Chapter 18
Sexual Behavior and Anatomy in Porpoises

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Abstract Among the taxonomic family of porpoises (Phocoenidae), mating behavior in nature has been described in detail only for the harbor porpoise (*Phocoena phocoena*). We review this species' unusual mating habits based on a study in San Francisco Bay, California, USA, and present new data from across its range in the North Pacific, North Atlantic, Black Sea, and managed care. Results confirm the

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male's unique laterality oriented solely to the female's left side as contact occurred both in nature and managed care. The male's high-energy sexual approach to the female led to splashy aerial behavior at the surface in nature. Drone footage provided observations of subsurface mating behavior, including evidence of male–male sexual interactions and a male calf interacting sexually with its mother. Harbor porpoise reproductive anatomy is also presented, with new comparative information on the vaquita (*Phocoena sinus*). The harbor porpoise's lateralized behavior and anatomy (i.e., long asymmetric penis, large testes size, convoluted asymmetric female reproductive tract) may have coevolved. We note gaps in knowledge, suitable platforms for future investigations (drones, bridges, boats, and coastal cliffs), and what is known about mating behavior in other porpoise species, including hybridization. We conclude with conservation implications for porpoises and encourage researchers to recognize and report mating behavior as baseline data valuable for establishing marine conservation areas.

Keywords Dall's porpoise · Harbor porpoise · Hybridization · Laterality · Mating behavior · Mating strategy · Mating tactics · Narrow-ridged finless porpoise · Social behavior · Sperm competition · Vaquita

18.1 Introduction

The porpoises (Phocoenidae) comprise a modest sized family of seven species that are among the smallest cetaceans. Unique features of porpoise anatomy that appear to play a role in sexual behavior include small, raised epidermal tubercles on the back or dorsal fin.[1] Porpoises in managed care at times rub each other with their tubercles, which may be important in social exchanges, serve a sensory function, and also assist in molts (Amundin and Amundin 1971; Liu et al. 1986; Kasuya 1999; Teilmann and Sveegaard 2019). Another porpoise characteristic is the weak spade-

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[1] Tubercles are a phocoenid feature, and a morphological analogue may exist in the genus *Cephalorynchus*, which can display serrations along the leading edge of the flipper (Baker 1978 referring to "rugose nodules"; Best 1988; Goodall et al. 1988). These are more prevalent in males and have a tactile function in social interactions (Johnson and Moewe 1999).

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shaped teeth that differ from the stout conical teeth of most dolphins, which may be the reason porpoises are not known to use their teeth to rake conspecifics in social and sexual interactions, as is common in many dolphin species (Martony 2020).

Porpoises are widely distributed from subpolar to tropical waters. Despite the coastal presence of nearly all porpoise species, except some populations of harbor porpoise (*Phocoena phocoena*), Dall's porpoise (*Phocoenoides dalli*), and spectacled porpoise (*Phocoena dioptrica*), many remain poorly known (Jefferson et al. 2015; Nielsen et al. 2018). Most porpoises are shy and inconspicuous, routinely altering their behavior and moving away from vessels. Only Dall's porpoises regularly approach boats to travel in the bow wave (Jefferson 1991). Porpoise group sizes are generally small, ranging from solitary animals to small groups (< 10), and rarely to several hundred in the harbor porpoise (Jefferson et al. 2015; Butler et al. 2017). The distribution, behavior, and group composition of porpoises pose a major impediment to researchers seeking to understand the sex lives of porpoises.

Mating behavior has never been described for the southern hemisphere Burmeister's porpoise (*Phocoena spinipinnis*), nor the critically endangered vaquita (*Phocoena sinus*) in the Gulf of California. Burmeister's porpoises exhibit greater length in males than females at sexual maturity (sexual size dimorphism), but whether this difference remains at physical maturity is inconclusive (Reyes and Van Waerebeek 1995). Vaquitas show reverse sexual size dimorphism, in which the female is larger than the male (Torre et al. 2014). Based on limited observations in nature, mate guarding behavior has been suggested for the sexually dimorphic spectacled porpoise and Dall's porpoise (Sekiguchi et al. 2006; Willis and Dill 2007; Frandsen and Galatius 2013). The slightly sexually dimorphic finless porpoises (*Neophocaena*) of Asia have undergone a recent taxonomic split (Jefferson and Wang 2011); narrow-ridged finless porpoise (*N. asiaeorientalis*) reproduction has been relatively well studied, but less is known about the Indo-Pacific finless porpoise (*N. phocaenoides*; Hao et al. 2006). Even the familiar and widespread harbor porpoise, which is reverse sexually dimorphic, in size has not been intensively observed in all its habitats (e.g., the Black Sea, northwest Africa), and behaviors of harbor porpoise hybrids with Dall's porpoise are poorly understood. More specimens of all species are needed to advance studies of reproductive physiology, anatomy, and genetics, which could shed light on life histories, including mating systems. In these efforts, beach-cast carcasses are of value. Several species of porpoises, notably harbor porpoises and narrow-ridged finless porpoises, have been kept in managed care facilities and have been a source of additional information. Although porpoise calves have been born in managed care and some have survived, limited attention has been given to sexual behaviors including their onset in individuals reared in managed care facilities.

This chapter primarily focuses on the harbor porpoise, which based on cetacean species studied so far, demonstrates a unique combination of lateralized and aerial sexual behavior. We review existing information available for the species and present new mating behavior data from the North Atlantic and Black Sea, with additional records from the North Pacific. We include the first photo-documentation of mating behavior for the Black Sea subspecies, and observations of male–male and mother–calf sexual interactions. Original research on the sexual behavior of animals in managed care facilities increases our understanding of the development of lateralized sexual behavior. New information is also presented on reproductive anatomy in the harbor porpoise and vaquita, along with a discussion of harbor porpoise anatomy that may provide insights on mating behavior patterns. We discuss effective approaches to collecting porpoise behavioral data using drones, bridges, land, small boats, and video cameras (including smartphones), and underwater cameras for animals in managed care.

18.2 Narrow-Ridged Finless Porpoise

The mating habits of the narrow-ridged finless porpoise have been studied in China, where conservation research has focused on the endangered Yangtze River subspecies (*N. a. asiaeorientalis*) either in enclosed oxbow lakes (Wei et al. 2002) or aquaria (Wu et al. 2010). The first birth in an aquarium was reported in 2005 (Wang et al. 2005). Chasing, synchronized swimming, and rubbing of genital slits with dorsal tubercles preceded ventrum-to-ventrum mating (Hua et al. 1994). The mating event lasted 30–60 min, of which copulation was only 2 min. Females sometimes responded to males that chased them with a tail-slap directed at the male (Hua et al. 1994). Sexual activity occurred throughout the year with peaks in April–July and September (Wang 2005). Increased testes size was positively correlated with the frequency of sexual behavior, but may have also been influenced by other factors such as social rank and water temperature (Wu et al. 2010). Socio-sexual (non-conceptive) behavior was prevalent (Zhang et al. 2015), and group hierarchies may influence how animals position themselves during physical contact (Platto et al. 2017). Most (65%) socio-sexual behaviors were cooperative male–male interactions thought to be related to the formation of coalitions (Zhang et al. 2015). Such behaviors begin early in life; a male calf's interaction with adults of both sexes was primarily ventrum-to-ventrum contact (Xian et al. 2010).

Knowledge of the mating behavior of the other subspecies of narrow-ridged finless porpoise, the East Asian finless porpoise (*N. a. sunameri*), is comparatively limited. Mating behavior occurred between March to September in the Inland Sea when group sizes increased; it was common to see mother–calf pairs followed by one or two adults, presumed males attending the female as she approached her estrous cycle (Kasuya and Kureha 1979). This attending behavior was also evident in managed care settings, where dominant males spent significant time with females engaged in pre-copulatory behaviors (mouthing, nudging) and both sexes rubbed their sensitive dorsal tubercules across the body of other porpoises (Liu et al. 1986; Nakahara 2009). During copulation, males positioned themselves ventrum to ventrum below the female. Females sometimes evaded the approach of a dominant male, giving a subordinate male an opportunity to copulate. However, paternity analyses revealed that only the dominant male sired calves despite having seasonally enlarged testes that suggest sperm competition (Nakahara, 2009).

18.3 Dall’s Porpoise: Mate Guarding

Dall’s porpoises are sexually dimorphic, displaying male secondary sexual characteristics (Jefferson 1990; Amano and Miyazaki 1993). The only other porpoise species with well-developed male secondary sexual characteristics is the spectacled porpoise that has a greatly enlarged dorsal fin in adult males compared to females (Goodall and Schiavini 1995). The female’s reproductive tract is notable for its weakly developed vaginal folds (Morejohn and Baltz 1972). The physical features of male Dall’s porpoises (larger than females, secondary sexual characteristics, relatively small testes) suggest they may compete for females through contest competition and polygyny is inferred (Kenagy and Trombulak 1986; Jefferson 1990; Ferrero and Walker 1999). Most females calve each summer and enter estrus a month later (Kasuya and Jones 1984; Ferrero and Walker 1999). Dall’s porpoises in the Salish Sea in the Pacific Northwest formed male–female pairs following summer calving, when a mother accompanied by her neonate calf often associated with an adult male (Willis and Dill 2007). This pairing behavior, which may last hours or days, is consistent with mate guarding in which a male remains close to a female during her estrous phase to reduce the chance of copulations by other males. Male–female pairs ($n = 18$) stayed together longer, maintained distances closer to each other, and surfaced in synchrony more than male–male pairs ($n = 24$). On six occasions, males actively chased other males away from females, which sometimes distressed their calves (Willis and Dill 2007); this mate guarding strategy may also be population-specific. In other regions, females with neonate calves occurred alone or with other female–calf pairs (Kasuya and Jones 1984; Jefferson 1987).

18.4 Harbor Porpoise

Harbor porpoises have been described as “living life in the fast lane” because they are one of the most short-lived cetaceans and females have a rapid (often annual) reproductive cycle (Read and Hohn, 1995). In the Gulf of Maine, few adults lived more than 10 years and females spent much of their adulthood pregnant and lactating (Read and Hohn 1995). The average age of sexual maturity is 3.6–4.6 years for females (131–154 cm) and 3–4 years for males (130–143 cm), with adults generally reaching lengths of 145–175 cm and weights of 50–75 kg (Gaskin et al. 1974; Hohn and Brownell 1990; Sørensen and Kinze 1994; ÓlafsdÓttir et al. 2002; Matsui et al. 2021). The species displays reverse sexual dimorphism in size, with females generally larger than males of similar ages. In most areas, females are on average approximately 8–10% longer and 20% heavier than males, and males lack obvious secondary sexual characteristics (Gaskin et al. 1984; Hohn and Brownell 1990; Read and Tolley 1997; Gol'din 2004; Galatius 2005, Murphy et al. 2020). The harbor porpoise mating system is polygynandrous, in which males and females copulate with multiple conspecifics (Bjørge and Tolley 2018), and reproductive peaks are seasonally synchronized (Lockyer 1995; Read and Hohn 1995). Gestation lasts 10–11 months and calves lactate for 8–12 months (Read 1990; Sørensen and Kinze 1994). Calves are typically born from May to September, depending on the region, followed by females entering estrus (Hohn and Brownell 1990; Read and Hohn 1995; Neimanis et al. 2000; Hasselmeier et al. 2004; Hall 2011; Norman et al. 2018). Hormone levels in female harbor porpoises in a managed care facility in Japan indicated the possibility of seasonal polyestry (Arai et al. 2017). Males undergo marked changes in testes size throughout the year, with maximum testes masses achieved in the summer when females are in estrus. Testes are inactive during the winter months (Neimanis et al. 2000; Kesselring et al. 2019). The very large testes-to-body mass ratio (4%, with combined testes weights of up to 2.7 kg; Gaskin et al. 1984), lack of secondary sexual characteristics, and reverse sexual size dimorphism, suggest a male mating tactic of sperm competition (Fontaine and Barrette 1997). Harbor porpoises ranked highest of 30 cetacean species in inferred level of sperm competition (MacLeod 2010). Noting their "megatestes," Fontaine and Barrette (1997) predicted males would mate with multiple females, attempt to mate many times with the same female, and not fight over access to females. Males grow fast and mature early at a minimum size enabling them to expend much energy into reproduction (Murphy et al. 2020).

18.4.1 Hybridization: Harbor Porpoise × Dall's Porpoise

Intergeneric hybridization of harbor porpoise with Dall's porpoise has been reported where their ranges overlap off the coast of British Columbia, Canada, and in the Salish Sea, Pacific Northwest, USA. Although the two species are sympatric elsewhere in the Eastern and Western North Pacific, no hybrids have been reported there. Multiple records of Salish Sea hybrids have been documented based on photo-identification, behavioral observations, strandings, and molecular analyses (Baird et al. 1998; Willis et al. 2004; Crossman et al. 2014, Morin et al. 2021). Hybrids generally had morphological traits intermediate between the two species, with individual variation that may lead to an underrepresentation of hybrids when using morphology to identify them (Willis et al. 2004; Crossman et al. 2014). It is possible that many abnormally pigmented Dall's porpoises, such as gray or white individuals (Morejohn et al. 1973; Joyce et al. 1982; Miller 1990), may be hybrids (Willis et al. 2004). Genetically identified hybrids (18 of 27) were mistaken for either parent species based on morphological assessment by experienced researchers (Crossman et al. 2014). The maternal parent of harbor porpoise × Dall's porpoise hybrids was consistently the Dall's porpoise (Willis et al. 2004). However, 30% of genetically identified hybrid porpoises had harbor porpoise mitochondrial DNA, indicating that at least sometimes harbor porpoises are the maternal parent (Crossman et al. 2014). Confirmed female hybrids with neonate calves mean that at least some female hybrids are fertile and can backcross with either species, but are more likely to do so with Dall's porpoises (Willis et al. 2004; Crossman et al. 2014). Given that most hybrids are born to Dall's porpoise mothers, it is likely these hybrids will behave like a Dall's porpoise and therefore would be more likely to mate with another Dall's porpoise rather than a harbor porpoise. This directionality of hybridization (in which the paternal parent is a harbor porpoise) may reflect the differences in the species' mating behaviors. Harbor porpoises may compete for females through sperm competition in contrast to the mate guarding and polygyny of Dall's porpoises, possibly resulting in polygynandrous male harbor porpoises indiscriminately pursuing females of either species (Willis et al. 2004).

18.4.2 San Francisco Bay Behavioral Case Study

Prior to recent work in San Francisco Bay, California, harbor porpoise mating behavior in nature was rarely reported. In the Bay of Fundy/Gulf of Maine, a site of long-term harbor porpoise investigations, copulation was only documented a total of five times over 5 years (Gaskin and Blair 1977) with no behavioral details provided. A brief early account of harbor porpoise mating behavior comes from a 1970 research expedition in the Black Sea in which two adults accompanied by a calf were encountered. The adults were observed for 5 min as they engaged in aerial behavior (repeated leaping) and also swam belly to belly for several seconds (Bel'kovich et al. 1991). During vessel surveys from 1987 to 1989 in Danish inner waters, mating behavior was seen only once. A male approached a mother–calf pair and separated the calf from the female, after which the adults engaged in chasing. Mating was then described near the surface producing "high splashes" (Kinze 1990).

Studies of harbor porpoise behavior in San Francisco Bay led to the systematic description of their mating habits, the first for any phocoenid (Keener et al. 2018). Over an 8 year period (2010–2018) in San Francisco Bay, photographs were obtained of 144 mating events from the Golden Gate Bridge. The males' rapid sexual approaches toward females were characterized by high energy and precision timing as males rushed to contact females. Males approached females with sufficient force and speed to result in male aerial behaviors (69% of copulatory attempts), which were observed exclusively in mating contexts (Keener et al. 2018). Males did not exhibit smooth head-first re-entries and instead made a splash as they contacted the water with their ventrum or flank. Typically, the duration of a mating event was 1–2 s (Keener et al. 2018). Remarkably, males always attempted to copulate by positioning their ventrum on the females' left side, even if the male began an approach while positioned on the female's right side (Keener et al. 2018). This extreme laterality in sexual approach is unique among cetaceans and mammals studied to date (Orbach et al. 2020; Lilley et al. 2022).

The penis was visible in 60% of the 96 mating events where the male's ventrum was visible (Keener et al. 2018). However, intromission was seen rarely (2 events) and was observed as the copulating pair was positioned crosswise at the surface with the male's ventrum pressed against the female's left flank (Keener et al. 2018).[2] Males also engaged in displays without attempting to copulate, consisting of postures in which males rolled their bodies to present their ventrum toward the females (with or without extruding the penis), an activity that could be seen while the animals were below the surface. Males initiated all mating events, based on photographs, videos, and observations, and mostly approached lone females (62.5% of events) or females with a calf (25% of events; Keener et al. 2018). Males generally ignored the presence of calves, and calves swimming on the mothers' left side were temporarily separated from their mothers by the fast-approaching males. In one instance, a male drove away a female's calf before pursuing her. Males did not herd nor coerce females and there was no evidence of mate guarding. Other adults of unknown sex were seen near some mating events, but none of them interfered with a mating male nor sexually approached the female. No male–male competition was observed and males occasionally approached one or more females repeatedly (Keener et al. 2018). These findings validate some predictions made about the behavior of harbor porpoises based on their reproductive biology and anatomy, supporting the hypothesis that males compete primarily by sperm competition (Fontaine and Barrette 1997; MacLeod 2010). In the absence of contest competition, the male's smaller body size than the female's may be useful for maneuverability in rapid sexual approaches (Murphy et al. 2020).

Females were sexually approached by males when at the surface (95% of occurrences; Keener et al. 2018). Males likely timed their approaches to coincide when females were taking a breath, possibly to make it more difficult for the female to maneuver during the brief moment of contact. Females generally appeared to be unaware of a male's presence until he was in immediate proximity, potentially indicating that males did not advertise their presence acoustically. Based on an analysis of 28 events captured on video, females reacted to male sexual approaches with high-intensity evasive behaviors such as fluke lifts ($n = 9$), dives ($n = 20$), and occasionally with passive receptive behaviors including no reaction or listless floating ($n = 5$; Orbach et al. 2019). Females also engaged in behavioral responses with ambiguous functions including dives ($n = 20$), peduncle curls ($n = 15$), body rolls ($n = 20$), and direction changes ($n = 5$; Orbach et al. 2019). Compared to other odontocete species and in contrast to the findings of MacLeod (2010), Orbach et al. (2019) evaluated multiple aspects of harbor porpoise anatomy and sexual behavior and reported that harbor porpoises had an intermediate level of sperm competition.

Despite the synchronized summer estrous cycle and winter regression of testes, mating activity in San Francisco Bay harbor porpoises occurred year-round (Keener et al. 2018). The stock of harbor porpoises studied, a distinct population with an

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[2] Hector's dolphin (*C. hectori*) males sometimes contact the flank of the female with chest or ventrum, referred to as a sexual "pounce" (Slooten 1994).

estimated abundance of <8000 animals (Forney et al. 2020), is non-migratory unlike many other populations across the species' range; it is not clear if stable residency facilitates out-of-season mating attempts. Because this description of harbor porpoise mating behavior was based on the small San Francisco Bay Area stock, we assessed whether the same pattern of high-energy lateralized and aerial mating occurred in other populations and subspecies of harbor porpoises.

18.4.3 Range-Wide Harbor Porpoise Mating Patterns in Nature

Solicitations of harbor porpoise mating behavior data across the species' entire range in the northern hemisphere resulted in a compilation of photo-documented observations from 1999 to 2022 from 23 locations where three reproductively isolated subspecies inhabit major marine basins: the North Pacific (*P. p. vomerina*), North Atlantic (*P. p. phocoena*), and Black Sea (*P. p. relicta*; Table 18.1; Fig. 18.1). Free-swimming harbor porpoise aerial behavior or mating events (sexual approaches or attempts to copulate) were photographed primarily by researchers or naturalists affiliated with organizations engaged in the study of local coastal environments (91% of contributions, $n = 21$). All data (e.g., date, GPS location, platform) were checked by a member of our research team. Of the 138 mating observation events contributed, half ($n = 69$) were on video totaling 19 min 21 sec and half ($n = 69$) were captured in 133 still photographs (Table 18.1). Digital photography platforms included land (46%, $n = 63$), drones (42%, $n = 58$), vessels (12%, $n = 16$), and a bridge ($n = 1$). A consensus-based process was used to evaluate potential mating events ($n = 135$) after analysis by an experienced team. Specifically, behavior was assessed for contact between male and female, the male's position with respect to the female during a sexual approach, male aerial behavior (>1/3 body above water), female response, and occurrence at or below the surface. When the sex of an individual could not be determined by observation of a penis, genital slit, or dependent calf, sex was presumed based on the typical mating behavior described in Keener et al. (2018). Of the 138 mating events, three were reviewed separately for non-reproductive socio-sexual behavior.

A mating event typically lasted 1–2 s ($n = 64$ videos). Mating events occurred in all months of the year, with a range of 2–40 events per month (January = 2, February = 7, March = 4, April = 40, May = 17, June = 5, July = 5, August = 6, September = 7, October = 8, November = 10, December = 6). April was a high outlier due to numerous drone-based videos collected over a 4 day effort in Denmark. The occurrence of mating behavior in all months, also found in San Francisco Bay, California (Keener et al. 2018), was surprising given the seasonal regression of testes and presumably low male hormone levels. It is plausible that constant year-round practice of sexual approach maneuvers could be an important activity for males as their mating behavior is a high-intensity, precisely timed activity.

Table 18.1 Images evaluated for free-swimming harbor porpoise mating behavior. Data were contributed from 23 locations ($n = 138$ events). The map # refers to locations indicated on Fig. 18.1

Map #	Waterbody	Location	Nation	Year	Format	Events	Contributor	Affiliation
1	NE Pacific	San Francisco Bay, CA	USA	2021	Still	1	W Keener	The Marine Mammal Center
2	NE Pacific	Monterey Bay, CA	USA	2015	Still	1	D Bianchetta	Monterey Bay Whale Watch
3	NE Pacific	Burrows Pass, Salish Sea, WA	USA	2014–2022	Still	14	C Elliser, K MacIver	Pacific Mammal Research
4	NE Pacific	Puget Sound, Salish Sea, WA	USA	2018	Still	1	D Anderson	Cascadia Research Collective
5	NE Pacific	Puget Sound, Salish Sea, WA	USA	2022	Video	4	C St. Ours	Pacific Mammal Research
6	NE Pacific	Howe Sound, Salish Sea, BC	Canada	2015, 2019	Still/video	13	A Hall	Porpoise Conservation Society
7	NE Pacific	Morse Basin, Prince Rupert, BC	Canada	2015	Still	1	C Birdsall	Ocean Wise Research
8	NE Pacific	Kachemak Bay, AK	USA	2019, 2022	Still/video	4	M Webber, DD Tobin	The Marine Mammal Center, University of Alaska
9	NW Atlantic	Gulf of Maine, ME	USA	2018	Still	1	K Pielmeier	Allied Whale/College of the Atlantic
10	NE Atlantic	Mount’s Bay, Cornwall	England, UK	2013–2015	Still/video	3	D Jones, R Knee	Marine Discovery Penzance
11	NE Atlantic	Bristol Channel, Devon	England, UK	2011	Still	1	D Jenkins	Seawatch Foundation
12	NE Atlantic	Scarborough, Yorkshire	England, UK	2015, 2021	Still	3	S Baines	Seawatch Foundation
13	NE Atlantic	Flamborough, Yorkshire	England, UK	2017	Still	1	J Hood	Flamborough Bird Observatory
14	NE Atlantic	St. George’s Channel, Pemb.	Wales, UK	2016–2020	Still	19	H Dunn	Sea Trust Wales

15	NE Atlantic	Gulberwick Bay, Shetland Is	Scotland, UK	2018–2019	Video	16	N McCaffrey	Southspear Media & Surveys
16	NE Atlantic	Inner Sognefjord	Norway	1999	Video	1	F Graner	Sealife Productions
17	NE Atlantic	Nordvika	Norway	2020	Still	1	C Mignot	Photographer
18	NE Atlantic	Kattegat	Sweden	2013	Still	1	T Edenborg	Photographer
19	NE Atlantic	Romsø Sound	Denmark	2018–2022	Video	42	ST Ortiz, H Hamel, D Brennecke	University of Southern Denmark
20	NE Atlantic	Little Belt	Denmark	2020	Video	1	L Kondrup	Natur & Ungdom Fredericia
21	NE Atlantic	Eastern Scheldt	Netherlands	2021	Still	3	F Zanderink	Stichting Rugvin
22	Black Sea	Constanța, W Black Sea	Romania	2020	Still	5	R-M Paiu	Mare Nostrum NGO
23	Black Sea	Zonguldak, S Black Sea	Türkiye	2019	Video	1	N Uluduz	Zonguldak Bülent Ecevit University

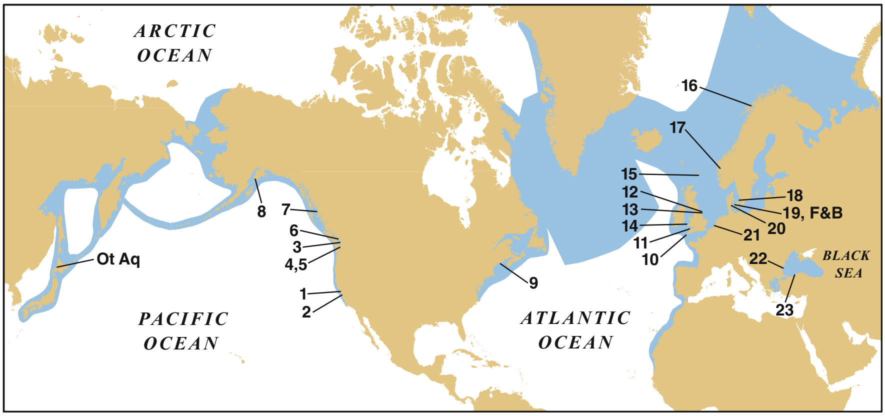

Fig. 18.1 Harbor porpoise global distribution map and locations that contributed mating/aerial behavior images for this species (numbers from Table 18.1). Two managed care facilities are also indicated (Fjord&Bælt, Denmark and Otaru Aquarium, Japan). Porpoise range information from Jefferson et al. (2015) and Nielsen et al. (2018). Map: Nina Lisowski

Photographs from land, bridge, and vessel platforms comprised 80 events with mating behavior exclusively at the surface. In contrast, drone-based videos revealed that 42 mating events occurred underwater. Of the 135 mating events evaluated, aerial behavior that appeared to be unrelated to mating ("high leaps"- single, high arcing, head-first, re-entry leaps) in 18 events was excluded from the mating behavior analysis. High leaps occurred for unknown reasons, possibly functioning in non-sexual social interactions or foraging, and mostly when no other adult porpoise was near the aerial individual (Fig. 18.2a). A similar type of high leap, which did not look like the serial leaping ("porpoising") of traveling dolphins, was observed in Denmark (Amundin and Amundin 1973). An additional 10 events were excluded in evaluating lateralization criteria because the male's position in proximity to the female was blocked by an animal's body or by splashes, or in some instances the male halted his approach well before reaching the female. It was possible to determine the sex of at least one porpoise engaged in mating behavior in 38 events as a penis was visible in 31 events (Fig. 18.2b) and a dependent calf was present in 10 events (Supplemental Video 18.1). The sexes of both adult male and female porpoises were known in three events. The terms *female* and *male* include both confirmed and presumed members of the sex.

Our observations confirm extreme laterality in the male harbor porpoise's mating behavior and are consistent with results in Keener et al. (2018) from San Francisco Bay, in which males attempted to contact the female's left side, and in some instances the penis remained erect immediately following a mating approach (Fig. 18.2c, d). In 100% of range-wide mating events, males attempted to contact the females' left side ($n = 107$). The male made physical contact with the female in 71% of events ($n = 76$), typically touching his ventrum on the female's left flank during his approach from behind angled crosswise to the female's body. The male's

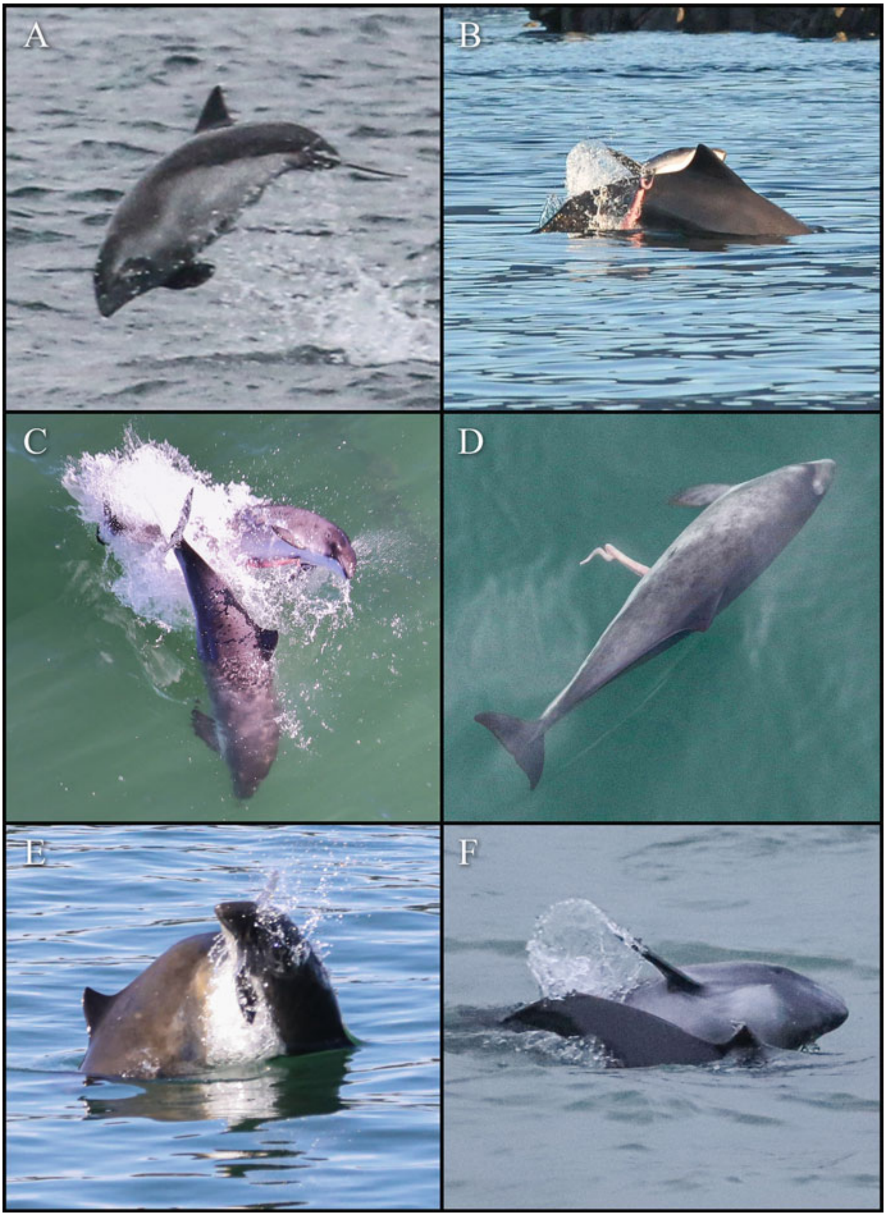

Fig. 18.2 Harbor porpoise behavior in nature. (**a**) High leap, English Channel, UK. (**b**) Male left-sided mating approach with penis on the female's right side, Prince Rupert, Canada. (**c**) Energetic male left-side mating approach, penis erect, female fluke lift and partial body roll, San Francisco Bay, California, USA. (**d**) Male with erect penis immediately after a left-sided mating approach, San Francisco Bay, California, USA. (**e**) Male left-sided approach perpendicular to the female, Salish Sea, Washington, USA. (**f**) Typical male mating approach to left side of the female, Black Sea, Romania. Photos: (**a**) Rebecca Knee/Marine Discovery Penzance; (**b**) Caitlin Birdsall/Ocean Wise Research; (**c**) Joey Meuleman/The Marine Mammal Center; (**d**) Marc A. Webber/The Marine Mammal Center; (**e**) Cindy R. Elliser/Pacific Mammal Research; (**f**) Romulus-Marian Paiu/Mare Nostrum NGO

energetic sexual approach led to his aerial behavior in 52% of 117 events ($n = 61$) (Fig. 18.2e, f). No copulations with confirmed intromission were observed. In 8% of events ($n = 10$), the male was most proximate to the female at the surface, and in 39% of events ($n = 46$) his approach was executed entirely underwater. The subset of surface events photographed only from land, bridge, or vessels ($n = 62$) revealed aerial behavior by the male in 89% of events ($n = 55$; Supplemental Video 18.2). The male's partial or full body breach usually terminated with a conspicuous splash. Of the 38 events in which the sex of an animal was determined, all 31 confirmed males executed left-sided approaches to the presumed females, and included aerial behavior in 74% ($n = 23$) of those events; ten confirmed females were approached from the left by males, and 5 of those males exhibited aerial behavior.

Males appeared to initiate all sexual approaches and predominately (91%, $n = 107$) approached single target porpoises (presumed females). Most mating events occurred when the female was at the surface (66%, $n = 76$). Two events were excluded because the female's position could not be ascertained. Female responses to the male's approach varied across a spectrum from little reaction to tail-slapping. Female behavioral responses most frequently included body rolls (47%, $n = 52$ of 110 events that could be evaluated for this criterion) and fluke lifts (43%, $n = 47$), which could occur simultaneously. Fluke lifts often appeared to function in evading or deterring the male's approach. Females were observed rapidly lifting their flukes, reaching a vertical position with the tailstock straight up in the air, simultaneously rolling on their long axis, occasionally resulting in a slap contacting the male. The females' rapid and energetic fluke lifts generated a considerable splash that slightly preceded the re-entry splash created by the males (Fig. 18.2c, e). Little or no reaction by a female occurred in 25% of events ($n = 28$). Other non-mutually exclusive female behavioral reactions included changes of direction (13%, $n = 14$), acceleration (4%, $n = 5$), or an immediate dive ($n = 1$). The subset of ten confirmed females did fluke lifts in seven events, body rolls in four events, and changed directions/accelerated in two events.

In one instance, a male porpoise made repeated sexual approaches towards a female. A male was photographed in the Black Sea off Romania energetically rushing to contact the same female's left side five times over a period of 9 min. In cases where females were accompanied by calves, males appeared to ignore the calves' presence as they approached females. Socio-sexual (non-conceptive) behavior collected by drone from the Shetland Islands, UK, showed a male–male interaction; a male hooked his fully erect penis around the tailstock of a target porpoise, a confirmed male based on its genital slit (Supplemental Video 18.3). The target male remained relaxed and did not exhibit any of the typical evasive behaviors used by females. He was a distinctly marked individual and was observed in a subsequent video exhibiting typical male behavior as he rushed to the left sides of other individuals. This is the first confirmed instance of male–male sexual behavior in harbor porpoises. While same-sex behavior was never documented in the San Francisco Bay study, it was expected due to its ubiquity among other species, including finless porpoises (Zhang et al. 2015; da Silva and Spinelli 2023, this book; Ham et al. 2023, this book). To date, there is no record of an interaction where more than one male in a group simultaneously has an erect penis. In Denmark, a dependent male calf, estimated to be aged 9–10 months and therefore not yet weaned, was observed via drone sexually interacting with its mother. He approached the left flank of his mother three times within 2 min, twice with his penis visible. In one contact event that lasted 5 s, he rolled underneath her until they were positioned ventrum-to-ventrum. This type of early sexual activity parallels that seen in other odontocetes, including Indo-Pacific bottlenose dolphins (*Tursiops aduncus*, Mann 2006; Supplemental Video 18.4).

18.4.4 Harbor Porpoise Mating Behavior in Managed Care

Harbor porpoises have been maintained in recent decades in managed care facilities in Denmark, the Netherlands, Japan, and Canada. Successful births have been reported since 2007 (Blanchet et al. 2008b). Information on the sexual behaviors of porpoises has been reported from the Fjord&Bælt (marine research center and aquarium) in Denmark and the Dolfinarium Harderwijk in the Netherlands. Numerous mating events observed in multiple projects at these facilities suggested a seasonal mid-summer peak during which males were the initiators of activity, but a female could determine the outcome of an approach by rolling her body away from the male (Benham et al. 2001; Desportes et al. 2003). Males attempted to mate indiscriminately, did not form male alliances, and did not dominate other males (Delgado-García 2009). We report the first investigation of harbor porpoise mating behavior in managed care facilities focused on lateralized sexual approaches by the male.

At Fjord&Bælt, three harbor porpoises were housed in an outdoor enclosure (30 × 20 m, average depth 3–4 m), with netting allowing for natural water to flow in from the adjacent harbor and Great Belt. The animals are exposed year-round to natural environmental conditions of tidal currents, temperature, and light. “Eskild” (male) and “Saga” (female) were born in nature in 2019, bycaught, and brought to the facility in winter 2020 (aged approximately 1.5 years; Fig. 18.3). “Freja” (female) was born in 1995 and was extremely old at the time of the study; she gave birth twice, unsuccessfully in 2006 (Blanchet et al. 2008a) and successfully in 2007 (Blanchet et al. 2008b). Eskild was first observed exhibiting sexual activity in August 2021 when he was 2 years old and 117 cm in length. During the summer and fall of 2021–2022, mating behavior was recorded using GoPro video cameras (Hero9 Black or Hero7 Silver models equipped with a wide-angle Max lens). For underwater observations, the camera was attached to a pole held 1 m below the surface in proximity to the porpoises. For above-water observations, the camera was suspended 8 m above the pool enclosure.

A total of 47 observational sessions from August 19, 2021 to September 14, 2022 amounted to 11 h 45 min of effort and resulted in 101 mating behavior events recorded. Subadult Eskild sexually approached both females, but showed a preference for subadult Saga (82% of events, $n = 83$). His penis was visible in 71% of

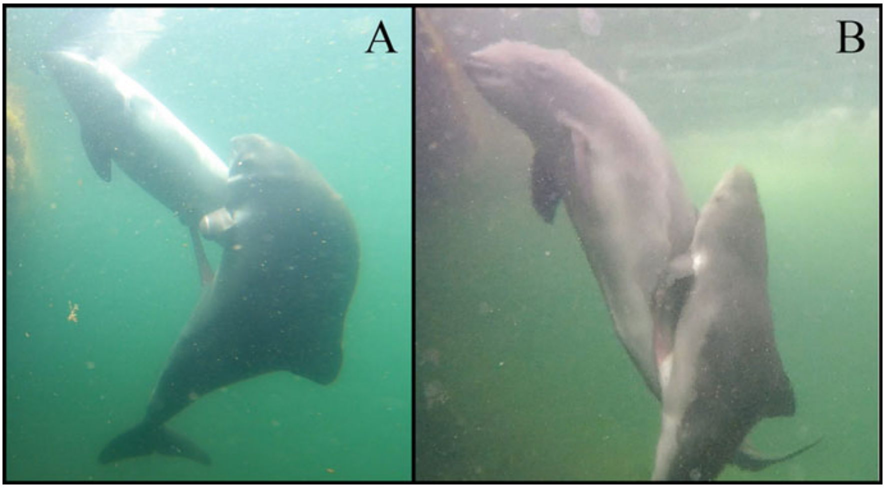

Fig. 18.3 Harbor porpoise mating behavior observed at Fjord&Bælt in Kerteminde, Denmark. Females were stationed at the surface near the edge of the pool enclosure. (**a**) Subadult male "Eskild" copulates with subadult female "Saga." (**b**) Subadult male rubs penis against left flank of adult female "Freja." Photos: Freja Jakobsen/University of Southern Denmark

events ($n = 72$). Eskild's sexual approaches usually resulted in contact with the target female ($n = 82$; Fig. 18.3a, b). His rapid approaches were initiated from the female's left side in 84 events and from below in 11 events. In six events, the angle of approach could not be discerned because of poor water clarity or camera angle. The male was positioned on the left side of the female at the closest point of approach in 100% of events, consistent with findings of free-swimming harbor porpoises in San Francisco Bay (Keener et al. 2018) and range-wide results reported here. Typically, Eskild attempted to copulate by approaching a female while she was stationary at the surface and positioned vertically at the edge of the pool with her attention directed toward a trainer. In nature, males tend to time their sexual approaches when females are swimming horizontally. When approached, the females showed avoidance behavior in 30% of events ($n = 29$); they turned their ventrum away from Eskild by executing a body roll or tilt or swam away. In one instance, Freja tail-slapped Eskild. Most sexual approaches appeared to be attempts to copulate but penetration was difficult to observe because the male's body position often blocked the view. Copulation with intromission was clearly observed only once, with Saga. Although Eskild was young, his frequent sexual behavior supports the hypothesis that males show interest in approaching females before reaching sexual maturity. Although one may speculate that the left-sided mating approach is innate as it was documented in a young male in a managed care facility, Eskild lived his first 9 months in nature where he may have encountered males sexually approaching his mother or nearby females, providing many learning opportunities. Manitzas Hill et al. (2023, this book) provide additional information on odontocete sexual behavior in managed care facilities.

At the Otaru Aquarium in Otaru, Japan, a visitor in an underwater glass-walled viewing room recorded 61 s of video footage in 2017 that captured harbor porpoise mating behavior. The pool housed two adult males, one adult female, and one subadult female, all bycaught in the Western North Pacific. A male with an erection made two sexual approaches to a female, both times targeting her left side at his closest point of contact. The first copulatory attempt may have resulted in intromission. These events were followed by grooming (using his dorsal fin to contact the female) without the penis extruded. The target female then increased her speed as the male with an erect penis followed her.

18.4.5 Harbor Porpoise Sexual Anatomy

Features of the harbor porpoises' reproductive anatomy were described by Meek (1918) from stranded specimens in the UK. The structure of the vagina is complex, characterized by multiple internal folds, spirality, and bilateral asymmetry (Orbach et al. 2020). Out of 20 cetacean species assessed, the harbor porpoise has the most vaginal folds (up to 13; Orbach et al. 2017b, 2023, this book). Orbach et al. (2020) used innovative techniques such as geometric morphometrics to quantify 2D variation in shape and photogrammetry of vaginal lumen endocasts (silicon molds) to quantify 3D directional asymmetry of the vaginal canal in specimens from California; the internal vaginal lumen showed variations between individuals and was highly asymmetric due to complex 3D spirals and deeply recessed vaginal folds (Orbach et al. 2020, 2021). A vagina from a harbor porpoise from the Eastern North Atlantic, reported here for the first time, showed similar extensive vaginal folding to specimens from the Eastern North Pacific (Fig. 18.4). The harbor porpoise penis is long for a small odontocete (~50 cm) and consists of a fibro-elastic shaft and a distal filiform tip (Meek, 1918; Orbach et al. 2017a). Meek (1918) described the shaft, which can be quickly extruded as rigid while the distal part remains pliable, presumably to better pass into the vagina. Based on the shapes of the genitalia, the bodies of the male and female may rotate as they copulate. Three artificially distended harbor porpoise penises were found to be asymmetric, with tips that originated on the left sides of a blunt knob and bent to the left (Fig. 18.5, upper right). The asymmetric shapes of the vagina and penis were both left-canted with similar angular bends that mirrored one another (Orbach et al. 2020).

The asymmetry apparent in female and male harbor porpoise genitals corresponds with the unique lateralized mating approach of the male, the result of an intersexual evolutionary "arms race" to control paternity (Orbach et al. 2019). The similarity in both North Pacific and North Atlantic female reproductive tracts (Fig. 18.4) supports new behavioral data presented here that confirm range-wide lateralized mating approaches by males. Vaginal folds and spirals may inhibit the depth or direction of penile penetration and semen movement, and the asymmetric penis appears to have coevolved to circumvent protruding vaginal barriers (Orbach et al. 2017a). To increase the chances of a successful copulation that achieves fertilization, males use

Fig. 18.4 Similarities in extensive vaginal folding of sexually mature harbor porpoises from the North Pacific (Alaska) on the left and the North Atlantic (Germany) on the right. Vaginal structures show asymmetry as a gauntlet for penis or sperm before reaching the cervix (truncated at top of images). Animals in dorsal recumbency with incision along ventral midline. Photos: Dara N. Orbach/Texas A&M University-Corpus Christi (left); Alexandra Rieger/University of Veterinary Medicine Hannover (right)

a left-sided sexual approach and contact females only with the optimum angle and body orientation. Females may respond by evasive maneuvers (e.g., body rolls, energetic fluke lifts) during copulation that could misalign the angle of penetration and prevent semen from reaching the cervix (Orbach et al. 2019). The harbor porpoise is a striking example of the coevolution of behavior and anatomy in which both sexes adapt and counter-adapt to control paternity.

18.5 Vaquita Sexual Anatomy

Although mating behavior of the vaquita has (to our knowledge) not been documented in nature, the semblance in male genital morphological shape with the harbor porpoise (Fig. 18.5) suggests that similar evolutionary pressures may be acting on genital form. Whether male vaquitas sexually approach females exclusively on the female's left side remains unknown. No insights could be derived from female morphology as a vaquita vagina recently assessed was dissected with a dorsal incision, instead of along the ventral midline, preventing direct comparisons with harbor porpoise reproductive tracts. One study of the vaquita ($n = 56$ specimens)

Fig. 18.5 Penises of post-mortem sexually mature vaquita (lower left) and harbor porpoise (upper right), artificially inflated to simulate erection. Ruler = 15 cm. Photo: Dara N. Orbach/Texas A&M University-Corpus Christi

concluded that lifespan, age at sexual maturation, seasonal reproduction, large testes size, and reverse sexual size dimorphism are all similar to the harbor porpoise (Hohn et al. 1996). Yet, based on residual testes mass, the vaquita ranked 18th of 30 cetacean species in terms of inferred level of sperm competition (MacLeod 2010).

18.6 Conclusions and Recommendations

Our data confirm that the harbor porpoise male's high-energy sexual approach to the female is oriented exclusively to her left side at the moment of contact, both in nature and in managed care facilities. Images from locations across the harbor porpoise's range suggest that this pattern of lateralized behavior is pervasive in all three subspecies. Comparisons of female reproductive tracts from the North Pacific and North Atlantic demonstrate similarities in internal structures, supporting our observed range-wide mating behavior pattern. Drone-based observations revealed underwater mating behavior events without evidence of activity at the surface.

In nature, energetic mating activity at the surface often leads to splashy aerial behavior due to the female's rapid reactive fluke lifts and the male's re-entry to the water at an oblique angle. Although visual observations were not used in our analyses, personal experiences by the authors suggest that because mating events happen suddenly at the surface, more could occur in an area than can be captured by camera. Researchers should be aware that aerial behavior accompanied by a brief intense splash may be a sign of mating rather than foraging. Resource managers should factor observations of such behaviors into decisions affecting potential mating hotspots. Because breeding is a key life history parameter, recognition of lateralized aerial behavior at the surface and locations where this activity is prevalent could help support the designation of marine protected areas or implementation of conservation measures.

Our new findings were possible because of contributions from investigators across the harbor porpoise's global range, an international collaboration that exemplifies the fruitful working relationships needed for the conservation of widespread porpoise species. Additional avenues of inquiry about porpoise mating behavior should be pursued, such as using acoustic recordings to augment photography. For example, detecting bioacoustic signals during mating attempts may address whether harbor porpoise males ambush oblivious females. Porpoises are less common in managed care facilities than dolphins, but more detailed behavioral work with known age harbor porpoises, including ones born in facilities, could elucidate whether certain sexual behaviors are learned or innate. Morphological studies can fill knowledge gaps for lesser-known species like the Burmeister's porpoise, spectacled porpoise, and vaquita. At the subspecies level, penis shape and reproductive tract structures are still not reported for Black Sea harbor porpoises.

We recommend considering options for observation platforms in field work on porpoise behavior. Harbor porpoises can be wary around boats (particularly powerboats, less so near kayaks and sailboats); therefore, drone, land, and bridge-based observations may reduce the potential for interference with natural behaviors. While aerial platforms (drones, bridges) could capture mating occurring underwater, some surface activity may be missed due to splashes. Regardless of platform, imagery techniques and equipment are important and still photos were more difficult to evaluate than video clips because photographers rarely photographed an entire behavioral sequence from beginning to end, capturing only an instant of the action. Mating events are brief, especially when observed at a low angle from vessels or shore; they happened without warning, which often resulted in images partially obscured by surface splashing. Our collective experience supports the value of high-resolution digital cameras with zoom lenses (100–600 mm) from land, vessel, and bridge platforms.

Drones In Denmark, the mating behavior of harbor porpoises in nature was recorded using a drone from March to October 2018–2022 during annual field surveys around the Island of Funen. Mating attempts were observed in the Romsø Sound, Kerteminde Bay, and the Great Belt. The drone (DJI Phantom 4 Pro V2.0) was launched from the beach or from a small boat in clear weather (wave height <0.1 m and wind <36 km/h) and above shallow waters (depth <10 m) to facilitate the tracking of porpoises underwater. Best results were achieved when the surface was flat calm. Flights lasted less than 25 min at altitudes between 10 and 30 m above sea level, depending on group size and water clarity. No negative reactions to the drones by porpoises or other wildlife (e.g., foraging seabirds) were observed, but usually the aircraft was flown to the side of the porpoises rather than directly overhead to minimize noise disturbance. Drones not only enabled observations without disturbing the natural behaviors of porpoises at the surface; they also captured action deep (to ~5 m) in the water column. Behavior transpiring below the surface offered new insights on same-sex behavior and the age at which sexuality is expressed. See Torres Ortiz et al. (2021) and Ramos et al. (2023), this book.

Land Because harbor porpoises usually are coastal, land-based observations are feasible where the species is regularly seen. Since 2014, mating attempts have been photographed from 6 m above sea level overlooking a narrow (400–500 m) stretch of water known as Burrows Pass near Anacortes, Washington, USA. The waters are generally calm, providing excellent conditions for viewing harbor porpoises that occur year-round (Elliser et al. 2018). The partial elevation provides a better vantage point compared to being on a small boat, allowing tracking of groups and activity that may occur prior to a mating event. Mating behavior occurred both in isolated instances (with no prior clues) and during heightened activity at the surface (foraging, aggregating in small groups displaying energetic movements and splashing).

Vessels Although harbor porpoises tend to avoid powerboats, researchers have had some success photographing the behaviors of a semi-enclosed, small population (~50) in the Eastern Scheldt (Oosterschelde), the Netherlands. Best practices were to idle or turn off the motors and to turn off all boat electronics (e.g., depth finder/fish finder). Similarly, in Kachemak Bay, Alaska, USA, mating behavior was photographed with digital still cameras from a vessel with engines and electronics turned off, while also tracking porpoises with a wide-angle video camera (even a mobile phone) to continuously capture surface action.

Bridge Bridges with pedestrian walkways that span porpoise habitat may be productive and economical photography platforms. Harbor porpoises have been photographed from the Golden Gate Bridge in San Francisco Bay, USA, since 2008. The bridge crosses a 1.5 km strait, with observation sessions conducted during high tides from the bridge's eastern public sidewalk, 70 m above sea level. The platform's chief limitation was that focal follows of socially active harbor porpoises could not be continued once they swam beneath the deck of the bridge.

All porpoise species face a variety of threats in a world increasingly modified by humans in the Anthropocene. The few remaining vaquita could be killed incidentally by unchecked gillnet fishing in the last small area where they survive in the upper Gulf of California. All species are confronted by habitat degradation from some combination of coastal and nearshore development, resource extraction, marine litter, chemical pollution, noise pollution, vessel traffic, bycatch in fisheries, direct harvests, and overfishing of shared resources (Mesnick et al. 2023, this book). Insufficient attention has been paid to the accelerating coastal habitat alterations associated with climate change and its effect on porpoises. Such challenges underscore the need for more studies on porpoise reproduction and sexual behavior that could inform management decisions affecting the survival, recovery, and long-term health of these small cetaceans.

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