*). The flesh in the pictures looks pale, and as the female was entangled in active salmon fishing gear, it is likely that the species was pink salmon.

Salmonid species are typically larger in length and mass than the majority of prey species known to be consumed by harbor porpoises. Average fork length (measured from the snout to the end of the middle caudal fin rays) of mature salmon for five species commonly found in the Salish Sea ranged from 53.8 to 80.0 cm, while wet mass ranged from 1,858 to 7,807 g (O'Neill et al., 2014). The Alaska Department of Fish and Game documents that pink salmon (the smallest salmon species in the Pacific found in North America) range from 45.7 to 63.5 cm and weigh 1,360 to 2,495 g. Additionally, American shad (which was introduced to the U.S. West Coast in the 19th century), like salmon species, are larger than the most common prey items consumed by harbor porpoises. The U.S. Fish and Wildlife Service describes American shad adult females as averaging 61.7 cm, adult males averaging 50 cm, and both weighing up to 5,500 g. Even if harbor porpoises consume juvenile/subadult individuals of either species, they would likely be, on average, larger than more common prey species such as Pacific hake (*Merluccius productus*), Pacific herring (*Clupea pallasi*), northern anchovy (*Engraulis mordax*), rockfish (*Sebastes* spp.), walleye pollock (*Theragra chalcogramma*), and various squid species (Jones,

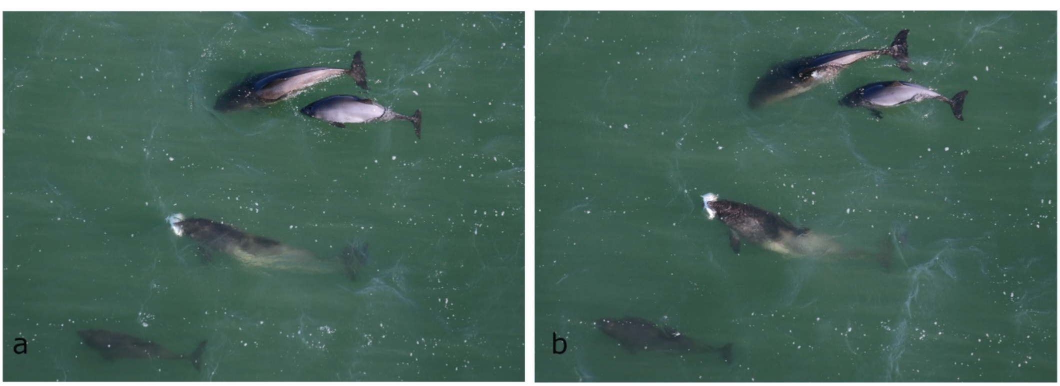

Figure 6a-b. Female harbor porpoise with calf carrying an American shad at the surface in San Francisco Bay, California, on 19 October 2016 (Photographs by Marc Webber)

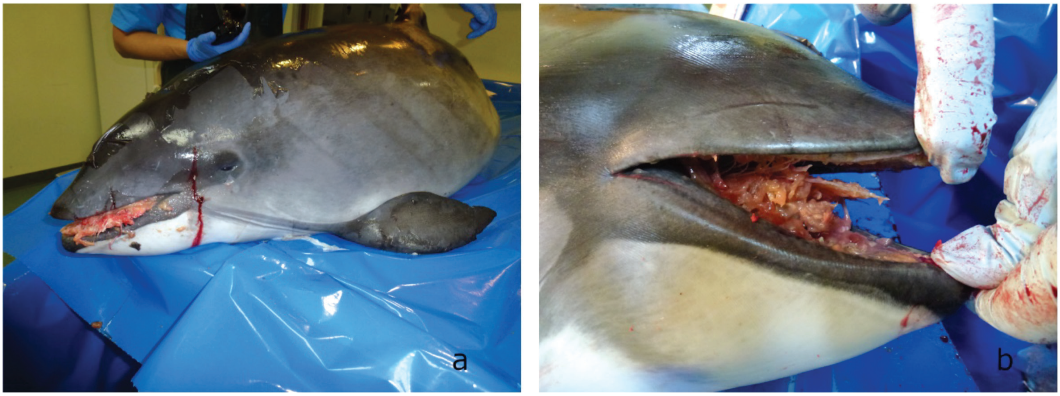

Figure 7a-b. Lactating female harbor porpoise with partially digested salmon (likely pink salmon) in throat. Female drowned in drift net of active salmon fishery in Cook Inlet, Alaska, on 8 August 2014. (Photographs by Marc Webber; MMSHRP Permit #932-1905/MA-009526 and Prescott Grant #NA12NMF4390162)

1981; Dorfman, 1990; Walker et al., 1998; Toperoff, 2002; Nichol et al., 2013; Oliaro, 2013). For example, four common prey species documented for harbor porpoises in the Salish Sea had fish lengths (estimated from body length–otolith length relationships) ranging from 7.8 to 36.4 cm, and mass ranging from 12.6 to 247.7 g (Nichol et al., 2013). However, prey length and mass may be underestimated when using otolith remains due to erosion, and the rate at which otoliths erode varies by prey species, so some species may be missed or underrepresented (Nichol et al., 2013). It is also worth noting that infrequently caught prey items may be missed completely by dietary analyses, particularly if part of the prey is not ingested. For example, if Smith & Gaskin's (1974) suggestion that harbor porpoises bite larger fish at the gills without consuming the head of the prey is correct, these types of captures would be missed in diet studies based on otolith remains. Two of the noted diet studies from California reduced this bias by utilizing other techniques that do not rely on visual and/or microscopic description—stable isotope ratios (Toperoff, 2002) and PCR-based molecular techniques (Oliaro, 2013).

Despite the limitations, diet analysis studies available along the U.S. West Coast and the Salish Sea (Jones, 1981; Dorfman, 1990; Walker et al., 1998; Toperoff, 2002; Nichol et al., 2013; Oliaro, 2013) spanned over 30 years (1981 to 2012) and documented variation in both prey type and frequency of consumption yet did not document salmonids or American shad in harbor porpoise diets. Interestingly, to our knowledge, American shad has not been noted in diet studies along the U.S. Atlantic coast where that species is native; only one study showed a related species, the bigeye herring (*Alosa pseudoharengus*), present in their diet (Recchia & Read, 1989).

Harbor porpoise diet can vary in prey selection and size (Andreasen et al., 2017) and in prey quality (Booth, 2019) in relation to seasonal fluctuations. Thus, it is possible that observations of capture of larger prey items may indicate changes in environmental/oceanic conditions or other influences (like fishing pressure) that may alter abundance of historically common prey and cause harbor porpoises to choose other prey items. This cannot be confirmed due to the limited observations available in this current study; however, this should be considered for discussion as future research/observations are documented.

Multiple studies have documented that large prey (in length and/or mass) can be ingested by harbor porpoises (Fontaine et al., 1994; Aarefjord et al., 1996; Víkingsson et al., 2003; Sveegaard et al., 2012; Andreasen et al., 2017). Larger prey can offer substantially greater energy gains because mass is a cubic function of fish length, and the caloric value of the fish is a product of their mass (Booth, 2019). When successful, the consumption of large prey items can provide high caloric value. For example, in Nichol et al.'s (2013) study, Pacific hake, which was estimated to be the longest and heaviest fish species documented, constituted only 2% of the diet by mass for harbor porpoises in the Salish Sea but made up 11% of their caloric intake. Harbor porpoises have a high metabolic rate (Kanwisher & Ridgway, 1983; Gallagher et al., 2018; Rojano-Doñate et al., 2018) but are limited in the amount of energy they carry and can only survive relatively short periods without feeding (Brodie, 1996; MacLeod et al., 2007a); thus, the high nutritional payoff may be worth the investment made in catching a large prey item. This may be of greater importance to pregnant and lactating females. Bioenergetic models show that they have the highest energetic costs compared to other sex/life history stages (Gallagher et al., 2018), and another study showed that lactating and postpartum females require increased food intake up to 80% by increasing foraging time and length of fish consumed (Yasui & Gaskin, 1986). Our observations revealed multiple cases of lactating females (the female porpoise in Alaska was lactating, and the 19 October 2016 pictures from the Golden Gate Bridge show a female with a calf); this indicates support for the idea that pregnant and/or lactating females may sometimes target larger prey items.

However, there are inherent risks involved. The unique morphology of the upper respiratory tract in odontocetes may make them more vulnerable to esophageal obstruction that can lead to asphyxiation (MacLeod et al., 2007b). This is especially true when large fish are ingested, although it can also occur with smaller fish that have significant dorsal spines (Stolen et al., 2013). Cases of harbor porpoises dying from asphyxiation due to laryngeal displacement and airway obstruction after attempting to ingest large fish have been documented in German and Irish waters (scad [*Trachurus trachurus*]: Ryan & Bolin, 2014; sole [*Solea solea*] and cod [*Gadus morhua*]: Roller et al., 2017), along the outer coast of Washington (American shad: Scheffer & Slipp, 1948; Scheffer, 1953), and in San Francisco Bay, California (gray smoothhound shark [*Mustelus californicus*]: Orr, 1937). Similar asphyxiation events on large fish and/or those with significant dorsal spines have occurred in other odontocetes (Byard et al., 2003, 2010; Watson & Gee, 2005; Mignucci-Giannoni et al., 2009; Stolen et al., 2013; IJsseldijk et al., 2015).

Another possibility is that the live harbor porpoises in our observations did not intend to consume the fish. If so, this could then have been an instance of object play or display. Play with other species, including chasing fish without consuming them, has been documented in many wild and captive cetacean species (Paulos et al., 2010). Captive harbor porpoises have been documented in play behaviors, including chasing live fish, tossing their food playfully, and playing with sea stars in their tank (Defran & Pryor, 1980; A. van den Berg & E. Everaarts, pers. comm., 26 February 2019). Information on play behavior is very limited for harbor porpoises, particularly in the wild. Since the ultimate fate of the fish was unknown in our observations, we cannot confirm whether play or display was involved. However, due to the information available from the stranded/asphyxiated porpoises described above, it is clear that they do try to ingest larger prey items on occasion, and our observations were most likely of foraging behavior.

Booth (2019) determined that for harbor porpoises, metabolizable energy intake estimates were most strongly affected by variations in target prey size (followed by foraging intensity) and that consideration of prey species, target size, and energy content is critical in assessing how a species exists in its ecological niche. Understanding the type and size of prey is critical to modeling energetic calculations and assessments of vulnerability (Booth, 2019). Harbor porpoises sometimes take larger than average prey items, and, thus, it is imperative to update our knowledge of harbor porpoise prey choices, and the quality of that prey, to better understand their energy needs and ecology.

This short note provides unique insights into previously undocumented harbor porpoise behavior and diet. We document the addition of two new species as harbor porpoise prey items along the U.S. West Coast (pink salmon and American shad) and one in the Salish Sea (coho salmon, salmonid sp.). Little research on this species has focused beyond group size, population abundance/distribution, presence/absence in relation to use of specific habitats (Elliser et al., 2018), and mating behavior (Keener et al., 2018); thus, wild harbor porpoise behavior remains poorly understood. Reports such as this are important to improve our knowledge of this difficult to observe species and highlight the need for further research and monitoring to fully understand their behavioral repertoire and ecological relationships.

Acknowledgments

We would like to acknowledge all staff, volunteers, and supporters of Pacific Mammal Research. Funding was provided by the Orange County Community Foundation and Andeavor Community Foundation. We would like to thank Steve Elliser and Linda Rogers for their continued funding and support. We thank Kathy Burek, James Ervin, James A. Hobbs, Levi Lewis, NOAA NMFS Alaska Stranding Network, William Walker, Annemarie van den Berg, and Eligius Everaarts for their help, data, and personal communications that improved the manuscript. We appreciate the suggestions by the anonymous reviewers which also improved the manuscript.

Literature Cited

Aarefjord, H., Bjørge, A. J., Kinze, C. C., & Lindstedt, I. (1996). Diet of the harbour porpoise (*Phocoena phocoena*) in Scandinavian waters. *Oceanographic Literature Review*, *10*(43), 1041.

Andreasen, H., Ross, S. D., Siebert, U., Andersen, N. G., Ronnenberg, K., & Gilles, A. (2017). Diet composition and food consumption rate of harbor porpoises (*Phocoena phocoena*) in the western Baltic Sea. *Marine Mammal Science*, *33*(4), 1053-1079. https://doi.org/10.1111/mms.12421

Booth, C. G. (2019). Food for thought: Harbor porpoise foraging behavior and diet inform vulnerability to disturbance. *Marine Mammal Science*, *36*(1), 195-208. https://doi.org/10.1111/mms.12632

Brodie, P. F. (1996). The Bay of Fundy/Gulf of Maine harbour porpoise (*Phocoena phocoena*): Some considerations regarding species interactions, energetics, density dependence and bycatch. *Oceanographic Literature Review*, *10*(43), 1041.

Byard, R. W., Gilbert, J. D., Gibbs, S. E., & Kemper, C. M. (2003). Cetacean café coronary. *Journal of Clinical Forensic Medicine*, *10*(2), 85-88. https://doi.org/10.1016/S1353-1131(03)00009-9

Byard, R. W., Tomo, I., Kemper, C. M., Gibbs, S. E., Bossley, M., Machado, A., & Hill, M. (2010). Unusual causes of fatal upper aerodigestive tract obstruction in wild bottlenose dolphins (*Tursiops aduncus*). *Forensic Science Medicine and Pathology*, *6*, 207-210. https://doi.org/10.1007/s12024-010-9143-3

Defran, R. H., & Pryor, K. (1980). The behavior and training of cetaceans in captivity. In L. M. Herman (Ed.), *Cetacean behavior: Mechanisms and functions* (pp. 319-362). Krieger Publishing Company.

DeRuiter, S. L., Bahr, A., Blanchet, M-A., Hansen, S. F., Kristensen, J. H., Madsen, P. T., Tyack, P. L., & Wahlberg, M. (2009). Acoustic behavior of echolocating porpoises during prey capture. *Journal of Experimental Biology*, *212*, 3100-3107. https://doi.org/10.1242/jeb.030825

Dorfman, E. J. (1990). *Distribution, behavior, and food habits of harbor porpoises* (Phocoena phocoena) *in Monterey Bay* (Master's thesis). San Jose State University, San Jose, California. https://scholarworks.sjsu.edu/etd_theses/44

Elliser, C. R., MacIver, K. H., & Green, M. (2018). Group characteristics, site fidelity, and photo-identification of harbor porpoises, *Phocoena phocoena*, in Burrows Pass, Fidalgo Island, Washington. *Marine Mammal Science*, *34*(2), 365-384. https://doi.org/10.1111/mms.12459

Fontaine, P. M., Hammill, M. O., Barrette, C., & Kingsley, M. C. (1994). Summer diet of the harbour porpoise (*Phocoena phocoena*) in the estuary and the northern Gulf of St. Lawrence. *Canadian Journal of Fisheries and Aquatic Sciences*, *51*(1), 172-178. https://doi.org/10.1139/f94-019

Gallagher, C. A., Stern, S. J., & Hines, E. (2018). The metabolic cost of swimming and reproduction in harbor porpoises (*Phocoena phocoena*) as predicted by a bioenergetic model. *Marine Mammal Science*, *34*(4), 875-900. https://doi.org/10.1111/mms.12487

Gearin, P. J., Melin, S. R., DeLong, R. L., Kajimura, H., & Johnson, M. A. (1994). Harbor porpoise interactions with a chinook salmon set-net fishery in Washington State. *Reports of the International Whaling Commission*, *Special Issue 15*, 427-438.

Heide-Jørgensen, M. P., Iversen, M., Nielsen, N. H., Lockyer, C., Stern, H., & Ribergaard, M. H. (2011). Harbour porpoises respond to climate change. *Ecology and Evolution*, *1*(4), 579-585. https://doi.org/10.1002/ece3.51

IJsseldijk, L. L., Leopold, M. F., Bravo Rebolledo, E. L., Deaville, R., Haelters, J., IJzer, J., Jepson, P. D., & Gröne, A. (2015). Fatal asphyxiation in two long-finned pilot whales *Globicephala melas* caused by common soles (*Solea solea*). *PLOS ONE*, *10*(11), e0141951. https://doi.org/10.1371/journal.pone.0141951

Jones, R. E. (1981). Food habits of smaller marine mammals from northern California. *Proceeding of the California Academy of Sciences*, *42*(16), 409-433.

Kastelein, R. A., Staal, C., Terlouw, A., & Muller, M. (1997). Pressure changes in the mouth of a feeding harbor porpoise (*Phocoena phocoena*). In A. J. Read, P. R. Wiepkema, & P. E. Nachtigall (Eds.), *The biology of the harbor porpoise* (pp. 279-291). De Spil Publishers.

Kanwisher, J. W., & Ridgway, S. H. (1983). The physiological ecology of whales and porpoises. *Scientific American*, *248*(6), 110-120. https://doi.org/10.1038/scientificamerican0683-110

Keener, W., Webber, M. A., Szczepaniak, I. D., Markowitz, T. M., & Orbach, D. N. (2018). The sex life of harbor porpoises (*Phocoena phocoena*): Lateralized and aerial behavior. *Aquatic Mammals*, *44*(6), 620-632. https://doi.org/10.1578/AM.44.6.2018.620

Leopold, M. F. (2015). *Eat and be eaten: Porpoise diet studies* (Doctoral dissertation). Wageningen University, Wageningen, Netherlands. http://edepot.wur.nl/361729

MacLeod, C. D., Santos, M. B., Reid, R. J., Scott, B. E., & Pierce, G. J. (2007a). Linking sandeel consumption and the likelihood of starvation in harbour porpoises in the Scottish North Sea: Could climate change mean more starving porpoises? *Biology Letters*, *3*, 185-188. https://doi.org/10.1098/rsbl.2006.0588

MacLeod, C. D., Reidenberg, J. S., Weller, M., Santos, M. B., Herman, J., Goold, J., & Pierce, G. J. (2007b). Breaking symmetry: The marine environment, prey size, and the evolution of asymmetry in cetacean skulls. *The Anatomical Record*, *290*, 539-545. https://doi.org/10.1002/ar.20539

Mignucci-Giannoni, A. A., Rosario-Delestre, R. J., Alsina-Guerrero, M. M., Falcon-Matos, L., Guzmán-Ramírez, L., Williams, E. H., Jr., Bossart, G. D., & Reidenberg, J. S. (2009). Asphyxiation in a bottlenose dolphin (*Tursiops truncatus*) from Puerto Rico due to choking on a black margate (*Anisotremus surinamensis*). *Aquatic Mammals*, *35*(1), 48-54. https://doi.org/10.1578/AM.35.1.2009.48

Miller, L. A. (2010). Prey capture by harbor porpoises (*Phocoena phocoena*): A comparison between echolocators in the field and in captivity. *Journal of Marine Acoustic Society Japan*, *37*(3), 156-168.

Nichol, L. M., Hall, A. M., Ellis, G. M., Stredulinsky, E., Boogaards, M., & Ford, J. K. B. (2013). Dietary overlap and niche partitioning of sympatric harbour porpoises and Dall's porpoises in the Salish Sea. *Progress in Oceanography*, *115*, 202-210. https://doi.org/10.1016/j.pocean.2013.05.016

Oliaro, J. F. (2013). *Identification of harbor porpoise (*Phocoena phocoena*) prey species using PCR based* *molecular techniques* (Master's thesis). San Francisco State University, San Francisco, California.

O'Neill, S. M., Ylitalo, G. M., & West, J. E. (2014). Energy content of Pacific salmon as prey of northern and southern resident killer whales. *Endangered Species Research*, *25*, 265-281. https://doi.org/10.3354/esr006311

Orr, R. T. (1937). A porpoise chokes on a shark. *Journal of Mammalogy*, *18*(3), 370. https://doi.org/10.1093/jmammal/18.3.370

Paulos, R. D., Trone, M., & Kuczaj II, S. A. (2010). Play in wild and captive cetaceans. *International Journal of Comparative Psychology*, *23*, 701-722.

Recchia, C. A., & Read, A. J. (1989). Stomach contents of harbour porpoises, *Phocoena phocoena* (L.), from the Bay of Fundy. *Canadian Journal of Zoology*, *67*(9), 2140-2146. https://doi.org/10.1139/z89-304

Rojano-Doñate, L., McDonald, B. I., Wisniewska, D. M., Johnson, M., Teilmann, J., Wahlberg, M., Højer-Kristensen, J., & Madsen, P. T. (2018). High field metabolic rates of wild harbour porpoises. *Journal of Experimental Biology*, *221*(23), jeb185827. https://doi.org/10.1242/jeb.185827

Roller, M., Gross, S., Reckendorf, A., Andreasen, H., Wohlsein, P., & Siebert, U. (2017, May). *Fatal asphyxiation with laryngeal displacement caused by platvissen in harbour porpoises*. 31st Annual Conference of the European Cetacean Society, Middelfart, Denmark.

Ryan, C., & Bolin, V. (2014). Stranded harbour porpoise (*Phocoena phocoena* (Grey)) with throat obstructed by a scad (*Trachurus trachurus* (L.)). *The Irish Naturalists' Journal*, *33*(2), 155.

Santos, M. B., & Pierce, G. J. (2003). The diet of harbour porpoise (*Phocoena phocoena*) in the northeast Atlantic. *Oceanography and Marine Biology: An Annual Review*, *41*, 355-390.

Scheffer, V. B. (1953). Measurements and stomach contents of eleven delphinids from northeast Pacific. *Murrelet, 34*(2), 27-30. https://doi.org/10.2307/3535867

Scheffer, V. B., & Slipp, J. W. (1948). The whales and dolphins of Washington State with a key to the cetaceans of the West Coast of North America. *American Midland Naturalist*, *39*(2), 257-337. https://doi.org/10.2307/2421587

Smith, G. J. D., & Gaskin, D. E. (1974). The diet of harbor porpoises (*Phocoena phocoena* (L.)) in coastal water of eastern Canada, with special reference to the Bay of Fundy. *Canadian Journal of Zoology*, *52*(6), 777-782. https://doi.org/10.1139/z74-102

Stern, J. S., Keener, W., Szczepaniak, I. D., & Webber, M. A. (2017). Return of harbor porpoises (*Phocoena phocoena*) to San Francisco Bay. *Aquatic Mammals*, *43*(6), 691-702. https://doi.org/10.1578/AM.43.6.2017.691

Stolen, M., St. Leger, J., Noke Durden, W., Mazza, T., & Nilson, E. (2013). Fatal asphyxiation in bottlenose dolphins (*Tursiops truncatus*) from the Indian River Lagoon. *PLOS ONE*, *8*(6), e66828. https://doi.org/10.1371/journal.pone.0066828

Sveegaard, S., Andreasen, H., Mouritsen, K. N., Jeppesen, J. P., Teilmann, J., & Kinze, C. C. (2012). Correlation between the seasonal distribution of harbour porpoises and their prey in the Sound, Baltic Sea. *Marine Biology*, *159*(5), 1029-1037. https://doi.org/10.1007/s00227-012-1883-z

Toperoff, A. K. (2002). *Examination of diet of harbor porpoise (*Phocoena phocoena*) from central California using stomach content and stable isotope analysis from multiple tissues* (Master's thesis). San Jose State University, San Jose, California. https://scholarworks.sjsu.edu/etd_theses/2337

Víkingsson, G. A., Ólafsdóttir, D., & Sigurjónsson, J. (2003). Geographical, and seasonal variation in the diet of harbour porpoises (*Phocoena phocoena*) in Icelandic coastal waters. *North Atlantic Marine Mammal Commission (NAMMCO) Scientific Publications*, *5*, 243-270. https://doi.org/10.7557/3.2829

Walker, W. A., Hanson, M. B., Baird, R. W., & Guenther, T. J. (1998). *Food habits of the harbor porpoise,* Phocoena phocoena*, and Dall's porpoise,* Phocoenoides dalli*, in the inland waters of British Columbia and Washington* (Alaska Fisheries Science Center [AFSC] Processed Report 98-10). National Marine Fisheries Service.

Watson, A., & Gee, L. E. (2005). Laryngeal displacement and asphyxiation by a beheaded sheepshead (*Archosargus probatocephalus*) in a bottlenose dolphin (*Tursiops truncatus*). *Aquatic Mammals*, *31*(4), 447-452. https://doi.org/10.1578/AM.31.4.2005.447

Yasui, W., & Gaskin, D. E. (1986). Energy budget of a small cetacean, the harbour porpoise, *Phocoena phocoena* (L.). *Ophelia*, *25*, 183-197. https://doi.org/10.1080/00785326.1986.10429749